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Editors
P.S. Wagenmakers
W. van der Werf
Ph. Blaise

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PROCEEDINGS OF THE FIFTH INTERNATIONAL SYMPOSIUM ON COMPUTER MODELLING IN FRUIT RESEARCH AND ORCHARD MANAGEMENT

Editors

P.S. Wagenmakers
W. van der Werf
Ph. Blaise

Wageningen, the Netherlands
28-31 July, 1998

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The Fifth International Symposium on Computer Modelling in Fruit Research and Orchard Management

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FOREWORD

The fifth symposium on modelling in fruit research and orchard management was held at Wageningen (the Netherlands) from 28 to 31 July 1998 under the auspices of the ISHS (International Society for Horticultural Science) and the IOBC-WPRS (International Organisation for Biological Control-West Palearctic Regional Section). It was organised by members of the Working Group on Computer Modelling in Fruit Research and Orchard Management of ISHS and the Study Group on Critical Assessment of Quantitative Approaches in Crop Management of IOBC-WPRS. The meeting was lively, and characterised by a stimulating team spirit. In addition to the papers, there were highly interactive poster sessions and computer demonstrations. The extensive discussions were constructive, open and critical. Thanks are due to the participants who contributed much to make this meeting successful.

Modelling has helped to understand processes underlying fruit production and to elucidate the consequences of management choices for fruit crop productivity. The systems approach could function as a bridge between fundamentally oriented and applied science. This concept functioned as a guiding principle throughout the meeting. Many of the presented models were research models dealing with fruit growth or crop protection, and aimed at understanding processes rather than predicting them. Some were presented as a decision support system. A special workshop was organised to discuss the possibilities and restrictions of models as a tool to increase insight in eco-physiological processes and to provide decision support for growers. This workshop was organised by the IOBC. Inventories were circulated among contributors to the workshop in such a way that effectiveness of modelling could be discussed. This inventory, the according papers and a report of the general discussion are included in this volume. Economic aspects were underexposed during the meeting. In the future, we will need more interaction and linkage between quantitative approaches in crop production, protection and economics. Systems approaches with wider goals are envisaged. New information technologies, especially the Internet, will enable actual application of models. Members of the working group believe in the contact between scientists of different disciplines. It will be a challenge to reflect this in the coupling of models for fruit growth and quality, crop protection, and economics. An intensive use of the working group's web site (http://ishs.ethz.ch) is an opportunity to continue the discussions and may stimulate co-operative ventures. Looking forward to the next meeting in California, in 2001!

Patricia S. Wagenmakers, Wopke van der Werf and Philippe Blaise

PREFACE

This volume of Acta Horticulturae is the proceedings of the ISHS/IOBC Fifth International Symposium on Computer Modelling in Fruit Research and Orchard Management.

Authors of offered oral papers and posters had the opportunity to submit their manuscripts for publication in this volume of the series Acta Horticulturae.

Submitted manuscripts were reviewed by at least two members of the Editorial Board and amended according to the referee suggestions prior to acceptance.
The Editorial Board could not accept all manuscripts submitted for publication.

The ISHS acknowledges the cooperation received from the Editor and Editorial Board on reviewing the manuscripts which was a significant contribution to the overall quality of the publication.

The ISHS Board of Directors

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M.J. Groot and W.A.H. Rossing made valuable contributions to the organisation of the conference, and the editorial skills and efforts of T.A. Atkins, E. Costes, Th.M. DeJong, and R. Habib were essential to get this volume published. We are very grateful for their thorough assistance. The organisational skills of Mrs H.R.M. Kentie and her colleagues of the International Agricultural Centre have been of great value before and during the conference. Mr C. Kortleve gave an enthusiastic tour to research stations and fruit farms, and the rest of the Netherlands. This tour contributed to the understanding of the strengths and weaknesses of the Dutch fruit sector. The sponsorship of the Dutch Fruit Growers Association (NFO) and Horti Bureau Wageningen (Bodata) has contributed considerably to make this meeting successful, and is therefore gratefully acknowledged. The Koninklijke Nederlandse Akademie van Wetenschappen (Royal Dutch Academy of Sciences) aided by a subsidy grant.

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Session 1

General introduction

SYSTEMS APPROACHES AND ECOLOGICAL MODERNISATION OF HORTICULTURAL PRODUCTION SYSTEMS

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Abstract

During the last decades horticultural science started a transition from an empirical, trial and error based science into a scientific discipline which is based on understanding and process knowledge. In the same period, society began to re-assess the role of horticulture using a much wider range of criteria than the traditional achievements of amount of physical product or production value. For horticultural science to contribute to these issues old paradigms need to be replaced by new concepts. In this paper the new challenges and perspectives are described and it is shown how renewal of agricultural and horticultural sciences will enable them to contribute to a new mission in a dynamic society.

1. Introduction

Horticultural science is confronted with a new mission: contributing to ecological modernisation of horticultural production systems. Ecological modernisation may be interpreted as the development of food production systems designed to maintain renewable resources, use non-renewable resources with foresight and recognise the intrinsic value of the environment while providing a decent living for farm families and satisfying the increasing demand for agricultural products (Rabbinge, 1997). The new mission is multidimensional. The old mission, in contrast, emphasised amount of physical product and production value. This new mission takes horticultural science into new domains of knowledge and calls for re-thinking of traditional ways of generating and disseminating information. There are ample opportunities. In this contribution we will explore the changing role of agriculture and horticulture in society, and investigate changes in horticultural research and practice that are needed in response. We will outline traditional concepts in agricultural and horticultural sciences and introduce their successors, radically different concepts, such as used in production ecology, based on systems thinking. Such re-orientation will not only lead to more effective understanding of biological phenomena, but also to better targeting of research at the relevant scales, field, farm and region, as well as at the relevant partners, students, growers and policy makers.

We expect the role of systems approaches in this renewal process to be considerable as they combine a holistic perspective with the power of the reductionistic analysis.

Examples of exploratory, predictive and explanatory studies based on a systems approach will be presented to provide underpinning. The lessons learned from these studies help in setting the research agenda in such a way as to affect the policy agenda in which explorative studies play an important role.

2. Old methodologies and new challenges

Methodologies in agricultural and horticultural science have been inspired upon the successes of farmers and growers who experimented by applying different treatments to their crops and comparing results, primarily crop yield. Until far into the twentieth century agricultural research built upon this approach and focused on 'dose-response' (or, treatment-yield) relations by experimentation at the field level only. Statistics provided a sophisticated toolkit for experimental design and enabled widely applicable recommendations with given confidence limits to be inferred from a limited set of experiments. Discoveries in biological and technical sciences were taken up by agricultural scientists and turned into new opportunities through field experimentation by disciplines such as plant breeding, engineering or crop protection. Key words in this approach were decision, action and recommendation orientation. How much nitrogen to apply, what pest and disease control measures to take, when and how to carry out land preparation, how to prune most timely and most effectively in fruit orchards, when and how to irrigate, what characteristics of new varieties or cultivars were most promising? These were questions, which were addressed with studies and experiments at the field level alone. The success of this approach is apparent from productivity increases in many products and regions all over the world.

The emphasis in agricultural research on widely applicable relations by studying responses at the system (=field) level only, has results in a number of undesirable simplifications: 1., ignoring heterogeneity, 2., ignoring *increasing* returns to *combinations* of inputs and, 3., ignoring integration levels other than the field. The aim of drawing general recommendations from a limited set of experiments at the system level caused heterogeneity in soil, crops or management to be considered a liability. The paradigm of the average reigned. Homogeneity was pursued by stimulating land development, propagating genetically uniform crops, and generic recommendations on uniform, high levels of fertiliser or pesticide supply.

When the response of crop growth to different levels of a *single* input is studied, the result is decreasing input productivity at increasing levels of input. This result, the so called law of diminishing returns, is valid only when one factor is changed under the ceteris paribus assumption that other factors remain constant. In practical agriculture, such conditions are usually not fulfilled in the longer term because investments in one production factor, e.g. improved plant nutrition, will only be made in conjunction with investments in other production factors, e.g. improved water availability or drainage, resulting in synergy between production factors and increasing productivity at increasing levels of input. The law of diminishing returns is a typical example of the field-oriented, statistical approach. Due to this dose-response approach this law of diminishing returns has been over-emphasised at the expense of the phenomenon of increasing returns which constitute an important and fundamental trait of dynamic agricultural production systems. Ignoring this trait constitutes a second serious limitation of the traditional research approach.

The third caveat of the traditional field-oriented approach in agricultural science is the lack of attention for integration levels other than the field. Studies that describe phenomena at the field level in terms of their (cor-)relation to other phenomena at the same level are descriptive in nature and fail to explain causes of observations. As a result, these studies do not offer much more than an analysis of the status quo. Similarly, upscaling to the farm or regional level is usually not pursued, leaving integration of the fragmented information to the farmer or policy maker.

These old concepts are challenged by new approaches. Through better understanding of basic physical, bio-chemical, physiological and ecological processes in plants it becomes possible to base interventions at the system level on insights at process level. The scientific challenge is not only to generate insights at process level, but, particularly, to integrate or synthesize such reductionistic knowledge to the system level. Examples of such integration are found in modern plant breeding which utilizes biotechnology and functional genomics. Processes that have been identified as having a major effect on a crop's field performance are traced to their genetic 'roots' using new molecular and statistical methods such as QTL mapping (Jansen, 1995). Also, behaviour of crops under different climatic conditions, e.g. in other parts of the world or even conditions that are projected to prevail in the future such as increased CO_2 levels, may be inferred from responses of constituent processes. Thus, understanding of functioning of the 'system', whether a plant, a crop or a cropping system, provides a rational basis for predicting system behaviour under new conditions.

Heterogeneity as a liability may be replaced by heterogeneity as an asset when spatially explicit information at the field level can be combined with process-based knowledge. Local fine-tuning of measures, such as timing of harvest or fertilizer and pesticide application, will improve the response at the larger spatial scales. A valuable concept in designing better crop management systems is the target-oriented approach. In this approach, target yield levels are defined on basis of the production situation, i.e. the prevailing conditions for crop growth that can not be changed within one growing cycle, and the ambition level of the grower, in our terminology the production orientation (Rabbinge and Van Ittersum, 1997). These target yields are used to derive the optimal mix of required inputs. Thus, output determines inputs. Usually, a range of output levels is defined in this way. The concept of production situation refers to biophysical factors which cannot be controlled by the grower in the short term but which affect the efficiency of interventions. In poor production situations, e.g. due to adverse climate or poor drainage, input efficiencies per unit product and per unit area will be negatively affected compared to good production situations (Van Ittersum and Rabbinge, 1997). Distinction of yield defining, limiting and reducing factors helps to prioritize crop growth factors and further structures thinking about the impact of interventions (Fig. 1). Target oriented approaches are becoming increasingly possible as the understanding of basic processes increases. They have already proved their usefulness in integrating information and designing new production systems (Rossing *et al.*, 1997b). Scientific problems to be addressed concern the upscaling and downscaling from process to systems level and the other way around. Thus, interventions and improvements based on insight and knowledge may be developed in an iterative and interactive way. The heuristic value of this approach is considerable (Rossing *et al.*, 1997a; Roetter *et al.*, 1998).

3. Society, horticulture and production ecology

The horticultural sector can no longer justify its existence solely by pointing out its achievements in terms of amount of physical product or production value. Society also expects top achievements with regards to external and internal product quality and quality of the production system and its ecology. These quality goals have operational definitions that differ among countries. Whatever form they take, these goals dictate the constraints and limitations within which horticulture has to operate. The renewed mission of horticulture is therefore the development of agro-ecosystems that are productive, efficient and effective in bio-technical, environmental and economic sense and utilize the options and possibilities at crop, farming (cropping) system and eco-regional levels. We have called this new mission 'ecological modernisation'.

To remain relevant for horticulture, horticultural science has broadened its knowledge domain considerably. Research projects dealing with production volume and product quality are supplemented with studies related to resource use: water and pest resistance conservation along with minimisation of external inputs per unit product and unit area. As we argued in the previous section, integrated evaluation of different options in relation to a range of goals has received little attention to date, particularly at integration levels above individual crop production systems. Important unused opportunities for development of modern horticultural systems exist at the farm and eco-regional levels and can be identified through land use studies. Such land use studies put into perspective current comparative advantages of a region, identify limits to achievement of goals and reveal constraints for improvement.

Today, horticultural science still is a discipline-oriented science. The types of studies we advocate typically require synthesis of information as is done when adopting a systems approach. To draw together agronomic, biological and technical knowledge and design new horticultural systems requires unifying concepts, such as the notions of production situation, production orientation and production level described above or the concept of target oriented approaches. We have found these concepts developed in production ecology to be highly valuable for organizing thinking about production systems, for prioritizing process-oriented research and for structuring information from very different disciplinary backgrounds, such as genetics, ecology, plant nutrition, biophysics and molecular biology (Rabbinge, 1993; Rossing and Heong, 1994; Van Ittersum and Rabbinge, 1997).

4. To explain, to predict and to explore using systems approaches

Systems approaches may be used for three purposes: explanation, prediction and exploration. In explanatory studies, systems analysis and simulation are used to gain understanding of the functioning of systems. Integration of basic knowledge and prioritisation of process studies are powerful features of this approach. A structured approach in explanatory studies comprises various phases and steps (Fig. 2). An interactive process of problem identification is followed by phases of quantitative systems modelling and systems design & management. In each of the phases various steps may be distinguished that have been described in detail elsewhere (Rabbinge *et al.*, 1989).

The tools used for analysing system behaviour in explanatory studies, usually simulation models, are often not suitable for the purpose of prediction. The amount of detail needed to explain system behaviour becomes a burden when prediction is the aim because of propagation of errors and input requirements. As a result, predictive (decision support) systems that make use of explanatory models are rare. Nevertheless, systems approaches may contribute to predictive models in two ways. First of all, knowledge of processes determining systems behaviour may lead to informed construction of regression models. Rather than establishing statistical correlation between variables and crop yield or other variables to be predicted in a purely trial and error manner, regression equations may be based on crop ecologically plausible predictors. Alternatively, explanatory simulation models may be used to generate information on systems behaviour under a wide range of external conditions *in lieu* of field experiments. Results may be summarised by regression for use in decision support systems.

Where predictions aim at probable futures, explorative studies sketch possible futures (Rabbinge *et al.*, 1998). In explorations, biophysical limits to horticultural production are confronted with goals and constraints imposed by politics, value systems or individual preferences. Thus, consequences of subjective choices are made visible and trade-offs between objectives or sociological constraints are shown. Options, utopia and dystopia may be made visible and the playing field can be identified. Examples of such studies exist at the level of farms (e.g. flower bulb production systems, Rossing *et al.*, 1997b) and regions (e.g. agricultural production in Europe, Rabbinge *et al.*, 1994). Below we will illustrate the various purposes of systems analysis in case studies.

5. Case studies

5.1. Explanatory studies

To understand the population dynamics in acarine systems, various process and system studies have been done (see e.g. Helle and Sabelis, 1985; Hardman *et al.*, this volume). In an early population dynamical study, Rabbinge (1976) analysed life cycle and interaction in the mite : predator system, *Phytoseiulus persimilis* and *Amblyseius potentillae,* in apple in the Netherlands. Empirical evidence had indicated that the native phytoseiid predators were able to control the phytophagous mite species, but no information was available on the robustness of biocontrol. Measurements on life table parameters were collated in simulation models of population dynamics of pest and predator. Predation was analysed in terms of predator satiation, 'hungry' predators being more voracious than predators with higher degrees of gut filling. The model was tested successfully with experiments on single trees in greenhouses and experiments in an orchard. Based on this understanding of the dynamics of the system, it was demonstrated that biological control could be expected for a wide range of predator-prey ratios, thus corroborating the empirical trust in the self-cleansing potential of the system.

5.2. Predictive studies

To help sugar companies plan their harvest campaign, predictive models of regional sugar yield have been developed (Vandendriessche and Van Ittersum, 1995). The models are usually based on regression of crop yield on one or more environmental variables. The availability of large databases enables evaluation of any combination of regressors with respect to predictive power of the regression equation. However, knowledge of crop growth processes may help to speed up the identification of useful regression models. For predicting the date of full ground cover, Spitters *et al.* (1990) took into account that rates of plant emergence and leaf appearance and leaf area expansion are nearly linearly related to temperature until the stage that plants start to compete for light. The length of the period between sowing and full ground cover was on average 75 days, with a coefficient of variation of 11%. When using the temperature sum approach, variation could be reduced to 5%. To describe production of sugar these authors used a regression model based on intercepted radiation, with radiation use efficiencies calibrated per region. For the major production regions, 77% of the variation in sugar yield between years was explained. The model is proposed as a tool in forecasting sugar beet yields. Results of periodic harvests can be used to update current model predictions.

A methodologically different approach was taken by Rossing (1991) to predict yield losses by cereal aphids in winter wheat. He developed an explanatory simulation model of winter wheat growth and included the major damage mechanisms of cereal aphids, reduction of leaf photosynthesis parameters and uptake of assimilates containing both carbon and nitrogen. The model was found to perform satisfactorily when evaluated using field data from specifically designed experiments. Next, damage by cereal aphids was calculated assuming a hypothetical 'representative' aphid infestation and running the model with different initial crop conditions to create yield levels ranging between 3 and 10 ton/ha. These 'artificial' data were used in regression equations to calculated yield loss per aphid-day (the entomological analogue of degree-day). Compared with other, empirical, damage models, the accuracy of these simulation-based regression equations was found to be similar to the best empirical model when evaluated with 21 sets of field data from different locations.

5.3. Explorative studies

In apple and pear production systems, planting systems were known to affect fruit growth and fruit quality (Wagenmakers, 1991a). Some multi-row systems performed better than single row systems, while the performance of others was inferior to single row systems. The causes of these results were poorly understood and, because of the multitude of interacting factors, hard to approach purely experimentally. In addition, an experimental result at the field level would not yield conclusive insight into the causes of variation between planting systems. Wagenmakers (1991b) used a systems approach to develop a 3-D simulation model of light interception and distribution, which explained performance of orchards differing in tree shape, planting density and planting system. The model was validated with light measurements in different apple and pear planting systems for a range of planting densities and pruning regimes. Deviations between model results and experimental findings were less than 10%. When used to explore various planting designs, the model showed so-called full-field systems with a low rectangularity of planting (ratio of between-row and within-row spacing) to have superior performance. Reasons included the high efficiency of light interception per unit ground area and the advantageous distribution of light inside the canopy. However, current mechanisation is not suited to full-field systems, which do not have tractor alleys, and even multi-row systems are currently under debate because they do not allow use of tunnel sprayers. As a next best solution, the model showed that single rows may perform as good as the theoretical, full-field optimum on the condition of an adapted (larger) tree height. Roughly, single-row trees should be 0.5 m taller than trees in multi-row systems to achieve similar light interception at a given planting density. The model illustrated further that trees planted in a triangular design would require very strong reductions, not only in tree height but in diameter as well, to allow for a light climate comparable to the full-field planting systems. Without these alterations, substantial shading in the centre of these systems would cause serious reductions in fruit growth and aspects of quality. This case study illustrates the role of a quantitative systems approach in testing hypotheses, and using the insights for defining ideotypes of planting systems as well as tree shapes. It was felt that the study increased research efficiency considerably, by greatly reducing the need for field experiments on planting systems and tree shapes, and by providing a tool to organise future thinking about strategic decision making.

An example from a different field, pest management, stems from Van der Werf *et al.* (1996). In a small, illustrative study of crop response to feeding injury by two-spotted spider mite (*Tetranychus urticae*) in cucumber, these authors combined detailed measurements of the effect of the pest on leaf photosynthesis parameters with different scenarios on mite injury distribution over the canopy profile. Specific aim of the study was to investigate the importance of vertical distribution of the pest for designing sampling plans with the purpose of estimating the relationship between injury and damage. The well tested, process-based crop growth model ASKAM (Gijzen, 1992) was used. Total mite injury of 25% of leaf area was distributed over the canopy profile according to 5 different patterns (Fig. 3) and gross photosynthesis and maintenance respiration was calculated for a crop with leaf area index 3, for high and low light intensities. The highest reduction of photosynthesis occurred when injury was concentrated in the top of the canopy. In practice, injury by *T. urticae* will commonly be concentrated in lower leaf layers, or be distributed more or less evenly throughout the canopy. The simulations indicated that for these cases, the shape of the injury profile only marginally affects the relationship between injury and photosynthesis. This suggested that precise observations on the vertical distribution of injury will not be necessary to calculate damage. The simulations also indicated that injury levels up to 40% result in only marginal reduction of crop photosynthesis, provided injury is in lower layers and LAI is not less than 3.

6. Outlook

In this paper we have argued the position that changes in the role of horticulture in society call for renewal of horticultural sciences. Possibilities for such renewal exist and we have outlined the changes in research aims and methodologies needed. In summary, the new research approach can be described as an HRH sandwich at different integration levels (Bouma, 1997), where HRH stands for Holistic - Reductionistic - Holistic. Reductionistic, disciplinary work will help to amplify the scientific basis of horticulture and open up new avenues for development. Explanatory studies, prediction and exploration each have their own role in further developing horticulture and stimulating informed decision making by growers and policy makers.

Renewal of horticultural science will also require scientists with new skills. Disciplinary depth is a necessary but no longer sufficient qualification for horticulturists. There is an urgent need for scientists with T-shaped skills. Familiarity with cutting edge reductionist science in a particular field alongside the capacity to integrate and use information in a larger setting. Context knowledge and understanding of problem identification through interaction with stakeholders are necessary skills of these systems oriented horticultural scientists. There are ample opportunities and rewards for these transitions. There is a demand in society, science becomes more rewarding and the broadening of horizons is stimulating. The opportunities are here to exploit, thus starting a new era of horticulture science in the next century.

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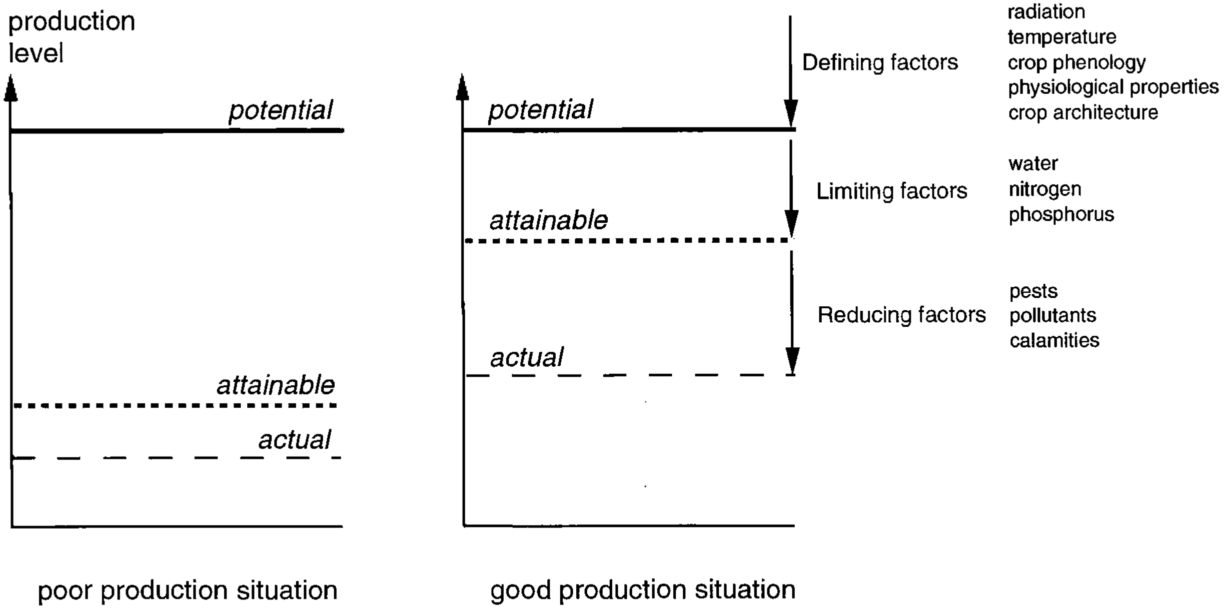

Figure 1 - Production situations, production levels and associated growth factors (from Rabbinge, 1993).

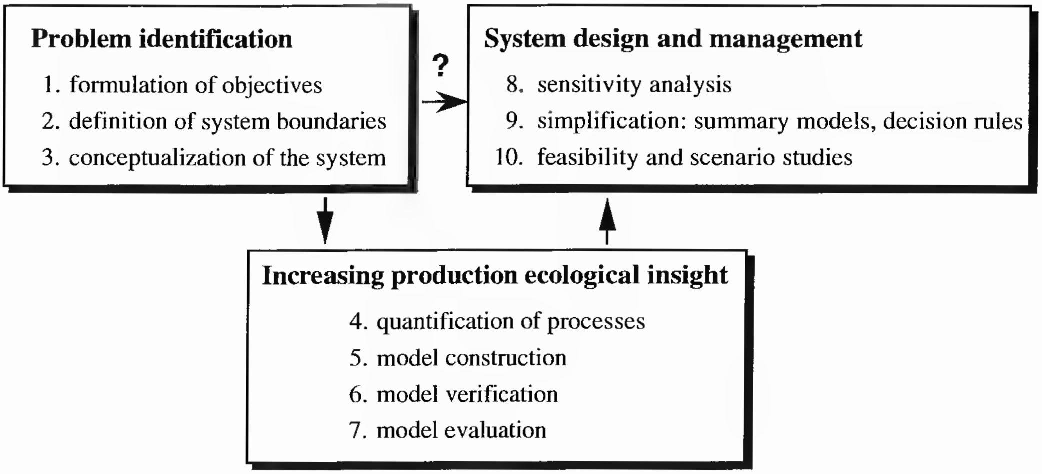

Figure 2 - Developmental phases in systems research (from Rossing and Heong, 1997).

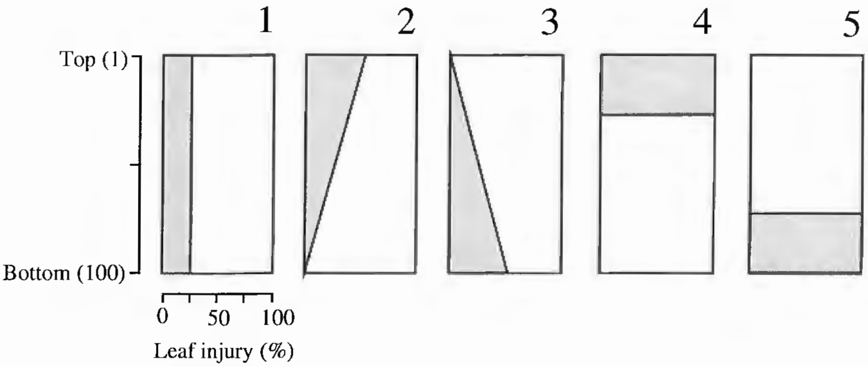

Figure 3 - Five injury profiles used in the simulations of the effect of mite injury on crop photosynthesis of cucumber. Here, the profiles represent a total injury of 25% leaf area.

DIRECTIONS IN MODELLING FRUIT GROWTH AND ORCHARD PROCESSES

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Abstract

This paper is a personal view of the future of modelling in research and technology transfer related to fruit and fruit production systems. The roles that modelling will play in horticultural research and technology transfer will be influenced and enhanced greatly by the availability of new technologies including those for the acquisition, management, and visualisation of data in 3 dimensions; the development of embedded systems technology with communications to central databases for information exchange and updating, principally via Internet or Intranets; and by the will and whims of the funding agencies.

A number of factors currently favour an increase in the use of modelling techniques in research, research management, and technology transfer. I believe we will see a renewed interest in use of models and modelling techniques, though they are likely to continue to be under-utilised as frameworks for managing research programmes and assessing research programme funding decisions. A limit to the use of a modelling approach will be that the educational system will continue to produce insufficient numbers of modellers, and horticultural specialists with generally inadequate IT and quantitative skills.

1. Introduction

Simulation and mathematical modelling have made significant contributions to our understanding of the processes involved in the growth and development of fruit, and the orchard systems which we manage as horticulturalists, and to the extension and application of new technologies in the management of the orchard system. Most of these advances have taken place within the context of broader research and extension programmes. And this is as it should be - modelling is a tool to be utilised for a variety of purposes, especially in horticulture as an applied science. However, it is worthwhile examining modelling directly as an activity in its own right. In this way we can sharpen our use of this tool by developing new techniques, looking for new opportunities for application, and exploring new technologies which may integrate with the modelling approach. By taking a fresh look at modelling activities we can examine modelling from a strategic perspective, and make decisions on directions and needs. Rather than provide a review of the literature, I will identify what I believe to be the areas in fruit research and orchard management which will benefit most through a modelling approach over the next decade.

2. Areas of Contribution

Simulation and mathematical modelling techniques offer significant benefits to a wide range of research and extension activities, and provide benefits in a range of areas including:

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2.1. Synthesizing knowledge

If modern science - heralded by the 'scientific method' - has had a weakness it is in its reductionist approach and philosophy. A consequence of practising 'good science' is to generally isolate the area of study; or as one axiom puts it, to learn more and more about less and less! We can generate immense amounts of information and knowledge about isolated parts of a process or system, but not address the interaction of these elements. As horticultural scientists and extenstion workers we are ultimately interested in understanding and improving the system. Models provide an excellent framework for synthesizing our knowledge about a system or about processes, and enable us to better address the importance of linkages and hierarchies within those systems and processes.

The formal construction of models also forces us to explicitly declare our assumptions about how the process or system works. We are required to separate hard knowledge from commonly held beliefs. With its long history, horticultural science is rife with 'truths' - more so with older established crops such as apples than for a newer crop such as kiwifruit. As a formalisation of our knowledge about a system, and processes within that system, models offer an excellent means of gathering together knowledge into a framework in order to separate assumption from fact, and to identify contradictory ideas and research gaps.

2.2. Generation and testing of hypotheses

Modelling offers an excellent means of generating new hypotheses which can then be tested through experimental means. The framework provided by process and system level models can be used to identify alternate hypotheses or pathways which can be explicitly tested experimentally. In some instances modelling can also be used to test hypotheses. For example, models can be used to provide expected behaviour to be compared against treatment behaviour where controls are expensive or impossible to maintain, and can be used to provide baseline information where the entire system is being affected.

2.3. Developing technologies for the fruit production system

As an applied science, we are concerned with the behaviour of a complex system. We manipulate the orchard system in a number of ways to improve a range of outputs including profitability and environmental impacts. While our research may focus on one element of the overall system, ultimately our impact is dictated by performance of the overall system. Systems level models allow us to evaluate new and proposed technologies. We can gain insight into the likely benefit:costs even before beginning a line of investigation, and we can identify the technical issues most likely to affect implementation of a new technology and so improve likelihood of successful introduction.

2.4. Prediction engines for inclusion in Decision Support Systems

Most Decision Support Systems (DSS) bring together information from a range of sources, often being parameterised with user-supplied information. Models can provide significant, tailored information to DSS including biological and economic outcomes.

3. New directions

Gazing into a crystal ball and predicting where a field of endeavour is going is a risky business - just ask the CEO of a well known major Information Technology company who was once paraphrased as saying he did not believe anyone would seriously be interested in communicating via modem! Despite the dangers of forecasting the directions of technology and scientific endeavour, I think we can see some clear trends which need to be identified.

One of the great drivers of where modelling goes and where it takes us over the next decade is new technologies. There is a natural coupling of modelling with IT-based technologies. The introduction of a new computer technology - Geographic Information Systems (GIS) for instance - removed specific limits to the application of modelling techniques. For example when GIS first became a widely available technology we saw a spate of studies where GIS-supplied information was processed through models of biological and physical systems and the results were then integrated and presented via the GIS format. GIS removed barriers to accessing certain types of information, and to the presentation of modelled outcomes.

Another significant driver of how modelling techniques will be applied is the funding agencies. Modelling goes through cycles of popularity with funding agencies, though the acceptance of modelling as a tool is becoming more generally widespread. The biggest determinant of modelling application of course must be the directions of the science being undertaken at any time - modelling is a tool, not an end in its own right in the horticultural sciences. The following examines what I believe are to be some of the directions that modelling will take over the next decade, and where modelling will take us.

3.1. Resurgence of production systems research

Molecular biology and biotechnology will continue to be significant drivers of scientific endeavour in horticulture over the next decade. Many countries have increased their capacity in these areas at the cost of "traditional" production technology research. At risk of sounding nostalgic, I believe we will see a resurgence of interest in production systems research for two reasons: the need to improve the rate at which new varieties - and indeed entirely new horticultural crops - can be adopted by growers; and the increasing concern of consumers with the environmental consequences of the production system used. Rapid introduction of new varieties and environmental consequences will both become even more dominant factors in the success of horticultural production systems than is the case currently. Models, especially system models, will become increasingly important to meet the time frames involved in the rapid introduction of new varieties and in achieving the efficiency required for profitable production.

3.2. Greater spatial and temporal resolution

It is important to recognise the start and stop nature of research progress. Strong progress in an area of research will be followed by a lull when the relevant measuring and analysis technologies become limiting. An often unrelated breakthrough in technology will then allow the area to advance strongly again. New technologies in acquiring, managing, manipulating, and displaying spatial - and temporal - data will be amongst the most significant in changing the modelling landscape over the next decade. These new technologies - including GIS, 3-D structure-descriptive languages, instruments such as data gloves for the acquisition of high resolution spatial data, and image analysis - allow us to effectively model the next level of increased complexity in the hierarchy of plant and community structures. We will be able to operate explicitly at the level of interest for most orchard management and many fruit growth processes giving much better validation and opening new avenues of research in many of the traditional areas of fruit and orchard modelling such as pests and disease, and phenology. In essence where we currently use stochastic representations of populations of leaves, nodes, pests, etc., we will be able to model explicitly enabling interactions to be considered at a higher level of resolution. Some of the biggest advances over the next decade will come from the linkage of work being done in tree structure and morphology with that being done in pest and disease population dynamics and the physiological processes of fruit growth and development.

3.3. Visualisation and interactivity

An interesting phenomenon in areas of Research & Development such as pharmacology is the advances brought about when information is presented to the researcher as 3-dimensional images instead of numbers, and even more so when tactile feedback is provided in a full immersion virtual reality environment. Literally seeing and touching a representation of the system being studied enables the researcher to draw more meaningful conclusions and to gain deeper insight into the system's workings. As we move away from stochastic representations of populations at the organ level - as discussed in the previous section on resolution - the opportunities for benefits from "visualisation" will significantly increase. Decreasing costs of visualisation hardware and improved software mean greater accessibility to visualisation and immersive virtual reality technology for research, education and technology transfer. The impact of visualisation will be significantly leveraged with the work currently being undertaken on descriptive languages and related statistical analysis methods.

In the area of horticultural education and technology transfer, the use of modelling techniques has been somewhat limited. Widespread use of visualisation techniques will make the benefits from modelling much more accessible for these applications.

3.4. Agricultural economics

Whatever happened to Agricultural Economics?! Models offer an excellent opportunity for examining the economic implications of new technologies prior to development, and for economic optimisation once implemented. However, this is generally a grossly under-utilised feature of system models. In an era of accountability, benefit:cost analysis etc. we see relatively little use being made of system models for the evaluation of technology and the identification of technology needs.

3.5. Modelling techniques

A case in point - why does the ISHS Fruit and Orchard Modelling Working Group exist? Why not just attend for example the IFP conferences or crop-specific conferences? The reason is we need to work beyond the disciplines, to integrate disciplines, and address generic problems of modelling and technique development. Some funding agencies have been reluctant to directly fund the development of new modelling techniques for horticultural application. I expect that over the next decade more effort will need to be made in the development of modelling techniques as the new technologies previously discussed come on stream, and funding agencies will belatedly provide funding to enable techniques to catch up with need.

3.6. Education and technology transfer

Decision Support Systems (DSS) have been seen as an excellent means of transferring technology to industry users, and to assist with its implementation and day-to-day usage. The reality is that relatively few DSS are successfully adopted into long term use. My prediction is that we will see a resurgence in popularity of more prescriptive expert systems using models as significant sources of information, and a reduction in the provision of information directly from models without embedded expertise. This will be accelerated greatly when we see breakthroughs in knowledge representation systems currently being researched in other sectors. I also expect to see an increase in the social research being done on the adoption of DSS to more properly address the reasons behind successful and unsuccessful introductions. A further trend in technology transfer will be a greater use of embedded systems with communications to centralised databases. Embedded systems technology (a good example of which is the computer embedded in your washing machine or microwave) makes sophisticated purpose-built "black boxes" possible. While the concept of converging technologies suggests that there should be a move away from stand alone systems, I believe that many orchardists will continue in their preference for black boxes over at least the first half of the next decade, especially if communications systems such as the Internet enable these black box systems to be routinely and seamlessly updated.

3.7. Who is doing the modelling

We have now had simulation languages such as Stella and Oberon for over a decade, but they have had little impact in horticultural modelling. These types of languages were once perceived to be the way in which discipline scientists would be able to easily take advantage of modelling benefits. I see little scope for change in the type of scientists and technology transfer specialists involved in modelling until the education system which produces them incorporates more Information Technology (IT) and quantitative methods into the training process! Over the next decade we will see a gradual movement towards more use of models in research and technology transfer programmes, but this movement will be limited by the availability of appropriately skilled researchers and technology transfer specialists.

3.8. Framework for research programmes

I believe that modelling will continue generally to be under-utilised as a method of synthesizing knowledge within a field and helping to identify the areas of best endeavour in research programmes from both a scientific and funding perspective. Historically there has been little use of models as programme frameworks in horticulture, and with the quantitative sciences continuing to be generally under-represented in the ranks of the decision makers and funding agencies there is little to suggest that this will change in the near future.

3.9. Communications

The next decade will obviously be focussed in many ways on the exchange of information (principally via the Internet and Intranets) and use of information regionally. We can expect to see models being used increasingly by policy makers using regional databases compiled in real time, and monitoring and forecasting programmes sharing information between regional sites.

4. Conclusions

Modelling in fruit research and orchard management is about to enter another growth phase - driven in orchard management by the use of software to package technology for use by orchard managers and the need for speedy uptake of results; and in fruit research by the use of new technologies for the acquisition, management, and visualisation of model data inputs and outputs, system level environmental consequences of orchards, and the increasing need for more cost-effective research and timely transfer of knowledge to the industry.

Most of the directions I have projected will come about as a natural consequence of ongoing activities. The main areas where there is a need to actively address shortcomings is (1) in the training of scientists and technology specialists who generally get insufficient grounding in IT and quantitative methods; and (2) lobbying of funding agencies to inform them of the benefits available through a modelling approach - including the use of models as frameworks in the setting of research directions and evaluation of technology benefits.

Session 2

Fruit growth and quality

MODELLING FRUIT SET, FRUIT GROWTH AND DRY MATTER PARTITIONING

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Keywords: abortion, allocation, cucumber, simulation, sink strength, pepper, tomato

Abstract

This paper discusses how fruit set, fruit growth and dry matter partitioning can be simulated by models where sink strength (assimilate demand) and source strength (assimilate supply) are the key variables. Although examples are derived from experiments on fruit vegetables such as tomato, sweet pepper and cucumber, the theoretical basis holds for a wide range of crops including fruit trees. Dry matter partitioning is the end result of the flow of assimilates from source organs via a transport path to the sink organs. It appears to be primarily regulated by the sink strength of the sinks, with fruits being the major sinks in fruit trees or fruit vegetables. Source strength has only an indirect effect on dry matter partitioning through effects on the number of fruits on a plant. The transport path is only of minor importance for the regulation of dry matter partitioning at the whole plant level. The growth rate of a fruit depends on the source strength and the fraction of the assimilates partitioned into it.

Dry matter partitioning was modelled as a function of the sink strengths of the plant organs, where sink strength of an organ is defined by its potential growth rate (potential capacity to accumulate assimilates). The potential growth rate has been shown to quantitatively reflect the sink strength of an organ. The potential growth of a fruit is a function of both its age and temperature. In several experiments and for different treatments it was shown that dry matter partitioning into a fruit can be simulated as a function of its sink strength relative to that of the other plant organs.

The number of fruits set per plant has a great impact on the dry matter partitioning and fruit growth. Several experiments have shown that fruit set increases with source strength and decreases with sink strength. Consequently fruit set could be reasonably successful modelled as a function of sink and source strength.

Finally it is shown how a photosynthesis-based model combined with submodels for fruit set, fruit growth and dry matter partitioning can be used for predictions of yield and fruit size.

1. Introduction

Although there is considerable information on the operation of individual processes in plants such as photosynthesis, sugar metabolism, translocation, and cell expansion, the controls which actually regulate the partitioning of dry matter at the crop level are still only poorly understood (Wardlaw, 1990). However, there has recently been quite some progress in quantifying and modelling dry matter partitioning in fruits (e.g. Wermelinger *et al.*, 1991; Grossman and DeJong, 1994) and fruit vegetables (e.g. Dayan *et al.*, 1993; Marcelis, 1994; De Koning, 1994; Heuvelink, 1996).

Besides genotype, developmental stage of the plant, many growth conditions and internal regulation by the plant may all affect dry matter partitioning (e.g. Marcelis, 1996). Only the dry matter partitioned into the harvestable organs contributes to the yield of the crop, indicating the importance of correctly simulating dry matter partitioning. However, for rapid growth of small (young) plants and for early leaf formation in fruit trees dry matter partitioning into the leaves is important, because a large fraction of the light is not yet intercepted by the leaves. Besides, in many fruit crops where harvestable organs are produced over an extended period of the crop's lifetime, an optimum balance between partitioning into the harvestable organs (short-term productivity) and the other plant parts (vegetative parts: future production capacity) should be maintained. Palmer (1986) suggested that for a regular perennial production pattern of apple fruits the fraction of assimilates partitioned into the fruits should not exceed 60-65%. In addition, partitioning relates to product quality, e.g. number versus size of individual fruits.

In this paper the importance of the source, the transport path and the sinks in the regulation of fruit set, fruit growth and dry matter partitioning is discussed. Potential growth rate as a measure of sink strength is evaluated. Models for fruit set, fruit growth and dry matter partitioning are presented in which sink strength (assimilate demand) and source strength (assimilate supply) are the key variables. Finally it is shown how a photosynthesis-based model combined with submodels for fruit set, fruit growth and dry matter partitioning can be used for predictions of yield and fruit size. Although examples are derived from experiments on fruit vegetables such as cucumber, sweet pepper and tomato the theoretical basis holds for a wide range of crops including fruit trees.

2. Regulation of dry matter partitioning

Dry matter partitioning is the end result of the flow of assimilates from source organs via a transport path to the sink organs. Source organs are defined as organs with a net export and sink organs as organs with a net import of assimilates. In cucumber no noticeable relationship between the fraction of dry matter partitioned into the fruits and solar radiation of the same day or week was observed during a growing season (Liebig, 1978; Marcelis, 1992a). However, a large change in solar radiation seemed to induce a change in dry matter partitioning to the fruits, but the time lag between the change in radiation and the change in partitioning was variable (Marcelis, 1992a). The limited direct effect of irradiance on dry matter partitioning, is substantiated by an experiment where cucumber plants of identical size and with a fixed number of fruits were shaded for 4 days (Marcelis, 1993c). Total plant growth rate decreased by 60%, but the partitioning between generative and vegetative growth was not significantly affected. Heuvelink (1995b) also concluded for tomato that source strength, varied by plant density, had no direct effect on dry matter partitioning between generative and vegetative parts.

Although effects of source strength (radiation) in the short term may be limited, in the long term increased source strength may increase the number of fruits on the plant and hence indirectly effect the dry matter partitioning (Marcelis, 1993c).

Despite the fact that, in some cases, partitioning is related to the relative distance between sinks and sources (Cook and Evans, 1983), distance is generally not an important factor in dry matter partitioning at the whole plant level (e.g. Marcelis, 1996). It has been shown that increasing the distance between source leaves and fruits had no effect on fruit growth in apple (Hansen, 1977) and cucumber (Schapendonk and Brouwer, 1984). Heuvelink (1995c) showed that in tomato plants with two shoots and a shoot length of more than 2m dry matter partitioning between vegetative and generative parts was not affected whether the fruits were located on only one shoot or whether the same number of fruits were divided over the two shoots.

The fruits appear to be the major sinks in fruit crops and the dry matter partitioning into the fruits positively correlates with the fruit load (number or weight of fruits on a plant) (Marcelis, 1992a; 1993b; Heuvelink and Buiskool, 1995). In tomato, Heuvelink (1995a), observed no direct effect of an increase in temperature on dry matter partitioning in the short term. However, De Koning (1994) and Marcelis (1993b) observed an increased dry matter partitioning into the fruits with increase in temperature in the short term for tomato and cucumber. In the long term this effect diminished, because the fruit load decreased with increasing temperature (De Koning, 1989; Marcelis, 1993b). Bhatt and Srinivasa Rao (1989) also observed that in the long term temperature had no effect on dry matter partitioning in pepper.

As discussed in more detail by Marcelis (1996) it can be concluded that neither the source (assimilate supply) nor the transport path between source and sink organs are dominating factors in regulating dry matter partitioning at the whole plant level and that dry matter partitioning among plant organs is primarily regulated by the sinks.

3. Potential growth rate as a measure of sink strength

As partitioning is primarily regulated by the sinks, for a simulation model it is necessary to find a parameter that quantitatively reflects the sink strength. The term sink strength used here refers to the competitive ability of an organ to attract assimilates and is defined as the potential demand or potential capacity of an organ for assimilate accumulation. This potential capacity can be quantified by the potential growth rate of a sink, i.e. the growth rate under conditions of non-limiting assimilate supply. Conditions for potential growth can be created by growing plants at a high irradiance and/or reducing the number of sinks on a plant. Sometimes problems may arise in measuring the potential growth rate of the vegetative parts (Marcelis, 1994; Heuvelink, 1996), while in sweet pepper potential growth rate of the fruits is hardly measurable as in many fruits blossom-end rot occurs when assimilate supply is high (Marcelis, unpublished). As the potential growth rate of vegetative parts is hardly measurable, Marcelis (1994) and Heuvelink (1996) indirectly estimated the vegetative potential growth from calculated potential fruit growth and from measured dry matter partitioning between fruits and vegetative parts.

Potential growth rate is not a static parameter but may change with e.g. developmental stage or temperature, but not with factors such as light intensity or CO_2 concentration which are assumed to affect only the availability of assimilates. In seeded fruits the potential growth rate may also increase with number of seeds set (Marcelis and Baan Hofman-Eijer, 1997). During development of an organ the potential growth often shows a sigmoid growth pattern (Marcelis, 1992b). Effects of temperature on growth rate are often confounded with effects of the developmental stage. Marcelis and Baan Hofman-Eijer (1993) showed that the development of a cucumber fruit was closely related to the temperature sum and that the effect of temperature on the growth rate of a fruit could be separated from developmental effects by considering growth as a function of the temperature sum. As development is related to temperature sum, the growing period (in days) decreases with increasing temperature. The growth rate of organs usually increases with increasing temperature (Marcelis and Baan Hofman-Eijer, 1993). However, Heuvelink and Marcelis (1989) and De Koning (1994) did not observe a significant effect of temperature on potential growth rate of tomato fruits. When growth of a cucumber fruit was not limited by assimilate supply, the increase in growth rate with increasing temperature was much higher than at a lower level of assimilate supply (Marcelis and Baan Hofman-Eijer, 1993). As the level of assimilate supply affects the magnitude of the response of the growth rate to temperature, final organ size at a high assimilate supply may increase whereas the final size at a low assimilate supply may decrease with increasing temperature (Marcelis and Baan Hofman-Eijer, 1993).

Cell number has often been proposed to be an important determinant of sink size. However, in cucumber fruits grown at non-limiting assimilate supply, a small number of cells, due to a low assimilate supply during early fruit development, was to a great extent compensated by an increased expansion rate of individual cells (Marcelis, 1993d). Therefore, cell number seems not to be an important determinant of fruit size, although fruit size often correlates positively with cell number (Marcelis, 1993d).

As in many situations the size correlates with the age of an organ, often an apparent relationship between sink size and sink strength is observed. However, the actual growth rate of a cucumber fruit appears to depend on its age rather than its size (Marcelis, 1993d). Different weights of cucumber fruits were achieved by retaining no or 6 competing fruits during 6, 12 or 18 days. Despite strong differences (>300%) in fruit weight, a few days after removal of the competing fruits the small fruits grew almost at the potential rate, i.e. the growth rate of fruits which were grown without competing fruits throughout (Fig. 1). A small size was fully compensated by an increased relative growth rate, indicating the sink strength is reflected by the potential growth rate rather than the potential relative growth rate. Comparable results were observed for tomato fruits (De Koning, 1994). However, in peach generally fruit growth did not fully reach the potential growth rate after removal of competing fruits (Grossman and DeJong, 1995).

4. Simulation of dry matter partitioning

Sink regulation models are most suitable for simulation of dry matter partitioning in fruit crops (Marcelis, 1993a; Marcelis *et al.*, 1998). These type of models have been described in detail for cucumber and tomato by Marcelis (1994) and Heuvelink (1996). In these models the plant is considered to consist of a set of sink organs which receive their assimilates for growth from one common assimilate pool, which is replenished by photosynthesis in the source organs. Part of the assimilates from this pool is used for maintenance respiration and the remaining assimilates are available for growth. Growth respiration of an organ is linearly related to its growth rate. The growth rates of the organs are determined by the amount of assimilates in the assimilate pool and sink strengths of the organs. Differences in growth rates between sink organs and hence dry matter partitioning depend on differences in sink strengths.

The time step of the model is one day. Firstly the number of fruits on the plant is calculated as a function of the rates of fruit appearance, fruit abortion and fruit harvest. The age of each fruit is determined and the sink strengths of the organs are calculated. Then the available assimilates are distributed among the sinks; the fraction of dry matter distributed to a sink i (f_i) equals its sink strength (S_i) relative to the total sink strength of all sinks together (ΣS):

$f_i = S_i / \Sigma S$ (Eqn. 1.)

The sink strength or potential demand for assimilate accumulation is quantified by the potential growth rate of the organ (as described above). The potential growth of an organ is a function of its age and temperature (Heuvelink and Marcelis, 1989; Marcelis and Baan Hofman-Eijer, 1993, 1995; De Koning, 1994). Some authors (e.g. Buwalda, 1991) used the potential relative growth rate as a measure of sink strength instead of the absolute potential growth rate. Moreover, in some models sink strength also depends on the current size of the organ (e.g. Grossman and DeJong, 1994; Goldschmidt et al., 1992).

The potential growth rate of the vegetative parts has been simulated either as a constant or a function of plant developmental stage (Heuvelink, 1996) or a function of the temperature (Marcelis, 1994). For cucumber fruits, the simulation of partitioning among individual fruits was improved when the sink strength of each fruit was not only dependent on its potential demand for assimilates but also on its affinity or priority for assimilates (Marcelis, 1994).

The growth rate of a sink organ (Y_i) is obtained by multiplying the total dry matter production of the plant (*source*) by the fraction of dry matter partitioned into the fruits (f_i) or by multiplying the sink strength of the organ (S_i) by the source/sink ratio ($source/\Sigma S$):

$$Y_i = source \times f_i$$
$$Y_i = source \times S_i / \Sigma S$$
$$Y_i = S_i \times (source / \Sigma S) \quad \text{(Eqn. 2.)}$$

When the daily assimilate supply exceeds the daily total potential growth rate, the growth rate of each sink occurs at its potential rate. In that case the assimilate pool is not totally depleted (reserves are formed). For cucumber and tomato, negative feedback on photosynthesis does not need to be included in the model, because in these crops this phenomenon does not seem to occur under normal growing conditions in greenhouses (Marcelis, 1991; Heuvelink and Buiskool, 1995).

The number and timing of fruits on a plant has a strong impact on the total sink strength of a plant and hence on dry matter partitioning. For instance in sweet pepper strong fluctuations in fruit harvest could be ascribed to strong fluctuations in fruit abortion two months prior to harvest (Marcelis, Dogliotti and Heuvelink, unpublished). The formation rate of non-aborting fruits is one of the weakest features of explanatory crop models.

In several reproductive crops like apple (Baumgärtner *et al.*, 1986), citrus (Goldschmidt *et al.*, 1992), cucumber (Marcelis, 1994), grape (Gutíerrez *et al.*, 1985; Wermelinger *et al.*, 1991), kiwifruits (Buwalda, 1991), peach (Grossman and DeJong, 1994), sweet pepper (Marcelis, Dogliotti and Heuvelink, unpublished) and tomato (De Koning, 1994; Heuvelink, 1996) dry matter partitioning has been successfully simulated by models based on sink strengths. For tomato, cucumber and sweet pepper this approach has proven its validity for simulating both the dynamics and average level of dry matter partitioning in a number of experiments covering effects of planting date, plant density, number of fruits per truss (Fig 2), number of trusses and shoots per plant and temperature. Besides partitioning between vegetative and generative plant parts, individual organ growth like tomato trusses (Heuvelink, 1996; Fig. 2) or cucumber fruits (Marcelis, 1994) could be predicted reasonably well. Modelling dry matter partitioning based on sink strengths of organs is promising, as it is a generic, dynamic and flexible approach, showing good agreement between measurements and simulation for a range of conditions.

5. Simulation of fruit set

Abortion of flowers and fruits may increase with decreasing number of seeds per fruit (Picken, 1984; Marcelis and Baan Hofman-Eijer, 1997), decreasing air humidity (Bakker, 1991) or increasing temperature (Picken, 1984; Marcelis, unpublished). However, the main determinant of fruit abortion appears to be the source/sink ratio during a short period before and after anthesis, as observed in tomato (Kinet, 1977), cucumber (Schapendonk and Brouwer, 1984; Marcelis, 1992a) and sweet pepper (Marcelis, unpublished).

In several experiments with sweet pepper and cucumber it was tested whether fruit set can be modelled as a function of the sink and source strength. Total dry matter production was used as a measure for source strength and potential growth rate of the plant organs as a measure for sink strength. A decrease in plant source strength by decreasing inter-plant distance, light intensity or by leaf removal led to a decrease in fruit set in sweet pepper (Marcelis and Heuvelink, unpublished). In a glasshouse experiment the average fraction of fruits that set was 8, 10 and 16% at a within-row plant distance of 0.27, 0.40 and 0.80 m, respectively. In a glasshouse experiment where 0, 20, 40, 60 or 80% of the leaves were removed in an early stage, fruit set was 78, 69, 67, 50 and 50%, respectively. In a climate room experiment (13 flowers were retained per plant) fruit set was 25, 38, 54 and 92%, at light intensities of 1.1, 1.8, 2.8 and 4.8 MJ PAR m^{-2} d^{-1}, respectively. While fruit set increased with increasing source strength, it decreased with increasing plant sink strength. In an experiment with 0, 1, 2 or 4 early formed fruits, fruit set of six later formed fruits was 78, 56, 28 and 6%, respectively (Marcelis and Heuvelink, unpublished).

As can be seen in Eqn. 2 the growth rate of an organ is proportional to the source/sink ratio $(source/\Sigma S)$ when its sink strength (S_i) is constant. Assuming sink strength of the vegetative parts to depend only on temperature, at constant temperature conditions the vegetative growth rate is proportional to the source/sink ratio. As it is easier to measure the vegetative growth rate than the source/sink ratio, we experimentally quantified the relationship between vegetative growth rate and fruit set or abortion at constant temperature. In cucumber the fluctuations in fruit set during a growing season correlated with the variations in growth rate of the vegetative plant parts and hence with the source/sink ratio (Marcelis, 1992a). Usually we observed that a decrease in growth of the vegetative parts was accompanied by a decrease in number of young non-aborting fruits, while a time lag often occurred between an increase in vegetative growth and number of young cucumber fruits. In sweet pepper we also observed a positive correlation between fruit set and vegetative growth rate. However, a decrease in vegetative growth rate as a result of more competing fruits had a stronger impact on fruit set than as a result of a decreased number of leaves (source strength). This may indicate that some hormonal control due to dominance of competing fruits might be involved.

Fluctuations in fruit set during a growing season could be reasonably predicted from the source and sink strength in sweet pepper (Fig. 3). Although the average rate of fruit set in cucumber and sweet pepper could be reasonably predicted from the source and sink strength, for individual plants this relationship showed a large variation.

In conclusion, the average rate of fruit set can be reasonably predicted from the source and sink strength. Nevertheless, a better understanding of fruit abortion is necessary to improve the simulation of fruit set as this has a strong impact on the simulation of dry matter partitioning. Maybe stochastic elements or hormonal control should be incorporated in these models. Developing a truly predictive submodel of fruit set still is a great challenge.

6. Prediction of yield and fruit size

The market as well as modern farm management require prediction of yield and quality of harvested fruits in advance. For cucumber a mechanistic photosynthesis-based dynamic growth model was developed to predict the weekly fresh weight yield and the fresh weight and developmental stage of the individual fruits at harvest (Marcelis and Gijzen, 1998a). The latter two being major criteria of fruit quality. The model consists of modules for greenhouse light transmission, light interception by the crop, leaf and canopy photosynthesis, assimilate partitioning, dry matter production, fruit growth, fruit dry matter content and fruit harvest. Dry matter partitioning was simulated as a function of sink strength and fruit set as a function of the source/sink ratio. The model was validated by comparing simulation results based on actual climate data with production data of 10 commercial growers (Marcelis and Gijzen, 1998a). Input data used for validation were week numbers of planting and removing the crop, weekly data on global radiation outside the glasshouse and glasshouse air temperature and daytime CO_2 concentration. The average error of the weekly prediction of the fresh weight yield averaged over all growers was 12.6%, while the error of the annual yield was only 0.3%. The simulated average fruit size corresponded reasonably well with growers' data, showing an average weekly error of 6.6%.

For predictions of production long-term average weather data were used (Marcelis and Gijzen, 1998b). Only the date of planting of the crop and date scheduled for the last harvest were used as input to the model. To keep the use of the model as simple as possible, average values were assumed for all other factors, e.g. plant density, fruit pruning, frequency of harvesting, cultivar properties. Depending on availability of data and objective of the prediction, the model calculations can be based on more or fewer input data. The average error of the weekly prediction of the fresh weight yield averaged over all growers was 14.9%, while the error of the annual yield was 2.8% in 1996 (Fig. 4A). The predicted average fruit size corresponded reasonably well with growers' data, showing an average weekly error of 6.5% (Fig. 4B).

Marcelis and Gijzen (1998a,b) showed that a mechanistic photosynthesis-based dynamic growth model can be applied for accurate predictions of cucumber yield and fruit size. Such predictions can be used for optimising the price setting, logistic arrangements and marketing of the produce. As growth as well as farm specific conditions are variables of the model, such a model is also a promising tool to control the quantity and quality of the produce such that it better fits to the demand by retailers or consumers. For instance, effects of future cultivation measures and climate set-points on crop growth and harvest can be calculated, so that the most appropriate strategy can be chosen.

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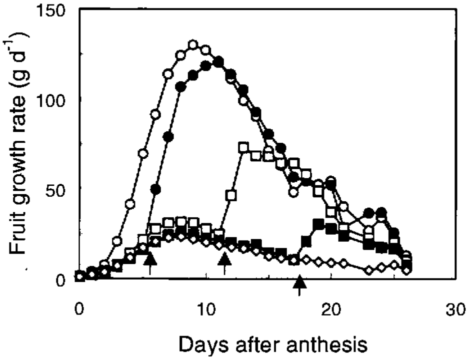

Figure 1 - The fresh weight growth rate of cucumber fruits when growth was constrained by assimilate supply for 0 (○), 6 (●), 12 (□), 18 days (■) or continuously (◇). Assimilate supply was constrained by retaining six competing fruits (from Marcelis, 1993d). Arrows indicate when competing fruits were removed.

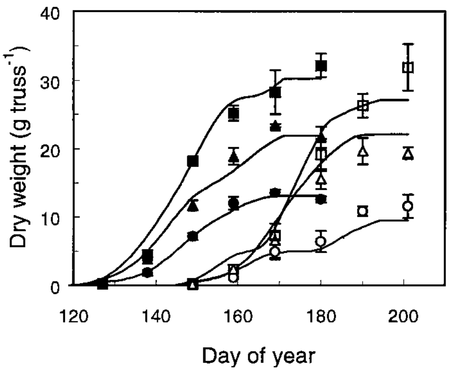

Figure 2 - Measured (●,▲,■: 3rd truss; ○, △, □ : 7th truss) and simulated (—) truss growth curves for tomato plants with 3 (○,●), 5 (△,▲) and 7 (□ , ■) fruits per truss. Daily plant biomass increase and greenhouse air temperature were input in the model, partitioning was simulated based on potential growth rates (from Heuvelink, 1996).

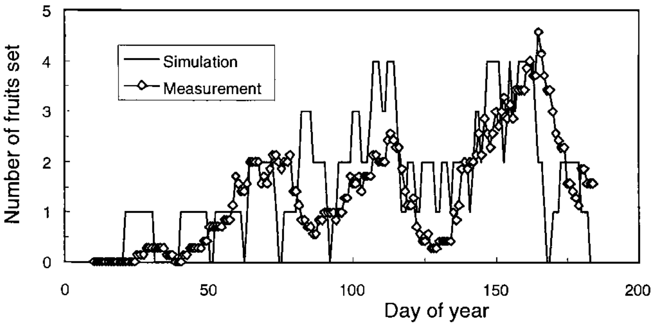

Figure 3 - Measured and simulated fruit set in sweet pepper. Fruit set was simulated as a function of source and sink strength (Marcelis, Dogliotti and Heuvelink, unpublished)

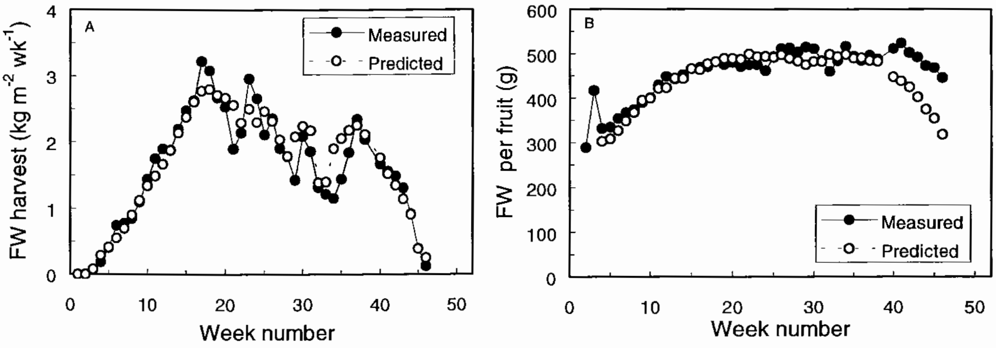

Figure 4 - Predicted and measured weekly fresh weight harvest (A) and average fresh weight per fruit (B). Data are means for 10 commercial growers. Predictions are based on long-term average weather data (from Marcelis and Gijzen, 1998b).

A SIMULATION PEACH GROWTH MODEL AT THE SHOOT BEARING FRUIT LEVEL: FRUIT GROWTH VARIABILITY AND RESERVE KINETICS

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Keywords: Prunus persica, fruit growth, vegetative growth, carbohydrate partitioning, reserve kinetics, model

Abstract

A simulation model of carbon supply and demand for vegetative and reproductive growth of peach was developed for shoots bearing fruit. The model considers three compartments: the one-year-old stem, the leafy shoots and the fruits. The model simulates daily and seasonal photosynthetic carbon assimilation using canopy light interception and demand effect on potential photosynthesis. Carbon partitioning and organ growth are simulated using organ-specific potential growth of each organ type, and allocation rules. The model takes into consideration the reserve kinetics with phases of mobilisation and accumulation depending on the supply-demand differences. The model reproduced a great part of the fruit growth variability observed on different experiments conducted on early and late maturing peach cultivars. Results from simulations undertaken with different leaf-to-fruit ratios are discussed highlighting on photosynthesis regulation, reserve kinetics effects and dry weight partitioning.

1. Introduction

Nowadays, fruit quality is an important challenge for fruit growers, who are especially induced to improve the homogeneity of products. An important variation of fruit size is observed at different levels of organisation: within the tree, among trees in an orchard and among orchards. A key level is the tree level, where most of the variation emerges (Marini and Trout, 1984, Dann and Jerrie, 1988), and because the tree is the target of most of technical interventions. Thus, modelling fruit growth with emphasis on within-tree variability is a crucial step for helping the management of fruit quality through horticultural practices.

Many models of carbohydrate assimilation and partitioning have been proposed for deciduous fruit crops (for example: Seem *et al.*, 1986; Abdel-Razik, 1989; Buwalda, 1991; Wermelinger *et al.*, 1991; Grossman and DeJong, 1994). These models are useful but they handle organ groups in the tree (fruits, leaves, stems, roots, etc.) and thus do not account for any within-tree variability. One way to address this serious limitation is to consider a level of organisation lower than the tree. Shoots bearing fruit are convenient subunits because they are large enough to subsume most important physiological processes on the one hand, and they are basic units for the most important horticultural interventions on the other hand. Moreover, they can be considered as relatively autonomous subunits concerning carbon flow

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(Sprugel *et al.*, 1991). Thus, we propose that the shoot bearing fruit is a useful unit for understanding the within-tree variability and we suggest that modelling isolated shoots is needed in a first step for the sake of clarification.

The objective of this paper is to present a model of assimilation and partitioning of carbohydrates at a shoot bearing fruits level isolated from the rest of the tree which is able to reproduce the fruit growth variability. The paper points out the internal behaviour of the model and especially the reserve kinetics.

2. Materials and Methods

The shoot bearing fruit is subdivided into three compartments: fruits, one-year-old stem and leafy shoots. The two last compartments are subdivided into a structural part and a reserve part. The model runs on a daily basis, except for photosynthesis that is computed hourly. The physiological processes considered are leaf and fruit photosynthesis, reserve mobilisation, maintenance and growth respiration of organs, growth of leafy shoots and of fruits, and finally allocation of reserves to the storage parts (Fig. 1).

The model calculates the carbon assimilation by the leaves, based on the total leaf area, light interception and the level of reserves in the leaves. The amount of reserve on the leaves for a given day determines the leaf light saturated photosynthesis for that day. The calculation of the photosynthesis rate uses the equations of Higgins *et al.* (1992). During that calculation a separation of the total leaf area into a sunlit and a shaded component is made. Carbon assimilation by fruits is calculated similarly (monomolecular response of photosynthetic rate to radiation and separation of sunlit and shaded fruit).

Carbon partitioning is based on organ demands and priority rules. Maintenance respiration costs, which are calculated on the Q10 concept basis, have first priority as in other models (e.g., Buwalda, 1991; Wermelinger *et al.*, 1991; Grossman and DeJong, 1994) to account for the fact that the first priority is to maintain the system. The vegetative growth and the reproductive growth are given second and third priority, respectively. This choice is based on different experiments on peach girdled shoots bearing fruit where no effect of fruit crop on leafy shoot dry weight was observed (Ben Mimoun *et al.*, 1998).

The daily carbon demands for growth (including growth respiration costs) are based on analytical formulations of the potential growth in terms of degree-days. The corresponding equation is linear with an effect of the initial weight for the leafy shoots, and is a mixture of logistic (in terms of accumulated growth) and temporal factors for the fruits.

The model considers also the mobilisation and accumulation of reserve on a daily basis. If the amount of carbohydrate assimilated for a given day is larger than the total demand of the organs and the maintenance respiration, an accumulation of assimilates occurs. The reserves are accumulated first in the leafy shoot compartment and when this compartment is saturated (dry weight of reserves in leaves exceeds a fixed fraction of the total dry weight of leaves), the remaining reserves are allocated to the one-year-old stem.

If the total demand is larger than the assimilation, a mobilisation of assimilates happens. Reserve are mobilised first from the leafy shoot and after from the one-year-old stem.

A complete description of the model including the different equations can be found in Lescourret *et al.* (1998).

3. Results

The model was tested using data from 7 experiments on vegetative and reproductive growth performed in two locations, Avignon (southern France) and Gotheron (120 km north of Avignon), during the years 1992 to 1996 and concerning two peach cultivars: 'Alexandra', an early maturing cultivar, and 'Suncrest', a late maturing cultivar.

The data presented in this paper concern only data from Avignon 1994 for the Suncrest cultivar (denoted SunAv94 in the following) both for test and simulation. The simulation starts at the beginning of the second stage of fruit growth (350 dd after bloom) and for three levels of leaf-to-fruit ratio (L:F): 5 leaves per fruit at the beginning of the simulation (6 fruits per shoot bearing fruits), L:F=15 (2 fruits) and L:F=30 (1 fruit). It uses the conditions of SunAv94 (light, temperature, and initial dry weights of the organs of the monitored shoots).

3.1. Fruit growth variability

The model reproduces successfully the fruit growth variability observed in the experiments between the different shoots bearing fruits (Fig. 2).

3.2. Carbohydrate assimilation

Carbohydrate assimilation increases throughout the season (Fig. 3). This increase reflects the increase of the leaf area. The production of assimilates on L:F=5 is higher than in the other treatments.

3.3. Carbohydrate partitioning

Fruit growth is the most important sink (Fig. 4). Forty to 65% of the total amount of carbohydrates, depending on the L:F ratio, is used by the fruit. The amount of carbohydrate partitioned to the fruit increases throughout the season before decreasing with the fruit maturity. Vegetative growth is the second sink.

3.4. Reserve kinetics

For the reserve simulation, the minimum, maximum and mean initial dry weights of organs are used. All the initial reserves are mobilised for both L:F=5 and L:F=15 treatments (Fig. 5). In both cases, an accumulation of assimilates occurs when the fruit reaches maturity. For the L:F=30 treatment, there is a reserve mobilisation in the case of minimum and mean initial dry weight during some days of the simulation with low solar radiation. Most of the time there is an accumulation of assimilates in both the one-year-old stem and the leafy shoot.

4. Discussion

The model was developed as a tool to analyse the effect of environmental factors and horticultural practices on fruit growth and quality. The model partly reaches this aim because it allows the simulation of the variability between shoots bearing fruits according to environmental conditions and leaf to fruit ratio, which is determined by thinning. The model allows testing the effect of modifications in the environmental factors and the source-sink relationships, which could help understanding the different factors behind the fruit growth variability and their respective importance (Génard *et al.*, 1998).

The model is also an interesting tool to understand the functioning of the whole system and analyse the interrelations between carbohydrate assimilation and partitioning. For example, the higher assimilation simulated by the model for L:F=5 indicates that photosynthesis rate is higher for that treatment since the leaf area is the same than in the other treatments. This result is to relate to the absence of reserve in the leaf (Fig. 5) which causes a higher light saturated photosynthesis rate. For L:F=15, the assimilation rate is also important and there is a high fruit growth rate. This indicates that the efficiency of the system is higher for that treatment than for the two others since on L:F=5 the photosynthesis rate is at its potential but the fruit growth rate is low. On L:F=30 the fruit growth is at its potential but the assimilation rate is low.

For the reserve kinetics, the model shows that an accumulation or a mobilisation of reserve could happen throughout the whole season. This result is interesting to consider for reasoning the horticulture interventions. Presence of more assimilates than the demand (accumulation of reserve) during the summer could affect the bud initiation for the next season and so the production of next year. The model could be used to find L:F ratio where such conditions exist throughout the season.

In conclusion, this model represents an interesting step to understand the fruit growth variability, but it needs to be pursued at the tree level taking into account the interrelations existing between the different shoots bearing fruits and also with the roots.

