Review

Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation

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ABSTRACT

Forest trees are exposed to a myriad of single and combined stresses with varying strength and duration throughout their lifetime, and many of the simultaneous and successive stress factors strongly interact. While much progress has been achieved in understanding the effects of single stresses on tree performance, multiple interacting stress effects cannot be adequately assessed from combination of single factor analyses. In particular, global change brings about novel combinations of severity and timing of different stresses, the effects of which on tree performance are currently hard to predict. Furthermore, the combinations of stresses commonly sustained by trees change during tree ontogeny. In addition, tree photosynthesis and growth rates decline with increasing tree age and size, while support biomass in roots, stem and branches accumulates and the concentrations of non-structural carbohydrates increase, collectively resulting in an enhancement of non-structural carbon pools. In this review, tree physiological responses to key environmental stress factors and their combinations are analyzed from seedlings to mature trees. The key conclusions of this analysis are that combined stresses can influence survival of large trees even more than chronic exposure to a single predictable stress such as drought. In addition, tree tolerance to many environmental stresses increases throughout the ontogeny as the result of accumulation of non-structural carbon pools, implying major change in sensing, response and acclimation to single and multiple stresses in trees of different size and age.

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1. Introduction

Forest environments are characterized by strongly fluctuating conditions for tree growth and development. Sustained deviation of any environmental condition beyond the optimum range reduces plant potential productivity, constituting a stress for the plant. Stressful conditions are part of "normal" plant life in the field, and therefore, understanding the limits of stress tolerance and acclimation to stresses is of great fundamental and practical value in predicting the potential and realized limits of plant productivity (Lichtenthaler, 1998; Isebrands et al., 2000). A key environmental limitation in forest understory is light availability, especially for developing seedlings and saplings (Valladares and Niinemets, 2008). In addition to light, excess water availability and drought, either sustained or periodic, are common stress factors of different types of forests (Franco and Lüttge, 2002; Irvine et al., 2002; Dale and Ware, 2004; Niinemets and Valladares, 2008). Limited nutrient availability is another key environmental limitation significantly curbing growth at many forested areas (Sampson and Allen, 1998; Bergh et al., 1999), whereas often several nutrients such as nitrogen and phosphorus may be simultaneously limiting for plant growth (Niinemets and Kull, 2005; Ågren, 2008). In field environments, often various chronic stresses occur in correlated and interactive manner, for instance, low light in forest understory combined with low soil nutrient availability can be limiting in old growth forests (Jozsa and Brix, 1989; Walters and Reich, 1997; Bergh et al., 1999). Predicting stress responses is especially relevant under current globally changing environmental conditions, i.e., elevated atmospheric CO_2 concentration and air temperature and enhanced probability of drought and stress interactions in world ecosystems (Hobbs et al., 2006), already now being characterized by major shifts in forested biomes (Peñuelas and Boada, 2003; Dobbertin et al., 2005; Grund et al., 2005; Walther et al., 2005; Peñuelas et al., 2007).

Given the relevance of stress on plant performance, extensive work is currently being conducted to understand plant responses, tolerance and acclimation to key environmental stresses (e.g., Mittler, 2006; Günthardt-Goerg and Vollenweider, 2007; Jones and Schofield, 2008; Jackson et al., 2009; Paoletti et al., 2010). Analyzing the influence of stress on plant performance in the field is complicated by occurrence of multiple successive and/or simultaneous stresses, often influencing plant performance interactively, either amplifying or ameliorating the plant responses (Pell et al., 1994; Valladares and Pearcy, 1997; Isebrands et al., 2000; Alonso et al., 2001; Niinemets and Valladares, 2004; Valladares et al., 2005; Mittler, 2006; Rennenberg et al., 2006). Given that global change involves modification of a series of environmental factors concurrently and changes in the severity of different stress factors, knowledge of how plants acclimate to multiple successive or multiple combined stresses is of key significance in understanding the effects of future climates on vegetation.

A further complication in understanding stress responses of forests is that naturally regenerating forest stands typically consist of multiple tree age classes ranging from seedlings to large trees. Numerous tree structural and physiological characteristics change throughout tree ontogeny, including reductions in net assimilation rate and stem hydraulic conductance (Ryan and Yoder, 1997; Bond, 2000; Niinemets, 2002; Mullin et al., 2009), increases in leaf dry mass per unit area (Niinemets and Kull, 1995; Sack and Grubb, 2001; Niinemets, 2002) as well as accumulation of support woody biomass and non-structural storage pools of carbon (Hoch et al., 2003; Sala and Hoch, 2009). In addition to profound structural and physiological changes, the combinations of stresses commonly sustained by forest trees change during tree ontogeny. For example, establishing trees in the understory gradually intercept more light as they increase in size and reach the canopy, and thus, the limitation of carbon gain by low light is gradually relieved (Givnish, 1988). Yet, enhanced radiation interception together with reduced hydraulic conductance leads to greater water limitations of carbon gain in large trees (Ambrose et al., 2009; Mullin et al., 2009).

The way trees sense stress also varies throughout the ontogeny. In particular, there is evidence of overall greater resistance to drought and ozone stress and biotic stress in large non-senescent trees compared with seedlings and saplings (Fredericksen et al., 1995, 1996a; Kolb et al., 1997; Fleischmann et al., 2005, 2009; Nunn et al., 2005a). In fact, large trees are infrequently killed by even long-term single stress events such as drought (e.g., Bréda et al., 2006) that result in massive mortality of undergrowth (Frazer and Davis, 1988; Donovan et al., 1993; Poorter and Hayashida-Oliver, 2000). Massive decline of large forest trees is commonly associated with multiple sustained stresses (Wargo, 1996; Walters and McCarthy, 1997; Adams et al., 2009a; Allen et al., 2010; Paoletti et al., 2010), highlighting the importance of multiple stresses in understanding the mortality of mature trees.

So far, most of the work on tree stress resistance has been carried out with young plants, most often with first-year seedlings (e.g., Walters and Reich, 1999). Given the changes in stress combinations and overall stress resistance with increasing tree size, the lack of stress studies on older plants is an important deficiency. This synthesis article first provides an overview of the complex environmental setting in forests, effects of single and multiple stresses on plant performance, and the interactions of past and present stresses and tolerance and acclimation to stress combinations under current and predicted future conditions. This paper further analyzes the modifications in stress responsiveness from seedlings to mature trees, and finally provides a short summary of currently used methods and novel promising tools to characterize stress in forest trees of varying size, and to scale the responses to entire trees and forest ecosystems. This analysis collectively suggests that the severity of various single stresses and stress combinations varies throughout tree ontogeny. Furthermore, future climates may be characterized by novel combinations of severity of various stresses. Understanding tree responses to such ontogeny- and global change-driven modifications in stress combinations is needed to predict forest stress responsiveness in current and future climates.

