Forest ecotone response to climate change: sensitivity to temperature response functional forms

Craig Loehle

Abstract: Past simulation studies using a variety of models have generally agreed that climatic warming could have adverse effects on forests, including large-scale diebacks in some regions and drastic range shrinkages of many species. These effects should be most evident at biome transition zones. Other studies have pointed out, however, that past models have used a parabolic temperature response function that is based on geographic range limits rather than functional responses or data and that this parabolic model could exaggerate dieback effects. A new model is proposed for growing degree-days temperature response, which is asymptotic rather than parabolic. In this new model, tree height growth rate increases and then levels off with increasing growing degree-days. Species from more southern regions have a higher asymptote. It is shown that this model can be derived from the integration of a parabolic growth response to temperature over a year-long sinusoidal temperature regime. The SORTIE forest simulation model was modified to incorporate this response function. An ecotonal region was simulated under a warming scenario. The traditional parabolic temperature response model produced a wide zone of dieback following warming. In contrast, the new asymptotic response function produced no dieback and a stable ecotone that migrated north at <100 m/100 years.

Résumé : Des études antérieures de simulation utilisant différents modèles arrivent généralement à la même conclusion que le réchauffement du climat pourrait avoir des effets néfastes sur les forêts, incluant des dépérissements à grande échelle et de fortes réductions de l'aire de répartition de plusieurs espèces. Ces effets devraient se manifester surtout dans les zones de transition des biomes. D'autres études cependant ont souligné le fait que les modèles antérieurs utilisaient une courbe parabolique de croissance en fonction de la température qui est basée sur les limites géographiques de l'aire de répartition plutôt que sur des données ou des réactions fonctionnelles et que ce modèle parabolique pouvait exagérer les effets de dépérissement. Cet article propose un nouveau modèle de croissance asymptotique plutôt que parabolique qui est fonction de la température exprimée en degrés-jours de croissance. Dans ce nouveau modèle, le taux de croissance en hauteur des arbres augmente puis plafonne avec l'augmentation des degrés-jours de croissance. Les espèces des régions plus au sud ont une asymptote plus élevée. On démontre que ce modèle peut être dérivé à partir de l'intégration d'une courbe de croissance parabolique en fonction de la température pour un régime sinusoïdal de température sur une période d'un an. Le modèle de simulation SORTIE utilisé en foresterie a été modifié pour y intégrer cette fonction de croissance. Une région écotone a été simulée en adoptant un scénario de réchauffement. Le modèle parabolique traditionnel de croissance en fonction de la température produit une large zone de dépérissement suite au réchauffement. Par contre, la nouvelle fonction de croissance asymptotique n'engendre pas de dépérissement mais un écotone stable qui migre vers le nord à raison de <100 m/100 ans.

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Introduction

Climate change could have serious effects on forested ecosystems. A number of past simulation studies (e.g., Bonan et al. 1990; Botkin et al. 1989; Dale and Franklin 1989; King and Neilson 1992; Lindner et al. 1996; Overpeck et al. 1991; Pastor and Post 1988; Prentice et al. 1993; Price and Apps 1996; Reed and Desanker 1992; Smith and Shugart 1993; Solomon 1986; Sykes and Prentice 1996; Urban and Shugart 1989; Urban et al. 1993) have suggested that impacts in a variety of forest types could include geographic range shrinkages, conversion to grassland, and catastrophic forest decline or dieback.

C. Loehle. National Council for Air and Stream Improvement, 552 S. Washington Street, Naperville, IL 60564, U.S.A. e-mail: cloehle@ncasi.org

As Loehle and LeBlanc (1996) have noted, however, results of past studies are critically dependent on the temperature response functions used in the models. Most past models have been based on a parabolic temperature response function that varies from 0 to 1 and back to 0 as a function of growing degree-days (gdd, 5°C base), with the lower and upper temperature limits determined by the geographic range's northern and southern limits. As Bonan and Sirois (1992), Loehle (1996), Loehle and LeBlanc (1996), and Schenk (1996) have shown in some detail, this model cannot be verified either mechanistically or empirically.

A new model of temperature response proposed by Loehle (1998) is based on a trade off between cold tolerance and growth rate. In this model, plants grow faster with an increase in gdd up to a plateau that does not change as temperature increases further (Fig. 1). Species from more southern regions have a higher minimum temperature and a higher asymptote (a faster maximum height growth rate). This model

is based on data showing a trade off between cold tolerance and maximum height growth rate (Loehle 1998). Loehle (1998) argued that faster growth rates of southern types lead to their competitive superiority in warmer environments. According to predictions of Loehle and LeBlanc (1996), such a temperature response should produce much less dieback and slower rates of change than the parabolic response model. This new model forms the basis for the present study. A theoretical justification is offered for this model and then the model is applied to a simulated ecotone under a warming scenario.

Ecotone response: theory

A number of authors have argued that ecotones could be sensitive regions for detecting climate change impacts (e.g., di Castri et al. 1988; Neilson 1993; Risser 1995; Solomon 1986; Dyer et al. 1988; Hansen et al. 1992). In an ecotone, a change in climate could cause a measurable shift in species composition, whereas in the middle of a broad forest zone such a change might not occur. Some ecotones, however, may not be suitable indicators of climate change impacts. Forest–grassland boundaries may be particularly unsuitable because these boundaries are usually determined by fire (Puyravaud et al. 1994; Loehle et al. 1996). A second ecotone type that may not be an appropriate zone for monitoring climate change impacts is the montane ecotone (tree line). Kupfer and Cairns (1996) and Noble (1993) argued that montane ecotones are not suitable locations for monitoring climate change, as the trees grow very slowly because of the extreme conditions, and only rarely reproduce successfully. Furthermore, the effects of avalanche damage may dominate in these ecotones. Under these conditions, ecotone response to warming will be very slow.

A temperature-based ecotone within a large forested region is perhaps more likely to demonstrate interpretable and measurable changes as a result of climate change. This is the situation modeled in this study. A pure temperature gradient is modeled, assuming that no moisture gradient is evident over the ecotonal region. For eastern North America, over the distances at which species replacement occurs at their range margins, this simplification is not unjustified. Churkina and Svirezhev (1995) modeled the general situation described above, with a uniform substrate and an environmental variable such as temperature that varies along a gradient. The authors modeled a transect along this gradient. The biomass density dynamics of each vegetation type were considered as a sum of dispersal of vegetation and competitive interaction between two types of vegetation, as follows:

$$[1] \quad \frac{\delta N_1}{\delta t} = D_1 \frac{\delta^2 N_1}{\delta x^2} + N_1[\varepsilon_1(x,t) - l_1 N_1 - c_1 N_2]$$

$$[2] \quad \frac{\delta N_2}{\delta t} = D_2 \frac{\delta^2 N_2}{\delta x^2} + N_2[\varepsilon_2(x,t) - l_2 N_2 - c_2 N_1]$$

Here $N_1(x,t)$, $N_2(x,t)$ are biomass densities of vegetation types; D_1, D_2 represent their diffusivities (radius of individual activity); $\varepsilon_1(x,t)$, $\varepsilon_2(x,t)$ denote individual growth coefficients; and l_1, l_2 and c_1, c_2 are coefficients of intra- and interspecies competition, accordingly. The results show that for symmetric competition, a soft ecotone is formed with a gradual change in species across it. For asymmetric competition, a hard ecotone that is subject to hysteresis is formed. Jesse (1999) applied this approach specifically to the forest–tundra ecotone and found that ecotone movement was much slower than that predicted by steady-state models. This model does not apply to simulations based on the parabolic temperature response function, because in such a model the species are unable to grow in each other's zones rather than being excluded by competition. In a forest, asymmetric competition is the competitive mode because taller trees overtop and shade shorter trees, which means that competition coefficients are not proportional to biomass but are asymmetric, with taller plants having larger competition coefficients. Hysteresis means that a colder climate will cause a faster southward retreat of a range's northern limit compared with the northward expansion of a range's northern limit following warming. Based on this theoretical framework, it can be predicted that the combination of height growth competition asymmetries across an ecotone and long tree life-spans will produce a hard ecotone subject to hysteresis under climate change for the asymptotic model used in this study.

