



Review and synthesis

Carbon implications of current and future effects of drought, fire and management on Pacific Northwest forests[☆]B.E. Law^{*}, R.H. Waring

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ARTICLE INFO

Article history:

Received 9 September 2014
 Received in revised form 18 November 2014
 Accepted 23 November 2014
 Available online 10 December 2014

Keywords:

Forest carbon
 Drought effects
 Tree mortality
 Climate mitigation
 Carbon management
 Pacific Northwest

ABSTRACT

Climate change has already begun to impact the structure and function of forest ecosystems in the Pacific Northwest by altering the frequency, intensity, and duration of droughts and heat stress, with implications for widespread environmental and socio-economic change. A major realization is that accumulated physiological stress can ultimately lead to tree mortality and changes in species distributions, particularly in areas away from maritime influences. To ameliorate the effects of drought, insect outbreaks, and reduce the risk of crown fires, various strategies are being tested. To make some of these strategies economical, biomass is proposed as an alternative energy source. At the same time that an increase in harvesting is being considered, there is a desire to increase carbon sequestration by forests to offset, at least in part, greenhouse gas emissions. Assessments are needed to determine current and future impacts of climate change, and to evaluate management options while considering carbon storage benefits and sustainability of ecosystem structure and function. Here we provide an overview of research results from the Pacific Northwest region where forests dominate the landscape and contain among the highest biomass on earth. In this review, we present findings that challenge common assumptions, and suggest a way to predict outcomes of changes in climate and land management in the future. The approach includes the use of observation-driven land system models that integrate the extent that forests are vulnerable to climate change, management practices, and economic considerations. It also requires increased emphasis on in situ and remotely sensed observations and experiments to initialize and test the model, and to track trends in forest condition.

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[☆] This article is part of a special issue entitled "Carbon, water and nutrient cycling in managed forests".

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1. Introduction

Over centuries, human activities have altered forests profoundly, changing their distribution, structure and productivity across landscapes and regions. Now, climate change attributed to rising greenhouse gas emissions is beginning to impact forests as the frequency and severity of droughts and extreme heat events increase (Joyce et al., 2014; Allen et al., 2010). An increase in disturbance affects the carbon balance of forests. More frequent and extensive disturbances reduce the ability of forests to sequester carbon and partially offset greenhouse gas emissions. The complexities of multiple interacting factors have prompted efforts to predict where forests are likely to be vulnerable to natural disturbances, and the carbon consequences of actions that land management might take in response.

The Pacific Northwest (PNW) domain of this synthesis includes British Columbia, Washington, Oregon, and Northern California (Fig. 1). Climate in the PNW is strongly influenced by the Pacific Ocean and mountain ranges, and two large-scale oscillations, the El Niño/Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO). When both oscillations are in a warm phase, the possibility of a warmer and drier winter increases (Dalton et al., 2013).

There is a strong eco-climatic gradient from the Coastal Range temperate rainforests (~2500 mm precipitation) inland to the Klamath Mountains and Sierra Nevada (1500 mm), East Cascades (~500 mm), and the Columbia Plateau and Northern Basin (250 mm; Fig. 1). Warming has led to ~20% loss of winter snowpack since 1950 (Mote, 2006), and spring snowmelt has occurred 0–30 days earlier depending on location (Stewart et al., 2005). Although the annual precipitation has not changed significantly, winters are becoming drier while the springs are generally wetter (Abatzoglou et al., 2014). The region is expected to experience progressively hotter and longer summers with a 10% reduction in summer precipitation (Mote and Salathé, 2010; Mote et al., 2014). Because Pacific Northwest summers are already dry, a 10% reduction in precipitation, particularly in the semi-arid part of the region, could further stress forests and increase the area burned. Such projections on the region's valuable forests are of great concern.

Carbon cycle research in Pacific Northwest US has focused on understanding how forests respond to climate and subsequent disturbances from the individual tree, upward through ecosystem, landscapes and regions. Some results challenge conventional thinking, and need to be highlighted as land managers and policy

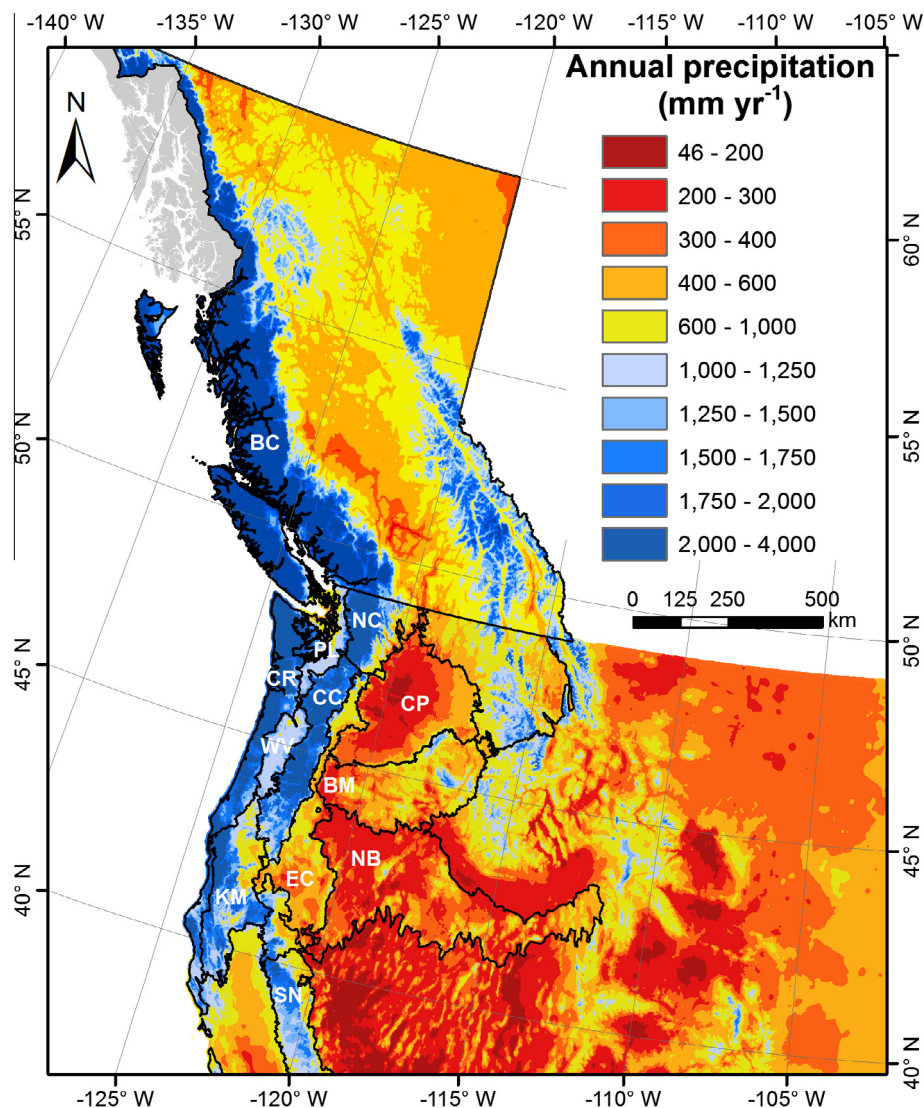


Fig. 1. Thirty year mean annual precipitation (1961–1990) in the Pacific Northwestern US. Note the strong gradient from the coast inland. Data are courtesy of Oregon Climate Service, map by Logan Berner.

makers attempt to minimize impacts on forests and manage them for a variety of ecosystem services.

Recent studies aim to determine the vulnerability of forests to a shift in climatic conditions and the potential increase in the kind, frequency and size of disturbances. They also endeavor to assess the effects of changes in management practices on carbon and water cycling, and upon biodiversity. Obtaining these objectives is aided by advances in technology that provide continuous measurements of ecosystem carbon and water fluxes from towers, track changes in forest structure from orbiting satellites, and utilize sophisticated land system models to generate predictions of ecosystem responses at a range of scales.

Here we highlight major carbon cycle research findings in Pacific Northwest over the past two decades, identify knowledge gaps, and needs for future research.

2. Carbon storage in PNW forests

The amount of carbon stored in forests, which primarily resides in wood and soil, plays an important role in regulating atmospheric carbon dioxide. Carbon stocks are higher in older forests, while younger forests take up carbon at a faster rate per unit of ground area. There is a growing body of evidence that forests can continue to accumulate carbon in live biomass and soils and serve as large carbon sinks for hundreds of years (Luyssaert et al., 2008). For example, a 450–500 year old Douglas-fir forest at Wind River, Washington has ~400 Mg ha^{−1} of carbon stored in tree biomass, close to average for old forests in the cool temperate moist region of North America, and the forest continues to take up carbon from the atmosphere annually (total net primary production 6 Mg ha^{−1} – year^{−1} of carbon), thanks in part to a well-developed understory of younger western hemlock and western red-cedar trees (Waring and McDowell, 2002; Harmon et al., 2004).

