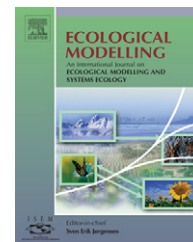


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## Bridging the gap between ecophysiological and genetic knowledge to assess the adaptive potential of European beech

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### ARTICLE INFO

#### Article history:

Received 25 April 2007

Received in revised form

23 April 2008

Accepted 14 May 2008

Published on line 21 June 2008

#### Keywords:

Adaptive potential

Ecophysiology

Genetics

*Fagus sylvatica* L.

Forest management

ForGEM

### ABSTRACT

In this study we aimed to combine knowledge of the ecophysiology and genetics of European beech to assess the potential of this species to adapt to environmental change. Therefore, we performed field and experimental studies on the genetic and ecophysiological functioning of beech. This information was integrated through a coupled genetic–ecophysiological model for individual trees that was parameterized with information derived from our own studies or from the literature. Using the model, we evaluated the adaptive response of beech stands in two ways: firstly, through sensitivity analyses (of initial genetic diversity, pollen dispersal distance, heritability of selected phenotypic traits, and forest management, representing disturbances) and secondly, through the evaluation of the responses of phenotypic traits and their genetic diversity to four management regimes applied to 10 study plots distributed over Western Europe. The model results indicate that the interval between recruitment events strongly affects the rate of adaptive response, because selection is most severe during the early stages of forest development. Forest management regimes largely determine recruitment intervals and thereby the potential for adaptive responses. Forest management regimes also determine the number of mother trees that contribute to the next generation and thereby the genetic variation that is maintained. Consequently, undisturbed forests maintain the largest amount of genetic variation, as recruitment intervals approach the longevity of trees and many mother trees contribute to the next generation. However, undisturbed forests have the slowest adaptive response, for the same reasons.

Gene flow through pollen dispersal may compensate for the loss in genetic diversity brought about by selection. The sensitivity analysis showed that the total genetic diversity of a 2 ha stand is not affected by gene flow if the pollen distance distribution is varied from highly left-skewed to almost flat. However, a stand with a prevailing short-distance

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doi:10.1016/j.ecolmodel.2008.05.004

gene flow has a more pronounced spatial genetic structure than stands with equal short- and long-distance gene flows. The build-up of a spatial genetic structure is also strongly determined by the recruitment interval. Overall, the modelling results indicate that European beech has high adaptive potential to environmental change if recruitment intervals are short and many mother trees contribute to the next generation.

The findings have two implications for modelling studies on the impacts of climate change on forests. Firstly: it cannot be taken for granted that parameter values remain constant over a time horizon of even a few generations – this is particularly important for threshold values subject to strong selection, like budburst, frost hardiness, drought tolerance, as used in species area models. Secondly: forest management should be taken into account in future assessments, as management affects the rate of adaptive response and thereby the response on trees and forests to environmental change, and because few forests are unmanaged. We conclude that a coupled ecophysiological and quantitative genetic tree model is a useful tool for such studies.

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## 1. Introduction

Global change is likely to exert strong evolutionary pressure on trees over the coming decades (Parmesan, 2006). Some authors have expressed concern that trees are unable to adapt to such changes because the rate of climate change is rapid relative to the longevity of individual trees (Davis and Shaw, 2001), trees may not have adequate genetic diversity to adapt to the changing environmental conditions (Davis and Kabinski, 1992), and trees may not be able to disperse to newly available habitat fast enough to outstrip the rate of global change, as the landscape they have to cross is highly fragmented (Jump and Peñuelas, 2005). Other authors, however, point to evident characteristics that uniquely empower trees to withstand environmental changes (Hamrick and Godt, 1996): trees have high phenotypic plasticity that allows them to withstand large environmental fluctuations during their lifetime (Rehfeldt et al., 2002); there are high levels of genetic diversity for allozymes and nuclear markers within – rather than between – populations (Buiteveld et al., 2007; Leonardi and Menozzi, 1995); and gene flow – especially of pollen – occurs over large distances, thereby exchanging favourable genetic variants between isolated stands (Petit and Hampe, 2006). Some paleo-ecological evidence indicates that large fluctuations in species range have been accomplished without apparent loss of genetic diversity (Hamrick, 2004; Magri et al., 2006). On the other hand, the spatial distribution of nuclear DNA markers of beech shows a severe loss of diversity from ice-age refugia to Western Europe (Comps et al., 2001). A possible reason for these conflicting results could be that, as chloroplast markers indicate, the most genetically diverse populations were not located in refugia of beech in the south of Europe, but at intermediate latitudes as a consequence of the admixture of divergent lineages that recolonized the continent from separate ice-age refugia (Petit et al., 2003).

The two key questions are whether tree species have the potential to adapt to rapid environmental changes such as the current climate change, and what role forest management could play in maximizing the rate of adaptation. It is important to recognize that the rate of adaptation of trees to environmental change depends not so much on the longevity of individual trees but rather on successful recruitment events during a tree's lifetime (Hamrick, 2004). Trees have overlapping genera-

tions and at regular intervals produce seeds in high numbers. During the first decades of forest development, tree numbers decline from several millions per hectare to a few hundred or less (Geburek, 2005). Thus during that stage, besides strong genetic drift, most of the selection and adaptation takes place (Finkeldey and Ziehe, 2004; Lefèvre, 2004). Virtually all temperate zone forests are managed in some way, hence it is the forest management that determines, or at least attempts to do so, which tree species and individuals regenerate where and when. Even if the forest manager does not deliberately and proactively select traits that may be suited to a future climate, forest management is a major force in allowing adaptation to occur, via the interval imposed between recruitment events. Furthermore, the selective response of trees to environmental changes depends on the heritability of functional traits: for example, a highly adaptive phenotypic trait such as budburst phenology has a high narrow-sense heritability up to 0.7 (Billington and Pelham, 1991; Howe et al., 2000; Wuehlisch et al., 1995) which is expressed as early as the seedling stage, thereby allowing the species to adapt that feature relatively quickly if needed.

During the EU-funded project DynaBeech were the interactions between selection, gene flow and management practice studied to evaluate the impacts of forest management on the dynamics of genetic and ecological diversity of European beech, *Fagus sylvatica* L. (Kramer, 2004). The overall aim was to assess the adaptive potential of beech as a model tree species to environmental changes, based on its genetic and ecophysiological characteristics. Three subsidiary aims were formulated: (i) the development of a coupled genetic–ecological individual-tree model and its parameterization with information derived either from field studies and experiments performed during the project or obtained from the literature; (ii) the evaluation of the adaptive response of a beech stand to environmental changes through sensitivity analyses of: (a) initial genetic diversity; (b) pollen dispersal distance; (c) heritability of selected phenotypic traits; and (d) forest management; and (iii) the evaluation, by model simulation, of the responses of selected phenotypic traits and their genetic diversity to a range of management regimes applied to the study plots.

As the genetic base of many of the critical parameters related to the tree's response to climate change is still to

be determined, we did not attempt to include a climate change assessment. Instead, we evaluated the role of forest management on adaptive response of selected traits, because we expected that forest management would have an important, albeit often neglected, impact on adaptation.

## 2. Material and methods

To meet the aims mentioned above, highly polymorphic genetic markers were developed for beech during the DynaBeech project (Pastorelli et al., 2003) to estimate effective pollen dispersal distances (Powell et al., 1995). The heritability of a number of ecological and ecophysiological tree features was determined, using an earlier established open-pollinated half-sib trial (i.e. in which the mother tree of an offspring is known but the father tree is unknown) (Teissier du Cros et al., 2004) and a hand-pollinated full-sib trial (i.e. in which both the mother and father trees of an offspring are known) (Scalfi et al., 2004). Five study sites were established in beech forests throughout Western Europe, each comprising two plots that were very similar, but were subjected to different management regimes: one was intensively managed, the other was extensively managed. The characteristics of the stand, climate, soil and management of each approximately 2 ha plot were recorded (Forstreuter, 2004) (see Section 2.6.2). A range of realistic forest management scenarios was defined in collaboration with local forest managers. The results of the field studies were integrated into an individual-based tree model, referred to as ForGEM, an acronym of FORest Genetics, Ecology and Management.

The ForGEM model includes descriptions of the following processes: (i) light interception by individual crowns; (ii) photosynthesis; (iii) growth, including the allocation of the net primary production over the plant components, and the increment of the tree's height, diameter and stem volume; and (iv) the establishment, growth and competition for light of seedling cohorts.

To assess the impacts of environmental change on the adaptive potential of trees, the functional phenotypic traits as described in the individual-tree model need to be linked to a genetic model. This model also includes gene flow through dispersal of pollen and seeds.

Resource-related mortality is an important aspect to describe and parameterize, as a differential genetic make-up leads to differential mortality through the tree's ability to exploit resources. Furthermore, as forest management can be expected to be a major driver by allowing adaptation to occur through its effect on regeneration, a model that aims to evaluate effects of climate change on the adaptive potential of forests needs to include a realistic representation of how forest managers treat their forests.

The following subsections describe: the approach to link a process-based individual tree model to a genetic model; resource-related mortality; and forest management regimes. See Kramer et al. (2001, 2004) and references therein for the classical processes in tree modelling, including interception of light, photosynthesis and respiration.

### 2.1. Linking phenotypic traits with a genetic model

Our modelling of the genetic control of a functional quantitative phenotypic trait was based on the following assumptions: (i) the trait is genetically represented by a multi-locus, 2-allele genetic model (i.e. neither mutation nor immigration of new alleles into the population); (ii) each locus contributes equally to the phenotypic trait without interaction with other loci and this contribution is constant in time (i.e. no linkage and no epistasis); (iii) there is an additive-linear relationship between the trait and the contribution of the allele to the phenotypic value of the trait, without interactions with other alleles (i.e. neither dominance nor pleiotropy).

Two steps need to be taken in order to represent a phenotypic trait by this genetic model: (i) initial frequencies must be assigned to the alleles, and (ii) the allelic effects must be distributed over the alleles, given the initial allele frequency distribution obtained under (i). This genetic model is set up independently for each selected quantitative trait and for each simulation. The allelic effects are kept constant throughout the simulation.

#### 2.1.1. Initial allele frequency

Allele frequency distribution in trees is typically U-shaped for polymorphic loci: alleles are usually very common (frequency approaching unity) or very rare (frequency approaching zero), but seldom have a frequency in the population of around 0.5 (e.g. Hamrick, 2004; Chakraborty et al., 1980). As no information was available to us on the frequency distribution of alleles of adaptive traits, we used an equilibrium allele frequency distribution of neutral traits to initiate the genetic model (Crow and Kimura, 1970). Once the simulation starts, evolutionary forces such as selection, random genetic drift and migration act upon these frequencies and will change allelic frequencies through time. These genetic processes are described mechanistically in the model. Mutation is assumed not to occur during the 300 years simulated time horizon.

