

SPECIAL FEATURE

Forest biogeochemistry in response to drought

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Abstract

Trees alter their use and allocation of nutrients in response to drought, and changes in soil nutrient cycling and trace gas flux (N₂O and CH₄) are observed when experimental drought is imposed on forests. In extreme droughts, trees are increasingly susceptible to attack by pests and pathogens, which can lead to major changes in nutrient flux to the soil. Extreme droughts often lead to more common and more intense forest fires, causing dramatic changes in the nutrient storage and loss from forest ecosystems. Changes in the future manifestation of drought will affect carbon uptake and storage in forests, leading to feedbacks to the Earth's climate system. We must improve the recognition of drought in nature, our ability to manage our forests in the face of drought, and the parameterization of drought in earth system models for improved predictions of carbon uptake and storage in the world's forests.

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Introduction

Historical records of drought extend to Biblical times, when lack of rainfall reduced crop yields, leading to famine and mass human migrations. Studies of tree rings also show periods of reduced forest growth that can be linked to historical records of low rainfall. In these examples, drought is taken to result from low rainfall, but in some cases, this linkage is too simple. Some trees may access deep sources of water that allow forests to avoid all but the most catastrophic periods of reduced rainfall. In other cases, extreme warmth can lead to drought-like symptoms even when rainfall is normal. In many cases, direct observations of plant responses to drought, as seen in lower leaf conductance to water loss or early leaf abscission, are better indications of drought than changes in meteorological or soil variables alone.

Changes in the forest canopy due to drought have impacts that extend throughout the ecosystem, affecting the input of organic materials to the soil and subsequent response of the soil microbial community. The thresholds of physiological response may differ consid-

erably between higher plants and soil microbes, with biogeochemical cycling often continuing in the soil long after severe drought has caused a reduction in physiological activities in the aboveground plant tissues. As most biogeochemical cycling occurs in soils, advances in our understanding of drought will come from studies that consider the response of entire ecosystems to limited water availability, which is likely first manifest in plants and then progress to soils.

Often, drought affects forest biogeochemical cycling through indirect pathways. Many drought-stressed trees are susceptible to insect attack, which can alter the movement of essential elements (e.g., N and P) from plants to the soil. And severe drought makes fires more likely, which release essential elements from live and dead organic matter in ecosystems to the atmosphere and to runoff waters. It may take many years to replace the nutrients that are lost from a single fire.

This study attempts to summarize what we know about the effects of drought on forest biogeochemistry. Much of what we know derives from observations during prolonged droughts and from field experiments that have imposed artificial drought on ecosystems (Wu *et al.*, 2010). These experiments offer a glimpse of what we should expect to occur more frequently in a warmer and drier world of the future and what climate

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change will mean for forest productivity and management. The literature reviewed is largely drawn from studies in North America, but the conclusions should be applicable worldwide.

Drought and forest biogeochemistry

The degree to which droughts impact nutrient cycling in vegetation depends on multiple factors: the severity and duration of the drought; the morphology, phenology, sensitivity, and physiology of the dominant trees; and the nutrients of interest. Prolonged droughts originating early in the growing season, for example, may induce some tree species to lose leaves (and possibly roots) prematurely – a process that would reduce nutrient uptake and accelerate nutrient losses from plants. Most nutrients are mobilized and transported in soil water, so water stress may lead to nutrient stress.

Nutrient uptake

The acquisition of nutrients by plants requires the availability of water. Nutrients move toward the surface of an absorptive root by diffusion and mass flow and are taken up and transported through the plant as a result of water potential gradients between root, xylem, and leaf cells. Thus, as soils dry during prolonged drought, nutrient uptake is generally reduced, resulting in lower leaf nutrient concentrations and reduced photosynthetic activity (Rustad *et al.*, 2011; He & Dijkstra, 2014). However, the impact of drought on nutrient uptake is species- and nutrient-dependent (Grabarova & Martinikova, 2001). Hanson *et al.* (2003) reported that after 6 years of experimentally induced drought (33% reduction in throughfall), foliar nitrogen (N) was reduced in some tree species (relative to controls) but not in others. Some species respond to drought by reducing their leaf area, but show little or no change in the nutrient content in their remaining leaves (Pilon *et al.*, 1996). In an experimental plantation of Norway spruce, Nilsson & Wiklund (1994) reported higher nutrient concentrations and greater nutrient uptake in drought treatments, relative to controls.

A possible explanation for sustained nutrient uptake under drought conditions may be related to below-ground responses of trees to water stress. Hanson *et al.* (2003) reported that some species likely accessed water and nutrients from deep soil via tap roots or by preferentially allocating carbon (C) to subsurface roots (Joslin *et al.*, 2000).

Allocation of C to mycorrhizal fungi may also represent a rooting strategy for overcoming water/nutrient stress (Hawkes *et al.*, 2011; Lehto & Zwiazek, 2011; Rapparini & Penuelas, 2014). Mycorrhizal fungi can

access water in soil micropores and hydraulically redistribute water to nutrient-rich surface soils (Querejeta *et al.*, 2007; Neumann & Cardon, 2012). Moreover, deciduous hardwood forests may differ in their sensitivities to drought based on the abundance of trees associating with arbuscular mycorrhizal (AM) relative to ectomycorrhizal fungi (ECM), as AM trees are generally less tolerant of water stress than ECM trees (Brzostek *et al.*, 2014).

In N-fixing trees, reduced nutrient uptake from the soil appears to be at least partially compensated by increased N-fixation in root-associated symbiotic bacteria. In experimental studies, drought increased nodule biomass in *Alnus* (Tobita *et al.*, 2010) and nitrogen fixation in *Robinia pseudoacacia* (Wurzburger & Miniat, 2014), potentially increasing nitrogen inputs to forest ecosystems.

Aboveground nutrient cycling

While less quantitatively important than uptake by roots, some plant canopies acquire a small amount of nutrients directly from precipitation and gases (Schlesinger & Bernhardt, 2013). As such, drought may exacerbate nutrient stress by reducing foliar uptake of growth-limiting nutrients such as N and some trace micronutrients. Drought-induced reductions in foliar uptake are likely to depend on the morphology of the crown (a function of the species, age, and stand structure), but may also depend on the availability of nutrients in soil relative to inputs in precipitation. In regions of the world where much of the N in soil is found in slow-degrading soil organic matter, for example, reductions in foliar N uptake owing to drought may be ecologically significant (Lockwood *et al.*, 2008; Sparks, 2009).

Rain can also enhance nutrient losses from the canopy by leaching nutrients from leaves (throughfall) and stems (stemflow); as such, decreases in rain can reduce the cycling of mobile nutrients such as potassium (K) (Gundersen *et al.*, 1998).

Retranslocation

The reabsorption of nutrients from senescing leaves (i.e., retranslocation) plays a critical role in nutrient retention, as trees generally reabsorb ~50% of N and P from leaves prior to senescence (Aerts, 1996; Vergutz *et al.*, 2012). While retranslocation rates are highly species- and site-dependent, there is some evidence that resorption efficiencies are sensitive to changes in soil moisture (Boerner, 1985; Minoletti & Boerner, 1994; Killingbeck, 1996). Resorption of amino acids was more efficient in *Quercus rubra* subjected to drought treatments (Suseela *et al.*, 2015), but nutrient resorption may

be less efficient if foliage senesces prematurely as a consequence of water stress (Estiarte & Penuelas, 2015). Drought may impact retranslocation by altering the physiology of leaves in ways that impair nutrient resorption prior to senescence (Suseela *et al.*, 2015).

Differences in the drought response of deciduous trees may also relate to the plant's overall strategy for dealing with water stress. Mesophytic tree species (e.g., *Acer*, *Liriodendron*, *Prunus*) may be more likely to drop leaves early during a drought than xerophytic tree species (e.g., *Quercus*, *Carya*), which often do not close stomates during drought and operate close to the margin of hydraulic failure (Choat *et al.*, 2012). In one of the few studies offering a direct examination of the effects of drought on leaf senescence and retranslocation, Marchin *et al.* (2010) found that 4 of 18 tree species in the southeastern US dropped leaves early during drought. The early senescence of leaves resulted in greater reabsorption of N, P, and K (relative to species that retained their leaves), and enabled these trees to reabsorb nutrients before the leaf desiccated.

