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Title:

Mixture enhances productivity in a two-species forest: evidence from a modelling approach

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Abstract:

The effect of mixture on productivity has been widely studied for applications related to agriculture but results in forestry are scarce due to the difficulty of conducting experiments. Using a modelling approach, we analysed the effect of mixture on the productivity of forest stands composed of sessile oak and Scots pine. To determine whether mixture had a positive effect on productivity and if there was an optimum mixing proportion, we used an aggregation technique involving a mean-field approximation to analyse a distance-dependent individual-based model. We conducted a local sensitivity analysis to identify the factors which influenced the results the most. Our model made it possible to predict the species proportion where productivity peaks. This indicates that transgressive over-yielding can occur in these stands and suggests that the two species are complementary. For the studied growth period, mixture does have a positive effect on the productivity of oak-pine stands. Depending on the plot, the optimum species proportion ranges from 38% to 74% of oak and the gain in productivity compared to the current mixture is 2.2% on average. The optimum mixing proportion mainly depends on parameters concerning intra-specific oak competition and yet, intra-specific competition higher than inter-specific competition was not sufficient to ensure over-yielding in these stands. Our work also shows how results obtained for individual tree growth may provide information on the productivity of the whole stand. This approach could help us to better understand the link between productivity, stand characteristics and species growth parameters in mixed forests.

Keywords: Mixed forest - Niche complementarity - Overyielding - Individual-based model - Model Aggregation

1 Introduction

It is currently admitted that plant diversity and ecosystem functioning are interrelated, and that greater plant diversity can lead to greater productivity (Hector et al. 1999; Loreau et al. 2002; Hooper et al. 2005; Thebault and Loreau 2006). One of the mechanisms that has been put forward to explain the greater productivity at higher diversity is the "niche complementarity" (Loreau et al. 2001) that may result from inter-specific differences in resource requirements and uses or from positive interactions between species.

The principle of complementarity has been widely studied for herbaceous species in applications related to agriculture (de Wit 1960; Vandermeer 1989). However, although mixed forests are being promoted more and more, results on tree species complementarity are quite scarce particularly because of the difficulty of conducting long-term experiments (Kelty and Larson 1992; Piotto 2008; Pretzsch 2009). A classical way to study the effect of mixing proportion on productivity is to establish "replacement series" experiments (Jolliffe 2000). In these experiments, rather well-adapted to the study of two-species mixtures, the proportions of species vary while the overall density is maintained constant. This type of experiment can also be applied in forestry (Luis and Monteiro 1998; Garber and Maguire 2004) but they are more difficult to conduct because, for most tree species, results are available only after a period of many years. The use of large-scale forest inventory data (Vila et al. 2007; del Rio and Sterba 2009) and studies based on modeling (Pretzsch and Schutze 2009) are two alternative approaches to fill in the gaps in knowledge of the mixed-forest productivity.

Here we focused on the case of mixed forests with two species which are widely distributed throughout Europe (MCPFE et al. 2007). For a two-species mixed stand, we can use replacement diagrams to define and represent three main types of productivity response to the mixing proportion (Figure 1).

Figure 1 here

The effect of mixing proportion on productivity clearly depends on the species that are combined (Kelty 2006). For a given pair of species, the first issue is to know what kind of response occurs (positive, negative or no influence on productivity). The second challenge is to determine whether the productivity of the mixture can exceed the productivity of the most productive species in a pure stand - in other words, whether productivity peaks when an optimum mixing proportion is reached (right side of Figure 1). This phenomenon is called "transgressive over-yielding" and reflects mechanisms of facilitation or a strong complementarity between species for resource use (Hector et al. 2002; Hector 2006; Schmid et al. 2008).

The answers to these questions should be strongly linked to the relationship between intra-specific and inter-specific competition (Harper 1977). For example, based on the Lokta-Volterra theoretical model of inter-specific competition, Loreau (2004) showed that inter-specific competition for both species must be lower than intra-specific competition for transgressive over-yielding to occur. Intra- and inter-specific competition can be quantified empirically using local competition indices in a distance-dependent individual-based model (Biging and Dobbertin 1992; Canham et al. 2004; Uriarte et al. 2004; Stadt et al. 2007). The challenge is to link the results obtained at the individual tree level with the results that concern the whole stand. That is what we did in the present study.

In this article, we investigate whether the mixture of two tree species can improve the productivity of the stand. To address this question we used a distance-dependent individual-based model developed in a previous study for mixed stands of sessile oak (*Quercus petraea* L.) and Scots pine (*Pinus sylvestris* L.) (Perot et al. 2010). We used an aggregation technique to analyse this model and to answer the following questions: 1) Does mixture have a positive effect on stand productivity? 2) What is the optimum mixing proportion in terms of productivity? 3) What are the factors that most influence the results for questions 1) and 2)?

