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Modeling mid-elevation Scots pine growth on a volcanic substrate

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Abstract

The aim of this study was to set up a deterministic and individual-based growth model of natural Scots pine (*Pinus sylvestris* L.) forests on a volcanic mountain located in the French Massif Central. In order to take the trees' competitive status into account, isolated trees were first distinguished from trees within a stand. Then trees within stands were assigned to one of the three categories of competitive status: trees characterized by a maximum competitive advantage to their neighbors (dominant trees), trees with a maximum competitive disadvantage (suppressed trees), and trees undergoing an intermediate level of competition (co-dominant trees). The modeling was achieved in three steps:

(i) Trees from the different categories were first measured and cores collected and analyzed in order to establish growth models of trunk-circumference, height, and crown-width. Radial growth curves for trees within a stand showed a similar pattern for the three competition categories, with a maximum growth value reached at age three. Growth values appeared to be strongly dependent on the tree's competitive status. Circumference curves were computed on the basis of radial increment values. Models predicting circumference and height with time were computed using a Von Bertalanffy–Chapman–Richard's model. Isolated tree-height and crown-width models were established using circumference as predictor.

(ii) Competition was measured on four stands ranging from young and dense to old and sparse. Each tree of the stands was mapped by its *X*, *Y* coordinates and its dimensions were recorded. Eleven distance-dependent competition indexes based on vertical or horizontal angle sums were computed and their correlation to tree dimensions was analyzed for the four stands.

(iii) Two competition indexes were selected and related to growth model parameters to produce a model predicting height and circumference from the age and the competition indexes. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: *Pinus sylvestris*; Growth model; Competition; Volcanic mountain

1. Introduction

Scots pine stands (*Pinus sylvestris* L.) are widely distributed in the Chaîne des Puys, a volcanic massif

located in the French Massif Central (Fig. 1). Most of them naturally developed after pastoral abandonment during the second half of the past century (Bazin et al., 1983). The colonization of heathlands and lawns is weaker at present, but may start again if there is a new decrease of grazing pressure. Scots pine natural establishment raises the problem for land managers to forecast the natural afforestation process — in order

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Fig. 1. Location of the study area (Chaîne des Puys) in the French Massif Central.

to keep the remaining heathlands still opened — and also the way to manage these current natural Scots pine stands that are frequently replanted by their owners with spruce, leading to a degradation of the landscape and a loss of biodiversity.

Currently, little is known of these natural forests: how they were established on former grasslands or heathlands (i.e. seed production and dispersal, seedling establishment), their dendrometric characteristics, and how these stands evolved. In this context, a modeling and simulation tool can be useful to forecast extension of Scots pine and to predict growth and evolution of present secondary Scots pine forests. Such a model implies studying two major components of the natural forest dynamics: recruitment and growth. The purpose of this paper, which only focuses on growth, is to establish a deterministic model of Scots pine growth. The proposed growth model is individual-based for three reasons. First, this kind of model has the advantage of examining individual tree characteristics as well as stand parameters by aggregation (Dale et al., 1985). Second, it can easily take into account competition that is the major cause of the natural forests structuring and a key component to describe growth. Third, it is well suited to integrate reproduction processes, and it is the reason why individual-based models were used to study forest dynamics (Ek and Monserud, 1979; Pacala et al., 1996), especially in the case of invasive species like pines (Higgins and Richardson, 1998). It is intended to integrate this model into a global one taking into account both regeneration, growth and death using Discrete Event Simulation (Coquillard, 1995; Coquillard and Hill, 1997).

Growth models corresponding to different categories of competition status have been distinguished (Prévosto et al., 1999). First, isolated trees were separated from trees within a stand. Then, for trees within stands, two growth models were established according to two extreme competition categories: dominant and suppressed trees. Finally, a third case was examined dealing with trees characterized by an intermediate competitive status (co-dominant tree). Competition was described with the help of distance-dependent competition indexes, widely used in previous studies (Pukkala and Kolström, 1987; Tomé and Burkhart, 1989; Rouvinen and Kuuluvainen, 1997), which are based on the distances and aerial characteristics of neighboring trees.

The study aims at emphasizing the growth pattern differences between various categories of trees undergoing extreme competition values, and not forecasting a yield including silvicultural interventions. Consequently, stands were intentionally sampled free of any silvicultural treatment (naturally established stands) and comparable in terms of site index.

2. Material and methods

2.1. Study area

The study area is located in the southern part of the Chaîne des Puys, a volcanic massif of the French Massif Central (Fig. 1). The Massif of the Chaîne des Puys consists of a range of about one hundred volcanoes forming a band of 40-km length and 5-km width entirely located at mid elevation (mean altitude: 850–1100 m). The climate is mountainous with oceanic influences. Annual mean precipitation is 1000 mm, but with strong variation from west to east and north to south, and annual mean temperature is 7°C. Soils are developed on various substrates: trachytic or basaltic ash-fall deposits or lava blocks. Both, the nature of the bedrock and the altitude influence the podzolization process (Hétier, 1975).

This region, which is presently included in a regional park, was traditionally used for extensive sheep production and thus maintained as an open landscape. The decline of this pastoral system after the Second World War enhanced the colonization of former heathlands and lawns by ligneous species, especially hazel

(*Corylus avellana* L.), silver birch (*Betula pendula* Roth), and Scots pine, which is by far the most widespread species on level areas or moderate slopes. Natural Scots pine stands are of varying age and structure, but stands of about 30–40 years old occur most frequently and correspond to a period when land abandonment was maximal.

The understory vegetation is abundant and diverse under mature stands, but rare under dense young stands. It is mainly composed of herbaceous species from the initial stages of colonization (lawn or heathland) mixed with beech (*Fagus sylvatica* L.) or beech-oak (*Quercus robur* L.) forest species. In fact, these monodominant Scots pine stands are only a transitional stage in the vegetation dynamics leading to a climatic beech forest.

2.2. Tree measurements

Measurements of different tree categories were carried out in order to establish growth models of circumference, height, and crown width.

On the basis of a previous phytoecological survey of Scots pine natural forests in our study area, we selected 57 stands (mean surface: 400 m²) located on comparable site conditions: similar substrate (basaltic scoria), altitude between 900 and 1000 m and level topography or moderate slope. A dendrometric inventory was carried out for the 57 stands and the circumference at breast height of 2434 trees was recorded.

