PROCESS-BASED MODELING OF SPECIES' DISTRIBUTIONS: WHAT LIMITS TEMPERATE TREE SPECIES' RANGE BOUNDARIES?

XAVIER MORIN,1,3 CAROL AUGSPURGER,2 AND ISABELLE CHUINE1

1Centre d’Ecologie Fonctionnelle et Evolutive, Equipe BIOFLUX, CNRS, 1919, route de Mende, 34293 Montpellier Cedex 5, France
2Department of Plant Biology, University of Illinois, 505 S. Goodwin Avenue, Urbana, Illinois 61801 USA

Abstract. Niche-based models are widely used to understand what environmental factors determine species’ distributions, but they do not provide a clear framework to study the processes involved in defining species’ ranges. Here we used a process-based model to identify these processes and to assess the potential distribution of 17 North American boreal/temperate tree species. Using input of only climate and soil properties, the model reproduced the 17 species’ distributions accurately. Our results allowed us to identify the climatic factors as well as the biological processes involved in limiting species’ ranges. The model showed that climatic constraints limit species’ distributions mainly through their impact on phenological processes, and secondarily through their impact on drought and frost mortality. The northern limit of species’ ranges appears to be caused mainly by the inability to undergo full fruit ripening and/or flowering, while the southern limit is caused by the inability to flower or by frost injury to flowers. These findings about the ecological processes shaping tree species’ distribution represent a crucial step toward obtaining a more complete picture of the potential impact of climate on species’ ranges.

Key words: climate; fundamental niche; geographical distribution; limiting factors; North America; phenology; process-based modeling; temperate trees.

INTRODUCTION

Which environmental factors determine the range boundaries of species and by which mechanisms? This question, which led to the foundation of both ecology and biogeography (Humboldt 1807, Lomolino et al. 2005), is particularly challenging today because of current global changes in climate (Parmesan et al. 1999, Johnstone and Chapin 2003). Indeed, an accurate understanding of how environmental conditions shape species’ distributions at the continental scale is necessary to predict future range shifts of species and their consequences for changes in biodiversity.

Two classes of factors affecting species’ distributions are classically recognized (Brown et al. 1996, Sax 2001). First, “historical” factors point out the role of (1) location that reflects temporal changes in geology, climate, and other environmental variables, and (2) lineages that reflect changes in characters that are phylogenetically constrained. These factors are also called “ultimate” factors as they depend on the evolution of biological traits. They reflect the effects of natural selection on species’ geographical distributions (Brown et al. 1996). Second, “proximate” or functional factors refer to environmental factors that prompt the response of individuals of a species and determine the present distribution of a species (Lomolino et al. 2005).

If ultimate factors are necessary to understand biodiversity patterns, e.g., the number of species present in a certain location, then current distribution limits of each species can be fully grasped only through an understanding of the response of organisms to environmental and biotic factors.

Since the definition of the niche by Hutchinson (1957), it has been generally accepted that many factors interact to define the set of conditions suitable to a species. Extrapolating the local niche definition, the geographic distribution of a species (“realized distribution”) is classically defined as the “fundamental” (or potential) distribution, dependent on physical conditions, reduced by biotic factors (species interactions) and dispersal limitation (Leibold 1995, Pulliam 2000). However, the realized distribution can also be larger than the fundamental distribution in the case of source–sink dynamics (Pulliam 2000). These dynamics occur when “source” populations located within the species’ fundamental distribution disperse individuals into “sink” populations, which are maintained only by a constant flux of new migrants, usually because site conditions do not allow individuals to produce offspring. At the continental scale, however, the role of dispersal in explaining present distributions has received little support (Fenner and Thompson 2005, Morin and Chuine 2006).

