# REVIEW

**Matthias Dobbertin** 

# Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review

Received: 9 December 2004 / Accepted: 27 April 2005 / Published online: 8 November 2005 © Springer-Verlag 2005

Abstract The intensive monitoring plots (Level II) of ICP Forests serve to examine the effects of air pollution and other stress factors on forest condition, including tree vitality. However, tree vitality cannot be measured directly. Indicators, such as tree growth or crown transparency, may instead be used. Tree growth processes can be ranked by order of importance in foliage growth, root growth, bud growth, storage tissue growth, stem growth, growth of defence compounds and reproductive growth. Under stress photosynthesis is reduced and carbon allocation is altered. Stem growth may be reduced early on as it is not directly vital to the tree.Actual growth must be compared against a reference growth, such as the growth of trees without the presumed stress, the growth of presumed healthy trees, the growth in a presumed stress-free period or the expected growth derived from models.Several examples from intensive monitoring plots in Switzerland illustrate how tree-growth reactions to environmental stresses may serve as vitality indicator. Crown transparency and growth can complement each other. For example, defoliation by insects becomes first visible in crown transparency while stem growth reaction occurs with delay. On the other hand, extreme summer drought as observed in large parts of Europe in 2003 affects stem growth almost immediately, while foliage reduction becomes only visible months

Communicated by Hans Pretzsch

M. Dobbertin (⊠) Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland E-mail: dobbertin@wsl.ch Tel.: +4-44-510 6423725)

*Present address*: M. Dobbertin Department of Environmental Sciences, Policy and Management, University of California, Berkeley, 213 Mulford Hall, Berkeley, CA 94530, USA later.Residuals of tree growth models may also serve as indicators of changed environmental conditions. Certain stresses, such as drought or insect defoliation cause immediate reactions and are not detectable in five-year growth intervals. Therefore, annual or inter-annual stem growth should be assessed in long-term monitoring plots.

**Keywords** Tree growth  $\cdot$  Vitality  $\cdot$ Crown transparency  $\cdot$  Stress factors  $\cdot$  Drought.

## Introduction

The extensive and intensive forest monitoring (Level I and Level II) of ICP Forests (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests of the United Nations Economic Commission for Europe) serve to examine the effects of air pollution and other stress factors on the condition of forests (Lorenz et al. 2004). The vitality of the trees is one of the most important indicators of forest condition (Innes 1993). Several definitions of tree vitality can be found in the literature (Gehrig 2004, Brang 1998, Shigo 1990). As vitality cannot be measured directly, various indicators can instead serve to describe vitality (Gehrig 2004). Next to the assessments of biochemical indicators at plant cell level (Larcher 2001), field practical methods are of great importance in long-term monitoring. Field methods include crown foliage or transparency assessments (Eichhorn et al. 2004), crown morphology (Roloff 1987), tree stem growth measurements (Waring et al. 1980), nutrient content analysis of needles (Stefan et al. 1997) or sapwood (Joos 1997), electric cambial resistance (Kucera 1986), needle size or shape (Kozlov and Niemela 1999), chlorophyll fluorescence (Lichtenthaler and Rinderle 1988) or luminescence analysis (Schmidt and Schneckenburger 1992), needle emission analysis (Lewinsohn et al. 1991, Abeles and Abeles 1972) and electric potential (Goldstein and Gensler 1981).

# **Objectives**

One of the aims of forest growth assessment on Level II plots is to estimate the response of individual tree and stand growth to environmental factors (Dobbertin 2000). The main objective of this review is to evaluate the usefulness of growth measurements as indicators of either the vitality status of trees or the stress trees are subjected too. I will give special emphasis to the growth variables assessed in the intensive monitoring plots (Level II) of the ICP Forests Programme. I also examine how growth relates to the variable tree crown transparency or defoliation, which is currently the main indicator of tree vitality used in the monitoring programme, and if both variables could complement each other. I will first propose a definition of tree vitality and stress. I will briefly discuss various indicators for tree vitality and present tree growth variables as assessed on the Level II monitoring plots. Then I will review studies of stem growth as indicator of trees with assumed reduced vitality, affected by stress or disease (evaluated against reference growth), and illustrate the findings with examples from Swiss Level I and II plots. Finally, I will make a suggestion for the use of growth or additional indicators of tree vitality.

#### Definitions and indicators of tree vitality

#### Definitions of vitality and stress

The vitality of a plant is a theoretical concept. Random House Webster's College Dictionary (1992) defines vitality as 'the capacity for survival, power to live or grow', while Merriam-Webster's Collegiate Dictionary (1994) defines it as 'the capacity to live and develop' and the American Heritage College Dictionary (1993) as 'the capacity to live, grow or develop'. Shigo (1990) distinguishes between 'vigour' as 'the capacity to resist strain; a genetic factor, a potential force against any threats to survive' (cannot be changed) and 'vitality' as 'the ability to grow under the conditions present' (dynamic action). Brang (1998) defines vitality as 'the capacity of an organism to assimilate carbon, to resist stress, to adapt to changing environmental conditions and to reproduce'. Gehrig (2004) on the other hand, sees plant vitality in a triangle between 'stress tolerance', 'longevity' and 'growth and reproduction'.

Important for the assessment of tree vitality is to assess the effect of external stress because the resistance to stress is an important criterion in all vitality concepts (see above). Larcher (2001) defines stress as a significant deviation from the condition optimal for life. Vitality becomes weaker as stress persists. Larcher's definition distinguishes between stress as the action leading to the deviation from the plant condition optimal for life, and 'stressed' or 'under stress' as the condition of the organism following the stress action. In the following I will also use stress as the action and not the status of the plant.

Stress leads to a phase of immediate reaction usually followed by a recovery phase. Various authors have depicted the effects of stress and the response of the plant as a function of time (Fig. 1 adapted from Gehrig 2004, Larcher 2001, Pedersen 1998a, 1998b, Manion 1981). Overcoming stress, either by increased plant efforts to repair damage or by increased resistance to further stress, results in change in carbon allocation (Waring 1987). If stress continues, the capability of a tree to overcome further stress or to survive diminishes, i.e. vitality decreases (see Fig. 1). At a certain point irreversible damage or tree death occurs. Manion (1981) developed a tree decline concept of predisposing, inciting and contributing stress factors which in combination lead to tree decline. Pedersen (1998b) argues that predisposing stress and inciting stress alone can lead to subsequent decline of tree vitality up to tree death.

Unfortunately, the hypothetical optimal tree vitality is not known (Fig. 1). Only tree death, the minimum tree vitality, can in most cases clearly be identified. Therefore, only changes in certain indicators of tree vitality can be observed (Fig. 1). During a stress the tree reacts to it (Fig. 1, cases 1-3, reaction phase, Larcher 2001). When the stress continues the tree adapts (restitution and hardening phase) and can reach either lower levels of stress resistance (Fig.1, case 2 b) identical levels of resistance (case 1) or even higher levels than before the stress (Fig.1, case 2 a), adjustment phase, see also Kozlowski and Pallardy 2002). If the stress persists over a long time or if a second stress occurs the tree may fall below a resistance threshold where irreversible damage occurs (Fig. 1, case 3, exhaustion phase, Larcher 2001). Permanent damage may mean a lower level of vitality or tree status or may mean that no recovery is possible (Pedersen 1998a, 1998b). The difficulty in field studies is first to identify and measure the suitable indicator of vitality, second to assess the strength and duration of the stress and third to determine the absolute or relative level of the vitality indicator (Fig. 1). As the absolute level of vitality can usually not be determined from the indicator, a relative value is commonly used.

Indicators of tree vitality and reactions to stress

If tree vitality is assessed in the forest, field-practical and cost-effective methods are needed. Biochemical indicators on the plant cell level such as phytohormones or enzymes may best reflect the reaction of trees to various environmental stresses (Larcher 2001). Unfortunately many such indicators cannot readily be extracted in the field or are very expensive. Gehrig (2004) analyzed several indicators for Norway spruce (*Picea abies* Karst. L.), such as transparency assessments, needle length, luminescence, needle odour emissions, cambial electric resistance and electronic potential. He compared the variables with each other **Fig. 1** Schema of tree vitality and the impact of stress, freely adapted from Gehrig (2004), Larcher (2001), Pedersen (1998a), Manion (1981)



and evaluated their practicability. He found that needle length, although useful to distinguish between fertilized and non-fertilized plots (Flückiger and Braun 1995), was not well correlated with crown transparency, and varied highly between sites. Luminescence analysis was difficult to calibrate and cost-intensive for field assessments. Electric potential measurements were highly influenced by soil water and weather conditions. In addition to crown transparency assessments Gehrig recommended to use electric cambial resistance and needle emission analysis as additional stress indicators in the field. Gehrig did not evaluate tree growth.

