Historical forest changes in the western United States

by Craig Loehle¹

ABSTRACT

Changes in factors such as temperature, precipitation, fire regimes, ozone, atmospheric CO₂, and nitrogen deposition may have altered forest growth over the past century. Determining changes in forest growth over long intervals is complicated by constantly changing growing conditions due to tree maturation, stand self-thinning, disturbance, and other factors. Because a comprehensive review is lacking, results from publications examining forest growth trends in the western United States over the past 100 years were evaluated. Across the region, upper elevational forest ecotones have been expanding upward in many but not all locations, possibly due to warming and reduced snowpack. Across most of the region, both growth increases and decreases are localized and spatially dispersed. For the inland West, historical photography and long-term inventory data show clear densification and expansion of ponderosa pine (*Pinus ponderosa*) and mixed conifer forest across the region, mostly due to reduced fire incidence. However, a recent drought, probably linked to ocean cycles and exacerbated by warming, has caused a growth setback and mortality, especially in the Southwest. Forest densification due to altered fire regimes does not equate to enhanced growth *per se*. Aspen (*Populus tremuloides*) dieback has been noted due to recent drought and local conifer mortality caused by drought has also been documented in several locations. Regeneration after recent fires appears to be inadequate in many localities. Except for local increased growth at some high elevation and coastal sites and possible periodic drought effects in the Southwest, it is difficult to detect any growth trends with available data.

Key words: climate change; environmental factors; forest growth and yield; forest growth trends; inventory data; treeline; western United States

RÉSUMÉ

Les modifications relevées au niveau des facteurs comme la température, les précipitations, les régimes des feux, l'ozone, le carbone et l'azote atmosphériques, peuvent avoir affecté la croissance des forêts au cours du dernier siècle. L'identification de ces changements au niveau de la croissance des forêts au cours de longues périodes de temps est complexe du fait des conditions de croissance sans cesse modifiées par la maturation des arbres, l'auto-éclaircie des peuplements et d'autres facteurs. Compte tenu de l'absence d'un examen complet de la littérature, les résultats des publications portant les tendances de la croissance des forêts dans l'ouest des États-Unis au cours des 100 dernières années ont été évalués. Partout dans cette région, les écotones forestiers d'altitude supérieure se sont développés vers les sommets dans plusieurs mais pas dans tous les sites, possiblement à la suite du réchauffement et de la diminution du couvert de neige. Dans la majeure partie de la région, tant la croissance que la réduction de la croissance se sont avérées être spatialement localisées et dispersées. Dans le cas de la partie intérieure de l'Ouest, les photographies d'archives et les données d'inventaire à long terme indiquent une densification évidente et une expansion marquée du pin ponderosa (*Pinus ponderosa*) ainsi que des forêts résineuses mélangées dans toute la région, probablement par suite de la réduction de l'incidence des feux. Cependant, une sécheresse récente découlant probablement des cycles océaniques et amplifiée par le réchauffement, a provoqué un recul de la croissance et de la mortalité, spécialement dans le Sud-Ouest de la région. La densification forestière découlant de la modification des régimes de feux ne signifie pas implicitement une croissance accrue. Le dépérissement du tremble (*Populus tremuloides*) a été noté à la suite de la récente sécheresse et la mortalité des conifères a été relevée dans plusieurs localités. La régénération apparue après les récents feux de forêt semble être inadéquate sur plusieurs sites. Mis à part une croissance accrue localement à des altitudes plus élevées ainsi que sur des sites de la Côte ouest, et des effets probables des sécheresses périodiques dans le Sud-Ouest, il est difficile d'identifier les tendances de croissances à partir des données disponibles.

Mots clés : changement climatique, facteurs environnementaux, croissance et rendement des forêts, tendances de croissance forestière, données d'inventaire, ouest des États-Unis

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Introduction

Forest health is of critical interest to the public, forest landowners, and the forest products sector. Many studies have reported changes over the past century in climate-related and other environmental factors that have the potential to influence forest health and growth, such as fire frequency, ozone levels, nitrogen deposition, atmospheric CO₂ concentrations, tempera-

ture, and precipitation (Loehle *et al.* 2016). The magnitude and pattern of reported changes in some of these factors have varied regionally. For example, Pederson *et al.* (2015) reported that the 20th century has been anomalously wet in the eastern US. Kim *et al.* (2012) detected increasing non-frozen seasons for Northern Hemisphere soil during 1979 to 2008. Mote *et al.* (2018) and Bishop *et al.* (2019) documented long-term winter drying in the mountainous west whereas Siler *et al.* (2018) documented stable snowpack since the 1980s. Bishop *et al.* (2019) also found spring increases in precipitation in western coastal regions of the US. A 431-year reconstruction of western Colorado snowpack from tree rings (Woodhouse 2003) did not reveal any trends. Because of the multiplicity of potential causal pathways and interactions, general discussions of effects of environmental changes on forests (e.g., Peñuelas *et al.* 2013), such as the benefits to tree growth from nitrogen (N) or phosphorous (P) deposition or from rising CO₂, how multiple factors have been interacting to affect tree growth cannot be deduced from first principles but is rather an empirical question.

Various authors (Allen *et al.* 2010, 2015; Anderegg *et al.* 2015; McDowell and Allen 2015; McDowell *et al.* 2016) have predicted that changing conditions will lead to widespread forest mortality and/or dieback, especially in drier forest types, and may already be doing so. On the other hand, global surveys combining various types of data suggest that, on average, forest growth is increasing (e.g., Boisvenue and Running 2006; Campbell *et al.* 2017; Pretzsch *et al.* 2017). Schulte-Uebbing and de Vries (2017) and Wang *et al.* (2017) showed that N and P depositions have been increasing forest growth worldwide. These studies sometimes do not separate forest regrowth (e.g., after fire) or forest age effects from growth rate changes *per se*.

