Ecohydrological Implications of Drought

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Introduction

Ecohydrology focuses on the interactions and interrelationships between hydrological processes and the structure and function of vegetation (Breshears 2005, Rodriguez-Iturbe 2000). It builds on a long history of watershed science that quantified how changes in vegetation (e.g., through purposeful manipulation, succession, or natural disturbances) alters water and streamflow dynamics at catchment scales (Bosch and Hewlett 1982, Vose and others 2014). Recent papers have broadened the scope to include understanding soil moisture dynamics (D'Odorinco and others 2010, Emanuel and others 2010), human-dominated landscapes (Jackson and others 2009), and the sensitivity of ecosystem transitions after disturbance (Viglizzo and others 2014). In this chapter, we focus on how drought affects the interrelationships among forest structure and function, hydrologic processes, and streamflow dynamics.

Forests naturally grow where water is sufficient to support perennial woody vegetation, as forest evapotranspiration (ET) is typically much greater than other vegetation types (Frank and Inouye 1994, Sun and others 2011). Where precipitation (P) inputs substantially exceed ET losses, surface water draining forest land is typically of high quality and supports many human uses, including drinking water, agriculture, and industrial activities (Binkley and Brown 1993, Vose and others 2011). Forests also maintain relatively clean and cold water and are important for supporting aquatic ecosystems, particularly coldwater fishes (Peterson and others 2013, Rieman and others 2003). In addition to being important for providing high-quality surface water supply, forests modulate the quantity and timing of streamflows by intercepting and transpiring precipitation (Sun and others 2011) and influence snowmelt timing (Cristea and others 2013). Forests are also commonly important areas for groundwater recharge (Price 2011) and flood mitigation (Beschta and others 2000, Jones and Perkins 2010).

In simple terms, drought means less water—less water for plants and less water for streams. In some regions, seasonal droughts are common, and forest and stream ecosystems often adapt to these somewhat predictable disturbances through various physiological, morphological, and behavioral adaptations (Lytle and Poff 2004, McDowell and others 2008). In contrast, multiyear or severe droughts are less predictable, and hydrological

and biogeochemical responses can be substantial (Lake 2003). This is especially true when very low precipitation is combined with warmer temperatures (Diffenbaugh and others 2015). The relationships among drought, surface water flow, soil water availability, and groundwater recharge are not straightforward for most forest ecosystems due to several factors, including the role of vegetation in the forest water balance. Hydrologic responses to drought can be either mitigated or exacerbated by forest vegetation depending upon vegetation water use and how drought affects forest population dynamics.

We can conceptualize a simple framework for assessing the drought sensitivity of a forest catchment by describing it as a series of four hydrologic pools: (1) vegetation, (2) soil, (3) groundwater, and (4) streams (fig. 10.1). Examining the sensitivity of streamflow to drought can be framed by looking at the duration that water is held in each pool and how much evaporative or transpiration losses occur from those pools. The first pool to intercept P is the vegetation surface (i.e., leaves, stems, boles). Some of the intercepted P (10–40 percent) evaporates back into the atmosphere. The wide range in intercepted P lost to evaporation is primarily related to vegetation surface area and rainfall characteristics, with a greater percentage of P intercepted with larger surface area and during light rain events (Eagleson 2002, Waring and Schlesinger 1985). Precipitation that is not intercepted (i.e., throughfall and stemflow) enters the forest floor where some (or all) may evaporate from the litter layer, or it may
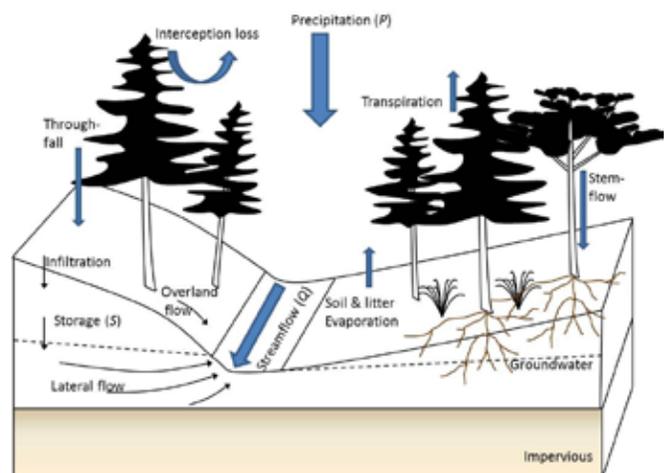
Figure 10.1—Conceptualization of major water pools and fluxes in a forested catchment. The catchment water balance can be viewed as partitioning of precipitation into evapotranspirative and drainage fluxes.

move across the leaf/soil surface as overland flow. The remainder enters the soil water storage pool. Stored soil water can be evaporated or transpired by plants before becoming streamflow or recharging groundwater. While some water is temporarily stored in the roots and boles, most of the soil water taken up by tree roots moves through the internal vegetation pool quickly and returns to the atmosphere. For some forests, roots capture much of the water that does not freely drain to groundwater within a brief period after precipitation (Brooks and others 2009). If roots can access groundwater, they can deplete groundwater pools. However, when groundwater pools contain sufficient water, they can provide long-term base flows (Tague and Grant 2009), buffering streamflow against long periods without P.

The connections among the pools can be expressed using a simple water balance equation:

$$Q = P - ET - \Delta S$$

where Q represents streamflow and is the balance of precipitation inputs (P) after losses to evapotranspiration (ET), which is the sum of interception, transpiration, and soil evaporation, and changes in storage (ΔS). Over the short term, all four variables can change dramatically; however, over the long term (e.g., annually), change in ΔS is typically minor and is therefore often assumed to be zero. Thus, Q can be estimated as P minus ET. The assumption that changes in storage are zero under severe drought conditions may not be correct in some instances and may yield incorrect interpretations of the impacts of drought on Q using $P - ET$ approaches (Creutzfeldt and others 2012, Vose and Swank 1994). Regardless, Q can change in response to drought directly through reductions in P and indirectly via ET responses to changing evaporative energy and water availability; however, these responses are especially complex.

For a particular watershed, drought effects on Q can vary greatly in space and time depending on the timing of reduced precipitation inputs (growing season versus nongrowing season), the magnitude of precipitation deficit, and watershed characteristics (e.g., vegetation, watershed size and configuration, terrain features, soil depth and storage capacity, and hydrogeology). For example, on shorter time scales, ET can exceed P, particularly when water used in ET is derived from soil water stores or deeper groundwater stores, rather than recent or local P (Loheide and others 2005, Lubczynski and Gurwin 2005).

In this chapter, we (1) review the relationships between meteorological and hydrologic drought; (2) examine how differences in forest species composition and structure impact evapotranspiration, and we interpret these changes in the context of mitigating or exacerbating hydrologic drought; and (3) discuss the impacts of hydrologic drought on watershed processes and water quality.

Relationship Between Meteorological Drought and Hydrologic Drought

Meteorological drought is defined as the degree and duration of dryness relative to the average (chapter 2); the effects of meteorological drought on streamflow may differ across and within forest ecosystems. Hydrologic drought, defined as decreases in streamflow below a threshold level (chapter 2), is complex and difficult to relate to meteorological drivers. In this section, we describe how catchment characteristics and precipitation patterns influence the relationship between meteorological and hydrologic drought.