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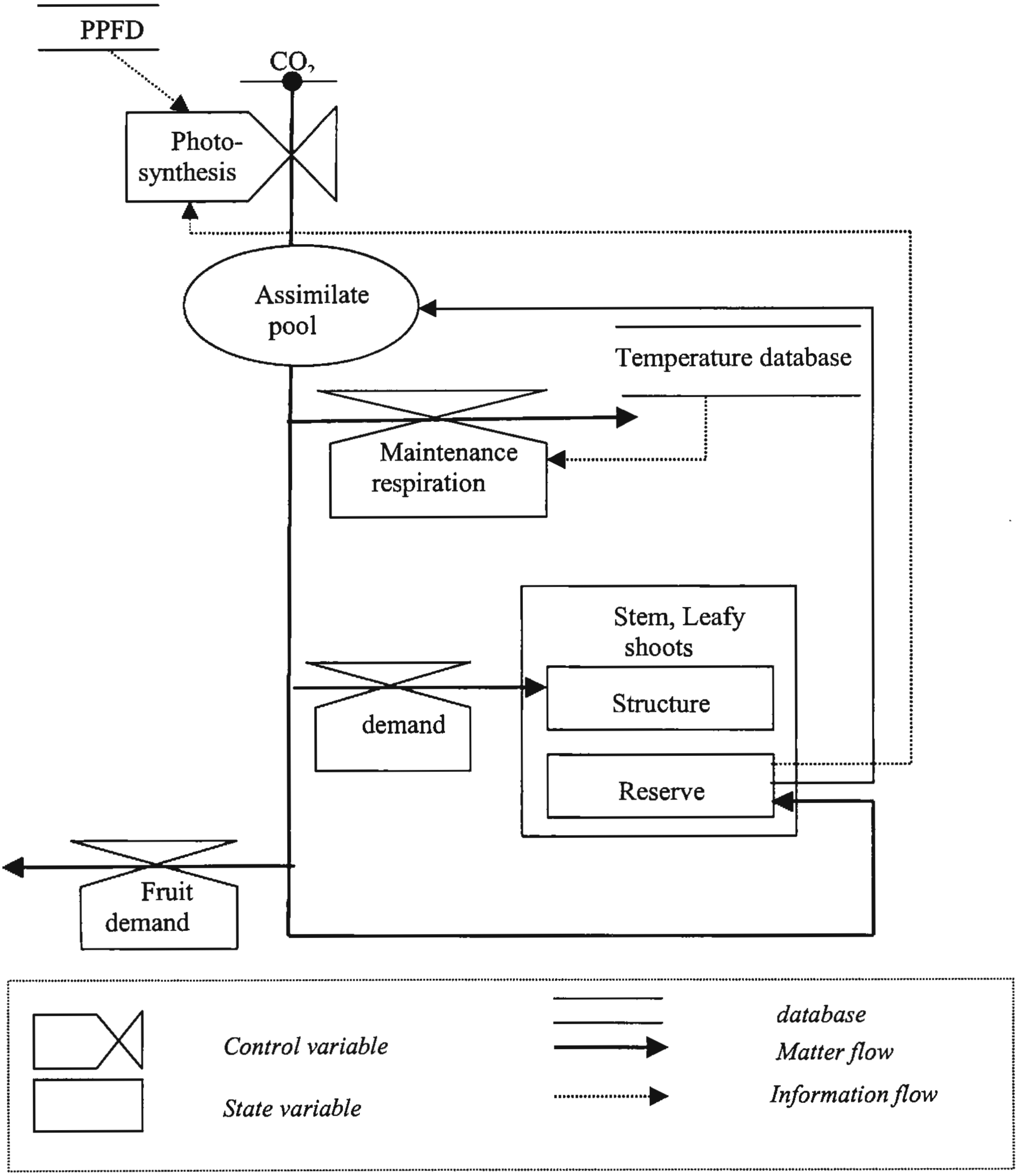

Figure 1 - Schematic representation of the model.

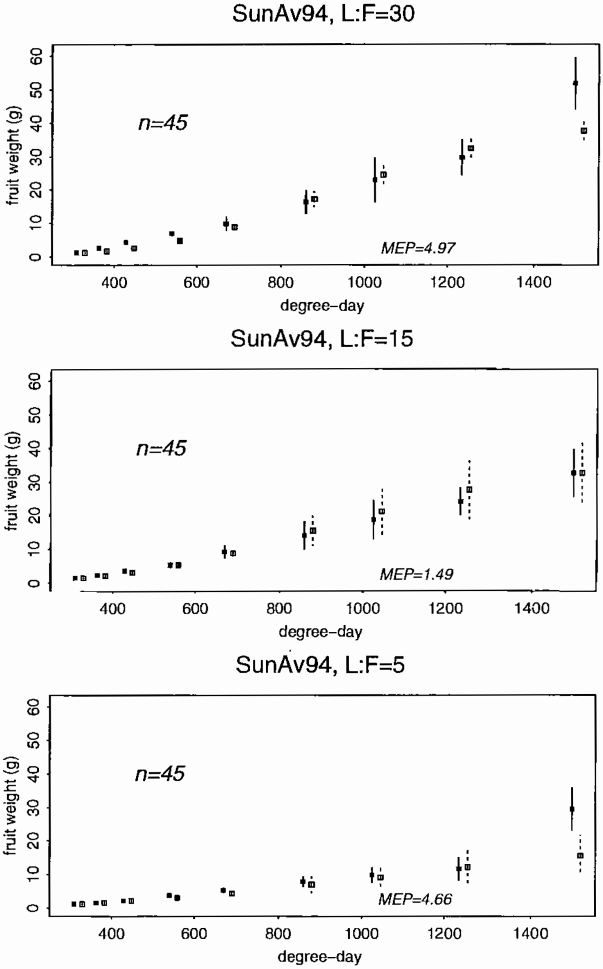

Figure 2 - Test of the model against the SunAv94 experimental data, for several leaf-to-fruit ratios: variation of mean fruit growth among monitored shoots according to degree-days (mean ± sd), either observed (black squares and full lines) or simulated (white squares and dotted lines), and mean error of prediction (MEP).

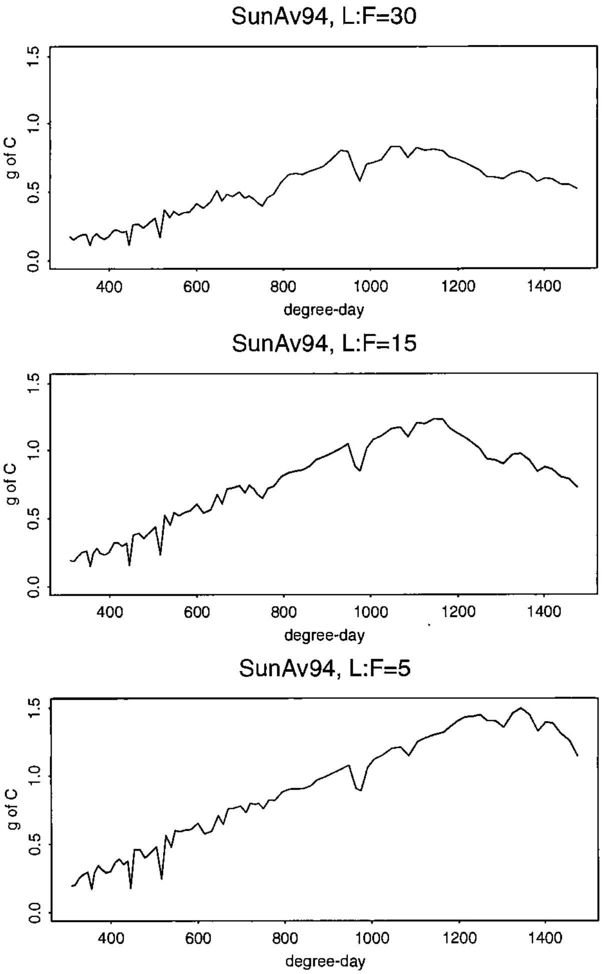

Figure 3 - Model simulation of daily carbohydrate assimilation during the period of growth (dd after bloom).

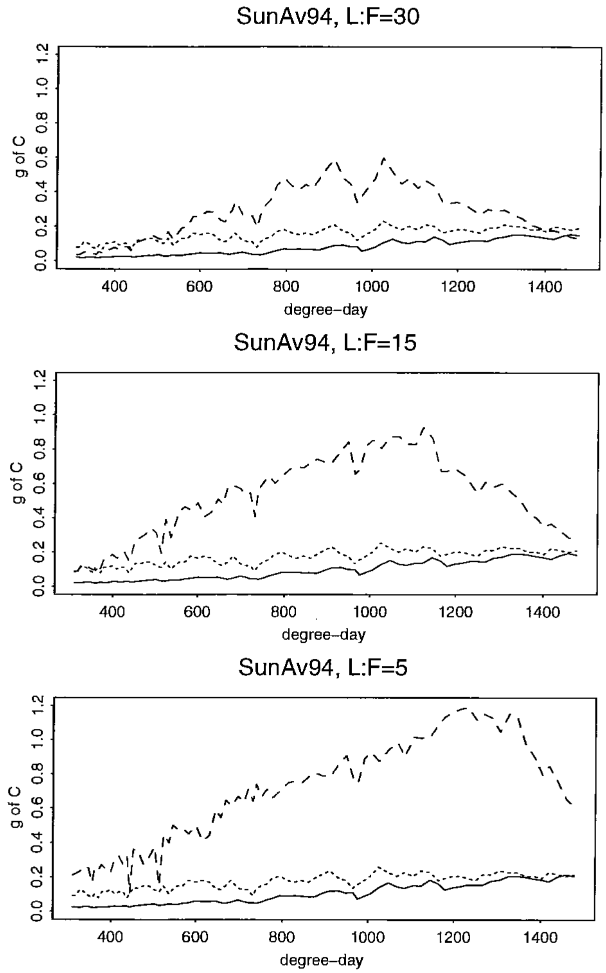

Figure 4 - Model simulation of daily carbohydrate partitioning among maintenance respiration (full lines), leafy shoots (dotted lines), and fruits (dashed lines), during the period of growth (dd after bloom).

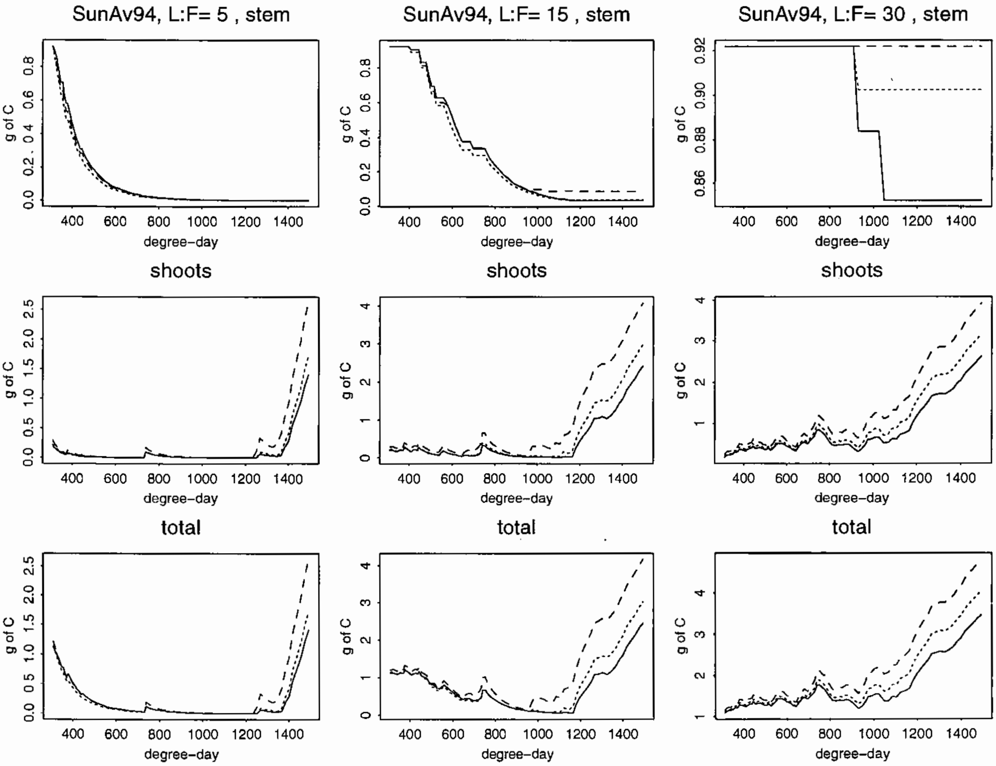

Figure 5 - Model simulation of daily reserve kinetics during the period of growth (dd after bloom) for minimum (full lines), mean (dotted lines) and maximum (dashed lines) total system initial dry weight.

SIMULATION OF THE EFFECT OF FRUIT THINNING ON PEACH QUALITY

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Keywords: *Prunus persica*, fruit growth, sugar, model

Abstract

A model of fruit quality described by fruit weight, percent dry material and sugar content was developed for peach. The application of the model is restricted to shoots bearing fruits considered as independent units. It is composed of three sub-models describing the dry matter, the fresh matter and the sugars accumulation, respectively. The inputs are the temperature, the global radiation and the intensity and date of fruit thinning. The first sub-model considers three compartments: the one-year-old stem, the leafy shoots and the fruits. It simulates the carbon assimilation, the respiration, the carbon storage and the growth of leaves and fruits. The carbon partitioning is based on organ demands and priority rules. The second sub-model computes the fresh weight of fruits from their dry weight through allometric relationships. In the third sub-model, the assimilates supplied to the fruit are partitioned in sucrose, sorbitol, glucose and fructose. The rates of change of these sugars are depending on supply, transfer functions between them, and use for respiration and synthesis of insoluble material. The effect of different periods and levels of thinning was analysed. As noticed in experiments, the fruit thinning increases the fruit weight, and the dry material and sugars concentrations in the flesh of the fruit. The fruit weight and sucrose concentrations are the parameters of fruit quality the most sensitive to thinning.

1. Introduction

Nowadays, the improvement of fruit quality and the increase of the homogeneity of products, which are recommended by the new market organisation for fruits and vegetables of the European Community, are important challenges for growers. They require an adaptation of the horticultural practices that influence the biological processes implicated in quality build-up.

Current agricultural practices and cultivars result in a wide variability of fruit quality from one part of the plant to another (Dann and Jerie, 1988). Various factors such as micro-climatic gradients (Corelli-Grappadelli and Coston, 1991) and heterogeneity in the leaf to fruit ratio (Génard, 1992) cause this variation. Training system, pruning and thinning are important practices for fruit quality because they determine the carbon supply to the fruit through their action on the leaf to fruit ratio. Abundant experimental work has been done, which describes the effect of these cultural practices on fruit production and quality. However, these works are difficult to use in practice, because they are often specific to given environmental and plant conditions.

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To go further, we need models of fruit production and quality sensitive to practices and micro-climatic gradients within the tree.

Several interesting models of fruit tree ecophysiology have recently been built (Buwalda, 1991; Grossman and DeJong, 1994), but they consider neither the within tree variability of growth, nor the gustatory quality of fruit. That is why a model of shoot bearing fruit sensitive to fruit load and to the variation of microclimate within the plant has been proposed for peach tree by Ben Mimoun *et al.* (this volume). This model simulates the carbon assimilation, the respiration, the carbon storage and the growth of leaves and fruits. In the present paper, we linked this model with a model of fresh weight accumulation and a model of sugar accumulation within the fruit, proposed previously (Génard *et al.*, 1996). The resulting model of fruit growth and sugar accumulation was used to analyse the effect of light environment and thinning intensity and date on peach size and sugar content, which are important parameters of quality for this species.

2. Model

The model is composed of three sub-models describing the fruit dry matter, fresh matter and sugars accumulations, respectively (Fig. 1). The inputs are the temperature, the global radiation, the sunlit fraction of leaves and the intensity and date of fruit thinning.

The first sub-model is presented in detail in Ben Mimoun *et al.* (this issue). It simulates the carbon assimilation and allocation in a shoot bearing fruit divided into three compartments: fruits, one-year-old stem, and leafy shoots. Equations of photosynthesis incorporate a feedback inhibition through the leaf storage reserves. The reserve pool can be used or restored according to supply and demand. The carbon partitioning is based on organ demands and priority rules. Maintenance respiration costs, vegetative and reproductive growth is given first, second and third priority. Daily carbon demands for the vegetative and reproductive organs are based on an analytical formulation of the potential growth rate.

The second sub-model is based on observations of xylemic and phloemic flows. Huguet *et al.* (1998) showed that the xylemic flow to the fruit is equal to the fruit transpiration under well-irrigated conditions. The consequence of this equality is that the fruit growth rate in fresh weight (*GRf*) is equal to the phloemic flow. Considering as a first approximation, a constant sugar concentration in the sieve, it implies that *GRf* varies in the same way as the fruit growth rate in dry weight (*GRd*). Indeed, we found a strong relationship between *GRf* and *GRd* (Fig. 2):

$$GRf = -2.38 + \frac{7.76}{1+e^{-3.78(GRd-0.18)}} \qquad (R^2 = 0.95)$$

Thus, the dry matter accumulation computed with the first sub-model can be converted in fresh matter accumulation using the above equation. The hypotheses of xylemic flow and transpiration equality are only valid for well-irrigated conditions, which is a strong limitation of this model.

The objective of the third sub-model was to predict carbon partitioning within the fruit flesh in order to compute the sucrose, sorbitol, glucose and fructose contents, and hence fruit sweetness. The model is dynamic and deterministic and was designed to be driven by the growth curve of the flesh dry weight, the flesh water content, and by temperature data. It uses differential equations where the state of the system is defined by state variables that describe how much carbon is present as each form of sugar and as other compounds (acids and structural carbohydrates). The rates of change of these amounts of carbon depend on the current values of corresponding state variables and on the transfer functions between them. Each flow exiting from a compartment i (except respiration) to a compartment j is the product of the carbon content in i by a coefficient F_{ij} . These coefficients are defined in Génard and Souty (1996) by rate constants k_{ij} and by functions of degree-days *dd* after full-bloom. To improve the accuracy of the model, the fruit weight and the respiration were added as variables in these coefficients to take into account the increase of sucrose accumulation with fruit weight and the decrease of cell wall synthesis with that of fruit activity (indicated by respiration per unit of fresh weight).

The temporal variation of carbon amount in a compartment j is the balance between the carbon flows entering and exiting this compartment:

$$\frac{dC_j}{dt} = Ej + \sum_{i \neq j} F_{ij}\left(k_{ij}, dd\right) \times C_i - Rj$$

where *Ej* and *Rj*, which can be equal to zero, are the carbon flow from the phloemic sap and the carbon outflow to the respiration, respectively.

The sugar concentration for a sugar x (*SCx*) is computed as:

$$SCx = \frac{100C_x}{c_x FW}$$

where c_x is the carbon content of 1 g of this sugar and *FW* is the flesh fresh weight.

3. Simulations

The effect of thinning intensity and date on fruit growth and sugar accumulation was analysed for a global radiation curve corresponding to a mean situation within the tree (Figs. 3 and 4). The seasonal variation of fruit growth, dry matter and sugar contents are in accordance with usual experimental results (Génard and Souty, 1996). The sucrose increases, when the fructose and the glucose decrease and the sorbitol fluctuates to finally decrease until reaching zero at harvest.

The fresh weight and the dry matter contents increase with the intensity and the precocity of thinning. The fresh weight at harvest is multiplied by 1.6 when the fruit number per shoot decreases from 5 to 1. The inhibition of leaf photosynthesis through the leaf storage carbohydrates and the buffer role of reserves included in the model (Ben Mimoun *et al.*, this issue) can explain this fact, as the storage in the shoot and in the stem is more important for 1 fruit/shoot. It is clear that glucose and fructose concentrations are independent from thinning pattern. Sorbitol content increases with thinning, but its value is zero at harvest. The sucrose is the more sensitive sugar to thinning with an increase of almost 2 g/100g when the shoot is thinned from 5 to 1 fruit. The sucrose content also increases with the precocity of thinning. The implications for the consumer are an increase of the fruit sweetness (g sucrose equivalent/100 g fresh pulp; see Kulp et al., 1991) with the thinning precocity and intensity.

To evaluate the response of quality due to the variation of light interception within the tree, the model was run for a set of light environments representative of the light heterogeneity within the tree. The simulations show that light heterogeneity has strong implications on fruit weight and sweetness (Fig. 5).

Considering 50 shoots bearing fruits issued from a tree and having each its own light environment, we analysed the effect of thinning intensity on fruit weight and sweetness (Fig. 6). As noted previously, the fresh weight and the sweetness increase at harvest with thinning. But the variability of these components of quality decreases with the increasing thinning intensity.

4. Discussion

Our objective was to illustrate how the aggregation of several models can be of interest for reasoning horticultural practices. The originality of our approach is to consider the fruit composition and to simulate the elaboration of fruit quality on a single shoot bearing fruit. This last point is determinant to account for the variability of fruit quality within the tree. The case presented here was very simple because only thinning was considered. However, it is well known that fruit quality also depends on other practices such as training, pruning and irrigation. Their effects and interactions should be incorporated into the model. Modelling bases exist that could be exploited in this way, which concern for example the effect of training and planting system on light interception (Wagenmakers, 1995), or the effect of pruning on tree growth (Génard *et al.*, 1998). Concerning irrigation, the hypotheses of xylemic flow and transpiration equality retained in our model are only valid for well irrigated conditions, which is a strong limitation. More sophisticated models of fruit water and dry matter accumulation have to be used in the case of water limitation. Such of model has been proposed by Fishman and Génard (this volume).

Our challenge for the future will be to complete and use the model to support the choice of orchard management techniques to produce fruits of good quality. For example, the fruit sweetness depends on sugar accumulation and on water accumulation in the fruit. If we want to increase sweetness, we will have to propose management techniques that favour water accumulation less than sugar accumulation (e.g. thinning). Going deeper into the analysis we could look for strategies that increase sugar accumulation. It can be done by increasing the photosynthesis (linked to light interception and thus to training, and to reserve accumulation and thus to thinning) or by decreasing the number of sinks (through thinning or pruning). The respective importance of each technique for fruit quality (including its variability) could be analysed according to its time of application and its intensity thanks to a model such as the one presented here.

An important point is that shoots bearing fruits cannot be considered as independent units as it is done in this model. Our intention for the future is to consider the links between shoots bearing fruits. To do that, we think that it is important to consider the roots and their interactions with fruits and shoots. The term "interaction" means here that each organ can act on carbon partitioning within the plant. Either of shoots, roots or fruits can preferentially use the carbon depending on the nutritional or hormonal equilibrium within the plant. This can be accounted for in models without any assumption on the nature of the equilibrium within the plant. A recent model focusing on root-shoot interactions, which integrates architectural and ecophysiological approaches, has been proposed for young peach tree (Génard *et al.*, 1998). Our future developments on modelling peach growth and quality variability within the tree will be based on the same philosophy. This will open the way to consider the effect of practices such as pruning.

Acknowledgements

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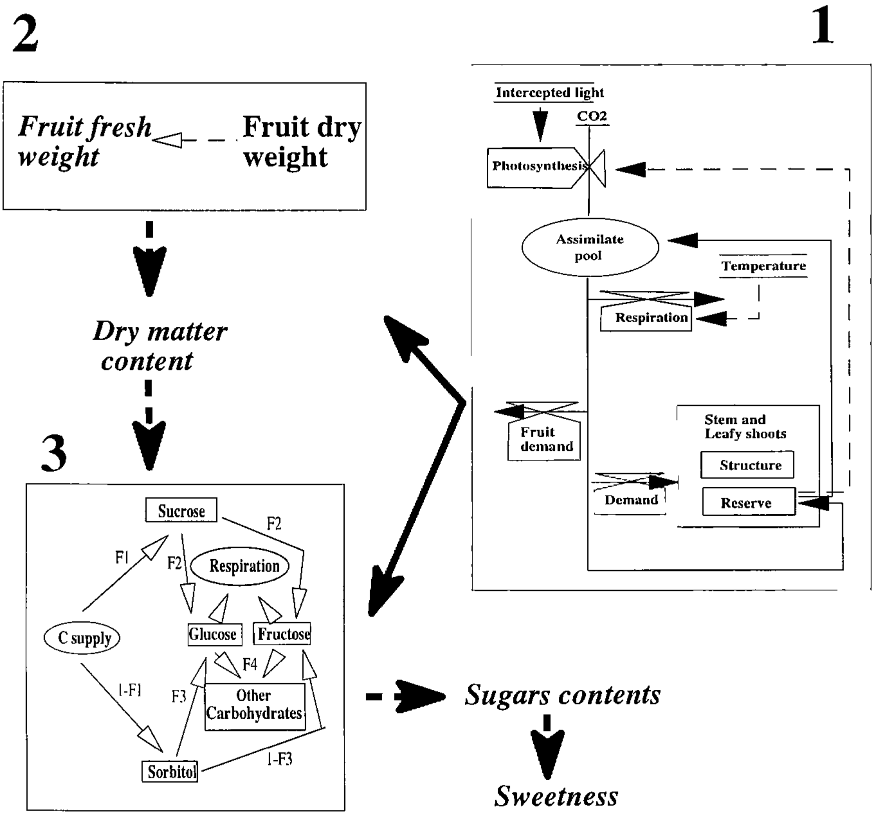

Figure 1 - Diagram illustrating the three sub-models and their links. The quality variables are in italics. Solid lines represent flow of matter and dashed lines represent flow of information.

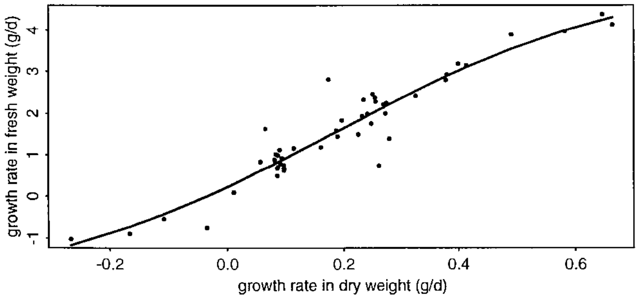

Figure 2 - Relationship between fruit growth rate in fresh weight (*GRf*) and dry weight (*GRd*) considered in the sub-model of water accumulation.

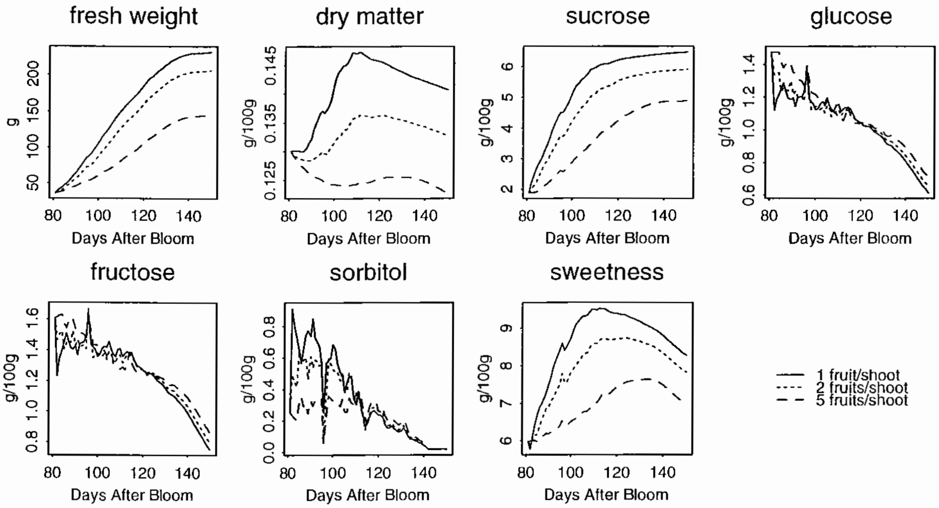

Figure 3 - Simulation of the effect of thinning intensity (1, 2 and 5 fruits per shoot) on seasonal variation of fruit growth, dry matter content, sugars contents and fruit sweetness.

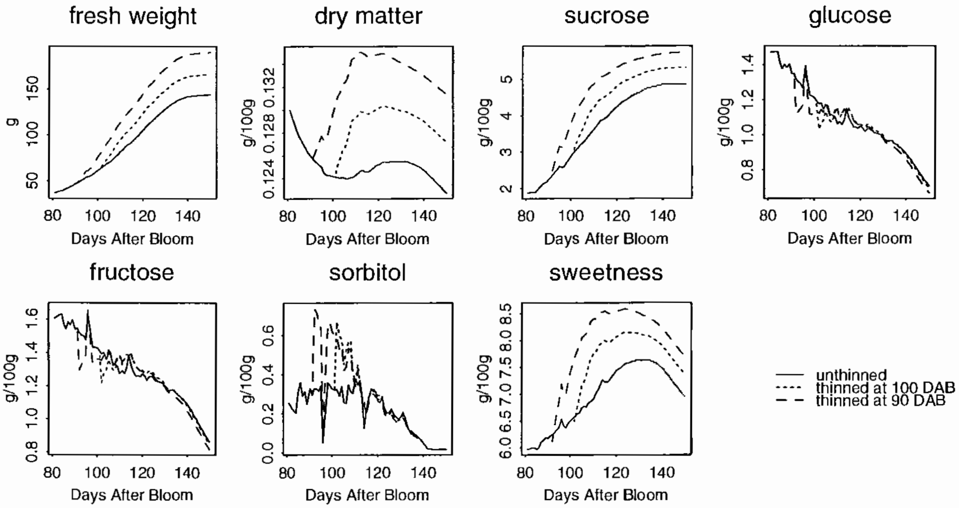

Figure 4 - Simulation of the effect of thinning precocity (no thinning, thinning from 5 to 1 fruit per shoot at 100 DAB and 90 DAB) on seasonal variation of fruit growth, dry matter content, sugars contents and fruit sweetness.

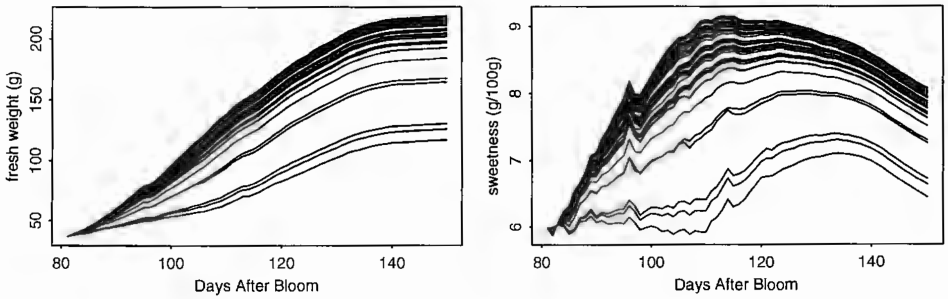

Figure 5 - Simulation of the effect of light interception on seasonal variation of fruit growth and sweetness. Each curve corresponds to the mean fruit of a shoot bearing fruit with a specific light environment. The range of light environments, expressed as the number of hours per day during which the shoot is fully sunlit, is 2-14 h day^{-1} (mean=10).

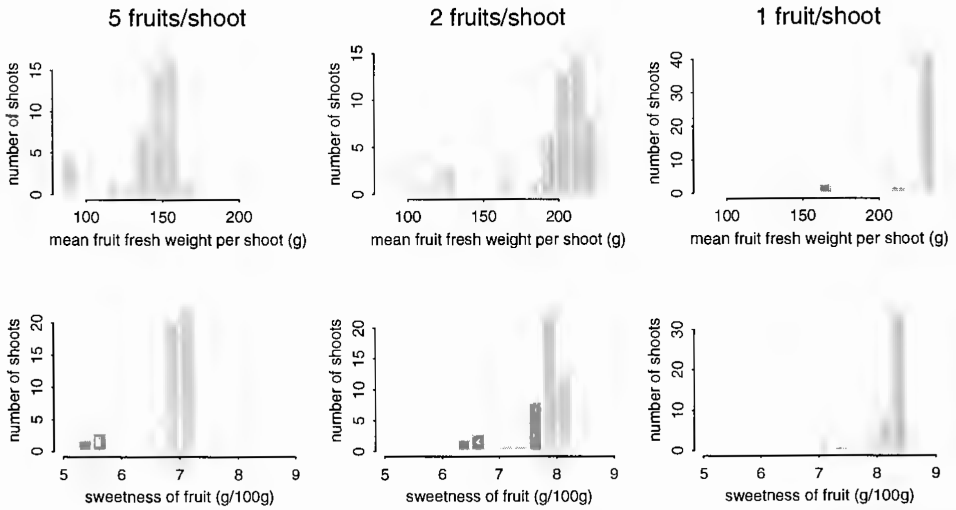

Figure 6 - Simulation of the effect of thinning intensity on the distribution of fruit weight and sweetness at harvest. Each histogram corresponds to a set of 50 shoots, having each its own sunlit fraction of leaf.

PROGRESS IN THE DEVELOPMENT OF 'CITROS' - A DYNAMIC MODEL OF CITRUS PRODUCTIVITY

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Keywords: carbohydrate, *Citrus paradisi*, Effective Heat Unit (EHU), Relative Growth Rate (RGR), simulation, sink, source

Abstract

The foundations of the Citrus productivity model 'CITROS' were laid by Goldschmidt and Monselise (1977). The model is based on the assumption that where all other needs (water, fertilizer, etc.) are managed at, or close to the optimum, dry matter production and allocation become the fundamental processes that limit tree productivity. The purpose of the model is to identify and quantify productivity problems, predict yields and devise means for optimization of Citrus crop production. Data from the literature supplemented by new field photosynthesis measurements were used to obtain reasonable estimates of daily and annual photoassimilate production by a Citrus tree canopy. The potential relative growth rate (RGR) of reproductive organs was followed through the growing season and the cost of fruit production was calculated. A model for an effective heat unit (EHU) was constructed to improve and refine the expression of temperature effects on fruit growth. Respiratory losses, including temperature effects, were also evaluated. This quantitative information was incorporated into a series of mathematical functions that provide estimates of carbohydrate demand and consumption by the reproductive organs (flowers and fruit) within a citrus tree. The carbon consumption of other tree organs (particularly roots) and the management of carbohydrate reserves should also be incorporated into the model. Matching the daily available amount of photoassimilates with reproductive organ demand for carbon, the model predicted that a shortage of carbohydrates might already occur during bloom. While early fruit development appears to be sink-limited, at least in certain cultivars, all subsequent stages of fruit growth and maturation are source-limited.

Yield predictions by the model fall within a reasonable range, but the problem of trade-off between fruit number and fruit size (during the fruit set and abscission period) requires further investigation. Actual differences in the performance of grapefruit (*Citrus paradisi* Macf., cv 'Marsh seedless') orchards from different climate regions were successfully predicted by the model. The model, which is already a powerful diagnostic and predictive tool, may gain further strength by incorporation of the effects of management practices (e.g., drip irrigation) and frequently encountered environmental stresses.

1. Introduction

The basic question in modelling fruit trees is what factors determine the yield and its quality. The availability of carbohydrates to different consuming organs is at the core of

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growth and development of any plant. Therefore, efforts should be made to accurately assess the balance between supply and demand for carbohydrates within the tree.

In many fruit crop species the number of fruit is more or less stable after fruit set, and the question is how to optimize the yield components. Citrus may represent a group of subtropical fruit tree species which tend to produce extremely large numbers of flowers and fruitlets, most of which abscise during the 2-3 months following bloom. Better understanding of the processes during that early period of fruit set might improve the ability of the grower to control the components of the yield. Zucconi *et al.* (1978) indirectly concluded that in citrus, the waves of fruit abscission are related to temporary changes in the ability of the tree to fulfil the overall demand for carbohydrates.

Goldschmidt and Monselise (1977) laid the foundations of a citrus productivity model. They analyzed the physiological knowledge existing at that time and suggested a schematic model that described the interrelations between the plant organs relevant to the determination of yield during an annual cycle. They suggested three stages in which "a decision should be taken by a tree" in quantitative terms: how many flowers to produce, how many fruit to set, and how much the fruit will enlarge. Following that, a primary mathematical model was developed based on empirical assumptions and semi-quantitative information. This model successfully described some principal processes as alternative bearing (Harpaz *et al.*, 1990), and even predicted responses of the yield of a Citrus tree to fruit thinning (Goldschmidt *et al.*, 1992). The success of this preliminary model encouraged its further development on a broader and deeper physiological basis, to provide a sharper description and more precise quantitative predictions. The purpose of the present model, 'CITROS', is to identify and quantify productivity problems, predict yields and devise means for optimization of citrus crop production.

The model is based on the assumption that, where all other needs (water, fertilizer, etc.) are managed at or close to the optimum, dry matter production and allocation become the fundamental processes that limit tree productivity (DeWit, 1986). Our approach in the present study is also based on the assumption that a relatively accurate estimation of the carbohydrate supply available for the reproductive organs, along with a reasonable assessment of their carbohydrate demand for maintenance and growth – should provide good estimates for the yield of a citrus tree.

It should be noted, that solid quantitative estimates are not yet available for several important components of the carbon balance (root growth and turnover, vegetative growth, reserves). The 'CITROS' version presented here is, therefore, still at an early stage and should be regarded as a basis for further development, defining the problems and areas where additional research is required.

2. The model

This chapter describes and discusses the principal components of the present model. A partial mathematical description of the model program is provided in the appendix.

2.1. Fruit demand for carbohydrates

The daily demand of an individual fruit is defined as the amount of carbohydrates required to satisfy the entire growth potential of that fruit according to its stage of development, the environmental conditions, and respiratory requirements.

2.1.1. Potential relative growth rate

The potential growth rate of a fruit was determined by measurements of individual fruit growth under sink-limited conditions (Pavel and DeJong, 1993). Sink-limited growth has been obtained by reducing the number of fruitlets from about 250 to 25 per branch at anthesis. Later on, at about 80 days after anthesis (DAA), sink-limited growth was achieved by trunk girdling combined with fruit thinning from about 400 to 40 fruit per tree (Bustan *et al.*, 1996a). Thus, the potential relative growth rate (RGR_P) has been elucidated, and serves as the major experimental input to the demand function (Bustan *et al.*, 1996a).

2.1.2. The effect of temperature on fruit growth

Nevertheless, these RGR_P data reflect the environmental conditions that prevailed during that specific year at that specific location (1992, Rehovot, Israel). To define a growth function that would be valid for broader environmental conditions, an RGR function that describes fruit growth under continuous optimum conditions is required (RGR_{OPT}).

Temperature, as the dominant environmental factor, has been commonly used for estimations of physiological time. The daily degree-day (DDD) is one of the methods frequently used in models. This unit is usually based on a minimum temperature threshold above which growth is assumed to linearly respond to temperature (Zalom *et al.*, 1983). This assumption might be correct for many plant species, including peach (DeJong *et al.*, 1996), however, fruit growth responses to high temperatures are not taken into account. We have suggested a method that counts physiological time in Effective Heat Units (EHU) and is based on an optimum response curve of citrus to temperature (Fig. 1). Although based on a general description of citrus response to temperature (Reuther, 1973), the EHU method predicts the negative effect of above-optimum temperature on citrus fruit growth (Fig. 2) (for a detailed description see Bustan *et al.*, 1996b).

2.1.3. Growth rate and fruit demand for growth

The RGR_{OPT} function of a grapefruit fruit has been calculated by dividing RGR_P by a temperature coefficient k_T, which expresses the ratio between the actual EHU accumulated during **n** days and the maximum EHU (24n). The resulting RGR_{OPT} (Fig. 3) are much higher than RGR values measured in the orchard, but their purpose is to serve as a basic function on which any set of temperature data can be projected.

The potential growth rate function (GR_{POT}) of a grapefruit fruit can be expressed at any point along fruit development as the product of RGR_{OPT} , the current fresh weight of the fruit (w_c), and the current temperature coefficient (k_T).

Glucose has been preferred in 'CITROS' as the common unit to express demand, supply, and respiratory losses. Therefore, to produce fruit demand for growth (DEM_{GR}), growth rates are converted from g FW per day to g glucose per day, using k_{DM} as a conversion coefficient from fresh to dry matter, and $1/Y_G$ as the conversion factor of dry matter to glucose (McDermitt and Loomis, 1981). These two coefficients, k_{DM} and $1/Y_G$, have been obtained by curve fitting functions based on measurements conducted along the growth season.

2.1.4. Respiratory losses

In respiratory losses one may distinguish between maintenance and growth respiration. Amthor (1990) addressed that problematic issue in his comprehensive study on plant respiration and suggested several alternatives for direct and indirect measurements. In the present model we adopted the subtraction of growth respiration from total respiration to obtain the maintenance respiration, r_m. Growth respiration is calculated from the dry weight composition (McDermitt and Loomis, 1981), and is assumed to respond to temperature in the same way as growth rate. r_m was significantly influenced by fruit stage of development (see appendix). Its response to temperatures in the range of 15-35°C, followed a Q_{10} within the range of 1.95-2.15. The demand for glucose by fruit maintenance respiration (DEMr) is expressed by the product of fruit dry weight (w), r_m, and k_{dTr} (temperature response coefficient), divided by 1.466 (to convert CO_2 to glucose).

2.1.5. Total fruit demand for carbohydrate

The sum of DEM_{GR} and DEMr reflects the demand for carbohydrate presented by the individual fruit (DEM_T). It should be stated here, that in the model priority is given to the fulfillment of DEMr, and only the remaining carbohydrates are available for growth. The total amount of carbohydrates required daily (DEM_{TOT}) is dependent upon DEM_T and upon the current number of fruit (N_{Fr}) borne by the tree. As already mentioned, unlike most fruit tree species modeled until now, the number of fruit on a citrus tree changes dramatically during the first months of fruit development. This phenomenon presents an additional challenge in the modelling process.

2.2. Photoassimilate supply

Since many efforts have been made in recent years to estimate the overall carbon exchange rate of a citrus tree canopy, we decided to adopt the concepts and results as presented by Syvertsen and Lloyd (1994). However, the environmental differences between Florida and semiarid regions like Israel must be taken into account. Syvertsen and Lloyd (1994) estimated the daily carbon exchange rate of the canopy of an average citrus tree at 340 g glucose. In our simulation we have used this value as an upper threshold. To adjust photoassimilation estimates to the local conditions we used the EHU method, for a rough calculation of the environmental effects on photosynthesis. The average daily estimate of photoassimilates was 250 g glucose for coastal plain locations, and only about 170 g for more arid inland locations. Although roughly estimated, the results obtained by the model were in a reasonable range.

2.3. Matching supply and demand

The model predicts source-limiting conditions during most of the growing season of the grapefruit yield. The estimated demand for photoassimilates was higher than the supply already during bloom (Bustan and Goldschmidt, 1998), when most of the flowers drop prior to, or immediately after anthesis. However, the number of remaining fruitlets was high enough to cause carbohydrate shortage at about 10-20 DAA. As already mentioned, the abscission of most of the fruitlets during the early 80 DAA requires special attention. Since we assume that fruit abscission is a direct result of carbohydrate deficiencies, a mechanism of self-thinning, which responds to carbohydrate shortage, has been incorporated into the model, in an attempt to imitate the natural process. A simulation in which only the number of fruit is affected by the stress brings about to a small number of huge fruit. On the other hand, where only fruit size is controlled, a tremendous number of tiny fruit is produced (according to the model). The key question is, therefore, how carbohydrate deficiency simultaneously controls the number and size of the fruit on a tree. The mechanism of that trade-off process is not yet known. In 'CITROS', we have used some technical coefficients, which are based on information about the patterns of fruit drop and the physiological mechanisms involved in fruit abscission. Although the final simulation results are satisfactory, research is still required to provide an explanatory ability to this part of the model. A promising direction of research might be the exploration of limitations imposed by the translocation system on fruit growth (Bustan *et al.*, 1995).

3. Results and validation of the model

3.1. Simulations of yield, fruit size, and fruit number

Since most of the parameters of 'CITROS' have been defined by relying on experiments conducted in Naan, in the Israeli coastal plain, the first test was carried out for that location, but under conditions of the subsequent year (1993). In the test year, the harvest was relatively early (Mid November), the number of fruit per tree was about 400, and the average fruit size was 330 g FW (about 53 Mg ha^{-1}). Usually, the harvest takes place much later and the yields are correspondingly higher. In spite of these limitations, 'CITROS' accurately predicted the growth rate of an individual grapefruit fruit, under source-, as well as under sink-limiting conditions (Fig. 4). Although root demand has not yet been included in 'CITROS', some effects of it appear indirectly in the results; when the number of fruit was reduced to 40, the model predicted a much higher growth rate than the actual one, but that growth rate was in accordance with the rate observed when trunk girdling was combined with fruit thinning (Fig. 4).

The model maintains a steady level of yield over a wide range of initial fruit numbers per tree (Table 1). The predictability of fruit size is quite reasonable within a range of initial fruit numbers.

The simulation results lead us to conclude that, while bearing a normal number of fruit, the grapefruit tree suffers from a continuous source-limiting condition. If harvested later, in January, the same orchard would have produced about 70 Mg ha^{-1} while much higher yields (100-120 Mg ha^{-1}) have, in fact, been reported for outstanding orchards in Israel. We assume that the reason for that discrepancy might be due to higher availability of carbohydrate, resulting from better environmental conditions. Partial support for this assumption arises from the simulation in which the level of potential daily supply has been changed (Table 2). According to the model, where the daily amount of photoassimilates actually available is about 340 g glucose, the yield would increase to the aforementioned record levels.

3.2. Effects of climatic conditions on grapefruit yields

Two different climatic regions in Israel have been chosen to test the environmental effects on yields; Naan, in the relatively mild coastal plain, and Massada, in the hot and dry inland Jordan Valley. As mentioned, temperature is the only environmental factor so far incorporated into the model.

The yields of orchards of the inland regions tend to be lower than those of the coastal plain, mainly due to small fruit size (Fishler, 1985). 'CITROS' provides some explanation for these problems. The model predicts lower levels of photoassimilates supply for a tree in Massada in comparison to Naan. However, the most significant difference is in the demand; the overall daily demand for carbohydrates was predicted to be much higher in Naan than in Massada (Fig. 5). This difference is mainly due to the higher demand of the individual fruit throughout most of the growing season (Bustan *et al.*, 1996b), but also due to the smaller number of fruits remaining on a tree under the conditions of the Jordan Valley. Actual fruit growth rates commonly agreed with values predicted by the model (Bustan *et al.*, 1996b). These successful predictions are directly related to the advantages of the EHU method used in the model.

The increase in respiratory losses under the higher temperature in Massada (Table 3) only slightly compensated for the dramatic decrease in fruit demand. However, the estimated seasonal amount of glucose consumed for maintenance respiration of a grapefruit fruit was higher in Massada than in Naan, in absolute as well as in relative values (Table 3). The estimated maintenance cost of a single fruit was 11.5 g glucose, about 21% of its overall glucose consumption until harvest. The corresponding value for a fruit in Naan was only 15.5%. This may serve as an example for the power of the model as an explanatory tool.

4. Conclusions

The ability of the model to accurately calculate and predict the carbon demand of an organ under a broad range of environmental conditions, different stages of development and fruit loads, has been significantly improved over previous versions. The predictions of yield levels are within a reasonable range, although more efforts are required to incorporate modules for other consumer organs and for the mechanism of carbon allocation between them. 'CITROS' identifies periods of carbohydrate shortage within the tree. The influence of that deficiency on the trade-off between fruit number and fruit size appears to be rather complicated and requires further research.

Acknowledgements

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Table 1 - Effect of initial fruit number per tree on number, size and fresh weight yield of fruit at harvest, simulated for Naan, 1993. The average daily amount of photoassimilates available was set to 250 g tree^{-1} (400 trees/ha).

Number of fruit per tree		**Average final fruit size**	**Yield**	**Yield**
Initial	Final	**(g)**	**(kg tree^{-1})**	**(Mg ha^{-1})**
50000	562	216	121	48.5
30000	479	253	121	48.5
20000	427	284	121	48.5
10000	**346**	**350**	**121**	**48.5**
5000	283	429	121	48.5
1000	189	642	121	48.5
500	160	759	121	48.5
100	100	1207	120.7	48.3
50	**50**	**1676**	**83.8**	**33.5**
1	1	1676	1.7	0.7

Table 2 - Sensitivity of the simulated yield of a grapefruit tree to different maximum levels of C availability. The estimated level of daily available photoassimilates within a tree was adjusted according to EHU accumulated each day.

Carbon availability (g glucose day^{-1} tree^{-1})		**Initial fruit number** (fruits tree^{-1})						
Max.	Actual	**10000**		**20000**		**50000**		**Yield**
		Fruits tree^{-1}	**g fruit^{-1}**	Fruits tree^{-1}	**g fruit^{-1}**	Fruits tree^{-1}	**g fruit^{-1}**	**kg tree^{-1}**
250	**198**	280	**319**	342	**260**	456	**195**	**89.3**
300	**224**	318	**337**	391	**273**	516	**207**	**107.3**
340	**254**	346	**350**	427	**284**	562	**216**	**121**
350	**261**	353	**353**	435	**287**	573	**218**	**125.2**
400	**298**	388	**368**	478	**299**	628	**227**	**142.4**
450	**336**	423	**380**	519	**309**	681	**236**	**160.3**
500	**373**	457	**390**	559	**319**	733	**243**	**178.1**

Table 3 - Absolute and relative costs of the maintenance respiratory losses (r_m) of an individual fruit, simulated for Naan and Massada, 1993.

Location	Harvest	Fruit dry weight	Glucose consumption			% of glucose consumed for r_m
		g fruit^{-1}	g fruit^{-1}			
			Growth	r_m	Sum.	
Massada	15/09/93	34.39	44.02	11.49	55.51	20.7
Naan	15/09/93	36.29	46.45	8.51	54.96	15.5
Naan	15/11/93	51.69	66.16	11.88	78.04	15.2

Figure 1 - Effective heat units (EHU) - a theoretical response curve of Citrus fruit growth to temperature.

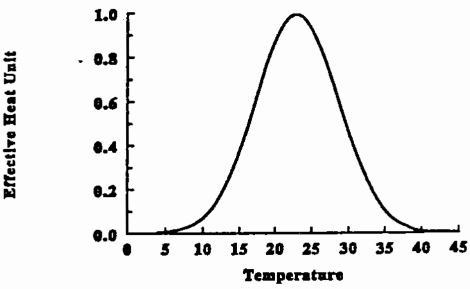


Figure 2 - The daily pattern of temperature (line) and EHU accumulation (bars) during 12/04/92. Although the average temperature (24.8°C) was close to the optimum, the environmental conditions during that day were quite extreme and unfavorable for fruit growth. Only 8.3 EHU were accumulated, indeed indicating a low growth rate. Such kind of temperature stress is not reflected by the daily degree method (17.8 DDD).

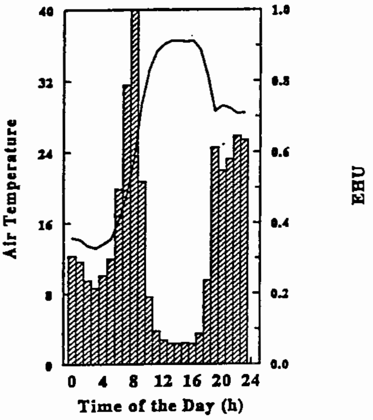
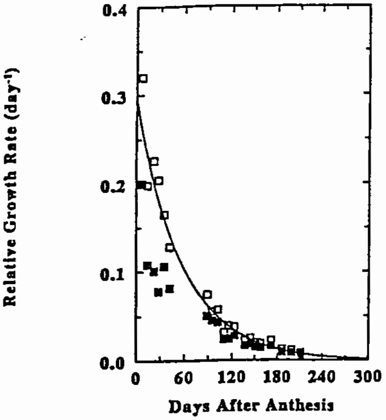


Figure 3 - The relative growth rate of a grapefruit fruit under conditions of non-limited carbohydrate supply and ambient temperature (RGR_P, ■). RGR_P, when divided by the temperature coefficient k_T yields the RGR under steady optimum temperature (RGR_{OPT}, □), which has been fitted (r^2=0.96) by the function (solid line): $RGR_{OPT} = 0.297 * e^{-0.018 * DAA}$ (DAA, days after anthesis).



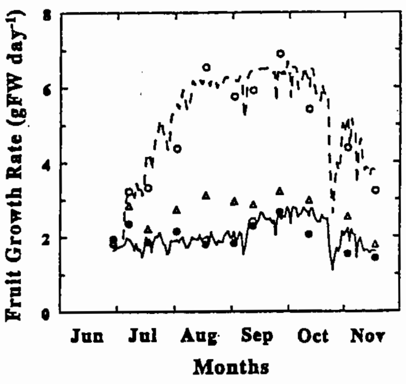


Figure 4 - Simulated absolute daily growth rate of an individual grapefruit fruit, where the number of fruits per tree was reduced to 50 (dashed line), as compared with 400 fruits per control tree (solid line) and actual growth rate of an individual fruit as measured in an experiment in which the number of fruits per tree had been reduced to 40 (Δ), or trunk girdled and thinned as well (O), compared to control (●). Treatments were performed at 80 DAA for both the experiment and the simulation.

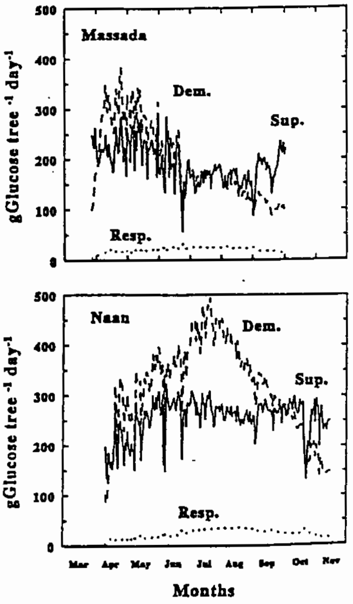


Figure 5 - Total daily fruit demand (dashed line) for carbohydrates, total daily supply (solid line) of photoassimilates, and that portion of fruit demand accounted for by maintenance respiration (dotted line), as simulated for a grapefruit tree along the growing season for two different climatic locations: the coastal plain (Naan), and the inland Jordan valley (Massada). The execution terms were similar for both locations, except for the temperature data and some minor adjustments concerning the sensitivity of fruit to carbon deficiency.

Appendix

Mathematical description of the model CITROS

Initial conditions	
W	Initial fruit size (g FW)
N_{Fr}	Number of fruits per tree
Temperature effects	
$EHU = e^{-((T-T_{OPT})/T_0)^2}$	Effective heat unit (hourly)
$k_T = (\Sigma_1^{24} EHU)/24$	Coefficient of temp. effect on fruit growth
$K_{dTr} = \Sigma_1^{24}((Q_{10}^{(T-25)/15})/24)$	Coefficient of temp. effect on fruit r_m
Fruit demand functions (g glucose· fruit^{-1}· day^{-1})	
$RGR_{OPT} = 0.297 \cdot e^{-0.0176 \times DAA}$	Maximum relative fruit growth rate (day^{-1})
$GR_{POT} = RGR_{OPT} \cdot w \cdot k_T$	Potential fruit growth rate, affected by temp. (g FW day^{-1})
$k_{DM} = 37-(20 \cdot DAA/160)$	Conversion coef. of fruit fresh into dry weight
$1/Y_G = 1.63-2.85 \cdot 10^{-3} \cdot DAA+6 \cdot 10^{-6} \cdot DAA^2$	Conversion coef. of fruit dry weight into glucose
$DEM_{GR} = GR_{POT} \cdot k_{DM} \cdot 1/Y_G$	Carbohydrate demand for growth of a single fruit (g glucose day^{-1})
$r_m = 44.3 \cdot e^{-0.0146DAA}$	Fruit r_m function (mg CO_2 g DW^{-1} day^{-1})
$DEM_r = W \cdot r_m \cdot k_{dTr}/1.466 \cdot 10^3$	Carbohydrates consumed by r_m of a single fruit (g glucose day^{-1})
$DEM_T = DEM_{GR} + DEM_r$	Total demand of a fruit (g glucose day^{-1})
$DEM_{TOT} = DEM_T \cdot N_{Fr}$	Carbohydrate demand by all fruits on a tree
Photoassimilate supply (g glucose· tree^{-1} · day^{-1})	
$SUPP = SUPP1 \cdot k_T$	Whole canopy photoassimilation, affected by temperature.
Daily balance between supply and demand	
$AVAIL1 = SUPP/N_{Fr}$	Amount of photoassimilates available for a fruit before updating the number of fruits per tree (g glucose fruit^{-1} day^{-1})
$AVAIL2 = SUPP/n_{Fr}$	Amount of photoassimilates available for a fruit after updating the number of fruits per tree
Adjustment of fruit numbers to carbon availability	
$DEF = MAX.(0,((DEM_T-AVAIL1)/W)/1/Y_G)$	Identification of carbohydrate deficiency
$k_{SENS} = \alpha \cdot e^{\beta \cdot DAA}$	Coef. of fruit sensitivity to deficiency
$THRES = MAX.(DEF-k_{SENS}),0)$	Threshold for activating fruit number update
$OKDRP = IF(THRES = 0,1,UPDT)$	Terms for fruit number update
$UPDT = MIN.(1-((DEM_{TOT}-SUPP)/DEM_{TOT} \cdot \gamma),1)$	Adjusting fruit drop to the level of deficiency
$n_{Fr} = OKDRP \cdot N_{Fr}$	Updated number of fruits per tree
Fruit growth	
$W = w \cdot k_{DM}$	Fruit dry weight before daily growth (g DW)
$GR = MIN.(GR_{OPT}, GR2)$	Fruit growth rate (g DW day^{-1})
$GR2 = (AVAIL2-DEM_r)/k_{DM}/1/Y_G$	Fruit growth rate as permitted by deficiency (g DW day^{-1})
Updating state variables for the next day	
$w = w+GR$	Fruit size (g DW)
$N_{Fr} = n_{Fr}$	Number of fruits per tree

Input variables and coefficients	
$SUPP1 = 340$ (g glucose tree^{-1} day^{-1})	Maximum canopy photoassimilation
T (℃)	Temperature (hourly)
$T_{OPT} = 23$ ℃	Optimum temperature for fruit growth
$T_0 = 8$ ℃	Minimum temperature for fruit growth
$Q_{10} = 2.05$	coef. of r_m response to temperature
DAA	Days after anthesis
$\alpha = 0.008$, $\beta = 0.0123$, $\gamma = 0.25$	Adjusting parameters

EXAMINATION OF 'HIERARCHICAL' AND 'PROPORTIONAL' DRY MATTER PARTITIONING MODELS WITH POTTED CITRUS TREES

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Keywords: Calamondin (*C. reticulata cv. Austera x Fortunella spp.*), defoliation, sink, source

Abstract

The mode of dry matter partitioning among organs of higher plants is as yet poorly understood. Two kinds of partitioning models have been proposed: a) A 'hierarchical' model, assuming absolute organ priorities. b) A 'proportional' model, in which every organ gets a fixed portion of the photosynthate supply. Pot-grown, fruiting Calamondin (*C. reticulata cv. austera* x *Fortunella spp.*) trees were used to examine the agreement of fruit/root partitioning data with the two models. Half of the trees were 50% defoliated to reduce the supply of photoassimilates (source manipulation). Half of the plants were transferred to larger pots to induce and enhance growth of new roots (sink manipulation). Thus, four treatments were obtained: small pots with full (S-100), or half (S-50) foliage, and large pots with full (L-100), or half foliage (L-50). In defoliated trees total growth (g dry weight) was reduced by ca. 50%. Transfer to larger pots invariably increased the portion of dry matter allocated to new roots. In trees with young fruitlets, 7 DAFS (days after fruit set), defoliation strongly interfered with fruit growth (55% reduction), but growth of new roots was not affected. In trees with older fruit (30 DAFS), the relative portions allocated to fruit and roots were not altered by defoliation. Large developing fruits dominated dry matter distribution, yet, significant emergence and growth of new roots occurred following transfer to large pots. In addition, the 50% defoliation changed the fruit size distribution, causing about 50% of the fruit to remain small. A computer simulation model was developed to test the hierarchical against the proportional approach. The data, as well as the simulation model, suggest that both kinds of partitioning models may be realistic. It is concluded, however, that the existence of a hierarchical mechanism of dry matter partitioning is essential in order to allow for the emergence and development of new plant organs.

1. Introduction

The partitioning of photoassimilates is a critical link in the chain of processes, commencing with leaf photosynthesis and winding up with fruit development and ripening. A partitioning mechanism is, therefore, an inherent part of every crop yield simulation model. Assumptions regarding the mode of dry matter partitioning must be made, based mostly on hypothetical grounds, in order to enable the model to be put to work.

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In some models an attempt was made to set sink priorities according to a hierarchical scale of organ types. The priority of a sink organ could be absolute (Gutierrez *et al.*, 1985), or weighed according to defined developmental stages of the plant (Penning deVries and van Laar, 1982). Practically, in models where the hierarchical approach was favored, the demand of the dominant sink organs was fulfilled sooner than that of other sinks, which receive less than demanded, or nothing at all, as long as source limitations prevail. The hierarchical approach was based on analyses of photoassimilate distribution in many crops during plant development and at harvest (Wardlaw, 1990). In general, experimental evidence supports the concept that fruit and seed growth dominate the growth of vegetative tissues (Eaton, 1931; Wardlaw, 1990). Shoot growth was generally found to have a higher priority than root growth, but underground storage organs revealed similar ability as fruit to efficiently compete for photoassimilates (Wardlaw, 1968). Yet, no physiological explanation was provided concerning the nature and origin of that hierarchy.

Other modelers preferred the proportional approach, in which every sink organ receives a fixed portion of supply, according to its relative sink strength. The term sink strength, although defined as the product of sink size and sink activity (Wareing and Patrick, 1975), remains conceptually unclear (Farrar, 1993) and sometimes difficult to use. Defining the potential relative growth rate of an organ along its development under non-limiting source conditions, enabled the design of a function of demand and improved the descriptive power and predictability of models (Grossman and DeJong, 1994; Marcelis, 1994).

Partitioning models have very rarely been put to an experimental test (Fick *et al.*, 1973). Most models followed a set of hypothetical assumptions, as long as the simulations obtained seemed reasonable. In the present study we designed an experimental system which, supposedly, might distinguish between hierarchical and proportional modes of partitioning. The results enable a deeper insight into the physiological significance of the alternative partitioning mechanisms.

2. Materials and Methods

2.1. Plant material

Calamondin plants (*C. reticulata cv. Austera x Fortunella spp.)* were grown in small pots (0.9L) in the nursery. Flowering was induced by withdrawal of irrigation for several days during August of the second year. After bloom and initial fruit set, plants were transferred to a greenhouse sheltered by a 30% shading net. Plants were drip irrigated 2-4 times a day. Fertilizer (Sheffer 7:3:7) was supplied continuously with the irrigation water at 100 $mg \cdot L^{-1}$ of nitrogen. The experiments were conducted during September-October of 1993 and 1994. A new set of plants was used each year.

2.2. Experiments

In 1993 the experiment started 14 days after initial fruit set (DAFS). In 1994 two experiments were conducted. One experiment started 7, and the other 30 DAFS.

Four representative plants were examined at the beginning of each experiment to determine the initial status of the plants. Thirty-two plants were divided into 4 groups, two of which (16 plants) were transferred to 4.2L pots. At the same time 8 plants of the small pot group, and 8 plants of the large pot group were 50% defoliated. Thus, four treatments were obtained: plants in small pots with full (**S-100**), or half (**S-50**) foliage, and plants in large pots with full (**L-100**), or half foliage (**L-50**). All new vegetative or reproductive growth was removed daily by manual pinching. The follow-up terminated 30 days after treatment and the plants were dismembered and analyzed.

2.3. Measurements

The projection area of the canopy of each plant was measured using photographs taken from a top position. The leaf area of each plant was measured at the end of the experiment, using a Delta-T leaf area analyzer. Plant leaf area was divided by its projection area, to estimate the leaf area index (LAI) for each plant.

The carbon exchange rate of single leaves was measured weekly during the experiment. Three leaves per plant were measured during the morning (09:00-11:00 am), under light intensity (PAR) of 800-1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, using a LiCor 6250 system.

Plants were dismembered into fruit, leaves, woody skeleton, and roots. Young, developing roots, distinguished by their white color, were separated from older, brown roots. Fresh and dry weight of each group of plant organs was determined. Fruits were counted to determine the number of fruits per plant and weighed individually to determine the size distribution.

Plant material was ground to fine powder and samples were taken for determination of soluble sugar and starch, which add up to the non structural carbohydrate (NSC) content (Schaffer *et al.*, 1985).

2.4. Model development

Two simple models were developed to simulate the dry matter partitioning within the potted calamondin plants to test the hierarchical versus the proportional approach. The model was based on the assumption that photoassimilate availability limits growth. Whenever the demand for photoassimilates exceeds the supply, the partitioning mechanism, hierarchical or proportional, is activated.

The available amount of photoassimilate was estimated at 0.333 $g \cdot d^{-1}$ (dry matter) for intact plants, and 0.168 $g \cdot d^{-1}$ for 50% defoliated plants. These daily estimates were based on the total dry weight gained by the trees during the entire experiment.

For the sake of simplicity it was assumed in the model that there are no differences among fruits and within roots. Thus, each sink type, fruit or new roots, was simulated as a single organ that represents the demand of its group.

In the model hierarchy is expressed by the fulfillment of the entire demand of the dominant organ, while only the rest of the daily supply is allocated to other sinks. If the demand of the dominant sink organ exceeds the total daily supply its growth rate declines, while the growth of other sink organs ceases altogether.

In the proportional approach, each organ gains dry weight according to its portion of the overall daily demand. Since the relative growth rate (RGR) of both fruit and new roots is assumed to be equal, the distribution of dry matter is dependent upon the ratio of their initial dry weight.

As mentioned, RGR is similar and constant (0.15 d^{-1}) for fruit and new roots, for both the hierarchical and the proportional approaches. Since no relevant data exist to support contradicting assumptions, it is presumed here that hierarchy is not expressed as as a higher RGR (!). A constant RGR yields exponential functions of demand; however, the actual growth rates are determined primarily by the availability of substrate.

In accordance with the experiments, the models simulate a period of 30 days, beginning 7, or 30 DAFS. The initial fruit dry weight is known and set as 0.2 g and 3 g, for 7 and 30 DAFS, respectively. On the other hand, the initial weight of new root meristems is unknown, hence a sensitivity test of the model to this parameter was necessary. Since an increase in soil volume has been found to promote the emergence of new roots, the initial dry weight is doubled for plants transferred to large pots. The influence of the above mentioned assumptions on the simulated behavior of the plants in comparison to that of real plants used for validation was evaluated.

The models were developed using Microsoft Excel 5.0 electronic spreadsheet. The mathematical determinations and functions used in the model appear in the Appendix.

3. Results and discussion

3.1. Effects of partial defoliation and increased soil volume on carbohydrate pools

The carbon exchange rate (CER) of a single calamondin leaf remained quite stable throughout the experimental period, ranging from 4 to 7 $\mu molCO_2 m^{-2} s^{-1}$. Leaf CER was not significantly affected by the enlargement of the soil volume, by the removal of half of the foliage, or by fruit growth.

Partial defoliation (50%) (on the basis of the number of leaves, total leaf area, or calculated leaf weight per plant) brought about an uneven leaf area index (LAI). In fact, the best index for the activity of the foliage, as a producer of dry matter was its dry weight, as measured at the end of the experiment (Fig. 1).

The linear, positive correlation between leaf mass and dry matter production throughout the defoliation and soil volume treatments (Fig. 1) suggests a lack of root restriction or fruit-induced interference with photosynthesis in our experiments.

The amount of carbohydrate reserves in the plant did not undergo a meaningful change during the experimental period. A slight accumulation of reserves occurred in plants with full foliage, whereas no reduction could be observed in the reserves of the 50% defoliated plants. Carbohydrate consumption for fruit growth (Table 1) was far larger than the amount of stored carbohydrate at the beginning of the experiment (data not shown). It seems, therefore, that at least for the stages of fruit development followed in the present study, fruit growth depends almost exclusively on current photosynthesis, and not on reserve carbohydrates.

3.2. Effects of 50% defoliation on the number and size of fruits

The 50% defoliation affected the number of fruit per plant to some extent. When leaves were removed 7 DAFS, the number of fruits per plant had not yet stabilized. Fruit drop occurred in all plants, but was more pronounced in the defoliated ones. The final number of fruits was significantly reduced in those plants (Table 2). In plants defoliated 30 DAFS, the number of fruits was already fixed, hence no effect on fruit number could be observed (Table 2).

The partial defoliation treatment clearly influenced fruit development, as revealed in the fruit size distribution pattern. In the 14 DAFS experiment, where plants were 50% defoliated, the population of fruitlets was divided into two well-distinguished very small versus large fruits (Fig. 2). These size distribution patterns were apparent irrespective of the soil volume treatments (Fig. 2). This somewhat unforeseeable response of the plant to partial defoliation demonstrates the plant's ability to cope with shortage of photoassimilates in a variety of ways.

3.3. Effects of 50% defoliation and increased soil volume on new root growth

Transfer of plants to larger pots resulted in an immediate burst of growth of new, white roots. However, some growth of new roots was also observed in plants remaining in small pots (Tab. 1). The response of new root growth to 50% defoliation was dependent upon the developmental stage of fruit. Defoliation 7 DAFS had no effect on the amount of dry matter allocated to growth of new roots. Quite to the contrary, 50% defoliation 30 DAFS reduced new growth by 50% or more (Tab. 1).

3.4. The partitioning of new dry matter between fruits and roots

The distribution of the dry matter produced during the experimental period was extremely sensitive to partial defoliation and new root growth, particularly during the early stages of fruit development (7 DAFS). The partitioning ratio (PR) between the net increase in fruit and root dry weight was about 6.4 for plants in small pots and full foliage (S-100) (Table 1), indicating a strong, preferential allocation of photoassimilates to the fruit. Where intensive growth of new roots was made possible by the transfer to larger pots (L-100), PR dramatically declined (Table 1). The 50% defoliation reduced the partitioning ratio by about 60% for both S-50 and L-50 treatments (Table 1). The effect of partial defoliation at an early stage of fruit development (7 DAFS) was confined to the fruit; no difference in root growth was apparent between S-100 and S-50, as well as between L-100 and L-50 plants.

At later stages of fruit development (30 DAFS), the patterns of dry matter distribution changed significantly. The PR was not affected by 50% defoliation, in spite of the sharp decrease in the available photoassimilates. This was also true where root growth was allowed through the increase in soil volume. Although the PR declined from 14 to less than 4, the same PR prevailed irrespective of the defoliation treatment. This may be taken as an indication for a 'proportional' mode of partitioning which is unaffected by the amount of available photoassimilates.

3.5. Predictions of dry matter partitioning between fruits and new roots by proportional versus hierarchical simulation models

An estimate of the initial dry mass of root meristems is a prerequisite condition for the model to run. Since no solid data exist to support an estimate as such, the model was run for a wide range of NRIDW (new root initial dry weight), within 0.0001 - 1g per plant. Small values of NRIDW are more likely to represent the real situation at the emergence of new roots. Thus, NRIDW values of 0.02 and 0.04g per plant were defined in the simulations of small and large pot experiments, respectively.

The simulation conducted for the 7 DAFS experiment estimated photoassimilate deficiencies at 17, or 22 days after fruit set, depending on the foliage condition (50% defoliated, or intact plants, respectively). Until that stage, the model indicated the existence of sink-limited growth.

In general, the simulations of the 7 DAFS experiment unequivocally supported the hierarchical pattern of photoassimilate allocation between fruit and new developing roots (Table 3). Only the simulation of the S-100 experiment yielded somewhat exceptional results in that the real PR had an intermediate value between the values predicted by the proportional and the hierarchical models. A model that renders complete priority of new roots over very young developing fruit appears to agree with the experimental results.