Stand ages in the PNW vary from less than one to over 1000 years, and stand biomass per unit ground area continues to increase after 600 years in the Klamath Mountains and after 300 years in the Coast Range, West Cascades and Sierra Nevada ecoregions (Hudiburg et al., 2009). Cool, temperate, moist forests can attain higher biomass carbon than tropical and boreal forests (Table 1; Gonzalez et al., 2010). Data from over 8000 inventory plots show that an upper limit to biomass in Oregon, Washington and Northern California is 440 and 520 Mg ha^{−1} of carbon (averages of 240 and 370 Mg ha^{−1}) for stands older than 200 years in the Klamath Mountains and Coast Range ecoregions (Van Tuyl et al., 2005; Hudiburg et al., 2009). The values are comparable to an average of 300 Mg ha^{−1} of carbon estimated for primary forests in the Tongass

National Forest in Southeast Alaska (Leighty et al., 2006). The average for primary forests across the cool temperate moist biome is about 450 Mg ha^{−1} of carbon, which is higher than biome averages for tropical moist and wet forests (Table 1; Keith et al., 2009). In Oregon, soil carbon to a depth of 1 m reaches an average of 360 Mg ha^{−1} of carbon in Coast Range Sitka spruce/hemlock forests and approaches an asymptote at about 150–200 years (Sun et al., 2004; Law et al., 2001). An average of 40–55% of forest carbon is stored in the soil (ecoregion means; Law et al., 2004).

3. Natural disturbances and forest carbon

An objective of carbon cycle science is to quantify transfers of carbon from the atmosphere into live biomass, and to follow the transformation into dead biomass and eventually through the decomposition process to where carbon dioxide is emitted to the atmosphere. Drought-related mortality, fires, and insect outbreaks speed up the rates that carbon is transferred through the cycle, and all of these natural disturbances vary in intensity, spatial extent and patchiness.

Inventory data for Oregon and Northern California in the 1990s indicate that as a percentage of live biomass, mean annual mortality ranged from 0.5%, 0.35%, and 0.35% for young (<80 years), mature (80–200 years), and old stands (>200 years) in the Coast Range to a high of 1.2% and 1.3% in young and mature stands in the Sierra Nevada, and 1.35% for old stands in the Blue Mountains of Northeastern Oregon (Hudiburg et al., 2009). These values are consistent with historical averages and background levels (Franklin and DeBell, 1988; Franklin et al., 1987).

A linkage between drought and wildfires has been shown in several studies. For example, high pre-fire water deficits (potential minus actual evapotranspiration) were related to higher post-fire tree mortality (van Mantgem et al., 2013). Since 1984, there has been an increase in the number of large fires (>4 km²) per year in the Cascade, Klamath and Sierra Mountains ecoregions, and the northern Rocky Mountains ecoregion, coinciding with increased severity of drought (Dennison et al., 2014). However, the increase in number of large fires is less than one fire per year (Dennison et al., 2014).

Recent Pacific Northwest wildfires have emitted less carbon to the atmosphere than previously thought. This is mostly due to previous overestimates of combustion losses by fire (Campbell et al., 2007), and uncertainty in remotely sensed estimates of burnt areas in different severity classes (Meigs et al., 2009). In mixed conifer forests of western North America, nearly all contemporary fires are mixed-severity.

Table 1
Comparison of live tree biomass carbon in the Pacific Northwest with that of different regions and biomes shows the PNW forests hold biomass equivalent to or larger than tropical forests.

Region	Live tree biomass carbon ^a (t ha ^{−1})	Calculation	Source
<i>Cool temperate moist</i>			
Coast Range ^b	370 (520)	Age > 200 years	Van Tuyl et al. (2005)
Klamath Mountains ^b	240 (440)	Age > 200 years	Hudiburg et al. (2009)
Sierra Nevada ^b	150 (194)	Age > 200 years	Hudiburg et al. (2009)
Alaska (Tongass NF)	300	Primary forests	Leighty et al. (2006)
Biome average	450	Primary forests	Keith et al. (2009)
<i>Tropical moist</i>			
Amazon (Tapajos ^c)	180 (250)	Primary forests	Gonçalves (2014)
Biome average	220	Primary forests	Keith et al. (2009)
<i>Tropical wet</i>			
Costa Rica (La Selva)	162 (195)	Primary forests, 18 plots	Dubayah et al. (2010)
Biome average	210	Primary forests	Keith et al. (2009)

^a Mean (maximum), except for Amazon and Costa Rica, which are median (max) values.
^b From FIA inventory plots in Oregon, Washington, California ecoregions.
^c Tapajos – assumed 50% of tree biomass is carbon, and coarse root biomass is 21% of aboveground biomass.

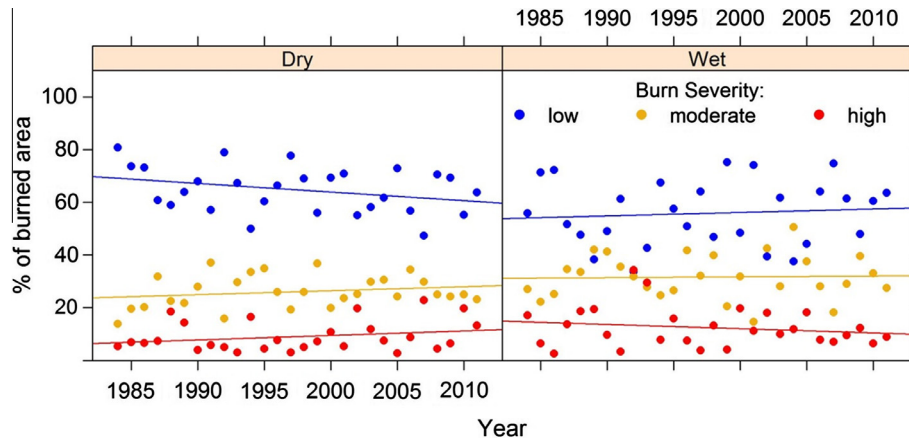


Fig. 2. The percentage of total area burnt within each burn severity class from 1984 to 2011 for dry (left panel, less than 600 mm year⁻¹) and wet (right panel) ecoregions in the Pacific Northwest. High severity fire accounted for an average of 9–12% of the total burn area and did not change significantly over time. Estimates are from the Monitoring Trends in Burn Severity database (Eidenshink et al., 2007). Summary statistics for each burn severity class are presented in Table 2, graphs by Logan Berner.

A study in the Sierra Nevada showed a 4.5% increase in percent high severity burnt area in yellow pine-mixed conifer from 1984 to 2010 (Miller and Safford, 2012). However, synthesis of Monitoring Trends in Burn Severity data (MTBS; Eidenshink et al., 2007) across the PNW, including the Sierra Nevada, shows that high severity fire (mortality of woody species >70%) represents only a small portion, 12–14%, of the total burnt area in the region and no increasing trend for dry and wet regions from 1984 to 2011 (Fig. 2, Table 2). The exception is percent moderate severity burnt area in dry regions, which increased 0.23% per year due to fires in the Sierra Nevada (excluding the Sierra Nevada, there was no significant increase in the trend).

In a comparison of pre- and post-fire carbon pools on a 200,000 ha mixed severity fire, only 1–3% of stem carbon was combusted in trees larger than ~8 cm diameter, and the percentage only increases up to 12% on large standing dead stems (Campbell et al., 2007). In four fires in Oregon, stand-scale carbon combustion averaged 22% of prefire carbon pools, and live tree stem combustion was a trivial amount, averaging 1.24% (Meigs et al., 2009). In this study, low- and moderate-severity fire released 58% and 82% as much carbon emissions, respectively, as high severity fire. In all five fires small trees, understory shrubs, litter and duff represented the majority of material combusted. In general, dry forest floor litter is more likely to burn than large stems with moist sapwood.

The biomass killed in fires eventually decomposes, slowly releasing carbon to the atmosphere over decades to centuries (Law and Harmon, 2011; Campbell et al., 2011). About half of the carbon remaining on site after a fire stays in soil for about 90 years, and the other half persists for more than 1000 years as charcoal (Singh et al., 2012).

Most fires do not kill all trees. What happens to the biomass that survives wildfires? In four fires in Oregon, 50–75% of live biomass survived low and moderate severity fires combined, which accounted for 80% of the burnt area (Meigs et al., 2009). In ponderosa pine forests, moderate severity fire killed only 34% of the trees larger than 20 cm in diameter, which accounted for most of the wood production two years after the fire (Irvine et al., 2007). Physiological measurements and tree cores shows many of these trees remain alive and productive 10 years after fire (Irvine et al., 2007; Waring, 2005; Becker, 2012), whereas standard surveys led to overestimation of mortality and a policy of removing healthy trees that could serve as shade or aid seedlings by hydraulically redistributing water from deep in the soil (Brooks et al., 2002). Removal of surviving trees reduces carbon storage, and adversely impacts regeneration in many cases.

Most tree mortality across the Pacific Northwest is attributed to mountain pine beetle (MPB) killing lodgepole pine. This insect killed 0.2–3.4 M ha of forests from 1997 to 2010 in the western conterminous US (Meddens et al., 2012). But in the PNW US, only about 2% of the forest area was affected; most of the impacted area was in British Columbia where critical winter temperatures of less than -40 °C no longer occur to keep beetle populations in check (Bentz et al., 1991) (Fig. 3).

