# REPORT

# Phenology is a major determinant of tree species range

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## Abstract

Global warming is expected to have a major impact on plant distributions, an issue of key importance in biological conservation. However, very few models are able to predict species distribution accurately, although we know species respond individually to climate change. Here we show, using a process-based model (PHENOFIT), that tree species distributions can be predicted precisely if the biological processes of survival and reproductive success only are incorporated as a function of phenology. These predictions showed great predictive power when tested against present distributions of two North American species – quaking aspen and sugar maple – indicating that on a broad scale, the fundamental niche of trees coincides with their realized niche. Phenology is shown here to be a major determinant of plant species range and should therefore be used to assess the consequences of global warming on plant distributions, and the spread of alien plant species.

## INTRODUCTION

Plant ecologists agree that the distribution of plant species is strongly influenced by climate (Parker 1963; Woodward 1987; Stephenson 1990) and in particular temperature (Parker 1963) and moisture regime (Stephenson 1990; Pigott & Pigott 1993). Several studies have addressed this issue at different scales (Pigott & Huntley 1981; Richardson & Bond 1991; Barton 1993; Pigott & Pigott 1993; Criddle *et al.* 1994; Comes & Kadereit 1998; Sollins 1998) and several biogeography models have been developed using either the correlative approach (Huntley *et al.* 1989; Lenihan & Neilson 1993; Myklestad & Birks 1993; Shao & Halpin 1995; Iverson & Prasad 1998), the process-based approach (Neilson 1995) or a mix of both (Neilson *et al.* 1992; Prentice *et al.* 1992; Burton & Cumming 1995; Sykes *et al.* 1996). Greater accuracy in plant biogeography models can be achieved by (i) working at the species level because species have been shown to react independently to climate change (Huntley 1991), and by (ii) using process-based models that simulate the plant responses to biotic and abiotic factors (Huntley 1991). Most importantly, as the primary application of such models is to get simulations of the distributions of species or ecosystems for past periods and predictions of these distributions for future climatic scenarios, their predictive power needs to be assessed accurately.

Here we present a model, called hereafter, PHENOFIT, a process-based model, which predicts deciduous tree species distributions, and is adjusted independently from present species distributions. This model focuses on survival and reproductive success as a function of the match between a plant's life cycle and local seasonal fluctuations in climate, rather than on productivity and competition as in other models (Prentice *et al.* 1992; Burton & Cumming 1995; Haxeltine & Prentice 1996; Sykes 1996). However, the seasonal coordination of phenology to climate does impact on competitive relationships via its influence on vegetative and reproductive performances (Lechowicz & Koike 1995). A mismatch between the life cycle and seasonal fluctuations in climate may result in (i) frost injuries to leaves or flowers if leafing or flowering occur during frost periods, (ii) drought injuries if severe seasonal drought occurs during the growing season, and (iii) failure to produce mature fruits and seeds if autumnal frosts occur before maturation or if summers are too cool or too short (Pigott & Huntley 1981) (Fig. 1). Reproduction and phenology have never been considered explicitly in plant distribution models even though, clearly, a species can be present in an area only if individuals are able to survive and produce viable seedlings in that area. Phenology has been shown to be a major component of plant fitness (Primack 1980; Mitchell-Olds 1996; O'Neil 1997), and hence may contribute to changes over time in tree distribution and abundance. Phenology is also important in research on global climate change (Menzel & Fabian 1999; Schwartz 1998), because it affects the global carbon seasonal cycle and seasonal outflows of water, and
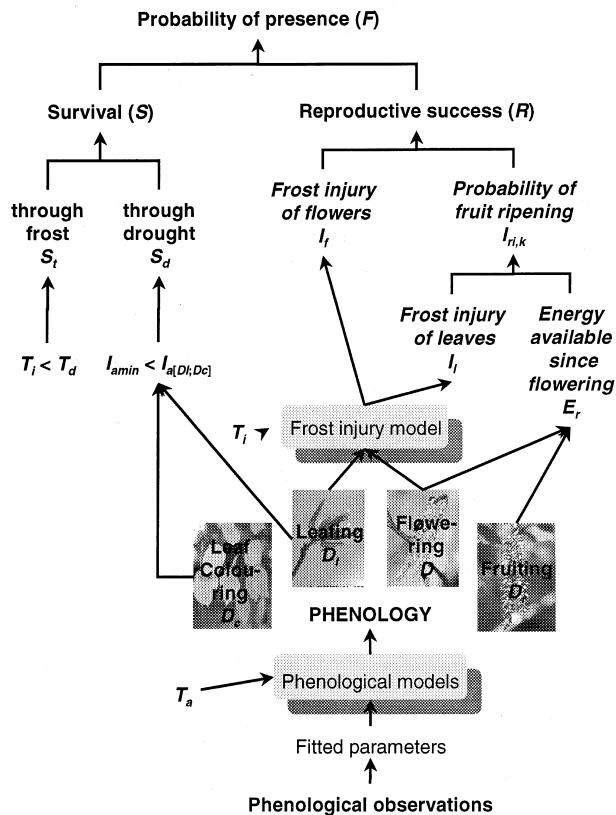
**Figure 1** Description of PHENOFIT. Photographs are leafing, flowering, fruiting and leaf colouring of quaking aspen. Legend as in Table 1 and $I_a[D_l; D_c]$, moisture index between leafing ($D_l$) and leaf colouring ($D_c$).

can be monitored at the global scale with satellites (White *et al.* 1997).

