

Height growth rate tradeoffs determine northern and southern range limits for trees

CRAIG LOEHLE* *Environmental Research Division, Argonne National Laboratory, Argonne, IL 60439, U.S.A.*

Abstract. Identifying the biological determinants of range limits of trees is an unsolved problem of critical importance for predicting the effects of climate change on forests. Data showing that many boreal trees can grow in temperate climates indicate that southern range limits do not necessarily result from excessive temperature *per se*. A growth tradeoff could exist between freezing tolerance and height growth rate if adaptations to tolerate cold climates interfered with growth. Analysis of height growth rate versus freezing tolerance for twenty-two North American trees provided evidence for such a tradeoff. Provenance trials of

numerous tree species also showed that a tradeoff exists within species, indicating a genetic basis for these traits. The result of this tradeoff is that at their southern range margins most species do not suffer from too much heat but rather face competitors with a faster growth rate. The implication for future climate change is that forests will not suffer catastrophic dieback due to increased temperatures but will rather be replaced gradually by faster growing types, perhaps over hundreds of years.

Key words. Biogeography, trees, range limits, ecotone, climate change, North America.

One of the unresolved questions of biogeography concerns the factors governing the geographic range limits of tree species. Given that many species can grow from subtropical to almost boreal conditions, it seems puzzling that species should be limited at all by climate. Traditionally, an optimal temperature has been assumed to exist for the growth of a tree species, with higher or lower temperatures being detrimental to growth. An entire literature of forest growth models (e.g. Botkin, Janak & Wallis, 1972a,b; Solomon, West & Solomon, 1981; Shugart, 1984; Pastor & Post, 1985; Kienast, 1987; Martin, 1992; Botkin, 1993; Levine *et al.*, 1993; Fischlin, Bugmann & Gyalistras, 1995; Urban, Harmon & Halpern, 1995) is based on a unimodal growth response to a measure of temperature such as heat sum or growing degree days, or produces such a response from its photosynthesis function (e.g. Bossel, 1996), as noted by Schenk (1996) and Loehle & LeBlanc (1996). Growth in these models typically declines to zero at the temperatures corresponding to the northern and southern range boundaries. In fact, for many species the best growth is achieved at the southern range limit or even south of this (Farr & Harris, 1979; Roberds *et al.*, 1990; Schenk, 1996). In this paper, I show that the assumption that growth necessarily declines at higher temperatures is invalid and that northern and southern range boundaries result primarily from a tradeoff between cold hardiness and maximum height growth rate.

Growth rate is easily shown to decline as one approaches the typical northern range limit of a tree species (Schenk,

1996; Woodward, 1987). In the northern hemisphere, the most severe constraint a tree faces north of its usual range results from frost damage. Extreme winter cold, particularly when accompanied by wind, can destroy terminal buds, crack trunks, cause scald on the bark, and freeze-dry needles of conifers. Cold temperatures can also limit reproductive activities (Woodward, 1990). Early spring growth is particularly susceptible to late frosts because the tissue is actively growing and is not lignified (Larcher & Bauer, 1981). Although frost damage has been shown to occur in many studies when trees are planted north of their usual range (e.g. Ying, 1991; Mátyás & Yeatman, 1992), why southern species should lack cold hardiness is not obvious. I propose that this deficiency results from a genetically based cost to cold tolerance.

At least three major aspects of cold tolerance can cause reduced growth, including structural investments, physiologic responses, and conservative growth strategies.

Structural aspects of growth response to cold climates involve adaptations to prevent freezing damage. Northern conifer species have needle traits, including increased lignification and internal structural supports, that help prevent the needle from deforming when it is frozen, which would damage the tissue and burst cells. In all types of plants from cold regions, increased dry matter per unit leaf area can be observed resulting from 10 to 40% greater leaf thickness, 20 to 200% greater cell wall thickness, and 50 to 600% greater cuticular thickness (Körner & Larcher, 1988), which, no doubt, are adaptations to cold (particularly at night) during the growing season. Such leaves have a higher production cost, which slows the overall growth rate (Chabot & Hicks, 1982).

