Growth models of silver birch (*Betula pendula* Roth.) on two volcanic mountains in the French Massif Central

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Abstract

Silver birch woodlands of two volcanic mountains (altitude 850 m and 1450 m) were studied in order to establish a growth model of birch. Height, radial increment and crown width were measured on both sites taking into account two situations: isolated birch or birch within a stand. For the latter case two categories were sampled considering the competition status of the tree: birch suffering the most severe competition (suppressed tree) were distinguished from trees facing the lowest competition (dominant tree). Measures of competition were also made using plots where each tree was located by its coordinates and its height, trunk circumference and crown width recorded. Examination of radial growth curves showed similar patterns for the two sites for the same category of tree. Radial growth was always inferior for the site located at the highest altitude but tree lifespan was about two-fold longer. Radial increment data were used to calculate circumference as function of tree age. Models predicting circumference with time were then established for each category of tree (dominant, suppressed or isolated) using Chapman–Richards' model. Height and crown width models were produced using circumference as the predictor. Competition indices based on vertical or horizontal angles weighted by the distance were calculated for birches in stands. Indices using vertical angles appeared to be more resistant and robust to characterize local competition. Competition index was then associated with the parameters of Chapman-Richards' growth circumference model for the two sites and models predicting the circumference from the age of the tree and its competition index are proposed.

Introduction

Birch is an early successional tree with a high productive capacity, a wind seed dispersal, a wide climatic and edaphic range and a limited tolerance to shade (Gimingham 1984; Perala & Alm 1990). These features explain the ability of birch to invade heathlands and grasslands after pastoral abandonment. In the French Massif Central the colonization of *Calluna* heathlands free of any grazing and the settlement of natural birch stands (*Betula pendula* Roth. and more rarely *Betula pubescens* Ehrh.) are frequent occurrences. Nevertheless, the modeling of the functioning and changing of these heathlands from the initial stages – an heathland scattered with rare birch trees –

to a mature birch woodland is a complex process that requires examining the three main following models:

(i) The functioning model of *Calluna* heathland: life expectancies, age distributions, layering probabilities, annual growth are needed to simulate the dynamics of a *Calluna* stand and thus to estimate the resistance of heathland to birch invasion. Recent work in our study area gave elements for these different parameters.

(ii) The recruitment model: demography and reproductive capacity of birch. Many other studies and field experiments have analyzed seed production and dispersal, germination, seedlings establishment for a various variety of climate, site and vegetation con-

ditions (Aradóttir et al. 1997; Kullman, 1986, 1993; Perala & Alm 1990; Skoglund & Verwijst 1989).

(iii) The growth models: radial growth, height growth and crown development for conditions ranging from isolated trees to birch stands including competition factors. At present, to our knowledge, no growth model exists for birch. One possible explanation lies in the fact that tree rings are very hard to discern for this species (see Materials section).

The purpose of this paper is to analyze this latter point and to set up a deterministic model of individual silver birch growth taking into account competition factors. This model is intended to be used in a more global mixed stochastic and deterministic model taking into account both demographic and dynamic processes of *Calluna* heathlands and birch stands by using a Stochastic Discrete Event Simulation (Coquillard 1995; Coquillard & Hill 1997). We present here the main results of circumference, height and crown diameter growth models for birch natural stands located in two middle volcanic mountain sites: the Chaîne des Puys (850 m) and the site of La Plate (Massif du Sancy, 1450 m). The altitude difference (i.e. 600 m) reflects a difference of about 3 °C in mean temperature and can be used to forecast birch growth in case of temperature increase due to the greenhouse effect forecasted by meteorologists.

Because individual tree growth depends strongly on the level of the competition the tree is facing (Connell 1990; Tomé & Burkhart 1989; Dale et al. 1985) results are given considering the relationships between the subject tree and its neighbors.

Three cases were distinguished according the competitive status of the subject tree:
 — isolated tree undergoing no competition as no neighbors surround the subject,
 — tree within a stand with a maximal competitive advantage to its local neighbors, called a dominant tree,
 — tree suffering from the most severe conditions of competition, called a suppressed tree.

Materials

Study areas

Two sites were studied in the French Massif Central (Figure 1). The first is localized in the central part of the Chaîne des Puys at an altitude of 850 m and the
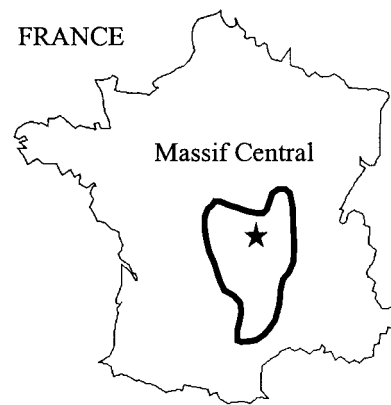

Figure 1. Situation of the study areas in the French Massif Central.

second is located in a neighbor volcanic massif (Massif du Sancy) at an altitude of 1450 m (La Plate site).

The bedrocks are of volcanic origin: trachytic ash-fall deposits in La Plate, basaltic lava and pyroclastic ejections in the Chaîne des Puys. Slopes range from 0 in the Chaîne des Puys to 30 deg (exposure south-west) in La Plate.

The climate of the region can be considered as a mountain one with strong oceanic influences. Precipitation ranges from about 900 mm (Chaîne des Puys) up to 1500 mm (La Plate) regularly spread throughout the year. Mean annual temperature is estimated at about 7 °C in the Chaîne des Puys but reliable data are unfortunately lacking for the site of La Plate. At both sites soils are of andic type, but influenced by podzolisation process in altitude (Hétier 1975).

