INVITED REVIEW: PART OF AN INVITED ISSUE ON TREE NUTRITION

Global climate change and tree nutrition: influence of water availability

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Summary The effects of global climate change will regionally be very different, mainly causing considerable changes in temperature and water availability. For Central Europe, for example, increased temperatures are predicted, which will cause increased frequencies and durations of summer drought events. On the other hand, the predicted changes in precipitation patterns will lead to enhanced rainfall during winter and spring, thereby increasing the risk of flooding in Central and Northern Europe. Depending on the sensitivity to reduced water availability on the one hand and oxygen depletion due to waterlogging on the other, physiological performance, growth and competitive ability of trees may be adversely affected. Both drought and excess water availability impair the mineral nutrition of trees by influencing on the one hand the nutrient availability in the soil and on the other hand the physiology of the uptake systems mainly of the mycorrhizal tree roots. Extreme water regimes also change interaction patterns among plants and between plants and microorganisms, and alter the carbon balance of trees and ecosystems. Here we summarize and discuss the present knowledge on tree nutrition under altered water availability as expected to be more common in the future. The focus is on tree mineral nutrient uptake and metabolism as well as on the interaction between carbon allocation and the mineral nutrient balance as affected by reduced and excess water availability.

Keywords: drought, global climate change, nutrient uptake, tree nutrition, waterlogging.

Introduction

Water availability in a future climate

Global climate change has significantly increased the amounts of rainfall during winter and spring in Northern Europe (Bardossy and Caspary 1990). According to climate models, this trend will be further enhanced in the future when even higher precipitation during winter and spring has to be expected in these regions, leading to a considerably higher risk of flooding events (ICPR 1998, IPCC 2007). Consistently, significantly less rainfall is predicted to occur in Central and Northern Europe in future summers. Accordingly, recent studies have shown significant summer warming and a trend towards an increased frequency of summer drought events in Europe in recent decades (Fink et al. 2004, Pal et al. 2004, Schaer et al. 2004, Seneviratne et al. 2006). Moreover, the climate models predict a stronger inter- and intra-annual weather variability, which will cause an increased risk of extreme events (heatwaves, heavy drought and precipitation events). Therefore, although the total amount of rainfall will decrease in many regions of Europe during summer, there will be a higher risk of heavy rainfall events at the same time. This will cause flooding not only during spring and winter but also during the vegetation period (Christensen and Christensen 2003, Meehl and Tebaldi 2004, Kundzewicz et al. 2005, Milly et al. 2005, Frei et al. 2006), particularly at sites with restricted permeability for water (e.g., clay-rich soils).

Tree nutritional aspects

The acquisition of inorganic nutrients by tree roots from the soil on the one hand depends on the nutrient availability and on the other hand depends on the capability and physiological efficiency of the uptake systems of mainly the mycorrhizal roots of trees (cf. Gessler et al. 2005). In addition, the absorbing root surface area is crucial for the tree- and stand-based nutrient uptake and for the exploitation of soil volume. Nutrient availability on the ecosystem scale is mainly influenced by the turnover of organic matter—accomplished by soil microorganisms—or the de novo input of nutrients into the ecosystem. It is, on a smaller scale, also a function of the spatial distribution of nutrients vertically in the soil profile and horizontally as affected by soil heterogeneity and canopy gaps. Thus, the three-dimensional distribution of roots in the

soil as related to gradients of varying nutrient concentrations is crucial. In this context, the ability of roots to actively exploit the soil space for nutrients (i.e., the foraging capacity) determines the resource acquisition efficiency.

The capability of a plant root to efficiently take up the nutrients available in the rhizosphere can be defined by the kinetic characteristics of the nutrient transporters (i.e., transporter affinity and maximum uptake capacity) (e.g., Glass et al. 1990). When focusing on plant species or plant functional groups in forest ecosystems, biotic interactions causing either competitive interference or facilitation become important for both nutrient availability and nutrient uptake efficiency. These interactions occur not only among plants but also between plants and microorganisms. Depending on the nature of the interactions, nutrient availability for and/or uptake efficiency of roots might increase or decrease (Rennenberg et al. 2009).

Both extremes of water availability, flooding and drought, affect the above- and belowground physiology of trees as well as soil properties. Besides negative effects on the water and carbon balance of trees and forests (e.g., Ciais et al. 2005), mineral nutrition will be another highly important factor influenced by extreme water conditions in the future.

Recent reviews assessing the effects of the predicted climate change have mainly concentrated on temperature effects on tree nutrition (Bassirirad 2000). Reviews taking into account excess water supply or drought have mainly focused on competition between microorganisms and tree roots for one particular element (Rennenberg et al. 2009) or on one particular species (Gessler et al. 2004, 2007a, b). With this review, we will give a more general picture and seek to explore differential effects of drought and waterlogging in forest ecosystems on nutrient availability as well as on the efficiency of roots to take up the nutrients from the soil. We will also include in our review the effects of biotic interaction with water stress—due to either drought or waterlogging—and will relate the acquisition of mineral nutrients of trees with stress-induced changes of the carbon balance.

Drought

Effects of drought on soil nutrient availability for plants

Even though it is more and more acknowledged that organic forms of nitrogen in soil and the rhizosphere play an important role in supplying trees with nitrogen especially in boreal and temperate ecosystems (Näsholm et al. 1998, 2009), the availability of inorganic nitrogen forms, i.e., nitrate and ammonium, is still assumed to be crucial (e.g., Lucash et al. 2007). Inorganic sulphate is the most important sulphur source to be taken up by plant roots from the soil (Herschbach 2003), and most of the other elements are available to plants mainly in inorganic mineral forms (Marschner 1995). Thus, any negative drought effect on the microbial mineralization activity—which will in turn influence the amount of the inorganic nutri-

ents available for plant uptake—has the potential to impair mineral N nutrition of trees. Even when we might assume that organic nutrients—i.e., mainly N in the form of amino acids—are taken up by tree roots, microbial depolymerization of proteins/peptides is still essential (Rennenberg et al. 2009).