The contradiction between predictions that changing conditions should be having adverse effects on forests and evidence to the contrary needs resolution. It clearly affects estimates of current and future forest health, the status of forest resources, carbon sequestration, and effects on wildlife habitat and other ecosystem services. The question of forest health is particularly acute in the western US, where recent drought, insect outbreaks, and large fires have caused widespread tree mortality. This region is thus the focus of this review. Two companion reviews cover Canada (Loehle and Solarik 2019) and the eastern United States (Loehle, *In Review*).

Given a warming planet, what historical trends might be expected? At a coarse scale, one might expect a rise in the treeline and infilling of patchy, high-elevation forest. How-

ever, treeline climates are complex. Aspect and exposure to wind can alter growing conditions in addition to temperature effects alone. Rising CO₂ might be expected to increase tree growth (angiosperms more than gymnosperms) and increase drought tolerance via a rise in water use efficiency (Loehle *et al.* 2016). There is some global evidence for this (Gedalof and Berg 2010). Rising temperatures could increase growth in regions that are not water-limited, such as some coastal forests in the Pacific Northwest of the US (Loehle 2018). In contrast, at dry ecotones (usually lower elevations in the West), warming and/or drying could lead to reduced growth and range retreat upslope via drought, insect, or fire-caused mortality (citations above; Loehle *et al.* 2016). All these processes are spatially distributed and may be gradual, making change detection difficult.

Several types of historical data exist which may be used to reconstruct long-term forest changes. Historical photography can be compared to recent images to assess major changes. Fire scar data can be used to assess historical fire size and frequency. Forest surveys and permanent plots can be used to assess changes in density, biomass, and species composition and their relationship to climate. For treeline, age of regeneration with distance from the forest edge can be used to assess invasion rates. Pulses of tree establishment can be related to climate.

Remote sensing data can provide information on forest growth rates. However, some serious inconsistencies have been found between and within (over time) remote sensing products (e.g., Guay *et al.* 2014; De Kauwe *et al.* 2016; Jiang *et al.* 2017) and between remote sensing results and Earth system model calculations (Smith *et al.* 2016). For these reasons, remote sensing studies of trends are not evaluated here.

Fire has historically been an important governing force determining forest/shrub or forest/grassland ecotone boundaries. Decreased fire frequency or intensity can allow forest to expand at the dry range limit and become denser. Historically, fires in North America, and the West in particular, were more common 100 years or so ago due to recent fire suppression (Doerr and Santín 2016; Taylor *et al.* 2016; Addington *et al.* 2018; Klimaszewski-Patterson *et al.* 2018). Nineteenth century fire regimes in much of the drier West appear to have been dominated by frequent, low-intensity fires (Hagmann *et al.* 2013; O'Connor *et al.* 2014; Margolis and Malevich 2016; Swetnam *et al.* 2016; and citations below). The National Interagency Fire Center (https://www.nifc.gov/fireInfo/fireInfo_stats_totalFires.html) shows that recent decades exhibit fewer acres burned than the early 20th Century, though early data is less reliable. Compared to the period 1970-1999, the most recent 17 years have roughly twice as many burned acres per year according to this database (see also Singleton *et al.* 2019). I attempt below to distinguish fire impacts on ecotones from other causes.

Because of changes in precipitation, temperature, fire regimes, CO₂, and other factors, attribution of changes can be complex and often requires evaluation of several types of evidence. In the studies described next, more than one environmental factor often could have caused the observed changes in forest area or growth rates. In such cases, authors sometimes made inferences from historical data on climate (e.g., seasonal/annual changes in temperature/precipitation) and/or fires to help clarify causation.

Fig. 1 Study area. Stippling indicates forest. Different forest types form local zonation at fine scales as a result of topographic moisture and temperature gradients

Study area

The study area was the western United States (Fig. 1). In this mountainous region, topography plays a key role in forest presence. Precipitation arrives mostly from the west, leading to high tree productivity in the coastal Pacific Northwest. Precipitation declines to the south and inland. Orographic effects lead to moisture gradients with elevation which, in concert with temperature gradients, lead to dry pine (*Pinus* spp.) forest at low elevations and to the south, and moister forest types at higher elevations, with rain shadow effects on the east side of mountain ranges. At higher elevations in the higher mountains, cold and snow create alpine treelines. Lower interior elevations (e.g., the Great Basin) are generally not forested due to dryness. Summers across the region tend to be dry. The continental climate means that local temperatures tend to be dominated more by altitude than latitude (Rochefort *et al.* 1994).

Across the West, a limited set of tree species and forest ecotypes dominate. At lower elevations where it is hotter and drier, ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) is found across the region, with some lodgepole pine (*P. contorta* Dougl. ex Loud.) and quaking aspen (*Populus tremuloides* Michx.) on sites that have burned. Moving upslope to cooler zones, Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), true firs (*Abies* spp.), and hemlock (*Tsuga heterophylla* (Raf.) Sarg. and *T. mertensiana* (Bong.) Carrière) dominate. The subalpine zone is comprised of silver fir

(*A. amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes), limber pine (*P. flexilis* James), subalpine fir (*A. lasiocarpa* (Hook.) Nutt.), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). In the very wet Washington coastal zone, hemlock and Sitka spruce (*P. sitchensis* (Bong.) Carrière) join Douglas-fir. Many other species, e.g., sugar pine, *P. lambertiana* Dougl. and western white pine, *P. monticola* Dougl. ex D. Don) are minor components or are locally abundant. The same dominant species span the entire zone and respond mainly to elevation and rainfall gradients, creating consistent elevational bands and sometimes large mono-specific stands (Burns and Honkala 1990).

Methods

The scientific literature was searched for references to long-term growth trends of forests in the western US. Woodlands and shrublands were considered out of scope. As an initial entry to the literature, the complete contents of Forest Science (2015-2018), Canadian Journal of Forest Research (2014-2018), Forest Ecology and Management (2013-2018), Global and Planetary Change (2014-2018), and Global Change Biology (2012-2018), (over 6000 articles), were manually searched for all papers that might touch on growth trends, mortality trends, or geographic trends, and then the literature was searched in Google Scholar using “alpine tree-line”, “forest history”, “carbon sequestration”, “forest NPP”, “forest inventory”, “forest greening”, “forest browning”, “forest dieback”, “forest mortality”, and “forest growth” as keywords. The International Tree-Ring Data Bank (ITRDB) was also searched. The cited literature in each publication identified in the searches was then searched.

