2 Forest Responses and Vulnerabilities to Recent Climate Change

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Abstract: Climate is a critical factor affecting forest ecosystems and their capacity to produce goods and services. This chapter reviews published studies of climate-forest relationships with emphasis on indications and mechanisms of change during recent decades. Effects of climate change on forests depend on ecosystem-specific factors including human activities, natural processes, and several dimensions of climate (temperature, drought, wind, etc.). Indications of recent climate-related changes in ecosystem processes are stronger in boreal forests than in other domains. In contrast, constraints on adaptive capacity that increase vulnerability to climate change are generally more severe in subtropical and tropical forests than in temperate and boreal domains. Available information is not sufficient to support a quantitative assessment of the ecological, social and economic consequences of recent forest responses to human influences on climate. The complexity of natural and human systems is a formidable barrier to impact quantification and predictability. For example, effects of land use practices and invasive species can overshadow and interact with effects of climate change. Nevertheless, substantial progress has been made in defining mechanisms of climate-change impacts on forest ecosystems. Knowledge of impact mechanisms enables identification and mitigation of some of the conditions that increase vulnerability to climate change in the forest sector.

Keywords: forests, climate, impacts, vulnerability, disturbance, complexity, adaptation, sustainable forest management, UNFCC, IPCC

2.1 Introduction

Many published reports have presented evidence that climate changes over the past half century have affected many aspects of forest ecosystems, including tree growth and dieback, invasive species problems, species distributions and migrations, seasonal patterns in ecosystem processes, demographics and even extinctions (IPCC 2007a). Effects of recent climate change appear to be greater in boreal forests than in other domains. In contrast, several factors that increase vulnerability to climate change appear to be more prevalent in subtropical and tropical domains than in boreal and temperate domains (Table 2.1).

Available information is not sufficient to support a quantitative assessment of the ecological, social and economic consequences of recent forest responses to human influences on climate (Backlund et al. 2008). Barriers to quantifying the impacts of anthropogenic climate change include: (a) lack of information about the nature, extent and causes of forest ecosystem change in most countries (FAO 2007); (b) uncertainty about the relative contributions of climate change and other factors to observed changes in forests (Sparks and Tryjanowski 2005); and (c) uncertainty about the relative contributions of natural and human factors to climate change and extreme weather events at the regional and sub-regional level at which ecosystem changes are usually measured (Solomon et al. 2007).

Table 2.1 Assessment of recent climate impacts and current vulnerabilities (IPCC 2007a).

Factors	Assessment
Exposure to recent climate warming	Generally higher in boreal forests
Plausible hypotheses about impact mechanisms	Plausible hypotheses have been described for all forest domains
Empirical evidence of ecosystem change consistent with impact hypotheses	Evidence stronger for boreal and temperate domains than other domains. However, this may be due in part to greater investments in research in boreal and temperate domains
Deforestation (increases vulnerability by reducing forest resilience and capacity for adaptation)	Deforestation rates generally higher in subtropical and tropical domains
Endemic forest types may have relatively high vulnerability to climate change because their limited extent may reduce resilience	Endemic forest types are more common in non-glaciated zones, including tropical and subtropical domains and warmer parts of the temperate domain
Adaptive capacity	Human dimensions of adaptive capacity in the forest sector are generally high in boreal and temperate domains; they are more variable in subtropical and tropical domains due to constraints on access to capital, information and technology

2.2 Natural History of Forest Response to Climate Change

The extent of world forests has undergone dramatic changes in response to past climate changes (Ritchie 1987). During the last ice age, which ended around 15 000 to 11 000 years ago (ice lasted longer in some areas), the world was much drier. Tropical forests were drier and fragmented. Low carbon dioxide (CO_2) levels increased physiological dryness and converted some forests to woodland (Loehle 2007). Large portions of regions now occupied by boreal forests were either under ice or occupied by tundra or cold grassland (Ritchie 1987). As the ice melted and the climate became wetter, forest expanded rapidly at all latitudes where temperatures were sufficient for tree growth.

Although rapid on a geologic timescale, the pace of forest advance in response to glacial retreat was limited by rates of seed dispersal and tree growth. In contrast, worsening conditions for tree growth and survival can cause relatively rapid retreat of the forest boundary (e.g. Tinner et al. 2008). There is, therefore, an expected hysteresis effect at forest ecotones: slow expansion of tree species boundaries as climate conditions become more favourable, and more rapid retreat in response to lethal episodes of climate-mediated stress (e.g. frost, drought) (Noble 1993).

During the current interglacial period, natural climate changes at various scales have had substantial effects on ecosystems. For example, Kröpelin et al. (2008) provide an example of a dramatic change from dry savanna to Saharan desert in response to long-term climate change over the past 6000 years, and Kobori and Glantz (1998) discuss the role that climate change has played in increasing the aridity of the Aral Sea area of central Asia. In both cases, long-term 'creeping' declines in precipitation have resulted in desertification over vast areas. Effects of climate change can be exacerbated by human activities, as in the Aral Sea basin where water use for irrigation has contributed to shrinkage of the Sea and desertification of the landscape (Kobori and Glantz 1998).

Where long-term climate changes are less extreme, the long lifespan and broad ecological tolerance of many trees means that internal forest ecotones (those between forest types rather than between forest and non-forest) are likely to respond slowly to changing climate (e.g. Loehle and LeBlanc 1996, Loehle 2003, Morris et al. 2008). For example, Eastern hemlock, a tree with poor dispersal, has been documented as still spreading north west of North America's Great Lakes in a lagged response to the end of the most recent ice age (Parshall 2002). Disequilibrium with climate has similarly been observed in forests of central Europe (Tinner and Lotter 2001).

Photo 2.1 Conversion of forests to agriculture has been and continues to be a major cause of forest loss. For example, large areas of tropical rainforest in northern Queensland, Australia, have been converted to sugar cane (shown here).

2.3 Factors Other than Climate Affecting Forests and People

2.3.1 Introduction

Parry et al. (2007, p. 31) suggest, 'In comparison with other factors, recent warming has been of limited consequence in the agriculture and forestry sectors.' In the forest sector, important factors affecting ecosystems and people include land use and land-use change, invasive species and rapid expansion of global trade.

2.3.2 Land Use

Over the past several thousand years, land clearing for agriculture and other purposes has been a dominant force affecting the extent and condition of the world's forests. According to Bryant et al. (1997, p. 2), 'Almost half of Earth's original forest cover is gone, much of it destroyed within the past three decades.'

FAO (2007) provides estimates of recent trends in forest extent and makes the following observation about progress in slowing deforestation. 'The analysis reveals that some countries and some regions are making more progress than others. Most countries in Europe and North America have succeeded in reversing centuries of deforestation and are now showing a net increase in forest area. Most developing countries, especially those in tropical areas, continue to experience high rates of deforestation and forest degradation. The countries that face the most serious challenges in achieving sustainable forest management are, by and large, the countries with the highest rates of poverty and civil conflict.' (FAO 2007, p. v).