## MATERIALS AND METHODS

### Description of the model

PHENOFIT has been developed for deciduous tree species and is described thereafter for two north American species, *Populus tremuloides* Michx. and *Acer saccharum* Marsh. It outputs a probability of presence over several years for an individual of a particular species, estimated by the product of a probability to survive until the next reproductive season and the probability to produce viable seeds by the end of the annual cycle (reproductive success) (Fig. 1). PHENOFIT is based on different process-based models: phenological models (Chuine 2000), a frost-injury model (Leinonen 1996), a survival model and a reproductive success model. All parameters of these models, except that for survival to drought for which data do not exist (Table 1), are derived from observations of the different traits involved in the model rather than from present distributions of the species. The frost injury, survival and reproductive success models are based on the match between the simulated development and climate seasonality, e.g. survival is reduced if severe drought occurs between leafing and leaf colouring, reproductive success is reduced if frost occurs during flowering.

Each year $k$ at location $n$, the probability to survive and reproduce ($F_{n,k}$) of an individual of a particular species is

**Table 1** List of variables used in PHENOFIT

|  | Name | Definition |
|---|---|---|
| Input variables: | $T_a$ | average daily temperature (°C) |
|  | $T_i$ | minimum daily temperature (°C) |
|  | $P$ | daily precipitation (mm) |
|  | $I_a*$ | daily moisture index |
|  | $N$ | night length (hour) |
| Output variables†: | $F$ | probability of presence |
|  | $R$ | probability to produce fully developed seeds |
|  | $S$ | probability to survive |
|  | $S_t$ | probability to survive frost |
|  | $S_d$ | probability to survive drought |
|  | $D_l$ | date of leafing (day of the year) |
|  | $D_f$ | date of flowering (day of the year) |
|  | $D_r$ | date of fruiting (day of the year) |
|  | $D_c$ | date of leaf colouring (day of the year) |
|  | $I_l$ | leaves frost injury index |
|  | $I_f$ | flowers frost injury index |
|  | $I_r$ | Index of fruit maturation |

*$I_a = A/E$, where $A$ is the actual evapotranspiration and $E$ is the potential evapotranspiration.
†Calculated each year at each location.

estimated as the product of its survival ($S_{n,k}$) and reproductive success ($R_{n,k}$):

$$F_{n,k} = S_{n,k} R_{n,k} \qquad (1)$$

*Survival*

The probability to survive year $k$ is the product of the probability to survive frost ($S_t$) and the probability to survive drought ($S_d$):

$$S = S_t S_d \qquad (2)$$

with

$$S_t = \prod_{j=0}^{365} S_{tj} \qquad (3)$$

Lethal frost occurs when the daily minimum temperature drops below a species-specific threshold temperature ($T_d$). Frost hardiness has been widely studied for forest trees, and Sakai & Weisser (1973) report a threshold temperature for lethal frost of –85 °C for quaking aspen, and –80 °C for sugar maple, and we therefore used these values for our predictions.

$$S_{tj} = \begin{cases} 0 & \text{if } T_i \leq T_d \\ 0.5 & \text{if } T_d < T_i \leq 0.9 T_d \\ 1 & \text{if } T_i > 0.9 T_d \end{cases} \qquad (4)$$

We considered that drought should significantly affect survival during the growing season only, i.e. from the date of leafing ($D_l$) to the date of leaf colouring ($D_c$). As the focus of the model was the match between climate and phenology as a determinant of species range, and because no experiment in the literature reports how much drought affects survival of quaking aspen and sugar maple, we decided to apply a very simple and general rule to estimate the probability to survive drought. Quaking aspen lives in very different type of ecosystem from boreal to deciduous forest, which are characterized by a moisture index (eqn 8) greater than 0.2 (Budyko 1974). Sugar maple is part of the deciduous forest, which is characterized by a moisture index between 0.8 and 1 (Budyko 1974). The probability to survive drought ($S_d$) was thus:
Sugar maple:

$$S_d = \begin{cases} 0.1 & \text{if } I_a < 0.8 \text{ or } I_a > 1 \\ 1 & \text{if } 0.8 \leq I_a \leq 1 \end{cases} \qquad (5)$$

Quaking aspen:

$$S_d = \begin{cases} 0.1 & \text{if } I_a < 0.2 \\ 1 & \text{if } I_a \geq 0.2 \end{cases} \qquad (6)$$

$$I_a = \sum_{j=D_l}^{D_c} A_j \bigg/ \sum_{j=D_l}^{D_c} E_j \qquad (7)$$

$E_j$, the daily potential evapotranspiration, was calculated using the Priestley-Taylor equation (Priestley & Taylor 1972) and specific Priestley-Taylor coefficients (Sykes 1996). $A_j$, the daily actual evapotranspiration, is given by

$$A_j = \beta E_j \text{ with } \beta = \begin{cases} 1 & \text{if } W_j > W_c \\ W_j / W_c & \text{if } W_j \leq W_c \end{cases} \qquad (8)$$

with $W_c = 0.5 W_m$, where $W_m$ is the total holding water capacity (mm), and $W_j$ is the daily ground water (mm).

*Reproductive success*

The probability to produce viable seeds was estimated by the product of the proportion of flowers uninjured by frost ($I_f$) and the probability that fruits will ripen ($I_r$): $R = I_f I_r$.