Results

Seventy-seven relevant publications were located. Fourteen studies documented changes in forest extent or density, 27 documented elevational expansion, 15 addressed changes in mortality, six documented regeneration trends, two studied geographic range shifts, and 13 evaluated changes in growth rates. Multiple studies were found that evaluated tree-ring records but most were trying to reconstruct historical climate or hydrologic signals and did not contain data on growth trends *per se*. Thus, they could not be used. Because different approaches yield different types of information, the literature was next summarized by type: changes in extent; changes in mortality; and growth trends.

Changes in forest ecotones, area, and density

The most common response of forests globally over the past 100+ years has been expansion and/or densification (Stevens *et al.* 2017; Nelson and Reams 2017). Expansion at cold margins can be an indication of warming or altered precipitation but, at dry margins, could result from fire regime changes, CO₂ enrichment, precipitation increases, grazing changes, or some combination of these factors. Adult trees and seedlings may not respond the same to changing conditions. Blowing ground snow can kill seedlings but, once they are tall enough, this effect diminishes. Snowpack may prevent seedling establishment (Franklin *et al.* 1971) while the same snow aids adult trees via melt during the summer.

Millar *et al.* (2015) found that at multiple sites across four mountain ranges in the western Great Basin, upper elevation

pinus had experienced a pulse of recruitment between 1963 and 2000 for limber pine and between 1955 and 1978 for bristlecone pine (*P. longaeva* D. K. Bailey). Pines were found to have expanded above the current treeline, downslope into grass or shrub communities, and laterally at mid-slope into treeless zones. Average extension over all cases was 225 m. These recruitment pulses were correlated with complex, lagged responses to increases in precipitation and higher minimum temperatures at those times. Smithers *et al.* (2018) found these same two species to be expanding their ranges, especially limber pine, which is expanding on all sites across the Great Basin.

Several studies at Glacier National Park, Montana, found contrasting results. Bekker (2005) found rates of advance of alpine treeline linear features (ribbon forest) of 0.28 to 0.62 m/y, with an establishment pattern of extension dating back to the 1700s. More recent establishment was farther downwind of existing trees than in the past. Butler *et al.* (1994), using historical photography, found mostly stable alpine treeline ecotones, with some increase in tree size and some seedling establishment upslope. Klasner and Fagre (2002) found visible thickening of tree patches but no ecotone shift in the same park. Alftine *et al.* (2003) found alpine forest expansion but not after 1980. Butler and DeChano (2001), also using historical photography at the park, found rates of lateral infilling of up to 9 m/y and expansion upward of 1.5 to 4 m/y. These contrasting results in the same location no doubt reflect complex topographic effects on disturbance, exposure, wind, soils, and differences due to methods.

Several additional studies show rising treelines across the West. Moore and Huffman (2004) found tree encroachment onto meadows on the North Rim, Grand Canyon National Park, Arizona at rates of 0.35–0.47 m/y over the period 1930–2004. On the Colorado Front Range, Daley and Shankman (1985) found some evidence of seedling advance. As this study is 34 years old, a revisit to this site might be informative. In Lassen Volcanic National Park, California, Taylor (1995) found that trees had been expanding since the mid-1800s. Seedlings became established preferentially in years of low snowpack and warmer temperatures, but established trees did better with elevated temperature and precipitation. The patchy expansion was mostly on the order of 100 m over the period since the mid-1800s. An unusual case exists in the Valles Caldera, New Mexico (Coop and Givnish 2007) where lower elevation meadows are subject to cold air drainage such that trees are limited at both upper and lower elevations by cold, though changes in fire regimes may have also contributed to forest expansion. Based on aerial photography in 1935 and 1996, they found that meadows had decreased by 18% over the period, or 0.3%/y. Additional studies have documented tree invasion of alpine meadows or expansion of the treeline in California (DeBenedetti and Parsons 1979; Vale 1981; Helms 1987; Taylor 1990; Millar *et al.* 2004), Colorado (Billings 1969; Shankman and Daly 1988), New Mexico (Dyer and Moffett 1999), Oregon (Franklin *et al.* 1971; Halpern *et al.* 2010; Haugo and Halpern 2010; Rice *et al.* 2012), Washington (Franklin *et al.* 1971), and Wyoming (Dunwiddie 1977; Vale 1978; Jakubos and Romme 1993; Moir *et al.* 1999;). Note that none of the studies cited here randomly sampled meadows or clearings to obtain an estimate of frequency of invasion. Rather, these studies were

focused on the invasion process where it was found. The studies were, however, clear that invasions they documented were in areas devoid of signs of recent occupation by trees (i.e., not recent burns). In some cases, authors did note that not all treelines were extending. For example, Dyer and Moffett (1999) in New Mexico found that south slopes in spruce-fir forest had been continuously invaded since the 1930s but that northeast slope ecotones were stable over this period.

It is generally believed that fire was historically rare in wet, high elevation forests of the West and, if it occurred, it was high intensity. Reilly and Spies (2016) documented this rarity in a large dataset for Oregon and Washington. DeRose and Long (2012), for example, documented historical drought and high-intensity fires in subalpine forests in southern Utah. Sibold and Veblen (2006) documented that high intensity subalpine fires in the Colorado Front Range since 1650 were related to oceanic cycles such as the Pacific Decadal Oscillation (PDO). However, it has been found that, at least in the Jemez Mountains of New Mexico, the moist mixed conifer forests did experience periodic low-intensity fires (Margolis and Malevich 2016). Such low-intensity fires could have created or helped maintain the upper treeline and high elevation meadows. However, data are sparse on this issue. Fire in upper treeline forests seems most likely to have played a role in maintaining meadows where upper elevation forests are still rather dry, such as at the Grand Canyon sites studied by Moore and Huffman (2004) or in Lassen Volcanic Park, California (Taylor 1995). Where alpine meadows are bordered by mature fire-sensitive species (e.g., *Abies* spp., *Tsuga* spp.), fire-maintained meadows seem unlikely. Some alpine meadows are clearly maintained by persistent snow (Billings 1969) and wet meadows may even resist fire except in the driest years (DeBenedetti and Parsons 1979). Finally, large alpine fires may result in long-lasting meadows due to slow reinvansion (Shankman and Daly 1988). Further subalpine fire history reconstructions would be useful.

