Temperate forests are extensive in the mid-latitudes of Earth and include a broad range of forest types and climates. Temperate forest soils reflect the seasonal variability in temperature and precipitation that make them productive and highly variable. Temperate forest soils also reflect the forest vegetation under which they develop. The extent, distribution and characteristics of temperate forests and forest soils are described in this Chapter, as well as their sensitivity to climate change. Because temperate forests are often located near large human populations, they are also affected by human intervention, such as pollution, management, introduction of pests and diseases, and local and national conservation policies. We consider the effects of changing temperature and precipitation regimes, and their interactions on temperate forest soils. Also, changes in frequency and severity of extreme events, as well as changes in length and timing of the growing seasons, can significantly affect the forests and forest soils.

Introduction

Temperate forests occur in the mid-latitude areas between tropical and polar regions (approx. 25—50 degrees north and south of the equator). The temperate climatic regime defining these forests include eleven of the 38 Holdridge BioClimate zones (Holdridge, 1967, Fig. 6.1). The temperate bioclimatic zones constitute about 766 million hectares (Pan et al., 2011) or about 25% of the earth’s forests (Bouwman, 1990; FAO, 2015). That the area of temperate forests is unchanged or increasing over time is significant, since most other forest types have been decreasing in extent since assessments began.

In this Chapter, we describe temperate forests and their distribution, structural and functional characteristics, and associated soils. We also evaluate the sensitivity of temperate forest soils to climate change, and identify some specific challenges and management opportunities particularly associated with this dominant forest type.
FIG. 6.1

Temperate BioClimate Zones with forest vegetation.
Temperate forests include deciduous, broadleaved and coniferous evergreen trees, and are found in North America, northeastern Asia, western and eastern Europe, and Oceania. Temperate forests experience a temperate climate, which means generally 3–4 seasons with distinct temperature and precipitation regimes. Temperatures range from −40 to 30 °C during the year, and annual precipitation ranges from 500 to 4000 mm. Some temperate forests receive enough precipitation (2000–8000 mm) to be classified as rainforests. Temperate rain forests are rare, and are limited to seven regions around the world - the Pacific Northwest of North America, the Validivian forests of southwestern South America, the rain forests of New Zealand and Tasmania, the Northeastern Atlantic (small, isolated pockets in Ireland, Scotland, and Iceland), southwestern Japan, and those in the eastern Black Sea region.

Temperate forests include planted and natural stands with management ranging from highly-managed plantations to vast wilderness. Overall, the extent of temperate forests is stable, with forests in Europe and China gaining cover, Australia and North Korea losing forest cover, and other temperate forest regions remaining stable. Temperate forests in the northern hemisphere are expanding, largely through “re-wilding” following abandonment of agricultural lands, or through the establishment of forest plantations that are usually intensively managed (FAO, 2015). Large areas of industrial forest plantations have been established with the planting of Sitka spruce (Picea sitchensis), Norway spruce (Picea abies), lodgepole pine (Pinus contorta), Douglas-fir (Pseudotsuga menziesii), radiata pine (Pinus radiata), loblolly pine (Pinus taeda) and Eucalyptus species across Britain, Ireland, Spain, Portugal, and the United States. Significant areas of natural temperate forests have been converted into forest plantations in countries such as New Zealand and Chile (P. radiata, P. taeda and Eucalyptus sp.; FAO, 1999).

Temperate forests also are found where there are large human populations and in close proximity to urban/developed areas, and therefore experience a number of stressors that stem from extensive human impact, described by Gilliam (2016) as the “large and deep footprint” of humanity. These stressors include pollution, land use changes, introduction of non-native invasive pests and pathogens, management (and mis-management) all of which can interact to create novel, difficult-to-predict ecosystem responses to changes in climate. For example, fire suppression on a large scale in North America, coupled with harvesting of large fire-resistant trees, grazing, and conversion of more open stands into denser, smaller diameter forests, have set the stage for more severe fire and insect problems now and into the future.

Temperate forest harvest regimes can vary in intensity through both harvest type and length of cutting cycle. High intensity clearcut harvests and shelterwood harvests are common in both deciduous and conifer forests, along with lower-intensity single-tree and group selection in the deciduous forest type (Duguid and Ashton, 2013). Common rotation lengths in natural temperate forests can vary from about 50 years to over 150 years, depending on site quality and dominant tree species (Gibbons et al., 2010). For uneven-aged methods, cutting cycles of 15–25 years are common (Nyland, 1996).

1Most tree species can be categorized as either deciduous (drop their leaves annually) or evergreen (retain their foliage for more than one year, and may shed older foliage). Generally, deciduous trees are broadleaved—though there are deciduous conifer trees (e.g., Larix)—and evergreen forests are general comprised of coniferous trees (although Eucalyptus retain their leaves year round). Nonetheless, we will use these terms interchangeably, as general descriptors, recognizing that there are exceptions.
Wood production is generally greater in plantations (20–30 m³ ha⁻¹ wood annually) relative to natural forests (2–3 m³ ha⁻¹ wood annually), and is a significant management goal for many temperate forests (Arets et al., 2011). Rotation lengths can range from 10 to 60 years in plantations and generally are much shorter (hence short-rotation) for species such as *Populus* species/hybrids, and warm temperate *Pinus* and *Eucalyptus* species, than for natural forests. Increased timber yields in managed planted forests are achieved through the use of genetic improvement, improved greenhouse culture, effective site preparation including control of competing vegetation with herbicides, irrigation where water is limiting, and nutrition management (Fox et al., 2007; Rubilar et al., 2018).

Soil ecosystem processes that may be affected by the practices of plantation forestry begin with the absence of decaying wood in the ecologically young stands, and also include altered carbon (C) cycling, water movement, and vegetative succession. Note, however, that sustainability practices, including in managed forests certified by the Sustainable Forestry Initiative (SFI), include the practice of leaving dead wood on-site, both as standing snags and downed woody debris (Woodall et al., 2013). A meta-analysis by Guo and Gifford (2002) found that soil C stocks declined by 12 to 15% when native deciduous forests were converted to conifer plantations. However, going from native forest to broadleaved plantations had no effect on soil organic carbon (SOC). Another meta-analysis by Liao et al. (2010) indicated that in addition to decreased soil C stocks (decline of 28%) following replacement of deciduous forest with conifer plantations, fine root and microbial biomass, and soil nitrogen (N), phosphorus (P), and potassium (K) concentrations each declined in planted forests relative to natural forests. Supporting these analyses, a global meta-analysis of soil C stock following afforestation showed that soil C stock increased following afforestation with hardwoods (e.g., *Eucalyptus*), but did not change following afforestation with pine species (Li et al., 2012).