The proportions of uninjured flowers ($I_f$) depend on the date of flowering ($D_f$) and the daily minimum temperature during this period ($T_i$). The probability of fruit maturation success ($I_r$) depends on the proportion of uninjured leaves ($I_l$), which produce the assimilates accumulated into the fruits, and on the amount of thermal energy available since the date of flowering ($D_f$). The proportion of fruits reaching maturity follows a normal distribution (Lescourret *et al.* 1999). $I_r$ was thus calculated as the cumulated probability of the normal distribution ($E_c, \sigma_m$), with $E_c$, a fitted parameter, being the average amount of energy needed to reach maturation (see the "fruit maturation" model).

$$I_r = \sum_{t_f}^{t_m} \frac{1}{\sigma_m \sqrt{2\Pi}} e^{\frac{\left(E_{tl}^t - E_c\right)^2}{2\sigma_m^2}} \qquad (9)$$

$$E_{tl}^t = \sum_{t1}^{t} P_h(T_0, t) I_a \frac{1}{1 + e^{-10(I_l - I_{50})}} \qquad (10)$$

$P_h(T_0, t)$, the photosynthetic activity, is a function of the daily air temperature (Budyko 1974),

$$\sigma_m = E_{D_r - 4}^{D_r},$$

$I_{50}$ is the critical proportion of remaining leaves for which the photosynthetic activity of the tree is reduced by 50% (we assume a sigmoid relationship between the number of leaves and the photosynthetic activity of the tree), and $t_m$ and $t_f$ are days when $E > E_c + 3\sigma_m$ and $E < E_c - 3\sigma_m$, respectively.

*Frost injury*

Frost injury on leaves and flowers was simulated according to the model of Leinonen (1996) using daily minimum temperatures, night length, specific parameters (Table 2) (Sakai & Weisser 1973) and the bud development simulated by the phenological models.

*Phenology*

Phenological models use the daily mean temperatures ($T_a$) from bud dormancy initiation (late summer of the previous

**Table 2** List of parameter values per species and population

| | | Sugar maple | | Quaking aspen | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Ottawa | Wauseon | Halifax | Ottawa | Winnipeg | Saskatoon | Edmonton | Wauseon |
| Frost injury model | $F_{rmax1}$ | −10 | −10 | −10 | −10 | −10 | −10 | −10 | −10 |
| | $F_{rmax2}$ | −50 | −50 | −50 | −50 | −50 | −50 | −50 | −50 |
| | $F_{lmin}$ | −5 | −5 | −6 | −6 | −6 | −6 | −6 | −6 |
| | $F_{fmin}$ | −3 | −3 | −12 | −12 | −12 | −12 | −12 | −12 |
| | $T_1$ | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| | $T_2$ | −16 | −16 | −16 | −16 | −16 | −16 | −16 | −16 |
| | $Ft_{lmax}$ | −60 | −60 | −62 | −62 | −62 | −62 | −62 | −62 |
| | $Ft_{fmax}$ | −60 | −60 | −62 | −62 | −62 | −62 | −62 | −62 |
| | $Fp_{lmax}$ | −20 | −20 | −22 | −22 | −22 | −22 | −22 | −22 |
| | $Fp_{fmax}$ | −20 | −20 | −22 | −22 | −22 | −22 | −22 | −22 |
| | $NL_1$ | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| | $NL_2$ | 16 | 16 | 16 | 16 | 16 | 16 | 16 | 16 |
| Phenological model leafing | $a$ | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 |
| | $b$ | 10.000 | 10.000 | 6.621 | 6.621 | 6.621 | 6.621 | 6.621 | 6.621 |
| | $c$ | −5.607 | −5.607 | −8.402 | −8.402 | −8.402 | −8.402 | −8.402 | −8.402 |
| | $d$ | −14.998 | −14.998 | −1.695 | −1.695 | −1.695 | −1.695 | −1.695 | −1.695 |
| | $e$ | −7.089 | −7.089 | −9.658 | −9.658 | −9.658 | −9.658 | −9.658 | −9.658 |
| | $w$ | 155.955 | 155.955 | 1000 | 1000 | 1000 | 1000 | 1000 | 1000 |
| | $z$ | −0.014 | −0.014 | −0.029 | −0.029 | −0.029 | −0.029 | −0.029 | −0.029 |
| | $C_c$ | 46.514 | 46.514 | 94.924 | 94.924 | 94.924 | 94.924 | 94.924 | 94.924 |
| | $t_c$ | 224 | 224 | 225.9 | 225.9 | 225.9 | 225.9 | 225.9 | 225.9 |
| Flowering | $a$ | 0.366 | 0.554 | 0.012 | 0.012 | 0.637 | 0.929 | 0.186 | 0.012 |
| | $b$ | −17.531 | −4.457 | 9.978 | 9.978 | −26.963 | 2.762 | 6.249 | 9.978 |
| | $c$ | 24.131 | 1.980 | −5.417 | −5.417 | 28.811 | 7.384 | −1.000 | −5.417 |
| | $d$ | −0.294 | −15.000 | −15.000 | −15.000 | −0.701 | −7.089 | −0.483 | −15.000 |
| | $e$ | −10.518 | −11.203 | −7.070 | −7.070 | −4.080 | −4.849 | −4.717 | −7.070 |
| | $w$ | 1470.365 | 107.483 | 447.954 | 447.95 | 114.40 | 15.96 | 511.48 | 447.95 |
| | $z$ | −0.025 | −0.081 | −0.033 | −0.033 | −0.012 | −0.063 | −0.042 | −0.033 |
| | $C_c$ | 124.12 | 14.09 | 66.33 | 66.33 | 150.97 | 1.33 | 65.01 | 66.33 |
| | $t_c$ | 186 | 106 | 186 | 186 | 195 | 100 | 158 | 186 |
| Fruiting | $F_c$ | 15.59 | 15.59 | 3.42 | 3.42 | 3.42 | 3.42 | 3.42 | 3.42 |
| | $E_c$ | 8639 | 8639 | 1489.33 | 1489.33 | 1489.33 | 1489.33 | 1489.33 | 1489.33 |
| | $T_o$ | 14.73 | 14.73 | 12.762 | 12.762 | 12.762 | 12.762 | 12.762 | 12.762 |
| | $o$ | 27.25 | 27.25 | −3.1923 | −3.1923 | −3.1923 | −3.1923 | −3.1923 | −3.1923 |
| | $p$ | −19.06 | −19.06 | −14.234 | −14.234 | −14.234 | −14.234 | −14.234 | −14.234 |
| | $\sigma_m$ | 360 | 360 | 149 | 149 | 149 | 149 | 149 | 149 |
| | $I_{50}$ | 0.4 | 0.4 | 0.4 | 0.4 | 0.4 | 0.4 | 0.4 | 0.4 |

