

Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century

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Abstract

Changes to forest production drivers (light, water, temperature, and site nutrient) over the last 55 years have been documented in peer-reviewed literature. The main objective of this paper is to review documented evidence of the impacts of climate change trends on forest productivity since the middle of the 20th century. We first present a concise overview of the climate controls of forest production, provide evidence of how the main controls have changed in the last 55 years, followed by a core section outlining our findings of observed and documented impacts on forest productivity and a brief discussion of the complications of interpreting trends in net primary production (NPP). At finer spatial scales, a trend is difficult to decipher, but globally, based on both satellite and ground-based data, climatic changes seemed to have a generally positive impact on forest productivity when water was not limiting. Of the 49 papers reporting forest production levels we reviewed, 37 showed a positive growth trend, five a negative trend, three reported both a positive and a negative trend for different time periods, one reported a positive and no trend for different geographic areas, and two reported no trend. Forests occupy $\approx 52\%$ of the Earth's land surface and tend to occupy more temperature and radiation-limited environments. Less than 7% of forests are in strongly water-limited systems. The combined and interacting effects of temperature, radiation, and precipitation changes with the positive effect of CO₂, the negative effects of O₃ and other pollutants, and the presently positive effects of N will not be elucidated with experimental manipulation of one or a few factors at a time. Assessments of the greening of the biosphere depend on both accurate measurements of rates (net ecosystem exchange, NPP), how much is stored at the ecosystem level (net ecosystem production) and quantification of disturbances rates on final net biome production.

Keywords: climate change, climate change impacts, forest growth, forest productivity, forest vegetation, review of changes in forests

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Introduction

Forests and forest production have been an integral part of society throughout human history. In 1662, the Interregnum and English civil war caused a crisis for sources of wood and threatened the restored monarchy. John Evelyn's *Silva* report (1664), addressing the request of the Royal Society for pertinent information about cultivating trees as quickly as possible, was probably

the first book published on silviculture and forest production (<http://instruct.uwo.ca/english/234e/site/chrnlg2.html>). The quest for understanding our environment has, over centuries, given us an insight into the mechanisms governing forest systems. In the 1640s, the work of both Johannes (Jan) Baptista van Helmont (1577–1644), an English clergyman, and physiologist Stephen Hales indicated that plants require air and water to grow (Sinha, 2004).

Documented changes in climatic conditions since the middle of the last century (Jones & Mann, 2004), coupled with our knowledge of the controls of forest

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production from forest physiology research, lead us to believe that the conditions under which forests have developed in the recent past, conditions that drive production, have changed. However, the impacts of environmental changes on global forest production are uncertain. M.G.R. Cannell's book *World Forest Biomass and Primary Production Data* (1982), provides a thorough compilation of forest stand level biomass and production data up to 1981.

The main objective of this paper is to review documented evidence in the scientific literature of the impacts of climate change trends since the 1950s on forest productivity. Any references to modelling speculations or experimental manipulations have not been considered in this review; only observed and documented impacts on forests have been incorporated. Forests respond to both short-term and longer-term variations in the environment (Innes & Peterson, 2001) and because of the blurred separation between natural and anthropogenic atmospheric changes (Innes & Peterson, 2001; IPCC, 2003), we make no distinctions between the two in this paper.

Three types of data form the basis of this review: satellite findings, field-based data from carbon sequestration research, and field-based data from forest management planning and activities. Satellites provide a broad overview of forest production at the regional to global scale (Running *et al.*, 2004), whereas field observations of the impacts of climate change on forest production give regional and local estimates. Recent monitoring of carbon through net primary production (NPP), net biome production (NBP), net ecosystem production (NEP) and net ecosystem exchange (NEE), promoted by the increasing interest in carbon sequestration, provides a picture of forest productivity status at regional to global scales. An important source of observations of change is aboveground biomass measurements such as diameter, height, and tree or stand volume, the common basis for stand-level studies and inventories, which are the basis for forest management planning around the world.

The distinction among NPP, NBP, NEP, and NEE is often unclear in the literature. We interpreted our findings following the IPCC (2003) definitions of these carbon measurements. The IPCC (2003) defines NPP as the rate of carbon accumulation in plants after losses from plant respiration and other metabolic processes (necessary to maintain the plant's living systems) are taken into account. It can be calculated as gross primary production (GPP) minus autotrophic respiration. NEP takes into account heterotrophic respiration such as decomposition of dead organic matter, and thus can be measured from the changes in carbon stocks in vegetation and soil or by integrating fluxes of CO₂ in

and out of the system (NEE) (Goulden *et al.*, 1996; IPCC, 2003). NEP is the accumulation of carbon over a whole ecosystem and over a whole season or other time period (IPCC, 2003). NBP refers to the net production of organic matter (e.g. biomass) in a region containing a range of ecosystems (e.g. a biome), including disturbances (IPCC, 2003). It can be calculated by summing ecosystems-level NEP over a region and subtracting losses due to disturbances. At the ecosystem scale, carbon losses due to disturbances are relatively infrequent and difficult to quantify. At the biome scale, however, disturbances such as fires and forest harvest can be considered processes as they occur on a regular basis in one area or another of the biome (Georgii & Yoshiki, 2002). NBP seems to be the most appropriate way to analyze long-term, large-scale changes in carbon (often referred to as a carbon sink or source), whereas NPP and NEP are more useful measures of carbon at an ecosystem or forest stand level. Many publications report aboveground NBP (ANBP) without specifying that measurements only considered aboveground carbon. In our review, we have incorporated the distinction between NBP and ANBP.

In this text, we first present a concise overview of the climate control of forest primary production. We then provide evidence of how the main controls have changed since the 1950s, followed by the core section of our review, our findings of observed and documented impacts on forest productivity. Finally, we present a brief discussion of the complications inherent in interpreting trends in NPP.

Climate and forest production

Although all biological activity in plants is ultimately dependent on absorbed solar radiation, it is obvious that solar radiation alone does not determine primary productivity. All plants require sunlight, carbon dioxide, and water for photosynthesis. Beyond these basic requirements, the amount of foliage, the light-use efficiency of this foliage, water availability, ambient temperature, availability of soil nutrients, and the adaptations of species to extreme temperatures and efficient use of water and nutrients are finer controls of forest productivity (Schulze *et al.*, 2002; Hopkins & Hüner, 2004).

The main abiotic controls of primary production (temperature, radiation, and water) interact to impose complex and varying limitations on vegetation activity in different parts of the world (Churkina & Running, 1998; Nemani *et al.*, 2003; Running *et al.*, 2004). Physiological responses to changes in climate are highly dependent on the limiting factors of a particular site to forest growth. For example, increasing temperature

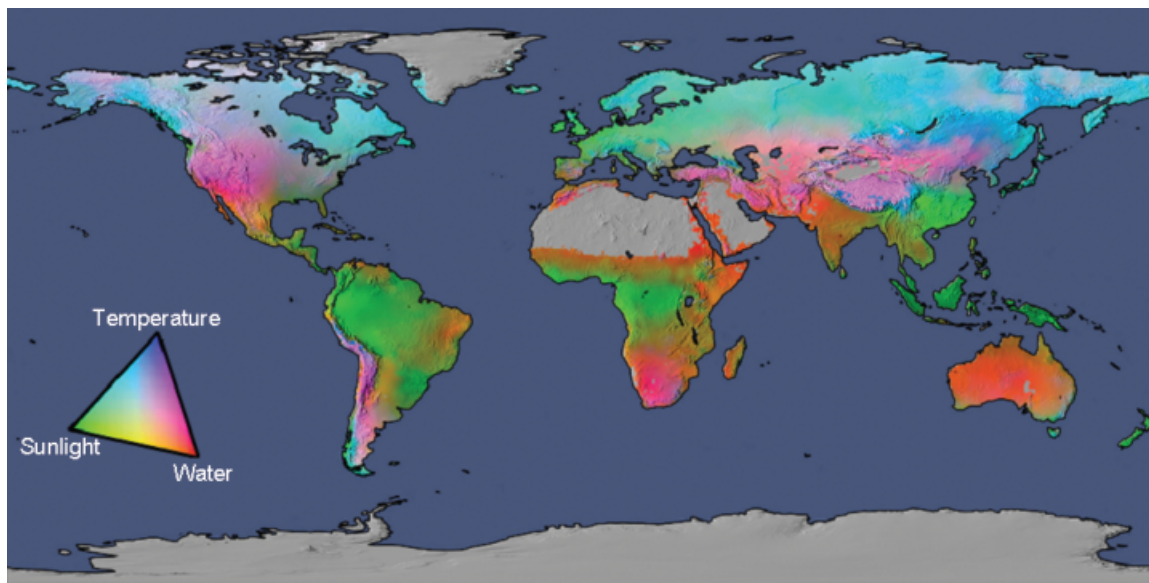


Fig. 1 Potential limits to vegetation net primary production based on fundamental physiological limits by vapor pressure deficit, water balance, and temperature (from Churkina & Running, 1998; Nemani *et al.*, 2003; Running *et al.*, 2004).

may also increase vapor pressure deficit (VPD) of the air, and thereby increase transpiration rates, resulting in adverse effects on dryer sites, unless stomata close in response to other changes such as an increase in CO₂, or if increases in night-time temperature exceed increases during the day (Kirschbaum, 2004). Figure 1 depicts the distribution of the limiting factors to primary production in terms of water, sunlight, and temperature on a global scale. Very few forest types in Fig. 1 are solid colors, expressing variability in the dominance of limiting factors within a given year. For example, the productivity of temperate forests of northwestern North America may be radiation and temperature limited in winter, temperature limited in spring and water limited by midsummer. These controls depend on climate and are expressed as a mosaic of regionally varied impacts on forest systems.