While the net area of temperate forests is stable, net productivity is increasing, so they are currently a C sink (they sequester rather than emit C) of about 0.2–0.4 Pg of C per year, accounting for 37% of global C uptake (Fahey et al., 2010). Annual C sequestration rates have been shown to peak in temperate forests between 11 and 30 years of age, although net C storage is greatest in older stands, which can contain up to 2 or 3 times more C than younger stands. Soil organic matter (SOM) comprises the largest C pool in many forests and forest soils represent an immense store of potentially volatile C. Thus, forest soils serve as a buffer against atmospheric CO₂ increases and as a potential sink for mitigating excess atmospheric C, as a net function of photosynthesis, respiration by vegetation and soil microbes, and stabilization processes of C in soils (Trivedi et al., 2013).

**Temperate deciduous forests**

Temperate deciduous forests are identified in the eastern United States, much of Europe, eastern Asia and Australia, New Zealand, and the southernmost portion of South America, in areas that receive between 750 and 1500 mm of rain per year and with average summer temperatures of around 21 °C, and winter temperatures often below freezing. Temperate deciduous forests experience distinct seasons, and trees shed leaves in the autumn and regrowth occurs in the spring (Ichoku, 2018). Trees are mostly broadleaf tree species including oaks (*Quercus*), hickories (*Carya*), maples (*Acer*), and beeches (*Fagus*), and commonly a diverse community of multiple strata of understory trees and shrubs, perennial herbs, and mosses. In the southern hemisphere, southern beeches (*Nothofagus*) and *Eucalyptus* are prominent genera of broadleaves.
**Temperate evergreen forests**

Temperate evergreen forests are found in the United States, Canada, Europe, and Asia, in areas that generally receive between 300 and 900 mm of rain per year and with seasonal temperature extremes ranging from -40 to 20 °C. Climate differences occur between the northern and southern evergreen forests, where in northern areas, winters are commonly long, cold, and snow dominated, relative to the more southern coniferous forests, where precipitation and temperatures are more evenly distributed throughout the year (Ichoku, 2018). Vegetation includes coniferous-evergreen tree species that produce cones and needles, dominated by spruce (*Picea*), pine (*Pinus*), fir (*Abies*), and hemlock (*Tsuga*) species, and the trees retain at least some of their needles year-round. In the southern hemisphere, conifer genera also include *Araucaria* and *Podocarpus*, which are widespread and common.

**Soils in the temperate forest**

Temperate forest soils reflect seasonal variability in temperature and precipitation — as well as the aboveground vegetation under which the soils develop. Many soil orders and suborders can be found within major temperate forest types. Table 6.1 shows the FAO Major Soil groupings (1988), the US Soil Taxonomy equivalents (Soil Survey Staff, 2014) and the area in each of those groups (developed from Bouwman, 1990). The majority of temperate forest soils fall into the Alfisols and Inceptisols categories (37.3% of the total areal extent), and about 18% of all soils are Lithic subgroups, meaning the soils are shallow with hard rock near the surface.

It is difficult to disentangle the influence of particular tree species or forest types on the development of specific soil properties from other factors affecting soil formation, including climate, parent material, and topographic influences (Binkley and Fisher, 2012). However, tree species can influence soil properties through: variation in the amount and chemical makeup of the organic material produced that could alter soil pH and rate of organic matter decomposition, the depth of rooting and allocation differences to above-ground and below-ground pools, and available water content through differences in water use and canopy structure that could alter mineralization and nutrient availability. Differences in soil properties may also arise as a result of intensive management activities in planted forests relative to natural forest cover.

**Temperate deciduous forest soils**

Dominant soil orders common to the temperature deciduous forest include Entisols and Inceptisols (or Luvisols and Cambisols, respectively), Alfisols and Ultisols (or Luvisols, and Acrisols, respectively). Entisols and Inceptisols (Fig. 6.2) are identified as very young soils, with weakly defined horizons, and encompass a broad range of characteristics, as they are formed on steep slopes from colluvium parent material and in floodplains from alluvial parent material. Globally, Alfisols (Fig. 6.2) encompass 9.6% of ice-free land and are distinguished by having a relatively high base saturation (>35%), fine texture, and are located in the more humid and cooler areas of the temperate region (Osman, 2013). Alfisols are recognized as nutrient-rich and fertile soils, and commonly have significant accumulation of clay in
Table 6.1 Comparison of FAO and USDA soil groups with Holdridge bioclimatic group.

