

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/311094181>

The role of nutrients in drought-induced tree mortality and recovery

Article in *New Phytologist* · November 2016

DOI: 10.1111/nph.14340

CITATIONS

70

READS

554

3 authors:



Arthur Gessler

Swiss Federal Institute for Forest, Snow and Landscape Research WSL

328 PUBLICATIONS 11,054 CITATIONS

[SEE PROFILE](#)



Marcus Schaub

Swiss Federal Institute for Forest, Snow and Landscape Research WSL

132 PUBLICATIONS 2,953 CITATIONS

[SEE PROFILE](#)



Nate McDowell

Pacific Northwest National Laboratory

213 PUBLICATIONS 16,232 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Climate and Insect Outbreaks [View project](#)



Bridging in Biodiversity Science (BIBS) - Novel ecosystems [View project](#)



Tansley insight

The role of nutrients in drought-induced tree mortality and recovery

Author for correspondence:
Arthur Gessler
Tel: +41 44 7392 818
Email: arthur.gessler@wsl.ch

Received: 9 June 2016
Accepted: 8 October 2016

Arthur Gessler¹, Marcus Schaub¹ and Nate G. McDowell²

¹Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland; ²Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM 87545, USA

Contents

| | | | |
|---------------------------------------------------------------------------------------------------------------------------|---|------------------|---|
| Summary | 1 | Acknowledgements | 6 |
| I. Introduction | 1 | References | 6 |
| II. Integrating nutrients into the hydraulic framework predicting mechanisms of drought survival, mortality, and recovery | 2 | | |
| III. Integration | 5 | | |

New Phytologist (2016)
doi: 10.1111/nph.14340

Key words: Birch effect, carbon starvation, feedbacks, hydraulic failure, nitrogen, predisposition, tree height.

Summary

Global forests are experiencing rising temperatures and more severe droughts, with consistently dire forecasts for negative future impacts. Current research on the physiological mechanisms underlying drought impacts is focused on the water- and carbon-associated mechanisms. The role of nutrients is notably missing from this research agenda. Here, we investigate what role, if any, forest nutrition plays for survival and recovery of forests during and after drought. High nutrient availability may play a detrimental role in drought survival due to preferential biomass allocation aboveground that (1) predispose plants to hydraulic constraints limiting photosynthesis and promoting hydraulic failure, (2) increases carbon costs during periods of carbon starvation, and (3) promote biotic attack due to low tissue carbon: nitrogen (C : N). When nutrient uptake occurs during drought, high nutrient availability can increase water use efficiency thus minimizing negative feedbacks between carbon and nutrient balance. Nutrients are released after drought ceases, which might promote faster recovery but the temporal dynamics of microbial immobilization and nutrient leaching have a significant impact on nutrient availability. We provide a framework for understanding nutrient impacts on drought survival that allows a more complete analysis of forest ecosystem responses.

I. Introduction

Research on the physiological mechanisms of drought-induced mortality has grown significantly in recent years as observations and simulations have increasingly pointed to the growing threat of climate change impacts on forests (reviewed recently in Allen *et al.*, 2015). The logical impacts of drought and warming on plant carbon (C) and water economies have driven research to focus almost exclusively on these factors, with additional emphasis on

insects and pathogens (McDowell, 2011; Hartmann *et al.*, 2013; Anderegg *et al.*, 2015 and many others). Our understanding of the mechanisms of drought-induced impairment of plant functioning and subsequent mortality, as well as tree and ecosystem recovery after mortality events, has grown enormously via this international-scale effort (Lloret *et al.*, 2012; Allen *et al.*, 2015; Box 1).

Plant growth and distribution has traditionally focused not only on the C and water cycle mechanisms, but also on the critical role of soil available nutrients (e.g. Oren *et al.*, 2001; Box 1). Nutrient

Box 1 Brief history of nutrient and drought research in forest ecosystems

Nutrients and growth Nutrients are major limiting factors for plant and forest productivity (Fisher *et al.*, 2012) even though water limitation might be of similar and growing importance (Craine *et al.*, 2012). Amongst the essential nutrients, nitrogen (N) plays a major role in limiting growth and productivity of forests (Vitousek & Howarth, 1991). Excessive anthropogenic N input into forests might, however, not only increase growth but also lead to nutrient imbalances and chronic damages (e.g. Schulze, 1989). N, together with sulfur (S) and phosphorus (P), also controls the shoot-to-root ratio, leading to relatively greater biomass allocation to roots when these nutrients are limiting (Marschner *et al.*, 1996).

Drought mortality Classic texts on the impact of climate on forest mortality originated from Manion (1981), Franklin *et al.* (1987) and Waring (1987), that were later put into physiological frameworks (Martínez-Vilalta *et al.*, 2002; McDowell *et al.*, 2008, 2011). According to these, drought forces plants to narrow their C and hydraulic safety margins to points where they may be at risk of physiological failure or failure to defend against biotic attacks (McDowell *et al.*, 2011). Evidence to date supports this framework, with most plants that die of drought experiencing a large degree of hydraulic failure (McDowell *et al.*, 2013; Anderegg *et al.*, 2015; Sperry & Love, 2015) and often but not always, a significant decline in carbohydrate stores (H. Adams *et al.*, unpublished). This hydraulic framework did not consider the impact of nutrient availability (the word 'nutrient' is not mentioned in McDowell *et al.*, 2008, 2011).

availability influences productivity of forests through photosynthetic, allocation, and stoichiometric effects (Sardans *et al.*, 2015). However, despite the strong legacy of research on forest nutrition and the rapidly growing literature on drought-induced mortality, there are few publications investigating the interaction between drought and plant nutrition (review by Gessler *et al.*, 2004) and the role of nutrients in drought survival and mortality (Royo & Knight, 2012; Wang *et al.*, 2012; Sargent *et al.*, 2014). In this paper, we argue that consideration of nutrients may give a more complete understanding of plant drought survival and post-drought growth. We review the potential role of nutrient availability before, during, and after drought on the likelihood of drought-induced mortality and survival, and on the ability of ecosystems to recover growth after drought-induced mortality events. In the following sections we are using terms high and low nutrient availability, but we acknowledge that nutrient availability occurs along a gradient from high to low.