Catchment-Scale Sensitivity to Meteorological Drought

The catchment water-balance equation provides a conceptual framework for evaluating differential sensitivities of ET and Q to drought. In general, sensitivity depends most strongly on temporal and spatial storage in soil and groundwater pools, as well as snowpack in snow-dominated ecosystems. For example, in places with deep soils and hence greater soil water storage, there may be an apparent reduced sensitivity of ET and Q to reduced precipitation (Boggs and others 2013, Ohnuki and others 2008) that may help enhance resilience to drought (Taylor and others 2013). In contrast, steep, coarse, and shallow soils that cannot retain water may represent systems with high ET and Q sensitivity to reduced precipitation. If accessible by trees roots, soil stores are more vulnerable to ET, so they deplete more rapidly and approach a state of near zero discharge much sooner (Fan and Miguez-Macho 2011).

The sensitivity of low flows to meteorological drought in places with deep or substantial groundwater storage should be thought of in two ways (Tague and Grant 2009). In terms of absolute flow, they are more sensitive than systems with little storage because they generally sustain greater baseflow than systems with shallow and tight bedrock, and even a small fractional decline in low flows can be a large amount of water. In

contrast, places with little baseflow cannot decline far in absolute terms, simply because there is already so little runoff. However, when cast as a percent change due to either drought duration or precipitation recharge, the systems with greater groundwater storage are less sensitive. This differs from sensitivity to variations in the soil store, as we defined it, because water stored in soils (generally places where roots are more abundant) is vulnerable to ET, but deep groundwater is not.

Streamflow from forests where the snowpack makes up a large proportion of annual P is more sensitive to precipitation declines. When the annual precipitation is delivered as meltwater in one relatively large pulse, runoff generation is more efficient, and variations in potential ET have little effect on the total annual runoff, which is essentially dependent on how much snow accumulates and then melts. Similarly, if most of the precipitation falls in the cold season, it is less vulnerable to evaporation and is converted more efficiently to runoff. In such cases, ET may vary little as a function of precipitation, but variations in P will be transmitted to runoff reliably on an annual scale (Berghuijs and others 2014, Wolock and McCabe 1999), similar to more humid

locations (Milly and Dunne 2002) and locations with greater seasonality in P (Wolock and McCabe 1999).

High degrees of snow heterogeneity caused by drifting or large elevation ranges in a basin provide substantial buffering of Q variation through the year because deep drifts and high-elevation snowpacks do not melt until late in the summer (Luce and others 1998, Wolock 2003). Snowpack meltwater is slowly released during warmer periods in these systems, making them less vulnerable to variations in summertime precipitation. Buffering from snow heterogeneity is probably most pronounced in the high mountains of the Western United States (Clark and others 2011). We illustrate the spatial variability of drought sensitivity impacts on water yield as a response to a uniform reduction of precipitation in figure 10.2 (Sun and others 2015).

Interactions With Precipitation Patterns
Reduced P not only affects Q through the amount of water available, but also through its timing. For example, in snowpack-dominated areas of the Western United States, a low snowfall winter creates a shallower snowpack that takes less time to melt and can create

Percent reduction in water yield
- -33 to -20
- -19 to -10
- -9 to -5
- -4 to 0
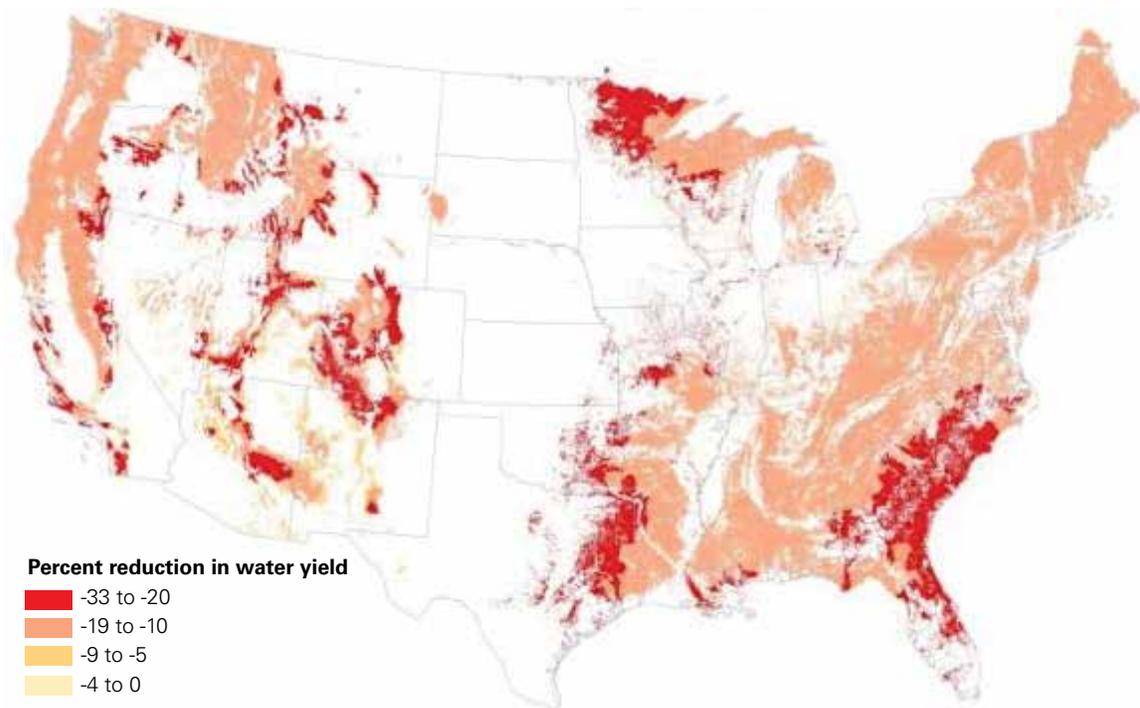
Figure 10.2—Spatial distribution of annual forest water yield response (percent reduction in water yield) to a 10-percent decrease in precipitation across the conterminous United States. Darker shades represent a greater percent reduction relative to lighter shades. Simulation results at the U.S. Geological Survey HUC-8 scale are presented at 1-km resolution by a mask of forest land cover (Source: Sun and others 2015).

an expectation for lower flows in late summer (Cayan and others 2001, Stewart and others 2005, Tague and Grant 2009). While low elevation snowpacks are more sensitive to temperature in determining the melt timing (Mote 2006), the effect of P variability on center of timing of outflow can be quite pronounced from high elevation basins (Luce and Holden 2009). Warming can also shift the elevation of the transition zone between rain and snow, and rain on snow events (Surfleet and Tullos 2013), both of which impact streamflow timing. The synoptic weather patterns giving rise to prolonged drought can also shape the nature of P events, making the relationship between hydrologic drought and meteorological drought dynamic (Potter and Chiew 2011). If limited ET occurs due to dry land surface conditions, convective storms may produce less intense P and less P during a given storm. The reduction in P has implications for a greater proportion being intercepted by canopies or held in soil, reducing runoff. Water added to wet soils or vegetation is more likely to contribute to recharge compared to periodic wetting of a relatively dry soil or canopy. Higher interception evaporation maximizes the potential for recirculation of water between land and atmosphere, but also exacerbates Q responses during prolonged dry periods.