2. Stress in forests

2.1. Occurrence of single and multiple stresses

According to classical stress concepts, every environmental factor deviating from the optimum constitutes a stress to the plants. While every factor can be individually controlled in lab experiments, a plethora of abiotic and biotic factors fluctuate simultaneously in field environments. The severity and timing of different stresses varies among different ecosystems and during the growing season as outlined in Fig. 1 for temperate bogs supporting low stature conifer tree cover, temperate conifer forests with high stature forest cover and Mediterranean savannas supporting
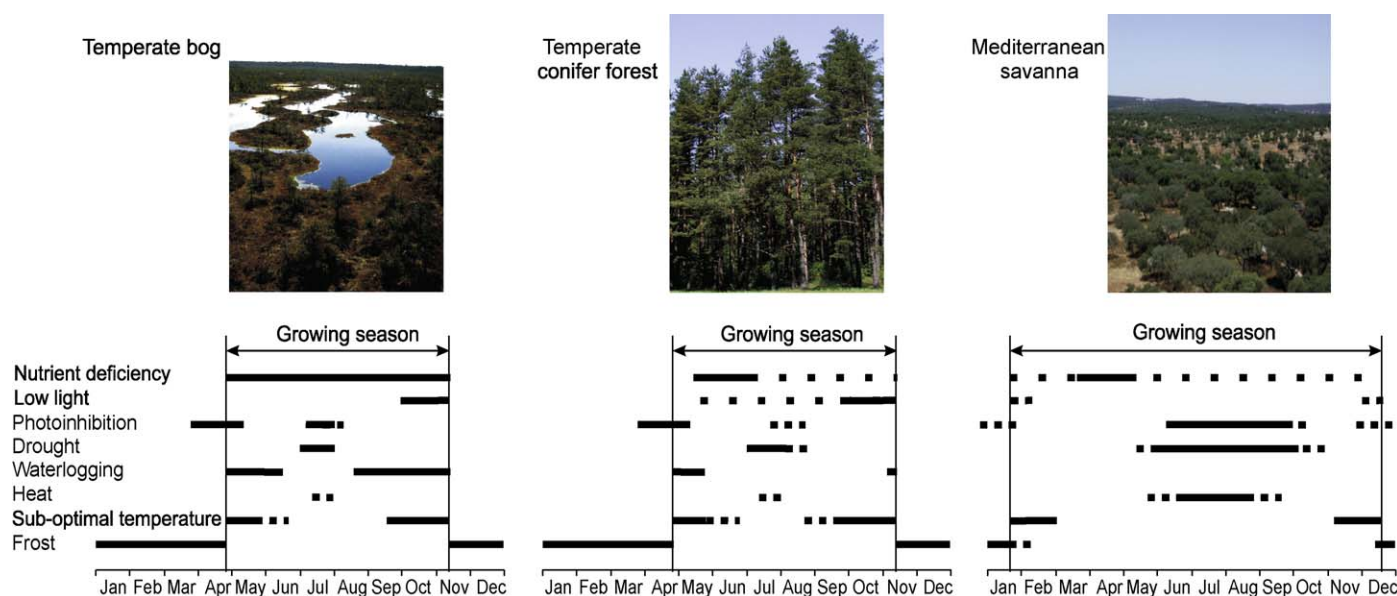
Fig. 1. Generalized illustration of occurrence of severe frequent stresses (solid vertical lines), and mild or sporadic stresses (dotted lines) in three contrasting Northern hemisphere temperate ecosystems dominated by evergreen tree species. Plants mainly sustain stress during the growing period and are less susceptible to stress during the winter frost period when the plants are dormant, especially in cool temperate ecosystems. However, frost stress in cool temperate species can be associated with premature dehardening in response to warmer periods in the middle of winter, resulting in major winter dieback (Ögren, 1996, 1997). The importance of various stress factors varies throughout the growing season in each ecosystem in a characteristic manner as explained in detail in Section 2.1. Sample images of a temperate bog (Männikjärve bog, Estonia, 58°52′N, 26°15′E) and a temperate forest (Ihaste Forest, Tartu, Estonia, 58°21′N, 26°47′E) both dominated by evergreen conifer *Pinus sylvestris*, and a Mediterranean savanna (montado) dominated by evergreen sclerophylls *Quercus suber* and *Q. ilex* (Mitra, Évora, Portugal, 38°34′ N, 7°54′W) are also shown.

sparse evergreen tree cover. Temperate bogs are characterized by chronic nutrient deficiency throughout the growing season (Small, 1972; Damman, 1990; Niinemets et al., 2001). Differently from the bogs, nutrient limitation is not always a chronic severe stress in temperate and Mediterranean forests. Severe nutrient limitations can still occur in the beginning of the growing season during new foliage formation (Weikert et al., 1989; Marschner et al., 1997; Saur et al., 2000), and moderate nutrient deficiency can be present during most of the season, especially in forested areas on soils not considered suitable for agricultural crops (Linder, 1987; Carreira et al., 1994; Rambal, 2001; Maroco et al., 2002).

The other key stress in the bogs is anoxia (waterlogging) during a major part of the growing season (Fig. 1). However, as the bulk of the roots occupies the upper 5–15 cm soil layer, mid-seasonal reduction of water table depth can also result in severe drought in bogs (Portsmuth et al., 2005, Portsmuth and Niinemets unpublished observations, Fig. 1) and the reduction in water availability can lead to photoinhibition (Fig. 1, Murray et al., 1989, 1993; Hájek et al., 2008). In temperate forests, drought and photoinhibition can significantly limit productivity, although the importance of these stresses strongly varies between the years in unpredictable manner (Linder, 1987; Rosenqvist et al., 1991; Niinemets et al., 1999b; Niinemets and Kull, 2001). In the Mediterranean environments, prolonged drought and photoinhibition are among the most severe stress factors (Flexas et al., 2001; Werner et al., 2001; Chaves et al., 2009; Unger et al., 2009). In ecosystems with dense canopy, different stresses can be prevalent in the upper (e.g., photoinhibition) and the lower canopy (shading) (Valladares et al., 2005, 2008; Valladares and Niinemets, 2008).

In addition to these stress factors, sub-optimal temperatures constitute a major environmental limitation in the cool temperate ecosystems (Troeng and Linder, 1982), while supraoptimal temperatures occur sporadically (Niinemets et al., 1999a). In contrast, heat stress is a major environmental limitation in the Mediterranean ecosystems (Gratani, 2000; Valladares and Niinemets, 2007;

García-Plazaola et al., 2008), although sub-optimal temperatures can also be limiting for the productivity during winter months (Beyschlag et al., 1987; Harley et al., 1987), and limit the plant survival especially at the northern margin of the Mediterranean evergreens (Larcher, 1981, 2000).

In all these three ecosystems analyzed, the plants commonly sustain multiple stresses, episodically even three or more environmental factors may be beyond the plant optimum. For example, in the bog, nutrient deficiency, waterlogging and photoinhibition, and nutrient deficiency, drought and photoinhibition can co-occur (Fig. 1, Murray et al., 1989, 1993; Tømmervik et al., 1994; Hájek et al., 2008), while the key co-occurring stresses in the Mediterranean ecosystems are drought, heat and photoinhibition (Fig. 1, Valladares and Pearcy, 1997, 2002; Valladares et al., 2005). Apart from the multiple co-occurring stresses, plants often also sustain multiple successive stresses such as cycles of drought followed by heat spells or waterlogging (Fig. 1, Liu and Dickmann, 1993; Fan et al., 1994; Conrath et al., 2006). For such successive stresses, order, duration and severity of different stresses can significantly vary, resulting in unique stress patterns. In addition to abiotic stresses, various biological stresses such as insect and pathogens attacks are further often superimposed on these key environmental limitations in all forested ecosystems (Schoeneweiss, 1981b, 1983; Kurz et al., 2008). As with the abiotic stress factors, the severity of different biotic stresses can also vary among different ecosystems (Walter, 1992; Kittredge and Ashton, 1995; Zavala et al., 2000; Anthony et al., 2002; Baier et al., 2002) further diversifying the stress patterns.

This evidence collectively demonstrates that forest trees are frequently exposed to a variety of stresses, making the prediction of plant physiological responsiveness to variations in environmental and biotic drivers a formidable task. As the result of common stress factors such as lack of nutrients, water and sub- or supraoptimal temperatures, the realized carbon gain of many forests has for long been recognized to be much less than the potential productivity (Jarvis, 1985; Landsberg, 1986; Linder, 1987).
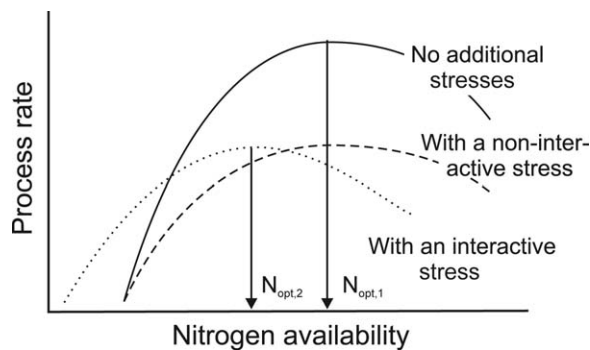
Fig. 2. Illustration of the concept of additive and interactive stresses. Classical stress studies have demonstrated that the rate of plant physiological processes (e.g., photosynthesis, growth) depends on resource availability, e.g., on nutrient availability, according to a bell shaped curve. Under optimum conditions, the level of a given resource is not limiting for plant performance, while super- and supraoptimal resource levels result in reduced plant performance. Typically, any additional stress, e.g., drought, further reduces plant performance. In the case of an additive effect (dashed line), the plant performance is reduced at any given nutrient availability to a similar degree. In the case of an interactive effect (dotted line), the effect of the second stress varies in dependence on the level of the first stress factor. For nutrients, the interactive effect typically implies changes in the form of the response curve, i.e., alteration in the shape of the reaction norm, visible in the shifted optimum nutrient availability ($N_{opt,1}$ for the responses without an additional stress and with an additive stress and $N_{opt,2}$ for the interactive stress).

2.2. Stress combinations, interactions and implications for reaction norms

Multiple stresses can occur simultaneously or successively. In the case of simultaneous stresses, seldom one encounters a situation with two or more limitations occurring at exactly the same time. More frequently, an episodic stress factor is superimposed on an already existing stressor. For instance, heat stress events are superimposed on drought-stressed plants, or shaded plants in understory experience seasonal drought. The difference between the two multiple stress situations is that previous exposure to the first stress can result in acclimation responses to this first stressor that, in turn, can alter the plant response to the superimposed stress, while such acclimation effects are absent for the overlaying stresses. Thus, tolerance and acclimation to the underlying stress can importantly alter the overall plant response to the combined superimposed stress (Section 3). The circumstances are similar with successive stresses, where acclimation to the first stress can occur during the recovery periods intervening the different stresses.

