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Individual-based modelling of *Pinus sylvestris* invasion after grazing abandonment in the French Massif Central

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Abstract

In the Chaîne des Puys, a mid-elevation volcanic mountain of the French Massif Central, Scots pine proves to be an 'invasive' species colonizing abandoned lawns or heathlands, and forms in a few years monospecific natural forests. Most of the abandonment occurred 30 to 40 years ago and this process has now stopped. Thus, we lack data on the very first phase of tree colonization. We anticipate that a simulation tool could bring an appreciable help in (i) rebuilding the entire colonization process – including the initial phase – of pine settlement and (ii) answering questions about the origin of the narrow and unimodal distributions of age of pine stands we observed. In addition, such a simulator could help managers to forecast extension of Scots pine and to predict growth and evolution of present secondary forests. A spatially explicit individual-based model is presented. The model takes into account both space and time and includes growth of trees, seed production and seed dispersal, death and competition between individuals. The influence of the initial parameters are analyzed and elements of validation given. The model was then used to predict tree settlement and stand establishment using the initial conditions from a natural stand studied in the field whose characteristics before abandonment were known (number and age-distribution of trees, location of mother trees, time of abandonment). Three simulations were achieved by using the same initial conditions but following different scenarios for the recruitment process. The scenario of a fluctuating resistance of the resident vegetation (that controls the susceptibility of the environment to tree establishment) seemed as one of the most probable to explain the actual stand characteristics. We thus concluded that dynamic models could be improved by taking into account the resistance of the vegetation to colonization as a fluctuating parameter instead of a static and permanent attribute.

Introduction

Woodlands cover 15 million hectares in France and the forest cover increases each year by about 40 000 ha. Although quantification is difficult to assess, several studies emphazise the important role of natural afforestation in this process. It has been estimated that currently only 16% of the annual gross forest extension is due to artificial planting, and consequently, the natural colonization by woody species represents the driving force of forest extension (DERF 1995). Scots pine is an important component of natural afforestation especially in mountain and mediterraean areas in southern France (Barbéro et al. 1998). Pine invasions on previous grasslands lead to a major shift in life-form dominance, increase in biomass (with implications for hydrology and fire behaviour) and changed patterns of nutrient cycling (Richardson and Higgins 1998). The control and the prediction of invading pines have thus received more and more attention in regions where these species naturally occur as well as in regions far removed from their natural range (Richardson 2000).

In the Chaîne des Puys, a mid-elevation volcanic mountain of the French Massif Central, the decline of grazing after the second world war has enhanced the colonization of former heathlands and lawns by pioneer trees like silver birch (*Betula pendula* Roth.) or Scots pine (*Pinus sylvestris* L.). The latter, which is not a natural species in this part of France, is by far the most widespread one on plane areas and gentle slopes especially in the southern part of the region. It proves to be an 'invasive' species colonizing abandoned lawns or *Calluna vulgaris* heathlands and to form monospecific natural forests within a few years. Because land use as well as agricultural and pastoral practices are very diverse in space, abandonment and then colonization often occur on small surfaces (about 1 ha). Tree colonization of former pastoral or agricultural lands leads to afforestation of the remaining open heathlands on volcanic slopes of the Chaîne des Puys, which are considered to be a highly valuable landscape. Therefore, land managers are particularly interested in a management and predictive tool in order i) to control the colonization process and, ii) to collect information about the new woodlands that have been naturally established.

The very first phase of Scots pine settlement occurred 30 to 40 years ago and consequently only young to mature stands are encountered in the field at present whereas the juvenile stages are lacking. In contrast to the usually reported continuous age distribution in natural single-species stands (González-Martínez and Bravo 2001; Oliver and Larson 1996), current pine stands are characterized by narrow and unimodal distributions of age. We thus want to test in particular whether the resistance of the vegetation in place (*i.e.* the resident vegetation), which partly determines the susceptibility of the environment to tree invasion (Lonsdale 1999; Davis et al. 2000), and that is considered as continuous and regular in the case of heathlands, is a consistent hypothesis (Coquillard 1995; Coquillard et al. 2000) to obtain such distributions.

The objectives of the paper are the following:

1. to establish a model of Scots pine colonization and rebuild the entire dynamics from the pioneer up to the mature stages. The model has been designed to take into account the major processes of natural afforestation: growth, competition, mortality and recruitment,
2. to study the general behavior of this model, its sensitvity to some major initial parameters of the colonization process, and to provide some elements of validation,
3. to determine the initial conditions required to obtain a narrow and unimodal distribution of age of pines that were usually recorded for many stands in this region.

Methods

Model description and parameter estimation

Modelling technique and implementation choices

The objectives we defined above lead us to develop a model which allows us to generate i) the number of trees and the age distribution at different time steps of the colonization process, ii) the changing of the main classical dendrometric variables (average stand height, average basal area and average girth) through time, and iii) the velocity of colonization. It was also important to take into account competition between trees. This factor does not solely control growth but also influences mortality and recruitment processes. Lastly, three assumptions were included: (i) the system is supposed to be isolated e. g. there is no influence of external factors, (ii) there is no occurrence of any particular events such as parasitic outbreaks, windthrows and other catastrophic circumstances, (iii) substitution by the beech tree was not implemented.

Because the colonization process we propose to model concerns small areas (1–25 ha) and takes place within a short period (some decades) we did not use the gap-model approach (Botkin et al. 1972; Shugart 1984) which is more suitable for predicting long-term forest dynamics on large forest units. Thus, we decided for an individual-based model approach (Huston et al. 1988; De Angelis and Gross 1992). This type of model has been widely used to study growth integrating competition among trees (Pukkala and Kolström 1987; Tomé and Burkhart 1989; Urban and Shugart 1992; Rouvinen and Kuuluvainen 1997), forest dynamics (Pacala and Silander 1985; Pacala et al. 1996) and, more recently, colonization by invasive species (Higgins and Richardson 1998).

In such conditions, we used the discrete event simulation technique integrating both stochastic and deterministic processes (mixed model). The fact that we have a stochastic model implies the computation of

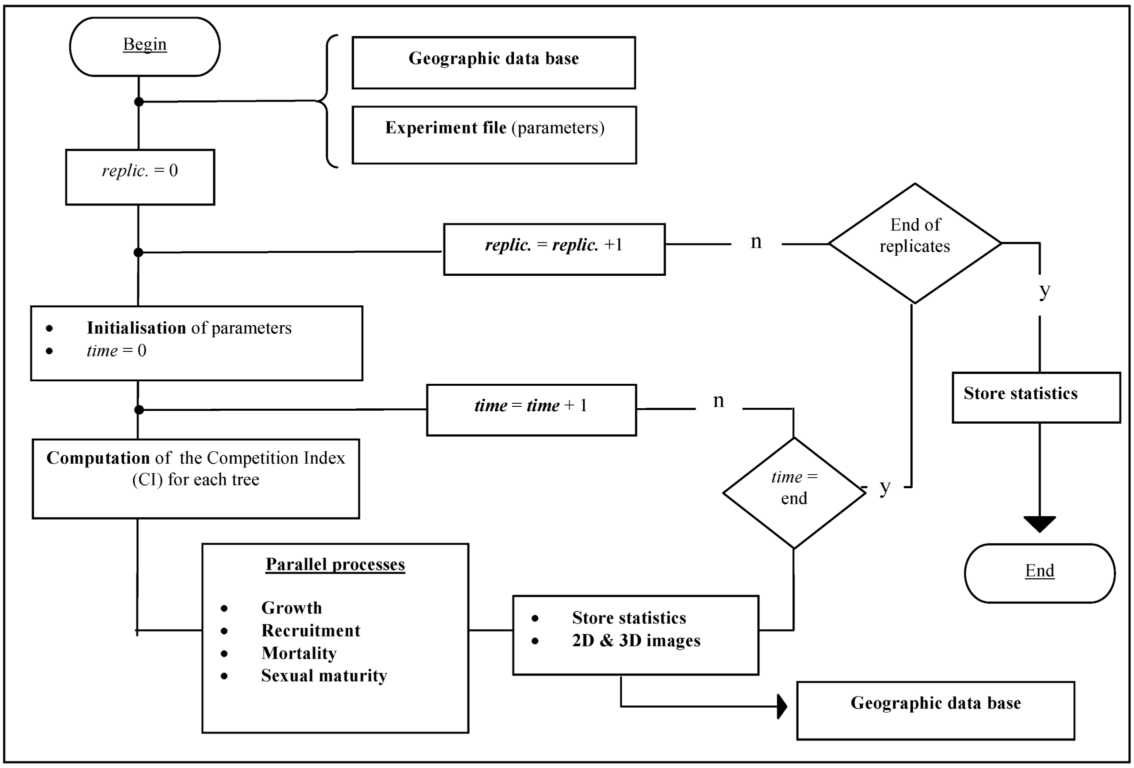

Figure 1. Simplified flow chart of simulation routine. Runs start using initial values of parameters from an experiment file (built by user) and a repartition of trees (age and (x,y) coordinates). Each year, the competition index is calculated for each tree by exploration of its neighbourhood. Next, five parallel processes are activated: Growth and Mortality of trees are computed from current dendrometric values, competition index values (CI) and age; Sexual maturity is estimated by means of the age of trees; Recruitment process takes into account the rate of reproduction and the immediate neighbourhood of the seeds. At the end of each year, several statistics are stored: number of individuals per age class, number of individuals per CI class, number of mature and juvenile individuals dead, basal area, height, girth and geographic repartition of trees.

