Germination base temperature and relative growth rate of 13 weed species - comparing populations from two geographical origins

Basistemperatur der Keimung und relative Wachstumsrate von 13 Unkrautarten im Vergleich der Samen aus zwei mitteleuropäischen Herkünften

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Abstract

Two experiments were conducted to test parameter validity of a simulation model under North German conditions. At the moment, the model is stocked with life cycle parameters of 25 annual weed species. These were obtained from experiments in the region Burgundy and from literature. Such parameters may vary strongly between geographical regions.

Base temperature for germination was studied in one experiment for North German seeds of ten species. Mostly, base temperatures were between 1.5 and 2.7 °C higher than the parameters from French experiments. The second experiment, on Relative growth rate of 19 species, yielded similar values for most species in French and German seed populations.

In respect to using the model for simulations under North German conditions, adaptations should be undertaken for the germination base temperature. Growth rates can be kept unchanged, but for some species it needs to be clarified whether differences between parameters can be explained through seasonal variations in seed collection or experiment.

Keywords: Early growth, FlorSys, weed biology

Zusammenfassung

Es wurden zwei Experimente durchgeführt, um die Validität von Modellparametern eines Unkraut-Simulationsmodells für norddeutsche Bedingungen zu testen. Es umfasst zurzeit Parameter zum Lebenszyklus von 25 annuellen Unkräutern, die entweder durch Experimente in der Region Burgund erhoben oder aus der Literatur entnommen wurden. Solche Parameter können sich in Populationen verschiedener geographischer Herkunft erheblich unterscheiden.

Im Experiment zur Basistemperatur für die Keimung wurden norddeutsche Samen von zehn Arten untersucht. Die meisten von Ihnen wiesen Basistemperaturen auf, die ca.1.5-2.7 °C höher lagen, als die Basistemperaturen der französischen Experimente. Das Experiment zur Relativen Wachstumsrate mit 19 Arten zeigte für die meisten Arten ähnliche Werte in französischen und deutschen Populationen.

Für eine Nutzung des Modells in Norddeutschland sollten die Basistemperaturen angepasst werden. Wachstumsraten können beibehalten werden, wobei für einen kleinen Teil an Arten zu klären ist, ob Unterschiede durch saisonale Verschiebungen bei Samenernte und Experiment zu erklären sind.

Stichwörter: FlorSys, Unkrautbiologie

Introduction

Modelling and simulation are powerful scientific tools, accompanying experimental work and field monitoring with the possibility to forecast possible future developments, or to evaluate a range of contrasting scenarios. The validity of model results is usually limited to the domain in which the model's processes and parameters were analysed during model building. Extrapolating to conditions that were not included by the data sourcing may yield strongly false conclusions. To use a simulation model in conditions different to the originally tested ones therefore requires an evaluation of the model parameters' validity under the new conditions.

We conducted experiments to test the validity of germination and growth parameters of the crop: weed model FlorSys for Northern German conditions. The aim is to use the model in future simulation studies for this region. FlorSys simulates a virtual field on which cropping systems can be experimented and a range of crop, weed and environmental measures estimated. The life cycle of annual plants is modelled by processes that connect the essential stages from seed to mature plant and new seeds adding to the seedbank, both for crop and weed plants.

FlorSys was developed in Burgundy, France, and has been tested successfully for other French regions. Currently, the model contains parameters for 25 frequent and contrasting weed species. The parameters were either determined in experiments with seeds mainly collected in the region or researched from published literature. Two of the first processes in plants' life cycle are germination and early growth. They both depend largely on individual seed traits, for example dormancy status or resources expressed in seed weight.

Apart from the variation of such traits between individual seeds in a seed lot they can also vary between seed lots depending on region of origin, ripening time, or conditions under which the motherplant grew (pre-conditioning effect).

We conducted two experiments on species-specific germination and early growth traits in Rostock, Mecklenburg-Vorpommern, Germany. We used seeds collected from fields in the region as well as seeds from the original French seed lots. The experimental plan allowed to

1) compare species-specific parameters between seed lots from France and Germany,

2) expand the species list with species more prevalent under Northern climate and

3) control for errors caused by experimental set-ups and handling by comparing results obtained for the same French seed lots in the two places.