Due to the acclimation responses and variations in tolerance to different environmental limitations (Section 3) the influence of superimposed and successive environmental stresses is often not additive, but different stresses can interact (Fig. 2). Interactions among the stress factors mean that any additional stress factor alters the reaction norm for any given environmental driver (Fig. 2). The interactions can be either negative, implying amplification of the plant response to the given stressor by an additional stress, or positive, leading to the reduced plant responsiveness to the given stress factor by an additional stress. As an example of negative interactions, in some studies, drought has been found to be more sever under shading (i.e., a negative drought-shade interaction, Valladares and Pearcy, 2002), while in other studies, plants under excess light have been shown to be more vulnerable to drought (a negative drought-high light interaction, Valladares and Pearcy, 1997; Aranda et al., 2001). As another example, waterlogging affected tree saplings more strongly under high light than under low light (Wagner and Dreyer, 1997). Negative interactions are also common for combined abiotic and biotic stresses. Trees exposed to a certain environmental stress factor, e.g., to severe drought or frost, are much more vulnerable to pathogen attacks than plants

not exposed to severe environmental stress (Schoeneweiss, 1981a, 1983; Appel, 1984).

As examples of positive interactions, studies demonstrate that drought-stressed plants are often more resistant to heat stress than plants under optimum water availability, reflecting the positive effects of enhanced content of sugars and other osmotically active compounds in drought-stressed plants in preserving membrane integrity under heat stress (Seemann et al., 1986; Hüve et al., 2006). Drought also leads to stomatal closure, and reduces the uptake of pollutants via stomata, thereby ameliorating the effects of gaseous pollutants, e.g., ozone (Chen et al., 1994; Ollinger et al., 1997; Löw et al., 2006). As a further positive interaction, nitrogen fertilization can reduce the impact of several stresses, e.g., waterlogging stress (Liu and Dickmann, 1993).

3. Stress responsiveness of trees in the current and future climates: tolerance, acclimation and stress history

3.1. Tolerance of single and multiple limitations

Tree stress responses depend on the plant resistance to any given stress and to any combination of stresses. Stress resistance depends on the tolerance of the specific stress, and on the degree of acclimation to the specific stress. Tolerance is a relative term that characterizes the species capacity to tolerate a given environmental limitation relative to the other species of the same ontogenetic stage (Niinemets and Valladares, 2008). In the past, tolerance was commonly characterized by a qualitative ranking, e.g., very tolerant, tolerant, mid-tolerant, intolerant and very intolerant (e.g. Baker, 1949 for qualitative shade tolerance rankings). Nowadays, quantitative numerical rankings based on combining and cross-calibrating the qualitative rankings or based on species abundance along environmental gradients are becoming increasingly more used (Ellenberg et al., 1991; Hill et al., 1999; Niinemets and Valladares, 2006).

Tree species widely differ in the tolerance to different environmental factors (Niinemets and Valladares, 2006 for tolerance rankings of Northern hemisphere species for light, flooding and drought). While the structural and physiological traits responsible for single factor tolerance are becoming increasingly well understood (Eissenstat, 2000; Lusk and Del, 2002; Sánchez-Gómez et al., 2006; Hallik et al., 2009), we currently poorly understand the factors responsible for the tolerance to multiple environmental drivers. However, there is evidence that multifactor tolerance is rare among the woody plants. In a study investigating the tolerance to shade, drought and waterlogging in Northern hemisphere temperate species, at most 10% of species were tolerant at least to two environmental factors, and ca. 0.4% of species were moderately tolerant to all three environmental factors. In fact, negative correlations between shade and drought tolerance (Fig. 3), shade and waterlogging tolerance and drought and waterlogging tolerance have been observed, suggesting that polytolerance is inherently constrained in temperate woody species (Niinemets and Valladares, 2006). Such negative correlations between tolerances to different stresses likely reflect different combinations of structural and physiological traits required to tolerate given environmental limitation (Smith and Huston, 1989; Hallik et al., 2009).

Although the tolerance of several chronic stresses is rare, the capacity to tolerate short-term biotic and abiotic stress events superimposed on a chronic environmental stress such as shade, can be critical to survive under the main chronic environmental limitation. For instance, fungal pathogen attacks have been shown to limit recruitment of tree seedlings in shade (O'Hanlon-Manners and Kotanen, 2004). The capacity to survive short-term additional biotic and abiotic stresses under shade has been linked to the size
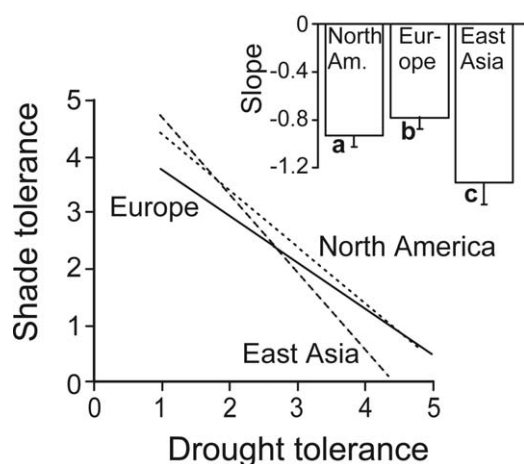
Fig. 3. Relationships between shade and drought tolerance (standardized major axis regression lines) among the Northern hemisphere temperate tree species from Europe ($n = 262$, solid line), North America ($n = 364$, dotted line) and East Asia ($n = 211$, dashed line). The inset shows the comparisons among the slopes according to the maximum-likelihood ratio test of Warton and Weber (Falster et al., 2003; Warton et al., 2006). Both the shade and drought tolerance are defined as numerical relative rankings between 1 (lowest tolerance) to 5 (highest tolerance). Modified from Niinemets and Valladares (2006).

of the storage pool of non-structural carbohydrates (Myers, 2005; Myers and Kitajima, 2007; Poorter and Kitajima, 2007). Greater pool of non-structural carbohydrates can contribute to the survival of the episodes of additional stresses both by directly covering plant metabolic requirements as well as by fuelling structural and metabolic acclimation to additional stresses (Amthor and McCree, 1990).

3.2. Influence of acclimation, stress priming and stress sequence on the resistance to multiple stress episodes

Stress acclimation is defined as full or partial recovery of plant functioning during environmental stress and lower stress responsiveness compared to non-acclimated plants. The degree of plant acclimation to the given stress depends on plant phenotypic plasticity and the time available for stress hardening. Therefore, past stress history can importantly alter plant responsiveness to environmental stresses. Exposure to mild stress typically results in induction of acclimation responses leading to greater resistance to a given type of stress (Conrath et al., 2006). For instance, a mild drought stress episode enhances the tree resistance to a subsequent more severe drought stress (Liu and Dickmann, 1993; Fan et al., 1994). Analogously, an early defoliation event results in greater contents of protective chemicals, thereby enhancing the resistance to subsequent herbivory episodes (Stevens and Lindroth, 2005). This so-called stress priming may enhance the resistance not only to a given stress, but to several subsequent stresses. For example, acquired resistance to pathogens can result in development of resistance to herbivory (Heil and Silva Bueno, 2007; Frost et al., 2008; Niinemets, 2010b) or even to abiotic stresses such as drought (Fujita et al., 2006).

For sequential multiple stresses, plant response may critically depend on what stress comes first and on the degree to which the plant has acclimated to this first stress factor. For example, the plants already acclimated to long-term low light conditions in the understory and having large leaf area and a low fraction of biomass in roots are expected to respond more strongly to drought (e.g., Valladares and Pearcy, 2002) than the plants recently overtopped by other competing plant individuals and not yet having substantially altered allocation of biomass to leaves at the expense of roots.

As a further example, plants exposed to long-term drought and having depleted the carbon reserves will have low resistance to pathogen attacks (Schoeneweiss, 1981a), while pathogen attacks preceding drought stress may activate defence pathways that can contribute to drought resistance as well (Fujita et al., 2006, see also below). In particular, accumulation of the stress hormone abscisic acid in pathogen-infected leaves can lead to stomatal closure and water conservation (Lee et al., 1999; Flors et al., 2005; Asselbergh et al., 2008). However, the patterns largely vary for different pathogens, and in some cases, pathogen attack can force stomatal opening, resulting in greater vulnerability to subsequent drought events (Allègre et al., 2007; Prats et al., 2007).

In addition to the stress sequence, stress severity and duration of stress events can also drive the overall plant response. Exposure to a severe stress in the past may reduce plant immediate capacity to cope with any subsequent event of the same type of stress or different stress. This is because a severe stress can deplete plant storage carbon reserves, leading to exhaustion of plant resistance to stress (Lichtenthaler, 1998). In most experimental stress studies, only one stress cycle has been applied. However, experiments with repeated stress cycles have demonstrated that multiple successive stress cycles impair plant performance more strongly than a single stress cycle (e.g., for drought stress cycles, Alcocer-Ruthling et al., 1989; Liu and Dickmann, 1993; Stewart et al., 1995). It takes increasingly more time to recover from the next stress cycle (Alcocer-Ruthling et al., 1989; Liu and Dickmann, 1993; Stewart et al., 1995), reflecting the exhaustion of plant resistance by recurrent stress episodes. This evidence suggests that apart from induced mechanisms of stress resistance, the availability of carbon reserves at the beginning of each stress episode plays a major role in determining the resistance against a further stress of the same type or an additional stress. Thus, repeated past stress events intervened by short periods of recovery insufficient to fill up the carbon reserves reduce the plant performance to any subsequent stress. However, when sufficient time is available between the stress episodes for recovery, priming responses may enhance plant resistance against further stresses. Thus, a delicate balance seems to exist between priming for stress resistance and depletion of carbon reserves, jointly determining the way the plant stress history alters the plant response to subsequent stresses. At any rate, these examples demonstrate that duration, severity and the order of different stresses importantly alter the overall effect of multiple stresses on plants.