* Present address: National Council for Air and Stream Improvement, 552 G. Washington St., Suite 224, Naperville, IL 60540, U.S.A.

A number of physiologic adaptations are involved in cold resistance. Cryoprotectants noted to accumulate in cold-tolerant species include unsaturated lipids, sugars, sugar alcohols, membrane proteins, and ATP (Levitt, 1980; Nakagawara & Sagisaka, 1984; Santarius, 1984; Woodward, 1987). The accumulation of these substances clearly is energy intensive and therefore inhibitory to growth. Furthermore, the accumulation of sugars in leaves might directly inhibit photosynthesis (Larcher and Bauer, 1981). Thus, the physiologic responses that help provide protection against frost damage simultaneously reduce growth rate (Beck, 1988).

Perhaps the biggest single component of the growth tradeoff response is the adoption of an inherently conservative growth strategy by plants growing in cold climates. The small stature and slow growth of plants from cold regions cannot be attributed to their photosynthetic capacity, which is similar to that of plants from warmer regions (Körner & Larcher, 1988), nor exclusively to growing season length. Taylor, Aarssen & Loehle (1990) argued that in impoverished environments, plants should adopt a conservative growth strategy. Because of the short growing season, such plants cannot afford much risk, because regrowth might not be possible. These plants should therefore invest energy in components of growth that reduce risk, such as herbivore defenses and increased frost tolerance. These investments further reduce growth rate. These defense and structural investments will be most worthwhile for evergreen conifers if they keep their needles for many years, as many northern conifers do.

A second feature of conservative growth in relation to cold hardiness involves phenology. In northern regions, daytime temperature is not a good predictor of frost risk (Larcher & Bauer, 1981). Warm days can be accompanied by frost at night, and several weeks of warm weather in spring can be followed by frost and even snow. Northern species have thus evolved a risk-averse strategy that involves delaying bud burst until either a certain amount of cold weather has passed or a substantial heat sum has accumulated. If spring were predictable, we would expect bud burst to be more rapid in the North because of the shorter growing season, but it is not.

Examination of year-to-year variability reveals the same type of problem on a different scale. An initially warm spring, which causes the tree to begin growing very rapidly and to draw down starch reserves to a low level, puts the tree at great risk, because the weather can suddenly get cool, or fall can come early, before the tree has replenished its carbohydrate reserves. The same problem can occur between years; a very good year that allows rapid growth can be followed by a very cool year. A tree that responds fully to the good year might be unable to keep up with respiratory demands in the cool year that follows. Inadequate carbohydrate reserves can interfere with freezing tolerance (Larcher and Bauer, 1981) and can directly cause crown and root dieback.

The net result of these factors is a conservative growth strategy that tracks the long-term average or the worst conditions and fails to respond to enrichment or favourable growing conditions. Trees using such a strategy will maintain

higher minimum carbohydrate levels during flushing, which means that growth is not maximized. Similar conservative growth regimes are exhibited by arid zone species. Studies have shown that the slow growth of northern species is inherent (genetically determined) and cannot be increased much in the greenhouse (Langlet, 1971; Sakai & Larcher, 1987). A northern tree that follows a much less conservative strategy, trembling aspen, typically has many more dead branches in its crown than do nearby spruce and fir (e.g., in the Upper Peninsula of Michigan) and has a much shorter stem life span (though clones persist much longer).