In some forested regions, it is possible to document changes in forest type and structure over time that are consistent with histories of human use that include major disturbances such as forest clearing, cultivation and farm abandonment leading to afforestation (e.g. Zhang et al. 2000). Urban sprawl is a relatively recent phenomenon that has created vast exurban areas in which forest ecosystems are altered in various ways (Radeloff et al. 2005). While such areas may remain forested to some extent, the land is often no longer available for traditional uses (e.g. wood production, hunting) and has characteristics such as high densities of paved roads and domestic animals that can be detrimental to many species. It can be difficult to find a 'climate impact signal' in the noise of land use history.

2.3.3 Invasive Species

In forests throughout the world, invasive species are exerting dramatic effects on all facets of ecosystem structure and function (Wilcove et al. 1998, Levine et al. 2003, Moore 2005, Asner et al. 2008). For example, invasive diseases and pests such as Chestnut blight (*Cryophonectria parasitica*) and Dutch elm disease (*Ophiostoma ulmi*) have caused major changes in the composition of forests in eastern North America over the past century (Tomback et al. 1995, Williams and Liebhold 1995, McNeely et al. 2001, Anderson et al. 2004, Logan et al. 2007, Anulewicz et al. 2008, Wingfield et al. 2008). Noteworthy invasive species affecting forests outside North America include the pine wood nematode (*Bursaphelenchus xylophilis*) in Asia and now Europe (Dwinell 1997, Naves et al. 2007) and sirex woodwasps (*Sirex noctilio* F.) in the southern hemisphere (Hurley et al. 2007).

The mechanisms for forest change in response to biological invasion vary with the system and the invasive species, but generally relate to competition with endemic species, lack of natural enemies, use of vacant niches, loss of fundamental processes such as mutualism, hybridization with genetically similar species, alteration of the physical and chemical characteristics of soils, modification of habitats, and vectors for pests and diseases (Christian 2001, McNeely et al. 2001). At the species level, direct effects of alien invasive species occur through processes such as predation, competition, and transmission of pathogens and parasites to individual organisms, eventually leading to population declines and species extinctions (CBD 2003, Loehle 2003, Chornesky et al. 2005).

The impacts of alien invasive plant species at the ecosystem level include changes to trophic structures, changes in the availability of resources such as water and nutrients, and changes in disturbance regimes (McNeely et al. 2001, CBD 2003). Systems that are rich in species are often, but not always, high in exotic species as well, possibly owing to high productivity of the system (Levine et al. 2002). In temperate forests in New Zealand, however, Ohlemuller et al. (2006) found no relationship between alien species richness and endemic species richness, suggesting that at least in those systems, climate and land use were the most important factors in invasive species success.

There are many incidences of invasive species in disturbed tropical and sub tropical systems (e.g. Richardson 1998, Moore 2005). There is evidence that natural tropical non-montane forests are less prone to invasion by alien species than disturbed forests, possibly owing to lack of available niches (Connell and Slatyer 1977).

Closed forests in general may be more resistant to invasion than forests with many canopy gaps created by disturbances (Richardson et al. 1994, Webb et al. 2000). Loehle (2003) modelled tree invasion and suggested that the more disturbance there is, the higher the probability that alien trees could invade a forest system. However, some invasions of alien species into closed forests have occurred; notably Chinese tallow (*Sapium sebiferum*) in the south-eastern USA (USDA 2000, Conway et al. 2002).

Variation in presence and abundance of invasive species in forests is not fully explained by measures of disturbance and native species diversity. This suggests that invasion depends not only on forest characteristics but also on the ecology of the invading species, including habitat preferences, food requirements, climate tolerance and presence of enemies (Mack et al. 2000, Ward and Masters 2007).

The spread of invasive species is facilitated by expansion of global trade, road networks and human presence in forests (Coffin 2007, Ding et al. 2008). Introduction of non-native trees for plantations (FAO 2007) has been an important source of invasive species in some countries (Richardson 1998, van Wilgen et al. 2001, de Wit et al. 2001, CBD 2003, Richardson and Rejmánek 2004, Moore 2005).

Alien invasive species are causing major impacts on biodiversity (Wilcove et al. 1998, Sala et al. 2000), ecosystem processes (Levine et al. 2003) and the production of ecosystem goods and services (FAO 2001, Moore 2005). Through direct impacts on species or indirectly through alterations of habitats, invasive species are responsible for placing many species at risk of extinction (Baillie et al. 2004). Loss of species as a result of alien invasive species ranks behind only habitat loss among threats to biodiversity (McNeely et al. 2001, Perrings et al. 2002, Richardson and Rejmánek 2004).

2.3.4 Global Trade in Wood Products

Production of industrial wood has risen around 1.1% per year globally since 1961, although the annual rate of growth has clearly not been constant (Figure 2.1). Output has grown the most in Latin America, southern Africa and Oceania. Growth in these regions is largely attributed to investments in new timber plantations and associated manufacturing facilities. Many of these plantations have been established with non-indigenous species, which have been found to achieve substantially higher growth rates compared to local indigenous species. Daigneault et al. (2008) estimated that non-indigenous forest plantations contribute around 13% of current global timber supply.

Rapid expansion of global trade in forest products has enhanced the economic efficiency of plantation

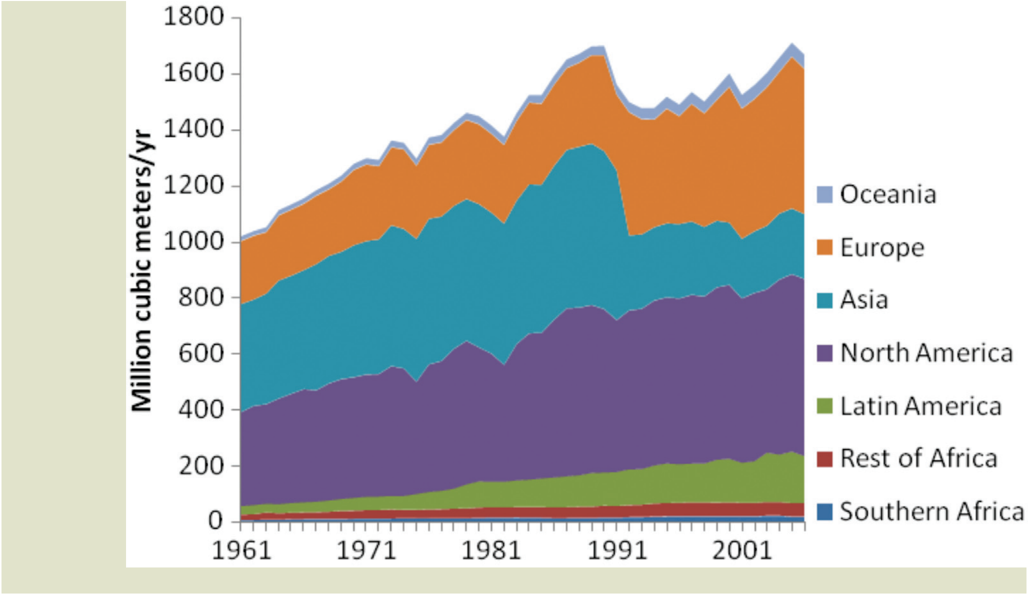

Figure 2.1 Historical wood harvest patterns by region (FAOSTAT 2008).

establishment. Between 1970 and 2001, the value of trade in forest products increased 7.5% per year (Laaksonen-Craig 2004). With increasing trade, some countries were better able to take advantage of local growing conditions and specialize in the production of fast-growing species. As a result, foreign direct investment in timber plantations and milling capacity has increased dramatically. In 1980, foreign direct investment in the forestry sectors of the USA, Canada, Brazil and Chile amounted to only about USD 2.5 billion, but by 2001, it was closer to USD 30 billion (Laaksonen-Craig 2004), implying an increase of nearly 12% per year.

