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Drought disturbance from climate change: response of United States forests

Paul J. Hanson[a,*], Jake F. Weltzin[b]

[a] *Oak Ridge National Laboratory, P.O. Box 2008, Bethel Valley Road, Building 1059, Oak Ridge, TN 37831-6422, USA*
[b] *University of Tennessee, Knoxville, TN 37996-1610, USA*

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Abstract

Predicted changes in climate have raised concerns about potential impacts on terrestrial forest ecosystem productivity, biogeochemical cycling, and the availability of water resources. This review summarizes characteristics of drought typical to the major forest regions of the United States, future drought projections, and important features of plant and forest community response to drought. Research needs and strategies for coping with future drought are also discussed. Notwithstanding uncertainties surrounding the magnitude and direction of future climate change, and the net impact on soil water availability to forests, a number of conclusions can be made regarding the sensitivity of forests to future drought. The primary response will be a reduction in net primary production and stand water use, which are driven by reductions in stomatal conductance. Mortality of small stature plants (i.e. seedlings and saplings) is a likely consequence of severe drought. In comparison, deep rooting and substantial reserves of carbohydrates and nutrients make mature trees less susceptible to water limitations caused by severe or prolonged drought. However, severe or prolonged drought may render even mature trees more susceptible to insects or disease. Drought-induced reductions in decomposition rates may cause a buildup of organic material on the forest floor, with ramifications for fire regimes and nutrient cycling. Although early model predictions of climate change impacts suggested extensive forest dieback and species migration, more recent analyses suggest that catastrophic dieback will be a local phenomenon, and changes in forest composition will be a relatively gradual process. Better climate predictions at regional scales, with a higher temporal resolution (months to days), coupled with carefully designed, field-based experiments that incorporate multiple driving variables (e.g. temperature and CO_2), will advance our ability to predict the response of different forest regions to climate change. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Forest; Drought; Climate change; Precipitation

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[*] Corresponding author. Tel: +1-865-574-5361; fax: +1-865-576-9939.
E-mail address: hansonpj@ornl.gov (P.J. Hanson).

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1. Introduction

The Intergovernmental Panel on Climate Change (IPCC) concluded that climate has changed over the past century, that human activities have had an influence on these changes, and that climate is expected to continue to change in the future (Houghton et al., 1996). Depending on the emission scenarios assumed, continued increases in concentrations of greenhouse gases in the atmosphere are expected to induce an additional 1–3.5°C increase in average global surface temperatures by the year 2100 (Kattenberg et al., 1996). These temperature increases are expected to modify global hydrologic budgets leading to increased winter precipitation at high latitudes, more extreme temperature days, and more or less droughts or floods depending on location (Rind et al., 1990; Kattenberg et al., 1996). These predicted changes in climate have raised concerns about potential impacts on terrestrial ecosystem productivity, biogeochemical cycling, and the availability of water resources (Melillo et al., 1990; Kirschbaum and Fischlin, 1996).

The response of forests to decreased water availability from postulated increases in future drought conditions is considered a key issue in climate change scenarios (Wigley et al., 1984), and concerns regarding vegetation impacts have been amplified because rates of change are expected to occur much faster than past successional processes and species dispersal rates (Overpeck et al., 1991; Pastor and Post, 1988). The actual directions and magnitude of expected changes in precipitation are highly uncertain and specific scenarios for regional climate change are only preliminary (Schneider, 1989). Notwithstanding this uncertainty, Gregory et al. (1997) concluded that future climate predictions point to an increase in the severity of drought conditions. This review summarizes current drought characteristics of forests throughout the conterminous United States and describes future drought disturbance projections. It summarizes important features of plant and forest community response to drought and discusses projections of the impacts of climate change-induced droughts on forests. Finally, the paper summarizes important research needs and discusses strategies for dealing with future drought. As this review is one in a series of articles on forest disturbance resulting from climate change (Dale et al., 2000), readers are referred to companion articles on fire (Flannigan et al., 2000) and insect outbreaks (Ayers and Lombardero, 2000) for details on those related disturbances.

2. Current drought conditions and future predictions

Drought is defined as the ‘absence of rainfall for a period of time long enough to result in depletion of soil water and injury to plants’ (Kramer, 1983). According to this definition, droughts occur in nearly all US forests, although the frequency and intensity of drought varies both between and within systems. In addition, drought is superimposed on climate, which varies predictably across the US. Generally, the majority of the western US is characterized by periodic drought, in the form of chronic aridity, regular seasonal drought, or stochastic drought occurring in seasons when water has historically not been limiting. As such, water stress is a dominant feature of many western forests. As one moves east across the US, rainfall becomes more plentiful and the occurrence of annual droughts declines. In the wettest regions of the east droughts occur randomly and may be totally absent in some years.