The goal of the present study is to assess the sensitivity of climate change impact projections to the temperature response function used. To do this, a simulation experiment is needed in which only temperature varies, preferably across an ecotone. To meet this objective, I have focused on a region where current temperature gradients are not strongly related to a moisture gradient: eastern North America south of the boreal zone. In this region, precipitation increases with temperature, such that net annual water balance (precipitation – potential evapotranspiration) ranges from 0 to 100 mm more or less randomly across the entire region, except locally because of orographic effects (Kemper et al. 1994). This region is thus suitable for study, because we can model a modest temperature increase along a temperature gradient without confounding a moisture gradient with a temperature gradient. The results of this study may also be relevant to eastern China and other regions. Certain other ecotones do not satisfy the requirements specified here. For example, in Europe as one proceeds to the southeast it becomes both hotter and drier (in terms of moisture deficit). In such a region the shifts in species along this gradient are due as much to moisture-stress differences as to temperature response.

Model description

The basic model used was SORTIE (Pacala et al. 1993, 1996; Ribbens et al. 1994), a spatially explicit individual tree simulator. SORTIE is similar to other forest simulators in that individual trees grow, compete, and die, but it is more realistic because individual trees have specific locations and compete with all neighbors. SORTIE is a hybrid mechanistic–empirical model. Light availability, for example, is calculated mechanistically as an average of seasonal and diurnal sky brightness in all directions from a point, as attenuated by passage through intercepting crowns. Tree crowns are defined as cylinders, with crown width, crown depth, and crown light transmissibility being species-specific parameters based on field data. This calculated value is used to construct a modeled fisheye photograph that is compared with growth rates

measured in the field and calibrated against actual fish-eye photographs. The diameter growth rate determined in this way is used to calculate empirically determined height growth rates (from height–diameter field measurements). Diameter increment also determines mortality rate, though mortality also has a random component. Recruitment is specifically distance dependent, as determined by field data on seed shadows. This spatial component to seed dispersal is a key feature of SORTIE relative to the purpose of this study. Movement of an ecotone in response to climate change will necessarily be limited by seed dispersal distance. Previous models using universal seed rain could not assess recruitment limitation effects or calculate realistic migration rates. SORTIE has been extensively tested (Pacala et al. 1993, 1996; Ribbens et al. 1994).

SORTIE is parameterized from field measurements obtained in Connecticut for *Fagus grandifolia* Ehrh*., Tsuga canadensis* (L.) Carr. (eastern hemlock), *Acer saccharum* Marsh. (sugar maple), *Acer rubrum* L. (red maple)*, Betula alleghaniensis* Britt. (yellow birch)*, Pinus strobus* L. (white pine)*, Quercus rubra* L. (red oak)*, Prunus serotina* Ehrh. (black cherry), and *Fraxinus americana* L. (white ash). This is a fairly complete set of dominant species for New England forests. For the present study, a second set of species that grow farther south was needed. A spatial simulation across a long transect was also needed. Unfortunately, these ideal conditions could not be met, as a 1000 km long transect would take far too long to run with SORTIE. Furthermore, no data set for more southerly species is available. One of the drawbacks of a model like SORTIE is that the fieldwork required to parameterize a new set of species is laborious. These difficulties were overcome as follows: A compressed temperature gradient was used that spans 1800 m and the Connecticut species set was used to create "northern" and "southern" sets of species, with identical parameters except for their growth responses to temperature. Because of the spatial nature of both dispersal and competition in SORTIE, competitive shifts at the ecotone and invasion processes can be specifically modeled.

To simulate a warming scenario, it is generally considered necessary to model drought stress effects directly, because higher temperatures increase evapotranspiration and therefore possible drought stress, and because many forest transition zones have gradients of both temperature and moisture. SORTIE does not incorporate moisture stress. Several factors, however, allow us to ignore moisture-stress effects here. Where effective moisture remains constant across an ecotone, it is possible to ignore moisture stress. If a higher temperature regime is applied across the entire transect and the transect has no moisture gradient, then the ecotone response will be governed mainly by the temperature change, though total net primary productivity across the entire ecotone could decrease somewhat. There is reason to believe that in many regions a warmer climate will also be wetter (e.g., Hennessy et al. 1997; Mahlman 1997; Neilson and Drapek 1998). The goal of this study in any case is to evaluate this temperature response as a single factor, unconfounded by moisture gradients. The model is not intended to model all climate change impacts. Once the realism of alternate temperature response functions has been evaluated, it is possible to model the combined impacts of

temperature and moisture regime changes (see Bugmann and Cramer 1998).

SORTIE does not include a temperature effect on growth. Two temperature response models are compared in this study: the standard parabolic model (used in studies that have predicted dieback) and a new asymptotic model.

Parabolic response function

The standard model is the parabolic response function used in many models:

[3] $f(T) = \max[0, f(D)]$
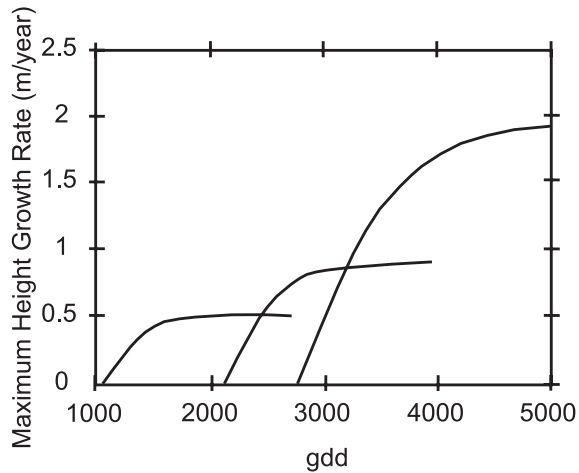
[4] $f(D) = \dfrac{4(D - D_{min})(D_{max} - D)}{(D_{max} - D_{min})^2}$

Here D is degree-days at the site in question, D_{min} is the lowest gdd value the species can tolerate, and D_{max} is the highest value (D_{min} and D_{max} are usually determined from range maps). Note that this model is typically used with a time step of at least 1 year for calculating growth response. For this model, $D_{min} = 800$ and $D_{max} = 3000$ for the northern species group, and $D_{min} = 2000$ and $D_{max} = 5000$ (typical values based on Schenk (1996)) for the southern species group, with all other parameters held constant. It has been asserted (e.g., Loehle 1996; Loehle and LeBlanc 1996) that this model will produce a sharp ecotone subject to diebacks of northern types following warming. The curves of northern and southern types cross at about 2577 gdd, which should be the ecotone transition point.