Trees planted north of their ranges suffer from the cold, and many have assumed that trees planted south of their ranges would suffer from the heat. Results of planting studies (e.g. Wright, 1976), however, show notable asymmetry in that trees can be planted successfully much farther south of their southern range limits (200–1000 miles) than north of their northern range limits (50–100 miles). Here 'planted successfully' means that in gardens or plantations, the trees will grow to maturity. For example, the northern species *Larix gmelinii*, *Larix laricina*, *Picea glauca*, and *Pinus sylvestris* can all grow hundreds of miles south of their natural ranges, rainfall permitting (Woodward, 1987, 1988). Certain species of the forests of the eastern United States, such as *Cornus florida* and *Nyssa sylvatica*, can be found in eastern Mexico in isolated locations (Dressler, 1954), perhaps having been carried there by birds. Many alpine and arctic plants are extremely tolerant of high temperatures, and in general one cannot distinguish between arctic, temperate, and tropical-moist-habitat types on the basis of heat tolerances, with all three types showing damage at 44–52°C (Gauslaa, 1984; Lange and Lange, 1963; Levitt, 1980; Kappen, 1981). Only a few desert groups of higher plants, such as *Agave* and cactus, have lethal temperatures in the range 55–65°C and may thus be considered truly heat tolerant. This anomaly might result because the soil surface and near-soil air can get quite hot in all regions, and seedlings even of arctic species must therefore be capable of enduring high temperatures. In addition, leaf temperatures on sunny days can exceed air temperatures by 12°C or more (Levitt, 1980). Only a few species have been shown to be limited directly by high temperatures at their southern range limits (Kappen, 1981).

Trees planted south of their normal ranges in the Northern Hemisphere might well encounter increased moisture stress. Over most of North America and Eurasia, more southern regions are increasingly arid, with eastern North America being a notable exception. Thus, in planting trials, the failure of northern species or provenances at southern sites could often result from moisture stress rather than high temperatures. Results of such studies must therefore be interpreted with care.

GROWTH TRADEOFFS

I argue here for the existence of a tradeoff between cold hardiness (in terms of both frost tolerance and growth at low temperatures) and maximum height growth rate. Such a tradeoff would explain the inability of any tree to span all climatic regimes. The general concept that tree species'

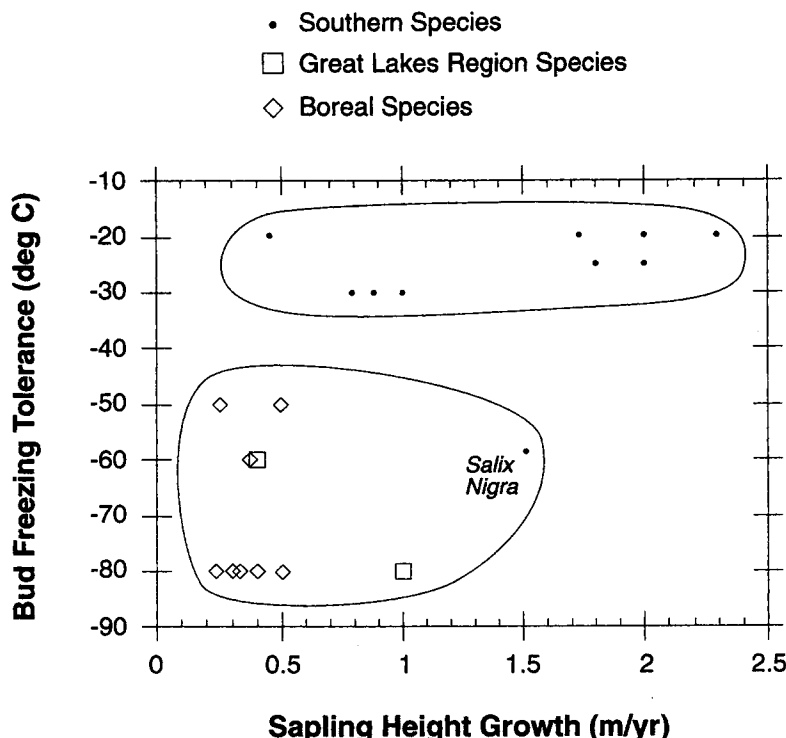


FIG. 1. Bud freezing tolerance versus maximum sapling growth rate for trees from three regions. See text for species. Circled regions depict groupings identified by cluster analysis. *Populus deltoides* cluster off the graph to the far right. *Salix nigra* identified as the only misclassified species (discussed in text).

southern limits might be governed by competition rather than temperature has been proposed before (e.g. Schenk, 1996; Woodward, 1987, 1988); however, (1) the nature of the competitive interaction has not previously been specified, and (2) the vast majority of forest growth models have assumed that temperature or moisture limitation is the determinant of southern range limits.