Susceptibility to insect attack

Insect defoliation increases the rate of biogeochemical cycling in forests and may ultimately lead to the mortality of trees and to forest fires, which have huge impacts on ecosystem biogeochemistry (Schlesinger & Bernhardt, 2013).

Forest ecologists have long recognized that when trees are stressed, such as by drought, they are more vulnerable to insect attack. Some tree species are less able to allocate photosynthetic resources to the synthesis of protective compounds, such as terpenes, during droughts (Waring & Schlesinger, 1985; Bonello *et al.*, 2006; McDowell *et al.*, 2013). Experimental drought, for example, stimulated insect attack on pinyon pine (Gaylord *et al.*, 2013) and Norway spruce (Netherer *et al.*, 2015). Mortality of oak in Arkansas and Missouri is related to drought and insect attack by oak borer (Fan *et al.*, 2008). Recent widespread bark beetle attack on western coniferous forests may be related to the drought-stress encountered in recent warmer, drier conditions (Kurz *et al.*, 2008). Tree-ring records show that periods of spruce beetle attack have been correlated with drought in Colorado since 1650 C.E. (Hart *et al.*, 2014). When trees are defoliated, there are major changes in the form and rate of nutrient return to the soil, especially by reducing the retranslocation of nutrients before leaf abscission (Lovett *et al.*, 2002).

Recent mountain pine beetle activity in the Rocky Mountains states was synchronized by regional-scale drought conditions that occurred around 2002 (Chapman *et al.*, 2012; Creeden *et al.*, 2014). In lodgepole pine,

mountain pine beetles introduce blue-stain fungi to the tree's vascular system that blocks water uptake within weeks of a successful attack and causes drought-like symptoms and tree mortality (Hubbard *et al.*, 2013). Along with reduced water uptake, plant-available soil N pools increase soon after beetle attack (Morehouse *et al.*, 2008; Clow *et al.*, 2011). Deposition of N-enriched litter is a common feature of beetle attacks in various forest types. Needle fall beneath beetle-infested ponderosa pine (*Pinus ponderosa*) contained 1.1% N compared to 0.6% in uninfested stands in Arizona (Morehouse *et al.*, 2008). Similar patterns occurred following infestation of lodgepole pine (0.75% vs. 0.45% N for beetle-infested and healthy trees; Griffin *et al.*, 2011) and Douglas-fir (1.4% vs. 0.9% N; Griffin & Turner, 2012).

Drought-related insect outbreaks that reduce leaf area or kill trees can also have a substantial impact on ecosystem C cycling (Weed *et al.*, 2013). For example, Clark *et al.* (2010) found that gypsy moth defoliation (75% canopy defoliation) reduced net ecosystem annual CO₂ exchange by 41–55% in upland forests, and severe bark beetle outbreaks (40% to >80% trees impacted) in the western United States reduced aboveground woody C production by 20–60% (Hicke *et al.*, 2012). In severe cases, insect outbreaks can switch a forest from being a C sink to a source, at least over the short term (Amiro *et al.*, 2010).

Cycling of elements in soils

Drought and consequent reductions in soil water have myriad of direct and indirect effects on the cycling of elements in soils. These include consequences for belowground microbial activity, nutrient availability, and solid and solution phases of soil chemistry. Changes in the timing and reductions of precipitation associated with drought also affect soil aeration and erosion by runoff, with effects on soil nutrient status.

For aerobic soil conditions, studies report a decline in rates of microbially driven processes such as N mineralization, nitrification, respiration, and litter decomposition with declining moisture, particularly as soil moisture falls below critical thresholds (Tate *et al.*, 1988; Pilbeam *et al.*, 1993; Burton *et al.*, 1998; Arnold *et al.*, 1999; Rustad *et al.*, 2000; Rey *et al.*, 2002; Emmett *et al.*, 2004). Stark & Firestone (1995) observed that ammonium oxidizers are sensitive to dry conditions, so during drought the rate of nitrification and nitrate losses in runoff decrease (Wetselaar, 1968). Schimel *et al.* (2007) estimated that osmolyte production by soil microbes during dry conditions immobilizes 10–40% of the N mineralization in grasslands and perhaps a similar

amount in forests. Nitrous oxide production is also lower in dry soils (Davidson *et al.*, 2008; Schlesinger, 2013), and there is evidence that forest soils can even become net sinks for N₂O under drought (Goldberg & Gebauer, 2009). Experimental drought treatments also show greater methane consumption by soils (Castro *et al.*, 1995; Borken *et al.*, 2006; Davidson *et al.*, 2008).

Declines in soil microbial processes during drought lead to reduced availability and leaching of C, N, P, and base cations (e.g., Ca²⁺, Mg²⁺, K⁺). Some of these effects are transient. For example, for red maple (*Acer rubrum*), O'Neill *et al.* (2003) reported that lower rates of decomposition during a precipitation exclusion in the spring were matched by higher rates of decomposition under normal precipitation regimes later in the year, so that the annual rate of decomposition was similar in drought and control plots. These observations probably derive from the long-noted effect of wetting and drying on soil microbes, where microbial activity fluctuates with moisture availability (Stevenson, 1956; Sorensen, 1974).

In hydric soils such as wetlands, where soils are permanently or seasonally saturated by water, oxygen is limiting, and anaerobic processes dominate (Brady & Weil, 2008). Here, drought can actually induce more favorable conditions for aerobic microbial processes by increasing the oxygen status of the soils (Emmett *et al.*, 2004). Concurrently, rates of anaerobic processes, such as methanogenesis and denitrification, will decline.

Changes in the biomass, distribution and physiology of plant roots have direct impacts on the cycling of elements in soils by altering plant nutrient uptake, root respiration, root-mycorrhizal interactions, and below-ground detrital inputs via the turnover of roots (Burton *et al.*, 1998; Bryla *et al.*, 2001; Borken *et al.*, 2002; Rey *et al.*, 2002). Drought can decrease fine root biomass due to decreased root elongation, and increased root cavitation and mortality (Jackson *et al.*, 2000; Joslin *et al.*, 2000). Field studies suggest that tree root systems respond to water stress by vertically and temporally shifting growth rates. This can result in less root growth in shallow soil layers (where moisture stress is greatest) and more root growth deeper in the soil (where moisture can be more available) or increases and decreases in root growth over time tracking changing soil moisture conditions (Jackson *et al.*, 2000; Joslin *et al.*, 2001). A decrease in fine root biomass during droughts is sometimes compensated by greater production during more favorable times of the year, as was shown at the Walker Branch Throughfall Displacement Experiment in Tennessee (Joslin *et al.*, 2000).

Over longer periods of time, trees adapt to dry climate regimes or longer-term drought by increasing fine root biomass, increasing root:shoot ratios, and

increasing rooting depth. Evidence for these responses to drought is apparent at the biome scale. Plants growing in xeric environments tend to have higher root:shoot ratios and deeper root systems compared to plants occupying more mesic environments (Schenk & Jackson, 2005). In all cases, the redistribution of roots in response to water stress will directly affect the cycling of C, N, P, base cations, and trace elements in soils.

Soil water status directly affects solid- and solution-phase soil chemistry. In addition to changing the availability of elements through the biologic processes described above, changes in soil moisture also impact abiotic processes associated with ion-exchange reactions, leaching, diffusion, and weathering. Declines in soil water, for example, will increase ionic concentration in soils, resulting in intensified soil surface exchange reactions (Sverdrup, 1990). Decreased soil water also decreases rates of ion diffusion within soils, leaching loss of elements, and rates of mineral weathering (Schlesinger & Bernhardt, 2013).

The rate of soil erosion by wind and water is typically low under closed-canopy forests, due to the moderating influence of the canopy on the energy of raindrops and threshold friction velocity of wind (Waring & Schlesinger, 1985). Erosion increases dramatically after forest harvest and forest fire, when soils are bare (Bormann *et al.*, 1974). These losses could be further exacerbated if a long period of drought is followed by intense rainfall. Globally, the greatest rates of erosion are typically when such events occur in semi-arid climates (Langbein & Schumm, 1958).