The standard parabolic model has been assumed to be based on biological principles, using two different arguments. In fact, neither of these arguments holds up under scrutiny. The first argument is based on the well-known fact that photosynthesis measured on short time scales shows a unimodal response to temperature. It is then argued by extension that the overall growth response to temperature should also be unimodal. This is of course true if one grows plants for the same number of days at a range of temperatures from too cold to lethal, with the temperature held constant as in a growth chamber. In the context of models with time steps of 1 year or greater, however, it is not obvious that the heat sum can be substituted into a photosynthesis relation for temperature in a simple way. Schenk (1996) showed that if one models net photosynthesis over the growing season using a daily time step and a unimodal photosynthesis response, there is no adverse effect of a warmer climate and no evidence for a parabolic model. Even if some days are too hot for photosynthesis to be optimal, there are also more days when photosynthesis can occur in a warmer region (e.g., the southeast U.S.A.). The second argument is based on the logical assumption that latitudinal banding results from temperature responses of growth–mortality. While it is true that northern limits (in the Northern Hemisphere) are governed by cold tolerance (Woodward 1987, 1988), there is no evidence for a «heat limit» at southern range margins (see Loehle 1998). Pacala and Hurtt (1993) argued against calibrating a model based on data such as geographic distributions. The option of directly calibrating the parabolic model from growth data across the species' geographic range has never been attempted. Growth rate data from planting trials provide no support for the parabolic model. In

Fig. 1. Replacement series showing that species from warmer habitats have a higher maximum height growth rate (data from Loehle 1998). Slope angles and inflection points are qualitative. From the left, the three curves represent southern boreal, midwestern, and southern U.S species, respectively.

fact, boreal species often experience the best growth at their range's southern margin. Bonan and Sirois (1992) derived a gdd curve for black spruce (*Picea mariana* (Mill.) BSP) from a physiological response model. Their response curve was a very broad parabola with a peak at the southern range limit of the species, and with good growth to at least 3000 gdd. Studies across a transect from the Great Lakes north (Larsen 1965; Mitchell 1967) showed that black spruce has optimal growth at its range's southern margin, and a flat response function between 1000 and 2000 gdd. Similar responses have been found for white spruce (*Picea glauca* (Moench) Voss) (Burns and Honkala 1990). A provenance study of white ash (Roberds et al. 1990) could not detect a downturn in height growth even at 5500 gdd.

Asymptotic response function

The new temperature response model developed by Loehle (1998) provides an alternative hypothesis for the determinants of range limits. This model hypothesizes that trees growing south of their normal geographic ranges do not suffer a growth decline but rather face competitors with a faster height growth rate (Fig. 1). It appears that there is a trade off between cold tolerance and maximum height growth rate, according to data in Loehle (1998). The reason for this trade off is that physiological and morphological adaptations to cold are at the cost of rapid growth. This means that species in the far north are inherently limited in their growth rates and cannot be induced to grow faster than this maximum, even in optimum habitats with longer growing seasons. For example, white spruce grows at 0.2 m/year (sapling rate) or less at its northern limit, but at 0.4 m/year at its southern limit (Burns and Honkala 1990). The rate found at this location cannot be increased by growing the species farther south or in a greenhouse, but growing the species farther south does not damage the trees, if adequate water is provided. In contrast, trees in the southeastern U.S.A. have maximum juvenile height growth rates exceeding 2 m/year but cannot tolerate the same degree of cold. To

take it to the extreme, most boreal species can be planted in the far southern U.S.A. and will survive if there is adequate water, but grow so slowly that they are quickly covered by vines and other growth. While it is logical to assume that there is some daily maximum temperature that will kill trees, this lethal temperature is not reached in regions where forest dominates, and in fact, all tree species have a very similar lethal temperature of about 47°C (Loehle 1998). Only desert species such as cacti have lethal temperatures above 50°C. There is no indication that greater gdd are necessarily harmful to a tree per se. A warmer climate mainly has a longer growing season, but no risk of direct heat lethality to most trees (though a few herbaceous species may so suffer). It is only when warmer is associated with drier that northern species may suffer from drought stress. Otherwise, northern species will maintain their maximum height growth rate in a warmer climate if water permits. The declines in growth that can be observed at higher gdd are modest and occur far south of the species southern range limit and thus do not influence competition or dynamics at the ecotone.
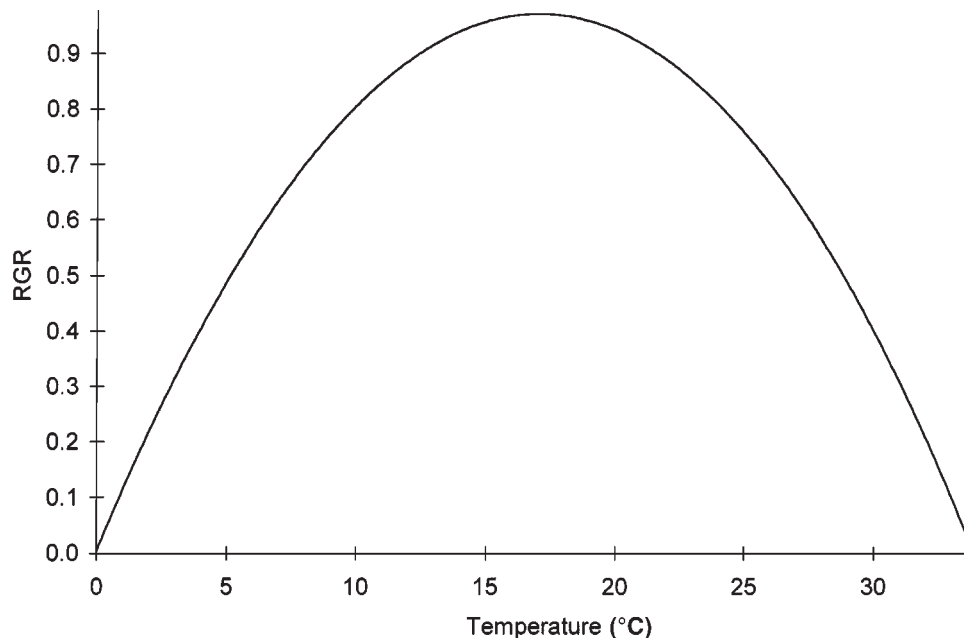
It is possible to derive the new asymptotic function for gdd directly from the temperature response to growth. A traditional model for the temperature response of photosynthesis or whole plant growth is a parabolic response function. This model is well-supported experimentally for short-term measurements of photosynthesis or for whole plants growing under a constant temperature regime. The model is

[5] $$G = PB(t)\left[\frac{4(T - T_{min})(T_{max} - T)}{(T_{max} - T_{min})^2}\right] - RB(t)Q_{10}^{T - T_{ref}}$$

where G is short-term (e.g., daily) growth rate, P is per mass photosynthetic rate, $B(t)$ is biomass at time t, R is respiration rate, T is temperature, T_{min} is minimum temperature for photosynthesis (e.g., 0°C for boreal species and 10°C for southern species), T_{max} is maximum temperature for photosynthesis (35 and 45°C, respectively), Q_{10} is a value such as 2.3, and T_{ref} (the reference temperature for respiration) is 5°C. For a unit biomass, when $P = 1.0$ and $R = 0.02$ (both in g/g), the growth function is parabolic (Fig. 2). Note that the growth rate becomes zero before the maximum photosynthesis value is reached, because of the respiration effect, and can have a negative value reflecting respiration losses at high temperatures.

When applying this growth function to real forests we must incorporate seasonal temperatures. Schenk (1996) showed that the response of such a model to a climate with a given mean temperature is not equivalent to the response of the model to a fixed temperature with the same mean value. A seasonal climate is simulated here with a sinusoidal function that has an increasing mean (and therefore maximum), but a decreasing amplitude as a constant in the model is increased (Fig. 3). The higher between-season temperature difference of boreal vs. temperate regions is captured by this model. Growing degree-days can be summed for each of these curves to find the yearly descriptive statistic. This function is ranged across 0 to 10 000 gdd to derive a gdd function response. If $S(d)$ is the seasonal temperature function value at day d (from Fig. 3), then the total growth Y (in some unit) over the year is

Fig. 2. Instantaneous growth response to temperature (from eq. 5).

[6] $$Y = \int_{d=1}^{365} PB(t)\left(\frac{4[S(d) - T_{min})(T_{max} - S(d)]}{(T_{max} - T_{min})^2} \right)$$

$$- RB(t)Q_{10}^{S(d) - T_{ref}}$$

where negative growth (wasting) is allowed to account for respiratory costs to reserves for high temperatures, but not for low temperatures. Y is computed over a range of gdd values. Assuming an evergreen conifer, the response to gdd for the northern and southern types defined above is shown in Fig. 4.