The simulation of the 30 DAFS experiment showed that the demand for carbohydrate exceeded the supply during the whole experimental period. Thus, the partitioning mechanisms were active from the beginning of the simulation. PR predictions were less accurate in the 30 DAFS simulations than in the 7 DAFS, nevertheless, those of the hierarchical approach were much closer to the experimental values (Table 3). Although the predictions of the proportional model for final fruit dry weight were sometimes in better agreement with actual data than those of the hierarchical one, it failed to predict the growth of new roots (Table 3). According to the proportional approach, no growth of new roots is possible concomitantly with active fruit growth.

4. Conclusions

The present study represents one of the very few attempts to put photoassimilate partitioning models to an experimental test, followed by simulation analysis.

In the Calamondin system, sink-organ priorities as well as responses to source and sink manipulations varied according to the stage of fruit development.

Although fixed, proportional fruit:root partitioning ratios may prevail for certain periods of time, experimental as well as simulation results indicate that hierarchical modes of partitioning play a predominant role. Hierarchical partitioning mechanisms appear to be indispensable for emergence and development of new plant organs.

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Table 1 - The distribution of new dry matter between developing fruits and new roots during 30 days following 50% defoliation and the enlargement of soil volume. The experiment was conducted 7 and 30 DAFS. Growth is presented by g DW per plant, ±SD. Treatments were: S-100, small pot, full foliage;. S-50, small pot, 50% foliage; L-100, large pot, full foliage; L-50, large pot, 50% foliage.

7 days after fruit set	**S-100**	**S-50**	**L-100**	**L-50**
Fruits	6.19 ± 0.70	2.85 ± 1.29	6.33 ± 0.93	2.84 ± 0.83
New roots	0.97 ± 0.12	1.09 ± 0.25	2.82 ± 0.52	2.80 ± 0.39
Total	7.16 ± 0.58	3.94 ± 1.09	9.15 ± 0.93	5.64 ± 0.54
Fruits to new roots partitioning ratio	6.40	2.60	2.24	1.01
30 days after fruit set				
Fruits	10.22 ± 1.44	5.36 ± 0.61	8.93 ± 1.43	3.05 ± 0.62
New roots	0.74 ± 0.20	0.37± 0.07	2.29 ± 0.13	0.87 ± 0.14
Total	10.96 ± 1.26	5.73 ± 0.65	11.22 ± 1.55	3.92 ± 0.71
Fruit to new roots partitioning ratio	13.81	14.48	3.90	3.51

Table 2 - The effect of 50% defoliation and the enlargement of soil volume on the number of calamondin fruit, 30 days after treatment. Experiments started 7, 14, and 30 DAFS. Data present number of fruit per tree, ± SE. Treatments are as indicated in Table 1.

	Number of fruits per plant				
DAFS	**Initial**	**Terminal**			
		S-100	**S-50**	**L-100**	**L-50**
7	38.6 ± 10.0	19.8 ± 1.2	15.5 ± 1.4	25.7 ± 2.8	15.0 ± 1.6
14	55.3 ± 4.8	42.7 ± 1.1	30.2 ± 1.5	34.6 ± 1.3	35.3 ± 2.5
30	29.4 ± 1.1	27.3 ± 0.6	24.5 ± 1.8	24.3 ± 2.5	23.8 ± 1.5

Table 3 - Predictions of dry matter distribution between developing fruits and new roots in potted calamondin trees, made by computer simulation model. Proportional (P) versus hierarchical (H) models were tested and compared with the experimental result (C). The simulation model was run for the experiments started 7 and 30 DAFS. Treatments are as indicated in Tab. 1. The value of NRIDW (new root initial dry weight) was defined in the simulation as 0.02 and 0.04 g per plant, for small and large pot treatments, respectively. (For further information concerning the simulation see appendix).

	7 DAFS											
	S-100			**S-50**			**L-100**			**L-50**		
Partition type	**P**	**H**	**C**	**P**	**H**	**C**	**P**	**H**	**C**	**P**	**H**	**C**
Fruit DW	5.79	5.22	6.19	3.65	2.86	2.85	5.48	4.28	6.33	3.43	2.14	2.84
New root DW	0.58	1.15	0.97	0.36	1.15	1.09	1.10	2.30	2.82	0.69	1.98	2.80
PR	10.0	4.53	6.40	10.0	2.48	2.60	5.00	1.86	2.24	5.00	1.08	1.01

	30 DAFS											
	S-100			**S-50**			**L-100**			**L-50**		
Partition type	**P**	**H**	**C**	**P**	**H**	**C**	**P**	**H**	**C**	**P**	**H**	**C**
Fruit DW	9.60	8.54	10.2	4.80	3.70	5.36	9.54	7.40	8.93	4.77	2.89	3.05
New root DW	0.06	1.13	0.74	0.03	1.13	0.37	0.13	2.26	2.29	0.06	1.98	0.87
PR	150	7.54	13.8	150	3.27	14.5	75	3.27	3.90	75	1.49	3.51

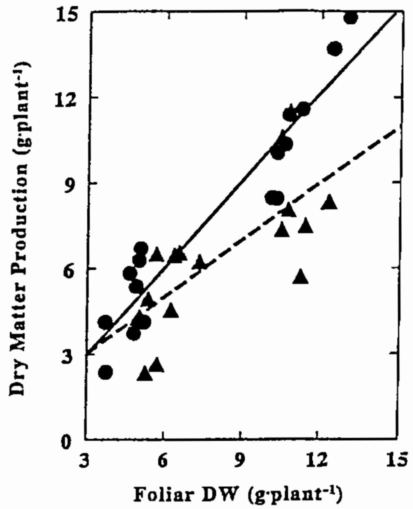

Figure 1 - The effect of different amounts of leaves, as measured by leaves DW per plant, on the production of dry matter during 30 days after treatment. Experiments were conducted 7 (triangles), and 30 (circles) days after initial fruit set. The regression lines were $y = 1.04 + 0.66x$, $(r^2 = 0.73)$ for the 7 DAFS and $y = -0.089 + 1.021x$, $(r^2 = 0.95)$ for the 30 DAFS experiment.

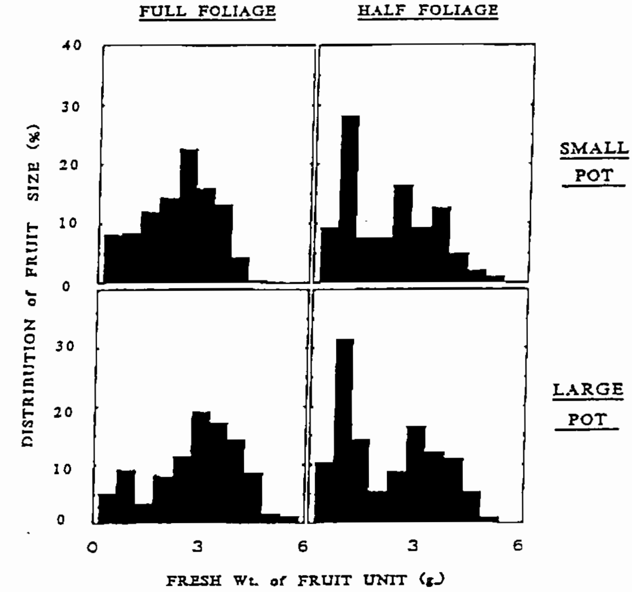

Figure 2 - The effect of 50% defoliation and enlargement of soil volume applied 14 DAFS on the distribution of fruit size in potted calamondin plants. Fruits were weighed 30 days after treatments.

Appendix

Concepts and formulas of the simulation model

		Modeling approach	
Initial parameters	**Explanation**	**Proportional**	**Hierarchical (new roots are dominant)**
FrDW	Fruit dry weight	0.2, or 3.0 g per plant*	0.2, or 3.0 g per plant*
RtDW (NRIDW)	New roots dry weight	0.02, or 0.04 g per plant*	0.02, or 0.04 g per plant*
RGR	Fruit and new roots relative growth rate.	0.15 day^{-1}	0.15 day^{-1}
TOTSUP	Total daily supply of photoassimilate	0.333, or 0.168 gDW per plant**	0.333, or 0.168 gDW per plant**
Variables		Model formulas	
FRDEM	Daily fruit demand for dry weight	FrDW*RGR	FrDW*RGR
RTDEM	Daily demand of new roots for dry weight	RtDW*RGR	RtDW*RGR
FRDEM+RTDEM	Total daily demand for dry weight (fruit and new roots)	FRDEM+RTDEM	FRDEM+RTDEM
FrGR	Fruit growth rate	IF(TOTDEM?TOTSUP,FRDEM,FRSUP)	IF(TOTDEM?TOTSUP,FRDEM,FRSUP)
FRSUP	Actual daily supply of dry matter to fruit	IF(TOTDEM?TOTSUP,0,KFR)	IF(TOTDEM?TOTSUP,0,KFR)
KFR	**Allocation coefficient to fruit**	**FRDEM*TOTSUP/TOTDEM**	**TOTSUP-RTSUP**
RtGR	New roots growth rate	IF(TOTDEM?TOTSU,RTDEM,RTSUP)	IF(TOTDEM?TOTSUP,RTDEM,RTSUP)
RTSUP	Actual daily supply of dry matter to new roots.	IF(TOTDEM?TOTSUP,0,KRT)	IF(TOTDEM?TOTSUP,0,KRT)
KRT	**Allocation coefficient to new roots**	**RTDEM*TOTSUP/TOTDEM**	**IF(RTDEM?TOTSUP,RTDEM,TOTSUP)**

* Simulations for 7, or 30 DAFS, respectively.

** Simulation for plants with full, or 50% foliage, respectively.

MODIFYING 'PEACH' TO MODEL THE VEGETATIVE AND REPRODUCTIVE GROWTH OF ALMONDS

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Keywords: Almond simulation model, carbon budget, carbon assimilation, carbon demand, organ growth potential, carbon partitioning

Abstract

A carbon budget computer simulation model for almonds has been developed by modifying the existing PEACH model (DeJong *et al.*, 1996). The model simulates, on a daily basis, the seasonal carbon supply and demand for reproductive and vegetative growth. The concept behind the model is that the tree grows as a collection of semiautonomous interacting organs competing for carbohydrates, whose partitioning is dependent on the organ growth potentials. Although peaches and almonds are closely related, they have some architectural and physiological differences due both to genetic and management-induced (e.g. pruning and training systems, thinning, etc.) causes. These differences required modification of the parameters of some of the equations used in the main parts of the model, the carbon *supply* and *demand* modules, although the main structure of the PEACH model was not changed. Carbon assimilation (supply) is simulated as a function of solar radiation, minimum and maximum temperatures, degree-days, tree light interception, and leaf photosynthetic rates. Respiration and growth are simulated to determine the various organ carbon demands; carbon partitioning is simulated based on sink strength (organ growth potential) and source-proximity of tree organs as well as on carbohydrate availability. The model provides a framework for integrating environmental and physiological factors controlling carbohydrate supply and demand for growth of almonds at the orchard level and indicates potential avenues of research related to growth and productivity. Results of the first model simulations are presented.

1. Introduction

Carbon budget computer simulation models have been used to relate plant growth to environmental conditions for several years (Thornley, 1990). Unfortunately, very few of these models have been developed for fruit tree crops, particularly on a whole tree basis (DeJong and Grossman, 1992, 1994). PEACH was developed in the last years as an attempt in this direction (Grossman and DeJong, 1994). PEACH simulates, on a daily basis, the annual carbon supply and demand for reproductive and vegetative growth of peach trees. It is a state variable simulation model in which fruit, leaf, stem, branch, trunk and root weight are the state variables, and minimum and maximum air and soil temperatures, degree days, solar radiation and canopy light interception are the driving variables.

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The central concept behind PEACH is the hypothesis that trees are collections of semi-autonomous but interacting organs whose carbon partitioning is driven by competition based on their growth potential, their source proximity and carbohydrate availability (DeJong and Grossman, 1992; Grossman and DeJong, 1994). The way the model simulates carbon supply and demand as well as carbon partitioning can be reviewed in detail in previous publications (Grossman, 1993; Grossman and DeJong, 1994; DeJong *et al.*, 1996). The assimilated carbon represents the "supply" part of the model; this carbon pool is available for growth and respiration, which represent the "demand" part. Carbon assimilation is simulated as a function of the seasonal patterns of canopy light interception, photosynthesis, and daily maximum and minimum air temperatures. Organ growth simulation is based on experimentally determined maximum achievable growth in trees growing with no limitation of water or nitrogen in which the fruit load was manipulated to minimise competition for carbohydrates (potential growth rates).

Carbon partitioning is simulated first by satisfying the maintenance respiration needs; then, carbon is allocated to organ growth based on sink strength (potential growth rates), source-proximity (fruits, leaves, stems and branches first, then trunk, and roots last), and carbon availability (for details see Grossman, 1993 and Grossman and DeJong, 1994). During the first 200 degree-days, fruits, leaves stems and branches are left to grow at their potential growth rates, and their cost is subtracted from the trunk and root reserves. The code of the model is written in Visual Basic^{TM}.

Field validation has shown that PEACH simulates the vegetative and reproductive growth of peach trees growing under different fruit loads and environmental conditions reasonably well (Grossman and DeJong, 1994; DeJong *et al.*, 1996). Current research is being done in order to adapt PEACH to other fruit tree species. One might presume that PEACH should be easily adapted to species such as almonds, which are closely related to peaches. However, some architectural, anatomical and physiological differences can be observed between these species, requiring modification of the two main parts of the model, the *supply* and *demand* modules. We gave special attention to those characteristics in which these species differ when trying to make the model adaptation.

The scope of this study was to develop the first version of an ALMOND carbon budget model and run the first simulations of the carbon supply and demand for reproductive and vegetative growth of almond trees. At the same time, this study serves as a test of the feasibility of adapting the PEACH model to different fruit tree species.

2. Materials and methods

2.1. Modifications to the PEACH model

2.1.1. Model parameterisation

The almond trees used to parameterise the model were 'Nonpareil' grafted on 'Nemaguard' rootstocks growing in a high yielding orchard at the Paramount Farming Company, Shafter, CA (35°N 117°E). The trees are planted 6.5 x 6.5 m in a North-South orientation .The orchard included 'Nonpareil' rows (50%), alternately with 'Monterrey' (25%) and 'Price' (25%) pollinizer rows.

Four eight-year-old trees were excavated at the end of the growing season in October 22 of 1996 to determine the initial values of biomass corresponding to the various tree organs including fruits, leaves, stems, branches, trunk and roots (baseline data). The nut yield was determined after shaking the trees in August 13, 1996; the leaves that fell because of the shaking were accounted for as well as those that the trees dropped prior to the excavation. The initial number of fruits per tree was estimated by considering the final number of fruits per tree at harvest as well as data on fruit set 22.06 % measured for that season (1996). For the simulations, the number of fruits was assumed to decline according to a power curve $y = at^k$ from the full bloom date to May 1, where y = number of fruits per degree day, a = initial number of fruits (at bloom), t = accumulated degree days, and K constant = -0.2378.

2.1.2. Carbon supply and demand modifications

The main change to the carbon supply module was the modification of the surface response curve describing the daily and seasonal tree light interception. New curves were obtained by monitoring tree light interception of Nonpareil almonds over the growing season of 1996. In the initial simulations, no changes were made to the leaf photosynthesis parameters, but work is ongoing to develop more realistic daily and seasonal patters of almond leaf photosynthesis.

Regarding the carbon demand module, all the organ growth potential curves were replaced by those obtained for almonds. Fruit growth potential was obtained by monitoring fruit growth in 10 'Nonpareil' trees with a very low fruit load (<500 fruits per tree) growing at Davis, CA during the season of 1995. Leaf canopy and trunk growth potentials were assessed by manually manipulating/adjusting the fruit load of 10 trees, which were heavily thinned at bloom in Shafter, CA in 1997, and measuring growth over the growing season; the main branches were assumed to grow similar to the trunk. The stem weight obtained from the excavated trees was assumed as the highest value of the growth curve; stem growth was monitored during the 1997 season. Fruit growth in trees with normal fruit load was also monitored in Shafter, CA during the 1996 season for model verification/validation. No changes were made to the organ maintenance respiration functions except to that of the branches. Since the almond branches are more massive than those of peach, the peach trunk respiration parameters were used for almond branches. Carbon partitioning was simulated as in the PEACH model (Grossman and DeJong, 1994). More data about organ growth and respiration are currently being collected, so these data can be re-evaluated in the future.

2.2. Environmental data

Minimum and maximum air and soil temperature and solar radiation data were obtained from the California Irrigation Management Information System (CIMIS) weather station located in Shafter, CA for the year 1996, and used for the model simulations (Fig. 1). Data from Davis (1995) and Shafter (1997) were also used to obtain some of the calibration equations as described in last paragraph. The calculation of degree-days was done by the single sine, horizontal cut-off method, with critical temperatures of 7 and 35 °C (Zalom *et al.*, 1983; DeJong and Goudriaan 1989).

3. Results and Discussion

3.1. Input variables

Table 1 shows the values of the parameters used in the model simulations. The results of the excavation as well as the calibration equations describing the organ growth potentials are also given.

Compared to the values of the parameters used in the original PEACH model (Grossman and DeJong, 1994), almonds have a bigger tree size than peaches; also, almonds exhibit a proportionally more dense aboveground structure (trunk, scaffolds, and primary and secondary branches) than peaches, which reflects the less intensive pruning in almonds. Genetic differences surely also account for these differences. Stems, on the other hand, are proportionally more dense and bigger in peaches than in almonds and the water sprouts represent a greater fraction of stem dry weight in almonds than in peaches. Other aspects in which both species differ markedly are related to fruits; the number of fruits per tree is much greater in almonds whereas the fruit size is much larger in peaches. The fruit growth patterns are also distinct in both species, particularly during the last stage of development, in which the growth of the fleshy mesocarp accounts for most of the accumulated dry matter in peaches whereas the dry matter accumulates mostly in the kernel in the case of the non-fleshy almond fruits. The growth pattern of almond fruits as well as that of the other organs is described by the calibration equations of Table 1. The modifications done to the PEACH model in this first trial were based on these differences.

Degree-days rather than calendar days were used to obtain the equations of Table 1. Degree-day accumulation and the other driving environmental variables used as basic inputs in the model simulations are shown in Fig. 1. As the season progressed, a higher accumulation of degree-days occurred due to a parallel temperature increment; some cloudy days were present during the season and caused variation in radiation and temperature. These variations were reflected in fewer degree-days accumulated per day and ultimately in the simulated carbon assimilation shown in Fig. 2.

3.2. Model simulations

Simulation of the seasonal pattern of daily carbon assimilation is shown in Fig. 2. The maximum rates of daily assimilation were similar to those reported for peach and other C_3 crops (Grossman and DeJong, 1994; Ng and Loomis, 1984). These results indicate that the model modifications done to the tree light interception resulted in reasonable estimations of carbon assimilation for a C_3 crop.

At the beginning of the season, most of the assimilated carbon was used for growth; however, as the season progressed, the fraction of the gained carbon going to growth decreased (Figures 2 and 3). The total organ growth represented a carbohydrate cost of 52.6% of the carbon assimilated until the harvest (August 13th); the rest of the assimilation was used in maintenance respiration, which is represented by the difference between both curves in Fig. 2. The carbon allocated to maintenance respiration, as opposed to growth, was more prominent at the end of the simulated season because of the higher temperatures and the progressive accumulation of dry matter (Fig. 1 and 3). The cost of growth was probably underestimated since, in comparison with peach, almond fruit growth exhibits an important accumulation of dry matter in the kernel rather than in the mesocarp during the last phase of growth. At this time, lipids, which are more expensive to produce, accumulate in the kernel (Hawker and Buttrose, 1980). Adjustments to fruit growth due to the lipid conversion were not done in this preliminary version of the model.

In the case of fruit growth, the model was tested with field data for fruits growing in trees with normal fruit load at Shafter, CA in 1996 (Fig. 4). The model predictions corresponded reasonably well to the observed values, with some apparent overestimation in the 300-1000 degree-day period. Final individual fruit weight on normal cropped trees at Shafter (1996) was 24% less than on thinned trees at Davis (1995) and the model simulated this difference quite well (Fig. 4). We are currently collecting the growth data for other organs to verify/validate the model simulations shown in Fig. 2 and 3. However, these results indicate that the modifications done so far allow the model to reasonably simulate fruit growth.

The model provides a framework for integrating environmental and physiological factors controlling carbohydrate supply and demand for reproductive and vegetative growth of almonds at an orchard level and provides a method to evaluate future potential avenues of research related to growth and productivity of almonds.

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Table 1 - Various tree organ biomass, initial values of state variables, and organ growth potential calibration equations used in the model simulations.

Variable	Organ biomass dry weight (g/tree)	Initial values	Calibration equation[X] (g of organ dry weight per dd)
Fruit number at bloom		24516	
Final fruit number		5410	
Individual fruit			$=\exp(-5.07 + 0.036dd - (7.16 \times 10^{-5})dd^{2} + (4.75 \times 10^{-8})dd^{3} - (dd>500)(4.75 \times 10^{-8})(dd-500)^{3} + (dd>1450)(8.5 \times 10^{-11})(dd-1450)^{3})$
Total fruit	24077		
Leaves	17618		$=\exp(95.85 - (1039.48/dd))^{0.5}$
Stems	4300		$=\exp(70.81 - (26982.7/dd^{1.5}))^{0.5}$
Trunk	154443	154443	$=\exp(154443 + (2.53 \times 10^{-5})dd)$
Branches[Y]	86313	86313	$=\exp(86313 + (5.50 \times 10^{-5})dd)$
Root	54438	54438	

[Z] Includes stump and main scaffolds

[Y] Woody parts other than trunk, stems and roots

[X] dd = degree days

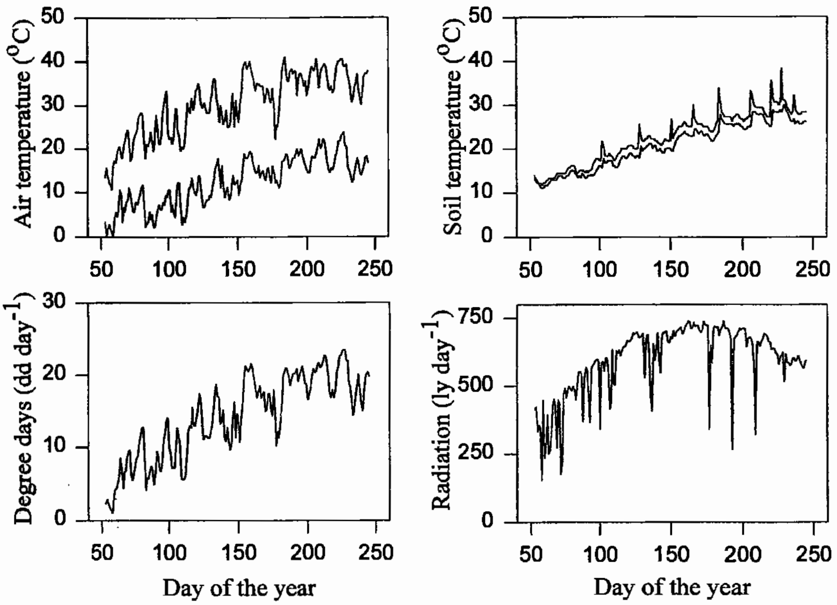

Figure 1 - Seasonal patterns of minimum and maximum air and soil temperatures, degree-day accumulation and solar radiation at Shafter, CA. 1996.

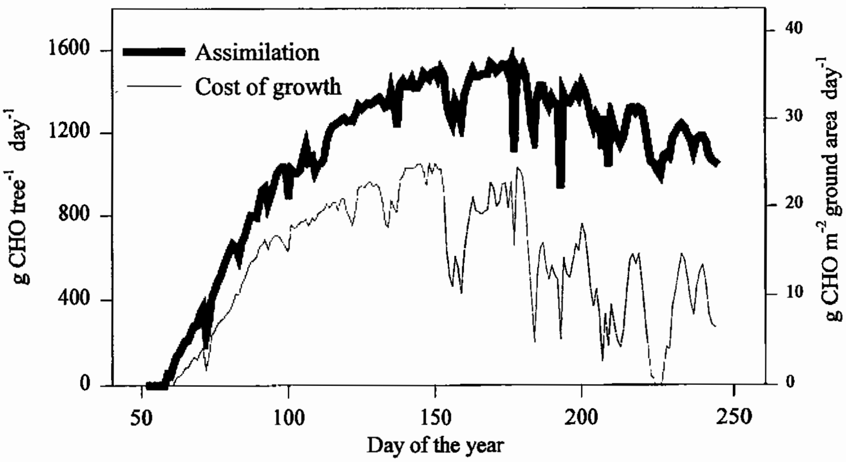

Figure 2 - Simulated seasonal patterns of daily carbon assimilation and daily cost of growth for almond trees at Shafter, CA.

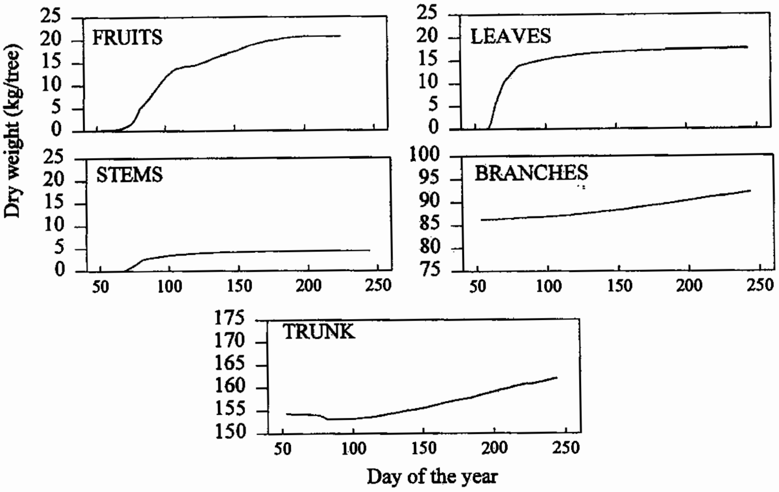

Figure 3 - Simulated seasonal patterns of organ dry weight accumulation per tree for almond trees in Shafter, CA during the 1996 season.

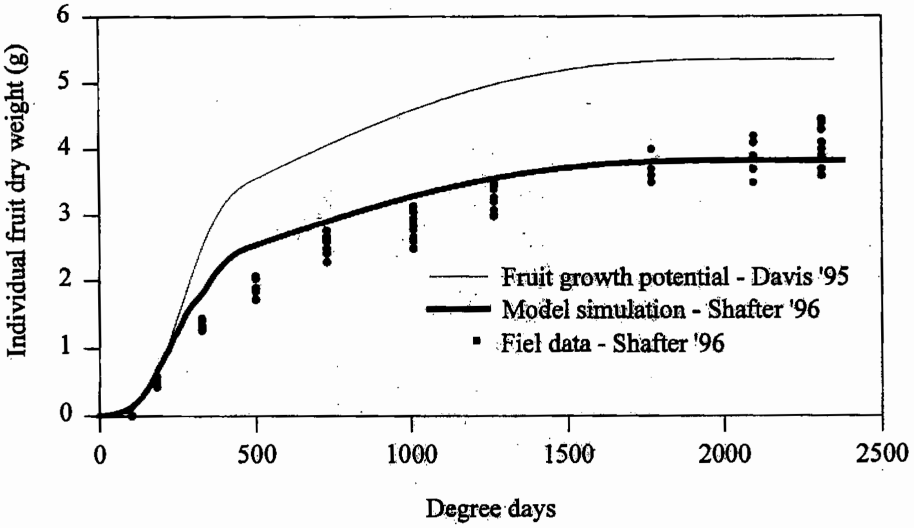

Figure 4 - Fruit growth potential obtained from almond trees growing with a very low fruit load at Davis, CA in 1995, and model-simulated and actual field growth data of individual almond fruits growing in trees with a normal fruit load at Shafter, CA in 1996.

MODEL OF FRUIT GROWTH BASED ON BIOPHYSICAL DESCRIPTION OF MAIN CONTRIBUTING PROCESSES

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Abstract

A theoretical framework is suggested for the description of fruit growth. The stages of fruit development are considered when cell division is finished and the fruit can be approximated by a community of growing cells; this criterion enables us to clarify the relationship among the basic mechanisms. The fruit is treated as one compartment, separated from two external compartments - the parent plant and the ambient atmosphere - by composite membranes. The composite membrane approximates a set of transport barriers, arranged both in series and in parallel, as a single barrier with combined transport characteristics. Cell growth is related to the turgor pressure exerted on the wall, by an equation based on experiments that revealed a threshold turgor pressure, below which no extension occurs. The model was applied to the calculation of seasonal and diurnal growth of the peach (*Prunus persica* (L.) Batsch) fruit. The growth, as determined by dry and fresh mass dynamics, was calculated under conditions of water stress for various crop loads. The model also enables us to calculate the hydrostatic and osmotic pressures in the fruit, and to compare the contribution of xylem and phloem flows to the fruit water budget.

1. Introduction

The dynamics of fruit mass result from the balance between the incoming and outgoing flows of water and solutes. These flows depend on the biophysical and biochemical state of the fruit and on the external conditions. Agrotechnical treatments influence the water and solute accumulation in the fruit. The processes involved in fruit growth and development are strongly correlated. Use of a model based on the thermodynamic analysis of the acting forces may help us to understand these interrelationships and to evaluate the roles of meteorological conditions and agrotechnical treatments in determining the yield and quality of fruits. Molz and Ferrier (1982) analysed the movement of water in plant tissue through two distinct pathways: the symplasmic and the apoplasmic. The possibility of carbohydrate import via the two paths was discussed by Patrick (1997). Steudle (1993) proposed to describe the tissue as a composite membrane, by treating the set of transport barriers, arranged both in series and parallel, as a single barrier with combined transport characteristics. The root was treated as one compartment, separated from the outside by a composite membrane, for which the water transport characteristics were studied (Steudle *et al.*, 1993). Studies of sugar uptake by fruits (Milner *et al.*, 1995; Vizzotto *et al.*, 1996) revealed an important role of an active and/or facilitated mechanism. Recently, a fruit growth model was developed, which considers the fruit as one compartment separated by composite membranes from two external compartments: the parent plant and the ambient atmosphere (Fishman and

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Génard, 1998). The model calculates the balances of water and sugars in a growing fruit and takes into account the influence of turgor pressure on the growth rate. It was calibrated and validated for peach (*Prunus persica* (L.) Batsch) fruit using weather data collected by INRA Avignon. The meteorological station was situated close to the experimental orchard. The aim of the present work was to demonstrate the generality of the qualitative results of the model and to evaluate the roles of the meteorological and agrotechnical conditions. The reported simulations were performed using sinusoidal functions for the meteorological data, with a maximum for the temperature and a minimum for the humidity at midday, approximating the daily variations of these parameters.

2. Model description

The stages after cell division had ceased, when fruit growth was due mainly to cell enlargement, were modelled. This justifies the consideration of the fruit as a cell community with a constant number of cells (or as a one-cell compartment) and use of the equation describing the hydrostatic pressure effect on the irreversible cell wall expansion, which was elaborated originally for a single cell (Lockhart, 1965). Treating the fruit as one compartment enabled us to simplify the theoretical analysis and to clarify the feedback relationships of the basic mechanisms. From the viewpoint of thermodynamics, the fruit is an open and autonomous system: there is exchange of material and energy with two surrounding compartments. The growing fruit exchanges water and solutes with the parent plant through the phloem and xylem systems of the pedicel. The connection with the ambient atmosphere proceeds via respiration, transpiration and heat transfer through the fruit surface (Fig. 1). The rate of exchange is restricted by kinetic barriers. The fruit compartment is separated from two external compartments by composite membranes. The composite membrane approximates the set of transport barriers, arranged both in series and parallel, as a single barrier with combined transport characteristics (Steudle *et al.*, 1993). The solution flows across the membrane are described by equations of nonequilibrium thermodynamics, driven by the difference between the chemical potentials of the respective species on the two sides of the membrane (Katchalsky and Curran, 1965). Coupling of fluxes of different materials has been taken into consideration by means of the equations of nonequilibrium thermodynamics, resulting in appearance of the reflection coefficient in the flow equations, as a measure of impermeability of the membrane to the solute. As a driving force for the transpiration losses, the difference in relative humidity between the intercellular spaces of the fruit and the ambient atmosphere was used (Nobel, 1974). The transport of sugar from phloem to fruit mesocarp is described by three possible mechanisms: (i) mass flow, which is proportional to the solution flow; (ii) passive diffusion, with the difference between the sugar concentrations as a driving force; (iii) the active (and/or facilitated) mechanism described by the Michaelis-Menten equation. From a mathematical viewpoint, the model is closed. Its main dynamic variables are the dry and fresh weight of the fruit. Auxiliary variables, such as sugar concentration, solution flows, osmotic and hydrostatic pressures etc., may be calculated from the main dynamic and input variables. A 1-h time step was employed to describe the diurnal and seasonal changes of the dynamic variables.

3. External signals

Environmental conditions, such as the temperature and relative humidity in the ambient atmosphere, intercepted solar radiation and water status in the soil, influence the processes involved in fruit growth. The effects of the temperature and relative humidity in the ambient atmosphere are immediate. Consideration of the fruit as an autonomous system, having contact with the parent tree through the pedicel, necessitates the inclusion of the branch (or stem) water potential as an external signal, which, in turn, reflects the soil water status. Solar radiation can be considered similarly. At first, we ignored the contribution of peach photosynthesis to their total growth carbohydrate requirements. This contribution is 5-9%, depending on the fruit exposure to light (Pavel and DeJong, 1993). The concentration of carbohydrates in the branch is used as an external signal, which depends on the leaf photosynthesis, influenced by the interception of the solar radiation by the leaves. To clarify the roles of the meteorological and agrotechnical conditions, the simulations in the present study were executed with sinusoidal functions for the inputs to represent the daily variations of the real values. The temperature and relative humidity of the ambient atmosphere were used as a sinusoidal function for each of the signals, with a maximum for the temperature and a minimum for the humidity at midday (Fig. 2a, b). The maximum and minimum temperatures were 25 and 15°C, respectively, and the maximum and minimum values of relative humidity were 0.95 and 0.40, respectively. The difference between the sugar concentration in the phloem during the light and the dark periods was assumed to be 0.08, as reported for the phloem of *Salix* spec. (Peel and Weatherley, 1962). The diurnal smooth variation of sugar concentration from 0.17 to 0.09 that was used as input, is presented in Fig. 2c. Diurnal fluctuations of the water potential in the stem of the peach tree were reported to range from -0.2 MPa in the morning to -1.0 MPa at midday in a normally irrigated orchard (Garnier and Berger, 1986). Water potential changes during the day, whereas at night changes are negligible. Therefore, this input was represented by a sinusoidal function during the day and a constant at night (Fig. 2d).

4. Results and discussion

Seasonal and diurnal fruit growth, as determined by the dry and the fresh mass, were calculated under conditions of normal irrigation and water stress, and under three different crop loads. Crop load was simulated by the concentration of sugar in the phloem. For a high crop load, lower concentrations of sugar were used as input: 0.12 and 0.04 for the maximum and minimum concentrations, respectively. For a low crop load, the maximum and minimum concentrations were 0.22 and 0.14, respectively. The seasonal fruit growth patterns under conditions of high, medium and low crop load (HC, MC and LC, respectively) are shown in Fig. 3. To simulate fruit growth under water-stress conditions, the curve of the stem water potential was reduced, the maximum and minimum being -0.5 and -1.4 Mpa, respectively (Fig. 2d). A comparison between seasonal fruit growth patterns under control (CT) and under water-stress (WS) conditions is presented in Fig. 4. Obviously, the fruit growth was reduced under stress conditions. The decrease in fresh mass (Fig. 4a) was much more pronounced than that in dry mass (Fig. 4b), which means that sugar concentrations of the fruit were enhanced under water-stress conditions. The concentrations under control conditions were calculated to vary during the season between 0.06 and 0.08, whereas under water-stress conditions they ranged from 0.085 to 0.1.

The calculations of the seasonal fruit growth under water stress were performed to demonstrate the potential sensitivity to changes of water status rather than to simulate a real orchard situation. In addition, we simulated a more realistic case in which the water stress was imposed for several days, after which a normal water regime was resumed (Fig. 5a). The smooth curve simulates the seasonal growth under control conditions, whereas the other curves correspond to treatments in which stress was applied for 4 days, staring at day number 21. The curve marked with black dots corresponds to maximum and minimum stem potentials of -0.5 and -1.4 MPa, respectively; the curve marked with white dots corresponds to maximum and minimum stem potentials of -0.6 and -2.4 MPa, respectively ("severe stress"). Fig. 5a shows that the growth stopped during the days of stress and fruit weight even diminished during severe stress, but as soon as the normal watering regime was resumed, the fruit growth restarted. By the end of the season, the growth delay that occurred during the stress period was compensated for. This compensation effect was a result of increased sugar concentration caused by the stress, leading to an increased difference between the osmotic pressures inside and outside the fruit, which, in turn, is followed by an increase in incoming solution flow. The diurnal patterns of processes showed that the fruit shrinkage during the day was greater and the growth during the night was slower with stronger stress (Fig. 5b). The intensive nighttime growth and the midday fruit shrinkage, which depend on plant water status, are consistent with observations (Huguet and Génard, 1995). These effects can be explained by analysis of the fruit water budget. The total income of water was simulated as a function of the water status in the tree and in the ambient atmosphere. A dual effect of transpiration is demonstrated by the calculations. On the one hand, it diminishes the internal hydrostatic pressure, and so leads to a maximum influx of solution when the transpiration is maximal, but, on the other hand, the water losses are so high that they may lead to a negative water balance in the fruit. It can be concluded that the model is able to describe fruit growth on the diurnal and the seasonal scales taking into account the basic associated phenomena, and is able to reveal interrelationships among these processes and the effect of meteorological conditions and agrotechnical treatments on fruit growth.

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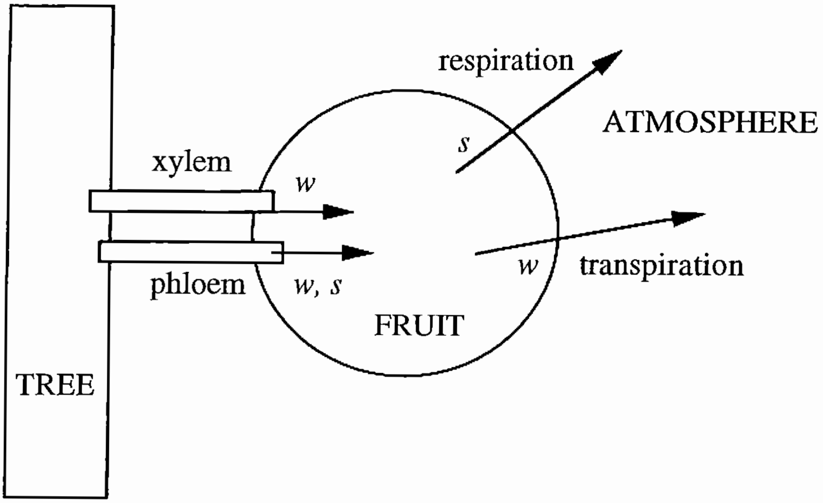

Figure 1 - Schematic presentation of the model. Arrows represent flows of water (w) and dry materials (s).

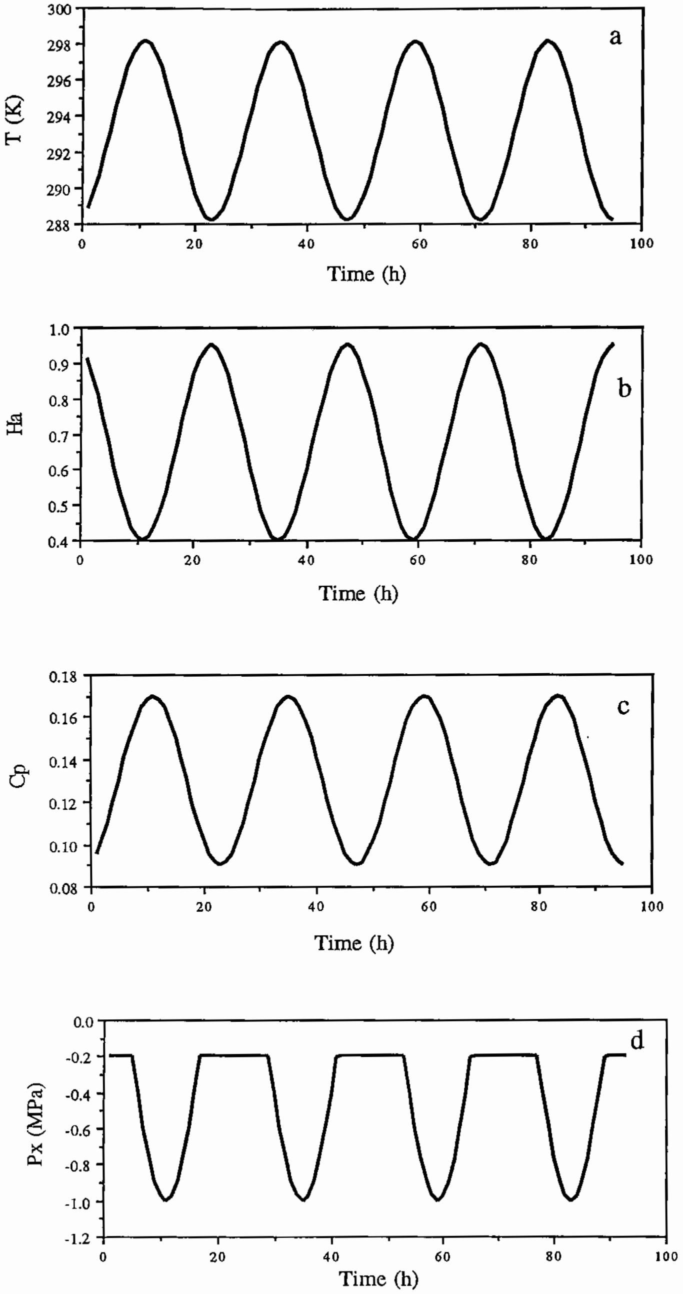

Figure 2 - Input variables as functions of time: (a) temperature (K), (b) relative humidity in ambient atmosphere, Ha (dimensionless), (c) sugar concentration in the phloem, Cp (dimensionless) and (d) water potential in the stem, Px (MPa).

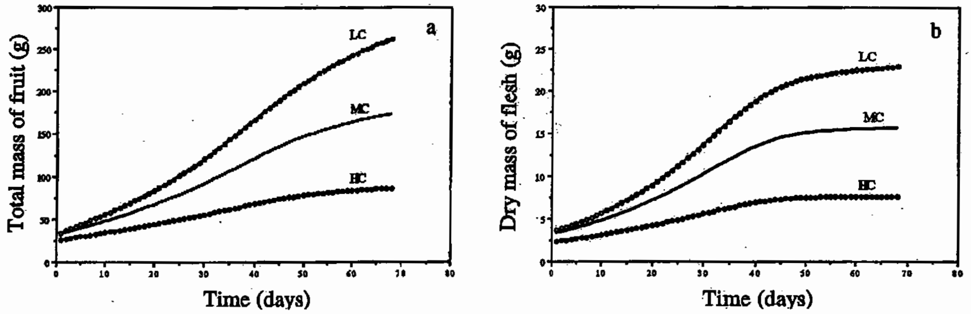

Figure 3 - Seasonal growth of (a) fresh mass of fruit (g) and (b) dry mass of flesh (g) as influenced by the crop loadings: low crop load (LC), moderate crop load (MC) and high crop load (HC).

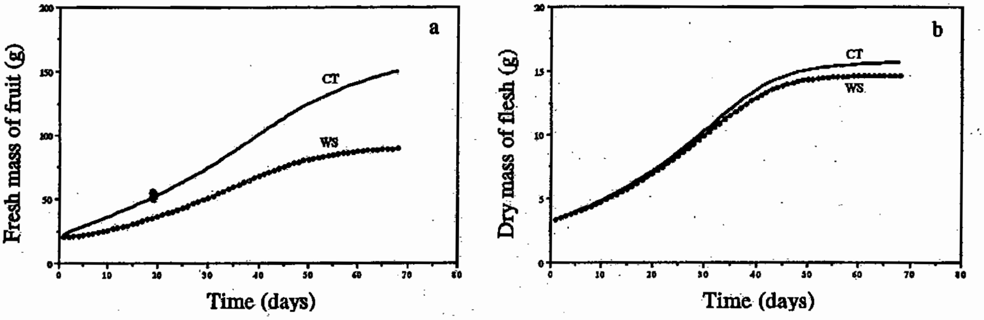

Figure 4 - Seasonal growth of (a) fresh mass of fruit (g) and (b) dry mass of flesh (g) as influenced by the water status in the stem: the normal watering treatment (CT) and the water-stress condition (WS).

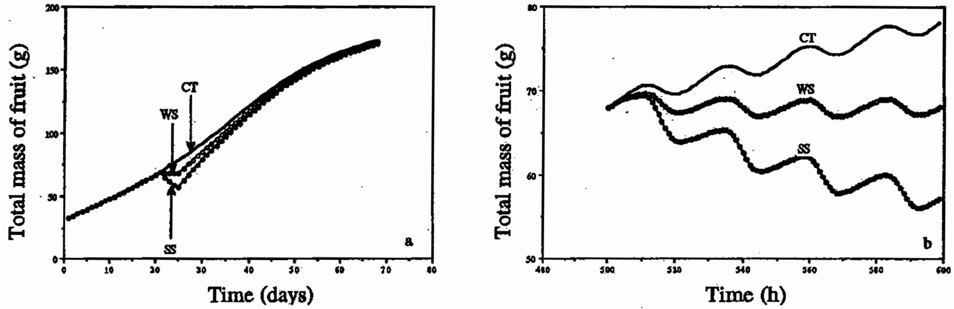

Figure 5 - (a) Seasonal dynamics of total fruit weight (g) simulated for normal watering conditions CT) before day #21 and after day #25. During the 4 days, #21 to #25, water stress (WS) and "severe" water stress (SS) were applied. (b) Diurnal dynamics of the fruit mass for the 4 days, #21 to #25, under the control (CT), stress (WS) and the severe stress (SS) conditions. The midday shrinkage increased with increasing stress.

USING THE RELATION BETWEEN GROWING DEGREE HOURS AND HARVEST DATE TO ESTIMATE RUN-TIMES FOR *PEACH*: A TREE GROWTH AND YIELD SIMULATION MODEL

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Keywords: Growing degree hour, harvest day, peach simulation model, yield

Abstract

The hypothesis that Growing Degree Hour (GDH) accumulation affects the length of the fruit growth period was tested on different stone-fruit cultivars. A strong correlation was found between the accumulation of the GDH during thirty days after bloom and the harvest date. This relation is introduced on PEACH, a computer simulation model of annual carbon supply and demand for reproductive and vegetative growth of peach trees. In previous versions, the PEACH model used the degree-day (DD) accumulation to predict the harvest date. The revised model uses the daily minimum and maximum temperatures to calculate the GDH accumulation during the first month of fruit growth and estimates the number of growing days for the specific year and cultivar. The GDH relation improves the model prediction of the harvest date and simultaneously improves the ability of the PEACH model to predict yield. Results are discussed for early and late peach cultivars and for different years and locations.

1. Introduction

Carbon budget computer simulation models have been used to relate plant growth to environmental conditions for several years (Thornley, 1990). Few of them have been developed for deciduous fruit crops (Seem *et al.*, 1986; Abdel-Razik, 1989; Buwalda, 1991; Wermelinger *et al.*, 1991; Grossman and DeJong, 1994). Most of them use degree-days to estimate fruit growth run-times. Organ growth depends on the temperature accumulation from the bloom and fruit maturity is reached after having accomplished a fixed amount of degree-days. This solution allows to simulate and compare different years and locations.

One of these few whole-tree-basis models developed is *PEACH* (Grossman and DeJong, 1994). *PEACH* is a computer simulation model, on a daily basis, of the annual carbon supply and demand for reproductive and vegetative growth of peach trees. It is a state variable simulation model in which fruit, leaf, stem, branch, trunk and root weight are the state variables, and minimum and maximum air and soil temperatures, degree days, solar radiation and canopy light interception are the driving variables. *PEACH* uses the degree-days to estimate run-times.

Another tool to estimate the temperature accumulation is the growing degree hours (GDH) (Anderson *et al.*, 1986). This concept was first developed to estimate the chilling and heat requirements of different deciduous tree species (Anderson *et al.*, 1986; Caruso *et al.*, 1992). The GDH concept is based on a higher effect of the temperature at the optimum and a high decrease of this effect after that optimum.

The scope of this study was to find a relation between the GDH and fruit growth period and to integrate it in *PEACH* for the run-times estimation.

2. Materials and methods

2.1. Temperature - GDH relation

To test the relation between the GDH and harvest date, data of full bloom and harvest date from different locations in California (Fresno, Stanislas and Yolo counties) and for different years (from 1988 to 1997 depending on the locations) were collected from growers. The data concerned different cultivars of prune, peach, cling peach and nectarine.

For each year, location and cultivar, the sum of GDH from full bloom until 30 days after bloom was calculated using the hourly temperature based on the GDH equation presented by Anderson *et al.* (1986). The hourly temperatures were obtained from the California Irrigation Management Information System (CIMIS) weather stations closest to the data location.

For each cultivar, all relative data was used together to find the relationships between the sum of GDH one month after bloom and the number of day of growth (number of days between the full bloom and the harvest date).

2.2. Modifications to the *PEACH* model

The relation obtained between the sum of GDH one month after bloom and the number of days of fruit growth was integrated to *PEACH* for three cultivars: Spring Lady (early maturating peach), CalRed (late maturing peach) and Ross (cling peach). The model computes the sum of GDH one-month after bloom and uses the relation between GDH and number of days of growth to estimate the fruit harvest date. The GDH used only that estimation, all the model equations for growth in dry weight still running with degree-days.

For each year and cultivar, *PEACH* was run using first with degree-days to estimate the harvest date (without modification) and second with the GDH relation (with modification). The harvest date estimated by the model in both cases was compared to the real harvest date. The simulated fruit yield was compared with data when simulation stopped on the observed harvest date.

3. Results

3.1. GDH - Day of Growth relationship

An important correlation was found between the sum of GDH one month after bloom and the number of growing days for 10 cultivars of cling peaches (Fig. 1). The number of growing days decreased with increase of GDH sum one month after bloom. The same results were found for five peach cultivars (Fig. 2), four nectarine cultivars (Fig. 3) and six plum cultivars (Fig. 4). The slopes of the different equations are of the same order for each species.

3.2. Model simulation

3.2.1. CalRed

For all fives simulated years, using the GDH – growing day relationship, the estimation of the harvest day is closer to the real date of harvest than using the degree-days (Table 1). This difference affects the estimated yield per tree. The difference between the estimated yield using the real harvest date and GDH is less than 5%.

3.2.2. Spring Lady

For three years (out of four) of simulation, by using the GDH, the model estimates the real date of harvest correctly (Table 2). The model running with the degree–days, makes a mistake of 3-4 days with the real date of harvest, which induces a difference on the estimated yield per tree superior to 20%.

3.2.3. Ross

In all four years of simulation, a better estimation of the harvest day is found using GDH instead of degree-days (Table 3). The difference on estimated yield is less than 7% with GDH, but more than 17% when degree-days are used.

4. Discussion

The relation observed between the sum of GDH one month after bloom and the date of harvest confirmed the importance of temperature during the early time of fruit growth found by Weinberger (1948) on peach or Bergh (1990) for apple. It seems interesting that the slope of the different equations is in the same order. Further investigations need to be made to verify this result which could indicate a specific species answer to temperature increase during the period following bloom on the decrease of number of day of fruit growth.

Using the relation between GDH and harvest date, *PEACH* makes a better estimation of the number of growing days and the simulated yield per tree. This effect is greater for early cultivars (Spring Lady). In that case, the number of day of growth is low (85 days) and two or three days of growth could have an important effect on the yield. The fruit growth rate is high during that period.

For Ross, the real data used to be compared with the simulation were from other locations than the location used to fit the model fruit growth equations. Local differences in environmental conditions (temperature) could explain the results obtained.

In both cultivars Spring Lady and Ross, the simulated fruit yield per tree based on degree-days can be 20% higher than the simulation results with real data. This indicates the high sensitivity of *PEACH* to the date of harvest, especially for early cultivars and when *PEACH* is used for other environmental conditions than the ones fit for.

The effect on fruit harvest date affects also the carbohydrate balance of the tree. Since the fruit is the most important sink, its absence (stop of growth) or presence (still growing) affects the partitioning of carbohydrate to the other sinks.

In conclusion, this works shows the problem of a good estimation of the harvest date for modelling and the sensitivity of PEACH to these factors. Using GDH improves the estimation in all cases. Further studies are needed to improve the results and to confront the simulation of the yield per tree with real data.

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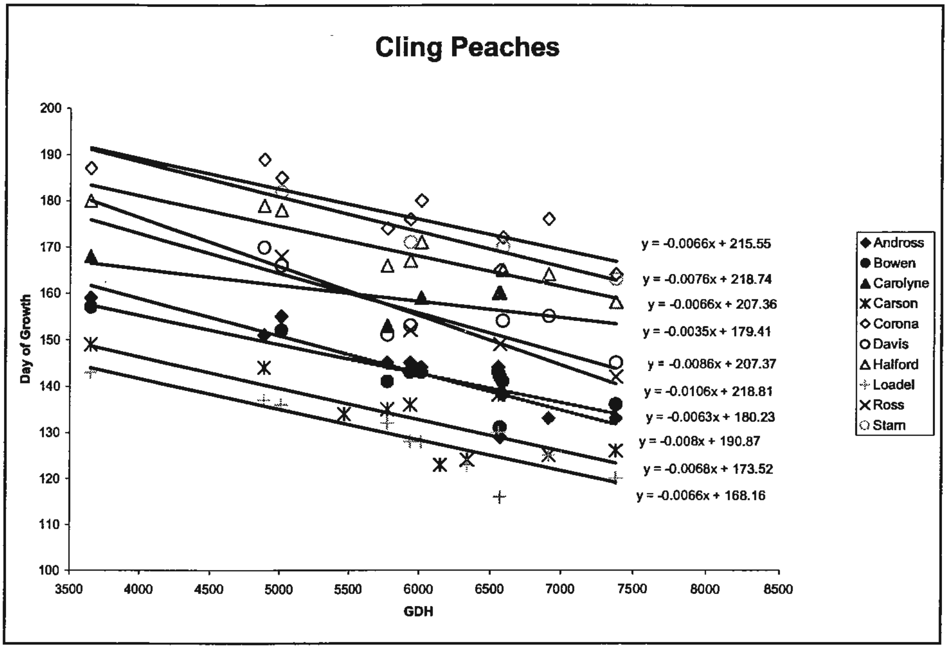

Figure 1 - Effect of sum of GDH one month after bloom on number of days of fruit growth on ten cling peach cultivars.

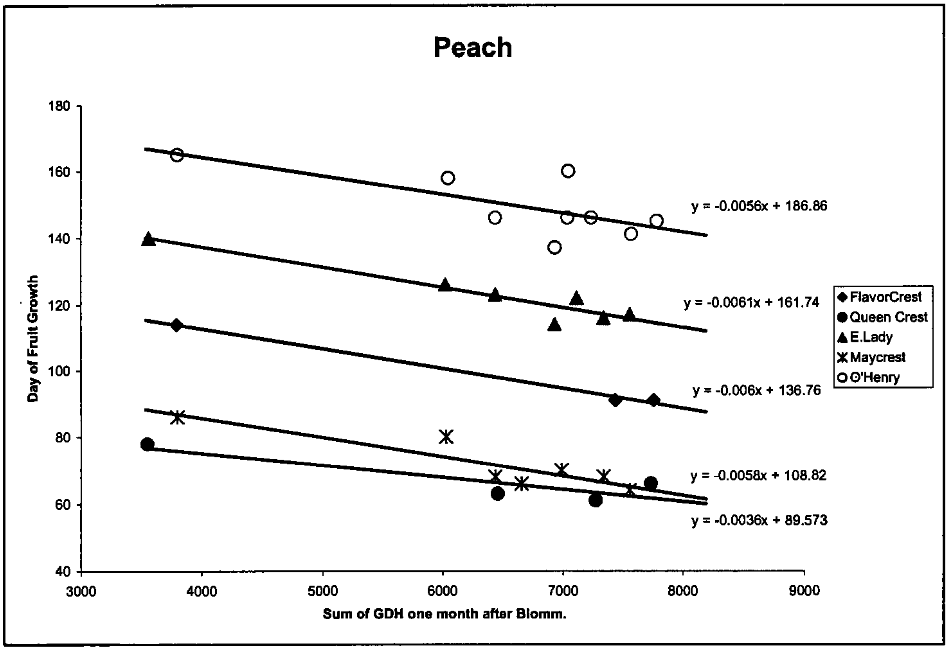

Figure 2 - Effect of sum of GDH one month after bloom on number of days of fruit growth on five peach cultivars.

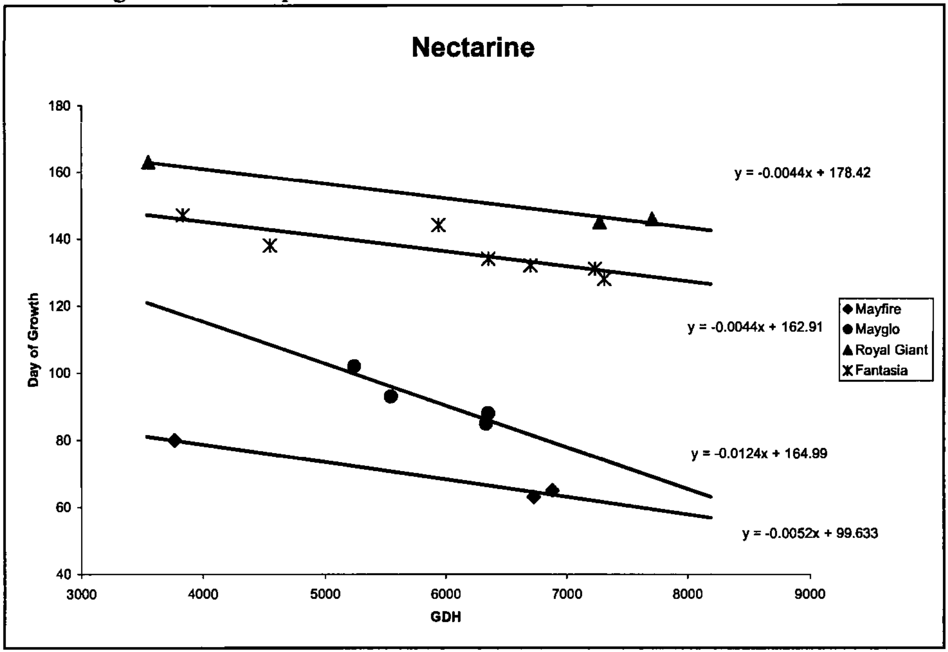

Figure 3 - Effect of sum of GDH one month after bloom on number of days of fruit growth on four nectarine cultivars.

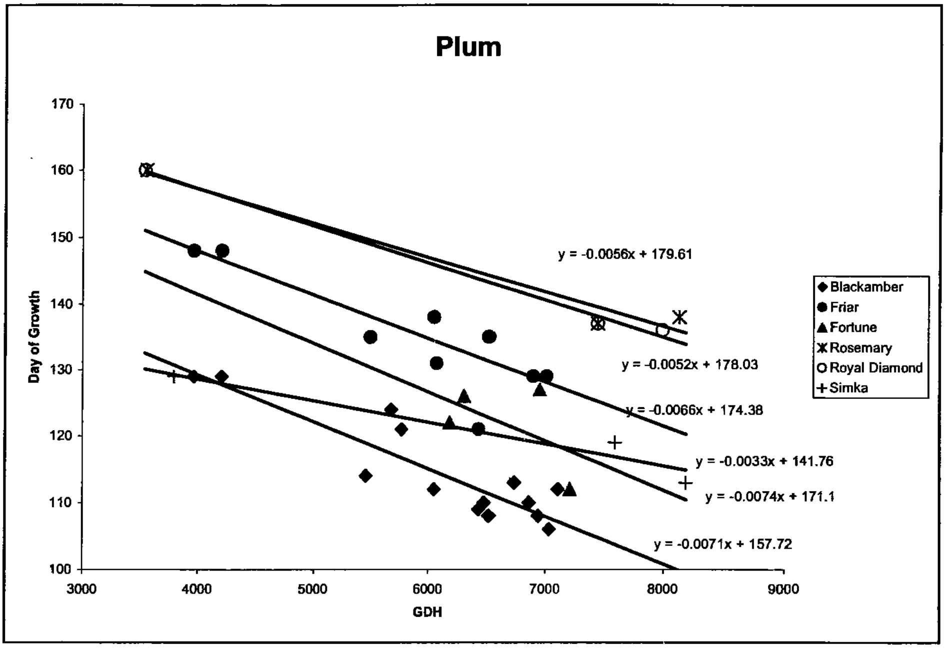

Figure 4 - Effect of sum of GDH one month after bloom on number of days of fruit growth on six plum cultivars.

Table 1 - *PEACH* simulation results using Degree-days (DD) and GDH and real data (RD) for CalRed for date of harvest and simulated yield.

	Day of Harvest			Estimated yield /tree (g DW)				
Year	RD	DD	GDH	RD	DD	%	GDG	%
1989	18 Aug	8 Aug	14 Aug	9866	8455	14	9339	5
1990	17 Aug	10 Aug	22 Aug	9462	8398	11	10163	7
1991	23 Aug	20 Aug	23 Aug	10512	10122	4	10512	0
1993	5 Aug	12 Aug	10 Aug	9033	10017	11	9717	8
1994	11 Aug	9 Aug	13 Aug	10041	9770	3	10300	3

Table 2 - *PEACH* simulation results using Degree-days (DD) and GDH and real data (RD) for Spring Lady for date of harvest and simulated yield.

			Day of Harvest			Estimated yield/tree (g DW)		
Year	RD	DD	GDH	RD	DD	%	GDG	%
1991	1 Jun	4 Jun	1 Jun	1796	2155	20	1796	0
1992	20 May	16 May	20 May	2370	1885	20	2370	0
1993	20 May	23 May	18 May	1721	2068	20	1511	12
1994	21 May	25 May	21 May	1728	2185	26	1728	0

Table 3 - *PEACH* simulation results using Degree-days (DD) and GDH and real data (RD) for Ross for date of harvest and simulated yield.

	Day of Harvest			Estimated yield /tree (g DW)				
Year	RD	DD	GDH	RD	DD	%	GDG	%
1994	12 Aug	30 Aug	18 Aug	9454	11797	25	10217	8
1995	16 Aug	29 Aug	14 Aug	9634	11292	17	9359	3
1996	15 Aug	21 Aug	20 Aug	9734	10428	7	10324	6
1997	30 Jul	13 Aug	5 Aug	9400	11384	21	10292	9

VALIDATING AN APPLE DRY MATTER PRODUCTION MODEL WITH WHOLE CANOPY GAS EXCHANGE MEASUREMENTS IN THE FIELD

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Keywords: photosynthesis, respiration, *Malus domestica* Borkh., light, temperature, seasonal gas exchange.

Abstract

The simplified apple dry matter production model developed by Lakso and Johnson (1990) was modified by inputing tree-specific parameters from a study of seasonal growth and gas exchange of 4-year-old Empire/M.9 apple trees, and light and temperature response curves developed for Empire apple organs. Measurements of the seasonal trend of diurnal net CO2 and canopy water vapor exchange were made at intervals on three four-year-old 'Empire'/M.9 slender spindle apple trees in the orchard from 10 days after bloom until 25 days after harvest. The tree canopies were enclosed in clear plastic "balloon-type" chambers (similar to Corelli and Magnanini, 1993) that was monitored continuously for more than 40 days with an automated control/datalogging system. The measurements over the season under different weather conditions and with late-season reductions in leaf photosynthesis due to pests gave a good range of values with which to test the model. In general, the model simulations showed the same seasonal patterns of gas exchange as the measurements, and gave actual values quite close to those measured. Variation in the canopy gas exchange rates after pest damage were not adequately reflected in the sampled single leaf gas exchange rates that were used as model inputs, suggesting that leaf sampling patterns should be adjusted for non-uniform pest damage.

1. Introduction

A simplified carbon production model was developed earlier as an integrator of short-term measurements of individual organ functions such as gas exchange (Lakso and Johnson, 1990). However, this model, as all models, required many assumptions and thus ultimately requires validation by direct measurement.

A measurement that integrates all the components of gas exchange of the top of a tree is a direct measurement of the whole canopy gas exchange. Clear, flexible plastic "balloon"-type chambers custom-fitted to the canopy as described by Corelli and Magnanini (1993) has simplified this technique. This allows the monitoring of gas exchange under near-ambient conditions in the field. With automated sampling and datalogging, such a system can monitor natural 24-hour patterns, and can provide integrated data useful to validate the gas exchange components of a dry matter production model. This report discusses some of the initial results of a model validation study in 1997 in which three apple trees were measured in balloon chambers for more than forty 24-hour periods during a growing season with an automated datalogger/controller (Lakso *et al.*, 1999a, 1999b).

2. Materials and Methods

2.1. Gas exchange measurements

The canopy gas exchange measurements were conducted during the 1997 season in an experimental orchard at the New York State Agricultural Experiment Station in Geneva, NY. Four balloon-type flexible plastic, flow-through chambers were built using 0.05 mm Mylar ® (DuPont Chemical) plastic film. The chambers were designed to fit closely around the canopies of four year-old dwarf 'Empire'/M.9 slender spindle apple trees, and were tied around the trunk to enclose only the canopy. The design was slightly modified from that described by Corelli Grappadelli and Magnanini (1993). The fourth chamber remained empty as a system baseline check. The chambers had a final volume of about 6200 l.

To allow continuous recording of multiple chambers 24 hours per day, a portable control and datalogging system was developed similar to the Wünsche and Palmer (1997) system (see details in Lakso *et al.*, 1999a and 1999b). Over 24 hours 92 sets of 3 minute-averages were logged per tree. Temperature of the inlet air and the outlet was recorded continuously by two different thermistors located at the bottom, before entering the chamber, and at the top before the air exited. Incident photosynthetic photon flux (PPF) above the canopy level was recorded each minute. Daily integrals of net CO_2 exchange and light-period versus dark-period could be calculated.

Due to equipment interference with pest management pest damage occurred at about 50-60 days after bloom. The primary pest was the spotted tentiform leaf miner (*Phyllonorycter blancardella*) that caused necrotic mines of 0.5 to 1.0 cm^2 area each. Also, necrotic spots (due to ???) occurred in significant numbers. Some European red mite (*Panonychus ulmi*) and white apple leafhopper (*Typhlocyba pomaria*) damage was also noted. The pests were killed by about 70 days after bloom, but the negative effects on leaf and canopy gas exchange persisted as discussed later. No defoliation or other growth effects were noted.

2.2. Model modifications

Since the original model was published (Lakso and Johnson, 1990), there have been slight modifications made in some parameters. The most important was to improve the leaf respiration by using a lower respiration rate intercept (i.e. less respiration at any temperature) since the original model only used respiration rates of exterior, exposed leaves. We have found that heavily-shaded leaves in the field have respiration rates only 20-25% as high as exposed leaves, and that the specific leaf dry weight density is a good predictor (Fig. 1). Also, since there was no apparent response to a sunny or cloudy day, the original connection of leaf respiration to daily photosynthesis was removed from the model. To take into account the lower respiration rates of shaded leaves we reduced the intercept of the leaf respiration by about 25% since in the young 'Empire' apple trees there were moderately shaded leaves, but few heavily-shaded.

The temperature response of leaf photosynthesis was found in other studies in our laboratory on 'Empire' to be less sharp than the original model estimate with higher rates than expected at low temperatures (Fig. 2). The high rates were confirmed with field measurements this season, although it is not clear why apple can photosynthesize so well at lower temperatures. The leaf area development sub-model was also modified by reducing the leaf area increment per degree day to better simulate the somewhat slower leaf area growth rates of the 'Empire' cultivar. The original leaf area increment parameter caused substantial over-estimates in the prebloom period compared to other independent studies. There is no current root submodel although one is under development.

2.3. Measurements for model inputs

The model had specific data inputs for this study: number of shoots and fruits, tree spacing, seasonal leaf photosynthetic maxima and response to low light (measured with a PP Systems, Inc. CIRAS-1 gas analysis system), wood surface area (estimated from regressions of surface areas to branch cross sectional areas). Leaf areas for each tree were determined by shoot counts and sampling for leaf area per shoot at intervals (Lakso, 1984). Daily light integrals, and maximum and minimum temperatures were obtained from a reference weather station 0.6 km away. For the days of comparison to direct canopy measurements, the chamber temperature maxima and minima were used.

3. Results and Discussion

The modified leaf area development model gave reasonable estimates of leaf area development although the final value was about 15-20% low (Fig. 3; model curve shown was using parameters for tree 2). Light-saturated leaf photosynthesis rates sampled from a range of representative leaves (including some immature leaves early in the season) on the test trees showed a rapid increase after bloom due to canopy development and a greater percentage of leaves reaching full-size, followed by a decline due to the pest damage, then a relatively slow decline until harvest in early October (Fig. 4). The maximum NCE rate values for the three trees showed a similar seasonal pattern (Fig. 5). The separation of the three trees in the whole canopy measurements was not, however, properly reflected in the single leaf readings, suggesting that leaf sampling patterns should be improved for pest damage that is apparently not uniform.

When the Stella model was run with averaged data for the three trees, the same pattern was seen although there was also a general decline related to decreasing total radiation later in the season (Fig. 6). This suggests that the model has reasonable behavior. Although full data analysis of the NCE measurements is continuing, early season maximum daily CO_2 fixation integrals were approximately 80 g/day while at harvest the values ranged from about 20-38 g/day. These values are reasonably close to the simulated values of about 90 g/day and 25 g/day at those times, respectively.

Since the model calculates the canopy photosynthesis and respiratory components separately, but the chamber measures the net exchange of all processes together, we could not directly compare the individual components of gas exchange. In mid-season on sunny days the canopy gas exchange rates at night were typically only 5-10% of the photosynthesis rates (on cloudy days night respiration rates were a higher percentage due to lower daylight NCE rates). The model suggests somewhat higher total daily respiratory loss of 15-20%. This discrepancy may be due to several factors. First, the model does not have a light response for fruit respiration and so it assumes dark respiration for the fruit in the daylight period. For exposed fruits this leads to an overestimate of the respiration as shown by Jones (1981) and Bepete *et al.* (1998). Also, respiration by fruit and wood that occurs in the daylight is calculated as respiration by the model, but would be manifested by a lowered daylight NCE in the balloon study.

4. Conclusions and Improvements Planned

Considering the simplicity of the model used, the initial validation results look promising. Further detailed tests with the whole canopy data will continue the validation of the dry matter production model. The next development will be to add a root respiration sub-model. Also to deal with the non-continuous restricted canopies of orchards we plan to evaluate the substitution of a measured percent light interception input for the current assumption of continuous canopy that uses e^{-kL} to estimate light interception as proposed by Charles-Edwards (1982). Light interception by orchards can be done relatively easily by the point grid method (Wünsche *et al.*, 1995), so errors associated with the leaf area submodel would be limited to the leaf area for leaf respiration. Eventually, shoot, fruit, root and wood growth components should be added for dry matter partitioning.