Global trends towards freer capital markets, and continuing efforts to make trade freer (GATT, WTO, European Union, NAFTA, etc.) have contributed to the internationalization of the forest products industry over the past 30 years. These trends have both beneficial and adverse effects on forest ecosystem resilience and the adaptive capacity of forest managers.

2.4 Conceptual Model of Forest Ecosystem Response and Vulnerability to Recent Climate Change

Understanding recent changes in climate and forest ecosystems is a complicated task. Many drivers and dimensions of environmental change have been operating simultaneously, including atmospheric CO_2 concentrations, nitrogen deposition rates (Högberg 2007), and tropospheric ozone concentrations (Karnosky et al. 2005) as well as land use practices, invasive species and global trade. These factors have caused considerable and measurable environmental change during the industrial period (Caspersen et al. 2000, Albani et al. 2006, Hyvönen et al. 2006). Further complicating the matter are the facts that: (1) these interacting, co-occurring factors can have positive, negative or synergistic consequences for forest ecosystems; and (2) these key environmental drivers may also interact with a number of natural disturbance agents that shape forest ecosystems such as insect or disease outbreaks, or with extreme weather events and fire (Kurz et al. 2008b).

Complexity notwithstanding, substantial progress has been made in defining mechanisms of climate change impacts on forest ecosystems (Fischlin et al. 2007). In general, impacts depend on ecosystem-specific factors and their interactions. Conceptually, changes in one or more dimensions of climate (e.g. temperature and precipitation regimes) affect ecosystem processes (e.g. photosynthesis, disturbance, etc.). Alteration of ecosystem processes can lead to impacts on biodiversity and ecosystem services.

Vulnerability to climate change impacts in the forest sector depends not only on exposure to climate change and other ecosystem-specific factors but also on adaptive capacity. Easterling et al. (2007, p. 279) wrote that, 'Adaptive capacity with respect to current climate is dynamic, and influenced by changes in wealth, human capital, information and technology, material resources and infrastructure, and institutions and entitlements.'

There is substantial variation within forest domains in most factors that influence climate impacts

Photo 2.2 Forest ecosystem resilience is the basis for SFM, which requires an understanding of the roles of natural disturbances and long-term processes within systems. The dynamic stability over time and space allows the use of ecosystems within limits without impairment of goods and services.

and vulnerabilities (IPCC 2007a). In the boreal domain, for example, recent climate warming is spatially variable, and human adaptive capacity, while generally high, is presumably low in remote, undeveloped areas. Forests in coastal, montane and arid regions appear to have relatively high vulnerability in all domains. The vulnerability of coastal forests is related not only to sea level rise but also to exposure to strong storms and effects of human population pressures. Montane forest types occupy relatively small, disjunct areas, are subject to disturbance by human influences associated with recreation and tourism, and may have limited potential to migrate in response to climate change. Forests in arid zones occupy niches that are almost too dry to support forests and may be vulnerable to changes in the severity or frequency of droughts.

2.5 Ecosystem Resistance and Resilience to Climate Change

Biological systems maintain a certain level of resistance to environmental change. This resistance is conferred at several levels, including through genetic diversity, species redundancy, species and ecosystem adaptability, and landscape distribution. For example, Amazon forests appear to be more resistant to recent drying events than climate models would predict (Saleska et al. 2007, Malhi et al. 2008), possibly as a result of the negative effects of drying being offset by greater production owing to higher levels of CO_2 (Malhi et al. 2008). Similarly, Newberry et al. (1999) suggested that the beneficial effects of understory plants on soil moisture regimes contribute to ecosystem resistance to drought in tropical forests of Malaysia.

However, climate changes may be of sufficient magnitude to overcome resistance and force forest systems into new states or even biomes (e.g. forest to grassland). Such impacts are likely to be exacerbated and less predictable across large landscapes that lack connectivity owing to habitat loss, forest fragmentation and the inability of species to migrate. This is especially the case in tropical, subtropical and temperate forest regions where human development is most common. Therefore climate change and land-use change are closely linked, as are the consequences for biological diversity and reassembly of biological communities under climate change (e.g. Hansen et al. 2001, Noss 2001, IPCC 2002, Brncic et al. 2007).

If perturbed, forest ecosystems often recover most, if not all, of their original properties unless environmental conditions have been changed markedly. Evidence for this resilience is abundant, with forest recovery following harvesting, fire or blowdown to the same or similar states. Indeed, such resilience is the basis for sustainable forest management, which requires an understanding of the roles of natural disturbances and long-term processes within systems. This dynamic stability in time and space, even if species assemblages change, is an important component of forested systems, and for human societies, because it allows use of the systems within limits without impairment of goods and services. However, as noted above, too great a change will disable the capacity for resilience and move the forest to another state, either a different forest ecosystem, or another state entirely such as grassland or even desert.

Biodiversity is important for long-term ecosystem persistence (Drever et al. 2006) and resilient ecosystems are characterized by functional diversity at multiple scales (Peterson et al. 1998). Changes in biodiversity can occur slowly or very rapidly in response to different environmental perturbations. In managed forests, insufficient attention to biodiversity can result in loss in resilience (Levin 2000, Drever et al. 2006) and thus increase vulnerability to climate change impacts.

A predicted component of climate change is unpredictability and an increase in severe events; hence the additional stress on systems may result in unexpected change. The capacity of a system to adapt to change may depend on the past history of environmental conditions, and complex systems and forests may often cycle among several stable states (Gunderson and Holling 2002).

Fjeldsa and Lovett (1997) suggested that biological communities adapted to stability are most at risk to increasing environmental change, and noted that many areas of the tropics may thus be threatened by climate change. This hypothesis has implications for long-term planning for adaptation to climate change, such as location of protected areas, and more generally the use of goods and services under a changing climate regime in the tropics.

Tropical stability can be contrasted with boreal forest short-term instability owing to frequent perturbations by fires, wind and insects. Within bounds, these forests have been, at larger scales of time and space, highly resilient to change. Nevertheless, many authors have cautioned about the cumulative effects of multiple stressors and the possibility of major change in managed boreal systems compounded by climate effects (Gunderson and Holling 2002, Drever et al. 2006, Chapin et al. 2007).

2.6 Effects of Climate on Forest Productivity and Phenology

Many studies of forest ecosystems have correlated recent climate trends with changes in phenology (the timing of seasonal activities of animals and plants) and forest productivity (Rosenzweig et al. 2007). It appears that climate warming has lengthened the growing season and increased tree growth rates in many boreal and temperate forests. However, results of several studies suggest that warming has contributed to reductions in productivity in some forests through interactions with drought, fire and biotic disturbance (see sub-chapter 2.8).