The two sites are at present free of any grazing pressure and have been colonized by silver birch (*Betula pendula*) forming natural birch woodlands. In the Chaîne des Puys the colonization of former *Calluna* heathlands is much older than in La Plate and therefore the majority of birch stands are mature whereas in La Plate various stands range from young and dense to old and sparse stands.

Growth measures and competition analysis

In the two sites three categories of birch were sampled: isolated, dominant and suppressed. The social status was evaluated in the field considering phenotypic characteristics: a tree was considered as suppressed when dead branches and abnormal length of twigs in the crown were observed. Its dimensions (circumference and height) were usually smaller than the mean of the stand. At the opposite, dominant birches were chosen

as the tallest and biggest trees of the stand. Isolated birches were those with no neighbors present less than 5 m from the edge of the crown.

In each site, trees of various dimensions (height, circumference, crown width) were randomly sampled. Height was measured with a SUUNTO tree-height meter or a measuring rod. Crown dimensions in two perpendicular directions, trunk circumferences at breast height and at the base, were measured too. Ages were determined by cutting at the base birches with a diameter less than 4 cm, or a core was taken as near the base as possible for larger trees. In the Chaîne des Puys site cores were taken at breast height for the trees were of much greater dimensions and often damaged at the base. In many cases several cores were extracted in the same birch until the heart of the tree was reached.

Sampled cores or pieces of trunk were polished or smoothed and observed under a stereo microscope in order to identify each ring (rings were often narrow and not easily visible, some cores could not be analyzed). Rings were then measured with a precision of 0.05 mm. As the aim of ring analysis was to point out the age/size correlation, no cross-dating (using characteristic rings) was carried out. After elimination of unreadable cores, a total of 99 cores or pieces of trunks were analyzed for La Plate site and 124 for the Chaîne des Puys.

The establishment of a competition index was based on data collected from randomly chosen plots in young and dense closed stands (La Plate site) or mature stands (Chaîne des Puys site). Trees were located using the XY coordinates of their crown center projection and their dimensions were recorded. Height, circumference of the trunk and crown width (measured in two perpendicular directions) of each tree were also recorded. Altogether 153 trees at the Chaîne des Puys and 87 trees at La Plate were analyzed.

Methods

Growth modeling of birch was achieved in three steps:

(i) The trunk circumference growth model as function of age was first established using the radial growth data for the three categories of birch (dominant/suppressed/isolated).

(ii) Circumference thus calculated was used as a predictor to produce height and crown width.

(iii) A competition index was then calculated and related to the circumference models.

Circumference modeling

Radial growth data were used to calculate under bark circumference growth using the following relation:

$$C(t) = 2\pi r(t) + C(t-1), \tag{1}$$

$C(t)$ and $C(t-1)$ are respectively circumferences (cm) at ages of t and $t-1$, $r(t)$ is the radial increment at age t.

Regression equations predicting tree circumference from age were then calculated by using Von Bertalanffy's model (1949, 1968) also commonly known in forestry as the Chapman-Richards' growth model (Chapman 1961; Richards 1959):

$$C = C_{max}(1 - e^{-bt})^\lambda, \tag{2}$$

where C_{max} is the asymptote circumference value (cm), b is the rate parameter, and λ is the shape parameter.

For isolated birches, due to a lack of circumference values for old age, computations were made with the same C_{max} value found for dominant birches. We made the assumption that when t approaches infinity, the maximal circumference reached was the same whether the birch was isolated or included in a stand with a dominant status.

Height and crown width modeling

Crown width was calculated as a linear function of the trunk circumference:

$$Cw = aC + b, \tag{3}$$

where Cw is the crown width (cm), C the circumference at the base of the trunk (cm), a and b are regression coefficients.

A Chapman–Richards' function was used to predict height of birches in a stand:

$$H = H_{max}(1 - e^{-aC}) \tag{4}$$

where H is the height (m), H_{max} is the asymptote value (m), C is the trunk circumference at the base (cm), and a is a coefficient.

For isolated birches, because of the narrow range of sampled circumference values (with time individuals in the heathland are no longer isolated but start facing competition from their neighbors), we computed a linear regression to produce height.
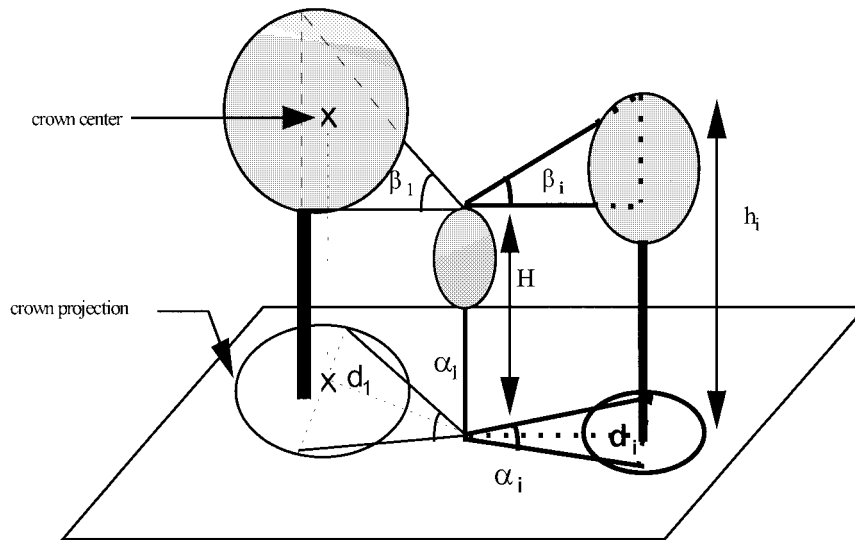
Figure 2. Principle for the computation of two competition indices using the horizontal angles sum ($\Sigma\alpha_i$) or the vertical angles sum ($\Sigma\beta_i$).