II. Integrating nutrients into the hydraulic framework predicting mechanisms of drought survival, mortality, and recovery

The hydraulic framework for drought-induced mortality suggests that the risks of hydraulic failure and C starvation result from whole plant regulation of water use and C uptake and use during dry and warm periods (McDowell *et al.*, 2008). Nutrients can have direct impacts on both C and water uptake and use, but integration of

nutrients into this framework has not been attempted (Box 1). Conditions of high (or low) nutrient availability can each have positive and negative impacts on the likelihood of forest survival during drought (e.g. Arquero *et al.*, 2006; Coomes *et al.*, 2007; Dzikdek *et al.*, 2016). The legacy of high vs low nutrient supply on the long-term, that is, before the direct impact of a drought event, will affect the predisposition of plants to drought. Large nutrient reserves can promote a plant's ability to recover from stresses (Waring, 1987), whilst the increase in shoot-to-root ratios and change of other plant traits under high nutrient supply could increase susceptibility to drought (Ewers *et al.*, 2000). During a drought event, the reduction of soil nutrient availability can promote impairment of the plant's nutritional status and thus of its general functioning and resistance (Kreuzwieser & Gessler, 2010). After drought, the ability of plants to restore nutrient uptake and allocation influences re-establishment of physiological functions and hence long-term resilience.

The role of nutrient availability before drought

Nutrient availability before drought has both positive and negative impacts on survival (Fig. 1a). Elevated nutrient availability can lower ratios of root area to leaf area ($A_r : A_l$) (e.g. Kozłowski & Pallardy, 2002), increase stomatal conductance (Fangmeier *et al.*, 1994), increase height growth (Wright *et al.*, 2011), widen vessel diameters (Hacke *et al.*, 2010), and reduce extramatrix mycelium/rhizomorphs (Wallander & Nylund, 1992). These shifts in plant hydraulic traits likely decrease the hydraulic safety margin of trees and promote hydraulic failure under drought. For example, Coomes *et al.* (2007) showed that conduit diameter and tree height were reduced at nutrient poor (and frost affected) sites leading to reduced cavitation risks. In addition, higher biomass accumulation under high nutrient supply increases the C costs during periods of C starvation if not compensated by higher C storage. Simultaneously, elevated nutrient availability causes lower carbon : nitrogen (C : N) ratios, thus increasing palatability to biotic agents (McDowell *et al.*, 2011). We emphasise that these nutrient-dependent predisposing traits may only develop when water availability is not the main growth limiting factor over the longer term. Under drought, different nutrient addition treatments may not affect biomass production and allocation (Wu *et al.*, 2008). This suggests that relatively mesic sites are most affected by nutrient interactions when they experience severe drought periods.

In contrast to the ways elevated nutrient availability before drought could promote mortality, there are also mechanisms by which it may promote survival, thus the balance of these processes must be resolved to predict the role of nutrients in drought-induced mortality and recovery. Elevated nutrient availability can also reduce vulnerability to embolism by decreasing stomatal conductance (Goldstein *et al.*, 2013) and increase production of N-based defense compounds (Coviella *et al.*, 2002). Growth is frequently correlated with survival (Bigler *et al.*, 2006) and nutrient availability promotes growth. In fact, Demchik & Sharpe (2000) showed that reduced growth as well as drought-induced mortality were associated with nutrient deficiency in *Quercus rubra*. However, negative correlations between growth and mortality have also been