Temperature (heat) controls the rate of plant metabolism, which in turn determines the amount of photosynthesis that can take place. Most biological metabolic activity takes place within the range of 0–50 °C (Hopkins & Hüner, 2004). There is little activity above or below this range. The optimal temperatures for productivity coincide with 15–25 °C; the optimal range of photosynthesis (Hopkins & Hüner, 2004) and lethal levels are between 44 °C and 52 °C (Schulze *et al.*, 2002). Photosynthesis depends on radiation, increasing with increasing irradiance. Water is a principal requirement for photosynthesis and the main chemical component of most plant cells. In dry regions, there is a linear increase in NPP with increased water availability (Loik *et al.*, 2004). In a study of systems with nearly steady-

state aboveground standing crop, Webb *et al.* (1983) showed an exponential decrease in productivity with decreased water availability. Knapp & Smith (2001) found a strong correlation between ANPP and annual precipitation across North America (22 study sites), but show the interannual variability in ANPP not to be related with precipitation. Contrary to Knapp & Smith (2001), Fang *et al.* (2001b) showed a significant positive relationship between the coefficient of variation (CV) of the normalized difference vegetation index (NDVI¹), used as a predictor of NPP, and that of precipitation. The differences in the scope of the data used in the Knapp & Smith (2001) vs. Fang *et al.* (2001b) analyses may be the source of the different findings; however, they may also stem from a difference in the time and space variability of productivity in relation to precipitation and, hence, may be a scale issue.

Forest soils and site productivity will likely be affected by changes in both site water balance and temperatures as these affect soil organic matter decomposition rates (Moore *et al.*, 1999; Barrett, 2002; Trofymow, *et al.*, 2002; Kirschbaum, 2004). Increased decomposition rates could result in more readily mineralized nutrients available to plants, which would likely increase photosynthetic carbon gain in nutrient-limited systems (Kirschbaum, 2004). An important contribution to forest soils may be the increase in atmospheric N deposition. Atmospheric depositions of N are likely to enhance growth for many temperate coniferous forests

¹NDVI = (NIR—VIS)/(NIR + VIS), where NIR is near infrared and VIS is visible light.

sites where N is considered to be the most common limiting nutrient (Breymer *et al.*, 1997).

The increase in productivity with an increasing amount of foliage is instinctive. The light-use efficiency of foliage, however, is thought to vary across forest types, and even within a single tree canopy, but how it varies across species and time scale is still under debate (Nichol *et al.*, 2002; Guo & Trotter, 2004; Lagergren *et al.*, 2005). In a comparison of aboveground NPP in deserts and forested ecosystems, Webb *et al.* (1983) found ecosystem type to have some control over abiotic factors in producing aboveground NPP but that this control was not large. Hence, forest ecosystems, like all other ecosystems, are mainly at the mercy of abiotic factors (radiation, water, temperature) with some adaptations having small effects, at least for aboveground NPP.

There is considerable variability in NPP controls across forests systems throughout the world. Changes in the rainfall patterns are likely to have large corresponding effects on forest productivity in regions where productivity is water limited (Kirschbaum, 2004). Similar statements can be made about radiation and temperature changes. Changes in temperature and precipitation can also change growing season length, an important determinant of NPP in temperate and boreal forests (Kimball *et al.*, 2004). Jolly *et al.* (2005) developed a phenological-control model using a combination of day length, VPD, and minimum temperatures. The model depicts well changes in growing season length regionally and globally, supporting the control that radiation, temperature, and water exert on growing season length. White *et al.* (2005) identified the regions of high-latitude North America and Eurasia as indicators of climate change as the productivity in these regions is limited by the combination of climatically controlled factors, is affected by compositional atmospheric changes but are relatively free of other driving forces of productivity changes such as urbanization, political changes, and other land-use changes.

Two patterns of climatic variability that have contributed to changes in rainfall and precipitation were prominent in the 20th century: the Pacific Decadal Oscillation (PDO) and the El Niño/Southern Oscillation (ENSO) (Bond & Harrison, 2000; Nemani *et al.*, 2003). ENSO- and PDO-influenced climate variables, such as temperature and precipitation, strongly influence inter-annual variability in NPP (Nemani *et al.*, 2003) and are referred to throughout the following sections. ENSO is the primary driver of temperature variations across the tropics and of precipitation fluctuations for large areas of the Americas and southeast Asia. PDO and ENSO display similar spatial climate fingerprints but have a very different behavior in time.

Evidence of climatic changes

Global temperature and precipitation trends

Global average has temperature increased by 0.6 ± 0.2 °C in the past 100 years, and global average precipitation has increased slightly (Barnett, 2001; Houghton *et al.*, 2001; Levitus, 2001). The greatest warming, up to 4 °C, occurred in winter. Jones & Mann (2004) refer to a recent large-scale warming and their assessment affirms the conclusion that late 20th century warmth is unprecedented at hemispheric and likely, global scales. They also point out the regional variability and the dramatic differences between regional and hemispheric/global past trends, which was confirmed by Feng & Hu (2004) who observed that changes in regional and local surface air temperatures and precipitation do not follow these global increases (Feng & Hu, 2004). Some regions, like Austria, exhibited no increase in temperature for latter parts of the 20th century (Hasenauer *et al.*, 1999) whereas others showed dramatic increases in valley bottoms but not at high elevations (Mote *et al.*, 1999; Innes & Peterson, 2001; Mote, 2003b).

Global radiation trends

Changes in incoming radiation have also been reported. Independent studies reported large increases in incoming solar radiation between the 1980s and the 1990s in parts of the world, mainly due to changes in cloudiness (Wielicki *et al.*, 2002; Nemani *et al.*, 2003). Contrary to these satellite analyses, ground-based measurements from thermopile pyranometers suggest that significant reductions in solar radiation reaching the Earth's surface have occurred during the past 50 years, termed 'global dimming' (Stanhill & Cohen, 2001). In an analysis of surface observations for the Northern hemisphere, Wild *et al.* (2005) showed the dimming not to have persisted in the 1990s but pointed rather to a widespread brightening since the late 1980s. Pinker *et al.* (2005) confirm this brightening in their analysis of the amount of solar radiation at the Earth's surface between 1983 and 2001, where they found a decrease until about 1990, followed by an increase in solar radiation. These discrepancies may be attributed to measurement, temporal and spatial scales of the databases analyzed, localized increases or decreases in radiation, and perhaps even to an increase in diffuse radiation due to Mount Pinatubo's eruption (Trenberth, 2002; Gu *et al.*, 2003; Clark, 2004; Lewis *et al.*, 2004a).

Global trends in CO₂

Although CO₂ is not the only pollutant that has increased since the 1950s, its multi-faceted role in primary

production, the potential for plant carbon sequestration, and the potential effect it has on global temperatures make CO₂ the focus of much research. Direct measurement of CO₂ at Mauna Loa Hawaii clearly shows a 55 µmol mol⁻¹ increase from 1959 to 2001, an increase of more than 16% during that time period (Keeling & Whorf, 2005). Of the approximately 760 Gt C in the atmosphere, photosynthesis by terrestrial vegetation removes approximately 120 Gt, almost 16% of the atmospheric content annually, but can return an equivalent amount through autotrophic and heterotrophic respiration (Prentice *et al.*, 2001; Schimel *et al.*, 2001).