Our approach was as follows. Nei (1987, p. 367) presents the stationary distribution,  $\phi(x)$ , of allele frequencies,  $x$ , over all loci in a population (Eq. (1)).

$$\phi(x) = \frac{\Gamma(M + M')}{\Gamma(M)\Gamma(M')} (1 - x)^{M-1} x^{M'-1} \quad (1)$$

where  $M = 4Nv$ ,  $M' = M/(k - 1)$ ,  $N$  is the effective population size,  $v$  is the mutation rate,  $k$  is number of alleles per locus,  $\Gamma()$  is the gamma function.  $M$  can be estimated from average heterozygosity ( $H$ ). If a large number of loci are examined  $M = H/(1 - H)$ . Good average values based on isozyme data are  $H = 0.25$  and  $k = 2$  (Comps et al., 1990, 2001; Leonardi and Menozzi, 1995). As it is only necessary to determine the initial set of allelic frequencies  $x$ , once during a simulation, we determined  $x$  by inverting the integral of  $\phi(x)$ , into  $\Psi(x')$ , for a given number of loci (see Press et al., 1999, pp. 287–288 for details on this approach). We used a 10-locus, 2-allele genetic model for each trait (Guevara et al., 2005; Lynch and Welsh, 1998). The initial allelic frequencies, after rounding, are as presented in Table 1.

**Table 1 – Initial allele frequencies (*p*, *q*, with *q* = 1 – *p*) of a quantitative genetic trait, over 10 loci**

Locus no:	1	2	3	4	5	6	7	8	9	10
<i>p</i>	A: 0.001	B: 0.006	C: 0.02	D: 0.045	E: 0.085	F: 0.14	G: 0.21	H: 0.3	I: 0.4	J: 0.5
<i>q</i>	a: 0.999	b: 0.994	c: 0.98	d: 0.955	e: 0.915	f: 0.86	g: 0.79	h: 0.7	i: 0.6	j: 0.5

2.1.2. Initial phenotypic values

It is necessary to find the distribution of allelic effects over the alleles under the constraint that the allelic frequencies follow the U-shaped initial distribution as described above. As currently insufficient information is available on the actual genes and alleles that determine quantitative phenotypic traits, our method entails taking a statistical approach, by designing for each trait a genotype distribution over the population of trees, such that the observed population mean and variance of the phenotypic trait are attained. When new knowledge becomes available on the candidate genes of the phenotypic traits considered, this procedure can be replaced by actual data on the genetic make-up of these traits.

The average phenotypic value of a population,  $\bar{y}$  can be obtained from the following formula (Falconer and Mackay, 1996) valid for a two-allele system (Eq. (2)).

$$\bar{y} = \sum_{i=1}^n a_i(p_i - q_i) + 2 \sum_{i=1}^n d_i p_i q_i \tag{2}$$

where *n* is the total number of loci determining the trait; *a<sub>i</sub>* is the allelic effect; *p<sub>i</sub>* and *q<sub>i</sub>* are the allelic frequencies; and *d<sub>i</sub>* measures the degree of dominance of locus *i*. The allelic effects of the alleles of a locus are assumed to be opposite in sign but of the same magnitude and are expressed as deviance from the population mean.

For a randomly mating population in equilibrium (neither linkage nor epistasis), the observed phenotypic variance, *V<sub>P</sub>*, is the sum of the additive and dominance genetic variance and the environmental variance, *V<sub>E</sub>* (Falconer and Mackay, 1996) (Eq. (3)).

$$V_P = 2 \sum_{i=1}^n p_i q_i [a_i + d_i(p_i - q_i)]^2 + 2 \sum_{i=1}^n (d_i p_i q_i)^2 + V_E \tag{3}$$

*V<sub>E</sub>* can be assessed from the observed phenotypic variance (*V<sub>P</sub>*) once the narrow-sense heritability (ratio of additive genetic variance to total variance) of the trait is known (*V<sub>E</sub>* = (1 – *h<sub>ns</sub><sup>2</sup>*)*V<sub>P</sub>*). If the trait is not known, a reasonable value for *h<sup>2</sup>* must be assumed, e.g. based on observations from related species. Fig. 1 gives an example of how this procedure yields an initial distribution of budburst in a simulated population that is consistent with an observed population.

Thus the value of *a<sub>i</sub>* in Eqs. (2) and (3) was determined given: (i) initial frequencies as presented in Table 1; (ii) environmental and genetic variance as determined by the heritability of the trait; and (iii) the mean and variance of the trait as observed in the population.

2.2. Gene flow by dispersal of pollen and seeds

Gene flow from adult trees to newly established seedlings can be described as a 3-stage process: firstly, the production of

pollen and its dispersal from the father tree to the mother tree; second, the production and dispersal of seeds; and thirdly, the survival of seeds and establishment of the seedlings dependent on local environmental conditions. These processes are described in the model as presented below.

2.2.1. Gene flow through pollen dispersal

The probability of gametes of a mother tree *M<sub>i</sub>* and father tree *F<sub>j</sub>* meeting can be estimated from the proportion of pollen from *F<sub>j</sub>* arriving at the location of *M<sub>i</sub>* relative to the proportion of pollen from all other known and unknown potential father trees. The amount of pollen from any father tree (*F*) reaching the location of a mother tree (*M*) depends on: (1) the amount of pollen produced by the *F* tree; (2) the distance between the target *M* and *F* trees; (3) the overlap in flowering phenology between the *F* and *M* trees; and the wind direction relative to the orientation of the *F* and the *M* trees.

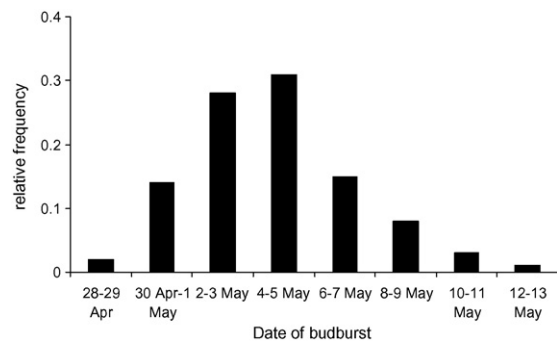
A Weibull distribution was used to describe the decline in the amount of pollen with distance. This is a generic and flexible distribution for describing this process (Kotz et al., 2000) (Eq. (4)).

$$D(M_i, F_j) = bc(bx)^{c-1} e^{-(bx)^c} \tag{4}$$

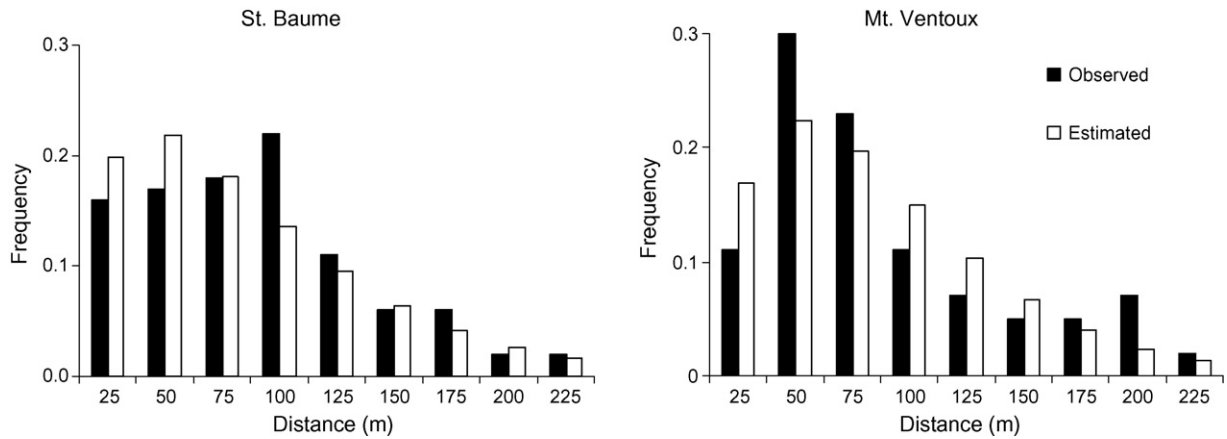
where *b* is a scale parameter, *c* a shape parameter, and *x* the distance to the father tree.

The overlap in flowering phenology between *F* and *M* trees determines what proportion of the pollen emitted by the father tree can actually pollinate a given flowering mother tree. Thus, the proportion of *F<sub>j</sub>* pollen arriving at position *M<sub>i</sub>* can be described (Eq. (5)).

$$P(M_i \times F_j) = \frac{Y_0(F_j)D(M_i, F_j)t(M_i, F_j)}{\sum_k (Y_0(F_k)D(M_i, F_k)t(M_i, F_k)) + E_{M_i}} \tag{5}$$



**Fig. 1 – Example of initial distribution of a quantitative phenotypic trait i.e. budburst over 235 trees using a 10 locus/2 allele genetic model as described in the text. Observed mean date of budburst is May 5; S.D. = 5d; *h<sub>ns</sub><sup>2</sup>* = 0.6. This genetic model was set up independently for each selected quantitative trait (see below).**



**Fig. 2 – Observed and estimated pollen dispersal curve in France. St. Baume (unmanaged,  $b = 0.0124$ ;  $c = 1.2892$ ) and Mt. Ventoux (managed,  $b = 0.0123$ ;  $c = 1.4334$ . See Eq. (4)).**

with  $Y_0(F_j)$ : amount of pollen from father tree  $j$  at distance = 0; and  $t(M_i, F_j)$ : overlap in flowering phenology; and  $E_{M_i}$ : the amount of external pollen arriving at mother tree  $F_i$ .

We assumed that: (i) the amount of pollen produced per  $m^2$  of canopy is the same for all flowering trees, (ii) stochastic variation in pollen production between years is the same for all trees, and (iii) the amount of pollen produced is proportional to the size of the tree’s crown. Consequently, to avoid modelling the amount of pollen produced per tree, we used the ratio of canopy sizes as an estimate of the ratio of the amount of pollen produced by father tree,  $F_j$ , to the amount of pollen produced by all other potential father trees.

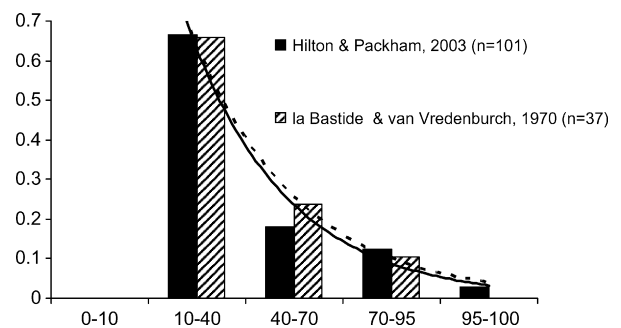
The pollen dispersal curves used in ForGEM were estimated based on a paternity analysis of seeds collected from mother trees in the two French plots Sainte Baume (the unmanaged plot) and Mt. Ventoux (the managed plot: Fig. 2). As no highly polymorphic microsatellites specifically for *Fagus sylvatica* L. were available at the start of the project and the markers identified for *Quercus* were not polymorphic for *Fagus sylvatica* (Streiff, 1998), we developed new microsatellites (FS4-46, MFC5, FS1-15, FS1-25, Pastorelli et al., 2003) to genotype the trees and their progeny. In Sainte Baume, 286 adults were genotyped and a sample of 190 seeds was collected from four mother trees. In Ventoux, 90 adults were sampled and 250 seeds were collected from five mother trees. The paternity analysis was performed using the Famoz software package (Gerber et al., 2003). The percentage of correctly assigned paternity was 66.2% for Sainte Baume and 65.6% for Ventoux. This value records how many times a father was found and it was the true one, or a father was not found because the father was actually outside the stand. The proportion of pollen originating from outside the stands was estimated to be 44.6% for Sainte Baume and 71.8% for Ventoux. Within the model, the genotype of the pollen from outside the area was assumed to be a random sample from the initial population.