Remarkably, the integration of a parabolic instantaneous temperature response with a sinusoidal temperature time function is a more or less linear function. Similar results have been obtained in other derivations (Bonan and Sirois 1992; Schenk 1996). This linear function results because even when some days exceed the maximum temperature for photosynthesis, other days may be near the optimum. As an example, conifers in the Pacific Northwest conduct a majority of their photosynthesis not during the hottest months but during the cooler months of spring and fall. This analysis covers the range of temperatures and degrees of seasonality experienced from the Canadian tree line to the southeast Gulf Coast. Over this very wide range, there is no evidence for a decline in growth rate, which could account for the elimination of northern species as we move south. In fact, the northern species should be superior competitors over the entire range.

Comparison of this result with growth data indicates that an additional factor must come into play. Figure 4 indicates that northern species should continue to grow faster as we move south of their normal range. Loehle (1998) proposed that tree height growth rates are a function of their zone of evolutionary adaptation and presented data to this effect. He showed that northern species have much slower maximum height growth rates than southern species (<0.5 vs. >2 m/year)
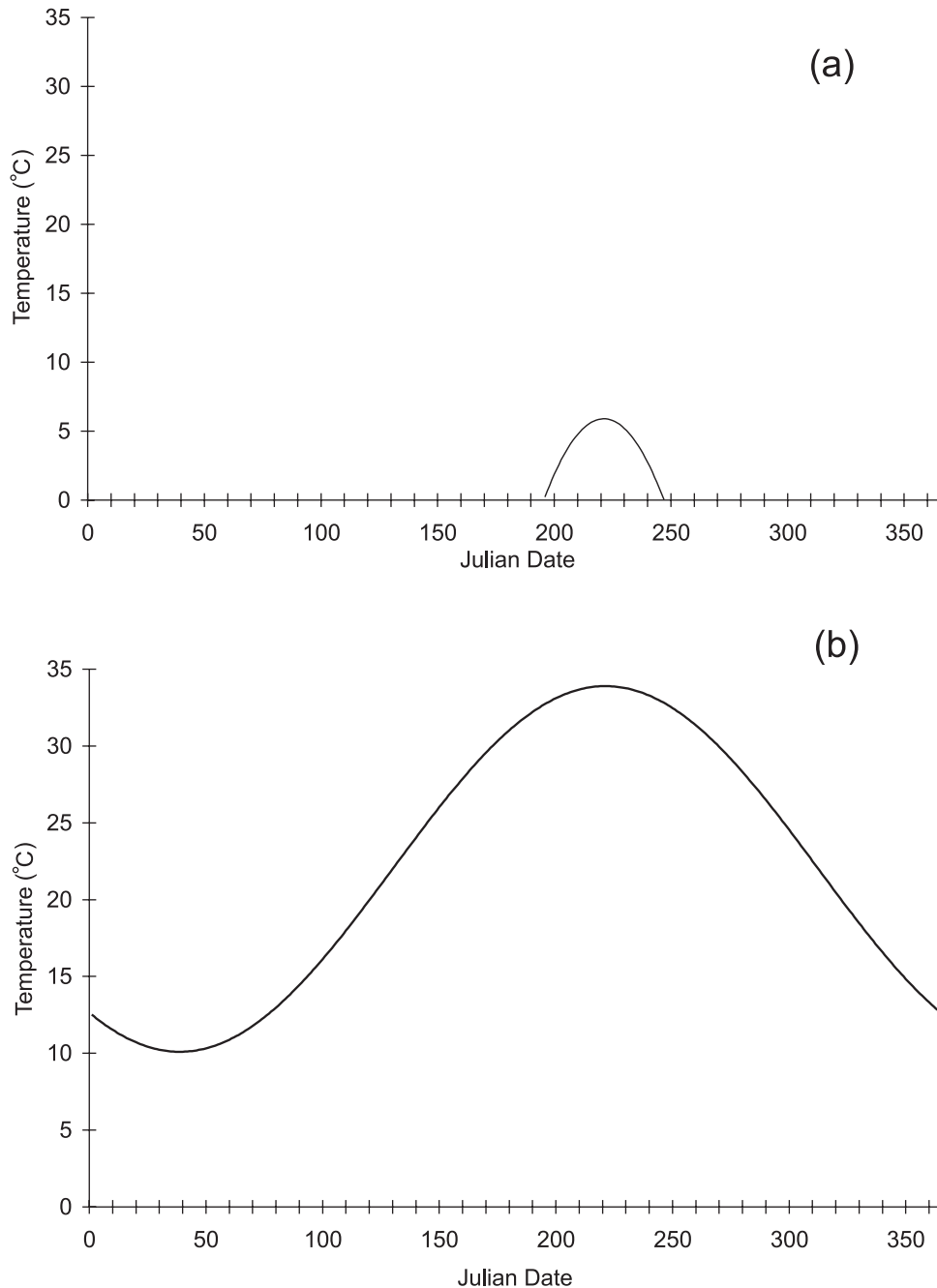
and argued that this is likely a conservative response that has evolved in harsh northern climates.

Based on this analysis, it is argued that when the photosynthetic rate over the year is such that maximum extension growth is achieved, then further photosynthesis is inhibited. Applying this assumption as approximately a simple ceiling function, with southern types having twice the extension limits of northern types, and with 100 units of photosynthesis being converted to 100 arbitrary height growth units, which is assumed to be the northern type's maximum extension rate, we obtain Fig. 5, where we clearly see that the competitive balance shifts from northern to southern types as gdd increases. The gdd value of the crossover is not far from the actual ecotone location for the transition from boreal forest to midwestern temperate forest. Note that in real forests the left-hand portion of the curves is somewhat truncated by the temperature at which freezing death occurs and by the minimum growth rate necessary to compete successfully with other vegetation. This ramp function is approximately the same as the asymptotic function of Loehle (1998).

In the flat region, the tree has an excess photosynthetic capacity; i.e., it is sink limited. This means that if R is larger than the value used here and there is a downward dip in Y at high gdd (as does occur by 10 000 gdd), there will still be an excess photosynthetic capacity relative to the amount necessary to achieve maximum extension growth. While there should perhaps be a dip in the curve as a high gdd value is approached, this does not occur anywhere near the ecotone for the species southern limit, in which range this study is being conducted.

There is some evidence for a response as proposed by this model. Brubaker (1986), for example, noted that tree ring response may be very insensitive to temperature fluctuations across the central portion of a tree's range. This is to be expected if the trees are sink (extension growth) limited. LeBlanc and Foster (1992) studied oaks in the Midwest, us-

Fig. 3. Seasonal temperature trend for *a*) most northern and *b*) most southern ends of the simulated gdd gradient. Only temperatures above freezing contribute to gdd calculations, so only positive temperatures are depicted.
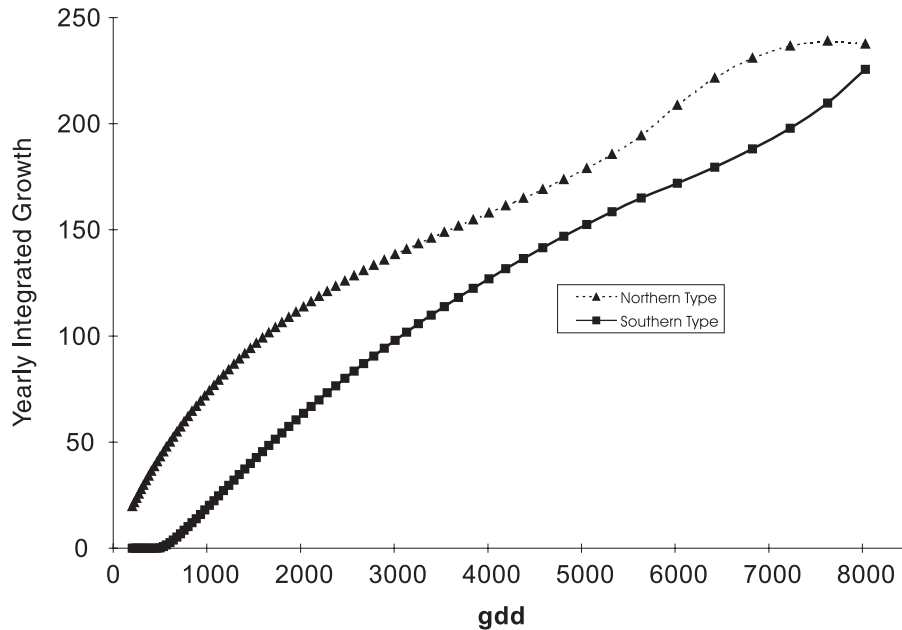

ing dendroecological correlations. They found that a day-to-day integration of growth comparing warmer and cooler years showed that in the warmer years the peak photosynthesis was reduced because of high temperatures, but the longer growing season compensated for this effect, producing little net effect of temperature (in contrast with precipitation, which had a strong effect). Bugmann and Solomon (2000) applied the asymptotic model in the context of a forest simulator to the forests of northwestern and northeastern North America and obtained realistic forest vegetation zones.