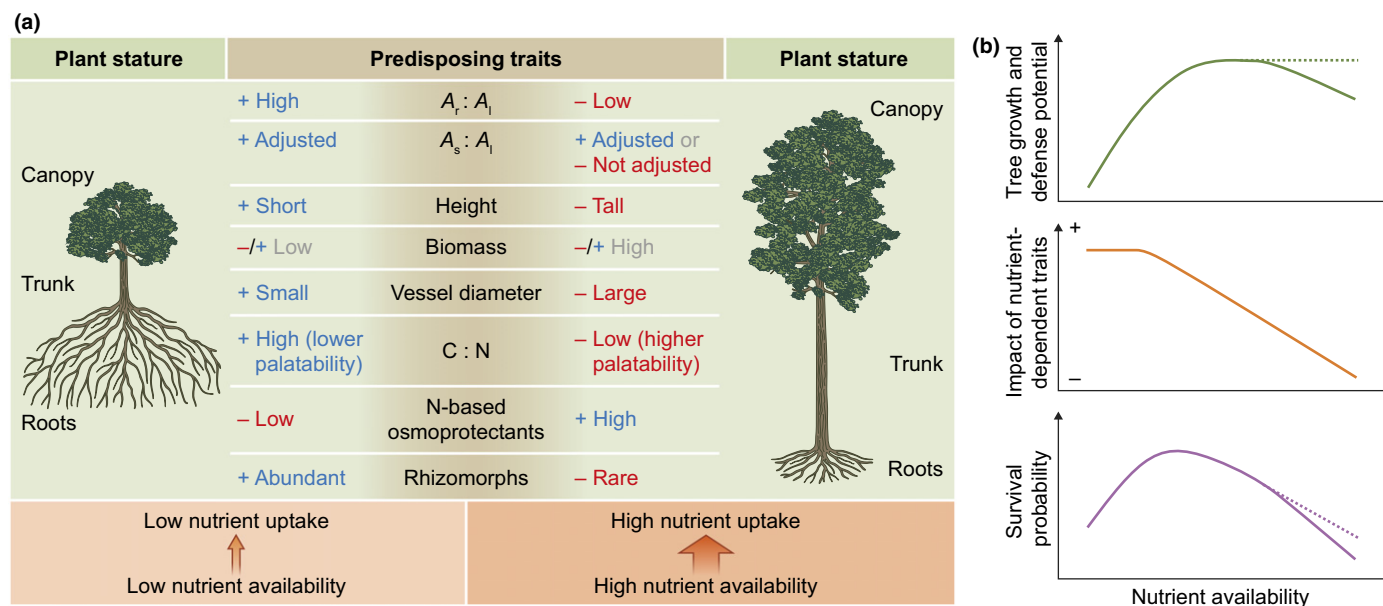


Fig. 1 Impact of long-term nutrient availability and uptake on predisposition attributes and drought survival probability. (a) High and low nutrient availability affect different anatomical and physiological traits over the long-term with positive (+ blue) and negative (– red) effects on plant survival during a drought event. (b) Relationships between nutrient availability and general plant growth and defense potential, formation of nutrient dependent traits with positive or negative effects on drought survival and the resulting survival probability. The x-axis represents a gradient of long-term nutrient availability across different sites. The top graph indicates that under low nutrient supply, an initial increase in nutrient availability may increase general tree growth and defense potential until a particular threshold is reached where nutrient imbalances might occur (e.g. Schulze, 1989). It is also possible that trees are not suffering from such imbalances and this alternative trajectory is given as dotted line. With increasing nutrient availability, the negative impact of nutrient dependent traits (see a) on drought survival increases (middle graph). The combined effect of both, determine the drought survival probability as depending on nutrient availability and predisposing traits (bottom graph). $A_s : A_l$, ratio of sapwood area to leaf area; $A_r : A_l$, ratio of root area to leaf area.

observed (Hentschel *et al.*, 2014), that is, individuals that grew best under high water supply were subjected to dieback as a consequence of drought. N-deposition within a particular range is known to promote tree growth (Högberg *et al.*, 2006) but conversely is also argued to have negative effects on forest trees by increasing water demand, reducing frost hardiness and increasing the risk to attract pests and diseases (Fangmeier *et al.*, 1994). However, it is unclear if atmospheric N-input promotes or mitigates drought-induced mortality (Dietze & Moorcroft, 2011) and the threshold at which excess nutrients could trigger mortality events (Magill *et al.*, 2004). There is experimental evidence that high N supply increases drought sensitivity of European beech mainly due to reduced root biomass (Dziedek *et al.*, 2016). Based on both theoretical considerations on the effect of nutrients on tree traits and direct observations, we conclude that an optimum balance of nutrient supply can support defense, thus decreasing the plant's mortality risk during a drought event (Fig. 1b). Very low nutrient availability and thus the lack of nutrient reserves impairs the plant's ability to sustain drought stress. Potassium deficiency for example is known to have detrimental effects on growth and survival under drought (Arquero *et al.*, 2006; Sardans & Peñuelas, 2015). However, when a nutrient threshold is exceeded, higher nutrient availability predisposes plants to drought-induced mortality due to morphological and physiological traits that are adaptive towards high nutrient supply but maladaptive for drought survival. Future research will need to define the optimal nutrient supply and stoichiometry, which allows optimum growth under 'normal' nonwater limited conditions and survival during drought events.

The role of nutrient availability and uptake on survival during drought

Direct and indirect effects of nutrient availability during drought have impacts on survival that are distinct from nutrient availability before drought. Fig. 2 provides a conceptual model of the direct (reduction of N availability and uptake) and indirect effects (effects conveyed via a reduction of stomatal conductance and assimilation, and various feedback loops) of drought on the balance of N – as the most important limiting nutrient – in plants. In contrast to the impact of the predrought long-term nutritional status on drought survival, abundant evidence suggests that low nutrient availability during drought should promote negative impacts on plant survival. This is because most processes that are negatively impacted by low nutrient uptake will also negatively impact plant survival (Fig. 2). Actual tree N uptake during one growing season makes up c. 10% of the total plant N stock in adult trees (Rennenberg & Dannenmann, 2015). Temperate trees use N storage reserves mainly for spring growth, but rely on root uptake during the rest of the growing season (Millard & Proe, 1992). Thus any restriction of soil N uptake during drought in summer, when drought periods most likely occur, is critical. One exception is the rise in tissue C : N ratio (leading to reduced palatability for biotic agents), which may reduce the risk of biotic attack but that effect might also be counteracted by a decrease in the content of N containing defense compounds.

