Critical limits of soil water availability (CL-SWA) for forest trees – an approach based on plant water status

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Abstract

Due to climate change, heat waves and drought are expected to increase in frequency and intensity in Central Europe. Thus, assessments of critical constraints of water supply in forest trees are needed to develop adequate forest adaptation measures. We present a novel 'critical limit' approach to soil water availability (SWA) for the major central European forest tree species based on the physiological plant water status. In regards to the conductivity of trees' xylem, three thresholds of pre-dawn water potential (ψ_{wp}) were chosen, referring to (i) slight conductivity loss (10 %), (ii) critical conductivity loss (50 %) and (iii) complete conductivity loss (> 90 %). In times of drought, pre-dawn water potential relates to the soil water potential at the lowest soil depth in which plant's root system is able to deplete water resources; the 'effective rooting depth' (ERD). The critical limit of soil water availability (CL-SWA) represents the proportion of plant-available water within the variable effective rooting depth (ERD) that meets both the critical soil water potential at the lower limit of the ERD and the critical plant water status. The CL-SWA-approach can be implemented in water budget models like BROOK90.

Keywords: Climate change, drought, adaptation, critical limit, xylem conductivity, pre-dawn potential, soil water potential, effective rooting depth

Zusammenfassung

Kritische Grenzen der Bodenwasserverfügbarkeit (CL-SWA) für Waldbäume – ein Ansatz auf Grundlage des Pflanzenwasserstatus

Aufgrund des Klimawandels werden sich sowohl Häufigkeit als auch Intensität von Hitze- und Trockenperioden in Mitteleuropa erhöhen. Die Beurteilung einer kritischen Wasserversorgung von Waldbäumen ist daher eine wichtige Grundlageninformation zur Entwicklung von Anpassungsmaßnahmen. Wir stellen einen neuartigen Ansatz zur Bestimmung von kritischen Grenzen der Bodenwasserverfügbarkeit (SWA) für wichtige Baumarten vor, der auf dem physiologischen Pflanzen-Wasserhaushalt basiert. Unter Betrachtung der Xylemleitfähigkeit wurden drei Schwellenwerte des Dunkelwasserpotenzials (Pre-dawn-Potenzial, ψ_{wp}) gewählt, die (i) zu geringem Leitfähigkeitsverlust (10 %), (ii) zu kritischen Leitfähigkeitsverlust (50 %) und (iii) zu komplettem Leitfähigkeitsverlust (> 90 %) führen. In Trockenzeiten steht das Dunkelwasserpotenzial in Beziehung zum Bodenmatrixpotenzial in jener Bodentiefe, in der die Wurzelsysteme gerade noch Wasserressourcen nutzen können; dies entspricht der ‚effektiven Wurzeltiefe' (ERD). Die kritische Bodenwasserverfügbarkeit (CL-SWA) stellt den Anteil an nutzbarem Bodenwasser dar, das sowohl zu einem kritischen Bodenmatrixpotenzial als auch zu einem kritischen Dunkelwasserpotenzial führt. Die kritischen Grenzen der Bodenwasserverfügbarkeit (CL-SWA) können in Wasserhaushaltsmodelle, wie z. B. Brook90 implementiert werden.

Schlüsselworte: Klimawandel, Trockenheit, Anpassung, Kritische Grenze, Xylemleitfähigkeit, Pre-dawn-Potenzial, Bodenwasserpotenzial, Effektive Durchwurzelungstiefe

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Introduction

Climate modeling projections for the next 100 years suggest that global annual temperatures will increase between 2 °C and 3 °C, when using medium severity scenarios (SRES B1 and A1B, IPCC 2007). Heat waves and drought will increase in frequency, intensity and duration (Schär et al., 2004; Tebaldi et al., 2006; Beniston et al., 2007). Together with projected higher probabilities of extreme storm events (Christensen et al., 2002; Leckebusch and Ulbrich, 2004; Leckebusch et al., 2006), these climatic changes will expose German forest ecosystems to environmental conditions that differ from those experienced in the past (Jansen et al., 2008). The forestry sector wants to respond to climate change by developing adaptive forest management measures in order to maintain forest resistance and resilience ability (Bolte et al., in press).