Drought and warmer temperatures can also accelerate the development and reproduction of bark beetles (Hicke et al., 2006). Drought stress can make trees more susceptible to attack because the trees cannot produce enough resin to pitch out beetles or wall-off infection from blue-stain fungi (Raffa et al., 2008; Christiansen et al., 1987). In Oregon and Washington, the climate variables with the largest effect on probability of an outbreak are minimum winter temperature (warmer is more favorable) and

Table 2

Mean annual burned area and trends in burned area by severity class from 1984 to 2011 for dry (<600 mm) and wet ecoregions in the Pacific Northwest.

Ecoregion precipitation ^a	Burn severity	Mean annual burned area (±1 SD)		Trend in total burned area			Trend in percent of total burned area		
		Total burned area (ha year ⁻¹)	Percent of total burned area	Slope (ha year ⁻¹)	P	R ²	Slope (% year ⁻¹)	P	R ²
Dry	Low	135,767 ± 86,888	58 ± 10	3837	0.06	0.13	-0.37	0.11	0.10
	Moderate	71,975 ± 56,338	28 ± 5	2952	0.02	0.19	0.23	0.04	0.16
	High	21,031 ± 43,575	14 ± 8	1709	0.09	0.10	0.14	0.44	0.02
Wet	Low	21,017 ± 25,751	56 ± 12	937	0.12	0.09	0.13	0.66	0.01
	Moderate	10,427 ± 9913	32 ± 8	385	0.10	0.10	0.03	0.88	0.00
	High	4287 ± 4322	12 ± 8	72	0.49	0.02	-0.16	0.37	0.03

^a Dry ecoregions included the Blue Mountains, Columbia Plateau, Eastern Cascade Slopes, Sierra Nevada and the Northern Basin and Range. Wet ecoregions included the Cascades, Coast Range, Klamath Mountains, North Cascades, Northern Rockies, Puget Lowland, and the Willamette Valley.

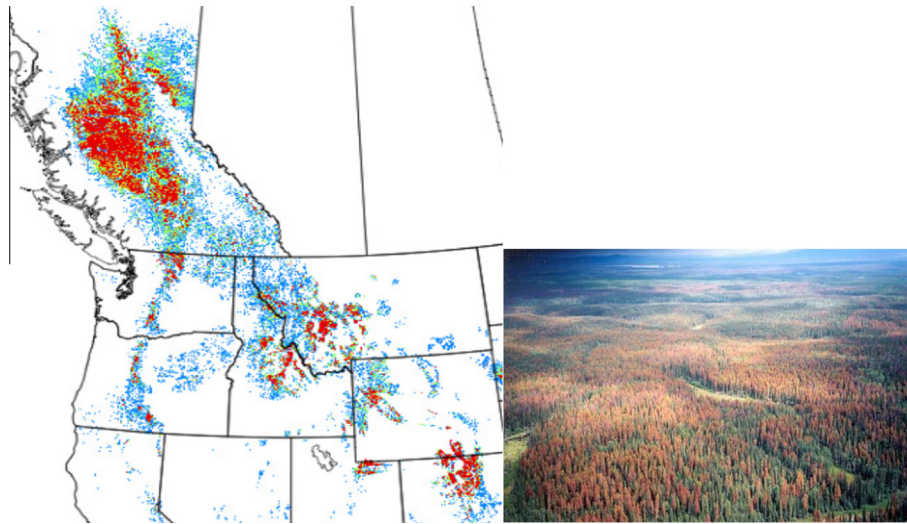


Fig. 3. Cumulative tree mortality caused by mountain pine beetles (US upper estimate, 1997–2010; British Columbia, 2001–2010); 2012, by Meddens et al. (2012). Mortality area within 1 km^{-2} grid cell – blue (0–5 ha), green (5–15 ha), red (>15 ha). Inset is “red attack” by MPB in British Columbia.

drought conditions in the year preceding the attack and during the attack (Preisler et al., 2012). Precipitation in the preceding year possibly influences brood size as well as tree vigor. Where drought occurs in the early stages of beetle outbreaks, relief from drought in the later stages does not result in declines in beetle populations.

The high humidity deficits that increase the likelihood of wild-fires, combined with soil drought, can also cause the death of mature trees. This appears to be the case with “sudden aspen decline” where a few years of unusually stressful conditions results in irreversible damage to the tree’s water conducting system (Anderegg et al., 2013, 2014).

4. Implications of current policies on the regional carbon balance

Even with an 82% reduction in wood harvest on U.S. National Forest land since 1993, the Pacific Northwest region, among all those in North America, records nearly the highest percentage of area harvested annually with the highest mass harvested per unit area. About 1.4% of total US forest area is harvested annually (Smith et al., 2009), with more than half of it as partial harvest (Masek et al., 2011). The highest intensities of roundwood volume per unit area harvested in western North America are in British Columbia ($\sim 400 \text{ m}^3 \text{ ha}^{-1}$) and the Pacific Northwest ($\sim 300 \text{ m}^3 \text{ ha}^{-1}$), followed by the intermountain region ($\sim 100 \text{ m}^3 \text{ ha}^{-1}$) (Masek et al., 2011). These rates of extraction partly reflect the relatively high growth rates ($5\text{--}15 \text{ Mg ha}^{-1} \text{ year}^{-1}$). Expressed as volume harvested per unit of forest area of each region, the Pacific Northwest coastal forests have the highest rate (2 to greater than $4 \text{ m}^3 \text{ ha}^{-1}$), followed by British Columbia ($1\text{--}2 \text{ m}^3 \text{ ha}^{-1}$; Fig. 4; Masek et al., 2011). In terms of carbon, merchantable wood removals (2001–2006) averaged 6.5, 5.1, and 2.7 Tg C for Oregon, Washington, and California, respectively (Hudiburg et al., 2011).

Factors that have influenced changes in harvest patterns include timber markets, which are increasing globally, and general economic activity as producers respond to changes in commodity prices (Howard and Westby, 2007). Short-term decreases in harvest rates respond to downturns in economic activity, as they did following 2008. Shifts in policy also affect harvest rates. For example, the implementation of the Northwest Forest Plan in 1993 and related policy changes, switched US northwest forests from a

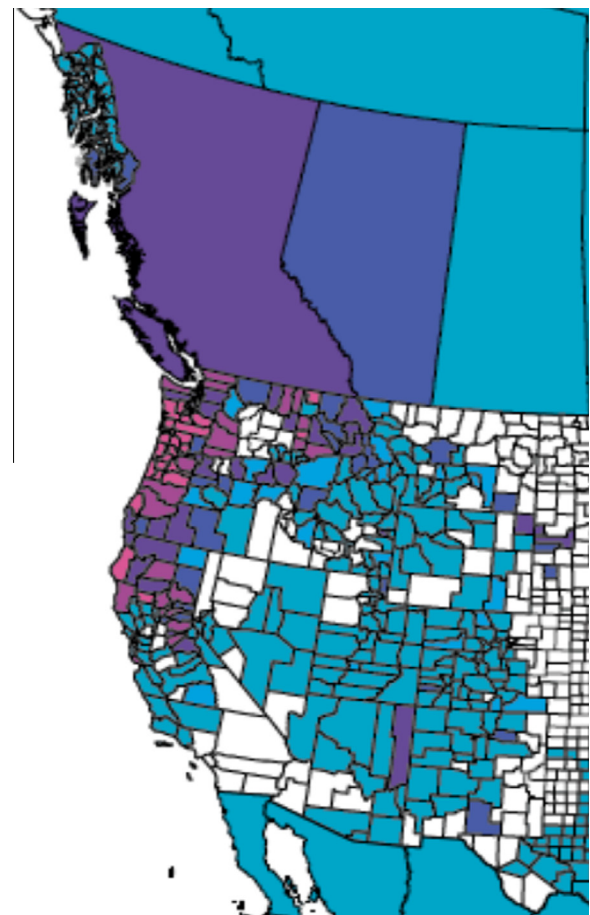


Fig. 4. Annual volume of roundwood harvest per unit of forest area. The highest rates are found in the Pacific Northwest US coastal forests (red = 2 to $>4 \text{ m}^3 \text{ ha}^{-1}$ forestland), followed by British Columbia (purple = $1\text{--}2 \text{ m}^3 \text{ ha}^{-1}$) in western North America, 2007, by Masek. The British Columbia data are net merchantable volume harvested, so the values may be relatively low compared to actual harvest volume. However, the data are assumed to be comparable to US data, which are derived from the Timber Product Output (TPO) analysis (Masek et al., 2011).

carbon source (negative net ecosystem carbon balance) to a carbon sink (Turner et al., 2011).

It would be theoretically possible, in the absence of disturbance, to increase regional forest carbon stocks significantly. For Oregon and Northern California, a reduction in the intensity of harvest, combined with an increase in the interval, could almost double carbon stocks from the current level of 3.2–5.9 Pg C, with an increase of 15% possible in 50 years (Hudiburg et al., 2009). It would take centuries, however, to make up for carbon that was lost through previous harvests (Schulze et al., 2012; Hudiburg et al., 2011; Harmon and Marks, 2002).