The role of nutrient impacts during drought starts with the limited availability of nutrients to plants and their crowns when soils are dry due to the reduced ion mobility and limited microbial

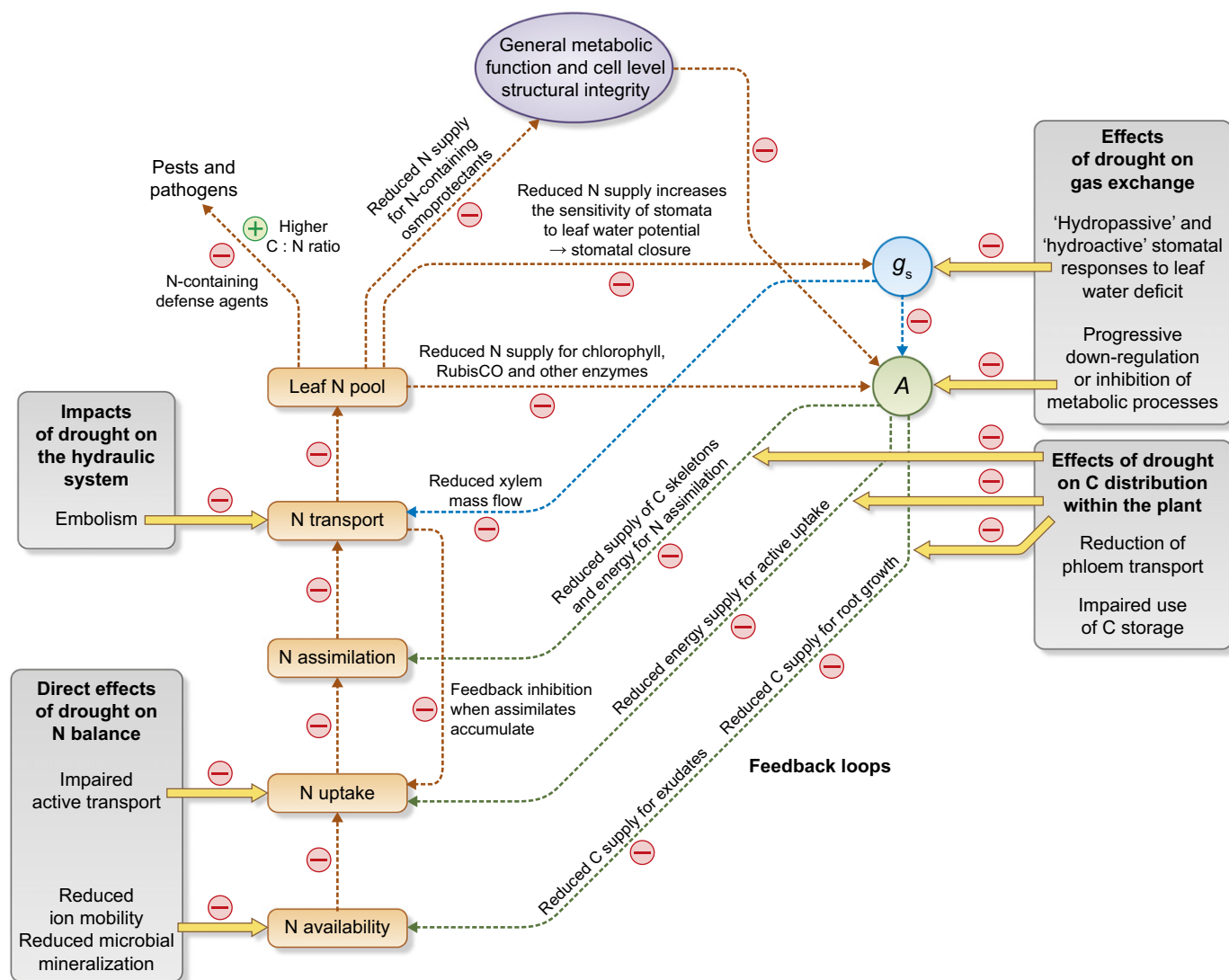


Fig. 2 Impacts of drought on the nitrogen (N) balance of plants during a drought event. Drought has mainly a direct effect on the nutrient availability in the soil by reducing the mobility of ions and the supply of inorganic N from microbial processes (grey panel on the left side, yellow arrows). The reduced availability further affects the plant internal N relations (light brown middle panel: N-uptake, N-assimilation, N-transport). Drought also affects stomatal conductance (g_s) and assimilation (A) (grey panel on the right side, yellow arrows) leading to lower transpiration and xylem mass flow on the one hand and to a reduced amount of new assimilates on the other hand with negative feedbacks on N-uptake, -transport and -availability. Reduced tissue N-contents also affect stomatal conductance and assimilation and thus various feedbacks link water-, carbon- (C) and nutrient-balance with potentially self-enhancing interactions. In addition, tissue N-availability affects resistance against pests and pathogens. Red minus signs indicate negative impacts and black plus signs indicate positive impacts on pools, fluxes, processes, and finally survival. Yellow arrows with black borders indicate direct drought effects on the N-, C- and water-balance; orange, blue and green arrows indicate plant internal effects driven by N-, water- and C-relations, respectively.

activity (Fig. 2; Kreuzwieser & Gessler, 2010; but see Cregger *et al.*, 2014). Impaired N uptake as well as decreases in tissue nutrients have been observed in drought-susceptible plants during droughts (Fotelli *et al.*, 2002).

Reduced transpiration (Gessler *et al.*, 2002) and drought-induced damage of membrane integrity reduce N-uptake rates, N-assimilation and consequently N-transport to the canopy. Reduced leaf N can intensify drought effects on photosynthesis and thus have potential impacts on C starvation (and its interdependence with hydraulic failure, McDowell *et al.*, 2011). Reduced N-supply increases stomatal sensitivity towards drought thus resulting in earlier stomatal closure (Ghashghaie & Saugier, 1989), triggers

protein degradation in leaves (Fotelli *et al.*, 2002) thus increasing repair costs and exacerbating C starvation (McDowell *et al.*, 2008) and decreases the content of N-containing osmoprotectants such as proline, which have positive effects on enzyme and membrane integrity (Ashraf & Foolad, 2007). Thus drought-induced N limitation can amplify C starvation, which can negatively feedback on hydraulic repair (McDowell *et al.*, 2011) and on N balance (Fig. 2a) due to the close integration between C and N metabolism. By contrast, reduced stomatal conductance under N limitation might reduce the risk of hydraulic failure. Reduced availability of recent assimilates as energy sources and C skeletons further impairs N-uptake and -assimilation under drought (Gessler *et al.*, 2005).