Tradeoffs are widely observed in studies of plant growth. Adaptations that favor survival under one set of conditions will generally reduce growth rate or survival elsewhere. For example, shade tolerance is traded off against growth rate and drought tolerance (Huston, 1994). Chemical and structural defenses that increase life span generally reduce growth rate (Loehle, 1988; 1996). In the case of the proposed tradeoff between cold hardiness and height growth rate, it is necessary to first obtain evidence that such a tradeoff exists, then to explain the tradeoff in terms of morphology and physiology.

To analyse the proposed tradeoff relationship (Figure 1), data on freezing tolerance were obtained from Sakai & Weiser (1973). Boreal and Great Lakes states species were sampled near Rhinelander, Wisconsin, and southern species in the Gulf Coast region. Buds were subjected to lower temperatures until they showed signs of damage. The coldest temperature tested was -80°C ; species with this level of tolerance might actually tolerate colder temperatures. Data on maximum height growth rate were obtained from Burns & Honkala (1990). Maximum growth rates were estimated from data for saplings and pole-sized trees growing on the best sites (highest site index), generally from the Upper

Midwest or Ontario for northern species and from Gulf Coast sites for southern species. Data were available for almost the complete set of major eastern boreal species: *Abies balsamifera*, *Betula papyrifera*, *Larix laricina*, *Picea glauca*, *Picea mariana*, *Pinus banksiana*, *Pinus resinosa*, *Populus balsamifera*, *Populus tremuloides*, and *Thuja occidentalis*. Height growth rate data for the two *Populus* species were estimated from descriptions in Burns & Honkala (1990) and the author's measurements. *Pinus strobus* and *Tsuga canadensis* were classified as Great Lakes states species rather than boreal because they occur as far south as the southern Appalachians. Data on freezing tolerance for the southern species *Acer rubrum*, *Fraxinus pennsylvanica*, *Liquidambar styraciflua*, *Magnolia grandiflora*, *Nyssa sylvatica*, *Platanus occidentalis*, *Pinus elliotii*, *Pinus palustris*, *Pinus taeda*, and *Salix nigra* were extracted from Sakai & Weiser (1973). No growth data were available for the three oaks from this study or for *Taxodium distichum*. Growth data for the pines are the author's estimates from field measurements.

The north-south comparison performed here requires uniform drought stress as one moves south. Eastern North America meets this condition, because moderate summer drought can occur across the whole region; however, precipitation increases as one moves south, compensating for increased temperatures. The net effect is that the region from eastern Texas and Missouri eastward and southern Canada southward (and including the Midwest) has nearly a constant net precipitation balance, with precipitation minus potential evapotranspiration varying from 0 to

100 mm/yr with no north–south trend (Kemper, Nicks & Corey, 1994). As a result, fully stocked stands on mesic sites have similar NPP, basal areas, maximum tree heights, and leaf areas across the entire region (Burns & Honkala, 1990; Huston, 1994). This is not true in western North America, Europe, or Central Asia. North–south comparisons in these regions would appear to show faster growth for species that are more cold tolerant, because the more southerly species are strongly limited by moisture where they grow. A growth rate tradeoff analysis requires that regions to be compared have similar moisture regimes.

The plot of these data (Fig. 1) shows a strong tradeoff between maximum height growth rate and cold tolerance, as hypothesized. The height growth rate data and bud freezing tolerance data are both for southern provenances of the species concerned (which should show the highest growth rates for the species), except for the two Great Lakes states species. The hypothesized trends are observed, with the Great Lakes states species being intermediate between northern and southern species. Examination of seedling height growth rates would show an even more extreme contrast, because the seedlings of many of the northern conifers can take 10 yr to reach a height of 0.3 m. One species violates the expected trend observed for these twenty-two species: *Populus deltoides* has maximum height growth rates exceeding 4 m/yr but also tolerates -80°C bud freezing (not plotted). Interestingly, this unusual species has the widest north–south range of the species considered here, with the plains variety extending well into Canada.