The ongoing project 'Adaptation Strategies for Sustainable Forest Management under Changing Climatic Conditions – Decision Support System 'Forest and Climate' (DSS-WuK)' develops models and methods to assist stakeholders within the forestry and environment sectors to find adequate forest adaptation measures to climate change. This work aims to compile and utilize existing knowledge about climate change impacts and their effects on the economic and ecological services of forests within a user-friendly decision support system (DSS). The DSS reflects site variation at a regional scale due to wind climate, drought and climate-induced biotic agents based on regionalized projections (CLM – Climate Local Model, REMO – Regional Model) for the above- mentioned IPCC SRES A1B and B1 scenarios. High-resolution maps showing projected climate variation as well as model outputs (including abiotic and biotic risk level, site-growth development and economic indicators) for major tree species (European beech, Peduculate/Sessile oak, Norway spruce, Scots pine and Douglas fir) provide decision support to the individual stakeholder (Jansen et al., 2008).

This paper presents and discusses a method to adequately assess the drought risk for the major tree species in Germany based on a 'critical limit' approach (UN-ECE 2004) for soil water availability (SWA) that is derived from plant water status. We focus on the sapling growth stage, due to the high susceptibility of trees to water stress in this regeneration phase (Czajkowski et al., 2005).

Methods

'Critical limit' definition

In vegetation ecology, critical loads and limits were first used to assess effects of air pollution on vegetation and forest ecosystems within the UN-ECE "Convention on Long-Range Transboundary Air Pollution" (UN-ECE, 1979). A critical load is defined as the maximum exposure "below which significant harmful effects on specified sensitive elements of the environment do not occur" (UN-ECE, 2004). A critical limit is a chemical criterion (e. g. the threshold of base cation to aluminium ion ratio [*Bc/Al*] in the soil solution) that is reached when the critical load is exceeded.

We adopt this concept for assessments of drought impact on young trees. A critical limit of plant water status occurs when cavitations in trees' xylem lowers the (stem) xylem conductivity considerably; we have chosen three thresholds referring to (a) slight conductivity loss (10 %), (b) critical conductivity loss (50 %, Bréda, 2006; Brodribb and Cochard, 2009) and (c) complete conductivity loss (> 90 %). We suggest to predominantly use the 50 % threshold (b) as the critical limit, since this limit is related to the maximum recoverable drought stress in conifers (Bodribb and Cochard, 2009), which meets quite well the criterion of a "harmful effect". Relationships between xy-

Table 1:

Xylem water potential (MPa) for three thresholds of xylem conductivity loss compiled from different literature sources. A loss of 50% of xylem conductance is regarded as the critical limit for desiccation response (Brodribb and Cochard, 2009)

	Xylem conductivity loss			
Tree species	**10 %**	**50 %**	**> 90 %**	**Source**
European beech *(Fagus sylvatica)*	2.0	**2.6**	4.0	Cochard et al., 1999; Hacke and Sauter, 1995; Lemonie et al., 2002a; Lemonie et al., 2002b; Lösch, 2001.
Pedunculate oak *(Quercus robur)*	2.0	**3.0**	4.0	Bréda et al., 1993; Bréda et al., 1995; Cochard et al., 1992; Cochard et al., 1996; Higgs and Wood, 1995; Lösch, 2001; Nardini and Pitt, 1999; Nardini and Tyree, 1999; Simonin et al., 1994; Tognetti et al., 1998; Tyree and Cochard, 1996
Sessile oak *(Quercus petraea)*	2.5	**3.3**	4.4	
Red oak *(Quercus rubra)*	1.5	**2.3**	3.5	
Norway spruce *(Picea abies)*	2.0	**3.5**	4.5	Cochard, 1992; Lösch, 2001; Lu et al., 1996; Martínez-Vilalta et al., 2004; Mayr et al., 2002; Mayr and Cochard, 2003; Rosner et al. 2006; Bond and Kavanagh, 1999; Cochard, 1992; Martínez-Vilalta and Piñol, 2002;
Scots pine *(Pinus sylvestris)*	2.5	**3.2**	5.3	
Douglas fir *(Pseudotsuga menziesii)*	2.5	**3.6**	5.0	Cochard, 1992; Domec and Gartner, 2001; Kavanagh et al., 1999; Piñol and Sala; 2000; Sperry and Ikeda, 1997; Stout and Sala, 2003.

lem conductivity and xylem water potential, derived for example from 'vulnerability curves' (Sperry et al., 1988; Tyree and Sperry, 1989; Kolb et al., 1996; Cochard et al., 2002; Cruiziat et al., 2002; Cochard et al., 2005), can be used for referring thresholds of conductivity loss to plant water status (Table 1). In this way, drought effects can be quantified using physiological criteria.