multiple runs within the same experimental framework (Shannon 1975; Kleijnen 1987; Coquillard and Hill 1997). Consequently, results are computed as means with confidence intervals. The simulation kernel is clock-based (time step equal to one year) and has a process approach. Sub models are detailed in next section. The software implementing the model is written with GNU ANSI-C++ (2.7.2) on Unix workstation or PC running a Linux system in a X-Windows graphic environment (X11R6). A graphical user interface was built, using the Gtk+ library for the management of experiment files, statistical data and results. Figure 1 presents a simplified flow chart depicting the simulation model behaviour.

Tree growth modelling

Individual growth models were established in a previous paper (Prévosto et al. 2000) and equations, given under their derivative form, are indicated in Appendix 1. We recall hereafter some of the characteristics of these models.

Growth models of trunk circumference, crown radius and height were established by distinguishing two categories of trees: isolated trees (*i.e.* trees with no neighbour) and trees within a stand. Models were derived from the Von Bertalanffy-Chapman-Richard's model and allometric relationships. They used tree age and a competition index as predictors.

The competition index retained, calculated for trees with neighbours within a fixed competition radius of 5 m, is based on a vertical angles sum (Fig. 2A) and is written as follows:

$$\begin{cases} CI(i) = \sum\limits_{\substack{j=1 \\ j \neq i}}^{n} \beta_j = \sum\limits_{\substack{j=1 \\ j \neq i}}^{n} \arctan[(h_j - h_i)/L_{ij}] \\ \text{if} \quad h_j \leq h_i - 5 \quad \text{then} \quad \beta_j = 0 \end{cases} \tag{1}$$

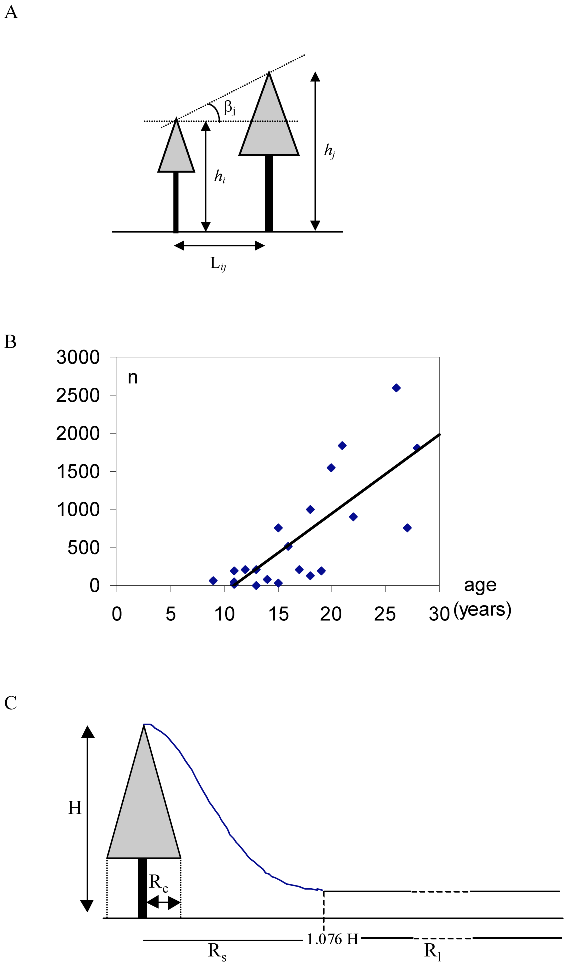

Figure 2. Model description.
A: Competition index construction. β_j is the positive or negative vertical angle from the subject tree i to the top of the competitor j.
B: Cone production with respect to tree age measured on 24 isolated trees. The regression line is indicated ($R^2 = 0.61$)
C: Seed dispersal around a tree. The short distance seed dispersal model is applied on the $R_s = [0, 1.076H]$ interval whereas long distance dispersal occurs on the $R_l = [1.076H, 1.5R_s]$ interval.

where

β_j is the positive or negative vertical angle from the subject tree i to the top of the competitor j (radian), h = height (m), L_{ij} = distance (m) between i and j, n is the number of competitors within a fixed competition radius of 5 m. Increasing the competition radius produces better results but these gains can be neglected given the associated increased computing time.

This index belongs to a set of indices based on vertical angles, which were already used in studies on Scots pine (Pukkala and Kolström 1987; Rouvinen and Kuuluvainen 1997). It can take negative or positive values so that the competition level of a subject tree is considered as the sum of its competitive advantages and disadvantages to its neighbours (Tomé and Burkhart 1989).

Lastly, the calculus of CI was modified in order to avoid extreme and artificial advantage of subject trees competing with small individuals. Considering that 5 m is the average difference in height between the smallest and tallest trees on the stands we sampled, the trees whose height h_j is such as $h_j \leqslant h_i-5$ are not taken into account in the calculus of CI(i).

Death process

Tree mortality is surely one of the most difficult processes to model because it is i) the result of complex interactions between the genetic status of the tree, environmental factors, age and dimensions of the tree which are in turn closely related to local competition from neighbouring trees and ii) it is a rare event and large data sets (like representative plots periodically remeasured) are needed to assess a model of mortality (Monserud and Sterba 1999).

It is the reason why mortality is classically modelled in a quite simple way. Higgins and Richardson (1998) assessed their mortality model on tree age and on the level of disturbance of the site. Shugart (1984) used a constant rate of mortality of 2% within a cohort, except for suppressed trees characterized by a higher probability of mortality. The mortality submodel developed by Pacala et al. (1996) was based on the individual growth rate over the past five years. Moravie et al. (1997) proposed mortality probabilities as a function of the class diameter and past growth.

In our model such a classical approach was used: the mortality of a tree was supposed to be a function of its age and of the level of competition the tree had undergone from its neighbours. These two factors were combined using the following relation:

$$P_i = P_i(Ma) + P_i(Mc) - P_i(Ma) \times P_i(Mc) \qquad (2)$$

where P_i is the probability of mortality of tree i, $P_i(Ma)$ is the probability of mortality linked to age and $P_i(Mc)$ is the probability of mortality linked to competition.

To our knowledge, there is no available data on life expectancy of *Pinus sylvestris* populations in south Europe at mid-elevation. Thus, we adopted a normal distribution of mean = 180 years and standard deviation = 10 years to compute $P_i(Ma)$. 210 years is the maximum age, *i.e.* $P_i = 1$ if age of tree i $\geqslant$ 210.

The exponential law is a classical model of the mortality process of a population (see Hawkes (2000) for a review of mortality algorithms). Let 'p' be the probability of death of a tree whose competitive advantage is maximal (*i.e.* $CI = CI_{min}$). We considered that the probability of death was equal to 1 for a tree which has a maximal disadvantage (*i.e.* $CI = CI_{max}$). According to previous measurements of competition indices values in naturally regenerated Scots pine stands (Prévosto et al. 2000) we put $CI_{max} = 14$ and $CI_{min} = -13$, then $P_i(Mc)$ is given by:

$$P_i(Mc) = \exp\left(\frac{-\ln(p)}{CI_{\max} - CI_{\min}}(CI_i - CI_{\max})\right) = \exp\left(\frac{-\ln(p)}{27}(CI_i - 14)\right) \qquad (3)$$

Using (Equation 2), the value obtained for tree i is compared to a random number r (r $\in$ [0; 1]). The death occurs if r $\leqslant P_i$. In the calibration phase, several runs gave a value of p = 1/10 000 to obtain realistic densities of pines.