5. Implications of shorter rotations on the regional carbon balance under a stable and changing climate

It is often thought that managing forests on shorter rotations (e.g. changing from current 80–90 year rotations to 40–50 years) would provide the most effective long-term carbon sequestration benefit. However, research in the region shows that long-term rotations or selective harvest are a better alternative on managed lands to maximize carbon sequestration (Harmon et al., 1990).

An important aspect of short-rotation forest management is that the carbon debt incurred on harvested sites is usually ignored, as is the fate of the wood once it is harvested. The combined carbon stored in ecosystems and products from the ecosystems is always lower when rotation intervals are shorter and harvest intensity is higher (Mitchell et al., 2012). That is, harvesting with greater frequency and intensity lowers carbon storage in forests and prolongs the time needed to recoup the carbon debt.

The full implications of shorter rotations was demonstrated in a regional analysis of Oregon's forest carbon stocks to year 2100 (Hudiburg et al., 2013a). This analysis provided an estimate of the net effect on forest carbon balances over the next 90 years under projected climate change, taking into account any gain from a continued increase in atmospheric levels of carbon dioxide. It also included a life-cycle assessment (LCA) once trees are harvested.

The analysis modeled shortened rotations from current to proposed levels in areas typically clear-felled. It applied multiple treatments into the future, and implemented thinning scenarios for bioenergy and fire-risk reduction activities in areas identified as having short intervals (<40 years) between fires. All of the intensified management scenarios significantly increased long-term carbon dioxide emissions to the atmosphere compared with business-as-usual management, with less increase in emissions from the semi-arid ecoregions.

Interestingly, the projected enhancement of forest productivity from warming and increased atmospheric carbon dioxide was more than enough to counterbalance a slight increase in fire emissions under current harvest levels. The amount of carbon lost from the treatments intended to reduce crown fire risk exceeded the gain from reducing burn probability and fire severity, even over long periods. Furthermore, the proposed harvest rates to reduce fire and drought impacts resulted in up to 2.2% of the forest area harvested annually. These harvest rates were not sustainable over the long-term because live biomass carbon did not recover to initial conditions before the next scheduled harvest. The result has implications for forest management and climate policy. Such analyses of proposed changes in land management compared with business-as-usual are needed in other regions.

A complete life cycle assessment (LCA) includes the land-based carbon (net biome production, accounting for fire emissions and decomposition after disturbance), and tracks carbon losses during transport, manufacturing, combustion, and fossil fuel substitution benefits. Two misunderstandings have occurred in conducting life

cycle assessments. First, such assessments cannot ignore carbon stocks present on the land, as these stocks influences the concentrations of CO₂ in the atmosphere and are clearly affected by land management (Schulze et al., 2012; Law and Harmon, 2011). Second, benefits attributed to product substitution are commonly overestimated. Substituting wood for aluminum and steel can displace fossil fuel emissions, but the displacement period needs to be part of the accounting. Displacement occurs until the building is replaced, and then the substitution can be renewed by a new building or it can be lost by using a material with a higher energy cost. In addition, it is often assumed that product substitution will reduce the demand for fossil fuel. However, due to human behavior and current economic systems that ignore adverse externalities, reducing resource consumption through substitution or improvements in efficiency rarely reduce fossil fuel use (York, 2012). Therefore, benefits may be substantially lower and the payback period much longer and smaller for the carbon debt from intensified management and avoided fossil fuel combustion than commonly assumed (Haberl et al., 2013).

Although much of the PNW region within the maritime influence of the coast is buffered against the influence of climate change (Waring et al., 2011), no place is immune. Much of British Columbia has already experienced unparalleled levels of disturbance by insects and diseases associated with climate change (Woods et al., 2010). This has led to harvesting rates that are unlikely to be sustainable. For the tree species that extend their northern limits into the province, the projected change in climate is so rapid that these species would have to migrate at >100 km per decade to keep up with the projected shift in their current climatic niche before the end of this century (Hamman and Wang, 2006; Rehfeldt et al., 2006, 2014). Although long-distance dispersal is certainly possible (Pitelka and Plant Migration Workshop Group, 1997), there are many barriers, both natural and those imposed by humans, that suggest that foresters will be involved in assisting the migration of species northward and upward in elevation (Bunnell and Kremsater, 2012). The likelihood that the composition of forests may be in continuous and rapid transition across much of the Pacific Northwest places additional challenges on managers and decision makers. It is likely that a new mix of species will continue to provide ecosystem services, but maintaining a sustainable harvest of wood products will be difficult.

In summary, recent science indicates that forests hold carbon much longer intact than when products from them are harvested and utilized. Harvested wood product can be stored at most on average 80–150 years in structural wood for housing or in landfills where it decomposes slowly, or short-term (e.g. paper), which decomposes rapidly. Pacific Northwest harvests generate merchantable wood that is about 50–60% of the total wood harvested and an average of 54% of the wood product remains in use or end up in landfills after 20 years where it decomposes (Smith et al., 2006). The remainder returns to the atmosphere within about 90–150 years and there are losses over time, not just at the end of product use. These loss rates are much higher than those from forests through the normal decomposition process and frequent harvesting increases these rates still further.

6. Predicting physiological condition and tree mortality

It is challenging to predict how different types of forests will respond to gradual shifts in climate or extreme events because the frequency and kind of disturbance may increase or decrease the fitness of one species compared to another. The most productive forests in the PNW support the densest canopies on earth (Waring and Franklin, 1979; Law and Waring, 1994; Waring et al., 2014). Having such dense canopies buffers these forests in

the maritime influenced areas against moderate disturbances because the increased exposure resulting from gaps in the canopy provide deeper penetration of light. As a result, the loss of 50% of the trees from a stand with a dense canopy may not reduce wood production more than a few percent because the leaves of surviving trees become more efficient, and as a result, the trees also become healthier and less susceptible to attack from insects (Waring, 1983). In more drought-stress regions where canopies are less dense, thinning is not as effective in improving residual wood production and tree growth efficiency, in part because of competition for water from competing shrubs (Campbell et al., 2009).

Physiological sensitivity to climate also varies with tree size. The relative sensitivity of leaf stomata to high evaporative demand is greater in young than old ponderosa pine (Irvine et al., 2004), and young trees are more susceptible to soil water deficits due to shallower rooting and their greater vulnerability of their roots to broken water columns (Domec et al., 2004). Over the course of dry summers, ~20%, 45% and 47% of water used by young, mature and old pine trees in sandy soils is extracted from below 80 cm depth (Irvine et al., 2004). Hydraulic redistribution from deep soil layers will be missed, along with the added storage capacity, if models that assume 1 m soil depth.

The effects of water deficits accumulate, increasing injury to a tree's water conducting system dependent on the duration and severity of drought (Miao et al., 2009; Mueller et al., 2005). During the extreme drought years of 2001 and 2002, old ponderosa pine trees in Oregon showed only a small decline in water transport efficiency to leaves (11–24%) whereas in mature pine, the efficiency declined by 46%, and for young pine, by 80% (Irvine et al., 2004). The ability of young pine to open their stomata more widely than older trees, increases the rate that water flows through a unit of their sapwood. As a result, younger trees risk the breakage of a larger proportion of their water columns, which may account for the high mortality in a young ponderosa pine plantation in California (Goldstein et al., 2000). On the other hand, large, old trees become progressively less efficient at assimilating carbon due to high resistance though elongating branches (Warren and Adams, 2000).

What kind of physiological properties need to be defined to identify thresholds of tolerance? One relation that differs among species and size classes is the vulnerability of the water conducting system, (expressed as loss of hydraulic conductance) to tension (expressed as negative water potentials) on the water column. During a typical summer drought in Oregon, mature Douglas-fir, ponderosa pine, and juniper trees lose ~80% of their hydraulic conductance (PLC), respectively, at predawn water potential (Ψ_{pd}) values of -2.0, -1.7, and -3.0 MPa (Law, 1993; Irvine et al., 2004; Miller, 1990).

A second relationship that matters is one between the humidity deficit of the air (vapor pressure deficit) and stomatal conductance of leaves. Stomatal conductance rates in Douglas-fir and ponderosa pine are much more sensitive than juniper to changes in Ψ_{pd} ; the latter is frugal at all times in transpiring water. The seasonal minimum Ψ_{pd} values for juniper in Oregon were not as low as those reported in the more arid Southwest US (-4.0 and -7.0 MPa in 2007 and 2008, respectively; Plaut et al., 2013). These relationships can be expected to differ among genotypes and species (Plaut et al., 2013).

A number of ecosystem process-based models have been developed that incorporate knowledge of physiological responses acquired from extensive field studies: Biome-BGC (Running, 1994; Thornton et al., 2002; Law et al., 2006), 3PG (Law et al., 2000; Coops et al., 2001), SPA (Williams et al., 2001), and the Community Land Model (CLM; Hudiburg et al., 2013a,b). These models have been tested across a steep eco-climatic gradient in Oregon.