Critical limits of soil water availability

The pre-dawn water potential (ψ_{wp}), measured just before sunrise, determines the plant water status in equilibrium with the soil water potential (ψ_m) within the plant rooting zone (Ehlers, 1996). According to this concept, plant water status relates to the soil water potential at the lowest soil depth in which plant's root system is able to deplete water resources, e. g. 140 cm depth (Bréda et al., 1995). This rooting depth meets the definitions of the 'effective rooting depth' (ERD) according to AK Standortskartierung (1996).

The critical limit of soil water availability (CL-SWA) describes the proportion of plant-available water within the effective rooting depth that meets both the critical soil water potential at the lower limit of the ERD and the critical plant water status. For the assessment of CL-SWA, specifications of effective rooting depth are very important. The architecture of root systems is mainly influenced by the parent material, the soil type, bulk density, the chemical soil conditions, the depth of ground water and species and age of trees. Due to this complexity, the root depth and the distribution in the soil profile are critical model parameters. For the estimation of the effective rooting depth we used the linking rule from Müller (2004) and Raissi et al., (2009). This rule was modified for shallow-rooting spruce on soils with unconsolidated rock by decreasing its rooting depth from 80 % of those of deeper-rooting species like Scots pine and oak to only 70 % (Table 2). This is in line with numerous publications (Rastin and Urlich, 1990; Heinze et al., 2001; Lehnardt and Brechtel, 1980; Kreutzer, 1961; Bolkenius, 2001; Osenberg, 1998). For water-saturated sites (with G, A, M layers, AK Standortskartierung, 1996) we kept to the rule that the depth of the groundwater table restricts the rooting depth.

Results and discussion

Root depth estimates

Use of the root depth estimation model is illustrated using input data for precipitation from the very high resolution interpolated climate data for Germany (Hijmans et al., 2005). For the spatially distributed simulation we used the digital soil map of Germany at a scale of 1:1 000 000 (Richter et al., 2007) and the digital metadata corresponding to the above soil map. Figure 1 shows the deeper rooting activity of Scotch pine in contrast to spruce. For both trees, the rooting depth in the mountainous regions is in general 100 to 120 cm. On sandy soils derived from unconsolidated rocks, where the soil depth is much greater than in the mountain regions, under poor precipitation conditions the effective root depth reaches a depth of about 2 m, this also being the lower limit of our soil profiles.

CL-SWA is modeled using water budget models (BROOK 90 model, Federer et al., 2003) using the variables (1) tree species, (2) effective rooting depth, and (3) the hydraulic properties of the soil (e. g. Clapp and Hornberger, 1978). The parameters of the water retention curve were deduced from soil texture (Clapp and Hornberger, 1978). More details on the CL-SWA modeling will be presented in a forthcoming paper.

Table 2:

Effective rooting depth on forest sites (ERD [dm]) according to Müller (2004, modified)

Soil substrate	**Age (a)**	**< 15**				**15 - 45**				**45 - 80 (100)**			
	Yearly prec. (mm)	**> 750**	**725**	**700**	**< 625**	**> 750**	**725**	**700**	**< 625**	**> 750**	**725**	**700**	**< 625**
Sand	Others	7.0	8.0	9.0	10.0	11.0	12.0	13.0	14.0	15.0	16.0	18.0	20.0
	Norway spruce	4.9	5.6	6.3	7.0	7.7	8.4	9.1	9.8	10.5	11.2	12.6	14.0
Loam	Others	8.0	9.0	10.0	11.0	12.0	13.0	14.0	15.0	16.0	17.0	19.0	21.0
	Norway spruce	5.6	6.3	7.0	7.7	8.4	9.1	9.8	10.5	11.2	11.9	13.3	14.7
Silt	Others	12.0	13.0	14.0	15.0	16.0	17.0	18.0	19.0	20.0	21.0	23.0	25.0
	Norway spruce	8.4	9.1	9.8	10.5	11.2	11.9	12.6	13.3	14.0	14.7	16.1	17.5
Clay	Others	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	13.0	14.0	15.0
	Norway spruce	5.6	6.0	6.3	6.7	7.0	7.4	7.7	8.1	8.4	9.1	9.8	10.5
Bedrock	Others		7.0				9.5				12.0		
	Norway spruce		6.0				8.0				10.0		