Relationships between climate changes and forest productivity are often complicated by simultaneous changes in other factors that affect productivity, including nitrogen deposition and atmospheric CO_2 concentration (Boisvenue and Running 2006). For example, a simulation study by Beerling and Mayle (2006) attributed recent observed biomass increases on Amazon rainforest plots to anthropogenic increase in CO_2.

Changes in phenology can affect ecological relationships, e.g. by creating a mismatch between plant flowering time and presence of insect pollinators (Humphries at el. 2002, Post and Forschhammer 2007, Rosenzweig et al. 2007). Interpreting the ecological consequences of phenology changes can be challenging, as illustrated by a study that documented variation in flowering responses to warming among related cherry species and their hybrids (*Cerasus* sp. or *Prunus* sp) growing at Mt Takao in Tokyo, Japan (Miller-Rushing et al. 2007).

2.7 Effects of Climate on Biodiversity

2.7.1 Displacement of Species and Communities

Distributional changes of species toward higher latitudes and elevations have been well documented and correlated with climate warming (Rosenzweig et al. 2007). In meta-analyses, Parmesan and Yohe

(2003) and Root et al. (2003) found that over 80% of species from many studies behaved as predicted (increased, declined or moved) with climate change, across multiple systems and regions.

There is no reason to expect that climate change would displace entire ecosystems to new locations with favourable climates (Hansen et al. 2001), except possibly for the northern taiga (Chapin et al. 2004). Formation of new species assemblages is more likely (e.g. Davis and Shaw 2001, Hannah et al. 2002, Davis et al. 2005), especially where thresholds are surpassed (Chapin et al. 2004). Any reorganization of species involving the addition of key competitors, the loss of key predators or of key functional species can have large consequences for plant community assembly, and hence for the goods and services that the system is capable of delivering in the future (e.g. Schmitz et al. 2003). Interactions of climate change and higher CO_2 levels may alter species assemblages and ecosystem processes with complex and non-linear effects on forest composition (IPCC 2002, Chapin et al. 2004, Fischlin et al. 2007).

If we ask whether forests have responded to recent climate warming, it is logical to look for evidence of forest expansion where low temperatures may be limiting factors, i.e. at mountain tree lines (e.g. Holzinger et al. 2008) and at the boreal tree line (e.g. Masek 2001). Movement of mountain tree lines can be influenced by changes in firewood cutting and grazing practices (e.g. Gehrig-Fasel et al. 2007), thus complicating interpretations of climate warming effects. Filliol and Royer (2003) suggested that the taiga has been advancing into the tundra zone at a rate of 12 km/year for the past decade, but some other studies have reported much smaller rates of tree-line advance (Suarez et al. 1999, Gamache and Payette 2004, Payette 2007). The presence of krummholz (Gamache and Payette 2004) can seem to amplify the rate of forest spread in response to climate warming. Trees do not actually disappear at a sharp demarcation at tree line, but gradually become reduced in stature and more scattered. At a certain point, trees (spruce particularly) adopt a krummholz form. These trees are shrubby and only reach a height where they are protected from winter desiccation by snow cover. When the climate warms, these trees can suddenly adopt an upright growth form and small scattered trees can grow larger, giving the appearance of a rapid ecotone movement.

Non-linear relationships between climate change and ecosystem processes can produce unexpected effects on forest species composition that ultimately have implications for forest goods and services (e.g. Chapin et al. 1997). Such changes appear to be already underway in boreal forests in North America and Europe. For example in eastern North America, white-tailed deer (*Odocoileus virginianus*) are distributed about 150–200 km north of where they were found in 1970 (Thompson 2000), and moose (*Alces alces*) have moved into coastal temperate forests in western North America (Darimot et al. 2005) owing to milder winters with less deep snow. Both ungulate species are capable of altering forest species composition and growth rates of trees, depending on their densities (Thompson and Curran 1993, Niemela et al. 2001, Tripler et al. 2005). Similarly, progression of mountain pine beetles into boreal forests with a warmer climate, from their montane forest habitat, is expected to alter the relative densities of pines and spruces (Logan and Powell in press). These effects may be unexpected and yet have large consequences for forest ecosystem structure over time.

2.7.2 Risk of Extinctions with Climate Change

Biodiversity on Earth has changed during many time periods owing to altered environmental conditions (e.g. Webb 1992). For example, large numbers of species went extinct during the global warming event at the end of the Pleistocene period. Many of these extinctions were directly attributable to the change in climate (Barnosky et al. 2004, Gutherie 2006). Even in tropical zones, there were changes in communities as a result of extinctions in montane areas (Rull and Vegas-Vilarrubia 2006).

Risk of extinction is generally related to a species' extent of distribution, habitat specificity, capacities to adapt to change and disperse, metapopulation dynamics, reproductive capacity, population size and multiple human-related factors (Thompson and Angelstam 1999). Climate changes can increase extinction risk by interacting with other risk factors.

Species with small distributions and high potential for range displacement are at a very high risk of extinction as a result of climate change (Midgely et al. 2002, Schwartz et al. 2006). Narrowly distributed species that are highly limited by climatic conditions and elevation have high potential for range displacement. Extinction risk for such species is greatest if predicted future ranges are disjunct from current ranges or absent altogether, such as in the case of Australian tropical forests (e.g. Williams et al. 2003). Narrowly endemic species that are limited by non-climatic factors (e.g. soil conditions) may also be at risk of extinction under climate change. For example, interactive effects of habitat loss and drought frequency could increase extinction risk for such species. It should be noted, however, that estimates of species losses from climate change depend on a number of assumptions, and that resilience of species may be greater than assumed (Botkin et al. 2007).

Malcolm et al. (2006) suggested that hotspots were at high risk for large extinction events owing to climate change, with up to 43% of species in some cases predicted to be lost, representing 56 000 endemic plants and 3 700 endemic vertebrates. They noted that estimates of habitat loss might be reduced depending on migratory capacity, although most species would not find surrogate habitats. In terms of broad range change, other studies suggested that higher latitudes of temperate and boreal forests will be most affected (Thuiller et al. 2005, Virkkala et al. 2008) with consequent effects of habitat loss of 60% or more for many species. Thomas et al. (2004) estimated that extinctions from climate change in forested systems will range from less than 1% in northern areas to over 24% in some temperate forest zones.

Amphibians generally seem to be at high risk and provide examples of extinctions that have been linked to climate change. For example, Pounds et al. (1999, 2006) concluded that climate change and a fungal pathogen were important causes of recent extinctions of the golden toad (*Bufo periglenes*) and harlequin frog (*Atelopus varius*) in Costa Rican cloud forests. Pounds et al. (1999) suggested that climate change contributed to extinction of these species by reducing the number of days when clouds are in the forest. Other authors, however, suggest that the links between amphibian extinction and climate change are too tenuous to state conclusively (Lips et al. 2008).