A statistical analysis was performed on the data in Fig. 1. Growth rate data were scaled to be comparable to the temperature magnitudes, so that a Euclidean distance cluster analysis could be performed for bud freezing tolerance and height growth rate. The cluster analysis found three clusters ($P < 0.001$). *Populus deltoides* clustered by itself. The northern plus midwestern species formed a cluster, and the southern species formed another, except that *Salix nigra* clustered with the northern species. Thus, twenty out of twenty-two species (91%) clustered according to geographic region.

The exceptions exhibited by *Salix nigra* and *Populus deltoides* to the expected growth tradeoff are also exhibited by some early successional species in Europe (J. Schenk, unpublished data). We can explain this observation in terms of growth strategies. The willow and cottonwood leaf out earlier than other species and exhibit indeterminate growth that continues later into the fall. This extended growing season contributes to the success of these extremely shade intolerant species, which must maximize their growth rates to avoid being overtopped, but this strategy necessitates greater frost tolerance than would be required for other species in the same locality. These two species subvert the expected growth tradeoff by being restricted to only the most favorable microsites, such as stream margins, which are both moist and nutrient rich. This habitat selectivity allows these species to have a much wider north–south range than other species and a faster growth rate than would be predicted from frost tolerance.

Provenance studies provide a second excellent source of data on possible growth tradeoffs. In a provenance study, seed from various geographic regions are planted across a

range of conditions. Those that evaluate a north–south gradient are of interest here. The results of a provenance study would support a tradeoff hypothesis if provenances performing best at colder temperatures performed worst at warmer temperatures, and conversely.

A white ash provenance study conducted by Roberds *et al.* (1990) (Fig. 2) provided exactly the expected result. Trees were grown for 6 yr across a range of temperatures. Of seventeen provenances, the two tallest provenances at 4500 degree days were the shortest at the coldest temperature. The tallest four provenances at the coldest temperature crossed over and became the shortest at 3400 degree days. The two provenances with greatest heat tolerance grew on average 0.72 m/yr over the first 6 yr at the warmest temperatures (peak growth rate), versus 0.27 m/yr for the four provenances with greatest cold tolerance at the warmest temperatures tested, a 2.7/1 ratio. This result quite clearly shows a genetic basis for the proposed tradeoff of growth versus cold tolerance.

A provenance study of lodgepole pine (*Pinus contorta*) in British Columbia, Canada (Ying, 1991) provided direct evidence of both cold hardiness and a growth rate tradeoff. Northern interior provenances were taken from various sites in northern British Columbia and the southern Yukon. Central interior provenances were collected from central British Columbia, and southern interior provenances came from southern British Columbia. All sites were from east of the coastal mountain range. For trees grown at the Klokut site in central British Columbia for 15 yr, the fastest height growth was achieved by the southern provenances and the slowest by the northern ones, with survival and freezing damage following the opposite trend (Table 1). By age 15, the northern provenances had 50% more trees surviving and with minimal frost damage. These results are further supported by a study on the related jack pine (*Pinus banksiana*) by Mátyás & Yeatman (1992) in which southern provenances had a faster growth rate at all sites but exhibited increasing mortality relative to northern types as they were planted farther north. Thus the genetically determined faster growth of southern ecotypes led to increased mortality under colder conditions.

The net effect of these several responses to cold climates is a greater allocation to biomass components that do not produce rapid growth and an overall conservatism that leads to slow height growth even under the best (e.g. greenhouse) conditions. This generalization holds even for trees that can reach 50 m when mature. It is this inherent tradeoff that determines the southern range boundary of a species. Even though southern ecotypes of northern species exhibit more rapid growth and less cold tolerance than northern ecotypes, as shown by the provenance studies cited above, gene flow through continuous populations limits the extent to which local adaptation can occur. Nevertheless, the widespread occurrence of north–south clines in growth rate/cold tolerance ecotypes does help to explain how so many tree species can be adapted to such a wide north–south range. No single genotype is this flexible. Regional ecotypes could help explain the extreme North–South range of *Populus deltoides*.