Recruitment process

Seed production

Krugman and Jenkinson (1974) reported that *Pinus sylvestris* is among the most precocious conifer (< 10 years). Lanner (1998) emphasized that many environmental factors, in addition to age and variety, can influence the date of sexual maturity.

Our observations and data sampling on 24 isolated trees of various ages show that cone production starts at about 10 years old and then increases with age with a considerable variation of cone numbers between individuals.

Thus we have modelled seed production with the following assumptions:

1. according to our field observations and data sampling, we consider that seed production starts at the age of 10 and we hypothesised that it reaches its maximum at 30 years old thus ignoring any decrease due to senescence,
2. seed production increases linearly between these two ages. This is a rough approximation. Indeed, Fig. 2B shows that cone production exhibits an obvious heteroscedasticity whose origin probably lies in size and past growth variations as well as microecological factors and genetics. Such a variation could have been easily introduced in the model by using a stochastic factor weighting the average production. However, this method would have introduced an additional element of uncertainty in the model and consequently results would have been made more difficult to interpret. In addition, the number of required replicates of runs needed to obtain satisfying confidence intervals of results would have been severely increased, thus leading to prohibitive computing times.

Numerous factors that can influence seed production and thus recruitment are still ignored. More realistic seed production models could be proposed, if data become available, by taking into account not only the age (though this factor has been recognized as a major one) but also environmental factors: growth rate, competition and predation (Lanner 1998). Moreover data are also lacking to express the fact that seed production is also decreasing when trees begin to senesce, and that it is widely affected by temporal variations as is proved by the existence of mast years. But concerning these two latter particular points realistic mathematical functions are still to be found (Greene et al. 1999).

Seed dispersal

Seed dispersal was modelled by means of a "dispersal kernel" composed of short and long distance components.

The short distance component represents a very localised dispersal: seed number is maximum at the source and then decreases quickly with distance. It is the most obvious component easy to measure by experimentation and the statistical models that depict this behaviour usually refer to the exponential model, the inverse power model or the gaussian model.

The long distance component takes into account the fact that a small amount of seed can travel over long distances under unusual wind conditions. It is a rare event but of a major importance to explain invasion speed (Clark 1998; Higgins and Richardson 1999; Neubert and Caswell 2000).

For the short distance component, we assumed that normal winds, without any preferential directionality, were the only dispersal vector and we adopted a gaussian distribution of seeds with parameters (m, σ) respectively mean and standard deviation. In a field study of Scots pine seed dispersal in the center of

France, Guittet and Laberche (1974) found that 93% of the seeds were spread within a radius of 18 m. In such condition, 99% of the seeds are spread within a radius $R_{max} = 3\sigma$ corresponding to a tree of maximal height H_{max}. In this case, we considered H_{max} as the maximal height reached by codominant trees = 27.6 m (Prévosto et al. 2000). This leads us to calculate the radius R_s of seed dispersal of a given tree of height = H with the relation:

$$R_s = H(R_{max}/H_{max}) = 1.076H \tag{4}$$

In addition, given that no seedling can survive under any crown according to our field observations (light competition, possible allelopathic factors...), the segment of R_s corresponding to the distribution of seeds is given by: [R_c; 1.076H], where R_c is the crown radius (Fig. 2C).

Long distance dispersal is classically based on the existence of "fat tails" in dispersal curves but their mathematical formulations are still debated certainly because direct data are extremely costly and difficult to obtain (Bullock and Clarke 2000). For instance, Bullock and Clarke (2000) have measured in the field long distance seed dispersal for two kinds of dwarf *shrubs* (*Calluna vulgaris* and *Erica cinerea*). Their data show that the tail of the distribution is fairly flat and is poorly modelled by classical empirical models (exponential and inverse power models) or the mechanistic models proposed by Greene and Johnson (1989).

As a consequence, we hypothesized that the number of seeds that can be long dispersed follows a uniform law (*i.e.* the tail of the distribution is exactly flat).

As the afforestation process in our study area operates at fine scale and because stand establishment is more concerned by short dissemination, we only considered long dispersal for each mature tree over a limited and fixed interval that was arbitrary put equal to R_l = [R_s, 1.5 R_s] for all the simulations. Moreover an unbounded uniform distribution would not have yielded a proper probability function, *i.e.* a function integrating 1 over its whole range.

Seedling establishment

Guittet and Laberche (1974) recorded that a mature Scots pine tree could produce 63 000 seeds per year but that only 204 seedlings of one year established and the rate of mortality after 5 years was about 83%. Consequently to avoid prohibitive computing time we have only considered the recruitment of 5 year old seedlings. It is also important to notice that, according to the fact that no seedling can survive beneath a crown, each seedling position was tested by comparison with those of trees in its neighbourhood.

The seedling establishment submodel consists of an algorithm that predicts the number and spatial locations of seedlings produced per maternal tree and per year.

The number of seedlings is controlled through a rate of recruitment parameter (denoted RC) expressed as the average number of young pines that established per mature isolated tree and per year. This parameter is thus a measure of the resistance of the ground vegetation to colonization: a low value of this parameter leads to a high resistance of the resident vegetation to colonization and *vice versa*. For instance according to previous works (Coquillard 1995; Coquillard et al. 2000) and additional field observations we consider that, on average, less than one seedling older than 5 years per mother tree and per year can settle in a *Calluna* heathland.

In the absence of any reliable data, we considered that the frequency of seedlings that establish at long distance was 0.5%.

Number of replicates required

We aimed first at computing the minimal number of replications necessary to estimate simultaneously the 4-dendrometric variables (Basal area, Number of trees, Height and Girth) with a 95% confidence level at least for each of them. In addition, we fixed the errors to a maximum of 5%.

According to Bonferroni's inequality [5] the probability for the 4 dendrometric means to be simultaneously included in their respective 99% confidence intervals is: 1−0.01×4 = 0.96, value which is therefore superior to our objective of 95% confidence level.

$$P(I_1 \leqslant \nu_1 \leqslant S_1, \ldots, I_r \leqslant \nu_r \leqslant S_r) \geqslant 1 - \sum_1^r \alpha_r \tag{5}$$

where $\{\nu_{1,}.,\nu_r\}$ are the means to estimate, I_r and S_r the inferior and superior confidence limits respectively.

The results we obtained with 10 replicates indicate that the errors never exceed 4.2% in estimating the variables, using a 99% confidence interval (Table 1). In such conditions, 10 replicates are sufficient to match our objectives.

Table 1. Computation of the confidence radius of each of the dendrometric variables (at the confidence level of 99%) and of the resulting error. Simulation: 30 trees from 20 to 24 years old randomly sparse on 1 ha, 10 replicates.

	Basal area (m^2)	Number of trees	Height (m)	Girth (m)
Mean	14.05	1113.5	10.57	0.35
Standard deviation	0.56	45.67	0.22	0.008
Confidence radius($=T^*_{0,01/2;\ 9}(s/n^{0,5})$)	0.57	46.93	0.22	0.009
Error % (= 100 × Confidence radius/mean)	4.1	4.2	2.1	2.5

Field application: measurements and simulation framework

In this part, the model is used to predict tree settlement and stand establishment using the initial conditions from a natural stand studied in the field whose characteristics before abandonment were known. Simulations were achieved by using the same initial conditions but following different scenarios of the recruitment process.

Field measurements

A set of enlarged aerial photographs of different dates (1962, 1974, 1984, 1989, 1999) was examined and used to select a 60×80 m Scots pine stand. The stand was located on a small volcano (minimum altitude: 1040 m, maximum: 1120 m) in the southern part of the Chaîne des Puys. This volcano was mapped as heathland in the French cadaster till 1831 and used for sheep grazing. A large part was abandoned 36 years ago and led to colonization by Scots pine that form at present natural and monospecific forests. The initial ground vegetation was mainly dominated by *Calluna vulgaris* and a few other bushes (*Genista pilosa*, *Cytisus scoparius*). Only a few and scattered Scots pine trees were present before abandonment.

Five Scots pines were present before abandonment on the plot (Fig. 3A). They represented the only parent trees as, at least for the first decade following abandonment, other trees were too far away to have a noteworthy influence on the colonization process within the plot.