Rare montane habitats without possibility of replacement at higher altitudes have seen extinctions in the past and are predicted to be at high risk in future (Rull and Vegas-Vilarrubia 2006). Finally, if the tropical areas are a cradle for evolution, owing in part to their past stability, and climate change causes species losses in these areas, especially in hotspots, then climate change has negative implications for future biodiversity at all latitudes (Jablonski et al. 2006).

There is a high degree of uncertainty surrounding consequences for forest goods and services from loss of species in forest systems. It is often not clear how species will move into vacated niches and reassemble into communities over time (e.g. Chapin et al. 2004), especially if alien species are advantaged. Further uncertainty stems from redundancy of functional roles among species, an unclear relationship between productivity and diversity, and also from the possibility of altered impacts of herbivores on plant species composition that can have unexpected effects on various goods and services, such as productivity (Chapin et al. 1997, Schmitz et al. 2003).

2.8 Effects of Climate on Disturbance in Forest Ecosystems

2.8.1 Introduction

All forests are shaped by disturbance regimes driven by climate variability in temperature, wind and moisture, which in turn affects fire, herbivory and other ecosystem processes. Forest structures, landscapes and functions at any point in time are dynamic disequilibria between maturation processes (e.g. tree growth) and disturbances at various spatial and temporal scales (e.g. Suffling 1995, Drever et al. 2006). Disturbances affect the size and age structure of trees and stands, species composition, ecosystem function and the socioeconomic value of forests. Fire, insects, pathogenes and invasive species are discussed below. In addition short term events such as storms and floods as well as large-scale circulation changes such as El Nino Southern Oscillation have effects on forest production (IPCC 2007a).

2.8.2 Fire

Climate-change influences on wildfire extent, severity and frequency depend on interactions among several factors including forest management history, drought frequency and severity, insect outbreaks and many others. There is evidence of both increase and decrease in fire activity at regional scales (Easterling et al. 2007). Forest thinning, controlled burning and other measures to reduce fuel loads and other aspects of wildfire hazard can be effective in reducing forest vulnerability to fire-mediated effects of climate change.

Effects of natural climate variation must be considered when interpreting observed changes in forest-fire regimes (Millar and Brubaker 2006). For example, a climate cycle known as the Pacific Decadal Oscillation can bring several decades of above or below average precipitation in south-western North America. During wetter periods, forest cover can expand and thicken, increasing fuel loads. Drought can then kill trees directly but can also create fires that clear large areas of trees.

Past human uses of fire should also be considered (Kay 2007). For example, intentional and accidental fires caused by humans have pushed back forest in forest-grassland ecotone regions and created parkland or savanna in others (e.g. McEwan and McCarthy 2008, Scheller et al. 2008). Conversely, human activities that exclude or suppress fire can allow encroachment of fire-intolerant species into previously fire-adapted ecosystems with adverse effects on biodiversity and risk of stand-replacing wildfires (Covington and Moore 1992).

2.8.3 Insects and Pathogens

Insects and pathogens (inclusive of native and exotic species) have major roles in forest disturbance regimes (Ayres and Lombardero 2000, Pimentel et al. 2000, Dale et al. 2001, Environment Canada 2004). Disturbance may take the form of tree mortality over large areas or scattered mortality that creates many small gaps in a forest.

Forest resistance to disturbance by insects and pathogens depends on many factors including tree species, stand ages and vigour, and climate. In some cases, investments in planted forests are impaired by damage from pests that are not significant problems in natural forests (Mack et al. 2000, Cock 2003, Wainhouse 2005). Reductions in tree diversity and high local densities of host trees seem generally to promote outbreaks of plant pests and pathogens (Jactel et al. 2005, Moreau et al. 2006). However, opportunities for early detection and effective management of pestilence are often greater in plantations. Where plantations are established using non-indigenous tree species, losses to pestilence can be low if the trees' native pests and pathogens are absent. This advantage can be reversed when invasions by native enemies occurs, and then the pestilence can be severe because pests and pathogens frequently have no enemies of their own in the new environment (Elton 2000, Lombardero et al. 2008).

Changes in climate can influence forest pestilence via relatively direct physiological effects on herbivores and pathogens, via effects on tree defences against herbivores and pathogens, and/or via effects on predators, competitors and mutualists of herbivores and pathogens. Forest pestilence can also produce feedback to the atmosphere by influencing fluxes of CO_2 (Kurz et al. 2008a) and probably water.

An emerging generalization is that inducible defences of plants tend to be positively correlated with environmental conditions that favour plant growth (e.g. increased precipitation leads to increased plant growth and increased efficacy of inducible plant defences), while constitutive defences tend to become less when water and/or nutrient availability increases (Lombardero et al. 2000a, Hale et al. 2005). This dichotomy may explain the frequent but variable effects of plant 'stress' on herbivore populations (Koricheva et al. 1998).

Interactions between forest pestilence and fire can be a primary determinant of ecosystem structure and function (Baker and Veblen 1990, van Mantgem et al. 2004, Parker et al. 2006). In some cases, the interactions produce a destabilizing positive feedback system. For example, fires can promote outbreaks of pests and pathogens (Thomas and Agee 1986, McCullough et al. 1998), and pests and pathogens can increase the probability of fires (Wood 1982, Raffa and Berryman 1987). In other situations, fires can reduce pest outbreaks (Hadley and Veblen 1993, Kipfmueller and Baker 1998, Holzmueller et al. 2008), and fire suppression can promote the development of large expanses of even-aged forests that have a high risk of epidemics from pests and pathogens (Meentemeyer et al. 2008, Raffa et al. 2008).

Several lines of evidence and argument support the hypothesis that recent changes in climate and other environmental factors have affected forest vulnerability to pestilence:

- The physiology of insects and fungi is highly sensitive to temperature, with metabolic rate, and therefore resource consumption, tending to about double with an increase of 10 °C (Gillooly et al. 2001, Clark and Fraser 2004). There is evidence that warmer is generally better for insects, even in climates that are already warm (Currano et al. 2008, Frazier et al. 2006). However, pestilence may tend to decrease in the warmer edges of contemporary distributions, as predicted by the model of climatic envelopes (Williams and Liebhold 1995). This model may help explain why the southern pine beetle has recently become less common in the pine forests of Texas and Louisiana even though it has been of great importance historically (Clarke et al. 2000, Friedenberg et al. 2008).
- The timing of life history stages (phenology) of many insect species has already been demonstrably advanced by warming temperatures (Harrington et al. 2001, van Asch and Visser 2007), and there are examples of insect distributions extending northward (Parmesan 2006). There are also reports of growing damage from some forest pests at the poleward and/or alpine limits of their historical occurrences (e.g. Jepsen et al. 2008, Lima et al. 2008).
- Climatic warming may generally reduce the risk to herbivore and pathogen populations of winter mortality (Bale et al. 2002, Battisti et al. 2005, Régnière and Bentz 2007, Tran et al. 2007). However, some insects that overwinter in forest litter may face higher mortality rates due to decreased snow depth (Lombardero et al. 2000b).
- Climate change may affect the frequency and intensity of extreme climatic events (IPCC 2007a). These events, such as ice storms and wind damage, may result in widespread disturbance in forest ecosystems, providing increased opportunities for invasive species to attack vulnerable trees and become established in disturbed areas (McNeely et al. 2001). Mechanical damage of plant tissue from storms can enable infection by pathogens (Shigo 1964).
- Increases in precipitation favour many forest pathogens by enhancing sporulation, dispersal and

host infection (Garrett et al. 2006). Drought stress can increase or decrease tree defences against herbivores and pathogens (Mattson and Haack 1987, Lombardero et al. 2000a, Hale et al. 2005).