Materials and Methods

Experiment on base temperature for germination

Seed germination of each species and seed lot was tested at four to five constant temperatures. Seeds were laid out in petri dishes lined with a double layer of filter paper and moistened with water. Four replicates of 50 seeds per treatment were placed in temperature chambers with light for 12 h per day. Petri dishes were checked for germinated seeds at least once a day and seeds considered germinated when the radicle was clearly visible. Experiments took place in 2017 and lasted for approx. 4 weeks each, or until no more germination occurred during 7 days. Temperature in the chambers was monitored and means of the measurements used for calculations.

Time-to-event models were fitted to the germination data. We used a nonlinear and nonsymmetric three parameter Weibull function following the equation

$$GP_t = GP_{final} * e^{-e^{(b*(\ln(t)-i))}}$$

where GP_t is the proportion of seeds germinated up to the sampling time t, GP_{final} the final proportion of seeds germinated out of the sample, t the time since water addition, i the time at which the inflection of the curve occurs and b a shape parameter. The parameter t50, which is the time to reach 50% of the final germination proportion, was calculated from the model parameters.

Germination rates (GR) were calculated as the inverse of t50:

$$GR = \frac{1}{t_{50}}.$$

The species-specific base temperature (BT) was then determined by a regression of the germination rates over all studied temperatures and is specified as the x-intercept of the regression line (ARNOLD, 1959).

$$GR_T = a + b * T,$$

$$BT = a/b.$$

Experiment on relative growth rate in seedling stage

Early growth is the phase in life cycle lasting from emergence to the beginning of competition between plants. Until then, growth is exponential and largely determined by the resources saved in the seed and the energy provided as temperature by the environment. Early growth was monitored in several greenhouse experiments between April 2016 and June 2017.

Seeds were placed in petri dishes, wetted with water and set to germinate under optimal conditions according to literature. When germination started, up to 20 seeds were placed in individual pots with standard garden earth. Pots were placed in green houses without heating, but with additional light when necessary to obtain min. 12 h light exposure. Pots were watered to ensure non-limited growth. Leaf area development was monitored by a non-destructive approach taking one photograph of each pot per day and analysing it via software. Some plants were harvested at 2-leaf, 4-leaf and 8-leaf stage respectively and their leaf area determined by a scan of all leaves. Leaf area values from the photographs were then corrected by a function determined from relations between scan and photograph on the same day.

Leaf area growth curves were fitted following the equation for exponential growth

$$LA_{TT} = LA_0 * e^{(RGR*TT)}$$

where TT is thermal time from emergence, LA_{TT} is leaf area at TT, LA_0 is leaf area at emergence and RGR the relative growth rate. Leaf area was log-transformed and parameters fitted by linear regression over TT.

Thermal time was calculated as

$$TT_d = \sum_{i=0}^{d} (T_i - T_b)$$

where TT_d is cumulated thermal time at sampling date d, T_i is the daily mean temperature and T_b is the species-specific base temperature. When the number of plants of a species with successful growth was not sufficient for the analyses, the experiment was repeated, and measurements pooled. Finally, the species-specific RGR was determined by averaging all RGRs from plants with good fits in the linear regression (expressed by $R^2 > 0.9$).

Species and seed material

Species from the FlorSys set were chosen for the experiments that are also prevalent in Northern German arable fields. The selection was completed with the most important species found in weed monitorings of the region that were not parameterised in FlorSys before. Seeds were sourced for these species from the experimental gardens and experimental fields of Rostock University, in a few cases from commercial suppliers. In early summer 2016, we additionally included some seed lots from Burgundy in the green house experiments, i.e. from the exact same seed lots that were used for the original parametrisation. Table 1 gives an overview of species, experiments conducted on these species and the seed sources.

Tab. 1 Species and seed sources for base temperature and relative growth rate experiments in Rostock, 2016 and 2017. Abbreviations: D – Germany, F – France, EG – experimental garden University Rostock, ES – experimental station Stover Acker, CS – commercial supplier, INRA – seed collection INRA Dijon. SP – spring, SU – summer, AU – autumn.