The five initial trees were easily recognisable in the stand due to their particular morphology: large crown, flexuous trunk with numerous big branches from the base. They were located by their X, Y coordinates, their dimensions and ages were recorded (respective age: 45, 47, 51, 58, 66). An exhaustive dendrometric inventory was carried out, trees were numbered and the circumference at breast height of each tree was measured. A total of 474 trees were recorded, 106 randomly chosen trees were cored at breast height and their age measured in order to establish the distribution of age for the stand. Furthermore the mean height of the stand was estimated by measuring 23 randomly located trees. Distribution of ages within categories is shown in Fig. 3B. As in many natural stands in our study area, age distribution is characterized by a dominant class: the age group [20–30] represents 43% of the total number of the stand and more than one third of the pines are aged between 27 and 31 years. On the other hand, tree distribution in circumference classes exhibits a broad range (Fig. 3C). This provides evidence for the deep influence of competition on growth in natural stands. The other main stand characteristics are the following: basal area 12 m^2 (*i.e.* 25 m^2/ha), mean height 9.8 m and mean circumference 0.50 m at breast height.

Presently, a clearing of about 920 m^2 mainly dominated by broom remains in the south corner of the stand and only a few scattered pines have settled. The boundary of the clearing was mapped and the isolated trees located (Fig. 3A). No pine seedlings were encountered within the clearing proving that the colonization process has actually stopped due to the strong competition of broom.

In order to limit edge effects, the different simulations were achieved on a larger area (100×100 m) but all the simulation statistics were exclusively collected within the 60×80 m stand.

Simulation framework

Simulations were run by using the initial conditions of the stand before abandonment, *i.e.* 5 initial trees with their corresponding age and coordinates as described above.

Simulations were made over 36 years (1964–2000) using 10 replicates.

Though we made careful investigations it was not possible to collect additional information to fix up the other main parameter of the simulation, that is the rate of recruitment. Instead of running multiple simula-

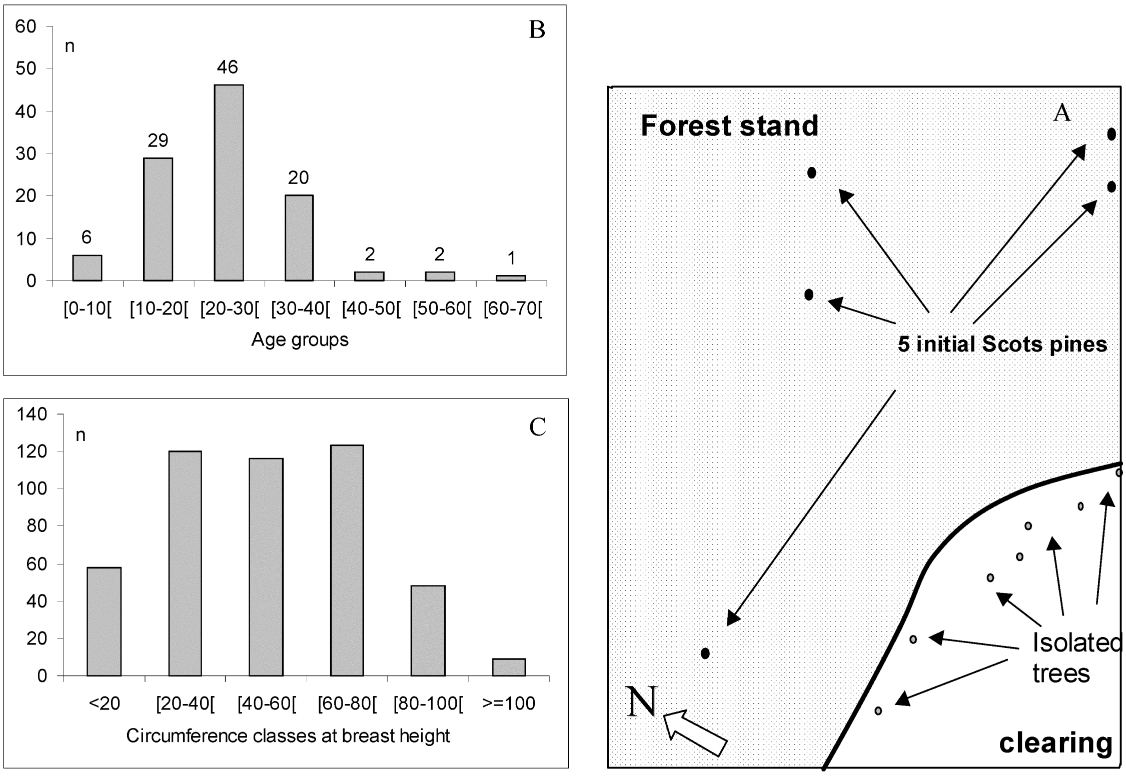

Figure 3. Present structure of the 60×80 m stand with position of the 5 initial trees within the stand (A), distribution of age classes for the 106 trees sampled (B), and distribution of circumference classes for the entire stand (C).

tions with a set of parameters randomly chosen we decided to test three scenarios of colonization that appeared to be the most probable given our field data:

1. the first scenario is based on a constant and regular resistance of the vegetation through time since abandonment. The rate of recruitment was put equal to 0.7 seedlings per year and per isolated mature tree. This value is supported by previous works on *Calluna* heathland colonization by Scots pine (Coquillard 1995; Coquillard et al. 2000). This scenario refers to simulation 1.
2. In the second scenario we hypothesized that the resistance was also constant but low, and consequently the recruitment was set up to an average rate of 5 seedlings per mature tree. This scenario corresponds to simulation 2.
3. We considered in the third scenario that the resistance of the vegetation could change with time: it was low the first 15 years (5 seedlings/tree/year) and high for the following years (0.7 seedlings/tree/year). This scenario refers to simulation 3.

Results

Influence of initial parameters

After numerous long-term simulations analysis (verification phase, data not shown), the behaviour and soundness of the model were found satisfactory to start the study of sensitivity to parameters. In this section, we attempted to estimate the importance of some parameters for the settlement process. Particularly, we considered whether (i) the initial number of trees, (ii) their distribution pattern within stands and (iii) the resistance of the area to pine settlement could constitute some key parameters to understanding the topics we raised in the introduction. Three series of experiments were done in which a single parameter was varied at a time. Table 2 shows that recruitment and distribution patterns have the greatest effect on the final density and basal area. In contrast, height and girth are less sensitive to these parameters.

The initial number of maternal trees obviously play an important role, especially in the initial stages of the colonization process (t = 20 and t = 40). At t =

Table 2. Influence of initial conditions of runs. Results at time (years) = 20, 40 and 80; 10 replicates. Runs initialised with 20–24 years old trees on a one ha area. Letters in parenthesis indicate statistical differences within some experiments ($p \leqslant 0.05$); in other cases each result is significantly different from all the others. RC is the rate of recruitment.

Experiments	Basal area (m^2)	Density (numb ha^{-1})	Height (m)	Girth (m)
Initial number of trees (Distribution pattern = random; RC = 0.7 seedling/mature tree/year)				
t = 20 yr				
30 pines	4.15	615	5.94	0.22
60 pines	7.30	907	6.51	0.24
90 pines	9.81	1024	7.01	0.26
t = 40 yr				
30 pines	15.23	1385	9.77	0.33
60 pines	19.27	1267	11.53	0.39
90 pines	20.72	1166	12.32	0.43
t = 80 yr				
30 pines	25.84	1052	17.01 (a)	0.52 (a)
60 pines	25.10	968	17.25 (a)	0.53 (b)
90 pines	24.47	919	17.22 (a)	0.53 (b)
RC seedling/mature tree/year (30 pines; Distribution pattern = random)				
t = 20 yr				
0.7	4.15	615	5.94	0.22
5	13.04	2080	7.07	0.24
t = 40 yr				
0.7	15.23	1385	9.77	0.33
5	34.15	1649	13.98	0.48
t = 80 yr				
0.7	25.84	1052	17.01	0.52
5	35.45	1154	18.34	0.57
Distribution Pattern (30 pines; RC = 0.7 seedling/mature tree/year)				
t = 20 yr				
1 cluster	2.91 (a)	223 (a)	6.49 (a)	0.28 (a)
3 clusters	3.37 (b)	370 (b)	6.39 (a)	0.25 (b)
6 clusters	3.90 (c)	530 (c)	6.03 (b)	0.22 (c)
10 clusters	4.14 (c)	610 (d)	5.99 (b)	0.21 (d)
Random	4.15 (c)	615 (d)	5.94 (b)	0.22 (c,d)
t = 40 yr				
1 cluster	6.85 (a)	673 (a)	8.33 (a)	0.29 (a)
3 clusters	9.90 (b)	964 (b)	8.92 (b)	0.30 (b)
6 clusters	13.55 (c)	1286 (c)	9.34 (c)	0.31 (c)
10 clusters	14.93 (d)	1368 (d)	9.68 (d)	0.32 (d)
Random	15.23 (d)	1385 (d)	9.77 (d)	0.33 (d)
t = 80 yr				
1 cluster	24.02 (a)	1298 (a)	13.65 (a)	0.44 (a)
3 clusters	25.64 (b)	1193 (b)	15.31 (b)	0.48 (b)
6 clusters	26.32 (c)	1086 (c)	16.68 (c)	0.51 (c)
10 clusters	26.52 (c)	1060 (d)	17.10 (c)	0.52 (c)
Random	25.84 (b)	1052 (d)	17.01 (c)	0.52 (c)