- Climate can affect concentrations of secondary metabolites and nutrients in plant tissues, with consequences for herbivores (Herms and Mattson 1992, Landsberg and Smith 1992, Bidart-Bouzat and Imeh-Nathaniel 2008). Moreover, climate can affect natural enemies of insect pests (Burnett 1949) and ecologically important symbionts (Lombardero et al. 2003, Six and Bentz 2007).
- Anthropogenic increases in nitrogen deposition and atmospheric concentrations of CO_2 and ozone can impact forest disturbance by insects and pathogens (Meadows and Hodges 1996, Karnosky et al. 2005, Burdon et al. 2006, Zvereva and Kozlov 2006). The suitability of plant tissue for herbivores tends to be decreased by increases in CO_2 (Stiling and Cornelissen 2007) and increased by nitrogen deposition (Throop and Lerdau 2004).
- Forest fragmentation can affect resistance to biological disturbance, but the effect can be to increase or decrease pestilence depending on the system (Roland 1993, Holdenreider et al. 2004, Ylioja et al. 2005).

Warm climate conditions have clearly contributed to some recent insect epidemics: e.g. bark beetles in North America (Berg et al. 2006, Tran et al. 2007, Raffa et al. 2008), defoliators in Scandinavia (Jepsen et al. 2008), aphids in the United Kingdom (Lima et al. 2008) and the processionary moth in continental Europe (Battisti et al. 2005, 2006). Some modelling studies suggest that many boreal forests are vulnerable to increases in tree mortality leading to an increased frequency of stand-replacing fires, exacerbated by a warming climate (e.g. Johnston et al. 2001, Kurz et al. 2008b). In temperate and tropical ecosystems, where gap dynamics are more important than in the boreal zone, the effects of warming on gap disturbances from invasive species are uncertain except that there will likely be shifts in forest species composition (Hunt et al. 2006, Brown et al. 2008).

Recent impacts of the native mountain pine beetle (MPB) (*Dendroctonus ponderosae*) in western North America are noteworthy for their scale, economic significance and apparent links to climate. The MPB had produced extensive mortality throughout 13.5 million hectares of lodgepole pine (*Pinus contorta*) by 2008, including in areas further north, east and at higher elevations than previously recorded (Aukema et al. 2006, Logan and Powell in press). This epidemic was facilitated by recent climatic patterns (mild winters and warm dry summers; Logan and Powell 2001, Carroll et al. 2004, Régnière and Bentz 2007) in combination with fire suppression during the last century that created extensive tracts of mature susceptible pine stands (Raffa et al. 2008).

It appears that warm climate conditions have transformed MPB into an invasive native insect based on: (1) intensified outbreaks within historical range; (2) range expansion to the north; (3) range expansion into endangered high elevation forests of whitebark pine (*P. albicaulis*); and (4) expansion into forests of jack pine (*P. banksiana*), which creates the potential for massive range expansions into north central and eastern North America (Logan et al. 2003, Logan and Powell in press). Moreover, the MPB epidemic has been progressing as predicted by Logan and Powell (2001) based upon models of climatic effects on beetle physiology. These models project an eventual northern range expansion of 7° latitude (780 km) under a warming scenario of 2.5°C.

2.8.4 Invasive Plants

Climate change can affect forests by altering environmental conditions and increasing niche availability for invaders (McNeely 1999, McNeely et al. 2001, Hunt et al. 2006, Ward and Masters 2007, Dukes et al. in press, Logan and Powell in press). Ecosystem susceptibility to invasion by alien plant species has been linked to species richness, ecosystem disturbance and to the functionality of species (Mack et al. 2000). Disturbance and loss of native species can open niches and reduce competition to invading species (Kennedy et al. 2002).

Rouget et al. (2002) noted that the current distribution of stands of invasive trees in South Africa was largely influenced by climatic factors. Climate change can facilitate the spread of invasive plant species by accelerating disturbance rates and contributing to the loss of native species while increasing the range and competitiveness of invasive plants (Schnitzler et al. 2007).

The complex interactions of climate change and invasive species make effects at the community level especially difficult to predict (Williams et al. 2000, Moore 2005). After climate change, dominant endemic species may no longer be adapted to the changed environmental conditions of their habitat, affording the opportunity for introduced species to invade, and to alter successional patterns, ecosystem function and resource distribution (McNeely 1999, Tilman and Lehman 2001).

James Miller: United States

Photo 2.3 Invasive species are among the most globally significant factors affecting forest ecosystems and biodiversity. Kudzu (shown here) invaded many forests in the southern United States after it was imported from Japan to reduce soil erosion. Controlling invasive species and other stress factors can reduce forest vulnerability to some aspects of climate change.

2.9 Insights from Experiments

2.9.1 Introduction

Controlled experiments are among our most important tools for measuring the separate and interactive effects on forests of climate change and air pollution. They provide exposure-response science support for interpretation of field observations and monitoring data. They also provide critical inputs for modelling impact mechanisms and future impacts of climate change.

2.9.2 Elevated CO_2 Experiments

Atmospheric CO_2 has risen some 33% since the pre-industrial period but remains well below the point of CO_2 saturation for photosynthesis in most tree species. There is considerable interest in the hypothesis that past and ongoing increases in atmospheric CO_2 are causing increases in forest productivity.

Across a host of experiments, increases in photosynthetic levels have averaged 40% in response to simulated increases in CO_2 from pre-industrial levels to 500 ppm, a concentration predicted for the middle of this century (Ellsworth et al. 2004, Ainsworth and Long 2005). For young temperate-zone forest stands exposed for nearly a decade to elevated CO_2 using Free-Air CO_2 Enrichment (FACE) technology, the increase in forest productivity has averaged 23% across a range of tree species tested on two continents (Norby et al. 2005). Relative growth enhancement varied by species (Karnosky et al. 2005), genotype (McDonald et al. 2002) and from year-to-year depending on climatic conditions (Kubiske et al. 2006, Moore et al. 2006). This increase in productivity is driven largely by the enhancement of photosynthesis, but it is also affected in some, but not all, species by increased leaf area (Karnosky et al. 2005), extended growing season (Taylor et al. 2008) and increased root growth, allowing for increased soil volume exploitation for available nutrients and moisture (Norby et al. 2004, King et al. 2005).

Increased water use efficiency can also contribute to productivity enhancement, particularly under water-limiting situations because elevated CO_2 causes a reduction in stomatal conductance (Medlyn et al. 2001). However, elevated CO_2 concentrations can also alter physical/chemical leaf defences against insects, leading to changes in leaf quality that result in changes in herbivory (Percy et al. 2002, Karnosky et al. 2003, Kopper and Lindroth 2003). Effects of elevated CO_2 or ozone (O_3) on insect performance as mediated through natural enemy populations may be more difficult to predict (Awmack et al. 2004).