In each stand, three or four trees were sampled considering their competitive status: one dominant tree, one suppressed tree (if present), and one or two intermediate trees (called co-dominant trees). A total of 223 trees were sampled. Tree distribution in circumference classes at breast height for the total set of the 57 stands and for the sample used for measurements is shown in Fig. 2. The status of the trees was evaluated in the field considering morphologic and dendrometric characteristics. The dominant tree was selected as the biggest tree of the stand. A tree was considered as suppressed when symptoms of decline were observed (dead branches in the crown, abnormal length of twigs, loss of needles), and each of its dimensions (trunk-circumference, height, crown-width) was smaller than the respective mean of the stand. Co-dominant trees were chosen among the most frequent circumference class in the stand. On each tree, a core was taken at breast height, and its dimensions were measured: the height, circumference at breast height and the crown width in two perpendicular directions. Tree rings were then counted and measured with a precision of 0.1 mm, however, some cores which were difficult to analyze were eliminated. Altogether, 51 cores from dominant trees, 77 from co-dominant, and 51 from suppressed trees were sampled.

Isolated trees were sampled within an area in the process of being colonized by Scots pine. Site conditions were comparable with those described for the

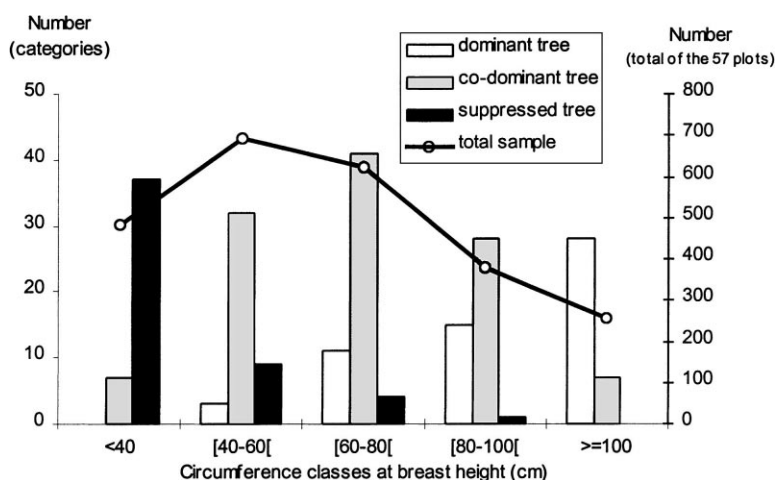


Fig. 2. Distribution of circumference classes for the sampled trees within stand. Bars indicate the number of trees (left axis) sampled for each category. The curve shows the total number (right axis) of trees measured in 57 stands.

sampled stands with some slight differences (altitude 1100 m, slope 21°, exposure Northeast). Fifty-three trees of various dimensions were measured and 42 cores analyzed.

2.3. Measurements for competition analysis

Competition is a factor that clearly influences radial growth, canopy structure, and branch characteristics, as well as biomass production of Scots pine stands (Pukkala and Kolström, 1987; Mäkinen, 1996; Rouvinen and Kuuluvainen, 1997). Distance-dependent competition indexes were shown to be reliable for taking competition into account (Bella, 1971; Tomé and Burkhardt, 1989; Ung et al., 1997), especially in natural stands where spatial heterogeneity can be important. Therefore, a knowledge of the location is of greater interest in these stands than in plantations characterized by a relatively controlled spacing.

Competition analysis was carried out in four mono-dominant Scots pine natural forests, ranging from young and dense to old and mature stands, that were located in similar site conditions. Trees of various competitive status (dominant, co-dominant or suppressed trees) are encountered in these stands. The stands' main characteristics are described in Table 1.

In all stands, each tree was characterized by the following measurements:

X and Y coordinates;
circumference at breast height;
height; and

crown projection dimensions in two perpendicular directions.

In all stands a strip alongside the plot was left as a buffer zone as in previous studies (Pukkala and Kolström, 1987; Rouvinen and Kuuluvainen, 1997).

2.4. Modeling

Modeling was achieved in three steps:

1. Development of growth models for the different categories of trees. Isolated trees were separated from trees within stands in which three categories — corresponding to competitive status — were distinguished: dominant, co-dominant, and suppressed.
2. Calculations and choice of distance-dependent competition indexes. The competitive status of a tree within a stand is described with a competition index, and no longer through categories.
3. Connection of competition indexes to growth model parameters in order to produce a growth model applicable to any tree within a stand.

Equations were fitted using the ordinary least squares method.

2.4.1. Growth models for the different categories of trees

2.4.1.1. Trunk-circumference modeling. For the four categories of sampled pines (isolated, dominant, co-

Table 1
Main stand characteristics used for competition analysis

	Stand 1	Stand 2	Stand 3	Stand 4
Plot dimensions (m)	7.2 × 9.7	15 × 15	24 × 24	30 × 30
Number of trees	58	127	91	49
Density (/ha)	8305	5644	1580	544
Height (m)				
Mean	5.0	10.8	15.9	16.9
SD	1.6	1.6	2.2	2.2
Circumference (cm) at breast height				
Mean	8	34.4	60.5	99.7
SD	10.8	12.8	16.8	25.6
Age at the base (year)				
Mean	13	25	36	49
SD	1.3	2.2	3.1	4.3
Buffer zone width (m)	1.5	3	5	6

dominant, and suppressed trees) trunk-circumference at breast height was computed on the basis of radial increments. Then a regression equation, derived from the Von Bertalanffy–Chapman–Richards growth model (Von Bertalanffy, 1949, 1968; Richards, 1959; Chapman, 1961), was computed to relate circumference to time:

$$C = C_{\max}(1 - e^{-b_1 t})^{\gamma_1} \quad (1)$$

where C is the under-bark circumference at breast height, $C_{\max}$ the asymptote value, b_1 the rate parameter, and γ_1 the shape parameter. In calculating the circumference model for isolated trees, we assumed that the asymptote value was the same as for dominant trees because data were lacking for old ages.

2.4.1.2. Height modeling. The height model was similar to the circumference model for trees within stands:

$$H = H_{\max}(1 - e^{-b_2 t})^{\gamma_2} \quad (2)$$

where H is the total height, $H_{\max}$ the asymptote value, b_2 the rate parameter, and γ_2 the shape parameter.