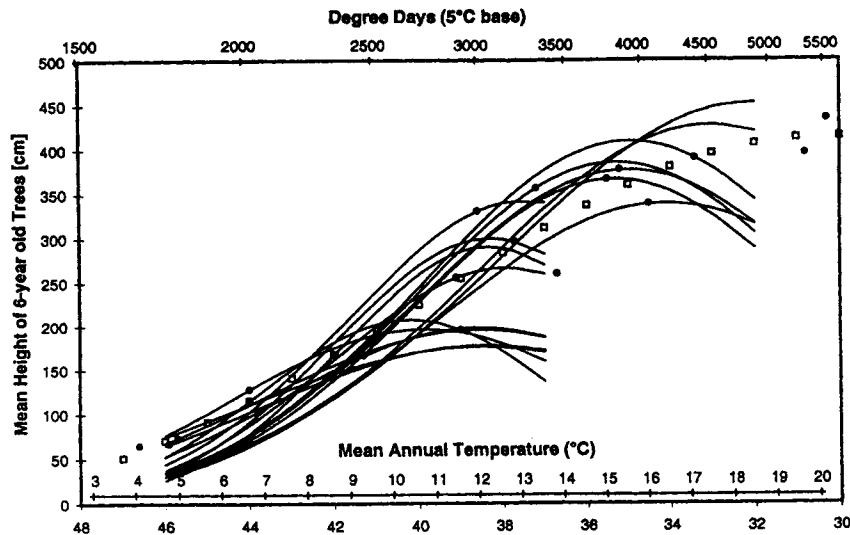


FIG. 2. Provenance study of white ash. Seed lots from different regions were grown under a range of temperature regimes. The plot shows that genotypes growing but under cold conditions grew worst under warm conditions, and conversely. From Schenk (1996) by permission, based on data in Roberds *et al.* (1990).

TABLE 1. Growth response and survivorship of lodgepole pine at Kloakut site in British Columbia at age 15 (data from Ying, 1991).

Provenance source	Height(cm)	Survival(%)	Surviving and undamaged (%)
N. Interior	240	88	60
C. Interior	275	80	51
S. Interior	286	68	42

It is particularly revealing to compare the average growth rates of regional groups of species across their geographic ranges and farther south on the basis of planting and provenance studies. Boreal species, (e.g. *Picea mariana*, *Picea glauca*, *Pinus resinosa*, *Larix laricina*) grow slowly, from <10cm in height per year in the far north to about 0.3m per year at their southern range limits. Although the growth of these species is clearly limited by growing conditions in the far north, in their southern ranges (e.g. Wisconsin, Michigan) it is not. In fact, although these species grow best at their southern range limits, they cannot be induced to grow faster when planted farther south. That is, their maximum height growth rate appears to be inherently slower than that of southern species. Their growth curve thus rises initially with temperature but levels off at a slow growth rate.

Midwestern trees on mesic upland sites typically have maximum height growth rates (for saplings) of about 1m/yr (Burns & Honkala, 1990). These species can typically be planted far to the south with good growth (Wright, 1976), but they will not do well more than 50–100 miles north of their current ranges. Thus, we again get a rising growth rate curve with increasing growing degree days that levels off and is flat across much of the geographic range, with only a slight decline at higher temperatures than those in the species' range. Many studies have shown trees to be

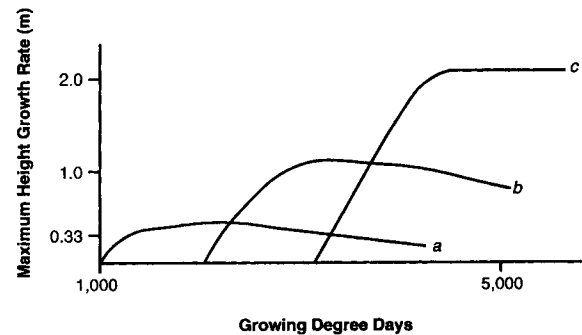


FIG. 3. Typical maximum sapling height growth rates for early successional members of regional U.S. tree floras: (a) boreal species, (b) Midwestern species, (c) southern species. Data from Burns & Honkala (1990) and Loehle (unpublished).

quite indifferent to temperature in the central parts of their ranges, as assessed by tree ring response (Brubaker, 1986).