Acknowledgements

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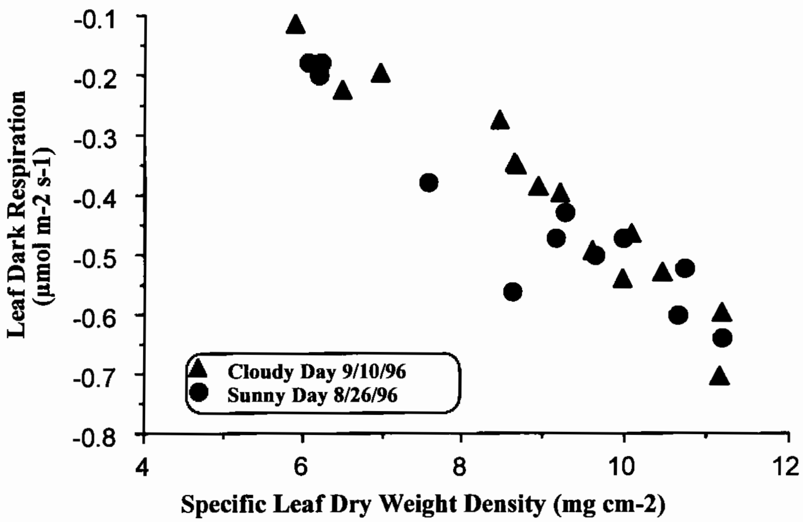

Figure 1 - 'Empire' apple leaf dark respiration rate at night at 20-22°C versus exposure-induced leaf dry weight density differences following a sunny and a cloudy day.

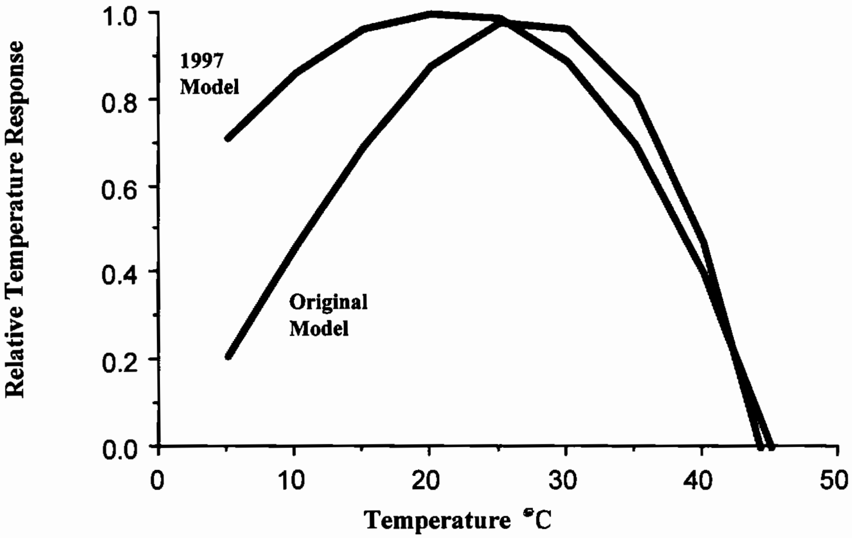

Figure 2 - Relative temperature responses for leaf photosynthesis used in the original model (estimated from data from literature) and in the current model after further studies and measurements in the field.

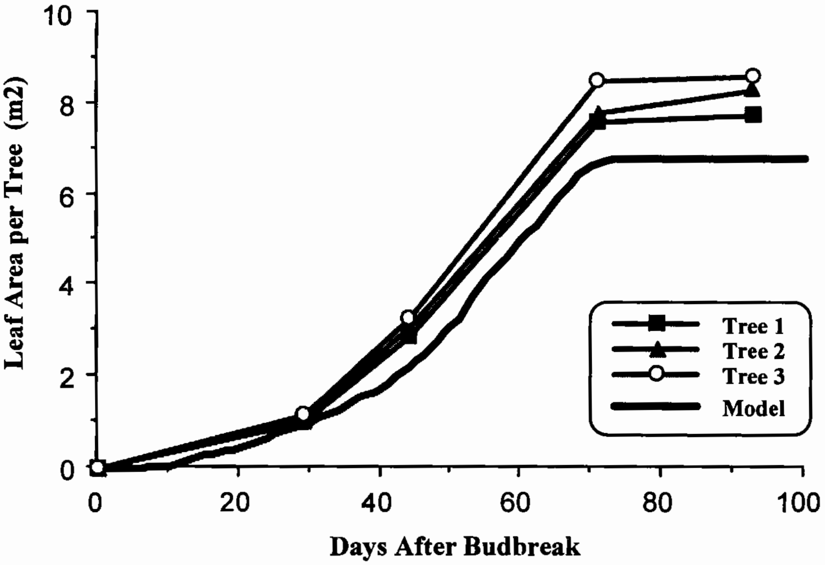

Figure 3 - Leaf area development patterns for the three measured 'Empire'/M.9 apple trees and the simulation from the model, using shoot numbers for Tree 2.

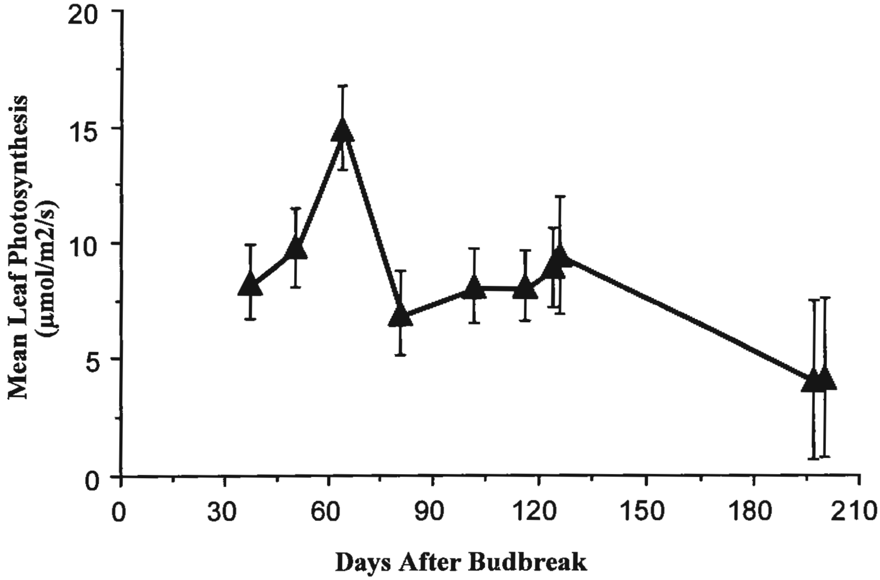

Figure 4 - Seasonal trends of mean leaf light-saturated photosynthesis rate of three 'Empire'/M.9 apple trees measured mid-day on sunny days.

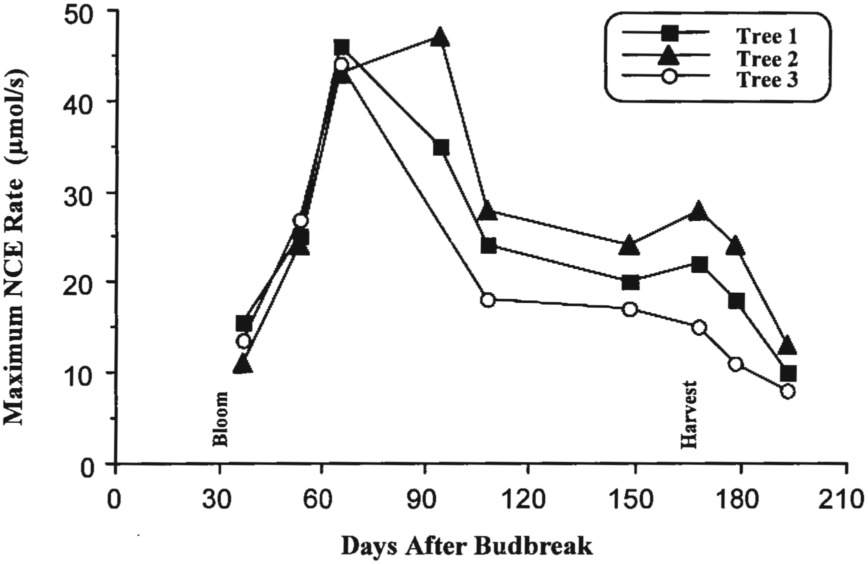

Figure 5 - Seasonal trends of maximum canopy NCE rates for three 'Empire'/M.9 apple trees under sunny conditions. Note mid-season decline due to pest damage.

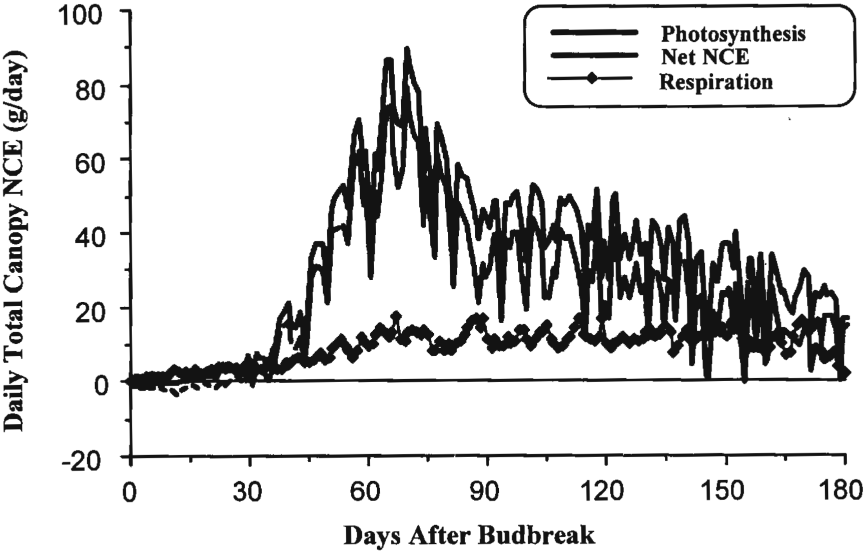

Figure 6 - Seasonal simulation of daily NCE integrals, canopy photosynthesis and respiration per tree for input data averaged for three 'Empire'/M.9 apple trees and actual weather data.

MODELLING CHEMICAL THINNING IN PEACH

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Keywords: *Prunus*, factor analysis, multivariate linear regression

Abstract

A statistical model was developed to make chemical thinning possible in the peach growing industry. The new concept behind this model is that, in addition to the obvious factors - active compound, concentration, volume and timing of the thinning application - an accurate prediction of the tree response should consider the plant's physiological status, and the environmental conditions following the application. The method of model building is presented as a factor analysis on three different sets of parameters - chemical thinning application, environmental conditions and physiological status of the tree - followed by a multivariate linear regression. The number of fruitlets remaining on the trees two weeks after the application was used as the predicted variable, while the predictors were the factors resulting from the factor analysis. Unnecessary variables were taken out of the factor analysis by a repetitive method. The influence of their removal was evaluated by checking the linear regression: prediction coefficient R^2, Marlow's total squared error Cp, and regression significance p. The correlations between the predictions of the model and observed results were highly significant. They varied between r=0.66 and r=0.85 when the model equation was applied on same-year observations, and between r=0.42 and r=0.81 when it was applied to those from another year or to data from the whole study.

1. Introduction

Peach tree response to chemical thinning has remained unpredictable for the last 40 years, despite numerous efforts to develop the method (Gautier, 1987). Many active compounds have been identified as effective in chemical thinning of peach, among them urea, which is inexpensive, environmentally inoffensive and resembles natural substances (Zilkah *et al.*, 1988). Although many promising thinners have been studied, the tree response to chemical thinning is still non-reproducible, indicating that the problem is inherent to the plant physiology (Zucconi, 1978).

In order to overcome this inability to forecast the chemical thinning results, we tried to model the tree response, taking into consideration three distinct aspects of the chemical thinning problem:

- the mode of application, including treatment parameters,
- the environmental conditions during the period following the application,
- the physiological status of the tree, reflecting past stress conditions, *e.g.* flooding and high temperatures during dormancy, former year's crop load, pests and diseases, etc.

The complexity of the interactions among all these factors led us to the building of a "black box" statistical model based on multivariate linear regression.

In the framework of multivariate linear regression, orthogonality (*i.e.,* independence) of the predictor variables is not necessary, but it is recommended, especially when a reduction in the dimension of the space of predictors is looked for (see, *e.g.,* Tomassone *et al.*, 1992). Quite obviously, such an orthogonality does not exist among the variables of the set of environmental conditions. Moreover, some parts of the mechanism underlying the physiological set of predictor variables are probably shared by several variables; those variables are, therefore, not entirely independent, and might even be redundant. Factor analysis of the measured variables enables us to overcome these flaws (*e.g.,* Tomassone *et al.*, 1992), and to use the resulting factors as reliable predictors of the linear regression.

2. Method

The methods for growing the plants and analysing the tissues have been described previously (Szafran *et al.*, 1997). The results from the 1997-98 season have been added to the previously presented data.

The predictor variables of the model were grouped in three sets of data. The treatment set included the phenological stage of the tree relative to full bloom, the urea concentration, the spray volume per tree and the resulting dosages of urea per tree and per flower. The environmental set included the chilling units accumulated during two weeks after treatment, computed in accordance with the dynamic model (Erez *et al.*, 1990), the minimal, maximal and average air temperature and relative humidity, both on the day of application and for two weeks following the application. The physiological set included the flowering intensity of the tree, the young leaf photosystem II fluorescence at the full-bloom stage, flower bud abscission force, water content and free proline levels, at both the pink-bud and the full-bloom stages. Induced nitrate reductase (NaR) activity, although previously studied (Szafran *et al.*, 1997), was not included because of missing data.

A factor analysis (proc factor) was performed separately on each set of predictors, by means of SAS software implemented on a personal computer. A multivariate linear analysis (proc reg) was carried out with the fruitlet load on the trees two weeks after the treatment as the predicted variable, and the factors resulting from the analysis as predictors. The process was carried out for each year (1996, 1997 and 1998) separately, and for the whole set of observations. Simplification of the equations was achieved by checking the effect of the elimination of each variable from the factor analysis, on the regression criteria: prediction coefficient, R^2; Marlow's total squared error, Cp; and regression significance, p.

Verification of the model was completed by computing the correlation between the expected and the observed fruitlet loads two weeks after treatment. The correlation was computed for every combination of equations and data: 1996 equation with 1996 data, 1996 equation with 1997 data, and so on.

3. Results

Different factors were obtained for each set of variables in different years, and even the number of retained factors was sometimes different. The correlation coefficients between the factors were not significant. The first factor computed from the physiological set for each year is illustrated in Table 1; correlation between these factors is not significant ($p>0.55$ for all three combinations of years).

The resulting regression equations also differed significantly from each other, as expected because of the different factors used as predictor variables. The final criteria of the regressions are presented in Table 2 (environmental conditions were not measured in year 1996, therefore the number of predictor factors is smaller for that year). Marlow's total squared error coefficient, Cp, equals the number of predictor factors in the regression (number of predictor factors plus one) for each equation, as expected from unbiased regression (Daniel *et al.*, 1980).

An attempt to eliminate redundancy from the equations was made by taking variables out of the factor analysis, and examining the resulting changes in the regression criteria. The results of this process are illustrated in Table 3. No simplification of the set of treatment variables was possible without impairing the regression criteria.

The model was verified by computing the expected fruitlet load two weeks after treatment and by comparing it with the observed fruitlet loads. The verification was made by using each year's regression model on all three sets of data. The results of the verification are presented in Table 4.

4. Discussion

The presented model concept is the first of its kind in the deciduous fruit growing industry. It is based on a functional concept. The response of peach trees to chemical thinning, extensively investigated for the last 40 years, is still not understood and remains unpredictable. An alternative, relatively short-term study is a "black box" approach: relying on statistical analysis and multivariate regression to forecast the behavior of the system.

The factors resulting from the factor analysis for each year are, for the most, not significantly correlated with those from other years (see Table 1). Even the number of significant factors differed from year to year, including the factors for the set of treatment variables. This apparent flaw in the experimental design resulted from the differing physiological status of the trees from year to year: the treatment was determined by the former year's regression equation, and the current year's physiological variables. The changing physiological status of the trees was reflected in a different set of variables (causing different results of factor analysis for each year), and changed treatment conditions led to different factors. The factors obtained from the environmental set of variables were expected to be different from year to year. This variance in the results of factor analysis is a major impediment in the attempt to find biological meaning in the retained factors, since temporary conditions seem to predominate. Longer data series would possibly provide more stable and biologically meaningful results.

The regression equations based on the retained factors for each year included different coefficients of the variables, and resulted in different values of the criteria when applied to the data from different seasons (see Table 2). However, the use of factors as predictor variables ensured unbiased equations, as demonstrated by Marlow's coefficient, and all models were highly significant. The low values of the prediction coefficient reflect the lack of significance of some variable coefficients in the regression equation.

Simplification of the equation (see Table 3) can be obtained by a repetitive method: cutting down the numbers of retained variables and factors by one third and one fifth, respectively. The reduction of the number of predictor variables is possible without diminishing the regression criteria, indicating a redundancy in the data studied. The increase of R^2 following the decrease in the number of predictors seems mathematically inconsistent. However, it is a consequence of the lack of independence among the measured variables. This simplification process should be of uttermost importance at the end of the model development, indicating the significant variables.

The model was tested (see Table 4) by using each year's equation to predict the fruitlet load for every season of the study. All correlations were significant, and the values of Pearson's coefficient, r, although too low for agricultural requirements, were nevertheless encouraging. The lower values obtained with the 1996 equation were apparently due to the fact that the measurement of environmental conditions began only in the 1997 season. The low correlation of the model prediction for 1998 based on 1997 data, (see Table 2), is still unexplained.

As it is, this first study in a new direction is already promising enough to support a better forecast of the peach tree response to chemical thinning, and it might be a helpful step towards the solution of the 40 year-old attempt to relieve the peach grower of hand thinning.

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Table 1 - First factor resulting from analysis of the physiological status indicators of peach plants for three consecutive years.

Variable	Year 1996	1997	1998
Flower density	-0.26	0.64	0.65
Proline, pink bud	-0.20	-0.47	-0.05
Proline, full bloom	0.73	-0.16	0.01
Abscission, pink bud	-0.66	0.66	-0.88
Abscission, full bloom	0.49	0.34	-0.03
Fluorescence	-0.64	0.45	0.13
Water, pink bud	0.68	0.45	0.72
Water, full bloom	-0.05	-0.57	-0.09

Table 2 - Overall criteria (prediction coefficient R^2, Marlow's total squared error Cp, and model significance p) of the linear regression of the treatment, environment and physiology factors over the number of fruitlets remaining on the trees two weeks after treatment.

	Factors year		
Data year	1996	1997	1998
1996 (n=53)	$R^2 = 0.44$ $p < 0.0001$ $Cp = 5$	$R^2 = 0.51$ $p < 0.0001$ $Cp = 7$	$R^2 = 0.59$ $p < 0.0001$ $Cp = 8$
1997 (n=68)	$R^2 = 0.55$ $p < 0.0001$ $Cp = 5$	$R^2 = 0.72$ $p < 0.0001$ $Cp = 9$	$R^2 = 0.22$ $p < 0.05$ $Cp = 8$
1998 (n=53)	$R^2 = 0.49$ $p < 0.0001$ $Cp = 5$	$R^2 = 0.66$ $p < 0.0001$ $Cp = 8$	$R^2 = 0.57$ $p < 0.0001$ $Cp = 8$

Table 3 - Criteria (see Table 2) for the regression equation, after elimination of redundant variables. The computations were based on 1997 data. The number of retained variables and factors is given for each set of variables separately.

	All variables	Final selection
Overall model	$R^2 = 0.57$	$R^2 = 0.57$
	$p < 0.0001$	$p < 0.0001$
	$Cp = 10$	$Cp = 8$
Stress set	$R^2 = 0.20$	$R^2 = 0.22$
	$p < 0.006$	$p < 0.0003$
	$Cp = 5$	$Cp = 3$
	8 variables in 4 factors	5 variables in 2 factors
Environmental set	$R^2 = 0.25$	$R^2 = 0.25$
	$p < 0.0003$	$p < 0.0003$
	$Cp = 4$	$Cp = 4$
	10 variables in 3 factors	6 variables in 3 factors

Table 4 - Model verification. Pearson's correlation coefficient, r, coefficient significance, p, and number of trees, n. The small number of trees in the overall model verification based on 1996 data is due to missing measurements with respect to later years.

	Model equation			
Data year	1996	1997	1998	All 3 years
1996	$r = 0.66$	$r = 0.71$	$r = 0.77$	$r = 0.74$
	$p < 0.0001$	$p < 0.0001$	$p = 0.0001$	$p < 0.001$
	$n = 54$	$n = 54$	$n = 54$	$n = 16$
1997	$r = 0.68$	$r = 0.85$	$r = 0.47$	$r = 0.64$
	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.001$
	$n = 0.69$	$n = 0.69$	$n = 0.69$	$n = 0.69$
1998	$r = 0.70$	$r = 0.81$	$r = 0.75$	$r = 0.65$
	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
	$n = 65$	$n = 65$	$n = 65$	$n = 65$
All 3 years	$r = 0.42$	$r = 0.79$	$r = 0.67$	$r = 0.59$
	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$
	$n = 188$	$n = 188$	$n = 188$	$n = 188$

MODELED SEASONAL PATTERN OF NITROGEN REQUIREMENTS OF MATURE, CROPPING PEACH TREES (*PRUNUS PERSICA* (L.) BATSCH)

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Keywords: carbon model, nitrogen demand

Abstract

Seasonal nitrogen (N) accumulation patterns of fruits, leaves, stems, branches, trunk and roots of mature, cropping peach (*Prunus persica* (L.) Batsch cv. O'Henry) trees were estimated by combining models of organ dry mass accumulation and seasonal organ N concentrations. Data for the models were collected from trees subjected to two different N treatments. The study estimates and compares the N demand of perennial and annual organs during the growing season for both treatments.

Although N demand was higher for N-fertilized trees, seasonal N accumulation patterns were similar for both treatments. Annual organs exhibited greater responses to N fertilization than perennial organs. The average daily N demand per tree remained nearly constant from 40 days after anthesis to harvest. Fertilized trees accumulated about 1 g $N \cdot tree^{-1} \cdot day^{-1}$, twice that of non-fertilized trees. For the orchard studied, a daily demand of approximately 1 kg $N \cdot ha^{-1}$ was estimated for fertilized trees while approximately 0.5 kg $N \cdot ha^{-1}$ was required for unfertilized trees. During the first 25-30 days, all N demand could be supplied by storage organs. The release of N from storage organs for current growth was apparently completed in about 75 days in both treatments.

1. Introduction

Nutrients are required for growth of various organs, and often must be available at specific times. Nitrogen is one of the most important macronutrients in crop fertilization and one that most often limits yield of peaches. The role of N reserves and current N applications in peach trees have been studied (Stassen *et al.*, 1982; Weinbaum *et al*, 1978, 1980, 1984a, b; Titus and Kang, 1982) but quantitative data are needed to determine the daily seasonal organ and total tree N demand in order to estimate the N supply required to balance that N demand. The goal of this research was to compare the simulated seasonal organ nitrogen demands and the total tree nitrogen utilization under low and high nitrogen conditions.

2. Material and methods

The PEACH computer simulation model, a model of the annual carbon supply and demand in peach trees (Grossman and DeJong, 1994) was used to predict changes in fruit and vegetative growth under different conditions of N supply. It is a state-variable model in which fruit, leaf, current-year stem, branch, trunk, and root mass are state variables, and minimum and maximum air and soil temperatures, degree-days, solar radiation and canopy light interception are the driving variables. Photosynthetic carbon assimilation and stored carbohydrates provide the supply of carbon that is demanded for maintenance respiration and growth. For N partitioning the same priorization as for dry mass in the PEACH model was followed.

Since the PEACH model assumes adequate N supply, high N (HN) simulations were run using default model data for photosynthesis and light interception. For low N (LN) treatment, the leaf photosynthesis rate was reduced to 86% and 63% for full sun and shade leaves, respectively, and light interception was reduced by 83% (Esparza, unpublished data on leaf photosynthesis and canopy light interception in a peach orchard receiving similar N fertilization).

The model was adjusted to give realistic vegetative growth output values, based on 1996 experimental data and previously recorded measurements from the same orchard. 'O'Henry' fruit dry mass values from 1996 were used to obtain the dry mass growth calibration curve for HN and LN treatments. The N treatments consisted of zero and 200 kg of $N \cdot ha^{-1}$, applied in April. The 1994 fruit dry mass values (Saenz, 1996) were used to validate the modeled curves. Previously-determined values for stem and leaf growth were used to estimate RGR in the model, and new coefficients for branch and trunk curves in the HN treatment and for leaves and stems in the LN treatment were used to adjust the model for decreases in vegetative growth caused by low N (Saenz, 1996; Berman, 1996; Niederholzer, unpublished data). These coefficients were obtained using data from trunk, scaffold and branch measurements and data from total current year growth (data not shown). Data from excavated trees during the dormant period in 1994 were used to develop input data for branch, wood, and root initial dry mass used in the model, and the data from the excavated trees (Niederholzer, unpublished data) were used to validate modeled values.

N concentration data for fruits, leaves and stems obtained in 1996 were used to develop seasonal N concentration algorithms for trees from HN and LN treatments. Furthermore, leaf and fruit N concentrations data from Saenz (1996) were used to validate the algorithms. Again data from trees excavated during the dormant period in 1994 were used to develop input data for branch, wood, and root initial N concentration (Niederholzer, unpublished data) and the seasonal patterns used for branch, wood and root N concentration were proportional on that reported by Stassen *et al.* (1983).

An inverse logistic function, ($y = (1+Be^{-kx})/M$) vs calendar days was fitted for all organ N concentration data using the non linear regression (PROC NLIN) procedure in SAS (SAS Institute, 1988).

Total N for each organ was estimated as the product of total organ dry mass, modeled for each day, and the simultaneous estimate of N concentration. N accumulation rate (NitAR) was determined using the equations described by Ryugo (1988) for dry mass:

$$\mathrm{NitAR} = (N_2 - N_1) \cdot (t_2 - t_1)^{-1}$$

where N_2 and N_1 are the total N organ content at time t_2 and t_1 respectively. N in current year growth organs resulted from adding NitAR in fruit, leaf and stem. N in storage organs was the result of combining branch, trunk and root NitAR.

Weather data for 1994 and degree-days used in the PEACH Model were obtained from the California Irrigation Management Information System (CIMIS) weather station located at the Wolfskill Experimental Orchard (WEO) in Winters. For 1996 data, CIMIS weather stations located at Davis and Winters were used.

3. Results and discussion

The result of combining the dry mass output data of the PEACH model for fruits, leaves, stems, branches, wood, and roots and the N concentrations from the fitted functions allowed an estimation of the seasonal N accumulation in each part of the tree. Although it was impossible to validate many aspects of the model, the model predictions for total organ dry mass and N content were within 3% and 8% of the values (for HN and LN respectively) from the whole-tree excavations. Although both treatments had similar patterns for the respective organs and few differences were obtained in the relative proportion of N in each organ, HN organ values were higher during the whole fruit growth period.

Because of high leaf N concentrations, leaves accounted for the highest accumulated N content among the current year growth organs during the season (Figs. 1 and 2). Only fruits in the LN treatment had a higher value than leaves at harvest due to the relatively higher yield per total biomass compared with HN trees.

Because of their storage function, the perennial organs started the season with a given amount of N. By the time of bloom there was already some depletion of storage N. During the growing season until harvest, these N contents decreased gradually in the trunk and the roots. Although a decrease after bloom was estimated for branches, it was very small, and just previous to harvest there was a slight increase.

For the period of this study, leaves and fruit were more N demanding than perennial tissues. Although lower values were obtained for LN trees during the season, a similar pattern was obtained with a slower increase due to a strong N competition from fruits.

The modeled NitAR of fruit increased sharply early in the season, particularly for LN trees (data not shown). The increase corresponded with the exponential DW increase in stage I of fruit growth. A period of decreasing fruit NitAR followed corresponding with stage II of fruit development (pit hardening). The rapid resumption of growth (cell enlargement) in stage III is parallel to an increase in N demand to satisfy fruit growth. There was an almost constant linear increase of NitAR values during the second half of the season with similar values for both N treatments.

The perennial tree tissues had very different NitAR patterns compared with current-year organs in both N treatments. Branch NitAR values remained close to 0 because of their low DW increase and small change in N content during the season. On the other hand, modeled root NitAR decreased for most of the season and the trunk released N for three and a half months after anthesis. After this time, the modeled values indicated a switch to positive or nul values. This pattern was apparently due to the net N release from storage organs to current-year organs. The N supplied by these organs decreased with time, apparently as increasing uptake from the soil occurred.

Model calculations for current year organ demand versus storage organ supply until calendar day 90-95 indicate that all N was coming from perennial organ release (Figs. 3 and 4, areas above and below the x-axis). This period corresponds to the period required for the first leaves to become photosynthetically active and N uptake was apparently minimal as a consequence of low N demand (Weinbaum, 1994). From that time on, N demand increased as a result of the vegetative growth, and the sum of fruit and stem N demand was fairly constant for the rest of the growing season. On the other hand, the model indicated that N release from storage organs was completed by calendar day 145-150 in both treatments and restorage presumably began after harvest, as soon as fruits, the main N sinks, were removed and leaves started N remobilisation back to the tree. The amount of N stored as reserves in postharvest would be expected to be similar to the N required for starting the next season.

Combining dry mass and N concentration data for each organ indicates that the total N content for each part of the tree was increased by N fertilization. Higher N contents for current year vegetative growth were obtained for HN trees while perennial organs had similar values for both N treatments. N content for each organ at harvest was higher for fertilized trees than for unfertilized trees. The final value for the whole tree N content was almost twice the amount of N for fertilized compared to unfertilized trees. Although higher values for N demand were obtained for N-fertilized trees, particularly for leaves and fruits, the seasonal pattern of the daily N increase for each organ was similar for both treatments, with higher values for HN tree organs. Annual organs from fertilized trees had greater response to N than perennial organs. The perennial tree tissues have very different patterns compared with current-year growth organs. Total tree N increment is an integrated value that takes into account the increases and decreases in N ratio and provides an estimate of the seasonal tree uptake. The average daily N increment from 40 days after anthesis to harvest was almost constant. For fertilized trees this value was about 1 g $N \cdot tree^{-1} \cdot day^{-1}$, twice that of non-fertilized trees. For the orchard studied, a daily increment of approximately 1 kg $N \cdot ha^{-1}$ was estimated for fertilized trees while approximately 0.5 kg $N \cdot ha^{-1}$ was required for unfertilized trees. During the first 25-30 days, virtually the whole N increment could be supplied by storage organs. The release of N from storage organs for current growth was apparently completed in about 75 days for both treatments.

Acknowledgements

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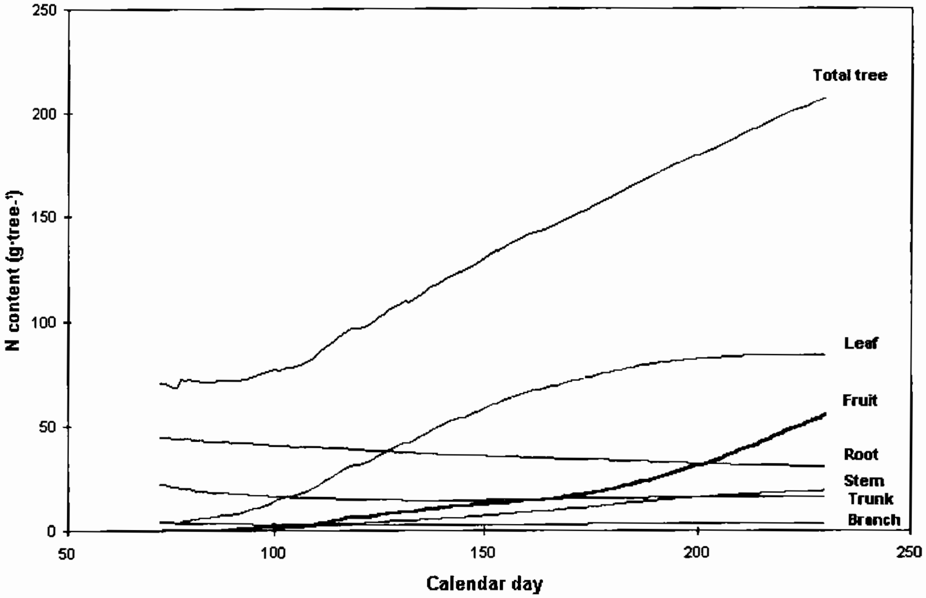

Figure 1 - Estimated seasonal patterns of total N distribution for the different parts of the tree in the high nitrogen treatment. Each curve value is the product of total organ dry mass modeled for each day, and the simultaneous estimate of N concentration for the respective organ.

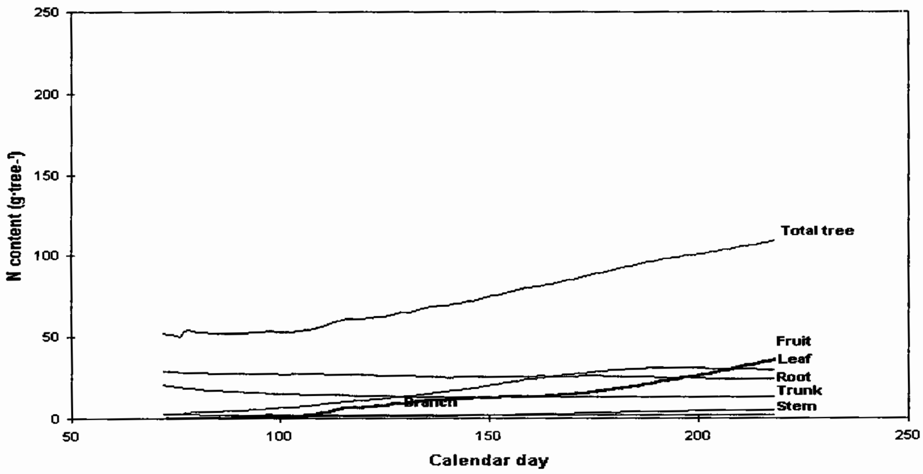

Figure 2 - Estimated seasonal patterns of total N distribution for the different parts of the tree in the low nitrogen treatment. Each curve value is the product of total organ dry mass modeled for each day, and the simultaneous estimate of N concentration for the respective organ.

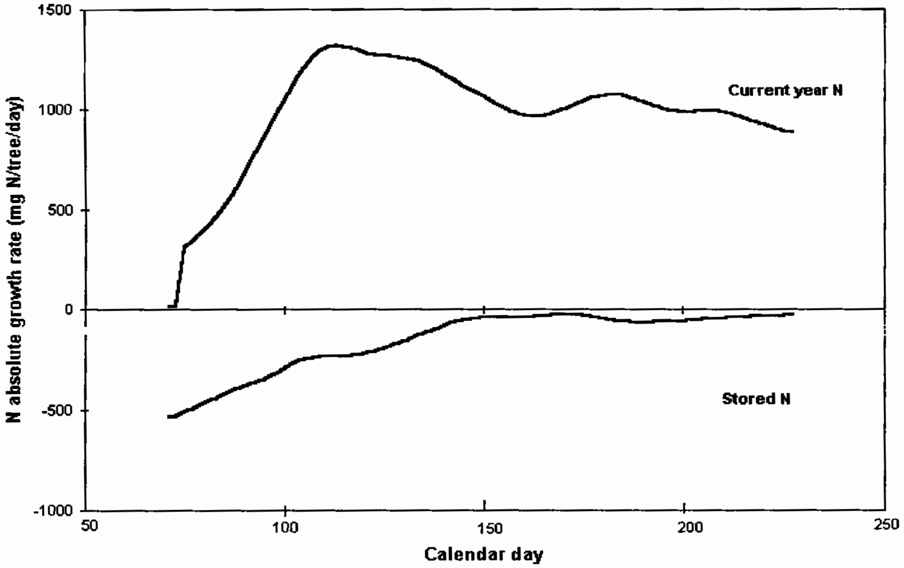

Figure 3 - Estimated seasonal patterns of nitrogen accumulation rate in current year organs vs storage organs for HN treatment.

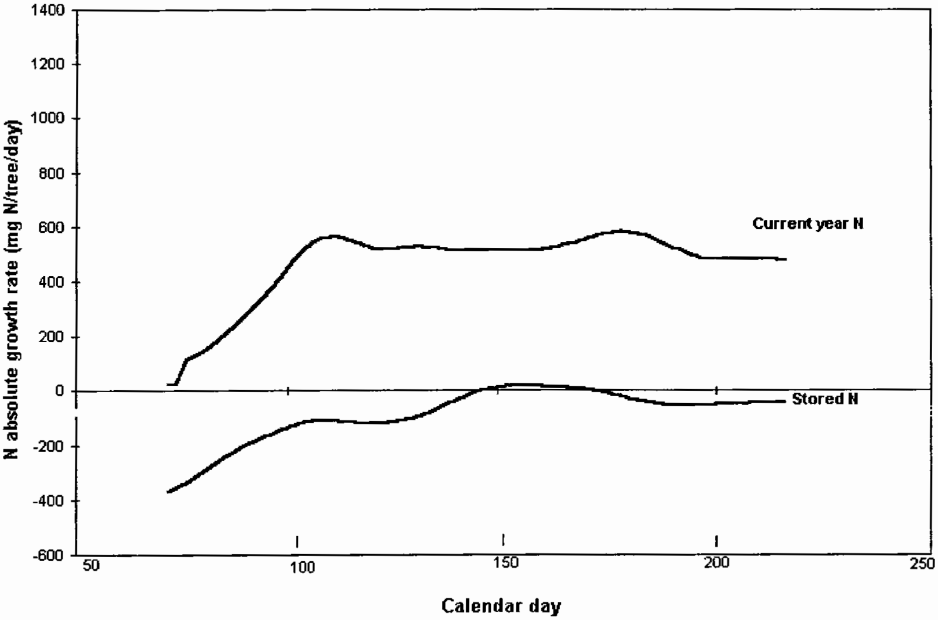

Figure 4 - Estimated seasonal patterns of nitrogen accumulation rate in current year organs vs storage organs for LN treatment. N in current year growth organs results from adding NitAR in fruit, leaf and stem. N in storage organs is the result of combining branch, trunk and root NitAR.

ANALYSIS AND MODELLING OF APPLE FRUIT GROWTH

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Keywords: *Malus communis*, fruit diameter, model simulation, yield forecast

Abstract

Crop management can be really improved by the analysis and modelling of crop growth. Particularly fruit growth represents a relevant element, because it is directly related with crop yield, and thus with the management of important techniques connected with harvesting, storing and commercialising. Fruit diameter is a very important index of fruit dynamics, and strongly related with the final yield. Moreover, it can be monitored non-destructively during the growing season. On these basis the analysis and modelling of fruit diameter was carried out on apple trees (*Malus communis*). Data sets were collected during several growing seasons in many orchards located in the northern regions of Italy. Fruit growth was analysed according to several indexes based on time after bloom. Moreover, simulation of fruit growth was attempted by means of several mathematical models. Finally the possibility to forecast harvest size of apple was evaluated on the basis of linear regression analysis of diameters measured during the growing season.

1. Introduction

The analysis of crop growth represents a very important step in the improvement of crop management. Cultivation methods, fertilisation, pruning system, harvest time, storage and commercialisation of yield can be planned with higher accuracy and their efficacy increased. Moreover, the development of mathematical models for growth simulation and yield forecast would give further advantages to crop management. Particularly, fruit growth represents an important process, because it is directly related with crop yield, and thus with the economical productivity of the crop.

Apple (*Malus communis*) represents in Italy, as well as in many other countries, a fundamental tree crop. Its cultivation is performed in the main horticultural areas. During the last decades, many papers (Pratt, 1988) and models (Moriondo *et al.*, 1998) have been published concerning crop growth processes, with specific attention to the analysis of fruit growth. This process has been described according to several indexes, such as fresh or dry weight, volume, and diameter. Among those, the latter can be considered very important, according to the correlation with the final size of fruit, both in terms of volume and weight, and thus with the quality and quantity of final yield (Welte, 1990). Moreover, the diameter can be measured during the growing season non-destructively, thus allowing an easy, fast monitoring technique with low variability.

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On the basis of these considerations, a preliminary analysis and modelling of fruit diameter was carried out on apple tree crops. Data sets were collected in orchards located in northern Italy. The analysis of fruit diameter dynamic was carried out considering the temporal trend starting from bloom. Several simulation models were applied and compared in order to verify their correspondence with the real system. Finally the possibility to forecast the final size of fruit was evaluated at different stages during the growing season.

2. Materials and methods

2.1. Field data sets

Fruit growth data were gathered from mature "Golden Delicious" apple trees in three orchards, located in some of the main horticultural areas of Italy: Bolzano (Alto Adige region) in a valley location and Trento (Trentino region) both in a valley and a hilly position. The period from 1987 to 1992 was considered. The crops had adequate nutrient availability in all the growing seasons, and climatic factors never imposed limitations to growth and development. However, stress monitoring was continuously carried out during the growing season. A normal cultivation and disease control programme was applied in all the studied orchards.

The data sets consisted of the mean of about 20 measurements of maximum fruit diameter performed by means of a calliper at regular intervals during the growing seasons. Measurements were performed on the same fruits chosen from adjacent trees with a similar structure, vegetative condition and crop level.

2.2. Models

Dynamic of fruit diameter was simulated considering the temporal trend starting from the blossom phase, generally occurring from the last decade of April to the first decade of May. Three simple models were chosen to describe the temporal increase of fruit diameter. (i) The model proposed by Winter (1969) simulates the diameter on the basis of the maximum possible diameter and parameters concerning variety and region. Welte (1990) later modified this model, to get a dynamic model, including the effect of climatic factors, such as temperature and day length. (ii) The logistic model is one of the most important for the simulation of many biological processes, such as disease epidemiology (Vanderplank, 1963) and leaf area growth (Sall, 1980). This model is based on the rate of fruit growth, variety parameter and the maximum possible diameter at the end of the season. (iii) The structure, as well as the sigmoid-shaped curve of the Gompertz function is quite similar to that of a logistic model. However, differences can be more readily apparent from the plot of the absolute rate versus the time (Campbell and Madden, 1990).

Recent approaches (Schechter and Proctor, 1993; Lakso *et al.*, 1995) to fruit growth simulation were not considered in this analysis, because they were proposed for the growth in weight or volume. Because weight, or volume, and diameter are related with exponential function (Mitchell, 1986), the simulation of their temporal trends must be performed with different models. However, the referred approaches showed a good correlation with the volume of apple fruits (data not shown) calculated converting the collected data sets of diameter to volume by considering the fruit as a sphere (Batjer *et al.*, 1957).

The forecast of harvest fruit size represents a very important element as well. In such a perspective, several approaches were proposed in the past which considered growth function or differential equation (Welte, 1990), as well as simple or multiple regressions with several growing parameters, such as the number of fruit per centimetre trunk circumference (Bergh, 1982) or the diameter measured during the growing season (Batjer *et al.*, 1957). The latter approach was evaluated in this study, using the data sets previously described.

The calibration and evaluation of the models were performed accordingly to widely applied tests. The average deviation of the simulated values from the measured values was evaluated calculating the mean absolute error (MAE) and the mean absolutes percent error (MA%E) according to Mayer and Butler (1993):

$$MAE = \frac{\sum\limits_{i=1}^{n}[xobs_i - xsim_i]}{N} \qquad MA\%E = \frac{100xMBE}{xobs_i}$$

where N is the number of observations, $xsim_i$ is the *ith* simulated value and $xobs_i$ is the *ith* observed value.

The linear regression analysis between simulated and observed values of fruit diameter was used for model validation.

3. Results and discussion

The analysis of apple fruit growth was performed on the basis of three main parameters describing the temporal dynamics of diameter: the growth - DG - (mm), the daily growth – DDG - (mm day^{-1}), the daily growth rate – DGR - (% day^{-1}). The period from bloom to harvest time was considered.

For DG, a typical trend was observed, characterised by several main stages (Fig. 1). The first showed a slow increase of diameter, followed by an exponential phase of growth that finally became linear with the maximum rate of growth. Finally, fruit grew slowly approaching the maturity with an average maximum value of about 80 mm. A low variability was observed among the years and the locations, with the exception of the data collected in Trento hilly orchard during 1990 and in Trento valley orchard during 1992.

The DDG increased for 30-40 days after bloom (Fig. 2). This time corresponds to the flex point of the sigmoidal trend of fruit growth (Fig. 1). Then, the DDG slowly and linearly decreased until harvest time. An higher variability among the collected data sets was observed, particularly in the first part of the growing season. The DGR increased for a short time after bloom (about 20 days from bloom), then decreased quickly during the first period, while a light reduction during the last months of the growing season was observed (Fig. 3).

In Fig. 1, the simulation of fruit diameter and the corresponding field data were presented concerning the Winter, logistic and Gompertz approaches. The models provided a good estimation of simulated process. However, he analysis of deviance showed that the model proposed by Winter provided better estimates than the other approaches (Table 1). Moreover, when the calibration was performed separately with data sets collected in each orchard, the errors were reduced even more. For example, data from Bolzano were simulated with a MAE of 1.86 mm (MA%E = 3.4%).

The Gompertz and logistic models showed higher values of errors (Table 1). However, the Gompertz model had a level of deviance close to that observed for Winter model. The error can be due to an overestimation during the first and the central part of the season and to an underestimation of the final size. The application of a logistic model increased the level of the errors mainly because of the symmetrical trend of the function (Fig. 1).

The linear regression analysis confirmed the previous results, showing a very good correspondence between observed and simulated data (Table 1). The significant values of R^2 and the analysis of the intercept (close to zero) and slope (close to 1) of regression functions were good indicators of the suitability of the considered models for the simulation of fruit diameters temporal trends.

Concerning the forecast of harvest fruit size, the correlation between fruit diameter measured at decade intervals from bloom and the corresponding harvest size was evaluated. Data sets were divided in two groups, one for the analysis of linear regression and the other for the application of the models. The results showed a very good correlation when data collected during the tenth decade or later were used. The comparison between the observed final sizes of apple fruits and the values calculated using the function derived from linear regression analysis showed that in correspondence of the tenth decade MAE approximates to 1 mm (Fig. 4), thus emphasising a good forecast of final diameter of fruit. The other statistical tests of deviance confirmed this consideration, with R^2 higher then 0.91, and a low level of MA%E (1.55 %).

4. Conclusions

The preliminary analysis of fruit diameter showed a sigmoidal trend in all the studied conditions (16 data sets). The analysis of several growth parameters showed a low variability in fruit dynamics among different years and locations, allowing to describe the trend of fruit size during the growing season. The application of several models allowed a good simulation of field data. The Winter model seemed to be most suitable for fruit size, being only slightly better than the Gompertz model. Concerning the forecast of harvest size, fruit diameters measured at the tenth decade were strongly related with the final diameters and the application of linear regression functions provided a good forecast of the harvest size, with a very low level of error.

This analysis represents the first step towards a global research project aimed at the analysis of fruit growth in several tree crops. Both the simulation of seasonal trend and the forecast of final size will be considered, because of their importance for improving cultivation techniques and thus of farmers decision making. The collection of weather data will allow the analysis of the effect of meteorological parameters on fruit growth and thus the improving of modelling activity.

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Table 1 – Statistical measures of model calibration.

	MAE	MA%E	R^2	Slope	Intercept
Winter	3.484	7.354	0.964	0.987	0.906
Gompertz	3.531	7.453	0.963	0.981	1.227
Logistic	4.095	8.644	0.957	0.999	0.005

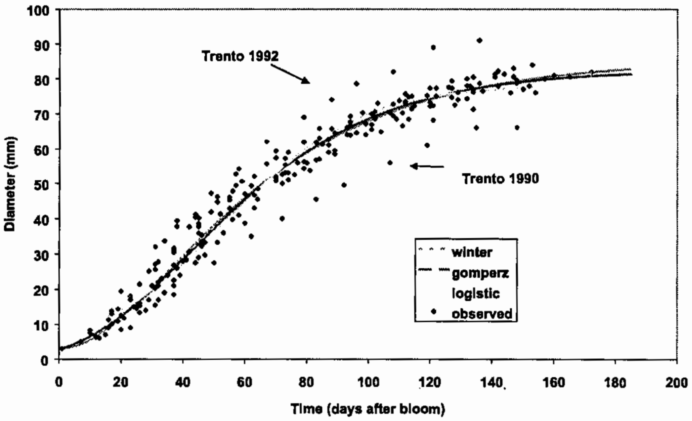

Figure 1 - Apple fruit diameter as a function of days after bloom. Observed data and fitted curves derived from applied models.

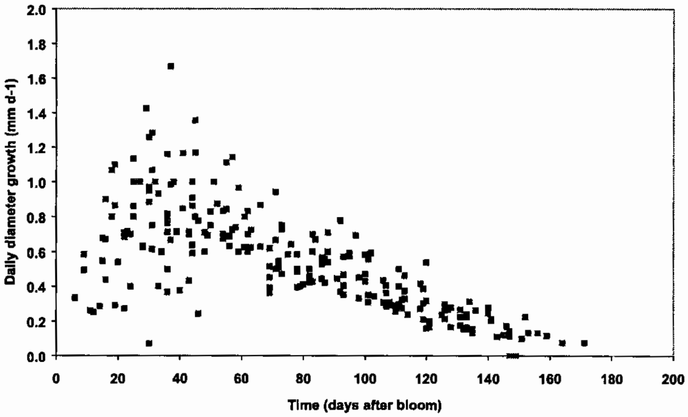

Figure 2 – Seasonal trend of daily diameter growth in Golden Delicious apple cultivar.

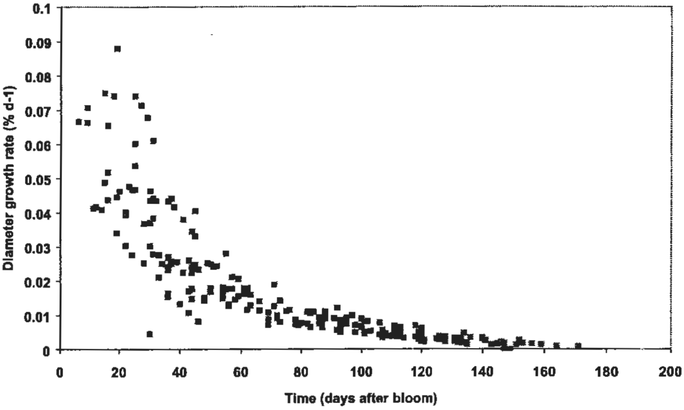

Figure 3 - Seasonal trend of daily rate of diameter growth in Golden Delicious apple cultivar.

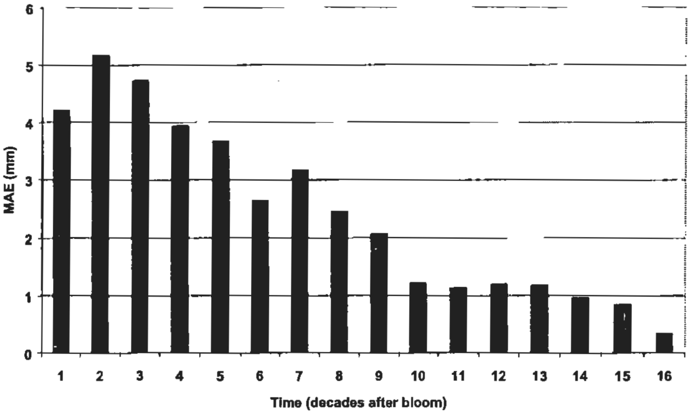

Figure 4 - Mean absolute error of final size forecast versus the decade of fruit diameter measurement.

Session 3
Critical assessment of modelling approaches

QUALITY OF MODELLING IN FRUIT RESEARCH AND ORCHARD MANAGEMENT: AN INTRODUCTION TO THE WORKSHOP

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1. Background

Models are used in research and extension, to draw together information and to suggest actions. In combination with computers, models constitute frequently used means of information transfer within and among groups of people in agricultural knowledge systems: researchers, farmers, policy makers, and consultants. Assessment of the effectiveness of models as means of communication is topic of a Study Group of the International Organisation for Biological Control, West Palearctic Section. To date, the Study Group has organised workshops together with groups working on greenhouse commodities (van Lenteren, 1996) and orchard management (this volume).

Decision support systems (DSS) provide a framework to structure ecological and management information and enhance efficient use of financial and natural resources. Despite these promising traits, the contribution of DSS to practical Integrated Crop Management (ICM) in orchards has been limited. Most DSS have been developed solely based on expertise and empirical information. The drawback of such a purely empirical approach to designing and managing ICM systems is that systems in new commodity groups or new additions to existing systems need to be made by trial and error. The area of validity is limited, but the actual limits are often not clear. Among the causes of failure, lack of clarity on the role of DSS in learning and decision making, as well as organisational problems related to user support and updating the model seem to stand out. The currently prevailing mismatch between demand for and supply of quantitative information is a problem for (applied) research and practice.

Within the research community, the wide-spread adoption of systems analysis and process-based modelling as research tools has its problems, too.

(1) Process-based models are often presented as new, even if they use ecological concepts that have been used many times before. The application in a specific system may be new, but the concepts may be well known and often applied. The newness and importance of process-based models is hard to assess unless explicit statements are made regarding relationships to existing models: ecological concepts, underlying data, and implementation (programming language, hardware requirements, etc.).

(2) Models are developed for specific purposes and environmental conditions, and are tested accordingly. However, lack of specification of the domain of validity may lead to applications for which the model was not intended. Disappointing results and

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rejection of basically sound approaches may ensue. The illiterate use of models as black boxes poses a threat to the credibility of models.

(3) Data for model validation are scarce and the input requirements of process-based models usually are substantial and require major experimental resources. The shortness of validation data hampers thorough evaluation of model performance in relation to model purpose.

The three problems noted call for a structured qualitative and quantitative evaluation of modelling approaches in orchard management, in relation to the objectives for which they were developed.

2. Aims of the workshop

i) To investigate reasons for low and high adoption rates of DSS in grower's practice, starting at the 'demand' side (growers or intermediates between growers and research).

ii) To evaluate the scientific contents of eco-physiological models on pest dynamics, crop growth and management, and their potential usefulness for growers.

3. Approach

Written contributions were invited (Blaise *et al.*, Boshuizen and van der Maas; DeJong; Graf *et al.*; Groot; Hardman *et al.*; Mols and Boers; Szafran *et al.*; van der Werf *et al.*; this volume). These contributions describe either (i) decision-support technologies for (a component of) orchard management (empirical models, not necessarily based on eco-physiological processes but used by growers or intermediates), or (ii) an application-oriented model based on eco-physiological processes in pest and/or crop dynamics (not necessarily used by growers or intermediates). To enable comparison of approaches, authors were asked to address the questions in Chapter 4 (DSS) or 5 (process-based models).

During the workshop the papers were reviewed using recent insights in factors governing successes and failures of such information technologies (Leeuwis, 1996; Rossing, 1996). The major part of the session was devoted to discussions among participants.

4. Questionnaire for Decision Support Systems

Problem context

- From whom does the initial idea for this DSS originate (research, extension, policy, growers, etc.)?
- To which problem is the DSS expected to be an answer/solution?
- Who is the 'problem owner'? To what extent are growers aware of the problem?
- Is the problem 'permanent' or 'once only'?

Strategy

- What is the concept behind DSS? How is it expected to contribute to problem solving?
- Which stages of learning, decision making or problem solving should be supported?
- What is the input required and output furnished by DSS?

Means

- Why has a DSS been chosen as a tool to help solve the problem?
- What other and/or competing means are available to users; have they been considered?
- What is the added value of DSS vis-a-vis other means?
- How complex are the models on which the DSS is based? (Range from very simple, straightforward to very complex.) Approximately how many variables are considered?
- Are concept and operation of the model easy to understand for users?

Targeting

- Who are the prospective users of the DSS?
- Which sub-categories of users exist, and to which sub-categories is the DSS directed?

Organisation

- What training activities have been carried out to make users familiar with DSS?
- What other support services are available to users in working with DSS?
- How much money must users invest for gaining access to appropriate hardware and software?
- On whose co-operation does the success of the DSS crucially depend?
- What activities are carried out to assess whether or not the DSS must be updated?
- Who is responsible for updating the DSS?
- How often has the DSS been updated?
- Are there any bottlenecks in updating the technology?

Development process

- Who have been directly involved in the development of the DSS?
- What software development method was used? A formal method? Prototyping?
- Did development start from scratch, or were already existing models used?
- How long did the development process last?
- How were prospective end-users involved in the development process?
- What forms of user and/or market research have preceded the development process?

Experiences

- How widely has the DSS been adopted by the prospective users?
- How long do users use the DSS? Do they continue to use it, or do they discontinue their use after a while?
- What unexpected forms of use, or unexpected events have occurred since the introduction of the DSS?
- Has the DSS been formally or informally evaluated?
- Which main conclusions can be drawn on the basis of evaluations?

5. Questionnaire for process-based models

Purpose of the model

- initial purpose and later purposes
- description of the problem and of the problem-owners
- description of the system

Application domain of the model
- study of system behaviour
- to be used in decision support system?
- to be used for deriving decision rules?

Structure of the model
- limits of the system: spatial, temporal, physical and geographic
- which basic ecological concepts are used to model the problem?

History of the model code
- versions, programming languages, computer platforms

Programming aspects
- hard- and software aspects
- availability

Sensitivity and uncertainty analysis
- parameters chosen, analysis of result

Evaluation of the model
- range of evaluation conditions
- evaluation criteria
- nature of evaluation: subjective or objective (statistical); partial or exhaustive
- conclusions of the evaluation: validity range

Usefulness of the modelling exercise
- were objectives reached
- more appropriate approaches in retrospect

Future plans
Outlook
Key publications

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QUALITY OF MODELLING IN FRUIT RESEARCH AND ORCHARD MANAGEMENT: ISSUES FOR DISCUSSION

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1. Introduction

The purpose of this paper is to highlight items for discussion during a one-morning workshop on Critical assessment of modelling approaches in Integrated Crop Management. This paper is based on information provided in nine papers that were submitted for this workshop (Blaise *et al.*, Boshuizen and van der Maas; DeJong; Graf *et al.*; Groot; Hardman *et al.*; Mols and Boers; Szafran *et al*; van der Werf *et al.*; all in this volume) in response to the questions listed in Rossing *et al.* (this volume). Distinction is made between process-based research models, which are considered in section 2, and decision support systems, which are addressed in section 3.

2. Research models

2.1. The process of model validation; when to stop and on which grounds?

The submitted papers indicate that building a research or DSS model helps researchers to systematize their knowledge. It leads to the identification of knowledge gaps and new research questions (e.g. Blaise *et al.*, Hardman *et al.*, DeJong). It seems, however, that one could continue forever to refine and expand a model. Even if the original research questions justified the investment in modelling, one can question whether this holds automatically for each subsequent question that is formulated in the process. If we automatically take up each research question raised by the modelling, we allow models to take over in setting the research agenda. An important issue therefore is how we should go about setting our research agendas, and in particular how we should evaluate research questions that are generated in the process of building a model.

One reason to expand and refine process-based models is the desire of researchers to make models that represent 'all' processes that they know to be relevant in the system. For instance, DeJong (this volume) mentions dry matter allocation to roots as such a refinement. Another reason for model expansion and refinement is the desire to obtain reasonable correspondence to observed data based on observed input functions, mechanistically sensible model structure and quantified relationships, without empirical (site-specific) fudge factors, because such a model could truly be called 'explanatory'. This is a high aim, which appears to be difficult to achieve in complex systems in the field. This is true both for models of multitrophic multi-species plant-pest-predator population interactions (Hardman *et al.*, this volume) and epidemiological processes (Blaise *et al.*, this volume) and for models of crop growth, dry matter accumulation and

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allocation, morphogenesis and architecture (DeJong, this volume). An important question, therefore, is at what point should we stop with refining model structure and increasing the number of input functions, in our attempts to make a model describe field experiments better?

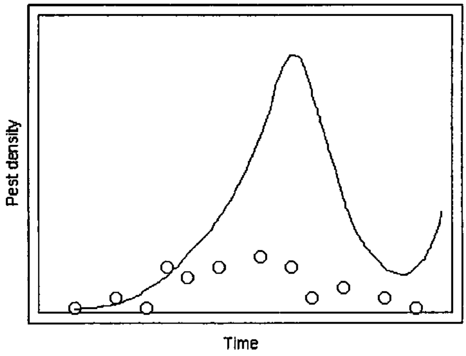

Figure 1 - A modeller's horror? Poor correspondence between simulation (drawn line) and field observations (circles). Causes for discrepancy may be manifold, including wrong model code, inappropriate or incomplete model structure, and lack of knowledge about external input functions and initial conditions.

A characteristic pattern in model development is to start off with a basic model and modify it as discrepancies between model predictions and validation trials suggest necessary changes (Fig. 1). The response to discrepancies between simulations and observations is generally threefold:

1. check the code
2. check the conceptual basis of the model for soundness and completeness
3. include more explanatory factors from outside the system in the modelling (Fig. 2).

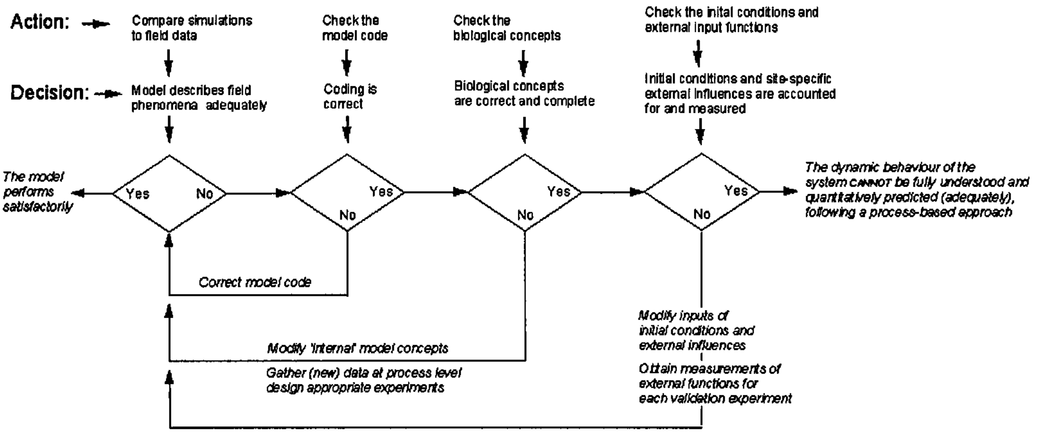

Figure 2 - Flowchart indicating actions and decisions in the cycle of model testing and improvement. The cycle can be said to spiral upward if knowledge and insight in the functioning of the modelled system are accumulated in the process. This learning process may be valuable, whether or not the final result is an adequate simulation of system behaviour.

The response process represents a learning cycle with repeated comparisons between field data and simulation results, to decide upon the effect of model modifications. The case study described by Hardman *et al.* (this volume) illustrates this developmental pattern and highlights the 'to-stop-or-to-detail' dilemma of researchers. Hardman c.s. initially constructed a basic age-structured and temperature-dependent predator-prey model, which is conceptually straightforward to build, but noticed that there were important discrepancies between the predictions of that model and what happens in actuality in the field. Considerable complexity and variability in the diet composition of the main predator mite, *Typhlodromus pyri*, was built into the model over a period of 10 years. Beside European red mites, the pest of interest, this predator can use rust mites (*Aculus schlechtendali*), pollen, phyllosphere fungi, and its own offspring as alternate food resources. Such food diversity stabilises predatory mite populations. It enhances an early and effective impact on pest mites and is therefore of considerable relevance to the success of biological control. In the framework of an explanatory model, the consequences of variable food availability on the predation on European red mites are difficult to calculate, due to lack of knowledge of the predator's foraging choices. Work to elucidate the 'rules' for foraging decisions has been undertaken, but it is a major endeavour. Moreover, when such rules are included in the model, extra input functions are needed to specify the time trends of the alternate food sources: rust mites and pollen. In experiments that were executed in the past, such measurements may not have been done; in new experiments, partly aimed at model testing, it may be too much work to collect such extra data. Therefore, a research and modelling program that is solely directed by the desire to get the model 'right' is doomed to get swamped in detailed research questions that might require decades of research work to answer.

Other examples might be chosen. At some point a researcher has to accept that there may be not enough site specific information and knowledge to simulate system dynamics under site-specific conditions, and that it is not practicable and scientifically advantageous to collect such information. The attempt to validate the model will then be open-ended, as the field data are site-specific, whereas the model might apply to an 'average' field, rather than one specific field. This poses a problem in a scientific culture that is based on the principles of 'success' (don't publish failures), 'newness' and 'publish or perish'. Models that do not provide an excellent fit to observed data do not seem to be worth publishing, or worse, authors may feel they have to cover up any discrepancies between simulations and field observations, or lack of independent validation data. Hiding the problems hampers scientific progress, which is critically dependent upon falsification of hypotheses and models. A question is therefore whether authors as well as scientific journals (editors and referees) should be encouraged to publish model falsifications.

There is substantial merit in the ability of process-based models to provide a mechanistically based prediction of system behaviour in response to environment and management. Even if a model cannot be validated, or only in part, due to the mentioned problems, simulation runs ('scenario studies') can be made to investigate options for managing the system under a range of initial and boundary conditions and forcing functions. The mechanistic basis of the model provides an inherent 'explanation' of model outcomes. Studying these explanations may suggest better management alternatives, thus generating new research questions to be investigated experimentally.

Specific questions:

- What are criteria to stop further model refinement?

- Are we satisfied with unvalidated models?
- Should we publish more model falsifications?
- How useful are models in setting the research agenda?

2.2. Relationships between modelling purpose, application and validity requirements

Four research models were presented in the workshop:

- Epidemiology of downy mildew, *Plasmopara viticola,* in grapes in Switzerland (Blaise *et al*., this volume)
- Growth and yield of peach, *Prunus persica,* in California (DeJong, this volume)
- Population dynamics of European red mite, *Panonychus ulmi,* and its predator *Typhlodromus pyri*, in Eastern North America (Hardman *et al*., this volume)

Population dynamics of woolly apple aphid, *Eriosoma lanigerum,* and its parasitoid *Aphelinus mali*, on apples in the Netherlands (Mols and Boers, this volume)

Three papers (Blaise *et al*., DeJong, Hardman *et al.*) emphasize use of the model to better understand system behaviour and to answer broad explorative questions on the effect of management (Table 1). Mols and Boers use a process-based model to answer a very specific research question: does a Canadian strain of *Aphelinus mali*, with lower temperature thresholds than Dutch strains, offer promise for more effective control of woolly apple aphid, due to an earlier impact on the pest in the cool early spring? The model is successful in providing an educated answer, providing a good example of the viability of the scenario approach. The other three models also offer the opportunity to ask such specific questions.

Table 1 - Comparison of four process-based research models with respect to model purpose, desired model attributes and validity requirements.

Model & authors	Model Purpose	Desired Model Attributes	Validation requirements
INSIM Mols and Boers	Comparison of biocontrol efficicacy of two parasitoid accessions from different climatic zones	Age-structured, temperature driven model for host-parasitoid interaction in orchard	No data available
VINEMILD Blaise *et al.*	Understanding mildew epidemics and timing fungicide sprays	Biologically sound, flexible, expandable system model	Epidemiology and damage consistent with general experience
PEACH DeJong	Develop integrated understanding of the annual C-budget of peach and simulate the potential effects of environmental factors, physiological processes and management practices on peach yield and fruit size	Usable for research and teaching	Acccuracy of built-in concepts more important than precise numerical predictions
MITESIM Hardman *et al.*	Understanding mite ecology; Exploring mite management tactics; Guidance in setting research priorities	Biologically sound, flexible, expandable system model	Ideally: valid at orchard level; but realistically representative for 'average' orchards

Specific questions

- Under which circumstances is a simulation model the best tool for asking specific questions, and when are manipulative or controlled experiments a better way?
- What is a better use of process-based simulation models: exploration or prediction?
- Are the validation requirements for a model different when predictive rather than explorative questions are asked?

3. Decision support issues

From an extension point of view, there are four dimensions of 'quality' with respect to DSS:

1. the way in which DSS are connected with learning and decision-making processes;
2. the relevance and validity of the DSS output;
3. the coherence of the built-in 'communication plan';
4. the quality of the DSS development process.

Using these four quality dimensions as section headings, we raise here below various points for debate.

3.1. Connection of DSS with learning and decision-making processes

Is there a need to 'model' learning and decision-making?

As the label 'DSS' suggests, the eventual aim of such computer models is to support human decision-making. It is interesting to note that in virtually all workshop papers 'decision-making' is used as a container concept that is not further refined into different categories. This is remarkable, because human decision-making in itself is a complex process that consists of many stages and sub-processes. Thus, in theory 'decision-support' could take many forms, and be geared towards enhancing very different stages and sub-processes, for example: observation, comparison, problem identification, problem analysis, translation, identification of alternative solutions, evaluation of solutions, experimentation, reflection, etc. Using 'decision-making' as a container concept suggests that developers of DSS wish to support every possible element in this process. The question emerges whether or not this is efficient and realistic. Would it make sense to investigate how decision-making processes evolve, and for which stage or sub-process support is most needed?

Supporting operational decisions or discovery learning?

Most of the DSS which are presented in the papers seem to be geared towards formulating specific advice on particular operational issues, for example on plant protection (Graf *et al.*, this volume) irrigation (Boshuizen and Van der Maas, this volume) and/or the use of agro-chemicals (Groot, this volume). The distribution of tasks here seems to be that the grower provides the data which are deemed relevant by the model, that the model does the reasoning and provides the advice, and that eventually the grower must decide whether or not to follow and/or adapt the advice (Graf *et al.*, this volume). It could be questioned whether or not a grower really learns something from this procedure if -as seems to be the case- the calculation model remains largely a black box. Does his or her understanding increase? Can we really speak of 'decision-support' when farmers take decisions on the basis of models they do not understand? Is there a discrepancy between the understanding gained by those who develop the DSS, and those who use it? How can DSS be adapted to support 'discovery learning' (i.e. probably the most effective educational strategy) by growers?

What types of problem situations are associated with sustainable and efficient DSS?

The investments that often go along with the development and maintenance of a DSS are considerable. Thus, one would think that it is important that DSS can be used for a prolonged time in order to obtain return on investment. This raises a number of questions with regard to the types of problems that justify DSS development. It was mentioned already that many of the DSS presented in the workshop address operational issues. It seems that the types of problems tackled (irrigation, plant protection, etc.) occur frequently enough (either within or among farming enterprises) in order to justify investment. However, a question which remains is the following: do these DSS continue to generate new answers to similar situations over time, or can their outcomes be summarised in simple rules of thumb which effectively make the models predictable (and therefore redundant) in a short while (i.e. do subtle differences in input generate large differences in output)?

3.2. The relevance and validity of the DSS output

Can and should we make a better problem definition?

Blaise *et al.* (this volume) note that 'In retrospect, a better analysis of the problem and a more precise definition of the objectives, with clear milestones to be reached would have increased the efficiency of the exercise'. This remark seems relevant to several other research and DSS models as well; in other cases too it can be observed that in the course of the development process the underlying research questions, objectives and activities change. A question that emerges is whether this phenomenon is an expression of necessary flexibility and learning, or the result of inadequate preparation and problem analysis.

In this respect it can be questioned *whose* problem models are dealing with: farmers' problems, researchers' problems, policy makers' problems? This question relates in part to the issue of agenda setting raised earlier, and also to the issue of targeting that is raised further on.

How to deal with validity problems?