For the purpose of this review, we classified US forests into three broad categories based on their frequency and predictability of drought (Fig. 1):

1. Random, occasional drought. Droughts in these forests occur, but the seasonality, intensity, and duration are not predictable using current numerical weather prediction models. Generally, these forests are located in the humid regions east of the Mississippi river. When droughts develop they are limited in duration and spatial extent, and tend to occur late in the growing season.
2. Common, late-summer drought. Droughts in these forests occur on an annual basis, usu-

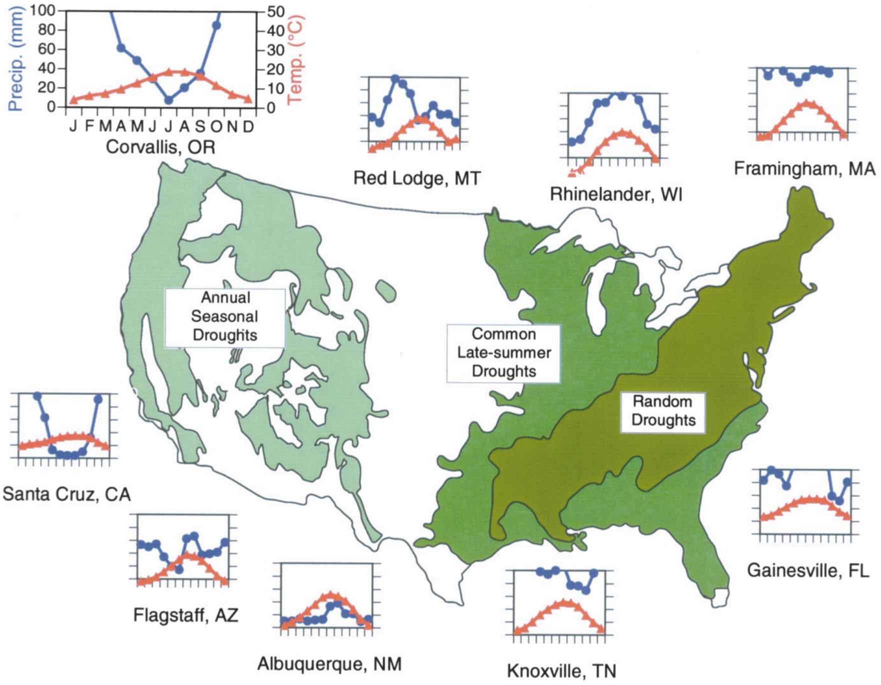

Fig. 1. Map of the United States showing the distribution of forest ecosystems according to their current drought occurrence characteristics. Climate diagrams (Walter and Lieth, 1960) showing monthly precipitation and temperature are provided for selected locations within each zone to illustrate the seasonal nature of drought potential (i.e. warm periods with low precipitation would exhibit higher average drought occurrence). Climate data are from NOAA 1985.

ally during the latter part of the summer growing season, and can be expressed on regional scales. Generally, these forests are located along the prairie–forest border at the eastern edge of the Great Plains. In addition, forests in more humid regions may experience effective late-summer droughts if they develop on relatively shallow soils or soils with low water availability (e.g. the SE coastal plain).

3. Annual, seasonal droughts. These forests are located primarily in the western United States, but the seasonality and intensity of drought vary from region-to-region depending on prevailing atmospheric circulation patterns coupled with large-scale topography. For example, forests and woodlands along the west coast of the United States are dependent upon precipitation that falls primarily during the winter months. Similarly, forests in the northern and western regions of the intermountain region receive the majority of their precipitation during the winter. Further south and east, the Arizona ‘monsoon’ brings summer precipitation in greater and more reliable amounts; forests in Arizona and New Mexico are relatively dependent upon precipitation received during the summer growing season.

In more arid ecosystems (e.g. lower-elevation shrublands, grasslands, and deserts), trees and forests are relatively uncommon, so we will not consider them herein. However, potential changes in disturbance regimes, management activities, and climatic conditions may cause a shift toward increased domination of these systems by woody plants, especially at ecotones or where habitats only marginally support woody species (Neilson, 1993; Weltzin and McPherson, 1995; Allen and Breshears, 1998). Ultimately, the impact of potential changes in drought or precipitation regimes will depend not only on the predicted scenario of change, but on the type of forest ecosystem and the climatic conditions to which it is currently adapted.