Isolated tree height was computed from the above bark circumference at breast height using a linear regression:

$$H = aC' + b \quad (3)$$

$C' = f(C)$ is the above-bark circumference at breast height computed from C by a single linear relation f ; a and b the regression coefficients.

2.4.1.3. Crown-width modeling. A previous study on Scots pine crown structure showed that crown width was already quite well described by the combination of diameter at breast height and height, and that the crown width model was only slightly improved by the knowledge of the local competition described through spatial competition indexes (Rouvinen and Kuuluvainen, 1997). Thus, crown width was produced by a linear regression using circumference and height as predictors. Trees within stands were distinguished from isolated trees:

$$C_w = a_1 C' + b_1 H + c_1 \quad (4)$$

C_w is the crown width, C' is the above bark circumference of the trunk at breast height, H the total height, a_1 , b_1 and c_1 the regression coefficients.

2.4.2. Competition indexes used

Local competition was described by 11 competition indexes (see formulas in Appendix A) computed for the four measured stands. Indexes CI_1 to CI_5 are based on vertical angle sums and indexes CI_6 to CI_{11} are based on horizontal angle sums. All have been used in previous studies of competition in Scots pine stands (Pukkala and Kolström, 1987; Rouvinen and Kuuluvainen, 1997). The general form of a competition index for a tree j is the following:

$$CI(j) = \sum_{\substack{i=1 \\ i \neq j}}^n \epsilon(i) \lambda_i \quad (5)$$

where n is the number of competitors, λ_i a vertical or horizontal angle from subject j to competitor i , and $\epsilon(i)$ is a coefficient that can take the values 0, 1, or -1 . Three cases can be distinguished:

1. $\epsilon(i) = 1$ if $X_i \geq X_j$, or 0 (CI_1 to CI_3 , CI_7 , CI_{10}). Only competitors with dimension X (trunk circumference, height, or crown width) greater than the subject's are taken into account;
2. $\epsilon(i) = 1$ (CI_6 , CI_9). All competitors are considered without any conditions;
3. $\epsilon(i) = 1$ if $X_i \geq X_j$, or -1 (CI_4 , CI_5 , CI_8 , CI_{11}). A competitor with dimension X greater than that of the subject places it at a competitive disadvantage, whereas a competitor with dimension X smaller than that of the subject places it at a competitive advantage. For a given tree, CI is, therefore, the sum of these competitive advantages or disadvantages (Tomé and Burkhart, 1989).

Only trees inside a fixed competition radius were considered as competitors and integrated in CI calculations. For each stand, the competition radius was set equal to the buffer zone width, so that no differences were induced by the location of the tree, in the plot center or at the edge of the buffer zone. Past studies suggested that competition radius is strongly dependent on the stand characteristics of density or age. In young *Pinus nigra* stands ranging from 2642 to 3661 stems/ha, De Luis et al. (1998) computed an optimal competition radius between 2 and 4 m. In mature Scots pines forest Pukkala and Kolström (1987) and Rouvinen and Kuuluvainen (1997) used a competition radius of 5 m; Piutti and Cescatti (1997) assessed

their growth model in old beech forests by using a fixed competition radius of 8 m. This is the reason why an increasing competition radius was chosen from young and dense to old and sparse stands.

Trees in the buffer zone were used as competitors in calculating competition indexes, but not as subject trees. Testing of CI indexes was achieved by examining the correlation coefficient obtained by plotting the competition indexes values of the different trees vs. their dimensions (circumference at breast height, height, and crown width, respectively). The effect of the competition distance on the correlation coefficient was also examined.

2.4.3. Relation of competition indexes to parameters of growth models for trees within stands

Height and circumference asymptote values and rate parameters computed using Eqs. (1) and (2) proved to be very different according to the tree competitive status. Thus, assuming that the asymptote value and the rate parameter of relations (1) and (2) were exponential functions of the competition index, we set:

$$b_1 = \alpha_1 e^{\beta_1 CI} \quad b_2 = \alpha'_1 e^{\beta'_1 CI} \quad (6)$$

$$C_{\max} = \alpha_2 e^{\beta_2 CI} \quad H_{\max} = \alpha'_2 e^{\beta'_2 CI} \quad (7)$$

The coefficients α_i , β_i and α'_i , β'_i were calculated for a given stand by using the two extreme values of CI found. The minimum value of CI (i.e. trees with a maximum competition advantage) was related to the asymptote value and rate parameter found for dominant trees, whereas the maximum value of CI (i.e. trees with a maximum competition disadvantage) was related to the same parameters, for suppressed trees. Using Eqs. (6) and (7), Eqs (1) and (2) can, therefore, be written as follows:

$$C = \alpha_2 e^{\beta_2 CI} (1 - e^{-t\alpha_1 \exp \beta_1 CI})^{\gamma_1} \quad (8)$$

$$H = \alpha'_2 e^{\beta'_2 CI} (1 - e^{-t\alpha'_1 \exp \beta'_1 CI})^{\gamma_2} \quad (9)$$

3. Results and discussion

3.1. Radial growth and circumference curves

The biological trend of radial growth linked with age is not affected by the competitive status for trees

within a stand. Ring width is maximized at three years old, and then growth decreases, first quickly and then more steadily for older ages, and nearly stabilizes between 30 and 35 years (Fig. 3). This is a pattern usually observed in dendrochronological studies (Fritts, 1976). In contrast, for a given age, growth appears to be strongly connected with the competition status; the more severe the competition, the lower the radial growth. Thus, maximum ring width is 7.4 mm for dominant, 6.0 mm for co-dominant and 4.2 mm for suppressed trees.

The main radial growth differences between isolated and dominant trees are:

1. a reduced growth during the first four years that can be explained either by climatic stress, such as lack of protection against wind by other trees, or by competition from the surrounding ground vegetation, which is dense and, therefore, slows down the establishment and the initial growth of young isolated Scots pines;
2. a superior growth after five years of age because the tree is not subjected to competition from neighbors;
3. a maximum radial growth reached at 11 years old (i.e. 8 years later than for dominant trees); and
4. a greater ring-width variability as shown by larger confidence limits. As competition effects are avoided, climatic effects on growth are emphasized. This is the reason why isolated trees are often sampled in dendroclimatological studies (Schweingruber et al., 1990).