As summarised by Kozlowski and Pallardi (1996), the requirements for tree growth are carbon dioxide, water, and minerals for raw materials, light as energy resource, oxygen, and favourable temperature for growth processes. The capacity for photosynthetic processes (i.e. foliar biomass) and the competition for resources are constraining tree growth. Tree growth processes can be ranked by order of importance in foliage growth, root growth, bud growth, storage tissue growth, stem growth and growth of defence compounds, and reproductive growth (Waring 1987). Under stress the photosynthesis and the subsequent carbon allocation of a tree may be altered in a way that the less important processes including stem growth are reduced first. Stress factors may either affect the photosynthetic processes directly (for example defoliation by insects or damage of foliage due to frost or air pollution) or indirectly via reduced resources (for example reduced water supply during drought, reduced nutrient uptake due to root damage or nutritional imbalance due to high acidic or N deposition).

Studies by Eckmüllner et al. (1988) and Kramer and Dong (1985) found close correlation between stem volume growth and needle mass. Foliage amount has also been found to correlate well with sapwood area at breast height or crown base (Waring et al. 1981), or with the sapwood area without the latewood (Eckmüllner and Sterba 2000). Decreasing rate of dry biomass growth with age has commonly been attributed to an increase in respiring tissue in proportion to photosynthetic tissues (Kozlowski and Pallardi 1996). Also, both stand leaf area index and individual tree foliage decline with age (Mitscherlich 1978). Stress such as high competition for light and resources may alter the relationship between sapwood area and foliage mass (Waring 1987). Shortterm stress could therefore be estimated in the deviation of sapwood area to basal area ratios or basal area growth to sapwood area ratios (Eckmüllner and Sterba 2000, Waring et al. 1981, 1980). Maguire and Kanaskie (2002) related crown length to sapwood area ratios corrected for stand density and age to Douglas fir stands infected by Swiss needle cast. If sapwood area is not known, the ratio of basal area growth to basal area may be used as vitality indicator (Bigler and Bugmann 2004, 2003).

As destructive assessment of tree foliage is rarely feasible, visual assessment of tree crowns and classification into transparency or defoliation classes has become a standard procedure in many parts of the world (Müller-Edzards et al. 1997, Hall 1995, Burkman and Hertel 1992). Crown transparency can be obtained costeffectively and relatively fast in field surveys. However, due to the subjectivity of the assessment, intense training courses and repeated control assessments are necessary (Wulff 2002, Solberg and Strand 1999, Dobbertin et al. 1997, Strand 1996). Crown transparency assessment has been criticized because it is highly subjective, because no absolute reference is known and instead often only site specific reference trees were used, and because transparency is not cause-specific (Ellenberg 1994, Innes 1993).

#### **Tree growth**

Tree growth measured within ICP Forests

Currently, the following parameters for tree and stand size and its changes are monitored at 5-year intervals on all intensive monitoring sites in Europe (Dobbertin 2004). Tree stem diameter (at least two perpendicular measurements required) or circumference at breast height is measured on all trees above the diameter limit, and tree height on at least a subsample of the trees. Crown size measurements have until now been optional. Guidelines for non-destructive continuous stem growth measurements, as well as for destructive measurements such as tree cores and stem disks in the buffer zone of the plots are also provided in the manual of ICP Forests (Dobbertin 2004). Annual or continuous stem circumference measurements on a subsample of trees or plots are also recommended and described in the manual, and are assessed in some countries. In some countries, such as Switzerland, stem diameter and tree height or crown measurements are also recorded on the extensive Level I monitoring network (Dobbertin, 1996).

# Finding the right reference tree growth

Any indicator of tree vitality in field studies needs to be defined against a reference because maximal or optimal vitality is not known. For crown transparency the reference is either an ideal tree with optimal foliage (absolute reference tree) or the tree with lowest transparency found under the local growing conditions (local reference tree, Eichhorn et al. 2004). For tree growth the question is similar: trees that are assumed vital or trees with assumed optimal growth may be used as a reference for growth. In tree growth models, commonly, opengrown trees are used as a reference to test for tree competition (Biging and Dobbertin 1995, 1992). Similarly, trees with lowest crown transparency can be used as reference (Solberg 1999). As tree survival can be seen as the ultimate indicator of vitality, the growth of trees that have died can be compared with that of surviving trees (Bigler et al. 2005, 2004, Bigler and Bugmann 2004, 2003, Pedersen 1998a,b). Also growth of trees with and without a disease or known stress can be compared (Cherubini et al. 2002, Standovar and Somogyi 1998). In some cases the growth of trees before, during and following a stress are compared and the change is used as vitality or mortality indicator (Bigler et al. 2005, 2004, Pedersen 1998b). And finally, the difference or residual of tree growth against mean growth or modelled growth of a population can be used to estimate the effect of environmental conditions on growth (Spitzbart and Sterba 2004, Solberg et al. 2004).

# **Recent Findings**

Comparing growth of assumed vital individuals with assumed non-vital individuals

Several authors could show that crown transparency correlates with subsequent tree mortality (Dobbertin and Brang 2001, Schmid-Haas 1993, Neumann and Stemberger 1990). Using data on Swiss Level I plots for

the period 1990 to 1997 Dobbertin and Brang (2001) found that next-year mortality rate increased exponentially with transparency. However on these plots, intermediate and suppressed trees in low transparency classes had a 10-times higher chance of dying than dominant and co-dominant trees in the same transparency classes, indicating a higher stress due to higher competition (Fig. 2). In higher transparency classes these differences diminished.

Based on crown transparency as indicator, many studies have grouped trees into vitality classes and tested the growth differences between the classes (Becker et al. 1990, Spelsberg 1988, Sterba and Eckmüllner 1988, Dong and Kramer 1987, Schöpfer and Hradetzky 1986, Kenk 1983). In the early years of the 'forest decline research' most of these studies used one-time crown assessments and retrospective tree-ring analysis. While many of these studies showed decreased growth with higher crown transparency, others could not find such a relation (Björkdahl and Eriksson 1989, Lorenz and Eckstein 1988, Eichkorn 1985, Pretzsch 1985). The problem was that no past crown transparency assessments were available. Meanwhile, monitoring data on growth and annual crown transparency estimates of trees have become available and can be compared. Solberg (1999) demonstrated that relative growth (i.e., growth of undefoliated trees was set to 100%) and defoliation of Norway spruce on permanent monitoring plots in Norway showed a linear decrease of growth with transparency. Similar results were found in the European Level II network (Dobbertin et al. in Lorenz et al. 2004).

In Figure 3 examples are given for Swiss Level II plots. Growth is computed as the annual basal area growth in percent of the original basal area at the beginning of a three- or four-year growth period. Each tree was allocated to a 10-% transparency class based on its mean transparency during the growth period. Each plot had more than 800 assessed co-dominant or dominant trees and at least 20 trees in a minimum of four transparency classes. Basal area growth of four conifer species (Norway spruce, Scots pine (Pinus sylvestris L.), silver fir (Abies alba Mill.) and mountain pine (Pinus mugo var. uncinata) is almost linearly related to crown transparency (Fig. 3a). For the mountain pines in the Swiss National park the cause of high transparency is assumed to be root rot (Dobbertin et al. 2001, Cherubini et al. 2002). For the other sites no specific causes for higher transparencies are known. Interesting to note is the increased growth percentage with decreasing altitude. The three deciduous broadleaved species (Common beech (Fagus sylvatica L.), Turkey oak (Quercus cerris L.), European hornbeam (Carpinus betulus L.) the relationship is weaker (Fig. 3b). For the displayed Common beech and Turkey oak sites decreased tree growth began with transparencies above 25%, while for European hornbeam only the trees with lowest transparency grew more than the others. However, this stand is a former coppice forest with little or no management, Fig. 2 Annual mortality rates of trees with standard errors in the Swiss Level I monitoring network 1990–2000 grouped by crown transparency categories and social tree position





and the degree of competition seems to be the dominating factor for tree growth differences. It should also be noted that most beech sites in Switzerland showed little variability in transparency. For European Level II plots growth decreases for beech were clearly correlated with transparency, but the slope was less steep than that found for Norway spruce (Dobbertin et al. in: Lorenz et al. 2004).