Based on Merzeau et al. (1994) who found 0% self-fertilization and Rossi et al. (1996) who found 2–6% self-fertilization, we assume beech is a 100% outcrossing species. After one year, Leonardi (data not published) found no surviving seedlings from self-pollinations in a  $4 \times 4$  diallel controlled cross (Scalfi et al., 2004).

### 2.2.2. Production of seeds

Usually, the amount of mast produced by European beech is low to moderate; only occasionally is it very high. The only data on seed production available to us were the long-term observations from La Bastide and Vredenburg (1970) – a 37-year time series – and from Hilton and Packham (2003) – a 101-year time series (Fig. 3). La Bastide and Vredenburg (1970) used a crop-rating scale ranging from 0 to 100, based on average seed production data in the Netherlands relative to the maximum attainable seed production know to them. Hilton and Packham (2003), on the other hand, used a 5-point scale based on a 7-min seed count. These different approaches mean that the classes used in the two studies are not fully compatible. Nevertheless, the trend lines through the data of both studies are very similar (Fig. 3). We simulated mast in the model by firstly, stochastically determining one of the four crop-rating classes indicated in Fig. 3 and then by stochastically determining the actual seed production within that class.

The actual amount of seeds produced by individual trees depends on the maximum number of seeds a fully grown adult tree can produce in a top mast year. Linnard (1987), Newbold and Goldsmith (1981) present a good estimate for this parameter: 600,000 beechnuts per tree. We scaled down the actual amount in proportion to the crown dimensions of the individual relative to the species’ maximum dimensions. Based on Watt (1923, 1925) and Evans (1984), we assumed that a tree



**Fig. 3 – Frequency distribution of average crop-rating of beech (*Fagus sylvatica* L.). Based on data from La Bastide and Vredenburg (1970) and Hilton and Packham (2003).**

starts producing seeds at an age of around 50–60 years. To make this parameter independent from the growing conditions at a site, it was determined as 70% of the maximum height possible at the site. Seed production continues until the maximum age of the tree is attained. This was set as 350 years (Koop, 1989; Tubbs, 2001; pers. comm. Ed Mountford).

### 2.2.3. Gene flow through seed dispersal

The dispersal rates of beech presented in the literature are that 90% of the seeds are spread within 25 m due to seeds falling, being blown by normal winds in a forest environment, and moved short distances by small mammals (Brown, 1953; Janßen, 2000; Jensen, 1985; Watt, 1925). Dispersal distances are simulated in the model using an exponential decline with distance, such that 90% of the seeds are dispersed within 25 m of the mother tree.

Over winter seed is lost because of unviability, infestation by insect larvae, destruction by animals and disease/decay, etc. This is expressed as a monthly loss rate. An accepted estimate of seed loss is 39% per month over a winter of 6 months (from data in Watt (1923) and Linnard (1987)), supported by the general view commonly held by UK foresters that beech seed is heavily predated, particularly by wood pigeons, mice/voles and grey squirrels, with most unburied seed taken (Bourne, 1945; Watt, 1923; pers. comm. Ed Mountford). The proportion of seeds left to germinate in spring is 60%, estimated from Gordon and Rowe (1982) based on an average percentage that germinated from 195 samples. Thus, a seed turnover during winter of 39% per month for 6 months and a 60% germination rate of the remaining seeds will leave 3.1% of seed overall.

The seedlings that do emerge from these surviving seeds can only establish if there is enough light at the forest floor. In beech, a shade-tolerant species, the minimum fraction of light required for seedling establishment and survival is 2% of the incoming global radiation on top of the canopy (Watt, 1923). Water availability for the seedlings was not taken into account in the version of the model used.

## 2.3. Mortality

From germination and establishment onwards, the seedlings in the model are prone to three causes of mortality: self-thinning; resource-related mortality; and age-dependent mortality. Resource-related mortality is particularly important when combining a genetic model on tree growth with an ecological model on tree growth, because genetic differences between trees in their growth will eventually result in differences in mortality and thus affect the genetic composition of the next generation. For computational reasons, the model assigns a genotype to an individual when it attains a height of 2 m. Thus, mortality due to self-thinning is independent from the genotype. Also, age-dependent mortality is not affected by individual characteristics.

Self-thinning is assumed to be operational during the seedling and sapling stage only, up to a height of 2 m. On a log–log scale, a linear relationship is assumed between the maximum number of individuals and the total plant biomass:  $\log^{10}(N_{\max}) = a \log^{10}(W) + c$  with  $a = -2/3$  and  $c = 2.3$  (e.g. Landsberg and Waring, 1997). If the actual number of individuals exceeds  $N_{\max}$ , the access numbers are randomly

removed until the biomass drops below the abovementioned self-thinning relationship.

We used an empirical mortality function that relates increased mortality to accumulated stress expressed as low diameter growth over the recent history of an individual tree (Wunder et al., 2006). Such empirical mortality functions have been shown to have better performance than theoretical mortality functions (Bigler and Bugmann, 2004). The method developed by Pacala, Kobe and co-workers was used (Kobe and Coates, 1997; Kobe et al., 1995; Pacala et al., 1993, 1996). Their approach is based on a functional relationship between the probability of mortality and the recent growth of saplings,  $m(g)$ , the parameters of which can be directly estimated from field data. They developed a maximum likelihood estimator for the parameters of this relationship, based on: (i) the probability of encountering  $D$  dead saplings in a total population of  $N$  individuals,  $P(D)$ ; (ii) the probability density function of growth rates prior to death; and (iii) the probability density function of growth rates for live individuals. The latter two functions are based on  $m(g)$ , and the probability density function of all growth rates found at the study site,  $h(g)$ , which is assumed to follow a 2-parameter Gamma distribution (Kotz et al., 2000). Pacala, Kobe and co-workers tested several functions for  $m(g)$  and recommended using (Eq. (6)):

$$m_t(g) = 1 - \exp^{-t \exp(-Bg)} \quad (6)$$

because it is flexible in the time interval,  $t$ , and can thus be decomposed to an annual basis that is suitable for inclusion in a forest dynamics simulator. Recent growth was represented by the 5-year average of dbh increment.

To test the approach of Pacala, Kobe and co-workers approach, we assigned scores to 20 dead and 143 living trees in 3 transects of 30 m × 4 m to determine  $P(D)$ , and we measured the diameter increment of 23 recently dead and 27 living individuals to determine  $h(g)$ . The result was:  $P(D) = 0.124 \pm 0.029$ . Fig. 4 shows the distribution of the 5-year diameter increment of recently dead and living trees. The overall distribution of growth rates,  $h(g)$ , fitted the Gamma distribution well, with  $\alpha = 5.529 \pm 0.901$  and  $\beta = 22.87 \pm 4.658$ .

Using the directive FITNONLINEAR of the GENSTAT statistical package resulted in  $B = 3.69 \times 10^{-2} \pm 2.859 \times 10^{-3}$ . Based on the abovementioned parameterization, the estimated mean growth of the recently dead trees was  $0.73 \pm 0.288$  mm/year;

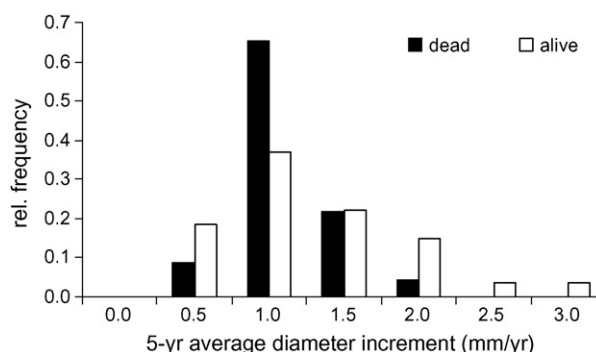


Fig. 4 – Observed distribution of 5-year average diameter increment of dead ( $n = 20$ ) and living ( $n = 143$ ) trees.

the estimated mean growth in the case of survival is  $1.31 \pm 0.507$  mm/year. Testing the model by submitting saplings (>2 m) to different simulated light levels resulted in 100% survival rate after five years of simulated growth at full light; 62% 5-year survival at 6% light; and 0% 5-year survival at 1% light. The average simulated survival duration at 1% light was less than 2 years. These results are consistent with the shade-tolerant behaviour of beech found in the field and in experiments (Bainbridge et al., 1966; Loach, 1970; Lyr et al., 1965; Mitscherlich et al., 1967; Röhrig, 1967). However, despite these differences between dead and living trees and the realistic survival rates, the relationship between growth of beech and mortality is weak for the sites studied. The residual sum of squares,  $SS_{\text{res}}$ , of the null-model is 121.8 ( $B=0$ ;  $m(g) = 1 - 1/e$ ), whereas the  $SS_{\text{res}}$  of the best fitting model is 122.3. Larger samples are needed, particularly of dead trees – though the latter are difficult to find, as most beech forests are subjected to management regimes that remove dead stems. See the Appendix A for how in ForGEM the increment of stem diameter is related to the allocation of net primary production to the stem, based on allometric relationships between tree height and stem volume.

Finally, age-related mortality was described by a linear increase in mortality rate from an arbitrary starting age until the maximum age, such that the integral of mortality over this phase of breakdown of the forest equals unity. As indicated above, a maximum age of 350 years was used, and the decline phase was assumed to start at an age of 200 years (pers. comm. Ed Mountford).

#### 2.4. Forest management

To model the implementation of alternative forest management regimes, we developed a user-defined harvesting algorithm (Arii et al., 2008) in ForGEM. In the terminology of Soderbergh and Ledermann, we used an empirical approach that allows for distance-dependent and distance-independent thinning, as well as for deterministic and stochastic thinnings and harvesting (Soderbergh and Ledermann, 2003). The definition of the management regime includes the formulation of the management objective, the rotation period and the quantification of the regeneration, tending, thinning, and harvest strategies (Matthews, 1999).

The *regeneration* determines the management interventions to promote the establishment of seedlings. The strategy is based on determining the timing of felling based on stem density or basal area; the gap-size distribution in a group selection is used to open the forest canopy. Additionally, the soil may be scarified to improve seedling survival rates and if the seedling density resulting from natural regeneration is below a given threshold, supplementary planting can be applied.

The *tending strategy* determines the management interventions during the sapling phase. Criteria for these interventions include the selection of the species and the average height at which their tending starts; the tending interval; and the density that should be attained after the tending operation.

The *thinning strategy* determines the management interventions concerning canopy trees. This includes criteria to start thinning, based on basal area or tree density threshold; the definition of a future tree (an *F*-tree: a tree selected early

in the rotation based on individual tree quality to produce the next generation of that species and high quality yield); and the selective thinning around the future trees.

The *harvest strategy* determines how many years after the start of the simulation the final harvest takes place.

For this study four management scenarios were evaluated (see also Table 2):

1. *No Management*: The benchmark scenario.
2. *Nature-oriented*: Management objective: transformation from even-aged into an uneven-aged and structurally heterogeneous beech forest, while preserving both large and dead trees for biodiversity.
3. *Conversion*: Conversion of even-aged stands into uneven-aged stands through a group selection system. Management objective: transformation from even-aged beech forest into uneven-aged and structurally heterogeneous beech forest.
4. *Sheltercut*: Management of even-aged stands through regeneration by sheltercut and thinning using an *F*-tree system. Management objective: sustainable production of high quality wood; rotation period 100–140 years.