Establishment of competition indices

Most competition indices are based on distances, diameters, angles and heights of neighboring trees (Rouvinen & Kuuluvainen 1997; Biging & Dobbertin 1995; Tomé and Burkhart 1989; Pukkala & Kolström 1987). Two indices were tested. The first one is based on horizontal angle sums and the second on vertical angle sums (Figure 2). Because most interactions among trees occurred at a local scale (Rouvinen & Kuuluvainen 1997; Kenkel et al. 1989) the two competition indices were both weighted by distance using an exponential function (see Tomé & Burkhart (1989) for the use of competition indices weighted by different kind of distance functions). They were calculated as follows:

$$CI_1(j) = \sum_{\substack{i=1 \\ j \neq i}}^{i=n} \alpha_i e^{-kd_i}, \tag{5}$$

$$CI_2(j) = \sum_{\substack{i=1 \\ j \neq i}}^{i=n} \beta_i e^{-kd_i}, \tag{6}$$

CI_1 and CI_2 are the competition indices for tree (j) with height H (m), n is the number of neighbors, α_i is the horizontal angle from the subject to the competitor i, $\alpha_i = 2\arctan(r_i/d_i)$ where r_i is the crown radius of i and d_i is the distance to i (m), $\alpha_i \in d_i\epsilon]0, \pi[$, β_i is the vertical angle from the subject to the competitor i which height is h_i (m), $\beta_i = \arctan[(h_i - H)/d_i]$,

it can take negative or positive values: trees with a competitive disadvantage are caracterized by negative values of CI_2 whereas these values are positive for trees with a competitive advantage, $\beta_i \in]-\pi/2, \pi/2[$, k is a coefficient that expresses the weighting by distance.

For a given neighbor i, CI is maximum when $d_i = 0$ and then can be neglected for neighboring trees beyond a certain distance depending on k value.

Relevance of the selected competition index was established by considering the regression coefficient R of the linear regression computed by plotting the competition indices values of different subject trees versus their circumferences. The higher the CI value is the lower the circumference should be and *vice versa*. We preliminarily verified that no significant relation was found between the age of the trees (when this data was collected) and their circumferences. The coefficient k was obtained by maximizing the regression coefficient R.

Relationships of the competition index to circumference growth models for birch within a stand

The competition index was then related to the circumference growth models by assuming that the asymptote value $C_{\max}$ and the rate parameter b of Equation 2 (2) were exponential functions of CI:

$$b = \alpha_1 e^{\beta_1 CI}, \tag{7}$$

$$C_{\max} = \alpha_2 e^{\beta_2 CI}. \tag{8}$$

The coefficients α_i and β_i were calculated for a given stand by using the two extreme values of CI found. The minimum value of CI was related to the $C_{\max}$ and b values found for dominant trees whereas the maximum value of CI was related to the same parameters found for suppressed trees.

Using relations (7) and (8), relation (2) can be written:

$$C = \alpha_2 e^{\beta_2 CI}(1 - e^{-t\alpha_1 e^{\beta_1 CI}})^{\lambda}. \tag{9}$$

Results

Radial growth

Birch stands Radial growth curves of birches sampled within stands are shown in Figures 3 and 4. For each site we distinguished dominant and suppressed trees. Confidence intervals were calculated and drawn, the variability in radial growth lies mainly in the variable climatic conditions of growth (each measure represents the mean of a minimum of 5 ring widths coming from different trees but for the same age). This variability is especially important for La Plate site because of harsher climatic conditions: birch woodlands were close to the upper limit of the forest, thus explaining that radial growth is very sensitive to climatic conditions (Brubaker 1986). However these curves indicate the main trend of the evolution of radial growth as a function of age: growth is maximum at the age of 11 for La Plate site and at 6 for the Chaîne des Puys considering dominant trees (Figure 3). Then growth regularly decreases as the competition between trees and the age increase to reach a threshold value of about 1.5 mm y^{-1} in the Chaîne des Puys at 40 years and 0.6 mm in La Plate at 80 years. Suppressed trees radial growth curve is very similar (Figure 4) to the dominant ones with weaker threshold values: about 0.6 mm y^{-1} in the Chaîne des Puys and about 0.5 mm y^{-1} in the case of La Plate.

It is important to emphasize that intraspecific competition occurred mainly in young birch stands (i.e., respectively inferior to 35 years old and 27 years old for La Plate and the Chaîne des Puys sites) as no suppressed trees were found in mature stands. The better conditions of growth in the Chaîne des Puys favoured the competition between trees and the elimination of suppressed trees occurred faster than in La Plate.

Isolated birches There were clear differences in growth pattern between birch within a stand and iso-

lated birch (Figure 5). Radial increment was low the first six years and then regularly increased with time. From these results we conclude that there is a different pattern of seedling establishment in *Calluna* stands. Isolated birches established inside dense or mature *Calluna* stands and had to undergo intense competition from surrounding vegetation. Growth increase was therefore slow the first years and regularly increased while competition from the vegetation was decreasing. Whereas, in the case of birch stands, regeneration probably occurred when gaps were formed (as observed when *Calluna* heads enter a degenerate phase) allowing *Betula* seedling establishment (Gong & Gimingham 1984).