Projected changes in climate regimes, including changes in surface temperature and precipitation amount and seasonality, are derived from general circulation models (GCMs). Current GCM models estimate climate changes from transient greenhouse gas forcing of coupled atmospheric-ocean global climate models that include the phenomenon of sulfate aerosol forcing (Kittel et al., 1997). Such GCMs developed by the Canadian Climate Center (CGCM1) and the Hadley Center in the UK (HADCM2) are being used to predict precipitation regimes for 2030 and 2095 for application to the United States National Assessment (VEMAP, 1995 and http://goldhill.cgd.ucar.edu/vemap/). The CGCM1 model predicts significant reductions in summer and winter precipitation in the Southeast and Great Plains regions by 2095. In contrast, HADCM2 simulations for 2095 show increased precipitation throughout most of the United States with the exception of summer reductions in the Southwest in both summer and winter. Other predictions derived from the MAPSS and MC1 models (Daly et al., in press), suggest that increased warming alone could increase evaporative demand and increase droughts in the Southeast, southern Rockies, parts of the Northwest, and the Gulf coast even though annual precipitation might increase.

Global-scale models provide a starting point from which to judge the likelihood of future drought conditions, but few global-scale models are designed to predict the net effect on soil water status needed to judge impacts on forest productivity and species survival. Furthermore, standard climatic expressions for drought applicable to all forest types are not available. A simple reduction in total annual precipitation might increase drought severity in the ‘annual, seasonal-drought’ regions which are dependent on dormant season precipitation and soil recharge, but it would not have the same impact on forests of the ‘random, occasional drought’ region where early season rainfall contributes greatly to total annual net primary production (Penninckx et al., 1999). Granier et al. (1999) concluded that day-to-day estimates of soil water content during the growing season were desirable for quantification of plant stress indices and appropriate biological response to drought. Short-term (perhaps daily) quantification of soil water availability as an indicator of drought within regional GCMs will require the use of detailed water cycle models that include root-specific extraction of water from the soil profile. Increases in model complexity will only be applicable for forest ecosystems where appropriate soil and root structural data are available, but they will provide a biologically meaningful description of drought response with generic application across divergent forest types.

3. Water stress, drought, and the individual plant

Detailed discussions of the response of plants and plant processes to water stress and drought are available elsewhere (Hinckley et al., 1981; Whitehead and Jarvis, 1981; Kozlowski, 1982; Kramer, 1983; Teskey and Hinckley, 1986), but a brief summary of individual plant responses to water stress is important for understanding forest community responses. Water loss from leaves to the atmosphere is an unavoidable consequence of CO_2 exchange in trees. The hydraulic architecture of the soil–plant–atmosphere continuum of individual trees plays a critical role in determining their response to drought conditions (Kozlowski et al., 1991). Hydraulic conductivity of the soil matrix, and especially the soil immediately adjacent to the root is an important constraint on water flux into roots from dry or drying soils (Stirzaker and Passioura, 1996). Once water is in the root, hydraulic conductivity of the root-to-leaf pathway represents an additional constraint on transpiration and is impacted by water stress in several ways. The xylem can be impaired by air embolisms that cause cavitation during periods of drought or high transpiration. The xylem water potential necessary to induce this cavitation varies widely among plants (Pockman et al., 1997), and has been shown to correlate with the lowest xylem water potentials that plants normally experience under natural conditions (Ewers, 1985). Plants tend to control stomata such that xylem water potential does not fall below cavitation-inducing pressures (Tyree and Sperry, 1988): as soil moisture declines, either transpiration is reduced or leaf-specific hydraulic conductivity is increased. In this way, plants balance the demand for transpirational water loss and carbon uptake by leaves with allocation to root absorption or stem conducting tissue (Givnish, 1995).

Altered levels of soil water resulting from changing regional precipitation patterns will have direct impacts on the water status of plant foliage leading to modifications of leaf conductance, rates of carbon assimilation and evapotranspiration (Briggs et al., 1986; Ni and Pallardy 1992). These alterations in physiology are in part determined by the genetic composition of the affected individuals. Genetic differences among individuals or species may lead to differential survival. Rapid biochemical feedbacks allow some forest species to regulate their metabolism for more competitive use of limited water resources (Abrams et al., 1990), while species without this capacity will suffer the most in the face of drought conditions. For example, *Quercus* species are expected to out-compete the more mesic *Acer* and *Cornus* in drying future climates (Hinckley et al., 1979; Bahari et al., 1985). In addition, direct detrimental effects of low soil water potential on assimilation and respiration impact understory plants earlier and to a greater extent than overstory trees, because understory plants have limited root extension and carbon reserves (Donovan and Ehleringer, 1991; Flanagan et al., 1992).

