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Tree and forest functioning in response to global warming

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Summary

Key words: global warming, physiology, phenology, tree and forest functioning.

Although trees have responded to global warming in the past – to temperatures higher than they are now – the rate of change predicted in the 21st century is likely to be unprecedented. Greenhouse gas emissions could cause a 3–6°C increase in mean land surface temperature at high and temperate latitudes. Despite this, few experiments have isolated the effects of temperature for this scenario on trees and forests. This review focuses on tree and forest responses at boreal and temperate latitudes, ranging from the cellular to the ecosystem level. Adaptation to varying temperatures revolves around the trade-off between utilizing the full growing season and minimizing frost damage through proper timing of hardening in autumn and dehardening in spring. But the evolutionary change in these traits must be sufficiently rapid to compensate for the temperature changes. Many species have a positive response to increased temperature – but how close are we to the optima? Management is critical for a positive response of forest growth to a warmer climate, and selection of the best species for the new conditions will be of vital importance.

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I. Introduction

There have been times in the past when vegetation responded to warming, and times when temperatures were higher than now. Consequently, trees are capable of adjusting to a warmer climate (Jacobson & Dieffenbacher-Krall, 1995). The novelty of the expected changes in the 21st century is the rate of increase in temperature (Flenley, 1998). A range of credible scenarios of greenhouse gas emissions could increase radiative forcing to cause a 3–6°C increase in mean land surface temperature at high and temperate latitudes this century (Houghton *et al.*, 1996; Kattenberg *et al.*, 1996).

Climate change will also involve uncertain changes in seasonal patterns of temperature, storms, fire, precipitation, air humidity, snow cover and frequency and severity of extreme events (Le Houérou, 1996; Michener *et al.*, 1997). As an example, storms are predicted to be more common in north-west Europe (Dorland *et al.*, 1999) breaking or uprooting increasing numbers of trees.

Although it is appreciated that temperature always interacts with other factors in producing an effect, we have necessarily limited our discussion of interactions with biotic and abiotic conditions, which are themselves affected by the global climate change. Mycorrhizal fungi, nodulating bacteria and defoliating insects are all (affected by) under the influence of rising temperature, which then indirectly affect the associated trees. In the context of global warming, increases in temperature will be inextricably linked to increases in [CO₂], drought, vapor pressure deficit (VPD) and in some regions fire frequency. Rising temperatures will affect nutrient availability, increase isoprene emission from trees in some regions, representing a carbon loss and a precursor for oxidant pollutants, and influence occurrence of air pollutants which affect frost hardiness.

Several reviews on trees and forest ecosystem responses to elevated [CO₂] and the future environment have been published in recent years by the Intergovernmental Panel on Climate Change (IPCC) and colleagues (Kramer, 1996; Kozłowski & Pallardy, 1997; Mohren *et al.*, 1997; Oechel *et al.*, 1997; Mickler & Fox, 1998; Saxe *et al.*, 1998). This review offers a new synthesis by singling out the effects of temperature, which are arguably the most important of the environmental responses of ecosystems. The review focuses on tree and forest responses at boreal and temperate latitudes.

II. Photosynthesis and respiration

Warmer temperatures increase rates of virtually all chemical and biochemical processes in plants and soils in a similar way if substrates are available, up to a point where enzymes disintegrate. The temperature dependencies of diffusion in the liquid phase and of mass flow driven by osmotic pressure are similar to those of metabolic processes (Thornley & Johnson, 1990). Thus, there is a commonality in the response of most

plant responses. Appendix I gives a brief introduction to temperature response functions. In this section, we focus on the two central processes of photosynthesis and respiration.

1. Photosynthetic processes

Temperature affects photosynthetic processes associated with light by altering the pigment content, light-saturated photosynthetic rate, the apparent quantum yield or photochemical efficiency of PSII and photoinhibition. On balance, the effect of warmer temperatures at temperate latitudes is positive.

The content of photosynthetic pigments is typically increased by warmer temperatures (Michelsen *et al.*, 1996; Ormrod *et al.*, 1999). An initial increase followed by a decline indicates that a warmer temperature induced an ontogenetic drift (Higuchi *et al.*, 1999).

The temperature dependence of light-saturated photosynthesis is of two kinds. There is an instantaneous response to temperature, which generally rises to a maximum in the range 25–40°C and falls rapidly to zero as protein functioning is impaired, and there can be acclimation to temperature over periods of days/weeks (Berry & Björkman, 1980). Acclimation can shift the temperature optimum by up to 10°C (Battaglia *et al.*, 1996). The general shape of the temperature dependence of light-saturated photosynthesis is matched by the temperature dependence of RuP2-limited photosynthesis (the maximum rate of electron transport) on which it mostly depends (Kirschbaum & Farquhar, 1984; Wang *et al.*, 1996).

In herbaceous plants, the apparent quantum yield (the slope of the curve relating CO₂ uptake to absorbed light) generally decreases between about 15 and 35°C (Cannell & Thornley, 1998). However, in evergreen trees subject to winter inhibition of photosynthesis, quantum yield changes during the year with seasonal variation in maximum photochemical efficiency of PSII (Leverenz & Öquist, 1987). This variation is largely explained by temperature and changes in pigments of the xanthophyll cycle (Roden & Ball, 1996; Faria *et al.*, 1998; Lundmark *et al.*, 1998; Verhoeven *et al.*, 1999). Warm temperatures increased apparent quantum yield in *Pinus sylvestris* when measured at high temperatures (20–30°C) while it was decreased when measured at low temperature (5–10°C) (Wang, 1996). Lewis *et al.* (1999) similarly found the apparent quantum yield and the light compensation point to increase at elevated growing temperature. Overall, we would expect higher temperatures to have a beneficial effect on quantum yield in trees, except during mid-winter and at extremely high temperatures where thylakoid membranes are injured in a species specific manner (Méthy *et al.*, 1997).

High light, together with low temperature, induces stress in trees because of photoinhibition, and down regulation of PSII, as well as desiccation (DeLucia *et al.*, 1991; Pavel & Fereres, 1998; Stecher *et al.*, 1999). Photoinhibition in *Pinus banksiana* was less when growing at relatively low temperatures. This was attributable in part to cold induced production

of filtering anthocyanin in the epidermis and in part because of increased photosynthetic capacity, most likely caused by an increased capacity at low temperatures to keep Q_A , the first stable quinone electron acceptor of PSII, oxidized at high irradiance (Krol *et al.*, 1995). Antioxidant enzymes also play a role in protecting against freezing temperatures (Tao *et al.*, 1998; García-Plazaola *et al.*, 1999), even in roots (Zhao & Blumwald, 1998). But if night time temperatures are too low, photoinhibition increases. Under such conditions a 1°C increase in average night-time temperature allowed *Abies lasiocarpa* seedlings to avoid photoinhibition during the day, and increased photosynthesis by 650% (Germino & Smith, 1999). By contrast, 80% shading increased photosynthesis by only 40%.

The high degree of co-ordination between stomatal behaviour, photosynthetic capacity and photo-protection mechanisms in trees growing in hot summer climates, may also help trees cope with climate change (Faria *et al.*, 1998). But clearly, there is a fine balance between success and disaster, where even small changes in temperature play a major role.

In C_3 trees molecular O_2 (resulting in photorespiration) and CO_2 (resulting in photosynthesis) compete for the same Rubisco enzyme and RuBP substrate. Photorespiration is stimulated by a high $O_2 : CO_2$ ratio, and by high temperature. At warmer temperatures the ratio of dissolved chloroplastic $O_2 : CO_2$ is increased (owing to the lower solubility of CO_2) and the specificity of Rubisco to CO_2 relative to O_2 increases. As a result, photorespiration tends to reduce net photosynthesis and the optimum temperature for light-saturated photosynthesis increases with increasing $[CO_2]$ (Long, 1991). In *Pinus taeda* photorespiration was stimulated more than photosynthesis when temperatures were increased from 25 to 35°C (Samuelson & Teskey, 1991), while in *Robinia pseudoacacia* photosynthesis and photorespiration increased simultaneously with rising temperature, so that it was dark respiration rather than photorespiration that contributed to the decline of net photosynthesis at above-optimal temperatures (Mebrahtu *et al.*, 1991). Carboxylation is not the only process which potentially limits photosynthetic dark processes – regeneration of RuBP may also be a bottleneck. Hikosaka *et al.* (1999) found that both the changes in the temperature dependence of carboxylation and regeneration of RuBP and the changes in the balance of these two processes altered the temperature dependence of the photosynthetic rate in *Quercus myrsinaefolia*.

2. Leaf level photosynthesis

Using path analysis, Bassow & Bazzaz (1998) demonstrated the relative importance of air- and leaf temperature, light, and relative humidity for photosynthesis and leaf level conductance measured over one growing season in four temperate deciduous tree species. Averaged over a season, temperature explained 12% of the photosynthetic variation in red oak

and 16% in yellow birch and even less in white birch and red maple. As a species average, variations in leaf temperature were only weakly correlated with variations in photosynthesis during the summer (June–Aug), while in September this correlation was relatively higher. Photosynthesis was mainly determined by light, and indirectly by light effects on stomatal conductance.

Out of 27 recent studies of temperature effects on net photosynthesis, only 12 studies had a measure for stomatal opening, and just a few gave information on vapour pressure deficit. Because of differences in plant age, measured needle class (Wang *et al.*, 1995), growing conditions, annual variation in response to temperature (Lewis *et al.*, 1999), and heating strategy (duration, soil or air heated) (Schwarz *et al.*, 1997) it is impossible to draw robust, general conclusions from all these studies. But with comparable conditions it was found that different species (Battaglia *et al.*, 1996; Sun & Sweet, 1996) and families (Mebrahtu *et al.*, 1991) responded differently to warming and heat stress. As an example *Quercus macrocarpa* took longer to recover after short-term heat stress than *Quercus muehlenbergii* (Hamerlynck & Knapp, 1996).

The 27 studies reinforced the expectation that rising temperatures will increase rates of net carbon dioxide assimilation to an optimum. In two studies out of three, photosynthesis increased in response to the moderately elevated temperatures expected to result from global warming in this century. Warming is likely to reduce net photosynthesis only in regions where it is already close to the optimum temperature, and/or it accentuates water stress. Some experimental data indicate that temperatures > 2–3°C above summer ambient may inhibit photosynthesis in European tree species, *Picea abies* and *Fagus sylvatica* (Leverenz *et al.*, 1999, J. Leverenz, unpublished). However, adaptation to the prevailing ambient growing temperature determines, to an extent, the temperature for optimal photosynthesis throughout the year (Battaglia *et al.*, 1996).

3. Autotrophic respiration

Estimates of the fraction of net photosynthetic production consumed by autotrophic respiration in trees lie in the range 40–75% (Edwards *et al.*, 1980; Ryan, 1991; Sprugel & Benecke, 1991; Ryan *et al.*, 1994, 1996a, 1997; Waring *et al.*, 1998; Amthor, 2000, Table 1). In a young *Pinus radiata* plantation, respiration of foliage at night, woody tissues, and roots varied from 10.5 to 17.8 Mg C ha⁻¹ yr⁻¹ (Ryan *et al.*, 1996a). By comparison, heterotrophic respiration varied from 2.6 to 7.1 Mg C ha⁻¹ yr⁻¹.

Over the short-term, respiration rates increase exponentially with temperature, and measurements of bulk respiration almost always display increases in response to short-term increases in temperature (Amthor, 1989). The response of respiration to temperature is usually modelled as resulting from a flux from the two components of construction and

maintenance (Amthor, 1989). Construction respiration varies with the amount of biomass grown and with the complexity and energy status of the chemical compounds in the biomass (Vertregt & Penning de Vries, 1987; Williams *et al.*, 1987). The rate of biosynthesis will increase at higher temperature, but the cost of biosynthesis will remain a fixed fraction of the compound synthesized and so is insensitive to temperature (Penning de Vries *et al.*, 1974). Maintenance respiration largely varies with the amount of living biomass, its enzyme content and temperature (Ryan, 1991). Respiration (presumably maintenance) may also vary with stress, and has been shown to increase with ozone fumigation (Gerant *et al.*, 1996) and decrease with water stress (Ibrahim *et al.*, 1997). Most process-based models of biogeochemical cycling estimate maintenance respiration first, subtract it from net photosynthesis as a tax, and allocate the remaining carbon to production, construction respiration, and storage (Vegetation Ecosystem Modelling and Analysis Project VEMAP Members, 1995; Ryan *et al.*, 1996b). No model includes the effects of stress on maintenance respiration. Only a few models couple respiration to the supply of photosynthates and hence to gross photosynthesis, so that the temperature response of respiration matches that of canopy photosynthesis when averaged over several days or more (Cannell & Thornley, 2000; Thornley & Cannell, 2000).

Because respiratory fluxes are large, if it is assumed that they respond exponentially to temperature, they play a large role in determining tree growth and forest production in response to warming. Models with this assumption predict that an increase in global temperature of 3–4°C *per se* will reduce productivity, as respiration increases more rapidly than photosynthesis (VEMAP Members, 1995).

For most forest species and plant parts (foliage, wood, roots) the Q_{10} value for the short-term respiration response to temperature is 1.8–2.5 (i.e. within the range of temperatures normally encountered in forests, short-term respiration rates will approximately double with a 10°C increase in temperature (Amthor, 1989, 2000; Ryan, 1991; Ryan *et al.*, 1994)). At temperatures > 35–40°C, damage to proteins could occur and reduce respiration, but the evidence that such declines occur is mixed (Amthor, 1989). Seasonal changes in temperature are often used to estimate the response of respiration to temperature. However, seasonal variation in respiration also incorporates phenological change (cellular activity, growth, changes in the amount of protein or living cells) in addition to temperature effects. Therefore, simulations of respiration using seasonally derived Q_{10} values are likely to give incorrect predictions for temperatures warmer or cooler than those during measurement, or for different annual patterns of temperature.