Multiple studies across the West have documented increased forest density and infilling in drier forest types. Brown *et al.* (2015) reconstructed forest age structure in the northern Front Range, Colorado, using tree-ring analysis. Fire history was reconstructed from 1667 to 2012. Fires were recorded in two or more plots during 1667–1859 (the date of the last such fire) on average every 8–15 years. In 1860 (the earliest that stand structures could be reconstructed), all trees were ponderosa pine and stand density was highly variable. Forests in 2012 were denser, had higher basal area, more smaller trees, and more Douglas-fir and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.). These changes are what would be expected from reduced fire frequency. Stine *et al.* (2014) presented photographs documenting similar changes in the Okanogan-Wenatchee National Forest in Oregon during 1934 to 2010.

Addington *et al.* (2018) conducted a detailed study of ponderosa pine forests of the Colorado Front Range using historical photography. They concluded that historical fire frequency was likely much higher before the mid- to late-1800s. A comparison of photographs from 1896, 1899, and 1905 to recent photography (past 20 years) showed ubiquitous and dramatic increases in tree density. Extensive historical photographs supporting these conclusions have been compiled (Veblen and Lorenz 1991). This trend was spatially

extensive and agreed with trends in the Southwest, according to the authors (and see Brown and Wu 2005). They noted that, in addition to fewer fires, a history of extensive grazing since settlement would have favored pine establishment by reducing grass competition with pine seedlings. The extent to which upper ecotone expansion has resulted from grazing is unclear because no references cited here documented grazing in their study areas. However, for grazing to have kept alpine meadows free of trees, grazing would have had to have had the opposite effect as at lower elevations and to have been ubiquitous. Lack of documentation makes this question impossible to resolve at this time.

Work by Stephens *et al.* (2015) extended evidence for densification of ponderosa pine and mixed conifer forest into the southern Sierra Nevada of California. In their study, they combined historical photography with inventories conducted in 1911. They found canopy cover to have increased from 25% to 49% in mixed conifer stands and from 12% to 49% in ponderosa pine stands. They attributed this change to altered fire regimes. Other work extends the areas where forest has become denser and less fire tolerant to Grand Canyon National Park (Mast and Wolf 2004); the San Juan Mountains of Colorado (Elliott and Baker 2004), where aspen has been infilling conifer stands since 1900 but more so recently; the San Francisco Peaks in Arizona (Cocke *et al.* 2005), especially in lower elevation zones; ponderosa and mixed conifer types in south-central Oregon (Hagmann *et al.* 2013); and the Medicine Bow Mountains of Wyoming (Andersen and Baker 2005), where forest openings on survey transects have shrunk 7.3% in the past 110 years. In addition, increased density has been documented in New Mexico (Margolis and Malevich 2016; Swetnam *et al.* 2016) and Arizona (O'Connor *et al.* 2014).

Based on the assumption that tree seedling density represents more recent climate responses than does adult density, Monleon and Lintz (2015) evaluated 46 species across California, Oregon, and Washington. More species had higher elevation and/or more northerly seedling distributions compared to adult distributions. Over all species, mean seedling distribution peaks (not range boundaries) were 26.58 m higher and 11.22 km farther north than adult trees. Note, however, that the recent drought in the Southwest could be partially responsible for this trend if dryness has inhibited seedling establishment more in the South and at low elevations. Whether this will continue is an open question.

Hanberry and Hansen (2015) evaluated areal coverage of species in latitudinal bands across the conterminous US based on forest inventory data. Trees were counted if >12.7 cm dbh and the survey interval was approximately 28 years. Of strictly western species, Englemann spruce, Rocky Mountain juniper, and white spruce (*Picea glauca* (Moench) Voss) had statistically significant areal expansion of adult trees in their northernmost band within the US and non-significant southern band changes. Limber pine expanded in both directions. Subalpine fir expanded to the south. Note that four of these five species are high elevation types. No species had a net significant range shrinkage. Fourteen species with adequate data (not too rare) showed no significant change.

In contrast to the extensive literature showing forest expansion and densification across the drier portions of the West and at upper elevations, there is evidence that recent

regeneration following severe fires has been deficient in Arizona (Roccaforte *et al.* 2012), Colorado (Chambers *et al.* 2016; Rother and Veblen 2016), New Mexico (Savage *et al.* 2013), Oregon (Dodson and Root 2013), and across the West (Stevens-Rumann *et al.* 2018). This is a result of the recent drought which has limited regeneration success, plus the total kill of adult trees in many areas which makes seed dispersal a limiting factor (see Roccaforte *et al.* 2012; Chambers *et al.* 2016; Rother and Veblen 2016). A cessation of the recent drought would enhance recovery, but dispersal limitation will remain an issue where large fires have removed all nearby seed sources. The extent to which trees are replanted will influence forest recovery. In the absence of seed sources or replanting, a likely pathway following fire is persistent shrub-fields (Savage *et al.* 2013) or grasslands.