Comparing growth of trees that have died with those that survived

The ultimate indicator of tree vitality is its capacity to survive stress. Various tree mortality prediction models include variables such as tree competition, tree size, tree vitality or tree growth (Monserud and Sterba 1999, Dobbertin and Biging 1998, Dursky 1997). Recently models have been developed to assess the probability of tree mortality based on tree-ring width (Bigler et al. 2005, 2004, Bigler and Bugmann 2004, 2003, Pedersen 1998a, 1998b,). Pedersen (1998b) used time series regression analysis and intervention models for tree rings of living and dead oaks to test for basal area growth difference prior and following possible intervention years, such as drought. Pedersen (1998a) applied a process-based model (Bossel 1986) to the same data to predict tree mortality. Bigler and Bugmann (2004, 2003) fitted a logistic regression model to dead and living Norway spruce in Switzerland using the log-transformed basal area increment in percentage of the total basal area and the slope of the log-transformed basal area growth of the previous five years. They achieved high prediction accuracy for spruce where competition was the dominant cause for mortality. In a similar study Bigler et al. (2004) used the same model for dead, declining and nondeclining silver firs in Slovakia as judged by their crown

condition in 1988. They showed that declining trees had higher probability to die than non-declining trees. In another study Bigler et al. (2005) demonstrated that reoccurring drought, as judged by a drought stress indicator, correlated well with modelled mortality probability for Scots pines in a dry inner-alpine Swiss valley.

For long-term growth and yield plots in the Black Forest, Germany, Spiecker (1990) found good correlation between computed 5-years drought stress (precipitation minus computed potential evapotranspiration) and tree growth of Norway spruce and silver fir as well as tree mortality. Tree growth, measured on the research plots, decreased and mortality, assessed on all public land, increased following above average drought stress. Even at high altitude (1000 m a.s.l.), believed to receive sufficient precipitation, drought seemed to reduce stem growth (Spiecker 1990, 1995).

At the Swiss Level II site 'Visp' (a dry site in the Swiss Rhone Valley) very high Scots pine mortality has been observed since the plot was installed in 1996 (Rebetez and Dobbertin 2004). The exact causes for this decline are not yet known, but droughts in the years 1996, 1998, 2000 and 2003 were found to be inciting factors (Bigler et al. 2005). Of all dominant and co-dominant trees that were alive at the time of the second measurements in late winter 1999/2000, basal area increment (BAI) for the years 1996–1999 was computed as the percentage of the basal area in 1996. Until summer 2003 31 trees had died and between summer 2003 and summer 2004 another 58 trees died. Trees that died before 2003 had significantly reduced stem growth (7.3% BAI versus 12.2% of the alive trees), while trees that died four years later, following the drought of 2003, displayed no differences in growth (12.3%, Table 1). Four-year tree growth was thus a good indicator of the drought stress that occurred during or at the end of the measurement period, but Fig. 3 Annual periodic basal area growth in percent of basal area at the beginning of the growth period as a function of crown transparency grouped in 10% classes for four conifer (a) and three broadleaved (b) tree species on Swiss Level II plots



Table 1 Diameter in 1996 (DBH96), stem basal area growth 1996–1999 of dominant and codominant *Pinus sylvestris* in percent of total basal area 1996 (BAI) and its standard deviation (Std. BAI) at the Swiss Level II plot 'Visp' for surviving trees and those which died between summer 2000 and summer 2003 or between summer 2003 and summer 2004

Tree	n	DBH96 (cm)	BAI (%)	Std. BAI	Kruskal-Wallis test*
alive died since summer 2003 died before summer 2003	158 58 31	17.4 15.8 19.4	12.2 12.3 7.3	9.8 6.5 5.1	0.256 0.001

\* test statistics for BAI of all alive trees versus the trees that have died

could not determine if trees were predisposed to die following the next severe drought. Bigler et al. (2005) concluded for data from the same region that in addition to growth level a variable describing the most recent growth trend is needed to adequately describe the tree mortality risk.

Comparing growth of trees under stress with those not under stress

The effect of stress on trees can also be evaluated by comparing trees under stress (with a disease for example) with those which are not diseased or under stress (Cherubini et al. 2002, Standovar and Somogyi 1998, Rosso and Hansen 1998, Schmid-Haas et al. 1997, Waring et al. 1992). Standovar and Somogyi (1998) compared stem growth of symptomatic and asymptomatic sessile oak (*Ouercus petrea* (Matt.) Liebl.) in a forest in Hungary affected by oak decline. Growth of seriously declining trees was reduced to almost half of the growth of healthy trees. However, incidence of oak decline and mortality was higher on more fertile sites with higher tree growth. Rosso and Hansen (1998) compared growth efficiency estimated from stem diameter growth and sapwood area of symptomatic and asymptomatic Douglas-fir (Pseudotsuga menziesii D. Don) in an experimental forest in Oregon affected by Armillaria ostoyae root disease. They found that trees that had recently died due to root rot or where symptomatic had reduced growth efficiency in the two to four years prior to death or before symptoms occurred in comparison with asymptomatic trees. However, no differences were found in growth periods more than four years before. They also found that growth efficiency and Armillaria disease incident were both higher on thinned plots than on control plots.

Cherubini et al. (2002) compared the growth of alive mountain pine trees at the Swiss Level II site 'Nationalpark' with trees that had recently died and were either infected with Armillaria spec. root rot or with Heterobasidion annosum root rot. They found that growth decreased in infected trees years before tree death occurred and observed frequent missing tree rings. However, the majority of the trees with Annosum root rot showed abrupt growth decline in the last years before tree death, while none of the trees infected by Armillaria had abrupt growth decline. Instead the trees infected by Armillaria, which were all below average in size, showed a steady decline in stem growth. They concluded that Heterobasidion annosum caused tree death of average sized trees, while Armillaria was either weakly pathogenic, or infected only trees that were dying due to increasing competition.

At the Swiss Level II site 'Visp' a majority of the Scots pines are infested by pine mistletoe (*Viscum album* ssp. *austriacum*, Dobbertin et al. 2005). Pine mistletoe, as a hemi-parasite, is able to photosynthesize but needs to take water and nutrients from its host tree (Calder

and Bernhardt 1983). The nutrient uptake of the mistletoe requires a high amount of water and thus increases water stress in host trees. During a drought, when the tree reduces its transpiration rates by closing its stomata, the mistletoe continues to transpire and increases the drought stress further (Fischer 1983). Basal area growth for the period 1996–1999 in percent of the basal area in 1996 was compared for pines assessed in 1998 as infected by mistletoe and those without mistletoe grouped by classes of similar size and crown transparency (Table 2). Trees with mistletoe showed lower relative basal area growth in each class, although the relation was not significant for medium- and large-size trees. Given the same defoliation class, trees with mistletoe displayed reduced growth, suggesting that mistletoe caused the observed growth reduction. These results agree with a study by Nötzli et al. (2003) who compared stem growth of silver fir without mistletoe (Viscum album ssp. abietis) infection with growth of infected trees before and after infection. They found no differences in proportion of trees with a negative growth trend between uninfected trees and infected trees prior to the start of the infection but significantly more declining growth trends for infected trees following the infection. The above studies show that tree growth can be used to differentiate between diseased and non-diseased trees. However, tree growth may not always be used to determine if trees are predisposed for a certain disease.

In addition to biological stress and climatic stress (see next chapter) changes in environmental condition can result in increasing stress to trees. Anthropogenic stress such as high concentrations of air pollution or high acidic or high nitrogen depositions may also affect tree vitality. On the Pan-European Level I grid crown transparency and its changes have been monitored and related to anthropogenic stresses, meteorological stress factors and soil conditions (de Vries et al. 2000). While most of the variation in crown transparency seemed to be due to methodological assessment difference between countries and tree age differences, some significant effects of anthropogenic stresses and climatic factors on defoliation were identified on regional levels (Klap et al. 2000). In order to contribute to a better understanding of the impact of air pollutions and environmental conditions on forest ecosystems, including forest growth, the Pan-European Level II Programme was implemented (de Vries et al. 2003a, b). A first calculation of wood volume and carbon pool storage in trees and soils and five-year changes on Level II sites is given in de Vries et al. (2003c). However, the implications of anthropogenic deposition on tree growth are often difficult to discern in correlative studies (van der Eerden et al. 1998).