Species Composition, Vegetation Dynamics, and Drought Interactions With Streamflow

Understanding and predicting the complex interactions among species, vegetation dynamics, and streamflow requires integrating atmospheric conditions, above- and belowground plant physiological processes, forest stand dynamics, soil water availability, and streamflow generation processes. Many of these components are discussed in detail in other chapters of this assessment (i.e., chapter 2 characterizes drought for forests and rangelands; chapter 3 summarizes the physiological responses of forest tree species to drought; and chapter 4 addresses drought impacts on forest structure, dynamics, and diversity).

Assessing the ecohydrological implications of drought requires quantification and understanding of how the individual components interact to determine hydrologic responses. Due to the challenges associated with linking ecological and hydrological processes, much of our insight into ecohydrologic feedbacks has been derived from quantifying short-term, species-specific physiological processes from experimental studies; linking and projecting long-term vegetation dynamics;

and interpreting long-term streamflow dynamics under varying ecohydrological conditions.

Vegetation structure and species composition directly impact the hydrologic cycle because they exert significant control on several hydrologic fluxes: evaporation, transpiration, canopy interception, forest floor interception, infiltration, overland flow, groundwater recharge, and streamflow (fig. 10.1). Given that transpiration can represent up to approximately 70 percent of ET (Schlesinger and Jasechko 2014) and ET can represent >100 percent of P (e.g., when ET includes stored soil water or groundwater sources) (Sanford and Selnick 2012), changes in transpiration (e.g., due to shifts in species assemblages) can substantially impact stand water balance and downstream water supply. If drought frequency and duration increase, these will likely lead to significant changes in vegetation structure and species composition. While some trees will die as a direct consequence of moisture stress and cavitation (chapter 3), the interaction between drought and other stressors such as insects and pathogens may be an even more important driver of drought-related mortality (chapter 6).

Extreme droughts and heat waves have already triggered widespread tree mortality globally (Allen and others 2010, Weed and others 2013), and there is observational evidence that forests across all biomes might be equally vulnerable to drought (Choat and others 2012). The detailed physiological mechanisms and thresholds that determine when mortality or dieback will occur for different species are addressed in chapter 3. Here we provide an overview of the potential impacts of drought on species assemblages and consequences for ecohydrological processes, while highlighting examples from different regions within the United States that illustrate possible scenarios for future change.

Generally, when mortality rates increase for a particular species or set of species, whether due to climatic, biotic, or other drivers, stand density of live mature trees decreases and stand leaf area index and productivity decline. This process may either occur abruptly, as in the case of rapid mortality in response to an acute stressor [e.g., eastern hemlock (*Tsuga canadensis*) mortality following attack by hemlock woolly adelgid (*Adelges tsugae*), or western juniper (*Juniperus occidentalis*) mortality following severe drought], or gradually, as in the case of chronic diseases that slowly diminish the health of host trees [such as with beech bark disease (*Neonectria* spp.) infecting American

beech (*Fagus grandifolia* Ehrh.)]. Extensive research in mesic forest ecosystems has shown that a reduction in forest cover generally reduces stand transpiration and leads to an increase in streamflow (Bethlahmy 1974, Bosch and Hewlett 1982, Hadley and others 2008, Stednick 1996, Zhang and others 2001); however, these forest-streamflow relationships are less well understood in semi-arid regions and are potentially very different than mesic regions (Wilcox and Thurow 2006). In northern temperate regions, the reduction in canopy cover leads to greater snow accumulation and more rapid snowmelt due to decreased canopy interception and increased solar radiation reaching the forest floor (Boon 2012, Pugh and Small 2012). Depending on the temporal and spatial dynamics of the die-off process, resources that become available after tree mortality are eventually utilized by existing co-dominant mature trees and/or existing or newly regenerating seedlings and saplings in the understory and mid-story; often (but not always) these changes are associated with a shift in species composition.

Because different species and functional groups vary in their ecophysiological traits that influence water use patterns (chapter 3), changes in species assemblages can alter hydrological processes from the stand to the watershed scales. Below, we highlight examples from different regions of the United States of species shifts resulting from global change drivers to illustrate the potential ecohydrological impacts.

Northeastern Region

Although the Northeastern United States is expected to experience an increase in total annual precipitation (mostly in the winter and spring), and an increase in large rainfall events, it is also projected to have more prolonged rainless periods, particularly in mid- to late-summer (Swain and Hayhoe 2014). While the mixed deciduous-coniferous forest ecosystems that dominate the Northeast are more limited by radiation and nutrients than water (Vadeboncoeur 2010), paleoecological evidence suggests that previous droughts have strongly influenced changes in species assemblages and ecosystem dynamics; consequently, such extreme events may be outside the range of species' capacities for adaptation and resilience (Pederson and others 2014). Future drought stress will likely be concomitant with biotic stressors that also may be outside the physiological tolerance of these forests (Dietze and Moorcroft 2011, Groffman and others 2012, Lovett and others 2006). Thus, the ecohydrological effects of tree mortality due to these multiple stressors are particularly

relevant for managing water resources in the Northeast. Here, we discuss two species affected by such climate change-biotic agent interactions specifically within the context of increasing drought stress and potential ecohydrological implications.

Eastern hemlock, an ecologically important species throughout much of its geographical range, is currently experiencing rapid decline due to the hemlock woolly adelgid (HWA), an exotic insect that has invaded forests from Georgia to Maine (Fitzpatrick and others 2012). The primary factor limiting the spread of HWA is overwintering temperatures; increasing winter temperature has accelerated the invasion process and associated hemlock mortality (Paradis and others 2008). Once attacked, eastern hemlock trees usually die within 4–5 years (Young and others 1995); thus, HWA infestations create an acute disturbance event that abruptly changes stand structure and composition.

The most likely scenario for these forests is that hemlock will be replaced by broadleaved deciduous species (Ellison and others 2005, Ford and others 2012). Research shows that this shift in the dominant species will result in higher annual transpiration rates and total ET, in turn causing small decreases in streamflow during the growing season and increased peakflow after large storm events in the dormant season due to decreased canopy interception (Brantley and others 2013, Brantley and others 2014, Ford and Vose 2007). Another hydrologic control of these dense evergreen canopies is their insulating effect on snowcover (Lustenhouwer and others 2012); consequently, hemlock loss and subsequent warming air temperatures will likely alter snowmelt and runoff dynamics during the winter-spring transition period. Post mortality regeneration may offset these impacts to some degree, but impacts will be long lasting if the evergreen canopy is replaced with a deciduous canopy. Finally, while the above studies show that hydrologic impacts of hemlock loss are likely, eastern forests may experience minimal long-term effects on carbon fluxes (Albani and others 2010) because although there can be rapid mortality of hemlock trees following HWA invasion, subsequent replacement by other species—such as red maple (*Acer rubrum* L.), birch (*Betula* spp.), oaks (*Quercus* spp.) and American beech (*Fagus grandifolia* Ehrh.)—also occurs relatively rapidly (Cobb 2010, Ford and others 2012).