Circumference modeling

Results giving the trunk circumference computed from the radial growth data using (1) function of the age are shown in Figure 6.

Regression equations found using (2) are the following:

Site of the Chaîne des Puys

Dominant trees $C_{bh} = 90.938(1 - e^{-0.0366t})$ (10)
$\qquad R^2 = 0.999 \quad Se = 0.64,$

Suppressed trees $C_{bh} = 28.17(1 - e^{-0.0564t})$ (11)
$\qquad R^2 = 0.998 \quad Se = 0.26,$

Isolated birches $C_{bh} = 90.938(1 - e^{-0.064t})^{2.53}$ (12)
$\qquad R^2 = 0.995 \quad Se = 1.05;$

Site of La Plate

Dominant trees $C = 86.339(1 - e^{-0.0142t})$ (13)
$\qquad R^2 = 0.999 \quad Se = 0.49,$

Suppressed trees $C = 36.51(1 - e^{-0.0286t})$ (14)
$\qquad R^2 = 0.996 \quad Se = 0.41,$

Isolated birches $C = 86.339(1 - e^{-0.0303t})^{1.88}$ (15)
$\qquad R^2 = 0.997 \quad Se = 0.65,$

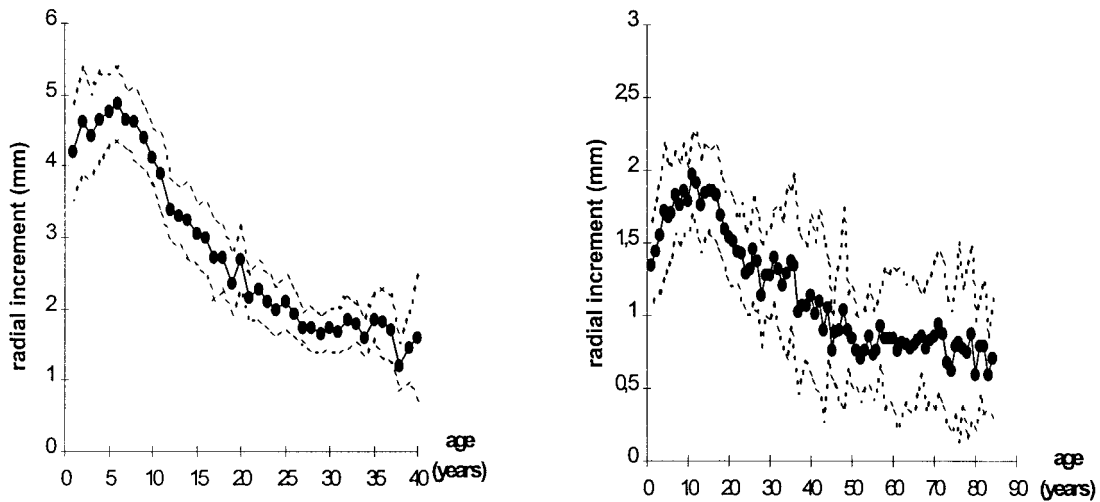where Se is the standard error of estimates and R the regression coefficient.

Figure 3. Mean radial growth for birch dominant trees. Left: Chaîne des Puys ($n = 43$). Right: La Plate ($n = 25$). Dotted lines indicate confidence intervals ($\alpha = 0.05$).

Height and crown width growth modeling

Data used are shown in Figure 7.

Height and crown width models using (3) and (4), as well as relations between circumference at breast height and circumference at the base of the trunk, are shown in Table 1. Models are given for the two sites considering the status of the tree: isolated or included within a stand. For this latter case, models can be applied irrespective of the competitive status of the tree (dominant or suppressed tree).

Either in the Chaîne des Puys or in La Plate, equations predicting crown width from the circumference are quite similar for dominant and isolated trees. This can be explained by the structure of our sampling: dominant trees were chosen among the tallest and biggest trees and had to suffer a minimum of competition from the neighboring trees such as isolated birches.

Height growth models are comparable for dominant and suppressed birches whereas isolated birch height is for a same circumference always inferior to the dominant one.

Competition index

Good linear relationships $CI_1 = f(C_w)$ (C_w: crown width and f a linear function) were found with data collected from local trees subsets in the studied stands, but no satisfactory relation was successfully established for the whole data combined. CI_1 is a competition index which seems to be too closely related to local stand parameters to be applied broadly.

Competition index CI_2 for a given tree appears to be a linear function of its circumference (Figure 8). The coefficient k was equal to 1.01 for the site of La Plate for a relatively dense and young birch stand and equal to 0 for the mature stand of the Chaîne des Puys. In this latest case, distance appears to have no longer influence on the competition index when the stand has reached an equilibrium stage.

Relationships of the competition index to circumference growth models

Values of coefficients α_i and β_i (relations (7) and (8)) and the parameters used for their computations are shown in Table 2.