Reduced soil water availability limits microbial activity in soils and, depending on the intensity and duration of the drought event, may lead to total inhibition of microbial metabolism (Borken and Matzner 2009). On the one hand, the diffusion of the organic substrates for microbe-driven mineralization or depolymerization becomes restricted (Schimel et al. 2007). On the other hand, the mobility of microorganisms in the soil as well as of the excreted exo-enzymes such as proteases decreases with increasing drought (van Meeteren et al. 2008). Also, intracellular processes of microbes are generally inhibited when water loss from the cells can no longer be avoided through countermeasures (e.g., increasing the osmotic potential). Drought events thus cause in a first step reduced bacterial activity accompanied by dehydration and, as drought prolongs, a dieback of soil microorganisms (Schimel et al. 2007). It is obvious that the decrease in microbial activity is related to the length and intensity of the drought period as well as to the adaptation potential of the microorganisms (Jensen et al. 2003). In general, the particular effects of drought on the process involved in mineralization and thus re-supply of inorganic nutrients are highly uncertain as the results in the existing literature are inconsistent. When taking nitrate and ammonium concentrations in soil solution as a proxy for plant or ecosystem N availability, Johnson et al. (2002) observed no effects of drought in a deciduous forest. Gessler et al. (2005) found even increased gross ammonification rates in summer on a drought-exposed beech site as compared with a cool-moist site. Beier et al. (2008) reported that carbon and nitrogen mineralization were affected differently by drought; whereas decomposition of organic carbon was mainly temperature sensitive, ammonification was only slightly dependent on temperature but strongly inhibited by reduced soil water availability. It has also been observed that the amount of dissolved organic nitrogen in the soil increases during drought events, presumably due to dieback of microbial biomass (Borken and Matzner 2009, Dannenmann et al. 2009). It has not been studied whether plants might benefit from this potential (organic) N source under drought conditions or whether diffusional limitations or other constraints prevent these compounds from being taken up. In conclusion, it is not clear to what extent drought events affect the re-supply of soil nutrients for plants by microorganisms. As a consequence, we need studies that systematically target gross and net nutrient mineralization fluxes in different forest ecosystems as affected by drought intensity and duration. It is also important in this context to assess the effects of drought on the spatial distribution of nutrients in the soil and relate this pattern to the foraging capacity of roots (i.e., the ability of roots to actively access soil regions with higher nutrient concentrations) as affected by reduced water availability. It is also important to differentiate between short- and long-term effects

of drought on nutrient availability in soils. Whereas occasional short summer drought periods and subsequent recovery times with sufficient rainfall might only lead to transient changes in soil nutrient conditions, severe longer term water restriction over years will most probably have more strong and lasting effects.

Impacts on uptake capacities of roots

Nutrient supply of trees is not only determined by the concentrations of nutrients in the soil and in soil solutions, which are strongly influenced by microbial activity, or by diffusion and mass flow of nutrients (Bassirirad 2000, Gessler et al. 2005). It also depends on the nutrient uptake kinetics of their (mycorrhizal) roots (Bassirirad et al. 1999). When global climate change effects on nutrient uptake kinetics of plants in terrestrial ecosystems are discussed, mainly increased temperature but not reduced water availability is focused on. This might be related to the experimental approaches used for characterizing the net uptake kinetics of intact roots (Lucash et al. 2007). In brief, roots from plants grown under field or controlled conditions are excavated from the soil—often without detaching them from the rest of the plant—and incubated in solutions containing the nutrients of interest (Gessler et al. 1998*a*, *b*). In order to determine the net uptake, either the depletion of nutrients in the solution or the enrichment of isotopically labelled elements in the roots is quantified (Gessler et al. 1998*a*, *b*, 2002, 2005). This approach requires roots to be removed from their surrounding soil with a given soil moisture and to be incubated in aqueous solutions where they might be re-hydrated quickly. However, other experimental approaches applied to characterize nutrient uptake by plants do not allow the distinction of the effect of reduced water availability on the different processes (i.e., diffusion and mass flow of nutrients vs uptake kinetics) involved in the nutrient nutrition of trees. Assessments of nutrient contents and concentrations in tree tissues (Peuke and Rennenberg 2004, Nahm et al. 2007, Sardans and Penuelas 2007, Sardans et al. 2008*a*) might allow the characterization of changes in mineral nutrient acquisition but do not give hints as to whether these changes are a consequence of altered nutrient availability or root uptake capacity or both.

The application of isotopically labelled nutrients (e.g., ^{15}N or ^{32}P; Zeller et al. 2000, Lehmann et al. 2001, Fotelli et al. 2004) or homologues such as Sr, which competes with Ca for common carriers (Fitter 1986), to the soil and the quantification of the accumulation of these traces in plant tissues have the same limitations as recently discussed in detail by Rennenberg et al. (2009).

Keeping in mind the limitations of the methods for assessing net nutrient uptakes from solutions, Gessler et al. (2005) observed effects of varying water availability on nitrate and ammonium uptake kinetics of non-excised intact mycorrhizal roots of adult beech trees. In detail, the maximum nitrate uptake rate but not the affinity of the transport system was strongly reduced in beech roots subjected to dry conditions

over the long term. Whether differences in mycorrhizal colonization in nitrate transporter abundance/activity and/or the expression of different nitrate transporters under drought are responsible for this reduction in nitrate uptake remains to be elucidated. There are several studies assessing the effect of drought on the expression level of (putative) ion transporters but mainly in herbaceous or grass species (e.g., Hu et al. 2006, Liu et al. 2006). Seki et al. (2007) observed several transporters including potassium transporters to be up-regulated under salt or drought stress in *Arabidopsis thaliana* L. (thale cress). In contrast, Ferrario-Mery et al. (1998) observed that drought stress reduced nitrate and amino acid concentration in tobacco leaves simultaneously with nitrate reductase activity. Salt stress is often seen and used in experiments as an analogue to drought stress (Bartels and Sunkar 2005). Transcriptome analyses revealed that NaCl exposure led to increased expression of Ca^{2+} and cation transporters in *A. thaliana* (Maathuis et al. 2003). It is, however, not clear whether this is a specific reaction towards the increased ion concentration and ion competition effects or an effect of water limitation by high salt concentrations. Dluzniewska et al. (2007) performed salt stress experiments with *Populus tremula×alba* (grey poplar) and observed a decrease in ammonium but not in nitrate net uptake and no change in the expression of the key enzymes of N assimilation.