Two lines of evidence suggest that predictions from Q_{10} estimates of the response of respiration to temperature will overestimate respiration. First, respiration rates may acclimate and adjust to new temperatures. Second, carbon budgets of forests (Ryan *et al.*, 1994, 1997; Waring *et al.*, 1998) and of

crop plants grown at different temperatures (Gifford, 1994, 1995; Tjoelker *et al.*, 1999a; Cannell & Thornley, 2000) suggest that partitioning of net photosynthesis to respiration and biomass production (generally expressed as carbon use efficiency (CUE) or the biomass fraction of net photosynthesis) is insensitive to temperature (Fig. 1).

Evidence for acclimation of respiration comes from studies where populations or species from cool environments have been shown to have higher respiration rates at a given temperature than those from warm environments (Criddle *et al.*, 1994; Reich *et al.*, 1996b), and sometimes, but not always (Collier, 1996), from studies of plants in controlled environments (Tjoelker *et al.*, 1999a, b). Acclimation of respiration rates strongly suggests that factors other than reaction kinetics regulate respiration over the long-term.

The current view is that, averaged over weeks to a year, autotrophic respiration is closely linked to net photosynthesis (Amthor, 2000; Cannell & Thornley, 2000; Thornley & Cannell, 2000). When enzymatically mediated reactions are insensitive to temperature, such processes are likely limited by substrate availability. Dewar *et al.* (1999) suggested the short-term increase in respiration with temperature is driven by the availability of labile carbon, but long-term respiration is constrained by the supply of substrate from photosynthesis. Thus, in the long term, respiration acclimates to substrate supply, not to temperature. Dewar (2000) has suggested a further model that couples respiration to the supply

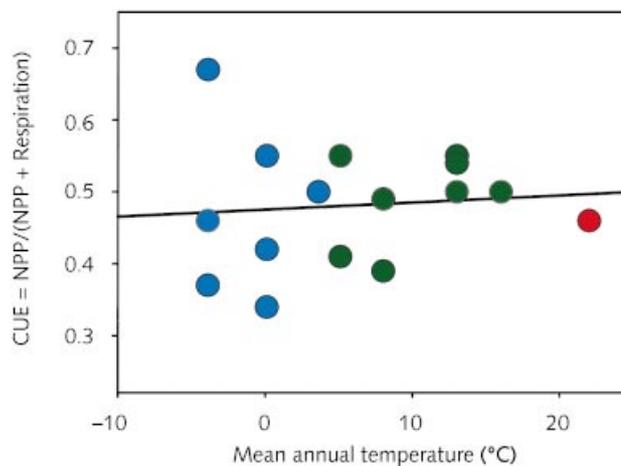


Fig. 1 Carbon use efficiency (CUE) of above-ground production in a range of different forests differing in mean annual temperature. Boreal (blue circles); Tropical (red circles); Temperate (green circles). Carbon use efficiency equals annual above-ground biomass production (NPP) divided by the net photosynthesis used for above-ground components. Net photosynthesis is estimated as the sum of above-ground production and above-ground autotrophic respiration. Sources for data are given in Ryan *et al.* (1997), Table 8. CUE was not related to mean annual temperature ($R^2 = 0.01$, $P = 0.74$).

of substrates which obviates the need to separate growth and maintenance functions.

Clearly, the view of autotrophic respiration as a tax that increases with temperature may be incorrect. Respiration is used by cells to generate energy for work, except in the rare cases where respiration is used for heating or perhaps to prevent the build-up of excess carbohydrate. Higher temperatures may mean that the work (biosynthesis or enzyme replacement) is accomplished faster, but there is little evidence that substantially more work is required at higher temperatures. For autotrophic respiration to use more net photosynthesis at higher temperatures, the protein turnover, maintenance of ion gradients, and cellular repair not associated with biosynthesis would have to increase. Experiments to determine these factors have yet to be done, although protein replacement has been shown to be a minor portion of what has been attributed to maintenance respiration (Bouma *et al.*, 1994). The growth-maintenance model of plant respiration does explain much of the short-term variation in respiration rates (Amthor, 1989; Ryan, 1991). However, 'maintenance' coefficients in the same species vary with growth (see discussion in Lavigne & Ryan, 1997), which suggests an inadequacy of this model even for short-term measurements. If respiration is substrate limited, and carbon use efficiency is constant with temperature, then over long time periods, all respiration for forests is growth respiration!

4. Conclusions

Warmer temperatures at boreal and temperate latitudes may enhance photosynthesis in trees by increasing the content of photosynthetic pigments, increasing light-saturated photosynthetic rate and possibly quantum yields, lessening the extent of winter inhibition. Effects on photoinhibition and photorespiration are more difficult to generalize. But overall, warming of up to 2°C is likely to be beneficial, although species may be expected to respond differently. There is likely to be adaptation, and in field conditions, associated factors such as water stress may have more influence on net photosynthesis than temperature *per se*. Furthermore, an increase in photosynthesis does not directly translate into increased growth (Brand, 1990; Chapin & Shaver, 1996; Roden & Ball, 1996).

Although autotrophic respiration responds exponentially to temperature in short-term experiments, with Q_{10} values in the range 1.8–2.5, in the long term respiration is limited by substrate supply and so must be linked to photosynthesis. The fraction of gross photosynthetic production consumed by respiration may vary within a narrow range when averaged over weeks to a year. Consequently, in the long term, the temperature response of autotrophic respiration may match that of gross photosynthesis. Studies of acclimation of respiration are likely to be confusing or complicated unless they are accompanied by information about photosynthesis and respiration of whole plants.

III. Soil organic matter decomposition and mineralization

1. Soil organic matter decomposition

Microbial ('soil') respiration rates have traditionally been characterized as exponential functions of temperature (Lloyd & Taylor, 1994) suggesting that rising temperatures will have significant impacts on rates of soil organic carbon (SOC) decomposition. The median Q_{10} value for global soils is reported to be 2.4 (range, 1.3–3.3), with Q_{10} values highest in cool regions, making them most vulnerable to warming (Raich & Schlesinger, 1992; Lloyd & Taylor, 1994; Peterjohn *et al.*, 1994; Kirschbaum, 1995; Van Minnen *et al.*, 1995). Models based on these Q_{10} values suggest that elevated temperature will increase CO₂ efflux from forest soils leading to declines in SOC (Jenkinson *et al.*, 1991; Rastetter *et al.*, 1992; Kwon & Schnoor, 1994; King *et al.*, 1997a; Peng & Apps, 1998). Forests worldwide would lose approx. 12 Pg of SOC with 1°C warming, and when excluding tropical forests, losses from mid- and high-latitude forests are expected to be on the order of 8–9 Pg °C⁻¹ (McGuire *et al.*, 1992). Schimel *et al.* (1994) estimated mid- and high-latitude rates of SOC loss on the order of 8–12 PgC °C⁻¹, but due to the quality of SOC pools in these regions losses may take > 100 yr to be fully realized.

Recently, it has been pointed out that the Q_{10} values used in current models were mostly derived from short-term laboratory incubations of disturbed soil or from *in situ* incubations of fresh litter, and that these values may not apply to old organic matter *in situ* (Giardina & Ryan, 2000). Liski *et al.* (1999) found that the amount of carbon in Finnish soils of both high and low productivity forest types actually increased with temperature, while Jarvis & Linder (2000) found that warming a soil by 5°C for 5 yr in northern Sweden has no effect on the CO₂ efflux. The decomposition rates of forest 'mineral' soil (excluding litter and metabolizable SOC) from 82 sites worldwide reveal little relationship with mean annual temperature (Giardina & Ryan, 2000). Respiration rates of European forests, based on eddy covariance estimates of whole ecosystem (plant + soil) respiration, appear to be independent of mean annual temperature (Valentini *et al.*, 2000). Since respiration rates of European forests are dominated by root and microbial respiration, these data suggest that latitudinal variations in mean annual temperature are not as important as, for example, biomass and litter production and soil moisture, for controlling broad latitudinal variations in SOC decomposition (Valentini *et al.*, 2000). Thus it seems possible that global soils will lose less carbon in response to warming than currently anticipated, because the decomposition of old organic matter is not greatly accelerated by increasing temperatures, maybe because microbes lack substrates, old organic matter is recalcitrant or increasing temperature increases physico-chemical protection.

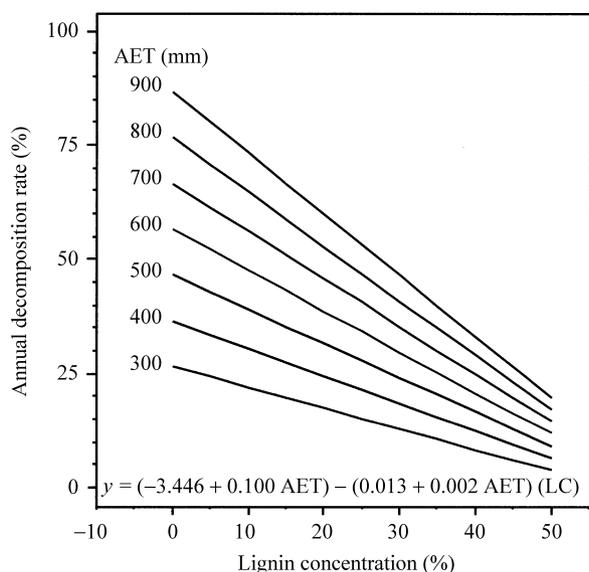


Fig. 2 Annual decomposition rate of leaf litter from a variety of ecosystems as a function of initial lignin concentration (LC) and actual annual evapotranspiration (AET), which is a surrogate for temperature and moisture. The regression equation explained 72% of the variability in regional litter decay rates. Redrawn from Meentemeyer (1978).

The decomposition of litter and metabolizable SOC is limited simultaneously by a variety of biotic and abiotic factors (Fig. 2). Field and laboratory studies find rates of litter and surface SOC decomposition (mass loss) positively correlated with temperature and moisture (Bunnell *et al.*, 1977; Meentemeyer, 1978; Dörr & Münnich, 1987; Belyea, 1996; Moore *et al.*, 1999), but studies differ as to the relative importance of the two – most likely depending on differences in forest type and region (Berg *et al.*, 1993). Data from 39 experiments from European and north-east American pine forests showed that annual rates of actual evapotranspiration (AET; an integrative variable for moisture and temperature) explained approx. 70% of the variability in mass loss rates (Berg *et al.*, 1993). The interactive effects of moisture and temperature on SOC decomposition may be due in part to moisture-induced alterations in the temperature sensitivity of soil respiration (Q_{10}) or a shift in the intercept of the temperature vs respiration curve (Bunnell *et al.*, 1977; Dörr & Münnich, 1987; Vourlitis *et al.*, 2000). Regardless of the mechanism, the close relationship between SOC decomposition and climate suggest that changes in moisture and temperature will enhance the decomposition of forest litter and labile SOC pools (Meentemeyer, 1978; Berg *et al.*, 1993; Schimel *et al.*, 1994; McGuire *et al.*, 1995).

Within a given region or site, initial litter represents an important predictor of the initial rate of mass loss (McClaugherty *et al.*, 1985; Ågren & Bosatta, 1987; Melillo *et al.*, 1989; Aber *et al.*, 1990; Schimel *et al.*, 1994; Belyea, 1996). High-quality litter (low C : N and/or lignin : N ratios) decomposes rapidly, and

as decay processes proceed, litter quality progressively declines as more recalcitrant carbon accumulates. Meentemeyer (1978) found that the annual rate of mass loss of 'high quality litter' (low lignin concentration) varied between 25 and 90% as AET increased from 300 to 900 mm yr⁻¹, while it varied between 5 and 25% with 'low quality litter' (Fig. 2). Thus, temperature and moisture effects on SOC decomposition vary quantitatively by orders of magnitude over the continuum of SOC quality and degree of degradation (Townsend *et al.*, 1995).

Clearly, the temperature increases anticipated under climate change have the capacity to stimulate rates of SOC decomposition, especially for the more labile surface SOC. However, the different responses of the various SOC pools to temperature (Melillo *et al.*, 1989; Schimel *et al.*, 1994; Giardina & Ryan, 2000) add uncertainty to predictions of future SOC decomposition. The magnitude and response of these SOC pools will also be altered by temperature-induced changes in soil water content, disturbance regime, net primary production (NPP) and vegetation composition (Bunnell *et al.*, 1977; Meentemeyer, 1978; Dörr & Münnich, 1987; Lloyd & Taylor, 1994; Schimel *et al.*, 1998; Kurz & Apps, 1999; Moore *et al.*, 1999). Although these interactions are beyond the scope of the present review, their effects on SOC decomposition are likely to be profound.

2. Mineralization

Of all the nutrients required for growth and survival, nitrogen (N) is needed in the largest abundance (Larcher, 1995), and forest productivity is more strongly affected by N availability than other nutrients (Pastor *et al.*, 1984; Oechel & Billings, 1992).

Any increase in SOC decomposition with global warming will enhance nutrient mineralization and availability (McClaugherty *et al.*, 1985; Rastetter *et al.*, 1992; Peterjohn *et al.*, 1994; Melillo *et al.*, 1996). But results from decomposition experiments indicate that although initial rates of mass loss of decomposing leaf litter are rapid, immobilization of N in microbial biomass can be large and prolonged. Rapid immobilization of N is typical for northern hardwood (Zak *et al.*, 1990) and coniferous forest soils (Hart *et al.*, 1994) and arctic tundra (Nadelhoffer *et al.*, 1991; Hobbie & Chapin, 1998). Rates of soil respiration (decomposition) may be correlated more with rates of gross mineralization and/or microbial immobilization than with net mineralization (Moorhead & Reynolds, 1993).