Equations (7), (8) and (9) can therefore be written:

Chaîne des Puys site

$$b = 0.0459e^{0.0047CI}, \tag{16}$$

$$C_{\max} = 49.14e^{-0.0128CI}, \tag{17}$$

$$C_{bh} = 49.14e^{-0.0128CI}(1 - e^{-0.0459te^{0.0047CI}}); \tag{18}$$

La Plate site

$$b = 0.0183e^{0.103CI}, \tag{19}$$

$$C_{\max} = 63.42e^{-0.127CI}, \tag{20}$$

$$C = 63.42e^{-0.127CI}(1 - e^{-0.0183te^{0.103CI}}). \tag{21}$$

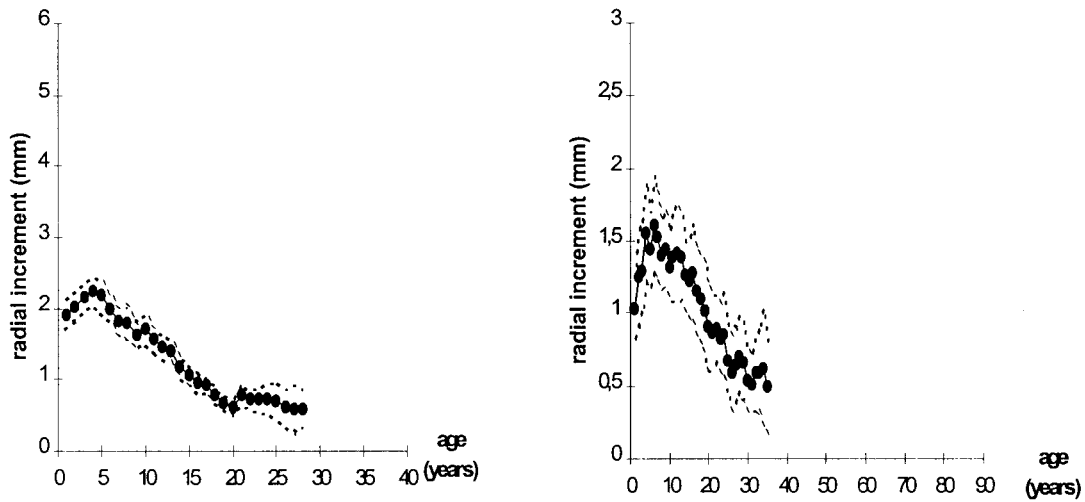*Figure 4.* Mean radial growth for birch suppressed trees. Left: Chaîne des Puys ($n = 62$). Right: La Plate ($n = 24$). Dotted lines indicate confidence intervals ($\alpha = 0.05$).
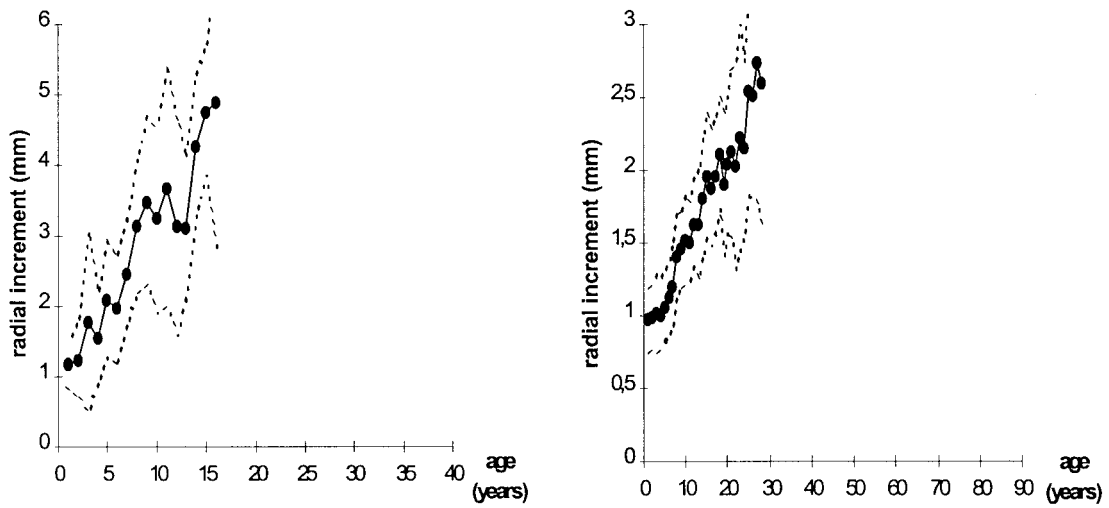

Figure 5. Mean radial growth for birch isolated trees. Left: Chaîne des Puys ($n = 19$). Right: La Plate ($n = 40$). Dotted lines indicate confidence intervals ($\alpha = 0.05$).
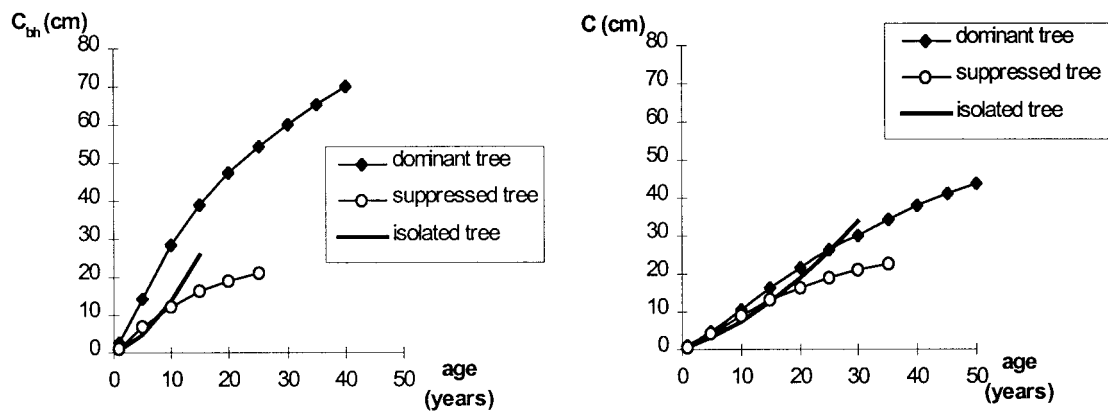