Trends by forest types

Analysis of station temperature trends during 1961–1990 indicate pronounced warming over substantial areas of the boreal forest in Alaska, northwestern Canada, and northern Eurasia (Chapman & Walsh, 1993). Air temperatures that regulate growing season dynamics have increased over temperature-limited regions of northwestern Europe (Myneni *et al.*, 1997) and an increase in temperatures and in growing degree days, defined for our purposes here as daily temperatures below 0 °C, of +1.7 °C and 16%, respectively, were documented for the northeast of British Columbia (BC), Canada (Mote, 2003a).

In the temperate forests of the Pacific Northwest of North America, changes in temperature (+0.8 °C) and precipitation (+14%) exceeded the global average during the 20th century. Even within that region finer scale regional variations depict the patterns of temperature in the Pacific Northwest more accurately: during the 20th century, average temperatures warmed by 0.6 °C on the coast of BC and 1.1 °C in the interior of the province (Mote, 2003a), and precipitation has been increasing by 2–4% per decade, primarily in the winter. A 50% increase in precipitation has been recorded in northeastern Washington and southwestern Montana during the 20th century (Mote, 2003a). A large part of the recent increase in temperature records reflects a rise in minimum temperatures, whereas maximum temperatures may remain stable or actually decrease, especially during the summer season. Hence, systems limited by maximum temperature (as the Canadian Cordillera may be) may not have shown any corresponding changes in productivity (Luckman *et al.*, 2004).

Over most of the western US, winter snow fall dominates the precipitation patterns (Mote *et al.*, 2005). Climate and snow data for the US and Canada showed a decline in mountain spring snow packs by approximately 30% since 1950, indicating earlier and/or winter melt (Mote, 2003). Analyses show climatic trends to be the dominant factor in snow pack decline,

as opposed to changes in land use, forest canopy, or other factors (Hamlet *et al.*, 2005; Mote, 2003a). Snow accumulation, along with soil storage and groundwater, are the primary mechanism by which water is stored and transferred to the relatively dry summer of western North America (Hamlet *et al.*, 2005) and hence, snow pack is a critical determinant to limitations imposed on tree growth and other ecological processes. The reported declines in snow pack are further corroborated by observed changes in stream flow toward earlier peak snowmelt, lower summer flow, and higher winter flow (Hamlet *et al.*, 2005; Mote, 2003, 2003a; Mote *et al.*, 2003, 2005). Taken together, these results emphasize that the North American West's hydrologic resources are already responding to changes in climate.

As in boreal forests, changes in temperature are reflected in a changing number of growing degree days in temperate forests. Growing degree days in BC increased by 13% on the coast and in the southern interior, and by 5% in the central interior of the province (Mote, 2003a). In a study of 88 years of data, White *et al.* (1999) showed that for individual sites in the eastern deciduous broadleaf forest of the USA, the length of the growing season regularly varied by more than 15 days. Hence, what consists of a change within the normal variability of growing season length requires careful consideration of the site or area's historic variability to be able to depict a trend. Nevertheless, Cayan *et al.*'s (2001) findings seem to confirm an advance in the timing of spring since about 1950 in much of North America, whereas Feng & Hu's (2004) results show an increase in growing season length across the western USA and a decreasing trend from the US Great Plains to the East Coast. A study by Inouye *et al.* (2000) showed no significant change in the calendar date of the beginning of the growing season at high altitude in the Colorado Rocky Mountains over the last quarter of the 20th century. Data from temperate eastern China show the growing season to have been extended by 1.4–3.6 day yr⁻¹ in the northern reaches and by 1.4 day yr⁻¹ across the whole area between 1982 and 1993 (Chen *et al.*, 2005). According to Peterson & Peterson (2001) and Peterson *et al.* (2002), the lighter snow packs of PDO periods in the Pacific Northwest brought an earlier start to the high-elevation growing season. However, at lower elevations where summer moisture stress limits productivity, growth was negatively correlated with PDO (Peterson & Peterson, 2001; Peterson *et al.*, 2002). In their analysis of temperate eastern China, Chen *et al.* (2005) found growing season length to correlate significantly with spatial patterns of mean air temperatures in the spring and autumn. The effects of an increased growing season length, much like precipitation and temperature, are dictated by regional conditions and site-specific limiting factors to productivity.

Tropical forest regions show temperature increases averaging $0.26 \pm 0.05^\circ\text{C}$ since the mid-1970s (Clark, 2004; Malhi & Wright, 2004) and a strong variation in long-term rain trends (Houghton *et al.*, 2001; Malhi & Wright, 2004). Overall precipitation appears to have declined in tropical rainforest regions at a rate of $1.0 \pm 0.8\%$ ($P < 0.05$) per decade since 1960 (Malhi & Wright, 2004). This pan-tropical decreasing trend in land surface measurements of rainfall, however, is primarily driven by a strong and significant decline in rainfall in the northern African tropics (3–4% per decade) (Houghton *et al.*, 2001; Malhi & Wright, 2004). Rainfall only declined marginally in tropical Asia and showed no significant trend in Amazonia (Malhi & Wright, 2004).

Productivity response

Given our knowledge of the mechanisms driving forest productivity and the changes outlined in the previous section, we expect to observe a detectable forest response to changes in climatic factors. Much like changes in temperature, precipitation, and radiation, productivity responses of forests have been measured at different time and spatial scales using a variety of measurement tools. In this section, we first outline reported changes in productivity at a large spatial scale, which mostly comprises satellite and global estimates, and then present regional and/or country-level estimates found in the literature, followed by trends from ground-based estimates. Table 1 summarizes the findings in this section.

Global and continental trends

According to Nemani *et al.* (2003), globally, NPP seems to have increased by 6% (3.4 Pg C) over 1982–1999 but with declines during all three major ENSO events. Other studies analyzing satellite-driven measures of vegetation greenness (NDVI), a surrogate for photosynthetic activity (Field *et al.*, 1995; Prince & Goward, 1995; Slayback *et al.*, 2003), also indicated reduced productivity in tropical ecosystems in warmer years (Braswell *et al.*, 1997; Asner *et al.*, 2000; Los *et al.*, 2001) which are associated with ENSO. NDVI is a remotely observed variable that responds strongly to healthy, green vegetation and is approximately linearly related to the fraction of photosynthetically active radiation absorbed by green vegetation (FPAR) (Sellers, 1987). It is, therefore, a good proxy for photosynthetic activity (Slayback *et al.*, 2003) and was shown to be highly correlated with NPP (Field *et al.*, 1995; Prince & Goward, 1995). NDVI measurements used for vegetation monitoring seem to also support an increasing trend in photosynthetic

activity during 1982–1999 (from 0.0015 to 0.0045 NDVI units per year), with trends generally higher in the 1990s than in the 1980s at global latitude bands from 35° to 75° north (Slayback *et al.*, 2003). According to Slayback *et al.* (2003), trends in North American and Eurasian for the 1980s were roughly comparable, whereas in the 1990s the North American trends were generally higher. Large areas of Canada, Europe, and northern Asia seemed to be experiencing a significant positive trend across all vegetated land covers (Slayback *et al.*, 2003), not just forest systems. The carbon balance of boreal deciduous and conifer forests has been shown to be sensitive to seasonal and interannual climatic variability (Arain *et al.*, 2002). White *et al.* (1999) confirm that a long growing season does increase NEP, GPP, and evapotranspiration (White *et al.*, 1999). Longer growing seasons reported increased carbon storage in aspen boreal forests (Chen *et al.*, 1999) and in northwestern Europe (Lucht *et al.*, 2002), where increased air temperatures have promoted earlier plant growth (Myneni *et al.*, 1997). Nemani *et al.* (2003) attributed the largest increase in NPP in the last two decades of the 20th century to tropical ecosystems. In this analysis, the Amazon rain forest accounted for 42% of the 6% global increase in NPP. Some studies attribute this increase to increases in solar radiation, owing to declining cloud cover in these predominantly radiation-limited forests (Trigo *et al.*, 2002; Wielicki *et al.*, 2002; Graham *et al.*, 2003; Nemani *et al.*, 2003), whereas others to more local changes in cloud cover as well as increases in CO_2 level and air temperatures (Lewis *et al.*, 2004b). Graham *et al.* (2003) attributed the response in productivity level to the more tightly coupled NPP and soil respiration processes in tropical climates compared with ecosystems in other latitudes.