Mortality events

Mass mortality may be a sign that forest growth has been negatively affected. Aspen is one species that has exhibited extensive mortality in some locations in the West. A severe drought during 2002–2008 caused extensive trembling aspen mortality in Colorado (Worrall *et al.* 2008, 2010; Anderegg *et al.* 2013). A complicating factor, however, is that aspen is a short-lived, disturbance-dependent species and thus older stands will be inherently more subject to mortality events. In an area of Colorado, for example, Binkley *et al.* (2014) found that most aspen stands at 100 to 140 years-old are approaching the maximum age for the species, with consequent dieback likely. The advanced age of these stands may result from low fire frequency in the 20th century that reduced stand establishment events. Worrall *et al.* (2013) concluded that across its range, aspen dieback was typically preceded by drought, tended to occur on marginal (i.e., drier) sites, and was exacerbated by insect and pathogen attack. While aspen appears to be sensitive to drought, there is also evidence that sucker regeneration is common in the understory of stands experiencing dieback (Frey *et al.* 2004). A key factor in aspen decline may be the influence of ungulate browsing on aspen regeneration. Beschta *et al.* (2016) found that historical data on exclosures in Yellowstone National Park and recent fluctuations in Rocky Mountain elk (*Cervus elaphus* L.) populations both point to herbivory as a limiting factor for aspen sucker success. In the northern part of the park, where elk abundance had declined, aspen stands were recovering. The following thus seems plausible: all aspen, but particularly old aspen stands and those on dry sites, are prone to dieback, and when there is excessive herbivory, are unable to recover. Aspen in some cases may also be lost due to successional processes (Bretfeld *et al.* 2016).

Millar *et al.* (2007) documented a mortality event in lower-elevation, young limber pine stands in the eastern Sierra Nevada range during 1985 to 1995. This was a period of high temperature and persistent drought in the region, according to their data. They noted that thinning caused by the drought led to increased resilience and no mortality during the subsequent 1999–2004 drought. Recent drought-caused mortality is also evident in subalpine forests of the Colorado Front Range (Smith *et al.* 2015). Allen and Breshears (1998), for a study area in northern New Mexico, documented that drought killed ponderosa pine and caused a several-kilometer shift upslope in the ecotone with piñon-

juniper woodland that persisted for more than 40 years as of their study date. Such shifts have not yet been documented to be widespread.

In subalpine zones of eastern California, mortality of whitebark pine (*P. albicaulis* Engelm.) was documented by Millar *et al.* (2012) to have occurred during the 2007–2010 drought. Stands with high mortality tended to have high density and to occur on lower elevations (mean 2993 m), on northerly aspects, and to have drier and warmer conditions relative to the typical condition for this species. Excess density may predispose stands to drought-caused mortality (Young *et al.* 2017).

Regional droughts can be extensive and have large impacts. Droughts have been ongoing in California (Guarín and Taylor 2005; Griffin and Anchukaitis 2014; Belmecheri *et al.* 2016; Robeson 2015) and the American West (Weiss *et al.* 2009) for the past decade or so. Oscillations in Pacific storm tracks (Dannenbergh and Wise 2017) can have a large impact on western precipitation patterns. Precipitation in California (Kirby *et al.* 2014) and the West generally (McCabe and Dettinger 2002) up into western Canada (Cayan *et al.* 1998; Steinman *et al.* 2014) are linked to Pacific Ocean cycles (Kadonaga *et al.* 1999; Gray *et al.* 2003). Mote *et al.* (2018) documented a downward trend in reconstructed western April 1st snowpack, and Belmecheri *et al.* (2016) showed that the 2015 Sierra Nevada snowpack was anomalously low compared to the past 500 years. However, in this same 500-year record, the past 100 or 50 years seem similar to the overall record. Considered as a multi-year event, the 2012–2014 or 2012–2015 periods were highly unusual (Griffin and Anchukaitis 2014; Robeson 2015) in California. As a result of this drought, tree mortality in California rose dramatically (Van Mantgem *et al.* 2009; Berner *et al.* 2017, 2019; Young *et al.* 2017). Discrete mortality events since 1984 have been better documented in Arizona and New Mexico due to fire and insect infestations (Williams *et al.* 2010). Hember *et al.* (2017) also documented small increases in drought-induced tree mortality across the Rocky Mountain and Cascade Ranges. Cohen *et al.* (2016) found a recent increase in western disturbance events.

Even on sites experiencing drought, however, tree mortality rates should be interpreted cautiously. Thorpe and Daniels (2012) noted that self-thinning and succession accounted for most of the mortality trends in their study in Alberta, Canada. Millar *et al.* (2012) and Young *et al.* (2017) showed that stands with higher density evinced higher mortality during droughts. The long-term trend toward higher density over the past century could thus be increasing western mortality during drought periods. In regions such as the Southwest subject to cyclical climate, a process of over-shoot and dieback can occur (Jump *et al.* 2017). During wetter decades and following fire suppression, trees can become established and grow faster, increasing forest density. When a dry period recurs, there is more biomass than can be supported and dieback or pathogen mortality will occur. Dieback in such cases will be more dramatic than in a dry, but stable, climate regime.

Mortality caused by insects and disease (pathogens) can be dramatic (Berner *et al.* 2017, 2019) but is difficult to interpret. Regional differences in pathogen-caused mortality, especially bark beetles, have been documented (Reilly and

Spies 2016; Berner *et al.* 2017, 2019). Due to lack of historical data, it is difficult to tell if pathogen incidence is increasing. There are known invasive pests which are causing mortality, but the recent droughts make separating this effect from total mortality problematic.

Growth trend reconstructions

Historical reconstructions based on permanent plots and or tree-ring records have the potential to provide estimates of changes in forest growth rates, although changes in stand age and density need to be considered. Stand-level biomass for even-aged (e.g., after fire) stands increases over time with a maximum yearly increment shortly after crown closure and a decline to minimal accumulation (i.e., steady state) for very old stands (e.g., Kashian *et al.* 2013). This age effect needs to be considered for growth trend reconstruction. Given the large historical increases in stand density documented in prior section, which could reduce individual tree growth due to water limitation (Biondi 1999) and crowding, care must also be taken that density over time is comparable in growth studies.