Increased soil water stress and drought will also have significant impacts on the cycling of elements in soils via indirect pathways, including changes in forest composition; pests and pathogens; and fire. Unless the drought is very severe, evapotranspiration remains relatively stable, and the reductions in water loss from the ecosystem are seen in runoff (Johnson *et al.*, 2001; Schlesinger & Jasechko, 2014). To the extent that drought reduces streamflow, a lower frequency of flooding will reduce nutrient inputs to floodplain forests, which are often subsidized by seasonal delivery of sediments (Mitsch & Rust, 1984).

Fire

Prolonged droughts increase the likelihood of fires in many ecosystems. Drought-induced wildfires cause periodic C and nutrient losses in gaseous and particulate forms released to the atmosphere (Raison *et al.*, 1985) and through leaching and erosion in runoff waters (Dunnette *et al.*, 2014). The biogeochemical consequences of wildfire are proportional to fire severity and depend on factors such as the amount of woody

fuel and forest floor consumed, the duration of combustion, the depth of heat penetration into the soil, and the spatial extent of the fire. Nitrogen losses from wildfires in conifer forests can range from 300 to 855 kg N ha⁻¹ (Johnson *et al.*, 1998), equivalent to 10–40% of the N in aboveground vegetation and forest floor layers (Schlesinger & Bernhardt, 2013). In contrast, low-intensity fires cause smaller N losses (e.g., 10–40 kg ha⁻¹ from southeastern pine forests; Wells, 1971; Richter *et al.*, 1982). Low severity surface fires (e.g., prescribed fires), which rarely cause mortality among canopy trees, may actually increase growth and C accumulation rates of the remaining trees due to reduced competition and temporarily increased nutrient availability (Fiedler *et al.*, 2010; Hurteau & North, 2010; Anning & McCarthy, 2013). Nevertheless, the cumulative nutrient loss from successive low-intensity fires may exceed that from a single large fire (Johnson *et al.*, 1998).

Recovery and regrowth of vegetation after fire restores carbon pools and the rate of nutrient cycling, such that long-term impacts on the ecosystem may be small (Kashian *et al.*, 2006; Ryan *et al.*, 2010; Wiedinmyer & Hurteau, 2010). However, wildfires that cause high postfire mortality (i.e., 'stand-replacing fires'), large fuel consumption, and slow postfire recovery can often result in large and long-lasting impacts on the magnitude and direction of carbon-cycling processes (Amiro *et al.*, 2010; Kolb *et al.*, 2013). Carbon lost from wildfires in forests of the continental United States can be substantial, with recent estimates ranging from 13.4 Tg C yr⁻¹ for the period 1990–1999 to 25.6 Tg C yr⁻¹ for 1980–1989 (Goetz *et al.*, 2012). For comparison, the NPP of forests in the United States is about 3500 Tg C yr⁻¹ (Xiao *et al.*, 2010) and total carbon sequestration is estimated at 100–200 Tg C yr⁻¹ (Zhang *et al.*, 2012).

Nutrient leaching usually increases after wildfire, although enhanced export to surface and groundwater is typically short-lived and small relative to losses to the atmosphere (Belillias & Feller, 1998; Johnson *et al.*, 1998, 2007). Combustion of vegetation and forest floor litter exposes the mineral soil surface and increases erosion of C and nutrients. In areas that receive high-intensity rain storms, postfire losses of forest floor C and nutrients by erosion can equal or exceed those from combustion. The consequences of these elemental losses are proportional to the extent of an area burned at high severity (Riggan *et al.*, 1994). For example, in the 2002 Hayman fire in Colorado, watersheds that sustained high severity wildfire on >45% of their area had streamwater nitrate and turbidity roughly threefold higher than other watersheds that were subject to severe burns on only 10% of their area (Rhoades *et al.*, 2011).

Wildfires induce biogeochemical transformations that commonly increase nutrient availability in soils, despite losses of C and nutrients from vegetation and soils (Raison, 1979; Wan *et al.*, 2001). Nutrients bound in vegetation and soil organic matter are released by combustion, adding inorganic forms of K, Ca, Mg, P, and N to the soil. Soil NH₄ is increased by oxidation of organic matter, ash inputs, and release of N from inter-layer clay exchange sites. Postfire soil NH₄ typically remains elevated for about a year and is followed by an increase in soil NO₃ (Certini, 2005). In addition to changes in the exchangeable forms of soil N, net N mineralization and nitrification can increase dramatically (DeLuca & Sala, 2006; Grady & Hart, 2006; Koyama *et al.*, 2010). Fires consume organic acids and release cations balanced by (bi)carbonates and hydroxides, reducing soil, and stream acidity. These changes are often short-lived (Cerdà & Doerr, 2008), although elevated soil pH may persist for years (Ulery *et al.*, 1993). Heating also affects the composition of the organic matter remaining after a fire. Fires consume a greater proportion of the labile C and leave stable pyrogenic C (charcoal) that has implications for long-term C storage and N cycling (DeLuca *et al.*, 2006; DeLuca & Aplet, 2008). Complex interactions between biotic and abiotic conditions in postfire environments influence the duration and spatial scale of biogeochemical changes within and among ecosystem types.

The pace of biogeochemical recovery from wildfires depends on the magnitude and extent of elemental losses and transformations caused by the fire, coupled with the growth rate and composition of postfire revegetation. Severe stand-replacing wildfires may reduce ecosystem N pools for decades to centuries (Certini, 2005; Smithwick *et al.*, 2005). Postfire recovery of plant and organic cover and nutrient demand relies on the persistence of soil microbes and vegetation capable of sprouting or germinating in burned soils or dispersing into burned areas. In Glacier National Park, rapid postfire growth of residual vegetation was credited for the return of summertime stream nitrate concentrations to preburn levels within 2 years (Mast & Clow, 2008). Conversely, dry conditions inhibited recovery of vegetation in Colorado ponderosa pine forests, and stream nitrate remained elevated for more than 5 years (Rhoades *et al.*, 2011).

The abundance of nitrogen-fixing herbaceous plants and shrubs usually increases after wildfire. These species are known to add 10–100 kgN ha⁻¹ yr⁻¹ and replace lost N within a few decades (Binkley *et al.*, 1982; Busse, 2000). Nitrogen-fixing plants may contribute an order of magnitude more N than atmospheric deposition in regions not impacted by industry (Johnson *et al.*, 2005).

Tree mortality and large fires have increased significantly in the western United States in recent years, likely in response to warmer and drier conditions (Van Mantgem *et al.*, 2009; Dennison *et al.*, 2014), but similar patterns are not yet apparent in the east (Dietze & Moorcroft, 2011). Landscape-scale patterns of species composition, vegetation structure, ground cover, and litter layer conditions contribute to long-term wildfire effects (Turner *et al.*, 2003; Giesen *et al.*, 2008). Patterns of forest succession after fire are well known for many ecosystems, yet the biogeochemical responses and recovery from the more severe and higher frequency fires projected under warmer, drier climates remain poorly understood.

Drought and carbon balance in forests

Large-scale droughts in recent decades have stimulated interest in field studies and simulation modeling to assess the effects of future droughts on the carbon balance of forests. Most field experiments that impose drought show reduced net primary production and net carbon exchange (Wu *et al.*, 2010). Drought led to reduced gross primary productivity and carbon sequestration across Europe in 2003 (Ciais *et al.*, 2005) and the Amazon Basin in 2010 (Gatti *et al.*, 2014). Global estimates of the long-term trends in forest NPP show a 1% decline during 2000–2009, largely as a result of droughts in the Southern Hemisphere (Zhao & Running, 2010). We can expect reductions in global NPP during the transient period of drought that is anticipated in most models of future global climate.

Severe drought in the Amazon Basin turned a system that is typically a carbon sink into a carbon source. Tian *et al.* (1998) reported losses of 0.2 Pg C yr⁻¹ carbon from the Amazon Basin during hot, dry years associated with El Niño conditions in 1987 and 1992. In 2005 and 2010, Amazonian droughts extended across 2–3 million km² of tropical forests. Lewis *et al.* (2011) estimate that the severe drought of 2010 reduced carbon uptake by ~2.2 Pg C, compared to a decrease of 1.6 Pg C during the 2005 drought. Gatti *et al.* (2014) report a net loss of 0.48 Pg C from the Amazon Basin during the 2010 drought, compared to a net uptake of 0.25 Pg C yr⁻¹ during normal conditions. This reduced carbon uptake during drought is large, equivalent to about 5% of total global carbon emissions from fossil fuel burning. In other regions, including Central America and Southeast Asia, field experiments and model simulations both suggest that the combination of increasing temperatures and drought could alter the balance of photosynthesis and respiration, leading to higher net CO₂ fluxes to the atmosphere and reducing carbon uptake (e.g., Cleveland *et al.*, 2010; Wood *et al.*, 2012; Moser *et al.*, 2014).