3.3. Global change and multiple stresses: CO_2, temperature and drought interactions

Predicted increases in temperature and changes in precipitation pattern (Meehl et al., 2007; Trenberth et al., 2007) are likely to lead to occurrence of novel combinations of stresses in ecosystems that have not encountered such stress combinations in the past as well as to novel combinations of severity of various stresses (Williams and Jackson, 2007). For example, enhanced temperatures can lead to occurrence of heat and waterlogging stress in bogs and more severe heat, drought and photoinhibition stress periods in temperate bog and forest ecosystems (Fig. 1). In future warmer climates, drought periods are generally expected to be longer and more severe (Breshears et al., 2005; Adams et al., 2009a; Allen et al., 2010).

Consideration of carbon reserves in plant stress resistance is particularly relevant in understanding the effects of key global change drivers on forest growth. This is because all global change associated modifications in environment occur at the background of CO_2 elevation, and typically, elevated CO_2 increases the non-structural carbon storage (Wullschleger et al., 1992; Roberntz and Stockfors, 1998; Tognetti et al., 1998; Vu et al., 2002), and enhances the resistance to several stresses. Plants grown in elevated CO_2 atmospheres

have been shown to be less vulnerable to drought (Conroy et al., 1986; Le Thiec and Dixon, 1996; Roden and Ball, 1996; Anderson and Tomlinson, 1998; Tomlinson and Anderson, 1998; Schwanz and Polle, 2001; Polley et al., 2002; Vu et al., 2002), maintaining higher growth rate under drought than plants under lower CO_2 atmospheres (Tschaplinski et al., 1995; Polley et al., 2002). Elevated CO_2 also enhances plant resistance to heat and frost stresses (Faria et al., 1996; Wayne et al., 1998; Taub et al., 2000; Vu et al., 2002; Darbah et al., 2010), likely reflecting greater concentrations of membrane-stabilizing sugars in the tissues (for sugar effects on heat stability of photosynthetic apparatus see Hüve et al., 2006) (for sugar effects on frost stability see Rütten and Santarius, 1988; Santarius, 1990).

Apart from these positive effects, elevated CO_2 commonly induces greater nutrient deficiency (for reviews see Curtis, 1996; Saxe et al., 1998). This in turn can led to accumulation of secondary carbon-rich chemicals such as tannins, improving plant resistance to herbivory attacks as observed in several studies (Roth et al., 1997; McDonald et al., 1999; Agrell et al., 2000; Mohan et al., 2006). On the other hand, if the content of secondary chemicals is not affected by elevated CO_2, greater leaf sugar concentrations may promote herbivory attacks under elevated CO_2 (DeLucia et al., 2008).

Predicting stress responses in the future climates is further complicated by concomitant modifications in temperature. Warming and associated increase in plant respiratory requirements can result in depletion of carbon reserves (Ahmed et al., 1993; Tjoelker et al., 1998, 2008; Campbell et al., 2007). This may enhance the vulnerability of plants to additional stresses such as to ozone stress (Riikonen et al., 2009) and drought stress (Xu et al., 2008; Adams et al., 2009a; Allen et al., 2010). Depletion of carbon reserves has been suggested to be the primary reason for the drought-driven mortality at warmer temperatures, reflecting "carbon starvation" (McDowell et al., 2008; Adams et al., 2009a). However, so far the evidence of enhanced carbon limitations under combined drought and warming treatment is lacking (Adams et al., 2009b; Sala, 2009; Sala et al., 2010). Furthermore, projected enhancement of tree mortality in future climates due to warming-drought interaction (Adams et al., 2009a; Allen et al., 2010) has not addressed the concomitant modifications in atmospheric CO_2 concentration (Sala et al., 2010 for a discussion). In fact, the combined effects of elevated CO_2 and warming on sugars has been examined only in a few studies. These experiments have consistently observed higher carbohydrate contents in plants grown under elevated CO_2 at both normal and elevated temperatures (e.g., Tjoelker et al., 1998; Vu et al., 2002), suggesting that the effects of elevated CO_2 on carbon reserves are dominating. This suggestion is supported by greater tolerance of simultaneous drought and heat stress episodes in plants grown under elevated CO_2 (Hamerlynck et al., 2000).

Alternative to "carbon starvation" hypothesis, greater mortality of trees under combined warming and drought treatment may be associated with hydraulic failure (McDowell et al., 2008) or/and with impaired long-distance transport of non-structural carbon from storage tissues to sinks (Sala et al., 2010), especially if drought occurs rapidly (Leuzinger et al., 2009). Lack of non-structural carbon pool data in trees undergoing drought- and warming-induced death makes it currently impossible to discriminate among the different hypotheses (Sala, 2009). Clearly, additional research on storage carbohydrate pools is needed for quantitative prediction of plant stress responsiveness in future conditions.

3.4. Multiple stresses in trees: use of storage carbon to gauge and predict stress responsiveness

Apart from the resilience to sustained chronic stresses mainly determined by species tolerance, tree response to environmental variability at any time during the growing season is also critically driven by tree acclimation capacity and the past stress history. Tree responses may be completely different depending on whether the past stress induces acclimation responses, possible only when there is enough time for recovery and acclimation, or whether the past stress results in depletion of carbon reserves. Given the unpredictability of the period and length of recurrent stress cycles during the growing season, the effects of past stress history have been so far particularly difficult to consider. I suggest that the effects of multiple successive and superimposed stresses and past stress history effects are best included in predictive models at the level of storage carbon dynamics. As storage carbon pool is one of the key players affected by elevated CO_2, dynamic simulation of plant carbon allocation and storage becomes especially relevant in predicting plant stress responsiveness under future climates (Constable and Friend, 2000 for review of models).

Measurements of storage carbon are not routinely conducted in tree studies, and there is an emerging consensus that more experimental research in tree carbon reserves is needed, especially under environmental stress (Adams et al., 2009b; Leuzinger et al., 2009; Sala, 2009; McDowell and Sevanto, 2010; Sala et al., 2010). Furthermore, only a few growth models consider the reserve carbon pool, and even in the models including the storage carbon, the dynamics of this pool is often considered in a limited manner, essentially as a "black box" without considering external and internal feedbacks (Le Roux et al., 2001). Even in fewer models, mediation of the stress effects at the level of carbon pools are considered (Chen, 1993; Chen et al., 1994; Weinstein and Yanai, 1994; Retzlaff et al., 1997). In addition to simulating the storage carbon pool, stress models should ideally also be able to simulate the investment in defence, for instance on the basis of carbon/nitrogen balance (Gayler and Priesack, 2007). Consideration of defence investments together with storage would make an important interface to consider plant resistance to biotic stresses as well.

4. Stress in forest trees: from seedlings to mature plants

4.1. Variation in stress combinations throughout tree ontogeny

The previous sections demonstrated the complexity of forest tree responses to various single and combined environmental and biotic stresses. Apart from the complex interplay between different stresses, important shifts in the severity of key stresses and modifications in tree stress sensitivity occur throughout the tree ontogeny. In particular, with increasing tree size, the depth of the tree root system commonly increases, resulting in access to deeper soil water supplies (Dawson, 1996; de Soyza et al., 1996; Drake et al., 2009). The water supply from these deeper water sources, in particular from groundwater reservoirs, is less affected by precipitation-free periods than the water availability in the upper soil layers; modifications of water availability in surface soil layers can already occur during short-term drought events (Dawson, 1996). This suggests that the water status of larger trees is less affected by lack of precipitation than the water status of smaller trees (Dawson, 1996). In fact, in open-grown woody plants, smaller plants have been shown to suffer from greater water deficiencies (Donovan and Ehleringer, 1992; de Soyza et al., 1996; Drake et al., 2009) and have greater drought-dependent mortality (Donovan et al., 1993) than larger plants.