Several studies appear to have detected a CO₂ growth response. Soulé and Knapp (2006) evaluated ponderosa pine growth on eight minimally disturbed sites across central Oregon and northern California. They matched time periods in terms of moisture stress. They found a growth enhancement at all sites after 1950 and significantly at most sites, which they attributed to CO₂ fertilization which increased drought tolerance. Growth was most enhanced during dry years and on the driest sites. They did not quantify the growth response *per se*. Gedalof and Berg (2010) also found some evidence for CO₂ fertilization effects. Using the global tree-ring database, they modeled tree-ring response to climate and examined residuals for a CO₂ signal. They found that 20% of sites globally exhibited a positive response to rising CO₂. They found that Douglas-fir and ponderosa pine appeared to be responding to CO₂ but at the bounds of detectability. Reed *et al.* (2018) evaluated lodgepole pine growth in west-central Montana and into Idaho for the period 1950–2015. They found stem biomass growth to be enhanced by rising intrinsic water use efficiency (iWUE) caused by rising CO₂ on dry sites. On wetter sites, rising iWUE was not adequate to compensate for falling snowpack, causing a slight growth decline.

Graumlich *et al.* (1989) found a large growth enhancement based on four sites in western Washington Douglas-fir-hemlock forests. Using reconstructions for stands without any obvious mortality (evident due to the slow decay of large trees in that locality), they inferred a regional increase in growth of 60% over the period 1880 to 1979. They ruled out a significant CO₂ effect and attributed most of the enhancement to warming, with precipitation having mainly short-term effects. This study is now 40 years old, so an update would be informative.

In contrast to Graumlich *et al.* (1989), Lee *et al.* (2016), also for Douglas-fir, found a 20th Century (to 2010) pattern of fluctuations due to the Pacific Decadal Oscillation and other cycles and periodic growth reductions due to Swiss needle cast (*Phaeocryptopus gaeumannii* (T. Rhode) Petrak) infection. The authors did attempt to reduce effects of tree ring detrending methods on suppression of long-term growth trends. They found no recent trend for three wet coastal sites,

a decline at low elevation interior dry sites since 1980 or 1990, and an increase since 1990 at high elevation sites, the latter two being responses to warming.

Salzer *et al.* (2009) found that bristlecone pine growth in the second half of the 20th century was unprecedented in the past 3700 years, but only in a narrow (~150 m) band at tree-line, regardless of elevation. Similarly, Hughes and Funkhouser (2003) found that bristlecone pine and foxtail pine (*P. balfouriana* Balf.) showed continuously increasing growth since the mid-1800s at upper ecotone sites but not lower ecotone sites in the Great Basin. The growth surge was positively associated with temperature. Note that these growth increases are very spatially restricted and match the ecotone expansions found by Millar *et al.* (2015) and Smithers *et al.* (2018). In contrast, Perkins and Swetnam (1996) found no unusual growth response for high elevation whitebark pine in the Sawtooth-Salmon River region of Idaho. Growth appeared to be dependent on snowpack depth. A small-scale study of foxtail pine near alpine treeline in Sequoia National Park, California (Bunn *et al.* 2005) found four wet sites to have an increasing growth trend since the mid-1800s and four drier sites to show no trend over the same period.

McIntyre *et al.* (2015) used US Forest Service forest inventory data from surveys in the 1930s vs. the 2000s to study changes in California forests. Over this time period, they found a 30% increase in tree density, fewer large trees, and a 19% reduction in basal area (an indicator of biomass). However, Roesch and Van Deusen (2010) showed that a change in survey methods across the two time periods had the effect of making large trees less observable. In addition, forest harvesting since the 1930s could have produced these same changes in structure by creating a younger forest.

Woolley *et al.* (2015) evaluated growth trends at eight sites in western Oregon. Annual biomass production (area basis) was estimated on permanent plots based on tree diameter increments and allometric equations over intervals from 12 to 32 years-long. Although age correction was not done, the relatively short interval between samples and the long periods during which these forests are highly productive make this only a minor issue. Of these sites, an old-growth site showed a decline in total annual bole biomass production, a mature site an increase, and the rest no trend. Individual tree responses were more coherent in younger stands, probably due to weather effects.

Tree-ring records from across the West were used by McKenzie *et al.* (2001) to evaluate growth trends during 1880 to 1980. They found a periodic signal in the Southwest, as discussed previously. They found large positive growth trends at a subset of high elevation and high latitude sites and no declines. However, Nehrbass-Ahles *et al.* (2014) concluded that the data selection method used by McKenzie *et al.* (2001) was likely to yield a positive bias to growth trends. It is likely that despite this bias, the study does provide some evidence for stable to increasing growth rates. It might be useful to update these 40-year-old data.

Del Grosso *et al.* (2008) simulated global net primary productivity (NPP) trends over the period 1901–2000, with fixed CO₂. They found that total NPP (TNPP) increased from 12% to 50% over virtually all of Canada and the central and western US (but not the US Rockies region from New Mexico up

through Colorado) over the 100 years, and 13% globally. Results from simulations such as these depend critically on reliability of interpolated older weather station records, realism of the growth models used, and whether CO₂ enhancement is included. Because CO₂ effects were not simulated, this study may be underestimating a growth response.

Case and Peterson (2007) constructed growth factor models for lodgepole pine in the North Cascades National Park based on detrended ring width series for the period 1930 to 2000. While the lower elevation sites (more limited by precipitation) showed an upward trend for 1945–1985 and a dip in the 1990s, there was no obvious long-term trend. Higher elevation sites (more limited by temperature) fluctuated around the mean over the entire 70 years. Because detrending may have removed any signal of slowly rising CO₂, small upward growth responses might have been concealed in this analysis.

Discussion

Some changes in western forests (elevational ecotones, growth rates) have likely resulted from more than one factor (Table 1). Forest aging, increased density, and drought can all affect mortality rates and growth rates. Results from the reviewed studies must therefore be synthesized carefully. For example, increase in density of dry forests across the West seems to be clearly the result of a change in fire regimes (Brown *et al.* 2015; Millar *et al.* 2015; Stephens *et al.* 2015; Addington *et al.* 2018; Klimaszewski-Patterson *et al.* 2018). Because of the dry climate and slow growth of trees, it has taken a long time for this change to occur. The expansion of forest at dry ecotones in the West is similar to global trends (Stevens *et al.* 2016; Nelson and Reams 2017) and may be the combined result of reduced fire incidence, grazing, and CO₂ fertilization, which favors trees over herbaceous species (Loehle *et al.* 2016), with some contribution from rising precipitation in some areas (Bishop *et al.* 2018). The interactions between forest density, fire, growth rates, drought, and forest extent (Fig. 2) are complex and play out over many decades.