To our knowledge, there are no studies combining transcriptomics, proteomics, metabolomics and nutrient uptake approaches to functionally assess the impact of drought on nutrient uptake and transport in trees. Against the background of the likely increase in duration and frequency of summer droughts in the future, we need research that is targeted at understanding of these mechanisms and processes.

An additional highly important factor that most likely influences the element uptake of trees and forest stands is not directly related to the physiology of transporters but to fine root dynamics. Low soil water availability and extended drought periods can strongly reduce the biomass of active fine roots (Mainiero and Kazda 2006, Cudlin et al. 2007, Konopka et al. 2007). As a consequence, the surface able to take up nutrients decreases. Since fine root turnover rates of trees can be >1.5 years (Ostonen et al. 2005), drought-induced fine root dieback might affect nutrient acquisition of trees over time periods much longer than the drought event itself.

Impacts of drought on the nutrient status of trees

Irrespective of whether changes in the availability of nutrients in the soil or in the characteristic of nutrient transporters in mycorrhizal tree roots are affected, drought causes in general an impairment of the nutrient content and concentrations in trees (Minoletti and Boerner 1994, Sardans et al. 2008*a*, 2008*b*). It has to be mentioned, however, that not all nutrients are affected in the same way. Sardans and Penuelas (2007) observed that a drought that lasted for 6 years caused an approximately one-third reduction in total stand biomass P content in *Quercus ilex* L. (holm oak). In contrast, no effect of

reduced water availability on K contents was detected. Peuke and Rennenberg (2004) observed that phosphorus and phosphate concentrations decreased in above- and belowground tissues in different European beech provenances after a 3-week drought treatment simulating a typical summer drought period. However, nitrogen and sulphur concentrations were not clearly affected in these experiments. In addition to nutrient-specific differences, different tree species show different stoichiometric plasticity in response to drought. Penuelas et al. (2008) compared the changes in element concentrations in response to reduced water availability for different woody Mediterranean species in order to define biogeochemical niches for different species in a multidimensional nutrient niche space. The authors observed that (i) nutrient/element stoichiometry is strongly different among co-existing species and that (ii) there is a species-specific plasticity concerning the total and relative nutrient content in response to drought. It was also observed that drought decreases nutrient content in aboveground biomass especially in the most drought-sensitive species, mainly through the decrease in growth and transpiration (Sardans et al. 2008b).

Studies focusing on drought effects on nitrogen nutrition of trees revealed that concentrations and compound profile of the soluble non-protein nitrogen compounds can be a sensitive indicator of short-term physiological responses, reflecting changes in their internal nitrogen status in much more detail than total N concentrations, which are constant over a wide range of climatic and nutritional conditions (Gessler et al. 2004). Moderately lower water availability caused reduced soluble nitrogen contents in various tissues of European beech and was assumed to indicate lower nitrogen uptake in summer and changes in nitrogen remobilization and storage patterns in spring and autumn, respectively (Nahm et al. 2006a, 2006b). However, an increase in the concentration of amino acids has also been observed in various tissues under reduced water availability (Fotelli et al. 2002). This was, however, due to the decomposition of proteins under severe drought as indicated by the simultaneous decrease in protein N content.

In conclusion, there is no straightforward picture of the effects of drought on tree nutritional status. In general, we observe an impairment of the nutrient contents and concentrations, but that might not hold true for all nutrients. As a consequence, we need more information on the combined effects of drought on the availability of and the plant uptake capacity for various elements. In addition, we need experiments assessing how changes in these parameters affect the whole tree nutritional status and growth. We also lack experiments that target the effects of dynamically changing drought conditions and assess the nutrient balance during repeated drought and recovery phases.

The interaction between carbon and mineral nutrient balance

Belowground nutrient acquisition of trees is influenced by multiple biotic interactions mainly among plant spe-

cies and between plants and microorganisms spanning from facilitation to competition. The effects of drought and drying–rewetting cycles on the direct competition among plant species and between plants and microorganisms related to nutrient acquisition/uptake have been reviewed recently (Rennenberg et al. 2009). However, much less is known about the effects of reduced water availability on the normally close coupling between assimilation in the canopy and all energy-demanding processes belowground in roots (including growth and nutrient uptake) and rhizosphere. Under severe drought stress, when the reduction in carbon assimilation in combination with direct adverse effects of water limitation on cellular functions restricts growth, changes in nutrient acquisition patterns might be secondary for plant performance. However, under short and/or moderate drought stress, the degree of coupling between assimilation and belowground processes might be central for the nutrition and, thus, for the growth of trees under water restriction.

The flux of recently assimilated carbon through trees and the transfer to soil microbiota have been assessed using manipulation experiments (e.g., girdling; Hogberg et al. 2001) by tracking the natural variation of stable isotope signatures through the different organic matter pools of a tree and to CO_2 emitted from plants and soil (e.g., Brandes et al. 2006, Gessler et al. 2007a, b, Kodama et al. 2008) and by the application of highly enriched isotope tracers in pulse labelling experiments (Hogberg et al. 2008).

The field-scale girdling experiment in boreal forests in Sweden (Hogberg et al. 2001) as well as trenching studies in Canada (Bond-Lamberty et al. 2004) have shown that the supply of new assimilates to tree roots is crucial for fuelling soil respiration. Cutting off this supply results in a rapid decline in belowground respiration within days to weeks. These experiments clearly show the close and immediate link between canopy assimilation on the one hand and heterotrophic energy gain and belowground metabolism of roots as well as of rhizosphere microorganisms on the other hand.

It is well known that drought reduces leaf- and canopy-level CO_2 assimilation by inducing stomatal closure and reducing carboxylation efficiency of Rubisco (Tezara et al. 1999, Flexas and Medrano 2002).

Beyond diffusional limitations to CO_2 or effects on Rubisco, not much information is available about the influence of the water balance on the carbon relations in trees (and the mechanisms behind it)—including the impacts of drought on phloem loading and transport, short-term partitioning and carbon storage—as well as on the transfer of carbon from trees to the soil microorganisms. Any change in the supply of assimilates to roots and microorganisms is, however, most likely to influence (i) energy-demanding nutrient uptake processes by roots and microorganisms, and (ii) fine root and mycorrhiza dynamics.