<table>
<thead>
<tr>
<th>FAO major soil groupings</th>
<th>FAO description</th>
<th>USDA soil taxonomy equivalent</th>
<th>Major Holdridge bio-climatic group</th>
<th>Extent in 1,000,000 ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Acrisols</td>
<td>Ultisols</td>
<td>Warm temperate moist forest</td>
<td>154</td>
</tr>
<tr>
<td>2</td>
<td>Chernozems, Phaezems, Greyzems</td>
<td>Mollisols</td>
<td>Cool temperate moist forest</td>
<td>166</td>
</tr>
<tr>
<td>3</td>
<td>Podzoluvisols, Albic Luvisols</td>
<td>Alfisols (Eutroboralfs)</td>
<td>Cool temperate moist forest (only)</td>
<td>75</td>
</tr>
<tr>
<td>4</td>
<td>Ferralsols</td>
<td>Oxisols</td>
<td>Warm temperate moist/wet</td>
<td>10</td>
</tr>
<tr>
<td>5</td>
<td>Histosols, Gleyosols</td>
<td>Histosols, Inceptisol/ Entisols (Aquepts/ Aquents)</td>
<td>Both warm and cool temperate</td>
<td>102</td>
</tr>
<tr>
<td>6</td>
<td>Lithosols/Leptosols</td>
<td>Lithic subgroups of most soil orders</td>
<td>All</td>
<td>324</td>
</tr>
<tr>
<td>7</td>
<td>Kastanozems</td>
<td>Mollisols</td>
<td>Cool temperate moist and warm temperate dry</td>
<td>56</td>
</tr>
<tr>
<td>8</td>
<td>Orthic Luvisols, Cambisols</td>
<td>Alfisols, Inceptisols</td>
<td>All</td>
<td>451</td>
</tr>
<tr>
<td>9</td>
<td>Nitrosols and Ferric Luvisols</td>
<td>Alfisols/Ultisols</td>
<td>Warm temperate moist and warm temperate dry</td>
<td>15</td>
</tr>
<tr>
<td>10</td>
<td>Podzols</td>
<td>Spodosols</td>
<td>Cool temperate only</td>
<td>18</td>
</tr>
<tr>
<td>11</td>
<td>Arenosols, Sandy Regosols</td>
<td>Psamments</td>
<td>Warm temperate only</td>
<td>7</td>
</tr>
<tr>
<td>12</td>
<td>Chromic Luvisols, Cambisols</td>
<td>Alfisols, Inceptisols</td>
<td>All (except wettest)</td>
<td>133</td>
</tr>
<tr>
<td>13</td>
<td>Solonchaks, Solonetz</td>
<td>Aridisols (Salorthids and Natric great groups)</td>
<td>Only warm temperate dry and moist</td>
<td>44</td>
</tr>
<tr>
<td>14</td>
<td>Andosols</td>
<td>Andisols</td>
<td>All</td>
<td>51</td>
</tr>
<tr>
<td>15</td>
<td>Vertisols</td>
<td>Vertisols</td>
<td>Only warm temperate</td>
<td>18</td>
</tr>
<tr>
<td>16</td>
<td>Planosols</td>
<td>Alfisols, Ultisols, Aridisols</td>
<td>Cool temperate moist and warm temperate dry</td>
<td>27</td>
</tr>
<tr>
<td>17</td>
<td>Xerosols</td>
<td>Aridisols, Entisols (Psamments)</td>
<td>Warm temperate dry</td>
<td>32</td>
</tr>
<tr>
<td>18</td>
<td>Yermosols</td>
<td>Aridisols, Entisols (Psamments)</td>
<td>Mostly warm temperate forest</td>
<td>54</td>
</tr>
</tbody>
</table>
the subsurface B-horizon, resulting in argillic (high clay), kandic (high clays underlying coarse textured material), or natric (exchangeable sodium >15%) horizons.

Ultisols (approx. 8% of ice-free land) are strongly weathered soils found in humid and relatively warmer regions of the temperate deciduous forest range, and are distinguished by relatively low base saturation and high acidity, and accumulation of simple clays in the subsurface B-horizon (USDA-NRCS). Most nutrients are found within the top few centimeters of soil and base saturation generally decreases with depth. Phosphorus (P) limitation of tree growth is common through occlusion of available P coatings by iron and aluminum compounds, and most temperate forests are believed to be limited by nitrogen (N), although the concept of nitrogen saturation from elevated atmospheric N inputs has been documented (Peterjohn et al., 1996; Aber et al., 2003).

**Temperate evergreen forest soils**

Conifer forests commonly thrive in less fertile soils relative to soils found beneath deciduous forests. In addition to Inceptisols and Entisols, the Spodosol soil order (or Podzols) is common in coniferous forests of cool temperate or wetter regions. Spodosols are recognized as having coarse texture and spodic/albic horizons from strong illuviation/eluviation processes (Fig. 6.2). The spodic horizons result in
a subsurface that is strongly acid with high amounts of humic substances, iron, and aluminum. Forests growing on spodic and other acidic soils are often phosphorus-limited, as available P is occluded by coatings of iron and aluminum.

**Distinctions between deciduous and evergreen forest soils**

The primary distinctions between deciduous and conifer forests are related to litter and forest floor dynamics. Mean annual litter mass is greater in deciduous forests (approximately 5.5 t ha\(^{-1}\) yr\(^{-1}\); range 5.0–6.3 t ha\(^{-1}\) yr\(^{-1}\)) relative to conifer forests (3.5 t ha\(^{-1}\) yr\(^{-1}\); range 3.0–3.7 t ha\(^{-1}\) yr\(^{-1}\); Landsberg and Gower, 1997). However, standing forest floor mass is generally greater in conifer forests relative to deciduous forests (approx. 18 and 45 t ha\(^{-1}\), respectively), resulting commonly in a mor-type forest floor in conifer, and a mull-type forest floor in broadleaf forests. Mor-type forest floors are characterized by matted accumulation of undecayed plant material, dominated by fungal decomposition, low pH, and distinct boundary between the mineral and organic horizon. Mull-type forest floor is characterized by strong mixing of organic material with the mineral component, dominated by bacterial decomposition, and strong granular structure (Fisher and Binkley, 2000). Turnover, or decomposition of organic material in temperate broadleaf forests occurs within about 4 years, and occurs within about 15 years in conifer forests (Waring, 2002). Turnover of deciduous organic material may occur even more quickly in forests impacted by high rates of N deposition (Gundersen et al., 1998) or invasive earthworm species (Ashton et al., 2005). Soil organic matter (SOM) stability and accumulation is commonly greater in conifer forests relative to deciduous, as a function of organo-mineral interactions, mostly with iron (Fe) and aluminum (Al) compounds in the subsurface (Gahagan et al., 2015; Ohno et al., 2017). Therefore, SOM content is commonly greater throughout the profile in conifer forest soils relative to deciduous soils (e.g., 943 and 631 g kg\(^{-1}\) soil for 0–50 cm soil depth, respectively, in Maine, USA; Ohno et al., 2017). SOM content will also vary with soil texture, with finer textured soils accumulating greater SOM pools through stronger aggregation forces (Rumpel and Kogel-Knabner, 2011). Generally, the maximum depth of rooting is greater beneath temperate conifers relative to deciduous forests (3.9 ± 0.04 and 2.9 ± 0.02 m, respectively; Canadell et al., 1996).

The type of mycorrhizal associations vary among dominant tree species, and are associated with differences in ecosystem processes of nutrient availability and C storage. Two main mycorrhizal types occur (ectomycorrhizal and arbuscular mycorrhizal; ECM and AM, respectively) with forest trees. Conifer species are commonly associated with ECM and deciduous trees can form associations with either AM or ECM fungal types. Recent studies suggest that ECM associations are correlated to slower litter decomposition, greater dissolved organic carbon (DOC) in soil solution and SOM content, lower mineralization and nitrification rates, and lower soil pH (Phillips et al., 2013; Averill et al., 2014). ECM fungal diversity also increases with stand age in some forests, and with stand development, at least up to crown closure, after which there is little difference between conifers and hardwoods (Twieg et al. 2007).