The models, implemented with measurements of key physiological properties for major forest types, have proven generally reliable as evaluated from measurements of productivity, biomass accumulation, and ecosystem fluxes measured from towers. Improvements in these models require more observations and experiments to identify the physiological thresholds of different tree species (and varieties) to drought and temperature extremes. There is also a need to obtain more precise estimates of the storage capacity of water available to trees with deep roots in drought-prone areas.

Recent analyses with climate-envelope models predict large changes in the area suitable for survival of Northwest tree species (Rehfeldt et al., 2006, 2014). In British Columbia, where climatic change is clearly underway (Xu et al., 2013), some species are predicted to have to migrate, or be assisted in migrating north at >100 km per decade between now and 2085 to remain within their climate niches (Hamman and Wang, 2006). Although long-distance dispersal may occur (Pitelka et al., 1997), mountainous terrain presents major impediments to migration, as do barriers created by human activities (Bunnell and Kremsater, 2012).

Some more process-based models take into account the importance of soil properties in defining the current, and presumably, future distribution of species (Mathys et al., 2014). Soil properties are obviously important when it comes to modeling changes in ecosystem carbon balances along with the mix of likely tree species (Kueppers and Harte, 2005).

Nitschke and Innis (2008) developed a gap model among the few models that considers how climate change affects the chance of successful regeneration for 17 PNW tree species by defining temperature limits for chilling, bud burst, frost tolerance and minimum for survival along with specific ranges in heat sums and tolerance to drought. The model was successful in identifying the degree of change in phenology and biophysical variables that largely control seedling establishment within an area in interior British Columbia where transition to new types of ecosystems are expected within a century.

In this section we recognized the need and the challenge to incorporate variation in sensitivity of physiological mechanisms into models to predict the response of tree species to climate change and continuing rising levels of atmospheric carbon dioxide. Species (and genotypes) respond differently, and size matters when it comes to evaluating what limits to set on models that predict growth, mortality, and distribution. The physiology of insects and pathogens cannot be ignored because their populations also respond to climate change, often more rapidly, and more damagingly than would be the case if climate alone were the only variable affecting ecosystem processes and biodiversity.

7. Future directions

The challenge for science is to predict the interactive effects of environmental change and management strategies on forest carbon and species distributions. Ideally, assessments should be conducted at scales appropriate for aiding policy and local management decisions (e.g. 1–4 km²). In the not-to-distance future, modeling at 10 km² resolution may be possible globally, but only if there are sufficient in situ and remote sensing observations available to account for the inherent variability among tree species, stand ages and soil conditions (Law, 2014; Bonan pers. comm.).

The challenge is multi-dimensional: to link biophysical and biogeochemical responses by forests with policy, economics, and management actions designed to mitigate the impacts of climate change across the region. Novel approaches are required, linking otherwise disparate fields of study, and stretching the comfort zones of scientists in different disciplines. Assessments of plausible

scenarios of climate and management change are needed to quantify carbon and water cycling and vegetation changes in the future.

The development of land system models that incorporate biophysics, biogeochemistry, and the demographics and structure of vegetation, such as the Community Land Model (Bonan et al., 2012; Lawrence et al., 2012; Fisher et al., 2010), allows integration of many of the mortality inducing processes (McDowell et al., 2013). CLM4.5 includes many plant functional types (PFTs) that can be surrogates for major forest types or species. The model provides an integrated set of data on transient land cover and wood harvest for the historical period (1850–2005), and the IPCC representative concentration pathways (RCP) or atmospheric CO₂ trajectories (2006–2100; Hudiburg et al., 2013a; Lawrence et al., 2012).

Short-comings of species distribution models are that they often lack interspecific competition and succession, which can have a large effect on species range expansion and contraction, and biodiversity in future climate conditions (Snell et al., 2014; Thuiller et al., 2013). Dynamic vegetation models that include these processes, as well as demography and mechanistic representation of dispersal, show promise for fine-scale applications (Fisher et al., 2010). Interactions and feedbacks between land-use, species range shifts, and climate can be simulated to better understand the likely consequences of a range of future scenarios of change.

Recent modifications of the Community Land Model (CLM4.5) include changes in mortality rate, refinement of physiological parameters for subgroups of species within plant functional types (e.g. foliage carbon to nitrogen ratios, specific leaf area), and rates of biological nitrogen fixation. For example, CLM4.5 is being modified to allow mortality and growth rates of trees to vary by PFT or species within ecoregions (Hudiburg et al., 2013a). Additional improvements to predicting mortality should account for mechanisms that lead to whole-system failure from the cumulative effects of climate, fire, and biotic stressors (insects, diseases, and competition among plants).

Other model improvements underway include predicting vulnerability to mortality from insect outbreaks and wildfires. New models are being developed to predict outbreaks associated with climate (Preisler et al., 2012), the mix of tree species and characteristics such as size and stand density. Earlier studies suggested tree vigor, defined by growth efficiency (productivity per unit of leaf area) was a good predictor of mortality due to mountain pine beetle (Waring and Pitman, 1985). A more mechanistic approach should consider depletion of tree carbohydrate supply, as this may occur during a drought, and might help predict epidemic phases of beetle populations (Safranyik and Carroll, 2006; Safranyik et al., 2010). The fire-effect module within CLM4.5 needs to continue to refine predictions of post-fire mortality, biomass combustion, and adjustment of land carbon pools and emissions (Li et al., 2012).

Both insect and fire modules should link to a land model's dynamic global vegetation model. This will require a more complete assessment of plant physiology representative of the changes that occur following disturbance, competition and succession (Thonicke et al., 2010; Fisher et al., 2010). Although land system models predict burn area, because fire severity is not explicitly defined for computing changes in carbon pools and emissions, this can lead to overestimation of carbon emissions. Realistic combustion factors are needed for more forest types and pool sizes and severities for process modeling.

There is also uncertainty associated with using downscaled climate data to interpret the output from regional climate models (Foley, 2010). To down-scale global climate simulations, for example from 50 km grid to 4 km, will require accounting for the land within the maritime influence of the Pacific Ocean, and the effects of mountainous terrain on wind patterns and the distribution of precipitation (rain shadows). One promising approach might

involve statistical downscaling that uses observation-based training data (PRISM; Daly et al., 2008) to remove historical biases and match spatial patterns in climate model output (Abatzoglou and Brown, 2012). Strategies to mitigate climate effects on forests and to reduce carbon emissions will need to include uncertainty estimates along with those obtained for climate projections.

Perhaps the largest uncertainties are in how humans will react to climate impacts on forest ecosystems and the services they provide. The social environment is almost certain to have even greater implications for forests and what happens to them. There have been surprises in PNW forests related to societal policy decisions, such as changes in the ownership of private lands with reduced harvest on public lands, and there will likely be many more. Changes in demographics and socio-economic values are difficult to predict, yet they are major drivers of environmental change. Historically, humans have lived through cycles of crisis and growth, and the projected increase in human population to 9 billion by 2042 and associated demands should lead to a range of possibilities in how we address climate change and its impacts.

Actions by land managers to mitigate climate change are part of this uncertainty. Feedbacks between potential harvests and economic factors ultimately drive harvest timing, intensity and locations. Economic considerations include knowledge of species available for harvest, biomass density, locations where harvest or thinning could improve forest condition as identified by predictions of vulnerability to mortality, transport distance to existing or proposed processing facilities, and market prices. Other important issues when considering land management change include potential impacts on ecosystem services including biodiversity, soil fertility, and stable water supply (Haberl et al., 2013). Some areas may serve as biodiversity reserves and corridors for migration to prepare for uncertainty of future climate impacts on forests and animal habitat. To date, these are rarely part of the decision-making process in simulating land management change scenarios, but they need to be.

Land models will continue to be improved, but will need continued observations to initialize, update, and evaluate the accuracy of a full array of predictions. Geographically explicit data layers will be required that geographically register species distribution, forest structure, foliar nitrogen, and how these and other properties change (Xiao et al., 2014). Improvements in testing the models await better satellite coverage with instruments that cannot only distinguish burnt areas from harvesting or insect activities (Kennedy et al., 2010; Meigs et al., 2011) but also update changes in biomass accumulation or loss e.g., LiDAR and RADAR (Treuhaft et al., 2004, 2010).

8. Conclusions

We have provided an overview and synthesis of research results on current and potential future effects of drought, fire and management on Pacific Northwest US forests, with an emphasis on forest carbon dynamics. Comprehensive assessments are needed to understand the consequences of land use actions on both the local and regional carbon balance. By accounting for more of the benefits and costs involved in reducing the risk of crown fires, modifying storage in long- and short-term products, and in substituting wood products for fossil fuel, we find that thinning existing forests to reduce crown-fire risk increases net carbon emissions to the atmosphere for many decades, but is likely to be less of an atmospheric impact in some dry forest regions that are highly vulnerable to fire.