However, the situation can be different in plants growing in closed forests. In closed stands, the foliage of larger trees receives gradually more light with increasing size. In addition to light, temperature is higher at greater heights in the forest canopy due to greater interception of solar radiation (Niinemets and Valladares, 2004 for a review). Higher temperatures in turn imply greater evaporative demands that can constrain water availability in the crowns
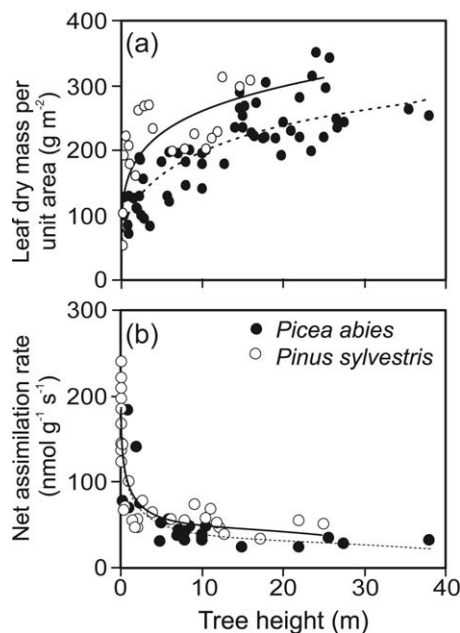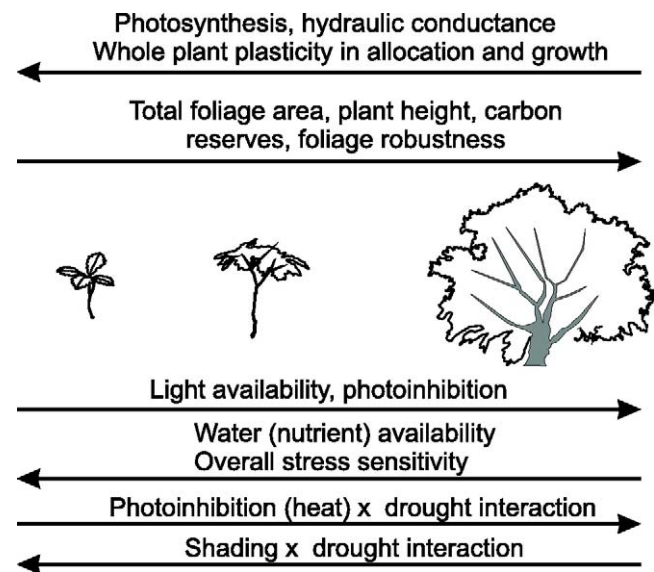
Fig. 4. Tree size-dependent increases in leaf dry mass per unit area (M_A, a) and decreases in photosynthetic capacity per unit dry mass (A_{mass}, b) in two wide-spread European conifer species (modified from Niinemets, 2002). Photosynthetic capacity per area ($A_{mass}M_A$) scaled also negatively with tree height, although the variation was narrower, 3–4-fold across the height range due to the opposite trends in M_A and A_{mass} (data not shown, see, Niinemets, 2002 for details).


Fig. 5. Generalized responses of tree size-dependent alterations in photosynthesis, stem hydraulic conductance (based on Niinemets, 2002; Koch et al., 2004; Woodruff et al., 2007, 2009; Mullin et al., 2009; Steppe et al., 2011), overall plasticity in growth and biomass allocation to environmental modifications, and severity and responsiveness to different stresses and stress combinations. In forests, young seedlings and saplings typically grow under low limiting light availabilities, but light availability gradually improves as the trees gain in size. With increasing radiation input, evaporative demand also increases. This, combined with reduced hydraulic conductance, potentially leads to greater water stress (e.g., Hubbard et al., 1999; Bond, 2000), and also commonly results in greater leaf temperatures (Niinemets et al., 1999a). However, the situation can be different for open-grown seedlings and saplings that commonly have shallower root systems than mature trees, and may therefore sustain greater drought-dependent mortality (Donovan and Ehleringer, 1992; Donovan et al., 1993). In old-growth forests, accumulation of limiting nutrients such as nitrogen in litter, soil organic matter and standing biomass may also result in reductions in stand growth (Gower et al., 1996). Simultaneous occurrence of drought and photoinhibition and heat stresses is expected to increase with increasing tree size, while shading and drought stress interaction is expected to be more important in seedlings and saplings (for shade–drought interactions in understory and photoinhibition–drought interactions in overstory see Valladares and Pearcy, 1997, 2002; Niinemets and Valladares, 2004). Due to larger carbon reserves, the overall stress sensitivity of large mature non-senescent trees is expected to be less than in seedlings and saplings.

of tall trees. In addition, gravitational component of water potential increases by 0.01 MPa m^{-1}. To compensate for this increase in water potential, and be able to maintain water supply to the top of the large plants, water potentials in the crowns of tall trees must be significantly lower than in smaller trees (Tobiessen et al., 1971; Koch et al., 2004). Furthermore, there is evidence that the hydraulic conductivity of larger trees is less than in smaller plants (Woodruff et al., 2007; Ambrose et al., 2009). Although the larger trees may have access to deeper soil water reservoirs, their lower water potentials, limited hydraulic conductivity, and greater evaporative demands can under certain conditions (e.g., under low atmospheric humidity) effectively uncouple the foliage at the top of the tree from the water in the soil, resulting in lower stomatal conductance in crowns of larger forest trees than in the smaller trees (Yoder et al., 1994; Fredericksen et al., 1996b; Bond, 2000). These reductions in stomatal conductance are partly responsible for lower rates of photosynthesis in larger trees (Fig. 4, Yoder et al., 1994; Bond, 2000).

Higher temperature and greater light itself can constitute a significant stress for larger trees, especially in conjunction with limited water availability at greater heights in the canopy. There is evidence that photoinhibitory damage to foliage photosynthetic apparatus is more severe under limited water availability and heat stress (Havaux, 1992; Flexas et al., 1999; Ishida et al., 1999), and significant photodamage in larger trees can occur in years with exceptionally severe additional stresses such as drought (García-Plazaola et al., 2008). On the other hand, extensive shading in the understory importantly curbs the carbon gain in tree seedlings and saplings, being the major limitation for forest regrowth (Walters and Reich, 2000; Valladares and Niinemets, 2008).

Among other environmental factors, nutrient availability has been considered limiting for the growth of larger trees in old-growth forests, where limiting nutrients can become largely fixed in standing biomass and soil organic matter (Gower et al., 1996; Murty et al., 1996). Thus, productivity of large trees in old-growth forests can be limited even by three chronic environmental

stresses: limited water and nutrient availabilities and excess light, while the productivity of undergrowth is limited by low light and nutrient availabilities.

This evidence collectively suggests that trees of varying size encounter different combinations of environmental limitations throughout their ontogeny (Fig. 5). Such ontogenetic modifications in the severity of various key stresses have important implications for transferring the knowledge of stress responses from the lab studies conducted with seedlings to the forest stands, as well as for prediction of forest tree growth and survival from seedlings to mature trees.

4.2. Effects of ontogeny on stress sensitivity

In addition to changes in the stress combinations, the stress sensitivity also importantly varies from seedlings to mature trees. With increasing tree size, the fraction of plant biomass in stems and roots increases, while the fraction of biomass in leaves decreases (Niinemets, 1998, 2010a; Jokela and Martin, 2000; Messier and Nikinmaa, 2000; Claveau et al., 2005; Portsmuth et al., 2005). In addition, the concentration of non-structural carbon also increases with increasing tree size (Fig. 6), possibly reflecting greater inhibition of growth than photosynthesis with increasing size (Körner, 2003; Sala and Hoch, 2009). Thus, together with the accumulation
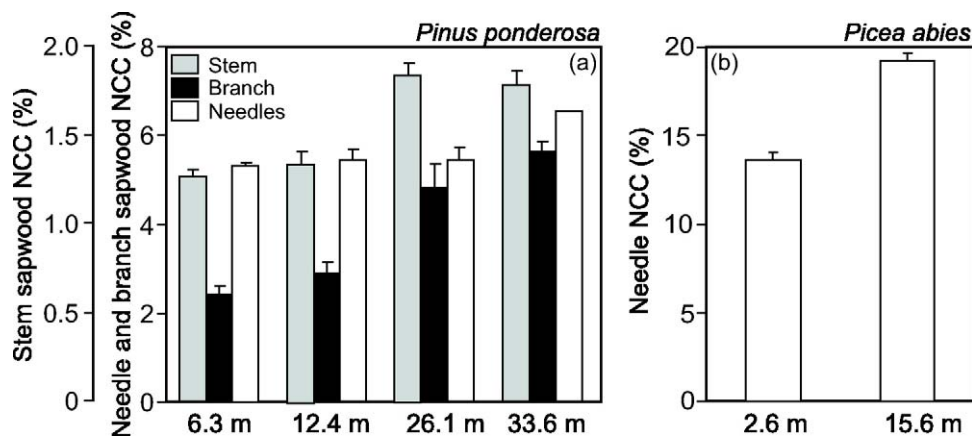
Fig. 6. Variations in stem sapwood, branch sapwood and 1-year-old needle non-structural carbohydrate concentrations (NSC, sum of sugars and starch) in different-sized trees of *Pinus ponderosa* (a) (dry site, Sala and Hoch, 2009), and in NSC in current-year needles of different-sized trees of *Picea abies* (Niinemets, 1997a,b). In *P. ponderosa*, the trend of increasing NSC with increasing tree height was significant for all three biomass fractions on the dry site shown here ($P < 0.014$), whereas on moist site, the trend was significant for branch sapwood (Sala and Hoch, 2009). In *P. abies*, the difference between the groups is significant at $P < 0.005$. The error bars show +SE ($n = 5$ for all tree size classes in *P. ponderosa* and for small trees of *P. abies* and $n = 3$ for large trees of *P. abies*).

of structural carbon in the woody biomass, the reserves of non-structural carbon (starch and soluble sugars) in stems and roots (concentration times the mass of roots and stem) increase with increasing tree size (Hoch et al., 2003; Körner, 2003; Würth et al., 2005; Sala and Hoch, 2009). In large trees, the non-structural carbon stocks may exceed several-fold the amount of carbon needed to form the entire canopy leaf area (Hoch et al., 2003; Würth et al., 2005).