The range of applicability of this model is across the boreal and temperate forest zones, such as in eastern North
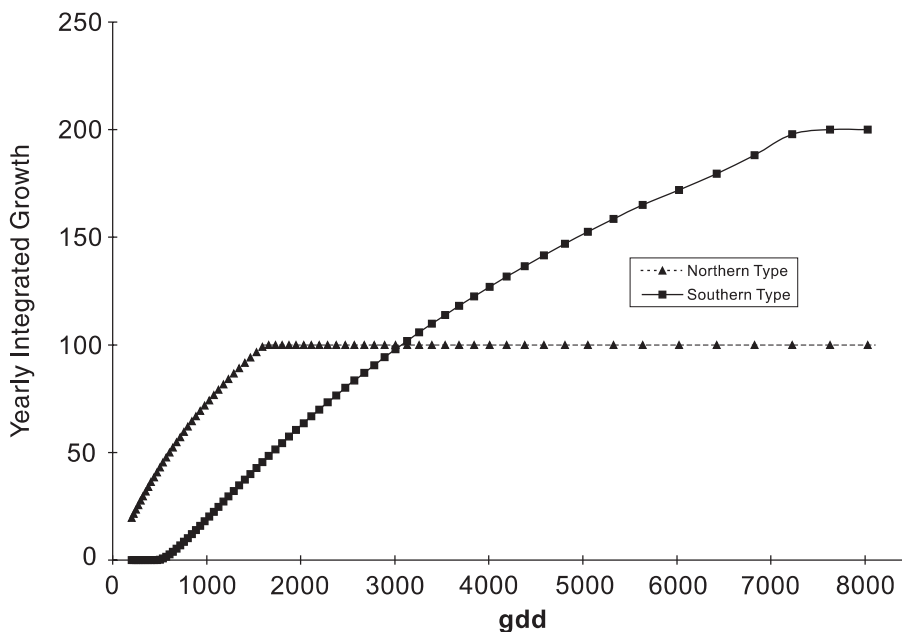
America where temperatures fluctuate seasonally. In the true tropics, a constant high temperature could result in net negative carbon balance because of respiration losses (if the temperature is over 35°C all year, for example) for the boreal species and be suboptimal (but not lethal) for temperate tree growth. Note that failure of the boreal tree to survive in the tropics would result from constant high temperatures and consequent respiration losses, not from temperature lethality per se.

For modeling, the implications of this model are clear. If a model is run using a daily or hourly time step, unrealistic conclusions will not be reached. However, when a yearly in-

Fig. 4. Integrated response (arbitrary units of height) to gdd for northern and southern types from theoretical qualitative model.

Fig. 5. Growth response (arbitrary units of height) to gdd assuming sink limitations from genetically fixed maximum growth rates. Example curves not those used in simulations.

dex like a heat sum or mean temperature is used for running a model on an annual time step, the nonlinearities of the biological processes are compromised and model results are likely to be grossly wrong, with adverse consequences, as Loehle and LeBlanc (1996) noted. Models used to predict climate change transient impacts have necessarily used time steps of 1 year or longer. I next use this new model to evaluate climate change impacts.

Simulation conditions setup

A growth curve is needed for the simulation to match the theoretical results above. Sufficient data do not exist to determine a detailed functional form, but a linear approxima-
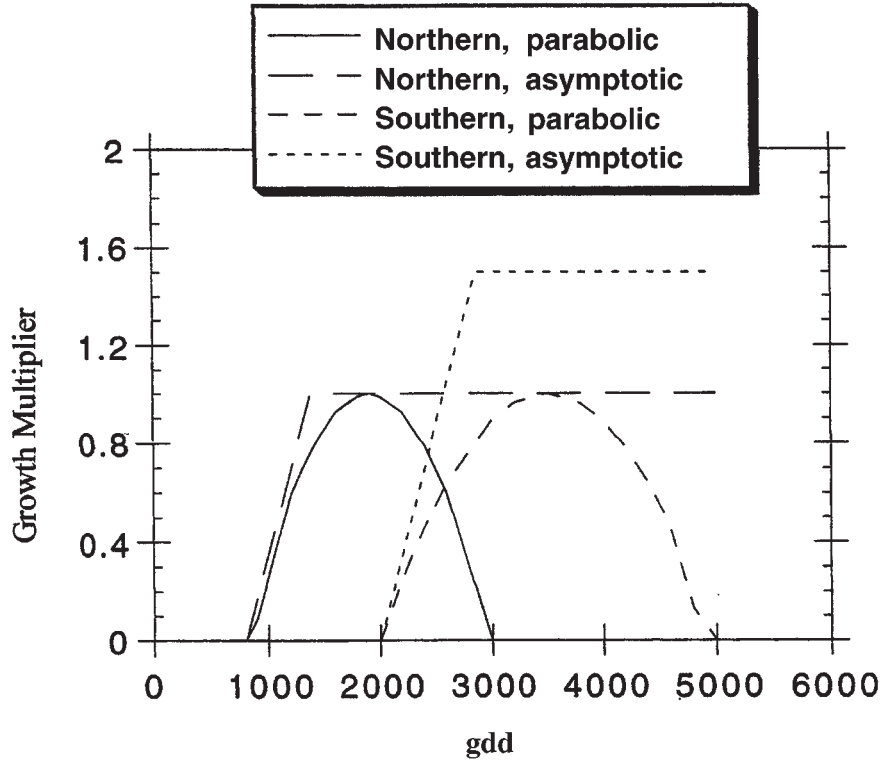
tion to the theoretical asymptotic model captures the essential features of the theoretically derived but cumbersome eq. 6 (Fig. 5). The model, approximated by a linear ramp from the minimum temperature used in the parabolic response model up to the asymptotic maximum growth rate, yields the following:

$$f(T) = \max[0, f(D)]$$

[7] $$f(T) = \min[\alpha, f(D)]$$

$$f(D) = \frac{D - D_{\min}}{\beta}$$

Fig. 6. Model growth multiplier for northern and southern ecotypes using the calibrated parabolic and asymptotic response functions. Representative growth curves are taken from previous models (parabolic) and Loehle (1998) (asymptotic). Growing degree-day range approximately represents the range from the boreal forest to the southeast in the U.S.A.

Table 1. Life-spans and annual mortality probabilities (m) for modeled species.

Species	Maximum life-span	m
Acer rubrum	150	0.045 0074
Acer saccharum	400	0.017 1211
Betula alleghaniensis	300	0.022 7628
Fagus grandifolia	400	0.017 1211
Fraxinus americana	300	0.022 7628
Pinus strobus	450	0.015 2333
Prunus serotina	250	0.027 2528
Quercus rubra	400	0.017 1211
Tsuga canadensis	600	0.011 4469

Note: Life-span data are from Loehle (1988).

as shown in Fig. 6. Here $\alpha = 1.0$ for northern species, and a multiplier is used for faster growth for southern species ($\alpha = 1.5$).