Long-term experimental studies can help to gain further knowledge. Tveite et al. (1990) examined experimental Scots pine plots treated with artificial acid rain and/or lime in Norway. They found in the first 2 years stimulated stem growth with increasing acid loadings, but after five years growth declined. Liming resulted in

Classes		No Mistletoe			With Mistletoe			Wilcoxon *	
		n	BAI	BAI Std. n	BAI	Std	P < Z		
DBH	11.5 < 14.5  cm	45	4.27	2.52	40	2.62	1.29	0.002	
	14.5 < 18  cm	30	3.04	1.53	52	2.58	1.79	0.051	
	≥ 18 cm	19	2.46	2.08	60	2.12	1.36	0.466	
transparency	0 - 20%	47	4.56	2.50	60	3.09	1.63	0.001	
	> 20%	47	2.47	1.40	92	1.97	1.26	0.021	

Table 2 Stem basal area growth 1996–1999 in percent of total basal area 1996 (BAI) *Pinus sylvestris* at the Swiss Level II plot 'Visp' by diameter at breast height (DBH) class, transparency class and mistletoe occurrence

\* Test statistics are for Wilcoxon's one-sided paired test with t approximation.

positive effects 9 years after treatment. The growth reactions seemed to correspond to the nutritional status of the trees. A long-term nitrogen fertilizer experiment (50 and 150 kg N/year and ha) at the Harvard forest LTER site resulted in decreased growth and subsequent high mortality in red pine forests, while the mixed hardwood forests originally responded with increased growth (Magill et al. 1997) However, following a severe drought the mixed hardwood forest with high N treatment is now also experiencing high mortality rates (Magill et al. 2004).

# Comparing tree growth before during and following assumed stress

The effect of stress on tree growth can be tested by comparing growth before, during and following a known stress, such as drought or defoliation by insects. Commonly tree-ring analysis has been applied to examine the effect of stresses on past tree growth (Bigler et al. 2005, 2004, Krause et al. 2003, Pedersen 1998b, Schweingruber 1996, Swetnam and Lynch 1993). Defoliation by insects has been shown to affect tree growth

Ring width (1/100 mm)

and can be reconstructed from tree rings (Rolland et al. 2001, Weber 1997, Kulman 1971). For example, periodic reoccurring insect outbreaks by larch bud moth (Zeiraphera diniana Gn) in the European Alps lead to reduced ring width in European larch (Larix decidua Mill, Rolland et al. 2001). Next to the Swiss Level II site Celerina the 7-10 year outbreak cycle (Baltensweiler and Rubli 1999) lead to substantially reduced ring width during and one year following the outbreaks (Fig. 4). The question is whether the reduced ring width is also an indicator of reduced vitality. During the severe 1972-74 outbreak with large reduction in tree-ring width, substantial tree mortality was reported in the vicinity of the site (Baltensweiler 1975). On the other hand the 1989 outbreak, collapsed in 1990 because of bad weather conditions (Baltensweiler 1993) and resulted only in a minimal growth reduction and no mortality. As the effect of the outbreaks is usually compensated during non-outbreak periods, the five-year growth intervals mandatory on Level II plots are not sufficient to detect the effect during outbreak years.

It is well established that tree stem growth is effected by the weather conditions of the growing season and of years prior to it (Schweingruber 1996, Spiecker 1995,



Fig. 4 Mean tree-ring width chronology of nine *Larix decidua* Mill trees next to the Swiss Level II site Celerina affected by periodic outbreak of the larch bud moth (*Zeiraphera diniana* Gn, Baltensweiler, Cherubini, Dobbertin, Müterthies, unpublished data) 1990). The severe drought during the temperature record-setting summer 2003 in Europe (Schär et al. 2004) also affected stem growth at long-term monitoring sites in Germany and Switzerland (Jolly et al. 2005, Kahle submitted, Meining et al. 2004, Bayerische Landesanstalt für Wald und Forstwirtschaft 2004). Meining et al. (2004) report reduced stem diameter growth rates in 2003 for all 10 spruce Level II sites in Baden-Württemberg ranging in altitude from 510 m to 1020 m. Growth in 2003 reached on average only around 50% of the growth in 2002 and on most sites an absolute minimum in stem growth was reported since measurements began. Kahle (submitted) also reports reduced growth in 2003 in comparison to 2002 for beech and spruce on four sites along an altitude gradient in the Black forest ranging between 220 and 1230 m in altitude. All sites, except beech growing at 1230 m altitude, showed reduced growth with an inverse relationship between growth reduction and altitude. In Bavaria growth in 2003 for all seven Level II spruce sites ranging in altitude between 415 m and 1110 m was reduced in comparison to 2002 (Bayerische Landesanstalt für Wald und Forstwirtschaft 2004). For beech, growth reduction was also found at low altitude sites (510 to 780 m), but above 800 m beech showed no growth reduction. On the other hand, European larch growing at 1500 m in the Bavarian Alps showed a 50% increased growth in 2003 as compared to 2002.

At Swiss Level II sites, permanent circumference bands had been placed in 2001 on 10 trees of the main species (stem basal area proportion > 10%) using a stratified random selection approach. Trees within each species were ordered by stem diameter and grouped into five classes from the smallest 20% of the trees to the largest 20%. Within each class two trees were randomly selected. Stem circumference at 1.4 m tree height was recorded annually to 1/10 mm following the end of the

growing season in October. Annual basal area growth weighted by species cover percent was calculated for the vears 2002 and 2003 for the 15 available sites and compared with plot altitude (Jolly et al. 2005, Fig. 5). Tree growth 2003 in percent of growth in 2002 decreased with decreasing altitude. At low altitude (< 1200 m) tree growth of all plots was reduced in 2003 as compared to the rather wet year 2002, while the trees on plots above 1200 m a.s.l. exhibited increased stem growth. Obviously, water availability in 2003 had been the limiting factor at low altitude, while higher temperature at high altitude had favoured growth in 2003 (Jolly et al. 2005). In contrast to tree stem growth, crown transparency in Switzerland and Southern Germany had not increased in 2003 in comparison to 2002. However, in 2004 a substantial increase in transparency was observed (Meining et al. 2004, Bayerische Landesanstalt für Wald und Forstwirtschaft 2004). Obviously, trees had reacted to the drought by reducing carbon allocation to stem growth, while foliar production and retention had been kept at their usual levels. However, allocation to bud growth and perhaps root growth had obviously been low in 2003, which resulted in increased crown transparencies in 2004.

The example given above also shows that the timing of the stress and the time selected to measure its effects are important. While spring drought affects the elongation and development of young needles and leaves (Grill et al. 2004, Raison et al. 1992), late summer drought results in insufficient storage for buds and causes reduced shoot length the following year (Lof and Welander 2000). Drought during the previous fall and current spring, and heat during the current summer can reduce current tree stem growth (Rigling et al. 2002, 2003), while summer drought may cause increased needle fall the following winter (Solberg 2004).

Fig. 5 Basal area growth 2003 in percent of basal area growth 2002 weighted by area proportion of the main tree species for 15 Swiss Level II plots as a function of altitude (filled circles: differences significant for a two-sided paired-t test (p < 0.05), open circles: non-significant ( $p \ge$ 0.05))



Comparing expected average growth with actual growth

Another way to determine reference growth is to develop tree growth models and to compare the differences of actual growth against predicted growth by the model. For example, an empirical individual-tree based regression model can be fit to account for tree size, stand density and site conditions to take into account the general growing conditions (Monserud and Sterba 1996). Deviations of actual growth from the model can subsequently be tested against other tree condition variables or changing environmental conditions or stresses (Spitzbart and Sterba 2004, Solberg et al. 2004, Solberg and Tveite 2000, Steyrer 1996). Spitzbart and Sterba adapted the empirical individual-based tree growth model Progneu (Monserud and Sterba 1996) to five-year growth data from Level II plots of Norway spruce and common beech in central Europe (Spitzbart and Sterba 2004). They included variables for tree size, current and past tree competition, plot density, site quality indicators and general climate factors. Residuals of the model, summed up per plot, were then compared with actual weather conditions during the five-year growing period and against deposition of sulphur and nitrogen. Actual growth for Common beech under high N or S deposition was less than estimated by the model suggesting reduced growth under high deposition loads. For spruce no clear correlation was found between growth residuals and deposition loads. Solberg et al. (2004) calculated 5-year basal area increment for Level I plots and other long-term observation plots ('officer plots') in Norway for Norway spruce and Scots pine and compared it with predicted increment from standard Norwegian growth models that use site index, stand age and stand density variables as input variables. They found that the actual growth in percent of the predicted growth was positively correlated with N deposition and soil N content and negatively with soil C/N ratio, suggesting a fertilizing effect of N.