***Tab. 1** Arten und Samenquellen für Basistemperatur- und Wachstumsraten-Experimente in Rostock, 2016 und 2017. Abk.: D – Deutschland, F – Frankreich, EG – Schau und Lehrgarten Rostock, ES – Versuchsstation Stover Acker, CS – gewerblicher Samenlieferant, INRA – Samensammlung INRA Dijon. SP – Frühjahr, SU – Sommer, AU – Herbst.*

Species	EPPO code	Country of origin	Seed source and harvest date	Temperature levels (°C) for base temperature experiment [a]
Alopecurus myosuroides	ALOMY	D	EG 07/2016	7; 11; 15; 16
		F	INRA	-
Amaranthus retroflexus	AMARE	D	ES 09/2015	-
		F	INRA	-
Anchusa arvensis	LYCAR	D	commercial supplier: Appels Wilde Samen 2016	-
Apera spica-venti	APESV	D	ES 08/2015	5; 7; 11; 16
Capsella bursa-pastoris	CAPBP	D	ES 06/2014	-
Centaurea arvensis	CENCY	D	EG 06/2016, CS 2016	7; 10; 12; 15
Chenopodium album	CHEAL	D	ES 2015	5; 7; 9; 13
		F	INRA	-
Echinochloa crus-galli	ECHCG	D	ES 08/2015	11; 13; 16; 17
		F	INRA	-
Galium aparine	GALAP	D	EG 07/2016	-
Geranium dissectum	GERDI	D	CS 2016	5; 7; 9; 11; 13; 16
Matricaria chamomilla	MATCH	D	ES 8/2015	5; 9; 11; 13; 16
Matricaria inodora	MATIN	D	ES 2015	5; 9; 13; 17
Papaver rhoeas	PAPRH	D	EG 07/2016	5; 9; 13; 17
Poa annua	POAAN	D	EG 2013	-
Setaria viridis	SETVI	D	EG 2011	-
		F	INRA	-
Solanum nigrum	SOLNI	D	ES 2011	-
		F	INRA	-
Stellaria media	STEME	D	EG 06/2016	5; 7; 9; 11; 13
Sisymbrium officinale	SSYOF	D	EG 9/2015	7; 10; 12; 15
Veronica hederifolia	VERHE	D	EG 2008	-
Viola arvensis	VIOAR	D	ES 06/2016	-

[a] Mean temperatures measured per chamber of a planned constant temperature level: 5: 6.0 °C; 7: 7.1 °C; 9: 8.6 °C; 10: 9.9 °C; 11: 11 °C; 13: 13.9 °C; 15: 15.0 °C; 16: 16.3 °C; 17: 18.4 °C.

Analysis

Calculations and statistical analyses were carried out with R, version 3.3.3 (R CORE TEAM, 2017). Fitting of germination curves was done with the R-package "drc" (RITZ et al., 2015).

Results and discussion

Base temperatures

All regressions of germination rates over temperatures had a good fit, obtaining R^2 between 0.88 and 0.99. For one out of the ten tested species, *Matricaria inodora*, the experiment resulted in nearly the same base temperature for the German seed lot (1.8 °C, Fig. 1) as it is recorded in the FlorSys data (1.9 °C).

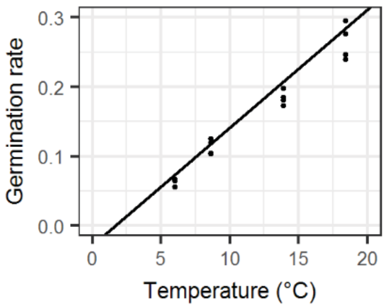

Fig. 1 Effect of temperature on germination rate of *Matricaria inodora*. Base temperature is determined as x-intercept of the linear regression line.

***Abb. 1** Effekt der Temperatur auf die Keimrate von* Matricaria inodora.

For one species, no reference value is included in FlorSys. The result for *Apera spica-venti* was the same in our experiment as reported by SCHERNER et al. (2017) obtained for a Danish seed sample. For six species, the base temperatures were clearly higher for the tested seed samples than was recorded for samples in Burgundy (Tab. 2). The difference was between 0.9 °C (*Stellaria media*) and 5.3 °C (*Geranium dissectum*). The only species with a lower base temperature in Germany was *Chenopodium album*. The German base temperature was 1.5 °C, which is more than 4 °C lower than the French value.

Tab. 2 Base temperature for germination of 10 weed species from North German seed lots.