Only a few studies of CO_2 enrichment effects have been completed on older trees. These trees have tended to be less responsive to elevated CO_2 than younger trees (Körner et al. 2005, Asshoff et al. 2006). However, because of the size of the trees involved, such studies have not been as statistically robust as have the younger tree studies.

2.9.3 Warming Experiments

Historical records show an increase in mean global temperature of 0.6ºC over the last 100 years (IPCC 2007b). Essentially all chemical and biological processes are affected by changes in temperature (Saxe et al. 2001), so it is axiomatic that warming has already had many effects on forest ecosystems. However, effects of warming in forests are confounded with effects of co-occurring increases in CO_2, land-use change and other factors such as drought and fires. Controlled experiments are useful in understanding effects of warming alone and in combination with other factors.

Scientists have conducted a vast array of diverse warming studies of trees and forests using growth chambers, mesocosms, open-top and closed-top field chambers, common garden studies across temperature gradients, and heated open-air plots. In addition, a number of soil-warming studies have been conducted using various methods: e.g. removing winter snow to create differences in spring soil warm up; placing passive covers over lower-statured vegetation to reduce night-time heat loss to the atmosphere; and heating the soil with electric cables buried in upper soil layers. Most warming experiments are restricted in their temporal scope – e.g. daytime only, night-time-only or seasonal – for budgetary and other practical reasons.

Interpretation of the warming experiment literature is constrained by the fact that investigators have used so many different experimental designs and methods. Nevertheless, some consensus from warming experiments is emerging as to how warming will impact forest ecosystems. Warmer temperatures at northern latitudes will likely enhance photosynthesis and growth through increases in maximal summer photosynthesis, and by increases in the seasonal duration of photosynthetic activity (Saxe et al. 2001, Norby et al. 2003, Danby and Hik 2007, Peñuelas et al. 2007, Slaney et al. 2007, Bronson et al. 2008, Post et al. 2008). Tropical forests remain largely unstudied from the standpoint of warming experiments (Fearnside 2004, Feeley et al. 2007). This remains an important research need as the tropical forests play a key role globally as carbon sinks, and recent studies have suggested this sink may be adversely impacted by climate change (Fearnside 2004, Feeley et al. 2007).

A second topic of major concern regarding global temperature increases is the potential for major shifts of tree species toward the poles, and upwards on mountain slopes (see sub-chapter 2.6). Some models indicate forest vulnerability to regional-scale dieback (Houghton 1996) and major changes in species ranges (Iverson and Prasad 2001, Parmesan and Yohe 2003). Other studies have raised questions about the validity of these models (Loehle 1996, Loehle and LeBlanc 1996). Warming experiments and associated modelling efforts provide useful insight into this scientific discussion as they have clearly demonstrated that there is large plasticity in response for many of the tree species examined (Rehfeldt 1988, 1989, King et al. 1999, Gunter et al. 2000, Rehfeldt et al. 2004, Reich and Oleksyn 2008). This growing body of research suggests that vegetation models designed to predict species' responses to global warming need improvement with respect to their capacity to evaluate the extent and structure of genetic variation.

Less scientific consensus has developed around forest vulnerability to impacts of warming on soil organic matter decomposition and on soil carbon accumulation and release (Davidson and Jansens 2006, Bronson et al. 2008). This is an important research question because models of temperature effects on soil organic matter decomposition derived from laboratory studies predict large decreases in global soil organic matter as a result of warming alone (e.g. 8–12 Pg C °C^{-1}) (Saxe et al. 2001). While some studies have found that warming significantly increases CO_2 efflux (Rustad and Fernandez 1998) from soils, others have shown substantially less CO_2 efflux than has been predicted by models (Niinisto et al. 2004, Bronson et al. 2008). Soil organic matter decomposition and CO_2 efflux from soils will likely be altered under global warming but the amounts will probably not be as great as lab-based models predict (Davidson and Janssens 2006).

2.9.4 Altered Precipitation Experiments

A key global change driver closely associated with warming is drought. Water availability affects almost all processes underlying forest tree growth and reproduction. Water stress due to drought is a key factor affecting limits of distribution of tree species. Even one or two seasonal droughts can trigger a cascade of events leading to dieback, decline or increased risk of fire (Jones et al. 1993, Hanson and Weltzin 2000, Asner et al. 2004, Nepstad et al. 2004, Breshears et al. 2005) or major pest outbreaks (Rouault et al. 2006, Dobbertin et al. 2007, Kurz et al. 2008a). Global change models suggest that there will be changes in drought occurrence and impacts in many areas of the world over the next century. Thus, water manipulation experiments can play a key role in evaluating model assumptions and results.

Throughfall exclusion experiments that alter rainfall amounts reaching the soil surface by 30–50% have been conducted in temperate oak forest in Tennessee (Wullschleger et al. 1998) and in the Brazilian tropics (Nepstad et al. 2002, Fisher et al. 2006). These studies have documented decreases in whole-plant water flux in response to simulated reductions in rainfall (Wullschleger et al. 1998, Romero-Saltos et al. 2005, Fisher et al. 2007, 2008). Few other responses to simulated changes in rainfall were detected in the temperate oak forest, despite intensive monitoring of growth, leaf area development, leaf duration and leaf senescence (Hanson et al. 2001, Wullschleger and Hanson 2006). In contrast, similar precipitation manipulations in the Brazilian tropics affected reproductive phenology, litterfall, wood production, below-ground carbon cycling and large-tree mortality (Brando et al. 2006, Nepstad et al. 2007, Brando et al. 2008).

There is no clear consensus yet as to long-term effects of droughts on soil CO_2 flux (Sotta et al. 2007). Interaction of deforestation and increased frequency of drought due to land-use change and climate change are predicted to also alter soil carbon efflux in the tropics (Nepstad et al. 2008). However, results from two major precipitation exclusion studies have shown mixed results in terms of soil CO_2 efflux. While a small increase (9%) in soil CO_2 efflux was measured over three years at the study in Santarén, Brazil (Fisher et al. 2007), there was a drought-induced decrease in soil CO_2 efflux in the Caxiuanã, Brazil study (Sotta et al. 2007). The authors speculated that different soil types and available soil moisture were likely to have caused these differences (Sotta et al. 2007).

As with responses reported for other global change drivers, there is a large genetic variation in response to drought (Ogaya and Peñuelas 2007, Slot and Poorter 2007, Meier and Leuschner 2008). It is clear that mechanisms of genetic control of drought tolerance are only beginning to be elucidated (Street et al. 2006).

2.9.5 Flux Tower Experiments

Ecosystem-level CO_2 exchanges between terrestrial ecosystems and the atmosphere are being monitored using eddy-covariance techniques from a network of over 500 tower sites worldwide. Monitoring data from these towers has improved understanding of the effects of extreme events that may occur with increasing frequency under climate change. For example, the gross primary productivity over Europe was reduced some 30% during the heat wave and drought of 2003 (Ciais et al. 2005, Peñuelas et al. 2007). Similar reductions in net ecosystem carbon exchange were detected for Portuguese forests during the severe drought experienced in 2004–2005 (Pereira et al. 2007).