#### Long-term growth changes

The scenarios of a general decline in forest growth in Europe in the 1980s have not materialized. On the contrary, since the early 1990s several reports of higher growth of forest stands in comparison with previously derived yield tables were published (Schöpfer et al. 1997, Spiecker et al. 1996, Spelsberg et al. 1995, Pretzsch 1992). The report by Spiecker et al. (1996) found growth increases for some Central European countries, while the studies on growth in the Nordic countries were not conclusive. However, neither the possible causes nor the consequences of the findings could be analysed. A second EU-project (RECOGNITION) was launched to gather more data and to determine the possible causes of these growth increases. The project included the retrospective analysis of height growth on selected ICP-Forests Level II sites. Herein, dominant trees next to Level

II sites in young and old stands with same site conditions were felled and their past height development was reconstructed from stem disks. The current height growth of young Scots pine, Common beech and Norway spruce was compared with that of older trees when they were of the same age. It was found for all species that growth was around 25% higher today than in the past (from Spiecker and Kahle in Lorenz et al. 2004, see example in Fig. 6). At the Swiss Level II site Othmarsingen the 50-year-old beech trees were found to be almost 30% taller than near-by 150-year-old beech trees when they were 50 years old around 1900 (data from RECOGNITION, Fig. 6). The authors of the REC-OGNITION project concluded that nitrogen deposition appears to be the main cause of the observed height growth increase (EFI 2002).

Independent of the possible causes for this increased height growth, the question arises of what this increase means in terms of tree vitality. Does increased stem growth automatically mean higher vitality? The question cannot directly be answered here, in particular as no information on the growth and vitality of the belowground tree parts is available (Brunner et al. 2002, Clemenssonlindell and Persson 1995a). Vitality, as defined earlier, includes the probability to survive stress. It is well known that, given the same age, the risk of wind damage increases with increasing tree height (Dobbertin 2002, König 1995). If nitrogen deposition will in the long run result in an increase in above-ground and/or belowground carbon storage or none at all is still controversial (see de Vries 2003c for a discussion). Results from nitrogen fertilizer experiments indicate that although above-ground stem growth increases, root growth may decrease (Clemenssonlindell and Persson 1995a, Clemenssonlindell and Persson 1995b) and root mortality may also increase (Persson and Ahlstrom 2002). Growth of woody tissues may be competing with production of defensive compounds (Baier et al. 2002, Waring 1987) and thus increased growth due to change in environmental conditions could mean reduced defence against pathogens or insect attacks. Increased growth due to increased nitrogen depositions may also reduce the frost and drought resistance of trees (Jonsson et al. 2004). However, other long-term studies on fertilizer experiments record increased growth and increased indicators of tree vitality in fertilized plots (Wargo et al. 2002, Weetman et al. 1997, Flückiger and Braun 1995, Filip et al. 1992, Waring et al. 1992, Proe et al. 1992, Spiecker 1990). Spiecker (1990) found only a short-term growth stimulation for Norway spruce in the Black forest following one-time N fertilization, while Ca- and Ca+Pfertilization resulted in long-lasting growth increases. The changing effects of the long-term N-fertilization experiment at Harvard forest on tree growth and mortality were discussed earlier (Magill et al. 1997, 2004). Comparable to the Harvard experiment, Juknys et al. (2002) report for Scots pines growing next to an N-fertilizer plant three distinct growth reaction periods: fertilization, depression and recovery following emission

Fig. 6 Mean height growth development of five young and five old common beech trees (*Fagus sylvatica*) against age on and next to the Swiss Level II site Othmarsingen (Data from RECOGNITION, Spiecker and Kahle) Tree height (m)



control measures. Most experimental studies with enhanced CO<sub>2</sub>-concentration on tree seedlings and saplings report a stimulation of stem growth in the first years of the experiment followed by an adaptation of growth in subsequent years (Janssens et al. 2005, Riikonen et al. 2004, Spinnler et al. 2003, Ceulemans et al. 2002, Broadmeadow and Jackson 2000), while carbon allocation to leaves and roots was often permanently increased (Janssens et al. 2005, Norby et al. 2002, Broadmeadow and Jackson 2000). The few studies on mature trees, either in field experiments or next to natural  $CO_2$ -springs, suggest either a response to  $CO_2$  in stem growth only for young trees (Hattenschwiler et al. 1997) or no response at all (Rasmussen et al. 2002, Tognetti et al. 2000). Therefore, growth changes due to changes in environmental conditions must be interpreted with great caution and with a long-term perspective.

#### Conclusions

International research results and examples from extensive and intensive monitoring plots in Switzerland illustrate how tree growth and transparency can serve as tree vitality or stress indicator depending on the type and extent of the stress factor. Depending on the time of the stress and the tree compartments affected by the stress, transparency or tree growth may complement each other as stress indicators. For example, defoliation by insects becomes first visible in crown transparency while stem growth reaction occurs with delay. On the other hand, extreme summer drought as in 2003 affected tree stem growth almost immediately, while foliage reduction occurred either late in the season or not at all.

Important for any potential vitality indicator is the comparison with a suitable reference. Depending on the

aim of the study the references used can be the growth of trees without a presumed stress, growth of presumed healthy trees, growth in a presumed stress-free period or expected growth derived from models. The general disadvantage is that no absolute growth reference is available.

Some stresses, such as competition, root rot or mistletoe occurrence are affecting the tree over longer time periods and can thus be detected in five-year measuring intervals. Other stresses such as drought or insect defoliation cause immediate reactions and are not detectable in five-year growth intervals. Therefore, annual or interannual stem growth assessment is needed in long-term monitoring plots. Annual tree-ring widths can be used, but their sampling has the disadvantage of being destructive and can therefore only be used retrospectively. However, they may allow estimation of survival probabilities of trees and add useful information to growth assessments on monitoring plots. Residuals of empirical tree-growth models accounting for tree size and between-tree competition with actual growth can also serve as indicators of changing environmental conditions.

The examples of various reactions of tree growth to environmental stress illustrate that tree growth can serve as a vitality indicator if reference growth or growth trends are available. It is noteworthy that not every stress is necessarily negative for the trees, but can instead induce increased resistance to stress (Kozlowsky and Pallardi 2002, Larcher 2001). Short-term stress reaction may therefore not coincide with long-term change in tree vitality. Growth changes must therefore be interpreted with a long-term perspective.

Tree growth and crown transparency may complement each other, but they are both not cause-specific indicators of stresses. It is therefore important to also monitor the possible stress factors and environmental conditions affecting tree growth and crown transparency.

Acknowledgements The Swiss Long-Term Forest Ecosystem Research (LWF) is part of the Swiss Forest Investigation Programme conducted by the Swiss Federal Institute of Forest, Snow and Landscape Research WSL in co-operation with the Swiss Federal Forest Administration. Many thanks to the various field teams and that have assessed the trees on the LWF plots, to Christian Hug for coordinating the fieldwork, to Michèle Kaennel Dobbertin and to the anonymous reviewers for helpful editorial comments.