#### 2.5. Genetic statistics

Summarizing statistics are needed to evaluate the impact of management on the genetic diversity of the simulated populations. ForGEM will calculate many statistics that characterize the genetic make-up of an individual and the genetic diversity of a population. Individual statistics include the genotype of individuals and their spatial distribution (Leonardi and Menozzi, 1996). We used the spatial autocorrelation and permutation test for significance as developed by Smouse and Peakall (1999).

The intra- and inter-population statistics include diversity measures, differentiation measures between populations, and fixation statistics (see Gregorius, 1978; Hanssen, 2000; Hattemer, 1991 for details on these genetic statistics). Here, to evaluate impacts of a management scenario relative to the benchmark scenario (No Management), we present the results on only two of these statistics: *hypothetical gametic multi-locus diversity* and *genetic distance*. Hypothetical gametic multi-locus diversity is a special case of genetic diversity that characterizes the adaptive potential of sexually reproducing populations. It is hypothetical in the sense that the absence of fertility selection is assumed, as well as the independence of the distributions of alleles at different loci (i.e. no linkage). The genetic diversity characterizes the heterogeneity of the distribution of genetic variants in a sample population. In this way, the allelic diversity of the  $k$ th locus or genotype diversity of a sub-population can be measured. The *genetic distance* characterizes the differentiation between two sub-populations by counting the number of genetic variants which the sub-populations do not share. If the genetic distance equals zero, then both populations have the same alleles or genotypes with the same frequency. The genetic distance equals unity if both populations have no alleles or genotypes in common. The genetic distance is a symmetrical statistic and the distance between populations  $X$  and  $Y$  cannot exceed the sum of their distances from a third population.

**Table 2 – Description of management scenarios as applied at the sites (Table 3)**

Scenario:	Sheltercut	Conversion	Nature-oriented
Regeneration strategy	Uniform regeneration (even-aged) under a shelter of beech; regeneration process is initiated at stand age of 100–120 by reducing the stand density to 70 trees ha <sup>-1</sup> (F-trees) ( <i>seeding felling</i> ); soil scarification after seed fall (mast year!); removal of the old stand in two stages, approximately 50% of the stand after 10 to 15 years ( <i>secondary felling</i> ) and the final harvest again 10–15 years later ( <i>final felling</i> ). Additional planting is optional after secondary felling	Group selection in combination with natural regeneration starting at age = 80 years; no fences; if necessary, additional planting; gap-size varies between 500 and 1500 m <sup>2</sup> , exceptionally 2000 m <sup>2</sup> . The first gaps are made at year 80; approximately every 10 years 15% of the area of the old stand is cut. Priority is given to merging old gaps and increasing the gap size in small gaps (up to 1000 m <sup>2</sup> )	As scenario 2. NB: preserve “over-aged” trees
Tending strategy	Favouring tree species other than beech, if present. Tending starts when average height of the regeneration is 5 m and continues until first thinning. Tending is aimed at keeping a maximum of 100 trees other than beech available ha <sup>-1</sup> (if possible, evenly distributed) as potential F-trees	As Management scenario 1	As Management scenario 1
Thinning strategy	Selective thinning in combination with F-tree thinning; first thinning at average height of 14 m (≈40 years), or earlier if the H/D ratio of the 50 trees with the largest dbh per ha exceeds 120; selective thinning (thinning intensity – 80% of the basal area increment); at age of 60, F-tree selection; 80 F-trees ha <sup>-1</sup> evenly distributed; thinning is aimed at keeping the F-trees free from strong competition. Species other than beech (if present) can be selected as F-tree. H/D ratio of F-trees should be <80. Neighbour trees are considered to be too strong competitors for F-trees if: (1) the distance between neighbour tree and F-trees is less than $c_1 + c_2$ dbh (relationship derived from yield tables can be a reference); (2) the neighbour tree is >80% of the height of the F-tree	As Management scenario 1	As Management scenario 1
Harvest strategy	F-trees are harvested in two successive cuts (see regeneration strategy)	F-trees are harvested if dbh >70 cm. The harvest of an F-tree could be the beginning of a gap which (depending on the size) can be extended	As Management scenario 2
Biodiversity strategy			20% of standing volume is lying and standing dead wood, dbh dead trees >30 cm; minimum of 5 “over-aged” trees per ha which will not be cut but will die naturally

F-tree – future tree, selected for final harvest; dbh – diameter at breast height (cm); H/D ratio: height to diameter ratio.

## 2.6. Model analyses

Four genetic traits were considered in the model runs: (1) a neutral trait, (2) budburst day, (3) spiral grain and (4) the potential rate of height growth. The *neutral trait* does not respond to any form of selection, so any trend in this feature indicates the degree of random drift only as a consequence of a small population size. The other traits are susceptible to both drift and selection. *Budburst day* is an important adaptive trait to local climatic conditions that is easily recognizable in the field and on which much information was collected in the project. It is assumed that seedlings and saplings are killed by frost if they flush when the temperature drops below  $-2^{\circ}\text{C}$ . Leaves are susceptible to frost up to 10 days after bud burst. In the model, adult trees are not killed by frost, but all flowers are assumed to be killed if damaging frost occurs during the frost-susceptible 10-day period (in beech, leaves and flowers flush at approximately the same time: Becker, 1981, p. 43). Thus, early flushing trees have a lower probability of producing offspring than later flushing ones. *Spiral grain* is a genetically determined wood quality factor (Teissier du Cros et al., 1980) which has no negative impact on the fitness of the tree. So there is no directional selection other than by management. It is scaled from zero (no spiral grain) to unity (maximal spiral grain) and therefore in the model is expressed on a logit scale. Both during the thinning and harvest of adult trees, in the management model it is assumed that the forest manager first removes the trees with the highest degree of spiral grain. Additionally, future trees are selected if they have the least spiral grain present in the stand. Finally, the *potential height growth rate* ( $\text{cm month}^{-1}$ ) was evaluated as an important adaptive trait on which there is both natural and artificial selection. Note that there is a constraint preventing unlimited selection on increased height growth: as the potential height growth rate increases, the radial stem increment at the same level of carbon gain will be reduced, and thus mortality increases, because the probability of mortality is inversely related to the 5-year average of diameter increment (see Section 2.3 and Appendix A explaining the relationship between height increment, stem volume increment and stem radius increment). The role of artificial selection on height and thus implicitly on potential height growth rate is explained in Section 2.4, and Table 2.

The four traits considered are assumed to have an equal initial narrow-sense heritability of 0.6. Narrow-sense heritability,  $h^2$ , is defined as the ratio of additive genetic variance to total phenotypic (genetic plus environmental) variance in the population (Falconer and Mackay, 1996). The  $h^2$  for budburst was determined within the project, using data from a previously established open-pollinated half-sib trial near Nancy, North-East France. In such a trial, the seeds collected have a known mother tree but an unknown father tree, seedlings are raised from the seeds, and the phenotypic value of the mother and her offspring is compared. Seventy mature beech trees that were at least 50 m apart (this to limit co-ancestry) were selected. Beechnuts were collected from the selected trees in 1996 and seedlings were raised in a nearby nursery, keeping records of their mother trees. In 1997 the one-year-old seedlings and grafted copies of the mother trees were planted in the forest from which the beechnuts had been collected, in 4 replications of plots containing 22 trees each, resulting in 88

seedlings per parent (=family). Only 48 families of the 70 originally harvested and sown remained; 22 families were lost due to lack of germination or high seedling mortality. Budburst was observed on the parent-grafted copies and on the offspring: three times in 2002 (from May 3 to 7) and four times in 2003 (from April 23 to 30), using a standardized scale (Teissier du Cros et al., 1981). This yielded estimates of  $h^2$  for budburst of 0.56 in 2002 and 0.58 in 2003. In the model we therefore used a value of  $h^2$  rounded to 0.6. Of the ecophysiological parameters considered in the trial, only  $V_{\text{cmax}}$ ,  $g_0$  and  $A_n/g_s$  displayed clonal variation. However, because the variance of the estimates was large between years and clones, none of the ecophysiological parameters displayed a significant broad sense heritability. The genetic model of ForGEM was therefore not applied to these ecophysiological parameters.

As the heritabilities of the other selected traits (spiral grain, potential height growth rate, neutral trait) were not determined within the project, we consulted the literature. The  $h^2$  of spiral grain had been determined in a much earlier study by Teissier du Cros and found to be 0.66 (Krahl-Urban, 1953; Teissier du Cros et al., 1980). Our literature search failed to find heritabilities for potential height growth rates for beech. However, recent observations under controlled condition on white spruce indicated a family heritability for potential height growth rate of  $0.717 \pm 0.107$  (Rweyongeza et al., 2004). An  $h^2$  of 0.6 seems therefore a cautious value for the potential height growth rate for beech. For consistency with the estimated values of the  $h^2$  of the other traits, the  $h^2$  for the neutral trait was also set at 0.6. Note that  $h^2$  is not a model parameter but that in the model it is used solely to assign the phenotypic values to the trees of the initial population (see Section 2.1.2). During the simulation,  $h^2$  changes, depending on the selection pressure exerted on a trait by the scenarios.

As no information was available on dominance of the genetic traits considered in this study,  $d$  was set to zero in Eqs. (2) and (3).

### 2.6.1. Sensitivity analysis

A forest stand's genetic diversity in the long term depends on a number of interacting factors and processes. These are: *the initial number of trees*, as this determines the genetic diversity to start with; *a trait's heritability*, as selective responses expressed in changed allele frequencies are low if the heritability is low, and vice versa; *the pollen dispersal distance*, as a strong selection decreasing genetic diversity at a given location can be counteracted by gene flow from areas that are genetically different or under a different mode of selection; and *the management regime*, as forest management is a main driver allowing adaptation to occur on newly established regeneration. We performed a sensitivity analysis to ascertain the importance of these four factors and processes on multilocus diversity. For this analysis, the model was initialized with a generated stand of 5, 10 or 100 trees, and the initial heritability of the four phenotypic traits was set at 0.00, 0.25, 0.50, 0.75 and 1.00. For the pollen dispersal distance the scale parameter (Eq. (4)) was varied such that the expectation of the Weibull distribution was approximately 2, 4, 8, 16, 32 and 64 m. These parameter values change the distance curve from very steep left-skewed to flattish. The shape parameter was fixed at 1.3613 (the average of the two French plots). The sensitivity