Southern species are generally intolerant of extreme cold but can have exceptional growth rates exceeding 2m for saplings (open grown, mesic sites) (Burns & Honkala, 1990). In Georgia and South Carolina, the author has measured annual growth rates of >2m for *Pinus taeda*, *Pinus elliotii*, *Pinus palustris*, *Populus deltoides*, *Liriodendron tulipifera*, *Salix nigra*, *Platanus occidentalis*, *Robinia pseudoacacia*, and *Liquidambar styraciflua*.

The maximum growth rate of saplings is critical to competitive success. During the sapling stage, a fast growing tree can establish a competitive asymmetry that eventually leads to the overtopping of close neighbors (Huston, 1994). This asymmetric competitive effect of height growth rate means that this growth trait strongly influences competitive interactions. When we plot the typical regional maximum sapling height growth rates described above as a function of temperature (Fig. 3) for boreal, midwestern, and southern

species, we see a replacement series type of response. As growing conditions become warmer, the northern species become unable to compete against faster growing midwestern species. Similarly, farther south the midwestern species cannot grow as fast as the southern species. The net effect of these differential growth responses is that northern range limits are determined by cool growing seasons and frost damage, but southern range limits are determined by faster height growth rates of southern species.

DISCUSSION

My primary focus has been on the assumption that high temperature determines southern range limits (in the northern hemisphere). This is the primary mechanism invoked in forest simulators, as noted in the introduction. Two other mechanisms are sometimes assumed to govern range limits: chilling requirements and drought stress.

Some recent models have included chilling requirements as determinants of range limits (Burton & Cumming, 1995; Prentice, Sykes & Cramer, 1993; Sykes & Prentice, 1995). For example, if a tree does not experience sufficient winter cold it will require a much greater heat sum before bud burst. While a few species may have some absolute requirement for extreme cold, particularly for successful reproduction, such cold requirements can not be universally used to explain broad trends in species ranges. Most alpine and boreal trees can be grown successfully in greenhouses or in mild climates. For example, the author has observed subalpine fir (*Abies lasiocarpa*) growing in Seattle where extreme frost never occurs. Planting trials have also shown that northern trees can be successfully planted quite far south of their usual range. Temperate and even alpine species have been planted in the tropics. An explanation for these contrary data may have to do with the cold hardiness mechanism. When trees are chilled in the fall, they initiate changes that lead to cold hardiness, commonly called winter dormancy. A certain amount of cold is required to break this dormancy. If strong winter dormancy is not initiated when a tree grows in a warm location, it may be that the cold (or warmth) necessary to break dormancy is not as extreme. This is why a tree can grow under conditions that do not meet the cold requirements estimated from its usual habitat where winter dormancy is more extreme.

A few recent models have used drought stress as a determinant of southern range limits (Prentice *et al.*, 1993; Sykes & Prentice, 1995). Care must be taken when using drought stress as a causal factor, because temperature and precipitation are often correlated with latitude locally. For instance, in Europe drought stress increases as one moves south and southwest. A drought stress factor in a model may produce a very good fit with current geographic ranges, but this may result from a spurious correlation between species range limits and drought, when the real limiting factor is growth rate or both growth rate and drought. Further, a drought-based model may not accurately reflect responses to future, altered climates. Locally, global warming-induced warmer climates can be accompanied by either drier or wetter conditions (Cushman & Spring, 1989). Under warmer and wetter conditions, trees will be affected

by higher temperatures but without any increased drought stress. A model must therefore include both temperature responses and drought stress to be able to predict responses to future altered climates.