# References

- Abeles AL, Abeles FB (1972) Biochemical Pathway of stress-induced ethylene. Plant Physiol 50:496–498
- American Heritage College Dictionary (1993) 3rd ed., Houghton Millton Company, Boston, New York
- Baier P, Fuhrer É, Kirisits T, Rosner S (2002) Defence reactions of Norway spruce against bark beetles and the associated fungus *Ceratocystis polonica* in secondary pure and mixed species stands. For Ecol Manage 159:73–86
- Baltensweiler W (1975) Zur Bedeutung des grauen Lärchenwicklers (Zeiraphera diniana Gn.) für die Lebensgemeinschaft des Lärchen-Arvenwaldes. Mitt Schweiz Entomolog Ges 50:15–23
- Baltensweiler W (1993) Why the larch bud-moth cycle collapsed in the subalpine larch-cembran pine forests in the year 1990 for the first time since 1850. Oecologia 1:62–66
- Baltensweiler W, Rubli D (1999) Dispersal: an important driving force of the cyclic population dynamics of the larch bud moth, *Zeiraphera diniana* Gn. For Snow Landsc Res 74:3–153
- Bayerische Landesanstalt für Wald und Forstwirtschaft (2004) Waldzustandsbericht 2004. Bayerisches Staatsministerium für Landwirtschaft und Forsten, Bayerische Landesanstalt für Wald und Forstwirtschaft LWF
- Becker M, Bräker OU, Kenk G, Schneider O, Schweingruber FH (1990) Kronenzustand und Wachstum von Waldbäumen im Dreiländereck Deutschland-Frankreich-Schweiz in den letzten Jahrenzehnten. Allg Forstz 45:263–266, 272–274
- Biging GS, Dobbertin M (1995) Evaluation of competition indices in individual-tree growth models. For Sci 41:360–377
- Biging GS, Dobbertin M (1992) A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For Sci 38:695–720
- Bigler C, Bräker OU, Bugmann H, Dobbertin M, Rigling A (2005) Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems (in press)
- Bigler C, Bugmann H (2003) Growth-dependent tree mortality models based on tree rings. Can J For Res 33:210–221
- Bigler C, Bugmann H (2004) Predicting the time of tree death using dendrochronological data. Ecol Appl 14:902–914
- Bigler C, Gricar J, Bugmann H, Cufar K (2004) Growth patterns as indicators of impending tree death in silver fir. For Ecol Manage 199:183–190
- Björkdahl G, Eriksson H (1989) Effects of crown decline on increment in Norway spruce (*Picea abies* (L.) Karst) in Southern Sweden. In: Brække H, Bjor K, Halvorsen B (eds) Air pollution as stress factor in the Nordic forests. Communications of the Norwegian Forest Research 42:19–36
- Bossel H (1986) Dynamics of forest dieback: systems analysis and simulation. Ecol Model 34:259–288
- Brang P (eds) (1998) Sanasilva-Bericht 1997. Gesundheit und Gefährdung des Schweizer Waldes - eine Zwischenbilanz nach 15 Jahren Waldschadenforschung. Berichte der Eidg. Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf
- Broadmeadow MSJ, Jackson SB (2000) Growth responses of Quercus petraea, Fraxinus excelsior and Pinus sylvestris to elevated carbon dioxide, ozone and water supply. New Phytologist 146:437–451

- Brunner I, Brodbeck S, Walthert L (2002) Fine root chemistry, starch concentration, and 'vitality' of subalpine conifer forests in relation to soil pH. For Ecol Manage 165:75–84
- Burkman W.G, Hertel GD (1992) Forest Health Monitoring A national program to detect, evaluate, and understand change. J For 90:27–28
- Calder M, Bernhardt P (eds) (1983) The Biology of Mistletoes, Academic Press, Sydney New York London Paris San Diego San Francisco Sao Paolo Tokyo Toronto
- Ceulemans R, Jach ME, Van de Velde R, Lin JX, Stevens M (2002) Elevated atmospheric CO2 alters wood production, wood quality and wood strength of Scots pine (*Pinus sylvestris L*) after three years of enrichment. Glob Chang Biol 8:153–162
- Cherubini P, Fontana G, Rigling D, Dobbertin M, Brang P, Innes JL (2002) Tree-life history prior to death: two fungal root pathogens affect tree-ring growth differently. J Ecol 90:839–850
- Clemenssonlindell A, Persson H (1995a) Fine-root vitality in a Norway spruce stand subjected to various nutrient supplies. Plant Soil 169:167–172
- Clemenssonlindell A, Persson H (1995b) The effects of nitrogen addition and removal on Norway spruce fine-root vitality and distribution in 3 catchment areas at Gardsjon. For Ecol Manage 71:123–131
- de Vries W, Vel E, Reinds GJ, Deelstra H, Klap JM, Leeters EEJM, Hendriks CMA, Kerkvoorden M, Landmann G, Herkendell J, Haussmann T, Erisman JW (2003a) Intensive monitoring of forest ecosystems in Europe - 1. Objectives, set-up and evaluation strategy. For Ecol Manage 174:77–95
- de Vries W, Reinds GJ, Vel E (2003b) Intensive monitoring of forest ecosystems in Europe-2: Atmospheric deposition and its impacts on soil solution chemistry. For Ecol Manage 174:97– 115
- de Vries W, Reinds GJ, Posch M, Sanz MJ, Kruase GHM, Calatayud V, Renaud JP, Dupouey JL, Sterba H, Vel, EM, Dobbertin M, Gundersen P, Voogd JCH (2003c) Intensive Monitoring of Forest Ecosystems in Europe, Technical Report 2003 ,UN/ECE and EC Forest Intensive Monitoring Coordinating Institute, Geneva, Brussels
- de Vries W, Klap JM, Erisman JW (2000) Effects of environmental stress on forest crown condition in Europe. Part I: Hypotheses and approach to the study. Water Air Soil Poll 119:317–333
- Dobbertin M (ed) (2004) Estimation of Growth and Yield. In: UNECE, Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests. Federal Research Centre for Forestry and Forest Products, Hamburg
- Dobbertin M (2002) Influence of stand structure and site factors on wind damage - Comparing the storms "Vivian" and "Lothar". For Snow Landsc Res 77:187–205
- Dobbertin M (2000) Forest Growth. In: Haußmann T, Lorenz M, Fischer R (eds). Internal Review of ICP Forests. UN/ECE, 2000, Fed. Res. Centre for Forestry and Forest Products pp 84– 102
- Dobbertin M (1996) Relationship between basal area increment, tree crown defoliation, and tree and site variables. In: Proceedings, IUFRO Conference on Effects of environmental factors on tree and stand growth, Berggiesshübel near Dresden, September 23–27, 1996. Dresden, Technische Universität, pp. 33–44
- Dobbertin M, Baltensweiler A, Rigling D (2001) Tree mortality in a mountain pine (*Pinus mugo* var. *uncinata*) stand in the Swiss National Park impacted by root rot fungi. For Ecol Manage 145:79–89
- Dobbertin M, Biging GS (1998) Using the non-parametric classifier CART to model forest tree mortality. For Sci 44:507–516
- Dobbertin M, Brang P (2001) Crown defoliation improves tree mortality models. For Ecol Manage 141:271–284
- Dobbertin M, Hilker N, Rebetez M, Wohlgemuth T, Zimmermann NE, Rigling A (2005) The upward shift in altitude of pine mistletoe (Viscum album ssp. austriacum) in Switzerland a result of climate warming? Int J Biometeorol 50:40–47

- Dobbertin M, Landmann G, Pierrat JC, Müller-Edzards C (1997) Quality of crown condition data. In: Müller-Edzards C, De Vries W, Erisman JW (eds), Ten years of monitoring forest condition in Europe. Studies on temporal development, spatial distribution and impacts of natural and anthropogenic stress factors. Technical background report. Geneva and Brussels, United Nations Economic Commission for Europe / European Commission pp. 7–22
- Dong PH, Kramer H (1987) Zuwachsverlust in erkrankten Fichtenbeständen. Allg Forst- Jagdztg 158:122–125
- Dursky J (1997) Modelling mortality in mixed spruce-beech stands. Allg Forst- Jagdztg 168:131–134
- Eckmüllner O, Halbwachs G, Schön B, Sterba H (1988) Vergleich von verschiedenen objektiv bestimmten Benadelungsmerkmalen und Schadklassenansprache bei Fichte. In: Führer E, Neuhuber F (eds) Waldsterben in Österreich: Theorien, Tendenzen, Therapien. FIW-Symposium, Wien, pp 259–260
- Eckmüllner O, Sterba H (2000) Crown condition, needle mass, and sapwood area relationships of Norway spruce (*Picea abies*). Can J For Res 30:1646–1656
- EFI (2002) Nitrogen deposition appears to be the main cause of increased forest growth in Europe. Press Release
- Eichhorn J, Szepesi A, Ferretti M, Durrant D, Roskams P (2004), Visual Assessment of Crown Condition. In: UN/ECE, Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests. Federal Research Centre for Forestry and Forest Products, Hamburg
- Eichkorn T (1986) Wachstumsanalysen an Fichten in Südwestdeutschland. Allg Forst- Jagdztg 157:125–139
- Ellenberg H (1994) Blatt- und Nadelverlust oder standörtlich wechselnde Ausbildung des Photosynthese-Apparats? Fragen zum Waldschadenbericht 1992. Schweiz. Z. Forstwes. 145:413–416
- Filip GM, Wickman BE, Mason RR, Parks CA, Hosman KP (1992) Thinning and nitrogen-fertilization in a grand fir stand infested with western spruce budworm. 3. Tree wound dynamics. For Sci 38:265–274
- Fischer JT (1983) Water relations of Mistletoes and their hosts. In: Calder M, Bernhard T (eds) The biology of Mistletoes. Academic Press, Sydney, pp 163–184
- Flückiger W, Braun S (1995) Revitalization of an alpine protective forest by fertilization. Plant Soil 169:481–488
- Gehrig M (2004) Methoden zur Vitalitätsbeurteilung von Bäumen. Vergleichende Untersuchungen mit visuellen, nadelanalytischen und bioelektrischen Verfahren. Diss. No. 15341, ETH Zürich
- Goldstein AH, Gensler W (1981) A physiological basis for electrophytograms. Bioelectrochemistry Bioenergetics 8:645–659
- Grill D, Tausz M, Pollinger U, Jimenez MS, Morales D (2004) Effects of drought on needle anatomy of *Pinus canariensis*. Flora 199:85–89
- Hall JP (1995) Forest health monitoring in Canada: how healthy is the boreal forest? Water Air Soil Pollut 82:77–85
- Hattenschwiler S, Miglietta F, Raschi A, Korner C (1997) Thirty years of in situ tree growth under elevated CO2: a model for future forest responses? Glob Chang Biol 3:463–471
- Innes JL (1993) Forest health: its assessment and status. Wallingford, Oxon, UK: CAB International
- Janssens IA, Medlyn B, Gielen B, Laureysens I, Jach ME, Van Hove D, Ceulemans R (2005) Carbon budget of Pinus sylvestris saplings after four years of exposure to elevated atmospheric carbon dioxide concentration. Tree Physiol 25:325–337
- Jolly M, Dobbertin M, Zimmermann NE, Reichstein M (2005) Divergent growth responses of Alpine forests to 2003 heat wave. Geophys Res Lett 32, L18409, doi:10.1029/ 2005GL023252
- Jonsson AM, Rosengren U, Nihlgard B (2004) Excess nitrogen affects the frost sensitivity of the inner bark of Norway spruce. Ann For Sci 61:293–298
- Joos K, (1997) Untersuchung der Zusammenhänge zwischen Nadeldichte, Zuwachsleistung und Nährstoffversorgung bei der Fichte unter besonderer Berücksichtigung des Ionentransportes im Splintsaft. Diss. ETH, No. 12117, ETH Zürich