There are many published studies that examine assimilate transport as affected by water supply under controlled and field conditions. However, the majority of the papers

focus on herbs or grasses (e.g., Plaut and Reinhold 1965, Wardlaw 1969, Palta and Gregory 1997) and/or only on particular processes of carbon allocation such as leaf assimilate export (e.g., Deng et al. 1990, Li et al. 2003). To understand the impact of summer droughts, which will increase in intensity and duration in temperate regions in the future, on the carbon balance of ecosystems, we need clear-cut information on how tree water relations affect carbon flux and partitioning.

In a ^{13}C pulse labelling study with wheat, the assimilate transfer to roots and the recovery of ^{13}C in soil respiratory CO_2 were higher under drought conditions compared with controls 2 days after the label application (Palta and Gregory 1997). In contrast, lower transfer of recently assimilated carbon to soil and microorganisms was observed in shrublands (Gorissen et al. 2004) a few days after a ^{14}C pulse label application. The main shortcoming of these two studies is their lack of temporal resolution as achieved in the more recent studies by Hogberg et al. (2008) and Carbone et al. (2007), which, in turn, did not assess drought effects.

Only recently, Rühr et al. (2009) have investigated the effects of drought on the translocation of recently assimilated carbon by pulse labelling 1.5-year-old beech tree microcosms with $^{13}CO_2$. The ^{13}C tracer signals in different organic matter pools of trees and soil microbes as well as in soil-respired CO_2 were determined for up to 10 days with daily resolution. Drought not only reduced C assimilation but also doubled the residence time of recently assimilated C in leaves from 2.4 to 5 days.

In phloem organic matter, the ^{13}C label peaked immediately after labelling then decayed exponentially in the control treatment, while under drought maximum label recovery was observed 4 days after the pulse labelling (Figure 1). The label peaked in soil microbial biomass 1 day after labelling in the control treatment, whereas under drought no peak was measured in soil microbial biomass within the 10 days of observation. The study with beech seedlings showed that drought can reduce the coupling between canopy photosynthesis and belowground processes. It is likely that the reduced inputs of labile carbon to the soil under drought as observed in the study of Rühr et al. (2009) result in a shift of the soil microbial community towards increased decomposition of soil organic carbon (Bradford et al. 2008). The reduced carbon transfer to the roots is also likely to constrain the supply of energy and carbon skeletons for plant nutrient uptake and assimilation. However, we need experiments directly targeting the effects of changed carbon allocation belowground on the factors affecting pedospheric nutrient supply—i.e., on changes in the absorbing fine root area as well as on the nutrient uptake and assimilation capacity.

In an experimental tree girdling experiment performed with ~90-year-old beech trees, a reduction in carbon transfer from the canopy to belowground plant organs resulted in a reduction in rhizodeposition and soil microbial biomass, whereas the abundance of the main mycorrhizal fungus was not affected and N net uptake by mycorrhizal roots even increased (Dannenmann et al. 2009). As a consequence, the authors hypothesized that reduced belowground carbon supply altered the competitive balance of N partitioning in favour of the tree species and its most abundant mycorrhizal symbiont at the expense of heterotrophic N turnover by free-living microorganisms in the soil. In addition, switches among different microbial processes might have affected the balance between root and microbial uptake. Reduced availability of labile carbon in the soil is also known to change the balance of heterotrophic ammonium-consuming microbial processes in forest soils in favour of autotrophic nitrification and additionally inhibits microbial nitrate consumption (Booth et al. 2005, Dannenmann et al. 2006).

Dannenmann et al. (2009) concluded that drought periods have potentially the same effects on N acquisition by plants at the expense of free-living microorganisms as girdling, but there is no direct experimental proof for this assumption.

Besides effects of changed carbon availability on competition patterns, carbon supply might also affect the interactions between plants and plant-growth-promoting rhizosphere bacteria. These organisms are associated with plant roots, and not only do they augment plant productivity and immunity but also elicit a so-called 'induced systemic tolerance' to drought and improve nutrient uptake capacity of plant roots (Yang et al. 2009). Plants shape their rhizosphere microbial community by exuding organic compounds into the rhizosphere (el Zahar Haichar et al. 2008). Rhizobacteria respond to root exudates by means of chemotaxis towards the exudate source, and competent, beneficial bacteria tend to modulate their metabolism towards optimizing nutrient acquisition and drought tolerance (Dimkpa et al. 2009). However, at present, we do not know to what extent especially longer drought periods affect the interplay between mycorrhizal roots and this type of bacteria, i.e., whether reduced root exudation causes changes in the bacterial community structure, which might reduce beneficial effects for nutrient uptake, and whether the increase in drought tolerance mediated by rhizosphere bacteria is only transient or is also a long-term effect.

In conclusion, we need more information for field conditions on how drought events affect the carbon supply of the mycorrhizal roots and of microorganisms not only competing for nutrients with plants root but also involved in mineralization and thus nutrient re-supply of plants and in promoting root functions. Such research has to include assessments of the drought response of different tree species and should characterize the effects of the length and severity of a drought period on belowground C allocation combined with nutrient uptake and turnover approaches.