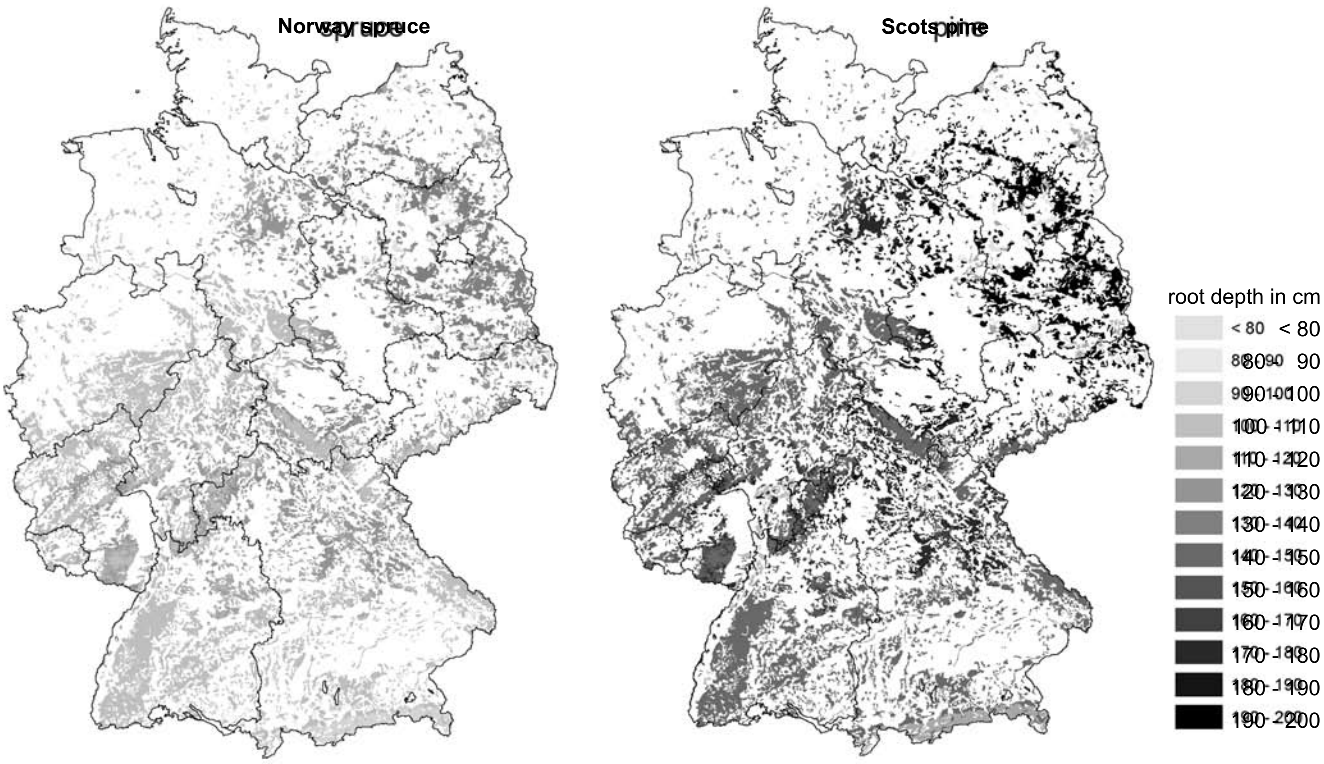

Figure 1:
Estimated effective rooting depth as a function of precipitation, soil texture and tree species

Options and constraints of the CL-SWA approach

To our knowledge, the present approach is among the first to combine the critical limit concept with plant water status and the related parameter of soil water availability. In our approach, plant water physiology is directly included in the indicator 'critical limit of soil water availability' (CL-SWA). Evident soil-plant interactions are reflected in CL-SWA indicator which determines the soil water potential that triggers a 50 % loss of xylem conductance and 95 % loss of leaf conductance. The latter indicates the maximum recoverable drought stress (Brodribb and Cochard, 2009).

Since plant water potential is commonly used for plant drought stress in terms of xylem conductivity loss (e. g. Kolb et al., 1996; Cochard et al., 2002; Cruiziat et al., 2002; Cochard et al., 2005), the inclusion of the CL-SWA indicator in large scale water budget modelling puts physiologically based drought stress estimates on a higher spatial scale and offers novel options for forest landscape assessments.

In contrast, Novák and Havrila (2006) based their ostensibly similar estimates of critical soil water content on the decrease of water extraction ability and yield of plants; criteria which differ considerably to our criteria for CL-SWA. Moreover, they used the 'relative transpiration index' (RTI) as an indicator of the (critical) state of soil water resource availability. RTI describes the ratio of actual transpiration to potential transpiration (RTI = ET_a/ET_p, Budagovskij and Grigorieva, 1991), and it is a commonly used indicator (e. g. Klap et al., 2002; Eccel et al., 2005), which may describe the stomatal control and thus adaptive behaviour of plants to water shortage rather than direct drought impact on plant water status.