- Juknys R, Stravinskiene V, Venecloviene J (2002) Tree-ring analysis for the assessment of anthropogenic changes and trends. Environ Monit Assess 77:81–97
- Kahle, HP (2005) Impacts of the drought and heat 2003 on forest growth. Submitted to Ann For Sci
- Kenk G (1983) Zuwachsuntersuchungen in geschädigten Tannenbeständen in Baden-Württemberg. Allg Forstztg 38:650–652
- Klap JM, Voshaar JHO, De Vries W, Erisman JW (2000) Effects of environmental stress on forest crown condition in Europe. Part IV: Statistical analysis of relationships.Water Air Soil Poll 119:387–420
- König A (1995) Sturmgefährdung von Beständen im Altersklassenwald. Ein Erklärungs- und Prognosemodell. Diss. Univ. München, Sauerländer's Verl., Frankfurt am Main
- Kozlov MV, Niemela P (1999). Difference in needle length A new and objective indicator of pollution impact on Scots pine (*Pinus* sylvestris). Water Air Soil Pollut 116:365–370
- Kozlowski TT, Pallardy SG (1996) Physiology of woody plants. 2nd edn. Academic Press, San Diego
- Kozlowski TT, Pallardy SG (2002) Acclimation and adaptive responses of woody plants to environmental stresses. Bot Rev 68:270–334
- Kramer H, Dong PH (1985) Kronenanalyse für Zuwachsuntersuchungen in immissionsgeschädigten Nadelholzbeständen. Forst- Holzwirt 40:115–118
- Krause C, Gionest F, Morin H, MacLean DA (2003) Temporal relations between defoliation caused by spruce budworm (*Choristoneura fumiferana* Clem.) and growth of balsam fir (*Abies balsamea* (L.) Mill.). Dendrochronologia 21:23–31
- Kucera LJ (1986) Kernspintomographie und elektrische Widerstandsmessung als Diagnosemethode der Vitalität erkrankter Bäume. Schweiz Z Forstwes 137:673–690
- Kulman HM (1971) Effects of insect defoliation on growth and mortality of trees. Annual Rev Entomol 16:289–324
- Larcher W (2001) Ökophysiologyie der Pflanzen. Ulmer Verlag, Stuttgart, 6. Auflage
- Lewinsohn E, Gijzen M, Croteau R (1991) Defense-mechanisms of conifers. Differences in constitutive and wound-induced monoterpene biosynthesis among species. Plant Physiol. 96:44– 49
- Lichtenthaler HK, Rinderle U (1988) The role of chlorophyll fluorescence in the detection of stress conditions in plants. J Plant Physiol 148:4–14
- Lof M, Welander NT (2000) Carry-over effects on growth and transpiration in *Fagus sylvatica* seedlings after drought at various stages of development. Can J For Res 30:468–475
- Lorenz M, Becher G, Mues V, Fischer R, Ulrich E, Dobbertin M, Stofer S (2004) Forest Condition in Europe – 2004 Technical Report. UN/ECE, Geneva
- Lorenz M, Eckstein D (1988) Wachstumsreaktionen von Einzelbäumen in Douglasien-, Fichten- und Kiefernbeständen in norddeutschen Waldschadensgebieten. Forst- Holz 43:8–12
- Magill AH, Aber JD, Currie WS, Nadelhoffer KJ, Martin ME, McDowell WH, Melillo JM, Steudler P (2004) Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. For Ecol Manage 196:7–28
- Magill AH, Aber JD, Hendricks JJ, Bowden RD, Melillo JM, Steudler PA (1997) Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. Ecol Appl 7:402–415
- Maguire DA, Kanaskie A (2002) The ratio of live crown length to sapwood area as a measure of crown sparseness. For Sci 48:93– 100
- Manion PD (1981) Tree disease concepts. Englewood Cliffs, Prentice Hall, New Jersey, USA
- Meining S, Schröter H, v. Wilpert K (2004) Waldzustandsbericht 2004. Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg
- Merriam-Webtser's Collegiate Dictionary (1994) 10th. Ed. Merriam-Webtser, Incorporated, Springfield, Massachusetts, USA
- Mitscherlich G (1978) Wald, Wachstum und Umwelt, vol. 1. J.D. Sauerländer's Verlag, Frankfurt am Main, 2nd ed

- Monserud RA, Sterba H (1999) Modeling individual tree mortality for Austrian forest species. For Ecol Manage 113:109–123
- Monserud RA, Sterba H (1996) A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. For Ecol Manage 80:57–80
- Müller-Edzards C, De Vries W, Erisman JW (eds) (1997) Ten Years of Monitoring Forest Condition in Europe. Studies on Temporal Development, Spatial Distribution and Impacts of Natural and Anthropogenic Stress Factors. UN/ECE, ICP Forests, Technical Background Report. Brussels, Geneva
- Neumann M, Stemberger A (1990) Über Ausmass und Verteilung der Mortalität: Gegenüberstellung von Ergebnissen der Waldzustandsinventur mit früheren Untersuchungen. Forstwiss Centralbl 107:63–99
- Nötzli KP, Müller B, Sieber TN (2003) Impact of population dynamics of white mistletoe (*Viscum album* ssp. *abietis*) on European silver fir (*Abies alba*). Ann For Sci 60:773–779
- Norby RJ, Hanson PJ, O'Neill EG, Tschaplinski TJ, Weltzin JF, Hansen RA, Cheng WX, Wullschleger SD, Gunderson CA, Edwards NT, Johnson DW (2002) Net primary productivity of a CO2-enriched deciduous forest and the implications for carbon storage. Ecol Appl 12:1261–1266
- Pedersen BS. (1998a) Modelling tree mortality in response to shortand long-term environmental stresses. Ecol Modelling 105:347– 351
- Pedersen BS. (1998b) The role of stress in the mortality of Midwestern oaks as indicated by growth prior to death. Ecology 79:79–93
- Persson H, Ahlstrom K (2002) Fine-root response to nitrogen supply in nitrogen manipulated Norway spruce catchment areas. For Ecol Manage 168:29–41
- Pretzsch H (1985) Wachstumsmerkmale Oberpfälzer Kiefernbestände in den letzten 30 Jahren. Vitalitätszustand, Strukturverhältnisse - Zuwachsgang. Allg Forstztg 42:1122–1126
- Pretzsch H (1992) Zunehmende Unstimmigkeit zwischen erwartetem und wirklichem Wachstum unserer Waldbestände. Forstwiss Centralbl. 111:366–382
- Proe MF, Dutch J, Miller HG, Sutherland J (1992) Long-term partitioning of biomass and nitrogen following application of nitrogen-fertilizer to Corsican pine. Can J For Res 22:82–87
- Raison RJ, Myers BJ, Benson ML (1992) Dynamics of *Pinus radiata* foliage in relation to water and nitrogen Stress. 1. Needle production and properties. For Ecol Manage 52:139–158
- Random House Webster's College Dictionary (1992), Random House, New York
- Rasmussen L, Beier C, Bergstedt A (2002) Experimental manipulations of old pine forest ecosystems to predict the potential tree growth effects of increased CO2 and temperature in a future climate. For Ecol Manage 158:179–188
- Riikonen J, Lindsberg MM, Holopainen T, Oksanen E, Lappi J, Peltonen P, Vapaavuori E (2004) Silver birch and climate change: variable growth and carbon allocation responses to elevated concentrations of carbon dioxide and ozone. Tree Physiol 24:1227–1237
- Rebetez M, Dobbertin M (2004) Climate change may already threaten Scots pine stands in the Swiss Alps. Theor Appl Climatol 79:1–9
- Rigling A, Bräker O, Schneiter G, Schweingruber F (2002) Intraannual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-Pinion in the Valais (Switzerland). Plant Ecol 163:105–121
- Rigling A, Brühlhart H, Bräker OU, Forster T, Schweingruber FH (2003) Effects of irrigation on diameter growth and vertical resin duct production in *Pinus sylvestris* L. on dry sites in the central Alps, Switzerland. For Ecol Manage 175:285– 296
- Rolland C, Baltensweiler W, Petitcolas V (2001) The potential for using *Larix decidua* ring widths in reconstructions of larch budmoth (*Zeiraphera diniana*) outbreak history: dendrochronological estimates compared with insect surveys. Trees 15:414–424
- Roloff A (1987) Morphology of crown development of *Fagus* sylvatica L. (beech) in consideration of new modifications. 1.