American beech has experienced decline since the early 20th century due to beech bark disease (BBD), which is caused by infestation by the exotic scale insect,

Cryptococcus fagisuga (Lind.), and subsequent infection by one or more fungi (Kasson and Livingston 2012). In contrast to HWA, BBD is a chronic disturbance that slowly diminishes the host tree's vitality and health, but usually does not directly cause mortality. Evidence also suggests that a prolonged period of mild winters and drier-than-normal late summers (including a major drought) triggered a significant growth decline and mortality in BBD-infected trees in Maine (Kasson and Livingston 2012); this suggests that the disease lowers the resistance of trees to other stressors. Predictions for future BBD-affected stands are that other associated or co-dominant species, particularly sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*), will replace this species (Forrester and others 2003, Hancock and others 2008, Lovett and others 2013).

Given the slow progression rate of BBD, the shift in forest structure and species composition is expected to also occur gradually, which is confirmed by the lack of a significant change observed in aboveground net primary production in BBD-affected stands in the Catskills region of New York (Hancock and others 2008). Consequently, impacts on the hydrologic cycle may also be gradual (Busby and Canham 2011). Moreover, because many of the associated species (e.g., sugar maple, yellow birch) have similar ecological characteristics and functions to American beech, including transpiration, leaf hydraulic traits, and vulnerability to cavitation (Hoffmann and others 2011, Wullschleger and others 2001), these changes may not significantly alter stand transpiration and, hence, runoff and streamflow dynamics, although effects will likely vary across different forests and geographic regions.

Western Mountain Region
Recent warming trends and more prolonged and frequent droughts have accelerated the spread and intensity of attacks by mountain pine beetle (MPB) (*Dendroctonus ponderosae*) and increased the susceptibility of host trees, resulting in widespread mortality of five-needle pine and affecting more than 600,000 km^2 of coniferous forests in western North America since 1996 (Weed and others 2013). Forests that are already water stressed appear to be more vulnerable to severe MPB attacks (Kaiser and others 2013). Because these outbreaks often kill nearly all of the canopy trees within forest stands, they influence the energy balance of the land surface and potentially affect many hydrologic processes (Potts 1984, Pugh and Gordon 2013). MPB-infested watersheds will likely experience a decrease in ET, but an increase in

snow accumulation and earlier and faster snowmelt; combined, these processes would lead to increases in runoff volume and a change in timing (Mikkelson and others 2013). As a whole, MPB-infested watersheds would be at greater risk for flooding in the spring and drought in the summer (Mikkelson and others 2013).

Similarly, increased wildfire in western U.S. forests (chapter 7) would be expected to change water yield, timing, and flood potential in basins after fire. Small basins (on the order of 10–20 km^2) have shown substantial increases in post-fire debris flows and flooding (Cannon and others 2001, Istanbulluoglu and others 2004, Moody and Martin 2009). However, increases in post-fire flooding have not been noted for large basins on the order of 2,000 km^2, despite a great enough portion of the basin burning to cause increases in basin water yield by 5 percent (Luce and others 2012).

Southwestern Pinyon-Juniper Woodlands
One region and vegetation type most severely affected by extreme drought and heat events— often in combination with associated increases in stress from biotic agents—is the pinyon-juniper woodlands of the Southwest United States. As a result of these extreme events, this vegetation type has experienced major changes in mortality rates and species composition throughout much of this region, with significant ecohydrological consequences. For instance, widespread mortality has occurred in pinyon pine populations, while western juniper trees have exhibited relatively high survival (Plaut and others 2012) (chapter 3 for mechanisms). During the 2000–2002 severe drought event, streamflow from southwestern watersheds decreased following tree die-off, likely due to increases in the understory vegetation after release from competition and shade, and subsequent reductions in overland flow (Guardiola-Claramonte and others 2011). Widespread vegetation die-off can have contrasting ecohydrological impacts in water-limited versus high rainfall regions; these observations underscore the need for more research to understand the vegetation-drought-hydrology interactions and feedbacks that determine watershed scale effects on streamflow dynamics (Adams and others 2012).

Southern Region
Extensive forest areas in the Southern United States have experienced severe droughts in recent years causing widespread tree mortality in many regions (Elliott and Swank 1994, Klos and others 2009). Some tree species and size classes are more vulnerable than others (chapter

4), suggesting the potential for drought-mediated shifts in both species composition and structure. For example, Klos and others (2009) reported higher drought-related mortality in pine and mesophytic species groups (e.g., *Liriodendron tulipifera, Acer* spp., *Betula, Fagus, Magnolia*) than in oaks (*Quercus* spp.). In contrast, Clinton and others (1993) documented a higher mortality in larger and older oak (especially *Quercus coccinea*) associated with interactions between drought and root pathogens.

Tree-level sapflow data suggest wide variation in whole-tree daily water use among species groups, and different sensitivities to water stress depending on xylem anatomy. A two- to three-fold difference among species (holding tree size constant) in mean daily water use can occur in these forests (Ford and others 2011b), with oaks (e.g., *Quercus rubra, Quercus prinus*) generally having lower water use than more mesophytic species (e.g., *Betula lenta, Liriodendron tulipifera*) (figs. 10.3 and 10.4). While oaks and hickories have a potential for high water use based on the diameter of their xylem conduits, field observations across the region suggest that these species operate under a fraction of this potential, thus lending support for their low observed water use (fig. 10.4). These tree-based data suggest that drought-related shifts in species composition may impact streamflow, as has been demonstrated by sapflow and ecohydrological studies on species such as eastern hemlock (discussed earlier), and in small paired

watershed studies of hardwood to pine conversions (Ford and others 2011b); however, drought-related changes in species composition may be much more difficult to detect, especially in diverse stands and at larger spatial scales (Patterson and others 2013).