However, results from field and laboratory experiments indicate that elevated temperature will increase rates of nutrient availability. In field experiments where soil temperatures of Alaskan black spruce forests were raised by on average 8–10°C over two growing seasons (May–Sept; Van Cleve *et al.*, 1990), the availability of N, P, and K was significantly increased by soil heating (Fig. 3). Concentrations of total

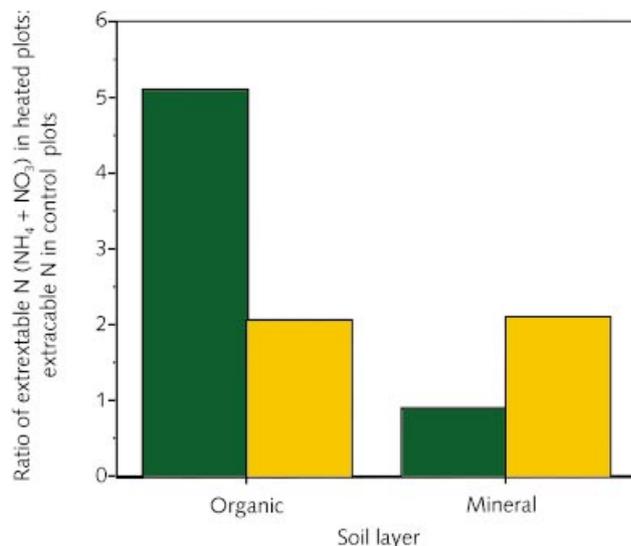


Fig. 3 The ratio of total extractable N ($\text{NH}_4 + \text{NO}_3$) in heated plots to the total extractable N in control plots from *in situ* experimental manipulations of soil temperature in the organic and mineral soil layers of black spruce (green bars) and mixed deciduous forests (yellow bars). Data from the black spruce forest are from Van Cleve *et al.* (1990), and depict the change in extractable soil N after approx. 4 months of soil heating where soil temperatures of the heated plots were elevated by 8–10°C over control plots. Data from mixed deciduous forest are from Peterjohn *et al.* (1994), and depict the change in daily rates of total N mineralization ($\text{NH}_4 + \text{NO}_3$) after approx. 4 months of soil heating where soil temperatures of the heated plots were elevated by approx. 5°C over control plots.

soil N in the organic surface soil horizons increased more than twofold, while 3–15-fold increases in exchangeable N (mainly NH_4) were observed over the 2-yr experiment (Van Cleve *et al.*, 1990). The higher N and P availability from soil warming caused a significant increase in tissue N and P concentrations and leaf photosynthesis (Van Cleve *et al.*, 1990) probably associated with faster growth (Oechel & Billings, 1992). Interestingly, NO_3 -N concentrations of the organic soil layers of the experimentally warmed plot declined significantly and, presumably, the decline of NO_3 -N in the warmed plot was caused by enhanced denitrification potential (Van Cleve *et al.*, 1990). In a similar experiment, a North American deciduous hardwood forest was exposed to a approx. 5°C soil heating treatment (Peterjohn *et al.*, 1994). After 6-months, heated plots exhibited twofold higher rates of N-mineralization in both forest floor (litter) and mineral soil layers (Fig. 3). Interestingly, N immobilization was not observed in warmed treatments (Peterjohn *et al.*, 1994), suggesting that elevated temperature may indeed enhance rates of *net* N mineralization (i.e. gross mineralization minus immobilization). The authors found no increase in the N_2O efflux from the heated plots; with no increase in nitrification or soil water N, the only alternative seemed to be an increased N uptake by plants.

As with SOC decomposition, simulations suggest that interactions between soil moisture and temperature produce

complex patterns of N availability, so that ecosystem responses are likely to be variable. For example, elevated temperature coupled with a decline in soil moisture is anticipated to cause a decline in N mineralization of temperate forest soils (McGuire *et al.*, 1992) but an increase in N mineralization in high-latitude soils (i.e. arctic tundra; Moorhead & Reynolds, 1993; McKane *et al.*, 1997).

Most experiments assess the effect of a large step-change in soil temperature, while actual warming will be more gradual. Laboratory experiments (Marion & Black, 1987; Nadelhoffer *et al.*, 1991) and simulation studies (Moorhead & Reynolds, 1993; Waelbroeck *et al.*, 1997) of arctic ecosystems indicated that a small temperature increase of 2–4°C can stimulate microbial respiration with little effect on net N mineralization. However, larger temperature increases, such as those simulated in the experiments described earlier, are enough to stimulate both microbial respiration and net N mineralization. Because there are many similarities in the C and N cycling dynamics of arctic tundra and boreal forest ecosystems (Oechel & Billings, 1992), these results may be applicable to climate-induced alterations in boreal forest N cycling. Transient climate change simulations under a variety of temperature forcing scenarios indicate that boreal forest net mineralization will be likely to fluctuate between positive and negative values during initial stages of climate change (up to 20 yr or an increase of 0.5°C; Xiao *et al.*, 1998). However, after an approx. 2.5°C increase in temperature over a 110-yr period (the so-called ‘reference warming rate’), net mineralization is estimated to increase by only 10%. Higher rates of warming, coupled with increases in precipitation, are anticipated to cause larger increases in boreal forests net N mineralization (Peng & Apps, 1998; Xiao *et al.*, 1998).

As with SOC decomposition, interactions between temperature, atmospheric change (elevated $[\text{CO}_2]$ and/or N-deposition), and vegetation change will undoubtedly alter rates of mineralization. Although beyond the scope of this review, changes in litter C : N ratio under elevated $[\text{CO}_2]$ exposure will potentially alter rates of net N mineralization (Curtis *et al.*, 1996; Johnson *et al.*, 1996; Körner, 1996; O’Neill & Norby, 1996).

Of potentially greater importance to future rates of N-mineralization is the interaction between temperature change and atmospheric N-deposition (Aber *et al.*, 1993). In theory, atmospheric N-deposition should increase N-mineralization by alleviating N-immobilization. However, N-saturation and/or soil acidification may cause a decline in ecosystem nutrient retention (Aber *et al.*, 1993; Asner *et al.*, 1997). Finally, the nature of vegetation change (i.e. how the vegetation change alters the ecosystem disturbance regime), N-fixation capacity, and nutrient use efficiency, will ultimately determine the long-term alterations to forest mineralization dynamics (Hobbie, 1992; Chapin *et al.*, 1996; Binkley & Giardina, 1998; Schimel *et al.*, 1998). These dynamics are hard to predict and are likely to vary significantly on local-to-regional spatial scales (Bazazz,

1996) and annual-to-century time scales (Oechel & Vourlitis, 1994; Chapin *et al.*, 1995).

3. Conclusions

The Q_{10} for soil organic matter decomposition, based on measurements of soils in laboratory experiments or fresh litter decomposition, is commonly in the range 1.4–3.3, being highest in cool climates. Models based on these values predict large decreases in global soil organic matter as a result of warming alone (e.g. 8–12 PgC °C⁻¹). However, recent evidence suggests that the decomposition of old organic matter *in situ* may not be responsive to warming, for reasons that are not yet clear, so global soil loss rates may be overestimated. There are well-established empirical relationships between litter decomposition rates and temperature, moisture (or AET) and litter quality. Global soil decomposition will also be affected by changes in elevated atmospheric [CO₂], vegetation cover and both natural and human disturbance – which may be more important than temperature *per se*. Any increased organic matter decomposition will mineralize N, but a large fraction of this N may be immobilized by microbes. Laboratory experiments, with slow soil warming, show little increase in net N mineralization, in contrast to forest soil warming experiments, with large step increases in temperature. Boreal forest net mineralization may, in fact, fluctuate between positive and negative in response to global warming. Overall, warming effects on mineralization may be much less than effects of continued N deposition, changes in vegetation composition and disturbance.

IV. Phenology and frost hardiness

Trees growing at temperate and high latitudes use temperature and night-length as information to regulate the cessation and onset of shoot growth and the development and removal of frost hardiness. For deciduous trees, light interception and growth are maximized by early leaf emergence more than by delayed leaf fall, so it is not surprising that the cues for budburst appear to be especially complex (Cannell, 1989a).

A crucial question is whether global warming will cause temperatures to rise outside the range in which trees can behave optimally, when regulatory mechanisms are so disrupted that there is incomplete exploitation of the growing season and perhaps increased frost damage. This question challenges our understanding of how plants use temperature and night-length to regulate their seasonal development, much of which is still based on classic work done between the 1950s and 1970s (Wareing, 1956; Vegis, 1964; Sarvas, 1974).

Before considering the role of temperature, it has to be recognized that trees follow a sequence of phenomena during each yr which seems to be partly internally regulated, almost regardless of the environment (Fuchigami *et al.*, 1982).

Thus, trees grown at a constant 15°C and constant day-length pass through seasonal phases of hardening and dehardening (Schwarz, 1968). This internal ontogenetic rhythm has been modelled to simulate realistic behaviour (Anisko *et al.*, 1994).

1. Shoot and bud growth cessation

In some tree species, the development of reproductive structures in the autumn may be entirely a function of accumulated day-degrees, more accurately termed ‘thermal time’ (Sarvas, 1974), and so may be vulnerable to damage by early frosts when development continues late into the autumn. It can be argued that trees can afford this risk, balancing a loss of seed in some years against the production of large, well developed seeds in others. By contrast, frost damage to vegetative shoots and buds is less easily compensated and near-complete avoidance may be of greater survival value. This may be why the timing of shoot and bud growth cessation seems to be more fail-safe against frost damage, using night length as the cue (Hänninen *et al.*, 1990) or in combination with temperature, such that sensitivity to night-length increases as temperatures fall (Heide, 1974; Koski & Sievanen, 1985). The dominant role of night-length as the trigger for shoot and bud growth cessation in trees is evident in the many reports of inherent differences in critical night lengths among provenances and individual genotypes (Cannell & Willett, 1976; Ekberg *et al.*, 1976).

Because night is often the dominant trigger for shoot and bud growth cessation, trees may fail to exploit the extended growing season as warming continues.

2. Frost hardening

The level of frost hardiness is commonly defined as the temperature which kills a defined fraction of tissues (e.g. lethal temperature for 50%, LT₅₀). Frost kills plant tissues primarily because cell membranes are damaged, causing electrolyte leakage into the apoplast (especially K⁺) and impairment of membrane transport properties (Arora & Palta, 1991). This damage always occurs when ice crystals form within cells. Intracellular ice formation may be avoided by supercooling to *c.* –10°C, and more exceptionally to –50°C in xylem parenchyma of tree species native to climatic zones where minimum temperatures seldom fall below –40°C (George *et al.*, 1974; Burke *et al.*, 1976). More commonly, shoot tissues harden to –50°C and below by allowing water crystallization only in the intercellular spaces. Ice crystallization there can be rendered harmless, provided cell structures acclimate to withstand both extracellular ice and the intracellular dehydration caused by lowered extracellular vapour pressure when water freezes. This acclimation involves changes in membrane lipid composition, accumulation of phospholipids and low-molecular cryoprotectants such as sucrose and raffinose,

water-binding to proteins and the production of antifreeze proteins (Sakai & Larcher, 1987; Palta & Weiss, 1993). These cellular aspects of frost hardening are beyond the scope of this review (Guy, 1990; Li *et al.*, 1997) but may help to explain why some authors distinguish two phases of shoot hardening – one occurring before and the other after intercellular ice crystallization.

The first phase of hardening is sometimes subdivided into two substages, the first induced by night-length alone and the second by temperatures cooling below 5°C (Sakai & Larcher, 1987). In experimental conditions it can be shown that lengthening nights alone can induce hardening to –20°C, at least in some broadleaved tree species, perhaps associated with substances translocated from leaves (Wareing, 1956; Weiser, 1970; Bervaeas *et al.*, 1978). But in nature the night-length response is normally indistinguishable from an effect of cooling temperatures, and hardening to *c.* –10°C often tracks the autumn fall in daily minimum air temperatures (Aronsson, 1975; Cannell *et al.*, 1985).

It is, perhaps, unhelpful to think in terms of environmental triggers, because it is known that hardening occurs to its maximum extent only when there is a progression and sequence of environments, from warm short nights to warm long nights to cool longer nights (Fuchigami *et al.*, 1971; Timmis, 1978). The important point is that cooling must occur at a particular time relative to increasing night-lengths in order to achieve maximum hardiness. This synchronization is likely to be disturbed by climatic warming. The expectation is that hardening, like growth cessation, will occur increasingly in response to night-length, earlier than is optimal in warm autumns. Also, warmer autumns and winters will induce shallower levels of hardiness than at present.

The second phase of hardening is considered to be induced by freezing temperatures, is independent of translocated substances and involves changes in cell constituents and structures that enable cells to withstand dehydration and the physical effects of ice formation in the intercellular spaces (Weiser, 1970). These changes may be the reason why the rate of hardening often seems to accelerate following the first severe frosts, even though minimum temperatures may fall no faster than before (Cannell *et al.*, 1985).