Morphogenetic cycle, abnormalities specific to proleptic shoots and leaf fall. Flora 179:355–378

- Rosso P, Hansen E (1998) Tree vigour and the susceptibility of Douglas fir to Armillaria root. Eur J For Pathol 28:43–52
- Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. Nature 427:332–336
- Schmid-Haas P (1993) Kronenverlichtung und Sterberaten bei Fichten, Tannen und Buchen. Forstwiss Centralbl 112:325–333
- Schmid-Haas P, Baumann E, Holdenrieder O, Keller W, Ramp B, Sepien E (1997) Infektionen der Stützwurzeln, Kronenverlichtung und Zuwachs bei Fichten und Tannen. Mitt. Eidg. Forschungsanstalt WSL 72, Birmensdorf
- Schmidt W, Schneckenburger H (1992) Time-resolving luminescence techniques for possible detection of forest decline: I. Long term delayed luminescence. Radiation and Environ Biophys 31:63–72
- Schöpfer W, Hradetzky J (1986) Zuwachsrückgang in erkrankten Fichten- und Tannenbeständen - Auswertungsmethoden und Ergebnisse. Forstwiss Centralbl 105:446–470
- Schöpfer W, Hradetzky J, Kublin E (1997) Wachstumsvergleiche von Fichte und Tanne in Baden-Württemberg. Forst- Holz 52:443–448
- Schweingruber FH (1996) Tree rings and environment. Paul Haupt, Bern
- Shigo AL (1990) Die neue Baumbiologie. Bernhard Thalacker Verlag, Braunschweig
- Solberg S (2004) Summer drought: a driver for crown condition and mortality of Norway spruce in Norway. For Pathol 34:93– 104
- Solberg S (1999) Crown condition and growth relationships within stands of *Picea abies*. Scand J For Res 14:320–327
- Solberg S, Andreassen K, Clarke N, Torseth K, Tveito OE, Strand GH, Tomter S, (2004) The possible influence of nitrogen and acid deposition on forest growth in Norway. For Eco Manage 192:241–249
- Solberg S, Strand L (1999) Crown density assessments, control surveys and reproducibility. Environ Monit Assess 56:75–86
- Solberg S, Tveite B (2000) Crown density and growth relationships between stands of *Picea abies* in Norway. Scand J For Res 15:87–96
- Spelsberg G (1988) Zur Frage der Wachstumsdifferenzierung bei vorherrschenden Fichten unter besonderer Berücksichtigung der Waldschäden. Forst- Holz 43:538–542
- Spelsberg G, Teske H, Graner M, Suntrup U (1995) Hohes Zuwachsniveau der Fichte in Nordrhein-Westfalen. AFZ 50:1097– 1098
- Spiecker H (1995) Growth dynamics in a changing environment -Long-term observations. Plant Soil 169:555–561
- Spiecker H (1990) Growth variation and environmental stresses -Long-term observations on permanent research plots in southwestern Germany.Water Air Soil Poll 54:247–256
- Spiecker H, Mielikäinen K, Köhl M, Skovsgaard JP (eds) (1996) Growth Trends in European Forests. EFI Res. Rep. 5. Springer, Berlin
- Spinnler D, Egli P, Korner C (2003) Provenance effects and allometry in beech and spruce under elevated CO2 and nitrogen on two different forest soils. Basic And Applied Ecology 4:467– 478
- Spitzbart G, Sterba H (2004) Application of the Tree Growth Model PrognEU to the Level II –plots of the European Forest Damage Monitoring Programme. Internal report
- Standovar T, Somogyi Z (1998) Corresponding patterns of site quality, decline and tree growth in a sessile oak stand. Eur J For Pathol 28:133–144
- Stefan K, Fürst A, Hacker R, Bartels U (1997) Forest Foliar Condition in Europe. Results of the large-scale foliar chemistry surveys (survey 1995 and data from previous years), Austrian Federal Forest Research Centre, EC, UN/ECE, Vienna Brussels Geneva
- Sterba H, Eckmüllner O (1988) Nadelverlust Zuwachsrückgang: doch eine Beziehung. Österr Forstztg 10:52–53

- Steyrer G (1996) Auswahl und Prüfung von Zuwachsparametern als Waldzustandsindikatoren - Einfluss des Kronenzustandes auf den Zuwachs. FBVA-Berichte / Forstliche Bundesversuchsanstalt Wien (Neumann M (ed), Österreichisches Waldschaden-Beobachtungssystem) 96: 121–135
- Strand GH (1996) Detection of observer bias in ongoing forest health monitoring programmes. Can J For Res 26:1692–1696
- Swetnam TW, Lynch AM (1993) Multicentury, regional-scale patterns of western spruce budworm outbreaks. Ecol Monogr 63:399–424
- Tognetti R, Cherubini P, Innes JL (2000) Comparative stemgrowth rates of Mediterranean trees under background and naturally enhanced ambient CO2 concentrations. New Phytologist 146:59–74
- Tveite B, Abrahamsen G, Stuanes AO (1990) Liming and wet acid deposition effects on tree growth and nutrition - Experimental results. Water Air Soil Poll 54:409–422
- Van der Eerden L, De Vries W, Van Dobben H (1998) Effects of ammonia deposition on forests in the Netherlands. Atmospheric Environment 32:525–532
- Wargo PM, Minocha R, Wong BL, Long RP, Horsley SB, Hall TJ (2002) Measuring changes in stress and vitality indicators in limed sugar maple on the Allegheny Plateau in north-central Pennsylvania. Can J For Res 32:629–641

- Waring RH (1987) Characteristics of trees predisposed to die. BioScience 37:569–573
- Waring RH, Newman K, Bell J (1981) Efficiency of tree crowns and stemwood production at different canopy leaf densities. Forestry 54:129–137
- Waring RH, Savage T, Cromack K, Rose C (1992) Thinning and nitrogen-fertilization in a grand fir stand infested with western spruce budworm. 4. An ecosystem management perspective. For Sci 38:275–286
- Waring RH, Thies WG, Muscato D (1980) Stem growth per unit of leaf area: a measure of tree vigor. For Sci 26:112–117
- Weber UM (1997) Dendroecological reconstruction and interpretation of Larch bud moth (*Zeiraphera diniana*) outbreaks in two central Alpine valleys of Switzerland from 1470–1990. Trees 11:277–290
- Weetman GF, Prescott CE, Kohlberger FL, Fournier RM (1997) Ten-year growth response of coastal Douglas-fir on Vancouver Island to N and S fertilization in an optimum nutrition trial. Can J For Res 27:1478–1482
- Wulff S (2002) The Accuracy of Forest Damage Assessments Experiences from Sweden. Environ Monit Assess 74:295–309