The variations in the size of non-structural carbon reserves bear important implications for understanding changes in stress resistance throughout tree ontogeny (Fig. 7). Typically, any stress results in the reduction of plant net carbon gain (Fig. 7). Influence of stress-driven reductions in net assimilation rate on plant survival apparently depends on the extent to which the total tree non-structural carbohydrate pool relies on immediate photosynthesis. In seedlings, the storage carbon pool size is relatively small, and a reduction in net assimilation rate leads to fast depletion of the storage reserves in plant maintenance processes (Fig. 7), further accentuating the stress effect on the plant. In contrast, in large trees, immediate carbon assimilation contributes only to a minor degree to the total tree non-structural carbon pools, and stress-dependent reduction in carbon uptake only moderately alters total tree carbon reserves (Fig. 7). As the result of these differences, seedlings that more strongly rely on immediate photosynthesis are expected to be more sensitive to prolonged stress events than large trees that are less strongly dependent on immediate photosynthetic production (Fig. 7).

Available evidence is in broad agreement with these predictions. The resilience of trees to fungal attacks increases significantly during the tree ontogeny (Fleischmann et al., 2005, 2009). Analogously, the responsiveness to ozone stress is higher (Fredericksen et al., 1995, 1996a; Kolb et al., 1997; Nunn et al., 2005a) and the overall antioxidative capacity (Wieser et al., 2003) is lower in seedlings than in mature trees. Tree water stress resistance also increases with increasing tree size, accompanying greater fractional investment of plant biomass in roots in larger plants (Anderson and Tomlinson, 1998; Tomlinson and Anderson, 1998). In fact, large trees can tolerate sustained drought periods extending over the entire growing season and even across multiple growing seasons (Epron and Dreyer, 1993), while such severe drought periods can lead to mortality of seedlings and saplings (for seedling physiological responses see Epron et al., 1993; Mendel et al., 1997; Mueller et al., 2005; Lopez and Kursar, 2007). The presence of large carbon reserves in mature plants can also allow for new shoot forma-

tion and resprouting (in resprouting species) following catastrophic events such as fire (Koskela, 2000; Langley et al., 2002) and breakage of branches or entire stem (Génard et al., 1998; Verdaguer and Ojeda, 2002; van Bloem et al., 2003; Wong et al., 2005; Vargas, 2009; Vargas et al., 2009). Thus, the availability of large reserves contributes to survival of and greater recovery after such devastating events. In contrast, lack of sufficient reserves to build a new stem and foliage following the death of above-ground plant part makes smaller plants highly vulnerable to biomass losses. In addition, larger plants have a greater capacity to tolerate sustained periods of combined stresses such as ozone and pathogen stress (Fleischmann et al., 2009). Due to greater antioxidative capacity under higher light in adult trees than in seedlings (Wieser et al., 2003), adult trees are expected to tolerate better the interactions of photoinhibition with other stresses such as ozone stress. In plants with limited content of antioxidants, such combined stresses have been shown to lead to extensive formation of reactive oxygen species (ROS) and extensive damage (Wise, 1995; Garcia-Plazaola and Becerril, 2001; Tausz et al., 2001; Wieser et al., 2001).

4.3. Determinate vs. indeterminate growth as an explanation for variations in stress tolerance with ontogeny

The reason for higher carbon pools in larger forest trees is partly associated with their access to greater light availabilities. In fact, given the lower photosynthetic rates and greater fraction of non-photosynthetic support biomass, tolerance of low light conditions decreases with increasing tree size (Valladares and Niinemets, 2008 for a review). However, even if grown in higher light under optimum conditions, the seedlings or the saplings partition less carbon in storage than the mature trees. This is because seedlings and saplings are commonly characterized by indeterminate biomass growth or multiple growth cycles during the growing season, while mature trees, especially in seasonal environments, have a determinate growth pattern characterized by a distinct period of rapid growth in the beginning of the favourable season (e.g., Borchert, 1991). Beyond the rapid growth period, much of the carbon produced is stored in large trees (Hoch et al., 2003).

The capacity for indeterminate growth implies that younger trees can more plastically respond to biomass losses (Stevens and Lindroth, 2005) and modify biomass allocation and construct foliage that is acclimated to prevailing conditions. Greater growth plasticity can be particularly advantageous in the acclimation to short stress events as well as in priming for future stress events
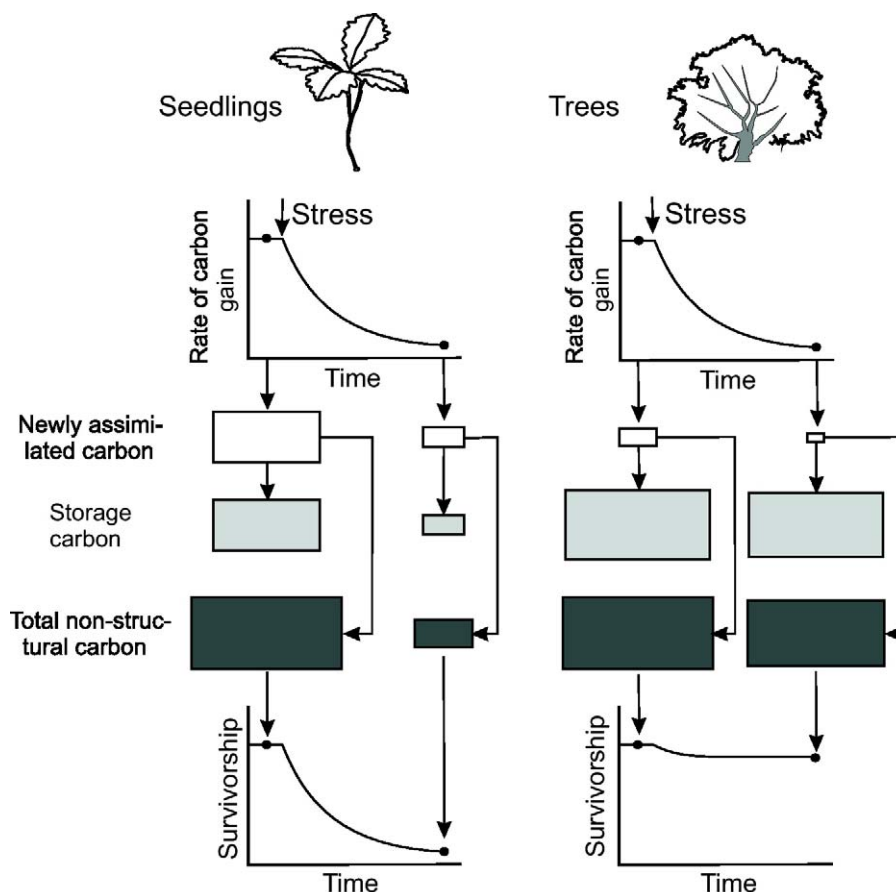
Fig. 7. Comparison of stress responses in seedlings and trees: a conceptual model. Most stress factors result in reduction in plant net assimilation rate, reducing the newly assimilated carbon pool present in leaves immediately after photosynthesis and further translocated to growing organs (developing leaves, fine roots, and woody structures) and used for maintenance respiration throughout the plant body possessing living cells, and also used to build up the storage carbon reserves. Apart from the newly synthesized carbon, all woody plants have significant non-structural carbon (sugars and starch) reserves in leaves, stem and branches and in roots (Fig. 1, Hoch et al., 2003; Myers and Kitajima, 2007; Poorter and Kitajima, 2007; Sala and Hoch, 2009) that can be used to support plant maintenance requirements throughout the stress periods when photosynthesis rates are low. In seedlings, a larger part of total non-structural carbon (newly assimilated carbon plus storage carbon) relies on newly assimilated carbon. Thus, reductions in the net carbon assimilation rate are essentially immediately reflected in plant survival. In contrast, mature trees have huge carbon reserves, even corresponding to several years growth (Hoch et al., 2003; Würth et al., 2005), and newly assimilated carbon contributes a small fraction to total tree non-structural carbon. Thus, the survival of trees during stress is less dependent on reductions in immediate rate of carbon gain. Boxes are not to scale.