There are also, however, constraints with our CL-SWA approach. One constraint is the use of pre-dawn water potential for characterizing the (critical) plant water status in order to interlink plant water and soil water status (Ehlers, 1996). Midday plant water potential, measured in times of highest evaporation pressure, often falls far below pre-dawn water potential. A correlation between the two traits is not always visible due to individual adaptation abilities to drought (e. g. Czajkowski et al. 2006). Thus, the probability of critical midday embolism is only in general reflected in the approach presented.

Another constraint is the relationship between plant water status and soil water status at the 'effective rooting depth' (ERD). The depletion depth of the plant rooting system varies due to the water-potential gradient between soil matrix potential and plant water potential (Hetsch and Heilig, 1981; Aussenac et al., 1984; Bréda et al., 1995; Tognetti et al., 1995; Laio et al., 2001; Porporato et al., 2001; Sperry et al., 2002; Sperry and Hacke, 2002; Bhaskar, 2006). In times of extreme drought, plants seem to be able to lower the depletion depth temporarily below the ERD (Joslin and Wolfe, 2003), but this cannot be included in our approach.

The main uncertainty of our approach relates to the determination of the 'effective rooting depth' (EDR) itself, since this is highly dependent on tree species, stand structure and soil characteristics (Bibelriether, 1966; Köstner et al., 1968; Lehnardt and Brechtel, 1980; Schmid and Kazda, 2002; Dannowski and Wurbs, 2003; Claus and George, 2005; Meier and Leuschner, 2008; Raissi et al., 2009). We lack data covering the whole variety of combinations of tree species, competition situations and soil characteristics. Thus, any general rule on ERD, like we have used for this approach and the following modeling, may consider average ERD, but not all specific situations.

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References

AK Standortskartierung (1996) Forstliche Standortsaufnahme : Begriffe, Definitionen, Kennzeichnungen, Erläuterungen. Eching : IHW-Verl, 352 p

Aussenac G, Granier A, Ibrahim M (1984) Influence du dessechement du sol sur le fonctionnement hydrique at la croissance du douglas (*Pseudotsuga menziesii* (Mirb.) Franco). Oecol Plant 5:241-253

Beniston M, Stephenson DB, Christensen OB, Ferro CAT, Frei C, Goyette S, Halsnaes K, Holt T, Julhä K, Koffi B, Palutikof J, Schöll R, Semmler T, Woth K (2007) Future extreme events in European climate : an exploration of regional climate model projektions. Clim Change 81:71-95

Bolkenius D (2001) Zur Wurzelausbildung von Fichte (*Picea abies* L. [Karst]) und Weißtanne (*Abies alba* Mill.) in gleich- und ungleichaltrigen Beständen. Freiburg : FVA, 155 p, Freib Forstl Forsch 35

Bolte A, Ammer C, Löf M, Nabuurs GJ, Schall P, Spathelf P Adaptive forest management : a prerequisite for sustainable forestry in the face of climate change. In: Spathelf P (ed) Sustainable forest management in a changing world : European perspective. Heidelberg : Springer (in press)

Bhaskar R, Ackerley DD (2006) Ecological relevance of minimum seasonal water potentials. Physiol Plant 127:353–359

Bibelriether H (1966) Die Bewurzelung einiger Baumarten in Abhängigkeit von Bodeneigenschaften. Allg Forst Z 21:808-815

Bond BJ, Kavanagh KL (1999) Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. Tree Physiol 19:503-510

Bréda N, Cochard H, Dreyer E, Granier A (1993) Field comparison of transpiration, stomatal conductance and vulnerability to cavitation of *Quercus petrea* and *Quercus robur* under water stress. Ann Sci For 50:571-582

Bréda N, Granier A, Barataud F, Moyne C (1995) Soil water dynamics in an oak stand : I. Soil moisture, water potentials and water uptake by roots. Plant Soil 172:17-27

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought : a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63:625-644

Brodribb TJ, Cochard H (2009) Hydraulic failure defines the recovery and point of death in water-stressed conifers. Plant Physiol 149:575-584

Budagovskij AI, Grigorieva NI (1991) The way to improve effectiveness of soil water resources utilization. Vodn resur 1:131-142

Christensen JH, Carter T, Giorgi F (2002) PRUDENCE employs new methods to assess European climate change. EOS 83:147

Claus A, Gorge E (2005) Effect of stand age on fine-root biomass and biomass distribution in three European forest chronosequences. Can J For Res 35:1617-1625

Clapp RB, Hornberger GM (1978) Empirical equations for some soil hydraulic properties. Water Resour Res 14(4):601-603

Cochard H (1992) Vulnerability of several conifers to air embolism. Tree Physiol 11:73- 83