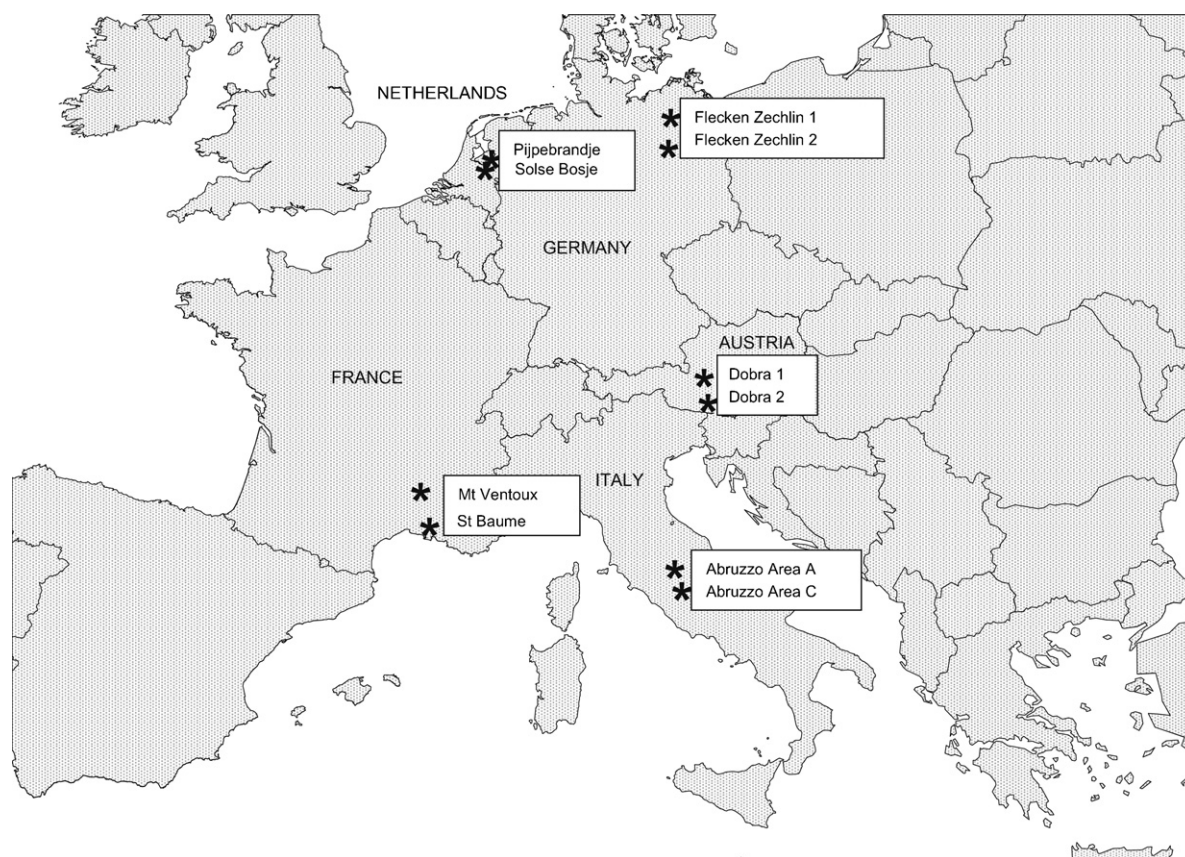


Fig. 5 – Geographical location of the sites.

analysis assumed that no pollen originated from outside the plot. Two management regimes were investigated: No Management and Sheltercut (see Table 2). The genetic diversity parameter analysed was the multilocus diversity at  $t = 300$  year since the start of the simulation. This simulation was reiterated 10 times, to estimate the variance of the genetic diversity per scenario. A new stand was generated for each iteration of a scenario.

The spatial autocorrelation, however, was based on a single run of the scenarios, in which pollen dispersal, management and initial number of trees were varied. Moreover, the genome was stored for a single trait only: the potential height growth rate. This was done because storing the genome of thousands of trees over 4 traits, 10 replicas, and 66 scenarios (30 heritability + 36 pollen dispersal) results in a huge database that is very time-consuming to analyse spatially. The spatial analysis of the pollen dispersal parameters, management regimes and initial number of trees took 2 days on a fast PC, and entailed 100 permutations to assess the confidence interval of the correlation coefficient of 5 m distance classes.

#### 2.6.2. Evaluation of management scenarios

The model was used to evaluate management scenarios at five beech study sites established during the project. Fig. 5 shows the location of the sites in Europe; Table 3 summarizes the site characteristics and the management scenarios applied and presents information on the climate at the sites. In collaboration with local forest managers, one or more forest

management scenarios relevant for the management of beech in their area were defined. At each plot the No Management scenario was analysed. The results of the other management scenarios were pooled over the plots, following the four scenarios indicated.

The effects of the management scenarios on the four traits considered are presented as normalized responses, as they operate at entirely different scales. For example, on most plots the budburst of individual trees varies between the 115th to the 135th day of the year, whereas spiral grain attains values between zero and unity. To make the responses of the traits comparable we subtracted the initial ( $t = 0$ ) population average and divided by the initial standard deviation. Thus, the normalized values present the number of standard deviations the population deviates from its initial situation.

### 3. Results

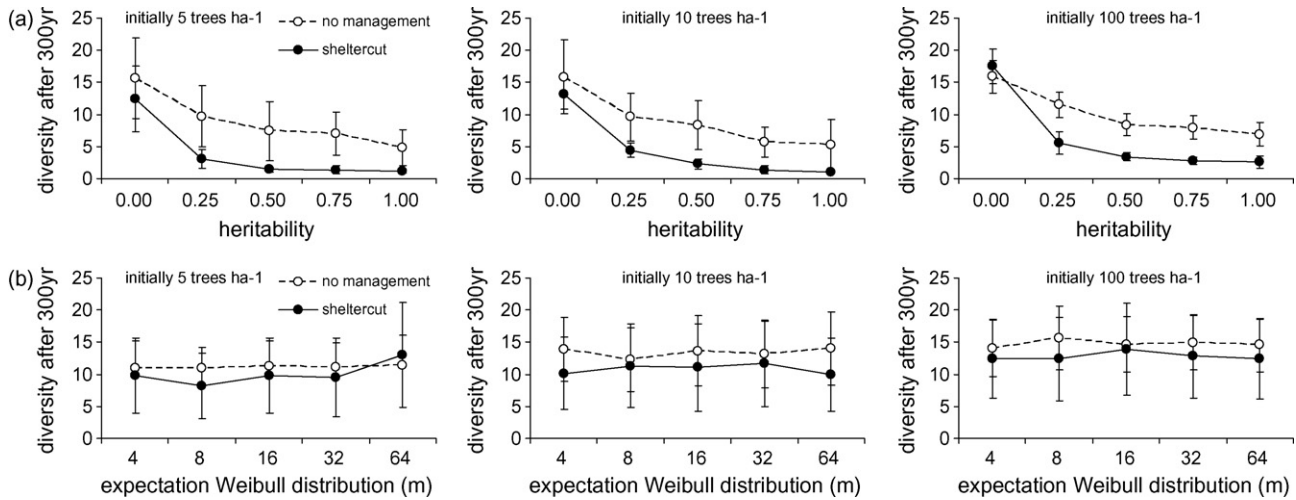
#### 3.1. Sensitivity analysis

The results of the sensitivity analyses are presented in Fig. 6a for the heritability and in Fig. 6b for the pollen dispersal distance. Fig. 6a shows that under the sheltercut regime, after 300 years of simulation the genetic diversity declines with increasing heritability of a functional trait. This inverse relationship is less pronounced for the No Management regime. The pattern appears to be uninfluenced by the initial number of trees.

**Table 3 – Plot characteristics**

Country	Site code/name	Location	Elevation (m, a.s.l.)	Type of stand	Avg T (°C)	Avg ppt (mm year <sup>-1</sup> )	Simulated management scenarios
The Netherlands	NL1 Pijpebrandje	52° 15'N 5° 43'E	50	Semi-natural	9.4	803	No Management Conversion
	NL2 Solse Bosje	52° 14'N 5° 39'E	50	Planted			No Management Conversion
Germany	G1 Flecken-Zechlin	53° 11'N 12° 43'E	85	Semi-natural	8.7	514	No Management Conversion
	G2 Flecken-Zechlin	53° 10'N 12° 44'E	85	Shelter cut			No Management Shelter cut
Austria	A1 Dobra	48° 35'N 15° 23'E	390–550	Natural	6.9	663	No Management Nature-oriented Conversion Shelter cut
	A2 Dobra	48° 35'N 15° 23'E	550–580	Shelter cut			No Management Nature-oriented Conversion Shelter cut
France	F1 Ste Baume	43° 19'N 5° 45'E	750	Natural	10.0	1118	No Management Shelter cut
	F2 Ventoux	44° 10'N 5° 16'E	1450	Colonized	7.7	1457	No Management Nature-oriented
Italy	I1 Area A	42° 30'N 13° 29'E	1270	Semi-natural	10.7	1026	No Management Nature-oriented
	I2 Area C	42° 30'N 13° 28'E	1155	Shelter cut			No Management Nature-oriented

Each plot is approximately 2 ha.

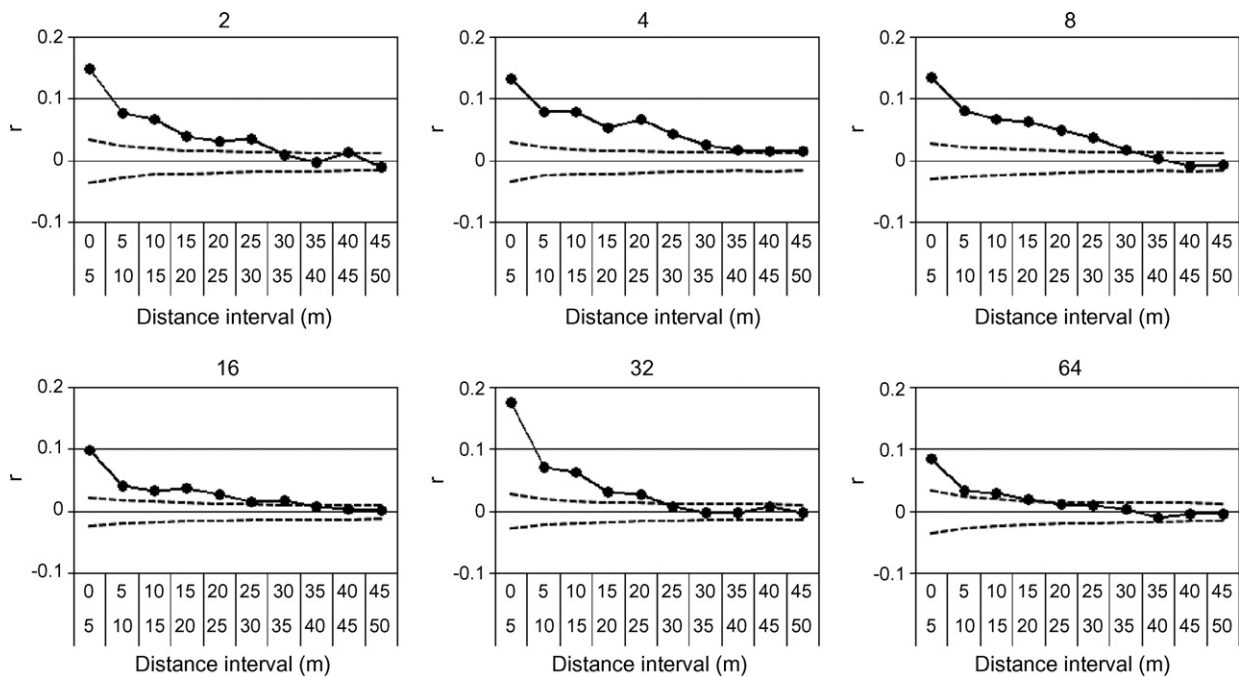


**Fig. 6 – (a) Effect of variation in the scale parameter of the pollen dispersal curve, initial number of trees and management regime on multi-locus diversity after 300 years simulation. (b) Effect of variation in the scale parameter of the pollen dispersal curve (b, Eq. (4)), initial number of trees and management regime on multi-locus diversity after 300 years simulation.**