While some suggest that shorter rotations would provide more effective carbon sequestration (e.g. changing from current 80–90 year rotations to 40–50 years), research in the PNW shows that the total carbon accumulated from longer rotations is superior to

that from e.g. 40- to 50-year rotations. When trees are harvested, the carbon released to the atmosphere from increased decomposition, and in the product chain needs to be accounted for when assessing carbon sequestration potential.

There is considerable potential for increasing carbon sequestration in PNW forests by using longer rotations, particularly in those forests dominated by Douglas-fir in climatically buffered areas, because they can continue, if undisturbed, to accumulate carbon for centuries. If rotations in managed forests were extended to 100+ years, the benefit would be significant in terms of carbon stocks per unit ground area. In addition, carbon markets that financially rewarded additional carbon storage in forests (e.g. carbon credits, discounts for uncertainty) could result in significant mid-term carbon storage (Law and Harmon, 2011).

There is a consensus among climate scientists that the region can be expected to experience progressively hotter summers with minimal change in annual precipitation but substantial loss of snowpack, which supplies water to many forests during the dry summers as well as to agriculture and communities.

There is still work to be done to develop improved predictors of species' responses to drought and heat extremes in specific environments. Human activities can exacerbate or improve the situation. Refined analysis of land management scenarios can help to reduce impacts of environmental change on forests.

Current models that combine climatic analyses with estimates of forest growth, and mortality have progressed in their sophistication and reliability, and are becoming useful for evaluation of many policies to counter or adapt to predicted climatic changes. We offer suggestions to improve models still further so that they provide more plausible evaluation of management actions to mitigate the effects of climate change on forests.

Both current and future assessments rely heavily on expanding in situ and remotely sensed observations. It is these sets of measurements that confirm or refute model predictions, and at the same time, provide a way of updating shifts in carbon stocks that otherwise might go unrecorded. Trend detection requires long-term observations over time, such as provided by Landsat data. Models also are in dire need of high quality data to define functional physiological relationships more accurately, and improved resolution maps of species distributions and biomass. Better integration of observations and models are essential to quantify changes over time and to predict forest conditions in the future in a way that significantly aids decision-making.

Acknowledgements

Many of the research findings resulted from support from the Office of Science (BER), US Department of Energy (DOE Grant No. DE-FG02-07ER64361). We gratefully acknowledge figure and table production by Logan Berner, and valuable comments from Jerry Franklin. This work was partially supported by grants from the Agriculture and Food Research Initiative of the USDA National Institute of Food and Agriculture (NIFA; Grant No. 2013-67003-20652), and Office of Science (BER) US Department of Energy (Grant No. DE-FG02-06ER64318). Support was also provided from the US National Aeronautics and Space Administration Program in Biodiversity and Ecological Forecasting to R.H.W. (Grant No. NNX11A029G).

References

Abatzoglou, J.T., Brown, T.J., 2012. A comparison of statistical downscaling methods suited for wildfire applications. *Int. J. Climatol.* 32, 772–780.
 Abatzoglou, J.T., Rupp, D.E., Mote, P.W., 2014. Seasonal climate variability and change in the Pacific Northwest of the United States. *J. Clim.* 27, 2125–2142.
 Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham,

R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684.
 Anderegg, W.R.L., Anderegg, L.D.L., Berry, J.A., Field, C.B., 2014. Loss of whole-tree hydraulic conductance during severe drought and multi-year forest die-off. *Oecologia* 175, 11–23.
 Anderegg, W.R.L., Plavcova, L., Anderegg, L.D.L., Hacke, U., Berry, J.A., Field, C.B., 2013. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Glob. Change Biol.* 19, 1188–1196.
 Becker, D., 2012 <<http://www.fseee.org/stay-informed/victories#trees>>.
 Bentz, B.J., Logan, J.A., Amman, G.D., 1991. Temperature-dependent development of the Mountain Pine Beetle (Coleoptera:Scolytidae) and simulations of its phenology. *Can. Entomol.* 123, 1083–1094.
 Bonan, G.B., Oleson, K.W., Fisher, R.A., Lasslop, G., Reichstein, M., 2012. Reconciling leaf physiological traits and canopy flux data: use of the TRY and FLUXNET databases in the Community Land Model version 4. *J. Geophys. Res.* 117, G02026. <http://dx.doi.org/10.1029/2011JG001913>.
 Brooks, J.R., Meinzer, F.C., Coulombe, R., Gregg, J., 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiol.* 22, 1107–1117.
 Bunnell, F.L., Kremsater, L.L., 2012. Actions to promote climate resilience in forests of British Columbia. *J. Ecosyst. Manage.* 13, 1–10.
 Campbell, J., Alberti, G., Martin, J., Law, B.E., 2009. Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada. *For. Ecol. Manage.* 257, 453–463.
 Campbell, J.L., Donato, D.C., Azuma, D.A., Law, B.E., 2007. Pyrogenic carbon emission from a large wildfire in Oregon, USA. *J. Geophys. Res.* 112, G04014. <http://dx.doi.org/10.1029/2007JG00045>.
 Campbell, J.L., Harmon, M.E., Mitchell, S.R., 2011. Can fuel-reduction treatments really increase forest carbon storage in the western US by reducing future fire emissions? *Front. Ecol. Environ.* 3, 314–322.
 Christiansen, E., Waring, R.H., Berryman, A.A., 1987. Resistance of conifers to bark beetle attack: searching for general relationships. *For. Ecol. Manage.* 22, 89–106.
 Coops, N.C., Waring, R.H., Brown, S.R., Running, S.W., 2001. Comparisons of predictions of net primary production and seasonal patterns in water use derived with two forest growth models in Southwestern Oregon. *Ecol. Model.* 142, 61–81.
 Dalton, M.M., Mote, P.W., Snover, A.K. (Eds.), 2013. *Climate Change in the Northwest: Implications for Our Landscapes, Waters, and Communities*. Island Press, Washington, DC.
 Daly, C., Halbleib, M., Smith, J.L., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int. J. Climatol.* 28, 2031–2064.
 Dennison, P.E., Brewer, S.C., Arnold, J.D., Moritz, M.A., 2014. Large wildfire trends in the western United States, 1984–2011. *Geophys. Res. Lett.* 41, 2928–2933. <http://dx.doi.org/10.1002/2014GL059576>.
 Domec, J.-C., Warren, J.M., Meinzer, F.C., Brooks, J.R., Coulombe, R., 2004. Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia* 141, 7–16.
 Dubayah, R.O., Sheldon, S.L., Clark, D.B., Hofton, M.A., Blair, J.B., Hurtt, G.C., Chazdon, R.L., 2010. Estimation of tropical forest height and biomass dynamics using lidar remote sensing at La Selva, Costa Rica. *J. Geophys. Res.* 115, G00E09. <http://dx.doi.org/10.1029/2009JG000933>.
 Eidenshink, J., Schwind, B., Brewer, K., Zhu, Z.L., Quayle, B., Howard, S., 2007. A project for monitoring trends in burn severity. *Fire Ecol.* 3, 3–20.
 Fisher, R.A., McDowell, N., Purves, D., Moorcroft, P., Sitch, S., Cox, P., Huntingford, C., Meir, P., Woodward, F.I., 2010. Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations. *New Phytol.* 187, 666–681.
 Foley, A.M., 2010. Uncertainty in regional climate modelling: a review. *Prog. Phys. Geogr.* 34, 647–670.
 Franklin, J.F., DeBell, D.S., 1988. Thirty-six years of tree population change in an old-growth Pseudotsuga-Tsuga forest. *Can. J. For. Res.* 18, 633–639.
 Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. *Bioscience* 37, 550–556.
 Goldstein, A.H., Hultman, N.E., Fracheboud, J.M., Bauer, M.R., Panek, J.A., Xu, M., Qi, Y., Buenter, A.B., Baugh, W., 2000. Effects of climate variability on the carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA). *Agric. For. Meteorol.* 101, 113–129.
 Gonçalves, F.G., 2014. Vertical structure and aboveground biomass of tropical forests from lidar remote sensing. PhD Dissertation, Oregon State University. 200pp.
 Gonzalez, P., Asner, G.P., Battles, J.J., Lefsky, M.A., Waring, K.M., Palace, M., 2010. Forest carbon densities and uncertainties from Lidar, QuickBird, and field measurements in California. *Remote Sens. Environ.* 114, 1561–1575.
 Haberl, H., Schulze, E.-D., Koerner, C., Law, B.E., Holtmark, B., Luyssaert, S., 2013. Response: complexities of sustainable forest use. *Global Change Biol. Bioenergy* 5, 1–2.
 Hamman, A., Wang, T., 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* 87, 2773–2786.
 Harmon, M.E., Bible, K., Ryan, M.G., Shaw, D.C., Chen, H., Klopatek, J., Li, X., 2004. Production, respiration, and overall carbon balance in an old-growth Pseudotsuga-Tsuga forest ecosystem. *Ecosystems* 7, 498–512.