To obtain equivalent ecotone locations with the two models, the northern and southern type's curves must cross at 2577 gdd. At this location, both northern and southern types have $f(D) = 1.0$; thus $\beta = 577$. A comparison of this model with the parabolic model (Fig. 6) shows a significant difference in the way growth rates change across an ecotone: the parabolic model assumes that species drop out because of growth failure as we cross an ecotone in the direction of higher heat sums, whereas the asymptotic model assumes that southern types have a faster growth rate at higher temperatures.

The growth multiplier determined from eq. 6 was multiplied by the nominal diameter growth rate calculated by

SORTIE. With the increased diameter growth rate, faster height growth resulted from the diameter–height correlation used by SORTIE. This height growth rate differential is the proposed mechanism by which southern species are more competitive at higher temperatures.

In the absence of disturbance, at 400 years into the simulation, SORTIE generated a beech–hemlock (63% of basal area) forest that eventually became pure beech, a situation that rarely occurs. Without disturbance, ecotone movement might also be unrealistically slow. Disturbance was therefore applied as follows: Each (10 m × 10 m) cell has a 0.001 probability of being disturbed per year (0.005 per 5-year time step). This is a fairly representative value for frequency of gaps of this size (Runkle 1982; Runkle and Yetter 1987; Tanaka and Nakashizuka 1997). For example, in Tanaka and Nakashizuka (1997) >80% of gaps were <100 m². Gaps smaller than this in the model also result from mortality of individual trees (demographic stochasticity). In a disturbed cell all trees die, opening the canopy. Because tree crowns extend outside a cell and overlap into the cell from adjacent cells, the death of all trees in a 10 m × 10 m cell will produce a range of gap sizes and shapes. Larger disturbances, clearings, and fire were not simulated. With this disturbance regime, all species remained in the simulation after 400 years, and beech and hemlock were much less dominant.

A second necessary change to SORTIE was in the mortality functions. The random mortality function in SORTIE gives each tree a 0.01 chance of dying per year, across all species. This means that 0.6% of the population of each species lives longer than 500 years with this function. For many of the species, this life-span is much too long. Life-span data

were therefore used to recalibrate random mortality. Assuming that very old individuals are rare, we can solve

$$[8] \qquad (1 - m)^n = 0.001$$

where m is the annual mortality probability and n is the number years in the species maximum life-span (from Loehle 1988). The results (Table 1) were used in the simulation. The relative ranking of longevities and the survivorship curves produced by the new model reflect realistic distributions. With the more realistic life-spans, sugar maple, red maple, white ash, and black cherry dropped out of the simulation after 300–400 years. Simulation experiments (not shown) indicate that certain larger disturbances return some of these species to the modeled forest. Thus, the final forest contained five species in both the northern and southern zones.

To test the model, a simulated temperature ecotone was created. A strip of land 650 m × 1800 m (65 × 180 cells) was simulated. In the length, the base number of gdd was 1500. This value was increased by 1 gdd/m up to 3300 gdd at 1800 m. This is a temperature gradient comparable to those found in steep mountain ranges. The model was run for 400 years to establish a growing forest. Initially all species (northern and southern) were seeded randomly across the entire transect, followed by competitive sorting out of zonation. At 400 years, the ecotone transition was well established at approximately 2577 gdd (1077 m). At this point, the temperature along the entire transect was increased by 800 gdd. This warming should cause a shift in the ecotone by 800 m. A comparison was conducted between the two growth models in terms of inertia of response, creation of a dead zone, and rate of movement of southern types.
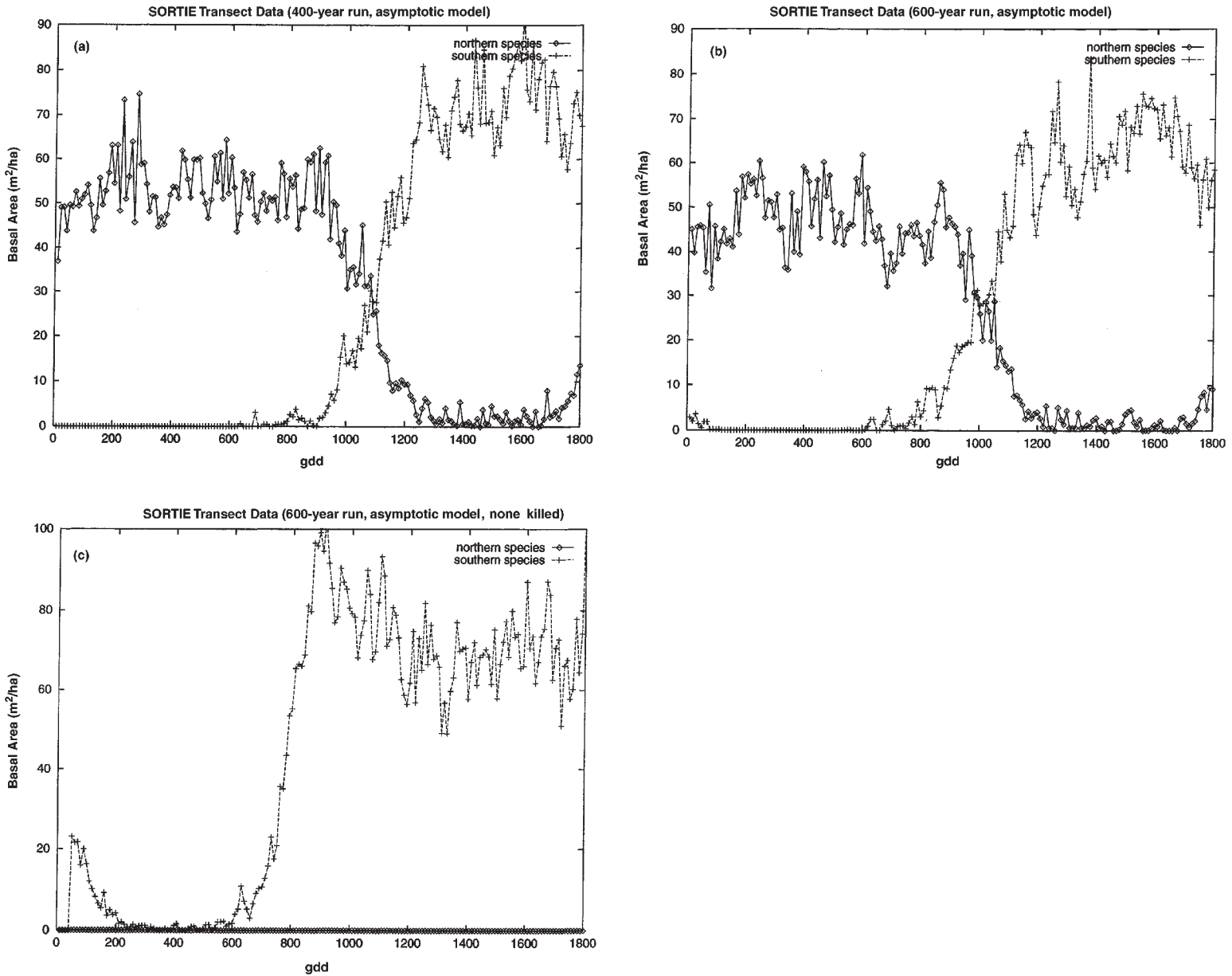
Results