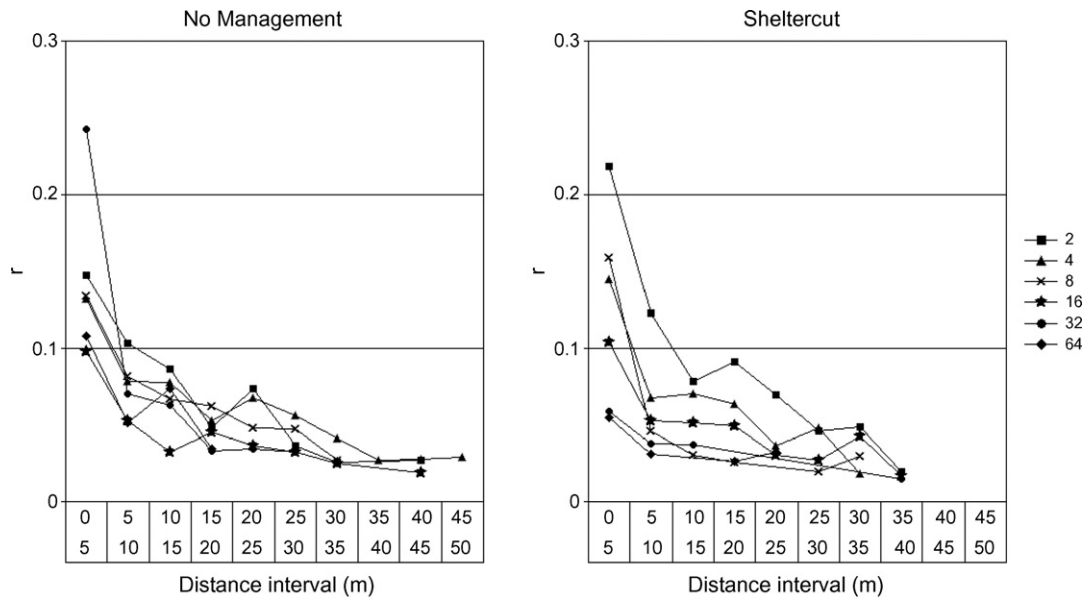
Fig. 6b shows that the overall genetic diversity of the stand is independent of pollen dispersal distance and initial number of trees, and that the No Management regime consistently has a slightly higher diversity compared to the Sheltercut regime.

Although the pollen dispersal distance appears not to affect the genetic diversity at this scale, it does affect the spatial genetic structure, which declines with increasing expectation of the Weibull distribution, that is increasing pollen dispersal distance, even when averaging over the two

management scenarios and the three initial tree number scenarios (Fig. 7). This pattern remains if the management scenarios are discerned, although it is clearer in the Sheltercut scenario than in No Management (Fig. 8). A probable reason for this difference between management regimes is that in the No Management scenarios, after 300 years the forest is just at the beginning of its second generation since the start of the simulation, when there was no spatial structure, whereas for the Sheltercut scenarios approximately three generations



**Fig. 7 – Effect of variation in expectation of the Weibull distribution (2–64 m. Eq. (4)) for pollen dispersal on spatial autocorrelation (r) after 300 years simulation. Values averaged over the scenarios for both initial number of trees (5; 10; 100) and management regime (No Management; Sheltercut). Dashed lines indicate 95% confidence interval within which the correlation coefficient is not significant, based on 100 permutations.**



**Fig. 8 – Effect of variation in expectation of the Weibul distribution (2–64 m. Eq. (4)) for pollen dispersal on spatial autocorrelation ( $r$ ) after 300 years simulation, per management regime. Average values over the scenarios with different initial number of trees (5, 10, 100). Only significant values are presented ( $P < 0.001$ , single-sided test), based on 100 permutations.**

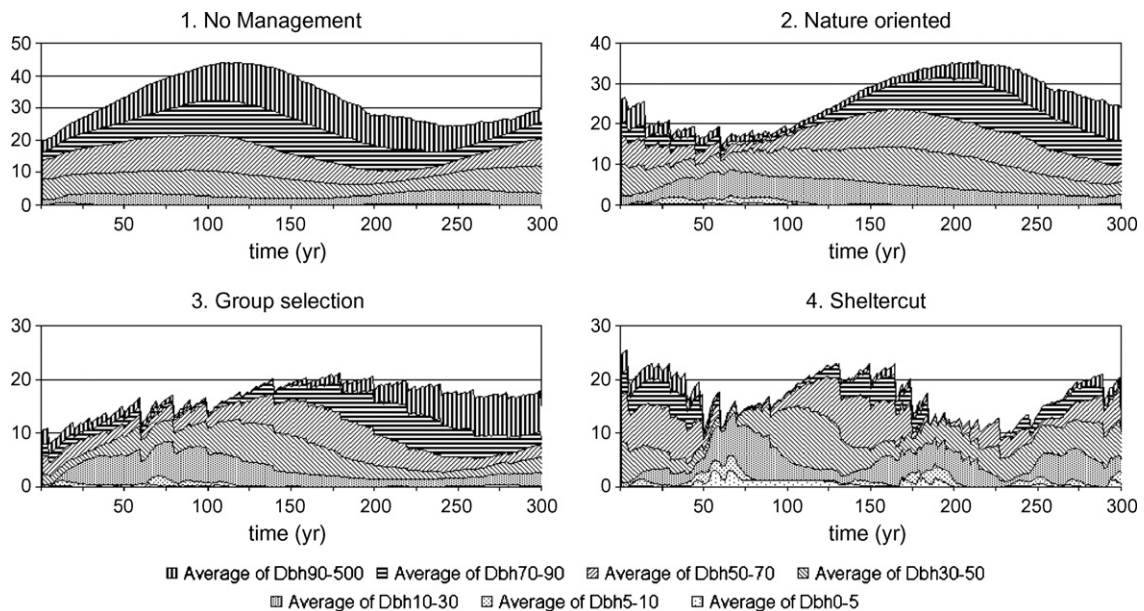
have passed, thus allowing spatial genetic structure to emerge (Fig. 9). Consistent with the results presented in Fig. 6, the initial number of trees did not result in a distinct spatial genetic structure (results not shown).

**3.2. Evaluation of management scenarios**

The effects of the different management regimes on basal area development are presented in Fig. 9. For the No Management regime there is a smooth pattern, in which the big trees (70–90; >90 cm) die from old age approximately 200 years after

the base year of the simulation, at which point the forest is on average 300–350 years old. This mortality of the old trees makes the expansion of young trees (5–10 cm) possible, so that a new forest generation emerges.

In the Nature-oriented management regime, there is first a 100-year conversion period in which group selection is applied in order to appreciably enrich the structure of the plot. Following that conversion period, a future-tree system is applied, in which management focuses on the thinning around F-trees. Fig. 9 shows that during the first 100 years of this regime there is a repeated management impact during which the selected



**Fig. 9 – Basal area of beech per dbh class for the different management regimes applied in the plots.**

groups are removed. Thereafter, the development of the basal area over time follows a similar pattern to that in the No Management regime. The large trees remaining in this regime are those that have been spared in order to enhance forest biodiversity.

The impact of the Conversion regime on the basal area development (Fig. 9) is that the group selection operates throughout the entire simulation. Thus, there are more opportunities for regeneration in the Conversion regime than in the Nature-oriented regime.

Finally, the Sheltercut management regime is quite different from the other management regimes. The general pattern is that the cycle of regeneration – build-up of the forest – harvest is greatly shortened (120 versus 250–300 years) and thus the dynamics of the basal area are much larger compared to the other management regimes (Fig. 9). It should be noted that pooling model output over the plots at which the Sheltercut regime is applied is somewhat confusing, as the moment of the subsequent regeneration cuts may differ by up to several decades, depending on the site. Thus, the series of harvests do not follow the same pattern in the same stand.

When the phenotypic responses of the genetic traits are normalized to the management regimes (Fig. 10) it is clear that of the traits evaluated, the feature with the highest selection response is the potential rate of height growth. The rate of response is the lowest in the No Management regime; the rates in the other three management regimes are similar in magnitude. Spiral grain is counter-selected in the three managed regimes but not in the No Management regime. Budburst day appears to advance slightly in the Sheltercut regime only. Finally, the neutral trait shows virtually no response to any of the management regimes applied.

Selection on a trait reduces its genetic diversity in the population, as unfavourable or undesirable alleles are removed from the population. The effect of management regimes on genetic diversity is presented in Fig. 11. Note that the simulated genetic diversity can only remain constant or decline

during the simulation, as the model does not simulate new mutations and the introduction of pollen and seeds from outside the area are assumed to have the same genetic make-up as the initial population. Fig. 11 shows that the two traits most selected, potential height growth rate and spiral grain, suffer the greatest loss in genetic diversity over time. The No Management regime shows the least loss in genetic diversity compared to the other management regimes: the loss is only in the potential height growth rate. Furthermore, the results in Fig. 11 indicate that the degree of loss of genetic diversity for spiral grain and potential height growth rate is of the same magnitude in all three managed regimes.

Populations can diverge in genetic composition due to selection or to random drift, even if the mean and variance of an adaptive genetic trait do not differ between two populations. The same mean and variance of a quantitative traits can be attained by different sets of alleles or by different frequencies of shared alleles. This degree of genetic diversion between populations is expressed in the genetic distance. The results for the genetic distances of the three management regimes to the No Management regime to the same plot are presented in Fig. 12. For all traits, there is an increase in time for the genetic distance between the managed regime and the No Management situation. For the two most selected traits, spiral grain and potential height growth rate, this deviance of genetic composition is the largest. The genetic distance in potential height growth rate appears to flatten after about 100 years since the start of the simulation. This might be the consequence of the loss in genetic diversity that occurs both in the No Management regime and the three managed regimes (see Fig. 11).