There are more complex interactions between the nutrients, C and the hydraulic system under drought (Fig. 2): drought is not only known to reduce C uptake but also assimilate transport and the remobilization of stored C (Sala *et al.*, 2010; Hartmann *et al.*, 2013). A shortage of C decreases N uptake and assimilation and also reduces the availability of sugars for xylem embolism repair (Zwieniecki & Holbrook, 2009). Drought induced embolisms further aggravate the reduction of N flow to the canopy and reduce the water circulation between xylem and phloem thus further impairing phloem transport.

The importance of interactions between the nutrient- and C-balance (and hydraulics) during drought depends on the duration and intensity of water restriction. This is partially because drought intensity modifies plant allocation to root growth and exudation. While long and severe drought will strongly retard C-allocation to roots and exudation, moderate drought can stimulate assimilate transport to roots and the rhizosphere belowground (e.g. Badri & Vivanco, 2009; Hommel *et al.*, 2016).

Owing to the fact that drought does not affect the uptake and transport of all nutrients to the same extent (Kreuzwieser & Gessler, 2010) and due to drought-induced changes in metabolic pathways and in growth rate capacities (Sardans & Peñuelas, 2013), restricted water supply also can cause changes in the element stoichiometry in plants. Across Europe, an especially strong P-deficiency in trees was observed (Jonard *et al.*, 2014) and higher drought frequencies might have driven the observed nutrient imbalances. Nutrient imbalances lead to impairment of physiological functions and to a reduction of growth (Schulze, 1989) and most likely add an important factor to C- and hydraulic-related mechanisms of plant mortality.

We predict that the reduced nutrient availability during drought negatively feeds back on the C balance (e.g. by reducing N supply for the photosynthetic apparatus, Heckathorn *et al.*, 1997) and on tree hydraulics (e.g. by impairing osmotic adjustment, Egilla *et al.*, 2005), intensifying hydraulic failure or C starvation.

The interaction of nutrient availability and drought on post-drought recovery

The trajectory of postdrought ecosystem recovery is influenced not only by the ability of plants to utilize resources during drought, but also their ability to capitalize on soil rewetting. Nutrient uptake is required for regrowth of tissues lost during drought (e.g. roots, stems, foliage) and for rebalancing nutrient stoichiometry. The key issue post-drought is then, can plants obtain available nutrients? There are postdrought shifts in both soil release and immobilization of nutrients as well as changes in plants' ability to acquire those nutrients after drought that interact to affect the nutrient uptake.

Soil rewetting after drought causes a burst of decomposition and N- and C-mineralization (Birch, 1964), thus resulting in an ephemeral increase in the nutrient availability for single trees and the whole stand. The transient nature of this 'Birch effect' and competition for nutrient acquisition with soil microbes as well as nutrient loss by leaching requires plant roots to rapidly exploit the nutrient resources after the drought release.

With a focus on the individual tree, the competition between roots and microorganisms for the nutrient pulse after rewetting is

crucial and depends on the ability of both to recover after the drought. For microorganisms, it is assumed that drying–rewetting cycles destroy microbial cells and therefore rewetting events provide plants a competitive opportunity as their roots, which are known to reestablish their functioning within hours (Volkman *et al.*, 2016), compete with a decreased microbial population and additional nutrients become available due to microbial cell lysis (Hodge *et al.*, 2000). The reestablishment of root functions will, however, depend on the intensity and duration of drought and thus the extent of root damage and mortality.

On the ecosystem level, drying–rewetting events decreased N-losses from a Norway spruce forest (Muhr *et al.*, 2010); however, more intensive rainfall events can also induce N loss by denitrification (Dick *et al.*, 2001). The intensity of the N-mineralization pulse depends on the general N-availability of the ecosystems, that is, high N stocks in soil organic matter increase the magnitude of N release after drought (Jarvis *et al.*, 2007). The cumulative N-mineralization upon rewetting is small compared with soil at optimum moisture, however, indicating that wetting pulses cannot compensate for reduced mineralization rates during drought periods (Borken & Matzner, 2009).

Partial mortality of a community of plants also alters nutrient supply of the surviving plants. It is, however, not clear whether the nutrients remain in the system and increase the supply for the remaining plants or if intensive leaching occurs (Xiong *et al.*, 2011) thus reducing the total nutrient stock of the system. There are indications that mortality in a stand may increase resource availability for the remaining plants, thus promoting growth of surviving plants after drought (Lloret *et al.*, 2012). To substantiate this assumption, the whole N cycle including N stocks and fluxes before and after dieback events needs to be quantified.

In summary, the mineralization pulse after drought release might supply surviving plants with additional nutrient resources and we postulate that sites with high nutrient stocks provide better conditions for tree recovery (e.g. Sergent *et al.*, 2014). We also suspect that the reduced availability and uptake during drought cannot be fully compensated afterwards and that nutrient losses might occur; if nutrients are limiting at a given site, a long-term, nutrient-driven growth reduction is thus to be expected. How such long-term changes in nutrient supply will affect the susceptibility of plants to pests and pathogens and needs also further attention.