Circumference curves computed using radial growth data are shown in Fig. 4.

3.2. Growth modeling of the different categories of trees

3.2.1. Circumference modeling

Equations for the circumference curves are:

$$\begin{aligned} \text{dominant trees} \quad C &= 120.65(1 - e^{-0.0355t}) \\ n &= 50, R^2 = 0.999, \text{ Se} = 0.83 \end{aligned} \quad (10)$$

$$\begin{aligned} \text{co-dominant trees} \quad C &= 77.62(1 - e^{-0.0426t}) \\ n &= 50, R^2 = 0.999, \text{ Se} = 0.83 \end{aligned} \quad (11)$$

$$\begin{aligned} \text{suppressed trees} \quad C &= 36.61(1 - e^{-0.0655t}) \\ n &= 42, R^2 = 0.995, \text{ Se} = 0.67 \end{aligned} \quad (12)$$

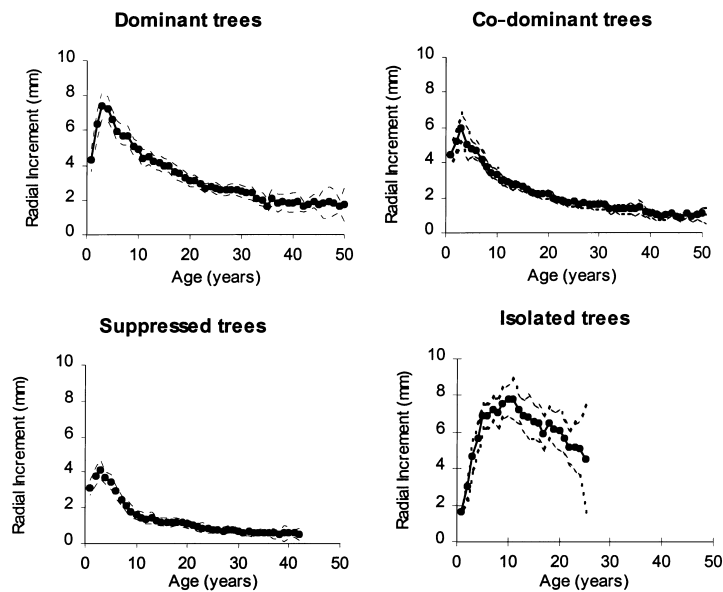


Fig. 3. Mean radial growth curves at breast height for the different categories of trees. Each point represents the mean of at least five samples, dotted lines show confidence limits ($\alpha = 0.05$).

$$\text{isolated trees } C = 120.65(1 - e^{-0.0849t})^{2.127} \quad (13)$$

$n = 25, R^2 = 0.999, \text{Se} = 1.05$

where n is the number of sample trees, Se the standard error of the estimate, and C the under-bark circumference at breast height (cm). Above-bark circumference (C') can be computed from under-bark circumference using Eq. (14):

$$C' = 7.107 + 1.1472C \quad (14)$$

$n = 143, R^2 = 0.89, \text{Se} = 10.5$

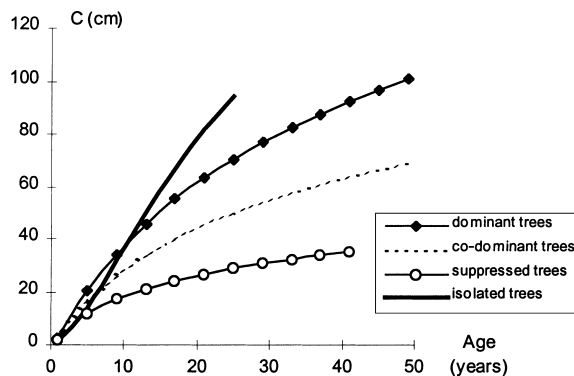


Fig. 4. Mean under-bark circumference growth calculated from radial growth data.

The very high values found for the coefficients of determination indicate that the model is well adapted, but mainly highlight the fact that the circumference was produced by using the mean of annual increments. The biological trend of growth linked with age is emphasized when the individual variability is removed.

Results prove that competition is a major factor contributing to growth variation when the effect of age is removed. When examining growth variability according to competitive status (dominant, co-dominant and suppressed) of a tree within a stand, we found that: circumference growth is lower when competition is greater, and competition effects appear early (Fig. 4). This can be explained because we sampled stands that established at high density and, therefore, competition, first for below-ground and then for above-ground resources, occurred very early after colonization. Competition effects would, most probably, have been observed later for relatively lower densities or for limiting edaphic conditions (Stoll et al., 1994).

3.2.2. Height modeling

Equations for height (H in meters) development are:

$$\text{dominant tree } H = 34.32(1 - e^{-0.0222t})$$

$$n = 57, R^2 = 0.73, \text{ Se} = 2.13 \quad (15)$$

$$\text{co-dominant tree } H = 27.60(1 - e^{-0.0276t})$$

$$n = 114, R^2 = 0.76, \text{ Se} = 1.69 \quad (16)$$

$$\text{suppressed tree } H = 17.95(1 - e^{-0.0423t})$$

$$n = 51, R^2 = 0.58, \text{ Se} = 1.97 \quad (17)$$

$$\text{isolated tree } H = 1.5468 + 0.0710C'$$

$$n = 51, R^2 = 0.91, \text{ Se} = 0.79 \quad (18)$$

Results are similar between height and circumference growth models. Height growth is also clearly affected by competition for trees within a stand; the stronger the competition to which the tree is subjected, the shorter the tree.

The tree-height model given for isolated trees is only applicable to the first stages following tree establishment because data are lacking for older isolated trees. It is also important to emphasize that the method used, i.e. measurement of single trees at one instant in time, is not optimal and that data from permanent plots are better suited to establish height models. But no permanent plots were available in such natural stands which were not previously studied. This is the reason why the above method was used.

3.2.3. Crown-width modeling

Result of crown-width model (C_w is the actual crown-width in meters) using Eq. (4) is the following:

Tree within a stand (all categories gathered)

$$C_w = 1.3306 + 0.0738C' - 0.1847H$$

$$n = 215, R^2 = 0.78, \text{ Se} = 0.89 \quad (19)$$

The model indicates:

1. the bigger the circumference, the wider the crown. Knowledge of the tree's competitive status contributes little additional information on crown width, since circumference already incorporates quite well the conditions of local competition (Fig. 5); and
2. the more slender (tall and thin) the tree, the narrower the crown.