***Tab. 2** Basistemperatur für 10 Ackerunkrautarten norddeutscher Herkunft.*

Species	**Base temperature obtained in experiment (°C)**	**Base temperature in FlorSys database (°C)[a]**
Alopecurus myosuroides	1.6	0
Apera spica-venti	0.6	-
Centaurea arvensis	3.0	1.5
Chenopodium album	1.5	5.8
Echinochloa crus-galli	10.2	6.2
Geranium dissectum	3.8	-1.5
Matricaria chamomilla	4.7	1.9
Matricaria inodora	1.8	1.9
Papaver rhoeas	3.5	0.8
Stellaria media	2.3	1.4

[a]GARDARIN et al. (2011)

The differences may be the result of adaptations both to climate and resulting cropping practices in the two regions, but also dependent on species' emergence patterns. *Matricaria inodora* and *Stellaria media*, the species with the most similar base temperatures between regions, are able to germinate all year around. The group of species that germinate mainly in autumn and early spring shows a higher base temperature in the German seed lots, but with an intermediate difference of about 1.5 to 2.7 °C. This may be an adaption to the lower temperatures in Mecklenburg during the emergence times. In autumn, germination in the German region would stop earlier than in the French region, leaving an appropriate amount of time for germinated seedlings to grow to favourable growth stages before the freezing period starts in winter. Likewise, germination in spring will start later than in the French region, lowering the risk for another spell of frost weather killing newly emerged seedlings.

Base temperatures also differ between seed samples taken at different times of the year. The early collection date of the German sample of *Stellaria media* in June suggests that these seeds were harvested from plants that emerged in autumn, and overwintered. Earlier germinating parts of a population may have lower base temperatures than seeds germinating later in the year. COLBACH et al. (2002) reported this for *Alopecurus myosuroides* for which they did not find an effect of seed source on base temperature, even with locations of different climate conditions. Yet, seeds were all collected in winter crops. The authors proposed that seeds from spring crops were produced by plants resulting from seeds germinating after winter and under warmer conditions, therefore might have different temperature requirements.

The large inner-specific trait variability of *Chenopodium album* has also been documented before. Base temperature values in the literature range from 2.0 °C (VLEESHOUWERS and KROPF, 2000) to 10.0 °C (GARDARIN et al., 2009). *Chenopodium album* exhibits a pronounced seed polymorphism with three categories of seeds (brown, black-reticulate and black-smooth) differing widely in their germination behaviour (WILLIAMS and HARPER, 1965). As the proportion of these seed categories varies between plants and growing situation of the mother plants, this leads to a high phenotypic polymorphism of seed samples and contributes to the variability of results from base temperature experiments as we found them.

Relative growth rates

The first part of the analysis was to compare relative growth rates that were determined with seeds from Burgundy in the two independent experimental set-ups in Dijon and Rostock. Growth rates of five species were similar between experiments (Fig. 2), mostly with similar medians. Even in the case of *Amaranthus retroflexus* where the Rostock experiment resulted in higher average growth rates, the values of the individual plants fall into the range of the Dijon experiment. It remains unclear so far, why growth rates of *Echinochloa crus-galli* were much smaller in the Rostock experiment. Altogether, it could be concluded that experimental set-up, conditions in green houses and handling were sufficiently similar between experiments to make comparisons of the results meaningful even if French and German seed lots were not tested in the same experiment.

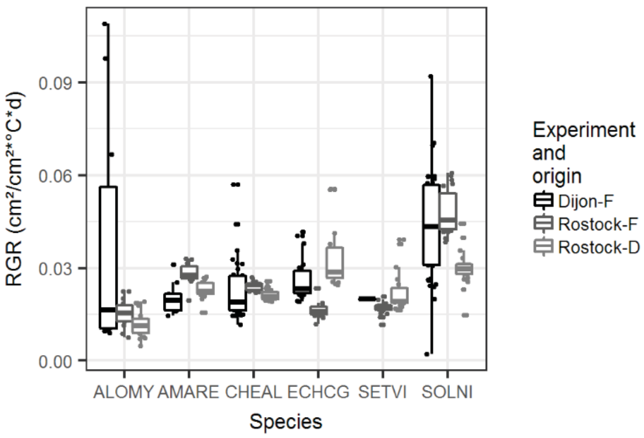

Fig. 2 Relative growth rate of leaf area of six weed species comparing two experiments (Dijon, Rostock) and two seed lots of different origin (F - France, D - Germany). Boxplots combined with values of all individual plants. For SETVI (Dijon) only a mean value was available.