III. Integration

High soil nutrient availability most likely pre-disposes plants to be more vulnerable to hydraulic failure when subjected to drought (Fig. 1) (and they would only become C-starved when the drought is both intense and long) as the traits developed in response to high nutrient availability implicate higher embolism risk due to imbalance in hydraulic supply and demand. Lower long-term nutrient availability restricts growth in height and leaf area thus minimizing plants proximity to the point of catastrophic hydraulic dysfunction, providing a broader safety margin (Choat *et al.*, 2012). Plants growing in stands with low nutrient availability might, however, be susceptible to long-lasting low intensity water stress even

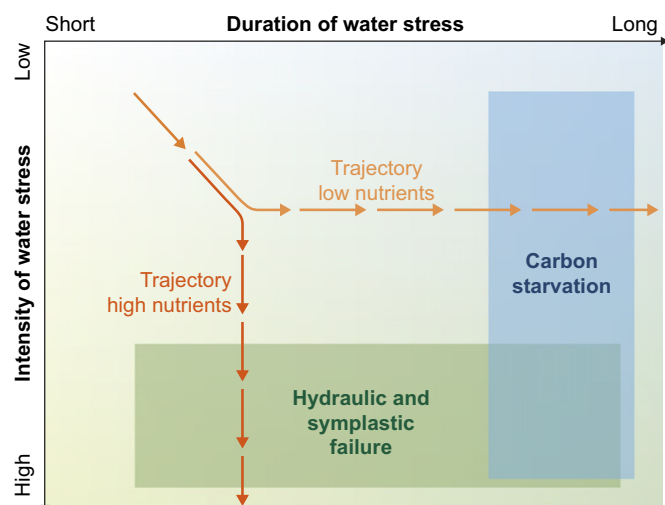


Fig. 3 Integration of nutrients into the carbon (C) starvation–hydraulic failure concept. Theoretical relationships according to McDowell *et al.* (2008) based on the hydraulic framework, between the temporal length of drought (duration), the relative decrease in water availability (intensity), and the hypothesized mechanisms (C starvation and hydraulic failure) underlying mortality. The arrows indicate likely trajectories of plants growing under high and low nutrient supply.

when the drought is not very intense if it is of sufficient duration. This is because in contrast to plants growing under high nutrient supply, they do not store considerable amounts of nutrients and will be more strongly affected by decreased nutrient availability during a drought event. We postulate that the reduced nutrient availability under drought (at least for lower intensity droughts) scales with the initial pre-drought availability aggravating any existing nutrient limitation. The close interrelation between N- and C-balance most likely increases the risk of drought-induced mortality under low nutrient supply (Fig. 2). High availability of nutrients during drought can have the opposite effect by increasing water use efficiency, effectively lowering the risk of C starvation, if nutrient uptake occurs during drought. When linking this nutrient availability concept with the framework of hydraulic failure and C starvation as developed by McDowell *et al.* (2008), high nutrient availability favors the trajectory to hydraulic failure under intensive water stress (Fig. 3) mainly due to the predisposition of the plant (Fig. 1). Low nutrient supply favors C starvation under long-term water stress (Fig. 3), mainly due to the effects of low nutrient availability and uptake on C metabolism during drought (Fig. 2). These trajectories can be additionally modified by biotic agents, that might be attracted by high nutrient concentrations in plant tissues (high nutrient trajectory) but also by lower allocation of N and C to defense compounds (low nutrient trajectory). Depending on the interaction of all these different factors the co-occurrence of C starvation and hydraulic failure (region of overlap between the two mechanisms in Fig. 3) as observed in previous studies (e.g. Sevanto *et al.*, 2014) might also occur. Plants are able to capture the nutrient pulses after the release of drought but for plants growing at sites with generally low

nutrient availability, this might not compensate the negative effects of drought on mineral nutrition.

Acknowledgements

A.G. acknowledges support from the SNF (31003A_159866). N.G.M. was supported by DOE's Office of Science and a WSL fellowship.

References

- Allen CD, Breshears DD, McDowell NG. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6: 129.
- Anderegg WRL, Flint A, C-y Huang, Flint L, Berry JA, Davis FW, Sperry JS, Field CB. 2015. Tree mortality predicted from drought-induced vascular damage. *Nature Geoscience* 8: 367–371.
- Arquero O, Barranco D, Benlloch M. 2006. Potassium starvation increases stomatal conductance in olive trees. *HortScience* 41: 433–436.
- Ashraf M, Foolad MR. 2007. Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and Experimental Botany* 59: 206–216.
- Badri DV, Vivanco JM. 2009. Regulation and function of root exudates. *Plant, Cell & Environment* 32: 666–681.
- Bigler C, Bräker OU, Bugmann H, Dobbertin M, Rigling A. 2006. Drought as an Inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems* 9: 330–343.
- Birch HF. 1964. Mineralisation of plant nitrogen following alternate wet and dry conditions. *Plant and Soil* 20: 43–49.
- Borken W, Matzner E. 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology* 15: 808–824.
- Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG *et al.* 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491: 752–755.
- Coomes DA, Jenkins KL, Cole LES. 2007. Scaling of tree vascular transport systems along gradients of nutrient supply and altitude. *Biology Letters* 3: 87–90.
- Coviella CE, Stipanovic RD, Trumble JT. 2002. Plant allocation to defensive compounds: interactions between elevated CO₂ and nitrogen in transgenic cotton plants. *Journal of Experimental Botany* 53: 323–331.
- Craine JM, Engelbrecht BMJ, Lusk CH, McDowell NG, Poorter H. 2012. Resource limitation, tolerance, and the future of ecological plant classification. *Frontiers in Plant Science* 3: 246.
- Cregger MA, McDowell NG, Pangle RE, Pockman WT, Classen AT. 2014. The impact of precipitation change on nitrogen cycling in a semi-arid ecosystem. *Functional Ecology* 28: 1534–1544.
- Demchik MC, Sharpe WE. 2000. The effect of soil nutrition, soil acidity and drought on northern red oak (*Quercus rubra* L.) growth and nutrition on Pennsylvania sites with high and low red oak mortality. *Forest Ecology and Management* 136: 199–207.
- Dick J, Skiba U, Wilson J. 2001. The effect of rainfall on NO and N₂O emissions from Ugandan agroforest soils. *Phyton* 41: 73–80.
- Dietze MC, Moorcroft PR. 2011. Tree mortality in the eastern and central United States: patterns and drivers. *Global Change Biology* 17: 3312–3326.
- Dziedek C, von Oheimb G, Calvo L, Fichtner A, Kriebitzsch WU, Marcos E, Pitz WT, Hardtle W. 2016. Does excess nitrogen supply increase the drought sensitivity of European beech (*Fagus sylvatica* L.) seedlings? *Plant Ecology* 217: 393–405.
- Egilla JN, Davies FT, Boutton TW. 2005. Drought stress influences leaf water content, photosynthesis, and water-use efficiency of *Hibiscus rosa-sinensis* at three potassium concentrations. *Photosynthetica* 43: 135–140.
- Ewers BE, Oren R, Sperry JS. 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. *Plant, Cell & Environment* 23: 1055–1066.
- Fangmeier A, Hadwiger-Fangmeier A, Van der Eerden L, Jäger H-J. 1994. Effects of atmospheric ammonia on vegetation – a review. *Environmental Pollution* 86: 43–82.