Figure 6. Mean circumference growth calculated from radial growth data. Left: Chaîne des Puys. Right: La Plate (C: circumference at the base, C_{bh}: circumference at breast height).
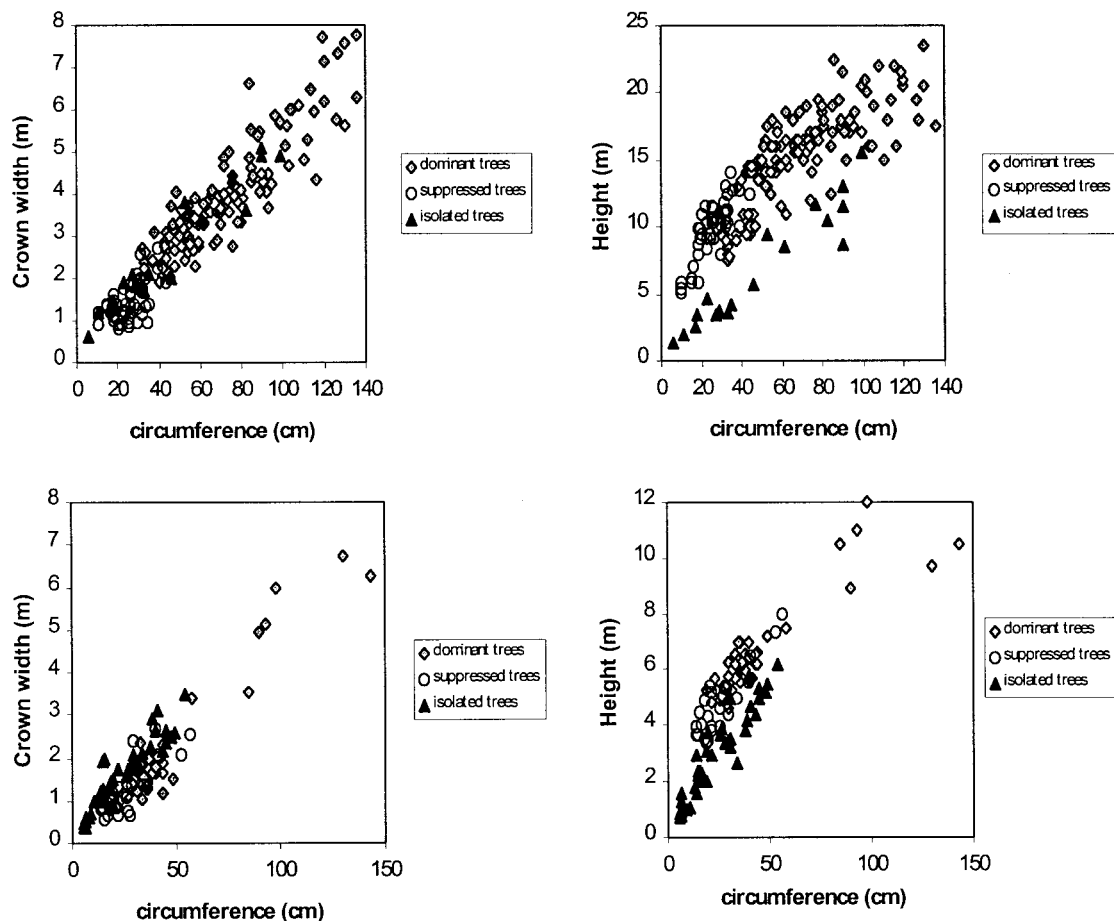
Figure 7. Crown width and height as function of the circumference at the base for the site of La Chaîne des Puys (above) and La Plate (below).

Table 1. Height and crown width models as function of the circumference at the base of the trunk (C in cm). Relation between C and C_{bh} (circumference at breast height) is also given (n: number of measured trees).

| Sites	Dimensions	Birch within stand	Isolated birch
Chaîne des Puys	Height: H (m)	$H = 21.58(1 - e^{-0.0198C})$ $n = 135$; $R^2 = 0.68$; Se $= 1.95$	$H = 0.13C + 0.468$ $n = 19$; $R^2 = 0.91$; Se $= 1.32$
	Crown width: C_w (m)	$C_{\mathbf{w}} = 0.0465C + 0.5762$ $n = 135$; $R^2 = 0.81$; Se $= 0.59$	$C_{\mathbf{w}} = 0.047C + 0.5455$ $n = 19$; $R^2 = 0.94$; Se $= 0.39$
	Circumference at breast height: C_{bh} (cm)	$C_{bh} = 0.868C$ $n = 135$; $R^2 = 0.98$; Se $= 3.60$	
La Plate	Height: H (m)	$H = 11.31(1 - e^{-0.0218C})$ $n = 48$; $R^2 = 0.83$; Se $= 0.71$	$H = 0.1205C + 0.5196$ $n = 39$; $R^2 = 0.88$; Se $= 0.55$
	Crown width: C_w (m)	$C_{\mathbf{w}} = 0.0513C - 0.1715$ $n = 48$; $R^2 = 0.91$; Se $= 0.40$	$C_{\mathbf{w}} = 0.0524C + 0.3486$ $n = 39$; $R^2 = 0.86$; Se $= 0.31$
	Circumference at breast height: C_{bh} (cm)	$C_{bh} = 0.757C$ $n = 73$; $R^2 = 0.97$; Se $= 3.51$	
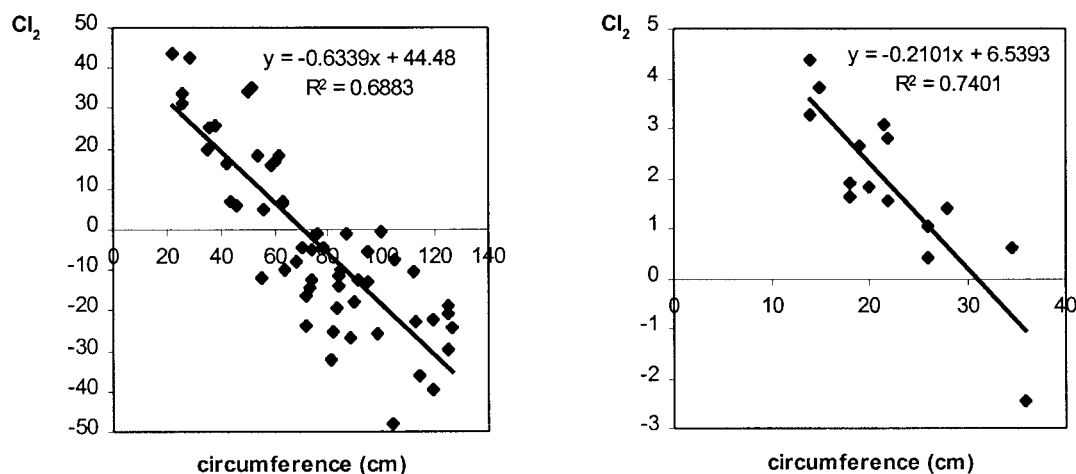
Figure 8. Relation between the competition index (CI_2) and the circumference of a tree. Left: Chaîne des Puys ($k = 0$). Right: La Plate ($k = 1.01$).