The progress of frost hardening of the shoot through both phases can be approximately simulated by assuming that, at any time, there is a 'stationary' level of hardiness that is dependent on daily minimum air temperature and night-length. Frost hardiness attains this level if temperatures and night-lengths remain constant (Repo & Pelkonen, 1986; Repo *et al.*, 1990); this level fluctuates as minimum temperatures rise and fall (Sakai & Larcher, 1987; Repo, 1992; Nilsson & Walfridsson, 1995) and the faster minimum temperatures fall the faster hardening occurs, with a certain delay (Greer, 1983; Cannell *et al.*, 1985). The relationship between the stationary level of frost hardiness and minimum temperature has been variously defined as a variable difference (Cannell *et al.*, 1985), as linear

(Repo *et al.*, 1990), logistic (Gay & Eagles, 1991, *Lolium perenne*) and piece-wise linear, with limits to the effective temperature range (Leinonen *et al.*, 1995). The effect of increasing night-lengths has generally been considered additive to the effects of temperature, as found in experiments (Bervaeas *et al.*, 1978; Christersson, 1978; Greer, 1983), either increasing the variable difference between minimum temperature and the level of frost hardiness or as an additional piece-wise linear relationship (Leinonen *et al.*, 1995). In order to make the models stable, it is further necessary to have a feedback control between the prevailing level of frost hardiness and the rate of hardening (Cannell *et al.*, 1985; Leinonen *et al.*, 1995).

These models give reasonable fits to observed natural patterns of hardening and some experimental results, but they are not mechanistic and do not deal with the requirement for a sequence of environments and the stages of development of frost hardiness. A significant advance would be made if it were possible to relate the temperature and night-length drivers to measurable processes at the cell level which accompany frost hardening, such as the increase in dry-to-fresh weight ratio (Ögren, 1999), total sugars (Ashworth *et al.*, 1993), low molecular weight proteins (Guy, 1990) and ice crystallization itself.

3. Rest (dormancy), growth competence and bud growth

In the autumn, buds enter a state of rest or dormancy and require chill temperature and maybe long night-length cues before they become responsive to warm temperatures (postrest or quiescence) after which they require a minimum accumulative thermal time above a threshold to develop to budburst. Efforts to predict the effects of climatic warming on budburst timing have prompted a re-examination of traditional ideas on these processes (Cannell & Smith, 1986; Hänninen 1990; Hunter & Lechowicz, 1992; Kramer, 1994a). Hänninen (1995) provided an overview of the literature by defining three physiological states of buds during winter: rest (dormancy); growth competence (ability to grow) and; actual growth and development.

The first physiological state, rest, shows that buds have a maximal state of rest (i.e. are most dormant) in the autumn when they are said to have 'set', meaning that cell division and growth have ceased and bud development is complete. Thereafter, the state of rest is diminished (or 'broken') by exposure to chill temperatures and short-nights can substitute for chilling, especially when the buds have received little chilling and so are most at rest (Nienstaedt, 1966; Cannell & Smith, 1983; Heide, 1993; Kramer, 1994a; Myking & Heide, 1995). The process of loss of rest, or 'rest break', involves changes in the balance between internal growth promoters and inhibitors, as well as other poorly understood biochemical processes (Rinne *et al.*, 1994). The state of rest at any time indicates the extent to which these processes have occurred.

This state can be gauged by measuring the concentration of gibberellic acid required to cause the buds to grow (Hatch & Walker, 1969; Couvillon & Hendershott, 1974) or more commonly, by the number of days it takes for the buds to grow in defined warm temperatures.

There is considerable uncertainty about the relationship between chill temperatures and the rate of rest break – that is, about the extent to which the state of rest is diminished after a unit time of exposure to given chill temperatures (Fig. 4a). Also, it is usually assumed that this relationship is constant, although there is evidence that the maximum effective chill temperature decreases as rest is broken, that warming can promote rest break in early winter but nullify it later, and that real-world fluctuating temperatures are more effective than constant temperatures (Overcash & Campbell, 1955; Campbell & Sugano, 1975; Erez & Couvillon, 1987; Hänninen *et al.*, 1990; Partenen *et al.*, 1998). The effects of alternating temperatures can be explained theoretically by hypothesizing a two-step process of rest break, where the first step is a reversible formation-destruction of a thermally unstable precursor substance and the second step is the fixation of this substance once it reaches a critical level, contributing to effective rest break (Fishman *et al.*, 1987). At high temperatures, the precursor is formed rapidly, but it is also broken down rapidly and so never amasses to a critical level; at chill temperatures the precursor is formed slowly but eventually amasses to the critical level where it becomes fixed and breaks rest; warm temperatures followed by chilling can accelerate step one and achieve step two in a shorter time.

The second physiological state, state of growth competence, defines the ability of the buds to grow in response to warm temperatures and varies from zero at maximal rest to one (maximum potential growth rate at warm temperatures) when rest is fully broken. Many authors assume that the relationship between the states of growth competence and rest is linear (Fig. 4bIIIa), in which case competence is already defined by the state of rest and the state of rest can be defined by the competence of the buds to grow at warm temperatures (Landsberg, 1974; Campbell & Sugano, 1979; Cannell, 1989b, 1990). However, others consider that buds attained full competence abruptly when rest was fully broken (Fig. 4aI; Sarvas, 1974; Richardson *et al.*, 1974), that competence falls to a minimum during rest break and then increases (Fig. 4bII; Kobayashi *et al.*, 1982), that competence remains low until a threshold state of rest is reached (Fig. 4bIIIb; Hänninen, 1990), or that competence is set in part by a night-length trigger (Nizinski & Saugier, 1988), maybe at a particular date in winter close to the shortest day (Häkkinen *et al.*, 1998; Partenen *et al.*, 1998). Clearly, there is a high degree of uncertainty.

The third state, state of bud growth and development, defines the visible change in size of the buds as cell division and enlargement progress in warm temperatures. The slope of the growth rate-temperature relationship depends on the growth

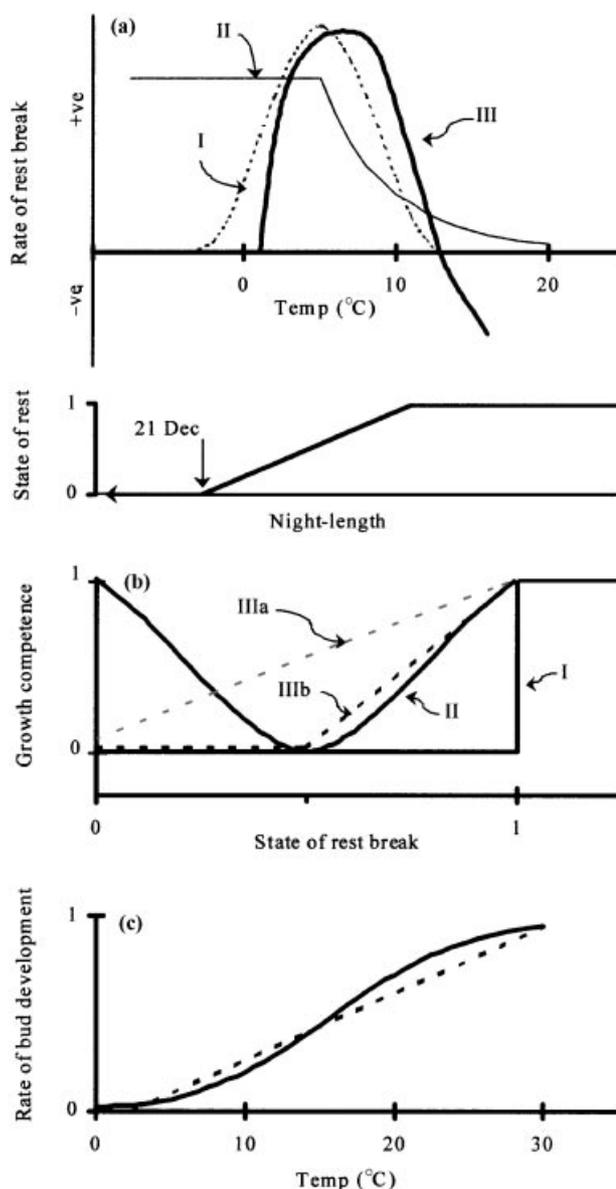


Fig. 4 Some contrasting, plausible, relationships which determine the timing of spring budburst. (a) Hypothesized effects of chill temperatures on the rate of rest break: (I) from Sarvas (1974) and used by Hänninen (1990, 1991) and Kramer (1994b); (II) from Landsberg (1974); (III) the 'Utah' model of Richardson *et al.* (1974). The lower graph shows the linear effect of night-length on the state of rest assumed by Hänninen (1995). (b) Hypothesized relationships between bud growth competence (ability to grow at warm temperatures) and their state of rest. (I) from Sarvas (1974); (II) after Kobayashi *et al.* (1982); (IIIa) from Cannell & Smith, 1983; (IIIb) from Hänninen (1990). (c) Sigmoidal and linear responses of bud growth rate to temperature (Hänninen, 1995).

competence. The shape of this response may be either sigmoidal or linear above a threshold (Fig. 4c; Hänninen, 1995).

Overall, there are at least 100 possible combinations of functions that can be used to describe rest break in response to temperature and night-length, growth competence as a

function of state of rest, and bud growth in response to temperature. This weakness is further confounded by the fact that the state of rest and growth competence cannot be measured directly (except perhaps by applying growth promoters). At present, bud phenology models are tested only by their ability to predict observed dates of budburst. With so many parameters and possible functions, it is not surprising that models can be constructed which accurately simulate past long-term records of dates of budburst (Kramer, 1994a, 1994b, 1995; Hänninen *et al.*, 1990). The problem is that different models, with substantially different assumptions, can give equally accurate postdictions (Hunter & Lechowicz, 1992; Hänninen, 1995; Hannerz, 1999). Also, within particular models, several combinations of parameter values can give equally accurate results, for example, by adjusting rate or threshold values, or by adjusting correlated parameters determining the rates of rest break and bud growth (Kramer, 1994a, 1994b).

A general conclusion is that our current understanding is sufficient to simulate past dates of budburst accurately, but models lack the realism required to predict the future, because there is little consensus or confidence in the way intermediate processes are represented or parameterized. The models have accuracy without realism (Hänninen, 1995). Little further advance may be possible until it is possible to measure the states of rest and growth competence directly, so that new, truly mechanistic models can be constructed.

Meanwhile, model predictions of the likely effect of warming on the date of budburst on trees vary from no change (Kramer, 1994a, 1995), much earlier with increased risk of frost damage (Hänninen, 1991; Guak *et al.*, 1998) to a variable response depending on the extent to which the chilling requirement for rest break is currently met (Cannell & Smith, 1986; Murray *et al.*, 1989). In general, work in recent years has emphasized the complex fail-safe mechanisms and plasticity that trees have to accommodate temperature variation (Hänninen, 1995; Kramer, 1995; Partenen *et al.*, 1998).

4. Elevated winter temperatures

Elevated winter temperature causing thaw can induce winter desiccation, but also stimulate photosynthesis in *Picea rubens*. Though the levels reached are only *c.* 37% of summer photosynthesis (Schaberg *et al.*, 1998), the early C-gain may prepare root growth for the onset of evapotranspiration with spring-time bud and needle sprouting, since mostly all C gained during winter and spring is allocated to the roots, and none allocated during and after bud burst (Hansen *et al.*, 1997). Current-year needles are lost when injured by severe or unexpected frost, which is the major cause of injury to *Picea rubens* in the eastern USA (and sugar maple in eastern Canada) (Robitaille *et al.*, 1995). The different response to winter warming of three different red spruce provenances indicated that one provenance could displace the others with a warmer climate (Schaberg *et al.*, 1995).

In Europe injury to conifers by high winter temperatures combined with low light intensities was first discussed by Prinz (1936). Though the symptom was loss of current-year needles it was not caused by winter desiccation. In *Picea abies* it was called 'top-dying' in the 1950s (Lees, 1991), 'subtop-dying' in the 1970s (Barklund, 1983), and the 'Red' decline syndrome in the early 1990s (Saxe, 1993; Saxe *et al.*, 2000). Skre & Nes (1996) confirmed that elevated winter temperature can increase needle loss in *Picea abies* and reduce growth the following season, particularly in northern provenances. Warmer winters may stimulate respiration more than photosynthesis at low temperatures (Hamerlynck & Knapp, 1996; Skre & Nes, 1996), cause premature dehardening (Section IV.4), and affect pest-pathogen activity (Jones *et al.*, 1993).

Thus, elevated winter temperatures may be as critical as elevated summer temperatures. Since temperatures in winter are expected to increase more than in summer under climate change (Kattenberg *et al.*, 1996), needle loss under elevated winter temperature may have important implications for the future productivity of northern coniferous forests.

5. Frost dehardening

Frost dehardening in spring is driven mainly by temperature and can occur at 0.5–1.5°C d⁻¹, much faster than hardening (Repo, 1992). Artificially short nights can hasten dehardening, but they are unlikely to be a major driver in nature (Leinonen *et al.*, 1997).

In midwinter, boreal conifers maintained at temperatures 5–20°C above ambient remain hardy to –40°C and so may remain frost protected in a warmer climate (Repo *et al.*, 1996). However, in some circumstances, sudden winter thaws can cause sufficient dehardening to cause injury during subsequent severe frosts, perhaps associated with increased respiration and loss of sugars (Ögren, 1997; Lund & Livingston, 1998).

During spring, temperature affects dehardening in two ways. First, it has a direct effect on the stationary level of hardiness, as in the autumn. Warm minimum temperatures decrease hardiness after a few days, thereby increasing the risk of subsequent frost damage, while low minimum temperatures can slow, halt or reverse dehardening, lessening the risk of frost damage (Repo *et al.*, 1990). Thus, fluctuating temperatures during early spring cause fluctuating levels of frost hardiness (Leinonen *et al.*, 1997). Second, warm temperatures during spring promote ontogenetic development towards budburst. This development is irreversible and once budburst begins the shoots can no longer harden in response to cool temperatures (Fuchigami *et al.*, 1982; Sakai & Larcher, 1987; Repo, 1991; Leinonen *et al.*, 1997). The minimum frost hardiness attained in northern conifer shoots during budburst varies from *c.* –2 to –10°C (Repo, 1991, 1992).