Not surprisingly, a recurring theme within several contributions is the issue of validation. Even if many models are validated for particular purposes and within particular environmental conditions, it seems almost inevitable -especially for DSS that are used in the field- that models are used in situations where their agro-ecological validity is questionable. This may hold even more for the validity of the advice that is being formulated on the basis of agro-ecological models. If one takes seriously that there exists strategic diversity in farming (see e.g. Van der Ploeg, 1990; Leeuwis, 1993), it may very well be that grower A needs a different solution to a given problem than farmer B. How can we tackle these types of problems? Should we try to solve them within our models, or should we make organisational arrangements in order to deal with this (e.g. one could imagine that that validity is assessed in mutual debate, rather than in refining a model)?

3.3. The coherence of the built-in 'communication plan'

From an extension point of view, DSS are a means of communication between those who develop it, and those who use it. Thus, one could argue that implicit to a DSS is (or should be) a particular 'communication plan'. Normatively speaking, a 'good' communication plan can be characterised as a plan in which a coherent balance exists between the following elements (see Van den Ban and Hawkins, 1996):

- goal
- message
- target audience
- media of communication
- organisation

As we have already discussed several issues that are related to 'goals' and 'message' in the preceding sections, we will raise a few issues in relation to the remaining three elements.

Why are prospective users a moving target?

Groot and Boshuizen & Van der Maas suggest that in the process of developing DSS, the target audience tends to shift from growers or grower study clubs to extension agents. Among communication planners this would be considered a very tricky thing, as one would expect that extension agents have different needs, problems and questions than growers, and operate in a rather different media environment. The underlying question here seems to be whether or not to select the target audience on the basis of the medium we use (i.e. computer models), or to select a medium on the basis of the target audience we want to reach.

Added value vis-à-vis other means of communication?

If one considers DSS a medium for communication, it becomes clear that DSS are only one out of several media that might be used to convey a particular message. Hence, it is important to think critically about the added value of this particular medium. From a viewpoint of communication science, the key advantage of DSS is that they incorporate both characteristics of mass media and interpersonal media. They allow for interaction between the software and the user so that -at least in theory- they combine a large coverage with a certain degree of message specificity. Other added values that are mentioned in the workshop papers include the increased speed of calculation (Groot, this volume), communication speed (Graf *et al.*, this volume) and the fact that models are less fragile and laborious than soil moisture measurement instruments (Boshuizen and Van der Maas, this volume). In the latter case it is interesting to note that the eventual introduction of less fragile and laborious tools has apparently not resulted in an abandoning of the idea to develop a DSS. In any case, it is perhaps relevant to think critically about the added values (but also the shortcomings) that we expect from DSS. Moreover, it is relevant to ask whether or not the added value expected really addresses a problem that has been observed. For example, is lack of communication speed really a problem in the current scab warning system (using phone and fax) described by Graf *et al.* (this volume), or are we really talking about the timeliness of monitoring? And if so, is the Internet really a solution?

What about the organisational design?

Some papers describe in some detail the way the DSS has been designed in software-technical terms. However, for a DSS to be effective all sorts of organisational arrangements are needed in order to guarantee the use and maintenance of the DSS. Some papers describe how they have tried to minimise the problems of regular maintenance (e.g. Groot, this volume; Boshuizen and Van der Maas, this volume). Little information is however provided on other organisational issues, such as the need for farmer and extension worker training, support services, financial arrangements concerning maintenance and use, organisational and/or disciplinary frictions during development processes, etc. Yet, one could argue that a viable 'organisational' design is of crucial importance (see also Leeuwis, 1993). Should we pay more attention to these issues? What are important lessons in this respect?

3.4. The quality of the DSS development process

Should we use research models as a basis for DSS development?

Blaise *et al.* and Hardman *et al.* (this volume) indicate that in the longer term the idea is to use these models as a basis for DSS development. First the emphasis is on increasing understanding, and then on application. At the same time, it transpires that such a shift in purpose may require important changes in the model, e.g. the inclusion of economic modes of reasoning in the case described by Blaise *et al.*. The implication here seems to be that growers may pose rather different questions than researchers, and that their considerations in taking decisions may cover a much wider (in the sense of multi-disciplinary) range than is covered by the 'mandate' of the researcher. Likewise, to develop a DSS for fruit thinning in peach, Szafran *et al.* (this volume) use statistical techniques which describe crop physiological responses observed in field trials under a variety of conditions, rather than modelling the physiological processes mechanistically.

A related issue is that during the 'research phase' the complexity of the models may increase continuously (due to the constant stream of newly emerging questions), whereas one can wonder if such complexity is required and/or helpful in case of a DSS. Van der Werf *et al.* (this volume) indicate that in the design process of sampling and monitoring methods, simple descriptive models are used rather than complex explanatory models. The question emerges whether or not it is a wise strategy to sequence DSS development as a follow-up on process-based models.

Do we need more user-participation in DSS design?

While reading the workshop papers, one gets the impression that many of the models are developed in relative isolation within the research community. An exception seems to be the case of IRRY, which has been developed using an interactive prototyping approach (Boshuizen and Van der Maas, this volume). Especially if the idea is to support growers, one could argue that it is essential to communicate intensively with prospective users in the development process, in order to identify needs and problems. Research has shown that information needs tend to be dynamic, and may very well alter and/or become more specific during a prolonged period of software-development and use (Leeuwis, 1993). Hence, discussing the pros and cons of user-participation may be an issue for debate.

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IRRY: A DECISION SUPPORT SYSTEM FOR THE WATER SUPPLY IN ORCHARDS

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Abstract

Several advisory systems are available for fertilisation in the Netherlands, but until recently, such support was not available for water supply of fruit trees. In 1990, Horti Bureau Wageningen/Bodata (HBW/B) and the Fruit Research Station in Wilhelminadorp (FPO-Wi) started to develop IRRY, a decision support system for water supply. Since 1994 six fruit growers in the province of Zeeland and the DLV, a large Dutch extension service, are involved. In 1998 a project has started in which 50 to 60 fruit growers will use IRRY. Within one or two years IRRY will be available to all Dutch fruit growers.

1. Problem context

In 1989, Horti Bureau Wageningen/Bodata developed a meteorological station and a DSS for apple scab control. HBW/B was also interested in using this weather station for irrigation control during the summer. During a discussion at FPO-Wi the initial ideas were formulated and a first outline of the model was drawn. By extending the weather station with a pyranometer measuring incoming radiation, evapotranspiration could be estimated. Using the Makkink formula (Makkink, 1957), crop factors for apples estimated by FPO-Wi (Kodde and Kipp, 1990), and soil hydrological information derived from the 'Staring reeks' (Wösten *et al.*, 1994), a straightforward water balance model for the rooting zone was built. This model forms the basis for the IRRY DSS for water supply.

In a humid climate such as in the Netherlands water was thought to be not a critical factor. However, it was found that in the last three years, water was limiting during one or more periods on several soil types. It also became clear that through lack of knowledge and advisory systems growers were not only solving problems by water supply, but creating them as well. Because a majority of fruit growers supply water in most years, without understanding of the effect on the growth and production of the tree, the problem has a permanent rather than an incidental character.

2. Development process

HBW/B develops software using the structured prototyping method. This means that an idea is implemented in a first working program as quickly as possible (first prototype) in order to give end-users and specialists the possibility to evaluate the program and underlying ideas. The experiences with the first prototype are used when a second prototype is developed. This structured prototyping approach leads to different prototyping cycles (stages) during the development process. In Table 1, the main characteristics of the development stages of IRRY are summarized.

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3. Strategy

The overall strategy in developing IRRY was to build a model that could be used as a DSS by fruit growers. However, at the start of the development cycle there was no certainty that the model would work and no market research was done. Moreover, it was not possible to foresee the time needed to develop the DSS and which technical bottlenecks were to be expected. Under such conditions the chosen strategy was to develop the DSS step by step. Each new step in the prototyping process was taken only if evaluation showed that we were still on the right track, and that development time (=budget), technology and expertise were available. Although there were times when the development process stagnated, there were also moments when new ideas were added to IRRY. Over the years, IRRY has developed towards a comprehensive, sophisticated water balance model for the rooting zone.

4. Means

When the development of IRRY was started, a model-based DSS was preferred over moisture measurements because using a model was expected to be more practical for growers. Tensiometers were considered too fragile and labour intensive. Another technique considered was Time Domain Reflectometry (TDR). TDR provides real time assessment of soil moisture on the basis of measurement of the travelling speed of electromagnetic pulses through the soil, in comparison to a reference. However, TDR is still very costly and therefore not practically applicable. During a workshop in Germany in 1994, watermarks (Irrometer Company, Inc., Riverside, California) were advocated as useful tools for growers to measure soil moisture status. Watermarks measure the electrical conductivity in a porous medium inside a sensor. The water pressure inside of the sensor is presumed to be in equilibrium with the soil surrounding the sensor. The watermark sensor is saturated with Calcium sulphate. We advise growers to install some watermarks to check the outcomes of IRRY and to calibrate the model from time to time. Watermarks are used more and more by fruit growers in the Netherlands.

5. Targeting

Originally fruit growers were expected to use IRRY on a daily basis. Later on the notion came up to run the model at the extension service and to communicate the results once or twice a week to growers by fax. There is some interest to use the model as a research and educational tool. Such applications would address a different category of users.

6. Organisation

From 1994 on, six growers have been involved in using and evaluating the DSS. During group meetings, instruction was given and problems were discussed. These meetings were highly effective as well as necessary, because most growers were not familiar with what goes on in the soil.

Little investment is needed to use IRRY, because meteorological stations, computers and communication facilities are already available, or can be used for multiple purposes. Operational costs are low and using IRRY doesn't cost much time of the grower. No specific bottlenecks in updating the technology were encountered, although the rapid developments in the computer and communication industry caused update problems from time to time. Close co-operation in supplementary trials and literature research between HBW/B and FPO-Wi helped to solve gaps in the knowledge about the irrigation process.

7. Experiences

Although experiences with IRRY in practice are limited to only four experimental stations, six growers and one advisory service, adoption by growers looks promising. During the Zeeland project, considerable attention was paid to the transfer of results to other growers by means of demonstrations and publications. As a result, the number of growers that wants to start with the system exceeds our possibilities at this moment.

Validation of (parts of the) model is considered a key factor. Therefore, in the near future, continued research support for IRRY by FPO is needed to extend IRRY's success.

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Table 1 - Development stages of IRRY.

Development stage	Year	Activities	Nr. of users	crops/varieties	new features added	validation	publications
First prototyping cycle	1990 1991	Concept : outline model Preliminary test FPO-Wi[1]	- 1	- Apple: Jonagold Discovery	- evapotranspiration crop factors drip irrigation	- photomobile	Makkink (1957) Wösten *et al.* (1994) Kodde and Kipp (1990)
Second prototyping cycle	1992 1993 1994	FPO-Ho, FPO-Wi, FPO-Ge, FPO-Ze [1]	4	Apple: Jonagold Elstar	Overhead sprinklers Minisprinklers	TDR[2] SHB[3] (93)	Weibel and de Vos (1994)
Third – sixth prototyping cycle	1995 1996 1997 1998	6 fruit growers in the province Zeeland FPO-Ho[1] FPO-Wi[1]	8	Apple: Jonagold/Elstar Pear: Conference Apple: Golden Delicious Blueberries	Capillary rise (95) soil transpiration(96) root distribution (97) multi column (97) local-uptake compensation (98) regulated deficit irrigation (97)	TDR Watermark closed lysimeter experiments with TDR monitoring	Unpublished Unpublished
Seventh prototyping cycle	1998 1999	Fruit growers in the provinces Limburg and Brabant FPO-Ho[1] FPO-Wi[1]	± 60		percolation profile (98) still under development: - user friendly - root pruning - growing on ridges	Watermark	

[1] FPO: Fruitteeltpraktijkonderzoek (Fruit Research Station); Locations: Wilhelminadorp (Wi), Horst (Ho), Geldermalsen (Ge) and Zeewolde (Ze).

[2] TDR: Time Domain Reflection. [3] SHB: Stem Heat Balance method.

Appendix

Description of the model

1. Dimensions

The model describes the water dynamics of a soil profile. It is a semi-two-dimensional model. The soil profile is described for every 10 cm layer. Vertical (one-dimensional) water movement between layers is described. When water is applied locally (e.g. through drip irrigation) two columns are defined: a relatively wet and a relatively dry column. The maximum number of columns that can be defined is four. Definition of layers and columns results in definition of soil compartments. Horizontal water movement is not described.

2. Boundary conditions

The upper boundary condition is specified by the rainfall and the soil evaporation. Calculations are made down to the depth of the ground water table if it is at less than 2 m. Otherwise, calculations are made to rooting depth plus 60 cm. The lower boundary condition is specified by a constant pressure head; 0 kPa in case of a groundwater table and 10 kPa for profiles without groundwater influence.

3. Initial input

The soil layers need to be described according to the classification of the 'Staring reeks' (Wösten *et al.,* 1994). In this classification, 14 topsoils (relatively high organic matter content and low bulk density) and 16 subsoils (relatively low organic matter content and high bulk density) are defined according to texture. For every soil the relationship between volumetric moisture content, pressure head and conductivity is given. When local information on these variables is available, a site-specific soil type can be defined in IRRY.

The depth of the groundwater table or the depth of constant pressure head and the water application rate (if necessary) need to be described. Usually a prediction is given for the whole simulation period. Values can be changed during the simulation period.

The following aspects needs to be described per parcel: crop, variety, planting date, planting distances (all needed to make a first estimate of the leaf area), rooting depth and the widths of the tree strip, root zone and wetted area. Finally an initial pressure head profile is needed.

4. Continuous input

To run the model, hourly data on temperature at 1.50 m height above the soil surface, incoming global radiation and precipitation are needed. When the depth of the groundwater table or the water application rate changes input on these variables needs to be changed as well.

5. Output

Output of the model is structured at three levels of detail which are accessible through a menu. The first and coarsest 'layer' of output gives the average (root length weighted) pressure head of the rooting zone at the end of the day (top screen). This average pressure head was found to have a direct relationship with the physiological processes in the tree (data not shown). The next layer shows the daily accumulated values for all water fluxes (transpiration, soil evaporation, leaching/capillary rise, water application, precipitation). At the deeper output 'layers' IRRY shows calculated water fluxes, pressure heads, volumetric contents and water volumes for every layer or compartment and per hour or day.

6. Present restrictions

The application of IRRY is restricted to trees on rootstock M.9 or rootstocks with similar growth potential and/or root distribution. IRRY cannot be used in case of root pruning or with trees planted in " ridges". When trickle irrigation is practised, the emitters must be placed within 10 to 20 cm from the tree. When soils show severe cracking when drying out IRRY probably miscalculates the relevant average pressure head and water fluxes. It is expected that in the near future IRRY will be extended to deal with these situations.

RECOMMENDATIONS FOR AN EFFICIENT PLANT PROTECTION PROGRAMME IN SWISS APPLE ORCHARDS: CURRENT STATE AND FUTURE DEVELOPMENT OF A DECISION SUPPORT SYSTEM

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1. General Objectives

Ecological awareness and economical constraints as well as the public request for a reduction in pesticide use compel the modern apple growers to further optimise their plant protection programmes. Direct control measures against pests and diseases have to be limited to a minimum. However, in order to avoid the risk of intolerable yield losses, growers and extension officers depend on reliable predictions of the phenology and the development of pests and diseases and corresponding risk assessments. Furthermore they need to be informed about the appropriate monitoring tools and adapted control measures. Since more than forty years the Federal Research Station in Wädenswil offers a warning service which has been constantly expanded and improved according to growers needs. It is designed as a centralised decision support system facilitating the timing of monitoring, management and control measures as well as the choice of appropriate methods and means. Today more than thousand apple growers regularly rely on this service which in the sense of indirect subsidies is offered to a very low price.

2. Current state

Currently the warning system depends on the close collaboration between different partners providing the necessary inputs such as the local weather data, tree phenology, the actual developmental stage and general population pressure of pests and the epidemiology of diseases as well as the appropriate monitoring and control measures.

2.1. Organisation

Basically four different partners are involved as provider and/or user of information: The Swiss Federal Research Station in Wädenswil FAW, the Swiss Meteorological Institute SMA, the Cantonal extension services and the fruit growers. A diagram of the flow of information between the partners is given in Fig. 1.

The Swiss Meteorological Institute is providing the data from five automatic weather stations (Basel, Güttingen, Vaduz, Wädenswil and Zürich) covering the different climatic zones of the apple growing area in Eastern Switzerland (Fig. 2). Based on these data the Federal Research Station is forecasting the phenology of various insect pests using models of different complexity. Additional mobile weather stations with integrated warning computer allow the prediction of scab infections on a smaller spatial scale. Model predictions are complemented with field observations on pest and disease incidents. The Cantonal extension services and the growers are strongly involved in the system not only as receiver but also as provider of information by monitoring pests and diseases at roughly 100 different sites (Fig. 2). This allows a general appreciation of the

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pest and disease situation with a rather high resolution. All the local information is gathered in Wädenswil. Based on the interpretation of model predictions and field observations recommendations for appropriate management strategies are established and communicated to the apple growers.

2.2. Weather data

The weather data are collected from the automatic weather stations of SMA on the one hand and from own mobile weather stations on the other. The main driving variables of the models such as air temperature, soil temperature (SMA only), relative humidity, precipitation and leaf wetness (own weather stations only) are recorded. Data are available with a maximal delay of 24 hours. Prospective weather development is take into account by means of a five day agricultural weather forecast.

2.3. Monitoring and forecasting tools

Various tools and methods are used for pest and disease monitoring. Aside from visual counts and phenological observations, pheromone and colour traps (Type Rebell®) are used for pest population estimates in the orchards. A special spore trap (Myco-Trap) has been developed (Siegfried *et al.*, 1996) in order to determine the beginning of potential scab infections in spring based on ascospore release at some typical sites.

The models used vary in their complexity and descriptive depth. They range from simple temperature sum approaches (e.g. for codling moth *Cydia pomonella* or apple aphids (Graf *et al.*, 1998)) to age structured phenology models including diapause (e.g. for apple sawfly *Hoplocampa testudinea* (Graf *et al.*, 1996a and 1996b). Scab warning is based on Mills' table and integrated in the warning computer of the mobile weather stations.

2.4. Communication

Communication is the crucial element within the warning system. The results of monitoring and field observations have to be transferred to Wädenswil, and the recommendations have to be sent back to the growers.

Typically field scouts and growers are checking their orchards weekly Sunday or Monday morning. The results of their visual counts and trap controls are communicated by phone or fax at the latest Monday afternoon. At the same time parallel observations are made in Wädenswil and the phenology models run with the most recent weather data which are permanently available by modem. Monday evening all the information from the different sources is interpreted and recommendations for timing, monitoring methods and control measures established. Tuesday morning a bulletin is edited and sent to the growers directly or via the Cantonal extension services either by ordinary mail, fax or e-mail. At the latest Wednesday morning all subscribers have the recommendations at their disposal.

3. Future development

At the moment different types of models and approaches are used for forecasting. A unification of the models towards an identical structure, analogous parameters for different species and a common platform for input and output is planed in order to facilitate and accelerate the handling. Embedding the models into a Geographical Information System (GIS) including local weather data would allow an enhancement with respect to the spatial resolution. In the near future an adaptation to modern communication technology has to be envisaged. Though only a small number of fruit growers have access to Internet yet, interactive computer communication will probably be the choice of the future. By these means communication could be sped up and time lags between updates could be shortened. This is particularly desirable with respect to an efficient scab management which requires an immediate reaction to short time weather changes.

Obviously the warning system can be significantly improved by implementing modern technology. However, the direct involvement and participation of the growers is probably the key element of its success and has to be maintained or even expanded in the future. Furthermore, even though the efficiency of the decision support tool can be enhanced, it will never dispense the growers from making their own observations and taking their own decisions.

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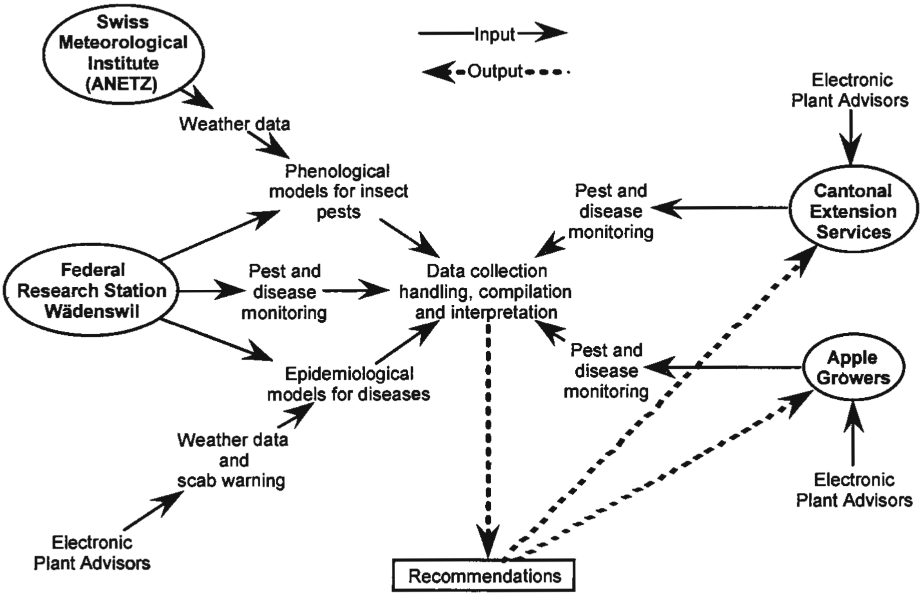

Fig. 1: Organisation of the forecasting and warning system for apple pests and diseases

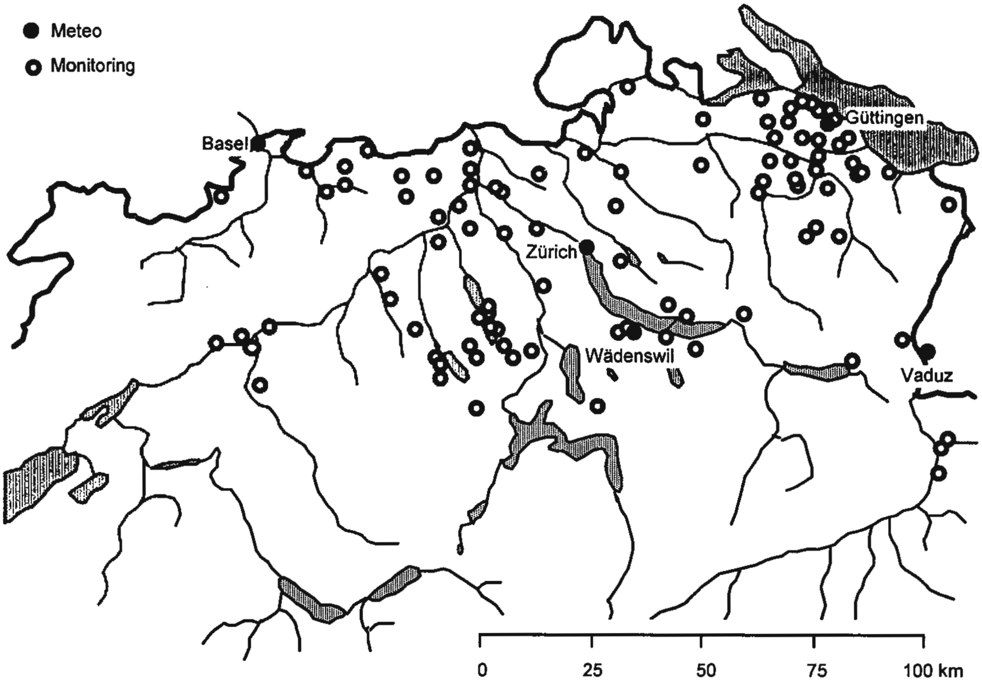

Fig. 2: Sites of observations and weather stations

A DECISION SUPPORT SYSTEM FOR ECONOMIC AND ECOLOGICAL CALCULATIONS FOR FRUIT CROPS

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1. Problem context

A pc-based decision support system (DSS) has been developed to calculate the effects of orchard management decisions on farm economics and environmental impacts. This is necessary because in 1991 the Dutch government presented a policy program that requires in 2000 44% reduction in the use of agrochemicals from the average during the period 1984-1988. Such a reduction can be achieved in many ways, resulting in the need for a DSS that enables growers to evaluate economic and ecological consequences of the various strategies that may be followed to reduce the input of chemicals. These strategies include growing other cultivars, economizing ways of crop protection, use of tunnel sprayers, planting of windbreaks on ditch banks, etc.

The idea for this DSS originated from research. Growers are highly interested in decisions affecting these strategies when a new planting is planned, or at times of other investment decisions. They are well aware of their financial problems and the demands from the government.

The problem "which decisions have to be made to satisfy both ecological and economic demands" has obtained a permanent character. Some decisions have to be made every time that a new planting is planned, or at times of investment decisions. At that time a grower, with the help of the extension service, has to choose between numerous possibilities. To make an informed decision the grower needs calculations about the economic and ecological consequences of all possibilities. Manual calculations are possible but time consuming and therefore expensive. The DSS is able to make calculations for a specific planting for one year (first part of the DSS) or for an orchard as a whole for a period up to a maximum of 15 years (second part of the DSS). The results are available within a few minutes and enable the grower to compare many different strategies to reduce the use of chemicals. Furthermore, it is possible to choose the strategy with the greatest reduction of chemical input and smallest financial loss.

2. Strategy

The DSS is expected to solve the problem of time-consuming calculations. With the computer calculations the effect of different aspects of the strategies are made clear, and a good understanding of these enables to take the right decisions. The DSS supports primarily the stage of learning. The DSS is meant to be used when the problem is identified and analysed and a grower needs the evaluation of different solutions.

The DSS is described in Groot (1996b). It consists of two parts. The first part (for short-term decisions) calculates the gross margin for a specified planting for one year. The gross margin calculation includes three different means of crop protection based on systems research for integrated fruit production at the Fruit Research Station. The second part of the DSS (for strategic decisions) makes calculations for the entire orchard. In this second part calculations can be made for a period up to 15 years to account for the perennial nature of apple and pear plantings. Economic results of the calculations are: costs, returns, gross margin per planting, investments in plantings and farm equipment, profitability, net farm results and growers income, savings and financing.

The required input differs for each type of calculation. For calculation of the gross margin, only a few characteristics of a planting are required. For a complete economic and ecological calculation of the orchard for a longer period, many economic characteristics are needed. The DSS is based on a data base, so that by specifying the cultivar, planting density, crop protection method and year of planting, the required labour hours, expected production, costs and so on are provided automatically.

The DSS calculates economic indicators as well as the following ecological/environmental indicators:

- use of active ingredients of agrochemicals in kilos per hectare
- spraying index (quantity of chemicals used, divided by the quantity of chemicals advised by the Extension Service)
- results according to the "Environmental Yardstick" that has been developed by the Centre for Agriculture and Environment (Utrecht, The Netherlands).These results are expressed in Environmental Impact Points with respect to water life, soil life, ground water in spring and autumn (Reus and Pak, 1993). Environmental Impact Points take into account the toxicity of a chemical.

3. Validation

Validation of the model is not considered an important issue, because the calculations are based on straightforward bookkeeping and application of accepted economic rules. Verification of model results is important, and this is accomplished through manual checking of the calculations. A significant issue is the quality of the input data used by the DSS. These include prices, costs, labour etc. in the Dutch fruit growing industry, and were compiled from various sources by Joosse and Besseling (1992). Data concerning experimental means of crop protection are taken directly from research at the Fruit Research Station, Wilhelminadorp/Randwijk.

4. Methods

To be able to make informed investment decisions it is necessary to carry out numerous calculations. The main problem is the need for data and the time necessary to make all calculations by hand. This DSS uses a large database providing standard input data; therefore, it is only necessary to choose or provide certain orchard specific data. Added values of the DSS are time saving, providing data and to make calculations so rapid that decisions can be based on many more data than would be possible with manual calculations.

This DSS is a straightforward model. All calculations are based on economic or arithmetic formulas. The number of input variables is approximately 30. With these input variables the DSS chooses the right data in the database in order to perform calculations. It is rather easy to use the DSS, but it is difficult to change the standards in the DSS. Plans are being made to devise a user-friendly menu for changing standard data.

5. Targeting

Prospective users of the DSS are individual growers or groups of growers united in study clubs, extension services, students and researchers. The latter can use it to evaluate new developments. In study clubs, farm data and experiences are exchanged and discussed in order to learn from each other. Existing study clubs focus, for example, on crop protection or economics.

6. Organisation

Until now there have only been demonstrations with the DSS and it is not yet ready to be further developed. A problem is the time required to regularly update the DSS data on all economic aspects of fruit growing. The DSS will be modified so that users can change these data themselves and use their own farm data.

7. Development process

Directly involved in the development process are the Fruit Research Station, the Agricultural Economics Research Institute (the Hague) and the Ministry of Agriculture, Nature Conservancy and Fishery. Model development started from scratch and no existing models were used. Firstly we developed the DSS by using Lotus 123. Due to the expected large number of formulae we chose a spreadsheet programme. Our main argument to go for Lotus was that it is known by the potential users. However, during the development process it became clear that a spreadsheet was not the right choice, because of the large quantity of data handling needed. Therefore, a switch was made to Microsoft Access.

The development process started in 1993 and involved important contributions by college and university students. Prospective end-users, other than researchers, were not involved in the development process, but by demonstrating parts of the DSS to prospective users, comments of growers and extension agents were obtained. This led to some changes. The most important comment was that growers wanted to be able to use farm specific data.

8. Experiences

As the DSS has only be used in demonstration projects, and not in actual management, genuine user experiences are lacking. Reactions to demonstrations showed that extension services are interested in using the DSS which leads to the expectation that the DSS will be used in future.

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COMPUTER-METHODOLOGY FOR DESIGNING PEST SAMPLING AND MONITORING PROGRAMS

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Abstract

This paper evaluates two distinct enterprises: (1) an ongoing attempt to produce an introductory book plus accompanying software tools on sampling and monitoring in pest management; and (2) application of the modelling approaches discussed in that book to the design of monitoring methods for European Red Mite in North America.

1. Introduction

Monitoring of pests over part of a growing season is often required to schedule interventions (biological, chemical or other) at the right time. To minimise sampling effort in monitoring programs, risks of a too late detection of damaging outbreaks must be balanced against the labour costs of frequent intensive monitoring. We developed a structured, simulation-based approach to design monitoring programs, which allows for a much wider exploration of management options than is possible in field-based studies, and which complements and supports an empirical approach by practitioners. In the simulations, the performance of candidate monitoring approaches is calculated by 'applying' them to computer generated stochastic population trajectories which are representative for pest dynamics in the field. The results of those simulations are summarised in a set of performance indicators. Such indicators include the probability of intervening, the number of samples in time and the size of those samples, as well as the damage caused by the pest and its density when the necessity of an intervention is 'detected'. Prototype monitoring programs with desirable performance in the simulations are tested in the field. The simulation approach has been successfully used to design monitoring programs for European red mite in apples under North East American conditions. By simulation we discovered possibilities to use higher actions thresholds, smaller sample sizes and longer sampling intervals than practitioners thought were feasible. Hence, the number of interventions and sampling effort could be reduced, with savings in costs while conserving natural enemies. The associated (small) risks were calculated. The methodology is widely applicable. User-friendly software tools are under development.

While our research focuses on the relatively unexplored area of monitoring, we work at the same time on a book and accompanying set of software tools that has a wider perspective. The book and software tools include basic sampling methods for decision making in pest management. These software tools are primarily aimed at researchers, to develop prototype sampling and monitoring protocols, and at students who want to become proficient in decision making for pest management. Therefore, researchers and

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well-informed extension specialists are the 'users' of the methodology. The end-users are the people who use the resulting protocols for practical surveillance in the field, such as scouts and growers. Our work gives therefore decision support at two levels: (1) the level of the scout in the field; and (2) the level of the designer (pest extension specialist) of sampling and monitoring protocols. When we address questions on decision support, we will most often answer them from the viewpoint of the extension officer.

Our work on sampling and monitoring cannot be easily classified as 'Research' or 'Decision Support' oriented; it can be viewed either way, and either way gives interesting and different perspectives on the usefulness of the approach. We therefore answer both questionnaires. We will first address the list of questions asked in the framework of Decision Support Systems (DSS). Further below, we address the questions asked in the framework of Research Models.

2. The DSS outlook

2.1. Problem context

From whom does the initial idea for this DSS originate? Cornell University (New York State) has responsibilities for research, education as well as extension. The New York State Agricultural Experiment Station, which resorts under Cornell University, specialises in research and extension in horticultural crops, including fruits (apples and grapes) and vegetables. Growers influence the programs of the station, as members of the planning boards. Integrated Pest Management is a major work area within the Department of Entomology, and work on sampling is an inextricable part of IPM.

To which problem is the DSS expected to be an answer/solution? The software tools are meant to allow researchers (and well-educated extension specialists) to design tailored sampling solutions for specific pest problems. The software allows integrating information on pest distribution, action threshold, and desired performance of the sampling method, acceptable and unacceptable risks, and sampling effort into a practically feasible sampling design.

Who is the 'problem owner'? There are problems and problem owners at two levels. At the one level the problem is how to set up a reliable and feasible sampling or monitoring scheme for use in practice under a variety of conditions. Here a researcher or extension specialist is the problem owner. At the crop level, the scout or grower is the problem owner. His problem is to take a correct management decision. He has to match effort and risk. Scouts and growers are generally not that interested in how a protocol is developed, only that it meets certain requirements of time and precision and even these are only vaguely understood and expressed.

Is the problem 'permanent' or 'once only'? Sampling is a recurring problem (or business) for a scout or pest management advisor. The design of a practical sampling method is in a sense a unique undertaking, because the sampling protocol, once developed, may be further developed in practice. However, as value judgements and perceptions change, the expectations about the performance of a sampling method may change, and hence it may require to be 'redesigned'.

2.2. Strategy

How is DSS expected to contribute to problem solving? The concept behind the DSS is that sampling may be simulated as a stochastic process. By repeating the simulations many times, an overview can be made of the 'overall performance' of the method by giving the distributions for a set of performance indicators. The performance depends upon the design parameters of the sampling method, e.g. the 'type' of protocol (e.g. fixed sample size, sequential sampling), the maximum sample size one is willing to collect, a threshold density, the distribution of the pest over sampling units, etc. Performance indicators are first of all the *operating characteristic (OC)* and *average sample number (ASN)* functions, which give – as a function of true pest density – the probability of *not intervening* and the *average number of sample units* that must be collected before a decision is taken. Measures of risk and effort can be derived from those primary performance functions. The main contribution to problem solving is that a clear link is provided between desired performance, biological properties of the pest (e.g. its distribution) and the sample plan parameters.

Which stages of learning, decision making or problem solving should be supported? The methodology supports the design process of sample plans, i.e. the initial steps towards formalising a decision process for the grower or pest consultant. Researchers and extension specialists, who use the design tools, are the main target group for learning. Secondly, the end-users, using tested sampling approaches under field conditions, have a learning experience, partly because the sampling and monitoring guidelines are provided with up to date information on the biology of pests and pictures of their life stages and injuries.

What is the input required and output furnished by DSS? At the design stage, required inputs are action thresholds for pest density, information describing the distribution of the pest over sample units, and desired performance (sample number and OC function). Under field conditions, the only information that is required is a chart or table with decision criteria and sample observations.

2.3. Means

Why has DSS been chosen as a tool to help solve the problem? The relationship between the parameters of a sampling protocol and its performance can be derived using statistical theory and stochastic simulation approaches which are too complex to 'write on the back of an envelope' and solve in a short-cut kind of way. Mathematical tools are needed to perform the underlying mathematical analyses and calculations. With the advance of modern fast personal computers and sophisticated mathematical software with a friendly user-interface, the stage is now set to provide the mathematical and simulation technologies to users.

What other and/or competing means are available to users? The main alternative to using the proposed structured approach to designing sampling plans is to proceed by trial and error, and evolve methods in practice. Such an approach is not basically unsound, but entails the risk that sub-optimal solutions are the end product and that implicit or hidden objectives guide the process. Moreover, the resulting product may not be easily transported to different conditions, because the boundaries within which they are valid may be unclear. At the other hand, the design process on the computer can result in a theoretically optimal product, which is practically not feasible or incompatible with other practices or grower's objectives. Therefore, field evaluations and computer explorations are complementary rather than competitive. An asset of the design approach using computer tools is that all the objectives and constraints are made clear in the process. This promotes awareness among researchers, consultants and other practitioners. For instance, when we made simulation analyses of thresholds for monitoring and control of red mite in apples, we realised during the simulations that one of our restrictions was that mite density should never be above 15 mites per leaf at the time an intervention was scheduled, because the age structure and persistence of such high density populations would hamper effective control. This restriction was 'built into' existing thresholds, but at first we did not consider this and based our threshold calculations only on damage relationships. Hence, we became more aware of the multi-faceted nature of the decision problem.

What is the added value of the DSS vis-à-vis other means? The computer simulation approach offers a sound theoretical underpinning, and allows running fast and cheap tests of alternative approaches that would be impossible to execute in the field.

How complex are the models on which the DSS is based? The statistical and stochastic models that are used are simple in a mathematical sense. Few variables and parameters are considered.

Are concept and operation of the model easy to understand for users? The details of the methods will be difficult to understand for users without a good grounding in mathematical statistics; however, the global results of the software tools should be accessible for interpretation. Nevertheless, the outcomes of simulations of sampling processes can be counter-intuitive and not so easy to understand. This gives in fact a strong argument for running such simulations! It shows the need for learning.

2.4. Targeting

Who are the prospective users of the DSS? Researchers with a task in extension.

Which sub-categories of users exist? Students of pest management courses at universities.

2.5. Organisation

What training activities have been carried out to make users familiar with the DSS? The software tools will be included in university courses on decision making in pest management.

What other support services are available to users in working with DSS? None.

How much money must users invest for gaining access to appropriate hardware and software? The situation on the soft- and hardware market is rapidly changing. As of June 1999, the expectation is that the tools (MathCad electronic books) will be placed on the World Wide Web at no cost, or a low service charge. MathCad, a sort of sophisticated mathematical spreadsheet program, is required to read those electronic books and run simulations. A powerful demo version of MathCad is available on the Web free of charge (www.mathsoft.com). MathCad runs under Windows95 on Wintel PCs.

On whose co-operation does the success of the DSS crucially depend? Success depends on the need of users to explore the theoretical performance of proposed sampling methodologies, and the ease of use and accessibility of the software. In addition, effective communication of the availability of the software is required.

What activities are carried out to assess whether or not the DSS must be updated? The DSS as we are developing it, is a set of tools (incorporated in an electronic book in MathCad) to design and evaluate sampling protocols. Updating may be required on the basis of user response. Sampling protocols developed using the DSS, may require regular 'redesigning' as the position of sampling in the context of whole crop management changes.

Who is responsible for updating the DSS? The authors.

How often has the DSS been updated? The current development of the design tools as an integrated MathCad electronic book is an innovation upon earlier – more limited – tools, developed in FORTRAN (Nyrop and Binns, 1991; Nyrop and van der Werf, 1994).

Are there any bottlenecks in updating the technology? The main bottleneck will be research money (i.e. time) and maintenance of a critical number of competent staff at research institutions. Changing research priorities, away from agronomy at the field level, and short-term allocation of research funds appear to constitute a threat.

2.6. Development process

Who have been directly involved in the development of the DSS? The main proponents of the theoretical work relating to sampling are Binns and Nyrop with publications in this area for more than a decade. They worked closely in co-operation with specialists on the control of specific pest-crop problems. Many of the theoretical advances were included with little delay in the yearly Pest Management Recommendations by Cornell Co-operative Extension (Anon., 1998).

What software development method was used? We did not follow a specific software development method. The basic structure of each 'chapter' in the electronic book is: Introduction, Input Parameters, and Results. The software program MathCad provides an interface for combining text, mathematical simulations and graphical presentation of results in a single environment.

Did development start from scratch? Developments in MathCad started from scratch, but calculation and simulation methodologies were reprogrammed with guidance from statistical literature and existing FORTRAN code.

How long did the development process last? For the MathCad electronic book: three years (1996-1999); for the earlier tools in FORTRAN: decades; for the original statistical and mathematical theory: centuries.

How were prospective end-users involved in the development process? They were not involved in the development process, other than through informal personal contacts in the frame of Cornell Co-operative Extension. End-user feedback can be obtained by active soliciting, and it does not come voluntarily easily. Users of development tools, such as extension specialists are involved more directly, due to co-operation within the New York State Experiment Station, where the decision guides are both developed and communicated to practice.

What forms of user and/or market research have preceded the development process? There was no user or market research.

2.7. Experiences

How widely has the DSS been adopted by the prospective users? Numerous well-designed sampling plans are available to growers and scouts (Anon., 1998). The new environment for developing sampling and monitoring guides, a DSS for applied researchers and extension specialists, is not yet readily available. It is planned to be available in the course of 1999.

How long do users use the DSS? Do they continue to use it, or do they discontinue their use after a while? The information in the Cornell Cooperative extension package is being updated and upgraded continually and keeps up with the demands of the market. Agnello et al. (1994) report that about 35% of 35 growers who had been trained to use a mite monitoring protocol developed by Cornell Cooperative Extension, continued to use it without modification. Another 60% monitored mites, but modified the protocol, usually by taking fewer leaves when they thought they could already predict the outcome. The remaining 5% abandoned the scouting procedure.

What unexpected forms of use have occurred since the introduction of the DSS? None.

Has the DSS been formally or informally evaluated? An evaluation of the adoption of decision support tools for insect pest management in 1993 was reported by Agnello *et al.* (1994).

3. Research model outlook

3.1. Identification of model and author(s)

This paper is not about a single model, but rather about a methodology, a way of thinking, as well as about a set of new tools to put that methodology into practice. The methodology will be published as a book with an accompanying electronic version on the World Wide Web. The provisional title is: *Sampling and monitoring in crop protection; the theoretical basis for designing practical decision guides.*

When arthropod pests (insects, mites) occur in annual or perennial field crops, season long surveillance may be required. To check the state of the system, a grower (or scout or pest management advisor) needs to go into the crop, collect a sample, and make a decision on pest management on the information contained in that sample. We assume that some kind of corrective intervention is possible, otherwise sampling makes no sense. That corrective action may be a pesticide application; it may also be a natural enemy release or a cultural action. We therefore refuse to see sampling as the bandwagon of pesticide spraying (although for judicious pesticide use, sampling cannot be dispensed with!). Sampling through time is monitoring. We make distinction between sampling and monitoring because monitoring has a time dimension which sampling lacks, with important consequences for the underlying design methodology.

3.2. Purpose of the model

The purpose of the research on the theoretical underpinnings of sampling and monitoring in crop protection is to strengthen the justification and appropriateness of sampling approaches used in practice. A theoretical approach helps to clarify objectives and means of sampling for pest management and ascertain that the chosen sampling or monitoring protocol has the expected performance and is the optimal approach in view of the objectives of management. A theoretical approach contributes to reducing the reliance on pesticides for pest control by explicitising risks. Practitioners may be more willing to accept risks if these can be quantified. Risk acceptance helps to increase pest density action thresholds, which lowers pesticide usage, conserves natural enemies, and contributes therefore to a more ecologically sound practice of crop protection.

3.3. Application area of the model

The prime objective of research on sampling methodologies is to develop more effective and efficient protocols for end-users: scouts, pest management advisors and growers. These protocols take into account both the growers objectives of sampling cost and risk of pest damage as the more public objective of reduced intervention with chemical products and restoration and conservation of natural enemy communities. Improved insight in the workings of sampling methods is an additional benefit that helps in designing methods for other systems. The modelling tools are used to derive decision rules.

3.4. Structure of the model

As an example, we summarise the conceptual framework, which was used by Nyrop *et al.* (1994). The methodology for developing and evaluating monitoring methods comprises five steps (Fig. 1).

1. The first step is the construction of a set sampling plans that are used to determine whether intervention is necessary or not. If no intervention is necessary, the time at which the pest should be resampled is indicated. For red spider mite in apples (*Panonychus ulmi* Koch), Nyrop *et al.* (1994) used sampling schemes that decided between immediate intervention, resampling after one week and resampling after two weeks (Fig. 2).
2. Monte Carlo simulation of the performance of each of the sampling plans in terms of 1) the probability of taking one of the possible decisions, and 2) the average number of sample units required to reach a decision (Fig. 3). These two criteria are functions of the true pest density only, assuming that the variance of population density is a function of the mean density. Nyrop *et al.* (1994) represented the sampling distribution of red spider mites over leaves with a negative binomial distribution, using a power relationship between the variance and the mean to calculate the dispersion parameter *k*.

Calculation of the performance of a chain of sampling plans used over a season to monitor density through time. Performance is calculated by combining the performance criteria of the sampling plans (functions of density) with simulated or observed trajectories of density over time. The performance of a monitoring protocol for a given set of population trajectories is characterised by five criteria:

1. the probability of intervening
2. the cumulative pest density up till the moment of intervention
3. the density at the moment of intervention
4. the total number of sampling bouts scheduled
5. the total number of samples taken in all bouts.

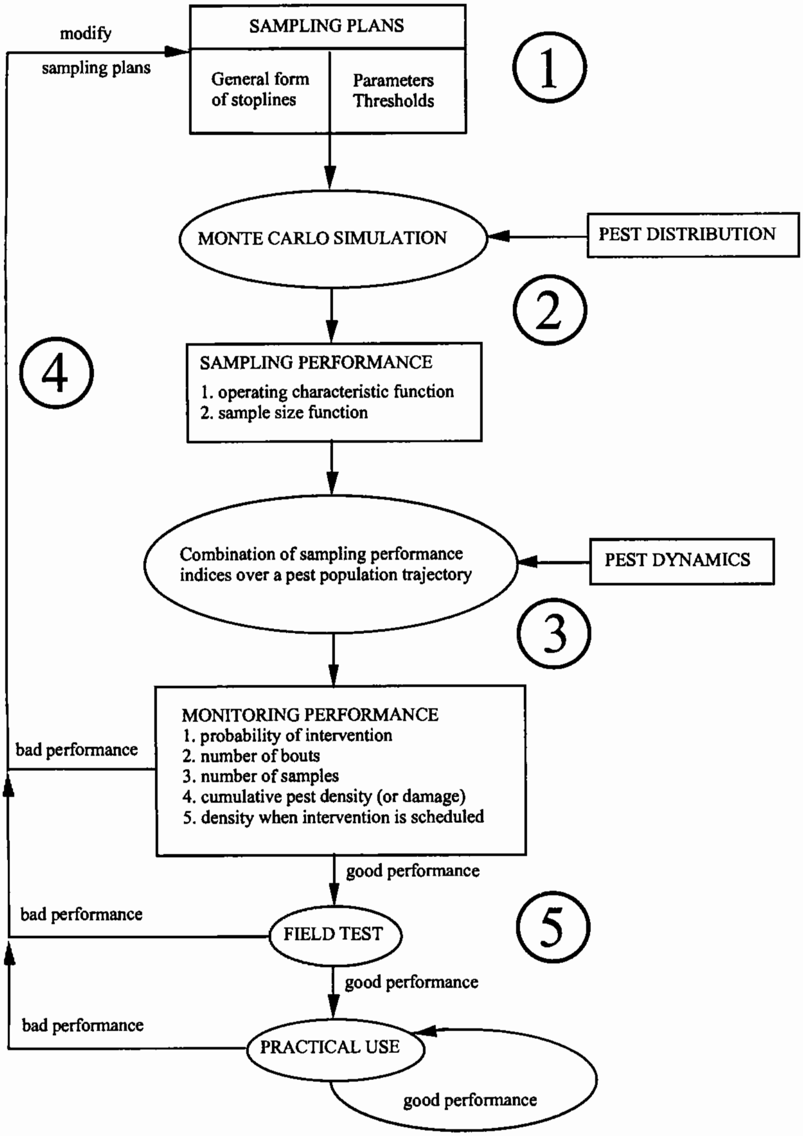

Figure 1 - Five steps in developing and evaluating a monitoring protocol

An example of simulated performance is given in Fig. 4. The overall performance depends on the performance of each of the sampling plans for given densities and on the population trajectorie(s). Monitoring protocols that have good performance for slowly growing pest populations (biological control!) might have bad performance for rapidly growing populations, and vice versa (Nyrop et al., 1994).

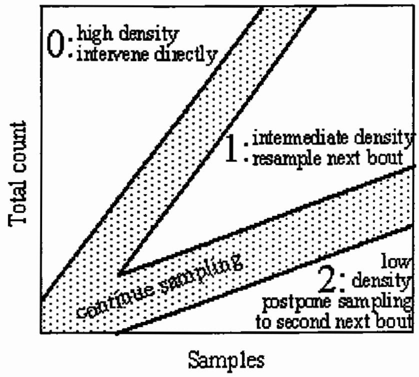

Figure 2 - Protocol for tripartite sequential classification. Leaves are inspected one by one. The cumulative number of 'positive' leaves (vertical axis) is plotted against the running total number of inspected leaves. As long as the point indicating the result of sampling is in the grey areas, sampling has to be continued. As soon as the point moves into one of the three white areas, the result of sampling is reliable enough to take a decision. The decisions are intervene (0), resample at next occasion (1), and resample at second next occasion (2).

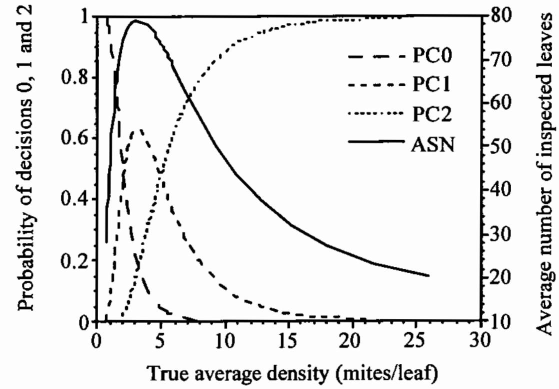

Figure 3 -Performance characteristics of a tripartite sequential classification sampling plan. Left axis: Probability of making one of three alternative Classifications: intervene (0) resample at next occasion (1), or resample at second next occasion (2). Right axis: ASN = average number of leaves inspected before taking a decision.

Next, the parameters of sampling plans constituting the monitoring protocol are varied, in order to identify the set of sampling plans that gives the most desirable performance. Thereby, the performance criteria are weighted by expert judgement.

The best monitoring protocol resulting from the iterative simulation process is tested in the field. If its favourable performance is confirmed, it can be extended to practice. The monitoring scheme developed by Nyrop *et al.* (1994) is currently recommended to and used by New York apple growers and field scouts (Anon., 1998).

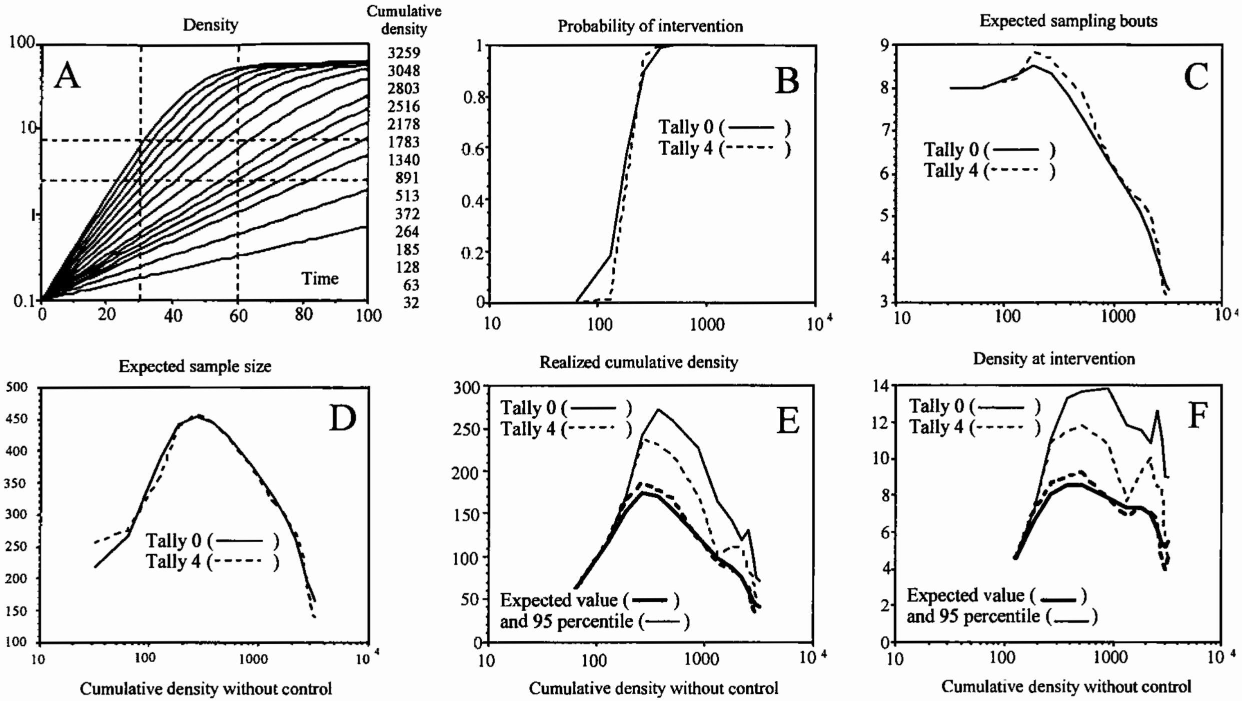

*Fig. 4: Simulated performance characteristics of two monitoring protocols, based on tripartite presence/absence classification, when monitoring mite populations over a period of 90 days. The comparison is made using logistic population trajectories with a maximum level of 50 mites/leaf and differing relative growh rates (A). Both protocols are based on critical densities of 2.5, 5 and 7.5. mites/leaf over the time periods 0-30, 31-60 and 61-90 days. Protocol 1 (**drawn lines**) is based on simple presence/absence monitoring (**tally 0**). Protocol 2 (**hatched lines**) is based on counting leaves with more than 4 mites/leaf (**tally 4**), which yields a more precise relationship between incidence and density, but is more laborious to execute in the field. The performance criteria are: (B) the probability of intervention, (C) the expected number of sampling bouts, (D) The expected total number of sample units, (E) the accumulated number of mite-days per leaf, and (F) mite density at the time of scheduled intervention. Performance criteria are quite similar for the two protocols, except for the 95th percentiles of density at intervention and cumulative mite density. These measures for 'risk' are higher for the less accurate presence/absence based monitoring method. Curves for the 95 percentiles are jagged due to the stochastic nature of the simulations.*

3.5. History of the model code and programming aspects

Versions, programming languages, computer platforms. Earlier versions of some of the software tools were developed in portable FORTRAN code, which could be compiled and executed on a range of computer platforms (including Macintosh computers, mainframes and IBM-compatible PCs). The current developments in MathCad run only under Windows95 on PCs. The existing FORTRAN code is directly available from the authors, while the newly developed MathCad electronic books will be published on the World Wide Web.

3.6. Sensitivity and uncertainty analysis

Sensitivity and uncertainty analysis, by way of simulation, is a main component of the design process (see above).

3.7. Evaluation of the model

Range of evaluation conditions. The only purely biological information that enters the model is the characterisation of dispersion among sample units. In theory, such dispersion may vary extensively depending upon local conditions, weather (rain showers), temperature, quality of the crop, pesticide applications, etc. The performance of sampling plans depends on the true distribution of the pest, and the sensitivity of the protocol to (un)expected deviations from an assumed 'nominal' dispersion model, should therefore always be investigated. The action threshold combines biological and economic information. In a strictly economic sense, the threshold should be decreased when the value of the crop is increased. Likewise, the threshold should increase when due to environmental conditions, there is less damage per unit pest.

Evaluation criteria. Performance indicators fall in two categories: (1) control quality, and (2) sampling effort. An optimal combination of performance indicators can only be determined by a personal evaluation.

Nature of evaluation. The calculation of performance indicators is strictly objective. On the contrary, the judgement of the appropriateness of optimality of a certain set of performance indicators is a strictly subjective value judgement. A bonus of this approach is that these subjective value judgements are brought to the forefront. Hence, following the theoretical design process towards sampling schemes promotes awareness of the 'true' objectives of the person developing the sampling protocol. Discussions with end-users may highlight what the end-user 'really wants'.

Conclusions of the evaluation: validity range. The framework for setting up and evaluating sampling and monitoring approaches is universally valid. For a specific pest problem, the validity range depends upon the variability of the biologically informed parameters of pest distribution and action threshold.

3.8. Usefulness of the modelling exercise

Were objectives reached? Yes. Sampling and monitoring protocols developed with the computer-methodology are included in the Cornell Pest Management Recommendations (Anon., 1998). They are used in practice and improve upon previous methodologies (e.g. Nyrop *et al.*, 1994; van der Werf *et al.*, 1997)

More appropriate approaches in retrospect. Empirical work in the field is an indispensable complement to the theoretical work, but not a substitute.

3.9. Future plans

A book and accompanying electronic book will be published in about a year after the Wageningen workshop.

3.10. Outlook

We expect demand for the book + electronic book at universities with courses in IPM throughout the world.

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VINEMILD: AN APPLICATION-ORIENTED MODEL OF *PLASMOPARA VITICOLA* EPIDEMICS ON *VITIS VINIFERA*

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1. Problem context

Since it was introduced in Europe in the last century, downy mildew caused by *Plasmopara viticola* is the major disease of grapevine under humid conditions. It affects leaves and clusters and beside destruction of the infected tissues, losses result also through a reduction of yield quality. The European cultivars being highly susceptible, favorable climatic conditions for the development of the fungus can result in a total loss of the crop. Since the discovery of the Bordeaux mixture, the disease has been therefore controlled mainly chemically in a preventive way. However, in years with unfavorable conditions, the disease may appear only late, causing no or little damage. Still, in a protective spraying scheme, the number of sprays will be the same. Considering the explosive and destructive character of the disease, the potential risk of loss resulting from an incorrect control strategy is in no relation to the gain from a reduced number of fungicide applications. Therefore, growers will only accept to reduce fungicide applications if they have the guarantee that the risk of an epidemic development of the disease is very low. There is however a pressure on growers to avoid unnecessary pesticide applications and consequently a demand for tools such as decision aids allowing to apply only necessary sprays.

Being confronted with this demand in the mid-eighties, we evaluated two models in use at that time, one in France and one in Germany, but none satisfied our requirements so that we initiated the development of a new one.

Our requirements, beside accuracy, were biological soundness, flexibility and expendability. Biological soundness was required because we were convinced that reduction of fungicides to the minimum requested a thorough understanding of the system. The development of an empirical model, which would have led to more immediate results, was therefore not taken in consideration. Flexibility and expandability were direct consequences from the fact that Swiss vineyards vary greatly due to the significant variations of the geotopographical environments: beside the use of different cultivars, planting density may vary from 4000 to 12000 plants per ha with different training and soil cultivation techniques while annual rainfall can be 500 mm in one location and 1500 mm in another.

2. History of the model

Our first idea was that if we were able to simulate the completion of the different epidemic events, we could quantify the risk of disease appearance and development. The first model was therefore a mechanistic model based on literature data mimicking the asexual life cycle of the fungus (Fig. 1A). The events taken into account were infection, sporulation and survival of the sporangia. From the weather data input, it produced a daily "risk factor" for the four events taken into account. The risk factor was expressed as a

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weight representing how often the optimal conditions necessary for the completion of the corresponding event had been fulfilled (Blaise and Gessler, 1990a).

We soon realized that if the occurrence of favorable conditions is necessary for the development of the fungus, the risk of damage caused by the disease depends mainly on

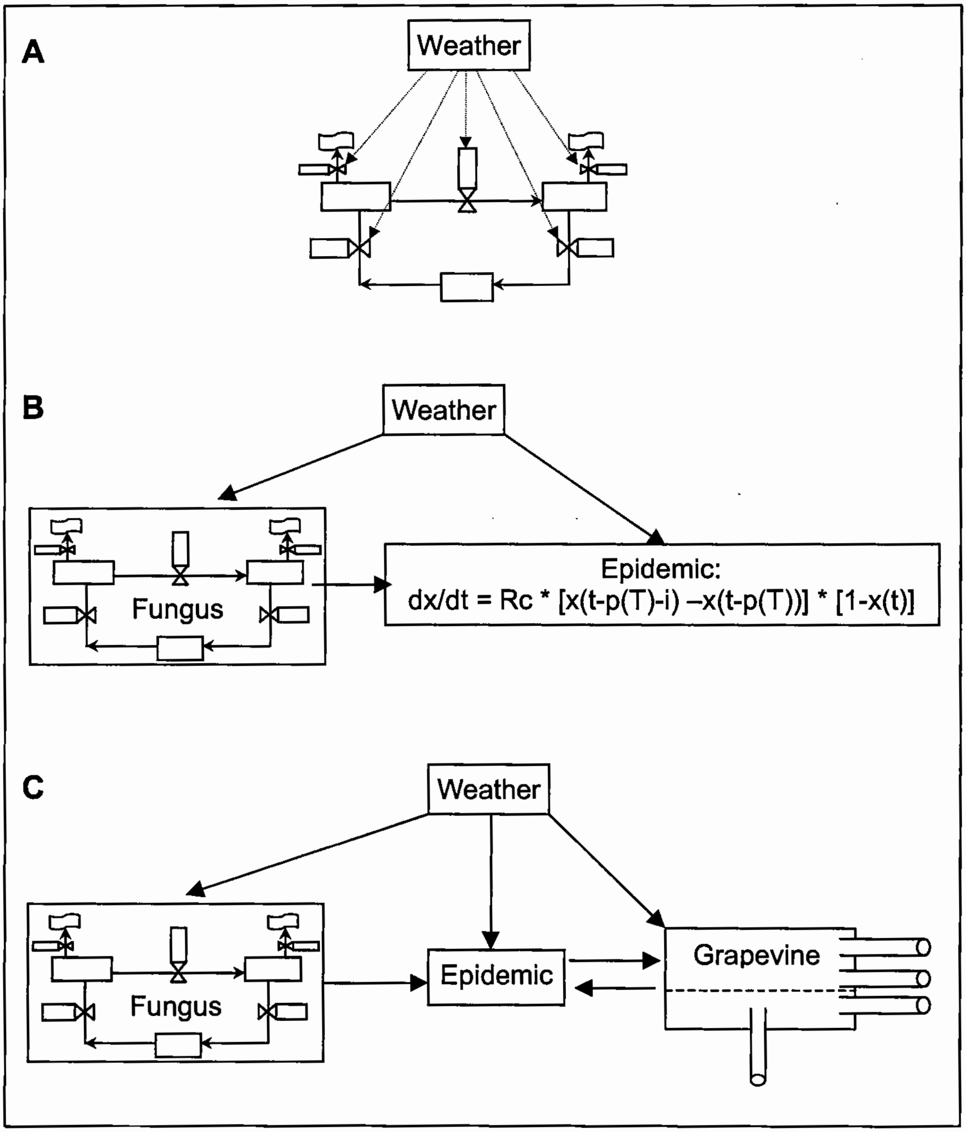

Figure 1 - Evolution of the structure of the Vinemild model. A) The original disease risk model. B) The risk model coupled with the epidemic model. C) Current version, including the grapevine growth model.

the severity level when the favorable conditions occur. The second step was therefore to simulate the actual level of disease present on the vineyard. To avoid the problems inherent to the simulation of disease dispersal, the epidemic development was simulated with an extended version of the classic progeny/parent ratio model proposed by Vanderplank, which is a synthetic, single differential equation model (Blaise and Gessler, 1992a). The output of the first model was used to drive the second (Fig. 1B). Since the disease development depends on the available host surface, we added a simple host growth model were growth is lineally proportional to day degrees (Blaise *et al.*, 1990).

At that point, the model gave satisfactory results when tested on historical data (Blaise and Gessler, 1990b), so that we considered it advanced enough to be used as a decision aid. For this purpose however, some functions for hypothesis testing had to be implemented and the interface to be adapted from a research oriented one to an user-friendlier, end-user oriented one (Blaise and Gessler, 1992b). As a result, the user interface became the largest part of the program. During this adaptation phase, it became obvious that the most important information necessary for the decision to apply a pesticide was missing: an economic injury level (EIL), i.e. we could not say if the disease level forecasted by our model was causing damages higher than the cost of a spray application.

The damages caused by downy mildew on yield quantity and quality being very different depending on the timing of the epidemic, an EIL for this disease can not be a fixed value and must be of a dynamic type. Considering the difficulty of field experiments with grapevine (perennial culture, different training and pruning techniques etc...) and the availability of a grapevine growth simulation model developed in our institute, the use of simulation to determine the EIL seemed a more feasible way.

The replacement of our simple host growth model with the physiological growth model describing assimilate partitioning within the grapevine developed by Wermelinger *et al.* (Wermelinger *et al.*, 1991) brought us a step further by allowing us to relate the disease development to the growth of the plant (Blaise *et al.*, 1996) (Fig. 1C). We are currently investigating the impact of the disease during the initial phase of berry ripening on the yield quality (Dietrich *et al.*, 1999).

3. Structure of the model

The model simulates development of downy mildew of grapevine on a homogeneous vineyard. Since the model requires input of weather data, its range of validity is theoretically limited to the area of the vineyard where these data approximate the actual weather. The time step is one hour. The three submodels Fungus, Epidemic and Grapevine are based on three different approaches. While the Fungus submodel simulates the development of the fungus in a mechanistic way, (i.e. sporulating lesions produce spores from which a part produce new lesions which may eventually produce new spores), the Epidemic submodel is a delayed diffential equation derived from a logistic growth function. They are both linked through the multiplication rate of the epidemic, which is modulated by the output of the Fungus submodel. The grapevine submodel is based on the metabolic pool approach. It is linked to the Epidemic submodel in two ways: i) the disease reduces either directly the amount of berries when infection occurs on clusters or the photosynthetically-active leaf area in the case of leaf infections and ii) the plant growth influences the available colonizable (healthy) area by the fungus, and leaves become less susceptible to infection as they grow older (ontogenic resistance).

4. The model code

The epidemic model as well as the grape growth model were developed on IBM PC-compatible computers in the Pascal programming language, which has been the standard programming language at our institution since its creation by N. Wirth. Although the graphical capabilities of the existing Pascal compilers were always limited, and the implementation of a graphical user interface required much programming work, the two models remained in Pascal until 1995. At that time, the two parts, which were distinct programs were coupled together. Since the coupling required important changes in the source code, we took this opportunity to partly rewrite and reorganize the code and to translate it into the Oberon programming language. The choice of Oberon was motivated by the fact that it is a descendant of Pascal, and therefore bears many similarities with its ancestor, and that it is an object oriented language. Moreover, we saw it as an advantage that the Oberon compiler allowed us to compile the same code for the MS-Windows and for the Apple MacIntosh platform, support for OS/2 and Unix being announced. The code of the two models were and are available on an "as is" basis.

5. Sensitivity analysis

Sensitivity analysis was done for each model separately. No sensitivity analysis was done with the combined model. Analysis was done with a given set of real weather data. Due to the simple structure of the Fungus and of the Epidemic model, the results of the sensitivity analysis were in agreement with general knowledge of the fungus. One notable exception was observed by testing the sensitivity of threshold values for the relative humidity necessary for sporulation. Although the fungus seems to be very sensitive to relative humidity in the laboratory, this parameter was quite robust in the simulation.

The complex structure of the metabolic pool made the sensitivity analysis of the grapevine submodels less straightforward than for the other submodels. We used the maximal leaf mass as an indicator for the influence of a given parameter and found not surprisingly the leaf production rate per degree-day per shoot to be the most sensitive parameter (effect 200x), while changing most other parameters had a small influence. A very critical point in the model is pruning, which influences greatly the development of secondary shoots.

6. Evaluation of the model

The fungus part of the model has been evaluated by comparing its output to field data collected in the control plot of our test vineyard during 10 years. Therefore, its validity range is restricted to this area. However, it must be noticed that it is situated in a region with the most favourable conditions for downy mildew in Switzerland. The evaluation criteria were subjective, and we only looked at the end of the season if the simulated epidemic corresponded to the field data. According to the explosive character of the disease, it was important that the simulation was not lagging behind the real epidemic and, considering the difficulty to determine precisely the actual disease level in the field, we felt that a visual agreement of both epidemic curves were sufficient. Moreover, we didn't require the simulation to be precise over a disease severity of 50-60% since such levels have no practical relevance.

Evaluation of the grapevine growth model is still going on. Up to now, we only required the model to reflect the trend, not the absolute values measured in the field. Again, the range of validity is limited to one cultivar in one specific vineyard.

7. Usefulness of the modelling exercise

Although the model has not yet left the laboratory and is still far from a decision support system, which was one of the main original objectives, it has been useful in several ways:

The requirement for calibration and control values forced us to design and conduct field experiments and to establish the relevant parameters to be measured. This resulted in a better observation of the disease and its development on the plant. It may be argued that this is not a direct benefit of modelling, still it brought us a better understanding of the disease dynamics.

The primary inoculum at the beginning of the season being unknown, our model requires input of at least one data point to be able to calibrate the disease severity level. We had therefore to study sampling schemes, so that any user would sample the disease level in an accurate way in a reasonable amount of time (Blaise *et al.*, 1993). After several experimental trials where we compared different sampling methods on mixed groups of samplers (Blaise and Gessler, 1995), we had to conclude that, at least for the cultivar Merlot which is the one we work on, asking a user to sample a low disease level with a reasonable precision is not feasible. As a consequence, we will direct our future reseach towards simulation of the sexual phase of the fungus, which is responsible for the primary inoculum.

One of the most important side effects was the recognition that, depending on the timing, even a relative high disease level not necessarily leads to a reduction of yield. This led us to distinguish between the influence of the disease on yield quantity and yield quality (Jermini *et al.*, 1994), the protection of which requires different spraying strategies.

The fact that disease not unavoidably means losses brought us to investigate the underlying phenomena. We could show that, although the plant does not seem to compensate the damage caused by the disease by increasing its photosynthetic activity, it does compensate by mobilizing carbohydrates from the roots i.e. an epidemic in one year influences also plant growth in the next year.

All in all, we still feel that the modelling approach is adequate to solve the problem of unnecessary sprays against downy mildew of grapevine. In retrospect, a better analysis of the problem and a more precise definition of the objectives, which clear milestones to be reached would probably have increased the efficiency of the exercise.

8. Future plans

The long-term objective, which was to develop a decision support system for the control of grapevine downy mildew, remains. However, at least two main parts are missing: i) a model of the sexual phase of the fungus allowing an early evaluation of the disease potential and a quantification of the primary inoculum and ii) a model of fungicide action and disappearance.

Our priority is currently on a better understanding of the impact of this disease on yield formation. On the other hand, we will invest in the next years in the modelling of the sexual phase of the pathogen. Since there is nearly no data available from the literature, we will have however first to generate these data.

Considering what remains to do and the fact that we have limited resources, we are seeking a cooperation with other groups especially in the area of crop growth modelling.