Microbial biomass is commonly greater in soils beneath deciduous trees relative to conifers (Priha and Smolander, 1997). For example, in northern Finland, significant differences in microbial biomass by tree species were noted, where microbial biomass beneath silver birch (*Betula pendula*) was approximately 17 g C kg\(^{-1}\) organic matter, and 9 g C kg\(^{-1}\) organic matter beneath Scots pine.
Total soil biomass of all soil fauna is greatest in mull-type deciduous forests (8.0 g g\(^{-1}\) C\(^{0}\) soil) relative to coniferous forest soils (2.4 g g\(^{-1}\) C\(^{0}\) soil) (Petersen and Luxton, 1982). Generally, temperate forests have a fungal-dominated microfauna relative to bacteria, and the ratio of fungal:bacterial biomass in deciduous forests can range from 5:1 to 10:1 and from 100:1 to 1000:1 in conifer forests (Ingham, 2018). Soil pH can be a strong predictor for microbial community diversity, structure, and function (Kaiser et al., 2016), with fungal dominance increasing with decreasing pH. Large earthworms are also ten times more abundant in deciduous forests than in conifer forests (Perry et al., 2008), thriving at soil pH values between 6.0 and 8.0.

Finally, water content of soils beneath conifers is generally lower than the deciduous counterpart, partly due to the common occurrence of conifers in more arid parts of the temperate bioclimatic zone. Also a year-round dense canopy of needles relative to leaves leads to greater annual evapotranspiration and interception rates in conifer forests (Waring, 2002). These differences in water availability, in turn, can influence microbial activity, decomposition and mineralization rates, and nutrient availability.

Sensitivity of temperate forest soils to climate change

Because temperate forests are so widely distributed, the effects of climate change on temperate forest soils and associated vegetation are likely to be of global importance. It is projected that there will be a 1–2 °C temperature increase from 1990 to 2050 in temperate forests. This is expected to have regional effects on precipitation patterns, with up to a 20% increase or decrease in annual rainfall, and with drier summers overall, drier winters in some areas and wetter winters in others (Yale Global Forest Atlas). Also, as climate change alters air temperature and precipitation patterns, soil thermal and moisture properties are likely to change. We may expect soil temperatures to increase with increasing air temperatures, however, soil temperatures also are influenced by precipitation (Brown et al., 2000; Houle et al., 2012). Precipitation is negatively correlated with soil temperature during the summer, and positively correlated with soil temperature during the winter. Higher temperatures are predicted to lead to warmer winters, meaning reduced regional snow packs, and lower water supplies for the following growing season. Therefore, summer water deficits may be even greater, leading to drought. Additionally, warmer winters may allow for greater reproduction and spread of insects and pathogens, further altering forests and soils that are already modified by other impacts of climate change or pollution. Forest disturbance processes likely to be affected or exacerbated by climate change include drought, insect outbreaks, blowdown and fires. Severe weather events (storms, hurricanes) also are expected to increase in frequency and severity.

There is a general consensus that in these mid-latitude temperate regions, site-specific conditions, as well as land use history, human management, air pollution, and biotic effects (e.g., herbivory) are likely to more directly control forest productivity, decomposition, and C balance than climate change or carbon dioxide (CO\(_2\)) enrichment (IPCC, 2001). However, the interactions among all of these, and these interacting factors coupled with climate change, make understanding and predicting the effects difficult. Ideally, experimentation would focus on the many factors affecting forest soils at one time, and would elucidate these interactions. However, for the sake of simplicity and experimental control, most research focuses on individual factors. We begin our discussion with the consideration of the effects of elevated CO\(_2\) levels on temperate forest soils, followed by the individual factors of temperature and precipitation. We also consider the interactions and implications of extreme events.
Effects of elevated carbon dioxide on temperate forest soils

Rising atmospheric CO₂ levels are considered to be the primary driver of climate change. Rising CO₂ levels not only affect climate, they also affect forest growth, C storage, and soil processes in temperate forests. Experiments have examined the impact of elevated CO₂ levels on forest growth and soil processes. Many of these experiments were free-air CO₂ enrichment (FACE) studies, such as conducted at the Duke Forest (Durham, North Carolina, USA; 35.970N, 79.080W) and Oak Ridge National Environmental Research Park (Oak Ridge, Tennessee, USA; 35.900N, 84.330W), and near Rhinelander, Wisconsin, USA (45.680N, 89.630W) and Viterbo, Italy (42.370N, 11.800E). The infrastructure associated with the FACE studies allowed for the control of CO₂ and other gases to determine the effect of elevated levels on the growth of field-grown trees of a variety of species (Fig. 6.3).

Findings from FACE studies have demonstrated that increasing the CO₂ concentration in the air increased the growth rate of individual trees and the overall net primary production measured in plots. Data from the Rhinelander FACE site showed that increasing the CO₂ concentration to about 120 ppm above ambient increased aspen (*Populus tremuloides*) height by 11%, diameter by 16%, and stem volume by 20% (Kubiske et al., 2006). Across the four FACE study locations, an increase of 200 ppm CO₂ above ambient levels produced a 23% increase in net primary productivity (Norby et al., 2005). Collectively, these studies suggest that the increased CO₂ has a fertilization effect that likely will increase net production in temperate forests, with concomitant effects on soils.

There is evidence that rising CO₂ levels may decrease litter decomposition rates for some tree species, which affects soil C and nutrient cycling, and water holding capacity, among other properties. For
example, Parsons et al. (2008) reported that the litter of aspen and paper birch (Betula papyrifera) produced under elevated CO2 levels decomposed more slowly than litter produced under ambient CO2. Reduction in the decomposition rate was related to the poorer quality of the litter produced under CO2 enrichment. Litter produced under elevated CO2 had a greater C:N, a greater lignin:N, and a higher concentration of condensed tannins than litter produced under ambient CO2. These findings suggest that the forest floor may be thicker and accumulate more biomass (and C) under elevated CO2.

Despite increased net primary productivity and the potential for accumulating a thicker forest floor, however, there has been no evidence to suggest that elevated CO2 will lead to increased C storage in the mineral soil of temperate forests. Increased net primary production was associated with an increased production of fine roots (Norby et al., 2002) or litterfall, which are subject to more rapid turnover than stem wood in the forest floor or the organic matter stored in the mineral soil. Zak et al. (2003) reported greater root turnover beneath trees grown under elevated CO2, as evidenced by higher microbial respiration rates (Phillips et al., 2002) and increased concentration of extracellular microbial enzymes in the soil (Larson et al., 2002). Thus, increased production from elevated CO2 levels may not lead to increased organic C stored in the mineral soil because of enhanced microbial activity and increased decomposition belowground, which results in greater fluxes back to the atmosphere.