Cochard H, Bréda N, Granier A, Aussenac G (1992) Vulnerability to air embolism of three European oak species (*Quercus petrea* (Matt) Liebl, *Quercus pubescens* Willd, *Quercus robur* L). Ann Sci For 49:225-233

Cochard H, Lemoine D, Dreyer E (1999) The effects of acclimation to sunlight on the xylem vulnerability to embolism in *Fagus sylvatica* L. Plant Cell Environ 22:101-108

Cochard H, Bréda N, Granier A (1996) Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism? Ann For Sci 53:197-206

Cochard H, Coll L, Le Roux X, Ameglio T (2002) Unraveling the effects of plant hydraulics on stomatal closure during water stress in walnut. Plant Physiol 128:282-290

Cochard H, Damour G, Bodet Ch, Tharwat I, Poirier M, Ameglio T (2005) Evaluation of new centrifuge technique for rapid generation of xylem vulnerability curves. Physiol Plant 124:410-418

Cruiziat P, Cochard H, Ameglio T (2002) Hydraulic architecture of trees : main concepts and results. Ann For Sci 59:723-752

Czajkowski T, Kühling M, Bolte A (2005) Einfluss der Sommertrockenheit im Jahre 2003 auf das Wachstum von Naturverjüngungen der Buche (*Fagus sylvatica* L.) im nordöstlichen Mitteleuropa. Allg Forst- Jagdztg 176:133-143

Czajkowski T, Bolte A (2006) Unterschiedliche Reaktion deutscher und polnischer Herkünfte der Buche (*Fagus sylvatica* L.) auf Trockenheit. Allg Forst-Jagdztg 177:30-40

Dannowski M, Wurbs A (2003) Räumlich differenzierte Darstellung maximaler Durchwurzelungstiefen unterschiedlicher Pflanzengesellschaften auf einer Feldgehölzfläche des nordostdeutschen Tieflandes. Bodenkultur 54(2):93-108

Domec JC, Gartner B (2001) Cavitation water storage capacity in bole xylem segments of mature and young Douglas-fir trees. Trees 15:204-214

Eccel E, Toller G, Ghielmi L (2004) The soil water balance of a mixed oak stand in the southern Alps. Studi Trent Sci Nat Acta Biol 81(Suppl 1):137-149

European Environmental Agency (2004) Impacts of Europe´s changing climate : an indicator–based assessment. Luxembourg : Office for Official Publications of the EC, 107 p, EEA-Report 2004,2

Ehlers W (1996) Wasser in Boden und Pflanze : Dynamik des Wasserhaushalts als Grundlage von Pflanzenwachstum und Ertrag. Stuttgart-Hohenheim : Ulmer, 272 p

Federer CA, Vörösmarty C, Feketa B (2003) Sensitivity of annual evaporation to soil and root properties in two models of contrasting complexity. J Hydromet 4:1276-1290

Hacke U, Sauter JJ (1995) Vulnerability of xylem to embolism in relation to leaf water potential and stomatal conductance in *Fagus sylvatica f. purpurea* and *Populus balsamifera*. J Exp Bot 46(299):1177-1183

Heinze M, Tomczyk S, Nicke A (2001) Vergleich von Rot-Buche (*Fagus sylvatica* L.) in sogenannten Grünen Augen mit benachbarten standortsgleichen Fichtenbeständen (*Picea abies* [L.] KARST.) des Thüringer Vogtlandes bezüglich Eigenschaften und Durchwurzelung des Bodens sowie Baumwachstum. Forstwiss Centralbl 120:139-153

Hetsch W, Heilig KH (1981) Der Wasserhaushalt von Fichte in Abhängigkeit von Boden und Atmosphäre. Z Pflanz Bodenkd 144:317-330

Higgs KH, Wood V (1995) Drought susceptibility and xylem dysfunction in seedlings of 4 European oak species. Ann For Sci 52:507-513

Hijmans RJ, Cameron SE, Para JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965-1978

IPCC (2007) Climate change 2007 : the physical science basis ; contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. New York : UNEP, 996 p

Jansen M, Döring C, Ahrends B, Bolte A, Czajkowski T, Panferov O, Albert M, Spellmann H, Nagel J, Lemme H, Habermann M, Staupendahl K, Möhring B, Böcher M, Storch S, Krott M, Nuske R, Thiele JC, Nieschulze J, Saborowski J, Beese F (2008) Anpassungsstrategien für eine nachhaltige Waldbewirtschaftung unter sich wandelnden Klimabedingungen : Entwicklung eines Entscheidungsunterstützungssystems "Wald und Klimawandel" (DSS-WuK). Forstarchiv 79:131-142