80, because of the saturation of the system, girth and height values are found not significant. Number of trees and basal area values, although significant, are less pronounced than in the initial stages.

High clustering of the initial pool of trees induces stronger competition between individuals and leads to lower values for height and girth at each time step and also for basal area except for the end of the colonization process.

Indeed, the best colonization, in terms of number of trees and of dendrometry at t = 20 and t = 40, is obtained using a random initialisation or a weak initial clustering. In these conditions, the system exhibits a decreasing number of trees at t = 80, whereas the density still rises in cases of stronger initial clustering.

This last effect is also apparent in the case of a weak resistance of the environment to colonization, a process that was simulated by increasing the rate of recruitment. While increasing the rate of recruitment, the differences in dendrometric values are largest in the first stages and become successively lesser when the stand gets older.

Elements for model validation

Precise historical data and multiple diachronic sampling would be required to obtain a complete and strong validation of a model like ours (Shugart 1984). Unfortunately, no accurate data were available to engage a validation of the model through time and space. Thus, we aimed at a partial validation on the basis of quantitative data obtained on stands independent of those used to elaborate the model.

We collected data from 51 plots (mean surface 400 m^2) measured within different natural Scots pine stands established on previous lawns. On each plot, the circumference at breast height of each tree was recorded; height and age by ring counting of 4 trees were also recorded.

The natural stands sampled were selected in similar site conditions but also to include a range of mean ages. They were characterized by a high density of trees and regularity (narrow dispersion of ages) on stands where an exhaustive age distribution was carried out (Prévosto et al. 1999). In such conditions, one can suppose that such stands were the result of a single abandonment of grazing followed by a sudden "blooming" of pine seedlings (in contrast to stands that established after a progressive decrease of the gazing pressure). Thus, we attempted to reproduce these circumstances with runs using the following initial conditions: trees of one year old randomly distributed, at an initial density varying from 1000 to 5000 individuals/ha; no recruitment (we hypothesised that tree establishment only occurred at the beginning of the abandonment); simulation length: 60 years; 10 replicates.

Results (Figure 4) show that the initial number of pine trees within the studied range greatly influences the basal area and density but has little importance for the average height and girth. In fact, most of basal area data are included between the extrema obtained by simulation, but a few stands exhibited some densities out of the range predicted by the model. The predicted average height and girth give reasonable values but hardly differ with the different scenarios. Observed values suggest however they scatter more widely for density and basal area than for mean height and girth. Several reasons discussed below, can explain the divergences observed between results and field data.

Field application

Dendrometric characteristics

Mean dendrometric values corresponding to the three different simulations are recorded in Table 3 for four time steps (t = 10, 20, 30 and 36).

Simulation 1 shows a low stand establishment due to a weak rate of recruitment. Consequently, though the number of trees is consistent with the actual stand density (respectively 454 and 474 trees) at the end of the simulation, the basal area as well as mean height and mean girth are largely under-estimated.

Conversely, results from simulation 2 show a rapid increase of the number of trees up to t = 20. From this time to t = 36 the density remains almost steady, thus proving that the plot is rapidly colonised and the final density quickly reached. However at time t = 36, both the number of trees (1100 trees) and the basal area (24.54 m^2) are clearly too large compared to present stand values (respectively 474 trees and 12 m^2). This simulation thus leads to a stand characterized by a much higher density and basal area than the values recorded in the field.

Simulation 3 shows a similar pattern with regard to density: a sharp increase during the first 15 years and then a slow change in the number of trees. Results at t = 36 prove that the main dendrometric values are reasonably estimated though the number of trees (752 trees) and the basal area (16 m^2) remain higher than the values recorded in the plot. Mean girth and, to a lesser extent, mean height are more correctly simulated.

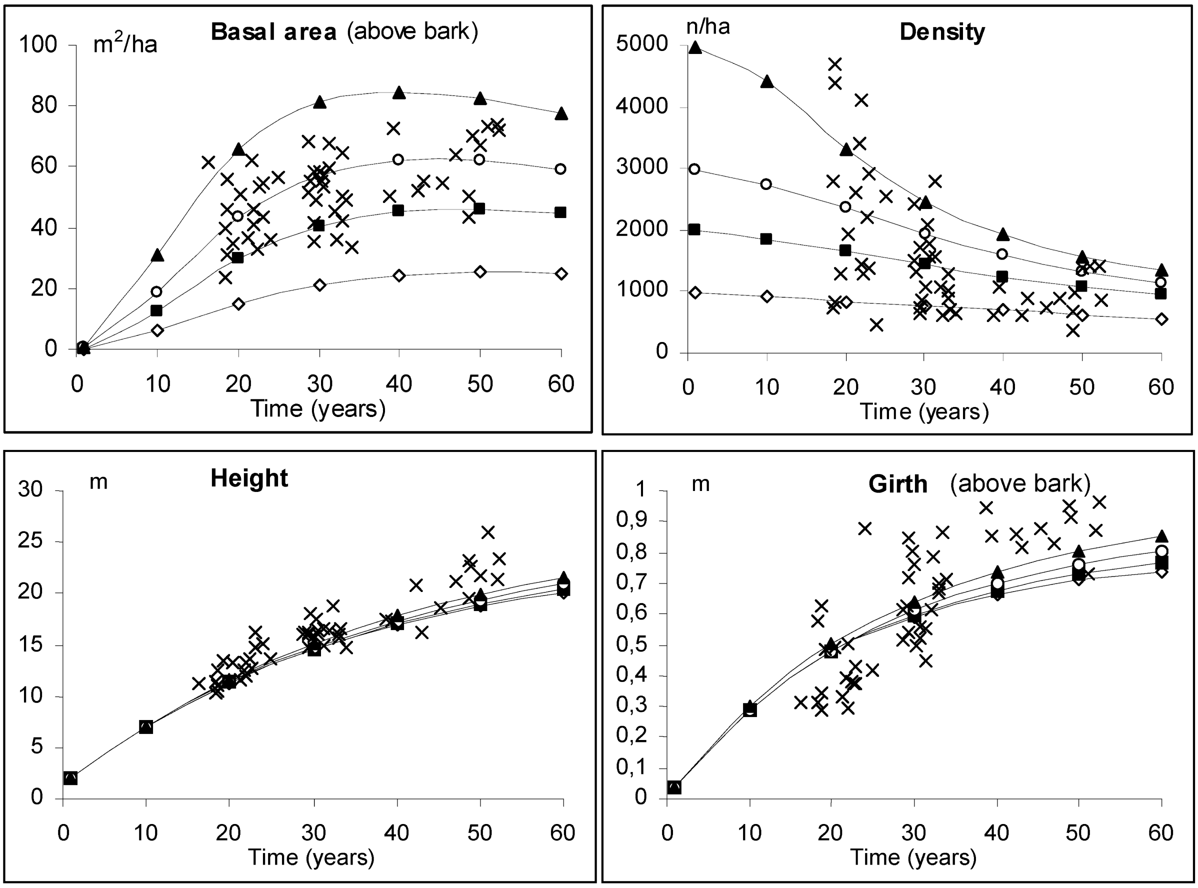

Figure 4. Element for model validation. Curves represent the trajectories of the 4 main dendrometric parameters along 60 year simulations. Four cases of initial densities of trees are studied: 5000 trees (▲), 3000 trees (○), 2000 trees (■), 1000 trees (◇) per ha. Ages of natural Scots pine plots established on former lawns (×) were estimated from core analysis and must be considered as approximate.