- Harmon, M.E., Ferrell, W.K., Franklin, J.F., 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247, 699–702.
- Harmon, M.E., Marks, B., 2002. Effects of silvicultural practices on carbon stores in Douglas-fir – western hemlock forests in the Pacific Northwest, USA: results from a simulation model. *Can. J. For. Res. – Revue Canadienne de Recherche Forestiere* 32, 863–877.
- Hicke, J.A., Logan, J.A., Powell, J., Ojima, D.S., 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *J. Geophys. Res.* 111, G02019. <http://dx.doi.org/10.1029/2005JG000101>.
- Howard, J. L., Westby, R., 2007. U.S. forest products annual market review and prospects, 2004–2008, Res. Note FPL-RN-0305, Forest Products Laboratory, Forest Service, U.S. Department of Agriculture, Madison, Wis. 8pp.
- Hudiburg, T.W., Law, B.E., Thornton, P.E., 2013b. Evaluation and improvement of the Community Land Model (CLM 4.0) in Oregon forests. *Biogeosciences* 10, 453–470.
- Hudiburg, T.W., Law, B.E., Turner, D.P., Campbell, J., Donato, D., Duane, M., 2009. Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. *Ecol. Appl.* 19, 163–180.
- Hudiburg, T., Law, B.E., Wirth, C., Luyssaert, S., 2011. Regional CO₂ implications of forest bioenergy production. *Nat. Clim. Change* 1, 419–423.
- Hudiburg, T.W., Luyssaert, S., Thornton, P.E., Law, B.E., 2013a. Interactive effects of environmental change and management strategies on regional forest carbon emissions. *Environ. Sci. Technol.* 47, 13132–13140.
- Irvine, J., Law, B.E., Kurpius, M., Anthoni, P.M., Moore, D., Schwarz, P., 2004. Age related changes in ecosystem structure and function and the effects on carbon and water exchange in ponderosa pine. *Tree Physiol.* 24, 753–763.
- Irvine, J., Law, B.E., Hibbard, K., 2007. Post-fire carbon pools and fluxes in semi-arid ponderosa pine in Central Oregon. *Glob. Change Biol.* 13, 1748–1760.
- Joyce, L.A., Running, S.W., Breshears, D.D., Dale, V.H., Malmshier, R.W., Sampson, R.N., Sohngen, B., Wood all, C.W., 2014. Ch. 7: Forests. *Climate Change Impacts in the United States: The Third National Climate Assessment*. In: Melillo, J.M., et al. (Eds.). U.S. Global Change Research Program. pp. 175–194 doi:<http://dx.doi.org/10.7930/J0Z60KZC>.
- Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon dense forests. *Proc. Nat. Acad. Sci.* 106, 11635–11640.
- Kennedy, R.E., Yang, Z., Cohen, W.B., 2010. Detecting trends in forest disturbance and recovery using yearly Landsat time series: 1. LandTrendr – Temporal segmentation algorithms. *Remote Sens. Environ.* 114, 2897–2910.
- Kueppers, L.M., Harte, J., 2005. Subalpine forest carbon cycling short-and long-term influence of climate and species. *Ecol. Appl.* 15, 1984–1999.
- Law, B.E., 1993. Remote sensing of radiation interception by vegetation to estimate aboveground net primary production across western Oregon. PhD dissertation, Oregon State University. 144pp.
- Law, B.E., 2014. Regional analysis of drought and heat impacts on forests: current and future science directions. *Glob. Change Biol.* <http://dx.doi.org/10.1111/gcb.12651>.
- Law, B.E., Harmon, M., 2011. Forest sector carbon management, measurement and verification, and discussion of policy related to climate change. *Carbon Manage.* 2, 73–84.
- Law, B.E., Thornton, P., Irvine, J., Van Tuyl, S., Anthoni, P., 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biol.* 7, 755–777.
- Law, B.E., Turner, D., Campbell, J., Sun, O.J., Van Tuyl, S., Ritts, W.D., Cohen, W.B., 2004. Disturbance and climate effects on carbon stocks and fluxes across Western Oregon USA. *Glob. Change Biol.* 10, 1429–1444.
- Law, B.E., Turner, D., Lefsky, M., Campbell, J., Guzy, J.M., Sun, O., Van Tuyl, S., Cohen, W., 2006. Carbon fluxes across regions: observational constraints at multiple scales. In: Wu, J. et al. (Eds.), *Scaling and Uncertainty Analysis in Ecology: Methods and Applications*. Columbia University Press, New York, USA, pp. 167–190.
- Law, B.E., Waring, R.H., 1994. Combining remote sensing and climatic data to estimate net primary production across Oregon. *Ecol. Appl.* 4, 717–728.
- Law, B.E., Waring, R.H., Anthoni, P.M., Aber, J.D., 2000. Measurements of gross and net ecosystem productivity and water vapor exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Glob. Change Biol.* 6, 155–168.
- Lawrence, P.J., Feddema, J.J., Bonan, G.B., Meehl, G.A., O'Neill, B.C., Oleson, K.W., Levis, S., Lawrence, D.M., Kluzek, E., Lindsay, K., Thornton, P.E., 2012. Simulating the biogeochemical and biogeophysical impacts of transient land cover change and wood harvest in the community climate system model (CCSM4) from 1850 to 2100. *J. Clim.* 25, 3071–3095.
- Leighty, W.W., Hamburg, S.P., Caouette, J., 2006. Effects of management on carbon sequestration in forest biomass in Southeast Alaska. *Ecosystems* 9, 1051–1065.
- Li, F., Levis, S., Ward, D.S., 2012. Quantifying the role of fire in the Earth system – Part 1: improved global fire modeling in the Community Earth System Model (CESM1). *Biogeosciences* 10, 2293–2314.
- Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P., Grace, J., 2008. Old-growth forests as global carbon sinks. *Nature* 455, 213–215.
- Masek, J.G., Cohen, W., Leckie, D., Wulder, M., Vargas, R., de Jong, B., Healey, S., Law, B.E., Birdsey, R., Houghton, R.A., Mildrexler, D., Goward, S., Smith, W.B., 2011. Recent rates of forest harvest and conversion in North America. *J. Geophys. Res.* 116, G00K03. <http://dx.doi.org/10.1029/2010JG001471>.
- Mathys, A., Coops, N.C., Waring, R.H., 2014. Soil water availability effects on the distribution of 20 tree species in western North America. *For. Ecol. Manage.* 313, 144–152.
- McDowell, N.G., Fisher, R.A., Xu, C., Domec, J.C., Hölttä, T., Mackay, D.S., Sperry, J.S., Boutz, A., Dickman, L., Gehres, N., Limousin, J.M., Macalady, A., Martínez-Vilalta, J., Mencuccini, M., Plaut, J.A., Ogée, J., Pangle, R.E., Rasse, D.P., Ryan, M.G., Sevanto, S., Waring, R.H., Williams, A.P., Yeepez, E.A., Pockman, W.T., 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytol.* 200, 304–321.
- Meddens, A.J.H., Hicke, J.A., Ferguson, C.A., 2012. Spatiotemporal patterns of observed bark beetle-caused mortality in British Columbia and the western United States. *Ecol. Appl.* 22, 1876–1891.
- Meigs, G.W., Donato, D.C., Campbell, J.L., Martin, J.G., Law, B.E., 2009. Forest fire impacts on carbon uptake, storage, and emission: the role of burn severity in the eastern Cascades, Oregon. *Ecosystems* 12, 1246–1267.
- Meigs, G.W., Kennedy, R.E., Cohen, W.B., 2011. A landsat time series approach to characterize bark beetle and defoliator impacts on tree mortality and surface fuels in conifer forests. *Remote Sens. Environ.* 115, 3707–3718.
- Miao, S.L., Zou, C.R., Breshears, D.D., 2009. Vegetation responses to extreme hydrological events: sequence matters. *Am. Nat.* 173, 113–118.
- Miller, J.D., Safford, H., 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau and southern Cascades, California, USA. *Fire Ecol.* 8, 41–57.
- Miller, P.M., 1990. Physiological ecology of western juniper (*Juniperus occidentalis* Hook. Subsp. *occidentalis*). PhD Dissertation, Oregon State University. 290pp.
- Mitchell, S.R., Harmon, M.E., O'Connell, K.B., Schneckenger, F., 2012. Carbon debt and carbon sequestration parity in forest bioenergy production. *Global Change Biol.* – *Bioenergy* 4, 818–827.
- Mote, P.W., 2006. Climate-driven variability and trends in mountain snowpack in western North America. *J. Clim.* 19, 6209–6220.
- Mote, P.W., Salathé, E.P., 2010. Future climate in the Pacific Northwest. *Clim. Change* 102, 29–50. <http://dx.doi.org/10.1007/s10584-010-9848-z>.
- Mote, P.W., Snover, A.K., Capalbo, S., Eigenbrode, S.D., Glick, P., Littell, J., Raymondi, R., Reeder, S., 2014. Ch. 21: Northwest. *Climate Change Impacts in the United States: The Third National Climate Assessment*. In: Melillo, J.M., et al. (Eds.). U.S. Global Change Research Program. pp. 487–513. doi:<http://dx.doi.org/10.7930/J0Z60KZC>.
- Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter III, R.T., Gehring, C.A., Whitham, T.G., 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *J. Ecol.* 93, 1085–1093.
- Nitschke, C.R., Innis, J.L., 2008. A tree and climate assessment tool for modelling ecosystem response to climate change. *Ecol. Model.* 210, 263–277.
- Pitelka, L.F., Plant Migration Workshop Group, 1997. Migration and climate change: a more realistic portrait of plant migration is essential to predicting biological responses to global warming in a world drastically altered by human activity. *Am. Sci.* 85, 464–473.
- Plaut, J., Wadsworth, W.D., Pangle, R., Yeepez, E.A., McDowell, N.G., Pockman, W.T., 2013. Reduced transpiration response to precipitation pulses precedes mortality in a piñon-juniper woodland subject to prolonged drought. *New Phytol.* 200, 375–387.
- Preisler, H.K., Hicke, J.A., Ager, A.A., Hayes, J.L., 2012. Climate and weather influences on spatiotemporal patterns of mountain pine beetle outbreaks in Washington and Oregon. *Ecology* 93, 2421–2434.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58, 501–517.
- Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., Evans, J.S., 2006. Empirical analysis of plant-climate relationships for western United States. *Int. J. Plant Sci.* 167, 1123–1150.
- Rehfeldt, G.E., Leites, L.P., St Clair, J.B., Jaquish, B.C., Sáenz-Romero, C., López-Upton, J., Joyce, D.G., 2014. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Clines in growth potential. *For. Ecol. Manage.* 324, 138–146.
- Running, S.W., 1994. Testing FOREST-BGC ecosystem process simulations across a climatic gradient in Oregon. *Ecol. Appl.* 4, 238–247.
- Safranyik, L., Carroll, A.L., 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L. et al. (Eds.), *The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, pp. 3–66.
- Safranyik, L., Carroll, A.L., Regniere, J., Langor, D.W., Riel, G., Shore, T.L., Peter, B., Cooke, B.J., Nealis, V.G., Taylor, S.W., 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. *Can. Entomol.* 142, 415–442.
- Schulze, E.-D., Körner, C., Law, B.E., Haberl, H., Luyssaert, S., 2012. Large-scale bioenergy from additional harvest of forest biomass is neither sustainable nor greenhouse gas neutral. *Global Change Biol.* – *Bioenergy* 4, 611–616. <http://dx.doi.org/10.1111/j.1757-1707.2012.01169.x>.
- Singh, N., Abiven, S., Torn, M.S., Schmidt, M.W.I., 2012. Fire-derived organic carbon in soil turns over on a century scale. *Biogeosciences* 9, 2847–2857.
- Smith, J.E., Heath, L., Skog, K.E., Birdsey, R., 2006. Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States. General Technical Report NE-343. Forest Service, U.S. Department of Agriculture, Northeastern Research Station, Newtown Square, PA. 216pp.