To understand the distribution of a species, one needs first to assess its potential distribution, i.e., environmental constraints on its global distribution. Among these constraints, the major role of climate at both continental
and regional scales has long been attested (Merriam 1894, Holdridge 1947, Budyko 1974, Brown 1984) and used to reconstitute paleoclimates from species’ distributions (Guiot 1994). The relationship linking climatic conditions and distributions is thus a basis for numerous statistical (niche-based) models that have been used to forecast present and future distributions of species (Austin 1985, Iverson et al. 1999b, Thuiller 2003, Thomas et al. 2004). Such models can quickly be developed and provide on a very short term predictions of shifts in distribution for a large number of species. These predictions should be viewed with caution, however, because of the possible flaws of these models, mainly the necessity of using the exact entire species distribution for calibration (information that may be very difficult to obtain) and the difficulty of performing an accurate external validation (Loehle and LeBlanc 1996, Bolliger et al. 2000, Fleishman et al. 2003, Thuiller et al. 2004). Thus, niche-based models are a powerful tool to provide predictions in the short-term, but they do not clearly identify the processes involved and may provide inaccurate predictions in the long-term (Loehle and LeBlanc 1996, Thuiller 2004).

Our knowledge of the underlying processes driving the effect of climatic variables on tree species’ geographic distributions at continental scale remains limited, and few examples have been documented (Pigott and Huntley 1981; and see examples cited in Lomolino et al. 2005). Given the difficulty of conducting experiments on the complete distribution of a species, process-based modeling is an alternative tool to study the impact of environmental factors (such as climate) on species’ ranges. Although very few process-based biogeography models currently exist (but see Kleidon and Mooney 2000, Chuine and Beaubien 2001) in comparison with niche-based models, they can bring relevant insights into the impact of climate on species’ ranges at continental and regional scales.

Focusing on trees, MacArthur (1972) proposed that the balance between physical and biotic factors in explaining species’ distributions was dependent on latitude. More precisely, considering the latitudinal gradient in species richness, he proposed that the northern distributional limits were due to physical environmental constraints (especially cold hardness), while the southern distributional limits were caused by competition. Abiotic factors have often been identified as limiting the northern or altitudinal range of species (Sakai and Weisser 1973, Gusta et al. 1983, Korner and Paulsen 2004). However, there is no clear evidence that competition explains the southern range limits at a global scale because some studies support this hypothesis (Loehle 1998, Pither 2003), while others do not (Sax 2001, Schwarz et al. 2003).

The objectives of this study were to show that process-based modeling can accurately account for species’ ranges using abiotic factors at the continental scale, and to address the following questions. Are species’ ranges in equilibrium with climate? Can interspecific competition and dispersal abilities shape species’ distributions at the continental scale? For this study, we used the species’ distribution process-based model PHENOFIT (Chuine and Beaubien 2001) to assess the potential distribution of 17 North American boreal/temperate tree species, using input variables of climate and soil properties and species specific parameters.

**Material and Methods**

**The model**

PHENOFIT is a process-based model that predicts tree species’ distributions at continental scale (Chuine and Beaubien 2001). The model relies on the principle that the adaptation of a tree species to environmental conditions depends on the synchronization of the timing of tree development to seasonal variation in climate. The model outputs a mean probability of the presence of an adult tree of the studied species after several years. This probability is assessed by the fitness of the individual, calculated as the product of its probability to survive until the next reproductive season and to produce viable seeds before the end of the annual cycle (reproductive success). More precisely, PHENOFIT simulates the probability of presence as the product of three indices ranging between 0 and 1, one index representing whole tree survival and two indices associated with reproductive success (fruit survival, fruit ripening) (Chuine and Beaubien 2001; see Appendices A and B for further details).