Range Shifts in Major Ecosystem Types in Response to Climate Change

Thus far we have focused the discussion on the ecohydrological impacts of tree mortality of certain species due to drought and interactions with biotic agents; but model projections and some empirical evidence suggest that entire communities will shift their range in response to climate change. In the New England region, models project that by the late 21st century 71–100 percent of boreal conifer forests will be lost; the range of mixed oak-hickory forests will shift northward by 100–200 km and expand by 149–431 percent; and northern deciduous hardwoods will decrease in area by 26 percent (Iverson and Prasad 2001, Tang and Beckage 2010, Tang and others 2012). However, within a community type, individual species' responses will depend on phenology and physiology, with some species benefiting more from decreased stomatal conductance and increased water use efficiencies in response to rising carbon dioxide (CO_2) (Tjoelker and others 1998).
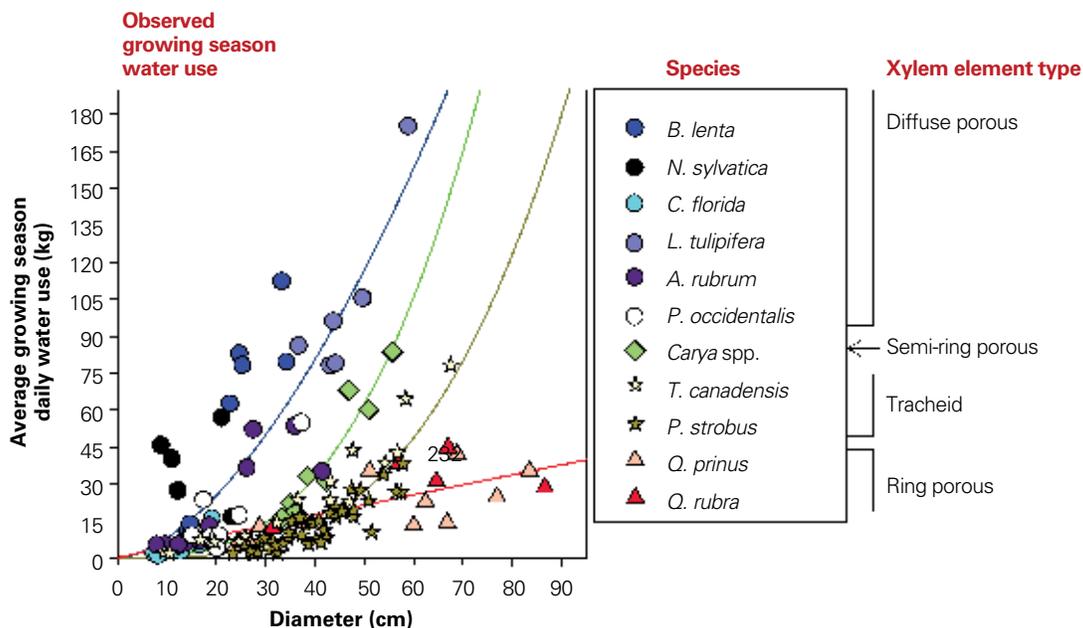
Figure 10.3—Average growing season daily water use across species sampled in the Coweeta Basin. (Source: Ford and others 2011).

(A) Southern Appalachian

(B) Piedmont
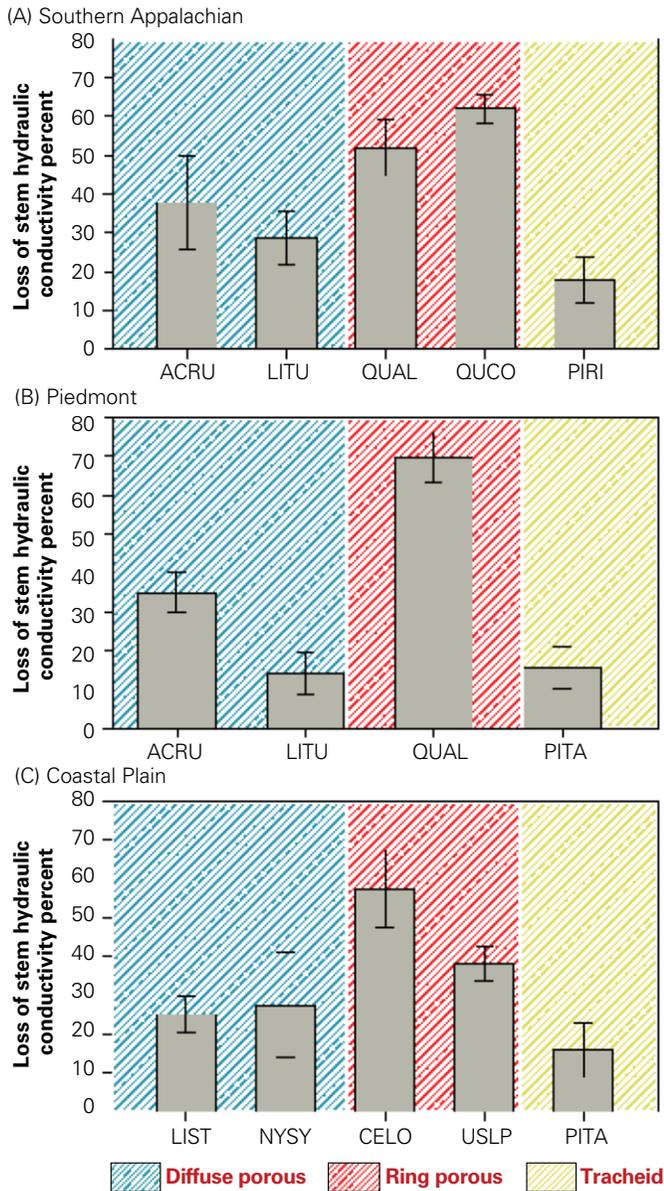
(C) Coastal Plain

Figure 10.4— Percent loss of hydraulic conductivity (PLC) for co-occurring species varied by xylem type across a regional gradient from (A) Southern Appalachian forests to (B) Piedmont forests to (C) Coastal Plain forests. Ring-porous trees had >50 percent dysfunction under the same soil water potentials as diffuse porous and tracheid-type species. Evidence suggests that mortality occurs when plants experience >80 percent dysfunction. Bars represent the mean PLC across five individuals from each species sampled three times throughout the growing season (May, August, and October 2010). Bars are standard error. PLC was determined using a flowmeter (Xyl'em, Bronkhorst,® France) and the following equation: {[ks(max)-ks(P)]/ks(max)}, where ks(P) is the hydraulic conductivity at the time of sampling from the field, and ks(max) is the conductivity determined after fully saturating the sample under vacuum for 24 hours or with high positive pressure. ACRU=red maple; LITU=tulip poplar; LIST=sweetgum; NYSY=black gum; QUAL=white oak; QUCO=scarlet oak; CELO=sugarberry; ULSP=American elm; PIRI=pitch pine; PITA=loblolly pine. (Source: unpublished data;C.F. Miniat and J.M. Vose. On file with: C.F. Miniat, Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Road, Otto, NC 28763; cfminiat@fs.fed.us).

For example, species with evergreen sclerophyllous leaves that characteristically have high mesophyll resistance are predicted to benefit more from increased CO_2 concentrations compared to deciduous broadleaved species (Niinemets and others 2011). The amount of time required for communities to reach a new equilibrium is uncertain; however, observations from past migration rates suggest that species may not keep pace with their climate envelopes (Loarie and others 2009).

Changes in future rainfall patterns may also affect the competitive interactions among species and thus affect the outcome of range shifts (Clark and others 2014a, Clark and others 2014b). For example, because northern deciduous hardwoods tend to be physiologically less drought tolerant than mixed oak-hickory, an increase in precipitation [as predicted by Swain and Hayhoe (2014)] may favor the former and enable them to persist to a greater extent within their current range. Because trees are long-lived, range shifts of forest ecosystems will be a slow process; however, initial shifts are already being detected in the understory regeneration. For instance, Fisichelli and others (2014) showed that seedlings and saplings of temperate forest tree species are establishing across local ecotones into boreal forest patches in central North America, a process facilitated by warmer temperatures.

Boreal conifer regeneration has been negatively correlated with the regional temperature gradient and only displayed high abundance at the boreal end of local ecotones at cool northern sites, suggesting a reduced range for boreal forests in the future (Fisichelli and others 2014). In the Western United States, models project shifts in major vegetation types in response to climate change (Bachelet and others 2001). In addition to climate, an overarching influence on future vegetation types for the Western United States is fire and biotic disturbances (Hicke and others 2012, McKenzie and others 2004). Using models that combine changing fire regimes and climate, Halofsky and others (2013) project an overall decline in cool needle-leaf and subalpine forest vegetation types, and an increase in xeromorphic shrubland types.