Excess water availability—waterlogging and flooding

Effects on nutrient availability

Strong rainfall events may lead to waterlogging if drainage is limited due to soil type or soil compaction. A surplus of water is the main environmental reason for oxygen deprivation in
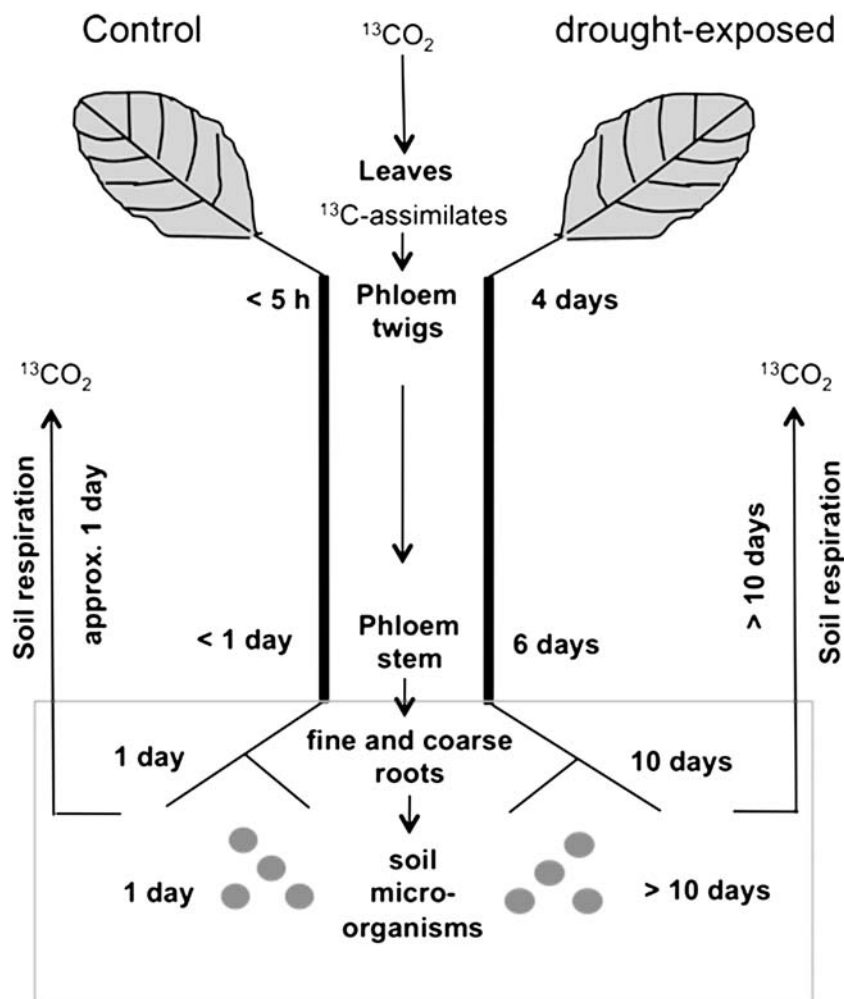
Figure 1. Carbon transport times in control and drought-treated beech seedlings. The times indicate the maximum (peak) occurrence of the ^{13}C label in either water-soluble organic matter or CO_2. The data are taken from Rühr et al. (2009).

the soil. At a steady consumption of oxygen in the soil by plant roots and microorganisms, the diffusion of oxygen into the soil is dramatically reduced due to a 10^5-fold higher diffusion resistance of oxygen in water than in air (Ponnamperuma 1984, Vartapetian and Jackson 1997). As soil oxygen concentrations are decisive for many pedospheric processes, nutrient availability is strongly influenced by waterlogging–drying cycles. The occurrence of regular periods of waterlogging has been extensively studied in floodplain ecosystems. In such areas, the flood water can carry a lot of nutrients into the ecosystem, thereby contributing to the high productivity of these forests (e.g., Beltman et al. 2007). On the other hand, soil physical and chemical properties are highly affected during a flooding event, which may lead to transient decreases or increases in individual nutrients. This is the result of flooding on the activity of microbial populations, which quickly respond to changes in oxygen availability and soil moisture. As an effect of waterlogging, often transient increases in phosphate concentrations are observed, which are due to bacterial transformations dependent on the altered soil redox status (Koerselman et al. 1993, Lamers et al. 1998, 2006). Together with such changes

in phosphate levels, often reduced levels of nitrate occur at the same time because of its loss by denitrification or its reduction to ammonium (Patrick and Reddy 1976, Laanbroek 1990, Baldwin and Mitchell 2000, Gusewell 2004, Alaoui-Sossé et al. 2005, Antheunisse and Verhoeven 2008). Concurrently, NO_3^- production by nitrification is inhibited because of the lack of oxygen (Haynes and Swift 1989, Pillips 1999). Other important nutrients affected in abundance by flooding are potassium and iron. Whereas iron concentrations may increase following soil inundation, potassium concentrations rather decrease most probably because of an exchange for other cations adsorbed onto soil particles (Antheunisse and Verhoeven 2008). A problem for plant performance during phases of waterlogging can be caused not only by the depletion of important nutrients but also by exposure to reduced minerals instead of oxidized ones. Reduction occurs consecutively according to a fixed sequence, with oxygen being the first compound to be reduced followed by nitrate, manganese (IV) oxide, ferric oxide, sulphate and carbon dioxide (Watanabe and Furusaka 1980, see Laanbroek et al. 1990). Submerged soils, therefore, have a low redox potential (Ponnamperuma

1984), and due to the transformations mentioned they are lacking nitrate and sulphate, but carbon dioxide, ammonium and sulphide are present in concentrations that might be problematic for the vitality of plants. Iron, manganese and phosphorus become soluble and are therefore more available to plants (Ponnamperuma 1984).

Tree nutritional status

The changes in nutrient availability and quality may have strong impacts on the performance of plants exposed to waterlogging. As a consequence of impacted soil fertility and because of decreased uptake capacities (see below), the nutrient status of plants may be affected. In leaves of highly flooding-sensitive cotton plants, reduced nitrogen, iron, potassium and phosphate contents but higher sodium concentrations were observed (Milroy et al. 2009), indicating an imbalance of ion uptake. On the other hand, the flooding-sensitive tree species *Eucalyptus grandis* and *Eucalyptus globulus* showed no or only very weakly changed concentrations of potassium and magnesium (but also higher levels of sodium and chloride) (Marcar et al. 2002). There is no clear correlation of the changes in nutrient content with the plant's flooding tolerance as many factors determine plant nutrient status. Comparing flooding-sensitive and flooding-tolerant oak species, Colin-Belgrand et al. (1990) found no waterlogging effects on the contents of potassium, phosphorus, calcium, magnesium and manganese but significantly lower nitrogen concentrations in flooding-tolerant *Quercus robur*, and the less tolerant *Quercus rubra* and *Quercus palustris*. Surprisingly, in the same study, *Q. robur* also showed lowered leaf sulphur concentrations, which were not observed in other oak species. The authors hypothesized that ongoing leaf growth of *Q. robur* led to sulphur depletion in this species, whereas the more sensitive species stopped growth during waterlogging periods and, therefore, did not develop any symptoms of sulphur deficiency (Colin-Belgrand et al. 1990). Consistent with this work, reduced sulphate concentrations in the roots of flooding-tolerant poplar trees were reported by Herschbach et al. (2005). Surprisingly, in the same study, increased levels of cysteine were found in roots and leaves. This phenomenon is most probably due to uptake of sulphide by the roots and incorporation into cysteine via the enzyme *O*-acetylserine (thiol) lyase (OASTL). Both OASTL activity and transcript abundance were strongly enhanced in waterlogged poplar roots.