Sustained changes in carbon assimilation and respiration induced by changes in soil water availability will lead to modified carbohydrate transport and carbon allocation to stem growth (i.e. wood production), production of leaves and fine roots, and will ultimately result in modified rates of detrital inputs to the soil. Waring and Pitman (1985) proposed a hierarchy of photosynthate allocation priorities for trees which considered stem growth to be a relatively low allocation priority, suggesting that stem growth is likely to be a sensitive indicator of drought stress. Like tree growth, dormant season carbon storage is an important, integrative measure of tree physiology. Carbon is stored throughout trees in the form of carbohydrates for later use as an energy resource and substrate for synthetic products (Kozlowski et al., 1991). Trees rely on carbon fixed during the growing season and stored through the winter to produce new organs for gathering light, water, and nutrients (Gholz and Cropper, 1991; Kozlowski et al., 1991). Effects of drought that lead to changes in carbon exchange rates should be cumulative over time (Chapin et al., 1990) resulting in degradation of stored non-structural carbohydrate pools. Dunn et al. (1987) and Parker and Patton (1975) have shown evidence of stress-induced carbohydrate reductions in *Quercus*.

Rooting profiles of plants illustrate different approaches to dealing with limited water in dry environments. For example, deeply rooted woody perennials can overcome periods of little or no rainfall during the growing season by using groundwater or water stored deep in the soil from prior rains (Dawson, 1996; Weltzin and McPherson, 1997). However, construction and maintenance of an extensive root system is energetically costly. Alternatively, shallow-rooted woody and herbaceous perennial plants are very effective at capturing moisture from growing season precipitation. However, they regularly experience wide fluctuations in soil moisture that limit photosynthesis to periods when water is readily available (e.g. after precipitation events). Consequently, seasonal patterns of water use, drought stress, and productivity vary widely between deep- and shallow-rooted plants even within a given habitat (Ehleringer et al., 1991; Weltzin and McPherson, 1997).

Preferential allocation to roots is a common response to water-stress in wild plants (Givnish 1986; Bazzaz, 1997). Theoretically, plants should allocate energy to the growth and maintenance of roots where soil moisture is available, as long as the physiological cost of this allocation is lower than the energy gained via photosynthesis from uptake of that moisture (Bloom et al., 1985). Unfortunately, there are few data to validate this hypothesis for native plant species (but see Nobel et al., 1992; Tschaplinski et al., 1998a).

The degree to which preferential allocation occurs to above- or below-ground plant components may depend on plant growth form. For example, evergreen oak seedlings (*Quercus emoryi*) grown from acorns in the field along a gradient of annual water inputs from 359 mm year^{-1} to 846 mm year^{-1} exhibited no reallocation response to watering treatments (Weltzin and McPherson, 2000). In contrast, deciduous *Q. douglasii* seedlings shifted root/shoot allocation ratios in response to resource manipulations in California (e.g. Gordon and Rice, 1993). This suggests that intrinsically low potential growth rates of evergreen plants may constrain their ability to respond to resource additions (Chapin et al., 1986).

Root growth patterns in mesic eastern forests (random-drought region) show similarities to the patterns described for seasonally dry forests. Joslin et al. (2000) demonstrated that root growth in an upland oak 'random-drought' forest is inhibited under severe drought conditions, but that forest trees appeared to have the flexibility to adjust for such reductions in subsequent wet growing seasons. In eastern forests, data on the spatial and temporal patterns of soil water uptake are seldom available for trees and shrubs (but see Dawson, 1993, 1996). However, seedlings (Holmgren, 1996) and saplings (Hanson and Todd, 1999) in eastern forests are often more susceptible to drought than are co-located mature canopy trees. Differential root depth and light availability likely interact to govern this response (Holmgren et al., 1997). Water uptake by plants is reviewed further in articles by Ehleringer and Dawson (1992) and Dawson (1993).

Phenologic patterns of growth and the occurrence of drought also play a role in the magnitude of plant response (Table 1). In hardwood forests that normally experience high annual rainfall without any strong seasonality (random-drought forests), annual growth may proceed to normal maximum values even though late season droughts occur. A large-scale precipitation manipulation study in the eastern United States (Hanson et al., 1995, 1998; Hanson and Todd, 1999) indicates that most tree species in a temperate upland oak forest complete growth early in the growing season and are unaffected by late season drought, even though forest physiological processes are dramatically altered (Gebre et al., 1998; Tschaplinski et al., 1998b; Wullschleger et al., 1998). Borchert (1998) has described the same pheno-

Table 1
Probable sensitivity of different response variables for individual trees within forests subjected to three different drought regimes[a]

Response variable	Drought regime		
	Random, occasional drought	Common, late-summer drought	Annual, seasonal drought
Physiological response (gs, A, Ψ)	Medium	Medium	High
Demographic response Seed production Seed germination Seedling establishment Recruitment	Low	Medium	Medium
Growth and production BAI NPP	Low	High	High
Mortality	Low	Low	Low

[a] The expected sensitivity is largely driven by the drought category's likelihood of drought occurrence. For example, a strong (high) physiological response would be expected in any given year in the 'annual, seasonal drought' region. In contrast, in any given year, there would only be a (low) chance of a growing season reduction in assimilation in the 'random, occasional drought' regime. Thus, morphological and physiological adaptations of the trees interact with the probability of drought to define the response of different plant processes.

menon for tropical rain forests, and similar growth patterns for a range of hardwood trees (*Acer, Fagus, Quercus*) can be seen in the studies of Buell et al. (1961), Phipps (1961) and Fritts (1976).