Demography

Distribution of trees in age classes is shown Figure 5. The comparison between simulation 1 at t = 36 and the stand shows two different patterns. Whereas present stand age distribution is characterized by a unimodal distribution that peaks at class [20–30], simulation 1 results exhibit an asymetric distribution: the number of individuals is maximal in the youngest class and progressively decreases in older classes (reverse J-shaped age distribution). From these results and the previous ones we can conclude that the assumption of a uniform resistance to colonization is inconsistent with the present age distribution and the dendrometric characteristics.

Simulation 2 and simulation 3 lead both to age-class distributions characterized by a maximum frequency in class [20–30] that are consistent with the observed data. This age distribution indicates that the colonization process has reached the stem exclusion stage (Oliver and Larson 1996) as observed in the field: the available space is fully occupied by young pines growing that compete with each other and new individuals cannot become successfully established.

Spatial pattern

Crown projections at the end of the different simulations were produced and compared with the present stand structure (Figure 6). Forest cover clearly and logically increases from simulation 1 to simulation 3 and simulation 2. It is important to emphasise that the bottom right corner of the simulated stands is always the least and most tardily colonized area of the plot. The location of the seed sources within the plot is thus a factor of major importance to explain the spatial pattern of tree colonization. However this part of the plot, corresponding to the present clearing of the stand free of tree settlement, is more likely to be colonized in simulation 2 than in simulation 3. The

Table 3. Mean dendrometric values. Results are given at time = 10, 20, 30, 36 (10 replicates). Letters in parenthesis indicate statistical differences within some experiments ($p \leqslant 0.05$), in other cases each result is significantly different from all the others.

Experiments	Basal area (above bark) (m^2)	Number of trees	Height (m)	Girth (above bark) (m)
$t = 10$				
Simulation 1	0.53 (a)	36	4.71 (a)	0.28 (a)
Simulation 2	1.20 (b)	315	4.10 (b)	0.16 (b)
Simulation 3	1.23 (b)	334	4.07 (b)	0.16 (b)
$t = 20$				
Simulation 1	1.12	117	5.56	0.25 (a)
Simulation 2	7.06	1026	5.92	0.25 (a)
Simulation 3	6.28	646	7.29	0.31 (b)
$t = 30$				
Simulation 1	2.70	306	6.28	0.26
Simulation 2	18.58	1180	9.14	0.40
Simulation 3	12.56	735	9.69	0.41
$t = 36$				
Simulation 1	4.46	454	6.98 (a)	0.29
Simulation 2	24.54	1100	11.08 (b)	0.49
Simulation 3	15.96	752	11.03 (b)	0.47
Stand	**12**	**474**	**9.8**	**0.50**

former simulation therefore seems to depicts the colonization process more accurately than the latter in terms of spatial structure. Summing up the results of a large number of replicates in a single representation of the frequencies constitues a discrete spectral analysis (Hill et al. 1996). Spectral analysis established for the stand (Fig. 6D) confirms that the south corner of the stand is characterized by low probability of colonization by Scots pine in contrast to the rest of the stand.

Discussion and conclusion

Model

The results show, in general, that the model can reproduce quite well the main traits of the afforestation dynamics of *Pinus sylvestris* in the context we studied. It gave some satisfying results as concern soundness and was capable to roughly reproduce growth and settlement of stands widely described in technical documents of forest managers. However, even if the quantitative results we obtained appeared realistic compared with available data, the model did not gave entire satisfaction in term of predictive values for density and girth. Consequently, we consider the model as partially valid only. This is probably the undesirable effect, of using a unique and constant weighted competition index through time (Biging and Dobertin 1995; Prévosto et al. 1999). Indeed, even if these indexes are helpful tools able to translate the effect of competition within short periods on a given stand, their use in long term simulation introduces some severe biases: the weight of competition diminishes at the same time as the stand reaches its equilibrium point. Improvements could be brought into the model by re-evaluating, for each time step, the local states of the stand and modifying the weight of the index or by adopting a more appropriate index.

The resistance of vegetation to pine colonization was first assumed to be constant in the model. This is a strong simplification and we must consider that several processes might modify the resistance to colonization. The most important are:

1. the internal dynamics of the system which can lead to an alternation of favourable and unfavourable phases for colonization. In particular, it is the case of *Calluna vulgaris* heathlands which often exhibit oscillations (Coquillard 1995; Coquillard et al. 2000),

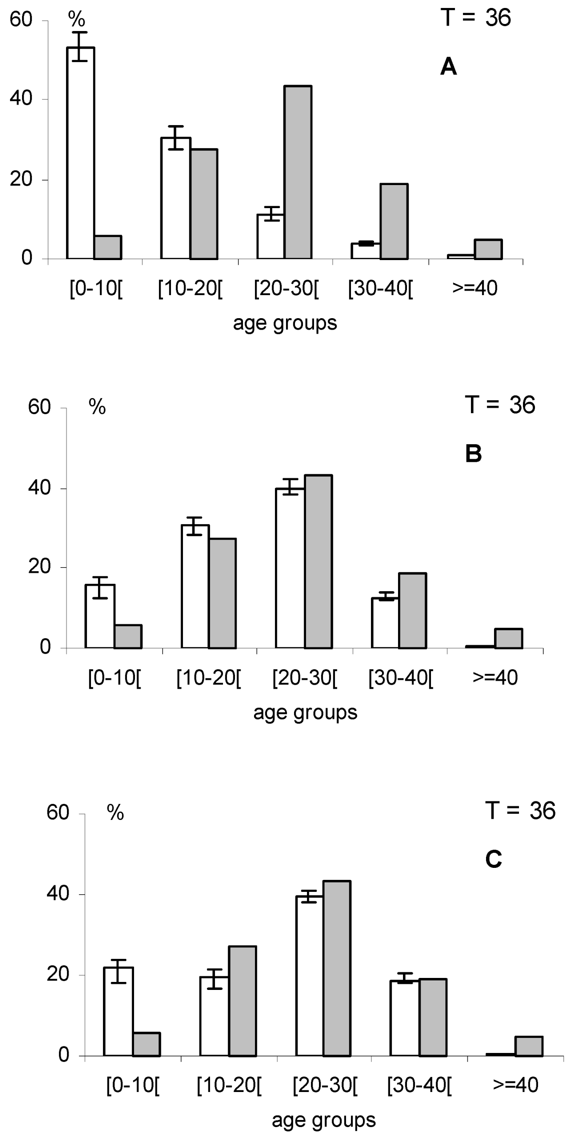

Figure 5. Distribution of age classes in frequency for the three simulations at time t = 36 (mean values and standard deviation). Present age distribution of the stand is indicated (grey bars). A: simulation 1 (high and constant resistance), B: simulation 2 (low and constant resistance), C: simulation 3 (variable resistance).

2. the competition for space with another species. In the study area and depending on the anterior agro-pastoral practices, the common broom *Cytisus scoparius* (L.) can quickly cover wide spaces after grazing withdrawal and, in doing so, can prevent colonization by pines over some periods. Thus, the first years after the abandonment of lawns are in most cases highly favourable to pine colonization, but can be followed by a less favourable period due to the presence of a dense shrubby vegetation.

Field application

Simulations

Our main goal was to determine the initial conditions of the colonization process that allowed the establishment of natural stands characterized by a narrow age distribution, this latter feature being frequently observed in many naturally regenerated Scots pine stands after field abandonment in the massif of the Chaîne des Puys. As the history of the colonization was unknown and impossible to rebuild, we decided to test only three main scenarios which seemed reasonable with respect to the knowledge we have about the colonization process of our study area, but which undoubtedly remain schematic.

The assumption of constant and high resistance of the resident vegetation to tree settlement can obviously be rejected because it produces irregular stands dominated by young age classes that establish too slowly. Conversely, a constant and low resistance produces stands too dense and formed too quickly as compared to present conditions. The hypothesis of a variable resistance with time appears the most probable scenario to explain the main dendometric characteristics, the age distribution and the spatial pattern. At this moment it is however important to stress that:

1. dendrometric and spatial parameters cannot be rightly predicted within a single simulation framework, thus suggesting that the biological models still require improvements,
2. tree establishment in our sampled stand is probably the result of a more complex scenario than the one proposed. In fact, a variation of only one factor of the initial conditions, such as year and season of abandonment in relation to tree seeds production or floristic composition of the ground vegetation, may significantly affect tree invasion.