Regional trends

The analysis of satellite data accompanied by process modelling showed an increase in China's NPP between 1982 and 1999 (Fang *et al.*, 2003). However, forests were only one contributor to this estimate and, although they are considered to be a large contributor to this increase in NPP (Fang & Wang, 2001), the spatial variability of NPP over the vast extents of China is very high (Yue *et al.*, 2005), with increases up to 31% in NPP in certain areas and losses in NPP in areas of rapid urbanization (Fang *et al.*, 2003). In an analysis based on forest inventory data, Fang *et al.*, (2001a) showed Chinese forests to have been a carbon source between 1949 and 1980 ($0.022 \text{ Pg C yr}^{-1}$) and planted forest a sink between the late 1970s and 1998 (up to $4.75 \text{ Pg C yr}^{-1}$ in 1998).

Table 1 Summary of published change in forest productivity under recent climate change. variables are: net primary production (NPP), net ecosystem exchange (NEE), net biome production (NBP), above-ground NPP (ANPP), above-ground NEP (ANEP), and above-ground NBP (ANBP)

Variable	Change	Time scale	Spatial scale	Data type	Reference
ANPP	+	1982–1999	Globe	Satellite	Nemani <i>et al.</i> (2003)
ANPP	–	ENSO years	Tropics	Satellite	Nemani <i>et al.</i> (2003)
ANPP	–	ENSO years	Tropics	Satellite	Braswell <i>et al.</i> (1997)
ANPP	–	ENSO years	Tropics	Satellite	Asner <i>et al.</i> (2000)
ANPP	–	ENSO years	Tropics	Satellite	Los <i>et al.</i> (2001)
NDVI	+	1982–1999	Northern hemisphere	Satellite	Slayback <i>et al.</i> (2003)
ANBP	+	Growing-season	Boreal aspen	Land-flux tower	Chen <i>et al.</i> (1999)
ANPP	+	Growing-season	North-western Europe	Satellite	Lucht <i>et al.</i> (2002)
ANPP	+	1982–1999	China	Satellite	Fang <i>et al.</i> (2003)
ANBP	–	1949–1980	China	Land biomass	Fang <i>et al.</i> (2001a)
ANBP	+	1970s–1998	Chinese planted forests	Land biomass	Fang <i>et al.</i> (2001a)
ANBP	+	1982–1998	North America	Satellite	Hicke <i>et al.</i> (2002)
ANBP	+	1945–1990	USA	Combined types	Houghton <i>et al.</i> (1999)
NBP	+	1980–1989	USA	Atmospheric and land-flux tower	Pacala <i>et al.</i> (2001)
		1990–1994			
NBP	+	1990s	European forests and grasslands	Combined types	Janssens <i>et al.</i> (2004)
ANPP	+	Recent	Canadian and Alaska boreal forests	Combined types	Innes & Peterson (2001)
ANPP/ANBP	–	1951–2000	Canadian prairies boreal aspen	Land biomass	Hogg <i>et al.</i> (2005)
ANPP	+	Since 1970	boreal/tundra forest	Land biomass	Gamache & Payette (2004)
NBP	+	1950–1999	European forests	Land biomass	Nabuurs <i>et al.</i> (2003)
ANPP	+	20th century	Canadian Cordillera	Land biomass	Luckman <i>et al.</i> (2004)
ANBP	+	During PDO events	Pacific Northwest	Land biomass	Peterson and Peterson (2001)
ANBP	+	During PDO events	Pacific Northwest	Land biomass	Peterson <i>et al.</i> (2002)
ANPP	–	1926–2001	Northwest Russia	Land-soil fluxes	Lawrence <i>et al.</i> (2005)
ANPP/ANBP	+	20th century	Scots Pine in Lapland	Land biomass	Mielikäinen & Sennov (1996)
ANPP/ANBP	0	20th century	Scots Pine southern Finland	Land biomass	Mielikäinen & Sennov (1996)
ANPP/ANBP	+	20th century	Sweden	Land biomass	Elfvig <i>et al.</i> (1996)
ANPP/ANBP	+	1953–1992	Swedish forest	Land biomass	Ericksson & Karlsson (1996)
ANPP/ANBP	+	Since 1960s	Scott Pine and Norway spruce in Sweden	Land biomass	Ericksson & Karlsson (1996)
ANPP/ANBP	+	1920s–1990	Danish beech forest	Land biomass	Skovsgaard & Henriksen (1996)
ANPP/ANBP	+	1975–2000	Eastern Germany spruce and beech	Land biomass	Unthelm (1996)
ANPP	+	Last 150 years	France	Land biomass	Wenk & Vogel (1996)
ANPP/ANBP	+	Since 1905	Toppwald Switzerland	Land biomass	Badeau <i>et al.</i> (1996)
ANPP/ANBP	+	20th century	Norway spruce in the Swiss Jura	Land biomass	Bräker (1996)
ANBP/NBP	+	1947–1995	Japan	Land biomass	Schneider & Hartmann (1996)
ANPP/ANBP	+	± 100 years	Various parts of Switzerland	Land biomass	Fang <i>et al.</i> (2005)
ANPP/ANBP	+	Since 1961	Austria	Land biomass	Zingg (1996)
ANPP/ANBP	+	Since 1961	Austria	Land biomass	Schadauer (1996)
ANPP/ANBP	+	1947–1990	Slovanian beech forests	Land biomass	Hasenauer <i>et al.</i> (1999)
					Kotar (1996)

Table 1. (Contd.)

Variable	Change	Time scale	Spatial scale	Data type	Reference
ANPP/ANBP	+	Last 150 years	Spanish forests	Land biomass	Montero <i>et al.</i> (1996)
NEP/NBP	+	110 years	European beech	Land biomass	Bascietto <i>et al.</i> (2004)
ANPP/ANBP	+	1970–1990	Portugal maritime pine	Land biomass	Tomé <i>et al.</i> (1996)
ANPP/ANBP	–	1970–1990	Portugal eucalyptus	Land biomass	Tomé <i>et al.</i> (1996)
NEP/NBP	+	1982–2001	Thuringian managed coniferous forests – high-elevation temperate conifer forests of Central Europe	Land biomass	Vetter <i>et al.</i> (2005)
ANBP	+	1970s and 1980s	Austria, Finland, Sweden, Germany, France, and Switzerland	Land biomass	Kauppi <i>et al.</i> (1992)
ANBP	+	1970s and 1980s	Austria, Finland, Sweden, Germany, France, and Switzerland	Land biomass	Spiecker <i>et al.</i> (1996)
ANPP/ANBP	+	1975–1996	Old growth tropical forests	Land biomass	Phillips <i>et al.</i> (1998)
NPP/NBP	+	1980–1989	Tropical forests	Land-flux tower	Malti and Grace (2000)
NBP	+	1990s	Northern extratropical areas	Land-flux tower	Schimel <i>et al.</i> (2001)
NBP	0	1980s	Northern extratropical areas	Land-flux tower	Schimel <i>et al.</i> (2001)
NBP	0	1980s and 1990s	Tropical land areas	Land-flux tower	Schimel <i>et al.</i> (2001)
ANBP	+	1971–2002	Tropical forests across South America	Land biomass	Baker <i>et al.</i> (2004)
NEP	–	1984–2000	Pará, Brazil	Land biomass	Miller <i>et al.</i> (2004)
ANPP/ANBP	+	1971–2002	Tropical forest across South America	Land biomass	Lewis <i>et al.</i> (2004b)

Regional studies in North America and in the USA reported increases in NPP of 2–8% between 1982 and 1998 (Hicke *et al.*, 2002). Changes in North America are thought to stem from increased growth by natural vegetation with increased precipitation and humidity, especially during the 1950–1993 period (Nemani *et al.*, 2002), and from the increase in air temperatures stated earlier that regulate the growth-season dynamics over temperature-limited regions (Myneni *et al.*, 1997; Lucht *et al.*, 2002). Reporting on the terrestrial carbon sink for the contiguous United States, Pacala *et al.* (2001) estimated a gain of 0.3–0.6 PgC a⁻¹ during the 1980s. Although this estimate is not exclusive to forests, forests are thought to be a major contributor (Pacala *et al.*, 2001; Janssens *et al.*, 2004).