The gradual loss of rehardening capability with ontogenetic development in spring may mean that climatic warming will increase the risk of frost damage more in spring than in

autumn (Repo *et al.*, 1996). However, at present, insufficient is known about the linkage between hardiness and development to represent this phenomenon mechanistically in models (Leinonen *et al.*, 1995).

6. Conclusions

Bud growth cessation in the autumn is triggered strongly by night-length (so occurs about the same time every autumn) and so may occur sooner than is optimal in a warmer climate. Autumn frost hardening may occur later, but disruption of the sequencing of cooling temperatures and lengthening nights may lead to incomplete hardening. However, models of the frost hardening process are largely conceptual; few describe processes at the cell level so their predictions are uncertain.

It is clear that sudden winter thaws can cause injury directly or after subsequent frost. Similarly, if early dehardening is accompanied by ontogenetic development, making rehardening more difficult, there may be increased risk of spring injury before budburst.

Models of the dormancy states of buds during winter are largely conceptual – usually assuming that buds have a state of rest influenced by chilling, a state of growth competence and a state of growth and development. The problem is that none of these states can be measured directly, so there remains uncertainty about, for instance, the relationship between rest and chilling and between rest and growth competence. This means that many model formulations and parameterizations can simulate historic relationships between budburst dates and temperature. But because the models are not mechanistic there is limited confidence in their ability to predict responses to future warming. Nevertheless, it is clear that trees have evolved complex fail-safe mechanisms to accommodate substantial shifts in seasonal temperature patterns.

V. Whole tree experimental responses to warming

1. Whole tree warming experiments

There are relatively few reports on how trees respond experimentally to moderately warmer air temperatures during the growth season (indirectly heating the soil). Growing five boreal tree species from seeds for one season at elevated temperature, Tjoelker (1997) found conifers (*Larix laricina*, *Picea mariana*, *Pinus banksiana*) had the highest mean relative growth rate (RGR) and mass at intermediate temperatures, while broadleaved species (*Populus tremuloides*, *Betula papyrifera*) exhibited the highest mean RGR and mass at the highest temperatures. By contrast, Bruhn (1998) in a similar study found that a conifer (spruce) had more to gain by elevated temperature than a deciduous species (beech) in terms of RGR, height increment, stem diameter and total dry mass (Fig. 5). From these observations we therefore conclude that

trees do not respond to temperature on a broad genetic basis such as conifers vs broad leaved trees, but on a more restricted level, such as species or even provenances. Though it is beyond the scope of this review, a strong synergistic effect of elevated temperature + [CO₂] on seedling growth was noted in recent experiments with beech and Norway spruce (Bruhn, 1998, D. Bruhn, unpublished).

Since warmer temperature affects ontogenetic drift (Farnsworth *et al.*, 1995; Tjoelker, 1997), growth stimulation is sometimes only an initial response, and in the long term it may turn into a decline (Olszyk *et al.*, 1998a,b; Higuchi *et al.*, 1999). As elevated temperature increase evapo-transpiration, trees growing at warmer temperatures need larger root systems to obtain the necessary water. But the literature does not clearly support the view that trees grow larger roots under these circumstances (Hawkins & McDonald, 1994; King *et al.*, 1996, 1997b). However, trees do adapt to high temperature stress in terms of tree canopy architecture, leaf size, shape, anatomy and orientation, and the morphology and architecture of the root system (Mahan *et al.*, 1997).

In soil heating experiments temperature strongly interacts with water and nutrients. Several studies have shown that increasing soil temperature stimulates tree growth differently according to species (Brand, 1990; Lopushinsky & Max, 1990; Graves & Aiello, 1997), which is one mechanism by which global warming will alter the composition of forest ecosystems (and move the borders of the natural distribution of tree species). At many sites, soil temperatures are presently still below the optimal values for growth. Warmer soils will therefore stimulate forest growth in most regions, but this could also be a result of rising [CO₂], higher atmospheric nitrogen deposition, warmer air, and improved management.

2. Conclusions

In relation to climate change, the growth response has been studied far less than frost tolerance. But when specifically looking at soil heating, Farnsworth *et al.* (1995) found that growth rather than phenology was affected in many tree species. In the limited number of experiments with elevated air + soil temperature, seedlings show a species-dependent, positive growth response to warmer temperatures up to an optimum. For European beech, however, there may be little to gain from warmer temperatures.

VI. Changes in species distribution at warmer temperatures

1. Geographic ranges

There is a good correlation between January isotherms and distribution of northern tree species. Low winter temperatures are the main limiting factor for frost-sensitive trees in continental regions, while high winter temperatures are an

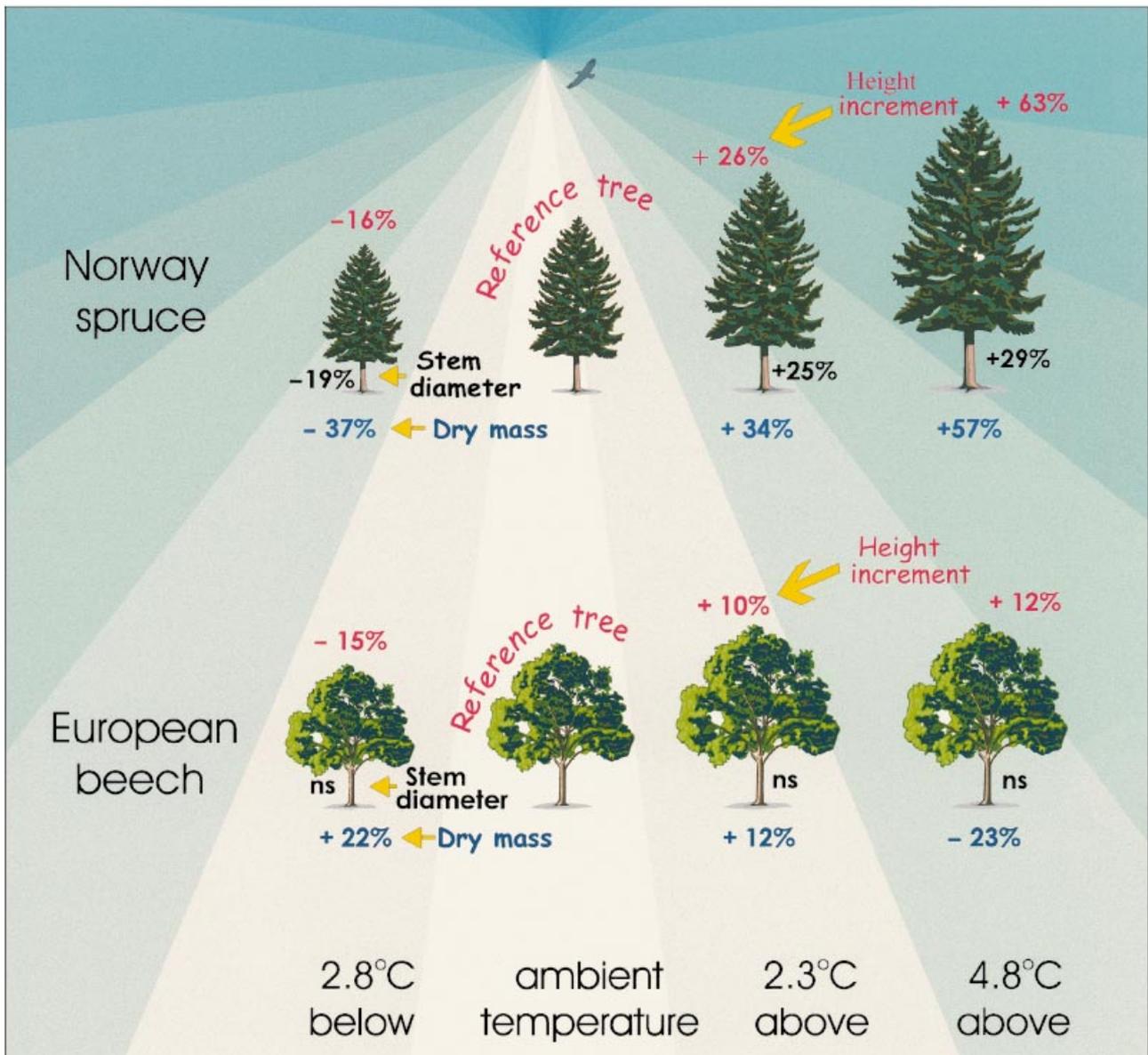


Fig. 5 The growth response of 1-yr-old *Picea abies* and *Fagus sylvatica* to 4 different temperatures. Red figures indicate height increment in percent of the reference tree that grew to spruce (90 mm) or beech (312 mm) over the first season. Black figures similarly indicate stem diameter increment (reference trees: spruce (3.2 mm) and beech (10.5 mm)). Blue figures indicate dry mass increment of root + stem + leaves (reference trees: spruce (1631 mg), beech (5609 mg)). The use of mature trees in this illustration should provoke the reader to question how – and if – the existing large volume of seedling data on temperature responses translates into responses of mature trees and forest ecosystems to global warming.

important limiting factor for some continental species that avoid coastal areas with mild winters.

In order to monitor future climate change Carter (1996) transplanted ecotypes of 10 north-east American temperate tree species from different latitudes and found the temperature difference between the provenance origin and transplanted site to account for 29% of height growth. But most latitudinal or oceanic/continental transfer experiments are applied to predict how trees will adapt to climate change, rather than to monitor such change. However, changes in day length,

soil type and immediate biotic environment will add to the effects of a warmer climate.

Oleksyn *et al.* (1998b) studied growth responses of *Pinus sylvestris* populations from a wide latitudinal range to temperature and photoperiod in growth chambers and in the field. In all populations, shoot elongation was most prolonged at low temperatures. Northern populations ceased height growth earlier than other populations in a southern photoperiod. In warm conditions growth cessation was regulated by the sum of day-degrees, not by photoperiod. Since the length of the

growing season is under strong environmentally mediated genetic control in Scots pine, potential climatic changes such as increasing temperature were projected to alter the length and timing of growth in above-ground tree parts towards a shorter growing season. This is in contrast to expectations used in previous models. A shorter period of shoot extension, however, does not mean that overall wood production will be negatively affected. But it is necessary to include such species and provenance-specific responses to acclimation and adaptation in future modelling on tree responses to climate change.

In Europe, however, the average growing season of a number of tree species has increased by 11 d (from Macedonia to northern Scandinavia) over the past 30 yr (Menzel & Fabian, 1999). But this does not allow us to predict how it will develop in the next 30 yr.

According to Persson (1994) and Ståhl (1998) *Pinus sylvestris* provenances transferred a few degrees southwards in Scandinavia have high survival rates and yields, but a low stem wood production. Based on predictions, trees will be straighter, have fewer spike knots and injuries, have thinner annual rings, fewer and thinner branches, less early wood, high basic density and slender thick-walled tracheids compared with local provenances. Northern material will thus produce higher quality timber, while southern material (transplanted north) will produce better wood for pulp and paper. Considering genetics is therefore important in forest management. Selection of appropriate species and provenances may be the best tool the forester has to meet the challenge of global warming.

2. Altitudinal ranges

Low summer temperature is the main limiting factor towards higher elevations for tree growth, but the altitudinal root zone temperatures of 5.5–7.5°C seem to be the critical lower limit for growth and development (Körner, 1998). Cold soil reduced height growth in *Pinus ponderosa* low-elevation ecotypes transplanted to higher sites, and budburst was delayed in transplanted firs and pines. But growth responded to increased temperature more in the low than in high elevation ecotypes (Lopushinsky & Max, 1990). Weih & Karlsson (1999) suggested that a similar weak growth response to increased temperature in high altitude mountain birch was functionally related to high leaf-N concentration, which is genetically determined and has an adaptive value in a cold environment. They believe that there is a trade-off between high N productivity at low temperature and a strong response of N productivity to temperature. In the reverse transplant of high altitude *Picea abies* ecotypes to 150 m, these retained a lower growth rate, with higher N-content, levels of chlorophyll, carotene, photosynthesis and dark respiration rates in needles than low altitude ecotypes (Oleksyn *et al.*, 1998a). They explained the low growth rate of the high altitude ecotypes at low altitude (higher temperature) by a reduced shoot-growth period, the high respiration rates, and

high allocation to roots, more than offsetting their higher photosynthetic rates.

In Scandinavia, low summer temperatures are the main limiting factor towards higher elevations for thermophile trees (Dahl, 1990). Evergreen conifers growing at high elevations or at high latitudes have longer-lived needles than trees of the same species growing elsewhere. A study of high altitude (*Picea abies*) and latitude (*Pinus sylvestris*) provenances in a common garden demonstrated that needle retention was not a genotypic but a phenotypic character (Reich *et al.*, 1996a). Needle retention therefore was not the cause of higher physiological rates in high altitude and latitude ecotypes grown in a warmer climate.

3. Models

Most models of temperate and boreal forest responses to climate change developed in the two decades up to the second IPCC assessment projected regional dieback (Houghton *et al.*, 1996). Loehle & LeBlanche (1996) pointed to several common weaknesses of these models, for example that forest management, climate tolerance and vegetative reproduction had been ignored, giving previous predictions a common multiplicative bias favouring drastic diebacks and geographical range shrinkages, even to the point of extinction. Management strategies are increasingly being incorporated into models of forest responses to climate change, and indicate that predicted losses may be partly mitigated (Lindner, 1999). Loehle (1996) claimed that changes in forests are far more likely to be gradual (over hundreds to thousands of years), to involve only local dieback, and due to management to result in far less economic loss than generally predicted.