Joslin JD, Wolfe MH (2003) Fine-root growth response. Ecol Stud 166:274-302

Laio F, Porporato A, Ridolfi L, Rodriguez-Iturbe I (2001) Plants in water-controlled ecosystems : active role in hydrologic processes and response to water stress ; II. Probabilistic soil moisture dynamics. Adv Water Res 24:707-723

Leckebusch GC, Ulbrich U (2004) On the relationship between cyclones and extreme windstorm events over Europe under climate change. Global Plan Change 44(1-4):181-193

Leckebusch GC, Koffi B, Ulbrich U, Pinto .G, Spangehl T, Zacharias S (2006) Analysis of frequency and intensity of European winter storm events from a multi-model perspective, at synoptic and regional scales. Clim Res 31:59-74

Lemoine D, Cochard H, Granier A (2002a) Within crown variation in hydraulic architecture in beech (*Fagus sylvatica* L.) : evidence for a stomatal control of xylem embolism. Ann For Sci 59:19-27

Lemoine D, Jacquemin S, Granier A (2002b) Beech (*Fagus sylvatica* L.) branches show acclimation of xylem anatomy and hydraulic properties to increased light after thinning. Ann For Sci 59:761-766

Lehnardt F, Brechtel HM (1980) Durchwurzelungs- und Schopftiefen von Waldbeständen verschiedener Baumarten und Altersklassen bei unterschiedlichen Standortverhältnissen : Teil I. Erfahrungen aus Geländearbeiten und Ergebnisse veröffentlichter Untersuchungen. Allg Forst- Jagdztg 151(6/7):120-127

Lösch R (2001) Wasserhaushalt der Pflanzen. Wiebelsheim : Quelle and Meyer, 595 p, UTB für Wissenschaft : grosse Reihe 8141

Lu P, Biron P, Granier A, Cochard H (1996) Water relations of adult Norway spruce (*Picea abies* (L) Karst) under soil drought in the Vosges mountains : whole-tree hydraulic conductance, xylem embolism and water loss regulation. Ann Sci For 53:113-121

Kavanagh KL, Bond BJ, Aitken SN, Gartner BL, Knowe S (1999) Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. Tree Physiol 19:31-37

Klap JM, Reinds GJ, Bleeker A, de Vries W (2002) Environmental stress in German forests : assessment of critical deposition levels and their exceedances and meteorological stress for crown condition monitoring sites in Germany. Wageningen : Alterra, 73 p, Alterra-rapport 134

Kolb KJ, Sperry JS, Lamont BB (1996) A method for measuring xylem hydraulic conductance and embolism in entire root and shoot system. J Exp Bot 47:1805-1820

Köstler JN, Brückner E, Bibelriether H (1968) Die Wurzeln der Waldbäume : Untersuchungen zur. Morphologie der Waldbäume in Mitteleuropa. Hamburg : Parey, 284 p

Kreutzer K (1961) Wurzelbildung junger Waldbäume auf Pseudogleyböden. Forstwiss Centralbl 80:356-392

Martínez-Vilalta J, Piñol J (2002) Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. For Ecol Manage 161:247-256

Martínez-Vilalta J, Sala A, Piñol J (2004) The hydraulic architecture of Pinaceae : a review. Plant Ecol 171:3-13

Mayr S, Wolfschwenger M, Bauer H (2002) Winter-drought induced embolism in Norway spruce (*Picea abies*) at the Alpine timberline. Physiol Plant 115:74-80

Mayr S, Cochard H (2003) A new method for vulnerability analysis of small xylem areas reveals that compression wood of Norway spruce has lower hydraulic safety than opposite wood. Plant Cell Environ 26:1365-1371

Meier I, Leuschner Ch (2008) Genotypic variation and phenotypic plasticity in the drought response of fine roots of European beech. Tree Physiol 28:297-309

Müller U (2004) Auswertungsmethoden im Bodenschutz : Dokumentation zur Methodenbank des Niedersächsischen Bodeninformationssystems (NIBIS). Stuttgart : Schweizerbart, 409 p, Arbeitshefte Boden / Niedersächsisches Landesamt für Bodenforschung 2

Nardini A, Pitt F (1999) Drought resistance of *Quercus pubescens* as a function of root hydraulic conductance, xylem embolism and hydraulic architecture. New Phytol 143:485-493

Nardini A, Tyree MT (1999) Root and shoot hydraulic conductance of seven *Quercus* species. Ann For Sci 56:371-377