Parameters of the frost injury model were fixed according to Leinonen (1996), whereas parameters of the phenological models were fitted to phenological observations.

year) to autumn, to simulate the development of vegetative and reproductive buds and of fruits. Parameters of the phenological models were fitted to time series of leafing, flowering, fruiting, and leaf colouring dates from Ohio and Ontario for sugar maple and Ohio, Ontario, Manitoba, Nova Scotia, Saskatchewan and Alberta for quaking aspen (Beaubien & Freeland 2000) (Table 3).

*Fruit maturation* An empirical model of prediction of fruiting dates ($D_r$) was defined according to experimental results (Kigel & Galili 1995) as follows,

$$D_r \text{ such that } \sum_{t_l}^{D_r} P_b(T_0, t) = E_c \tag{11}$$

$$t_l \text{ such that } \sum_{D_f}^{t_l} \frac{1}{1 + e^{o(Ta-p)}} = F_c \tag{12}$$

where $F_c$, $o$ and $p$ are fitted parameters.

**Table 3** Fit of the phenological models and test of genetic differentiation

| Species | PE | Populations | | | | $R^2$ | Genetic differentiation (%) | |
|---|---|---|---|---|---|---|---|---|
| | | N | Ob | Name | Location | | | |
| Acer saccharum | flowering | 2 | 22 | Ottawa, ON (a) | 45°19′; −75°40′ | 0.924*** | total | 11.2* |
| | | | 17 | Wauseon, OH (b) | 41°33′; 84°09′ | 0.609 ns | | |
| | leafing | 1 | 16 | Wauseon, OH | 41°33′; 84°09′ | 0.661 ns | | |
| | fruiting | 1 | 8 | Wauseon, OH | 41°33′; 84°09′ | 0.597 ns | | |
| Populus tremuloides | flowering | 6 | 14 | Halifax, NS (a) | 44°53′; −63°30′ | 0.809 ns | total | 36.1*** |
| | | | 21 | Ottawa, ON (a) | 45°19′; −75°40′ | 0.945*** | a-a | 17.9 ns |
| | | | 24 | Winnipeg, MN (b) | 49°54′; −97°14′ | 0.854*** | b-c | 11.8* |
| | | | 26 | Saskatoon, SK (c) | 52°10′; −106°41′ | 0.750** | c-d | 32.2** |
| | | | 26 | Edmonton, AB (d) | 53°18′; −113°35′ | 0.596* | b-c-d | 48.1*** |
| | | | 16 | Wauseon, OH (a) | 41°33′; 84°09′ | 0.841* | a-(b,c,d) | 1.7 ns |
| | leafing | 1 | 16 | Wauseon, OH | 41°33′; 84°09′ | 0.395 ns | | |
| | fruiting | 1 | 14 | Wauseon, OH | 41°33′; 84°09′ | 0.479 ns | | |

$R^2$, percentage of variance explained by the model; PE, phenological event; N, number of populations; Ob, number of observations. Populations followed by the same letter have not significantly different responses of their phenology to climate. total, percentage of genetic differentiation among all populations considered; a-a, percentage of genetic differentiation among populations of group a; b-c, percentage of genetic differentiation between populations of group b and group c; a-(b, c, d), percentage of genetic differentiation between populations of group a and all other populations (groups b, c and d). ***$P > 0.001$; **$P < 0.01$; *$P > 0.05$, ns, not significant.

*Leaf colouring* As no empirical model of leaf colouring exists so far, we used a linear function of latitude, fitted on leaf colouring dates of the northern and southern limits of the range of each species (Lamb 1915).

*Leafing and flowering* Dates of leafing and flowering were simulated according to the phenological model of Chuine (Unified model) (Chuine 2000) using daily mean temperatures and species-specific parameters (Table 2).