Isolated tree:

$$C_w = 0.3047 + 0.0544C' + 0.2712H$$

$$n = 51, R^2 = 0.95, \text{ Se} = 0.61$$

The model shows that:

1. the bigger the circumference, the wider the crown; and
2. the bigger and the taller the tree, the wider the crown.

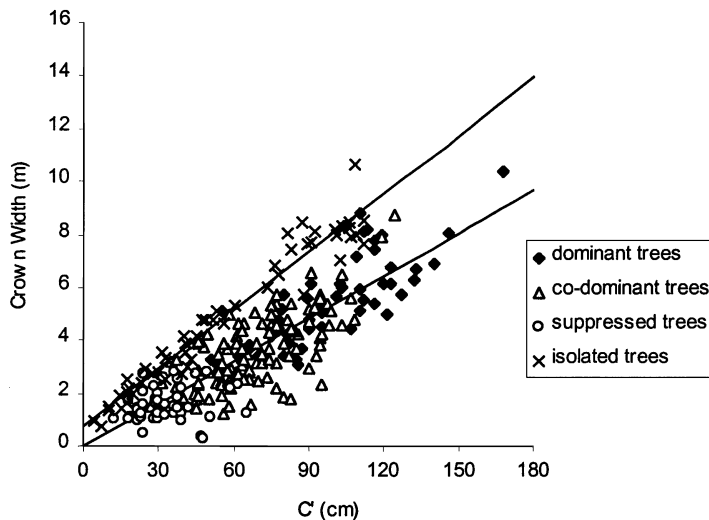


Fig. 5. Crown width vs. circumference at breast height for the different categories of trees. The two lines indicate linear regressions (crown width vs. circumference): the upper one is for isolated trees, the lower one is for trees within a stand (all categories aggregated).

Moreover, examination of data in Fig. 5 shows that, for a given circumference, isolated tree crown width is always superior to that of a tree within a stand.

3.2.4. Biological interpretations (circumference and tree-height models)

Circumference and height models were developed using the Von Bertalanffy–Chapman–Richards growth model that led us to consider, for our conditions and for trees within a stand, two parameters: the asymptote value and the rate parameter. The asymptote value is the maximum theoretical value reached when the age of the tree approaches infinity. The rate parameter expresses the velocity in reaching the asymptote value. Computation of these parameters for two extreme competitive status categories (dominant and suppressed) and for one intermediate status category (co-dominant) shows (Eqs. (10)–(12) and Eqs. (15)–(17)):

1. the more intense the competition, the lower the asymptote value; and
2. the more intense the competition, the greater the rate parameter.

These results can be explained by biological considerations: as the competition from neighboring trees increases, a tree already disadvantaged has its capacities to find new below-or above-ground resources reduced. Consequently, its maximum height or circumference is reduced and is more quickly reached. In contrast, a dominant tree is able to access more resources, and therefore achieve a more prolonged

growth, as long as its competitive advantage to its neighbors remains.

3.3. Growth modeling connected to competition

3.3.1. Competition analysis

Results of the correlation analysis between the main characteristics of the trees and the competition indexes are given in Table 2. Correlations are stronger for stands 1–3 that are characterized by intense competition, than for the older and sparser Stand 4, which is close to an equilibrium stage in terms of competition. In general, the best results are found for circumference, height, and crown width with competition indexes, respectively, based on circumference, height, and crown width angle sums. Indexes computed without any conditions on neighboring trees prove poor correlations (CI_6 and CI_9).

CI_{10} and CI_{11} , which correspond to horizontal-angles sums of neighboring trunks, correlate best with circumference at breast height. This result is essentially the same as found by Pukkala and Kolström (1987), who explained the competition index CI_{10} over 50% of the variation in five-year radial growth in naturally regenerated Scots pine stands in Finland. With the exception of the oldest stand, correlations were always better with CI_{11} because, with this kind of index, the competition status of neighbors was taken into account (Tomé and Burkhart, 1989). For similar reasons, correlation proves to be strong between height and CI_4 .

Table 2
Correlation coefficient, r , values between the competition index and tree dimensions

	Stand 1 ^a			Stand 2 ^a			Stand 3 ^a			Stand 4 ^a		
	C'	H	C_w	C'	H	C_w	C'	H	C_w	C'	H	C_w
CI_1	–0.86	–0.93	–0.86	–0.75	–0.93	–0.74	–0.78	–0.92	–0.66	–0.23	–0.83	–0.25
CI_2	–0.86	–0.88	–0.82	–0.77	–0.81	–0.80	–0.80	–0.92	–0.68	–0.38	–0.81	–0.36
CI_3	–0.87	–0.91	–0.85	–0.80	–0.88	–0.80	–0.80	–0.93	–0.68	–0.38	–0.81	–0.36
CI_4	–0.84	–0.96	–0.79	–0.72	–0.93	–0.71	–0.81	–0.98	–0.61	–0.19	–0.81	–0.13
CI_5	–0.85	–0.95	–0.79	–0.78	–0.87	–0.76	–0.83	–0.97	–0.70	–0.50	–0.62	–0.60
CI_6	–0.32	–0.17	–0.36	–0.34	0.05	–0.33	–0.13	–0.08	–0.33	–0.44	–0.11	–0.62
CI_7	–0.83	–0.75	–0.89	–0.70	–0.51	–0.88	–0.64	–0.52	–0.84	–0.44	–0.23	–0.83
CI_8	–0.84	–0.81	–0.90	–0.69	–0.62	–0.90	–0.70	–0.58	–0.85	–0.32	–0.23	–0.72
CI_9	–0.31	–0.18	–0.37	–0.15	0.12	–0.20	–0.14	–0.12	–0.32	–0.42	–0.22	–0.56
CI_{10}	–0.91	–0.85	–0.87	–0.84	–0.65	–0.84	–0.91	–0.78	–0.69	–0.80	–0.21	–0.50
CI_{11}	–0.93	–0.91	–0.86	–0.84	–0.73	–0.81	–0.96	–0.82	–0.63	–0.71	–0.13	–0.31

^a C' , above-bark circumference at breast height; H , height; and C_w , crown width.