The nitrogen status of plants is better reflected by the amino acid concentrations and composition than by total nitrogen content (Muller et al. 1996, Gessler et al. 1998*a*, *b*). The abundance of amino acids is often dramatically changed in waterlogged trees as compared with normally watered plants. Kreuzwieser et al. (2002) observed strongly decreased total amino acid concentrations in roots of flooding-sensitive *Fagus sylvatica* and moderately tolerant *Q. robur* trees, whereas it was unaffected in leaves. Accordingly, the abundance of many amino acids (e.g., serine, glycine, aspartate)

was lower in waterlogged roots than in normally watered controls, but the concentrations of individual amino acids [alanine, γ-aminobutyrate (GABA)] were higher. Such changes in amino acid abundance were found to strongly depend on the tree's flooding tolerance (Kreuzwieser et al. 2002). Nevertheless, depending on the duration and strength of the stress, the N status of flooding-tolerant species may also be affected. In a study with *Populus × canescens*, a tolerant tree species, many amino acids derived from pyruvate (e.g., alanine, leucine, valine) or intermediates of glycolysis (e.g., glycine, serine, tyrosine) accumulated during waterlogging. In contrast, decreased levels were observed for amino acids derived from tricarboxylic acid cycle intermediates (glutamine, glutamate, aspartate, asparagines) (Kreuzwieser et al. 2009). As in other tree species (Kreuzwieser et al. 2002, Jaeger et al. 2009), also in poplar the concentrations of alanine and GABA strongly increased as a consequence of waterlogging (Kreuzwieser et al. 2009). This pattern indicates the onset of the GABA shunt, a pathway considered a metabolic adaptation to cope with cellular oxygen deficiency (Crawford et al. 1994).

It is evident that adverse soil conditions together with impacted nutrient availability on the one hand and disturbed nutrient status of trees on the other will have consequences on the trees' biomass production. Growth of trees has often been demonstrated to be reduced due to soil oxygen depletion. Only highly adapted species do not (or only to a minor extent) suffer from waterlogging stress. This has been demonstrated in numerous studies with species from tropical (Parolin 2001, Mielke et al. 2005, Ferreira et al. 2007, de Oliveira and Joly 2010, Ferry et al. 2010) to temperate (Colin-Belgrand et al. 1990, Alaoui-Sossé et al. 2005, Parelle et al. 2006, Neatrour et al. 2007, Kreuzwieser et al. 2009) climates.

Impact on nutrient uptake and assimilation

As mentioned above, soil chemical properties quickly respond to a waterlogging event. Therefore, both nutrient availability and quality dynamically change with exposure to this stress; this requires a high degree of flexibility from the trees. Due to the complexity of real waterlogging scenarios, studies on nutrient uptake have been performed under defined conditions not considering dynamic changes in nutrient availability. Experiments taking into account much more realistic changing situations are strongly required in the future. There are only a few studies available that directly analyse nutrient uptake of trees as affected by waterlogging or flooding. In accordance with diminished nutrient concentrations in plant organs, these studies generally indicated that oxygen deficiency in the rhizosphere causes reduced nutrient uptake by the roots (Drew 1991, Vaast et al. 1998). A clear correlation of the inhibition of nitrate uptake, for example, with the plant's flooding tolerance was observed by Kreuzwieser et al. (2002). Reduced uptake of nutrients may have different reasons such as reduced availability of transporter proteins, repressed uptake capacity of an abundant transporter or energy limitation to maintain active transport processes. As oxy-
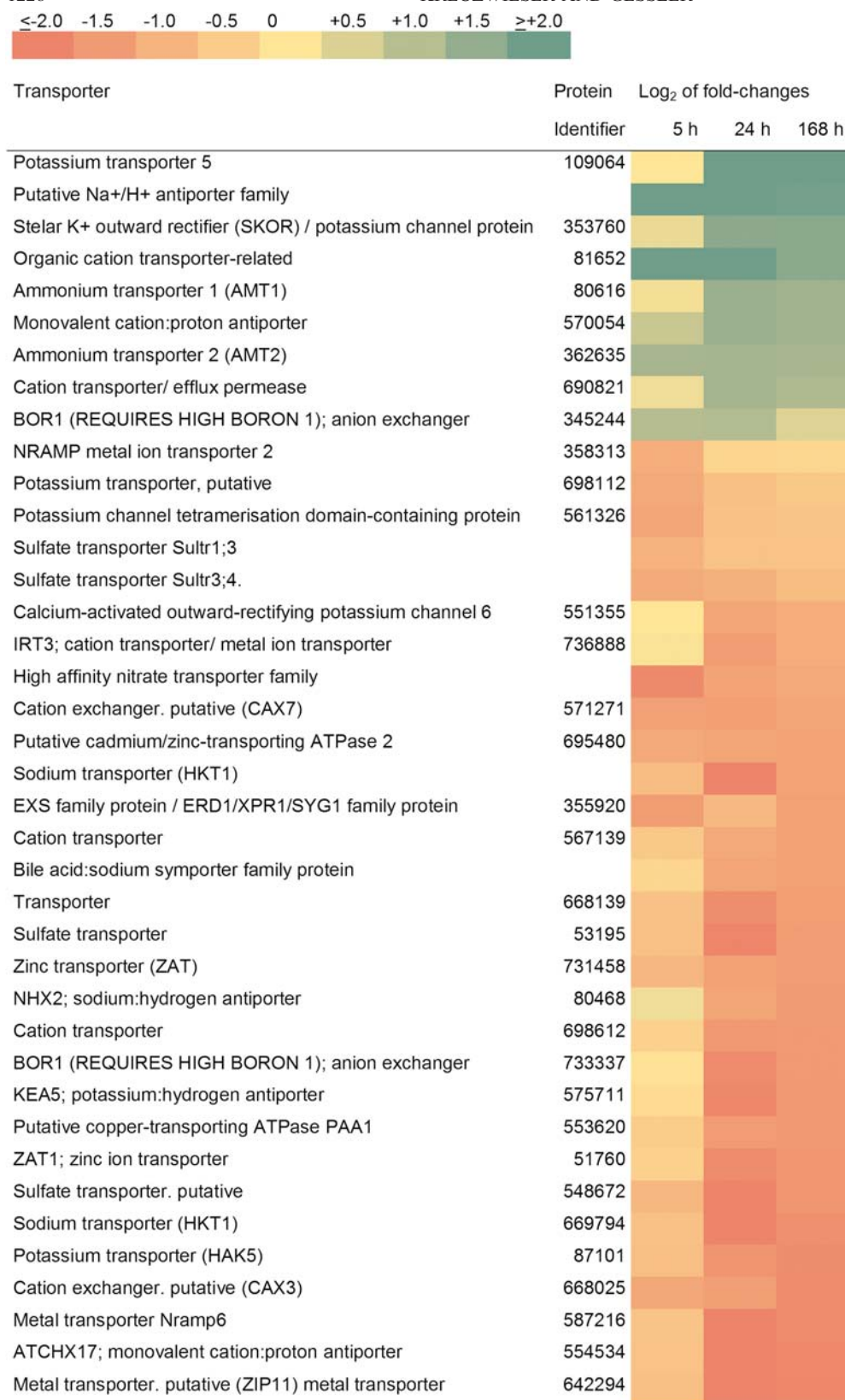
Figure 2. Effect of waterlogging on gene expression of assumed ion transporters in poplar roots. After 5, 24 and 168 h of waterlogging, roots were harvested and transcript levels determined by microarray analysis. The log_2 values of fold changes are displayed using the colour code indicated. Data are from Kreuzwieser et al. (2009).