Unified Model ($a, b, c, d, e, w, z, C_c, t_c$):

$$t_f \text{ such that } S_{f,t_f} = \sum_{t_1}^{t_f} R_{f,t} = F_c \tag{13}$$

$$R_{f,t} = \frac{1}{1 + e^{a(T_t - b)}} \tag{14}$$

$$t_1 \text{ such that } S_{c,t_1} = \sum_{t_0}^{t_1} R_{c,t} = C_c \tag{15}$$

$$R_{c,t} = \frac{1}{1 + e^{c(T_t - e)^2} + d(T_t - e)} \tag{16}$$

$$F_c = we^{-zS_{c,t_c}} \tag{17}$$

## Genetic differentiation

Genetic differentiation of phenology between populations may decrease the accuracy of model predictions across a species range if a single population is used to estimate the model parameters. Genetic differentiation of phenology can be estimated with phenological models (Chuine *et al.* 2000). Using observations from several populations of each species, we tested the differentiation in phenology among

these populations (Table 3). Wherever there was significant genetic differentiation among populations, each of the locations chosen for the model validation was assigned the phenological estimate of the closest population (Table 3). Plasticity and genetic differentiation have often been a preoccupation in plant distribution modelling, although it has usually been impossible to take them into account. PHENOFIT includes explicitly both plasticity (phenology is a plastic response to climate) and genetic differentiation of phenology quite readily given observations for different populations.

## Model validation

One of the main benefits of the process-based models (as soon as none of their parameters is fitted to the present distributions) is that they can be cross-validated (i.e. independent datasets are used to fit and test the model) using present distributions. Cross-validation is the primary requirement to assess model effectiveness and has been shown recently to be of major importance in assessing niche overlap between closely related animal taxa (Peterson *et al.* 1999). However, correlations and process-based models have so far usually been fitted, respectively, to present distributions, entirely (Iverson & Prasad 1998) or partially (Sykes 1996; but see Neilson 1995), and have thus very rarely been cross-validated (but see Beerling *et al.* 1995).

PHENOFIT can be cross-validated using present distributions that are not used to fit the model. PHENOFIT was tested on American tree species, because North America has

several climatic regions ranging from arctic to subtropical and from super-humid to subarid, and its biogeography is well described in comparison with other continents, and thus offers ideal conditions to test models based on the response of a plant to climate. Quaking aspen (*Populus tremuloides* Michx.) and sugar maple (*Acer saccharum* Marsh.) were chosen to test the performance of PHENOFIT because they have very different distributions (see Figs 2 and 3) and because sufficient observations were available to fit the phenological models. The probability of presence (*F*) after several years (50 years on average for the USA and 6 years elsewhere, i.e. Canada and Mexico) was estimated for each species at 92 locations in North America from local daily climate data. At each of the 92 locations, the probability of presence of the species was coded 1 if inside the distribution, 0.75 if inside yet close to a boundary (within 50 km), 0.5 if at the boundary, 0.25 if outside yet close to the boundary (within 50 km) or next to fragmented populations, and 0 if far outside the distribution. The log-likelihood (*L*) of PHENOFIT predictions was computed considering a binomial error for the presence/absence of a species at a given location:

$$L = \sum_n O_n \ln(F_n) + (1 - O_n)\ln(1 - F_n) \qquad (18)$$

where $O_n$ is the observed probability of presence at location *n*, and $F_n$ is the predicted probability of presence at location *n*.

$$F_n = \begin{cases} 0 & \text{if } \exists k \text{ such as } S_k = 0 \\ \frac{1}{k}\sum_k F_k & \text{if } \forall k\, S_k > 0 \end{cases} \qquad (19)$$

The likelihood of the null model was calculated as,

$$L_0 = \sum_n O_n \ln(\overline{O}) + (1 - O_n)\ln(1 - \overline{O}) \qquad (20)$$

where *o* is the average observed probability of presence. The Akaike Information Criterion is,

$$AIC = -2L + 2k \qquad (21)$$

where *k* is the number of fitted parameters in the model.

## RESULTS

### Prediction of sugar maple and quaking aspen distributions

The rule applied for survival to drought for sugar maple led to worse predictions than if survival to drought was simply not taken into account in the model. Among several conditions of moisture reviewed in the literature, only one led to slightly better predictions than if survival to drought was not taken into account, i.e. precipitation superior to 250 mm during the growing season (Holdridge 1947). Figures 2 and 3 show the distributions predicted by PHENOFIT for sugar maple and quaking aspen, respectively. The predicted distributions are in both cases very close to the observed distributions. The percentage of variance in the observed probabilities of presence explained by PHENOFIT (compared with the null model for which at each of the 92 locations $F_n = \overline{O}$, the average observed probability of presence) was 47.5% for quaking aspen and 58.5% for sugar maple. If survival to drought was not considered in the model, percentages of variance explained were 54.1% for sugar maple and 28.8% for quaking aspen. Sugar maple distribution is thus very weakly affected by moisture conditions. We performed a cross-validation test by comparing the AIC (Akaike 1973) of PHENOFIT for each species to that of the null model. AIC statistics allow the comparison of models based on their likelihood and degrees of freedom. The model with the lowest AIC fits significantly better if the difference between the two AICs is two or more (Akaike 1973). The AICs of PHENOFIT for sugar maple and quaking aspen were 38.6 and 60.6, respectively, vs. 95.0 and 117.4, respectively, for the null model. PHENOFIT is thus strongly supported and accurately predicts the distributions of quaking aspen and sugar maple.