From simulation results it is possible to put forward some parameters that play an important role in the colonization process.

The geometry of seed sources undoubtedly appears to be a key parameter that controls the colonization pattern. This result is in accordance with many previous studies on tree colonization. Lawson et al. (1999) found that recruitment is highly dependent upon seeds dispersed from adjacent forests and the

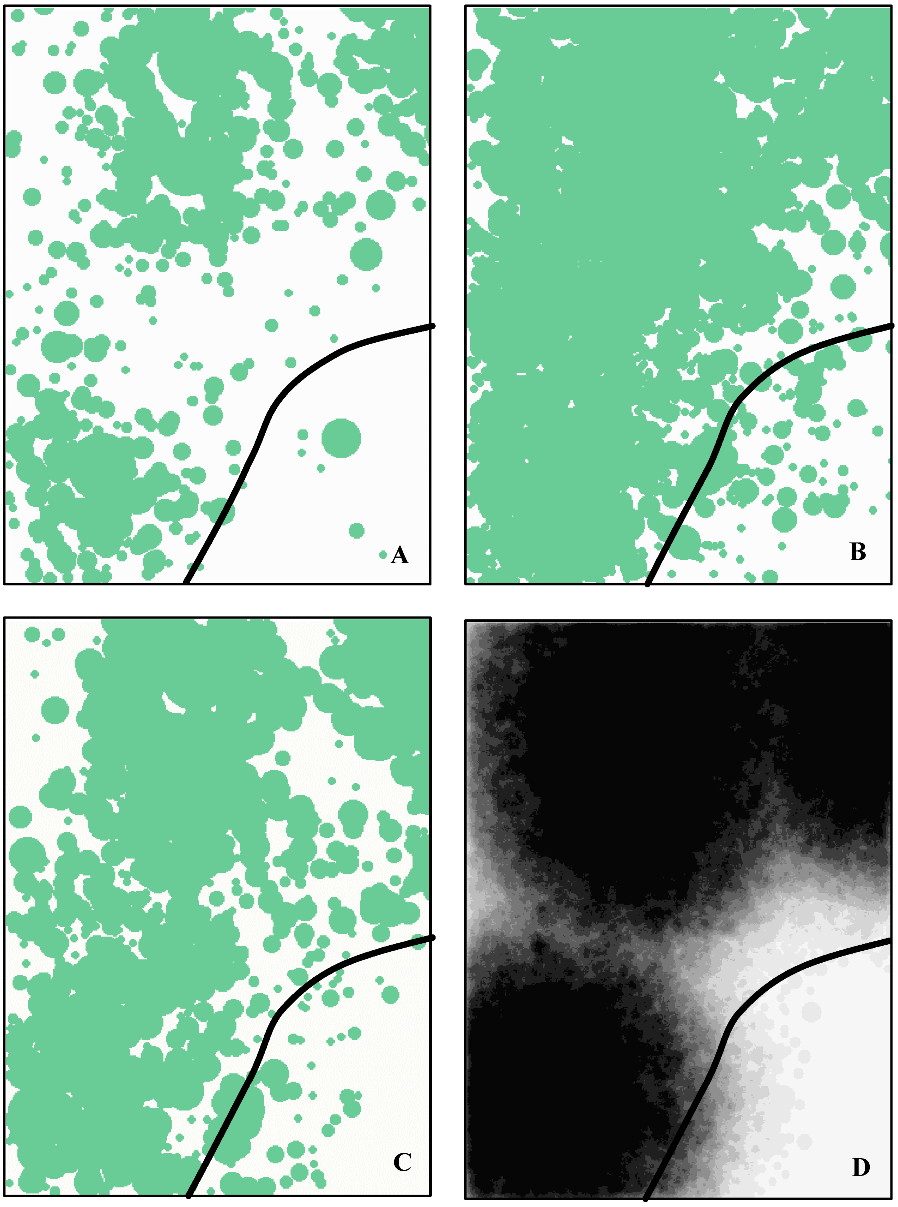

Figure 6. Crown projections for the different simulations at t = 36. A: simulation 1 (high and constant resistance, one replicate), B: simulation 2 (low and constant resistance, one replicate), C: simulation 3 (variable resistance, one replicate). D is the spectral analysis of the simulated stand for simulation 3 (100 replicates). The different range of greys correspond to 10% frequency intervals ranging from 0% (white) up to [90%–100%] (black).
Border of the clearing has been indicated in the different pictures.

influence of the degree of clustering and edge effects on the spatial pattern is also reported by Myster (1993).

Lastly competition that occurs within the stand controls the rate of growth and the number of trees through mortality. Results from the different simulations showed that density in the different age classes was difficult to fit proving that the use of a single and constant weighted geometric competition index and the calculus of a death probability are certainly insufficient to model such complex processes as competition and mortality.

Dynamics

The scenario of a fluctuating resistance of the resident vegetation, which emerges as the most probable from our simulation results, is supported by two considerations about *Calluna* ecology. First, it has been proved that *Calluna* heathland dynamics are cyclic: senescence phases with gaps favourable to tree settlement alternate with mature phases resistant to colonization (Khoon and Gimingham 1984; Coquillard 1995). Second, sheep grazing is likely to have produced a shorter heather as well as numerous gaps. These two factors were proved to favour seedling establishment: Steven and Carlisle (1959) and French et al. (1997), Scott et al. (2000) found that Scots pine regeneration was higher when heather was shorter. In any case the presence of gaps is commonly cited as an important requirement for seedling establishment (Miles and Kinnaird 1979; Booth 1984). Immediately after the withdrawal of grazing, these gaps with their size-reduced vegetation likely have offered opportunities for enhanced tree colonization during the first years following abandonment. Grazing cessation can be thus considered as the disturbance that has removed a ‘barrier’ to invasion as suggested by Johnstone (1986) and offered an opportunity for tree settlement. Scots pine seedlings previously controlled by grazing could establish in a vegetation characterized by a reduced *Calluna* cover and numerous safe sites. Trees gained dominance and once established may have shaded out the shade-intolerant *Calluna* plants. Afterwards the resistance of the ground vegetation was certainly restored. If not, this would have led to the colonization of the entire plot we have studied and the presence of a clearing would be difficult to explain. Moreover, Scots pine, in our field conditions, was not the only invader and broom proves to be also a competitor that could have progressively established especially in sites faraway from Scots pine seed sources. However, at this step, we cannot draw definite conclusions about the number and length of periods during which the resistance has fluctuated.

The proposed scenario is consistent with the concept of ‘windows’ (Gross 1980; Rankin and Pickett 1989) which represents regeneration opportunities that are episodically offered. These windows are periodically open but close quickly again (Myster 1993). Tree invasion is thus the result of a conjunction of events: seeds rain entering an environment that becomes temporarily favourable to tree settlement.

A recent theory proposed by Davis et al. (2000) puts forward the role of fluctuations of resource availability as a key factor controlling the susceptibility of an environment to invasion: a community’s susceptibility to invasion is submitted to fluctuations controlled by the level of resources available. In fact, the resistance to colonization by resident vegetation cannot be considered as a static and permanent attribute. To our mind, future predictions and models of tree colonization should take into account this latter proposition. They could therefore gain insight by focusing not only on the main ecological features of the invader species but also by considering dynamics and biological traits of the resident vegetation.

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Appendix 1

Equations used for circumference, height and crown radius modelling (after Prévosto et al. (2000))

Isolated trees:

$$dC = 0.21787e^{(age \quad 0.0849)}(1 - e^{(-age \quad 0.0849)})^{1.127}$$

$$dH = 0.0929dC$$

$$dR = (0.09179/2)dC$$

Trees within stands (all categories aggregated):

$$dC = 0.7075e^{(-0.0411CI)}0.0467e^{(0.0211CI)}$$
$$e^{(-age \quad 0.0467 \quad exp(0.0211CI))}$$

$$dH = 25.67e^{(-0.0223CI)}0.0296e^{(0.0222CI)}$$
$$e^{(-age \quad 0.0296 \quad exp(0.0222CI))}$$

$$dR = (0.067/2)dC$$

dC, dH, and dR are the respective increments for under-bark circumference at breast height, height, and crown radius. CI is the competition index.