gen deficiency dramatically impairs the energy metabolism of cells and plant organs, thereby causing an energy crisis for the tissues affected (reviewed by Bailey-Serres and Voesenek 2008), a lack of adenosine triphosphate (ATP) certainly is an important reason for the observed reduced uptake rates by waterlogged roots. Studies on different tree species clearly indicated that waterlogging causes slowed down assimilate translocation from shoots to the roots, thereby enhancing the situation of energy deficiency in the roots as the substrate for glycolysis becomes limiting (Kreuzwieser et al. 2004). As indicated by transcriptome analyses, it seems to be a main strategy of many waterlogged herbaceous (Klok et al. 2002, Geigenberger 2003, Liu et al. 2005, Loreti et al. 2005, Branco-Price et al. 2008) and woody (Kreuzwieser et al. 2009, Christianson et al. 2010) plants to slow down energy-consuming processes such as nutrient transport in order to cope with limited oxygen and therefore impaired ATP availability. These studies demonstrated that the expression of transporter genes seems to be down-regulated, indicating that reduced uptake rates are, in addition to limited energy supply, also caused by a lower protein abundance of transporter molecules. Although highly tolerant to oxygen deficiency, waterlogged $P. \times canescens$ trees showed significantly reduced transcript abundance of 42 assumed ion transporters (Figure 2; data from Kreuzwieser et al. 2009). Interestingly, two of the few exceptions with higher transcript abundance during waterlogging were ammonium transporters. If these transporters are involved in ammonium uptake, this pattern might reflect an adaptation of poplar to optimize nitrogen uptake as ammonium abundance increases in waterlogged soils (Alaoui-Sossé et al. 2005, Antheunisse and Verhoeven 2008). In good agreement with impacted nitrogen uptake in poplar roots, nitrogen assimilation seems to be affected by waterlogging (Kreuzwieser et al. 2009). This is suggested by the strongly down-regulated expression of the glutamine synthetase gene and the gene encoding a ferredoxin-dependent GOGAT isoform. However, a NADH-dependent GOGAT isoform was up-regulated; this enzyme is discussed to be important for re-assimilation of ammonium derived from degradation of proteins and other N-containing compounds (Aurisano et al. 1995, Mattana et al. 1996). As seen for nitrogen assimilation and consistent with reduced uptake, the assimilation of sulphate was strongly reduced in poplar roots. Herschbach et al. (2005) observed a complete disappearance of activity and transcript of adenosine 5-phosphosulphate (APS) reductase, the key enzyme of the sulphate assimilation pathway. Reduced transcript abundance of APS isoforms together with lower levels of ATP sulfurylase, cysteine synthase and methionine synthase transcript levels was also observed in poplar roots by Kreuzwieser et al. (2009).

Flooding and its effect on mycorrhizae

Plants benefit from the association with mycorrhizal fungi as both ectomycorrhizae and AM mycorrhizae improve plant water supply (Hardie 1985, Boyle and Hellenbrand 1991, Faber et al. 1991, Davies et al. 1993, Morte et al. 2001, Marjanovic et al. 2005) and influence nutrient uptake (Marschner 1994, Smith and Read 1997, Kreuzwieser and Rennenberg 1998, Kreuzwieser et al. 2000, Chalot et al. 2002, Allen and Shachar-Hill 2009). Moreover, the fungal sheath of ectomycorrhizae provides protection against pathogenic microorganisms (Branzanti et al. 1999). An important feature of tree performance, therefore, is the stability and vitality of mycorrhizal symbioses. The few studies on the effect of waterlogging on mycorrhizae surprisingly indicate that already existing mycorrhizal symbioses are relatively stable and can be maintained even during longer periods of oxygen deficiency. Even AM mycorrhizal colonization does not seem to be significantly disrupted during (short-term) waterlogging events (Sah et al. 2006). Consistently, Lodge (1989) observed AM colonization of *Populus* and *Salix* trees over a wide range of soil moisture including flooded soils. Other studies with AM mycorrhizae clearly showed that the trees profit from existing mycorrhizal systems as biomass production is increased and nutrient uptake clearly improved compared with trees without established mycorrhizae (Rutto et al. 2002, Muok and Ishii 2006). Rutto et al. (2002) therefore propose that AM infection confers limited tolerance to flooding. In contrast to AM mycorrhizae, ectomycorrhizae seem to react more sensitively to high soil moisture or flooding (Lodge 1989). The few existing studies indicate that this type of symbiosis is rare in waterlogged soils (Theodorou 1978, Lodge 1989) and that the vitality of ectomycorrhizal fungi drops as a consequence of waterlogging (Gadgil 1972, Bougher and Malajczuk 1990). Accordingly, Lodge (1989) observed that plants growing in periodically inundated areas almost exclusively formed endomycorrhizae, whereas the same species formed ectomycorrhizae when growing in better drained soils. Nevertheless, it was also reported that some fungal species (*Thelephora terrestris*, *Laccaria laccata*, *Hebeloma crustuliniformae*) developed mycorrhizae with *Pinus sylvestris* even during periods of flooding, whereas other species (*Suillus flavidus*, *Suillus bovines*) were highly sensitive (Stenström 1991). The aforementioned studies mainly focused on abundance and establishment of mycorrhizal symbiosis. However, more information on the performance of existing mycorrhizae under conditions of waterlogging, particularly regarding nutrient uptake, is still strongly needed.