Unlike eastern deciduous hardwoods, conifer species exhibit a stem growth pattern which is sustained throughout a greater portion of the growing season in the absence of moisture stress (Zahner, 1968; Fritts, 1976; McLaughlin and Downing, 1996). This seemingly inherent and genetically controlled difference leaves conifer species open to the effects of late season droughts. Fig. 2 shows how the growth pattern for eastern hardwoods and pines differ in their sensitivity to late season droughts in the random-drought region of the eastern United States. When periods of growth activity do not overlap with the predominant periods of drought occurrence (as for hardwoods), basal area growth is relatively unaffected even though drought impacts on physiological processes may be pronounced.

In forests where annual production is not impacted by severe drought, it has been hypothesized that reductions in stored carbohydrate levels and/or nutrient uptake lead to altered leaf or fine root production in subsequent growing seasons (Tainter et al., 1984; Kohyama and Hara, 1989; Pedersen, 1998a). Such hypotheses are the basis for the suggestion that severe drought years may represent 'inciting stresses' that lead to eventual tree mortality (Pedersen, 1998b) which may take decades for large trees. However, an analysis of mortality of mid-western overstory oaks located in the random-drought region did not support this hypothesis (Pedersen, 1999).

4. Water stress, drought, and the plant community

Water stress has been often been cited as the ultimate constraint on the distribution and abundance of plants. Chronic and episodic droughts

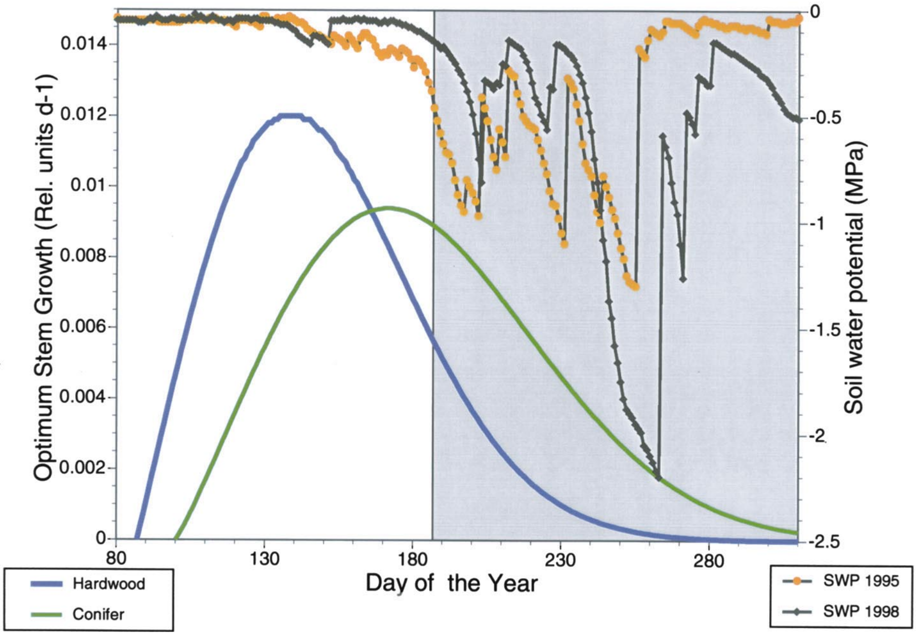

Fig. 2. Stem basal area growth patterns for the mean of several eastern deciduous hardwood (*Acer, Quercus, Liriodendron, Nyssa*) and for a conifer (*Pinus*) species are plotted for typical growing seasons without water stress. The figure also includes data for surface soil water potential (0–35 cm) in an upland hardwood forest of eastern Tennessee (Hanson et al. 1998) for the drought years of 1995 and 1998. A comparison of growth and soil water potential curves shows that annual hardwood stem growth is nearly complete before late season droughts develop in the random-drought occurrence region.

that affect soil water availability constrain seedling establishment (Osmond et al., 1987), mediate plant–soil and plant–plant interactions, and limit forest productivity on a world-wide basis (Schulze et al., 1987). For example, in one of the earliest systematic scientific investigations of natural ecosystems, Merriam (1898) invoked water stress as the primary factor influencing the distribution of dominant plants in the mountains of the south-western United States. Merriam's conclusions have been supported by contemporary research (e.g. see Whittaker, 1975; Niering and Lowe, 1984). Generally, moisture-controlled differences in recruitment, establishment and survival are often the dominant cause underlying the distribution and extent of forest ecosystems, as well as their internal structure and function (e.g. Neilson and Wullstein, 1983; Cornelius et al., 1991; Bowman and Panton, 1993).