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PEACH: PEACH CROP YIELD AND TREE GROWTH SIMULATION MODEL FOR RESEARCH AND EDUCATION

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1. Purpose of the *PEACH* model

The initial purpose of the model was to develop an integrated understanding of the annual carbon budget of peach fruit growth and crop production and to simulate the potential effects of environmental factors (temperature, light, etc.), physiological processes (leaf photosynthetic rate, respiration rate, organ developmental rates) and management practices (pruning system, fruit thinning, etc.) on peach fruit size and yield. As an environmental physiologist with the responsibility of trying to develop techniques for improving the production and management efficiency of growing fruit crops, I needed to develop an integrated, quantitative understanding of fruit crop production. Crop simulation modelling appeared to be one approach to developing that understanding. There have been very few previous attempts to develop quantitative, physiologically-based simulation models of tree fruit production because most of the early crop models depended on empirically-derived, sequential harvest data of whole plants and this approach was not feasible for large, long-lived tree crops. In 1985 the project was begun by simply trying to quantify the seasonal carbon costs for growth and respiration for fruit of early and late maturing peach cultivars (DeJong *et al.*, 1987). This lead to the development of a relative growth rate model for describing the developmental growth potential of individual growth of peach fruit (DeJong and Goudriaan, 1989) and eventually to an integrated simulation model for the whole tree using a carbon supply and demand approach for accumulating and partitioning carbon on a daily basis throughout the growing season (Grossman and DeJong, 1994; DeJong and Grossman, 1994). The approach we used for simulating carbon partitioning was developed independently but is similar to the approach used by Marcelis (1994) for cucumbers.

2. Application of area of the model

After the initial development of the model it appeared to have educational value for demonstrating some of the interactions between environmental conditions, tree physiology and orchard management to students and growers. Consequently the program was rewritten into a more user-friendly "windows" environment. Since that time it has been used in undergraduate pomology classes to demonstrate the consequences of fruit thinning time and severity on crop yield and fruit size. It has also been used to demonstrate the relationship of leaf photosynthetic capacity to crop yield in peach, and the effect of cultivar harvest date on yield potential (Berman *et al.*, 1998). At the same time the model was used to re-examine and refine some of our existing concepts about how carbon is partitioned in plants. This lead to a number of additional field studies to test these hypotheses (Saenz *et al.*, 1997; DeJong and Grossman, 1996; Grossman and DeJong, 1994, 1995a, 1995b, 1995c; Berman and DeJong, 1997a, 1997b)

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3. Structure of the model

3.1. Design assumptions

PEACH is a state-variable in which fruit, leaf current-year stem, branch, trunk, and root weight are the state variables, and minimum and maximum air and soil temperatures, degree-days, and solar radiation are the driving variables. The rate variables that characterise carbohydrate supply and demand are derived from previous studies on photosynthesis, respiration, and growth potential in peach trees (DeJong and Goudriaan, 1989b; DeJong *et al.*, 1990; Grossman and DeJong, 1994a, 1994b, 1995a, 1995b). The model assumes that the trees are optimally irrigated and fertilised. Further information on the model is published in Grossman and DeJong (1994b).

3.2. Carbohydrate supply

The photosynthetic carbon assimilation submodel was modified from an annual crop growth model, SUCROS '86 (Simple and Universal Crop Growth Simulator, van Keulen *et al.*, 1982; van Kraalingen and Spitters, 1986), which explicitly simulates total daily canopy photosynthesis using Gaussian integration of the instantaneous rate of leaf photosynthesis over canopy depth and diurnal light conditions (Goudriaan, 1986; Kropff *et al.*, 1987). The assimilation module of SUCROS '86 was modified to account for the discontinuous canopy within a peach orchard using empirical data on the seasonal pattern of daily light interception within peach orchards to adjust the effective leaf area index throughout the day (DeJong and Goudriaan, 1989b). The light-saturated instantaneous photosynthetic rate (DeJong and Doyle, 1985; DeJong *et al.*, 1989) is adjusted for the effect of air temperature (Grossman, unpublished data), leaf age (DeJong and Doyle, 1984) and light exposure with canopy depth (DeJong and Doyle 1985). Leaf area index is calculated from simulated leaf weight using an experimentally determined average specific leaf area.

3.3. Carbohydrate demand

3.3.1. Maintenance respiration

Leaf maintenance respiration rates were estimated from previously determined leaf specific respiration by the mature tissue method (Amthor, 1989; Grossman and DeJong, 1994a). Stem, branch and trunk maintenance respiration rates at 20°C were estimated using the regression method:

$$RS = RM + (G * RGR)$$

where RS is the specific respiration rate (g carbohydrate g^{-1} second), RM is the maintenance respiration rate (g carbohydrate g^{-1} $second^{-1}$), G is the growth respiration coefficient (g carbohydrate g^{-1}), and RGR is the relative growth rate (g g^{-1} $second^{-1}$) (Amthor, 1989). The growth respiration coefficient, G, for peach fruits was used in the calculation (0.211 g carbohydrate g^{-1}, DeJong and Goudriaan, 1989a). Current year stems, branches and trunk specific respiration rates, RSs, and relative growth rates, RGRs, were obtained experimentally as previously described (Grossman and DeJong 1995a, 1995b). The maintenance respiration rate for roots was set to the rate determined from branches of similar size.

The model calculates temperature and maintenance respiration hourly because maintenance is sensitive to temperature, approximately doubling when the temperature increases from 20 to 30°C (Amthor, 1989; Grossman and DeJong,1994a). Hourly temperatures are calculated from air and soil minimum and maximum temperatures assuming a sinusoidal temperature pattern during the day and an exponential temperature decline during the night (van Kraalingen and Rappoldt, 1987). The daily carbohydrate cost of maintenance respiration is determined as the sum of the products of the hourly respiration rates and the dry weights for each organ type.

3.3.2. Growth

The model determines daily potential net sink strength for each organ type from experimentally determined seasonal patterns of organ growth potential (Grossman and DeJong, 1995a, 1995b). The daily conditional net sink strength, reflecting the effect of temperature on growth, is determined from the potential net sink strength and the number of degree-days accumulated on each day. The carbohydrate cost of daily growth is calculated as the sum of the carbohydrate equivalent weight of the dry weight added by growth (sink strength) and the respiratory cost of that growth:

$$CG = (CEDM * DM) + (G * DM)$$

where CG (g carbohydrate day^{-1}) is the carbohydrate cost of the dry matter added, CEDM (g carbohydrate g^{-1}) is the carbohydrate equivalent weight of the dry matter, DM (g day^{-1}) is the weight of the dry matter added, and G (g carbohydrate g^{-1}) is the growth respiration coefficient. The carbohydrate equivalent weights of leaves, current-year stems, trunk and roots were determined by pyrolysis at the Microanalytical Laboratory, Department of Chemistry, University of California, Berkeley, CA.

3.3.3. Partitioning

PEACH simulates carbohydrate partitioning on a daily basis. The model supplies carbohydrate for maintenance respiration requirements before supplying carbohydrate for growth (Crapo and Ketellapper, 1981). The carbohydrate requirements for growth are satisfied based on the conditional net sink strengths of the growing organs and their proximity to the source. Similar approaches to partitioning have been taken in modelling the growth of potatoes (Ng and Loomis, 1984), grapevines (Wermelinger *et al.*, 1991), and kiwifruit (Buwalda, 1991). All carbohydrate partitioning is characterised in terms of dry weight gain, representing the weight of structural growth and carbohydrate storage reserves.

Sink strength is calculated by grouping organs of the same type together although it is recognised that transport occurs to individual growing organs. The fruits, leaves, stems, and branches are modelled as being closest to the source, followed by the trunk, and finally the roots. Daily carbohydrate availability after maintenance respiration, and the carbohydrate cost of daily potential fruit, leaf, stem, and branch growth are calculated. Growth occurs at the potential rate if sufficient carbohydrate is available. If this is not possible, the fraction of potential growth that can be supported is calculated as the ratio of carbohydrate availability after maintenance respiration to carbohydrate requirement for potential growth. This fraction is multiplied by the daily potential growth of each organ type to determine organ growth. Trunk growth is determined by calculating the ratio of carbohydrate available after fruit, leaf, stem, and branch growth to the carbohydrate cost of daily trunk growth potential.

The daily carbon budget is balanced by assigning remaining carbohydrate to root growth. No attempt is made to account for loss of carbohydrate from the roots by fine root turnover, exudation, and increased respiration during active transport of nutrients. For this reason, although the model calculates root growth, the values should more reasonably be attributed to root function, including metabolic processes and structural and storage biomass gain.

Until the "storage day," fruits, leaves, stems, and branches are allowed to grow at their conditional growth rates unrestricted by carbohydrate availability. If the carbohydrate available from current photosynthesis is not sufficient to support this growth, it is provided by stored carbohydrate and deducted from the dry weight of the trunk and roots (Ryugo and Davis, 1959; Johnson and Lakso, 1986). During the rest of the season, the carbohydrate demand is met by daily carbon assimilation.

3.3.4. Organ growth potential

The organ growth potential is the genetically determined growth attained when an organ is grown under optimal environmental conditions in the presence of a nonlimiting supply of carbon and other resources (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975; Ho, 1984, 1988). Under these conditions, organ growth is limited only by endogenous characteristics of the organ, and is termed sink-limited growth (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975). In contrast, growth that is limited by resource supply is termed source-limited growth. The organ growth potential determines the potential net sink strength, the maximum rate at which an organ can accumulate dry matter per unit time(Warren Wilson, 1967, 1972; Wareing and Patrick, 1975; DeJong and Goudriaan, 1989a; DeJong and Grossman, 1992).

3.3.5. Potential net sink strength

The potential net sink strength is the maximum rate at which an organ can accumulate dry matter per unit time (Warren Wilson, 1967, 1972; Wareing and Patrick, 1975; DeJong and Goudriaan, 1989a; DeJong and Grossman, 1992). The potential net sink strength is the product of sink size and potential sink activity expressed as the relative growth rate:

potential net sink strength = sink size x potential sink activity

3.3.6. Potential gross sink strength

The potential gross sink strength is the sum of the potential net sink strength and the respiratory losses of the growing organ:

potential gross sink strength = potential net sink strength + growth respiration + maintenance respiration

4. Model parameterisation

The trees used in the development and testing of the model were a mid-August maturing peach cultivar *(Prunus persica* (L.) Batsch cv. Cal Red) planted in 1984 at the University of California Kearney Agricultural Center in Parlier, California. Calibration data on fruit and vegetative growth potentials were obtained on trees that had been heavily thinned and defruited at bloom, respectively (Grossman and DeJong, 1995a, 1995b)

Minimum and maximum air and soil temperatures, and solar radiation was obtained from the California Irrigation Management Information System (CIMIS) weather station located at the Kearney Agricultural Center. Degree-days were calculated using the single sine horizontal cut-off method, with critical temperatures of 7 and 35°C (Zalom *et al.*, 1983; DeJong and Goudriaan, 1989a).

5. History of the model code

The modelling effort began using CSMP when the fruit growth "demand" submodel was being developed in conjunction with parts of the Wageningen SUCROS model that were revised for simulating carbon assimilation in tree crops. When the comprehensive model was developed, it was first written in FORTRAN, and subsequently in VISUAL BASIC for the "Windows" environment. The current system requirements are: Windows 3.1 or greater, DOS 5.0 or greater, processor with 4 megabytes of RAM (preferably a 486 DX with 8 megabytes of RAM), 10 Megabytes of free hard disk space and a VGA (or better) monitor. (The program, with source code, is available for a small fee, by contacting tmdejong@ucdavis.edu)

6. Sensitivity and uncertainty analysis and evaluation of the model

Because of the complexity of the model and the system that is being modelled there has been no systematic attempt to analyse the sensitivity or uncertainly of the model. During the initial development of the model, the model's ability to predict various reproductive and vegetative rowth parameters was tested and it was found to be relatively successful (Grossman and DeJong, 1994). Subsequently, the model has been used to predict the effect of environment on growth, respiration and yield of peach trees growing in different locations or with different maximum leaf photosynthetic capacities (DeJong *et al.*, 1996). Since it is impossible to actually do these experiments in the field, it is impossible to empirically test the modelled results. However, in every case the results subjectively appeared to be reasonable. Recently the model was used to predict the differences in potential yield of seven clingstone peach cultivars and the results corresponded to practical experience in the field (Berman *et al.*, 1998). At this stage in the development of the model, I have become convinced that, for a model for this type, the precision of the model for quantitative prediction is not as important as the accuracy of the concepts incorporated in the model. Since the empirical precision and variability of the input variables are always major limitations to obtaining precise results the model will probably never be useful for precise quantitative predictions. However, the model has already proved its value in forcing the development of a unified concept of tree growth and carbon partitioning and providing a mechanism to qualitatively test the influence of various physiological, environmental and management factors on tree performance.

7. Future plans

The model, as it is currently written, is also clearly deficient in its handling of growth and storage functions in the root. It currently only partitions carbon for growth and storage to the root after the above-ground needs of the tree are met. Experiments are being currently conducting to better understand the control of carbon partitioning to the root. The model will be modified to more accurately accommodate root growth when a mechanism for doing so is identified.

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MODELLING MITE DYNAMICS ON APPLE TREES IN EASTERN NORTH AMERICA

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Abstract

The model described in this paper simulates seasonal dynamics of *Panonychus ulmi* and the phytoseiid predator *Typhlodromus pyri* on apple trees in Eastern North America. It was originally developed to understand the effect of weather, predation, cannibalism, alternate food for the predator, and uneven mite distribution among leaves on mite dynamics. Overwintering mortality of *T. pyri*, cannibalism, and the uneven distribution of predators and prey among leaves were found to stabilize the predator/prey interaction. The availability of alternate foods for *T. pyri* minimizes the likelihood of predator extinction at the whole-tree level, as is seen in orchards. The model was used to guide tactics of mite management. Early simulations involving optimal times to apply miticides indicated that if there are high densities of *P. ulmi* winter eggs, and mite counts are not done until June, there would be significant damage before the mites are noticed and treatments applied. This insight was relayed to growers who now monitor *P. ulmi* eggs in April and apply treatments if needed to prevent early-season damage. Growers also accepted simulations which suggested that post blossom applications of the miticide Apollo would be more effective than applications made before bloom. Other simulations validated the empirical decision rule that biological control is effective with a *T. pyri*: *P. ulmi* ratio of at least 1:10. The model also indicated the value of introducing *T. pyri* into orchards early in the summer to maximize speed of colonization and biological control. Finally, the model has served to guide research. Discrepancies between simulated and observed densities of mites were usually due to factors not yet included in the model such as aerial dispersal of adult *P. ulmi*, leaf quality, sublethal effects of pesticides on *T. pyri*, feeding competition among predators, and availability of alternate food for *T. pyri*. Considerable research has been done on these factors.

1. Introduction

This model simulates the seasonal dynamics of populations of the European red mite *Panonychus ulmi* Koch and the predatory phytoseiid mite *Typhlodromus pyri* Scheuten on

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apple trees in eastern North America, especially Upstate New York, USA and Nova Scotia, Canada. In the 1980's, three different *P. ulmi* models were developed independently by mite researchers: Dan Johnson in British Columbia, Mike Hardman in Nova Scotia and Jan Nyrop in New York. Each wanted to study system behaviour, i.e. to understand the relative importance of factors such as weather, predation, cannibalism, alternative food for the predator, prey dispersal, and mite distribution among leaves on mite dynamics. Starting in 1985 Hardman began blending these models. Two new applications were found for the model: refining tactics of mite management and guidance in setting research priorities.

2. Applications of the model

2.1. Application in guiding management

2.1.1. 1989

Often models point out the obvious, which implies developing a model is a waste of time- we should spend more time thinking. But researchers, and practitioners alike, sometimes miss the obvious and models have therefore been helpful. The obvious arose from simulations with a *P. ulmi*/miticide model which suggested that if there are high counts of *P. ulmi* winter eggs and the mite counts are not done until June, there could be economically significant damage before the mites are noticed and treatments applied (Hardman, 1989). The obvious was told to the provincial entomologist.who alerted growers and a pest monitoring company. As a result many growers started applying petroleum oil to prevent early-season damage and *P. ulmi* winter eggs are now monitored in many orchards (Rogers, 1992).

2.1.2. 1990-1991

The model suggested post blossom applications of the miticide Apollo would be more effective in controlling *P. ulmi* and avoiding resurgence than application after bloom. This was for three reasons: 1) leaf surfaces expand less after bloom than before bloom (less growth dilution); 2) more vulnerable life stages are present after bloom; and 3) there is less time for mite populations to recover from treatment. Another insight was the importance in having the predator mite *T. pyri* present in an orchard: even an extremely low density would be sufficient to prevent a population of *P. ulmi* from resurging after treatment. These insights presented at the 1990 annual meeting of Nova Scotia Fruitgrowers Association were widely accepted by growers and extension personnel. As a result, Apollo use in Nova Scotia is nearly always postbloom and growers became more motivated to obtain and conserve *T. pyri*.

2.1.3. 1992

Simulations with the 1992 version of the model indicated that the decision rule for expecting effective biological control with a predator prey ratio of at least 1:10 (Nyrop, 1986) was sound (Van der Werf *et al.*, 1994).

2.1.3. 1993

Observations of Dutch entomologists and output from simulations using the mite model, convinced Hardman of the value of introducing *T. pyri* into orchards early in the summer to maximize speed of colonization and biological control. Observations in 1996 have confirmed model findings: colonization from dormant prunings placed on trees in March-April is at least one year faster than with summer prunings placed on trees in August.

2.2. Application in understanding system dynamics and guiding research (1991-1992)

Cannibalism, the ability of *T. pyri* to survive on alternate foods and the uneven distribution of predators and prey among leaves were seen to be stabilizing factors in interactions between *T. pyri* and *P. ulmi*. Winter survival of *T. pyri* was also considered (Walde *et al.,* 1992). At this point publication of output from the model had two consequences: 1) it spurred researchers to get new data to fill in crucial gaps in knowledge, and 2) it encouraged further development and applications of the model.

The model has been a valuable tool to guide research. It revealed gaps in knowledge which warranted further study including factors that were not known to be so important. Often invalidations, discrepancies between simulated mite densities and those observed in orchards, played an important role in this learning process. Invalidations were usually due to external factors not yet included in the model such as those listed in Table 1. Considerable research has now been done on these factors.

Table 1 - Recent studies that were stimulated by the mite model

Type of data	References
Biological residual life of Apollo on apple leaves	Marshall *et al.* (1994)
Nitrogen content of apple leaves	Hardman *et al.* (1998)
More accurate estimation of *T. pyri* density	Hardman *et al.* (1997)
T. pyri density and reduced rate of feeding	Wei (1996)
Interactions between predators Z. mali and *T. pyri*	Magagula (1993), Wei (1996)
Overwintering survival of *T. pyri*	Moreau (1996), Hardman *et al.* (1997), Nyrop *et al.* (1998)
Pollen availability and reduced feeding of *T. pyri* on *P. ulmi*	Wei and Walde (1997)
Sublethal effects of pyrethroids on *T. pyri* predation and oviposition	Moreau and Hardman (unpub. data)
P. ulmi density and residence time of *T. pyri* on leaves	Lawson and Walde (1993)
Aerial dispersal of *P. ulmi* and *T. pyri*	Lawson *et al.* (1996)
Time series of densities of *P. ulmi*, *T. pyri* and other mites	Walde *et al.* (1997), Moreau and Hardman (unpub. data)
Sampling mites and assessing risk of economic losses	Rogers (1992), Nyrop *et al.* (1994), van der Werf *et al.* (1994)

3. Description of the model

3.1. Spatial, temporal and geographic limits of the system

The model is deterministic and is considered applicable to a single tree or to a uniform block of trees. However, the effects of spatial variability on predation are taken into account by simulating events on different classes of leaves using probability models as described below. Simulations may cover dynamics from early March, when trees are still dormant, to leaf fall in October, though shorter intervals (e.g. summer months) may be chosen. Multi-year simulations may be run by using end of season mite densities from one year as input for initial mite densities in the following year after applying an arbitrary value for overwintering survival. This approach was used in Walde *et al.* (1992).

There are definite geographic limits to the model. Firstly, populations of both species of mites in one region of the world differ in temperature responses from populations in other regions. This is true for *P. ulmi* from the cool, moist climate of Nova Scotia in Eastern Canada versus *P. ulmi* from the warm, dry Okanogan Valley of British Columbia in Western Canada. However, New York and Nova Scotian *P. ulmi* seem to have similar temperature responses. With *T. pyri* there are contrasts between populations in Nova Scotia and those in northwestern Europe (Hardman and Rogers, 1991). Secondly a host of site-specific abiotic and biotic factors affect dynamics of *P. ulmi* and *T. pyri* on apple trees. Several of these factors must be measured and included as external functions used as input for the model. Abiotic factors include: rainfall (mm/d), daily maximum and minimum temperatures (°C), and day length (h), which may also be calculated from latitude. Pesticide applications must also be accounted for. Necessary data include dates of application (up to 5), initial concentration of pesticide (ppm), toxicity to each of the life stages of *P. ulmi* and *T. pyri*, and rate of decrease in toxicity due to weathering and decreasing biological availability. Additionally there are parameters for the degree of suppression of predator feeding and oviposition caused by contact with the pesticide. Biotic input data include initial densities and age structures of populations of *P. ulmi* and *T. pyri;* densities of adults and older nymphs of *Zetzellia mali* which feed on eggs of *P. ulmi* and *T. pyri*; immigration of adult female *P. ulmi* ; mortality of *P. ulmi* due to insect predators; pollen availability (alternative food for *T. pyri*); and nitrogen content of apple leaves, which affects fecundity of *P. ulmi.*

3.2. Simulating age structure, development, mortality and reproduction

The method to simulate age structure and development, taken from Johnson and Wellington (1984), resembles the boxcar train with no dispersion as decribed by Goudriaan and van Roermund (1989). Populations of *P. ulmi* and *T. pyri* consist of physiological age classes of individuals, grouped into the life stages eggs, larvae, protonymphs, deutonymphs, young females, ovipositing females and males. The stage-specific rate of development of *P. ulmi* is solely a function of hourly temperature. The rate of development of *T. pyri* is affected by temperature and prey ingestion. Mortality factors for the various life stages of *P. ulmi* include low temperatures, old age, rainfall, crowding, predation by *T. pyri, Z. mali* and insect predators, and pesticides. Mortality factors for *T. pyri* include ageing, starvation, cannibalism (adult females and deutonymphs sometimes feed on larvae and protonymphs), predation by *Z. mali* on eggs, and pesticides. Reproductive rates of female *P. ulmi* depend upon temperature and physiological age of the adults, crowding, leaf injury (which increases with accumulation of mite-days per leaf), and nitrogen content of leaves. Nitrogen content is computed as a function of Julian date. As temperatures decrease and day length shortens in late summer, an increasing proportion of *P. ulmi* nymphs mature into females that lay diapausing eggs which will not hatch until the following spring. Leaf injury, as indicated by an accumulation of *P. ulmi* mite-days, also increases the proportion of females that lay diapausing eggs. For *T. pyri* the age-specific rate of oviposition is a function of temperature, the per capita feeding rate, and any suppression due to direct contact with pesticide or with pesticide residues. Short day length induces reproductive diapause where a decreasing proportion of *T. pyri* lay eggs.

3.3. Effects of alternate sources of food on predation and mite dynamics

Alternate foods for *T. pyri* include pollen, the apple rust mite *Aculus schlechtendali*, the two-spotted spider mite *Tetranychus urticae* Koch and any other edible mites besides *P. ulmi*. If *T. urticae* are present their sampled densities may be interpolated to provide estimates of daily densities which represent another food source for *T. pyri*. The model treats motile life stages of *T. urticae* as having the same food value and catchability for *T. pyri* as equivalent stages of *P. ulmi*. However, *T. urticae* eggs are edible, whereas those of *P. ulmi* are not. The availability of *T. urticae* enhances development, survival and reproductive rates for *T. pyri* and lessens the intensity of predation on *P. ulmi*. Pollen is particularly difficult to include in the functional response equation because its absolute quantity is not known in field studies. Yet, its effect is considered of major importance. A full pollen supply is considered equivalent to providing each nymph and adult *T. pyri* on a leaf with a fully satiating diet of *P. ulmi*. For an adult female this would be equivalent to ingesting 2.5 adult female *P. ulmi* or 10 *P. ulmi* larvae per day at 20°C. In the model, pollen supply declines linearly from a full supply in early summer to a small supply (10% of initial value) by September, as was observed in German vineyards (Eichorn and Hoos, 1990).

3.4. Simulating predation and cannibalism

Predation is calculated for mites on two classes of leaves where class is defined according to occupancy by *T. pyri* and *P. ulmi* (see below). The motivational (hunger) status of predators is not simulated in this model. Single prey functional responses were fitted with the integrated form (Royama, 1971) of the rate equation:

$$dN/dt = b\,(1 - \exp(-a\,N\,/\,b))$$

where b = maximum predator feeding rate, a = initial slope of the functional response, N is the density of prey, aN is prey supply, and b is predator demand. The supply/demand ratio $R = aN/b$ measures in how far a 'supply' of a prey stage (aN, considering prey density and catchability) meets the 'demand' of the predator (b; based on predator voracity and handling speed). The parameters a and b are different for each prey-predator combination. When multiple prey are present, the rate at which a prey is eaten is:

$$E_{kj} = b_{kj} * R_{kj} / R_{.j} * (1 - e^{-R_{.j}}) * A_l * P$$

where E_{kj} is the number of prey of life stage k that are eaten per unit time by a predator of life stage j, b_{kj} is predator demand (maximum potential kills of prey of class k per unit time), $(1 - e^{-R_j})$ is fulfilment of predator stage j's demand by all classes of prey, R_j is the sum of all supply/demand ratios for predator stage j, R_{kj}/R_j is the proportion of demand met for predator stage j that comes from eating prey of class k, A_1 is a proportion that quantifies the effect of pollen feeding on mite feeding and P is a proportion that represents the reduction in feeding due to a pesticide application. The model in its standard form assumes that *P. ulmi* has priority over cannibalism when meeting the demand of *T. pyri*. The equation for cannibalism is:

$$E_{kj} = b_{kj} * R_{kj}/R_j * (1 - e^{-R_j}) * A_1 * A_2$$

where k indicates *T. pyri* larvae or protonymphs and where A_1 and A_2 are correction factors accounting for the fraction of demand met by pollen and *P. ulmi* respectively.

3.5. Spatial considerations and predation

Based on a large data set (Nyrop, 1988), probability distributions describing the allocation of mites among leaves are used to calculate the coincidence of predators and prey on leaves. Six classes of leaves are distinguished (Table 2). Average densities of mites on different classes of leaves are reset every day. Class frequencies are based on negative binomial distributions. The model assumes statistical independence of the distributions of *P. ulmi* and *T. pyri*, so that the proportion of leaves occupied by both species is the product of the proportions occupied by either alone (Nyrop, 1988). For both species, a negative binomial distribution is used with the variance equal to a power function of the mean (Walde *et al.*, 1992).

Table 2 - Classes of leaves as defined by mite occupancy

	Number on leaf		
Leaf class	P. ulmi	T. pyri	Diet composition
1	0	0	-
2	0	=1	Alternate food
3	0	>1	Alternate food, cannibalism
4	≥1	0	-
5	≥1	=1	*P. ulmi*, alternate food
6	≥1	>1	*P. ulmi*, alternate food, cannibalism

3.6. Simulating effects of pesticides

The model simulates effects of miticides such as clofentezine and pyrethroid insecticides such as cypermethrin. Selective miticides cause high mortality of *P. ulmi* but not *T. pyri*. Pyrethroid insecticides do not cause mortality among *P. ulmi* or pyrethroid-resistant strains of *T. pyri* but there are sublethal effects: for a period of time, rates of feeding and oviposition of the predator are suppressed. Residues of these pesticides decline exponentially. Half-lives of residues can be reliably estimated based on determinations of biological activity of residues on field collected leaves sampled at different intervals after an application (e.g. Marshall *et al.*, 1994). Dilution of pesticide residues due to growth and expansion of leaves is also taken into account. Leaf area is a logistic function of physiological time.

4. Availability of the model

In the course of 1998, the model, implemented as an executable FORTRAN computer program, will be made available on the internet at:

http://res.agr.ca/kentville/personal/hardmanm.htm.

The program is structured so that the main program largely deals with input/output and makes calls to biologically meaningful modules, the subroutines. A technical report that includes the FORTRAN code and data files is under development and will be published on the internet when finished. This report shows how to use the program and indicates the data sources for the assumptions used in the model.

5. Evaluation of the model

So far, all evaluations of the model have been at the 'whole system level' where simulated densities of mites were compared with densities observed at 7-14 day intervals on apple trees in orchards in Nova Scotia and New York. Observed means per leaf were based on samples of 10-25 leaves per tree from 4-10 trees per treatment. Comparisons were based on the researcher's subjective judgement of agreement or discrepancy between graphs of the two time series. Thus evaluations of the model were both preliminary and partial. Invalidations sometimes occurred, especially where external factors not yet included in the model had a strong effect on mite dynamics. These factors included aerial dispersal of adult *P. ulmi*, leaf quality, sublethal effects of pesticides on *T. pyri* and availability of alternate food for *T. pyri*. One by one effects of these factors were incorporated in the model and, where possible, measurements taken of the external factors. But much data still has to be taken.And even with these additions a problem remains. Due to these degrees of freedom, the model can be made fit as well as one wants to, except when all relevant external functions have been measured in validation experiments, but this is rarely the case. Therefore it remains uncertain whether similarity of model results and observations is due to calibration or to structural correctness of the assumptions, processes and external influences functioning in the simulation. For this reason it is also difficult to delimit situations where the model will or will not be usable. The model may be used to answer many questions but the reliability of the results is unclear.

6. Usefulness of the modelling exercise

The objectives of modelling- to gain a better understanding of mite dynamics, to refine tactics of mite management and to help guide research- were met. The model was particularly useful in raising the consciousness of researchers: first, by pointing out the 'obvious' as in the miticide studies, and second, by highlighting gaps in knowledge which needed further study, including factors that were not known to be so important. Often discrepancies between simulated mite densities and those observed in orchards played an important role in this learning process. Invalidations led to literature searches, data gathering and refinements to the model, then to new evaluations in an ongoing cycle. Was usage of the model cost effective? The answer is yes. Insights from the model led to changed practices of mite management in Nova Scotia including increased sampling, greater use of dormant (petroleum) oil and refinements in use of Apollo. It is likely that the economic benefits from these practices alone (which are ongoing) may pay for the modelling effort, expensive as it may seem. Would other approaches have been sound alternatives for simulation? Probably not. We don't know of other approaches that complement experimentation so well and allow one to explore the effects of numerous factors on mite dynamics. We believe that simulation and experimentation should proceed in parallel.

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MODELLING PEACH RESPONSE TO CHEMICAL THINNING

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1. Purpose of the model

The primary purpose was to characterize the physiological state of peach trees, thus enabling peach growers to forecast the trees' response to chemical thinning. Thinning of the reproductive organs is an essential practice to ensure commercial value of the crop in deciduous fruit orchards. Hand thinning is compulsory in a peach orchard, since the peach trees' response to chemicals is still unpredictable. Chemical thinning, as customary in other deciduous fruit trees, should consume much less time and work. The system during the model development consisted of potted peach plants, cultivar AprilGlo (188), grown in a greenhouse in Volcani Center, ARO, Bet Dagan, Israel. The expected system of model application will be any commercial peach orchard.

2. Application area of the model

The model is to be used both to study the system behavior, for early detection of developing stress conditions in the orchard, and as a decision support system, enabling deciduous fruit growers to adapt a chemical treatment to the physiological conditions of their trees, in order to achieve a required thinning response.

3. Structure of the model

Being part of a Ph.D. research study, the model was restricted to the reproductive organs of potted plants, cultivar AprilGlo, during the reproductive period, for three consecutive years. The adopted concepts were the dependence of several plant responses to stress conditions, including physical and biochemical measurable responses, and the stress-like action of chemical thinning treatments like urea spray.

4. History of the model code

The model was developed on an IBM-PC compatible, using statistical (SAS) and worksheet (Borland's QuattroPro for Windows) programs.

5. Programming aspects

The model core might be represented as a multivariate linear regression, and is thus usable on any hardware as sophisticated as a portable calculator.

6. Sensitivity and uncertainty analysis

The model was built separately on three growing seasons - 1995/96, 1996/97 and 1997/98, and the parameters off all three versions were computed by the way of factor analysis and multivariate linear regression. Sensitivity analysis was conducted, as usual, by introducing "outliners" predictors and checking their influence on the model's parameters.

7. Evaluation of the model

All three versions of the model were checked on the other seasons' data. The evaluation was made under semi-natural conditions, with identical growing conditions for all plants during the experiment season (budbreak to fruit ripening) and differential irrigation regimes after fruit picking. The evaluation criteria were the correlation between the model's predicted variable (fruit load at the end of the treatment-induced fruitlets drop) and the observed results. The model was valuable when applied on potted plants of the cultivar AprilGlo, but the parameters were unfit for application on other cultivars, or in commercial orchards.

8. Usefulness of the modelling exercise

The main purpose of the model, enabling the peach grower to forecast the trees' response to chemical thinning, has not been achieved yet, and we plan on three more seasons to enlarge the model to all cultivars and agrotechnical conditions. But the basic conception of this model, that the characterisation of the trees physiological condition enables us to forecast its reactions, is already more promising than the conventional researches on peach chemical thinning. A possible improvement of the model, in the same conception, could be a more appropriate chose of the biochemical or physical variables to characterise the tree's condition.

9. Future plans

Our plans are mainly in three directions; one is the research of more appropriate indicators of the plant physiological status, and more practical and accurate methods of measuring those indicators; the other one is the determination of adequate parameters for the application of the model to all other peach cultivars, in commercial orchards under any agrotechnical regime; the last field to develop will be the sampling method necessary to characterise a whole orchard without analysing each individual tree.

10. Outlook

In our opinion, a ready-to-use version of the model should be available in three more years, providing the peach grower a reliable tool for improving the financial compensation of his efforts.

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QUALITY OF MODELLING IN FRUIT RESEARCH AND ORCHARD MANAGEMENT: REPORT OF A DISCUSSION

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Abstract

A discussion was organized on the topic of Critical Assessment of Modelling Approaches in Integrated Crop Management. Process-based models, used as research instruments, were discussed separately from Decision Support Systems, which are basically used as media for information exchange with growers and agricultural consultants. With respect to process-based models, the discussion centered on social aspects (team work, reward systems and return on investment), project management (when is a model finished?), and model presentation. With respect to Decision Support Systems, the discussion focused on how DSS are used (for learning or for decision support *sec*), communication with end-users, and on specificity, validity and adoption of DSS. Some of the main points brought forward in this discussion are reviewed in this report.

1. Introduction

During the Conference on Computer Modelling in Fruit Research and Orchard Management, 28-31 July 1998 in Wageningen, a discussion was organized on the topic of *Critical Assessment of Modelling Approaches in Integrated Crop Management.* The purpose of the discussion was to exchange ideas about aspects of modelling and software development in integrated crop management that get less attention in published work, yet are decisive for the success of the work. Distinction was made between 'research models' and 'decision support systems'. Research models comprise a group of models based on eco-physiological processes of pest and/or crop dynamics developed and used by applied researchers. Decision support systems involve computer-based technology for orchard management, using more or less detailed representation of biology and management, used by farmers or agricultural consultants. The discussion focused on
(*process-based models*:)
social aspects of modelling; team work, reward systems and return on investment;
when is a model finished; how to present models;
(*Decision Support Systems*:)
what is supported; decision making or learning; communication: involving the end-user; specificity, validity and adoption of DSS.

The items that were discussed correspond partly with the discussion items in Van der Werf *et al.* (1999a). Some items listed in that paper were discussed very little, while other were discussed more. This was largely determined by the interest of the participants in the discussion. The bottom line in the discussion was: *How can we achieve the proximate and* *ultimate goals of our modelling efforts effectively and successfully?* Proximate goals are those goals that are listed in the documents that describe our projects, while ultimate goals relate to the impact on society and the personal careers of the model makers. This paper summarizes the discussion, including some thoughts from the papers submitted to the workshop (Blaise *et al.*, Boshuizen and van der Maas; DeJong; Graf *et al.;* Groot; Hardman *et al.*; Mols and Boers; Szafran *et al.*; van der Werf *et al.,* 1999b*;* all in this volume) and from other literature sources.

2. Process-based models

2.1. Social aspects of modelling; team work, reward systems and return on investment

A concern of researchers is whether their investments in process-based modelling will be duly rewarded. Will the investment in modelling yield publications and further career development? Some 'threats' are:

- Systems-oriented studies, involving modelling, are multidisciplinary team work with an integrative and applied focus. Results of such studies may be difficult to get published in scientific journals which favour a disciplinary focus and an analytic approach;
- It is difficult to earn personal credit from team work;
- Modelling is time-consuming, model validation may be an iterative process taking many seasons (*cf.* Fig. 2 in van der Werf *et al.,* 1999a), while models which are not validated successfully are difficult to publish. Experimental studies which are required for model validation may be labour intensive (season long monitoring) but scientifically unrewarding.
- Agricultural Research Institutions around the world are focusing more on results that may be 'sold' on a research market. Long term multi-year research programs, aimed at profound systems understanding and public interest, need to fight for their place in the institute budgets.

These threats may be counterbalanced by positive developments. In some countries (e.g. New Zealand), the reward system in Agricultural Research Institutions has been adapted to encourage team work. Researchers using modelling approaches may team up nationally or internationally, helping each other be productive. They may also form (inter)national consortia to conduct validation trials, e.g. through Research Programs of the European Union.

Two contrasting solutions were offered for the problem of maximizing return on investment:

- stick with a model for a long time, and adjust experimentation to it, even if the experimental work would be temporarily out of phase with other ongoing work and shifts of interest (Hardman *et al.*, this volume). It will pay off in the end;
- use a model only for a specific question; when done, discard it and build a new model as need arises.

It is clear that the latter approach would work better for simple, concise models, towards the theoretical and conceptual end of the spectrum, than for the elaborate and detailed models, which are common in the agricultural sciences (this workshop), and which are considered useful because they take relevant details into account.

2.2. When is a model finished?

In textbooks on systems analysis and modelling (e.g. Leffelaar, 1993) prospective modellers are urged to carefully consider the objectives of the study, as these determine the required accuracy of representation of biological phenomena. Although in scientific reports the objectives of modelling may be stated, the implications for the required accuracy and precision of model results are usually not addressed. This applies also applies to the process-based model accounts in this volume. Although correspondence between observed results and simulations is always an issue that receives attention, a quantitation of the deviations, and a setting of upper limits for errors in relation to model application, is seldom if ever practiced. Such a technical engineering approach is apparently not effective in biological sciences in which variability and stochasticity play a prominent role.

Sinclair and Seligman (1996) emphasise the role of (crop) models as heuristic tools to aid our interpretation of reality. According to their interpretation of the role of models in science, models provide a framework in which to explore crop response to environmental, structural, functional, or parameter change. In addition, models may allow the discovery of faulty reasoning or interesting implications about a crop. With respect to criteria to judge the acceptability of a model, they conclude that these are rather ambiguous in a research setting. High predictive capability may be less important than the need to identify weaknesses in the conceptualisation of biological reality. ‘Validation’ in a research setting is more likely to be concerned with trends and patterns of model output compared to reality than with precise quantitative predictions. Clear support for this viewpoint is found in the contributions by DeJong (this volume) and Hardman *et al.* (this volume). DeJong states that ‘..the precision of the model for quantitative prediction is not as important as the accuracy of the concepts incorporated in the model...’ and ‘...the model will probably never be useful for precise quantitative predictions. However, the model has already proved its value in forcing the development of a unified concept of tree growth... and providing a mechanism to qualitatively test the influence of various (...) factors on tree performance.’. Hardman *et al.* add that this type of usage of their model was cost-effective.

During the discussion, the idea was expressed that modelling is a slow process, the major reason being the difficulty to get models 'right' with respect to representation of the field situation. A model could never be called finished, however, when the purpose would be to describe a system in all its detail and possible intricacies. A model should therefore never be an end in itself, and clear statements of project aims, and the role of models in achieving it, are indispensable to determine when the goals have been achieved. Models become difficult to validate when numerous site-specific conditions affect system behaviour, as in complex multi predator-multi prey interactions. Validations are also difficult to present clearly and convincingly in research papers because the modelled systems are often complex and many factors are involved. And there is always the risk that a model gives the right result for the wrong reason. This adds to the problem of getting model-related papers published. To reduce the risk of right results for the wrong reasons, it is important to check and publish intermediate model results.

As suggested at the outset, it is probably not practical in the biological sciences to decide when a model is finished on the basis of monitoring the actual 'goodness of fit' in comparison to a target 'goodness of fit' that is defined at the start of a project. Another criterion, used more often perhaps than any other, is that the model is considered 'finished' when the project money has ran out. A meaningful and publishable contribution to the literature would be defined as the amount of work that a competent and diligent researcher would be able to achieve in a time frame of two to three years, if it involves field work. Another, only vaguely defined, criterion would be that the model or the insights gained from it are 'new' enough to be published. The two latter criteria would suggest publications of models, whether the model is validated or not. Another suggestion was made to guide further model development by the objective to expand the domain in which the model is evaluated, rather than improving the goodness of fit.

2.3. How to present models

Even within a small group of competent researchers, all working on models in fruit research and orchard management, a Babylonic confusion of speach is not easily avoided. There are so many schools of thought regarding ecological modelling, there are so many possible objectives, and there are so many different mathematical approaches to building models. Within a certain school, objectives, concepts and mathematical approaches may be so well accepted and shared, that they go without saying; however, when presentations are given to outsiders, these objectives, concepts and approaches must be explicitly stated. It was felt that it would be useful to provide a checklist on how to present models, in order to help researchers to make themselves understood when presenting models.

Two such lists are given in Appendices 1 and 2. The first list focuses on the mathematical content and technical aspects of models. The second list is more geared towards function and presentation. A third set of check lists, focusing on purpose, function and process, is provided by the inventories that were produced for the workshop (Rossing *et al.*, this volume). There is not a single recipe for giving a clear presentation on models to audiences. However, if one keeps the audience in mind, works from clearly stated objectives, and uses the four checklists that are provided, the level of understanding should not be bad. Some research groups have developed their own media for documenting modeling concepts, data and model code. The C.T. de Wit Research School of Production Eoclogy at Wageningen Agricultural University, has developed a culture of documenting concepts, data and model code in the form of books (e.g. the old Pudoc Simulation Monographs series and the current series on Current Issues in Production Ecology by Kluwer) and internal reports (Quantitative Applications in Systems Analysis). However, the scientific appreciation for such publications is unfortunately (and unjustifiably) not as high as of that of refereed journal publications, and it is also felt that 'nobody reads the code' (DeJong). Therefore, concepts and conclusions should be emphasized, rather than code and technique. Nevertheless, internal and external documents explaining the 'nuts and bolts' of the modelling are highly useful and indispensable resources furthering the development of systems approaches in agricultural science.

3. Decision support systems

3.1. What is supported: decision making or learning?

One important lesson from the past is the realisation that DSS may be used by farmers and consultants as learning tools, rather than as decision support aids. The consequence is that users stop using the decision support system as soon as they have learned what they needed to know. A well known example is the Dutch EPIPRE system for advise on disease and pest control in winter wheat (Zadoks, 1989). Growers were typically involved in EPIPRE for about three seasons. In that period, they learned to recognize the diseases, and they figured out what 'rules' were used by the big computer in Wageningen that provided the control advise. After quitting the system, they continued to do observations, and made interpretations on their own. EPIPRE had succeeded as an instrument for learning and behavioural change; yet, it made itself redundant in the process. As a commercial undertaking, in which direction EPIPRE gradually developed, it became a failure. Newer approaches in decision support take the lesson to heart and provide glasshouse horticulturists with ever changing actual data, e.g. on climate conditions, disease pressure, prices and yield data of colleague (competitor) growers in the neighbourhood (Leeuwis, 1993), such that the system keeps generating new opportunities for comparison and learning. It was noted that databases of registration material may have a greater lasting value than specific decision support models, as the data can be used for learning on new problems, while specific models tend to deal with yesterdays learning needs.

Decision support systems are especially useful for growers if they give information on variables that are difficult to observe directly, e.g. soil water status (Boshuizen and van der Maas, this volume). One and the same decision support system may be used in different ways by different users. Rajotte noted that a decision support system that was used 'quick in and quick out' by experienced growers in Pennsylvania, was used for longer session times by less experienced growers. It was concluded that the less experienced growers used the system to look up information and learn, while the more experienced growers were using the same system to obtain confirmation for decisions they had already made. Indeed, one and the same system was used for learning and decision support (see also Leeuwis, 1993). Growers differ in their information needs; many prefer simple and staightforward suggestions on what to do (Atkins, Gussakovski), but others like explanations and backgrounds (Braun). Institutions with public funding are able to invest in systems that further objectives of public importance, such as environmental protection, while the private sector by its nature has to focus on objectives related to profit. Private sector DSS has therefore to go towards the 'information pull' while public sector DSS may also give some information 'push', and be on the lookout for the pull (DeJong).

3.2. Communication: involving the end-user

Two major errors in developing decision support products are to build a system that provides answers to questions that are not asked, or to present the information in a way that does not appeal to the users. To avoid these pitfalls, a prototyping approach is useful. User feedback is requested throughout the development of a DSS product, so that user requirements become more articulate, and can be optimally taken into account (Boshuizen and van der Maas, this volume; Groot, this volume). Confidence in the outputs of decision support systems is increased by showing intermediate calculation results, and this also enables learning. Scope for the use of DSS products will increase as more weather stations become available and as the Internet provides easy access, as well as a straightforward way to put DSS software updates in place. The option of quick implementation of updates is essential for systems supporting disease control decisions, e.g. when new unexpected events happen such as the appearance of a more virulent strain of a plant pathogenic fungus. The idea that researchers are information 'sources' and growers 'sinks' has been largely abandoned in Europe and North America, but has not been eradicated everywhere. In Japan, a top down approach still prevails in agricultural extension. In France, however, efforts are made to build a DSS by collecting and integrating farmers experiences. A succesful Dutch DSS product (Teletuin; WWW.DACOM.NL) does little more than collect and redistribute information on management and yields among growers.

3.3. Specificity, validity and adoption of DSS

Although growers find it tedious to put in large amounts of data, they are not unwilling to do so, if it gives them an overview of the economics of their enterprise. Input of farm data makes the result specific and more useful (Groot). Farm specific calibration and updating of predictions from DSS is a sound possibility to improve validity and farm-specific relevance of DSS (van der Maas). Nevertheless, an unvalidated DSS may be adopted if there is nothing better (Atkins). Interestingly, although DSS is meant to improve farm productivity, efficacy, efficiency, profitability, etc., fruit growers in California may not be all too interested in DSS, because they are looking for a 'silver bullet', i.e. a special approach or management tactic, that will give them a competitive edge over their neighbours in a highly competitive marketplace (DeJong). Products that are available to everybody are therefore not of great interest. DSS does not need to be thoroughly validated in order to be adopted. In New Zealand, a warning system for Botrytis fruit rot in grapes was quickly adopted by growers, even though the system had been little tested (Tustin). The pressures stimulating adoption were (1) value of the crop; (2) high potential impact of the disease; (3) lack of alternative sources of information (Atkins).

According to Rajotte, 'regulation is the mother of adoption', referring to governmental regulation as the major force affecting behavioural change away from pesticides and towards implementation of IPM and DSS as a part of IPM. According to DeJong, researchers at institutions have the opportunity and the responsibility to be pro-active in developing tools for more environmentally friendly farming for which there is no market (yet), such that, when regulation arrives, the tools exist. A pesticide averse attitude among growers is one of the reasons for high adoption rates (75%) of the program Orchard 2000 in New Zealand, even though implementation of this program at farm level would not be economically advantageous, at least not in the short run (Atkins). Another most effective instrument for behavioural change is provided by demonstration projects. An issue in pest management DSS is the question of action thresholds for multiple pests (Lakso). If management tactics (chemical or biological controls or cultural measures) affect multiple pests, the density at which action is worthwhile would be lower than when single pests were targeted. The problem is little studied and thresholds are more often rules of thumb, based on experience and risk avoidance considerations, than anything else. However, when farmers avoid their private risk of yield loss due to pest impact, by using a pesticide, they are likely to increase the public risks of environmental contamination, resistance development, and region wide impacting on natural enemy populations (Leeuwis).

4. Conclusions

It is a difficult and risky task to summarize three and a half hours of discussion in a few lines of conclusions, considering the diversity of view points expressed. Probably the following statements are underscribed by the majority of participants:

- Process-based models and Decision Support Systems are altogether different things. Effective DSS need not be based on a process-based model, and Decision Support is not a strong point of process-based models, due to their information-hungriness.
- Process-based models are useful instruments for scenario studies that may feed decision support systems during the development phase, or on-line.
- There is a need for better and clearer documentation of process-based models, both at the technical and at the conceptual level. Checklists appended to this paper and van der Werf *et al.* (1999a) give suggestions for preparing clear accounts of modelling studies.
- Validation has been reduced too much to a search for statistical correspondance between simulation results and observed field data. The value of process based models is also in the accuracy of concepts. A broader and richer interpretation of modelling purpose, and, therefore, model validity is needed, in view of the complexities of real systems in the open field and the impossibility of including all the details in a process-based model.
- Decision Support Systems must be developed with a diversity of users in mind; this can best be realized by means of user participation in the design process. Top down approaches in extension are being replaced by a networking approach. The rapid development of the Internet as a equitable network for information exchange is boosting this social trend.
- The need for learning from Decision Support Systems may be greater than the need for decision support *sec.* Supporting learning poses different demands on a system than supporting decision-making. As learning needs change continuously, greater flexibility must be provided. Moreover, the organization of opportunities for communication and debate must receive greater priority when improved learning is the aim.

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Appendix 1

Blank form for the CAMASE Register of Agro-ecosystems Models (Plentinger and Penning de Vries, 1996)

A. General overview

Name and version:
Title:
Update:
Date first profile:
Date last profile:
Program type:
☐ Simulation model or module (fill out A, B, D)
☐ Simulation tool (e.g. statistical method, data base, simulation environment, simulation language)(fill out A, B, D when relevant)
☐ Optimization model (linear programming or interactive multiple goal linear programming)(fill out A, C, D; otherwise fill out A, B, D)
☐ Other
Purpose:
Research 1 2 3
Education 1 2 3
Application 1 2 3
New releases expected: Yes/No
Subject:
☐ Crop science
☐ Soil science
☐ Crop protection
☐ Forestry
☐ Farming systems
☐ Environmental science
☐ Agricultural economics
☐ Land use studies
Aggregation level:
☐ Organ
☐ Plant/animal
☐ Crop/herd
☐ Cropping system/animal husbandry system
☐ Farm
☐ Region
☐ Supra region
☐ Other, ...
Description (< 200 words):

B. Scientific specifications of simulation models

Rate variables (< 25 words):
Number of rate variables:
State variables (< 25 words):
Number of state variables:
Input data (< 25 words):
Number of input data:
Output data (< 25 words):
Number of output data:
Time interval of simulation:
Basic spatial unit:
References general validation:
Stand alone model: Yes/No
Parentage:
Check internal consistency or material balance present?: Yes/No.
Input check in model?: Yes/No.

C. Scientific specifications of optimization models

Type of optimization model: Linear Programming or Interactive Multiple Goal Linear Programming
Type of variables/activities (< 25 words):
Number of variables/activities:
Type of constraints (< 25 words):
Number of constraints:
Type of objective functions (< 25 words):
Number of objective functions:
Basic spatial unit:
Time horizon:
Optimization interval:
Stand alone model: Yes/No.
Parentage:

D. Technical specifications

Hardware:
Programming language:
Other software requirements:
User's guide available:
Technical reference manual:
Application reports:
Source code available: Yes/No.
Executable available: Yes/No.
User contract mandatory: Yes/No.
Costs:
Comments:
Contact:
Address:
Telephone:
Telefax:
E-mail:
Co-authors:

Field definitions for the CAMASE Register of Agro-ecosystems Models

A. General overview

Name and version	The code name of the model, which is often an acronym; add the version number, if there is any. Every registered model must have a name
Title	The acronym of the title spelled out
Update	The last date on which the model was updated
Date last profile	The last date at which this profile was updated
Program type	Indicate if it is a simulation model or module (part of a model), a simulation tool (e.g. data bases, simulation environment, simulation language, statistical methods), an optimization model (part of a model) or something else (other)
Purpose	There are three categories of uses of models distinguished: for research, for teaching, and for application. For each category, score '1' if very relevant, and '3' for little relevant.

New releases expected	Answer 'yes' if the model is in development, and 'no' if it is completed under this title
Subject	Indicate the broad subject class in which the model falls: crop science, soil science, crop protection, forestry, farming systems, environmental science, agricultural economics, land use studies, other.
Description	Describe the model by using relevant keywords in the text (as users of the data base can search for them), mention a typical use of the model, and indicate over what range of conditions the model is valid. Specific but non-standard techniques or (sub-)models mentioned can be entered as separate issues in the database, and will then be labelled with an *.

B. Scientific specifications of simulation models

To indicate the complexity of the model, we ask about:

Rate variables	Give names (of types) of rate variables
Number of rate variables	Give approximate number of rate variables
State variables	Give names (of types) of state variables
Number of state variables	Give approximate number of state variables
Input data	Give names (of types) of input data
Number of input data	Give approximate number of input data
Output data	Give names (of types) of output data
Number of output data	Give approximate number of output data
Time interval of simulation	The value or range
Basic spatial unit	e.g., m^2, ha, 1000 ha, (watershed), irrigation system, nation
References general validation	As in journals
Stand alone model	Yes or no
Parentage	Indicate in a few words whether the model is derived from or based on other models, if there is/are any. We aim to have all models mentioned in the list included in the data base
Check internal consistency or material balance present	Yes or no
Input check in model	Yes or no

C. Scientific specifications of optimization models

Type of optimization model: Linear Programming or Interactive Multiple Goal Linear Programming. To indicate the complexity of the model we ask about:

Type of variables/activities	Give names (of types) of variables and activities
Number of variables/activities	Give approximate number of variables and activities
Type of constraints	Give names (of types) of constraints
Number of constraints	Give approximate number of constraints
Type of objective functions	Give names (of types) of objective functions
Number of objective functions	Give approximate number of objective functions
Basic spatial unit	The basic spatial unit for which variables/activities have been quantified; e.g., m^2, ha, 1000 ha, (watershed), irrigation system, nation

Time horizon	The value or range
Optimization interval	The value or range
Stand alone model	Yes or no
Parentage	Indicate in a few words whether the model is derived from or based on other models, if there is/are any. We aim to have all models mentioned in the list included in the data base

D. Technical specifications

Hardware	The minimum requirements and recommended configuration
Programming language	The official name and supplier
Other software requirements	The official name(s) and supplier(s)
User's guide available	If there is an user guide available, give the full reference
Technical reference	If there is a technical reference available, give the full reference
Application reports	Mention important articles of the model
Source code available	Yes or no
Executable available	Yes or no
User contract mandatory	Yes or no
Costs	Approximate value of purchase in US$
Comments	Any comment by the author, up to 200 words
Contact	The full name of the contact person
Address, telephone, telefax, and e-mail	The postal and e-mail address of the contact person
Co-authors	The names of the co-authors (and their e-mail addresses)

Appendix 2

Some suggestions on presenting research-oriented modelling studies. Presenters of models pay surprisingly little attention to specify their goals and approaches clearly. This causes a lot of misunderstanding because there are so many purposes, methods and schools of modelling; you may be communicating with somebody from another school. You can use these guidelines as a checklist for items you may wish to address in a presentation of a study that involves modelling.

- What is the problem?
- Why is a modelling approach chosen to address the problem?
- What purpose is the model specifically serving? In a general sense, is the purpose explanation, exploration, prediction or .....
- In which way does reaching that purpose help to solve the initial problem?
- What is the conceptual structure of the model; is it a state-variable based model, an optimization model, an individual based model, etc.
- what are the components (state variables, structures (for individual based model), independent and dependent variables; etc.)
- How are the relationships between the components of the model specified (differential equations, arithmatic relationships, linear or non-linear, difference equations, integro-difference equations, partial differential equations, etc., logical rules as in an expert system)?
- Is the model process-based and mechanistic (i.e. does it links processes to system behaviour) or merely descriptive of the behaviour of the system as a whole. Of course, there is a gradual scale here.
- Is the model theoretical/conceptual, i.e. is the purpose to investigate ‘general’ phenomena, or is it system-specific, aiming at characterizing the processes in and the behaviour of a specific system? Is the model site- and situation-specific; i.e. is there a lot of site and situation-specific data input necessary to run the model?
- How were parameter values of the model arrived at; by expert judgement, least squares regression, maximum likelihood, some sort of optimization technique, calibration 'by hand', etc.
- The level of detail required in answering all these questions cannot be generally specified. Answers to the above need to be given to such an extent that the structure and purpose of the model are somewhat clear.
- Comment on the general validity of this sort of model for reaching the specified purpose and solving the kind of problem
- If the model has earlier versions, say so.
- Always store the version of a model that you use for a publication in some safe place for future reference, so people may be able to find the errors in your code. Make a technical documentation, in the first place for yourself, so when using it later, you are still aware of what is in the model. Few people are likely to read technical documentation, but it is of enormous value for yourself and for anybody who would like to do further work on the basis of your model. Without technical documentation, if your model is very complex and has many pages of code with few comments, it will have to be recoded. Because you are not able to put all the technical details in a journal article, the recoded model will be different. (This may not be a problem if the concepts are more important than details.)

- Validation: Be explicit about what criteria are used to judge the usefulness of your model. The purpose of the model determines the requirements. Theoretical and conceptual models only neeed to produce 'realistic' (acceptable) trends. Predictive (regression) models must often be accurate (at least give a competitive edge). 'Models' that help you to make decisions don't need to be accurate in the predictive sense, as long as they result in the right decision or in appropriate advise. In process-based mechanistic models, a model may primarily act as a learning tool for the investigator. However, if the model along with sensitivity and scenario analyses of it are presented, the whole world will learn from it; at least that should be the case if the researcher has been asking questions that are amenable to answering by using models.
- Especially if detection of knowledge gaps is an objective, sensitivity analysis and uncertainty analysis are useful techniques, to guide research to those activities where the biggest 'gains' are to be expected. Here again, the 'learning function' may be extended by a general audience by publishing the results.
- Do not overpromise prediction capabilities of the model (avoiding disbelief and underdelivery), but do not overstate uncertainties and weaknesses either (to avoid indifference)
- Be very clear, concrete and explicit about what insights or application options the model or its use gives that could otherwise not have been obtained. State its niche in comparison to experimentation, logical reasoning, surveys, etc.
- Realize that a model will always be incomplete in some sense. Incompleteness is very practical, because it keeps a model simple. Comprehensive models are cumbersome to work with due to amount of code, data input that is required to run, data output you need to look at to evaluate model behaviour. At any stage of development, results from modelling may be worth publishing. It is not advisable to wait until the model is 'finished', unless you have a practical and feasible definition of the finished stage. If 'finished' implies perfect correspondence to experimental results, you may never reach that stage.
- If you use the word prediction, make clear what you mean: is it 'explaining' system behaviour on the basis of model structure, model equations and forcing functions, or making a statement about the future. The first type of 'prediction' may better be called 'analysis' or 'reconstruction'.
- Be as explicit as you can about the range of situations about which the model is considered to make valid statements.
- Explain what will be your next steps.

Session 4
Tree architecture

SIMTECK : A SIMULATION MODEL FOR TECHNICAL OPERATIONS IN KIWIFRUIT ORCHARD MANAGEMENT

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Abstract

In this paper, we describe a simulation model designed for studying orchard management in kiwifruit. It considers both fruit number and the distribution of fruit size at harvest in orchards in relation with some combined technical operations (plantation scheme, pruning, thinning and irrigation). The model attempts to account for fruit size variability by considering factors of variation taking place at different levels of organisation (flower, cohort of flowers, shoot, cane, vine, and plot). This is an important difference of design with the previous model of Doyle *et al.* (1989).

We will exemplify the use of the model by comparing several management options, using the cost of the technical operations and the expected value of the crop to build an economical criterion for evaluation.

1. Introduction

Numerous models have been produced in fruit research, that generally concern one part of the plant production cycle. Some of them, which deal especially with organ growth, relate explicitly or implicitly biological processes to cultural practices (Buwalda, 1991; Grossman and DeJong, 1994; Génard and Huguet, 1996). Other models try to cover the whole cycle (Doyle *et al.*, 1989; Testolin and Costa, 1990) but they are not always enough mechanistic to allow a sufficient portability, according to Dent *et al.* (1994). Moreover, except for a few attempts (e.g., kiwifruit: Testolin and Costa, 1992), models rarely incorporate the variation of criteria of fruit quality, not even the (simple) variability in fruit size at harvest. Our general purpose is thus the design of biotechnical simulation models at the orchard level devoted to fruit crop management studies in a somewhat process-based manner, with emphasis on between-fruit variability. This supposes to address explicitly complex system modelling, including the technical choices the producers are facing.

We will summarise the way the system analysis and modelling were performed in the case study of a kiwifruit orchard, and present the way the technical operations are incorporated into the global model. Then, we will exemplify the use of the model by comparing several management options, using the cost of the technical operations and the expected value of the crop to build an economical criterion for evaluation.

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2. System analysis and modelling

2.1. Model description

The consideration of the different levels where fruit variability is structured has inspired the choice of the main biological objects considered in the model (Fig. 1): the orchard (between-vine variability), the vine (between-cane variability), and the fruit (within-cane variability).

The second step was to identify the main limiting factors of kiwi fruit production, and to render them consistent with the model structure. Kiwifruit vine is a dioecious species, and the period of overlap of female and male flowering constrains pollination. After fruit set, fruit drop rarely occurs, and fruit growth depends on the result of the pollination process, the number of seeds in the fruit, as shown by the well-documented relationships between fruit size at harvest and seed number per fruit (Lescourret *et al.*, 1998b). Hence, the model was planned to be composed of three submodels linked in a dynamic and functional way. It describes flowering at the flower/cane/vine level, pollination at the vine/orchard level integrating the spatial distance (planting scheme) between male and female vines, and fruit growth at the fruit level, respectively (Fig. 1). Finally, the individual fruit sizes at harvest are aggregated at the orchard level. These submodels have been extensively described in other reports (Agostini, 1995; Lescourret *et al.*, 1998a), and will not be presented here.

2.2. Integration of management practices in the model

Concerning management practices, we focused on planting scheme, considered in the pollination submodel, on cane pruning considered in the flowering submodel, and on flower/fruit thinning and water management, considered to occur during fruit development, in the fruit growth submodel. Our effort was here to identify explicitly the model parameters and variables affected by the management practices we considered. The connections of cultural operations to the model are presented in Fig. 1. Altogether, these operations correspond to ca. 66% of the in-season production cost of kiwifruit in Corsica.

2.3. Building of an economic criterion for the evaluation of cultural operations

We consider here only the cost of the cultural operations taken into account in, or affected by, the simulation model. In a reference plot in Corsica, input costs of cultural operations taken into account in the simulation model represent ca. 2/3 of the F.O.B. cost (Fig. 2) (note that there is no need for pest control for kiwifruit in Corsica). Harvesting that is also accounted for, as it varies with yield, represents 25% of the F.O.B. cost. The figures in Fig. 2 are calculated on a per ha basis for a 500 vines/ha density, with a male/female ratio of 0.24, producing ca. 17000 kg/ha.

The cost of packaging and transport are also accounted for in the evaluation criterion, since they are affected by the size distribution of the harvested fruits. They account for ca. 40% of the total cost of the reference plot.

The value of the harvested crop is calculated by using current selling prices in Corsica, according to the distribution of fruit size. Therefore, the evaluation criterion is calculated as the difference between the total cost (input + harvesting + packaging +

transport costs) and the total value of the harvested crop. Thus, the total cost is a function of the cultural operations and the distribution of fruit size. The crop value is a function of the distribution of fruit size only.

It should be noted that the criterion value is not equal to the total economical balance of the crop, since several costs (e.g. fertilisation, herbicide, fixed charges, ...) are not accounted for. Furthermore, the model has not yet been tested for on-farm applications. Therefore, only the large differences of criterion values between simulated experiments can be interpreted.

3. Simulations

3.1. Case study 1

In kiwifruit, planting schemes define the number of productive (female) plants per ha, and the ratio and spatial position between male and female vines. They are strategic decisions that cannot be modified. Therefore, it could be interesting to evaluate how tactical operations like pruning and thinning can be managed to render as close as possible the crop performance of two plots characterised by different planting schemes. We simulated several technical situations on plots having the same area, climate, soil and crop conditions and operations (except those changed for the need of simulation as explained hereafter) than the reference. Vines were always well watered.

In the reference plot A, the male/female ratio was 1:5. This situation was highly favourable to pollination. The pruning was fairly light (60% of replacement canes kept) as was thinning (only the aberrant shaped flower buds removed). The total yield was 24.6 tonnes/ha and both percentage and number of fruits were high in the best grades (Tab. 1).

In case B, the male/female ratio was 1:11, a situation unfavourable to pollination. Situation B1 consisted of trying to compensate the effect of the anticipated poor pollination on fruit growth by reducing as much as possible the vine crop load. Pruning and thinning were severe (40% of replacement canes kept, aberrant shaped and lateral flower buds removed). The simulated number of seeds per fruit was dramatically lowered in B1 compared to A. The reduction of the number of flowers, which was stressed by thinning, was not sufficient to make up the deficit of fruit growth. On the contrary, the resulting small number of fruits was a critical point. The yield was poor (15 tonnes/ha) as was the number of fruits in the best grade: about 2 times less than for A though these fruits represented a high percentage of the yield (Tab. 1). The results of B1 indicated that pruning and thinning were too severe. In B2, vines were pruned and thinned like in A. With seed conditions similar to B1 and crop load conditions similar to A, fruits grown in B2 were slightly lighter. However, the yield was largely improved (23.6 tonnes/ha) as was the number of fruits in the best grade (80% of the number corresponding to case A), though the percentage of such fruits in the total yield decreased (Tab. 1).

These effects are dramatically expressed in the criterion values (Tab. 2), from where it comes under modelling assumptions that no technical alternative may overcome the error in the planting scheme. More interesting is the difference between case B1 and B2. Although this difference may change with climatic variations, it is large enough to assess that the technical choice in case B1 decreases dramatically the corresponding expected profit. This can even turn negative if other costs are to be taken into account (data non presented).

3.2. Case study 2

In this case study, we consider two neighbouring plots A1 and A2 with the same climatic conditions and different soil characteristics, each irrigated from the same water reservoir. Plot A1 is almost the same as plot A in the preceding case study, with soil readily available water (RAW) equal to 180 mm. The only difference is that irrigation is considered to occur from fruit set to harvest for plot A, and is restricted to 4 months for plot A1. Plot A2 differs from A1 by the age of the vines, which are supposed to be younger in A2, and by RAW that is 90 mm. The vine age is characterised by the mean number of canes after pruning that is 27 in A1 and 12 in A2.

The irrigation period is considered to take place between the 1rst of June and 30 September, therefore corresponding to a total of 32 weeks for the two plots. We consider here a water shortage of four weeks within the irrigation period, a situation that may appear in Corsica. Thus, the problem comes to allocate this water shortage either to only one plot, either to both of them. We will not here use some optimisation technique to find the 'best' solution, but exemplify the use of the model as a tool to learn the presumed consequences of some tactical choices.

We first verified that the irrigation model was able to reproduce the experimental data of Vannière and Huguet (1991). They compared the effects of two periods of application of deficit irrigation to a well-irrigated control in kiwifruit vine. The first period was between the 29th May and 12th July. The second period was between12th July and 29 September. Their data showed a significant effect of deficit irrigation, with a larger decrease in fruit growth at the end of the season with the second period of deficit irrigation. The model simulates well these results (data not shown).

Then, we used the model to compare the effects on fruit growth of four different ways of applying the 4-week water shortage (WS) during the 16-week (4-month) irrigation period in plot A1. WS treatments were defined as follows:

WS1, no irrigation during the first 4 weeks of the irrigation period (i.e., in June);

WS2, no irrigation in the middle of the irrigation period (i.e., from mid-July to mid-August);

WS3, no irrigation during the last 4 weeks (i.e., in September);

WS4, no irrigation each second week of the 4-month irrigation period.

Arbitrary fruits were chosen, characterised by their number of seeds and the load of the vine where they were supposed to grow. The 1997 climatic conditions were used in the simulations. In Fig. 3, the general pattern is presented for a 1000-seed fruit growing on a vine loading 1000 fruits. The growth curve of a control fruit without any water shortage is also presented for sake of comparison. It is obvious from Fig. 3 that the sooner the water shortage (WS1) the larger the decrease in fruit growth. On the contrary, WS3 has the smallest negative effect, very close to WS4. WS2 has an intermediate effect. If one could choose the period of water shortage, one would probably choose WS4, since it further minimises the risks of some climatic accident over the growing season. Nevertheless, WS2 type of water shortage (i.e. in summer) is the more likely to occur in Corsica.

We will compare hereafter the economical consequences of the application of WS2 to A1 and/or A2 plots. Three different cases were studied: (i) water shortage of 4 weeks in A1 from mid-July to mid-August, no water shortage in A2, (ii), water shortage of 4 weeks in A2 from mid-July to mid-August, no water shortage in A1, (iii) water shortage of 2 weeks in A1 and A2 applied from the last week of July to the first week of August. Results, summed up for the two plots, are presented in Tab. 3. It is obvious from Tab. 3 that the best choice is to apply the 4 weeks water shortage to A1. The performance of orchard A1 is indeed much better than that of A2. Therefore, it is globally better to accept a small decrease in A1 production, and to maintain A2 production.

We set the same problem to an expert. His first opinion was that the application of the water shortage to the two plots would minimise the global risk. However, he came in conclusion that he would prefer finally to promote fruit size in the potentially 'best' orchard (A1) in order to promote the global benefit. In fact, the model calculated a loss in A2 higher than the gain in A1, leading to the reverse solution.

4. Conclusions

The method we proposed here to study the effects of several orchard management options on the economical performance of the crop is based on the mathematical modelling of the underlying processes. The structure of the model allows easy consideration of other management variables (such as nutrient supply, sensitivity to pest, effects of growth regulators, ...), as well as other outputs than fruit size (such as refractometric index). Although not yet used for on-farm application, this model has proved to be efficient to simulate the variability in kiwifruit production in a way that exacerbates the role of management practices, and seems to offer real opportunities to better reason the combination of cultural practices to reach a given production goal.

Furthermore, the methodology of model construction presented here should be only part of a systemic analysis of orchard management. For instance, the kiwifruit model should also be linked to an existing economical model (e.g. in a framework described in Attonaty *et al.*, 1996), in order to investigate the financial consequences at the farm level of various strategies. Linking such sub-systems is likely to promote the evolution of the basic models.

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Table 1 - Distribution of fruit numbers (row percentages in brackets) among size grades (70 and 90 g are EEC thresholds for 'First choice' and 'Extra' grades) for three simulated technical situations. The male/female ratio is 1:5 for A and 1:11 for B; the ratio of replacement canes kept at pruning is 60%, 40% and 60% for A, B1 and B2, respectively; thinning concerns the aberrant shaped flower buds for A and B2, plus the lateral buds for B1.