#### 4. Discussion

In this study we have attempted to link ecophysiological and genetic knowledge on trees in order to assess a species' adaptive potential to environmental change. Both ecophysiology

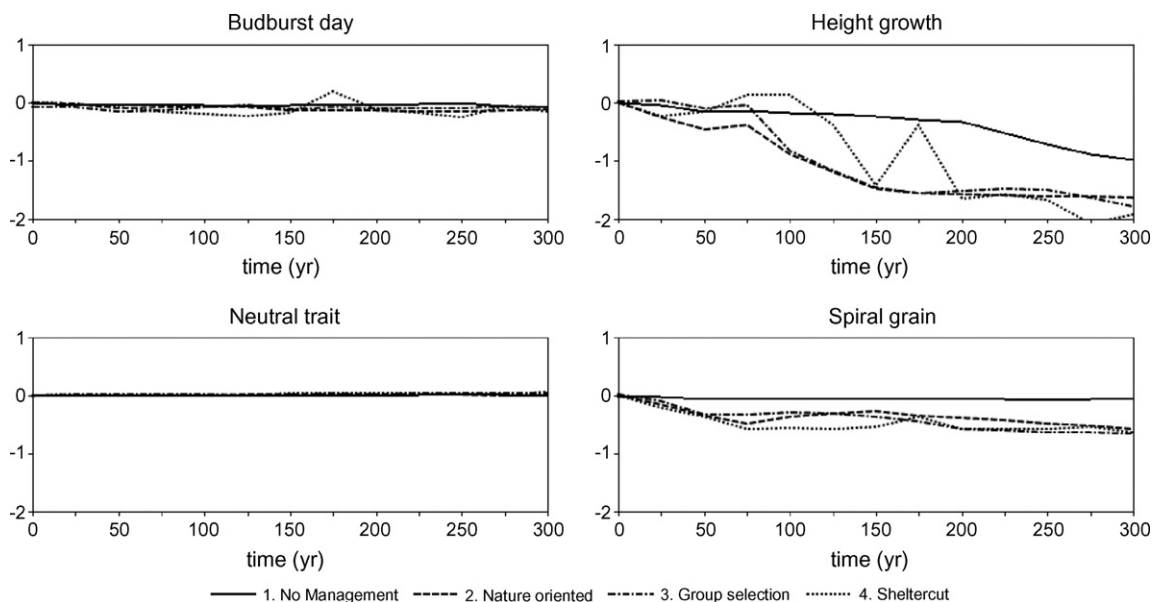
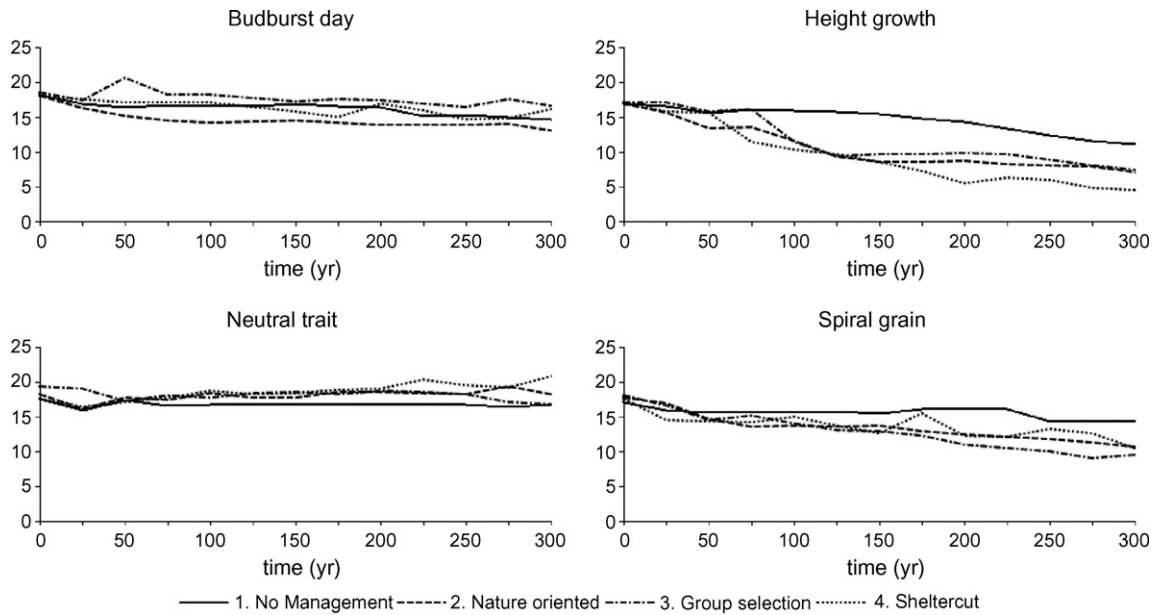


Fig. 10 – Normalized response of the four phenotypic traits for the different management regimes applied to the plots, relative to the phenotypic values at t=0. Y-axes in standard deviations.

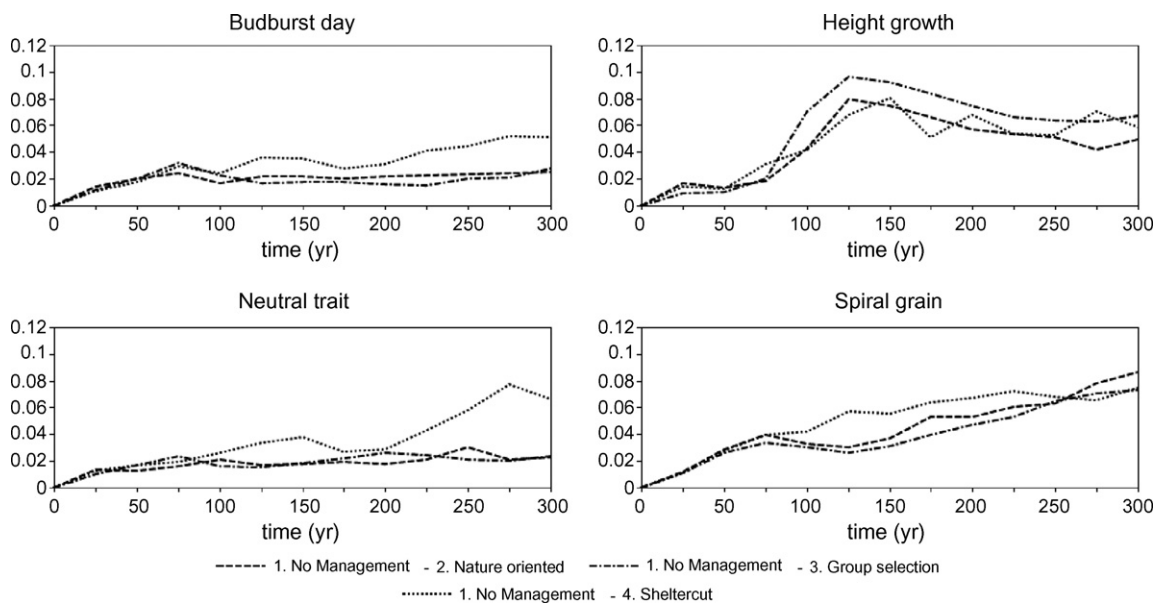


**Fig. 11 – Genetic multi-locus diversity of the four phenotypic traits for the different management regimes applied to the plots.**

and genetics entail large bodies of data and furthermore, in both disciplines insight is essential in order to determine whether the concern that trees are unable to adapt to climate change (Davis and Kabinski, 1992; Davis and Shaw, 2001) is justified or whether we can be confident that they can adapt (Hamrick, 2004). Our approach entailed integrating extensive field and laboratory studies with the modelling of the life cycle of individual trees. Much emphasis was put on the determination of reliable parameter values under field conditions for mechanistic descriptions of the genetic, eco-

logical and ecophysiological key-processes driving whole-tree functioning.

Beech was selected as model species, because the intensive management of beech forests in the past may have reduced its genetic diversity in Europe. This is because the management regime widely applied to regenerate beech, the sheltercut regime (Matthews, 1999; Teissier du Cros et al., 1981), results in only a few dozen trees per hectare remaining after thinning to contribute to the next generation (Matthews, 1999), hence possibly reducing the genetic diversity in subsequent gener-



**Fig. 12 – Genetic distance between “No Management” and the other management regimes of four phenotypic traits for the different management regimes applied to the plots. The same randomization was applied to the stochastic factors in the model in all simulations.**

ations. Despite that, we are aware that high levels of genetic diversity are typically found within beech stands ((Buiteveld et al., 2007; Konnert, 1995; Leonardi and Menozzi, 1995; Sander et al., 2000, 2001).

The adaptive potential of species to environmental change cannot be measured directly on individuals. It can only be assessed by experimentally changing the species' environment, as is done in provenance trials (König, 2005) or by means of process-based simulation. In this study we opted for the latter approach. Using the ForGEM model we evaluated the role of a number of interacting factors and processes on the adaptive response of a beech stands, defined as the rate of change of genetic composition in the population for adaptive traits, including:

- (i) *gene flow* from areas that are genetically different or under a different mode of selection. This can counteract the local loss of genetic diversity by selection or drift (Hamrick, 2004). In beech, pollen dispersal is an especially important mechanism for bringing new genetic variants into a population, because gene flow through seed dispersal is limited (more than 90% of the seeds are dispersed within 30 m of the adult tree: Janßen, 2000; Watt, 1923, 1925). At European scale, however, incidental long-distance dispersal may play an important role (Petit et al., 1997). In our study we found that a substantial proportion of the pollen originated from outside the stands (44.6% and 71.8% for the Sainte-Baume and Ventoux sites, respectively: Vendramin et al., in preparation). The results of the sensitivity analyses show that for stands of about 2 ha, the genetic diversity is independent of pollen dispersal distance and management regime (Fig. 6b). Nevertheless, a family structure is likely to build up. Based on microsatellites and isozymes and using distance classes of 10 m (Povillon, 2002; Teissier du Cros, 2006), we found a significant positive spatial autocorrelation up to 20 m in Ventoux and up to 30 m in Sainte-Baume. The correlation coefficients for the 0–10 m distance class were about 0.06 for the unmanaged stand, Sainte-Baume, and 0.12 for the managed stand, Ventoux. This corresponds to an effective pollen dispersal of up to 32 m, assuming no import of pollen (Figs. 7 and 8).
- (ii) *heritability* of phenotypic traits. Selective responses are low, therefore the loss of genetic diversity is high if the heritability is low, and vice versa. The results of the sensitivity analysis show that genetic diversity does indeed decline with the increasing heritability of a functional trait under the Sheltercut regime (Fig. 6a). In that regime, selection on emerging recruitment is allowed to operate about every 120 years, thereby removing poorly adapted saplings and thus reducing genetic diversity. Such a trend is much less apparent in the No Management regime because the selection moments are determined by the longevity of beech: about 250 years.
- (iii) *selection pressure on a trait*. A given environmental change will not affect all traits similarly. In this study we evaluated four types of traits: a neutral trait, that is not selected for or against and that changes solely in response to genetic drift; budburst day, which changes solely in response to natural selection; spiral grain, which changes solely in response to artificial selection; and potential height growth rate, which changes in response to both natural and artificial selection. Based on the simulated responses we can conclude that the selection pressure imposed on the selected traits increases in this sequence (Fig. 10), and genetic diversity decreases proportionally to the selection pressure (Fig. 11). Of the adaptive traits, budburst day shows a small response, whereas potential height growth rate shows a strong response even though the heritabilities were set the same (see Section 2.6). The small response of budburst day is attributable to a trade-off between two factors. Firstly, with advancing budburst, the probability of late frost damage increases. In the model it is assumed that in the juvenile stage frost below  $-2^{\circ}\text{C}$  kills seedlings and saplings with emerged leaves. As this is a rather low level of frost tolerance (Larcher, 1975; Sakai and Larcher, 1987), it results in a strong selection against advancing budburst. However, modelling experiments with  $-5^{\circ}\text{C}$  as the threshold for frost that is fatal for seedlings yielded very similar results. The second factor is that the gains in light interception and hence in growth and survival achieved by advancing budburst day are small: at most, a few percent of the light available during the growing season (Kramer, 1995). Thus, the balancing selection by these forces on budburst day is asymmetrical, resulting in a small genetic gain and a small loss of genetic diversity. The strong response of potential height growth rate in all management scenarios (Fig. 11) indicates that it is an important adaptive trait affecting competition and mortality from the seedling stage onwards. In the model, the response is determined by balancing the selection of increased growth due to increased light interception against the increased mortality if diameter increment lags behind height increment (see Section 2.3). Here, diameter increment depends on the allocation of net primary production to the stem (see the Appendix A).
- (iv) *recruitment interval*. The rate at which trees adapt to environmental changes depends not so much on the longevity of individual trees, but rather on successful recruitment events during a tree's lifetime (Hamrick, 2004). In most forests the recruitment interval is determined by the management practice rather than through natural forest dynamics. Our modelling analysis on the effects of forest management at 10 study sites showed that the loss in genetic diversity is directly related to management activity, which increases in the sequence from No Management, Nature-oriented, Conversion, to Sheltercut (Fig. 11). The results indicate that selection mainly operates during recruitment events. Hence, the duration of the interval between the recruitment events is an important factor determining the adaptive ability of the forest. In the No Management regime, a significant regeneration occurs only approximately every 200–250 years when the forest breaks down due to the age-related mortality of large adult trees. In the Sheltercut regime, the regeneration interval is every 120–140 years – less under more intensive management in which seedlings are cut. However, compared with the No Management regime, fewer adult trees contribute to the next generation.
- (v) *initial genetic diversity*. The sensitivity analysis indicates a small but not significant trend in increasing genetic

diversity after 300 years of simulation with increasing initial number of trees (Fig. 6). Furthermore, the variance in genetic diversity diminishes with increasing initial number of trees for the No Management regime (most clearly presented in Fig. 6a for the No Management regime). Thus under the conditions set up for these simulation runs, the initial size of the population and thereby initial genetic variation does not have an important impact on the genetic diversity 300 years later in the simulation.