The effects of drought have been increasingly visible in boreal forests during the last decade. Boreal forests cover more than 10 million square kilometers of the earth's surface and contain >50 Pg of biomass C (Pan *et al.*, 2013). Tree mortality in Canada's boreal forests increased 4.7% per year from 1963 to 2008, with recent climate change and drought-induced water stress estimated to be the dominant cause of this mortality (Peng *et al.*, 2011; Ma *et al.*, 2012). Drought stress decreased biomass accumulation particularly in western Canada, where moisture deficiency was greater, and increased annual tree mortality from <0.5% of biomass in the early 1970s to 1.8% more recently (Peng *et al.*, 2011; Pan *et al.*, 2013). If the results apply to all of Canada's boreal forests, then the reduction in the carbon sink from mature forests would be 7.3 Tg C yr⁻¹, equivalent to ~4% of Canada's fossil fuel emissions (Ma *et al.*, 2012).

In boreal forests, individual species show different vulnerabilities and potential for large-scale die-back as a result of drought. Michaelian *et al.* (2011) used a combination of remotely sensed and field data and model simulations to examine mortality of aspen (*Populus tremuloides*) across 115 000 km² (~45 000 mi²) of Saskatchewan, Canada. The severe drought of 2001–2002 led to >50% aspen mortality across large portions of the region, reducing aboveground biomass by 20% and having consequences similar to those of a large scale of fire. In the southern part of the region where the drought was most severe, one-third of the aspen trees died. Overall, the amount of dead biomass was estimated to contain ~45 Mt C.

Each year forests in the United States accumulate enough C (833 Tg C yr⁻¹) to offset approximately 16% of U.S. fossil fuel emissions (National Climate Assessment 2014); however, the rate of C accumulation varies from year to year due to climatic variability, disturbances, and management practices (Xiao *et al.*, 2011), and drought can substantially decrease carbon accumulation rates (Schwalm *et al.*, 2012). Brzostek *et al.* (2014) reported that droughts can reduce the C sink of deciduous forests in the United States by as much as 17 percent – a decrease in C capture that translates to an additional 1–3 days of global C emissions from fossil fuel burning each year. Further, the authors found that drought impacts can offset C gains of longer growing seasons as a result of warmer climate. For example, using decade-long records of climate and tree growth at the Morgan Monroe State Forest in Indiana, Brzostek *et al.* (2014) found that despite 26 more days per year of C assimilation owing to milder temperatures, drought caused a loss of 42 days of wood production over the same period, resulting in a 41% decrease in the amount of C stored in woody biomass. The impacts of drought on forest carbon balance would be expected to vary

considerably across the continental United States due to differences in the biophysical environment, species composition, and management intensity. In most instances, the effects of severe drought persist for several years after the return of normal rainfall (Anderegg *et al.*, 2015).

Simulation models and long-term eddy covariance studies that include drought years provide estimates of the net effects of drought on ecosystem carbon balance and suggest causal factors. These models suggest different carbon-cycling responses depending on the climate regime, where humid sites (such as in the eastern United States) were generally less responsive to lower precipitation than drier sites (such as in the western United States) (Gerten *et al.*, 2008). In the southeast United States, Powell *et al.* (2008) reported little change in the net ecosystem production (NEP = gross ecosystem productivity minus ecosystem respiration) during drought in *Pinus elliotii* due to the counteracting effects of decreased canopy photosynthesis and soil respiration. Elsewhere in the Southeast, NEP in a *Pinus taeda* plantation was reduced by drought, primarily through decreased canopy and whole-tree leaf conductances (Noormets *et al.*, 2010), without a corresponding decrease in ecosystem respiration. In forests of the western United States, net CO₂ uptake reported from eddy-flux towers during a prolonged drought indicated a reduction in NEP of 63 g m⁻² yr⁻¹ and a decline of 30–298 Tg C yr⁻¹ in the current carbon sink in that region (Schwalm *et al.*, 2012). For western coniferous forests, NEP declined primarily as a result of decreased gross ecosystem production, whereas ecosystem respiration declined only slightly (Schwalm *et al.*, 2012).

Management implications

Forests will respond to existing and new disturbance regimes; however, the resulting forest structure and function may be inconsistent with the desired future conditions and associated ecosystem services. A key question is whether and how forest management can be used to maintain desired conditions and ecosystems services. Increased drought severity and frequency are likely to make forests more vulnerable to both direct (e.g., reduced growth and mortality) and indirect (insect outbreaks, pathogens, wildfire) impacts (Dale *et al.*, 2001; Choat *et al.*, 2012; Liu *et al.*, 2013; Weed *et al.*, 2013). Exactly how these impacts manifest will depend in large part on the nature of drought. For example, frequent low severity drought may selectively favor more drought-tolerant trees and create forests better adapted to future conditions without the need for management intervention. In contrast, severe drought (especially in combination with insect

outbreaks or fire) may result in large-scale changes that warrant substantial management responses. These responses range from reducing vulnerability to drought, facilitating postdrought recovery, or facilitating a transition to a new forest condition (Millar *et al.*, 2007). Here, we focus primarily on management options that reduce vulnerability.

Forest management actions to minimize drought impacts on biogeochemical cycling will require altering forest structure and function in ways that increase adaptive capacity and/or reduce vulnerability to drought. Management options are highly site specific and constrained by a wide variety of factors; however, from the perspective of biogeochemical cycling, maintaining forest cover and minimizing forest floor loss and soil erosion are key objectives. Reducing stand density by thinning may decrease water demand and subsequent drought stress (McDowell *et al.*, 2006; Dore *et al.*, 2012; D'Amato *et al.*, 2013), with the potential added benefit of reducing fuel loading and wildfire risk (McIver *et al.*, 2009). Stand structure can also be altered and managed using multi-aged systems that may create stands with higher water-use efficiency (O'Hara & Nagel, 2006). Some evidence suggests that younger (smaller) trees are more vulnerable to drought than older (larger) trees (DeLucia & Schlesinger, 1990; Hanson *et al.*, 2001 – tree size, Klos *et al.*, 2009 – tree age), indicating that stand age and size class distributions could be managed to decrease vulnerability. Our current understanding of differences in functional attributes related to transpiration demands (Ford *et al.*, 2011) and rooting characteristics (Joslin *et al.*, 2000; Schenk & Jackson, 2005) could be used to favor more drought-tolerant (or water-use efficient) tree species in existing stands and developing and planting more drought-resistant species for new stands.

In some regions of the United States, planting or favoring more drought-tolerant species may conflict with management objectives that favor rapid accumulation of biomass, as fast-growing woody species often use more water and exacerbate drought impacts (King *et al.*, 2013). Drought impacts could also be reduced by designing road and drainage networks to keep more of the water in the forest (Grant *et al.*, 2013), instead of moving runoff rapidly to the streams or concentrating it in small areas of the landscape as is typically the case (Kolka & Smidt, 2004). Successful forest management in the face of drought will likely require a combination of many approaches. For example, Grant *et al.* (2013) used simulation modeling to demonstrate the advantages of combining increased water availability, thinning, and mulching to reduce drought-stress-related mortality in ponderosa pine (*Pinus ponderosa*) during an extreme drought.

Representation of drought in ecosystem and global models

To anticipate how forest biogeochemistry will respond to future drought, it is important to assess the representation of drought in ecosystem and biogeochemical models as these are our primary means of extrapolating the response of ecosystems to novel or rare conditions. Particularly useful in this assessment are the results of model intercomparison projects (MIPs), where the performance of multiple models is judged against data from one or more sites or experiments. These give a better measure of the performance of the community of models, rather than assessing individual models tuned to individual sites. In a recent comparison of 22 ecosystem models against 44 eddy-covariance towers across North America, the biases and chi-squared error in the net ecosystem exchange of carbon (NEE) were only marginally higher under dry conditions, and this error was only apparent during the growing season (Schwalm *et al.*, 2010). This is encouraging because these errors were smaller than the errors across seasons or among biomes in the same models.