The model is composed of several sub-models: phenological models (leafing, flowering, fruiting, and senescence), a frost-injury model, a survival model, and a reproductive-success model. Each sub-model works at a daily time step, except potential evapotranspiration (PET) that is calculated using the Thornthwaite equation (1948) on a monthly basis (see Morin and Chuine 2005). All parameters are derived from observations of the traits and the processes involved, and not from the present distributions of the species. Thus, the calibration of PHENOFIT involves fitting the phenological model parameters with observations from native populations. Other parameters of the model are obtained from the literature. The inputs are daily climate variables (daily mean and minimum temperatures, and precipitation) and the water-holding capacity of a site. The model is cross-validated by comparing the predicted probability of presence to the observed presence. PHENOFIT has been previously calibrated and validated for two North American species, quaking aspen (Populus tremuloides Michx) and sugar maple (Acer saccharum Marsh) (Chuine and Beaubien 2001). See Chuine and Beaubien (2001) for further details concerning the model.

Here we developed, calibrated, and validated PHENOFIT for 15 North American temperate tree species representing 12 genera (see Table 1). We then used the model for the 17 species (with Acer saccharum and
The simulated cold hardiness of each organ varies as a function of a congeneric species with similar phenology (Chuine and Beaubien 2001). If two series from two locations were available for a species, a set of parameters was fitted for each location. For nine species, the length of the data series was insufficient to get an accurate model (five parameters) for the fruit maturation date. For these species, we used the parameters fitted for *Acer saccharum*, i.e., the maturation model with the best fit, which provided better predictions than the mean delay between flowering and fruit maturation. For *Pinus contorta* and *Pinus monticola*, we did not use the fruit maturation model described in Chuine and Beaubien (2001) because fruit maturation takes two years in pines. In the first year, fertilization does not occur and cone development is limited. In the second year, fertilization takes place and cone development is completed. We used the accumulated degree-days (from 0°C) from early April to late August at the northern range limit to determine whether cones could achieve their development. Model parameter estimates were optimized with a simulated annealing algorithm, the Metropolis algorithm (Metropolis et al. 1953). The goodness of fit (percentages of variance explained: $r^2$) ranged among species from 0.48 to 0.93 for the budburst date model, 0.69 to 0.92 for the flowering date model, and 0.42 to 0.88 for the fruit ripened date model.

No process-based model simulating the date of leaf senescence currently exists. We used a linear function of latitude, fitted on mean dates of leaf colouring at northern and southern limits of the species’ ranges from Lamb (1915). For eight species, mean colouring dates were not available for both northern and southern range limits. For these species, parameters of the linear function of a congeneric species with similar phenology were used.

Frost injury on leaves, flowers, and fruits was calculated according to the model of Leinonen (1996). The simulated cold hardiness of each organ varies

### Table 1. Specific presence threshold, i.e., the fitness value above which the model simulates the presence of a species (SPT); percentage of log-likelihood ratio of the simulations (LLR); area under the receiver operating characteristic curve (AUC); and percentage of grid points correctly predicted by the model, i.e., true-presence and true-absence (Agreement).