	<70 g	70-90 g	>90 g
A	1086 (1)	9382 (10)	88288 (89)
B1	4018 (6)	14315 (21)	49192 (73)
B2	6893 (6)	31318 (29)	70344 (65)

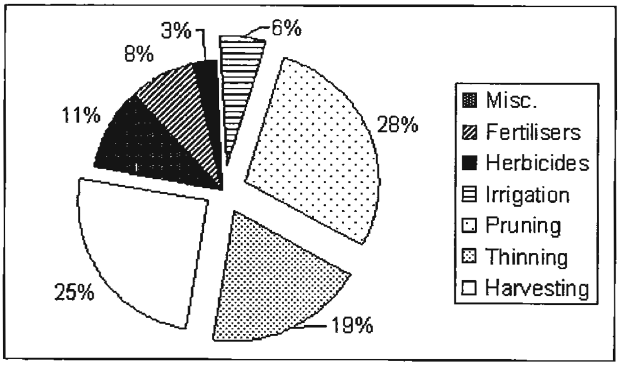
Table 2 - Calculation of the economical criterion value for the three simulated situations

	Orchard A	Orchard B1	Orchard B2
Irrigation	2048	2048	2048
Pruning	19266	19612	19612
Thinning	13889	15783	15783
Harvesting	12006	7264	11445
Packaging	22227	12701	19543
Transport	18896	10816	16541
Total cost	88332	68224	84972
Crop value	136406	76762	116590
Criterion value (FF/ha)	48074	8538	31618

Table 3 - Calculation of the economical criterion value for the three Water Shortage simulated situations

	Water Shortage in A1	Water Shortage in A2	Water Shortage in A1 and A2
Irrigation	4394	4364	4424
Pruning	35401	35401	35401
Thinning	25029	25029	25029
Harvesting	15526	15425	15420
Packaging	27147	24774	25103
Transport	22910	21025	21237
Total cost	130407	126018	126614
Crop value	161625	146442	149334
Criterion value (FF/2 ha)	31218	20424	22720

Figure 1 - Schematic diagram of the kiwifruit orchard management model, stressing the relationships between technical operations and the main modelled processes



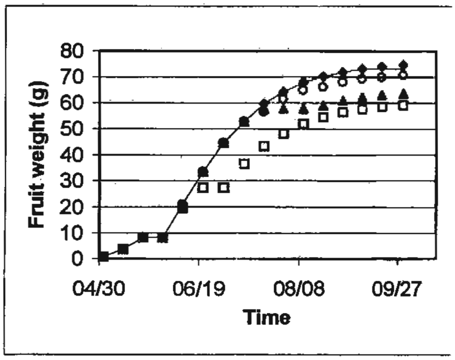


Figure 3 - Effects of deficit irrigation on a 1000-seed fruit grown on a 1000-fruit vine

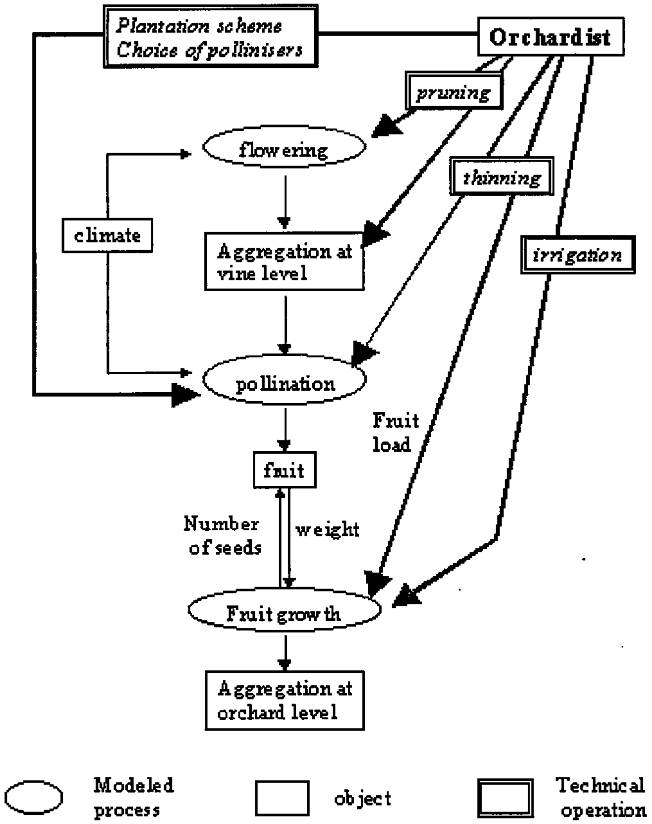


Figure 2 - Distribution of input and harvesting costs in % of F.O.B price.

A POLLINATION AND FERTILISATION MODEL FOR MULTI-SEEDED FRUIT AND ITS APPLICATION TO KIWIFRUIT.

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Abstract

A model describing flower pollination and ovule fertilisation was developed. It was designed for species that require pollination among different genotypes and where the number of seeds per fruit affects fruit quality, including their size. The outcome of the model varies with the climate, the number and phenology of flowers in an orchard, the planting scheme and the choice of pollenizers. The model takes into account the presence in the orchard of various pollenizer groups. The first step of the model is a Poisson-distributed deposition of pollen on the stigmas of flowers during the effective pollination period of these flowers. The intensity of the process depends on pollen production and release by pollenizers, which in turn depends upon the number and time-distribution of flowers that open; it also depends on pollen dispersal, which is assumed to vary according to the distance between the sources and the target. The second step is a binomially distributed selection of fertile pollen grains. The third step is a random fertilisation of ovules by the pollen tubes conditional on the presence of N ovules in the ovary. This requires knowledge on the distribution of ovule numbers per flower. The fourth step is a binomially distributed selection of fertile ovules. The combination of the four steps enables to calculate the probability that n ovules out of N present in a flower are fertilised and can become seeds. Fruit set can be deduced from the model outcomes using a probability calculated according to a logistic function in terms of seed number. The model was applied to kiwifruit, which is a dioecious species. It was used to point out knowledge gaps and to suggest further research.

1. Introduction

In fruit tree and vine species, the quantity and quality of the crop depend on numerous factors, among which the fertilisation of ovules, which is linked to the pollination process. Poor pollination is often cited to explain low fruit set as well as fruit drop before maturity. In multi-seeded fruits such as apple, pear, grape or kiwifruit, several quality criteria like fruit shape, fruit size and conservation ability depend on the number of seeds that is determined by the intensity and efficiency of pollination (Pyke and Alspach, 1986; Bramlage *et al.*, 1990; Boselli *et al.*, 1995).

Pollination among different genotypes is often required because of self-incompatibility (apple, pear) or dioecy (kiwifruit). Under such conditions, the success of pollination depends on technical choices concerning the planting scheme (planting ratio,

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planting distances,), the choice of pollenizers, and the management of all factors affecting pollen vectors, which can be insects (especially honey bees) and/or wind.

A model of pollination and fertilisation of flowers in fruit trees can contribute to improve our understanding of the variation of fruit quantity and quality in orchard crops. It can help to study results from the changes in the technical operations listed above on the intensity and success of pollination, and their consequences on fruit production. We present hereafter such a model, which has been partly developed for kiwifruit (Lescourret *et al.*, 1998a,b), in the general framework of multi-seeded fruit.

2. The model

The model operates at the flower level and not at the carpel level, under the assumption that the growth of pollen tubes in syncarpous species is not limited to the carpel associated with the stigma on which the pollen is deposited. Such an assumption was verified for kiwifruit by Vaissière *et al.* (1991) and Pan *et al.* (1997). The model describes four main steps:

(i) deposition of pollen grains on the stigmas during the effective pollination period of the flower;
(ii) selection of fertile pollen grains, i.e. the grains that produce tubes able to bring the male gametes to the ovules;
(iii) fertilisation of ovules conditional on the presence of N ovules in the ovary;
(iv) selection of fertile ovules.

The first process (i) is represented as Poisson-distributed. The Poisson distribution is currently employed to count things randomly dispersed in space, as can be assumed here for pollen grains in the space occupied by flowers. For the sake of simplicity, we suppose here that the population of pollenizers is homogeneous in regard to pollen fertility and pollen production per flower. The intensity λ of this Poisson process is supposed to depend on the date of anthesis of the flower to be pollinated with respect to the temporal pattern of pollen availability in the orchard. Thus, it is computed for each cohort (populations of flowers to be pollinated with the same day of anthesis) in each tree of the orchard. It is the sum over all the compatible pollen sources of the orchard of the pollen produced by these sources and received by the target (the stigmas of the flower) during the effective pollination period. Pollen production is distributed over the period during which a flower of a pollenizer releases pollen. We assume that pollen release is uniform balanced over this period. Pollen production depends on the number and time-distribution of flowers that open, and on the number of pollen grains produced per flower p, which is considered as a fixed input value and can vary with the cultivar. Pollen reception is a function that should describe the part of the pollen produced by a source that is transported on the target, according to various features among which the distance between the source and the target. This function may be different according to the species. We suggest a function for the case of kiwifruit (see section 3). Rain is assumed to stop temporarily the deposition process.

The model assumes that the second process (ii) is binomially distributed with parameter f (pollen fertility), considering that at each trial (selection of a pollen grain), either of two exclusive events can take place, i.e. the pollen grain is fertile (with a probability f) or not fertile (with a probability $1-f$). For the third process (iii), a basic hypothesis, formulated by Falque *et al.* (1995), is that pollen tubes reach ovules in a similar way whether or not these ovules have already been reached by another pollen tube. According to Falque *et al.* (1995), it results that the probability that a fertile pollen tube does not reach a given ovule i among a total of N ovules present in the ovary is $1-\frac{1}{N}$. Then, combining the Poisson process of intensity λ (i) and the binomial process of parameter f (ii) leads to the formulation of the third process, i.e. the calculation of the probability that ovule i is fertilised given a total of N ovules in the ovary (Lescourret *et al.*, 1998a):

$$P\left(i\ fertilised \mid N\right)=1-e^{\frac{-\lambda f}{N}} \qquad (1)$$

The model assumes that the fourth process (iv) is binomially distributed with parameter F (ovule fertility), for reasons similar to the case of the second process (selection of fertile pollen grains). Ovule i fertilisation by pollen and ovule fertility being assumed independent, the probability that i is fertile and fertilised is $F\left(1-e^{\frac{-\lambda f}{N}}\right)$. Now, the result of the combination of the four processes is viewed as binomially distributed, and the probability that n ovules out of N develop into mature seeds is thus:

$$P\left(n \mid N\right)=C_N^n\left[F\left(1-e^{\frac{-\lambda f}{N}}\right)\right]^n\left[1-F\left(1-e^{\frac{-\lambda f}{N}}\right)\right]^{N-n} \qquad (2)$$

provided that ovules in a flower are independent of each other with regard to fertilisation, as hypothesized for apple by Brain and Landsberg (1981).

To simulate management options, it is necessary to account for the presence of various pollenizer groups in the orchard. For extending the model to the case of k pollenizer populations, we assume that pollen distribution from the k groups of sources are independent, and that pollen fertilities are also independent. If $\lambda_1, \lambda_2, \ldots, \lambda_k$ are the intensities of the Poisson processes of pollen deposition of the k populations and $f_1, f_2, \ldots, f_k$ the fertilities, it can be demonstrated that the number of fertile pollen grains reaching the ovule obeys a Poisson distribution having as intensity $\mu = \frac{U}{N}$ where $U = \lambda_1 f_1 + \lambda_2 f_2 + \ldots + \lambda_k f_k$. Therefore, the probability that an ovule is fertilised given a total of N ovules in the ovary is $1-e^{\frac{-(\lambda_1 f_1+\lambda_2 f_2+\ldots+\lambda_k f_k)}{N}}$.

After equation (2), using the model requires knowledge on the distribution of ovule numbers per flower N. As for the function of pollen reception, the determination of N, which is linked to botanical features, may depend on the species. We suggest a simple law for the case of kiwifruit (see section 3).

Fruit set does not pertain *per se* to the model, but it should be deduced easily from its results if the model is to be used for studying the effect of pollination on fruit yield and quality. We propose to model fruit set in terms of seed number. The number of seeds played an important role in Brain and Landsberg's (1981) model of fruit drop in apples. The process can be simply described as the result of a Bernouilli trial with a probability calculated according to a logistic function, i.e. $\frac{1}{1+e^{snt-n}}$, where n is the number of seeds and *snt* (seed number threshold) a parameter representing the number of seeds for which the probability of fruit set is equal to 0.5 .

3. Application to kiwifruit

In kiwifruit, insects - especially honey bees - and wind are both responsible for pollination. However, their respective role is still debated (Craig and Stewart, 1988) and quantified relationships expressing the effect of various factors on their contribution are lacking. Because of these knowledge gaps, we gathered the contributions of the two pollen vectors to pollen deposition into a global ratio of pollen production, and we focused on the effect of the distance between the source and the target on this ratio. The equation of this effect was inspired from the experimental work of Testolin (1991). Thus, the intensity of the Poisson process λ_j^t, i.e. the mean amount of pollen deposited on the stigmas of a flower opened on day t on a female vine j over the effective pollination period t - $t+epp-1$, where epp was stated by Gonzalez *et al.* (1995) to be related to stigmatic receptivity, was represented as the sum over the males i of the orchard of pollen quantities deposited during this period:

$$\lambda_j^t = \sum_i \sum_{l=t}^{t+epp-1} r_{\max}^l \, e^{-g\left(d_{ij}-d_{\min}\right)} \times P_i^l \qquad (3)$$

P_i^l denotes the pollen released by the source i (male vine) at day l, $d_{\min}$ is the minimal planting distance, $d_{ij} \geq d_{\min}$ is the i-j distance, $r_{\max}^l$ the ratio of pollen produced by i at day l received by the stigmas of a flower of j when $d_{ij} = d_{\min}$, and g a shape parameter. This relationship is obviously rough and based on several hypotheses that are discussed in Lescourret *et al.* (1998a).

Concerning the distribution of the ovule number in kiwifruit, though it has not yet been investigated, literature data indicate that the numbers of carpels per ovary and of ovules per carpel are variable. Awaiting further studies, we suggest that ovule numbers could be simulated using Poisson distributions (because they are simple discrete laws) of the number of carpels per ovary and of the number of ovules per carpel.

On these bases, we studied the model behaviour (partly in Lescourret *et al.*, 1998b), using estimates of the model parameters originating mainly directly or indirectly from the kiwifruit literature. The graphical evaluation of the model was found satisfactory. For example, the model was able to reproduce the general pattern observed in the experiment of Testolin (1991) where a unique pollenizer was left in the centre of an orchard (Fig. 1). The model was proved to be sensitive to parameters such as pollen fertility and production per flower, f and p, and to the two parameters $r_{\max}$ and g of pollen reception (equation 3). Rough estimates of $r_{\max}$ and g obtained through graphical comparison of model outputs to the experimental results of Testolin (1991) for two years were very different from one year to another. The model response, expressed as the number of seeds per fruit after fruit set averaged per vine, was very different according to the value of the number of carpels per ovary and of the number of ovules per carpel (Fig. 2).

The ability of the model to study the effect of technical operations related to the pollination features on flower fertilisation is illustrated on Fig. 3. For the simulations, the pollination and fertilisation model was incorporated into a global biotechnical model of kiwifruit production (Habib *et al.*, this issue), which included models of flower anthesis (Agostini *et al.*, in press). The simulations were made for plots comprising 6 rows and 36 plants per row on a regular or diamond scheme (Fig. 3a) with planting distances equal to 5 or 7 m between rows and to 4 m within the row. The planting ratio was 1:8 and the male cultivar was Tomuri. On the regular scheme, the worst seed responses were those of plants at the periphery of the plot, the best ones were those on rows with males, and the responses were intermediate on rows surrounded with males (Fig. 3b). The response on the diamond scheme showed waves with crests corresponding to zones with males and hollows to zones without males. Though the response surfaces had different shapes, their overall level was similar (Fig. 3b). Contrasted planting spacings (5 or 7 m between rows) resulted in contrasted seed responses (Fig. 3b).

4. Conclusions

The design and the study of the model allowed to suggest further studies to improve our knowledge of the pollination and fertilisation of fruits in orchards. When applying the model to kiwifruit, we used an empirical relationship to describe the dependence of the amount of pollen grains deposited on the stigmas of a flower on the position of the female vines with respect to the pollen sources. However, we noted that the estimates of the parameters of this relationship (to which the model is sensitive) could vary a lot among years. Such differences could be attributed, at least partially, to changes in the respective impacts of the two pollination vectors of kiwifruit, wind and insects, as proposed also by Testolin (1991). This suggests further refinements of the model aiming at describing separately the contributions of the two vectors. From a general point of view, further studies allowing to incorporate the spatial behaviour of pollen vectors are needed to improve the model.

Similarly, we noted that the model response was sensitive to the number of ovules per flower, for which literature data are lacking. It was also sensitive to the pollen fertility f and production per flower p. However, pollen viability was shown to be variable between orchards and between vines within orchards (Meyer and Bliss, 1991). Moreover, most of the studies on pollen fertility are *in vitro*, and the model requires *in vivo* pollen fertility estimates. Further studies on the relationships between *in vitro* and *in vivo* pollen performance on one hand, and models of the variation of pollen fertility according to factors such as temperature (Jansson and Warrington, 1988), on the other hand, should help to refine the model. In the same way, explanations on the variation of pollen production per flower, which could be attributed to adaptations to growing conditions (Gonzalez *et al.*, 1994), would be helpful.

In fruit crops, the technical operations devoted to pollination are important (including the planting options that are established for the entire life of the orchard) and cannot be reasoned independently of other operations. Thus, this pollination and fertilisation model is also interesting as part of a global biotechnical model (for example: Habib *et al.*, this issue) that offers the means of simulating the consequences of technical changes or innovations. This is useful for fruit growers faced to significant and rapid changes in the socio-economic context.

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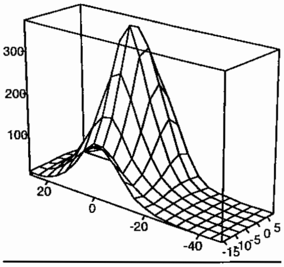

Figure 1 - Response surface plot of the total number of seeds per vine (× 10^{-3}) in a situation simulated through the model, close to Testolin's (1991) experiment where one male vine was left in the centre of a kiwifruit orchard. As in Testolin (1991), the intersections on the grids of response surface plots represent vines and x- and y-axes are between-row and within-rows distances (m) from the central male.

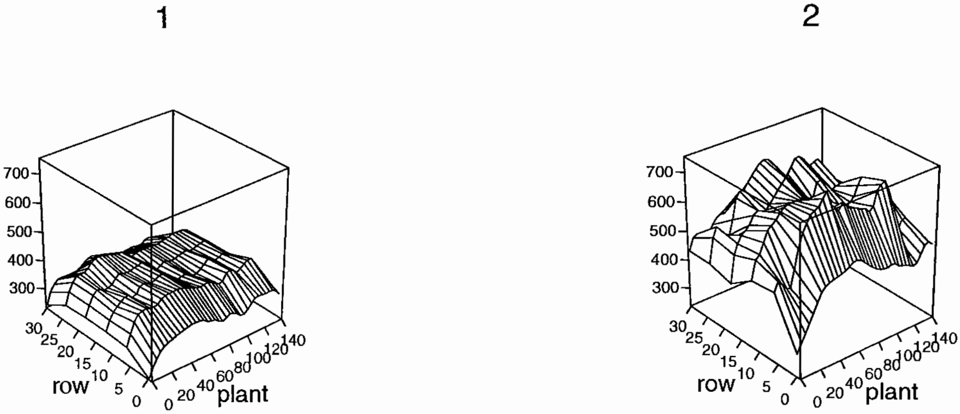

Figure 2 - Seed surface response (numbers of seeds per fruit averaged per vine) provided by the model on a simulated plot when the numbers of carpels per ovary and of ovules per carpel are 25 and 20 (1), and 40 and 40 (2). The x- and y-axes are distances (m) from the corner of the plot.

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Figure 3a - Regular (up) and diamond (down) planting schemes. 'F' denotes a female plant and 'M' a male plant.

regular scheme diamond scheme

short between-row distance long between-row distance

Figure 3b - Seed surface response (numbers of seeds per fruit averaged per vine) provided by the model on a simulated plot with a regular or diamond planting scheme up); or on a regular scheme with short (5m) or long (7m) between-row distances. The x- and y-axes are distances (m) from the corner of the plot.

WINTREE: A COMPUTER PROGRAM FOR CALCULATING CHILL AND ANTHESIS UNITS USED IN MODELLING FRUIT TREE PHENOLOGY

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Keywords: dormancy, apple, peach, rest, chill units, anthesis units

Abstract

WinTree is a collection of program modules designed to allow easy use of the 'Utah' and similar dormancy models. WinTree includes the following modules: database, data update (entry), data collection (text files), dormancy modelling, and a workbook (spreadsheet). The program, created with Delphi 1.0 (Borland International, Inc.), runs on Microsoft Windows 95 or Windows NT. WinTree uses the Borland Database Engine (BDE) to allow access to commercial database files (Paradox). Temperature data can be entered as daily maximum and minimum or hourly intervals. WinTree uses hourly or estimated hourly temperatures in calculations. Estimated hourly temperatures are generated using various sine-exponential or linear methods. Commonly, chill units (CU) are accumulated until the estimated end of endodormancy. Then, growing degree hours (GDH °C) are accumulated until the estimated time of bloom. WinTree can also be used to calculate only CU or GDH. The temperature requirements for determining chill units can be user modified. GDH are calculated using either linear or asymmetric-curvilinear (ASYMCUR) methods. The minimum, optimum, and critical temperatures used to calculate GHD are easily modified. Data output can be hourly, daily or seasonal. Output can be sent to the workbook module for additional calculations and transfer to spreadsheet programs.

1. Introduction

Dormancy models can be useful tools for estimating the end of dormancy and anthesis development of deciduous fruit trees from temperature data. Dormancy models make possible the scheduling and optimisation of cultural practices. However, user-friendly dormancy model programs are not available. WinTree was designed to fill this need.

2. Materials and methods

WinTree was coded employing Delphi 1.0 language (Borland International, Inc.). Delphi includes the Borland Database Engine (BDE) enabling access to commercial database files (Paradox and others). WinTree runs on Microsoft Windows 95 and Windows NT. WinTree can manage extensive meteorological databases using the BDE. Data can be typed in manually or converted from text files. The program includes a module for dormancy model computations. The WinTree program computes chill units (CU) according to the 'Utah' (Richardson *et al.*, 1974; Anderson and Seeley, 1992, 1993), and other similar models. Anthesis units, (growing degree hours (GDH), (Richardson *et al.*, 1975), or hours at the optimum temperature for growth and development or fractions thereof for each hour

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depending on temperature), are calculated by either the linear or ASYMCUR (Richardson *et al.*, 1982) methods. A workbook or spreadsheet module is included for data manipulation and direct access to the meteorological database. A toolbar is always present to allow the user to switch between program modules.

Hourly temperatures are required to calculate CU and GDH. Hourly data are used directly by the dormancy and anthesis models. Models are used to estimate the hourly course of temperatures when the data is restricted to daily maximum and minimum temperatures.

2.1. Database module

Data files in WinTree are defined and grouped according to their station or geographic origin. Any number of data files can be created for each station. Stations can be defined by country, state, county, or regional areas, or by geographic co-ordinates. Once the station has been created and defined, individual data files are created, with each having a descriptive name. Daily or hourly intervals can be selected. Once the file has been named and the interval has been indicated, data variable names are created. Variables represent the columns or fields in the data file. The variable names appear when the data file is accessed. The units of each variable can be indicated. Temperature data can be entered as either Celsius or Fahrenheit; however, Fahrenheit values are automatically converted to Celsius for CU and GDH calculations. A group of predefined units is included. These units can be modified or supplemented by the user. Once the data file has been created and variables named, a blank database file is created. After the database file has been created, neither the name nor the variable names can be changed. Units can be modified at any time. In addition to the variable name and unit columns, other columns are used for text file import instructions.

2.2. Manual data update module

This module consists of a grid to browse and edit the contents of a selected data file. Selecting an appropriate date is simple using a toolbar. Data can be changed by typing the new value directly in a cell. New dates can be appended at the end of the file (i.e. one record, one day, one week, or one-month intervals). Changing the date or time is allowed only after selecting the appropriate button or menu command.

2.3. Data collection module

The data collection module updates database files by collecting or extracting information from text files. WinTree can process text files where measurements are arranged in columns (i.e. separated by commas). Text files of this type are generated by data loggers, (i.e. CR10, Campbell Scientific, Inc.), and the U. S. National Weather Service. The user can select which rows and columns of data are to be extracted from the text file.

The station and data files to be updated are selected on one side and the text data files to be extracted are selected on the other. Variable records in the database module include information about how to parse the text file including data column positions, lines to read (ID), and how to read the date and time. Unit ranges (database module) are used to filter obviously erroneous data when importing data from text files.

2.4. Dormancy module

The dormancy module is divided in three sections: general, output, and parameters. The module is activated by opening a data file containing hourly or daily temperatures. The general section offers controls to select the starting and ending dates. Dates can be easily extended to cover several seasons by selecting a cycle option.

Traditionally, dormancy models begin by estimating CU until a given accumulation is reached. Then, anthesis units (GDH), are computed until enough units have accumulated for full bloom. CU and GDH values are easily changed manually. In addition, CU and GHD can be calculated independently. WinTree uses a step mode matrix to define each dormancy model. Predefined matrices include the 'Utah' Chill Unit Model, the North Carolina Model (Shaltout and Unrath, 1983) and the Variable Chill Unit Model (VCU) which is a three-dimensional extension of the 'Utah' Chill Unit Model developed for subtropical conditions (del Real-Laborde, 1989). Matrices can be created or modified to create new CU models.

In addition to several linear methods, WinTree includes a sine-exponential model to estimate hourly temperatures (Rojas-Martinez, 1994). Parameters of the sine-exponential model can be modified in the parameter section of this module. Rojas-Martinez (1994) has shown that the sine-exponential model is capable of generating chill estimations with a relative absolute error of less than 3.2% when compared with chill accumulations calculated using hourly temperatures.

Results can be created as hourly, daily, or seasonal (cycle) accumulations. These options can be modified. The results can be sent to the bottom half of the screen where they can be edited and copied, or they can be sent to the workbook module.

The parameters section allows selection of methods to estimate growing degree hours (linear or ASYMCUR). Minimum, optimum, and critical values are easily changed. Also, parameters used to estimate hourly temperatures can be modified here.

2.5. Workbook module

This spreadsheet module provides direct access to the meteorological database and data generated by the dormancy module. The workbook module is essentially a Microsoft Excel-like spreadsheet. By means of a flexible interface, a user can calculate temperature means, maximums, etc. over various time periods such as days, months, and years, etc. These files can be saved (Excel and other formats) for manipulation in other Windows programs.

3. Example

A new station was created for Farmington, Utah in the database module. Station geographic information was added. A new database file for the new station was created to store the daily meteorological information. Data was downloaded from the Utah Climate Center web page (www.climate.usu.edu) as a text file. Variable names were created and appropriate units defined according to the meteorological information contained in the text file. The data file was modified using search and replace to change some weather station identification numbers to a shorter identification used by the collection module. In order to read the text file, column locations were indicated and instructions on how to read the date information was set up. A new empty database file was created. In the data collection module we selected the station, database file, and then the modified text data file. The database file was updated. Switching to the dormancy module, we set up the initial dates from early fall

(9/1) to early summer (7/1) for the first year (1986-87), and set up 11 yearly cycles. CU and GDH information was added for both 'Delicious' apple and 'Redhaven' peach (Table 1). The output was sent to the workbook module, where we compared the predicted date of bloom with the observed date of bloom at nearby field plots [USU experiment station, Kaysville, Utah (Table 2)]. The model selected closely predicted peach bloom (±2.3 days, standard deviation). The model did not predict apple bloom dates accurately (±4.0 day), especially in 1989 when insufficient chill units were accumulated to predict the end of endodormancy. In 1989, delayed foliation was common in Utah (Anderson *et al.*, 1990). When endodormancy ended later than normal, the model would predict a later bloom date than was observed. We believe that this is due to insufficient chilling and/or heat accumulation during endodormancy.

4. Conclusions

The WinTree program is a user-friendly tool for calculating CU and GDH according to the 'Utah' and other similar dormancy models. As it is now, it is a research tool and needs further refinement before it can be used easily by most interested growers. Chill unit (CU) and anthesis unit (GDH) requirements for orchard cultivars need to be incorporated into the dormancy model for easy access and modification. Also, for the program to be predictive, some method needs to be incorporated to predict future temperatures from historic normal temperatures. Once the program completes the analysis of actual current data, it needs to be able to switch to historical normalise for the designated location in order to provide prediction of the end of endodormancy and anthesis phenology events for that location.

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Table 1 - Chill and heat units required for peach and apple rest completion and spring bud phenology as defined by the 'Utah' model

'Redhaven' peach

Chill units	Floral bud stage	Growing degree hours (°C)	Anthesis units*
870	1 First swell	1411	71
	2 Calyx green	2578	129
	3 Calyx red	3271	164
	4 First pink	3710	185
	5 First bloom	4174	209
	6 Full bloom	4926	246
	7 Post bloom	5491	275

' Delicious' apple

Chill units	Floral bud stage	Growing degree hours (°C)	Anthesis units*
1234	1 Silver tip	2061	103
	2 Green tip	2544	127
	3 Green ½ inch	3100	155
	4 Tight cluster	3939	197
	5 First pink	4856	243
	6 Full pink	5394	270
	7 First bloom	6172	309
	8 Full bloom	6933	347

* One hour at the optimum temperature for growth and development during anthesis

Table 2 - Comparisons of observed apple and peach full bloom dates (Kaysville, Utah) with dates predicted using the 'Utah' model (daily max/min temperatures, Farmington, Utah) as calculated with WinTree. The temperature data was downloaded from the web and imported into a database file in WinTree. Hourly temperatures were estimated using the sine-exponential method.

'Red Delicious' apple

Cycle	CU start date	CU end date	CU sum At end	GDH start date	Predicted full bloom date	GDH sum at end	Observed full bloom date	Difference
1	09/01/86	02/12/87	1244.5	02/13/87	04/25/87	6957	04/26/87	-1
2	09/01/87	03/22/88	1243.5	03/23/88	05/04/88	7040	04/29/88	5
3	09/01/88	06/01/89	909.5	12/30/99			04/22/89	DF
4	09/01/89	03/05/90	1246.0	03/06/90	04/20/90	7065	04/20/90	0
5	09/01/90	03/10/91	1234.5	03/11/91	05/12/91	6952	05/15/91	-3
6	09/01/91	03/07/92	1248.0	03/08/92	04/18/92	6999	04/15/92	3
7	09/01/92	04/11/93	1246.0	04/12/93	05/18/93	7078	05/11/93	7
8	09/01/93	02/18/94	1238.5	02/19/94	04/25/94	7052	05/02/94	-7
9	09/01/94	02/17/95	1244.0	02/18/95	05/02/95	6953	05/01/95	1
10	09/01/95	02/10/96	1237.0	02/11/96	04/29/96	6962	05/03/96	-4
11	09/01/96	02/11/97	1234.5	02/12/97	05/04/97	7160	05/06/97	-2
							Standard deviation	4.03

'Redhaven' peach

Cycle	CU start date	CU end date	CU sum at end	GDH start date	Predicted full bloom date	GDH sum at end	Observed full bloom date	Difference
1	09/01/86	12/05/86	886.5	12/06/86	04/17/87	5301	04/16/87	1
2	09/01/87	02/18/88	870.5	02/19/88	04/16/88	5139	04/17/88	-1
3	09/01/88	03/18/89	882.5	03/19/89	04/19/89	5175	04/19/89	0
4	09/01/89	01/25/90	876.0	01/26/90	04/11/90	5101	04/11/90	0
5	09/01/90	02/12/91	877.5	02/13/91	04/20/91	5048		M
6	09/01/91	02/12/92	887.5	02/13/92	04/07/92	5034	04/07/92	0
7	09/01/92	03/12/93	877.5	03/13/93	04/24/93	5013	04/29/93	-5
8	09/01/93	01/13/94	874.0	01/14/94	04/17/94	5088	04/19/94	-2
9	09/01/94	01/12/95	873.0	01/13/95	04/12/95	4995	04/08/95	4
10	09/01/95	12/15/95	889.0	12/16/95	04/11/96	5087	04/13/96	-2
11	09/01/96	12/29/96	883.0	12/30/96	04/19/97	5189	04/17/97	2
							Standard deviation	2.34

Session 5
Pest management

A NEW DEMAND FUNCTION FOR GRAPEVINE FRUITS IN VINEMILD

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Keywords: Growth, *Plasmopara viticola*, *Vitis vinifera*, simulation, dry matter

Abstract

The 'Vinemild' model simulates downy mildew development on grapevine and its influence on yield and is composed of a grapevine growth model coupled to a disease model. Due to unsatisfactory results, the original fruit demand function of the growth model was replaced by a new function. A two growth-curve model used for the simulation of pit fruits was selected and fitted to field data collected for this purpose in 1997. Simulation runs made with the new demand function were compared to runs made with the original function and to field data of berry dry weight collected in the two previous years. A function relating fresh weight of berries to dry weight was obtained by linear regression of 1997 data and used to transform the fresh weights measured in 1995 and 1996 into dry weight data. The simulations were always better with the new function, however the model failed to reflect the dry weight of berries in 1996, which was more than 50 % higher than in the other two years. It is concluded that the new function is an improvement over the original one, but that the problems of variations in berry number and weight will have to be addressed.

1. Introduction

The 'Vinemild' model, aimed at the evaluation of the risks of quantitative and qualitative grapevine yield losses due to the downy mildew fungus, *Plasmopara viticola,* is composed of a disease model coupled with a dynamic crop growth model of grapevine (Blaise *et al.*, 1996). Although the first simulations gave encouraging results (Dietrich *et al.,* 1998), reflecting the influence of the fungus on yield formation for the first test year, further analysis and comparison with other field data sets showed that, while the simulation of grapevine growth dynamics was realistic, the model failed to reproduce the correct level of fruit mass.

This led us to re-examine the components of the grapevine growth model and especially to adapt the demand function so that the model would reflect more accurately the yield level. Most literature data on the growth of reproductive organs are given in term of fresh weight; the allocation of photosynthates however is more accurately expressed on a dry weight basis, which is also the basis of the model output, so that specific field data had to be collected. We present here field data of berry growth of Merlot grapevine and the changes we made to the 'Vinemild' model to improve the simulation of grapevine yield formation.

2. Material and methods

2.1. Field data

In 1995 and 1996, monitoring of growth and yield factors has been made in a small experimental vineyard of Southern Switzerland planted with 20 years old *Vitis vinifera* cv. Merlot grapevines grafted on rootstock *Riparia* x *Rupestris* 3309. The training system was the Guyot double, usual in this part of Switzerland, with distances of 1.4 and 1.8 m within and between the rows respectively, resulting in a density of 3960 plants per ha. The number of shoots per meter row length has been regulated to 11. A first topping of the plants was done mid-June and a second one mid-July.

Two treatments were considered for the control of *P. viticola* on leaves: untreated and normal treatment schedule from the beginning of the season. The two plots, separated by a third one (not presented here), were sub-divided into six blocks of eight contiguous plants considered as six repetitions. To prevent quantity losses, in the untreated plot, only the clusters were treated once with a contact fungicide when the first disease symptom ("oil spot") was discovered on the leaves. Disease severity was estimated with an extended Horsfall scale (Horsfall and Cowling, 1978).

The evolution of the yield parameters was measured weekly from véraison (berry colouring) until harvest: for each treatment, 4 samples of 100 and 40 berries were taken in 1995 and 1996 respectively from which berry fresh weight was determined.

In 1997, monitoring of the disease and of plant growth and yield factors was done in an experimental vineyard near the one used in 1995 and 1996. It was planted with 6 years-old *Vitis vinifera* cv. Merlot grapevines grafted on rootstock *Riparia* x *Rupestris* 3309 trained as a double Guyot with a spacing of 2 x 1.20 m between and within the rows respectively (4166 plants/ha). The vineyard was divided in two plots treated as in the previous years. Disease severity evaluation began on May 27 and was done weekly until the last sampling, which was done just after harvest. Berry dry matter was estimated weekly from July 21 until harvest based on 3 random samples of 50 berries. For the six first sampling dates (out of 13), samples were pooled.

In order to get comparable results between the plots, in 1995, 1996 and 1997 the number of clusters was limited, based on the plot with the lowest potential, to result in a homogeneous theoretical production of 1.5 kg/m^2, 1.4 kg/m^2 and 1.3 kg/m^2 respectively.

2.2. Demand function

The function described by Génard and Bruchou (1993) for the growth of peach fruits was used:

$$Y(t) := P_1 * (1 - \exp(-P_2 * t)) + P_3 / (1 + \exp(-P_4 * (t - P_5)))$$

where Y is the dry weight of a berry at time t, and $P_1..P_5$ a set of parameters. Parameter estimation was done by fitting the function through field data from 1997 with the help of a curve-fitting tool (FitAll, MTR Software, Toronto ON, Canada).

The demand function δ_F is then found by deriving the function Y(t) with respect to t:

$$\delta_F = P_1 * P_2 * \exp(-P_2 * t) + P_3 * P_4 * \exp(-P_4 * (t - P_5)) / (1 + \exp(-P_4 * (t - P_5)))^2$$

2.3. Simulations

Simulation runs were made with weather data from an automatic weather station near the experimental vineyard. To eliminate differences due to unequal berry numbers in the different plots, the actual number of berries measured in the field was used for each run.

3. Results and discussion

Growth of grape berries is usually described as being divided into three phases, where two phases of fast growth are separated by a slow growing phase which length is cultivar specific (Coombe, 1980; Currle *et al.*, 1983). Field measurement of berry development in 1997 expressed as dry weight indicate that for the Merlot cultivar the duration of the first growth phase is around 200 day-degrees over 10° C (DD) after fruit set while the length of the other phases amounts ca. 200 DD and 600 DD respectively (Fig.1). Véraison occurred around 450 DD after fruit set, which corresponds to the beginning of the second phase of rapid growth. The average dry weight of a berry at harvest was 0.35g and 0.34g in the treated and the untreated plot respectively, which is clearly more than what Wermelinger *et al.*(1990) reported for Pinot Noir (0.273g).

Simulation of the growth of grapevine fruits has been done for Chenin blanc by Gutierrez *et al.* (1985) assuming a constant demand of the berries at two different levels, the threshold for level change being set at 1111 DD. This results in a two-phase linear growth, which can be only an approximation. In the original model for grapevine used in 'Vinemild', Wermelinger *et al.* (1991) used a quadratic function to simulate the fruit demand of Pinot Noir berries, leading to a sigmoid growth function (Fig. 2). The two approaches however fail to represent adequately the three phases of berry growth. Considering that this division of berry growth in three phases is very similar to the growth of pit fruits such as peach, the simulation of which has been successfully made by Génard *et al.* (1993) as well as other authors (cited by Génard *et al.*), we applied their model to the grapevine. This approach assumes a two-phase growth characterized by a two growth-curve model composed of a monomolecular and a logistic function, the phase of slow growth corresponding to the overlapping of the two curves.

Fitting the two-phase growth function to the field data allows to mimic adequately the growth of a berry (Fig. 1). The resulting parameters are given in Table 1.

Comparing the so obtained growth function and its derivative demand function with the growth respectively demand functions of the original model reveals that (Fig. 2): i) the function proposed for Pinot Noir underestimates the growth of Merlot berries and ii) the shapes of the demand functions are completely different for the first half of the growing period, being even opposite during the first growth phase.

To evaluate the new demand function within the 'Vinemild' model, simulations were done with weather data from 1995 and 1996 and compared with the corresponding field data collected in our trial vineyard. However, since the model output is expressed as dry weight and only berry fresh weight data was available for these two years, dry weight had to be estimated. The relation between fresh and dry weight of berries samples taken during the whole season 1997 was established by linear regression (Fig. 3). The linear function obtained was then used to calculate dry weight from berries sampled in the earlier years.

Simulation runs of the berry growth for the three years are presented in Fig. 4. Since the data from 1997 were used to calibrate the demand function, even if the growth rates are controlled by the interplay between photosynthate supply-demand it is not surprising that the simulation follows closely the field data for this season. Although only few data points exist for 1995 and 1996 and therefore no evaluation of the simulation of growth dynamics is possible, it can be seen that the newly implemented demand function performs always better than the original one. In 1995, although the dynamics of the last growth phase is not exactly reproduced, the simulation of berry dry weight is nevertheless satisfying, reaching the value measured in the field. In contrast, simulation for 1996 fails to reproduce the observed growth and highlights a main problem of the simulation of grapevine growth: the average size of the berries, which are the basic unit of fruit growth in the model can vary greatly from one year to the other. In 1996, the average berry was 54% heavier in the untreated plot than in 1995 (Table 2). Large variations in berry size were observed also by Coombe (1980), which attributed variations between berries on the same plant for a small part to competition between bunches but could not explain the large part of the variation.

Another problem is the variability in the number of berries per plant within a plot and between plots, which is not reproduced by the model. In 1995 and 1997, the different number of berries per plant is responsible for the greatest part of yield variation between plots (Table 2). Two explanations can be given for these discrepancies: i) an important factor for berry size variation between plots and years lays in the manual thinning for the regulation of crop load and ii) although it was not monitored, early infections of clusters by downy mildew may have lead to berry destruction.

Even if still not perfect, the two growth-curve model represents a significant improvement over the original quadratic model. Future work will have to concentrate on two directions: i) to master the problem of the berry number or to change the fruit unit and ii) to establish which factors may be responsible for the great variation in berry weight.

Acknowledgements

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Table 1 - Parameters of the new demand function obtained by fitting the two growth-curve model to the 1997 field data of berry growth.

P_1	P_2	P_3	P_4	P_5
4.95E-02	1.05E-02	3.08E-01	9.03E-03	6.27E+02

Table 2 - Components of yield of Merlot grapevine at harvest in three consecutive years in plots treated against *Plasmopara viticola* and untreated plots, and corresponding results of simulation with the 'Vinemild' model.

			DM / berry [g] (SD)	Berries / plant (SD)	DM / plant [g]
1995	Field	Treated	0.383 (0.026)	1771 (321)	680.1
		Untreated	0.366 (0.009)	1525 (228)	558.2
	Simulated	Treated	0.367	set to 1770	650.0
		Untreated	0.369	set to 1530	562.7
1996	Field	Treated	0.461 (0.010)	1309 (143)	603.4
		Untreated	0.563 (0.088)	1279 (257)	720.1
	Simulated	Treated	0.371	set to 1300	485.6
		Untreated	0.371	set to 1280	474.5
1997	Field	Treated	0.350 (0.014)	1478 (112)	551.3
		Untreated	0.342 (0.011)	1280 (176)	437.8
	Simulated	Treated	0.351	set to 1480	518.8
		Untreated	0.350	set to 1280	448.0

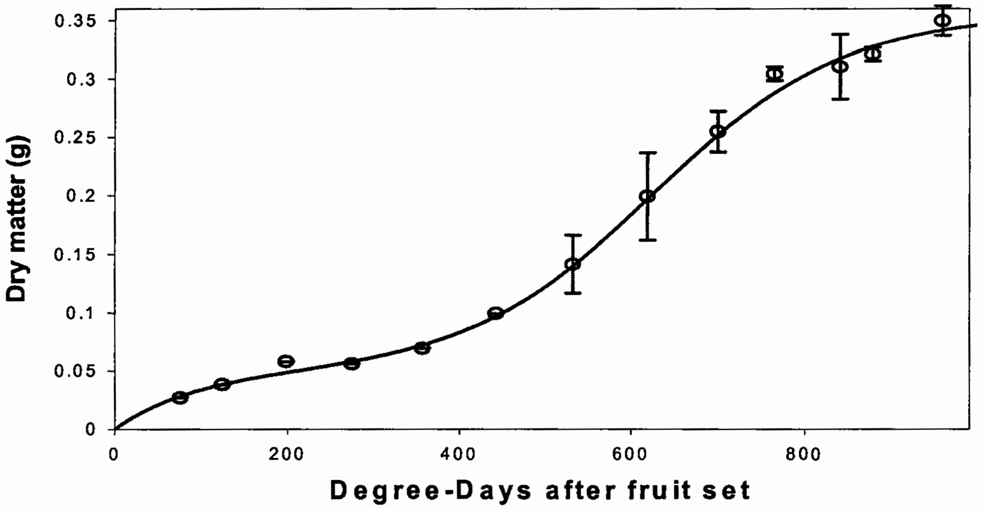

Figure 1 - Accumulated growth of a Merlot grapevine berry expressed as dry matter in 1997 (circles) and two growth-curve model (solid line) fitted to the data points. Except for the 6 first dates where samples were pooled, each value is the average of 3 measurements.

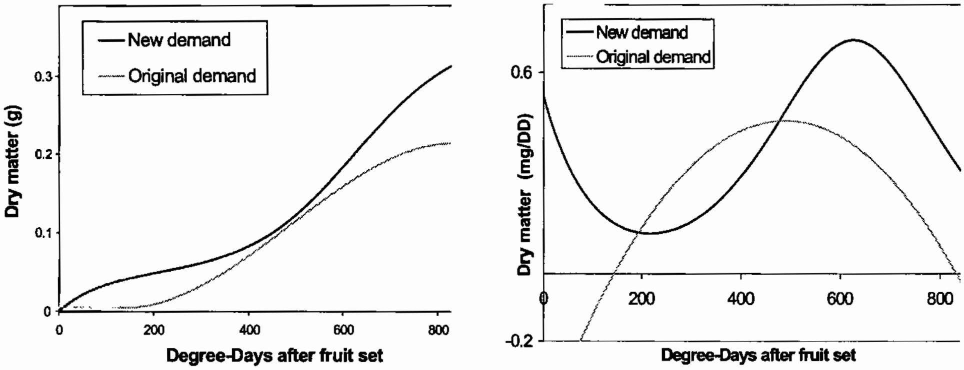

Figure 2 - Comparison of the original quadratic model for fruit demand and growth of Pinot Noir berries (gray line) and of the two growth-curve model fitted to the data from 1997 for Merlot. Left: cumulated growth of a berry. Right: demand rate of a berry (mg/DD).

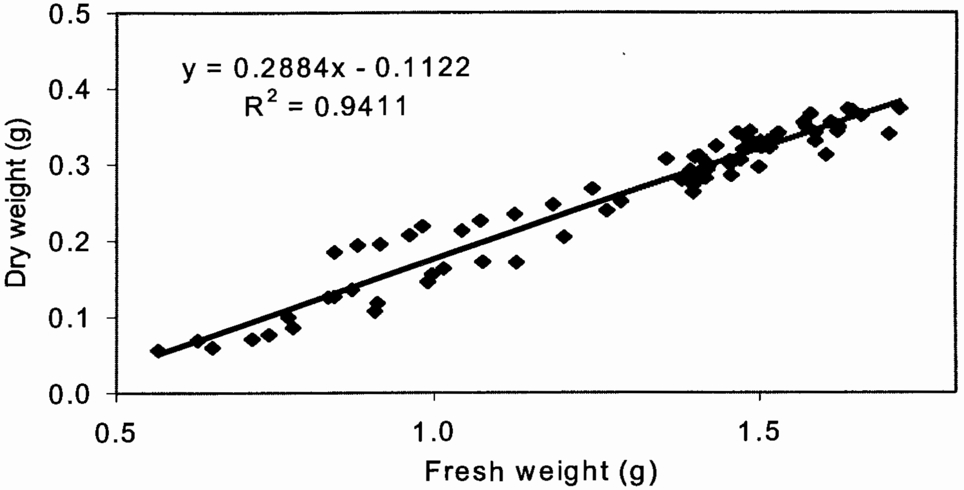

Figure 3 - Correlation between fresh and dry weight of Merlot berries sampled at weekly intervals in 1997. Each point represents the average weight of a berry in a sample of at least 50 berries.

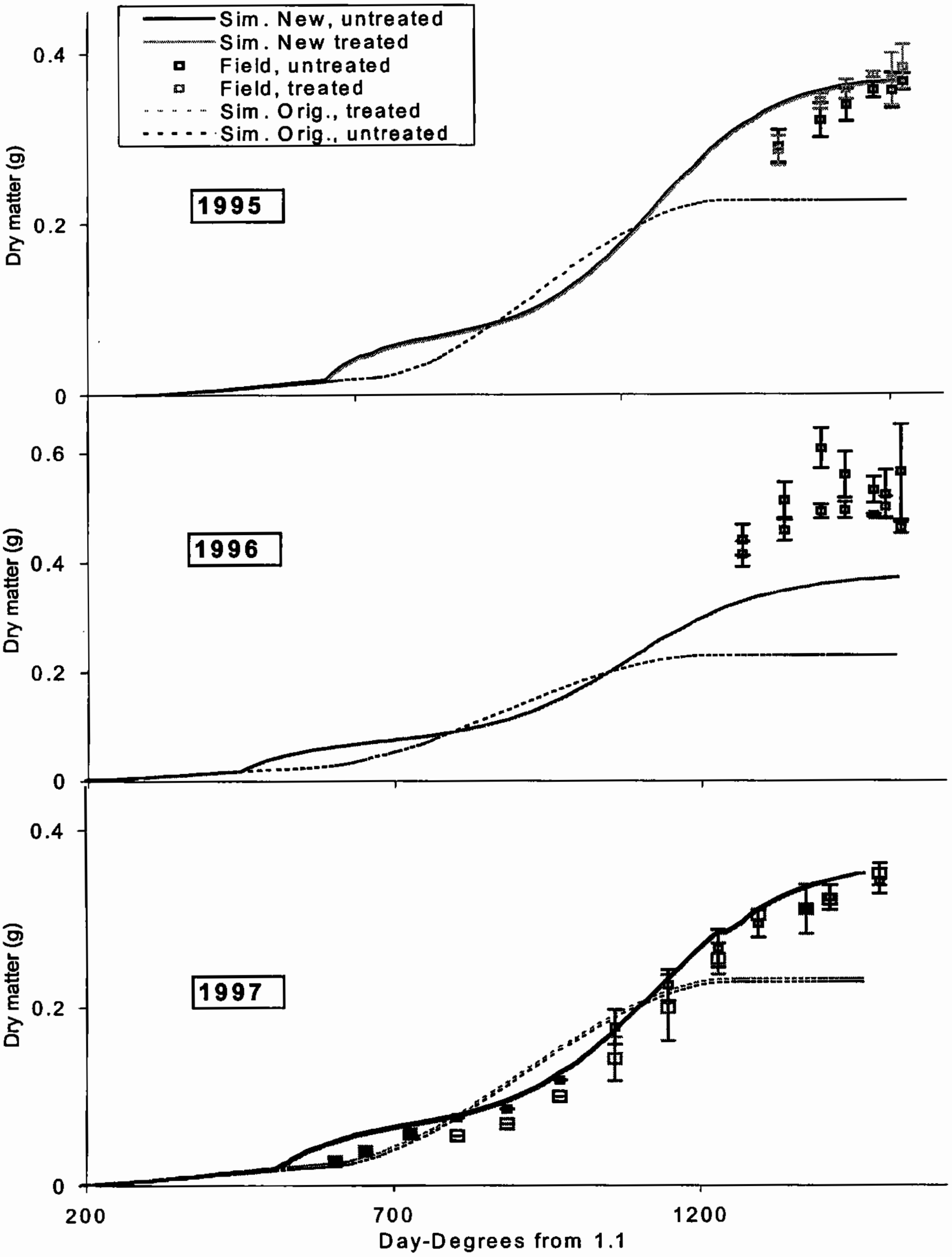

Figure 4 - Simulated development of the berry weight of Merlot grapevine and corresponding field data for three consecutive years. Dotted lines: simulation with the original demand function; Solid lines: simulation with the new demand function; Squares: field data. The black color corresponds to the treated, grey to the untreated plot.

A SIMULATION STUDY WITH A DUTCH AND A CANADIAN STRAIN OF THE PARASITOID *APHELINUS MALI* (HALD.) FOR CONTROL OF WOOLLY APPLE APHID *ERIOSOMA LANIGERUM* (HAUSMANN) IN THE NETHERLANDS

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Abstract

Woolly apple aphid (*Eriosoma lanigerum* Hausmann) is one of the major apple pests in the Netherlands. Weather conditions and natural enemies determine whether woolly apple aphid (WAA) will reach pest status. In some years WAA escapes control by natural enemies, and has to be controlled chemically. To prevent unnecessary spraying and to promote biological and natural control of WAA more knowledge has to be obtained about the role of natural enemies, weather and their interactions on the development of WAA. The monophagous parasitoid *Aphelinus mali* (Hald.) has been introduced in most of apple growing areas to control WAA with more or less success. In springtime, the parasitization level by *Aphelinus mali* is often too low to be effective in time for the farmer, but during summertime the parasitization level may be high (Mueller *et al.*, 1992).
The purpose of this research is to see whether strains of *A. mali* may exist that are better adapted to the 'Dutch' climate, which is characterised by a cool spring. The effectiveness of different strains of the parasitoid *A. mali* under Dutch climatological conditions is compared using a simulation model of the population interaction between woolly apple aphid and *A. mali.*

1. Introduction

1.1. Woolly apple aphid

Woolly apple aphid (*Eriosoma lanigerum* Hausmann) is an important apple pest in the Netherlands. Weather conditions and natural enemies determine whether woolly apple aphid (WAA) will reach pest status. In some years WAA escapes control by natural enemies and has to be controlled by means of spraying with Pirimicarb. To prevent unnecessary spraying and to promote biological and natural control of WAA, more knowledge has to be obtained about the role of natural enemies, weather and their interactions on the development of WAA populations. The woolly apple aphid *Eriosoma lanigerum* (Hausmann) is a native secondary pest of apple in the United States of America. In North America it has two hosts: the apple *Malus domestica* (Borkh.) and the elm *Ulmus americana* L. The elm serves as winter host.

The 'Dutch' WAA has only one host, the apple, since the American elm does not occur in Holland (Evenhuis, 1958). WAA infests both stem and roots of apple trees (Brown 1986), causing hypertrophy and gall formation. Stylet penetration to suitable tissues for

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feeding is a time- and energy-consuming process. Therefore the aphid usually remains sessile (Mueller *et al.*, 1992). Favourite penetration sites are wounds on the trunk and branches and new growth shoots (Mueller et. al., 1992; Evenhuis, 1958). The galls form ideal feeding sites for their offspring (Geoffrion, 1985), and they often result in the formation of densely packed colonies. The galls are also ideal places for infection by Apple canker (*Nectria galligena*), especially when they crack. Despite these seemingly ideal circumstances, the first instar nymphs ('crawlers') leave the colony to form new colonies mostly on new-formed shoots. Mortality of these emigrating nymphs is high, and only approximately 5% survive to find a new penetration site and found a new colony (Mols 1996). WAA reproduces asexually, giving birth to female offspring only. The size of the offspring differs between countries and probably also between climates. The monophagous parasitoid *Aphelinus mali* (Hald.) has been introduced in most of apple growing areas to control WAA with more or less success. The parasitization level by *Aphelinus mali* in springtime is often too low to provide effective control. However, the 'French' and 'Dutch' results are based on the introduction of only 3 and 4 females respectively. The purpose of this research is to see whether strains of *A. mali* exist that are better adapted to the Dutch climate. This is done with help of simulations to explore the effectiveness of this strain under Dutch conditions.

1.2. Biology of the parasitoid *Aphelinus mali* (Hald)

The above ground populations of WAA are attacked by many natural enemies of which the parasitoid *Aphelinus mali* is the most important. Parasitization level by *Aphelinus mali* in springtime is often too low to be effective in time for the farmer, although during summertime parasitization may be high (Mueller *et al.*, 1992). The parasitoid *Aphelinus mali* (Hald.) has been introduced to control WAA in most of the areas where WAA occurs. These introductions have met with more or less success, probably depending on the climatological conditions. The WAA has 10-11 generations per year, while the parasitoid has only 4-5.

The problem with the Dutch strain of *A. mali* is that, although in many years biological control seems to be efficient, in some years, especially when winters are relatively warm (average temperatures in January and February above zero degrees), the woolly apple population starts growing too early, reaching levels, at the moment that *A. mali* breaks diapause, that cannot be conquered by the parasitoid anymore. A strain of *A. mali* that becomes active earlier in the year, therefore has an advantage above one that breaks diapause later.

It is uncertain whether strains exist that are better adapted to the Dutch weather situations. The chance to find better adapted strains than the one now present in the Netherlands will closely coincide with prevailing weather conditions. Therefore, we searched an area in the origin area of WAA where weather conditions look like the Dutch climate and where the WAA-parasitoid complex exists. In Nova Scotia (Canada) we found such an area and we also did find *A. mali.*

In 1997 research was done concerning biological characteristics of *A. mali,* like post-diapause development and developmental temperature thresholds.

2. Modelling

2.1. The modelling environment

The model is implemented in the INSIM (INsect SIMulation) environment (Mols and Diederik, 1996). INSIM is menu driven and uses biological information of the insect species. INSIM generates age-structured models and therefore includes modules that calculate the number and development of insects by use of 'boxcars', to account for the variable speed of development ('dispersion') in insect populations (de Wit and Goudriaan, 1978). A so-called distributed-delay process then represents the flow of individual insects from one stage to the next. The core of the program is the so-called fractional boxcar train, which is used to mimic the dispersion of the individuals passing through a life stage (Goudriaan and van Roermund, 1989). The number of life stages determines the basic structure of the insect model. By means of tables, life-history data are read into the program. For a simple phenological or population model the information required is: life cycle, developmental rate and standard deviation of stage duration for each insect stage, sex ratio, life expectancy of the adult and age dependent reproduction. The stages are coupled to each other in a spreadsheet, which makes the program flexible. For the simulation of complicated interactions between prey and predators or parasitoids, an extra module is added. All code is written in Visual Basic.

The weather data, the minimum and maximum daily temperature, are stored in an environment file. The temperature for each time step is calculated from a sinusoidal curve through the daily minimum and maximum temperature. User-selected variables can be presented graphically or numerically on the screen.

2.2. Simulation of biological control of woolly apple aphid with *A. mali*

To gain more insight in the role of the various factors that influence biological control of WAA, research has been started to unravel the population dynamics of WAA and its natural enemies. To evaluate the role of these enemies, a basic simulation model is developed that simulates the growth of WAA under field conditions, and a model for the population dynamics and impact of the parasitoid *A. mali* is coupled to it. First, the relationships found for the Dutch strain of *A. mali* were included into the model and secondly those of a Canadian strain. With help of this model it is possible to simulate the population dynamics of both WAA and *A. mali* under several temperature conditions. The outcome of the model can be used to predict whether a Canadian strain of *A. mali* may be used for control of WAA in the Netherlands.

2.3. Bionomics of woolly apple aphid

- The developmental rates of the nymphal stages with their dispersion and adult longevity were derived from Walker (1985) and Bodenheimer (1937).
- Age dependent reproduction was derived from Walker (1985), Evenhuis (1958), Bonnemaison (1965) and Ehrenhardt (1940).

- Mortality, especially of the crawler stage, is related to temperature. Mortality in winter differs for the various stages of WAA. The younger the stage, the greater its resistance for frost, which may partly explain the greater chance of WAA outbreaks following soft winters (Jancke, 1935; Ehrenhardt, 1940; Kjellander, 1953).
- Above a threshold of 15°C the crawlers leave the colony and swarm out in search for young shoots, where they try to establish a new colony (Hoyt and Madsen, 1960). From our experiments it became clear that during this phase mortality is very high. In the laboratory 40% succeeded in founding a new colony, while in the field only 5-8% was able to do so, even when protected against natural enemies. Laboratory tests with an artificial rain maker with rain at various wind speeds did not give any significant relationship with colony founding success in the range tested (rain 20-25 ml/hour and wind of 0, 2, 7 and 18 m/sec tested for 5-30 min.). However, in the field, heavy rainstorms had a large effect in one year, while in another year no single weather factor had a significant influence on founding success, but a combination of factors was still important. In the model an average survival of 8 % is assumed for the crawler stage.
- The influence of the apple tree is not included in the model. However, the apple tree, as host plant of WAA, may have a strong influence on the performance of WAA by:
  1) Resistance. Apple varieties exist which are partially resistant to WAA. Resistant rootstocks inhibit the hibernation of WAA on the roots during winter. Relationships in the model hold for (at least) apple cultivars Golden Delicious and James Grieve.
  2) Plant condition (governed by fertilisation and moisture) may affect developmental rate and longevity.

2.4. Bionomics of Dutch and the Canadian strains of the parasitoid *Aphelinus mali*

In the model are included:

- Investigations on post diapause development and developmental thresholds of a Dutch strain of *A. mali* were done by Trimble *et al.*, (1990). They investigated post diapause developmental rate (Y) in relationship to temperature (T) for the Dutch strain and found a linear relationship, $Y = -0.00682 + 0.0073\ T$, which indicates a temperature sum of 136.4 degree-days and a developmental threshold of 9.6 °C.
- Adult longevity depending on temperature (Bonnemaison, 1964; Evenhuis, 1958).
- Parasitization rate in relation to weather factors and aphid density (Evenhuis, 1958). Data about a functional response were lacking. A linear Holling type I functional response is assumed with a plateau level depending on maximum parasitization/day in relation to temperature and aphid availability. The maximum egg production capacity is 85 eggs per female (Evenhuis, 1958). The maximal attained egg production per day depends on temperature and availability of aphids as host. A search rate, a', of 0.1 was used in both strains. The search rate, a', is the initial slope of the functional response and expresses the proportion of surface area of a tree searched by one parasitoid per day.

- Egg and larval development up to the mummy stage (Mueller *et al.*, 1992). These development rates in the host depend on temperature and on the age of aphid stages (Mueller et al, 1992). Development takes shortest time in fourth stage WAA nymphs and in adult aphids, and longest in first stage nymphs.
- Sex ratio depending on the size of the host stages (Mueller *et al.*, 1992). The sex ratio is strongly biased to males when small stages are parasitized and to females when eggs are deposited into adults.

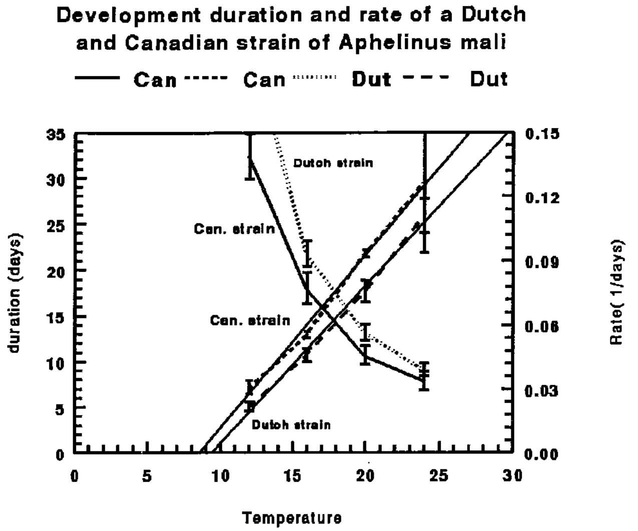

Figure 1 - Development duration and development rate of a Dutch and a Canadian strain of *Aphelinus mali* at constant temperatures

The results of the experiments concerning the Canadian strain indicate that the threshold of development of the Canadian strain is lower than that of the Dutch strain, 8.6°C vs 9.4 °C respectively. The temperature sum required for development of the Canadian strain is also lower than that of the Dutch strain: 123.5 vs 136.4 degree-days, because the relationship of the rate of development with temperature is steeper in the Canadian than in the Dutch strain. The other figures like fecundity, egg and larval development longevity, sex ratio and parasitization rate are kept the same as in the 'Dutch' strain. Sensitivity analysis is done concerning these factors.

2.5. Input for simulation

Normally the number of WAA is measured by an average surface covered by WAA because of the wax cover numbers are very difficult to be estimated in a non-destructive way. The relationship between WAA surface and numbers has been estimated experimentally to be 200 individuals per cm^2. The simulation starts each year at the first of January with the average WAA surface found in one tree for that time of the year: which is 1/2 cm^2 of WAA. This is on average 100 WAA in a stable age distribution: 65 N1, 16 N2, 8 N3, 6 N4 and 5 Adults.

With *A. mali* we started each year with 20 female mummies and 10 males per tree. This density is arbitrary and depends on the ability to control WAA during the summer in a normal year (Mols, 1997).

For the Canadian strain, the figures like fecundity, egg and larval development longevity, sex ratio and parasitization rate are kept the same as in the 'Dutch' strain of *A. mali.*

We did several simulations with the Dutch and with the Canadian strain, especially to be able to see the performance in different years. We used temperatures of the meteorological station in 'de Bilt', which is in the centre of the Netherlands. We selected 1990, 1995 and 1996, because these years show contrasting winters: 1990 had a warm winter, 1995 had an 'average' winter, while the winter of 1996 was exceptionally cold.

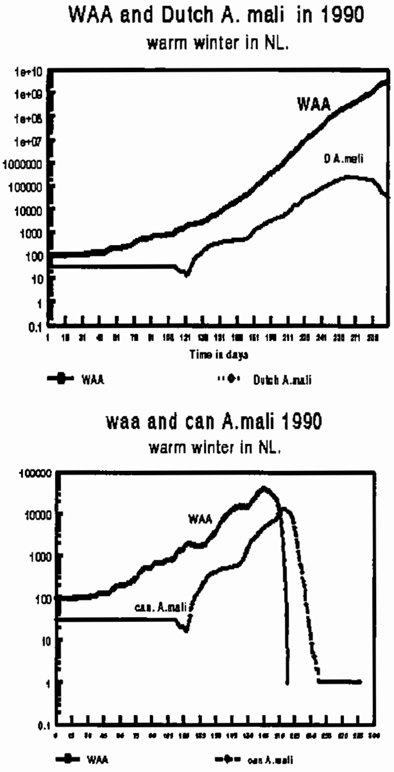

Figure 2 - Population development of woolly apple aphid in relation with a Dutch (upper figure) and a Canadian strain (lower figure) of its parasitoid *Aphelinus mali* for the year 1990. The winter of 1990 was relatively warm.

3. Simulation results

For the year 1990 we see that WAA completely outnumbers the Dutch strain of *A. mali* (Fig. 2). The Canadian strain performs much better after the relatively warm winter in 1990. We do not see the extreme exponential growth of WAA as we saw in the Dutch strain, but we see an onset to an exponential growth that is controlled by the Canadian strain in that year at day 195. For the years 1995 and 1996 a better control of WAA by the Canadian strain is obtained which is due to the colder winters in those years.

4. Discussion

Both temperature threshold and thermal constant values were lower for the Canadian strain compared the Dutch strain of *A. mali* 8.6°C against 9.4°C and temperature sums of 123.5 against 136.4 degree-days respectively. This is an indication that the Canadian strain may break diapause sooner than the Dutch strain and thus start activity earlier in the year as is shown by the simulations. This is a strong advantage of the Canadian strain. The Dutch winters are relatively mild while those of Canada are much colder and therefore cause higher mortalities (Jancke, 1935).

The question how large the winter mortality of the Canadian strain is, can only be answered by experiment. Other questions that remain are:

- Is the fecundity the same for the different strains? Up till now there are no indications from literature for differences in fecundity, but of course it has to be looked at.
- Does a difference exist between the strains in the rate of development of both the egg and larval stages in the host?
- How do the searching capabilities of the strains compare? We assume that it is the same for the two strains. Therefore, we used a Holling I curve with an a' of 0.1 in both strains. Changing the value of a' has a strong effect on the performance of the strains.

Ultimately, the proof of the pudding is by introducing the Canadian strain into the Netherlands and see how it performs.

5. Acknowledgements

We thank R Smit in Nova Scotia for giving Jan Boers the opportunity to do experiments at the station and we thank all the people who helped him. We thank Dick Diederik who programmed the model and many students who did an excellent job collecting data at experimental orchard 'de Schuilenburg' in Lienden, The Netherlands.

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Session 6
Orchard management

3D DIGITIZING BASED ON TREE TOPOLOGY : APPLICATION TO STUDY THE VARIABILITY OF APPLE QUALITY WITHIN THE CANOPY

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Keywords: *Malus domestica*, tree architecture, tree training

Abstract

For several years we have been addressing the problem of designing dedicated databases to quantitatively explore plant architectures. In a first step, plants were decomposed into constituents, at different levels of details, and their topology represented by specific models. In a second step, a geometric description of plant constituents was integrated into the databases. This paper illustrates how these databases can be used to study the variability of apple quality at harvest time, accounting for the relative location of both fruit and vegetative growth within the canopy.
Two training systems, i.e. bent and not bent, were compared for 'Fuji' variety. Two trees per modality were described. The topology was organized into four scales of details, including both fruits and different kinds of vegetative shoots. The geometry of each constituent was described with a few parameters that were measured in the field, and its spatial location was recorded using a 3D digitizer (3SPACE® FASTRAK®, Polhemus Inc.). Geometric parameters and spatial coordinates were considered as constituent properties and were attached to the corresponding constituents in the database. At harvest, the main usual quality parameters were analyzed for each individual fruit (height and diameter, refractometric and starch indexes, color, firmness). These parameters were integrated into the database, as variables attached to fruit entities.
Three-dimensional representations of the digitized apple trees were reconstructed using AMAPmod software. The visual comparison between 3D reconstructions and photographs gave us a natural feedback of the measurements, at whole plant scale as well as at branch scale. The fruit quality variability within the canopy was explored *a posteriori* building fruit samples, according to different criteria (spatial location, topological location, number of leaves of the associated bourse-shoot) and taking advantage of the multiscale description of the tree. This approach highlighted that fruit characteristics at harvest are influenced by the vegetative growth considered at different scales within the canopy: (i) the total vegetative growth of the whole tree, (ii) the relative arrangement of the shoots within the canopy and their location with respect to the fruits, (iii) the local vegetative context of the fruits.

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1. Introduction

The variability of fruit quality within the canopy handicaps orchard profitability: delays in fruit maturity force to multiply picking dates and differences in fruit weight and color force to sort the fruits. Previous researches showed that several factors are involved in fruit quality variability:

(i) The shade and the penetration of global solar radiation within the canopy are currently described as key factors for fruit coloration (Jackson *et al.*, 1971; Proctor *et al.*, 1975; Robinson *et al.*, 1983; Kappel and Neilsen, 1994). These parameters vary with spatial location (azimuth, height, distance to the trunk, etc.) (Tustin *et al.*, 1988; Voltz *et al.*, 1993; Génard and Baret, 1994) and, since they influence the photosynthetic activity of the leaves, they modify the carbon export to the fruits (Corelli-Grapadelli *et al.*, 1994).

(ii) The total number of leaves supplying carbohydrates to the fruits or the fruit/leaf ratio influences the carbohydrate content of the fruits (Corelli-Grapadelli *et al.*, 1994; Poll *et al.*, 1996).

(ii) The topological position, i.e. the relative position of an organ with respect to the other ones has also been shown to have a determinant effect on fruit size and maturity (Farhoomand *et al.*, 1977; Patten *et al.*, 1986; Barritt *et al.*, 1987).

To study the penetration of global radiation, the canopy structure (Norman and Campbel, 1989) and, more recently, the spatial arrangement of individual components of the plants were studied. Several digitizing methods were thus developed to locate fruits and leaves in space (Smith *et al.*, 1992; Smith and Curtis, 1995; Sinoquet and Rivet, 1997). On the other hand, to address the problem of designing dedicated databases to quantitatively explore plant architectures, we developed a method to describe the topology of plant components (Godin and Costes, 1995; Godin *et al.*, 1997a). Recently, a multiscale model of plant topological structures was proposed (Godin and Caraglio, 1998).

This paper describes how topological databases were complemented by spatial information and how these databases can be explored in order to study the factors involved in fruit quality variability within the canopy. Statistical analysis were performed on different fruit samples organized *a posteriori* according to different criteria (spatial location, topological location, local vegetative context of the fruits) and according to the different scales used for plant description. This approach aims at studying plant entities development, in the present case the final fruit quality, as a function of their location within the canopy taking into account their relative context of development.