We should further note that a drought stress function alone can provide no explanation for range limits of bog, swamp, or streamside species, nor of the often-noticed optimal growth of a species at its southern range limit. If a tree truly is limited by moisture at its southern range limits, it should show an increasing confinement to moist sites as one moves south. One such species might be northern white cedar (*Thuja occidentalis*), which becomes confined to scattered moist sites in the southern part of its range. Most species, however, do not evince this pattern. We must further note that interior boreal forests in North America are often quite dry and are dominated by lodgepole pine (*Pinus contorta*). In this case movement north is not accompanied by increased available moisture, but by the converse. There is an implicit assumption in these models that cold tolerant species need higher moisture. In fact, a number of boreal or alpine species of western North America are quite drought tolerant (white spruce, limber pine, bristlecone pine, lodgepole pine, jack pine). Such a combination yields behaviours that violate the assumptions of models that assume drought stress determination of southern range limits. For example, *Pinus contorta* is very tolerant of cold and drought, but grows slowly under even the best conditions. The lower elevations of western mountains are quite hot and dry, and are dominated by lodgepole pine. As one moves upslope, douglas fir and other rapidly growing trees grow faster than lodgepole under the cool, moist conditions there, and lodgepole is rare. Then, as it gets very cold at high elevations, lodgepole may become important again. In fact, lodgepole spans from nearly the coldest to the driest sites, but across that entire range grows very slowly, as I argue a tree with a conservative strategy should. In eastern North America, there is little if any net moisture change with latitude over quite a wide region, and yet species zonation still exists. Thus while a north-south drying gradient may govern range limits in Europe, drought can not be generally assumed to govern latitudinal gradients and may not be relevant to future climatic conditions.

IMPLICATIONS FOR CLIMATE CHANGE

The proposed explanation for tree geographic range boundaries has major implications for predictions of the effect of climate change on forests. The conventional wisdom (e.g. Houghton *et al.*, 1996) assumes, implicitly or explicitly, that trees cannot persist outside their current geographic ranges as determined by climate. This assumption leads to predictions of serious problems following warming, including forest dieback, range shrinkages, and increased insect outbreaks. However, this study suggests a different outcome. Warming moves a tree to the right along its temperature response curve (Fig. 3). This does not result in a major decline in growth rate (as long as net moisture stress remains constant). Thus, for existing adult trees it will be difficult to detect a change in growth. Invading southern species at the northern edge of their range will

have an increased growth rate as they move to the right on their response curves. However, seedlings of these southern species will not gain much competitive advantage from faster growth in the face of existing stands of northern species, because the existing adult trees have such an advantage due to light interception. Southern types must wait for gap replacement, disturbances, or stand break up to utilize their faster growth to gain a position in the stand. Thus, the replacement of species will be delayed at least until the existing trees die, which can be hundreds of years. A simulation of an ecotone using the growth model proposed here (Fig. 3) produced no dieback and a slow rate of ecotone movement north following warming (manuscript in preparation). Furthermore, the faster growing southern species will be initially rare and must spread, perhaps across considerable distances or from initially scattered localities. Thus, the replacement of forest (southern types replacing northern types) will be an inherently slow process (several to many hundreds of years). Although on an evolutionary time scale this replacement process could be catastrophic for species unable to migrate north fast enough, the lag of several hundred years is more than adequate for human mitigation activities to moderate the effects.

Many model studies of climate change effects on forests have assumed a net drying effect or an increased frequency of severe drought. With such scenarios, a focus on modeling drought stress would seem to be appropriate. However, past climate change trends do not vindicate such assumptions. At the last glacial maximum, most of the unglaciated land was both cooler and drier than today. Whether a future climate will be warmer and wetter (as some recent GCMs predict) or not, some local climates will certainly be warmer and wetter. Under these conditions, a proper model of temperature response is crucial. No forest growth models currently include an explicit growth rate tradeoff with height growth, as proposed here, nor have any models not based on the parabolic function succeeded in reproducing geographic trends in species distributions in a region where moisture stress is not correlated with latitude (such as in eastern North America). Proper inclusion of this tradeoff, including both mortality and growth rate considerations, could greatly increase the biological realism of forest models.

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