Other factors can mediate or offset some of the potential changes in tree growth or decomposition rate resulting from elevated CO2 levels. Particularly, site-related nutrient and/or water limitations can reduce the growth response associated with elevated CO2 levels (Oren et al., 2001; Norby et al., 2005). For example, Finzi et al. (2002) reported that tree growth under elevated CO2 levels was 1.4 times greater where N was abundant. Soil temperature can affect soil respiration even under elevated CO2 levels. Vose et al. (1997) showed that under elevated CO2 levels, soil respiration increased where soil temperatures were <18 °C but decreased markedly when soil temperatures exceeded this threshold. Therefore, in temperate forest soils, as soil temperatures rise with climate change, respiration may decrease where soil temperatures exceed 18 °C. Ozone (O3), an air pollutant known to negatively affect tree growth, has also increased in concentration due to increasing temperatures in temperate zones. These elevated O3 levels have been shown to reduce tree growth of some tree species even where CO2 was elevated (Kubiske et al., 2006). Elevated O3 levels have also been shown to reduce litter decomposition rates where CO2 levels are also elevated (Parsons et al., 2008), with effects on soil C (Loya et al., 2003).

Elevated CO2 levels in the air will also increase the quantity that is available to dissolve in rainwater. Once dissolved in rainwater, CO2 rapidly forms carbonic acid (H2CO3), a weak acid. The H2CO3 dissociates into HCO3− and CO32−, leaving H+ in solution. This process causes natural rainfall to be slightly acidic, even in the absence of atmospheric pollutants such as SO2 and NOx. Additionally, HCO3− is the companion ion associated with cation leaching, so increased leaching due to elevated HCO3− is possible. Under current atmospheric CO2 levels (about 405 ppm in 2018), the pH of rainwater is about 5.6. Rain pH has been projected to decrease to about 5.5 by adding an additional 300 ppm of CO2 (Bogan et al., 2009). However, the amount of CO2 that can dissolve in rainwater decreases with rising temperature, possibly offsetting the effect of rising CO2. Bogan et al. (2009) estimated that pH will increase 0.02−0.03 units per each 10 °C rise in temperature. While air temperature in temperate regions is projected to rise 1−2 °C during the next century, CO2 levels are projected to double. Thus, the effect of the increasing CO2 on the rainwater pH will be greater than the effect of the rising temperature. Despite these potential changes, pure rainwater is poorly buffered and alone is not
likely to change soil pH due to soil’s relatively high buffering capacity related to its cation exchange capacity.

**Effects of warming on temperate forest soils**

A variety of experimental manipulations have been used to assess the effect of changing temperature on forest soils (Aronson and McNulty, 2009; Melillo et al., 2017). *Ex situ* warming studies in greenhouses and growth chambers have been used to study C dynamics, nutrient cycling, and soil respiration. *In situ* experiments using heat lamps and buried resistance cables have also been used in several long-term ecosystem studies to evaluate impacts on soil and ecosystem processes (Melillo et al., 2011). Although, the results of these studies have been variable, most of the evidence suggests that soil warming increases C loss from the soil despite increases in C produced aboveground in plant tissue (Rustad et al., 2001; Wu et al., 2011; Melillo et al., 2011, 2017; Carey et al., 2016; Hicks Pries et al., 2017; Noh et al., 2016).

Generally, soil warming experiments have focused on impacts to soil C, and vegetation responses (e.g., changes in biomass and species composition). In temperate forests, soil C inputs come from leaf litter, root exudates and detritus, and belowground macro- and micro-biotic communities. Soil C losses are largely via gaseous efflux of CO2 and methane (CH4) in poorly drained soils, and leaching of DOC. However, gaseous losses are the most significant C flux in temperate systems (Chen et al., 2014).

Carbon dioxide is evolved from soils due to microbial decomposition of organic matter and root and mycorrhizal respiration (collectively referred to as “soil respiration”). Soil respiration generally increases with temperature, but this relationship is complicated by a number of factors. Specifically, soil moisture, nutrient availability, substrate quality, C supply, and microbial activity all affect decomposition of soil C. Changes in decomposition rate associated with elevated soil temperature may also show an acclimatization to warming over time. Therefore, while there is consensus that warming influences C fluxes to and from the soil (Chen et al., 2014), there is less agreement on the specific impacts or mechanisms (Conant et al., 2011; Crowther et al., 2016). In their 26-year warming study at the Harvest Forest, Massachusetts, USA, Melillo et al. (2017) demonstrated that warming induced a 17% loss of C in the upper 60 cm soil profile. However, C losses were not consistent over time, and two periods showed reduced or no losses. These periods of reduced or no C loss were attributed to changes in microbial biomass and community composition, substrate quality and availability, and thermal acclimation.

Soil changes may also be related to altered vegetative processes. In forested systems in the eastern US, a number of studies show significant increases in vegetation biomass associated with long-term warming (e.g., 5 °C) (Melillo et al., 2011; Keenan et al., 2011). Increased temperatures are expected to have positive impacts on plant growth, assuming other growth factors such as water are not limiting. In temperate forests, stand-level biomass may increase with warming (Saxe et al., 2001), although there are a multitude of factors that may affect such a response. For example, soil warming may increase nutrient availability, change phenology, and decrease soil moisture. To further complicate predictions, many of these responses are species-specific. Butler et al. (2012) showed a 45% increase in mineralization and a threefold increase in nitrification rates with soil warming over 7 years. In response, red maple (*Acer rubrum*) doubled its relative growth rates, red oak (*Quercus rubra*) accumulated the greatest total biomass, whereas white ash (*Fraxinus americana L.*) showed only a minor response.
Changes in understory vegetation have also been noted in response to increased soil temperatures (Farnsworth et al., 1995; De Frenne et al., 2010). Warming can decrease germination success of some native species (Willis et al., 2010; Haeuser et al., 2017), and can also affect understory biomass (Farnsworth et al., 1995; Lin et al., 2010). Specific reasons for these changes in vegetation community composition and growth are varied but generally involve increased availability of nutrients. Warming of soils is expected to accelerate organic matter decomposition and the mineralization of nutrients to plant available forms (Peterjohn et al., 1994; Rustad et al., 2001; Melillo et al., 2011, Kirschbaum, 1995.). In a long-term soil warming experiment (Melillo et al., 2011), soils heated to 5 °C above ambient conditions resulted in an additional 27 kg available N ha⁻¹ yr⁻¹. Increased N mineralization and nitrification due to soil warming resulted in increased foliar N concentrations and litter mass (Butler et al., 2012), both of which can result in greater aboveground productivity.