Within a given plant community, species can show differential responses to drought conditions (LeBlanc, 1998; Clinton and Yeakley, 1999). Similarly, Turner et al. (1993) contrasted the growth of *Quercus* and *Liriodendron* over a 25-year period including a characteristically wet and dry decade in the random-drought region. While *Liriodendron* showed a 50% reduction in growth during a period of abnormally dry years, *Quercus* did not. Orwig and Abrams (1997) used tree ring observations to study multiple species' response to drought. They concluded that *Liriodendron* was more sensitive than *Quercus*, but found that shaded canopy trees exhibited larger growth reductions during drought than canopy-dominant trees of the same species.

Results of a study of multi-year precipitation change in eastern upland hardwoods indicate that mature eastern trees (*Acer, Quercus, Liriodendron, Nyssa*) exhibit some reductions in growth associated with occasional severe late season droughts, but that they are highly buffered against changes in rainfall quantity in terms of survival (Hanson and Todd, 1999). In contrast, juvenile individuals of these species were sensitive to incremental changes in rainfall inputs. For example, dramatic mortality was documented for *Cornus* saplings during a late-season drought in plots that received 33% less precipitation than ambient experimental plots (Hanson and Todd, 1999).

For forests in the region of random-drought occurrence, disproportionate changes in seasonal patterns of rainfall will have a greater impact on plant productivity and survival than quantitatively similar decreases in total rainfall distributed equally throughout a year. This occurs because equally distributed precipitation events tend to limit drought severity (Hanson and Todd, 1999). As such, dramatic shifts in forest productivity and/or composition in the eastern United States as a result of intensification of drought over the next few decades are unlikely to be widespread. However, forests in the random-drought region growing in shallow soils with reduced water storage capacity, would respond more like forested regions with annual late-season droughts.

In contrast to projections of the limited response of forests in the random-drought region, reductions in precipitation in the regions of predictable seasonal droughts may cause major shifts in plant composition, distribution, and abundance (Stephenson, 1990), and may, under extreme circumstances, lead to dramatic mortality (Allen and Breshears, 1998). Furthermore, certain tree species in the western United States or along the prairie–forest ecotone, depend on winter rains or snowpack to fill the soil profile with much of the water needed for summer growth (Phillips and Ehleringer, 1995). Any reduction in this pool of available soil water will shorten the effective growing season.

Changes in soil carbon and nutrient availability of the forest soils may lead to altered nutrient uptake by forest vegetation (Foster et al., 1992) and feedback to changes in the assimilation potential of the forest canopy (Field and Mooney, 1986; Field et al., 1992; Johnson et al., 1998). In a future with less precipitation and reduced decomposition, immobilization of nutrients in soil organic matter may limit carbon assimilation through inhibition of nutrient uptake from soils (especially N and base cations). Johnson et al. (1998) showed that 33% reductions in precipitation to an upland oak forest were leading to immobilization and reduced leaching of base cations, and more recent data suggests the same pattern for nitrogen after only 6 years of precipitation manipulations (D.W. Johnson, personal communication).

Over multi-year periods, drought-induced changes in canopy leaf area and canopy structure will result in modified penetration of solar radiation and modified microclimates within the forest community. Altered understory microclimates suggest a potential for future changes in species composition over successional time scales (Holmgren et al., 1997).

5. Interactions of drought with other factors

Changes in the concentration of CO_2 in the atmosphere may directly mediate the response of trees to drought. With some exceptions, increasing atmospheric CO_2 reduces foliar conductance and plant water use (Eamus and Jarvis, 1989; Kimball et al., 1993; Tyree and Alexander, 1993; Ceulemans et al., 1999; Norby et al., 1999). Such reductions in water use may limit the duration and severity of droughts. Furthermore, enhanced carbon fixation during non-stressed periods, driven by the fertilization effect of elevated CO_2, may compensate for reduced availability of soil water. However, increasing temperatures will increase vapor pressure deficits and evapotranspiration which could lead to no change or even greater water use under future climate conditions.

Increases in fine root production under elevated CO_2 (Rogers et al., 1994) represent yet another mechanism whereby forests might adjust to future climates. If greater rooting density and/or depth is attained by forests in the future they may be able to tap into new water sources and maintain normal function under altered atmospheric conditions. The combined effects of future climate and elevated CO_2 are complex, and net responses by forests will need to be resolved through a combination of experimentation and model driven synthesis.

Changes in drought regimes are likely to affect the frequency and extent of wildfire, with ramifications for many forests where natural fire regimes have been suppressed by management activities. Similarly, relatively wet periods that cause a buildup of fine fuels can increase fire frequency and extent in subsequent dry years (Rogers and Vint, 1987; Swetnam and Betancourt, 1990). However, habitat fragmentation, livestock grazing, and fire suppression activities will probably continue to reduce the importance of fire as a factor in many forest ecosystems (McPherson, 1995). Flannigan et al. (2000) further review the importance of fire as a disturbance in forest ecosystems.