Predicting how these changes will impact hydrologic processes at larger spatial scales presents a considerable challenge. Although tree-level physiological data and small watershed studies suggest a strong interaction between vegetation type, structure, and hydrologic processes, we do not know how these interactions and gradual changes will play out at larger landscapes and longer time scales.

Groundwater Interactions With Drought

When available to tree roots, groundwater may help vegetation avoid drought-induced effects (Ehleringer and Dawson 1992). This strategy is well-known in groundwater-dependent ecosystems (Orellana and others 2012) such as wetlands and riparian forests (Busch and others 1992, Thorburn and others 1992), but has also been recognized in upland systems (Dickson and Tomlinson 1996, Miller and others 2010), which can be referred to as groundwater-influenced ecosystems.

Groundwater-dependent ecosystems dominated by phreatophytes, plants dependent on groundwater for their water supply (Meinzer 1927, Robinson 1958), are well studied. Examples include deep-rooted trees and shrubs including cottonwood (*Populus* spp.), willow (*Salix* spp.), salt cedar (*Tamarix* spp.), greasewood (*Adenostoma fasciculatum, Baccharis sarothroides, Glossopetalon spinescens, Larrea tridentate,* and *Sarcobatus vermiculatus.*), and mesquite (*Prosopis* spp.). Phreatophytes can be obligate or facultative depending on whether they rely on perennial access or intermittent access to groundwater to avoid drought (Smith and others 1998), with examples in the latter category including sagebrush (*Artemesia* spp.) and rabbitbrush (*Chrysothamnus* spp.) (Nichols 1994). Phreatophytes (particularly those in arid regions) also employ a diverse array of other drought-avoidance and drought-tolerance strategies to survive dry periods including control of the magnitude and timing of leaf area, osmotic potential, leaf conductance, and maintenance of turgor at low leaf water potential (Nilsen and others 1984).

The groundwater subsidies, as defined by Lowry and Loheide (2010), are provided to groundwater-dependent and groundwater-influenced ecosystems buffering them from adverse effects of drought. Maps depicting estimates of depth to groundwater (see fig. 4 in Fan and others 2013) reveal that it is generally <5 m across vast regions of the United States, which is within the critical range required to help offset the impacts of drought in forests and many other ecosystems (Lowry and Loheide 2010, Maxwell and Kollet 2008, Soylu and others 2014). Even when groundwater is not regionally shallow, riparian and other areas may have shallow groundwater (Fan and others 2013) resulting in local areas where groundwater is not sufficient to buffer drought. Heterogeneity in

groundwater depth across the landscape suggests the potential for management and protection strategies aimed at specific resources as the landscape becomes further fragmented into natural, urban, and agricultural systems (Jackson and others 2009).

Challenges to Predicting the Impacts of Drought on Hydrological Processes

Sensitivity analysis and empirical data suggest that the magnitude of hydrologic responses to droughts, due to climate warming or/and reduction in precipitation, vary tremendously under different regimes (Lu and others 2013, Ma and others 2008). Predicting short-term responses to moderate- and short-duration droughts is generally straightforward, especially if drought does not change above- and belowground forest structure. For example, at monthly or annual time scales over large areas, hydrologic models can capture much of the drought-related streamflow dynamics that occur simply as a direct result of reduced precipitation, or indirectly using an empirical soil moisture feedback (Caldwell and others 2012, Sun and others 2011).

In addition to climatic dryness (potential ET/P), terrain characteristics, land cover types, biomass, and soils all influence the potential impacts of droughts on watershed hydrology. This complexity poses considerable challenges for predicting the impacts of drought on hydrological processes. Adding leaf-level physiological responses (either mechanistically or empirically) and soil moisture dynamics can increase predictive ability (Hanson and others 2004), although often these are "big-leaf" models that homogenize canopy variation and belowground responses.

Considerable uncertainty can result if models are unable to accurately account for above- and belowground structural and functional vegetation responses that can occur after severe and/or long-term drought (Luo and others 2008, Tague and others 2013). Examples of long-term vegetation responses to drought include reduced leaf area index from abscission or mortality, altered root-to-shoot ratios (Joslin and others 2007), differential species responses in mixed species stands (Ford and others 2011a), and changing species composition (Anderegg and others 2013, Klos and others 2009). All of these factors drive or feed back to ET, ultimately influencing stand water balance and streamflow.

One of the limitations of physically based modeling approaches is that changes in vegetation structure (e.g., reduced leaf area, changing root distributions, etc.) and function (e.g., shifts to species with different mechanisms for regulation of water use) that may occur in response to severe drought are often not explicitly incorporated in the framework and require direct empirical investigation to understand (Powell and others 2013). For example, short-term droughts (e.g., <1 year) may dry up depressional forested wetlands in the Southeastern United States, but hydrologic processes recover quickly and trees are rarely subject to water stress due to changes in soil water storage in wetlands (Lu and others 2009, Sun and others 2010). However, long-term droughts could alter wetland hydrology to an extent that causes permanent changes in plant community composition and fire regimes (De Steven and Toner 2004) resulting in altered hydrologic processes at larger spatial scales. Furthermore, lumped parameter ecosystem models that intend to describe the effects of soil water on ecological processes such as carbon cycling, often treat soil water and nutrient movement in a rather simplified fashion. For example, lateral flow and topographic effects on soil water distribution on the landscape are usually not accounted for in ecosystem models (Govind and others 2009); however, modeling approaches that account for subsurface hydrologic connectivity suggest strong spatial controls on ecosystem processes (Emanuel and others 2010, Hwang and others 2009).

More accurate predictions of the impacts of severe and longer term drought (especially when vegetation changes occur) will require models that couple hydrologic and ecosystem processes in a dynamic context with appropriate feedbacks (Law 2014). It is expected that ecosystem-specific models are needed to more fully determine hydrologic responses to extreme droughts, especially recent observations of "exceptional drought" arising from the combination of very low precipitation and warmer temperatures (Diffenbaugh and others 2015). This is not a trivial expectation, as it requires models that couple leaf-level physiology, above- and belowground whole-tree responses, root dynamics and soil water access, stand level responses, and physical hydrology (Tague and others 2013) and usually results in complex models that are difficult to parameterize and calibrate over large spatial scales.

Drought Impacts on Water Quality

Droughts not only affect the quantity of water in and flowing from forest ecosystems, but also water quality, having important implications for stream ecosystem services. Drought affects water quality both directly and indirectly. Direct impacts are primarily physical, as reduced streamflow concentrates nutrients and sediment, and warms more quickly. Indirect effects include a combination of terrestrial, riparian, and instream processes that impact sediment and nutrient concentrations and fluxes. The impacts of drought on terrestrial biogeochemical cycling processes are discussed in chapter 5. Here we focus primarily how those and other drought-related impacts influence water quality in forest streams.