The same MIP found that model errors for estimates of gross primary productivity (GPP) were substantially higher under low-humidity conditions (Schaefer *et al.*, 2012). Furthermore, while all models captured the shape of the GPP response to moisture under high humidity conditions, for many models the shape of the GPP response curve was substantially different from observations, indicating underlying structural errors rather than simple miscalibration. Similarly, a MIP at the Duke and Oak Ridge FACE experiments showed substantial differences among eleven models that could be attributed to differences in moisture responses at the leaf level (stomatal closure), the whole plant level (water uptake), and at the stand level (boundary layer exchange of water vapor) (De Kauwe *et al.*, 2013). Likewise, a detailed analysis of the sources of uncertainty within a single model applied to four North American biomes and seventeen vegetation types found that water uptake and stomatal closure responses were the second and third (respectively) largest sources of uncertainty in predicting NPP (Dietze *et al.*, 2014). Sims *et al.* (2014) found that many deciduous forests do not lose their 'greenness' in remote-sensing images taken during drought, despite large reductions in photosynthesis at the canopy scale.

Given that satellite data products predicting GPP and NPP assume a relationship between greenness and photosynthesis, these data products may underestimate the magnitude of droughts in terms of net ecosystem balance. As a whole, there is pressing need to improve

the ecophysiological of plants to drought in ecosystem and global models.

Few MIPs have focused on belowground biogeochemical responses. Traditionally, heterotrophic respiration has been modeled as proportional to the size of the soil carbon pool and a temperature-varying turnover rate, with the effects of soil moisture entering as a scaling function (0–1) (Parton *et al.*, 1993). In such models, drought generally causes a substantial reduction in heterotrophic respiration. One recent MIP looking specifically at seven oak woodlands growing in Mediterranean climates found that across five models there was a tendency to overestimate ecosystem respiration during droughts (Vargas *et al.*, 2013).

In many cases, models impose a tight stoichiometric coupling between soil carbon and nitrogen; thus, the reduction in respiration also results in a slowing of the nitrogen cycle. Recently some models have considered microbial activity and soil enzymes more explicitly (Lawrence *et al.*, 2009; Allison *et al.*, 2010; Davidson *et al.*, 2011; Xu *et al.*, 2014). Such approaches improve predictions of transient fluxes that occur during post-drought rewetting (Lawrence *et al.*, 2009) and explain how drought can decouple the typical temperature-respiration responses (Davidson *et al.*, 2011). In contrast to soil CO₂, most models devote much less attention to the cycling of other nutrients in response to drought, largely because the biogenic greenhouse gas emissions considered by models are normally associated with wet conditions (N₂O, CH₄), while tree VOCs such as isoprene, which respond to heat stress, are seldom considered. Finally, many ecosystem models include a representation of fire, with fire probability explicitly a function of either fuel moisture or soil moisture, and thus generate an interaction between fire and drought. By contrast, insects and pathogens are absent from most models, or are limited to case studies, as more general approaches to modeling their impacts has been lacking (Hicke *et al.*, 2012; Dietze & Matthes, 2014). As such, models will in general miss the known interactions between drought and outbreak susceptibility.

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References

Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology*, **84**, 597–608.