Changes in air temperatures can also affect the phenology of temperate forests, with implications for soils. For example, a warmer climate may extend the growing season for temperate forests which may lead to greater productivity (Boisvenue and Running, 2006), providing additional C storage in vegetation and soils (Way et al., 2011). However, greater productivity resulting from a longer growing season may be offset by the increased risk of late spring frosts and freezing temperatures in the autumn before tissues have hardened (Norby et al., 2003; Fu et al., 2014), which also can potentially alter the amount and timing of C inputs to the soil. Inadequate chilling times may delay bud development and delay bud burst (Morin et al., 2009; Harrington and Gould, 2015); although, as others have suggested, species growth strategy, life-form or life stage also influence these effects (Farnsworth et al., 1995; Augspurger and Bartlett, 2003). The growing season has been increasing by about 2—4 days per decade in temperate forests in the US and Europe (Yue et al., 2015).

Finally, warmer winter temperatures also have a somewhat indirect, and seemingly contradictory, impact on temperate forests and soils. As temperatures increase, winter thaw events increase, and snowpacks are expected to decrease in extent and duration (Knowles et al., 2015). Decreased snowpack can lead to lower soil temperatures due to the loss of the insulating effect of snow cover, and result in frost damage to root tissues (Iwata et al., 2010; Campbell et al., 2014; Tatariw et al., 2017), resulting in altered soil moisture. In controlled snow removal treatments, sugar maple (Acer saccharum) trees showed increased root injury and decreased foliar cation concentrations compared to trees with an undisturbed snowpack (Comerford et al., 2013). Groffman et al. (2001) reported altered nutrient cycling and nutrient uptake by sugar maple, but no significant effects in yellow birch (Betula allegheniensis), as a result of late development of snowpacks. Changes in soil temperature regimes can also alter the availability of soil moisture in temperate forests through changes in evapotranspiration and surface evaporation.

While there has been a general decrease in snow cover in the US, significant seasonal trends are emerging. Since the 1960s, fall snow cover has increased, however spring snow cover has decreased to a larger extent (Easterling et al., 2017). Warmer winters generally result in precipitation in the form of rain rather than snow. However, in continental regions, elevated temperatures can increase mid-winter snowfall, assuming temperatures are still below freezing (Trenberth, 2011), which may extend spring snow cover extent.
Effects of altered precipitation on temperate forest soils

Precipitation affects soil moisture, soil processes, and tree growth. Severe and persistent drought events in temperate forests have resulted in increased tree mortality, reduced growth, shifts in species composition, and changes in belowground nutrient and C fluxes (Vose et al., 2016). Generally, as long as conditions remain aerobic, higher soil moisture increases microbiologically-mediated processes such as decomposition and nutrient cycling, and soil moisture is positively correlated with soil respiration (Davidson et al., 1998). For example, excluding throughfall in a Massachusetts, USA, a deciduous forest reduced annual soil respiration by 10%—30% (Borken et al., 2006), primarily as heterotrophic respiration, with implications for increased soil C stocks over time. Similarly, Schindlbacher et al. (2012) used throughfall exclusion treatments to induce 25-day drought effects over two growing seasons in a spruce (P. abies) dominated forest in Germany. Compared to ambient precipitation plots, annual respiration rates were about 18% lower where rainfall was excluded. This relationship is, however, sometimes confounded by other relationships. Lu et al. (2017) demonstrated that decreased precipitation produced only minor changes in soil respiration, purportedly due to increased autotrophic respiration rates. Also, Samuelson et al. (2009) and Zhang et al. (2016) demonstrated that CO2 fluxes from a loblolly pine (P. taeda) plantation in the southern US were relatively insensitive to water additions or removals. Others have noted that reduced decomposition rates during dry periods are compensated for by enhanced decomposition during wet periods (O’Neill et al., 2003). Additionally, because droughts reduce decomposition rates and promote accumulation of organic matter, they can lead to increased fire risk (Hanson and Weltzin, 2000), and increased fire intensities if they do burn (Lensing and Wise, 2007). Subsequently, intense fires can reduce infiltration (Certini, 2005), thereby increasing surface flow and increasing the risk of soil erosion.

Elevated precipitation is also expected to increase leaching of base cations and exports of N (Vose et al., 2016) from soil. Broadly, DOC and dissolved organic nitrogen (DON) fluxes increase with increasing annual precipitation (Michalzik et al., 2001). By contrast, N immobilization may occur with reduced precipitation and soil moisture (Johnson et al., 2002). However, a throughfall diversion study in North Carolina, USA indicated that either increasing or decreasing precipitation by 33% had little impact on N export after 3 years (Johnson et al., 2002).

Interactions of changing precipitation and temperature on forest soils

Although often considered separately for experimental purposes, temperature and precipitation have interactive effects on plants and soil processes. Temperature-induced drought stress associated with warming climates without a concomitant increase in precipitation can lead to significant mortality events (Van Mantgem and Stephenson, 2007; Allen et al., 2010). Dietze and Moorcroft (2011) found that some plant functional types/species were more sensitive to inter-annual variation in precipitation than to annual precipitation. Temperature and precipitation both impact soil respiration (Zhou et al., 2016), and therefore C cycling. Temperature effects dominate soil respiration patterns during periods when soil moisture is adequate. However, research suggests that as soil water content falls below about 15%, soil moisture availability has a greater control over rates of soil respiration rates (Yuste et al., 2003; Davidson et al., 1998). In a combined soil warming and rainfall exclusion experiment in Norway spruce (P. abies), Schindlbacher et al. (2012) reported a strong interaction between treatments. Soil warming produced large increases in soil respiration, whereas
reduced rainfall resulted in lower rates of soil respiration. The authors suggested that, in a warming climate, decreased precipitation can reduce the effects of elevated temperatures on soil respiration to ambient levels.

Effects of extreme events on temperate forest soils

Climate change models suggest that extreme events such as droughts, hurricanes and thunderstorms, and snow and ice storms are likely to occur with greater frequency (IPCC, 2001). These extreme events are likely to increase the frequency of record-breaking floods, increase blowdown in temperate forests, and exacerbate wildfire extent, frequency, and severity.