The southern borders of boreal forests are predicted within this century to move 500–1000 km north, as natural competition and management turn up to 40% of present boreal forests into broad leaved temperate forests. In the North Arctic tundra would gradually or by management be invaded by boreal conifers (Kellomäki & Karjalainen, 1997). Some countries, for example Finland, will have regions that may win and regions that may lose wood production (Beuker *et al.*, 1996; Talkkari, 1998). The Russian boreal forest which contains 20% of the world's timber resources and over half of all boreal forests are for economical and political reasons less likely to be managed productively to assist changes induced by climate change (Krankina *et al.*, 1997). If forests do not migrate, and planting in these regions is not sufficient to keep up with changing climate, carbon storage could be reduced, and the warming would induce a positive feedback to further increase atmospheric [CO₂] (Solomon & Kirilenko, 1997).

In the temperate forests of central Europe spruce is expected to decline (Von Heining, 1996), beech may be less dominant (Von Heinsdorf, 1999), though it could improve in some regions (Von Felbermeier, 1994), while broadleaved species like ash, birch, aspen, alder, maple, oak, hornbeam,

lime and conifers like pine and European larch would thrive (Von Ebert, 1996). Seasonal precipitation will have decisive influence on drought limitation of temperature and [CO₂] advantages (Herbst & Hörmann, 1998). Hogg & Schwarz (1997) studied *Picea glauca*, *Picea pungens* and *Pinus sylvestris* across a climatic moisture gradient in Canada and demonstrated the importance of soil water. A drier future climate in the southern boreal forest of western Canada could significantly reduce natural regeneration of the studied conifers in these regions. In Scotland, where soil water is not limiting, the area where *Picea sitchensis* can be profitably grown has doubled over the last 40 yr, and models predict that warming will again double this area in only 20 yr (Proc *et al.*, 1996). In the east North American forests, models predict that 30 of 80 studied tree species could expand their importance by 10%, while another 30 species would decline by 10%, and 36 of the species could shift at least 100 km north (Iverson & Prasad, 1998). Management would improve the migration through fragmented landscapes.

4. Conclusions

Global warming will make it possible for tree species to migrate (or be transplanted) northwards (in the northern hemisphere). Latitudinal transplanting experiments indicate that Northern trees will produce higher quality timber and probably at a higher rate. Though the length of the growing season will increase for many trees with warmer temperature, this does not seem to be the case for all species. Little is known about the importance of responses to photoperiod alongside increases in temperature.

Rising soil temperatures will induce low-elevation ecotypes to grow at higher elevations, but at a given elevation warmer temperature will not stimulate growth of local trees as much as trees migrating or planted from the warmer climate of lower altitudes. The high altitude ecotypes seem to have a genetically determined high demand for nitrogen.

Models indicate a potential for increased growth with increasing temperature and [CO₂], but it will be limited in regions with insufficient precipitation. Management is critical to a positive response of forest growth to a warmer climate, and selection of the best species and provenances for the new conditions will be of vital importance.

VII. Adaptation and evolution

1. Genetic adaptation and phenotypic plasticity

Temperature is probably the major selecting agent causing population differentiation along latitudinal and altitudinal clines (Sections VI.1–2). Langlet (1936) demonstrated that phenotypic variation among natural populations of *Pinus sylvestris* was arranged along clines that paralleled Scandinavian climates. Common garden plantations have since then provided

data for studies of the variability in adaptive traits among and within wild populations of forest tree species (Rehfeldt, 1988, 1989; Campbell *et al.*, 1989; Hannerz, 1998). These studies have shown that climatic adaptation seems to be the most important component in the evolutionary process of temperate and boreal tree species.

A heritable trait is interpreted as being adaptive if it fits these clines closely, and believed to be the product of natural selection. Warm temperatures may operate indirectly by dis-favouring genotypes with a delayed onset of growth in the spring and premature dormancy in the autumn. These genotypes will under-utilize a given site's resources, are categorized as having insufficient growth capacity (Heide, 1985), and could possibly be ousted by genotypes expressing longer-lasting growth (Rehfeldt *et al.*, 1999). On the other hand, low temperature extremes may severely injure genotypes with premature onset of vegetative growth in the spring and delayed growth cessation in the autumn (Heide, 1985). In general, one cannot assume that native populations are optimally adapted to minimize frost damage and yet utilize the full growing season in the face of varying temperatures (Rehfeldt *et al.*, 1999). This depends on how many generations each species has been present in a given region and adapted its growth phenology, the genetic variation within the adaptive traits of hardening, dormancy and dehardening, the selection pressure from temperature extremes, and the magnitude of gene flow among populations. It is beyond the scope of this review to discuss all the evolutionary forces involved (Endler, 1986; Eriksson, 1996, 1998a, 1998b; Hänninen *et al.*, 2000).

Bradshaw (1965) defined phenotypic plasticity as 'the amount by which the expressions of individual characters of a genotype are changed by different environments'. The many successful transfers of provenances have led to the assumption that long-lived conifers show a high degree of phenotypic plasticity towards mean temperature differences. The degree of expression of phenotypic plasticity is under genetic control (Hoffmann & Parsons, 1991), but in conifers pertinent information about its impact on variation pattern in adaptive traits is not known. Genotypes with a high degree of phenotypic plasticity have an enhanced probability of surviving fatal temperature extremes by activating those genes that produce phenotypes with better resistance to this particular stress. Such genotypes must have a flexible gene regulation system, and a species needs to attain a whole range of different phenotypes depending on the environmental conditions, to protect it from being eliminated by natural selection (Eriksson, 1996, 1998b), leaving more of the genotypes alive to breed, and hence contribute to the maintenance of a large within-population variation. On the other hand, species with a high degree of phenotypic plasticity should express less clinal and/or ecotypic differentiation. The only way to study the influence, magnitude and inheritance of phenotypic plasticity in adaptive traits, is to use clonally replicated trees from a pedigree family

hierarchy, and test these clones in trials along climatic gradients. Such trials have been established with Norway spruce in the Nordic countries, and they will assist prediction of effects of climate change (T. Skråppa, pers. comm.).

2. Fast formation of land races in forest trees

But to forecast temperature effects on tree and forest functioning we need information, not only on the population dynamics in the present tree generations, but also about the dynamic change from one generation to the next (Loehle & LeBlanc, 1996). We may learn something from migration history, from progeny performance from seeds produced in transferred provenance trials or plantings, and from experiences with seeds from translocated seed orchards.

After the last ice age, conifer species migrated at an average rate of 10–40 km per century (maximum migration rate for white spruce: 200 km per century; Schwartz, 1991). Norway spruce, a relatively young species on the Scandinavian Peninsula, may serve as an example. It migrated from the Russian retreat, through the forest area at the present border between Russia and Finland, and passed through Finland and northern Sweden into Norway in the period 3500–500 BC (Moe, 1970; Schmidt-Vogt, 1977). Kullmann (1995) suggested an earlier establishment of the species in some areas. The border area between Sweden and central Norway was crossed approx. 500 BC. In the southern part of Norway the earliest immigration took place in the area between the present border between Norway and Sweden in the years 400–200 BC. Eight hundred years later the species was established in the Norwegian south-eastern lowlands. The migration up the valleys to its present altitudinal boundaries was not completed until AD 1000–1300. Norway spruce has had a short time to adapt to local Norwegian climatic conditions, taking the long generation interval into account. Nevertheless, the Norwegian provenances show remarkably distinct and strong clinal variation in both bud-set (Kohmann, 1996) and frost hardiness in the autumn (Dæhlen *et al.*, 1995), a provenance differentiation that has evolved without numerous generations of strong natural selection in Norway, and a large within-stand variation in, for example frost hardiness during autumn has been maintained (Skråppa, 1991; Johnsen & Østreg, 1994).

Seedlings from seeds harvested in planted stands with transferred provenances perform differently from seedlings of their original provenance. In Denmark, seedlings from seeds harvested in first generation stands of *Picea sitchensis* have better survival and are less injured by climate than seedlings of the same provenances from direct import from North America (Nielsen, 1994). Similar experiences are found with *Abies normaniana* in Denmark (Nielsen, 1999). In Scotland, seedlings from first generation *Abies grandis* stands perform far better than direct import of the same provenance (Ennos *et al.*, 1998). In Germany, Douglas fir seedlings from German stands perform better than foreign provenances (Kleinschmit

et al., 1974). Thus, a fast formation of 'land races' (from one generation to the next) seems to occur in several conifer species.

Norway spruce provenances have been extensively transferred from southern to northern latitudes in Norway. Seeds that were collected in stands in West Norway (lat. 61°N) and in Central Norway (lat. 64°N) were established with seedlings of origin Harz, Germany (lat. 52°N). In one of the stands included in the study, the mean diameter of 15 trees of Harz origin was 24% larger than that of the 15 trees sampled in the adjacent stand of local provenance. In spite of this difference among the mother trees, large differences in the timing of bud-set were observed between the progenies from the northern located Harz stand and the original Harz provenance, but not between those of the northern Harz stand and the native northern provenances (Skråppa & Kohmann, 1997, Fig. 6). New tests have confirmed the very fast formation of 'land races' in Norway spruce, and it is believed that natural selection and pollen flow from the natural northern stands could not be the sole explanation for the very fast adaptation to local condition from one generation to the next (T. Skråppa, pers. comm.). All this points to low risk and good prospects for coniferous trees with increasing temperature, but it remains an open question whether or not a comparable speed of change from one generation to the next is also expressed in angiosperm trees.

3. The seed connection

Another phenomenon may contribute to our understanding of likely effects of climate change, in the light of the fast formation of land races in forest trees. Recent findings show that climate and weather conditions experienced by the parents during sexual reproduction influence the progeny in Norway spruce (Johnsen *et al.*, 1996; Johnsen & Skråppa, 1996, 1997; Balduman *et al.*, 1999; Skråppa & Johnsen, 2000). The phenomenon is expressed in seed orchards established by moving parent trees, propagated as grafts, from north to south, from high to low elevation, or from outdoor to indoor glasshouse conditions (translocated seed orchards). The seed produced under warm conditions gave rise to seedlings with a delayed dehardening and flushing in spring, an extended growth period and delayed growth cessation during summer, and later development of frost hardiness in the autumn compared with seedlings from seeds from the same parents reproduced under colder conditions. These after-effects on progenies endure for many years after sowing (Edwardsen *et al.*, 1996), perhaps throughout the lifetime of the trees. These results were confirmed with controlled cross families, making identical crosses in contrasting environments in outside seed orchards located at latitudes 62°N and 66°N in Finland (Skråppa *et al.*, 1994), inside a heated glasshouse, and in a nearby seed orchard in Norway (Johnsen *et al.*, 1995). The warm conditions in the south or inside the glasshouse gave seedlings a delayed development of autumn frost

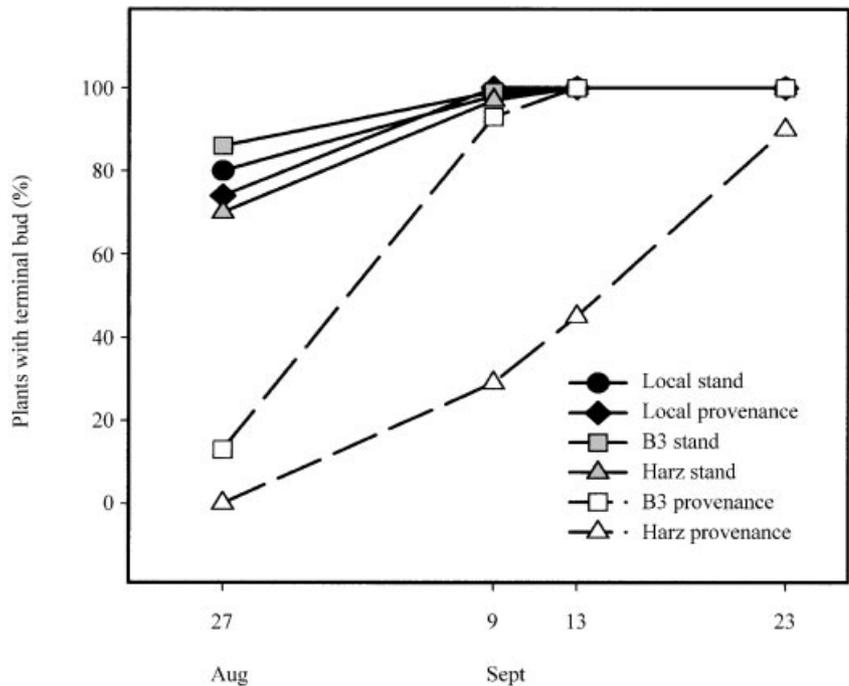


Fig. 6 Mean bud-set (%) development in a nursery in Stiklestad, Norway (64°N) for Norway spruce seedlings of seeds collected in three stands, and planted in central Norway with parent trees of original provenances from central Norway (64°N), south-eastern Norway (B3, 61°N), Harz in Germany (52°N), and seedlings from seeds collected from parent trees located in the original provenance regions (Skrøppa & Kohmann, 1997).