- Allison SD, Wallenstein MD, Bradford MA (2010) Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience*, **3**, 336–340.
- Amiro BD, Barr AG, Barr JG *et al.* (2010) Ecosystem carbon dioxide fluxes after disturbances in forests of North America. *Journal of Geophysical Research*, **115**, 1–13.
- Anderegg WRL, Schwalm C, Biondi F *et al.* (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, **349**, 528–532.
- Anning AK, McCarthy BC (2013) Long-term effects of prescribed fire and thinning on residual tree growth in mixed oak forests of southern Ohio. *Ecosystems*, **16**, 1473–1486.
- Arnold SS, Fernandez IJ, Rustad LE, Zibilske LM (1999) Microbial response of an acid forest soil to experimental soil warming. *Biology and Fertility of Soils*, **30**, 239–244.
- Belillias CM, Feller MC (1998) Relationships between fire severity and atmospheric and leaching nutrient losses in British Columbia's coastal western hemlock zone forests. *International Journal of Wildland Fire*, **8**, 87–101.
- Binkley D, Cromack K, Fredriksen RL (1982) Nitrogen accretion and availability in some snowbrush ecosystems. *Forest Science*, **28**, 720–724.
- Boerner REJ (1985) Foliar nutrient dynamics, growth and nutrient-use efficiency of *Hamamelis virginiana* in three forest microsites. *Canadian Journal of Botany*, **63**, 1476–1481.
- Bonello P, Gordon TR, Herms DA, Wood DL, Erbilgin N (2006) Nature and ecological implications of pathogen-induced systematic resistance in conifers: a novel hypothesis. *Physiological and Molecular Plant Pathology*, **68**, 95–104.
- Borken W, Xu Y, Davidson E, Beese F (2002) Site and temporal variation of soil respiration in European Beech, Norway spruce, and Scots pine forests. *Global Change Biology*, **8**, 1205–1216.
- Borken W, Davidson EA, Savage K, Sundquist ET, Stuedler P (2006) Effect of summer throughfall exclusion, summer drought, and winter snow cover on methane fluxes in a temperate forest soil. *Soil Biology and Biochemistry*, **38**, 1388–1395.
- Bormann FH, Likens GE, Siccama TG, Pierce RS, Eaton JS (1974) The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. *Ecological Monographs*, **44**, 255–277.
- Brady N, Weil R (2008) *The Nature and Properties of Soils*, 14th edn. Prentice Hall/Pearson Education, New York.
- Bryla DR, Bouma TJ, Hartmond U, Eissenstat DM (2001) Influence of temperature and soil drying on respiration of individual roots in citrus: integrating greenhouse observations into a predictive model for the field. *Plant, Cell and Environment*, **24**, 781–790.
- Brzostek ER, Dragoni D, Schmid HP *et al.* (2014) Chronic water stress reduces tree growth and the carbon sink of deciduous forests. *Global Change Biology*, **20**, 2531–2539.
- Burton AJ, Pregitzer KS, Zogg GP, Zak DR (1998) Drought reduces root respiration in sugar maple forests. *Ecological Applications*, **8**, 771–778.
- Busse MD (2000) Suitability and use of the ¹⁵N-isotope dilution method to estimate nitrogen fixation by actinorhizal shrubs. *Forest Ecology and Management*, **136**, 85–95.
- Castro MS, Melillo JM, Stuedler PA, Chapman JW (1995) Soil moisture as a predictor of methane uptake by temperate forest soils. *Canadian Journal of Forest Research*, **24**, 1805–1810.
- Cerdà A, Doerr SH (2008) The effect of ash and needle cover on surface runoff and erosion in the immediate post-fire period. *Catena*, **74**, 256–263.
- Certini G (2005) Effects of fire on properties of forest soils: a review. *Oecologia*, **143**, 1–10.
- Chapman TB, Veblen TT, Schoennagel T (2012) Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology*, **93**, 2175–2185.
- Choat B, Jansen S, Brodribb TJ *et al.* (2012) Global convergence in the vulnerability of forests to drought. *Nature*, **491**, 752–756.
- Ciais P, Reichstein M, Viovy N *et al.* (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.
- Clark KL, Skowronski N, Hom J (2010) Invasive insects impact on forest carbon dynamics. *Global Change Biology*, **16**, 88–101.
- Cleveland CC, Wieder WR, Reed SC, Townsend AR (2010) Experimental drought in a tropical rain forest increases soil carbon dioxide losses to the atmosphere. *Ecology*, **91**, 2313–2323.
- Clow DW, Rhoades CC, Briggs J, Caldwell M, Lewis WM Jr (2011) Responses of soil and water chemistry to mountain pine beetle induced tree mortality in Grand County, Colorado, USA. *Applied Geochemistry*, **26**, 174–178.
- Creeden EP, Hicke JA, Buotte PC (2014) Climate, weather, and recent mountain pine beetle outbreaks in the western United States. *Forest Ecology and Management*, **312**, 239–251.
- Dale VH, Joyce LA, McNulty S *et al.* (2001) Climate change and forest disturbances. *BioScience*, **51**, 723–734.
- D'Amato AW, Bradford JB, Fraver S, Palik BJ (2013) Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications*, **23**, 1735–1742.
- Davidson EA, Nepstad DC, Yoko Ishida F, Brando PA (2008) Effects of an experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous oxide, and nitric oxide in a moist tropical forest. *Global Change Biology*, **14**, 2582–2590.
- Davidson EA, Samanta S, Caramori SS, Savage KE (2011) The Dual Arrhenius and Michaelis-Menten (DAMM) kinetics model for decomposition of soil organic matter at hourly to seasonal time scales. *Global Change Biology*, **18**, 371–384.
- De Kauwe MG, Medlyn BE, Zaehle S *et al.* (2013) Forest water use and water use efficiency at elevated CO₂: a model-data intercomparison at two contrasting temperate forest FACE sites. *Global Change Biology*, **19**, 1759–1779.
- DeLuca TH, Aplet GH (2008) Charcoal and carbon storage in forest soils of the Rocky Mountain West. *Frontiers in Ecology and the Environment*, **6**, 18–24.
- DeLuca TH, Sala A (2006) Frequent fire alters nitrogen transformations in ponderosa pine stands of the inland Northwest. *Ecology*, **87**, 2511–2522.
- DeLuca TH, MacKenzie MD, Gundale MJ, Holben WE (2006) Wildfire-produced charcoal directly influences nitrogen cycling in ponderosa pine forests. *Soil Science Society of America Journal*, **70**, 448–453.
- DeLucia EH, Schlesinger WH (1990) Ecophysiology of Great Basin and Sierra Nevada vegetation on contrasting soils. In: *Plant Biology of the Basin and Range* (eds Osmond CB, Pitelka LF, Hidy GM), pp. 143–178. Springer-Verlag, New York, NY.
- Dennison PE, Brewer SC, Arnold JD, Moritz MA (2014) Large wildfire trends in the western United States, 1984–2011. *Geophysical Research Letters*, **41**, 2928–2933.
- Dietze MC, Matthes JH (2014) A general ecophysiological framework for modeling the impact of pests and pathogens on forest ecosystems. *Ecology Letters*, **17**, 1418–1426.
- Dietze MC, Moorcroft P (2011) Tree mortality in the eastern and central U.S.: patterns and drivers. *Global Change Biology*, **17**, 3312–3326.
- Dietze MC, Serbin SP, Davidson C *et al.* (2014) A quantitative assessment of a terrestrial biosphere model's data needs across North American biomes. *Journal of Geophysical Research: Biogeosciences*, **119**, 286–300.
- Dore S, Montes-Helu M, Hart SC *et al.* (2012) Recovery of ponderosa ecosystem carbon and water fluxes from thinning and stand replacing fire. *Global Change Biology*, **18**, 3171–3185.
- Dunnette PV, Higuera PE, McLaughlan KR, Deerr KM, Briles CE, Keefe MH (2014) Biogeochemical impacts of wildfires over four millennia in a Rocky Mountain sub-alpine watershed. *New Phytologist*, **203**, 900–912.
- Emmett B, Beier C, Estiarte M *et al.* (2004) The response of soil process to climate change: results from manipulation studies of shrublands across and environmental gradient. *Ecosystems*, **7**, 625–637.
- Estiarte M, Penuelas J (2015) Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency. *Global Change Biology*, **21**, 1005–1017.
- Fan ZF, Kabrick JM, Spetich MA, Shifley SR, Jensen RG (2008) Oak mortality associated with crown dieback and oak borer attack in the Ozark Highlands. *Forest Ecology and Management*, **255**, 2297–2305.
- Fiedler CE, Metlen KL, Dodson EK (2010) Restoration treatment effects on stand structure, tree growth, and fire hazard in a ponderosa pine/Douglas-fir forest in Montana. *Forest Science*, **56**, 18–31.
- Ford CR, Hubbard RM, Vose JM (2011) Quantifying structural and physiological controls on variation in canopy transpiration among planted pine and hardwood species in the southern Appalachians. *Ecohydrology*, **4**, 183–195.
- Gatti LV, Gloor M, Miller JB *et al.* (2014) Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature*, **506**, 76–80.
- Gaylord ML, Kolb TE, Pockman W *et al.* (2013) Drought predisposes pinyon-juniper woodlands to insect attacks and mortality. *New Phytologist*, **198**, 567–578.
- Gerten D, Luo Y, LeMaire G *et al.* (2008) Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*, **14**, 2365–2379.
- Giesen TW, Perakis SS, Cromack K (2008) Four centuries of soil carbon and nitrogen change after stand-replacing fire in a forest landscape in the western Cascade Range of Oregon. *Canadian Journal of Forest Research*, **38**, 2455–2464.
- Goetz SJ, Bond-Lamberty B, Law BE *et al.* (2012) Observations and assessments of forest carbon dynamics following disturbance in North America. *Journal of Geophysical Research*, **117**, 1–17.
- Goldberg SD, Gebauer G (2009) Drought turns a central European Norway spruce forest soil from an N₂O source to a transient N₂O sink. *Global Change Biology*, **15**, 850–860.
- Grabarova S, Martinkova M (2001) Changes in mineral nutrition of Norway spruce (*Picea abies* [L.] Karst.) under the impact of drought. *Ekológia (Bratislava)*, **20**(Suppl. 1), 46–60.