Historically, treelines across the West have fluctuated above and below the current elevation due to changes in both precipitation and temperature (Rocheffort *et al.* 1994). Dates of treeline changes (Rocheffort *et al.* 1994) are not obviously spatially synchronous over the past 10 000 years across the West. This can be explained by the various limiting factors at particular sites. For sites where wind scours the surface, killing plants and leading to local, large snow drifts (e.g., in ribbon forest, Billings 1969), a change in prevailing winter winds could alter the treeline in complex ways. Decreased snowpack could allow wet meadows to be invaded while making drier meadows less suitable. Very large alpine fires could create persistent conditions unfavorable to seedlings or require a long recovery (Billings 1969; Shankman and Daly 1988), thus causing a locally lowered treeline for long periods unrelated to climate. Sites with very thin soils or where snow is all blown away might require a much greater change in climate before trees could become established. These same factors lead us to expect that current treeline rise in the West should not follow a warming climate in a uniform way but should rather be both locally variable and intermittent in time (not continuous). This is what appears to be the case. Thus, while studies agree that treeline invasions or extensions began after the 1850s, the decade and pattern differs from

Table 1. Summary of Findings

Reference	Region	Period	Method	Finding
Multiple ¹	Alpine	Various to 1700s	Historical photography, tree ageing	Alpine meadow colonization
Multiple ²	Ponderosa pine, mixed conifer across the West	From 1860s	Historical photography, inventory data	Increased density
Monleon and Lintz 2015	CA, OR, WA	Recent	Seedlings vs. adult distributions	Upward and northward shifts in peak abundance
Hanberry and Hansen 2015	Conterminous US	Recent 28 year survey interval	Tree geographic change	Four spp. elevational expansion, 2 spp. to south, 14 spp. no change
Multiple ³	Across the West	Recent decades	Regeneration surveys	Inadequate regeneration
Multiple ⁴	Across drier West	Recent decades	Inventory data, surveys	Tree mortality events
Soulé and Knapp 2006	Central OR, northern CA ponderosa pine forest	20 th century	Tree-ring data	Enhanced growth post-1950 dry sites
Gedalof and Berg 2010	Across the West	20 th century	Tree-ring data	CO ₂ fertilization effect
Graumlich <i>et al.</i> 1989	Western WA moist forest	1880–1979	Stand growth	60% increase
Salzer <i>et al.</i> 2009; Hughes and Funkhouser 2003	CA, Great Basin	3700 yr	Tree rings	Pine increased growth in narrow elevation bands
Case and Peterson 2007	North Cascades National Park, WA	1930–2000	Tree rings	No net trend high or low elevation
Lee <i>et al.</i> 2016	OR	1890–2010	Tree rings	Mixed recent responses
Perkins and Swetnam 1996	ID	Historical	Tree rings	No change
Bunn <i>et al.</i> 2005	CA	Mid-1800s to present	Tree rings	Increased growth at 4 wet sites, no trend at 4 dry sites
McIntyre <i>et al.</i> 2015	CA	1930s–2000s	Inventory data	Decreased basal area but methods may have caused artifact
Reed <i>et al.</i> 2018	West-central ID, to MT	1950–2015	Tree-ring and isotope data, lodgepole pine	Increased growth on dry sites, reduced growth on wet sites
Woolley <i>et al.</i> 2015	Western OR	12–32 yr remeasure	Stand growth	No net trend
McKenzie <i>et al.</i> 2001	Across the West	1880–1980	Tree-ring records	Large positive trends at some high altitude and high latitude sites, no declines
Del Grosso <i>et al.</i> 2008	West	1901–2000	Modeled NPP	Increase in West except Rockies region

¹Alftine *et al.* 2003; Bekker 2005; Billings 1969; Butler and DeChano 2001; Butler *et al.* 1994; Coop and Givnish 2007; Daley and Shankman 1985; DeBenedetti and Parsons 1979; Dunwiddie 1977; Dyer and Moffett 1999; Franklin *et al.* 1971; Halpern *et al.* 2010; Haugo and Halpern 2010; Helms 1987; Jakubos and Romme 1993; Klasner and Fegre 2002; Millar *et al.* 2004, 2015; Moir *et al.* 1999; Moore and Huffman 2004; Rice *et al.* 2012; Shankman and Daly 1988; Smithers *et al.* 2017; Taylor 1990, 1995; Vale 1978, 1981

²Addington *et al.* 2018; Andersen and Baker 2005; Brown *et al.* 2015; Brown and Wu 2005; Cocke *et al.* 2005; Elliott and Baker 2004; Hagmann *et al.* 2013; Margolis and Malovich 2016; Mast and Wolf 2004; O'Connor *et al.* 2014; Stephens *et al.* 2015; Stine *et al.* 2014; Swetnam *et al.* 2016; Veblen and Lorenz 1991

³Beschta *et al.* 2016; Chambers *et al.* 2016; Dodson and Root 2013; Frey *et al.* 2004; Roccaforte *et al.* 2012; Rother and Veblen 2016; Savage *et al.* 2013; Stevens-Rumann *et al.* 2018

⁴Allen and Breshears 1998; Anderegg *et al.* 2013; Binkley *et al.* 2014; DeRose *et al.* 2012; Hember *et al.* 2017; Millar *et al.* 2007, 2012; Smith *et al.* 2015; van Mantgem *et al.* 2009; Williams *et al.* 2010; Worrall *et al.* 2008, 2010, 2013

Fig. 2 Causal interactions of fire, drought, and density on forest condition

place to place, in some cases by a century. Some sites show continuous and some episodic (e.g., Helms 1987) invasion. A general amelioration due to warming is evident but a climate signal cannot always be teased out of the response at any particular site. In fact, multiple studies have failed to find climate correlates of invasion success (e.g., Jakubos and Romme 1993; Halpern *et al.* 2010; Rice *et al.* 2012).