After a 400-year simulation, ecotones had become established. The plot of total basal area versus transect location (Figs. 7 and 8) shows a very similar ecotone structure for both temperature response functions tested. Variability along the transect resulted from both stochastic birth and death processes for individual trees and stochastic disturbances. A wider simulated transect would reduce this variability. In both cases, the abundance crossover point was very close to 1077 m (2577 gdd), as intended for the constructed growth curves. For the asymptotic model, the ecotone is quite sharp, or is a hard ecotone as predicted by eqs. 1 and 2 for the asymmetric competition case (Fig. 7). The southern ecotype with the asymptotic model had slightly higher basal area than either the northern half of its own ecotone or the southern forest type with the parabolic model, as expected (Fig. 7a). Total mean basal areas across the ecotone were within realistic ranges (Pacala et al. 1996) for both temperature response models. The parabolic model showed a curious dip in total basal area in the region of the ecotone (Fig. 8a). This is because the growth of both northern and southern types was well down the relative growth rate parabola from the peak value. When the original longer life-spans were used in SORTIE, the lower mortality rate caused this total basal area dip to be much less pronounced. The dip was also not very evident in the absence of disturbance. This result is thus one indication that the parabolic temperature response

approach is unrealistic because we do not observe a biomass dip at most ecotones. The only other major difference between the two models is the small amount of residual survival of northern trees across the entire reach of the transect in the southern half of the ecotone with the asymptotic model. Stohlgren and Bachand (1997) showed just such a pattern in Colorado montane forests. They established transects in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) stands and studied changes as lodgepole pine integrated with other types. Along the elevation (lower to higher) transects, lodgepole pine decreased abruptly at the upslope transitions to stands of both limber pine and spruce–fir types, but these other types decreased gradually downslope into lodgepole pine stands. The reason for this pattern is that the upslope species can grow adequately in the lodgepole pine zone if they are not overtopped when small, and will persist once established, since the higher temperatures at lower elevations do not cause a decrease in their height growth rate, whereas lodgepole pine cannot tolerate the cold at higher elevations. This asymmetric dominance shift might be characteristic of a temperature-governed ecotone for trees growing according to an asymptotic model. The parabolic temperature response model cannot produce such an asymmetric ecotone pattern, because upper elevation trees cannot grow at lower elevations according to that model.
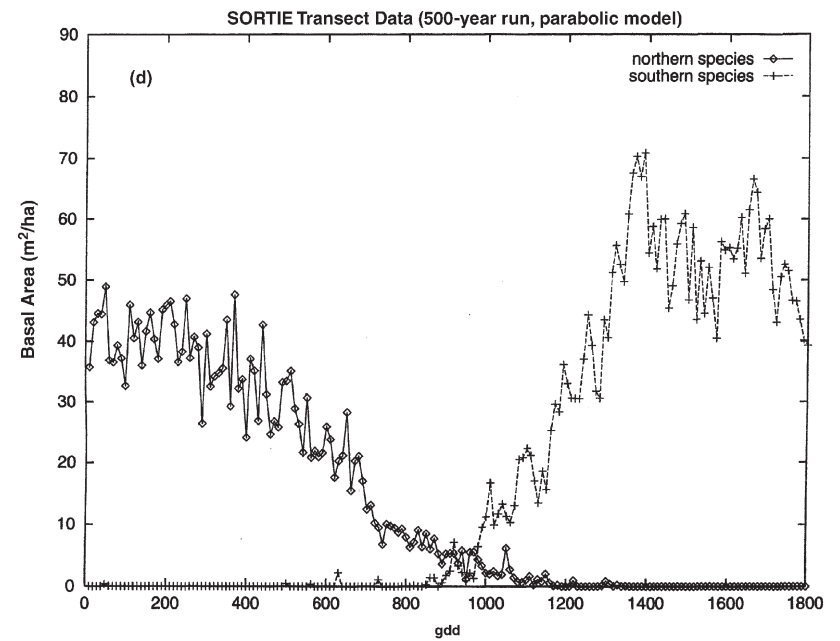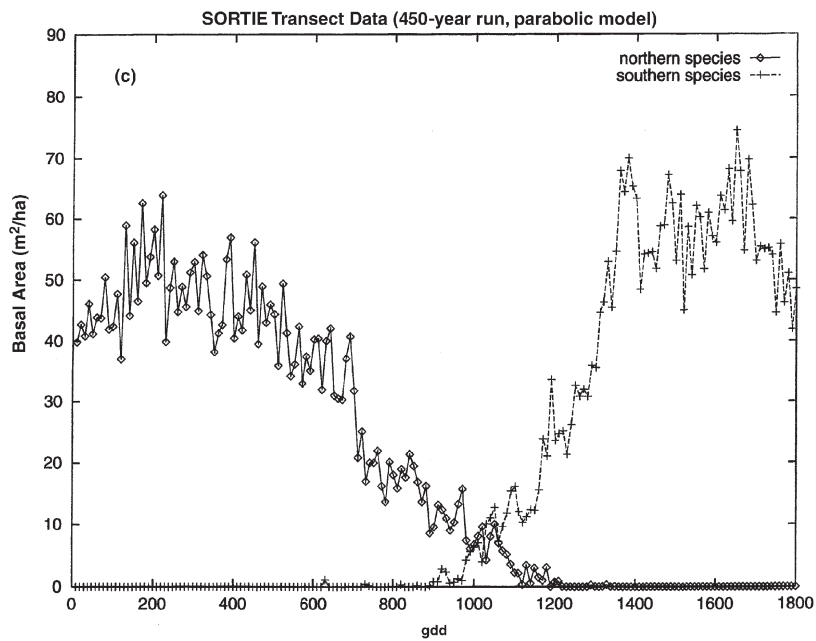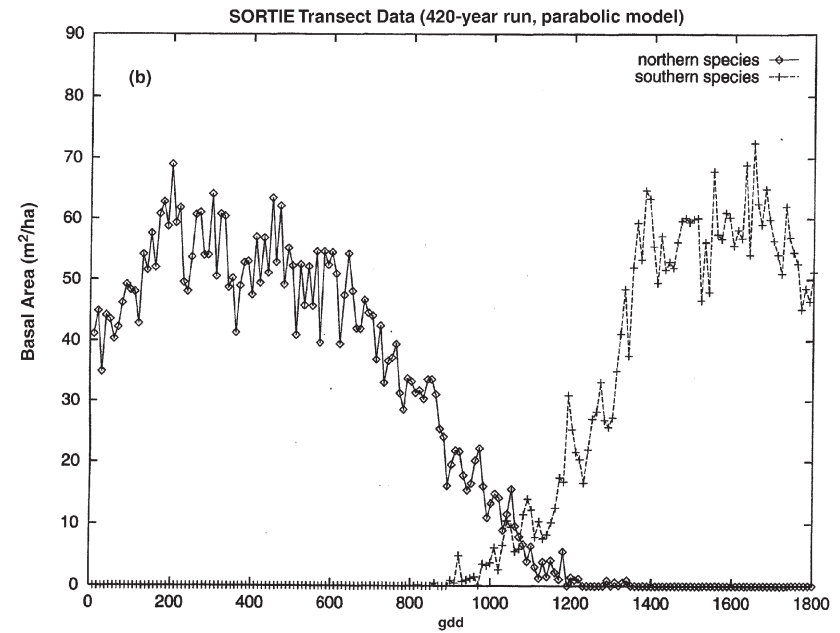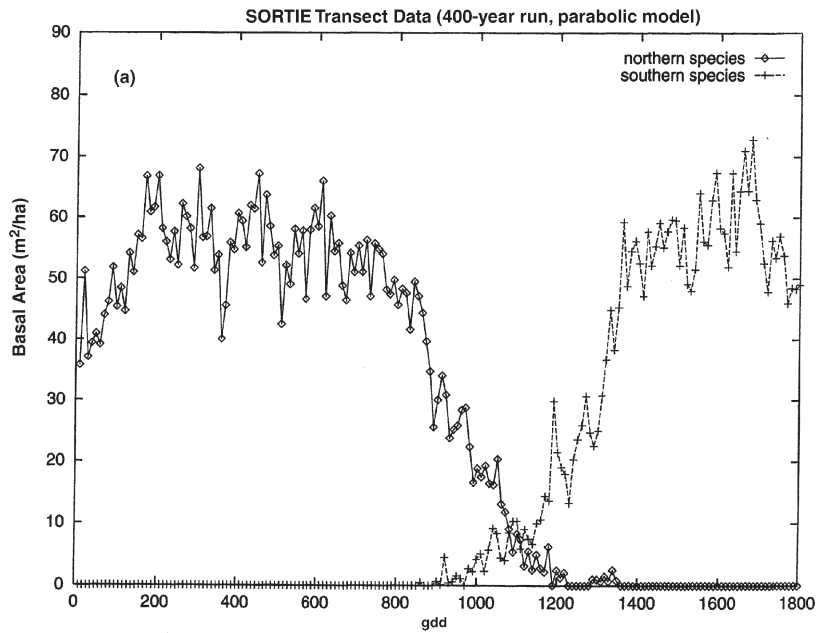
The next step in the experiment was to use the forest at 400 years as the initial condition, raise the temperature by 800 gdd all along the transect, and run the model again for 200 years. The asymptotic growth model showed very little change (Fig. 7b), except for a northern (left) shift of the ecotone by about 100 m. Because we expect the ecotone to shift by the full 800 m (800 gdd), the shift here was obviously a nonequilibrium situation, no doubt limited by the existing northern forest, which continued to grow at full vigor. This resistance to invasion might characterize most forests because of the long life-span of trees and the density dependence of invader population growth along the invasion front.
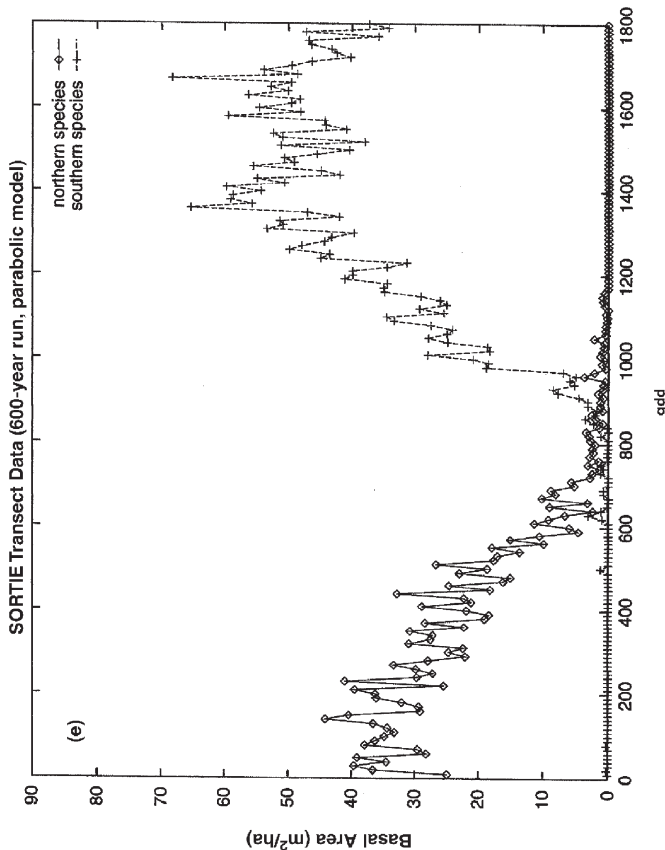
To assess how much the existing northern forest was slowing the spread of the southern forest, another simulation was run. With the 400-year established ecotone as input, all northern trees were removed. Southern species could then invade freely, as if into a large clearing. After 200 years, the southern forest had advanced 450 m. The advancing edge of the forest showed high basal area, because it was dominated by young, fast-growing trees. The blip at the northern end of the transect resulted from wraparound on the torus from the southern edge of the transect, which could not be prevented in the model (to prevent edge effects on the mapped grid, trees on the right edge dispersed seed to the left edge and vice versa for all map borders). This wraparound invasion was not, of course, counted as part of the real invasion process. Without the northern forest, invasion was much faster, which shows that the existing northern forest inhibited the rate of migration north. This is evidence for a hysteresis effect, again as predicted by the simple model (eqs. 1 and 2). We should not consider either of these migration rates to be a maximum rate. The SORTIE seed dispersal function is known to be accurate only for local dispersal. This function captures neither rare distant-dispersal events nor the wide dispersal often observed at forest edges, where wind veloci-