Forest pests may predispose a tree population to mortality caused by drought. For example, infestations of bark beetles (*Dendroctonus* spp. and *Ips* spp.) may have contributed to high mortality rates of *Pinus ponderosa* during the regional drought of the 1950s in northern New Mexico (Allen and Breshears, 1998). Variations in seasonal precipitation are tightly coupled with forest pest populations. In the south-western United States, western spruce budworm (*Choristoneura occidentalis*) populations have been shown to be positively correlated with the quantity of spring precipitation (Swetnam and Lynch, 1993). Interactions between drought and insect herbivory or pathogen proliferation have also been proposed as a mechanism whereby future climate change may lead to the decline of forest ecosystems (Wargo, 1996; Hogg, 1999). Additional details on the impacts of forest pests and pathogens on forests can be found in the companion article by Ayers and Lombardero (2000), and Schoeneweiss (1981) provides a complete review of water stress as a predisposing factor in plant disease.

6. Modeling forest responses to climate change

In the absence of adequate experimental manipulations or long-term observations of the impact of drought on the production and demography of different tree species, models are used to extrapolate available data on species-specific responses to larger forest scales. The PnET-II model was used by Aber et al. (1995) to investigate the impact of future climate and CO_2 regimes on a wide range of hardwood and conifer forests of the north-eastern United States. They concluded that the net effect of increased temperature (+6°C), reduced precipitation (−15%), and a doubling of CO_2 would increase forest net primary production but decrease regional water yield. McNulty et al. (1997) also used a version of the PnET-II model to evaluate response of *Pinus taeda* throughout the south-eastern United States to changes in air temperature and precipitation. Impacts on water use and leaf area production were strongly dependent on the climate change assumptions and the location of individuals within their range. *Pinus taeda* at the southern edge of its range was anticipated to suffer more in future climates than *P. taeda* at the northern edge of its current range.

Although a number of model predictions have suggested that future climate change (including drought) will lead to extensive forest dieback and effective species migration (Leverenz and Lev, 1987; Solomon, 1986; Pastor and Post, 1988), such sensitivity has been questioned (Fischlin et al., 1995; Loehle, 1996; Loehle and LeBlanc, 1996). In particular, Loehle (1996) suggested that current models of forest response might overestimate negative responses to climate change because of (1) differences between the realized vs. fundamental niches; (2) underestimation of tree longevity; (3) inappropriate or inadequate simulation of vegetative reproduction; (4) tolerance of established trees to climatic fluctuations; (5) assumptions that managed forests will be as sensitive as natural ecosystems; and (6) unique niches occupied by fire tolerant or edaphically specified species. In combination, these features of established forests cause them to be buffered against future climate change. Accordingly, Loehle (1998) concluded that forests would not exhibit catastrophic dieback, but would instead be replaced gradually by faster growing tree species over extended time periods.

Recently, Neilson and Drapek (1998) described the response of vegetation to climate change based on equilibrium and transient GCM simulations using an equilibrium biogeographic model, MAPSS (Neilson, 1995). They found that transient or stepwise changes in climate had beneficial rather than negative impacts on vegetation. However, they also indicated that the extent to which the world's vegetation would experience large drought-induced declines vs. expansions in early stages of climate change would be dependent on the degree to which elevated CO_2 will benefit vegetation. Ehman et al. (2000) used the JABOWA-II forest growth model to evaluate the impact of climate change on forest vegetation in the Southern Great Lakes region of the United States. Their analysis, which did not include direct effects of elevated CO_2, showed that northern species (e.g. *Acer saccharum* and other northern conifers) would decline in this region, but that intermediate range and southern species would prosper under future climate conditions.

7. Research needs

Considerable research has described the response of individual trees, tree populations, and forest communities to drought. However, the majority of this research has focused solely on the effect of drought or water availability, and has ignored potential interactions between water availability and other climatic variables likely to change as a result of human activities. In particular, increases in the concentration of atmospheric CO_2, and concomitant increases in surface temperatures, may ameliorate or exacerbate the effects of changes in drought regimes. A better understanding of the relative importance of such interactions requires research that incorporates all factors likely to affect water use and carbon fixation by plants. For example, the Jasper Ridge Global Change Project in the California annual grassland incorporates interactions between four factors: atmospheric $[CO_2]$ (ambient, approx. 2 × ambient), atmospheric temperature (ambient, +2°C), water (ambient, 150% of ambient), and nitrogen (ambient, $+7\ \mathrm{g\ m^{-2}\ year^{-1}}$) (C.B. Field, personal communication). Although this project is not within a forest ecosystem, and does not include a drought treatment, it is representative of the type of research approach needed to investigate the interactive role of drought with other changing environmental variables. A significant financial commitment will be required to surmount scale and engineering considerations implicit to conducting similar experimental research in forested ecosystems.