Better results were generally found with competition indexes that expressed competitive relationships of a tree to its neighbors as the sum of positive or negative values, according to the competitive status of the neighbor (Tomé and Burkhart, 1989). It is important to emphasize that previous studies have not found a distance-dependent or distance-independent competition index to be universally superior to all others (Martin and Ek, 1984; Daniels et al., 1986; Biging and Dobberty, 1995), and therefore other competition indexes, not tested in this study, may have more accurately described the competition process for this species in these specific situations.

Another characteristic of the chosen competition indexes is the number of selected competitors. Accordingly, the limiting competition distance has an influence on the competition index relationships with tree dimensions, which is usually improved when the limiting competition distance is great. Nevertheless, an excessive distance could be too expensive in terms of calculations, especially in the case of an individual-tree model aiming at describing the whole stand development from early to mature stages.

It is important to emphasize that the correlation values are dependent on the chosen competition radius. Previous studies have shown that when more competitors were selected, the correlations were better (Pukkala and Kolström, 1987; Tomé and Burkhart, 1989), even if the increase in the correlation values was slow beyond a given distance. This finding was also put forward by Biging and Dobberty (1995) to explain the superiority of some distance-independent indexes applied over an entire stand to distance-dependent indexes whose competition radius was usually small relative to stand size.

For this reason, we decided to widen the competition radius which was previously kept equal to the

buffer zone; results are given in Fig. 6 for the competition index CI_{11} . Indeed, we do observe an increase in the correlation coefficient with a wider competition radius, but gains can be neglected beyond a certain distance. In particular, our selected competition distances proved to be sufficiently significantly related to tree dimensions, except for Stand 4 where competition is accurately described only if a greater number of competitors is selected (corresponding to competition radius of ca. 15 m). This can be explained by the fact that tree size variability is low in old and mature stands in which competition is weak, whereas it is important in young and dense stands characterized by intense competitive relationships among trees.

3.3.2. Circumference model connected to competition (trees within stands)

According to Table 2, CI_{11} appears to correlate best to circumference and was, therefore, selected as competition index in Eq. (8).

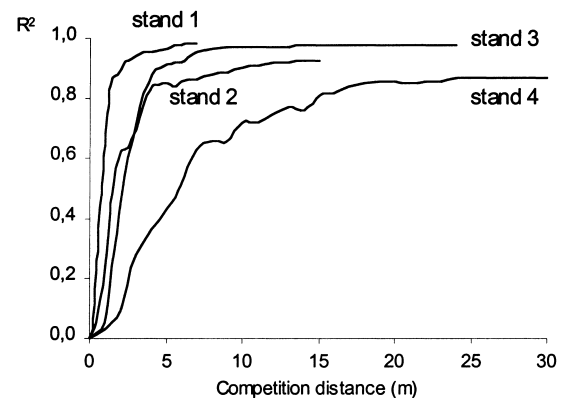


Fig. 6. Evolution of R^2 the coefficient of determination (circumference vs. competition index CI_{11}), with respect to the competition distance.

Table 3

Circumference growth model: computations of coefficients α_i and β_i and parameters used in the calculations

	Stand 1	Stand 2	Stand 3	Stand 4
Minimum CI_{11} value	-20.74	-33.92	-30.25	-22.52
Maximum CI_{11} value	30.39	40.49	13.77	24.04
Coefficient α_1	0.0455	0.0469	0.0475	0.0477
Coefficient β_1	0.0120	0.0082	0.0084	0.0132
Coefficient α_2	74.39	70.05	68.44	67.76
Coefficient β_2	-0.0233	-0.0160	-0.0163	-0.0256

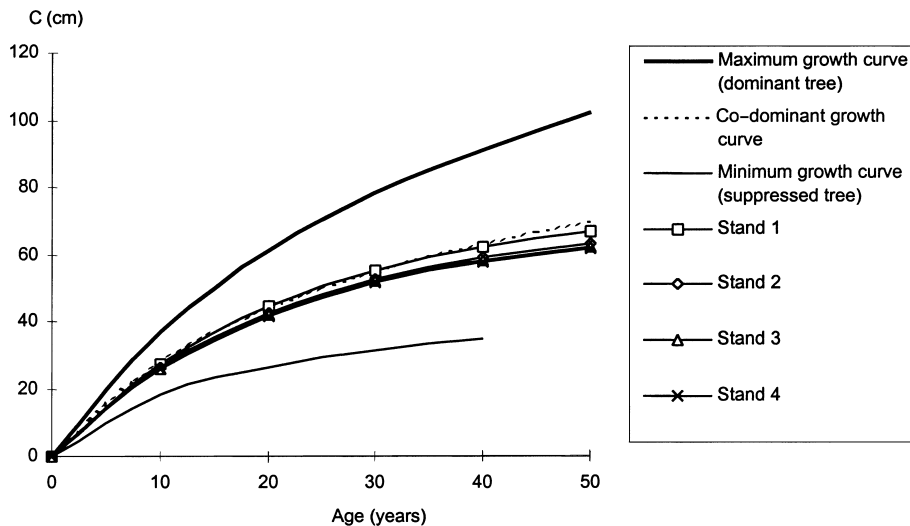


Fig. 7. Under-bark circumference model for the different categories of trees within stands. Growth curves related to stands 1–4 were established using Eq. (21).

Estimates of coefficients α_i and β_i are given in Table 3.

One possible way to test the model consistency was to consider trees without any competitive advantage or disadvantage over their neighbors. Such trees are, therefore, characterized by a competition index equal to zero. Setting $CI = 0$ in relation (8) gives, for a tree within a stand ($\gamma_1 = 1$):

$$C = \alpha_2(1 - e^{-t\alpha_1}) \quad (21)$$

Curves drawn for stands 1 to 4 using the above relation showed (Fig. 7):

1. all are between the maximum dominant growth curve and the minimum suppressed growth curve;
2. each of these curves separates trees favored in terms of competition in the superior region of the

graph from disadvantaged trees in the inferior region; and

3. curves are close to the co-dominant curve. This can be explained by the fact that co-dominant trees are characterized by an intermediate competitive status and, therefore, their competition index approaches 0.

3.3.3. Height model

The height models were then related to CI_4 in the same way and for the same reason as for the circumference model. Results are expressed in Table 4.