Trends from ground-based estimates

Boreal forests. Changes in vegetation over centuries to millennia in Alaska suggest that the magnitude of ecological response to global climate change is greater at high latitudes than at low latitudes (Ager, 1997). For example, paleoaeobotanical evidence indicates that 6000 years ago, boreal forests extended north of the modern tree line, apparently in response to high-latitude warming resulting from variations in the Earth's orbit (Foley *et al.*, 1994). The expanded boreal forest, which replaced the tundra, is also thought to have affected climate by significantly reducing surface albedo (Foley *et al.*, 1994). This apparent plasticity in boreal forests to changes in climate seems to be detectable in forest productivity measurements given the recent changes in climate. A number of phenomena have already been observed that suggest that Canadian and southern Alaskan forests are responding to recent warming. These include increases in boreal forest productivity, accelerated seasonal development of some insects, changes in the distribution of insect pests, and provenances from slightly warmer areas out-competing local provenances (Innes & Peterson, 2001). In northeastern BC, Canada, mature lodgepole pine trees are succumbing to *Dothistroma* needle blight, which is unprecedented (Woods *et al.*, 2005). Woods *et al.* (2005) identified a clear mechanistic relationship between observed climate trends and host–pathogen interaction. Although most documented evidence points to increases in productivity, decreases have also been reported. A tree-ring analysis of boreal aspen over a large track (1800 km × 500 km) along the northern edge of the Canadian prairies showed that during 1951–2000, the region's aspen forests underwent several cycles of reduced growth, when the mean stand basal area (BA) increment decreased by about 50% (Hogg *et al.*, 2005). This was partially due

to increased insect activity but was also attributed to climate changes.

Nugesser *et al.* (1999) suggest that current methods for forest productivity measurement may be underestimating productivity in boreal forests, and Wirth *et al.* (2002) maintain that changes in site productivity in fire-dominated systems like the boreal forest remain indiscernible due to the large variability in aboveground NPP caused by disturbances. In the northern forest-tundra sites of the province of Québec, Canada, a recent increase in height growth and a positive trend in leader shoot elongation were reported (Gamache & Payette, 2004). These increases were not observed in the southern forest-tundra, and suppressed height growth of spruce seemed to be more prominent in the southern parts of this systems. A European study by Sinkevich & Lindholm (1996) showed similar observations for the northern reaches of trees in taiga forests in the 1990s, with the increment variability in the mid-taiga zone presenting increments characteristic of the northern reaches of the taiga. The interpretation of these growth patterns in the southern taiga may be misleading as these forests have shown cyclical patterns of 30-year growth increment decreases between the mid-taiga and north-taiga stands (Sinkevich & Lindholm, 1996).

The general increasing trend in observed NPP is positive for boreal forests and supports the more general and global satellite-based analyses.

Temperate forests. Temperate forests have a long history of structured management and forest inventories, more so in European than North American forests. For the period between 1950 and 1999, Nabuurs *et al.* (2003) report an almost constant increase from 0.03 PgC yr⁻¹ in the 1950s to 0.14 PgC yr⁻¹ in the 1990s in NBP of European forests. The Canadian Cordillera did show an increase in growth but not in the two last decades as reported in satellite-based studies (Luckman *et al.*, 2004). Temperature-sensitive chronologies showed maximum growth in the mid 20th century rather than in the last few decades (Luckman *et al.*, 2004). These conclusions, however, are based on dendrochronological studies and are thought to reflect regional rather than local climate signals. Again, this illustrates the importance of scale in determining general trends. During a PDO event, which brings warm winters and light snow packs to the Pacific Northwest, USA, in sites where trees are not typically constrained by summer moisture stress, growth was positively correlated with PDO (e.g. near the upper tree line in Oregon and Washington) (Peterson & Peterson, 2001; Peterson *et al.*, 2002).

Lawrence *et al.* (2005) found a decrease in diameter growth and a suppression of climate-tree growth relationships in Norway spruce but this decrease coincided with a flux in local industrial pollution. Most studies in northern Europe showed an increase in productivity. In Lapland, Scots pine showed increases in diameter for most forests in the 20th century, with increments ranging from 0.85 to 1.5 mm, as compared with the 19th century, where increments ranged from 0.45 to about 1.4 mm, with more than half the observations below 1.0 mm (Mielikäinen & Sennov, 1996). Scots pine in southern Finland, where the nitrogen deposition is many times higher than in the north, showed no detectable trends in the radial increment while aging stands at sites near Saint-Petersburg, where N deposition has increased to 25 kg ha⁻¹ yr⁻¹, did not show the normally observed decrease in current annual volume increment of mature stands during the last few decades (Mielikäinen & Sennov, 1996).

The Swedish National Forest Inventory showed a highly significant annual increase in both height and BA growth (0.5–0.8%) for the period 1953–1992 (Elfving *et al.*, 1996), and site indices (SI), a measure of site quality, have increased for both Scots pine and Norway spruce during the last decades by 0.05–0.11 myr⁻¹ for spruce and with a difference of 2.5 m with expected SI in pine by the 1980s (Ericksson & Karlsson, 1996). SI of beech forests in Denmark also showed an increase between 1920 and 1990 of 3.6 m (at reference year 100) (Skovsgaard & Henriksen, 1996), and a general increasing trend in height growth within age classes was observed on both spruce and beech over the last quarter of the 20th century in eastern Germany (Unthelm, 1996; Wenk & Vogel, 1996). SI, despite its shortcomings (Nicholas & Zedaker, 1992), is a well-used measure of productivity in forest management (Vanclay, 1992). SI has been considered to be constant for species on a given site (Clutter *et al.*, 1983) and changes in this estimate undermine the premise that supports classical growth and yield projections.

In their analyses of Swedish long-term yield experiments, Ericksson & Karlsson (1996) conclude that site productivity has increased in most parts of Sweden during the last 30–40 years. The BA and height increases do not appear to have influenced the established height growth development patterns that continued to develop according to site curves on permanent sample plots both in Sweden and in Norway (Elfving *et al.*, 1996). Much like the previously mentioned Finnish and Russian studies, these increases are partly attributed to the increase in N atmospheric deposition (Elfving *et al.*, 1996; Ericksson & Karlsson, 1996). A comparison of average temperatures and

precipitation levels across Sweden from the earlier and latter parts of the century show no significant differences between the two time periods in either precipitation or temperatures (Eriksson, 1982, 1983). This lack of climatic trend either suggests that averages of daily temperatures and precipitation levels may not be good indicators of changes in site productivity and that the range and extreme events of both abiotic factors may play a more important role in the changes in productivity, or that other factors, such as growing season length combined with N deposition, may be partially responsible for the changes.

Dendrochronological studies in France showed an increasing growth trend in the past 150 years of +50% to +160% depending on species and location (Badeau *et al.*, 1996), with no specification of the portion of this change that occurred in the latter half of the 20th century. This surprising increase was scrutinized by the authors for biases and precorrected for the effect of aging. No overarching biases seem to undermine the reliability of data but some localized and potential biases were identified (Badeau *et al.*, 1996). It seems appropriate, given the authors' efforts to identify biases, to at least assume that the growth trend is positive and large. After removing the variation in growth caused by short-term climate fluctuations, a case study in Toppwald, Switzerland, also showed an improved growth trend since the beginning of the 20th century (from 4% to 49% of the growth variance) and increased growth in the 1980s (Bräker, 1996). An increase in the diameter and BA increment can be shown for various tree species and for various forest structures in different areas of Switzerland (Schneider & Hartmann, 1996; Zingg, 1996). In Austria, studies show current annual increment of BA to have increased since 1961 with a maximum increase in the 1970s and the 1980s of 17%, and a significant increase in diameter increment obtained from 1179 cores of Norway spruce across Austria with a long-term trend increasing in diameter growth over the 20th century (Schadauer, 1996; Hasenauer *et al.*, 1999). The increases in the 1970s and the 1980s were partially attributed to an increase during that time in the length of the temperature-controlled growing season (Hasenauer *et al.*, 1999). Variation in growth responses to increased precipitation between aspects, with some aspects showing higher sensitivity than others, has also been reported in tree line and timber line studies in Austria (Oberhuber, 2004), emphasizing that various site-specific controls are at play in these overall positive responses.

Beech forest in Slovenia have shown growth trends surpassing those of yield tables with current annual increment increases of $3.1 \text{ m}^3 \text{ ha}^{-1}$ in 1947 to $5.3 \text{ m}^3 \text{ ha}^{-1}$ in 1990 (Kotar, 1996). Spanish forest growth

trends have also been increasing for the last 150 years but Montero *et al.* (1996) only partly attributed the change to increased site productivity (Montero *et al.*, 1996). Analyses of carbon sequestration trends showed higher than expected levels of carbon sequestration in 110-year-old beech forests in Europe (Bascietto *et al.*, 2004). Forests in northern Spain were accumulating carbon at an average rate of $1.46 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ from 1972/1973 to 1986/1988 (Rodríguez Murillo, 1997), but changes in forest management and land use throughout the region make it hard to discern whether forest have actually increased in productivity. Rodríguez Murillo (1997) concludes that increases in the growing stock could be considered compatible with 'normal' stand evolution.