### Altitudinal distribution

Occurrence of quaking aspen could not be predicted in most of the Western USA where it lives at very high altitude (between 2100 and 3300 m), for which daily weather data are rare and records are usually incomplete, with few climatic variables recorded. We were thus compelled to use monthly statistics for several high elevation sites, from which daily data were derived using the CLIMGEN software developed by Washington State University (http://www.bsyse.wsu.edu/climgen/). The number of weather stations that stand within the right elevation belt (2100–3300 m) in each state was insufficient to allow a simulation of the complete distribution of quaking aspen in the Western USA. However, the altitudinal distribution was correctly predicted in other cases, i.e. a predicted presence between 2100 m and 3300 m in Wyoming and Colorado, a predicted absence under 1800 m in Idaho and Montana and a predicted absence under 2100 m in Arizona, New Mexico, Nevada and Utah. A high probability of presence was also estimated at Topeka, KA, where the species is currently absent. If this prediction is right, this illustrates the fact that quaking aspen may sometimes be absent from the Prairies because of biotic factors such as grazing, and not because of abiotic factors.

### Sensitivity analysis

A sensitivity analysis on the model parameters allowed to determine the proportion of variation in the species range
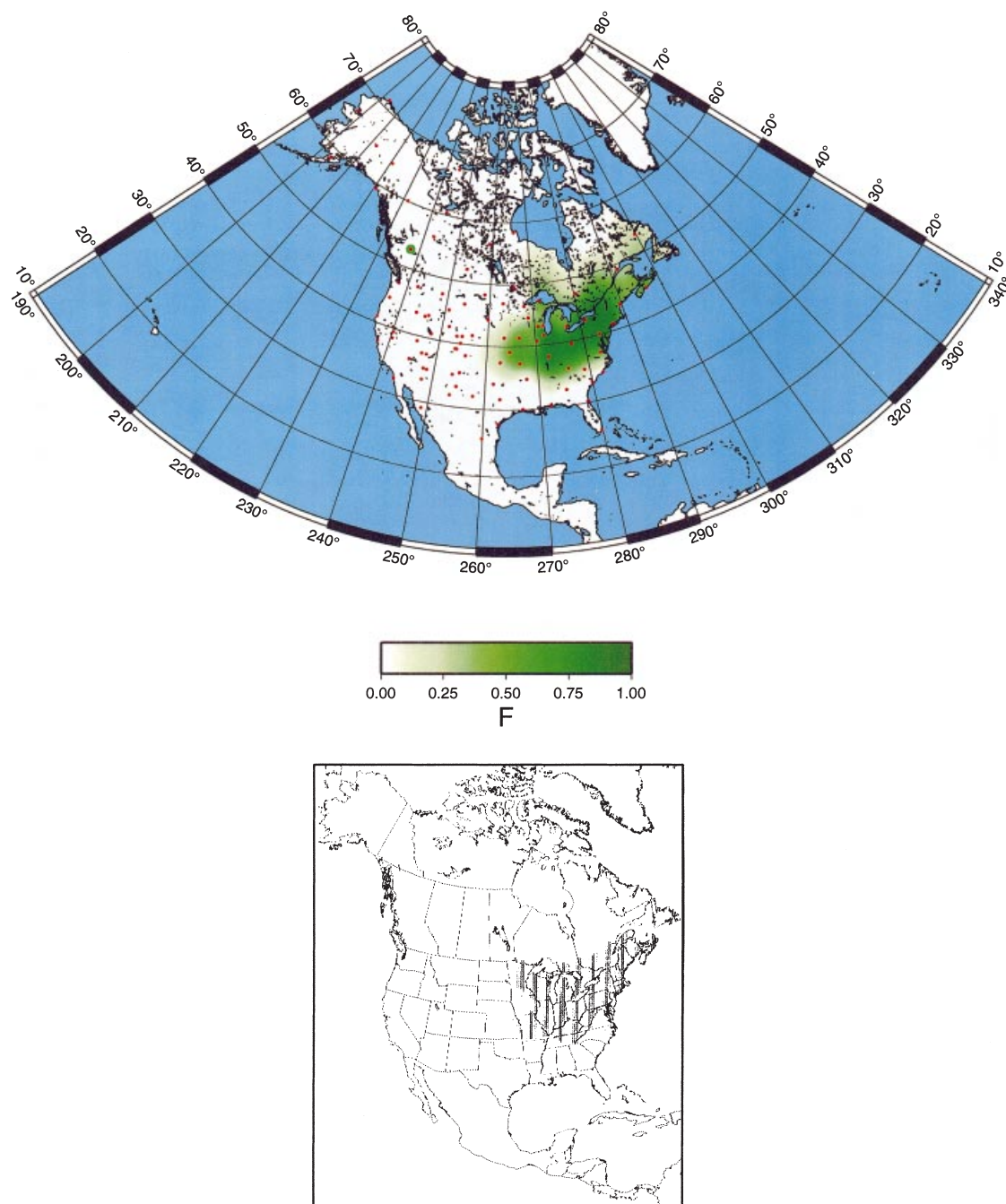
## Acer saccharum