Importance of Intermittent and Ephemeral Streams
Much of our understanding of the linkages among drought, streamflow, and water quality is derived from gauged perennial streams; less information is available on the impacts of drought on ephemeral and intermittent streams, despite the fact that these streams are a critical component of the hydrologic network in forested watersheds and river systems (Acuña and others 2014, Larned and others 2010, Lowe and Likens 2005). In terms of ecohydrological functions, intermittent and ephemeral streams serve critical roles for elemental cycling, connecting materials and energy exchange in watersheds (Lowe and Likens 2005) and river networks, and providing unique habitat for plants (Katz and Moore 2011) and aquatic and terrestrial species (McDonough and others 2011). They are most common in arid and semi-arid regions of the United States (Levick and Rogers 2008), but also occur frequently in the headwaters of forested watersheds in all regions (Hansen 2001, Larned and others 2010).

Intermittent streams are typically seasonal, and surface flows occur in response to snowmelt or elevated groundwater resulting from high precipitation or reduced ET, whereas ephemeral streams flow as a result of discharging groundwater and in response to runoff events (McDonough and others 2011). Due to their dependence on precipitation and/or snowmelt, intermittent and ephemeral streams are particularly vulnerable to drought (Palmer and others 2008). Increasing the duration or frequency of drought will

increase and alter periods of "no-flow" conditions and change hydrologic processes and aquatic habitats (Godsey and others 2014, Jaeger and Olden 2012).

These changing flow regimes are likely to have important implications for the timing and quantity of carbon, nutrient, and sediment exchanges with the perennial stream network, and alter habitat availability for fish and other aquatic organisms (Brooks 2009). Species that utilize ephemeral and intermittent streams already have adaptations to survive dry periods; however, whether these traits will allow for survival under longer, more frequent, and more extreme droughts is uncertain (Robson and others 2011) but of concern (Acuña and others 2014, Brooks 2009). For example, a prolonged drought had a much greater impact on fish and invertebrates in ephemeral and intermittent streams than in perennial streams in a Mediterranean climate (Beche and others 2009).

Stream Chemistry and Sediment

The terrestrial biogeochemical consequences of drought (chapter 5) are closely linked to changes in vegetation and hydrology (Dahm and others 2003). However, the effects on water quality can be highly variable depending on the characteristics of the site and broader region. The role of tree species on nutrient cycling is well documented (Finzi and others 1998, Pastor and others 1984); therefore, shifts in species composition may affect biogeochemical processes in soil that ultimately impact the chemical composition of streamwater (chapter 5). For example, Wurzburger and Miniat (2014) found that tree species that have the ability to form nitrogen gas (N_2)-fixing nodules in their roots do so more under conditions of moderate drought, adding a new source of nitrogen (N) into these systems that could be available for uptake and eventual leaching and stream export.

Drought may also affect the productivity of vegetation, having implications for stream chemistry. For example, Lutz and others (2012) suggested that streamwater nitrate concentrations are affected by temporal trends in fine root production and mortality during drought. In the early stages of drought, root production may initially increase as trees attempt to access soil water over broader areas (Hendrick and Pregitzer 1996), resulting in lower streamwater nitrate concentrations. Following drought, root mortality returns N to the system, resulting in higher stream nitrate concentrations. Secondary influences of drought on disturbances such as wildfire can also impact water chemistry and sediment (Goode

and others 2012, Smith and others 2011, Spencer and others 2003) (chapter 7 includes discussion of how drought affects fire severity and probability).

The combination of biological and hydrologic controls on water quality results in high complexity and spatial heterogeneity in response to drought. Concentrations of a particular solute in streamwater can increase at one location while decreasing at another. Droughts can have a concentrating effect on solutes in streamwater due to the limited volume of water. However, the flux of solutes in streamwater is generally lower during drought periods because less water is moving through the watershed. As streamflow declines, nutrients moving downstream are cycled more rapidly (Fisher and others 1998). This more rapid uptake of solutes within streams can have a strong influence on their concentration. For example, high streamwater silica concentrations are often observed during dry periods because silica is derived from mineral weathering and tends to increase when groundwater inputs dominate (Johnson and others 1969). However, several studies have reported declines in the concentration of dissolved silica during drought (Wall and others 1998, Williams and Melack 1997).

Wall and others (1998) determined that the low silica concentrations during a drought at Canajoharie Creek, New York, could only be attributed to instream processing, resulting from uptake by diatoms. Reduced streamflow velocity also enhances sediment and particulate organic matter deposition (Acuña and others 2007, Wood and Armitage 1999). Fine sediment deposition during drought has been shown to negatively affect stream organisms, such as macroinvertebrates and fish (Hakala and Hartman 2004, Kaller and Hartman 2004, Kemp and others 2011, Wood and Armitage 1997). In cases where streamflow ceases entirely, water becomes stagnant, and sediment, organic matter, and nutrients can accumulate in the pools that form. Severely reduced or eliminated flow, along with warmer temperatures, may promote algal growth (Caramujo and others 2008) and reduce dissolved organic carbon (DOC) in streams (Everard 1996). In most cases, the concentration and flux of DOC in streamwater are low during drought years compared to normal or wetter years. The reduced export of DOC during droughts has been attributed to factors such as diminished flow and changing flow paths (Eimers and others 2008, Portal and others 2009, Schindler and others 1997, Worrall and Burt 2008), decreased organic matter solubility during acidic episodes (Clark and others 2005, Clark and others

2006), and decreased production of DOC due to the inhibition of microbial processes associated with dry or acidic conditions during drought (Scott and others 1998).

Subsurface hydrologic flowpaths can also play a critical role in regulating the concentration of solutes in streamwater. During droughts, groundwater continues to travel along deep, long flowpaths, whereas less water flows along shallow groundwater paths. As the water residence time increases along these deep flowpaths, the contact time between groundwater and bedrock lengthens. This results in a higher concentration of streamwater solutes derived from geological weathering of bedrock. In contrast, during high flows, water tends to move more rapidly through upper soil horizons, resulting in higher concentrations of elements derived from organic matter, such as carbon (C) and nitrogen (N) (Raymond and Saiers 2010, Swistock and others 1989). Local lithology largely determines which elements will become more concentrated in streamwater during drought.

While it is typically difficult to determine when a drought begins, droughts are often punctuated by a more abrupt ending, at which point their biogeochemical impacts are most apparent. The first flush of water following drought has high concentrations of products that have accumulated in the soil (Burt and others 2014). Aerobic processes in the vadose zone produce nitrate, sulfate, and DOC that are transported to surface waters when a drought ends. The flushing of solutes can last for multiple storms, as saturated zones enlarge and hydrologic connections expand. Some solutes can have complex responses to drought, such as potassium, which has been shown to be influenced by changes in flowpaths, sediment transport, and the chemical properties of streamwater (Stott and Burt 1997). Other solutes with more predictable responses to drought are those that are sensitive to oxidation-reduction reactions. For example, sulfate and nitrate tend to exhibit the strongest and most predictable responses to drought, especially in streams that drain wetland and riparian zones, which are typically saturated.

Stream Temperature
Streamwater temperature is a critical water quality parameter that affects the chemical, biological, and ecological processes and functions of watersheds (Caissie 2006), and it influences the growth and distribution of aquatic organisms (Hester and Doyle 2011, Mohseni and others 2003). Droughts impact streamwater temperatures primarily by decreasing stream discharge (flow volume and velocity) and increasing solar radiation (exacerbating wildfires and limiting vegetation density), and to a lesser extent by changing atmospheric (precipitation, air temperature) and streambed factors (groundwater input). The low flows associated with droughts during warm periods cause stream temperatures to increase because thermal capacity is lower when flow volume decreases (Hockey 1982, Webb 1996, Webb and others 2003) and slower water velocities allow streams to more strongly equilibrate to local climatic conditions (Isaak and others 2012, Meier and others 2003).