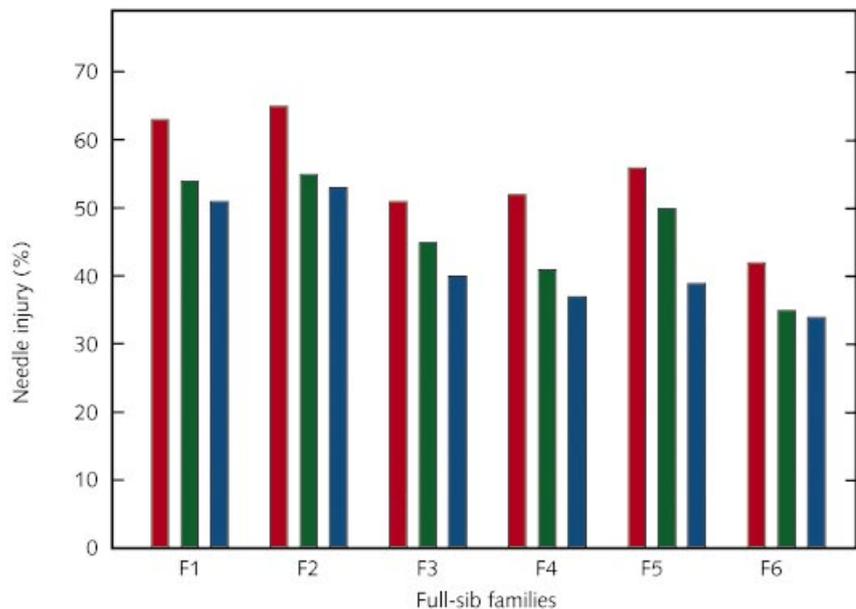


Fig. 7 Frost damage of six unrelated full-sib families as affected by the female reproductive environment. Pollination in the early indoor (red bars) crosses was performed in March, and the late indoor (green bars) and outdoor (blue bars) crosses were performed in May. All indoor grafts were moved out of the glasshouse in the middle of June (Johnsen *et al.*, 1996).

hardiness compared with their full-sibs produced in the northern seed orchard or the colder outside seed orchard. It was of great interest to verify whether this was an after-effect of the male, the female or the general parental environment. Experiments with potted grafts, which had identical growth conditions until the year of sexual reproduction, proved that the altered autumn hardiness of the progenies was not related to differences in temperature and photoperiod given during male meiosis, microsporogenesis and pollen maturation, but to the female reproductive environment (Johnsen *et al.*, 1996).

An early start of the reproductive process inside the glasshouse produced progenies which were less frost hardy than their full-sibs from late spring crosses inside the glasshouse, while the most frost hardy progenies originated from the outdoor, late spring crosses (Fig. 7). A regulatory mechanism was proposed, which senses temperature and/or photoperiod during the reproductive process in the female flowers, and modifies the expression of genes controlling adaptive traits in the progeny (Johnsen *et al.*, 1996). Recent results indicate that the after-effect of the female reproductive environment

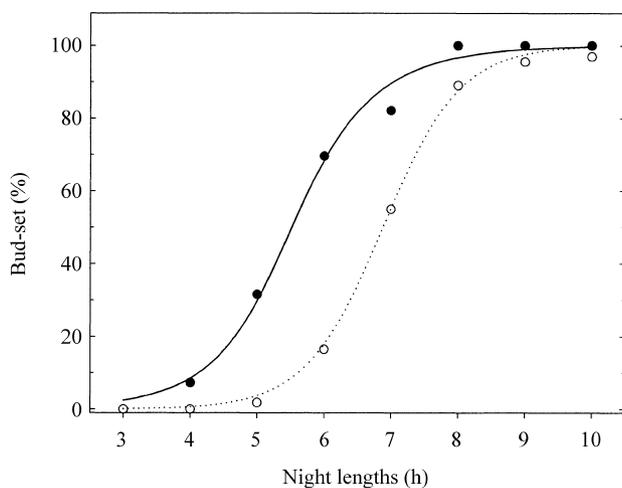


Fig. 8 The photoperiodic response of seedlings from bulked seeds collected from one seed orchard in a warm (1989, open circles) and a cold (1987, closed circles) seed year (Kohmann & Johnsen, 1994).

is a temperature response. Heat differences accumulate during the entire reproductive period from dormant seed cone buds to mature seeds, creating differences in the progeny performance (Ø. Johnsen *et al.* unpublished). Short periods of heat treatments during female meiosis, pollen tube growth and fertilization are not sufficient to affect the progeny. Consequences of these effects have been observed both in field trials and in plantations, resembling experiences of provenance transfers of Norway spruce. The progenies from translocated seed orchards generally show superior height growth, they suffer in early autumn frost events, but benefit in late spring frost due to a later bud flushing compared with the native provenance (Johnsen *et al.*, 1989; T. Skrøppa, unpublished).

Seed year effects within single seed orchards have also been reported. In two seed orchards, seedlings from seeds produced in a cool seed year formed terminal buds at shorter nights both in growth chambers and in nurseries than did seedlings from a warm seed year (Kohmann & Johnsen, 1994) (Fig. 8).

Effects of the female reproductive environment represent a non-Mendelian phenomenon in which phenology and hardiness of progenies are tuned to the characteristics typical for the genotypes native to the environment where reproduction takes place. Reproduction in cold climates under long day advances bud-set and frost hardiness development of the progenies, both hardening in the autumn and dehardening in the spring. Reproduction in warmer climates under shorter days delays these processes even if progenies are produced from the same parental material. Thus, provenance variation is not only influenced by classical evolutionary forces, but also by directional, maternal effects which deterministically influence the progeny according to climatic condition at the sites where the mothers are growing. Similar effects have also been observed in Scots pine (Lindgren & Wang, 1986; Dormling

& Johnsen, 1992; Andersson, 1994; Lindgren & Wei, 1994), white spruce (Bigras & Bonlieu, 1997; Stoehr *et al.*, 1998) and *Larix* spp. (Greenwood & Hutchison, 1996). Adaptive plasticity (Donohue & Schmitt, 1998) is a proper term for the reported effects. Applied to our results with Norway spruce, adaptive plasticity may create phenotypic clinal variation like natural selection. On the other hand, similar to phenotypic plasticity, it may enhance survival of progenies leaving more genotypes to breed and thereby maintaining a larger within-population variation and a different covariation pattern among traits within populations (Johnsen & Skrøppa, 2000). These complex seed connections have implications not only for tree responses to climate change, but on a broader level also about how evolution operates in nature (Jablonka & Lamb, 1995; Amzallag, 1999).

4. Conclusions

Adaptation to varying temperatures revolves around the trade-off between utilizing the full growing season and minimizing frost damage through proper timing of hardening in autumn and dehardening in the spring. In the face of global warming, the evolutionary change in these traits may be too slow to compensate for the anticipated increase in temperature, especially for those species exhibiting a long time between generations. A high degree of phenotypic plasticity could reduce the adverse effect of changing temperatures to some extent. Little is known, however, about the genetics of phenotypic plasticity in trees, let alone the importance of this characteristic relative to natural selection. A surprisingly fast formation of land races has been observed in several conifer species when progenies from first generation of provenance plantings have been tested. A recent discovery has shown that temperature conditions (and perhaps photoperiod) experienced by the female parents during seed production influence the adaptive potential of the progeny in some conifer species. In Norway spruce this non-Mendelian phenomenon tunes progeny performance to the characteristics typical for genotypes native to the environment where reproduction takes place. Reproduction in a cold climate or under cold weather conditions, advances bud-set and frost hardiness development in the autumn and dehardening and flushing in spring in the progenies. A warm climate or warm weather during seed production delays the timing of these processes. Together with natural selection, pollen flow from native populations and phenotypic plasticity, this non-Mendelian phenomenon may explain why conifers so rapidly adapt to new environmental conditions. It remains an open question whether or not this speed of change from one generation to the next is also expressed in angiosperm trees. Before attempts are made to predict and quantify the role of these fast adaptations to future warming, the nature of the environmental signals involved and the molecular mechanism underlying the non-Mendelian phenomenon need to be clarified.

VIII. Ecosystem level responses to warming

1. Net primary production

Net primary production (NPP) is the balance between gross primary production and autotrophic respiration (R_a). Temperature affects NPP mainly by changing rates of photosynthesis, autotrophic respiration, nutrient mineralization, and the period of foliation and frost hardiness (McGuire *et al.*, 1992, 1993; Lloyd & Taylor, 1994; Larcher, 1995; Van Minnen *et al.*, 1995; Melillo *et al.*, 1996). In boreal regions, the net effect is expected, potentially, to be an increase in NPP (Van Cleve *et al.*, 1990; Oechel & Billings, 1992; Van Minnen *et al.*, 1995; Peng & Apps, 1998), but the direct temperature effects on forest NPP will be substantially modified by corresponding changes in the disturbance regime and shifts in vegetation (Neilson, 1993; Melillo *et al.*, 1996; Kurz & Apps, 1999).

In northern forests, temperature effects on N availability may represent the most important control on forest NPP (Pastor *et al.*, 1984; Oechel & Billings, 1992). If C and N cycles remain coupled (i.e. a large fraction of newly available N is taken up by trees) then NPP should increase over the long-term, as changes in system N capital are mirrored by parallel changes in carbon capital (Rastetter *et al.*, 1992; Asner *et al.*, 1997). Thus, if N mineralized from a forest soil with a C : N ratio of 10–50 is taken up by vegetation with a C : N ratio of 60–600 (McGuire *et al.*, 1992), the redistribution of N from soil to vegetation will increase forest NPP (Rastetter *et al.*, 1992; Melillo *et al.*, 1996; Xiao *et al.*, 1998). In temperate deciduous and coniferous forest and taiga, where the vegetation C : N ratio is on average 15 times that of the soil (McGuire *et al.*, 1992), the increase in NPP is expected to range from small (5%; Peng & Apps, 1998) to relatively large (10–45%; Xiao *et al.*, 1998) depending on the climate change scenario. In tropical forests, where the vegetation C : N ratio is only approx. 6 times that of the soil C : N ratio (McGuire *et al.*, 1992), the temperature-induced increase in NPP is expected to be smaller (King *et al.*, 1997b; Xiao *et al.*, 1998).

If C and N cycles become uncoupled, then NPP may or may not increase due to climate change depending on what causes these cycles to become uncoupled (Rastetter *et al.*, 1992; Melillo *et al.*, 1996). Uncoupling resulting from enhanced atmospheric N deposition may increase NPP by alleviating N limitation (Kauppi *et al.*, 1992; Rastetter *et al.*, 1992) unless soil 'N saturation' induces acidification and limitations in other nutrients (Schulze, 1989; Asner *et al.*, 1997). Uncoupling also arises if rates of soil respiration (and N mineralization) respond more rapidly to temperature than rates of NPP and/or N uptake (Melillo *et al.*, 1996). In these situations, mineralized N may be lost from the system due to denitrification, and/or leaching, thus reducing the soil N capital and the forest NPP response. However, fine root

production is highly correlated with N availability and NPP (Nadelhoffer *et al.*, 1985; Nadelhoffer & Raich, 1992), so rapid root growth could counteract the potential for long-term losses of N from forest soils (Van Cleve *et al.*, 1990). Because soil microbes compete effectively with plant roots for mineralized N, prolonged immobilization of N in microbial biomass could also uncouple N mineralization and plant uptake (Zak *et al.*, 1990; Aber *et al.*, 1993; Moorhead & Reynolds, 1993; Hart *et al.*, 1994).

Simulations of the effects on ecosystems of business-as-usual climate change scenarios with elevated atmospheric $[CO_2]$ predict large potential increases in global forest NPP over the next 50–100 yr, especially at high latitudes (White *et al.*, 2000a) due principally to CO_2 and N-enhanced photosynthesis, increased N uptake and C : N ratio of vegetation (McGuire *et al.*, 1992, 1993; Rastetter *et al.*, 1992; VEMAP Members, 1995; Peng & Apps, 1998). In regions where temperature change may reduce soil moisture (i.e. Southern Europe, Southeast Asia, and Australia) (Fig. 9), elevated atmospheric $[CO_2]$ may increase NPP by increasing stomatal conductance and alleviating drought stress (McGuire *et al.*, 1992, 1993; Xiao *et al.*, 1998). However, the effects of elevated CO_2 on alleviating drought stress are unclear, because although elevated CO_2 can cause declines in stomatal conductance, the degree of stomatal closure may vary depending on environmental conditions (Heath, 1998; Bunce, 2000), and an increase in leaf area under elevated CO_2 may ultimately lead to a higher water use on a whole-plant basis (Heath *et al.*, 1997). If water use increases, then the interaction between temperature and elevated CO_2 may exacerbate soil water limitation, causing declines in NPP in arid and semiarid forests.

Temperature-induced changes in disturbance regimes could have a major impact on forest NPP because early and mid-successional species have relatively higher productivity than late successional species (Houghton *et al.*, 1998). Kurz & Apps (1999) argued that the productivity of Canadian forests is likely to decline in the future, regardless of climate change and/or elevated atmospheric $[CO_2]$, because forests are approaching older, less productive age classes. An increase in fire frequency with climate change, may reset many Canadian forests to more productive early and mid-successional age classes. But more frequent fires also lead to large losses in soil C and N, especially for tropical regions, causing NPP to decline (Asner *et al.*, 1997). Clearly, interactions between temperature, atmospheric $[CO_2]$, and disturbance have profound implications for forest NPP.