Increasing frequency of summer droughts represents a major threat to the vitality and productivity of forests in the temperate zone, with some tree species most likely to be affected along the margins of their natural ranges. For example, European beech (*Fagus sylvatica*), the most important tree species of Central Europe’s natural forest vegetation, is known to suffer from increased drought intensity at its southern distribution limits, but it is not known how this species is affected in the center of its distribution range (Knutzen et al., 2017).

In mixed-species temperate forests, chronic reductions in precipitation may lead to shifts to more drought-tolerant tree species composition (McDowell et al., 2016). During severe drought, trees associated with the more mesic sites can experience greater mortality (Kloeppel et al., 2003; Clark et al., 2016). Such species-specific responses have been reported following severe drought events, driving shifts in species composition in mixed deciduous hardwood forests in Europe (Cavin et al., 2013) and North America (Clark et al., 2016), and ultimately spatial shifts of forest types (Fei et al., 2017). A shift in dominant tree species will likely shift dominant mycorrhizal associations as well. Dry-site tree species would be more associated with ectomycorrhizal fungi (e.g., oak) relative to more mesic tree species and arbuscular mycorrhizal fungi (e.g., maple), with consequent associated rates of nutrient cycling and SOM storage. With changes in forest composition observed during the last 50 years across much of the eastern US to more mesophytic species, water stress may lead to significant reductions in ecosystem C storage (Brzostek et al., 2014).

Projected increases in drought frequency will likely also lead to increased fire frequency and severity, particularly in the western US (Vose et al., 2016), Australia, and Mediterranean temperate forests. More intense fires will consume more of the protective forest floor, decreasing infiltration (Certini, 2005), and causing the soil to be vulnerable to erosion, increased runoff, and to accelerated nutrient loss. Fire also affects nutrient cycling and the biological makeup of soils that mediate nutrient cycling and water quality (DeBano et al., 1998; Neary et al., 2005).

Droughts have received considerable attention because of their obvious, and often negative impacts on forest health and productivity. By comparison, less is known about ecosystem responses to increased precipitation (or increased variability of precipitation) (Weltzin et al., 2003). In a throughfall displacement experiment, Hanson et al. (2001) demonstrated positive basal area growth for sapling-sized trees subjected to increased precipitation, whereas trees >10 cm dbh did not respond significantly. Average annual precipitation of 1350 mm, coupled with deep soils, likely limited moisture stress for large established trees with deep root systems. A number of studies using irrigation to mimic increased precipitation suggest that elevated precipitation has limited effects on tree growth across a wide range of site conditions and regions (Albaugh et al., 1998; Wightman et al., 2016). However, these effects are somewhat species-specific. Allen et al. (2005) demonstrated that irrigation resulted
in increases in productivity for two hardwood species, but not pines, growing on an upland site in the southern US.

Increased frequency, severity or extended duration of flooding is also an anticipated effect of climate change that will influence temperate forests and soils. Although many temperate tree species are able to tolerate flooding for short periods during the winter and early spring, they are not able to tolerate extended flooding, particularly if it occurs during late spring and summer. During the most active part of the growing season, tree roots require large quantities of oxygen in the soil to utilize stored carbohydrates. Flood water limits the amount of oxygen that can diffuse into the soil and the anoxic conditions produced by flooding will cause increased mortality to all but the most flood-tolerant tree species. Catastrophic flooding will also affect erosional and depositional processes in bottomland forests. Large quantities of suspended sediments are deposited in the floodplain near the streambank as water leaves the channel. Scouring occurs elsewhere where floodwater is concentrated in the floodplain. Rare but catastrophic flood events have been shown to greatly alter floodplain geomorphology, soil patterns, and vegetation (Brakenridge et al., 1994; See Box 6.1).

Ice storms are common to temperate forests (Ding et al., 2008), particularly in North America (Changnon, 2003) and Europe. However, ice storms are likely to occur with greater frequency under a number of climate change scenarios (Rustad and Campbell, 2012). The weight of ice that accumulates during ice storms can cause tree branches to break and fall to the ground. Damage to the tree canopy increases the amount of light reaching the forest floor as well as the quantity of woody debris on the soil surface. Simulated ice storm experiments in temperate Northern Hardwood ecosystems suggest that even minor ice events produce canopies that are measurably more open and generate as much fine and coarse woody debris on the forest floor as would be expected to occur during an entire year without ice damage (Rustad and Campbell, 2012). It is not known whether short-term increases in the quantity of woody debris translate into increased soil C storage because some of the C increases will be offset by enhanced decomposition caused by the more open canopy.

Conclusions

Temperate forests supply important economic and ecosystem services, and must continue to do so in a changing climate. Therefore, maintaining healthy, productive soil is essential in the maintenance and management of healthy, productive temperate forests. Because of the proximity of temperate forests to large human populations, these ecosystems may be poised for resiliency in a changing climate. Temperate forests are generally increasing in area, partly due to recovery after being cleared for cultivation, and partly because of the large area of land being planted in production forests. Also, there is a robust understanding of temperate forests and soils based on extensive problem-related research (see Box 6.2). Many nations in the temperate regions have strong forest inventory programs that incorporate soils. Therefore, the close human proximity provides advantages of information, opportunity for pro-active management and response to issues, an extensive history of research related to soils and management, and considerable economic value derived from temperate forests and soils.

This same proximity and use by human populations can also present challenges. Some of these challenges are related to poor management practices of some forest areas—for a variety of uses, over extended periods of time. As demands for a variety of products from temperate forests grow,
Bottomland hardwood forests are some of the most dynamic forests in the world. These floodplain forests are common along larger rivers systems, and periodic seasonal flooding leads to the deposition of nutrient rich sediments and organic matter, the distribution of plant propagules, and in some cases, creates new growing space through physical disturbance (Friedman et al., 2006).

Species composition of these forested wetlands is a function of site-specific hydrology and deposition patterns, which are influenced by the frequency, duration, depth, and timing of flood events. Extreme precipitation events are increasing across the eastern US, leading to increased magnitude and frequency of flooding events. Increased sedimentation associated with these more frequent flooding events can have significant impacts on hydrologic functioning within bottomland hardwood forest systems.

As an example, in southern US bottomland hardwood forests, topography and drainage conditions produce unique tree species assemblage patterns similar to the figure below.

Adapted from Hodges (1997).