<table>
<thead>
<tr>
<th>Species</th>
<th>SPT</th>
<th>LLR (%)</th>
<th>AUC</th>
<th>Agreement (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acer saccharinum</em></td>
<td>0.13</td>
<td>65.6</td>
<td>0.92</td>
<td>90</td>
</tr>
<tr>
<td><em>Acer saccharum</em></td>
<td>0.18</td>
<td>71.6</td>
<td>0.95</td>
<td>92</td>
</tr>
<tr>
<td><em>Aesculus glabra</em></td>
<td>0.06</td>
<td>83.2</td>
<td>0.95</td>
<td>90</td>
</tr>
<tr>
<td><em>Carya ovata</em></td>
<td>0.02</td>
<td>41.8</td>
<td>0.93</td>
<td>82</td>
</tr>
<tr>
<td><em>Fraxinus americana</em></td>
<td>0.36</td>
<td>75.0</td>
<td>0.97</td>
<td>83</td>
</tr>
<tr>
<td><em>Fraxinus nigra</em></td>
<td>0.29</td>
<td>79.4</td>
<td>0.98</td>
<td>93</td>
</tr>
<tr>
<td><em>Juglans nigra</em></td>
<td>0.04</td>
<td>62.6</td>
<td>0.94</td>
<td>93</td>
</tr>
<tr>
<td><em>Ostrya virginiana</em></td>
<td>0.36</td>
<td>21.7</td>
<td>0.87</td>
<td>67</td>
</tr>
<tr>
<td><em>Pinus contorta</em></td>
<td>0.05</td>
<td>29.9</td>
<td>0.88</td>
<td>94</td>
</tr>
<tr>
<td><em>Pinus monticola</em></td>
<td>0.05</td>
<td>85.6</td>
<td>0.97</td>
<td>65</td>
</tr>
<tr>
<td><em>Populus deltoides</em></td>
<td>0.18</td>
<td>20.1</td>
<td>0.95</td>
<td>81</td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td>0.07</td>
<td>22.8</td>
<td>0.94</td>
<td>89</td>
</tr>
<tr>
<td><em>Quercus bicolor</em></td>
<td>0.13</td>
<td>85.4</td>
<td>0.96</td>
<td>85</td>
</tr>
<tr>
<td><em>Quercus macrocarpa</em></td>
<td>0.03</td>
<td>43.0</td>
<td>0.89</td>
<td>89</td>
</tr>
<tr>
<td><em>Salix nigra</em></td>
<td>0.26</td>
<td>47.2</td>
<td>0.92</td>
<td>68</td>
</tr>
<tr>
<td><em>Sassafras albium</em></td>
<td>0.17</td>
<td>81.5</td>
<td>0.98</td>
<td>99</td>
</tr>
<tr>
<td><em>Ulmus americana</em></td>
<td>0.04</td>
<td>35.0</td>
<td>0.95</td>
<td>96</td>
</tr>
</tbody>
</table>

*Populus tremuloides*) to identify which traits and processes are involved in limiting species’ distributions.

### Data sets

**Phenological data.—** We used phenological series of leafing, flowering, and fruiting dates from two sites: Wauseon, Ohio, USA (41°33’ N, 84°09’ W) (11 species: *Acer saccharinum*, *Fraxinus americana*, *Fraxinus nigra*, *Juglans nigra*, *Ostrya virginiana*, *Populus deltoides*, *Quercus bicolor*, *Quercus macrocarpa*, *Salix nigra*, *Sassafras albium*, *Ulmus americana*) (Smith 1915), and Urbana, Illinois, USA (40° N, 88° W) (five species: *Aesculus glabra*, *Carya ovata*, *Fraxinus americana*, *Quercus macrocarpa*, *Ulmus americana*) (C. Augspurger, unpublished data). The phenological series concerned the period 1883–1912 in Ohio and 1990–2003 in Illinois.

**Climatic data.—** We used the CRU TS 2.0 data set of monthly means of daily mean and minimum temperature and precipitation from 1901 to 2000 for a 0.5° × 0.5° grid resolution (Climatic Research Unit, University of East Anglia, UK). These data were obtained by interpolation of observed climatic data for more than 20 000 weather stations around the world (New et al. 2000). We generated daily data by following the classical method of generation of daily temperatures from monthly means used by weather generators, e.g., CLIGEN (Nicks et al. 1995). For further details, see Morin and Chuine (2005).

### Model parameters fitting

Parameters of the phenological models (budburst, flowering, fruit maturation) were fitted using daily mean temperatures and the phenological series from Ohio and Illinois. For *Pinus contorta* and *Pinus monticola*, we used phenological data from Chuine et al. (2006) and I. Chuine (unpublished data). For *Acer saccharum* and *Populus tremuloides*, we used the parameters from Chuine and Beaubien (2001).
between maximum and minimum hardness depending on the daily minimum temperatures, night length, and the state of development of the organ. Species’ maximum and minimum hardness of stems, leaves, and flowers was compiled from the literature (Sakai and Weisser 1973, Larcher 1975, Gusta et al. 1983, Calmé et al. 1994, Chuine et al. 2006). For eight species, these data were not available and maximum and minimum hardness from a congeneric species was used. Survival of drought stress was assessed through specific precipitation ranges following Russel et al. (1990) and Iverson et al. (1999a).