2. Net ecosystem production

Net ecosystem production (NEP) is the difference between NPP and heterotrophic ('soil') respiration (R_h) (Melillo *et al.*, 1996); if it is positive, there is an increase in the net C storage of the ecosystem. Because both NPP and R_h are large temperature-sensitive quantities, temperature change and

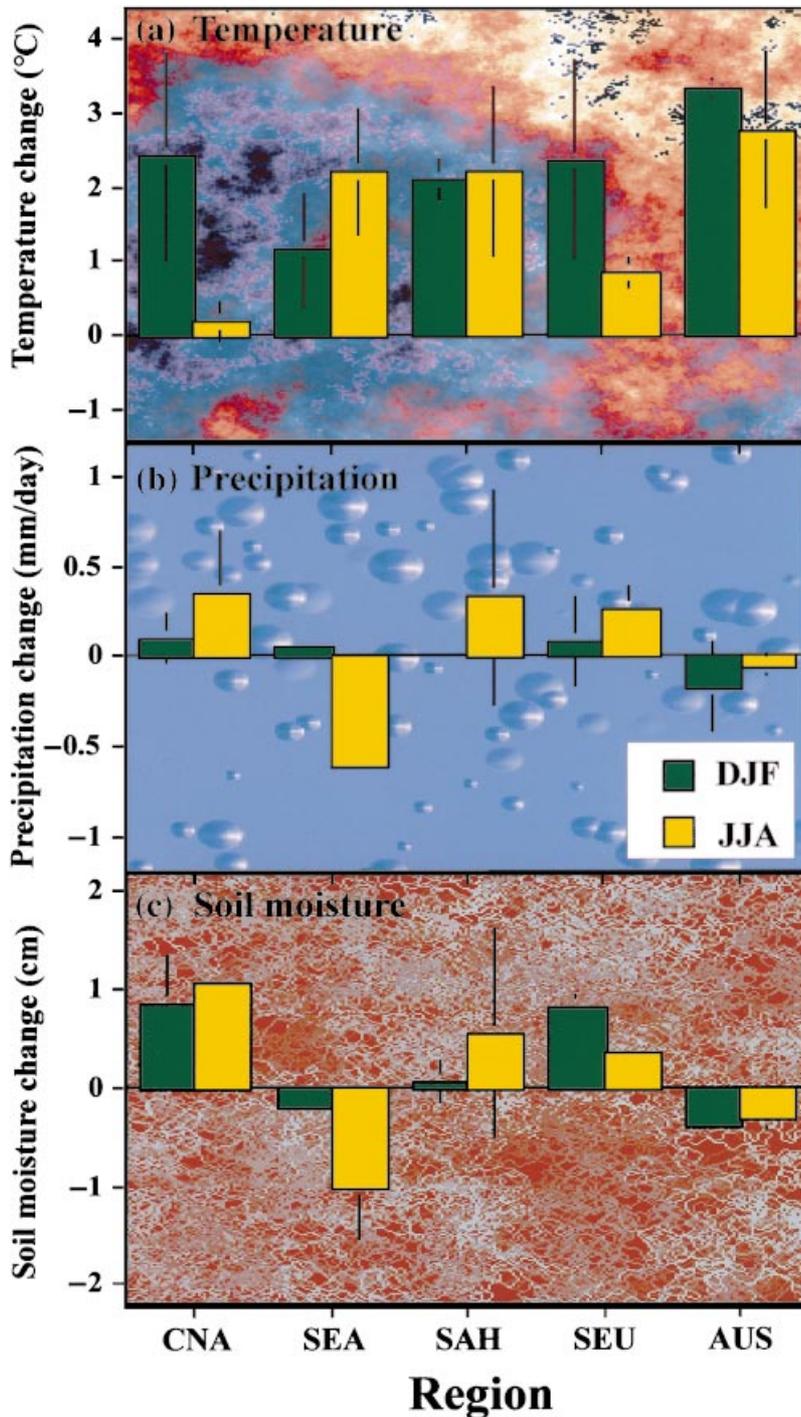


Fig. 9 Simulated winter (December, January, February (DJF), green bars) and summer (June, July, August (JJA), yellow bars) temperature (a) precipitation (b) and soil moisture change (c) for Central North America (CNA), South-east Asia (SEA), the Sahel (SAH), Southern Europe (SEU), and Australia (AUS). Data represent the average change in temperature, precipitation, and soil moisture from preindustrial to 2030–2050 due to atmospheric greenhouse gas and aerosol forcing as predicted by the UKMO-GCM and MRI-GCM. Redrawn from Kattenberg *et al.* (1996).

associated changes in hydrology and disturbance can profoundly alter NEP. Transient changes in the magnitude and direction of NEP may be large as ecosystem components adjust to climate change (Oechel *et al.*, 1993; Oechel & Vourlitis, 1994; VEMAP Members, 1995; McKane *et al.*, 1997; Xiao *et al.*, 1998).

There is considerable evidence that northern forests and other terrestrial ecosystems may currently be a carbon sink –

that is, NEP is positive, presumably in response to increasing $[\text{CO}_2]$, temperature and N deposition. Certainly, a terrestrial sink is required to balance the global carbon budget (Houghton *et al.*, 1998). There is evidence for a northern C sink from analyses of the global CO_2 flask network (Conway *et al.*, 1994), isotope tracers and both forward and inverse modelling of atmospheric $[\text{CO}_2]$ concentrations (Ciais *et al.*, 1995; Denning *et al.*, 1995; Enting *et al.*, 1995), direct measurements of NEP

from eddy covariance (Wofsy *et al.*, 1993; Goulden *et al.*, 1996a; Chen *et al.*, 1999; Valentini *et al.*, 2000; but see Goulden *et al.*, 1998), and the increasing seasonal amplitude of $[\text{CO}_2]$ at northern latitudes (Keeling *et al.*, 1996; Randerson *et al.*, 1997). Also, there is evidence that many forests are growing faster than hitherto, from analyses of growth data across Europe (Spiecker *et al.*, 1996), tree ring patterns average over northern regions and near the tree-line (Briffa *et al.*, 1998; Rolland *et al.*, 1998), satellite and ground observations of growing season length (Goulden *et al.*, 1996b; Myneni *et al.*, 1997) and forest inventories, which combine land use and climate effects (Dixon *et al.*, 1994; Houghton, 1996).

Most simulation models predict an increase in forest NEP with climate change and increasing $[\text{CO}_2]$ over the next 50–100 yr, especially at northern latitudes, although they differ in the extent to which photosynthesis is enhanced, water stress is alleviated, N mineralization, plant and soil respiration are increased and root allocation is increased – all of which are uncertain to varying degrees (Norby, 1987; McGuire *et al.*, 1992; Rastetter *et al.*, 1992; Polley *et al.*, 1993; Hudson *et al.*, 1994; VEMAP Members, 1995; Koch & Mooney, 1996; Melillo *et al.*, 1996; King *et al.*, 1997a; Peng & Apps, 1998; Xiao *et al.*, 1998; White *et al.*, 2000a). However, models differ considerably in their predictions of regional distributions in NEP and in the period over which NEP will be increased – as CO_2 enhancement of photosynthesis saturates and soil respiration increases with temperature (Cao & Woodward, 1998; White *et al.*, 2000b).

Climate change alone, without accounting for the direct effects of $[\text{CO}_2]$, is predicted by some models to result in a net loss of carbon (negative NEP) on the assumption that R_h will respond to warming more than NPP, but these estimates may need to be revised if soil respiration is not shown to be an exponential function of temperature (see Section III; VEMAP Members, 1995; White *et al.*, 2000a,b). Other models predict a positive effect of climate change alone on NEP in northern forests, because NPP is greatly enhanced by accelerated N-mineralization (Rastetter *et al.*, 1992; Hudson *et al.*, 1994; VEMAP, 1995; King *et al.*, 1997a; Xiao *et al.*, 1998).

Long-term measurements of NEP in the arctic tundra indicate that climatic warming and drying in the early 1980s resulted in substantial losses of terrestrial carbon (Oechel *et al.*, 1993, 1995). Although warming and drying have continued, net losses of ecosystem C have diminished, and the ecosystem has been a net C sink during warm, dry periods (Vourlitis & Oechel, 1997, 1999), perhaps indicating that the system has adapted metabolically to the change in climate (Oechel *et al.*, 2000). Although the mechanism is unclear, it is possible that ecosystem adjustment, increases in N availability and/or changes in plant community composition could stimulate NPP enough to compensate for C losses from decomposition (Rastetter *et al.*, 1992; Chapin *et al.*, 1995; McKane *et al.*, 1997).

Temperature-induced change in the distribution of species and vegetation types (Section VI) may have a significant

effect on NEP. The Hybrid model suggests that about 30% of the predicted increase in NEP at northern latitudes this century could potentially be attributable to increased forest area (White *et al.*, 2000a). Indeed, data collected from soil cores in northern Alaska indicate that soil C accumulation rates were substantially higher during the warm mid-Holocene ($6.7 \pm 1.6 \text{ g C m}^{-2} \text{ y}^{-1}$) compared with the cool late-Holocene ($1.2 \pm 0.3 \text{ g C m}^{-2} \text{ y}^{-1}$; Marion & Oechel, 1993). The increase in soil C accumulation was due in part to the migration of boreal forest vegetation during the warm mid-Holocene into regions that are currently dominated by wet-sedge arctic tundra (Billings, 1987; Marion & Oechel, 1993). Clearly, the magnitude of this effect depends on the rate and spatial distribution of vegetation change, the type of vegetation replacement, changes in the disturbance regime, land use change and climatic and atmospheric effects ($[\text{CO}_2]$ and pollution) on production (Melillo *et al.*, 1996). Some early models predicted large transient losses of C as forests die back, recruit, and redistribute (Neilson, 1993; Smith & Shugart, 1993). NEP in the temperate region might decline and/or become negative if deciduous forest were replaced by deciduous savanna, conifer forest, or 'mixed' forest, because these new vegetation types have lower rates of NPP than temperate deciduous forest (Van Minnen *et al.*, 1995; VEMAP Members, 1995; King *et al.*, 1997a). In contrast, boreal forest migration into arctic and subarctic tundra is likely to enhance C sequestration in regions currently covered by tundra (Billings, 1987; Marion & Oechel, 1993; Plöchl & Cramer, 1995; White *et al.*, 2000a).

Temperature effects on disturbance regimes (e.g. fire frequency) will also alter long-term C sequestration of forests. These changes will affect both NPP and SOM decomposition by altering the age distribution of forests, litter quantity and quality, soil C and N pools, nutrient availability, microclimate, and the potential for exotic species invasion (D'Antonio & Vitousek, 1992; Asner *et al.*, 1997; Kurz & Apps, 1999).

3. Conclusions

Increasing temperatures have the potential to increase the NPP of northern forests, depending especially on the extent to which additional N is mineralized and is taken up by the trees rather than immobilized or lost to the system. Most models predict that likely scenarios of climate change and increasing $[\text{CO}_2]$ will enhance global forest NPP over the next 50–100 yr, especially at high latitudes. However, changes in disturbance regime may prevent potential increases being realized in some regions, because, for instance, changes in forest age structure. There is considerable evidence that the NPP of northern forests currently exceeds heterotrophic respiration – that is, that they are currently contributing to the terrestrial carbon sink (positive NEP) required to balance the global carbon budget. Most models predict that this sink will persist for many decades in response to increasing $[\text{CO}_2]$ and climate change, but they differ in regional and temporal

detail. Climate change alone is often predicted to produce a carbon source (negative NEP), but this may not be the case if the temperature response functions for soil respiration need to be revised, if N-mineralization is greatly accelerated and/or ecosystems adapt to warmer temperatures, as may be occurring in the arctic tundra. Finally, NEP may be increased in the boreal region by the spread of conifer forests but decreased in temperate regions by the loss of deciduous forests.

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Appendix I. Temperature response functions

The theory of temperature responses of chemical reactions and plant processes has been elaborated by Johnson & Thornley (1985), and Ågren (1985, 1996) and colleagues. It is beyond the scope of this review to cover kinetic theory in any detail. However, this review would be incomplete without noting that, to account for the fact that a 3% increase of absolute temperature leads to a 2–300% increase in reaction rate in simple chemical reactions (Arrhenius, 1889, 1915) formulated his well known relationship between absolute temperature and the rate of a process. However, the Arrhenius function does not provide a convenient or accurate representation of the temperature dependence of biological processes. Arrhenius equations are monotonous functions of the absolute temperature, excluding the possibility of an optimum rate, which is typical for biological systems, where reactions are catalysed by enzymes that lose their catalytic function when denatured at high temperatures. After decades of Arrhenius-plots with added breakpoints to explain enzyme behaviour Kumamoto *et al.* (1971) and Sharpe & DeMichele (1977) formulated a uniform model of the temperature response of poikilotherms (plants, insects, microorganisms). It described the process rate in the whole temperature range and was assumed to have a general applicability for all processes controlled by

enzyme kinetics. The model was later reformulated by Schoolfield *et al.* (1981), and used by Van der Have & De Jong (1996) to describe growth rates and rates of cell differentiation. Various polynomial functions have been used to describe the temperature responses of plant and soil processes. The sigmoidal cubic function is, perhaps, the most transparent with the right overall shape – starting at zero at a minimum temperature, rising nonlinearly with a point of inflexion and a peak rate falling rapidly to zero at a maximum temperature (Cannell & Thornley, 1998). An empirical approach is to use Q_{10} , based on the observation that, over a restricted range, a given temperature increment often increases the reaction rate by a constant factor. The Q_{10} -equation can be algebraically reformulated into an Arrhenius equation (Johnson & Thornley, 1985) but it has no theoretical justification. It is just a convenient expression that has been widely used to describe temperature effects on nutrient- and carbon uptake, respiration and growth (Berry & Raison, 1981; Clarkson *et al.*, 1988; Long, 1991). The rate of development of plants and single organs is often conveniently described using the day-degree concept, where development is linearly related to an achieved temperature sum above a threshold (Laudien, 1973; Sharpe & DeMichele, 1977; Ingestad, 1979; Johnson & Thornley, 1985). This approach implicitly assumes that the development rate has a linear temperature response over the range considered.



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