(Stevens and Lindroth, 2005). For instance, drought tolerance has been associated with enhancement of root growth under moderate drought in small-seeded seedlings of several Mediterranean species (Padilla et al., 2007). However, under severe prolonged stress that strongly inhibits growth, it is not always clear whether the variation in plastic modifications in plant function (stronger vs. smaller reduction in growth rate) is associated with fitness. In fact, plants capable of growing in low-fertility habitats with chronic drought and nutrient stress have commonly low growth plasticity (Grime, 1989; Lambers and Poorter, 1992). Survival under shade has also been found to be even negatively associated with the plasticity in growth (Walters and Reich, 1996; Kaelke et al., 2001).

This discussion demonstrates that tree stress responsiveness is critically driven by both the dimensions of time (stress length, stress prehistory) and size (storage pool, exposure to different stresses). In the forest ecosystems, mortality is a frequent event in smaller tree size classes (Lorimer et al., 2001; Palahi et al., 2003; van Mantgem et al., 2009), reflected in massive reduction in stand density in early stages of stand development (Lorimer et al., 2001; Palahi et al., 2003). With increasing tree size, mortality rate commonly decreases (Lorimer et al., 2001; Palahi et al., 2003). Even extended periods of severe single stress typically do not lead to mortality of large trees (Bréda et al., 2006; Bigler et al., 2007). How-

ever, stresses co-occurring with extreme environmental events such as pathogen or herbivory attacks in drought-stressed plants with significantly exhausted pools of storage carbon can result in major forest decline episodes (Schoeneweiss, 1981a, 1983; Mattson and Haack, 1987; McLaughlin, 1998; Manion, 2003; Bréda et al., 2006; Kurz et al., 2008). Such catastrophic events can be more frequent in old-growth stands, reflected in enhanced mortality of older trees (Lorimer et al., 2001).

5. Towards adequate diagnosis of stress in forest trees: from single plant to ecosystem responses

5.1. Complexity of assessing stress in trees

Understanding the stress effects in trees and forest stands critically depends on the capacity to diagnose stress. A plethora of methods have been developed to study stress in plants (Fig. 8) and commonly a series of tools are used simultaneously to characterize tree physiological status in the field (Nunn et al., 2005b). However, trees largely vary in size throughout the ontogeny from seedlings to mature trees. While most methods can be applied to seedlings, saplings and larger trees constitute a major challenge
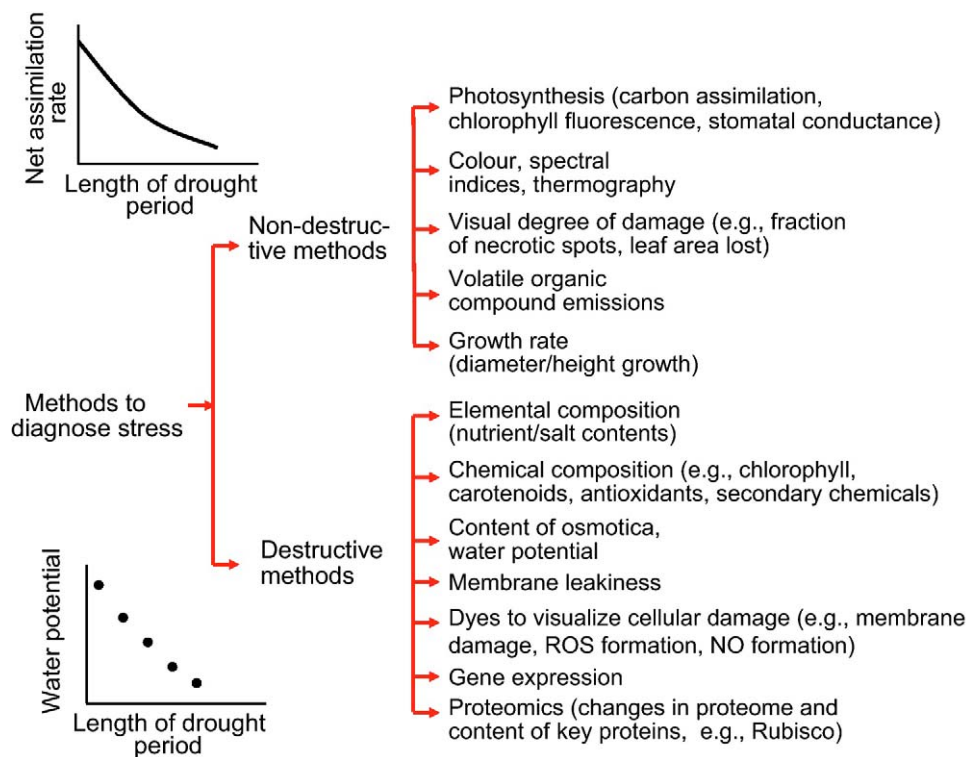
Fig. 8. Overview of the methods used to diagnose stress in plants. The stress diagnosis methods can be divided between non-destructive (commonly also non-invasive) methods that do not require harvesting of the plant or a plant part and destructive (always invasive) methods that require harvesting of the entire plant or a plant part (typically leaves). A plethora of methods exists within each sub-division, and here only the examples of widespread methods are provided. The advantage of non-destructive methods is that the same plant or the plant part can be repeatedly sampled and evolution of stress can be monitored essentially continuously (the inset for a sample relationship between net assimilation rate and time of drought treatment that can be assessed in the same plant or leaf). In the case of invasive methods, either new plants or new plant parts must be sampled at different times during stress development. This is associated with inherent variability between the samples and also entails that continuous monitoring is impossible (the inset for a sample response of leaf water potential and duration of drought, where each data point necessarily corresponds to an individual leaf). However, typically non-destructive methods provide an integrated estimate of plant performance and provide limited information of sensing the stress and modifications in plant metabolism, with some exceptions. For example, studies on volatile compound emissions (volatile plant hormones and the compounds released as the result of oxidative stress in the plant) can provide information of the time-kinetics of elicitation of stress-signalling network (Pichersky and Gershenzon, 2002; Martin et al., 2003; Beauchamp et al., 2005; Niinemets, 2010b).

for stress studies. In particular, strong environmental gradients of light and temperature exist in the crowns of large trees (e.g., Niinemets and Valladares, 2004). These gradients are accompanied by several-fold variations in foliage photosynthetic capacities and pigment contents (for reviews see e.g., Nunn et al., 2005b; Niinemets, 2007) as well as in variations in foliage sensitivity to environmental stresses (Niinemets et al., 2003; Aasamaa et al., 2004; García-Plazaola et al., 2004). Due to this large within-crown environmental and physiological heterogeneity, gaining insight into environmental limitations in large trees using conventional leaf-level methods requires large sampling effort and also models to integrate from leaf-level observations to the whole plant response (Matyssek et al., 2008; Paoletti et al., 2010). Some methods are also available to directly diagnose stress at whole plant or at entire ecosystem scale. However, as shown below, many of the available methods, especially large-scale methods, are relatively unspecific and may not always be sensitive enough in detecting early stress stages or an overall mild stress. In the following, a case is made that more specific methods need to be developed to diagnose early stages of stress and monitor stress development and recovery.

5.2. Traditional methods to diagnose stress

The available stress diagnosing methods can be broadly divided between non-destructive (commonly also non-invasive) methods that allow for repeated monitoring of the same plants or plant organs, and destructive (always invasive) methods that require

destructive harvesting of either the entire plant or plant organ (Fig. 8). Among the non-destructive methods, the simplest methods are various visual indices based on foliage colour, degree of leaf damage (necrotic spots, fraction of area removed by herbivores) and degree of full crown defoliation (crown transparency) (Innes and Boswell, 1990; Schmid-Haas, 1993; Tausz et al., 1997; Solberg, 1999; Wood et al., 2000; Nunn et al., 2005b; Vollenweider and Günthardt-Goerg, 2005; Aldea et al., 2006). However, these visual indices demonstrate already the presence of a severe stress, and are not suitable for diagnosing a mild stress. They also do not allow for reliable monitoring of the stress evolution kinetics. As an extension of visual estimates, various spectral indices have been constructed to monitor stress (Buschmann et al., 1991; Samson et al., 2000; Stylinski et al., 2002; Coops et al., 2003; Richardson et al., 2004; Porder et al., 2005; Schaepman-Strub et al., 2006; Jones and Schofield, 2008; Delaieux et al., 2009; Hilker et al., 2009). These spectral tools can be applied at scales ranging from leaves to whole tree canopies and ecosystems and provide an important means to assess stress using remote sensing techniques. Compared to visual estimates, spectral indices provide higher resolution into stress development kinetics. Using specific wavebands, the spectral methods can be used to simultaneously study various processes such as changes in foliage water content, chlorophyll and carotenoid content, foliage temperature, and elicitation of xanthophyll cycle as well as changes in canopy transparency (Stylinski et al., 2002; Coops et al., 2003; Schaepman-Strub et al., 2006; Jones and Schofield, 2008; Delaieux et al., 2009). However, the sensitivity of these spectral tools may be limited by the opacity of thick leaves

and dense canopies of many forest species, leading to signal saturation (Gamon et al., 1995; Asner et al., 2000; Porder et al., 2005; Kumar et al., 2010).