A great gap in our understanding of forest community responses to drought stems from limited research attention on plant–plant interactions (e.g. competition for water between individuals), plant–soil–water relationships (movement of water into the soil, across the soil–root interface, and though the plant), and ecosystem-level processes (soil water status, nutrient cycling). Although much has been published about the nature of future climates (i.e. more frequent drought episodes and/or more severe extended droughts), there is a dearth of knowledge about regionally specific climate change scenarios from which to develop critical experimental studies (Houghton et al., 1996). That said, it is not too soon to devise and implement experiments to test the sensitivity and range of the response of ecosystems to most-likely scenarios of climate change (McPherson and Weltzin, 2000).

Better GCM predictions (i.e. scenarios) at regional scales with minimum temporal resolution on the order of months, are required to adequately predict impacts for existing forest ecosystems throughout the United States. With such scenarios in hand, new field experiments should be considered for those forest ecosystems predicted to be highly sensitive (i.e. forests that exhibit significant growth reductions or mortality). Where feasible and cost-effective, experiments on changing precipitation regimes should include elevated CO_2 and increased temperature treatments to reflect the multiple interacting environmental changes that are expected to coincide with global change. Critical observations of patterns of response of different tree species to environmental perturbations (e.g. Falkengren-Grerup and Eriksson, 1990; Allen and Breshears, 1998) are needed, along with improved models of forest succession to expand confidence in our ability to make long range predictions about the fate of forest ecosystems over decadal time periods. Other topics that require future investigation include:

1. role of precipitation/drought in controlling secondary succession and carbon sequestration;
2. importance of precipitation regimes (frequency and severity) on structural and functional response of plant root allocation and architecture;
3. role of drought in increasing susceptibility to invasion by exotic plant species;
4. role/importance of precipitation seasonality, serial correlation, and extremes on ecosystem structure and function; and
5. role of precipitation on nutrient cycling and feedbacks to plant production.

Interactive effects of soil moisture and temperature on competitive interactions, particularly those involving different life forms, are largely unknown. For example, it is hypothesized that high temperatures of shallow soil layers during the summer months may limit root activity, thereby constraining uptake of water by tree roots to deeper soil depths, regardless of availability (Williams and Ehleringer, in press). This pattern would be further constrained by the amount and seasonality of precipitation, and the characteristics of the soil.

Research and field observations of forest responses to drought is almost exclusively based on naturally occurring droughts (both mild and severe) or chronic manipulations (i.e. droughts not resulting in the death of mature plants; Hanson et al., 1995, 1998). In contrast, there are few explicit experimental data on the duration and magnitude of drought needed to kill or severely constrain growth of mature forest trees (Borghetti et al., 1998 is an exception). In the absence of predictions of catastrophic changes in drought and precipitation regimes from GCM output, acute drought studies may seem superfluous. However, because current ecosystem models predict tree mortality and species displacement for incremental changes in precipitation amounts and/or frequency (Section 5), there remains a need for a better mechanistic understanding of the level of drought required to kill or severely constrain growth of mature trees.

8. Coping strategies

Climate change is perhaps the most critical factor facing the current generation of land managers who are concerned about the future condition of natural and managed ecosystems. Changes in climate are important to resource managers because: (1) directional change has occurred, and is virtually certain to continue; (2) potential impacts on vegetation can be profound; (3) effects will occur over larger areas, and have potentially greater impacts, than changes in forest management practices; and (4) the influence of management practices on vegetation will be difficult to predict or interpret without explicit consideration of relatively rapid climate change. Accurate prediction of ecosystem response to climatic change will facilitate proactive resource management. Conversely, if managers are unaware of potential and on-going changes in climatic conditions (i.e. means and extremes) and their associated effects on ecosystems, efforts to effectively manage those ecosystems could be severely handicapped.

Mitigative actions for minimizing impacts of future droughts are likely to range from the acceptance of change (i.e. doing nothing) to intensive manipulations to protect forest ecosystems of value to society. If future GCM outputs are able to provide reliable predictions of the direction and the geographic extent of alterations in regional climate, society may choose to undertake proactive responses. Such actions might include tree planting programs to accelerate natural succession and species migration. Alternatively, currently accepted silvicultural methods for plantation forestry might need to be modified to allow sustained use of existing species and forest lands (e.g. increasing the spacing between planted trees). For highly valued and/or rare ecosystems, irrigation might be considered. Such intensive solutions would likely represent only a temporary measure to support specific gene pools until new and stable environments are established for these systems.

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