Novák V, Havrila J (2006) Method to estimate the critical soil water content of limited availability for plants. Biologia (Bratislava) 61(Suppl 19):S298-S293

Osenberg M (1998) Wurzelbiomasse in zwei Beständen unterschiedlicher Baumart in der Montanstufe der Niederen Tauern. Wien : Universität für Bodenkultur (BOKU), 96 p, Diplomarbeit / Institut für Waldökologie

Piñol J, Sala A (2000) Ecological implications of xylem cavitation for several *Pinaceae* in the Pacific Northern USA. Funct Ecol 14:538-545

Porporato A, Laio F, Ridolfi L, Rodriguez-Iturbe I (2001) Plants in water-controlled ecosystems : active role in hydrologic processes and response to water stress. III.Vegetation water stress. Adv Water Resour 24:707-723

Raissi F, Müller U, Meesenburg H (2009) Ermittlung der effektiven Durchwurzelungstiefe von Forststandorten. Hannover : Landesamt für Bergbau, Energie und Geologie, 6 p, Geofakten 9

Rastin N, Ulrich B (1990) Durchwurzelungstiefe und Wurzelverteilung der Fichte auf drei unterschiedlichen Standorten. Forst Holz 45(22):665-668

Richter A, Adler GH, Fahrak M, Eckelmann W (2007) Erläuterungen zur nutzungsdifferenzierten Bodenübersichtskarte der Bundesrepublik Deutschland im Maßstab 1:1 000000 (BÜK 1000 N, Version 2.3). Hannover : BGR, 53 p

Rosner S, Klein A, Wimmer R, Karlsson B (2006) Extraction of features from ultrasound acoustic emissions : a tool to assess the hydraulic vulnerability of Norway spruce trunkwood? New Phytol 171:105-116

Schär Ch, Vidale PL, Lüthi D, Frei Ch, Häberli Ch, Liniger A, Appenzeller Ch (2004) The role of increasing temperature variability in European summer heatwaves. Nature 427:332-336

Schmid I, Kazda M (2002) Root distribution of Norway spruce in monospecific and mixed stands on different soils. For Ecol Manage 159:37-47

Simonin G, Cochard H, Delatour C, Granier A, Dreyer E (1994) Vulnerability of young oak seedlings (*Quercus robur* L) to embolism : responses to drought and to an inoculation with *Ophiostoma querci* (Georgevitch) Nannf. Ann For Sci 51:493-504

Sperry JS, Ikeda T (1997) Xylem cavitation in roots and stems of Douglas-fir and white fir. Tree Physiol 17:275-280

Sperry JS, Donelly JR, Tyree MT (1988) A method of measuring hydraulic conductivity and embolism in xylem. Plant Cell Environ 11:35-40

Sperry JS, Hacke UG (2002) Desert shrub water relations with respect to soil characteristics and plant functional type. Funct Ecol 16:367-378

Sperry JS, Hacke UG, Oren R, Comstock JP (2002) Water deficits and hydraulic limits of water supply. Plant Cell Environ 25:251-263

Stout DL, Sala A (2003) Xylem vulnerability to cavitation in *Pseudotsuga menziesii* and *Pinus ponderosa* from contrasting habitats. Tree Physiol 23:43-50

Tebaldi C, Hayhoe K, Arblaster JM, Meehl GA (2006) Going to the extremes : an intercomparsion of model-simulated historical and future changes in extreme events. Clim Change 79:185-211

Tognetti R, Johnson JD, Michelozzi M (1995) The response of European beech (*Fagus sylvatica* L.) seedlings from two Italian populations to drought and recovery. Trees 9:348-354

Tognetti R, Longobuco A, Raschi A (1998) Vulnerability of xylem to embolism in relation to plant hydraulic resistance in Quercus pubescens and Quercus ilex co-occurring in a Mediterranean coppice stand in central Italy. New Phytol 139:437-447

Tyree MT, Sperry JS (1989) Vulnerability of xylem to cavitation and embolisms. Annu Rev Plant Physiol 40:19-38

Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. New Phytol 119:345-360

Tyree MT, Cochard H (1996) Summer and winter embolism in oak : impact of water relations. Ann For Sci 53:173-180

UN-ECE (1979) Convention on long range transboundary air pollution [online]. Zu finden in <http://www.unece.org/env/lrtap> [zitiert am 28.04.2009]

UN-ECE (2004) Manual on methodologies and criteria for modelling and mapping critical loads and levels and air pollution effects, risks and trends [online]. Zu finden in <http://icpmapping.org/cms/zeigeBereich/11/manual_english.html> [zitiert am 28.04.2009]