- Grady KC, Hart SC (2006) Influences of thinning, prescribed burning, and wildfire on soil processes and properties in southwestern ponderosa pine forests: a retrospective study. *Forest Ecology and Management*, **234**, 123–135.
- Grant GE, Tague CL, Allen CD (2013) Watering the forest for the trees: an emerging priority for managing water in forest landscapes. *Frontiers in Ecology and Environment*, **11**, 314–321.
- Griffin JM, Turner MG (2012) Changes to the N cycle following bark beetle outbreaks in two contrasting conifer forest types. *Oecologia*, **170**, 551–565.
- Griffin JM, Turner MG, Simard M (2011) Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. *Forest Ecology and Management*, **261**, 1077–1089.
- Gundersen P, Boxman AW, Lamersdorf N, Moldan F, Andersen BR (1998) Experimental manipulation of forest ecosystems: lessons from large roof experiments. *Forest Ecology and Management*, **101**, 339–352.
- Hanson PJ, Todd DE, Amthor JS (2001) A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. *Tree Physiology*, **21**, 345–358.
- Hanson PJ, Todd DE, Joslin JD (2003) Canopy production. In: *North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes* (eds Hanson PJ, Wullschlegel SD), pp. 303–315. Springer, New York.
- Hart SJ, Veblen TT, Eisenhart KS, Jarvis D, Kulakowski D (2014) Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology*, **95**, 930–939.
- Hawkes CV, Kivlin SN, Rocca JD, Huguet V, Thomsen MA, Suttle KB (2011) Fungal community responses to precipitation. *Global Change Biology*, **17**, 1637–1645.
- He M, Dijkstra FA (2014) Drought effects on plant nitrogen and phosphorus: a meta-analysis. *New Phytologist*, **204**, 924–931.
- Hicke JA, Allen CD, Desai A *et al.* (2012) The effects of biotic disturbances on carbon budgets of North American forests. *Global Change Biology*, **18**, 7–34.
- Hubbard RM, Rhoades CC, Elder K, Negron JF (2013) Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. *Forest Ecology and Management*, **289**, 312–317.
- Hurteau MD, North M (2010) Carbon recovery rates following different wildfire risk mitigation treatments. *Forest Ecology and Management*, **260**, 930–937.
- Jackson RB, Sperry JS, Dawson TE (2000) Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science*, **5**, 482–488.
- Johnson DW, Susfalk RB, Dahlgren RA, Klopatek JM (1998) Fire is more important than water for nitrogen fluxes in semi-arid forests. *Environmental Science & Policy*, **1**, 79–86.
- Johnson DW, Sustalk RB, Gholz HL, Hanson PJ (2001) Simulated effects of temperature and precipitation change in several forest ecosystems. *Journal of Hydrology*, **235**, 183–204.
- Johnson DW, Murphy JF, Susfalk RB, Caldwell TG, Miller WW, Walker RF, Powers RF (2005) The effects of wildfire, salvage logging, and post-fire N-fixation on the nutrient budgets of a Sierran forest. *Forest Ecology and Management*, **220**, 155–165.
- Johnson DW, Murphy JD, Walker RF, Glass DW, Miller WW (2007) Wildfire effects on forest carbon and nutrient budgets. *Ecological Engineering*, **31**, 183–192.
- Joslin JD, Wolfe MH, Hanson PJ (2000) Effects of altered water regimes on forest root systems. *New Phytologist*, **147**, 117–129.
- Joslin JD, Wolfe MH, Hanson PJ (2001) Factors controlling the timing of root elongation intensity in a mature upland oak stand. *Plant and Soil*, **228**, 201–212.
- Kashian DM, Romme WH, Tinker DB, Turner MG, Ryan MG (2006) Carbon storage on landscapes with stand replacing fires. *BioScience*, **56**, 598–606.
- Killingbeck KT (1996) Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology*, **77**, 1716–1727.
- King JS, Ceulemans R, Albaugh JM *et al.* (2013) The challenge of lignocellulosic bioenergy in a water-limited world. *BioScience*, **63**, 102–117.
- Klos RJ, Wang GG, Bauerle WL, Rieck JR (2009) Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications*, **19**, 699–708.
- Kolb T, Dore S, Montes-Helu M (2013) Extreme late-summer drought causes neutral annual carbon balance in southwestern ponderosa pine forests and grasslands. *Environmental Research Letters*, **8**. doi:10.1088/1748-9326/8/1/015015.
- Kolka RK, Smidt MF (2004) Effects of forest road amelioration techniques on soil bulk density, surface runoff, sediment transport, soil moisture, and seeding growth. *Forest Ecology and Management*, **202**, 313–323.
- Koyama A, Kavanagh K, Stephan K (2010) Wildfire effects on soil gross nitrogen transformation rates in coniferous forests of Central Idaho, USA. *Ecosystems*, **13**, 1112–1126.
- Kurz WA, Dymond CC, Stinson G *et al.* (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature*, **452**, 987–990.
- Langbein WB, Schumm SA (1958) Yield of sediments in relation to mean annual precipitation. *Transactions of the American Geophysical Union*, **39**, 1076–1084.
- Lawrence CR, Neff JC, Schimel JP (2009) Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. *Soil Biology and Biochemistry*, **41**, 1923–1934.
- Lehto T, Zwiazek JJ (2011) Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza*, **21**, 71–90.
- Lewis SL, Brando PM, Phillips PL, van der Heijden GMF, Nepstad D (2011) The 2010 Amazon drought. *Science*, **331**, 554.
- Liu Y, Goodrick SL, Stanturf JA (2013) Future U.S. wildfire potential trends projected using a dynamically downscaled climate change scenario. *Forest Ecology and Management*, **294**, 120–135.
- Lockwood AL, Filley TR, Rhodes D, Shepson PB (2008) Foliar uptake of atmospheric organic nitrates. *Geophysical Research Letters*, **35**. doi:10.1029/2008GL034714.
- Lovett GM, Christenson LM, Groffman PM, Jones CG, Hart JE, Mitchell MJ (2002) Insect defoliation and nitrogen cycling in forests. *BioScience*, **52**, 335–341.
- Ma Z, Panga C, Zhub Q *et al.* (2012) Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 2423–2427.
- Marchin R, Zeng HN, Hoffmann W (2010) Drought-deciduous behavior reduces nutrient losses from temperate deciduous trees under severe drought. *Oecologia*, **163**, 845–854.
- Mast MA, Clow DW (2008) Effects of 2003 wildfires on stream chemistry in Glacier National Park, Montana. *Hydrological Processes*, **22**, 5013–5023.
- McDowell NG, Adams HD, Bailey JD, Hess M, Kolb T (2006) Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications*, **16**, 1164–1182.
- McDowell NG, Fisher RA, Xu C *et al.* (2013) Evaluating theories of drought-induced vegetation mortality using a multimodel- experiment framework. *New Phytologist*, **200**, 304–321.
- McIver A, Youngblood A, Stephens SL (2009) The national fire and fire surrogate study: ecological consequences of fuel reduction methods in seasonally dry forests. *Ecological Applications*, **19**, 283–284.
- Michaelian M, Hogg EH, Hall RJ, Arsenault E (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*, **17**, 2084–2094.
- Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications*, **17**, 2145–2151.
- Minoletti ML, Boerner REJ (1994) Drought and site fertility effects on foliar nitrogen and phosphorus dynamics and nutrient resorption by the forest understory shrub *Viburnum acerifolium* L. *American Midland Naturalist*, **131**, 109–119.
- Mitsch WJ, Rust WG (1984) Tree growth responses to flooding in a bottomland forest in northeastern Illinois. *Forest Science*, **30**, 499–510.
- Morehouse K, Johns T, Kaye J, Kaye M (2008) Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests. *Forest Ecology and Management*, **255**, 2698–2708.
- Moser G, Schuldt B, Hertel D, Horna V, Coners H, Barus H, Leuschner C (2014) Replicated throughfall exclusion experiment in an Indonesian perhumid rainforest: wood production, litter fall and fine root growth under simulated drought. *Global Change Biology*, **20**, 1481–1497.
- National Climate Assessment (2014) Forest Sector Report, <https://nca2014.globalchange.gov/report/sectors/forests>.
- Netherer S, Matthews B, Katzensteiner K *et al.* (2015) Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist*, **205**, 1128–1141.
- Neumann RB, Cardon ZG (2012) The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *New Phytologist*, **194**, 337–352.
- Nilsson LO, Wiklund K (1994) Nitrogen uptake in a Norway spruce stand following ammonium-sulfate application, fertigation, irrigation, drought, and nitrogen-free fertilization. *Plant and Soil*, **164**, 221–229.
- Noormets A, Gavazzi MJ, McNulty SG, Domec J-C, Sun G, King JS, Chen J (2010) Response of carbon fluxes to drought in coastal plain loblolly pine forest. *Global Change Biology*, **16**, 272–287.
- O'Hara KL, Nagel LM (2006) A functional comparison of productivity in even-aged and multiaged stands: a synthesis for *Pinus ponderosa*. *Forest Science*, **52**, 290–303.
- O'Neill EG, Johnson DW, Ledford J, Todd DE (2003) Acute seasonal drought does not permanently alter mass loss and nitrogen dynamics during the decomposition of red maple (*Acer rubrum* L.) litter. *Global Change Biology*, **9**, 117–123.