- Fisher JB, Badgley G, Blyth E. 2012. Global nutrient limitation in terrestrial vegetation. *Global Biogeochemical Cycles* 26: GB3007.
- Fotelli M, Rennenberg H, Gessler A. 2002. Effects of drought on the competitive interference of an early successional species (*Rubus fruticosus*) on *Fagus sylvatica* L. seedlings: ^{15}N uptake and partitioning, responses of amino acids and other N compounds. *Plant Biology* 4: 311–320.
- Franklin JF, Shugart HH, Harmon ME. 1987. Tree death as an ecological process. *BioScience* 37: 550–556.
- Gessler A, Jung K, Gasche R, Papen H, Heidenfelder A, Borner E, Metzler B, Augustin S, Hildebrand E, Rennenberg H. 2005. Climate and forest management influence nitrogen balance of European beech forests: microbial N transformations and inorganic N net uptake capacity of mycorrhizal roots. *European Journal of Forest Research* 124: 95–111.
- Gessler A, Keitel C, Nahr M, Rennenberg H. 2004. Water shortage affects the water and nitrogen balance in central European beech forests. *Plant Biology* 6: 289–298.
- Gessler A, Kreuzwieser J, Dopatka T, Rennenberg H. 2002. Diurnal courses of ammonium net uptake by the roots of adult beech (*Fagus sylvatica*) and spruce (*Picea abies*) trees. *Plant and Soil* 240: 23–32.
- Ghashghaie J, Saugier B. 1989. Effects of nitrogen deficiency on leaf photosynthetic response of tall fescue to water deficit. *Plant, Cell & Environment* 12: 261–271.
- Goldstein G, Bucci SJ, Scholz FG. 2013. Why do trees adjust water relations and hydraulic architecture in response to nutrient availability? *Tree Physiology* 33: 238–240.
- Hacke UG, Plavcová L, Almeida-Rodriguez A, King-Jones S, Zhou W, Cooke JEK. 2010. Influence of nitrogen fertilization on xylem traits and aquaporin expression in stems of hybrid poplar. *Tree Physiology* 30: 1016–1025.
- Hartmann H, Ziegler W, Kolle O, Trumbore S. 2013. Thirst beats hunger – declining hydration during drought prevents carbon starvation in Norway spruce saplings. *New Phytologist* 200: 340–349.
- Heckathorn SA, DeLucia EH, Zielinski RE. 1997. The contribution of drought-related decreases in foliar nitrogen concentration to decreases in photosynthetic capacity during and after drought in prairie grasses. *Physiologia Plantarum* 101: 173–182.
- Hentschel R, Rosner S, Kayler ZE, Andreassen K, Børja I, Solberg S, Tveito OE, Priesack E, Gessler A. 2014. Norway spruce physiological and anatomical predisposition to dieback. *Forest Ecology and Management* 322: 27–36.
- Hodge A, Robinson D, Fitter A. 2000. Are microorganisms more effective than plants at competing for nitrogen? *Trends in Plant Science* 5: 304–308.
- Höglberg P, Fan H, Quist M, Binkley DAN, Tamm CO. 2006. Tree growth and soil acidification in response to 30 years of experimental nitrogen loading on boreal forest. *Global Change Biology* 12: 489–499.
- Hommel R, Siegwolf R, Zavadlav S, Arend M, Schaub M, Galiano L, Haeni M, Kayler ZE, Gessler A. 2016. Impact of interspecific competition and drought on the allocation of new assimilates in trees. *Plant Biology* 18: 785–796.
- Jarvis P, Rey A, Petsikos C, Wingate L, Rayment M, Pereira J, Banza J, David J, Miglietta F, Borghetti M *et al.* 2007. Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the “Birch effect”. *Tree Physiology* 27: 929–940.
- Jonard M, Fürst A, Verstraeten A, Thimonier A, Timmermann V, Potočić N, Waldner P, Benham S, Hansen K, Merilä P *et al.* 2014. Tree mineral nutrition is deteriorating in Europe. *Global Change Biology* 21: 418–430.
- Kozłowski T, Pallardy S. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. *Botanical Review* 68: 270–334.
- Kreuzwieser J, Gessler A. 2010. Global climate change and tree nutrition: influence of water availability. *Tree Physiology* 30: 1221–1234.
- Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F. 2012. Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology* 18: 797–805.
- Magill AH, Aber JD, Currie WS, Nadelhoffer KJ, Martin ME, McDowell WH, Melillo JM, Steudler P. 2004. Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. *Forest Ecology and Management* 196: 7–28.
- Manion PD. 1981. *Tree disease concepts*. Englewood Cliffs, NJ, USA: Prentice-Hall Inc.
- Marschner H, Kirkby EA, Cakmak I. 1996. Effect of mineral nutritional status on shoot–root partitioning of photoassimilates and cycling of mineral nutrients. *Journal of Experimental Botany* 47: 1255–1263.
- Martínez-Vilalta J, Piñol J, Beven K. 2002. A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean. *Ecological Modelling* 155: 127–147.
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG *et al.* 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.