Exploratory analysis of growth trends in Portugal did not reveal positive growth trends for volumes of Maritime pine and eucalyptus poplar between 1970 and 1990 (Tomé *et al.*, 1996). Maritime pine did show positive trends in dominant height ($\approx 4.5 \text{ m}$ in dominant height) but the trends were negative for eucalyptus ($\approx 12 \text{ m}$ in dominant height). The negative trend seems to be related to decreasing amounts of precipitation on these dry sites during the growing season (spring and early summer) during those decades (Tomé *et al.*, 1996).

For Europe as a whole, forest growth trends are positive, although a few cases showed no trends, and some sites with extreme growth limitations such as increased temperatures on water-limited sites, showed a decrease in productivity (Lucht *et al.*, 2002). Based on a point-in-time estimate, the terrestrial carbon sink of Europe during the 1990s is believed to have amounted to $0.1\text{--}0.2 \text{ Pg C yr}^{-1}$ (Janssens *et al.*, 2003), and forests are considered a major contributor to this sink (Janssens *et al.*, 2004). Vetter *et al.* (2005) attributed the increase in productivity (measured in NEP) of high-elevation temperate conifer forests of Central Europe to the increase in N deposition between 1982 and 2001 and to the increase in CO_2 fertilization for conifer forests at mid- and low elevations.

Synthesis compilations of growth and yield data to identify changes in productivity in the light of recent climate change, such as the ones available for Europe, are scarce for other temperate regions of the world. Holman (2004) deciphered widespread positive growth correlations at large spatial scales in the forests of the Olympic Mountains of Washington, USA, suggesting that they are responding to an overarching climate-growth signal, despite the blurring effect of many growth-limiting factors acting at the local scale. A biomass accumulation analysis of Japan's forest from 1947 to 1995 showed an increase in both aboveground and total biomass ($26.7\text{--}43.2$ and $33.9\text{--}56.6 \text{ Mg C ha}^{-1}$, respectively) (Fang *et al.*, 2005). In a smaller scale study of a deciduous forest in New England, USA,

Goulden *et al.* (1996) attributed the variation to changes in photosynthesis and respiration with shifts in photosynthesis associated with the timing of leaf expansion and senescence, and respiration shifts with anomalies in soil temperature, deep snow in winter, and summer drought. The same mechanisms may be acting at the continental scale expressing themselves in overall trends within the local variation.

Data support forest productivity increases across temperate North America, Northern Europe, most of Central Europe, some parts of Southern Europe, and Japan (Kauppi *et al.*, 1992; Spiecker *et al.*, 1996; Myneni *et al.*, 1997; Fang *et al.*, 2005). This agrees with the initially stated increases in NPP detected from satellite-based analyses, although local conditions cause exceptions.

Tropical forests. Until recently, the prevailing view has been that old-growth tropical forests are likely to have been acting as a substantial carbon sink over the recent decades, increasing their NPP (Phillips *et al.*, 1998; Malhi & Grace, 2000; Prentice *et al.*, 2001; Schimel *et al.*, 2001; Baker *et al.*, 2004). Presently, there is much debate about the productivity of tropical forests, and existing data are insufficient to support any firm conclusion. Change in aboveground biomass is just one component of net forest carbon balance; it is the most commonly measured one due to ease of measurement, and to date, no tropical rain forest seems to have a complete assessment of total carbon stocks and their change through time (Clark, 2004; Houghton, 2005).

Data from a few eddy covariance (tower-based) studies of whole-forest CO₂ exchange have been interpreted as evidence that old-growth tropical rainforests are currently acting as moderate to very strong net carbon sinks (e.g. Malhi & Grace, 2000). Years of anomalously poor tree growth at La Selva rain forest site in Costa Rica were years of peak inferred net emissions from the terrestrial tropics, and both field-based and remotely sensed records were significantly related to annual temperatures and ENSO (Clark, 2004). Stand- and tree-level responses to annual climate variations have been recorded at La Selva (Clark & Clark, 1994; Clark *et al.*, 2003), with the greatest tree growth occurring during the two coolest years and the lowest growth rates during the record-hot ENSO year 1997/1998 with differences of 61–278% between years of greatest and lowest growth rates. Growth rates were intermediate in years of intermediate temperatures (Clark *et al.*, 2003). Baker *et al.* (2004) indicated a net increase of $0.59 \pm 0.31 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ in aboveground biomass in forest plots in western Amazonia and even greater net increases in forest plots

on river floodplains ($1.16 \pm 0.39 \text{ MgC ha}^{-1} \text{ yr}^{-1}$). Comparatively, in central and eastern parts of the Amazon, a small but significant net biomass increase was found ($0.37 \pm 0.34 \text{ MgC ha}^{-1} \text{ yr}^{-1}$) (Baker *et al.*, 2004). Biometrical measurements from an old-growth forest in Parà, Brazil, showed the forest to be either a source or a moderate sink between 1984 and 2000 (Miller *et al.*, 2004).

An analysis of 50 long-term monitoring plots across South America spanning from 1971 to 2002 showed increases in tree and stand BA ($0.1 \pm 0.04 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$) in this time period (Lewis *et al.*, 2004b). In relative terms, the pools of BA and stem density increased by $0.38 \pm 0.15\%$ and $0.18 \pm 0.12\%$ per year, respectively, and stem density (number of stems per hectare) increased significantly over time ($+0.94 \pm 0.63 \text{ stems ha}^{-1} \text{ yr}^{-1}$) (Lewis *et al.*, 2004b). The fluxes in and out of these pools increased by an order of magnitude more, and gains consistently exceeded mortality losses. The authors conclude that this implied a continent-wide increase in resource availability, which is increasing NPP and altering forest dynamics (Lewis *et al.*, 2004b). Field observations of mortality rates during 1982–1985 and 1985–1990 in Barro Colorado Island in Panama showed unexpected results: canopy trees showed the highest mortality of three group types studied during a dry 1982–1985 period, whereas small trees and shrubs showed no difference between the periods (Condit *et al.*, 1995). During drought years, forest-wide mortality rates were 2% more in the larger size class. Tropical forest plot data from both the neotropics and the palaeotropics show large increases in forest-wide tree mortality associated with the very strong ENSO events of 1982/1983 and 1997/1998 (Clark, 2004) and localized species-specific effects (Williamson *et al.*, 2001). Elevated mortality rates, which increased with tree size, were also seen in trees of unburned rainforest in East Kilimantan during the 1982/1983 ENSO, with 37% of trees >60 cm in diameter found dead on ridge tops and 71% on slope plots (Leighton & Wirawan, 1986). Clark (2004) states that tropical forests have already experienced notable shifts in floristic composition and in tree size structure owing to these selective mortality patterns of single strong ENSO. Clark (2004) interpreted the general finding of a sharp increase in tree mortality in the strong ENSO events of recent decades to mean that, around the world tropics, these old-growth forests are already being strongly negatively affected by current levels of temperature and drought stress.

Discussion

According to both field- and satellite-based data found in the literature, the climatic changes in the last 55 years

seem to have a generally positive impact on forest productivity on sites where water is not strongly limiting. The many interacting factors preclude the identification of one factor causing these changes as each site has specific, and possibly unique, combinations of factors; however, the changes in productivity correspond to reported changes in temperature, precipitation, and radiation. Our incomplete understanding of the mechanisms and processes in the forest system itself (Ryan, 1991; Ryan *et al.*, 1996; Thornley & Cannell, 2000; Landsberg, 2003; Mäkelä, 2003; Magnani *et al.*, 2004) is an important obstacle to the interpretation of these measured impacts. In this section, we outline some other considerations in the interpretation of these findings.

Forests within a changing atmosphere

CO₂. The atmospheric system has not only experienced changes in temperature, precipitation, and radiation, but in CO₂ concentration and pollutants between 1950 and 2005 (Keeling *et al.*, 1976; Keeling *et al.*, 1995; Innes & Peterson, 2001). Current global CO₂ is approximately 380 ppm, an increase of about 65 $\mu\text{mol mol}^{-1}$ since the 1950s (Keeling & Whorf, 2005). How forests will respond to rising levels of CO₂ in the long term is still uncertain but the present overall response is positive. A median increase of 23% in NPP has been recorded across sites exposed to elevated CO₂ (550 ppm) in comparison with control sites (370 ppm) since the inception of the FACE experiments (Norby *et al.*, 2005). Assuming a linear interpolation of these FACE site results, the 65 $\mu\text{mol mol}^{-1}$ increase since the 1950s would imply approximately a 4% increase in NPP.