2. Material and method

2.1. Plant material

Two blocks of twenty 'Fuji' trees, grafted on 'Pajam' rootstock, were planted at the INRA experimental station of Montpellier in 1995, after one year of growth in nursery. In 1995 and 1996, all the trees were trained in the same way, selecting long axillary shoots along the trunk. From spring 1996, the trees belonging to one block were trained according to the "Solaxe" system: all the long shoots and twigs were bent; the trunk itself was bent when it reached a wire located at 2.5 meters from the ground. The trees of the second block were let without shoot bending and, in the following, are said to be trained in "Free" system.

2.2. Fruit quality characteristics

All the fruits of the digitized trees were harvested at a single date, according to a given starch index. On each tree, the fruits were labeled and analyzed individually: their weight, diameter and height, refractometric index (RI) and starch index (from 1 to 10) were measured. The dry matter content was estimated from a sample of cortex weighted before and after drying in a ventilated chamber at 80°C. The firmness was measured by a manual penetrometer. The blush percentage was visually estimated. Red and green colorations and hue angles were estimated using a tristimulus Minolta CR-300.

2.3 Digitizing method

For each training system, two trees were digitized. The trees were decomposed into components organized into four scales: axes, annual shoots, growth units and metamers (according to White's definition, 1979). At growth unit (GU) scale, four types of entities were considered: long growth units (more than 20 cm); twigs (from 5 to 20 cm); short GU (less than 5 cm) and floral GU. Fruits were considered at metamer scale. Spatial coordinates and diameters were collected at metamer scale, but only each five leaves on the long GU and at the top of each axis. The coordinates were collected using a 3SPACE® FASTRAK® (Polhemus Inc.) and Diplami software (Sinoquet and Rivet, 1997). To simplify the observations, the short laterals were not decomposed into metamers and the spatial coordinates were collected only at their top. In the database, topology was encoded according to a specific code which preserves the topological relationships between entities (Godin and Costes, 1995; Godin *et al.*, 1997a). Diameter, spatial coordinates and fruit quality characteristics were considered as constituent properties and were attached to the corresponding entities. Then, the database was explored in AMAPmod, using a specific querying language (Godin *et al.*, 1997b).

3. Results

Since the studied trees were only four-year old and crop load was very low, only preliminary results are presented here. Consequently, this paper mainly focuses on the method evaluation and on its potentialities.

3.1. Plant 3D visualization

A 3D reconstruction of the digitized trees was done using the graphical module of AMAPmod (Godin *et al.*, 1996). 3D coordinates and dimensions of the nodes that were not measured were interpolated. The visual comparison with a photography shows that the reconstruction is accurate enough to recognize the different branches (Fig. 1). These reconstructions provide a graphical point of view on the database and were used to explore fruit quality variability. In figure 2, fruits were colored according to four classes of blush percentage at harvest. The visual comparison between two trees trained respectively in "Solaxe" and "Free" systems, highlights the effect of shoot bending on fruit coloration: on the tree in "Solaxe", the fruits with a high blush percentage are more numerous than on the tree in the "Free" system and the best colored fruits are located in high positions. This visual observation was formalized and confirmed by a statistical comparison of the mean values of blush percentages of fruits sorted according to four classes of height (Fig. 3).

3.2. Quality characteristics according to different fruit samples

For the other fruit quality characteristics, in particular those dealing with carbohydrates and water content, there was not such an obvious effect of the spatial location. The mean dry matter percentage and RI per tree did not exhibit differences depending on the training system but between trees 1 and 4 on one hand and trees 2 and 3 in the other hand (Tab. 1). We tried to explain these differences exploring the vegetative growth of each tree i.e. counting their vegetative entities at different scales (Tab. 2). The total number of leaves and their ratio to the number of fruits per tree was consistent with dry matter and RI differences only for the trees trained in "Free" system: tree 3 had a higher total number of leaves and a relative lower crop load compared to tree 4. On the contrary, the trees trained in "Solaxe" had a similar ratio of number of leaves per fruit but the arrangement of the leaves into different types of shoots was different: a higher number of long GU was found on tree 2 compared to tree 1. The same relative arrangement of shoot type was also observed on trees 3 and 4.

Several previous studies on carbon allocation to fruits showed that fruits are supplied by the leaves of the floral GU (spur) in the first weeks after bloom and thereafter by the extension shoots (i.e. long shoots), in particular bourse-shoots (Hansen, 1971; Ferree and Palmer; 1982, Corelli-Grapadelli *et al.*, 1994). Consequently, we built fruit samples according to the number of leaves of the bourse shoot (Tab. 3). It appeared that, on tree 1, more fruits than on other trees did not have any associated leaves and were fed by other sources of assimilates. These results suggest that, for a given global vegetative growth, the relative arrangement of the leaves into different kind of shoots within the canopy and their location with respect to the fruits influence the carbohydrates supply to the fruits.

On the other hand, the number of leaves of the bourse-shoot was strongly correlated to the topological location of the fruit (Fig. 4): most of the fruits without bourse-shoots were born in axillary position. Building fruit samples according to topological locations highlighted great differences in their characteristics at harvest (Tab. 4): fruits born in axillary position were smaller, less mature with respect to starch index but better colored. Fruits located terminally on long shoots were bigger but less colored. Finally, fruits located terminally on twigs had the best characteristics at harvest since their weight was similar to those on long shoots and their color to those in axillary position. In addition, small fruits (in particular those in axillary position) had a lower water content but no difference in RI (only a tendency to be more elevated) when they were compared to the two other classes of topological location within the same canopy. This results probably from the low crop load of the studied trees and suggests that other shoots were able to supply carbohydrates to these fruits. The same results were found for each individual tree and for both training systems. But, considering the most disadvantaged fruits, i.e. those without associated leaves, it can be seen that those born on tree 1 and 4 were even more disadvantaged than those born on tree 2 and 3 (Fig. 5). This suggests that the carbon supply to the fruits is adjusted by the vegetative growth at whole tree scale.

In short, our results suggest that the development of each individual fruits depends, in a first step, on its topological location for its final size, maturity and coloration. This last characteristic is also influenced by its spatial location and by the training system, which determines the form of the canopy. The dry matter and soluble sugar contents seem to depend on more global factors such as the global vegetative growth of the tree and on the relative arrangement of the shoots within the canopy. Nevertheless, these results needs to be confirmed by further observations on older trees.

Conclusion

This study showed that the method used is efficient for describing plant topology and geometry simultaneously. In addition, this approach allows us to describe the same trees several years successively since the database can be complemented at different dates taking benefit from the topological description, until the components can be recognized. However, since the data acquisition is time consuming (one to two days per tree for four-year old trees), such descriptions will probably not be done on a great number of trees, even if the method could be improved by increasing automatization. Consequently, it would be useful to explore such detailed databases in pluridisciplinary studies, and use them as tools to assess different biological assumptions or models.

The databases allowed us to build *a posteriori* samples according to many criteria and taking benefit of the multiscale description of the trees. This approach seems to be promising since the first results suggest that both the local context of the fruits and the vegetative growth at whole tree scale influence their characteristics at harvest.

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Table 1 - Main fruit quality characteristics: mean values and standard deviation per tree

Training system	Tree	Fruit number		fresh weight (g)	%dry matter	RI	Starch index
"Solaxe"	1	55	Mean	285.80	14.51 B	14.50 b	8.54
			Std	*67.98*	*2.19*	*1.72*	*1.50*
	2	63	Mean	307.62	16.13 A	15.06 A	8.37
			Std	*81.44*	*1.60*	*1.29*	*1.38*
"Free"	3	42	Mean	305.32	15.43 Ab	14.52 b	8.27
			Std	*71.37*	*1.87*	*0.86*	*1.29*
	4	48	Mean	294.20	14.65 B	13.74 C	8.29
			Std	*59.26*	*1.26*	*0.95*	*1.43*
				ns	**	**	ns

Newmans-Keuls Test: capital letters mean the test is significant at 1%, small letters at 5%

Table 2 - Counting of the total number of leaves and of the different type of GU

Training system	"Solaxe"		"Free"	
Tree number	1	2	3	4
Nb of leaves	4262	4893	3916	3468
Nb of fruits	57	66	44	51
Nb of leaves/fruit	68.74	68.92	75.31	53.35
Nb of long GU	56	**87**	**83**	64
Nb of brindles	74	86	97	49
Nb of short GU	**280**	**291**	183	190

Table 3 - Number of fruits per class of number of leaves of the bourse-shoots

	"Solaxe"		"Free"	
Nb of leaves of the bourse	Tree 1	Tree 2	Tree 3	Tree 4
0	**21**	12	10	13
1 à 5	4	10	4	10
6 à 15	10	18	7	8
more than 15	22	23	22	13
Total	57	66	44	51
Mean	9.2 AB	11.31 AB	11.63 A	7.86 B
Std	9.35	9.63	9.33	9.97

Newmans-Keuls Test: capital letters mean the test is significant at 1%, small letters at 5%

Table 4 - Fruit quality characteristics for three different topological locations

Topological location		weight (g)	RI	Starch Index	Firmness	Density	%Blush	Green hue	Red hue
Axillary	Mean	255.8	14.7	7.9	6.63	86.7	74.0	-15.6	31.3
	Std	*56.3*	*1.0*	*1.4*	*1.04*	*1.2*	*17.8*	*5.8*	*9.5*
Terminal On brindle	Mean	337.7	14.3	8.8	6.34	86.0	75.9	-16.0	29.2
	Std	*64.9*	*1.7*	*1.1*	*0.77*	*0.8*	*16.6*	*4.4*	*10.9*
Terminal On long GU	Mean	336.2	14.4	8.7	6.97	87.1	67.8	-17.3	23.7
	Std	*57.7*	*1.5*	*1.4*	*0.74*	*1.2*	*19.0*	*4.9*	*8.6*
		**	ns	**	**	**	**	ns	**

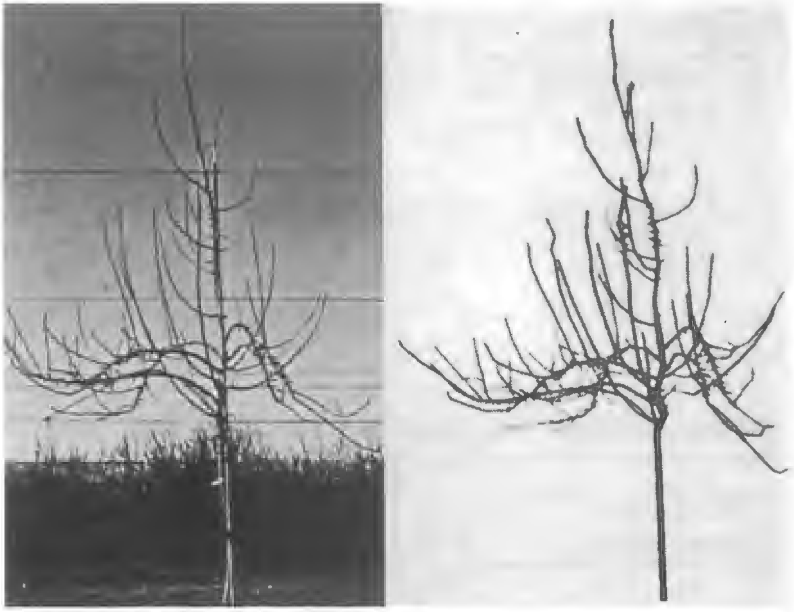

Figure 1 - Comparison of a digitized apple tree with its 3D reconstruction.

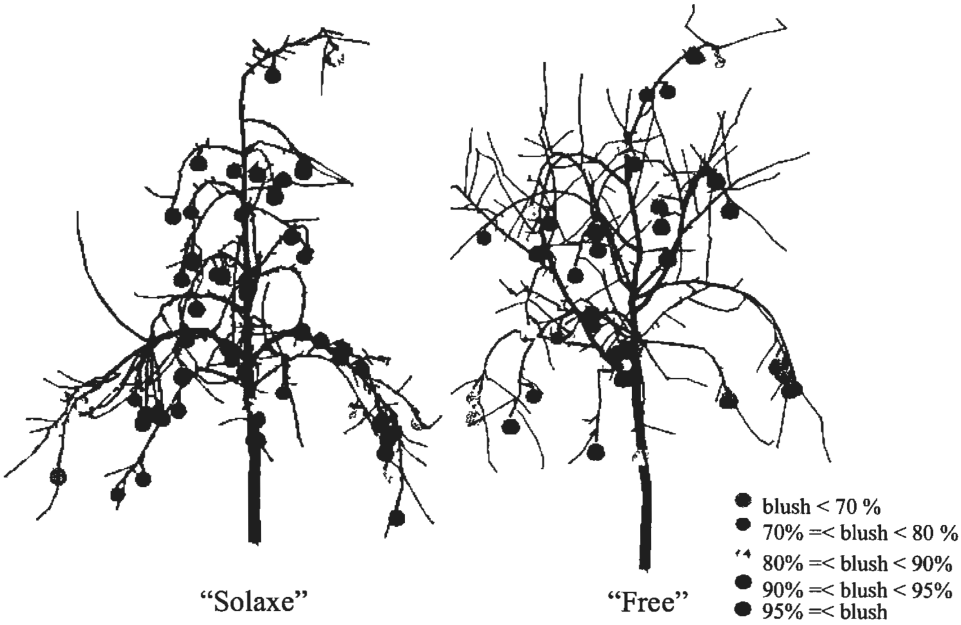

Figure 2 - Effect of the training system on blush percentage distribution within trees.

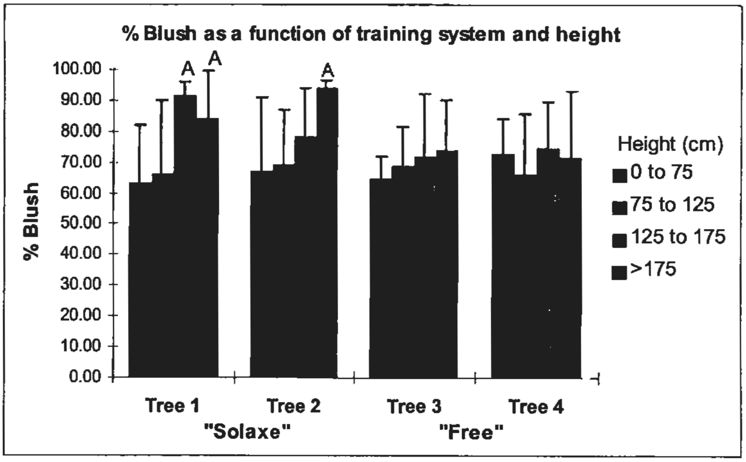

Figure 3 - Blush percentage of 'Fuji' apples in relation to their height within the canopy and the training system.

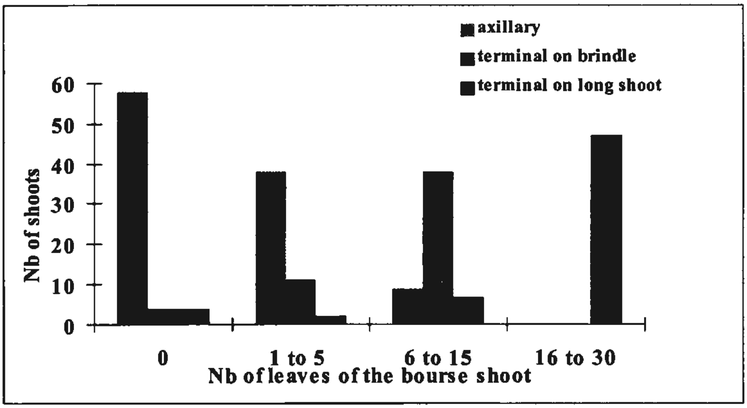

Figure 4 - Number of leaves of the associated bourse-shoot in relation to the fruit topological location

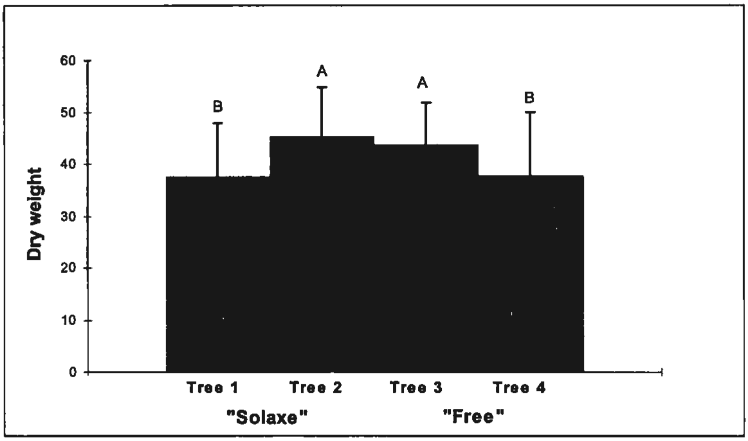

Figure 5 - Comparison of the mean dry weigth of the fruits without bourse shoot for the four different trees.

A STATISTICAL APPROACH FOR ANALYZING SEQUENCES IN FRUIT TREE ARCHITECTURE

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Keywords: Hidden semi-Markov chain, Kullback-Leibler divergence, plant breeding, sequence alignment

Abstract

The comparison of fruit tree cultivars on the basis of their architecture is addressed. We propose to extract sequentially structured data (sequences for short) from collected tree-structured data. Sequences realize a good compromise between the availability of statistical methods (which is the highest for unstructured data i.e. vectors) and the explicit representation of the structural information of plant architectures (which is the highest for tree-structured data). Different approaches are presented for the comparison of fruit tree cultivars relying either on the building of parametric models from samples of sequences corresponding to each cultivar or on the comparison of individual sequences. The strengths and weaknesses of each family of methods, referred either to as parametric or non-parametric, are discussed on the basis of the comparison of seven apple cultivars.

1. Introduction

In the framework of architectural analysis, data are organized in a tree form and different variables may be recorded for each elementary botanical entity (node, growth unit, annual shoot ...) (Godin *et al.*, 1997). These variables are either qualitative (e.g. type of axillary production chosen among latent bud, short shoot and long shoot) or quantitative (e.g. number of axillary flowers). The architectural analysis gives a high importance to discrete variables (qualitative or quantitative) that are very often of morphological nature compared to classical approaches, which focus more on continuous variables. Therefore, a statistical approach for architectural analysis should take into account both mixture of continuous and discrete variables (at a local scale) and structural information (at a more macroscopic scale).

We choose here to focus on sequences which correspond to a first level of simplification of the structural information contained in the collected tree-structured data. Successions of entities along axes or branches are naturally represented by sequences, the attached variables qualifying either the bearing entity in the sequence or the borne entities. For tree-structured data, few statistical methods exist whereas for sequences, a large panoply of statistical methods is available. These methods cover the main fields of statistical analysis ranging from exploratory analysis to model building and discriminant analysis. In particular, the following topics will be addressed:

- model building from a sample of discrete sequences illustrated by the analysis of the succession of transient phases along sequences using hidden semi-Markov chains,

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- comparison of models following the concept of Kullback-Leibler divergence and exploration of the resulting dissimilarity matrix,
- comparison of individual sequences by dynamic programming and exploration of the distance matrix resulting from the pairwise alignment of a set of sequences.

This statistical approach is mainly illustrated by the comparison of seven apple cultivars. The objective is to determine early predictors of the adult branching habit by comparing branching patterns on two-year-old trunks of apple cultivars.

2. Materials and methods

Seven apple cultivars (*Malus domestica* Borkh) corresponding to diverse growth and fruiting habits were planted in Montpellier, France. The seven cultivars were: 'Belrène', 'Elstar', 'Fuji', 'Imperial Gala ', 'Granny Smith', 'Reinette blanche du Canada' and 'McIntosh Wijcik'. Twenty trees per cultivar, bench-grafted on M.7 rootstock, were planted in the field and cut back to one bud one year after transplantation. Trees then were allowed to develop without pruning. The location of the sylleptic or immediate shoots was recorded after one year of growth while the location of one-year-delayed shoots was recorded after two years of growth. Among these one-year-delayed shoots, short shoots (no or a poor elongation of the internodes), long shoots (elongated internodes) and flowering shoots were distinguished. In this measurement, we qualified both the immediate branching which follows the establishment growth from the base to the top and the one-year-delayed branching which is organized by an acrotonic gradient from the top of the annual shoot. After an exploratory analysis of the sample of sequences, we chose to focus on the acrotonic gradient and describe the annual shoots node by node from the top to the base.

The measurements are illustrated by the three Reinette B. sequences in Figure 1 with the following coding of the five possible types of axillary production - 0: latent bud, 1: one-year-delayed short shoot, 2: one-year-delayed long shoot, 3: one-year-delayed flowering shoot, and 4: immediate shoot -. These sequences exhibit a succession of six well-differentiated zones. Each of these six zones is characterized by a given mixture of axillary productions: (1, 2) for the first zone, (0, 3) for the second, 4 for the third, 0 for the fourth, (0, 1, 2) for the fifth and 0 for the sixth. As in Costes and Guédon (1997), this branching structure can be modeled by a hidden semi-Markov chain, which is a hierarchical model with two levels of representation. At the first level, a semi-Markov chain represents both the succession of zones and the lengths of each zone. Each zone is represented by a formal entity called state and successions of zones are represented by transitions between states. The second level consists in attaching to each zone represented by a given state of the semi-Markov chain a discrete distribution, which represents the observed mixture of axillary productions.

The hidden semi-Markov chains built from the Reinette B. and Belrène sequences respectively are represented in Figure 2 with the following convention: each state is represented by a box which is numbered near its lower right corner. Boxes representing transient states are surrounded by a single line while the box corresponding to the final absorbing state is surrounded by a double line. The possible transitions between states are represented by oriented edges with the attached probabilities noted nearby. Oriented edges entering in states indicate initial states (states 0 and 1 for Reinette B. and states 0, 1 and 2 for Belrène). The attached initial probabilities are noted nearby. The occupancy distributions of the transient states which represent the lengths of the corresponding zones in terms of number of nodes are figured above the corresponding boxes. Finally, the possible axillary productions observed in each zone are indicated inside the boxes, the font sizes being roughly proportional to the observation probabilities (for state 1 of Reinette B., these probabilities are 0.45, 0.13 and 0.42 for latent buds, one-year-delayed short shoots and one-year-delayed long shoots respectively).

The evaluation of the accuracy of an estimated model relies on the fit of characteristics extracted from the measured sequences to the equivalent theoretical ones computed from the model parameters. The most obvious characteristics are the probabilities of the different axillary productions as a function of the node rank which give an overview of the overall structuring of the sequences in terms of successions of zones (Fig. 3).

The interpretation of the branching structure of a cultivar may also rely on the computation of the optimal state sequences deduced from the observed sequences by the so-called Viterbi algorithm (Guédon and Cocozza-Thivent, 1990). The optimal segmentation of three Reinette B. sequences is presented in Figure 1. States 1 to 6 clearly correspond to six well-differentiated successive zones. The lengths of the segmented zones and the axillary productions observed in these zones indeed reflect the corresponding state occupancy and observation distributions depicted in Figure 2a.

The parametric models built for each cultivar can be compared at a detailed level on the basis of their respective parameters and characteristic distributions but also globally by computing dissimilarity measures between pairs of hidden semi-Markov chains following the concept of Kullback-Leibler divergence (Juang and Rabiner, 1985). Basically, the Kullback-Leibler divergence measures the divergence of a target model θ with respect to a reference model θ_0 for a sample of sequences which is assumed to be generated by the reference model θ_0. A dissimilarity matrix between hidden semi-Markov chains corresponding to each cultivar is then obtained.

We have given above an overview of the capabilities of analysis and comparison of cultivars in the framework of a parametric approach, i.e. based on parametric models that synthesize the structure of the different cultivars. Now, we will consider the comparison of cultivars in the framework of a non-parametric approach. The basis of this new approach consists in computing distances between individual sequences. If we compare two sequences, the most obvious type of difference between them is the substitution of one element for another at the same rank in the sequence. Other types of difference include deletion of elements and insertion of elements. These are local differences. We define a distance between two sequences as the minimum sum of the costs attached to the three possible elementary operations, namely deletion, insertion and substitution, required for transforming one sequence into another (Wagner and Fischer, 1974; Sankoff and Kruskal, 1983).

Let ϕ denote the null element. The three possible elementary operations can be noted in rewriting rule form:

- deletion ('d') of x: $x \to \phi$
- insertion ('i') of y: $\phi \to y$
- substitution ('s') of x by y: $x \to y$ $(x = y \text{ or } x \neq y)$

where x and y are arbitrary elements.

The example in Figure 4 details the optimal alignment of two Reinette B. sequences. In the presentation of the optimal alignment, we have chosen to differentiate the substitution of one element for a different element ('s') from the exact matching of two elements. The result is presented on three rows. The upper row consists of the test sequence possibly interspersed with null elements. The middle row consists of the sequence of elementary operations ('d', 'i', 's', exact matchings are represented by vertical lines). The lower row consists of the reference sequence possibly interspersed with null elements. The null elements are represented by underscores (underscores in the test sequence correspond to deletions while underscores in the reference sequence correspond to insertions).

The main differences between the two Reinette B. sequences aligned in Figure 4 are located at the beginning of the sequences (corresponding to the top of the annual shoots) where there are more long shoots in the reference sequence (and also a longer flowering zone) and at the middle of the sequences where there are no immediate shoots in the reference sequence.

The sequence alignment procedure can be used at a detailed level to analyze the local differences between two sequences. Another possible use of this procedure consists in computing the distance matrix resulting from the pairwise alignments of a set of sequences.

3. Results and discussion

The detailed comparison of two apple cultivars (Reinette B. and Belrène) on the basis of model parameters and characteristics is illustrated in Figures 2 and 3. The main difference between these two cultivars lies in the locations of one-year-delayed short shoots. For Reinette B., short shoots are mainly located on the basal part of the main shoot (between ranks 40 and 70 counted from the top) while they are located mainly on the apical part of the main shoot for Belrène (before rank 25) (Fig. 3a and 3b). The structures of the two models are also very close, the main differences being the supplementary initial state (state 1) for Belrène and the different balances between short and long shoot in the basal and apical zones (state 1 of Reinette B. compared to state 2 of Belrène and state 5 of Reinette B. compared to state 6 of Belrène).

The seven cultivars can also be globally compared by two different means:

- the dissimilarity matrix between hidden semi-Markov chains built from each sample of sequences (Tab. 1),
- the matrix of average distances within a cultivar or between cultivars deduced from the distance matrix between individual sequences resulting from their pairwise alignment (Tab. 2).

The homogeneity/heterogeneity of the samples is expressed in the intra-cultivar distances deduced from individual sequence comparison (Tab. 2): Reinette B. is the most homogeneous (0.184), then Granny S., Belrène and I. Gala (with 0.187, 0.196 and 0.205, respectively). The most heterogeneous are Wijcik (0.225), Fuji (0.225) and Elstar (0.246).

The cultivars can be ordered by ascending average dissimilarity measure i.e. from the least (most central) to the most outlying (Tab. 1): Fuji (0.414), Elstar (0.436), Belrène (0.456), I. Gala (0.491), Granny S. (0.575), Reinette B. (0.668), Wijcik (1.146). This order is close to the one deduced from the non-parametric approach (Tab. 2, intra/inter cultivar distance ratio) except for the location of Belrène: Elstar (0.857), Fuji (0.812), I. Gala (0.743), Granny S. (0.67), Belrène (0.656), Reinette B. (0.655), Wijcik (0.544). The change in position of Belrène is due to the average length of the corresponding sequences (89.5) which is the highest among the seven samples of sequences (Elstar: 66.1, Fuji: 73.9, I. Gala: 70, Granny S.: 75.1, Reinette B.: 73, Wijcik: 57.3). The difference in length is actually strongly penalized in the algorithm of sequence alignment by deletion and insertion operations while the modeling by hidden semi-Markov chains present fewer constraints in this respect. The locations of Elstar and Fuji are also inverted but, in both cases, the distances or dissimilarity measures are relatively close.

4. Conclusions

This modeling approach can be extended to multivariate sequences as in the apricot tree example presented in Costes and Guédon (1996) where two variables - type of axillary production and number of axillary flowers - are recorded for each successive node. All the statistical techniques presented in this paper for analyzing and comparing samples of sequences are fully implemented in the AMAPmod software which also includes a database component dedicated to plant architecture measurement and various graphic interfaces and exploratory tools (Godin *et al.*, 1997).

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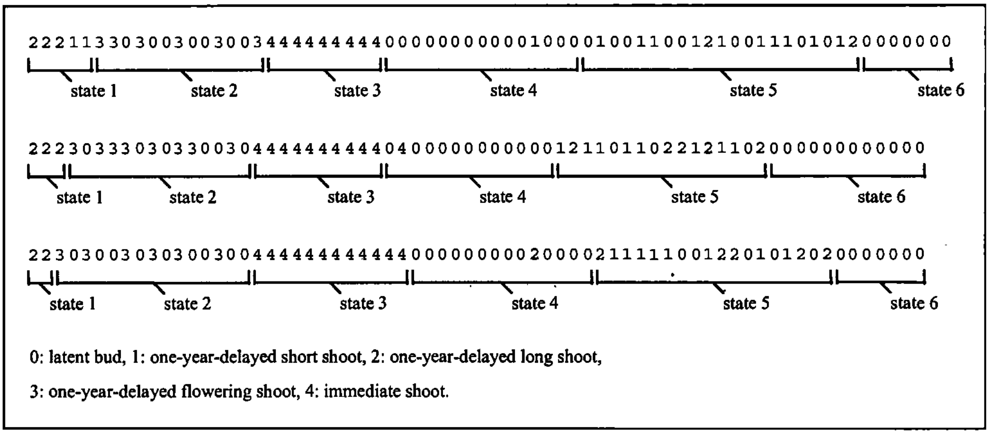
Table 1 - Dissimilarity measures between pairs of hidden semi-Markov chains

	Belrène	Elstar	Fuji	I. Gala	Granny S.	Reinette B.	Wijcik	Average
Belrène	0	0.34	0.233	0.325	0.491	0.434	0.958	0.456
Elstar	0.34	0	0.237	0.248	0.276	0.658	0.926	0.436
Fuji	0.233	0.237	0	0.304	0.35	0.376	1.065	0.414
I. Gala	0.325	0.248	0.304	0	0.302	0.72	1.13	0.491
Granny S.	0.491	0.276	0.35	0.302	0	0.617	1.503	0.575
Reinette B.	0.434	0.658	0.376	0.72	0.617	0	1.302	0.668
Wijcik	0.958	0 926	1.065	1.13	1.503	1.302	0	1.146

Table 2 - Distances between cultivars deduced from individual sequence comparison

	Belrène	Elstar	Fuji	I. Gala	Granny S.	Reinette B.	Wijcik	intra-cultivar	inter-cultivar	ratio
Belrène	0.196	0.293	0.269	0.262	0.262	0.269	0.431	0.196	0.299	0.656
Elstar	0.293	0.246	0.258	0.237	0.235	0.272	0.424	0.246	0.287	0.857
Fuji	0.269	0.258	0.225	0.247	0.251	0.245	0.388	0.225	0.277	0.812
I. Gala	0.262	0.237	0.247	0.205	0.222	0.252	0.424	0.205	0.276	0.743
Granny S.	0.262	0.235	0.251	0.222	0.187	0.262	0.429	0.187	0.278	0.67
Reinette B.	0.269	0.272	0.245	0.252	0.262	0.184	0.383	0.184	0.281	0.655
Wijcik	0.431	0.424	0.388	0.424	0.429	0.383	0.225	0.225	0.414	0.544



0: latent bud, 1: one-year-delayed short shoot, 2: one-year-delayed long shoot,

3: one-year-delayed flowering shoot, 4: immediate shoot.

Figure 1 - Optimal segmentation of three Reinette B. sequences

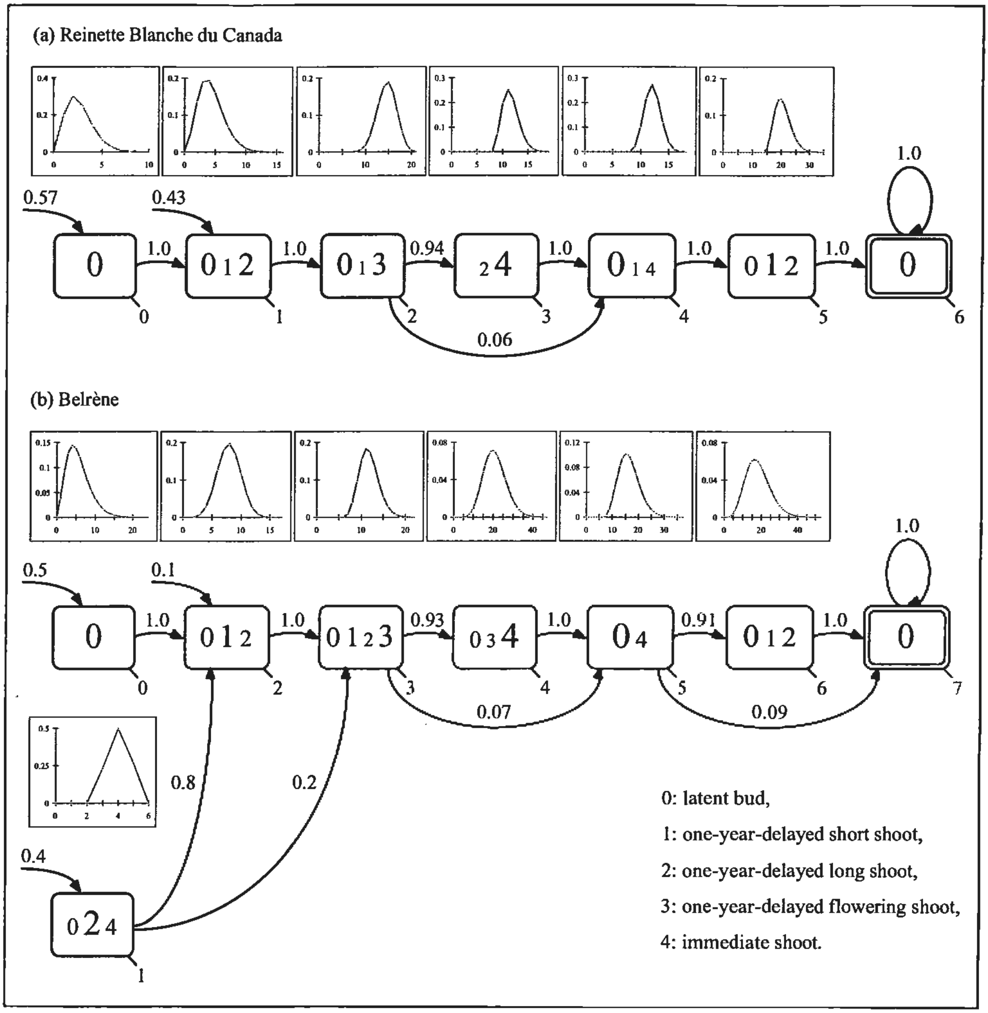
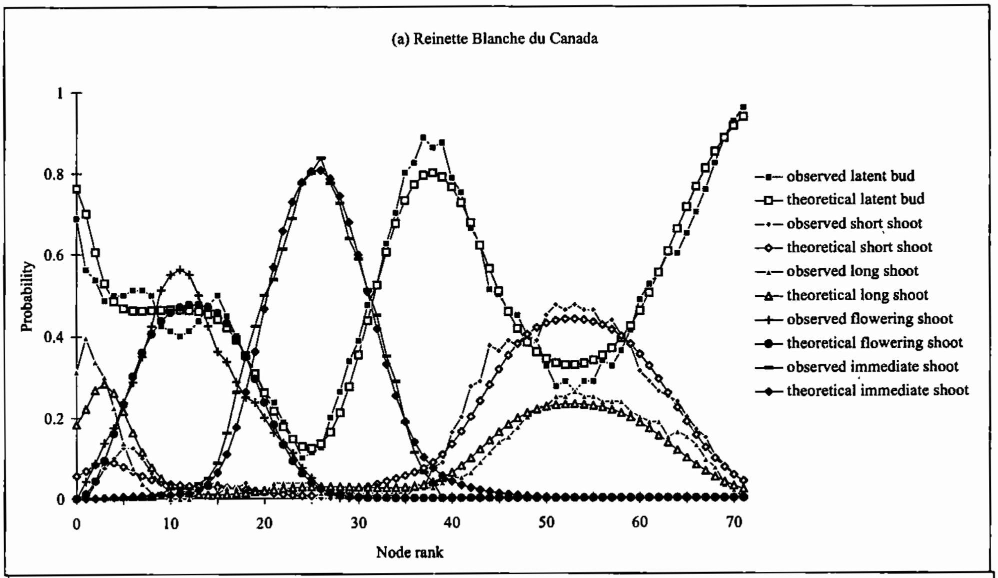


Figure 2 - Hidden semi-Markov chains estimated from the Reinette B. and Belrène sequences.


(a) Reinette Blanche du Canada

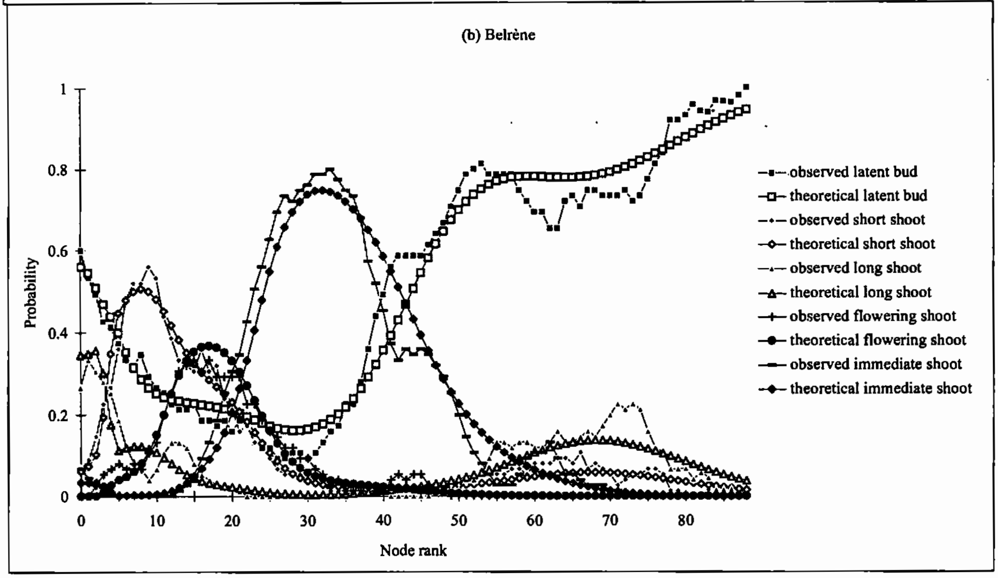
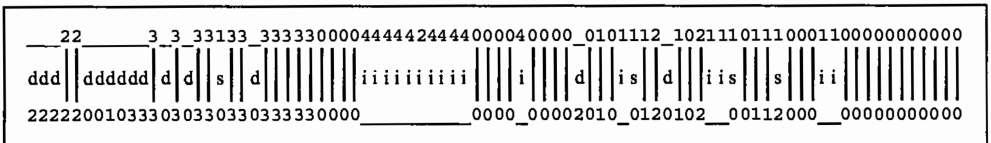

(b) Belrène

Figure 3 - Fit of characteristics for the cultivars Reinettte B. (top) and Belrène (bottom)



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___22_______3_3_33133_33333000044444244440000040000_0101112_1021110111000110000000000
2222200103330303303303333330000__________0000_00002010_0120102__00112000__00000000000
```

d: deletion, i: insertion, s: substitution (14 deletions + 16 insertions + 4 substitutions + 50 exact matchings)

Figure 4 - Optimal alignment of two Reinette B. sequences

COMPUTATIONAL MODEL FOR DIRECT SOLAR IRRADIATION OF CANOPY IN DENSE ORCHARD

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Keywords : *Star Ruby* grapefruit, *Valencia* orange, *Murcott* mandarin, fruit yield

Abstract

A computational model (formulations and computer program) was developed to estimate the energy of direct solar radiation incidence on canopies in dense orchards taking the shading by adjacent trees into account. The model considers direct solar irradiation, but not diffused or reflected light. The annual incident direct solar energy was calculated for experimental plots of *Star Ruby* red grapefruit, *Valencia* orange and *Murcott* mandarin, and compared with the respective fruit yield during 1992-1997. The annual direct solar energy calculated for three experimental citrus orchards was found to be closely correlated with the actual fruit yield for all species tested. The model allowed both to determine the efficiency of the side and top surfaces of the canopy in their contribution to the annual fruit yield and to predict the optimal plantation design at which the orchard productivity is expected to be maximal.

1. Introduction

Light is a major factor determining the tree vegetative growth and productivity. Many physiological processes are known to depend on both light intensity and quality. In dense orchards shading by adjacent trees significantly decreases the irradiance and may thus become the main limiting factor for growth and fruit production (Jackson and Palmer, 1977a,b; Seemann, 1979; Monteith, 1994). Fruit yield of trees in varying plantation designs could be attributed to the difference in solar irradiation and shading on individual canopies in the different designs (e.g. Ferree, 1989; Robinson and Lakso, 1991; Clayton-Greene, 1993).

To evaluate solar irradiation of canopies, actual light measurements by different types of sensors or fish-eye photography have been used (Jackson, 1980; Lakso, 1980; DeJong and Doyle, 1985; Avidan and Erez, 1986; Hanan and Bégué, 1995). Models for orchards and crops were described in respect to light interception by canopies (e.g. Jackson and Palmer, 1980; Cohen and Fuchs, 1987; Johnson and Lakso, 1991; Wagenmakers, 1991; Sinoquet, 1993; DeJong and Grossman, 1994), and the correlation of solar radiation interception by individual canopies with their fruit yield was studied (Jackson, 1978; Palmer, 1988; Robinson and Lakso, 1991).

The light interception by a canopy which can be described by the Beer's law (Jackson, 1980) is in fact an attenuation of the incident solar radiation. In the present study we have considered the level of direct solar incidence on opaque canopies and the limitation by adjacent tree shading in dense orchards, and developed a computational model for it.

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2. The computational model

2.1. Geometry of sunbeam and light incidence area

Let the y-axis correspond to the row direction, α be the angle between y-axis and the sunbeam, n be the normal to the sunbeam, and β be the angle between n and the x-axis (Fig. 1). According to the general definition, $x \cos\beta + y \sin\beta - r = 0$, where r is the distance between the sun/shadow line and the center of the plant (origin of the coordinate system, O). In our case, $r = \Delta R$ or $r = W - \Delta R$ which determines the shade on canopies of the same width $W = 2R$. Obviously, $\alpha = \alpha_b - \alpha_r$ where α_r and α_b are the azimuth angles of the row and sunbean, and $\beta = \pi - \alpha$. Then, the equation of the sunbeam becomes:

$$- x \cos(\alpha_b - \alpha_r) + y \sin(\alpha_b - \alpha_r) - r = 0 \tag{1}$$

The differential solar power $dP = P_0 \cos\gamma \, R \, d\gamma \, dh$ has a photobiological effect in a certain area $dA = R \, d\gamma \, dh$ of a canopy, γ being the angle of the sunbeam incidence and h the height of the canopy. The total effective solar power P incident on a total illuminated area within dh is the integral of dP ($\gamma = 0$ through π). It is equal to $d_h P = W P_0 \, dh$ which is simply a cross-section of the canopy per incident P_0, and the effective illuminated area is the projection of the canopy on a plane which is rectangular to the sunbeam.

2.2. Formulation for individual canopy

The azimuth (α) and zenith (Θ) angles determine the shaded area on a canopy in the horizontal and vertical directions, respectively. The shaded area in the horizontal direction is characterized by the projection length l_{cs} determining the horizontal size of the shade at a given zenith angle Θ:

$$l_{cs} = W - \sin(\phi - \alpha) \sqrt{x_i^2 + y_i^2} \tag{2}$$

where $\phi = \tan^{-1} |x_i / y_i|$.

The height h_{CS} of the shade on a canopy is determined by the zenith angle Θ and the height h_S of the adjacent canopy:

$$h_{cs} = h_s \acute{y} - [x_i \sin\alpha + y_i \cos\alpha - \sqrt{l_{cs}(2W - l_{cs})}\,] / \tan\Theta \tag{3}$$

This formula allows to calculate the shade height at each couple of azimuth and zenith angles. Evidently, the canopy side area which is shaded by any adjacent canopy, is $A'_{side} = h_{cs} \, l_{cs}$. This is valid in the case when no other canopy is situated between shaded and adjacent canopies.

In a dense orchard two adjacent canopies of the coordinates (x_1, y_1) and (x_2, y_2) can have their own shaded area A_1 and A_2. The total shaded side area is a simple sum $A_{side} = A'_{side1} + A'_{side2}$ when the shaded areas from both adjacent canopies do not overlap. Otherwise, we need to subtract the overlapping area. In this case we have:

$$A_{side} = A'_{side1} + A'_{side2} - h_{ci}\,[(x_1 - x_2)^2 + (y_1 - y_2)^2]\, \mathrm{Sin}^2(\kappa - \alpha) \qquad (4)$$

where $\kappa = \mathrm{Tan}^{-1}|(x_1 - x_2) / (y_1 - y_2)|$.

Shading the top surface will occur when the adjacent canopy is higher than the shaded canopy ($h_S > h_C$). The shade of the top surface area is estimated by a rectangle: $A_{top} = l_{cs}\, \Delta d_{cs}$ where $\Delta d_{cs} = (h_s - h_c)\, \mathrm{Tan}\Theta - d_a$ is the length of the shaded top surface.

The illuminated side and top areas of canopy are $S_{side} = W\, h_c - A_{side}$ and $S_{top} = \pi\, W^2 / 4 - A_{top}$. The effective direct solar power $P_{eff}(t)$ is the part of the incident power $P_o(t)$ which depends on the angle of the incidence. The effective energy incident on a surface, is the product P×area×time:

$$E_{eff} = E_{side} + E_{top} = P_o(t)\, t\, [(Wh_c - A_{side})\, \mathrm{Sin}\Theta + (\pi\, W^2 / 4 - A_{top})\, \mathrm{Cos}\Theta] \quad (5)$$

This effective energy determines the photobiological effects produced by direct sunlight. The incident direct sunlight $P_o(t) = I_o \exp[-E_m\, Tm(\Theta(t))]$ was estimated using Solar constant I_o, the mass $m = b / (760\, \mathrm{Cos}\Theta(t))$ of air transirradiated, the extinction coefficient E_m for the absolute air mass and the turbidity factor T (Seemann, 1979).

2.3. Formulation for continuous hedgerow

The side surface area of the hedgerow wall is simply a product of a length L and height H of the hedge: $S_{side} = LH$. The side surface shaded area depends on the azimuth angle α: no shade at $2\pi - \varepsilon < \alpha < \varepsilon$ or $\pi - \varepsilon < \alpha < \pi + \varepsilon$, where $\varepsilon = \mathrm{Tan}^{-1}(d_a / L)$ and d_a is a clear alley width. The shade appears at $\varepsilon < \alpha < \pi - \varepsilon$ or $\pi + \varepsilon < \alpha < 2\pi - \varepsilon$, resulting in a side surface illuminated area of $S_{side} = H\, d_a / \mathrm{Tan}\alpha + L_s\, d_a / (\mathrm{Tan}\Theta\, \mathrm{Sin}\alpha)$. The illuminated top area is simply the top surface $S_{top} = LW$ (when all rows in orchard are of the same height). The effective solar energy E_{eff} as a function of α and Θ, is:

$$E_{eff} = E_{side} + E_{top} = P_o\, t\, [S_{side}\, \mathrm{Sin}\alpha\, \mathrm{Sin}\Theta + S_{top}\, \mathrm{Cos}\Theta] \qquad (6)$$

2.4. Limitations

The model includes several limitations in order to avoid an over-complexity. The only principle limitation of the model is that it accounts for only the incidence of direct solar beam; neither sky-diffused nor reflected light were considered. The other limitations which can be avoided by respective changes in formulations and computer programs are: (i) canopies or hedgerows are opaque, (ii) cylindrical shape of canopy or rectangular shape of a hedge, (iii) calculated incident solar radiation based on Solar constant may be substituted by calculated or measured photosynthetically active radiation (PAR) as a function of zenith angle or time, (iv) flat horizontal soil surface.

3. Methods

The *Star Ruby* experimental orchard consisted of trees of 2.5 or 3 m height, 2.7-3.5 m width. Some trees were removed from 2×5 m rows oriented 52°N. As a result, several variants of tree canopy surrounding were formed in the orchard. The model for cylindrical shape of canopy was applied and the annual direct solar energies E_{side}, E_{top} and $E_{tot} = E_{side} + E_{top}$ were calculated according to the formula (5) for each variant of canopy size and surrounding canopies.

The original plantation design of hedgerows of *Valencia* orange and *Murcott* mandarin was 3.5×6 m (*Valencia*) and 3.5×5 m (*Murcott*) with azimuth angle of 16°N. The removal of some hedgerows a few years prior to the experiment, resulted in additional plantation designs: 7×6, 3.5×12 and 3.5×6 m (*Valencia*) and 3.5×10 m (*Murcott*). These variants were used to compare fruit yields with the calculated annual direct solar energy according the model. To calculate the energy, cylindrical shape of canopy (*Valencia* orange, 6×7 m) and rectangular shape of continuous hedgerows were assumed.

Zenith Θ and azimuth angles α_b were calculated using current time, latitude (Λ_a) and longitude correction (Λ_c) values as the initial parameters, and the time of solar noon, the solar declination and the equation of time as intermediate parameters (Campbell, 1981). $\Lambda_a = 33°1'$ and $\Lambda_c = 5°37.5'$ were used for the experimental orchard of *Star Ruby* grapefruit in kibbutz Gadot, Northern Israel, and $\Lambda_a = 31°16'$ and $\Lambda_c = 4°23'$ for the *Valencia* orange and *Murcott* mandarin commercial orchards in Besor dictrict, Southern Israel. The calculations were made with the QBASIC program SHADE based on the formulations described above. Integration for the diurnal and annual solar energy were made with increments of 10 min. and 5 days, respectively. Solar constant was assumed of 1370 $W \cdot m^{-2}$ (Drummond *et al.*, 1968). The diurnal integration was made with zenith angles $0 < \Theta < \pi / 2$.

4. Results

4.1. Comparison of fruit yield with calculated solar irradiation

Citrus canopies have a high leaf density and are essentially opaque. We applied the model to compare the annual fruit yield (per tree) of grapefruit, orange and mandarin with the calculated annual direct solar energy incident on the tree canopy in the orchard.

When the averaged actual fruit yield was plotted versus the calculated solar energy incident on total surface, a correlation between the yield and the incident energy became evident, with a mean correlation coefficient of 0.96 ± 0.04, 0.91 and 0.98 for *Star Ruby, Valencia* and *Murcott*, respectively. The results strongly supported the basic working hypothesis of the fruit yield (Y, kg) determined by the direct solar irradiation energy (E_{tot}, GJoule). In 1992-1993 the yield/light efficiency of *Star Ruby* was about 0.8-0.9 kg/GJoule per tree while it was found to be 1-2 kg/GJoule per tree for *Valencia* and *Murcott* during 1995-1997.

4.2. Efficiency of side and top surfaces of canopy for fruit production

Total energy presented as a sum $E_{tot} = E_{side} + E_{top}$, means that side and top surfaces have the same yield/light efficiency. However, this is not necessarily the case. If we assume different efficiency of the side and top surfaces, the yield/light relationship can be written as:

$$Y_p = \sigma E_{side} + \tau E_{top} \tag{7}$$

where σ and τ are yield/light efficiencies of side and top surfaces, respectively. Applying the least square analysis to equation (7), values for σ and τ were obtained. The results showed significant differences between σ and τ for the most cases studied. The obtained σ and τ values were applied to equation (7) to receive a calculated fruit yield (Y_p) which is expected to correlate with the actual fruit yield (Y_a). Indeed, the slope of the linear regression Y_p vs Y_a was found to be close to unity, with a high correlation coefficient (0.99). This correlation now allows to use equation (7) for prediction of fruit yield, if σ and τ values are known and the incident solar energy is calculated for side (E_{side}) and top (E_{top}) surfaces of tested hedgerow or individual canopies in a dense orchard.

4.3. Prediction of optimal plantation design

The model allows to calculate E_{side} and E_{top} for various parameters of the plantation design, and then to find the design resulting in the highest fruit yield Y_p according to equation (7). This is in fact a prediction of an optimal plantation design. The predicted fruit yield calculated per tree is expected to be increasing when lowering the plantation density due to a decrease of shading. However, lowering the plantation density leads to lower fruit yield per unit area. The model can predict the design for maximal fruit yield per unit area.

We tested the prediction procedure for *Murcott* mandarin plot of different plantation designs using the values of σ and τ obtained as mentioned above. As expected, increased row spacing led to higher predicted fruit yield per tree because of lower shading, and lower fruit yield per hectare because of lowering the plantation density for hedgerow width range of 2-4 m. Maximal fruit yield per hectare is anticipated at hedgerow spacing of 5-6 m when hedgerow width and height were of 3-4 and 3.5-5 m, respectively

In the *Murcott* mandarin plots redesigned from 3.5×5m to 3.5×10 m, the shading by adjacent hedgerow became lower, leading to higher actual fruit yield per tree of about 70%. However, the actual fruit yield per hectare dropped by about 14-17% because of the low plantation density. The prediction indicated that in this particular case, the hedge side pruning of the rows from width of 4-4.5 to 3 m (no topping) would not have affected the fruit yield per hectare while making the alley width more suitable for working machines.

Applying the prediction procedure to various hedgerow heights, it was found that tall and narrow hedgerows produced by pruning can give more productive orchard than the orchard redesign by row removal. The prediction procedure can be also used for optimal plantation design of new plots assuming the values of σ and τ are known for a given species.

5. Conclusions

The model presented here was based on a working hypothesis assuming that the productivity of dense orchards closely depends on the annually accumulated direct solar irradiation, which is limited by shading the canopies by adjacent trees. For simplicity we chose to ignore elements like diffused or reflected light, spectral changes, light penetration through canopy etc., since they all relate to the origin, namely the direct solar radiation. The strong linear correlation between the annual irradiation as calculated by the model, and the actual fruit yield obtained for different citrus varieties over a few years in two different locations, provide a good support for the working hypothesis and for the potential applicative importance of the model.

The model can be used to predict optimal plantation designs for new orchards, or optimal manipulation of over-densed existing orchards by redesigning canopy shapes or tree removal. It may allow to correlate not only the total solar radiation, but any specified wavelength range (for example, photosynthetically active radiation, PAR) or the radiation incident during a specified period of time (during the day or the season). The model is flexible to other assumptions as well, excluding the principle limitation mentioned.

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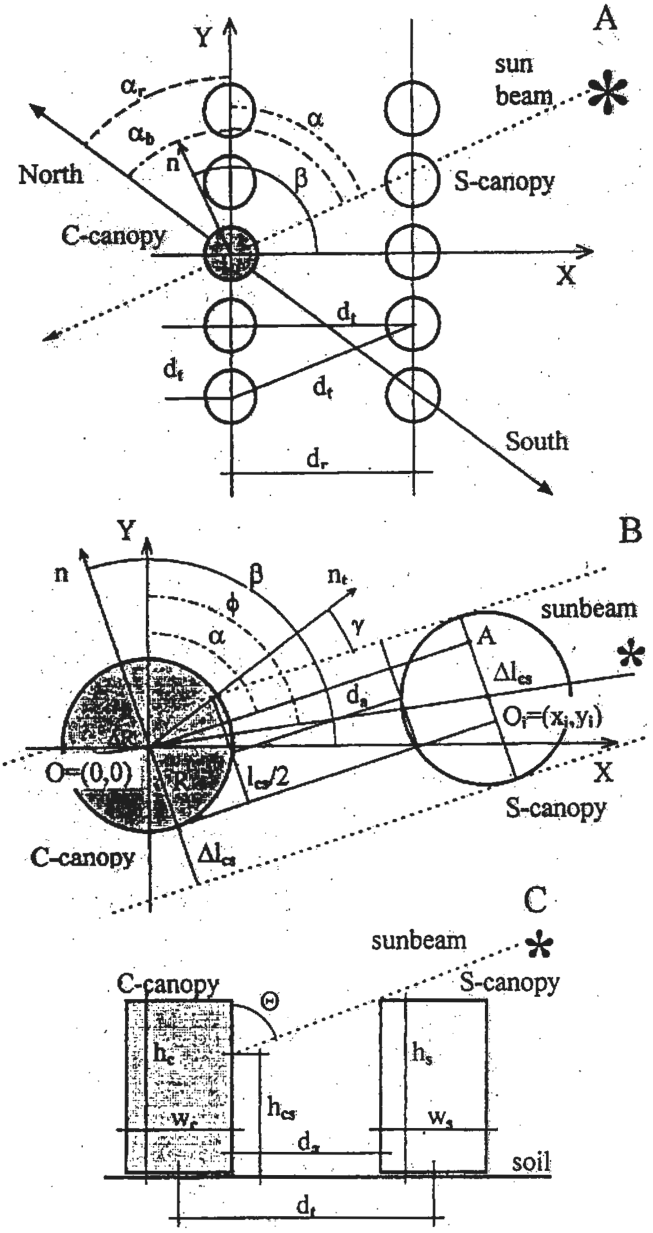

Figure 1 - Geometry of sunbeam and rows of canopies in the XY-orthogonal coordinates. Panels A and B, top view. Panel C, side view. α_b, and α_r, absolute azimuth angles of the sunbeam and row. Θ, zenith angle. n, the normal to the sunbeam. $C(0,0)$- and $S(x_i,y_i)$-canopies are the shaded and shading (adjacent) canopies, respectively. h and w, height and width of canopy. d_t, d_r and d_a, trunk, row and canopy spacing, respectively.

MODELLING LIGHT INTERCEPTION ON THE BASIS OF SUNFLECK MEASUREMENTS

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Abstract

Canopy light interception is related to productivity and fruit quality. Therefore, optimum light interception is of strategic importance for growers. Up to 70% diffuse light interception, the productivity of an apple or pear orchard increases without loss of quality. However, when more than 70% of the incoming light is intercepted, the total production per ha may increase but the production of fruit quality will be affected negatively. Measuring light with PAR sensors under diffuse conditions is a reliable method but not always practical because such weather conditions do not always prevail. Measuring under direct light conditions is, however, more complicated since date, time and row direction influence the results strongly. Sunfleck estimations on the orchard floor have been related to direct PAR measurements and model calculations of light interception over a range of dates and time. The model input parameters were solar inclination and declination, and orchard characteristics such as tree shape and dimension, leaf area, planting system, and row direction. The visual rating of sunflecks on the ground was linearly correlated with direct light records. Therefore, a reliable estimation of orchard light interception on the basis of sunflecks seems possible, providing that latitude, date, time and row direction are taken into account.

1. Introduction

The relationship between canopy production and light interception is widely accepted (Monteith, 1977). In fruit trees, not only the total production level is important but also fruit quality. Up to values of 80-90% light interception, the relationship with bulk production level of apple seems to be linear. However, several important aspects of fruit quality are negatively affected, such as red blush, size, and sugar content (Lakso *et al.*, 1989; Wagenmakers and Callesen, 1995). Apple orchards have therefore an optimum of light interception, where the production of quality fruit is maximal. This optimum has been reported to be about 70%, independent on the planting system and corresponds to an orchard leaf area index (LAI) of 3 (Verheij and Verwer, 1973; Wagenmakers, 1991; Wagenmakers *et al.*, 1995). Limited data are available for pear but point in the same direction as those for apple. The production of cultivar Conference was linearly related with light interception between 50 and 85%. In the same range of light interception, fruit weight decreased linearly (unpublished data).

The spatial distribution of light can be measured fast and easily when sky conditions are overcast, by relating absorbed light to incoming light over a representative canopy area (Palmer *et al.*, 1992). The method is, however, limited to the appropriate weather. Getting an impression of direct light interception is more complicated and more time-consuming because of interaction with time of day and dynamics of clouds. Therefore, alternative methods have been studied. Wünsche *et al.* (1995) compared several techniques for estimating light interception. They found fairly good agreement between a "point grid" method (counting shaded and exposed points on a grid under the canopy) and daily total light interception. This visual estimation of sunflecks is rapid, simple and inexpensive, but dependent on solar height and orchard configuration. By combining incidental measurements with model calculations, it should be possible to predict light interception at any time of the day for any row orientation. Several models of light interception have been developed with varying levels of complexity. Palmer (1977a) used a two-dimensional approach for hedgerow orchards. For orchard systems with within-row discontinuity, a three-dimensional approach has to be applied (van Kraalingen *et al.*, 1989; Wagenmakers, 1991).

2. Material and methods

2.1. Study site

The study was carried out in orchards situated at 51°30' N and 3° 45' E (the Netherlands) planted with Conference pear and Elstar apple trees in single rows. Row orientation was NS and NW-SE for pear and apple, respectively. The trees were full-grown and more or less parabolically shaped (slender spindle). The planting distance was 3.12 x 1.07 m and 3.00 x 1.00 m for pear and apple, respectively. Tree dimensions were recorded on the basis of two-year-old (bearing) wood, on three trees per plot in two replications. Tree height was recorded from bottom to top and maximum tree diameter was measured at 45 and 135 degrees to the row direction. Leaf area was recorded on three pear trees in one replicate by counting leaves and taking a sample of every 25th leaf. Apple leaf area was calculated using an exponential function of light extinction and leaf area, found experimentally (Wagenmakers and Callesen, 1995).

2.2. Light measurements

Light measurements were made instantaneously on clear and overcast days with two cosine-corrected, hand-held PAR quantum sensors (SKP 2200), one above the canopy to measure the incident light, and one below the canopy (Skye instruments Ltd., Powys, UK). The measurements were made with little or no wind. The under-canopy sensor was moved by hand along grid lines (normal and parallel to the row) at ground level with a sampling interval of 10 and 25 cm under direct and overcast skies, respectively. A rod with dots every 10 and 25 cm was used to enable the measurement. The grid covered a rectangular area between two rows and two trees within a row. The sensors were hand-held horizontally in 1997 and equipped with a level in 1998. The clear-sky records were made with a time interval of approximately 2 hours in 1997 (30 July) in the pear orchard and 1 hour in 1998 (22 June) in the apple orchard. The diffuse-sky records were taken in the same week as the direct-light records. Values of a sensor on the ground (I) were divided by the values of incident light (I_0) and averaged to obtain the fraction of canopy light penetration. Canopy light interception was assumed to be 1 minus light penetration. Visual records of shaded and exposed spots ("sunflecks") were made on clear days at ground level at 10-cm intervals, comparable to the method of the direct light measurements. Shaded and exposed spots were estimated as 100 and 0% light interception, respectively. The average of all grid values was considered to be canopy light interception.

2.3. Model structure

The light-interception model considers orchard systems in three dimensions. The leaves, branches, and fruit are assumed to be black and distributed uniformly throughout the crown, thus ignoring canopy reflectance and transmittance which is approximately 5% (Palmer, 1977b). Leaf-angle distribution is assumed to be spherical. Tree shape is assumed to be parabolical and light transmission on the ground is calculated as a fraction of incident light above the canopy for a horizontal plane. Light intensity is calculated numerically along a line between the ground and the sun. Light extinction is an exponential function of leaf area according to

$$I = I_0 \, e^{(-k \, LAD \, s)}$$

where I is light intensity at a given point on the line, I_0 is light intensity at the previous point, k is the extinction coefficient (the projection of leaves in the direction of the sun), LAD is leaf density (m^2 leaf area per m^3 crown volume), and s is path length through the canopy (m). The model has been described in Wagenmakers (1991). Diffuse light is calculated numerically for a standard overcast sky at ten-degree intervals over the hemisphere (9 inclinations, 36 azimuths). A longitude correction was made on the modelled data accounting for local time (+40 minutes). The yearly variation of the equation of time has been accounted for (Iqbal, 1983). This was a small correction, being not more than 6 minutes between May and September. Summer time (local time plus 1 hour) is not considered in this article.

3. Results

3.1. Pear, NS row

Orchard LAI was 3.2. Tree average height and radius were 1.9 and 0.97 m, respectively. Diffuse light interception was recorded to be 70%. This was very close to the 68% light interception calculated, under the assumption of 10% addition to the actual tree dimensions (representing annual shoot growth). Although the pattern of measured direct light interception was linearly related to the sunflecks (r^2=0.94, n=8), the values were underestimated by 23% (Fig. 1). By the end of July, the sunfleck records met the value of diffuse light interception at 10:40 am, 2 hours before noon (local time). The simulated direct light interception was linearly related to the sunfleck measurements, but the values were 9% higher. Owing to a lower solar inclination, the estimated light interception would be increased by 6% when recorded one month later (end of August), according to simulation results (Fig. 1). The estimated time that should fit with diffuse light interception would be about 30 minutes later by the end of August. Since the daily pattern is similar before and after noon in a NS row, additional times are given for afternoon estimations, considering noon at 12:40 plus a small correction for the equation of time (Tab. 1).

3.2. Apple, NW-SE row

The average tree height was 2.0 m. Actual tree shape was not parabolic in the lower tree parts, since the radius remained 0.75 m below 1 m. The model made use of a parabola with crown radius 0.75 at 1 m height and 0.95 m at the crown basis. The measured diffuse light interception was 68%. Orchard LAI, calculated from diffuse light interception, was 3. When assuming a parabolic shape with radius 1,0 and height 2,1 m, diffuse light interception was calculated to be 67%. Sunfleck records were strongly correlated with direct PAR measurements ($r^2 = 0.98$, n=5), the values being only 3% lower. The simulated values of light interception were again 10% higher than the sunfleck values (Fig. 2). Since row orientation was not NS but NW-SE, the minimum light interception was already before noon, and the daily pattern was not similar before and after this minimum. At 8:45 am, the sunfleck records met diffuse light interception (Fig. 2). Simulation revealed that this moment was achieved only 5 and 15 minutes later when estimating the light interception 1 and 2 months later, respectively (Tab. 1).

4. Discussion

Sunflecks under orchard treees appear to be well correlated with PAR light interception. However, a large difference was observed between measured and simulated values for direct light in 1997. This can be explained by the levelling of the sensors. Deviations of a few degrees from horizontal may cause significant errors in incident light (Salminen *et al.*, 1983). This was significantly improved in 1998 when the sensors were levelled. Because of large variations under clear conditions, in time as well as in space, it is recommended to repeat the measurements during a day. Light interception by sunfleck records may be considered a reliable method to estimate the light environment of orchards. However, day, time, and row orientation are important parameters and the current records hold only for latitude 51-52 degrees. Under diffuse conditions, the model data correspond with measured light interception. Since the relationship between sunfleck estimations and model calculations is good, the model can be very useful to supply rapidly light interception values under other time conditions or row configurations than those measured. The current calculations predicted that a suitable time of estimation should be closer to noon when measuring later in the season, and that this time varies with row orientation. To achieve a sound model prediction for a given orchard system, the simulated light interception must be compared with measured data. For general purposes it might be sufficient to run the model for a range of orchard systems. It is recommended to verify the current model predictions on estimated times later in the season (Tab. 1).

The simulated results show a 10% higher light interception, compared with the sunfleck method. This could be related to a penumbral effect. In short canopies with a relatively large individual leaf size, penumbras are minimized (Pearcy *et al.*, 1990). In apple and pear orchards, however, the presence of many small leaves in a relatively large canopy causes a penumbral effect that cannot be ignored. When the angular size of leaves and gaps in the canopy is smaller than the solar disk, penumbral effects can be important. This might explain why light interception according to sunfleck recordings is underestimated, compared with the simulation results. However, the PAR sensors do not account for penumbral effects. Still, there is a difference of approximately 10% between measured and simulated light interception in 1998. When simulating direct light, the diffuse components were not taken into account. Even on sunny days, there is a certain fraction of diffuse light. Assuming a given diffuse fraction, the simulated curve would be smoother, with lower values early in the morning and higher values around noon. The mean value of simulated interception, however, would not be changed considerably, and the contribution of diffuse light is probably not responsible for the difference between measured and simulated direct light. The simulation model does not account for transmission and reflection of light by the leaves, which should lead to higher values of light interception. However, under diffuse light conditions the comparison between simulated and measured light was good. If the contribution of reflected and transmitted light would be considerably higher under direct conditions compared with diffuse light, simulated light interception might be overestimated.

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Table 1 - Estimated local times when shadow patterns correspond with diffuse light interception in N-S and NW-SE row direction

	N-S	NW-SE
End of June	10:30 and 14:45	8:45
End of July	10:40 and 14:30	8:50
End of August	11:10 and 14:10	9:00

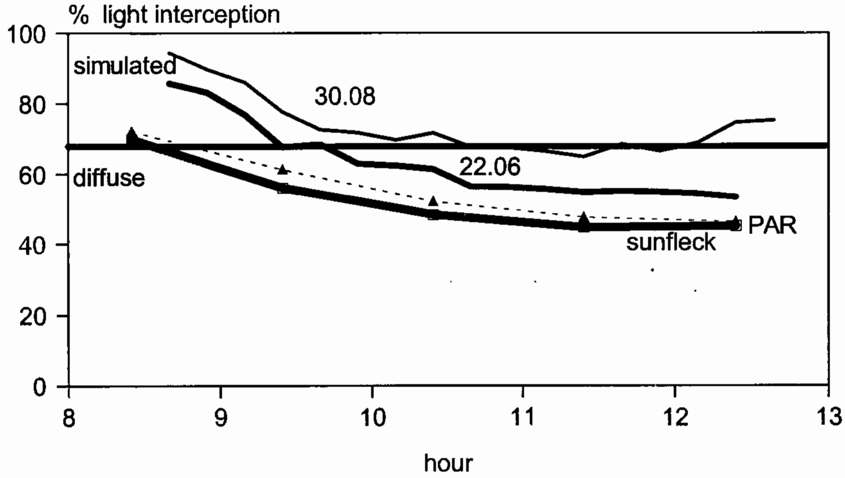

Figure 1 - Measured PAR and sunfleck method (30 July), and simulated direct light interception (30 July and 30 August) in a NS-oriented pear orchard. Measured and simulated diffuse light interception (horizontal line) was similar.

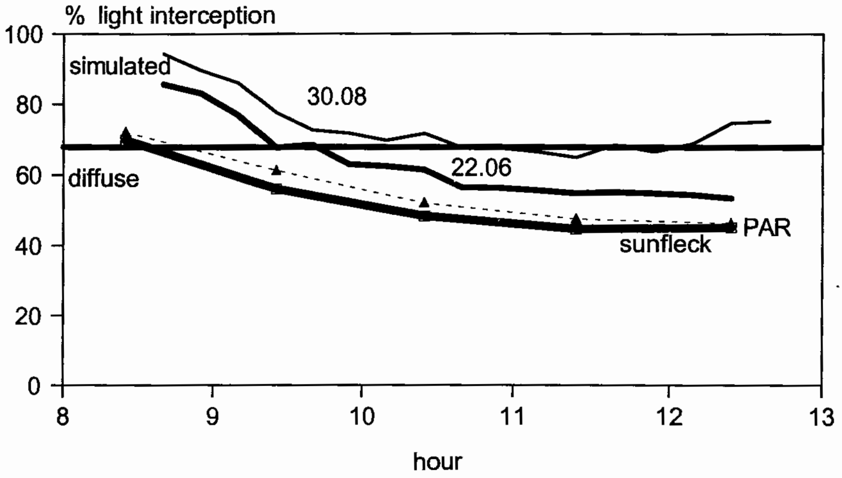

Figure 2 - Measured PAR (dotted line, 22 June), sunfleck method (solid line, 22 June), and simulated direct light interception (22 June, 30 August) in a NW-SE oriented apple orchard. Measured and simulated diffuse light interception (horizontal line) was similar.

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