On poorly-drained sites and at low elevation (i.e., swamps), bald cypress forests may persist for hundreds of years in the absence of deposition and major disturbance. However, with adequate sedimentation, these forests transition to other species (Hodges, 1997). The increased sediment deposition and increased frequency of these events can effectively “speed up” succession in bottomland hardwood forests.

Additionally, while bottomland hardwood systems are adapted to periodic flooding, changes in the hydro-period can greatly affect plant communities. Increased flood frequency may limit the amount and persistence of reproduction and potentially affect the future composition of bottomland hardwoods. As flood events increase in frequency and duration, anaerobic conditions in the soils also are important drivers of vegetation assemblages. The type of sediment (e.g., sand vs. silt textures) influence germination patterns and productivity of bottomland forests (Pierce and King, 2007).
and interact with the stresses of a changing climate, soil resources may be stressed. Also, proximity to human population centers means that temperate forests are more exposed to other stressors, such as introduced pests and pathogens.

One example of a forest soil challenge arising from the close proximity and interactions of temperate forests and humans, comes from central Europe in the 19th century, where the practice of litter raking of forests was common. Conifer litter was removed, sometimes as often as annually, from forests for animal bedding or other uses. Removing this nutrient-rich litter, often before much decomposition had occurred, resulted in considerable losses of nutrients (Ca, Mg, K) from the site, impoverishing the soil. These regions also experienced significant acidic deposition in the 20th century, due to human development and population growth, which further caused leaching of these nutrients from the soil. Hofmeister et al. (2008) calculated that the loss of base cations from litter raking in the 19th century was roughly equivalent to that removed by acidic deposition in the 20th Century. These nutrient losses led to forest decline and in some instances widespread tree death (e.g., “Waldsterben”) in the late 20th century. Extensive research on these issues led to policies and practices that improved forest health and productivity.

Altered temperature and precipitation regimes are likely to affect soil processes and soil health, particularly in the ecotones (edges between one forest type and another), and one persistent challenge is to further understand the potential interactive effects that the various stressors arising from a changing climate may have on forest and soil health. Altered disturbance regimes expected in temperate forests may be more of a challenge than changes in other climatic regimes. Where the climate becomes warmer and drier, drought and insect outbreaks, in addition to more frequent and severe fires, are likely to threaten functioning of temperate forest soils (Seidl et al., 2017). Where the climate is predicted to become warmer and wetter, an increase in wind storms and fungal blight pathogens are likely to be an important impact on forest health and subsequently soil function. A significant number of blight diseases have become widespread, impacting many tree species in the temperate zone, including beech bark disease and fusiform rust. All of these factors (stressors) can have effects on forest soils, as we have discussed.

There is a general consensus that at these mid-latitudes, site-specific conditions, as well as land use history, human management, air pollution and biotic effects (such as herbivory) are likely to be stronger controllers of forest productivity, decomposition, and C balances than climate change or CO₂.
enrichment (IPCC, 2001). While human impacts may be more significant than the individual changes in temperature, moisture, or CO₂ levels, the interactions among all of these, including human impacts, are likely to result in alterations of temperate forest soils and their function. Further research remains critical to maintain forest productivity as the expansive temperate forest undergoes many interacting changes.

References
Augspurger, C.K., Bartlett, E.A., 2003. Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. Tree Physiology 23 (8), 517–525.


Haeuser, E., Dawson, W., vanKleunen, M., 2017. The effects of climate warming and disturbance on the coloni-
Hanson, P.J., Weltzin, J.F., 2000. Drought disturbance from climate change: response of United States forests. The
Science of the Total Environment 262 (3), 205–220.
Hanson, P.J., Todd Jr., D.E., Amthor, J.S., 2001. A six-year study of sapling and large-tree growth and mortality
responses to natural and induced variability in precipitation and throughfall. Tree Physiology 21 (6), 345–358.
Pacific Northwest tree species. Frontiers of Plant Science 6 (120), 1–12.
Hicks Pries, C.E., Castanha, C., Porras, R.C., Torn, M.S., 2017. The whole-soil carbon flux in response to
warming. Science 355 (6332), 1420–1423.
(2–3), 117–125.
Hofmeister, J., Oulehle, F., Krám, P., Hruška, J., 2008. Loss of nutrients due to litter raking compared to the effect
of acidic deposition in two spruce stands, Czech Republic. Biogeochemistry 88 (2), 139–151.
Houle, D., Bouffard, A., Duchesne, L., Logan, T., Harvey, R., 2012. Projections of future soil temperature and
water content for three southern Quebec forested sites. Journal of Climate 25, 7690–7701.
Service, University of Illinois, Urbana-Champaign.
2001: Impacts, Adaptation and Vulnerability, Contribution of Working Group II to the Third Assessment
Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, and
Iwata, Y., Hayashi, M., Suzuki, S., Hirota, T., 2010. Effects of snow cover on soil freezing, water movement, and
Johnson, D.W., Hanson, P.J., Todd, D.E., 2002. The effects of throughfall manipulation on soil leaching in a
deciduous forest. Journal of Environmental Quality 31 (1), 204–216.
Driving forces of soil bacterial community structure, diversity, and function in temperate grasslands and
forests. Scientific Reports 6. Article 33696.
Keenan, T., Maria Serra, J., Lloret, F., Ninyerola, M., Sabate, S., 2011. Predicting the future of forests in the
Mediterranean under climate change, with niche-and process-based models: CO2 matters! Global Change
Biology 17 (1), 565–579.
global warming on soil organic C storage. Soil Biology and Biochemistry 27 (6), 753–760.
Kloepfel, B.D., Clinton, B.D., Vose, J.M., Cooper, A.R., 2003. Drought impacts on tree growth and mortality of
southern Appalachian forests. In: Climate Variability and Ecosystem Response at Long-Term Ecological
Knowles, J.F., Blanken, P.D., Williams, M.W., 2015. Soil respiration variability across a soil moisture and vegeta-
Knutzen, F., Dulamsuren, C., Meier, I.C., Leuschner, C., 2017. Recent climate warming-related growth decline
impairs European beech in the center of its distribution range. Ecosystems 20, 1494–1511.
Kubiske, M.E., Quinn, V.S., Heilman, W.E., McDonald, E.P., Marquardt, P.E., Teclaw, R.M., Friend, A.L.,
Karnosky, D.F., 2006. Interannual climate variation mediates elevation CO2 and O3 effects on forest growth.
Global Change Biology 12, 1054–1068.