We set $CI = 0$ in relation (9) for trees within stands ($\gamma_2 = 1$):

$$H = \alpha'_2(1 - e^{-t\alpha'_1}) \quad (22)$$

Table 4

Height growth model: computations of coefficients α'_i and β'_i and parameters used in the calculations

	Stand 1	Stand 2	Stand 3	Stand 4
Minimum CI_4 value	−12.98	−13.53	−11.73	−4.35
Maximum CI_4 value	16.02	13.74	5.82	8.13
Coefficient α'_1	0.0296	0.0306	0.0297	0.0278
Coefficient β'_1	0.0222	0.0236	0.0249	0.0517
Coefficient α'_2	25.67	24.88	25.59	27.38
Coefficient β'_2	−0.0223	−0.0238	−0.025	−0.0519

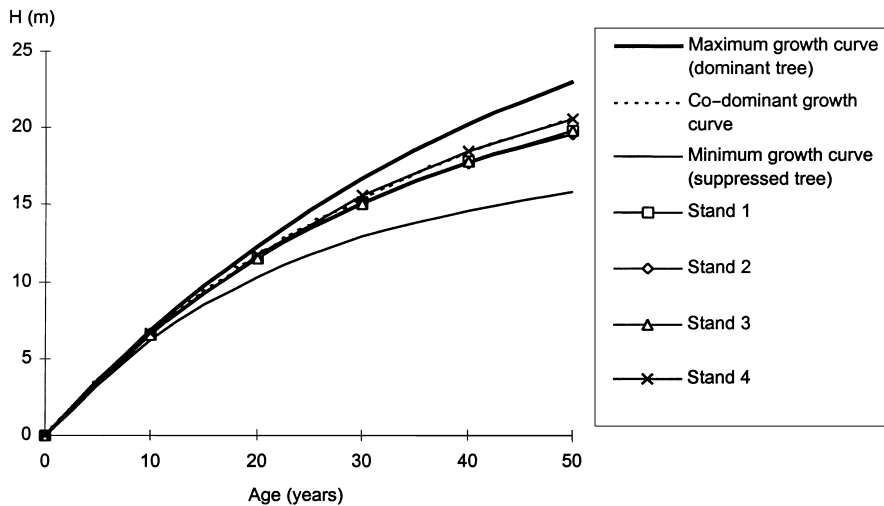


Fig. 8. Height model for the different categories of trees within stands. Growth curves related to stands 1–4 were established using relation (22).

Results given in Fig. 8 are similar to those found with the circumference model: each of the four curves computed for the stands are close to the co-dominant curve, and included between the dominant growth and the suppressed growth curves. Like circumference, height growth is under competition control. Nevertheless, circumference growth is more severely affected by competition. The more intense the com-

petition, the more slender the tree. This is particularly confirmed in young stands characterized by intense competition (Fig. 9).

The height and the circumference models allow us, for a given tree within a stand characterized by its age and two competition indexes, to produce its circumference and its height. Then its crown width is computed with the help of these two variables (Eq. (19)).

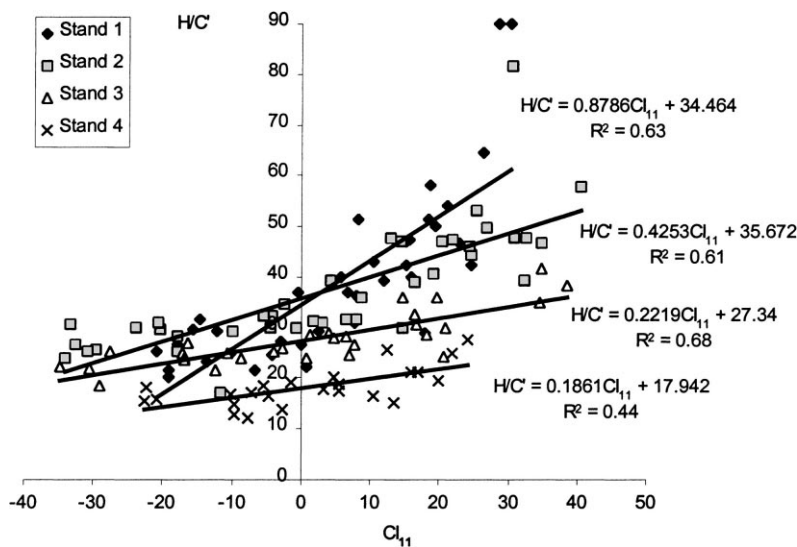


Fig. 9. Variation of the ratio height : circumference as function of competition index, Cl_{11} , for each stand. Correlation values are higher for the stands 1–3 ($R^2 > 0.6$), characterized by intense competition rather than for the oldest Stand 4 ($R^2 = 0.44$) where the competition is weak.

Growth of each tree within a stand is thus individualized, and not assigned the mean growth of the whole stand as in stand-level models.

4. Conclusion

Tree growth is under the control of age, genetics, site quality, and competition. In our study, we established a growth model as a function of tree age while considering local competition. We tried to eliminate site variation by choosing stands in similar edaphic, topographic, and climatic conditions. Stands were chosen among monodominant and dense natural Scots pine forests that were common in our study area. Under these conditions, height and circumference growth prove to be related to competition: for a given age, tree height and circumference are lower when the competition the tree faces is more intense. We preferred an individual tree-based model to a stand model because of the ability of the former to take into account the competition process, which is a major factor in determining natural woodland structure.

The proposed growth model is one of the two components needed to model the establishment and dynamics of natural Scots pine forests. The second component consists in characterizing the main parameters of the recruitment process: seed production, dissemination, germination and seedling mortality. Some aspects of the model still need more investigation; competition history, stand-establishment conditions, and site effects were not integrated. Moreover, the transition between the isolated trees model and the trees within a stand model was not studied. Nevertheless, the proposed model emphasizing the role of individual characteristics and variation is a first step toward a better understanding of natural stand development processes and growth.

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l'Alimentation (Direction de l'Espace Rural et de la Forêt).

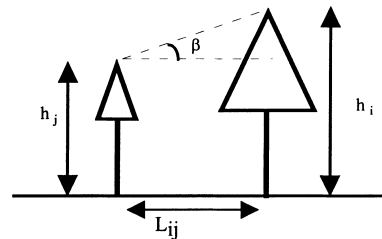
Appendix A. Calculation of the competition indexes

Formulas used for the calculation of the competition indexes. Index i denotes a competitor of subject tree j , and n the total number of competitors inside the chosen competition radius. The following parameters are defined: h , height; R , crown radius, r , trunk radius, L , distance, x_{opt} , coefficient $\in [0,1]$ computed to optimize the correlation coefficient between the competition index and the circumference at breast height, α and λ the horizontal angles and β a vertical angle.