Increases in tree mortality documented by multiple authors may not necessarily presage large-scale forest loss. For aspen mortality, stand aging and drought were noted above to be proximate factors, with failure to regenerate being perhaps due to ungulate grazing. Drought diebacks have been documented in the Southwest (Allen and Breshears 1998; Millar *et al.* 2007; Williams *et al.* 2010) and increased rates of mortality have also been documented by Smith *et al.* (2015), van Mantgem *et al.* (2009), Cohen *et al.* (2016) and Hember *et al.* (2017). The already-noted historical increase in stand densities in drier forests could have led to an overshoot condition (per Jump *et al.* 2017) in which too much biomass exists for trees to be tolerant of drought (Voelker *et al.* 2019). This would cause excess mortality in the event of drought. Increased density in dry forests could help convert a low-intensity fire to a high-intensity fire by making fuels more continuous. In a drought, higher recent densities could also lead to more likelihood of insect or disease attack if more trees are stressed. Vankat (2017) documented this type of dynamic in pinyon-juniper (*P. edulis* Engel., *Juniperus scopulorum*) woodland on the South Rim of Grand Canyon National Park, Arizona. In the core zone of this type, periodic droughts causing mortality followed by recovery were observed during 1935–2011. In contrast, at the ecotone with ponderosa pine, the forest was much more stable.

Drought and fire-caused dieback at dry ecotones is what is predicted to result from warming. The open question at this time is whether recent forest losses due to fire and drought, especially in California, will be permanent. The many decades required for forest to reoccupy burned areas (Stevens-Rumann *et al.* 2018), especially if large, make determination of permanence or not of dry margin losses a slow process.

This is especially true during an ongoing drought, when tree establishment is likely to be low. In some cases, large burns can convert forest to shrub fields (e.g., Guiterman *et al.* 2018), which may make tree establishment difficult or promote further fires (Fig. 2).

One test of whether tree ranges are shrinking is provided by Hanberry and Hansen (2015). In their 28-year resurvey of most of the abundant western tree species, none were found to have significant areal extent shrinkage (number of plots in which they were found) and five, mostly alpine species, had expanded. Resolution of their data did not allow for small changes to be detected. By this measure, whatever diebacks or fire losses occurred during their study period do not appear to be affecting tree spatial extents in the West at scales that are detectable.

Direct evidence of changes in productivity *per se* are sparse. A large increase since 1901 in productivity for the US, including the Pacific Northwest, was inferred by Del Grosso *et al.* (2008) by simulation, though not for the Rockies region. Graumlich *et al.* (1989) found a 60% increase in plot-scale NPP during 1880 to 1979 in Washington. This study, however, had end dates 40 years ago and thus cannot be considered indicative of current trends. A large growth spurt in bristlecone pine (Salzer *et al.* 2009) is very local. There is some evidence for modestly increased growth of trees due to CO₂ fertilization (e.g., Soule and Knapp 2006; Gedalof and Berg 2010; Reed *et al.* 2018). As it is likely, based on both experimental work and models of photosynthesis (see Loehle *et al.* 2016) that rising CO₂ should increase tree growth and drought tolerance, it would be beneficial if this aspect were studied more thoroughly. While there is some indication of increased tree growth at higher elevations (McKenzie *et al.* 2001; Bunn *et al.* 2005; Salzer *et al.* 2009; Lee *et al.* 2016; Millar *et al.* 2015; Monleon and Lintz 2015), this trend may soon be countered by reduced growth due to declining snowpack (Mote *et al.* 2018; but see Siler *et al.* 2018). In the inland Northwest, various authors found slight growth declines (Lee *et al.* 2016; Reed *et al.* 2018) and mostly stable growth (Case and Peterson 2007; Woolley *et al.* 2015). Between these tem-

perature extremes (hot and dry Southwest and subalpine zones), it is difficult to make any firm statements about growth trends from available data. The lack of clear growth trends is consistent with the lack of effective moisture trends over the past 70 years across the region (Greve *et al.* 2014). The ambiguity of existing growth studies means that increased tree growth cannot be directly invoked to explain elevational expansion in this region. Seedling establishment limitations due to snowpack may be the more parsimonious explanation (Franklin *et al.* 1971). Further studies of historical growth trends would be useful, with the effect of stand density changes being carefully considered.

An important open question is whether drought, particularly in the Southwest, will continue. For example, the California Department of Water Resources reported the seasonal (October 1, 2018 – February 28, 2019) precipitation to be 130% of average statewide, perhaps signaling an end to the drought. While some long-term climate patterns appear to exist (Kadonaga *et al.* 1999; Gray *et al.* 2003; Woodhouse 2003) that may have predictable impacts on tree growth (e.g., Gray *et al.* 2003; Lee *et al.* 2016), it is not yet possible to make forecasts based on these patterns. Precipitation trends will particularly affect regeneration after fire. Fire *per se*, however, will probably continue to be an issue even if the recent drought ends due to the higher than historical fuel loads and more spatially continuous fuel structures. Model-based forecasts of climate change effects (Loehle 2018) indicate both increased growth in many regions plus increased fire risk. Research needs include an assessment of the extent and rate of upslope forest movement, more studies of forest growth trends, and follow-up of regeneration in recently burned areas.

Forests provide a valuable carbon storage service. The documented increased density over the past 100 years in the West suggests a large increase in C storage over this period. This is particularly true because much of the region is not managed for timber. However, the increase in fire acreage since the 1980s, especially in California, calls into question the permanence of these gains. It may be necessary to consider whether lower density in fire-prone zones might help protect against forest loss. Careful analysis of this question would be required to determine an answer.

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