Nowak *et al.* (2004) tested several early hypotheses on the response of ecosystems to elevated CO₂. Among these were the hypotheses that acclimatization of photosynthesis would occur most prevalently where N is limiting, that productivity response would be greater in drier ecosystems and in drier years for more humid ecosystems, that NPP at air CO₂ enrichment (FACE) sites should vary around a mean increase of 20% (at 550 ppm) and that nonwoody functional groups should be more responsive than woody plants. As expected, the leaf CO₂ assimilation and the ecosystem primary production increased across all species. The primary production observations, however, are mixed and are overall less than the hypothesized 20%. Downregulation of photosynthesis occurred in a number of FACE experiments but not in all species and not consistently in species between sites. The hypothesis about differing responses depending on site water levels was not well supported but the

predicted increase in productivity enhancement with N availability was well supported. Nowak *et al.* (2004) found no consistent support for either the resource-based or the plant functional-type response model to CO₂.

Wittig *et al.* (2005) evaluated GPP of fast-growing *Populus* species (3 years from establishment to canopy closure) and found that GPP increased dramatically in the first year but markedly less so in the subsequent years. Similar results that support the accelerated growth of trees over a 30-year period of elevated CO₂ exposure, with most of the accelerated growth occurring at young stages of development, were found by Hättenschwiler & Körner (2003). The findings of Wittig *et al.* (2005) and Hättenschwiler & Körner (2003) suggest differing responses of trees at different development stages and add another obstacle to a blanket statement response of forest productivity to elevated CO₂. Hättenschwiler & Körner (2003) also suggest that trees exposed to higher CO₂ levels seem to be more tolerant to drought stress. Körner (2000) concluded that besides a stimulation of photosynthesis, the most robust finding on plant responses to elevated CO₂ are changes in active tissue quality (wider C/N ratio) and effects on community dynamics. In their 2005 analysis based on FACE data, Körner *et al.* (2005) found an immediate and sustained enhancement of carbon flux in mature temperate forest trees but, contrary to expectations, found no overall stimulation of growth or litter production after four years; hence, forests seem to be 'pumping' carbon through faster with no net gain in biomass (NEP).

More factors may be at play in CO₂ productivity responses. Kozovits *et al.* (2005) found the type of competition (intra vs. interspecific) to change the response of trees to elevated CO₂. Through scenario modelling of CO₂, O₃, temperature, and precipitation, Hanson *et al.* (2005) found a change in response direction of annual NEE between single factor and combined factors modelling and also found differing response when adjustments were made for observed physiological responses to these changes. DeLucia *et al.* (2005) found an increase in NPP and NEP in both loblolly pine and deciduous sweetgum forests, but also found an increase in plant respiration that reduced the NPP (not unlike Körner *et al.*'s (2005) finding of carbon 'pumping') and more so in the pine than in the deciduous forest. DeLucia *et al.* (2005) caution that greater allocation to more labile tissues may cause more rapid cycling of C back to the atmosphere.

The need to elucidate changes in stand-level biogeochemical cycling requires a focus on large-scale long-term experiments such as FACE sites. As the

literature shows, there is no clear answer as to whether rising CO₂ concentrations will cause forests to grow faster and store more carbon (Körner *et al.*, 2005). The response to increasing atmospheric CO₂ confounds our link from changes in temperature, precipitation, and radiation, to forest productivity response.

O₃ and pollutants. The photochemical oxidant O₃ and pollutants such as SO₂, have been shown to damage plants (Kita *et al.*, 2000; Potter *et al.*, 2002; Ashmore, 2005), and the combined effects of pollutants, CO₂ levels, temperatures, and changes in precipitation are not mechanistically well understood (DeLucia *et al.*, 1994; DeLucia *et al.*, 2000; Kirschbaum, 2004; Ashmore, 2005). Global annual background concentration of ground-level O₃ is about 20–25 ppb (McCarthy *et al.*, 2001). Background concentrations in Europe during the 20th century have increased from 10–15 to 30 ppb (McCarthy *et al.*, 2001). In the northern hemisphere as a whole, trends in concentration of O₃ since the 1970 show large regional differences: increases in Europe and Japan, decreases in Canada, and only small changes in the US (McCarthy *et al.*, 2001). Unlike the global and consistent CO₂ increase, the increase in O₃ and other pollutants is highly geographic.

O₃ affects leaf gas exchange (Cojocariu *et al.*, 2005). In localized studies, higher levels of O₃ and other pollutants were associated with insects-related disturbances (Jones *et al.*, 2004). O₃ was also found to interact with frost (Oksanen *et al.*, 2005), increasing the negative effects of frost on pigment loss and stomatal conductance. As indicated in the previous section, integrating O₃ with CO₂, temperature, and precipitation changes within models, resulted in different productivity predictions (Hanson *et al.*, 2005). There is no doubt that the increase in atmospheric O₃ will modify the response of forest to elevated CO₂, temperature, precipitation, and radiation.

N deposition. N deposition in the eastern US can reach 10 kg N ha⁻¹ yr⁻¹ and is estimated to have increased 10–20 times above preindustrial levels. Nine kg N ha⁻¹ yr⁻¹ have been reported in California, 1 kg N ha⁻¹ yr⁻¹ in the inland northwest of North America, whereas Europe can see deposition levels as high as 50 kg N ha⁻¹ yr⁻¹ (Galloway *et al.*, 2004). In the Great Smoky Mountains National Park of the USA, it is estimated that of the 28 kg N ha⁻¹ yr⁻¹ deposited from the atmosphere at high elevations approximately 10–20 kg N ha⁻¹ yr⁻¹ are lost in runoff. In the early 1990s, reactive N creation by anthropogenic activities was around 156 Tg N yr⁻¹ globally (Galloway *et al.*, 2004).

The increase in atmospheric N deposition onto forest soils may be an important contribution to carbon

balance of forests. Atmospheric depositions of N are thought likely to enhance growth for many temperate coniferous forests sites where N is considered to be the most commonly limiting nutrient (Breymer *et al.*, 1997). However, a saturation of N may occur, as per Verburg's (2005) findings, contributing or even accelerating the leaching of other essential nutrients such as calcium, magnesium, and potassium. To date, experiments indicate that an increase in N increases C sequestration (e.g. Adams *et al.*, 2005; Hagedorn *et al.*, 2005) but that the effects of N deposition are modulated by the biochemical characteristics of the dominant litter (Gallo *et al.*, 2005). Not only are atmospheric N deposition levels increasing but temperature increases also affect soil nitrogen content and availability. For certain regions, Körner (2000) speculates that the consequences of climatic changes and soluble N deposition are likely to be greater than CO₂ effects on the carbon balance of vegetation, and his prediction seems to befit the response of northern European forests to higher N deposition found in this review. Nowak *et al.*'s (2004) analysis of FACE site observations showed an increase in productivity with increasingly available N. C/N ratios are important in estimation of carbon in soils and hence changes in C/N ratios as a result of N deposition can greatly affect NE NBP estimates.

The contribution of N, much like O₃, is not completely decipherable from individual effects of temperature, precipitation, radiation, CO₂, or from its own interactions with other pollutants. All these interacting gases from the increase in pollution since the 1950s add to the already self-confounding climatic and photosynthetic role of CO₂, rendering the possible interactions and effects seemingly infinite and indecipherable. Multiple-factor analyses, such as those of Hanson *et al.* (2005) and Verburg (2005), may lead to clearer answers but none of the changes in polluting gas concentrations is occurring independently and experiments isolating the independent effect of one may not give us much insight into the effects of their co-occurrence. In an attempt to incorporate all known mechanistic interactions of CO₂ and stand age into a forest growth model, Kirschbaum (2005) concluded that there are no simple and general valid interactions between rising levels of CO₂ and forest age and cautions that this interaction must be further researched before any conclusions regarding the effects of CO₂ on forests may be made. Not only are the effects of CO₂ on growth and photosynthesis at various stages of tree and stand development not clear, they are not often incorporated in our models and experiments and neither are the known effects of other pollutants. The effects of these and other multiple,

interacting environmental factors must be elucidated through further research and modelling (Norby & Luo, 2004).