- Pan Y, Birdsey RA, Phillips OL, Jackson RB (2013) The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics*, **44**, 593–622.
- Parton WJ, Scurlock JMO, Ojima DS *et al.* (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles*, **7**, 785–809.
- Peng C, Ma Z, Lei X *et al.* (2011) A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*, **1**, 467–471.
- Pilbeam CJ, Mahapatra BS, Wood M (1993) Soil matric potential effects on gross rates of nitrogen mineralization in an Orthic Ferralsol from Kenya. *Soil Biology and Biochemistry*, **25**, 1409–1413.
- Pilon CE, Cote B, Fyles JW (1996) Effect of an artificially induced drought on leaf peroxidase activity, mineral nutrition and growth of sugar maple. *Plant and Soil*, **179**, 151–158.
- Powell TL, Gholz HL, Clark KL, Starr G, Cropper WP, Martin TA (2008) Carbon exchange of a mature, natural regenerated pine forest in north Florida. *Global Change Biology*, **14**, 2523–2538.
- Querejeta JL, Egerton-Warburton LM, Allen MF (2007) Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California oak savanna. *Soil Biology and Biochemistry*, **39**, 409–417.
- Raison RJ (1979) Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations—review. *Plant and Soil*, **51**, 73–108.
- Raison RJ, Khanna PK, Woods PV (1985) Mechanisms of element transfer to the atmosphere during vegetation fires. *Canadian Journal of Forest Research*, **15**, 132–140.
- Rapparini F, Penuelas J (2014) Mycorrhizal fungi to alleviate drought stress on plant growth. In: *Use of Microbes for the Alleviation of Soil Stress* (ed. Miransari M), pp. 21–42. Springer, New York, NY.
- Rey A, Pegoraro E, Tedeschi V, de Parn I, Jarvis PG, Valentini R (2002) Annual variation in soil respiration and its components in a coppice oak forest in central Italy. *Global Change Biology*, **8**, 851–866.
- Rhoades CC, Entwistle D, Butler D (2011) The influence of wildfire extent and severity on streamwater chemistry, sediment and temperature following the Hayman Fire, Colorado. *International Journal of Wildfire Science*, **20**, 430–442.
- Richter DD, Ralston CW, Harms WR (1982) Prescribed fire: effects on water quality and forest nutrient cycling. *Science*, **215**, 661–663.
- Riggan PJ, Lockwood RN, Jacks PM, Colver CG, Weirich F, DeBano LF, Brass JA (1994) Effects of fire severity on nitrate mobilization in watersheds subject to chronic atmospheric deposition. *Environmental Science and Technology*, **28**, 369–375.
- Rustad LE, Huntington TG, Boone RD (2000) Controls on soil respiration: implications for climate change. *Biogeochemistry*, **48**, 1–6.
- Rustad L, Lebrija-Trejos E, Beier C, Loik M, Huxman T (2011) The effects of changing precipitation on ecosystem carbon and nutrient cycling: A meta-analysis of global change experiments. Oral presentation at the 2011 annual meeting of the Soil Science Society of America.
- Ryan MG, Harmon ME, Birdsey RA *et al.* (2010) A synthesis of the science on forests and carbon for U.S. forests. *Issues in Ecology*, **13**, 1–16.
- Schaefer K, Schwalm CR, Williams C *et al.* (2012) A model-data comparison of gross primary productivity: results from the North American carbon program site synthesis. *Journal of Geophysical Research*, **117**. doi:10.1029/2012JG001960.
- Schenk HJ, Jackson RB (2005) Mapping the global distribution of deep roots in relation to climate and soil characteristics. *Geoderma*, **126**, 129–140.
- Schimel J, Balsler TC, Wallenstein MD (2007) Microbial stress-response physiology and its implications for ecosystem function. *Ecology*, **88**, 1386–1394.
- Schlesinger WH (2013) An estimate of the global sink for nitrous oxide in soils. *Global Change Biology*, **19**, 2929–2931.
- Schlesinger WH, Bernhardt ES (2013) *Biogeochemistry: An Analysis of Global Change*. Elsevier/Academic Press, Waltham, MA.
- Schlesinger WH, Jasechko S (2014) Transpiration in the global water cycle. *Agricultural and Forest Meteorology*, **189**, 115–117.
- Schwalm CR, Williams CA, Schaefer K *et al.* (2010) A model-data intercomparison of CO₂ exchange across North America: results from the North American Carbon Program site synthesis. *Journal of Geophysical Research*, **115**. doi:10.1029/2009JG001229.
- Schwalm CR, Williams CA, Schaefer K *et al.* (2012) Reduction in carbon uptake during turn of the century drought in western North America. *Nature GeoScience*, **5**, 551–556.
- Sims DA, Brzostek EP, Rahman AF, Dragoni D, Phillips RP (2014) An improved approach for remotely sensing water stress impacts on forest C uptake. *Global Change Biology*, **20**, 2856–2866.
- Smithwick EH, Turner M, Mack M, Chapin FS III (2005) Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. *Ecosystems*, **8**, 163–181.
- Sorensen LH (1974) Rate of decomposition of organic matter in soil as influenced by repeated air drying-rewetting and repeated additions of organic material. *Soil Biology and Biochemistry*, **6**, 287–292.
- Sparks JP (2009) Ecological ramifications of the direct foliar uptake of nitrogen. *Oecologia*, **159**, 1–13.
- Stark JM, Firestone MK (1995) Mechanisms for soil moisture effects on activity of nitrifying bacteria. *Applied Environmental Microbiology*, **1**, 218–221.
- Stevenson IL (1956) Some observations on the microbial activity of remoistened air-dried soils. *Plant and Soil*, **8**, 170–182.
- Suseela V, Tharayil N, Xing B, Dukes JS (2015) Warming and drought differentially influence the production and resorption of elemental and metabolic nitrogen pools in *Quercus rubra*. *Global Change Biology*. doi:10.1111/gcb.13033.
- Sverdrup H (1990) *The Kinetics of Base Cation Release Due to Chemical Weathering*. University of Lund Press, Lund, Sweden.
- Tate RL, Ross DJ, Feltham CW (1988) A direct extraction method to estimate soil microbial C: effects of experimental variables and some different calibration procedures. *Soil Biology and Biochemistry*, **20**, 329–335.
- Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich JVK, Moore B, Vorosmarty CJ (1998) Effects of interannual variability on carbon storage in the Amazon Basin. *Nature*, **396**, 664–667.
- Tobita H, Uemura A, Kitao M, Kitaoka S, Utsugi H (2010) Interactive effects of elevated CO₂, phosphorus deficiency, and soil drought on nodulation and nitrogenase activity in *Alnus hirsuta* and *Alnus maximowiczii*. *Symbiosis*, **50**, 59–69.
- Turner MG, Romme WH, Tinker DB (2003) Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment*, **1**, 351–358.
- Ulery AL, Graham RC, Amrhein C (1993) Wood-ash composition and soil pH following intense burning. *Soil Science*, **156**, 358–364.
- Van Mantgem PJ, Stephenson NL, Byrne JC *et al.* (2009) Widespread increase of tree mortality rates in the western United States. *Science*, **323**, 521–524.
- Vargas R, Sonnentag O, Abramowitz G *et al.* (2013) Drought influences the accuracy of simulated ecosystem fluxes: a model-data meta-analysis for Mediterranean oak woodlands. *Ecosystems*, **16**, 749–764.
- Vergutz L, Manzoni S, Porporato A, Novais RF, Jackson RB (2012) Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecological Monographs*, **82**, 205–220.
- Wan S, Hui D, Luo Y (2001) Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecological Applications*, **11**, 1349–1365.
- Waring RH, Schlesinger WH (1985) *Forest Ecosystems: Concepts and Management*. Academic Press, San Diego.
- Weed AS, Ayres MP, Hicke JA (2013) Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*, **83**, 441–470.
- Wells CG (1971). Effects of prescribed burning on soil chemical properties and nutrient availability. In: *Prescribed Burning Symposium Proceedings*, pp. 86–97. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, NC.
- Wetselaar R (1968) Soil organic nitrogen mineralization as affected by low soil water potentials. *Plant and Soil*, **29**, 9–17.
- Wiedinmyer C, Hurteau MD (2010) Prescribed fire as a means for reducing forest carbon emissions in the western U.S. *Environmental Science and Technology*, **44**, 1926–1932.
- Wood TE, Cavaleri MA, Reed SC (2012) Tropical forest carbon balance in a warmer world: a critical review spanning microbial- to ecosystem-scale processes. *Biological Reviews*, **87**, 912–927.
- Wu Z, Kijkstra P, Koch GW, Penuelas J, Hungate BA (2010) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology*, **17**, 927–942.
- Wurzburger N, Miniati CF (2014) Drought enhances symbiotic dinitrogen fixation and competitive ability of a temperate forest tree. *Oecologia*, **174**, 1117–1126.
- Xiao JF, Zhuang QL, Law BE *et al.* (2010) A continuous measure of gross primary production for the conterminous United States derived from MODIS and AmeriFlux data. *Remote Sensing of Environment*, **114**, 576–591.
- Xiao J, Zhuang Q, Law BE *et al.* (2011) Assessing net ecosystem carbon exchange of US terrestrial ecosystems by integrating eddy covariance flux measurements and satellite observations. *Agriculture and Forest Meteorology*, **151**, 60–69.
- Xu X, Schimel JP, Thornton PE, Song X, Yuan F, Goswami S (2014) Substrate and environmental controls on microbial assimilation of soil organic carbon: a framework for Earth system models. *Ecology Letters*, **17**, 547–555.
- Zhang F, Chen JM, Pan VD, Birdsey RA, Shen SH, Ju WM, He LM (2012) Attributing carbon changes in conterminous U.S. forests to disturbance and non-disturbance factors from 1901 to 2010. *Journal of Geophysical Research-Biogeosciences*, **117**. doi:10.1029/2011JG001920.
- Zhao MS, Running SW (2010) Drought-induced reduction in global terrestrial net primary production from 2000 to 2009. *Science*, **329**, 940–943.