Conclusion

Both reduced and excess water availability affect the mineral nutrition of trees in multiple ways. Not only does reduced availability of nutrients in dry or waterlogged soil impair the nutrient balance but also changes in the belowground carbon and thus energy balance play a central role as they drive the drought-mediated change in the nutrient uptake rate and capacity of roots as well as microbial activities (Figure 3). Drought, in general, decreases nutrient availability in the soil by restricting microbial activity and
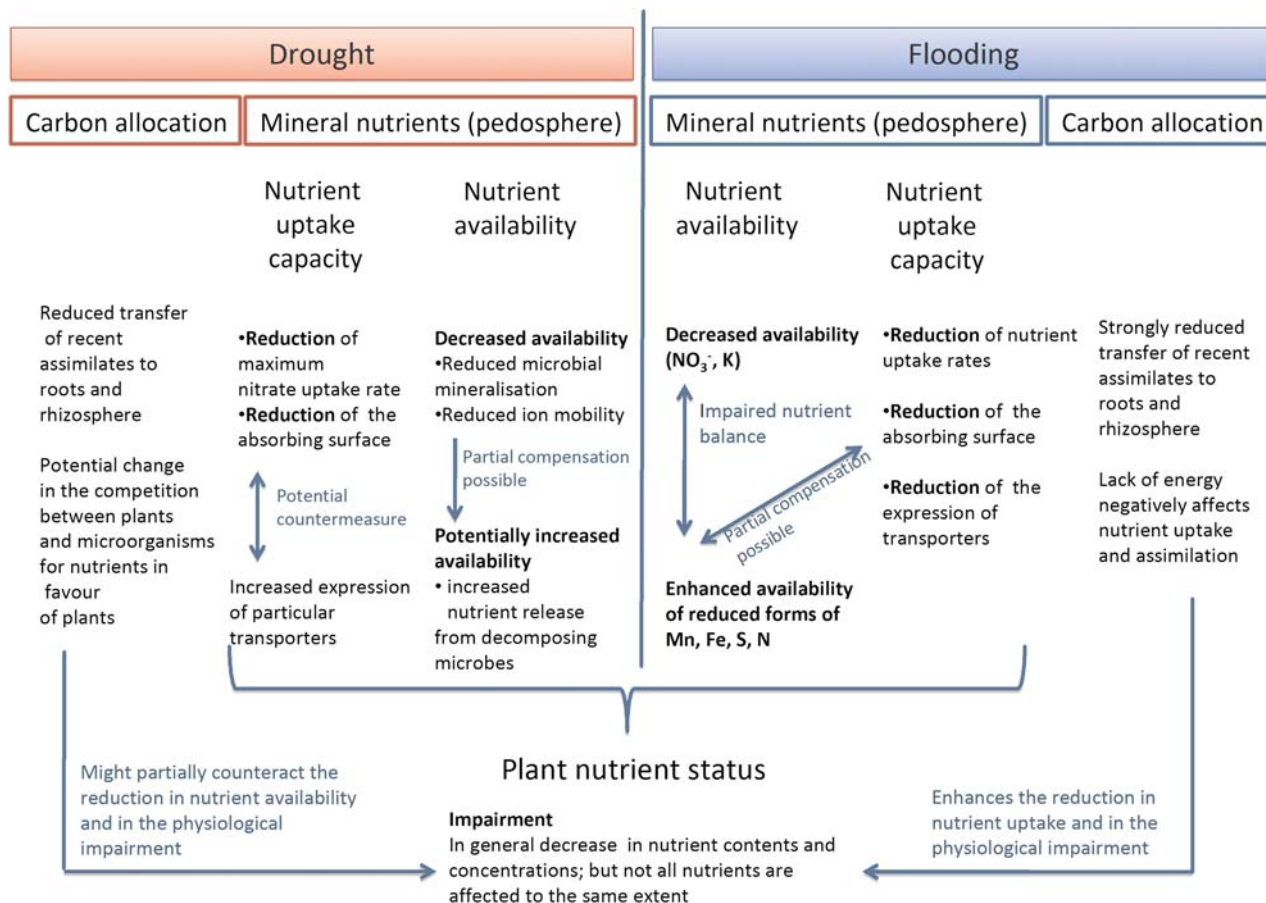
Figure 3. Effect of drought and excess water on tree nutrition. The main processes determining nutrient availability and uptake that are affected by changing water availability are summarized. This figure appears in color in the online version of *Tree Physiology*.

ion mobility. Whether the occasionally observed increase in nutrient release from decomposing microorganisms can compensate for the aforementioned effects remains to be elucidated. Drought also reduces the nutrient uptake capacity due to its effects on uptake rates and fine root biomass. On the one hand, the reduced transport of carbon to belowground tissues under drought might cause energy and carbon limitation and thus be one cause for the reduction in uptake rates and absorbing root surface. On the other hand, changes in the competition patterns between plants and microorganisms in favour of plants might partially counteract the reduced nutrient availability and the physiological impairment. The interplay between plant roots and microorganisms on the one hand and between carbon and mineral nutrient balance on the other is strongly affected by water availability and should thus be the central focus of future research assessing the effects of either drought or flooding and waterlogging on the nutrition of trees and forest ecosystems.

Acknowledgement

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