Biogeography

Synergistic interactions among factors will occur and so will species adaptation, both changing the NPP and carbon balance of a given site. Plants adapt to changes in environmental conditions. A good example of such an adaptation is found in a review of published studies from the Luquillo Mountains of eastern Puerto Rico. Productivity in that study declined while stem density increased with elevation, as is typical of other montane forests, with the exception of a mid-elevation floodplain palm stand with high levels of productivity (Waide *et al.*, 1998). High productivity in the palm-dominated floodplain forest is apparently explained by specific adaptations of palms to the conditions found in the floodplains (Frangi & Lugo, 1985). Another adaptation became apparent with the comparison of trees of the same species growing in different environments, where trees in warm dry sites had a lower leaf area to sapwood ratio than those in cool moist sites (DeLucia *et al.*, 1994; Mencuccini & Grace, 1994; DeLucia *et al.*, 2000; Maherali & DeLucia, 2000). In this case, changes in leaf to sapwood areas and in hydraulic conductivity seem to act together to maintain a similar water potential gradient (DeLucia *et al.*, 2000). Differing growth responses of species to drought at low- and high-elevation extremes have also been reported (Adams & Kolb, 2004). These few examples of studies of changing traits within a species under varying environmental conditions suggest that trees may be changing with the changing climatic conditions.

Genetic traits may also be changing; however, much of the genetic diversity in forests is within rather than among populations (Hamrick, 2004). Hence, adaptations to climate changes may not be apparent on the landscape by the loss of whole populations but may be occurring in specific traits of individual tree (Hamrick, 2004; Savolainen *et al.*, 2004). Genetic selection of traits happens at a slow pace (Savolainen *et al.*, 2004), and hence, the longevity of trees would not allow us to see changes in physiological or genetic traits over the past 55 years of climate change (Hamrick, 2004). Large changes in species composition that would affect productivity may therefore take a long time to be visible across many of our landscapes (Iverson & Prasad, 2002). Processes other than climate change may be causal to observed changes. For example, changes in lodgepole pine (*Pinus contorta*) distributions were observed by Johnstone & Chapin (2003) in the Yukon Territory of Canada (Johnstone & Chapin, 2003), and these phenom-

ena were attributed to climate change. However, Bergeron *et al.* (2004) caution that the northerly migration of lodgepole pine may not entirely be a climatic phenomenon, but rather a vegetation stabilization process still underway following the Holocene period.

Be it changes or losses in species traits, or species composition changes due to disturbances or other phenomena, changes are reported and affect the interpretation of and contribute to productivity responses to recent climate changes. For now, the time scale and the reversibility of future and present ecological changes as a result of global warming remain unclear (Maslin, 2005).

Measurement limitations

Limits of estimation methods of carbon accumulation and forest stand dynamics also hinder progress in accurately depicting climate effects on forest productivity. Tree bole growth is considered a sensitive indicator of total tree carbon balance because of its low priority for carbon allocation (Ryan *et al.*, 1996) and may be a good driver for productivity estimates, but even above-ground carbon accumulation can vary drastically over the development of a stand with accumulation rates increasing exponentially as trees increase in size and additional trees establish, and it can also be highly variable (Hicke *et al.*, 2004; Lagergren *et al.*, personal communication). In an attempt to estimate the carbon budget of Scots Pine forest in the Netherlands, Schelhaas *et al.* (2004) assessed the NEE of Scots pine using two different methods and found important discrepancies between the estimates. Using forest inventories, the carbon sinks of these forests were estimated at $202 \text{ g C}^{-1} \text{ m}^2 \text{ yr}^{-1}$ with a confidence interval of $138\text{--}271 \text{ g C}^{-1} \text{ m}^2 \text{ yr}^{-1}$, compared with $295 \text{ g C}^{-1} \text{ m}^2 \text{ yr}^{-1}$ using the eddy covariance method, with confidence intervals of $224\text{--}366 \text{ g C}^{-1} \text{ m}^2 \text{ yr}^{-1}$. This last study discredits measurement techniques that seem to lead to imprecise yield estimates or biased measurements. However, Krankina *et al.* (2004) showed a high degree of accordance between field and satellite estimates of both total live forest biomass and mean C sink (272 and 269 Tg C , and 0.36 and $0.34 \text{ Mg C}^{-1} \text{ ha}^{-1} \text{ yr}^{-1}$, respectively) for a site near St-Petersbourg in Russia. Schelhaas *et al.*'s (2004) findings may leave the actual amounts of increased productivity on uncertain footing, but the overall changes for temperate forests are still positive. Schmitz *et al.* (2003) further caution the use of either of the prominent methods to assess climate change effects, the first being empirical synthesis and modelling of species range shifts and life-cycle processes that coincide, and the second experiments examining plant–soil interactions under simulated climate

warming. Although both approaches indisputably point to changes occurring in our ecosystems due to changing climatic conditions, Schmitz *et al.* (2003) maintain that both approaches often provide conservative estimates of the effects of climate change on ecosystems. Schmitz *et al.* (2003) underline the lack of understanding of the interplay and feedback among higher trophic levels in ecosystems (top-down processes) and speculate that these may have a larger than presently estimated effect on plant species composition and ecosystem services such as productivity.

An important distinction must be made between measures of productivity such as NPP, NEP, NBP, and NEE. NPP implies an overall increase in production, a faster turnover rate, NEP, and NBP are net gains in biomass at different spatial scales, whereas NEE is a net CO₂ flux. As per the findings of Körner *et al.* (2005), in their analysis of four years of data at a FACE site, an increased NPP, where the added carbon was uptaken by trees at a higher rate, does not necessarily result in a net gain in biomass. Published findings sometimes support an increase in NPP and NEP in various stages of development under our changing climate conditions and sometimes do not (Law *et al.*, 2001). It seems that an analysis of the same data at different scales may show an increase in NPP at one scale, a decrease in NEP (adding heterotrophic respiration) at another, and overall NBP estimate varying with seemingly random disturbance patterns. The differences between full forest sector inventory-based methods that measure NBP, and flux-tower measurements (Van Tuyl *et al.*, 2005) suggest that the eddy-flux network overestimates long-term sinks because they do not take into account harvesting, and hence, assess NEP as opposed to NBP (Nabuurs *et al.*, 2003). Uncertainties in eddy-flux tower data (which are prominent in the tropics; Clark *et al.*, 2003), however, have been shown to be small (<3% annually) but sensitive to how low-frequency and non-horizontal flows are treated in their estimation. As per Cahill *et al.*'s (personal communication) conclusion after attempting to estimate carbon fluxes in temperate grasslands, it is extremely difficult to close the carbon balance in forests. Linking plot-level measurements of NPP to large-scale NBP estimates requires an estimate of disturbance rates, and a precise estimate of disturbance is not easy or simple to obtain. The magnitude and sign of NEP estimates are presently affected by uncertainties in estimating aboveground NPP as a whole and at different stages of stand development, below-ground NPP and autotrophic and heterotrophic respiration estimates. Hence, the question of how much carbon gets taken up and stored in forests remains.

Land-use estimates are also an unknown factor, especially at global scales. Although we mostly address

changes in growth rate as opposed to total growth of forest, the precise estimation of the forested status of a piece of land is important for evaluating a change in productivity through time as estimates are often calculated as means over a large area. This problem applies particularly to satellite-based estimates of production, where land classification further confounds the mechanistic and spatial uncertainties of NPP estimates (Greer *et al.*, 1998; Houghton *et al.*, 1999; FAO, 2000; Innes & Peterson, 2001; Pacala *et al.*, 2001; Lepers *et al.*, 2005).

Determination of current climatic responses of forests around the world will require careful annual monitoring of ecosystem performance in representative forests. A lack of reliable data for below-ground NPP and an incomplete understanding of mechanistic processes in forests, and between forest and the atmosphere, are major contributors to our inability to build reliable evidence or to agree on the evidence we do have on the impacts of climate change on forests. A main problem with experiments is that isolating one or a few factors and finding the effects of these throughout a predefined range of variability does not provide any insight into how the systems as a whole will behave with changing climatic conditions. The use of simulation models is essential for both research and management as some societal change or preventative management may help us avoid drastic changes in world climate. In the last half-century of climate change, methodological capacities in physiological research have grown tremendously and so has our understanding of physiological processes. Monitoring of physiological processes under climate change has only become a noteworthy issue in the latter portion of the 20th century and the growing focus on the effects of climate change combined with these advances will hopefully contribute to rapidly advancing our knowledge of our forest systems.

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