- Smith, W.B., Miles, P.D., Perry, C.H., Pugh, S.A., 2009. Forest resources of the United States, 2007. General Technical Report WO-78. Forest Service, U.S. Department of Agriculture, Washington, D.C. 336pp.
- Snell, R.S., Huth, A., Nabel, J.E.M.S., Bocedi, G., Travis, J.M.J., Gravel, D., Bugmann, H., Gutiérrez, H.G., Hickler, T., Higgins, S.I., Reineking, B., Scherstjanoi, M., Zurbiggen, N., Lischke, H., 2014. Using dynamic vegetation models to simulate plant range shifts. *Ecography* 37. <http://dx.doi.org/10.1111/ecog.00580>.
- Stewart, I.T., Cayan, D.R., Dettinger, M.D., 2005. Changes toward earlier streamflow timing across western North America. *J. Clim.* 18, 1136–1155.
- Sun, O.J., Campbell, J., Law, B.E., Wolf, V., 2004. Dynamics of carbon storage in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA. *Glob. Change Biol.* 10, 1470–1481.
- Thonicke, K., Spessa, A., Prentice, I.C., Harrison, S.P., Dong, L., Carmona-Moreno, C., 2010. The influence of vegetation, fire spread and fire behaviour on biomass burning and trace gas emissions: results from a process-based model. *Biogeosciences* 7, 1991–2011.
- Thornton, P., Law, B.E., Gholz, H., Clark, K.L., Falge, E., Ellsworth, D.H., Goldstein, A.H., Monson, R.K., Hollinger, D., Falk, M., Chen, J., Sparks, J.P., 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric. For. Meteorol.* 113, 185–222.
- Thuiller, W., Münkenmüller, T., Lavergne, S., Mouillot, D., Mouquet, N., Schiffrers, K., Gravel, D., 2013. A road map for integrating eco-evolutionary processes into biodiversity models. *Ecol. Lett.* 16, 94–105.
- Treuhaft, R.N., Law, B.E., Asner, G.P., 2004. Forest attributes from radar interferometric structure and its fusion with optical remote sensing. *BioSciences* 54, 561–572.
- Treuhaft, R.N., Gonçalves, F.G., Drake, J.B., Chapman, B.D., dos Santos, J.R., Dutra, L.V., Graça, P.M.L.A., Purcell, G.H., 2010. Biomass estimation in a tropical wet forest using Fourier transforms of profiles from lidar or interferometric SAR. *Geophys. Res. Lett.* 37, L23403. <http://dx.doi.org/10.1029/2010GL045608>.
- Turner, D.P., Ritts, W.D., Yang, Z., Kennedy, R.E., Cohen, W.B., Duane, M.V., Thornton, P.E., Law, B.E., 2011. Decadal trends in net ecosystem production and net ecosystem carbon balance for a regional socioecological system. *For. Ecol. Manage.* 262, 1318–1325.
- van Mantgem, P.J., Nesmith, J.C.B., Keifer, M., Knapp, E.E., Flint, A., Flint, L., 2013. Climate stress increases forest fire severity across the western United States. *Ecol. Lett.* 16, 1151–1156.
- Van Tuyl, S., Law, B.E., Turner, D., Gitelman, A., 2005. Variability in net primary production and carbon storage in biomass across Oregon forests – an assessment integrating data from forest inventories, intensive sites, and remote sensing. *For. Ecol. Manage.* 209, 273–291.
- Waring, R.H., 1983. Estimating forest growth and efficiency in relation to canopy leaf area. *Adv. Ecol. Res.* 13, 327–354.
- Waring, R.H., Franklin, J.F., 1979. Evergreen coniferous forests of the Pacific Northwest. *Science* 204, 1380–1386.
- Waring, R.H., McDowell, N., 2002. Use of a physiological process model with forestry yield tables to set limits on annual carbon balances. *Tree Physiol.* 22, 179–188.
- Waring, R.H., 2005. Court disposition, pp. 22–24 <http://www.fseee.org/attachments/013_highroberts-sjmemo.pdf>.
- Waring, R.H., Pitman, G.B., 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66, 889–897.
- Waring, R.H., Coops, N.C., Mathys, A., Hilker, T., Latta, G., 2014. Process-based modeling to assess the effects of recent climatic variation on site productivity and forest function across western North America. *Forests* 5, 518–534.
- Waring, R.H., Coops, N.C., Running, S.W., 2011. Predicting satellite-derived patterns of large-scale disturbances in forests of the Pacific Northwest Region in response to recent climate variation. *Remote Sens. Environ.* 115, 3554–3566.
- Warren, C.R., Adams, M.A., 2000. Water availability and branch length determine $\delta^{13}\text{C}$ in foliage of *Pinus pinaster*. *Tree Physiol.* 20, 637–643.
- Williams, M., Law, B.E., Anthoni, P., Unsworth, M., 2001. Use of a simulation model and ecosystem flux data to examine carbon–water interactions in ponderosa pine. *Tree Physiol.* 21, 287–298.
- Woods, A.J., Happner, D., Kope, H.H., Burleigh, J., MacLauchlan, L., 2010. Forest. *Chron.* 86, 412–422.
- Xiao, J., Ollinger, S.V., Frolking, S., Hurr, G.C., Hollinger, D.Y., Davis, K.J., Pan, Y., Zhang, X., Deng, F., Chen, J., Baldocchi, D.D., Law, B.E., Arain, A., Desai, A.R., Richardson, A.D., Sun, G., Amiro, B., Margolis, H., Gu, L., Scott, R.L., Blanken, P.D., Suyker, A.E., 2014. Data-driven diagnostics of terrestrial carbon dynamics over North America. *Agric. For. Meteorol.* 197, 142–157.
- Xu, L., Myneni, R.B., Chapin III, F.S., Callaghan, T.V., Pinzon, J.E., Tucker, C.J., Zhu, Z., Bi, J., Ciais, P., Tommerik, H., Euskirchen, E.S., Forbes, B.C., Piao, S.L., Anderson, B.T., Ganguly, S., Nemani, R.R., Goetz, S.J., Beck Bunn, A.G., Cao, C., Stroeve, J.C., 2013. Temperature and vegetation seasonality diminishment over northern lands. *Nat. Clim. Change* 3, 581–586.
- York, R., 2012. Do alternative energy sources displace fossil fuel? *Nat. Clim. Change* 2, 441–443.