The initial genetic diversity depends on how we determined initial allele frequencies (Section 2.1.1) and allelic effects (Section 2.1.2). Alternative options for attaining initial allele frequencies include: (i) starting with a random initial distribution and running the model without selection until an equilibrium is attained, and evaluating the effect of selection from that point onwards in the simulation. This was the approach taken by Savolainen et al. (2004), who found that it takes about 1000 years for Scots pine to discard excessive mortality in the first generations, (ii) starting with homozygotes for all loci and allowing new alleles in the population by mutation until a stable frequency distribution is attained. This was the approach Le Corre and Kremer (2003) took: it takes about 100,000 generations. These options are not available for the ForGEM model, as the model's run time is up to several minutes per simulated year. However, our approach is supported by Hill et al. (2008), who conclude that theory for neutral alleles can serve as reference point for complex traits, as the effects on fitness of genes at many loci influencing most quantitative traits are likely to be small.

An alternative option for determining allelic effects is to assume a normal distribution of effects, but the feasibility of this option is contentious (Lynch and Welsh, 1998). Savolainen et al. (2004) tested the consequence of different number of loci and normally distributed allelic effects and found no differences for the adaptive response of bud set and frost hardiness of Scots pine to climatic warming and cooling along a latitudinal gradient in Finland.

Overall, we found that the highest level of genetic variation is maintained in a forest if no forest management is applied. However, if environmental conditions change rapidly – for example, due to climate change – this regime is the least suitable, as the window of time in which adaptation operates most effectively is small, i.e. the recruitment stage. Windows of opportunity for adaptation occur more frequently in the Conversion and the Sheltercut regimes than in the No Management and Nature-oriented regimes, because the rotation is shorter. Consequently, the selective response of adaptive traits increases, as the regeneration phase is the only moment at which new genotypes enter the population – an event that is essential for an effective response to a changing climate. It is important to note that the simulations described in this study were performed on relatively small plots (1–2 ha) and that no account was taken of natural disturbances such as storms or forest fires. Ignoring such natural disturbances may have resulted in the adaptive response being underestimated, especially for the No Management situation, as these events will periodically create gaps in which regeneration will take place and thus selection on functional traits can occur. Selection, however, occurs at the cost of a reduction in genetic diversity

and the loss of potentially adaptive alleles (Namkoong and Koshy, 1997). The magnitude of the response depends, firstly, on how important the trait is for a tree's competitiveness and survival and, secondly, on how often selective events occur. With regard to the magnitude of adaptive response, models are required to assess the consequences of a wide range of climate scenarios. With regard to selective events, in most forests in the temperate and boreal zone it is the forest manager who determines regeneration interval through the length of the rotation period.

To conclude the results of this simulation study suggest that beech has high potential to adapt to environmental change if recruitment intervals are short relative to its longevity and many mother trees contribute to the next generation. The rate of adaptation depends on the amount of additive genetic variance (Falconer and Mackay, 1996) and will be less if dominance or pleiotropy is important for a particular trait. Due to lack of information we ignored these genetic interactions. However, Hill et al. (2008) concluded that both data and theory point to mainly additive genetic variance for complex traits, because allele frequencies are skewed towards extreme values. Thus, even though we had to ignore both dominance and pleiotropy in our study, we have probably not overestimated the rate of adaptive response.

To our knowledge, no other forest model currently exists that mechanistically links selection intensity on an adaptive trait with a quantitative genetic system. Existing models of forest genetics either require the user to define a phenotypic optimum and selection intensity on a trait (Austerlitz et al., 2000; Le Corre and Kremer, 2003; Savolainen et al., 2004), or focus on neutral traits, which do not experience selection, and use simple tree growth functions and competition indices for the effects of management on genetic structure (Degen and Scholz, 1998a,b; Phillips et al., 2004; Degen et al., 2006). We could not find any literature reference to an ecophysiological model on forest dynamics that includes a genetic submodel.

Our results have the following two implications for future projections of climate change assessments. Firstly, that it cannot be taken for granted that parameter values do not change during the period of a few tree generations. This is the case, for example, for the traits (shown in brackets) related to thresholds for species area modelling, such as the duration of the growing season (bud burst, timing of growth cessation), frost hardiness and drought tolerance (minimum leaf or soil water potential), which are important thresholds in both statistical and dynamic species area models (Bolliger et al., 2000; Austin, 2002, 2007). Such thresholds may change even during a rapid climate change; hence, the projected drastic consequences of climate change on the geographical distribution of tree species may need to be adjusted. Secondly, forest management should be taken into account. Modelling studies have shown more often that forest management affects genetic diversity and spatial genetic structure (Degen et al., 2006) suggesting that management affects the rate of adaptive response of trees to environmental change. Indeed, Savolainen et al. (2004) conclude that the reason for Scots pine adapting too slowly to match the rate of climate change is because of its low mortality. They assumed a constant mortality, expressed as the one over the longevity of the tree per year ( $1/150 \text{ year}^{-1}$ ). Our results indicate that simulating a more realistic rate of mor-

tality brought about by forest management will increase the adaptive response.

Overall, we conclude that a model that integrates genetic and ecological knowledge as presented here is a new and useful tool for assessing the interactions of environmental change and management on forest ecosystems.

## Acknowledgements

This project was co-funded by the EU (DynaBeech and EvolTree), the Dutch Ministry of Agriculture, Nature and Food Quality, and national funding agencies for the different partners involved. Among the many technicians who contributed to the collection of data in the field and performed the experiments were Alain Nassau, Bert van Os, Fabrice Bonne, Frédéric Jean, Geurt van Roekel, Jan Bovenschen, Jean Thévenet, Marie-Claire Boerwinkel, Pierre Legroux, René Mazet, Thomas Thalmayer, Triye Huijbers, Wim van Orden. Their input is gratefully acknowledged. Joy Burrough advised on the English of the draft paper.

## Appendix A

### A.1. Increment in height, diameter and volume

We used the Chapman–Richard function for height increment (Eq. (A1)). This function is a generalization of the Von Bertalanffy's growth model (Pienaar and Turnbull, 1973), which is based on fundamental allometric relationships between both anabolic and catabolic rates and the volume of an organism.

$$H = H_{\max}(1 - e^{C7t})^{C8} \quad (\text{A1})$$

$$\Rightarrow \frac{\partial H}{\partial t} = C7C8H \left( \frac{e^{C7t}}{1 - e^{C7t}} \right) \quad (\text{A2})$$

where height  $H$  is in m,  $t$  the tree age in years, and the values of  $C7$ : 0.01766; and  $C8$ : 1.33300 (Jansen et al., 1996).

For diameter increment we also used an allometric approach, as is used in virtually all forest growth models (Landsberg and Waring, 1997; Zianis et al., 2005). To derive diameter increment, we expressed volume as power function of both diameter and height (Eq. (A3)) (Peichl and Arain, 2007, their Eq. (3)):

$$V = D^{C1}H^{C2}e^{C3} \quad (\text{A3})$$

$$\Rightarrow \frac{\partial D}{\partial t} = \frac{D}{C1} \times \left\{ \frac{1}{V} \frac{\partial V}{\partial t} - \frac{C1}{H} \frac{\partial H}{\partial t} \right\} \quad (\text{A4})$$

where, volume  $V$  is in  $\text{dm}^3$  and diameter  $D$  in cm.  $e$  is the exponent of the natural logarithm. The values of  $C1$ : 1.86116 and  $C2$ : 1.04313 were obtained from Jansen et al., 1996, their Table 2, p 14).

The volume increment of the stem is then based on net primary production, NPP, the allocation to the sapwood,  $f_{\text{sw}}$ , and wood density,  $\rho_{\text{sw}}$  ( $579 \text{ kg m}^{-3}$ ) (Duursma et al., 2007, their

Eq. (2)):

$$\frac{\partial V}{\partial t} = \frac{f_{\text{sw}}}{\rho_{\text{sw}}} \times \text{NPP} \quad (\text{A5})$$

### A.2. Allocation

For the allocation of photosynthates among tree components we assume that the internal development of partitioning ratios depends on tree dimensions only (Grote, 1998). This assumption can be derived from pipe model theory and the principle of a functional balance between tree components (Mäkelä and Hari, 1986; Valentine, 1988). We derived the partitioning ratios of the weights of foliage ( $W_{\text{fl}}$ ), branch ( $W_{\text{br}}$ ), stem ( $W_{\text{st}}$ ) and roots ( $W_{\text{rt}}$ ) with total shoot biomass ( $W_{\text{sh}}$ ) using biomass data obtained from the literature. On a log–log scale, a polynomial function was fitted, relating the ratio of a plant component with the stem to the total shoot biomass:

$$\ln \left( \frac{W_{\text{fl}}}{W_{\text{st}}} \right) = C1 + C2 \ln(W_{\text{sh}}) + C3 \ln(W_{\text{sh}})^2 + C4 \ln(W_{\text{sh}})^3 \quad (\text{A6})$$

$$\ln \left( \frac{W_{\text{br}}}{W_{\text{st}}} \right) = C5 + C6 \ln(W_{\text{sh}}) + C7 \ln(W_{\text{sh}})^2 + C8 \ln(W_{\text{sh}})^3 \quad (\text{A7})$$

$$\Rightarrow \frac{W_{\text{st}}}{W_{\text{sh}}} = \frac{1}{1 + \ln(W_{\text{fl}}/W_{\text{st}}) + \ln(W_{\text{br}}/W_{\text{st}})} \quad (\text{A8})$$

Thus, we obtained:  $C1$ :  $-1.2040$ ;  $C2$ :  $-0.3404$ ;  $C3$ :  $-0.0232$ ;  $C4$ :  $0.0000$ ;  $C5$ :  $-0.5272$ ;  $C6$ :  $-0.1256$ ;  $C7$ :  $-0.0315$ ; and  $C8$ :  $0.0034$ . A constant fraction of 0.35 of the NPP is allocated to the roots. The fractions of NPP allocated to the other plant components are derived such that the tree strives for partitioning ratios as indicated by Eqs. (A6)–(A8).

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