Warmer waters hold less dissolved oxygen, and drought conditions concentrate aquatic organisms in smaller habitat volumes. Droughts, therefore, can cause significant stress to fish and other aquatic organisms by increasing metabolic costs and the intensity of interspecific competitive interactions. For some highly valued, coldwater species like trout and salmon, temperatures often define the geographic extent of their habitat, and drought conditions may temporarily constrain those habitats or even incur direct mortalities during extreme events. The lethal temperature limit for a coldwater trout species such as eastern brook trout (*Salvelinus fontinalis*) is approximately 25 °C (Bjornn and Reiser 1991, Hokanson and others 1977); but, reduced growth begins to occur at temperatures well below this limit. Most aquatic organisms are ectothermic, so the limitations imposed by temperature and dissolved oxygen during droughts have broad implications for the growth and survival of individuals in many species (Bjornn and Reiser 1991), including coldwater species.

Atmospheric, topographic, and vegetative shade; streambed; and stream and groundwater discharge factors all play a role in stream temperature dynamics. Atmospheric factors are most influential on larger streams and less so in smaller headwater streams. For example, Evans and others (1998) found that 82 percent of the heat energy exchange in a stream with a 109-km² drainage area in the United Kingdom occurred at the air/water interface, while 15 percent occurred at the streambed interface. In smaller headwater streams, temperature dynamics are more strongly controlled by the amount of local groundwater (Deitchman and Loheide 2012) and the role of topographic and vegetative shade in mediating the solar radiation that a stream receives (Johnson 2003, Luce and others 2014). Solar radiation is the single largest energy input to most streams, accounting for as much as 97 percent of the total energy gains (Evans and others 1998).

Management Options for Minimizing the Impacts of Drought on Water Quantity and Quality

The concept of managing forests to augment annual streamflow is not new (Douglass 1983); however, recent severe drought in many areas of the United States has increased awareness of the relationship among forest disturbance and management, drought, and streamflow (Ford and others 2011b, Jones and others 2012). Since harvesting often increases annual water yield, it has been suggested that the effects of drought could be mitigated by cutting forests (McLaughlin and others 2013). A major challenge in managing forests to enhance water supply is that a large proportion of the watershed has to be cut in order to increase annual runoff (Bosch and Hewlett 1982). Consequently, the potential increases in streamflow through forest cutting are minimal due to limitations on the amount of land that can be harvested at any given time (Kattelmann and others 1983).

Streamflow responses are often short term due to rapid forest regrowth (e.g., especially in the Eastern United States) (Swank and others 2014), and the aggrading post-cut forest may actually have lower streamflow than the uncut forest (Ford and others 2011b). Additionally, because of the unpredictable nature of droughts, it is impractical to plan the timing of harvesting operations so that the streamflow response occurs rapidly enough to offset the effect of drought. Furthermore, in contrast to management actions that are intended to augment streamflow, increasing drought stress in some forest ecosystems may warrant management strategies that retain water (and hence reduce streamflow) on the landscape in order to keep trees alive (Grant and others 2013).

Replanting cut forests with species that consume less water is a longer term solution that may be warranted in some cases, if it is economically feasible and does not adversely affect other forest management objectives, such as forest productivity, carbon sequestration, wildlife habitat, and water quality (King and others 2013). In snow-dominated, coniferous forests of the Western United States, small patch cuts and thinning have been shown to enhance snow accumulation by reducing snow interception and evaporation (Ffolliott and others 1989, Meiman 1987); however, these responses are transient as regrowing forests fill in the openings. Since much of the water supply in the West originates as snowmelt

from montane ecosystems, managing subalpine forests to enhance snow accumulation may alleviate the effects of drought in this region.

As with other natural disturbances, droughts are difficult to prepare for because they are unpredictable. However, there are management options that may be implemented to minimize the impacts of drought on water quality. In more developed areas, an obvious measure is to limit streamwater withdrawals (Meier and others 2003, Webb and Nobilis 1995) and wastewater discharge during periods of low flow, and encourage reuse of treated wastewater to help reduce higher temperature effluent volume from entering streams (Kinouchi and others 2007). In forested areas, efforts should focus on minimizing inputs of sediments and nutrients into the stream. It may be beneficial to plan the timing of management activities so they do not disturb streams during low-flow periods and to avoid vulnerable areas during droughts. Another management option is to practice riparian buffer conservation and restoration strategies that will maintain or increase shading from solar radiation (Burton and Likens 1973, Kaushal and others 2010, Peterson and Kwak 1999, Swift and Baker 1973); buffering stream temperatures against drought becomes important because removal and alteration of riparian vegetation increases stream temperatures (Beschta and others 1987, Groom and others 2011), particularly following timber harvest (Sun and others 2004, Swift and Baker 1973, Swift and Messer 1971, Wooldridge and Stern 1979) and wildfires (Dunham and others 2007, Isaak and others 2010). Other mitigation strategies, such as releases of cold water from the hypolimnions (i.e., the lower layers of water) of deep reservoirs, can have a significant cooling effect in downstream reaches (Null and others 2013), as can discharge of municipal wastewater from underground pipes, which may cool streams in the summer (Bogan and others 2003).

Conclusions

Forest vegetation has a strong influence over the water balance and biogeochemical cycling processes that determine streamwater quality. Hence, understanding and predicting how drought will impact hydrological processes requires linking vegetation drought responses across fine (e.g., stomatal regulation) and coarse scales (e.g., community dynamics at watershed scales). Where impacts are large and sudden, and species diversity is less complex (such as widespread drought-mediated mountain pine beetle mortality in the Western United

States), assessing short- and long-term responses may be possible with existing models (Tague and others 2013). However, where impacts are smaller scale and longer term (such as selective mortality in eastern U.S. forests), predicting impacts will be much more difficult and uncertain. If drought frequency and severity increases as expected (Swain and Hayhoe 2014), understanding the ecohydrological implications will become even more critical. To improve understanding, we recommend several areas of research need:

● Better understanding of species' differences in water use and sensitivity to drought, as well as the thresholds that determine species' physiological capacity to survive drought.

● Better understanding of competitive interactions among species, especially novel species combinations that might result with climate change or other disturbance regimes.

● Better understanding of belowground processes (e.g., root dynamics, hydraulic lift, and soil water access) that interact with drought responses.

● Improved ability to scale from tree-level, plots, and small watersheds to landscape scales in order to better understand and predict the ecohydrological consequences of tree-level responses to water balance and streamflow dynamics.

● Better understanding of the impacts of multiple co-occurring stressors on drought responses.

● Better understanding of how water quality is influenced by subsurface flow paths and hydrological connectivity.

● Improved ecohydrological models that couple hydrologic, ecosystem, and plant physiological processes in a dynamic context with appropriate feedbacks.

● Increased efforts to monitor the effectiveness of management options to mitigate droughts.

● Better understanding of the effectiveness of post-disturbance (e.g., direct and indirect effects of drought) restoration for improving watershed function.

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