Boreal forest ecosystems, which are large reservoirs of soil-held carbon, are particularly vulnerable to carbon release under global warming (Goulden et al. 1998). Recently, flux measurements have been useful in showing that the carbon balance of these northern ecosystems has been shifted to one of higher respiration, particularly in the autumn as these regions have warmed over the past two decades. Results indicate vulnerability to reductions in the capacity of northern ecosystems to sequester carbon as global warming continues (Piao et al. 2008).

2.9.6 Phenological Gardens

Phenological shifts (particularly bud break and flowering dates) have emerged as a prime indicator of forest responses to global warming in temperate and boreal forests (Menzel and Fabian 1999, Walther et al. 2002, Sherry et al. 2007). Important data sources include phenological gardens where investigators have monitored dates of spring bud break, flowering and autumnal foliar coloration (Menzel and Fabian 1999). Repetitive examination of keystone species in these gardens has documented advancements in dates of spring bud break ranging from 2.3 to 5.1 days per decade (Menzel and Fabian 1999, Chmielewski and Rötzer 2001, Wolfe et al. 2005, Menzel et al. 2006, Pudas et al. 2008). However, there is some evidence that part of this phenological change may be due to increasing atmospheric CO_2 concentrations as well as warming (Taylor et al. 2008).

Reported changes in phenology are generally greatest at higher latitudes and have been correlated with rising temperatures over the past several decades (Parmesan 2007). Interestingly, results from phenological gardens have correlated very well with satellite imagery used to follow seasonal green-up and with measurements of the variations in the timing and amplitude of the seasonal cycle of atmospheric CO_2 (Linderholm 2006), showing the value of phenological gardens in 'ground truthing' a key climate-change phenomenon. In the tropics, tree phenology is driven largely by seasonal water availability, so leaf out and leaf longevity are not useful indicators of climate warming (Borchert et al. 2005).

2.9.7 Research Needs

Experiments have provided important insights into the potential effects on forests of climate change variables and interacting factors. For example:

- Recent CO_2 increases and climate warming are consistent with (and may be contributing to) observed increases in forest productivity in some regions (Norby et al. 2005). Any increase in carbon sequestration due to elevated CO_2 occurs largely from enhanced tree growth, as increased soil respiration under elevated CO_2 results in little added soil carbon build-up (King et al. 2004).
- Effects of CO_2 on tree growth can be diminished by co-occurring effects of factors such as nutrient limitations (Oren et al. 2001), pest activity

or elevated tropospheric ozone (Karnosky et al. 2005). However, elevated CO_2 can mitigate impacts of drought on forests by increasing water use efficiency (Medlyn et al. 2001).

- Community structure can be altered by elevated CO_2 as different species and communities are favoured under elevated CO_2 compared to control conditions, both above ground (McDonald et al. 2002, Kubiske et al. 2007, Mohan et al. 2007) and below ground (Phillips et al. 2002, Zak et al. 2007).

It should be noted, however, that the vast majority of global change experiments have been conducted as single-factor studies with young temperate-zone trees. There is a need for more multiple-factor studies of the key climate-change drivers with tree species from boreal, subtropical and tropical domains (Karnosky et al. 2003, Hyvonen et al. 2006). These studies must be well-replicated, robustly designed, and run for the long term to allow for exposure under a range of local climatic conditions for stand dynamics and pest population cycles to operate so that the important role of global change drivers in predisposing trees to other biotic and abiotic stressors is better understood (Percy et al. 2002).

Very little experimental work with elevated CO_2, warming or drought has been done on mature trees, so this remains a large knowledge gap that hinders modelling of future impacts of climate change on forest productivity. Similarly, almost no experimental work has been done with warming or elevated CO_2 in tropical forests. Model predictions are that greater CO_2 enhancement will occur in tropical trees than has occurred in temperate forest trees (Hickler et al. 2008), but that warming effects on respiration will largely offset these positive effects (Lloyd and Farquhar 2008).

The interactions of climate-change drivers with nutrient dynamics and important air pollutants have not yet been adequately studied. The current theory of 'progressive nutrient limitation' suggests that long-term responses to elevated CO_2 will lower nitrogen availability (Oren et al. 2001) and thereby limit subsequent growth responses. This highly contentious theory has not been validated, particularly on relatively fertile sites (Finzi et al. 2007). Similarly, the role of tropospheric O_3 in limiting the sink strength of forest trees remains poorly understood (Reilly et al. 2007, Sitch et al. 2007) and is tightly linked to climate change (Vautard and Hausglustaine 2007). Elevated concentrations of tropospheric O_3 are predicted to affect large areas of the world's forests in this century (Felzer et al. 2007).

2.10 Conclusions

The complexity of natural and human systems is a formidable barrier to quantification of climate change impacts in the forest sector. For example, forests are strongly influenced by tree growth rates (via slow processes) and disturbance regimes (via rapid processes). Slow processes and rapid processes can be influenced simultaneously by a complex array of factors that includes several dimensions of climate (drought, temperature, wind, etc.). Changes in climate can influence forests simultaneously in opposing directions. For example, warming of mid- to high-latitude forests tends to increase productivity in the absence of disturbance, but also tends to increase forest disturbance. It is also necessary to consider cumulative effects and interactions of climate changes, forest management, air quality, invasive species and other factors.

Complexity often stymies quantification and predictability of climate change impacts, but also provides many different pathways to adaptation when local or scientific knowledge is sufficient to define the dimensions of climate change and their interactions with natural and human systems. It is known already that warming can influence the geographic range and behaviours of herbivore species, thereby altering plant community structures and disturbance regimes in forest ecosystems. Such knowledge of herbivore biology, ecology and management can inform the development of adaptive responses to climate change. For example, theory and experience support the general concept that thinning of overstocked stands can reduce climate impacts on forest productivity mediated by insects that feed on trees.

The resilience of forest ecosystems supports human adaptation but can be overcome by severe disturbance and sufficiently large changes in climate. Trees can die rapidly and en masse, but forest regeneration and regrowth are relatively slow processes. Therefore, small changes in disturbance regimes can have large, lasting effects on forest ecosystems. Sometimes, disturbance-related changes in forests are made more difficult to reverse by associated alterations in, for example, soils, seed sources, pollinators, seed dispersers, herbivores and local climates. Because of the relatively long time required for natural forest regeneration following disturbance, there can be advantages to proactive changes in management compared to reactive changes.

Proactive adaptation measures based on knowledge of climate impact mechanisms have potential to prevent reductions in ecosystem goods and services in forests managed actively for timber and non-timber forest products. Effective adaptation requires explicit recognition that climate is one of many drivers of ecosystem change (Vitousek 1997, Chapin et al. 2000, Hanson et al. 2001, Chambers et al. 2007, Chapin et al. 2008). Non-climatic factors can influence forest disturbance regimes via interactions with climatic effects. Such interaction can take the form of feedback systems that tend either to stabilize or destabilize forest ecosystems (Ayres and Lombardero 2000, Bonan 2008). Recognizing and managing these feedback systems offers a general pathway to adaptation of human interactions with forests subject to climate change.

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