Vertical angle sums are given as under:

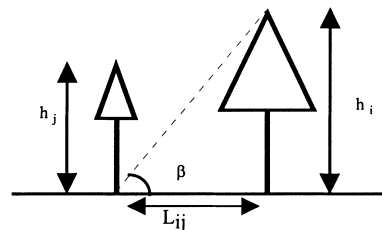
$$CI_1(j) = \sum_{\substack{i=1 \\ i \neq j}}^n \varepsilon(i) \beta_i \equiv \sum_{\substack{i=1 \\ i \neq j}}^n \varepsilon(i) \arctan \left[\frac{(h_i - h_j)}{L_{ij}} \right]$$

if $h_i \geq h_j$, $\varepsilon(i) = 1$ or 0



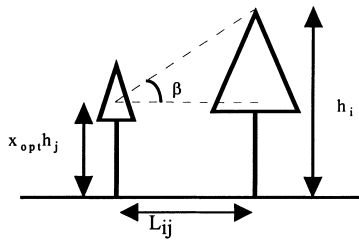
$$CI_2(j) = \sum_{\substack{i=1 \\ i \neq j}}^n \varepsilon(i) \beta_i \equiv \sum_{\substack{i=1 \\ i \neq j}}^n \varepsilon(i) \arctan \left[\frac{h_i}{L_{ij}} \right]$$

if $h_i \geq h_j$, $\varepsilon(i) = 1$ or 0



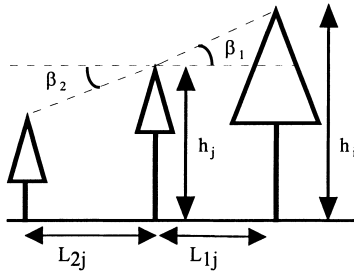
$$CI_3(j) = \sum_{\substack{i=1 \\ i \neq j}}^n \varepsilon(i) \beta_i \equiv \sum_{\substack{i=1 \\ i \neq j}}^n \varepsilon(i) \arctan \left[\frac{(h_i - x_{\text{opt}} h_j)}{L_{ij}} \right]$$

if $h_i \geq h_j$, $\varepsilon(i) = 1$ or 0



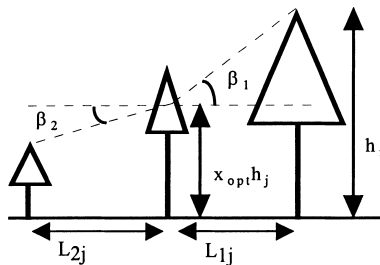
$$CI_4(j) = \sum_{i=1 \atop i \neq j}^n \varepsilon(i) \beta_i \equiv \sum_{i=1 \atop i \neq j}^n \varepsilon(i) \arctan \left[\frac{|h_i - h_j|}{L_{ij}} \right]$$

if $h_i \geq h_j$, $\varepsilon(i) = 1$ or -1



$$CI_5(j) = \sum_{i=1 \atop i \neq j}^n \varepsilon(i) \beta_i \equiv \sum_{i=1 \atop i \neq j}^n \varepsilon(i) \arctan \left[\frac{|h_i - x_{opt} h_j|}{L_{ij}} \right]$$

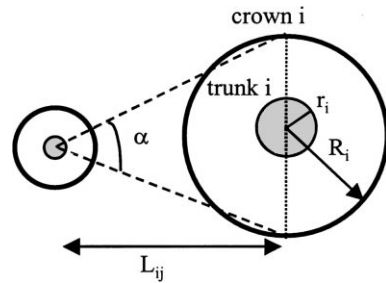
if $h_i \geq h_j$, $\varepsilon(i) = 1$ or -1



Horizontal angle sums are given as under:

$$CI_6(j) = \sum_{i=1 \atop i \neq j}^n \varepsilon(i) \alpha_i \equiv \sum_{i=1 \atop i \neq j}^n \varepsilon(i) 2 \arctan \left(\frac{R_i}{L_{ij}} \right)$$

$\forall i, \varepsilon(i) = 1$



$$CI_7(j) = \sum_{i=1 \atop i \neq j}^n \varepsilon(i) \alpha_i \equiv \sum_{i=1 \atop i \neq j}^n \varepsilon(i) 2 \arctan \left(\frac{R_i}{L_{ij}} \right)$$

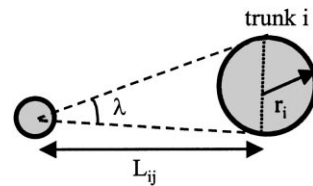
if $R_i \geq R_j$, $\varepsilon(i) = 1$ or 0

$$CI_8(j) = \sum_{i=1 \atop i \neq j}^n \varepsilon(i) \alpha_i \equiv \sum_{i=1 \atop i \neq j}^n \varepsilon(i) 2 \arctan \left(\frac{R_i}{L_{ij}} \right)$$

If $R_i \geq R_j$, $\varepsilon(i) = 1$ or -1

$$CI_9(j) = \sum_{i=1 \atop i \neq j}^n \varepsilon(i) \lambda_i \equiv \sum_{i=1 \atop i \neq j}^n \varepsilon(i) 2 \arctan \left(\frac{r_i}{L_{ij}} \right)$$

$\forall i, \varepsilon(i) = 1$



$$CI_{10}(j) = \sum_{i=1 \atop i \neq j}^n \varepsilon(i) \lambda_i \equiv \sum_{i=1 \atop i \neq j}^n \varepsilon(i) 2 \arctan \left(\frac{r_i}{L_{ij}} \right)$$

if $r_i \geq r_j$, $\varepsilon(i) = 1$ or 0

$$CI_{11}(j) = \sum_{i=1 \atop i \neq j}^n \varepsilon(i) \lambda_i \equiv \sum_{i=1 \atop i \neq j}^n \varepsilon(i) 2 \arctan \left(\frac{r_i}{L_{ij}} \right)$$

if $r_i \geq r_j$, $\varepsilon(i) = 1$ or -1

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