**Figure 2** Maps of the predicted and observed (grey shaded) distributions of sugar maple. Black dots indicate the 92 weather stations used. The predicted distributions was produced by interpolating the 92 average probabilities of presence (*F*) predicted at each location (except the 15 high elevation sites, represented by disks).
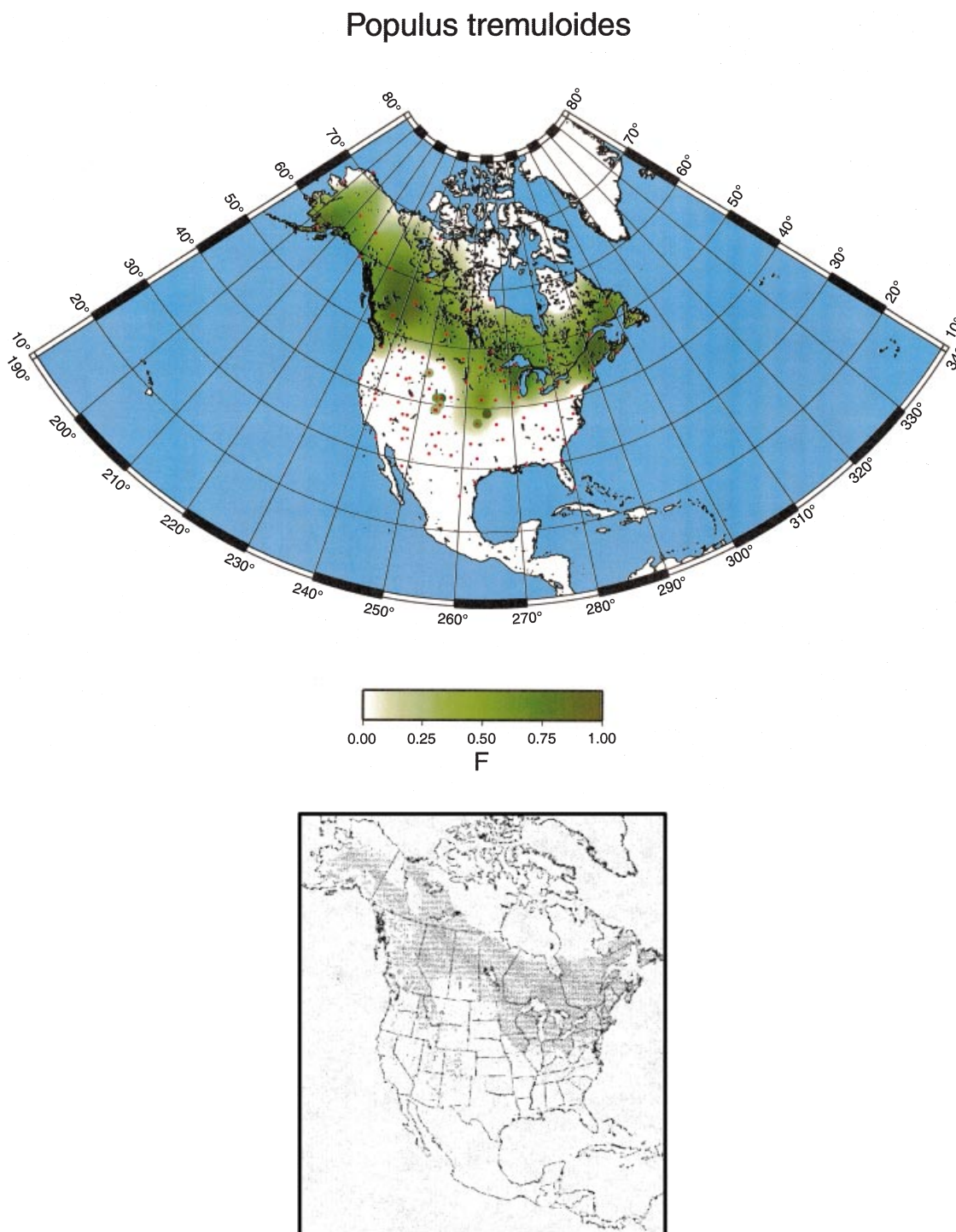
## Populus tremuloides



Figure 3 Maps of the predicted quaking aspen and observed (grey shaded) distributions of sugar maple. Legend as in Fig. 2.

sizes explained by one of the model components (Gaston 1996). Mortality due to lethal frost injury never influenced $F$ and thus had no effect on the two species distributions. This is because first, the minimum temperature that the tree can stand is always far below the temperatures reached anywhere, and second, because survival or reproductive success are affected before survival to lethal frost becomes an issue. Temperature is usually thought to have a greater influence on species range than drought. However, in quaking aspen $F$ was influenced by water stress as much as

phenology and frost during the active growth period (the dynamic of frost resistance is dependent on the dynamic of tissues development, and thus on phenology) (16.3% for phenology and frost and 21.9% for water stress), whereas in sugar maple $F$ was only slightly influenced by water stress (4.8% of the total variance) once phenology and frost injury during the active growth period were taken into account (50% of the total variance). This analysis has also revealed that most of the factors explaining the absence of quaking aspen and sugar maple outside their present distribution were the same. At high latitudes (above 60°N) and south of the distributions (below 37°N), $F$ was primarily limited by the inability of the two species to develop flowers and leaves. According to PHENOFIT this failure is due to temperature regimes that do not allow buds to break dormancy, or the subsequent completion of bud development. Elsewhere, $F$ was primarily limited by frost injury to leaves and flowers in sugar maple and by drought and frost injuries to flowers in quaking aspen. Thus, phenology appears to be of major importance in determining plant species' range.