Simulations

PHENOFIT was run on a grid covering North America with a 0.5° × 0.5° resolution (i.e., 15 888 points) over the period 1901–2000. The results of the simulations (i.e., phenology and indices of fitness, survival, reproductive success, and frost damage on leaves, flowers, and fruits) were averaged over this 100-year period. For those species where several sets of parameters were available (i.e., parameters from several populations), the model was run for each set, and the results of each simulation were averaged using means weighted by squared inverse-distance averaged. For a given point i, the probability of presence assessed by the model, $p_i$, is thus

$$p_i = \sum_j \frac{p_i^j}{X_i^j}$$

where $p_i^j$ is the model output simulated with the set of parameters fitted from the jth population, and where $X_i^j$ is

$$X_i^j = \frac{\sum_j d_{ij}^2}{\sum_j \sum_i d_{ij}^2}$$

and $d_{ij}$ is the distance between point i and the jth population.

Model accuracy

To validate model predictions, we used the species’ observed distributions from the U.S. Department of Agriculture Forest Service maps compiled by Little and Critchfield (Critchfield and Little 1966, Little 1971, 1976, 1977; maps available online).4 The Kappa index (Landis and Koch 1977) is a classic estimator used to quantify levels of agreement between observed and simulated distribution maps (Monsurud and Leemans 1992). However, this index includes flaws (Morin and Chuine 2005); thus we used two indicators of fit rather than the Kappa index. First, following the classical methodology (Thuiller 2003), we used a specific presence threshold (SPT) to assign the presence or absence of a species, and to choose the threshold that minimized the mean square error. We also used the area under the relative operating characteristics curve (AUC) to provide an assessment of the model accuracy independent of a specific threshold. The greater the AUC, the higher the agreement between observed and predicted distributions (for more details, see Fielding and Bell [1997]). AUC ranges from 0.5 to 1 where 0.9 means very good agreement (Swets 1988). However, because AUC provides a global estimation of model accuracy, does not depict local discrepancies, and applies only to presence/absence binary data, we also used the log-likelihood of the predictions calculated as described in Chuine and Beaubien (2001). We then computed a log-likelihood ratio (LLR) by dividing the log-likelihood of the simulations with the log-likelihood of a null model that predicts the random distribution of a species over the entire continent (for further details see Morin and Chuine 2005).

Limiting factors

The probability of presence simulated by the model is the product of three indices: survival, proportion of ripe fruit not killed by frost, and probability that a fruit ripens (see Chuine and Beaubien (2001); Appendix A and B). We consider that these three indices refer to constraints on survival, flowering, and fruit maturation, respectively. In PHENOFIT, these three indexes do not interact, except fruit maturation that depends on fruit survival, i.e., the flowering index. It is thus possible to identify which one of these three processes is responsible for the decreasing probability of presence at the distribution limits. We identified which of the three indices was the lowest in the grid points whose simulated probability of presence was lower than SPT + 0.1.

Results

The simulated species’ distributions were mapped (Fig. 1). AUC values were greater than 0.9 for all species (Table 1), except for Ostrya virginiana (0.87), Pinus contorta (0.88), and Quercus macrocarpa (0.89), indicating very good agreement between model simulations and observed distributions (Swets 1988; Table 1). The seven species showing the highest AUC (>0.95) also showed the highest LLR (>0.70; although not in the same order). LLR values were weak, however, for Ostrya virginiana, Populus tremuloides, Populus deltoides, and Pinus contorta (Table 1). The percentage of predicted presence inside the present distribution was greater than 80% for all species (Table 1), except for Ostrya virginiana (67%), Pinus monticola (65%), and Salix nigra (68%). Over-predictions of presence sometimes arose in the Great Plains region (Fig. 1), e.g., for Populus tremuloides and Pinus contorta, where the model predicts a low

4 (http://climchange.cr.usgs.gov/data/atlas/little)
probability of presence, although the species are not currently present in this region.