Table 2. Computation of coefficients α_i and β_i and parameters used for their calculation.

	Minimum CI value	Maximum CI value	b value (dominant tree)	b value (suppressed tree)	C_{max} value (dominant tree)	C_{max} value (suppressed tree)	α_i	β_i
Chaîne des Puys	−47.96	43.36	0.0366	0.0564	90.94	28.17	$\alpha_1 = 0.0459$	$\beta_1 = 0.0047$
							$\alpha_2 = 49.14$	$\beta_2 = -0.0128$
La Plate	−2.43	4.35	0.0142	0.0286	86.34	36.51	$\alpha_1 = 0.0183$	$\beta_1 = 0.103$
							$\alpha_2 = 63.42$	$\beta_2 = -0.127$

Putting $CI = 0$ in the relations (18) and (21) allows to establish the limit circumference between dominant and suppressed trees, we found:

Chaîne des Puys site
$$C_{bh} = 49.14(1 - e^{-0.0459t}), \qquad (22)$$

La Plate site
$$C = 63.42(1 - e^{-0.0183t}). \qquad (23)$$

The different circumference models are shown Figure 9.

Discussion

The circumference models

We have set up our growth model by establishing first the equation giving circumference as a function of time, using tree-ring analysis. Contrary to dendroclimatological studies aiming at extracting the part of tree ring growth due to climatic effects (high frequency signals) we have only considered the biological growth trend linked with age (low frequency signals). Because under a given set of climatic and edaphic conditions growth structure is closely related with competition, all possible situations for birch were sampled. Trees in a stand were first separated from isolated trees for which competition with neighbors for above and below resources does not exist. For this first case two categories were distinguished considering the competition level. Suppressed trees represent the part of the population suffering from the most severe competition conditions. Because they showed symptoms of decline and they are relegated to the lowest strata of the stand these trees are probably destined to die in the next few years. At the other extreme, birches with a dominant position in the canopy are facing the lowest competition and represent the fastest growing trees of the stand. Thus, the circumference growth curve for a given tree undergoing intermediate com-

petition lies between the two extreme circumference growth curves of suppressed and dominant trees. One can verify (Figure 9) for trees with $CI = 0$ (i.e., with no advantage or disadvantage in term of competition) this latter assertion.

Competition and connection to growth

Effects of competition quantified through competition indices on stand productivity, radial increment, crown structure, growth height have been widely reported in previous studies (Piutti & Cescatti 1997; Rouvinen & Kuuluvainen 1997; Ung et al. 1997; Tomé & Burkhart 1989, Pukkala 1989, Pukkala & Kolström 1987). Connecting a circumference growth model to competition implied choosing an appropriate competition index. The CI based on vertical angles weighted by distance give the best correlation coefficient between the calculated values of CI and the correspondent circumferences whereas the competition indices calculated with horizontal angles appear to be too sensitive to local stand structure. This can be explained considering light requirements which are crucial for shade intolerant species like birch. Light is essentially a vertically distributed resource whose interception depends on the crown structure and dimensions. Thus vertical angles probably describe light competition processes and conditions more accurately. Weighting by distance appears to be important in the young stages where the density is high and therefore competition among trees intense but can be neglected when the stand has reached an equilibrium: in the mature stand of the Chaîne des Puys competition appears weak and current tree size only reflects the past competition. Our CI, though related to the local stand for which it has been developed, seems to be effective to describe the competition of individuals in two different test stands.

Relations (10), (11) and (13), (14) show that the asymptote value C_{max} and the rate parameter b of equation respectively decrease and increase while competition becomes stronger. Assuming these two parameters depend on CI by an exponential function we found relations (17), (20) and (16), (19) that can also be explained by biological considerations.