Fig. 7. Ecotone response to asymptotic temperature response function. The ecotone is approximately the point where the northern and southern basal area curves cross. (*a*) 400-year base run. (*b*) 600-year run (for 200 years of higher temperature) with asymptotic temperature response, showing only a gradual ecotone shift. (*c*) 600-year run with northern forest removed at year 400, to show increased migration rate of southern forest with competition removed.

Fig. 8. Ecotone response to parabolic temperature response function. (*a*) 400-year base run. (*b–e*) Time progression of response to warming, showing expansion of dieback zone over time.

ties are high. SORTIE really represents typical dispersal rates in closed forest. In this context, it predicts migration rates of 225 m/100 years without competition and <100 m/ 100 years with competition, but actual rates are probably higher.

In contrast, the parabolic model ecotone showed a very distinct effect from a step increase of 800 gdd (Fig. 8). After 100 years (simulated year 500), a large dieback zone with very low basal area occurred north of the ecotone, where the northern ecotypes had suffered mortality. This result matches those from many previous studies, which predicted dieback to result from warming. After 200 years, the dieback zone persisted and worsened, the southern type had moved north by about 200 m, and a wide zone of northern forest showed reduced basal area. If these results are extended to a geographic scale from the compressed gradient used here, the model predicts that large geographic areas would become almost deforested.

To examine the speed of dieback, short runs of 20 and 50 years were conducted for the parabolic model (Fig. 8). After 20 years of increased temperature, dieback had begun but was not obvious. By 50 years, the southern edge of the northern forest showed decreased basal area. Thus, dieback was gradual over the 100-year period and resulted in part from the failure of patches to grow back after disturbances or tree death. Many past studies have predicted sudden dieback of forests (e.g., Bonan et al. 1990; Botkin et al. 1989; Dale and Franklin 1989; King and Neilson 1992; Lindner et al. 1996; Overpeck et al. 1991; Pastor and Post 1988; Prentice et al. 1993; Price and Apps 1996; Reed and Desanker 1992; Smith and Shugart 1993; Solomon 1986; Sykes and Prentice 1996; Urban and Shugart 1989; Urban et al. 1993). In these models, mortality is often a dichotomous function, with low-level random mortality above some minimum diameter increment and much higher (up to 100%) mortality below this level. A drop of growth rate in such a model will lead to sudden diebacks. In SORTIE, by contrast, mortality is an exponentially falling function of growth rate, and therefore, if there is slower growth it will lead to gradually increased mortality, as observed in the parabolic model simulation. The SORTIE mortality function is the more realistic representation of mortality processes. Thus, this result is consistent with past studies showing dieback when a parabolic temperature response model is used.

Conclusions

Past studies of climate change impacts on forests have depended on certain critical, but untested, model assumptions. The use of the current geographic range to parameterize a parabolic temperature response is an unwarranted modeling shortcut that cannot be supported either theoretically or empirically. Growth data and planting trials indicate an asymptotic temperature response, at least within the range of temperatures present in eastern North America. The parabolic model leads to a rapid (<100 years) forest dieback that can be extrapolated to a wide geographic zone of forest decline or even deforestation in some cases. Simplified mortality functions, in which all trees below some cutoff growth rate die, further accelerate this decline. In contrast, the more realistic temperature response (Loehle 1998) used here leads

to no dieback whatsoever and only a gradual ecotone movement north. A gradual rather than a step warming would of course produce an even slower response. Whereas studies based on equilibrium biogeography response or the parabolic growth model have suggested that drastic range shifts could cause extinctions of species, the results presented here suggest that ecotone shifts will take many hundreds to thousands of years, so that species will not face a risk of extinction.

Acknowledgments

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