**LIMITING PROCESSES**

Concerning processes limiting ranges, two main groups of species can be identified (Fig. 2). The first group of species has a distribution limited northward by fruit maturation and southward by flowering (*Acer saccharum, Aesculus glabra, Carya ovata, Fraxinus americana, Pinus contorta, Pinus monticola, Populus deltoides, Quercus macrocarpa, and Ulmus americana*). For these species, the northern limit is likely due to a late
fruit maturation date caused by a lack of degree days. In the south, flowering can be limited by two processes depending on species. The southern range of *Acer saccharum, Fraxinus americana, Populus deltoides,* and *Quercus macrocarpa* is limited by very late flowering (due to a lack of chilling preventing dormancy break); consequently the newly formed fruits are sensitive to frost events in autumn. The southern range of *Aesculus glabra, Carya ovata, Pinus contorta, Pinus monticola,* and *Ulmus americana* is limited by flowering too early, resulting in flowers being killed by frost. The second group of species has a distribution limited by flowering at both margins (i.e., northern and southern ranges) and fruit maturation at the southern margin (*Acer saccharinum, Fraxinus nigra, Juglans nigra, Ostrya virginiana, Quercus bicolor,* and *Salix nigra*). For these species, the northern range is limited by flowering too late due to a lack of degree days such that fruit maturation is prevented. The southern range is limited (1) by no flowering due to a lack of chilling that prevents...
dormancy break, or (2) by a late fruit maturing (Fraxinus nigra and Ostrya virginiana). Populus tremuloides cannot be assigned to any group as the processes limiting its distribution vary because of its large distribution. This species seems particularly limited by its failure to survive drought in the Great Plains region, where it is absent and where its simulated probability of presence is low.

According to these results, phenology appears to be the main factor limiting species’ geographic distributions, followed by survival of drought. Survival to low temperatures never limited species distributions in these
simulations. Limitation by drought arises in regions close to Mexico for *Acer saccharinum*, *Juglans nigra*, and *Populus tremuloides*, and in the Great Plains region for *Fraxinus americana*, *Fraxinus nigra*, *Populus deltoides*, *Populus tremuloides*, *Salix nigra*, and *Sassafras albidum*. Drought can also constrain species in high elevation zones, i.e., in the Rocky Mountains for *Pinus contorta* and *Pinus monticola*, or in the Appalachians for *Acer saccharinum*, *Aesculus glabra*, *Juglans nigra*, *Populus deltoides*, and *Quercus macrocarpa*.

**DISCUSSION**

**Vicariance vs. dispersal**

Our model simulated climatically suitable areas west of the Rocky Mountains for all species and east of the Rocky Mountains for *Pinus contorta* and *Pinus monticola*. **FIG. 2.** Continued.
Our simulations showed that species’ northern range limits were limited by degree-days for fruit maturation or flowering. This finding is in agreement with the hypothesis of thermal limitations at the northern edge of species’ distributions (Pither 2003, Wiens and Graham 2005, Morin and Chuine 2006), but the precise processes underlying this hypothesis have rarely been discussed and identified (Pigott and Huntley 1981, Gaston 2003, Lomolino et al. 2005).

Our simulations showed that species’ southern range limits were usually determined by flowering, either because of the lack of chilling preventing dormancy break, or, in a few species, flowering too early, causing frost killing of flowers. Thus, whereas at high latitudes the development of leaves and flowers can be compromised by insufficiently high temperatures during quiescence (Hänninen 1990), at low latitudes the development of leaves and flowers can be compromised by insufficiently low temperatures preventing dormancy break (Prentice and Helmisaari 1991).