Measurements of foliage photosynthesis rates either by monitoring carbon uptake or chlorophyll fluorescence provide an important tool to gaining insight into modifications in foliage physiological activity. The rates of photosynthesis have been frequently applied to diagnose stress in the field (Long et al., 1996; Chaerle and Van der Straeten, 2000; Maxwell and Johnson, 2000; Laisk et al., 2001; Long and Bernacchi, 2003; Nunn et al., 2005b), including mature trees (Nunn et al., 2005b). Detailed photosynthetic measurements separating between partial limitations of photosynthesis (e.g., Laisk et al., 2001) are possible only with single leaves, and replicate sampling coupled with models is needed to integrate from leaf-level measurements to whole plant (Jarvis, 1995; Infante et al., 1997; Ollinger et al., 1997; Karnosky et al., 2005; Matyssek et al., 2008). The sensitivity of photosynthesis to different stresses varies in dependence on plant tolerance, and this may make it difficult to relate the reduction in photosynthetic function directly to the severity of environmental limitation. For example, the degree of photoinhibitory reduction of photosynthesis is greater in more shade tolerant species (Krause et al., 2001; Valladares et al., 2002, 2005). A given soil water limitation also often reduces photosynthesis less in more drought tolerant species that can maintain stomata open at lower soil water potentials than the less tolerant species (Flexas and Medrano, 2002; Chaves et al., 2009).

For seedlings and saplings, whole plant measurements provide an alternative way to gain insight into the integrated alterations in plant photosynthetic process during stress (Klingeman et al., 2005; Baltzer and Thomas, 2007). Whole tree photosynthesis measurement systems enclosing 8–14 m^2 plant leaf area have been constructed (Corelli-Grappadelli and Magnanini, 1993; Lloyd et al., 1995; Wünsche and Palmer, 1997; Wallin et al., 2001; Medhurst et al., 2006). However, extensive cost, slow response time and alteration of ambient climatic conditions complicate the employment of such large systems to assess the tree carbon gain.

Alternatively, the physiological activity of large trees can be assessed by measuring sap-flow rate at the stem base using thermoelectric sensors (e.g., Granier et al., 1996; Köstner et al., 1998; James et al., 2002). Given the strong correlation between plant physiological activity and plant water use, these measurements can provide important insight into the development of stress in forest trees (e.g., Alsheimer et al., 1998; Pataki et al., 1998; Nadezhdina, 1999; Rothe et al., 1999; Tenhunen et al., 2001). From whole tree measurements of transpiration, estimates of canopy conductance can be derived (Ewers et al., 2001). These values of canopy conductance can be further used to estimate the uptake of gaseous pollutants such as ozone, making it possible to directly evaluate whole tree ozone stress (Matyssek et al., 2008).

At the ecosystem scale, stress-dependent alterations in the physiological activity of forest stands can be assessed by eddy covariance techniques (Baldocchi, 1997; Arneth et al., 1999; Law et al., 2001). However, as the latter method provides an integrated estimate of both the soil and the plant activities, separate measurements of the soil respiratory activity or modelling approaches are needed to separate the vegetation and soil contributions to whole ecosystem fluxes (e.g., Janssens et al., 2000). Growth studies using dendrometers (Breitsprecher and Bethel, 1990; Vogel et al., 1996; Schleppi et al., 1999; Nunn et al., 2005b) can also be used to gain insight into the environmental variations during tree growth period. Analyses of tree ring time series can further be employed to diagnose the biotic and abiotic conditions for growth during a specific year. However, the latter measurements have inherently low time resolution and are therefore hard to associate with climatic conditions during the given year. In addition, a significant part of fixed carbon is stored and not immediately used for tree stem growth (e.g., Fig. 7). Especially in seasonal climates, intensive diameter growth occurs over a limited time period even under optimum conditions. Thus, the growth measurements alone are not always strongly linked to stress effects on carbon assimilation.

Most methods outlined above provide an integrated estimate of tree physiological status, and do not necessarily allow separation of different stresses as well as gaining insight into various physiological processes affected by stress. A variety of invasive methods are available to diagnose stress-related modifications in plant metabolism, including analyses of plant elemental composition, pigment contents, antioxidant production and secondary chemistry and gene expression (Fig. 8). Some of the invasive methods such as analyses of foliage elemental composition, pigment contents and water potential are routinely used together with non-invasive methods to characterize plant physiological status. In addition to these methods, studies on gene expression and proteomics are becoming increasingly more often used in trees. Such detailed analyses provide important insight into the stress-dependent elicitation of defence pathways, accumulation of stress-elicited protective compounds and acclimation to stress (Mittler et al., 2001; Pelloux et al., 2001; Andersson et al., 2004; Keskitalo et al., 2005; Fracheboud et al., 2009). However, as discussed above, large sampling effort is needed to gain insight into the whole tree stress status from these detailed measurements that are necessarily conducted at the leaf scale.

5.3. Monitoring volatile organic compounds: a promising method for stress studies

Environmental and biotic stresses elicit a cascade of events starting with the oxidative signalling and concluding with the modification in plant phenotype (acclimation) or with the programmed cell death (Doke, 1997; Dizengremel, 2001; Vranová et al., 2002; Baier et al., 2005). During signal transduction, a plethora of signal compounds are formed, many of which are volatile, including NO, methyljasmonate, methylsalicylate and ethylene (Arimura et al., 2002; Degenhardt and Lincoln, 2006; Filella et al., 2006; Gas et al., 2009). Such emissions of volatile stress hormones have been monitored in response to heat (Ibrahim et al., 2006), ozone (Beauchamp et al., 2005) and waterlogging (Copolovici and Niinemets, 2010) stress as well as in response to various biotic stresses (Filella et al., 2006).

In addition, several volatile markers of the onset of stress-dependent metabolic pathways are also released from the stressed plants; some of these compounds can also be involved in propagation of stress signals (Arimura et al., 2009). For instance, methanol is emitted from the stressed plants as the result of demethylation of cell wall pectins by pectin methylesterases (Micheli, 2001), while lipoxygenase pathway products (LOX products, volatile C$_6$ aldehydes, so-called green leaf volatiles) are emitted as the result of the release of free fatty acids from membranes and activation of various lipoxygenases (Porta and Rocha-Sosa, 2002; Matsui, 2006). As the result of expression of different terpenoid synthases, both biotic and abiotic stresses can lead to elicitation of emissions of mono- and sesquiterpenes (Loughrin et al., 1997; Staudt and Bertin, 1998; Mandujano-Chávez et al., 2000; Steindel et al., 2005; Opitz et al., 2008; Copolovici et al., 2009). The emissions of key stress volatiles, such as LOX products, have been demonstrated to be quantitatively linked to the severity of the stress (Beauchamp et al., 2005; Steindel et al., 2005; Loreto et al., 2006). In addition, different volatile compounds are elicited at different times during stress development (Beauchamp et al., 2005). Thus, the measurements of volatile emissions provide a promising way to diagnose both the severity of the stress and to assess the kinetics of stress development.

Availability of rapid sensors to gauge the emissions of volatile compound emissions such as the Proton Transfer Reaction Mass

Spectrometer (PTR-MS, Lindinger et al., 1998) has made it possible to diagnose stress at leaf to ecosystems scales in the field (Niinemets, 2010b for a review). So far, PTR-MS combined with eddy co-variance methodology has been used to measure the emissions of stress volatile methylsalicylate from forest stands (Karl et al., 2008). These emissions were quantitatively correlated with heat spells (Karl et al., 2008), demonstrating that diagnosing forest stress by monitoring volatile compound emissions is principally possible.

6. Conclusions

Due to interactions among environmental drivers, forest stands exposed to different combinations of light, water and nutrient availabilities can have unique responsiveness to environmental modifications. Global change is further predicted to bring about novel interactions among the severity and timing of environmental limitations, cardinally shifting the degree of stress in different communities (Hobbs et al., 2006). The difficulties with diagnosing multiple stresses and assessing the effects on plants are associated with overall lack of knowledge of how the reaction norms to given environmental factor change in response to any additional simultaneous or successive stress and how the reaction norms change with tree ontogeny. More experimental work is needed to characterize the effects of various abiotic and biotic stress combinations and gain more quantitative insight into how reaction norms change during tree ontogeny.

Currently the effects of various stresses cannot be deconvoluted in field environments, but storage carbon size likely provides an important point of convergence of various stress pathways. The predictions based on non-structural carbon pools suggest that maintenance of higher storage carbon pools increases the tolerance of sustained stress episodes. The existing evidence indicates an increase in storage carbon pools with increasing tree size, likely explaining the enhancement of single and combined stress resistance during tree ontogeny. Thus, general predictive forest tree growth models including the effects of multiple stresses, past stress history and ontogeny can be principally developed on the basis of the dynamics of storage carbon pools.

Acknowledgements

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