- McDowell NG. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* 155: 1051–1059.
- McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution* 26: 523–532.
- McDowell NG, Fisher RA, Xu C, Domec JC, Hölttä T, Mackay DS, Sperry JS, Boutz A, Dickman L, Gehres N *et al.* 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist* 200: 304–321.
- Millard P, Proe MF. 1992. Storage and internal cycling of nitrogen in relation to seasonal growth of Sitka spruce. *Tree Physiology* 10: 33–43.
- Muhr J, Franke J, Borken W. 2010. Drying–rewetting events reduce C and N losses from a Norway spruce forest floor. *Soil Biology and Biochemistry* 42: 1303–1312.
- Oren R, Ellsworth DS, Johnsen KH, Phillips N, Ewers BE, Maier C, Schäfer KVR, McCarthy H, Hendrey G, McNulty SG *et al.* 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO_2 -enriched atmosphere. *Nature* 411: 469–472.
- Rennenberg H, Dannenmann M. 2015. Nitrogen nutrition of trees in temperate forests—the significance of nitrogen availability in the pedosphere and atmosphere. *Forests* 6: 2820–2835.
- Royo AA, Knight KS. 2012. White ash (*Fraxinus americana*) decline and mortality: the role of site nutrition and stress history. *Forest Ecology and Management* 286: 8–15.
- Sala A, Piper F, Hoch G. 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist* 186: 274–281.
- Sardans J, Alonso R, Janssens IA, Carnicer J, Vereseglou S, Rillig MC, Fernández Martínez M, Sanders TGM, Peñuelas J. 2015. Foliar and soil concentrations and stoichiometry of nitrogen and phosphorus across European *Pinus sylvestris* forests: relationships with climate, N deposition and tree growth. *Functional Ecology* 30: 676–689.
- Sardans J, Peñuelas J. 2013. Tree growth changes with climate and forest type are associated with relative allocation of nutrients, especially phosphorus, to leaves and wood. *Global Ecology and Biogeography* 22: 494–507.
- Sardans J, Peñuelas J. 2015. Potassium: a neglected nutrient in global change. *Global Ecology and Biogeography* 24: 261–275.
- Schulze ED. 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest. *Science* 244: 776–783.
- Sergent AS, Rozenberg P, Breda N. 2014. Douglas-fir is vulnerable to exceptional and recurrent drought episodes and recovers less well on less fertile sites. *Annals of Forest Science* 71: 697–708.
- Sevanto S, McDowell NG, Dickman LT, Pangle R, Pockman WT. 2014. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell & Environment* 37: 153–161.
- Sperry JS, Love DM. 2015. What plant hydraulics can tell us about responses to climate-change droughts. *New Phytologist* 207: 14–27.
- Vitousek PM, Howarth RW. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* 13: 87–115.
- Volkman THM, Haberger K, Gessler A, Weiler M. 2016. High-resolution isotope measurements resolve rapid ecophysiological dynamics at the soil–plant interface. *New Phytologist* 201: 839–849.
- Wallander H, Nylund JE. 1992. Effects of excess nitrogen and phosphorus starvation on the extramatrical mycelium of ectomycorrhizas of *Pinus sylvestris* L. *New Phytologist* 120: 495–503.
- Wang WF, Peng CH, Kneeshaw DD, Larocque GR, Luo ZB. 2012. Drought-induced tree mortality: ecological consequences, causes, and modeling. *Environmental Reviews* 20: 109–121.
- Waring RH. 1987. Characteristics of trees predisposed to die. *BioScience* 37: 569–574.
- Wright SJ, Yavitt JB, Wurzbarger N, Turner BL, Tanner EVJ, Sayer EJ, Santiago LS, Kaspari M, Hedin LO, Harms KE *et al.* 2011. Potassium, phosphorus, or

nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology* **92**: 1616–1625.

Wu F, Bao W, Li F, Wu N. 2008. Effects of drought stress and N supply on the growth, biomass partitioning and water-use efficiency of *Sophora davidii* seedlings. *Environmental and Experimental Botany* **63**: 248–255.

Xiong Y, D'Atri JJ, Fu S, Xia H, Seastedt TR. 2011. Rapid soil organic matter loss from forest dieback in a subalpine coniferous ecosystem. *Soil Biology and Biochemistry* **43**: 2450–2456.

Zwieniecki MA, Holbrook NM. 2009. Confronting Maxwell's demon: biophysics of xylem embolism repair. *Trends in Plant Science* **14**: 530–534.



About New Phytologist

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Trust, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <28 days. There are **no page or colour charges** and a PDF version will be provided for each article.
- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.
- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@lancaster.ac.uk)
- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**