### Table 2

<table>
<thead>
<tr>
<th>Species</th>
<th>Range</th>
<th>R/P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer saccharum</td>
<td>1059</td>
<td>0.59</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>1013</td>
<td>0.59</td>
</tr>
<tr>
<td>Aesculus glabra</td>
<td>387</td>
<td>0.39</td>
</tr>
<tr>
<td>Carva ovata</td>
<td>859</td>
<td>0.90</td>
</tr>
<tr>
<td>Fraxinus americana</td>
<td>1214</td>
<td>0.82</td>
</tr>
<tr>
<td>Fraxinus nigra</td>
<td>1027</td>
<td>0.67</td>
</tr>
<tr>
<td>Juglians nigra</td>
<td>859</td>
<td>0.51</td>
</tr>
<tr>
<td>Ostrya virginiana</td>
<td>1363</td>
<td>0.91</td>
</tr>
<tr>
<td>Pinus contorta</td>
<td>943</td>
<td>0.16</td>
</tr>
<tr>
<td>Pinus monticola</td>
<td>156</td>
<td>0.42</td>
</tr>
<tr>
<td>Populus deltoides</td>
<td>1657</td>
<td>0.78</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>4393</td>
<td>0.62</td>
</tr>
<tr>
<td>Quercus bicolor</td>
<td>369</td>
<td>0.43</td>
</tr>
<tr>
<td>Quercus macrocarpa</td>
<td>1089</td>
<td>0.47</td>
</tr>
<tr>
<td>Salix nigra</td>
<td>1373</td>
<td>0.99</td>
</tr>
<tr>
<td>Sassafras albidam</td>
<td>880</td>
<td>0.61</td>
</tr>
<tr>
<td>Ulmus americana</td>
<td>2380</td>
<td>0.74</td>
</tr>
<tr>
<td>Mean (SE)</td>
<td>0.62 (0.05)</td>
<td></td>
</tr>
</tbody>
</table>

Note: A total of 15888 pixels was possible.

**Equilibrium vs. disequilibrium**

For each species, we calculated the ratio between the number of grid points present in the distribution simulated by PHENOFIT and the number of grid points present in the observed distribution. We found a mean ratio of 62.4 ± 5.0% (mean ± SE; Table 2). This ratio is higher than the one calculated for European trees with a niche-based model (38.3 ± 30.3%) by Svenning and Skov (2004). Contrary to those authors, we do not claim that these results support the hypothesis that tree species are in disequilibrium with climate, because such a conclusion requires that the model predictions be very accurate and robust (Guisan and Thuiller 2005). Furthermore, as discussed beneath, such discrepancies can be due, in the case of process-based models, to genetic differentiation among populations that is insufficiently taken into account in the model.

**Competiton vs. climate**

Biological interactions, especially competition, have long been proposed to limit tree species’ distribution toward the equator (MacArthur 1972, Sax 2001, Murphy et al. 2006). Here we show that the southern distribution limits of species can in most cases be predicted solely by climate. The simulated southern limit for each species is quite close to the observed one, except for *Pinus contorta*, *Populus tremuloides* (eastern part), *Ostrya virginiana*, and *Salix nigra*. For *Pinus contorta*, the simulated distribution expands more southward than the observed one, although isolated populations are present. For *Ostrya virginiana* and *Salix nigra*, the model does not simulate the entire distribution, possibly because genetic differentiation is not taken into account for these species. Thus, based on 17 species, our results show that climate can be the main factor shaping the southern distribution limits of temperate trees at the continental scale. This finding does not...
necessarily imply that competition and disturbances, such as fire (Glenn-Lewin and van der Maarel 1992, Turner et al. 2003), do not play a role in shaping species’ distribution. Our results suggest, however, that these factors might be involved at a more regional or local scale, as previously proposed (e.g., Woodward 1987).