Parameter b expresses a velocity to reach the asymptote value. Equations (16) and (19) point out that the more intense the competition the higher b is. As the competition by neighboring trees becomes higher the capacities for suppressed trees to find new resources (light and nutrients) are reduced and thus the maximal circumference is quickly reached. On the contrary a dominant birch can grow more easily while competition by neighbors decreases, it is able to have access to new resources and therefore to a more sustainable growth. A similar argument can be proposed to explain that the higher the competition the lower the asymptote value is and *vice versa* (relations (17) and (20)).

Comparison between the two sites

The two study areas differ primarily from one another by climate, especially thermic conditions, although edaphic differences cannot be excluded. Because trees undergo extreme thermic conditions in La Plate, radial growth is always less important than in the Chaîne des Puys. Another major difference consists in the length of lifespan being two-fold longer for dominant birches in La Plate than in the Chaîne des Puys. In this latter case, once stands have reached a mature stage (about 50 years old), shade tolerant species (beech essentially) start successfully competing with birch. However growth patterns are very similar considering each category of tree and they appear to be tightly connected with competition conditions.

Integrating growth models of the Chaîne des Puys in the conditions of La Plate should enable us to simulate birch growth in case of a climate warming.

In conclusion, the above model can be classified according to the 'individual tree-based models'. This kind of model is more significant than stand models because 'age structure, spacing, and diversity as well as individual tree attributes can be examined' (Dale et al. 1985) and they are thus well suited to study forest dynamics.

The proposed growth model is one of the first dealing with birch and several improvements could be made. In particular the validity of our competition index should be tested for different birch stands and the weighting by distance clearly connected with the main parameters of the stand such as density or mean height. In addition the problem of individuals moving progressively from an isolated status to a status of tree included in a stand raises the problem of transition between the two models involved.

This deterministic model was set up to be included in a combined deterministic/stochastic model (using the Discrete Event Simulation method) dealing with birch colonization and growth on *Calluna* heathlands integrating the simulation of climatic modifications. Thus, further studies have to be carried out to establish the key parameters of the regenera-
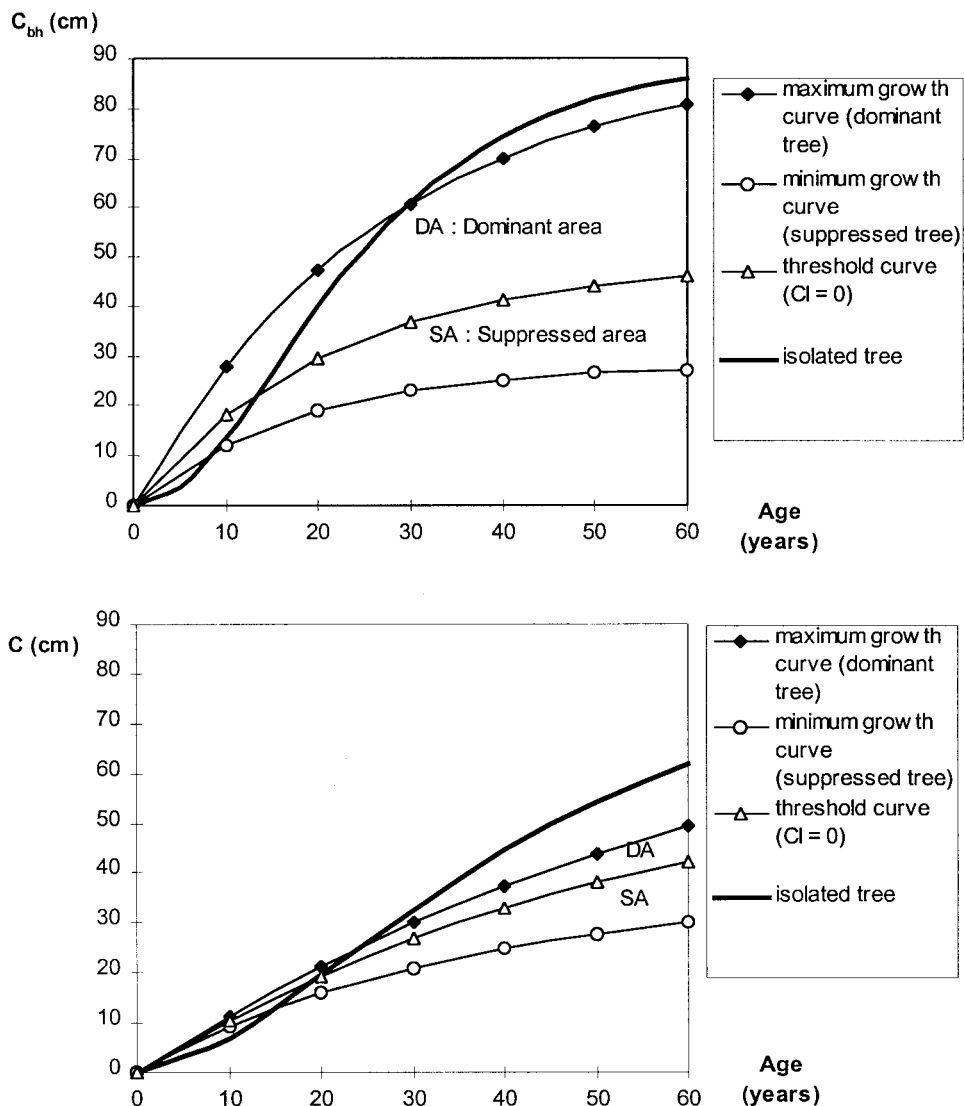
Figure 9. Circumference models of the different categories of trees for the Chaîne des Puys (above) and La Plate (below) sites. The two threshold curves were computed using relations (22) and (23). Further explanations in text.

tion process in our study area (seed production and dispersal, recruitment) and integrated in the model.

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