Abb. 2 *Relative Wachstumsrate der Blattfläche von sechs Unkrautarten, im Vergleich zwischen zwei zeitlich unabhängigen Experimenten (Dijon und Rostock) und zwei Samenherkünften (F – Frankreich und D – Deutschland). Boxplots unterlegt mit Werten aller Einzelpflanzen. Für SETVI (Dijon) war nur ein Mittelwert verfügbar.*

When relative growth rates from the experiment in Rostock were compared directly between French and German seed lots (Rostock-F and Rostock D in Fig. 2), four species showed similar rates between populations. Two species, namely *Echinochloa crus-galli* and *Solanum nigrum* had pointed differences. Yet again, even in these cases the results from Rostock all fall into the range of values from the Dijon experiment.

In the second part of the analysis, growth rates of the German seed lots (Tab. 3) were compared to the values included in the FlorSys model. Relative growth rates of ten German seed lots were similar to the growth rates of French seed lots. The exceptions were *Matricaria chamomilla*, *Galium aparine* and *Stellaria media*. In all three cases, the RGR in our experiments was markedly larger than in the FlorSys data. The larger RGR was combined with a smaller leaf area at emergence (data not shown).

Tab. 3 Relative growth rate of leaf area ($cm^2/cm^{2}*°C*d$) of 19 weed species in comparison between two experiments and differing seed samples. Values are means ± standard deviation.

Tab. 3 *Relative Wachstumsrate der Blattfläche ($cm^2/cm^{2}*°C*d$) von 19 Unkrautarten, im Vergleich zwischen zwei Experimenten und verschiedenen Samenherkünften. Mittelwerte ± Standardabweichung.*

Species	**Rostock, Germany**	**Dijon, France**
Alopecurus myosuroides	0.009 ± 0.002	0.037 ± 0.039
Amaranthus retroflexus	0.022 ± 0.004	0.019 ± 0.005
Anchusa arvensis	0.011 ± 0.001	-
Capsella bursa-pastoris	0.019 ± 0.002	0.023 ± 0.014
Centaurea arvensis	0.014 ± 0.001	-
Chenopodium album	0.021 ±0.002	0.022 ± 0.009
Echinochloa crus-galli	0.028 ± 0.002	0.028 ± 0.012
Galium aparine	0.020 ± 0.004	0.013 ± 0.004
Geranium dissectum	0.013 ± 0.001	0.012 ± 0.002
Matricaria chamomilla	0.026 ± 0.005	0.015 ± 0.006
Matricaria inodora	0.017 ± 0.002	0.015 ± 0.003
Papaver rhoeas	0.020 ± 0.002	-
Poa annua	0.012 ± 0.004	0.013 ± 0.008
Setaria viridis	0.019 ± 0.002	0.020 (sd n.a.)
Solanum nigrum	0.048 ± 0.007	0.046 ±0.016
Sisymbrium officinale	0.019 ± 0.004	-
Stellaria media	0.019 ± 0.002	0.011 ±0.003
Veronica hederifolia	0.007 ± 0.001	0.011 (sd n.a.)
Viola arvensis	0.013 ± 0.001	0.011 ± 0.007

These differences may be explained by two factors related to climate and vegetation season patterns in the different provenances. On one hand, many species show a seasonal variability in relative growth rate in experiments in spring vs. autumn (STORKEY, 2004). The author reported that plants which emerged before the winter had a lower relative growth rate than the ones that emerged in spring. When light availability was accounted for, the growth rates were the same.

This effect could explain our results on *Matricaria chamomilla*. The growth rates in Table 3 are averages from plants grown in two experiments in Rostock and Dijon respectively. Growth rates obtained only from very early spring experiments in March 2016 in Rostock and April 2011 in Dijon were 0,021 and 0,018 for the German and French seed lot. In contrast to that, an experiment in April 2016 in Rostock gave a rate of 0,031 and an experiment in July 2010 in Dijon a rate of 0,009.

On the other hand, high early growth rates may be an adaptation to length of vegetation periods. Especially in Northern latitudes with shorter vegetation periods, plants may need to be quicker in the development to successfully flower and reproduce. When higher base temperatures as we found them for *Matricaria chamomilla* and *Stellaria media* lead to a later vegetation start in spring, a higher growth rate might compensate for that late start.

In general, it can be concluded that for the large majority of tested species base temperatures were higher, but relative growth rates similar in plants from Northern German seed samples compared to the values that are included in FlorSys. Base temperatures should therefore be adapted before using the model for simulation under Northern German conditions. Relative growth rates can be used with the values that are included in FlorSys. For the species that showed large differences in growth rate it remains to be checked whether seed harvest and experiments were executed in the same season and if species have the same emergence season in both regions.

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