## DISCUSSION

### Fundamental vs. realized niche

According to Hutchinson's definition, PHENOFIT estimates the fundamental niche, or Grinellian niche of a species, i.e. the hyper volume defined by the environmental dimension within which that species can survive and reproduce (see Pulliam 2000 for review). Present distributions can be considered as the realized niches, in the sense of Hutchinson, i.e. the fundamental niche reduced by competition, disturbance regime and other biotic interactions. It is noteworthy that, at a global scale, the realized niche of the two tree species studied here is very close to their fundamental niche, suggesting that they may not be dispersal-limited, and may be currently at equilibrium with climate. However, if PHENOFIT were to be used at a regional or local scale, we would expect more discrepancies between its predictions and the present distributions, due to either interspecific competition (e.g. for light and nutrients) or disturbance regime (e.g. fire, human activity, pest) or source-sinks dynamics (Pulliam 1988), which are, to date, not taken into account into PHENOFIT. It is usually very difficult to define habitat suitability (fundamental niche), and thus to demonstrate that a species occurs in unsuitable habitats or is absent from suitable habitats. Pulliam (2000) highlighted in his review paper the need for measuring niches directly, i.e. measuring the environmental variables that directly influence population densities. PHENOFIT illustrates this point and may help in identifying cases where source-sink dynamics are involved in the realized distribution of a species.

## Range limits

The southern range limit of the two species were well predicted by PHENOFIT. Whereas northern range limits of plants have been widely attributed to either frost kill or inability to achieve adequate growth during a growing season because of adverse temperature conditions, southern range limits are far less understood and usually thought to be shaped by competition, although evidence for this hypothesis is weak (Woodward 1987). The sensitivity analysis showed that the inability to make new leaves and flowers for the new annual cycle primarily limited the range of sugar maple and quaking aspen northward and southward. This can seem strange, but is actually due to the duality of the response of bud growth and development to temperature. The phase of dormancy (during which bud growth is stopped despite adequate temperatures) can be broken by low temperatures (generally between 0 and 10 °C), whereas the subsequent phase of quiescence (that follows dormancy and during which bud growth responds to temperature) requires higher temperatures (generally from 5 to 20 °C) (Hänninen 1990; Kramer 1994; Chuine 2000). Thus, whereas at the high latitudes, leaves and flower development can be compromised by insufficiently high temperatures during quiescence to complete this phase of development, at latitudes, leaves and flower development can be compromised by insufficiently low temperatures during dormancy to break this latter. Damage due to water stress was also an important component of the definition of the westward and eastward limits. The Great plains actually play an important role in plant species distribution on North America. Most tree species are unable to sustain the high water stress of this region, which usually correspond to the western limit of tree species from Eastern USA, and the eastern limit of species from western USA, being also limited by the Rocky Mountains barrier.

### Ecological correspondence

PHENOFIT predicts the occurrence of sugar maple in British Columbia where it does not occur. Within a particular genus, the complexes of species occurring in Western and Eastern North America are not the same except for those species occurring at very high latitudes that were able to colonize both sides of the continent (e.g. quaking aspen, balsam poplar). Even though morphologically different, these species complexes are usually considered to be "ecologically corresponding", i.e. both complexes have similar ecological ranges of tolerance, and are able to survive in analogous habitats (Kornas 1972). Since PHENOFIT is based on ecological characteristics, the predicted presence of sugar maple in the West, where another maple species lives (i.e. *Acer glabrum* Torr.), is likely to be due to ecological

correspondence between these two species. Another discrepancy between the observed distribution and the predicted distribution, is the predicted absence of sugar maple in most of Wisconsin and Minnesota, which is probably due to inadequate estimates of the phenological models. The models indeed predict that the species will usually be unable to make leaves and flowers, although obviously it should. Inadequacy of the estimates is due to the genetic differentiation between the populations we used to fit the model and the populations from Wisconsin and Minnesota. The overall accuracy of the predictions would be greatly improved if more phenological data were available throughout the range of the species to take into account more precisely genetic differentiation between the populations.

PHENOFIT shows that process-based models can be very powerful, as this has already been argued in the literature, and that we should focus more on which traits are important to take into account in the model for the questions we raise. Here we show that the match of the phenology of a particular plant species to seasonal variation in climate is a major determinant of its distribution. Two major issues could benefit from PHENOFIT: biodiversity and global warming impact assessment. Competition from introduced species has now become the second cause of species extinction after habitat destruction in the USA (Wilcove *et al.* 1998), which costs 123 billion dollars annually. PHENOFIT could help in predicting the ultimate distribution of an invasive species in an ecosystem. Assessing the impact of global warming on plant ecosystems requires both effective General Circulation Models (GCMs) and plant biogeography models. Effectiveness of GCMs can be tested by comparing the distribution of past vegetation to that predicted by a plant biogeography model using the climate simulated by a GCM for this past period (Webb & Kutzbach 1998). The robustness of such tests relies on the effectiveness of the biogeography models, which can be increased by taking phenology into account as we have in PHENOFIT.

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**BIOSKETCH**

Isabelle Chuine is interested in the evolution of plant species range and the adaptation of plants to climate. Her research is currently focused on phenology modelling, plant species range modelling and response of plants to global change.

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