Limits of the model

For most species, PHENOFIT provides an accurate prediction of tree species’ distributions examined in this analysis. However, improvements in the modeling of some processes can make better predictions. First, the assessment of drought mortality can be more mechanistically modeled to incorporate strong seasonal variation in the water balance. The underestimation of drought mortality in the Great Plains region may be the reason why PHENOFIT over-predicts the distribution of *Pinus contorta* (Fig. 1). Second, parameters of cold hardiness and drought resistance can be measured for each species and several populations to take into account local adaptation of these parameters. Third, a process-based model of leaf coloring date remains to be developed. Latitude, incorporating temperature and photoperiod, is known to influence the end of the growing season (Lee et al. 2003), but no accurate models have been developed. A simulation of leaf coloring date using these variables may improve predictions of shifts in species’ ranges, especially in the context of climate change.

Generally, the simulated northern range limit is beyond the observed northern range limit. It should be noted, however, that for some species, isolated populations exist beyond the observed northern range limits, e.g., *Juglans nigra* (Fig. 1f), *Quercus bicolor* (Fig. 1m), and *Populus deltoides* (Fig. 1k). More generally, when the model predicts a false presence, isolated populations are present in the region (except for *Pinus contorta*), indicating that the continuous distributional limits may not represent the actual climatic limit of the species (Gaston 2003). Fragmentation of a species’ distribution may have been caused by human factors such as land use (Hall et al. 2002).

PHENOFIT can take into account the genetic differentiation of tree populations, and thus local adaptation, but in our simulations this was possible for only five species because of data limitations (*Acer saccharum, Fraxinus americana, Pinus monticola, Populus tremuloides*, and *Ulmus americana*). It is noteworthy that the predictions of the model were accurate for most species, despite not taking into account local adaptation. This result is consistent with several studies showing that tree species generally exhibit low levels of genetic differentiation among populations (see Hamrick 2004 for review). However, genetic differentiation may substantially increase at range boundaries, and may be the reason why the model does not accurately predict species’ presence at the southern range limit as it is the case for *Ostrya virginiana, Quercus bicolor*, and *Salix nigra*, and to a lesser extent for *Carya ovata* (as the populations used are usually located in the north of the species’ range). The northwestern part of the distribution of *Populus deltoides* is also not predicted with accuracy, but this problem probably arises because of inaccurate data about the current distribution of this species (Russell et al. 1990).

Conclusion

Species’ distributions result from many factors that vary according to the scale considered. Models are very useful in separating the different scales. At the landscape scale, theoretical studies have shown that the local distribution of individuals can result from gradients in habitat availability, colonization rates, and extinction rates of metapopulations (Maurer and Taper 2002). However, it is difficult to identify the processes responsible for the limitation at this scale. At the continental scale, we showed that a species’ physiology, especially its phenology, is a major factor that constrains tree species’ ranges.

As highlighted by Lawler et al. (2006), building mechanistic models for a large number of individual species is an enormous undertaking, especially in comparison with widely used niche-based models, because of the need to take into account species’ life histories and physiologies. Processes are crucially needed, however, to obtain a more thorough understanding of the potential impact of climate on species’ ranges (McDowall 2004, Wiens and Donoghue 2004), especially at their margins (Parmesan et al. 2005).

Acknowledgments

The authors thank David Viner (Climate Research Unit, University of East Anglia, UK) for providing climate data. They are very grateful to Georges Kunstler, Paul W. Leadley, Jacques Roy, and Martin T. Sykes for helpful discussions and comments on this paper, and to Hervé Bohbot for GIS help. They also thank two anonymous reviewers for their comments that substantially improved this paper. Support was provided to X. Morin by a Bourse de Docteur Ingenieur du Centre National de la Recherche Scientifique.

Literature Cited


Morin, X., and I. Chuine. 2005. Sensitivity analysis of the tree distribution model PHENOFIT to climatic input character-

APPENDIX A
A description of the model PHENOFIT (*Ecological Archives* E088-137-A1).

APPENDIX B
A descriptive figure of PHENOFIT (*Ecological Archives* E088-137-A2).