References

Barbéro M., Loisel R., Quezel P., Richardson D.M. and Romane F. 1998. Pines of the Mediterranean Basin. In: Richardson D.M. (ed.), Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, pp. 153–170.

Biging G.S. and Dobertin M. 1995. Evaluation of competition indexes in individual tree growth models. For. Sci. 41: 360–377.

Booth T.C. 1984. Natural regeneration in the native pinewood of Scotland: a review of principles and practice. Scott. For. 38: 33–42.

Botkin D.B., Janak J.F. and Wallis J.R. 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60: 849–872.

Bullock J.M. and Clarke R.T. 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. Oecologia 124: 506–521.

Clark J.S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and paleorecord. Am. Nat. 152: 204–224.

Coquillard P. 1995. Simulation of the cyclical process of heathlands. Induction of mosaics structures, evolution to irreversible states. Ecol. Model. 80: 97–111.

Coquillard P. and Hill D.R.C. 1997. Modélisation et Simulation d'Ecosystèmes. Des modèles analytiques à la simulation à événements discrets. Collection Ecologie, Masson, Paris.

Coquillard P., Gueugnot J., Michalet R. and L'Homme G. 2000. Heathlands functioning in a perspective of climate warming: estimation of parameters, elements for discrete event simulation. Plant Ecol. 149: 107–108.

Davis A., Grime P. and Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol. 88: 528–534.

De Angelis D. and Gross L.J. 1992. Individual-based Models and Approches in Ecology: Populations, Communities, and Ecosystems. Chapman and Hall, New York.

DERF 1995. Les indicateurs de gestion durable des Forêts Françaises. Ministère de l'Agriculture et de la Pêche, Direction de l'Espace Rural et de la Forêt, Paris.

French D.D., Miller G.R. and Cummins R.P. 1997. Recent development of high-altitude *Pinus sylvestris* scrub in the northern Cairngorm Mountains, Scotland. Biol. Conserv. 79: 133–144.

González-Martínez S.C. and Bravo F. 2001. Density and population structure of the natural regeneration of Scots pine (*Pinus sylvestris* L.) in the High Ebro Basin (Northern Spain). Ann. For. Sci. 51: 277–288.

Greene D.F. and Johnson E.A. 1989. A model of wind dispersal of winged or plumed seeds. Ecology 70: 339–347.

Greene D.F., Zasada J.C., Sirois L., Kneeshaw D., Morin H., Charron I. et al. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. 29: 824–839.

Gross K.L. 1980. Colonization by *Verbascum thapsus* (Mullein) of an old field in Michigan: experiments of the effects of vegetation. J. Ecol. 68: 919–927.

Guittet J. and Laberche J.C. 1974. L'implantation naturelle du pin sylvestre sur pelouse xérophile en forêt de Fontainebleau. II: démographie des graines et des plantules au voisinage des vieux arbres. Oecol. Plant. 9: 111–130.

Hawkes C. 2000. Woody plant mortality algorithms: description, problems and progress. Ecol. Model. 126: 225–248.

Higgins S.I. and Richardson D.M. 1998. Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. Plant Ecol. 135: 79–93.

Higgins S.I. and Richardson D.M. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. Am. Nat. 153: 464–475.

Hill D.R.C., Mazel C. and Coquillard P. 1996. Integrating Verification and Validation in the object-oriented life cycle of ecological modelling simulation projects. In: 8th European Simulation Symposium 96 (Simulation in Industry), Oct 24–26., Genova, Italy, pp. 21–25.

Huston M., De Angelis and Post W. 1988. New computer models unify ecological theory, computer simulation shows that many ecological patterns can be explained by interactions among individual organisms. BioScience 10: 682–691.

Johnstone I.M. 1986. Plant invasion windows: a time-based classification of invasion potential. Biol. Rev. 61: 369–394.

Khoon G.W. and Gimingham C.H. 1984. Birch regeneration in heath vegetation. Proceedings of the Royal Society of Edinburgh 85 B: 73–84.

Kleijnen P.C.J. 1987. Statistical Tools for Simulation Practitioners. Marcel Dekker Inc. Pub., New York.

Krugman S.L. and Jenkinson J.L. 1974. *Pinus* L. pine. In: Schopmeyer S.C. (ed.), Seeds of Woody Plants in the United States. USDA Forest Service Agriculture Handbook 450, Washington, DC, USA, pp. 598–638.

Lanner R.M. 1998. Seed dispersal in *Pinus*. In: Richardson D.M. (ed.), Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, pp. 281–295.

Lawson D., Inouye R.S., Huntly N. and Carson W.P. 1999. Patterns of woody plant abundance, recruitment, mortality, and growth in a 65 year chronosequence of old fields. Plant Ecol. 145: 267–279.

Lonsdale W.M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522–1536.

Miles J. and Kinnaird J.W. 1979. Grazing: with particular reference to birch, juniper and Scots pine in the Scottish Highlands. Scott. For. 33: 280–289.

Monserud R.A. and Sterba H. 1999. Modelling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113: 109–123.

Moravie M.-A., Pascal J.-P. and Auger P. 1997. Investigating canopy regeneration processes through individual-based spatial models: application to a tropical rain forest. Ecol. Model. 104: 241–260.

Myster R.W. 1993. Tree invasion and establishment in old fields at Huchestone Memorial Forest. Bot. Rev. 59: 251–272.

Neubert M.G. and Caswell H. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. Ecology 81: 1613–1628.

Oliver C.D. and Larson B.C. 1996. Forest Stand Dynamics. J. Wiley and Sons, New-York.

Pacala S.W. and Silander J.A. 1985. Neighborhood models of plant population dynamics. I. Single-species models of annuals. Am. Nat. 125: 385–411.

Pacala S.W., Canham C.D., Saponara J., Silander J.A., Richard K.K. and Ribbens E. 1996. Forest models by field measurements: estimation, error analysis and dynamics. Ecol. Monogr. 66: 1–43.

Prévosto B., Coquillard P. and Gueugnot J. 1999. Growth models of silver birch (*Betula pendula* Roth.) on two volcanic mountains in the French Massif Central. Plant Ecol. 144: 231–242.

Prévosto B., Curt T., Gueugnot J. and Coquillard P. 2000. Modeling mid-elevation Scots pine growth on a volcanic substrate. For. Ecol. Manage. 131: 223–237.

Pukkala T. and Kolström T. 1987. Competition indices and the prediction of radial growth in Scots pine. Silva Fen. 1: 55–67.

Rankin W.T. and Pickett S.T.A. 1989. Time of establishment of red maple (*Acer rubrum*) in early old field succession. Bull. Torrey Bot. Club 116: 182–186.

Richardson D.M. 2000. Mediterranean pines as invaders in the southern hemisphere. In: Ne'eman G. and Trabaud L. (eds), Ecology, Biogeography and Management of *Pinus halepensis and P. Brutia* Forest Ecosystems in the Mediterranean Basin. Backhuys publishers, Leiden, The Netherlands, pp. 131–142.

Richardson D.M. and Higgins S.I. 1998. Pines as invaders in the southern hemisphere. In: Richardson D.M. (ed.), Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, pp. 450–473.

Rouvinen S. and Kuuluvainen T. 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. Can. J. For. Res. 27: 890–902.

Scott D., Welch D., Thurlow M. and Elston D.A. 2000. Regeneration of *Pinus Sylvestris* in a natural pinewood in NE Scotland following reduction in grazing by *Cervus elaphus*. For. Ecol. Manage. 130: 199–211.

Shannon R.E. 1975. System Simulation the Art and Science. Prentice Hall, Englewood Cliffs, NJ, USA.

Shugart H.H. 1984. A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models. Springer-Verlag, New York.

Steven H.M. and Carlisle A. 1959. The Native Pinewoods of Scotland. Oliver and Boyd, Edinburgh.

Tomé M. and Burkhart H.E. 1989. Distance-dependent competition measures for predicting growth of individual trees. For. Sci. 35: 816–831.

Urban D.L. and Shugart H.H. 1992. Individual based models of forest succession. In: Glenn-Lewin D.C., Peet R.K. and Veblen T.T. (eds), Plant Succession, Theory and Prediction. Chapman & Hall, London, pp. 249–292.