2 Materials and methods

2.1 Growth data from mixed oak-pine stands

We collected the growth data in mixed oak-pine stands from the Orléans state forest. This forest is located in north-central France (47°51'N, 2°25'E) and covers 35 000 ha. Mixed oak-pine stands occupy an important position in French forests for three main reasons: they cover a relatively large area (Morneau et al. 2008); they have a heritage value for the public; and they are well-adapted to the sandy, water-logged soils common to central France.

Between 2006 and 2007, we established 9 plots (ranging in size from 0.5 to 1 ha) to study the growth of mixed oak-pine stands (Table 1). The nine plots included other broadleaved species (mainly *Carpinus betulus* L., *Betula pendula* R. and *Sorbus torminalis* L.) but they are in very small proportion (4% of the total basal area on average) and were not considered in the present study. These plots had been fully mapped in a previous in-depth study on horizontal spatial structure (Ngo Bieng et al. 2006). In each plot, we sampled 20 trees per species to take growth measurements. Sampled trees were cored twice to the pith in perpendicular directions at a height of 1.3 m. Cores were scanned and ring widths were measured to the nearest 0.01 mm (see Perot et al. 2010 for details). Because some trees were impossible to core and some cores were not usable, the growth analyses were based on a final total of 154 oaks and 179 pines. The mean oak age per plot ranged from 50 to 90 years, and that of pines from 50 to 120 years. In a plot, all trees of a species had approximately the same age indicating a single cohort for pines and a single cohort for oaks. Pines occupied the upper stratum of the stand while oaks occupied both the upper stratum and the understory, excepted in plot D78 where oaks were more abundant in the understory. Oak and pine populations had mainly experienced artificial thinnings but some natural perturbations may also have occured (*i.e.* storms, fires, and pest damages). Detailed information on past disturbances (natural or artificial) was not available in our plots (location and size of suppressed trees) so we chose the period from 2000 to 2005 to study growth because there were no human or natural disturbances during that time.

Table 1 here

2.2 The distance-dependent individual-based model

A distance-dependent individual-based model was developed in a previous work from the growth data presented above (Perot et al. 2010). We briefly recall model equations and refer to Perot et al. (2010) for details on model fitting and equation selection. Subscripts 1 and 2 are used in equations and in the following sections to indicate oak and pine species respectively. The distance-dependent individual-based model uses tree size and local competition indices calculated inside a circle centred on a focal tree to predict the radial increment of its trunk. Different competition indices and circle radii were compared for their ability to explain individual growth (see Perot et al. 2010 for details on competition index selection). A radius of 10 meters around the focal tree (neighbourhood radius) best explained growth variability. A plot effect was introduced to take into account the possible effects of factors acting at stand level such as site effect, total density or stage of development (young or old stand). The model was fitted separately for oaks and pines using the ordinary least squares method to obtain an individual growth equation for each species:

for oaks,

$$\Delta r_{i,k,1} = \alpha_{k,1} + \beta_{k,1} girth_{i,k,1} + \lambda_{1,1} N_{i,1,1} + \lambda_{1,2} N_{i,1,2} + \varepsilon_{i,k,1} \tag{1}$$

for pines,

$$\Delta r_{i,k,2} = \alpha_2 + \beta_{k,2} girth_{i,k,2} + \lambda_{2,2} G_{i,2,2} + \varepsilon_{i,k,2} \tag{2}$$

where $\Delta r_{i,k}$ is the radial increment (mm) over a six-year interval (2000-2005) of the *i*th tree in plot *k*, *girth* is the girth (cm) in 1999 and ε is the residual error. α_k and β_k are model parameters for plot *k*. For pine, results showed no plot effect on α which we simply denote α_2 (see Table 2). $\lambda_{j,1}$ and $\lambda_{j,2}$ are the coefficients associated with the competition indices calculated for oak and pine, respectively. $N_{i,1,1}$ is the number of oaks in the neighbourhood (*i.e.* at a distance less than 10 meters) of a focal tree *i* belonging to the oak species. $N_{i,1,2}$ is the number of pines in the neighbourhood of a focal tree *i* belonging to the oak species. $G_{i,2,2}$ is the basal area of pines in the neighbourhood of a focal tree *i* belonging to the pine species. For simplicity, $N_{i,1,1}$, $N_{i,1,2}$ and $G_{i,2,2}$ will be called the local density of oaks, the local density of pines and the local basal area of pines, respectively. These competition indices account for both intra- and inter-specific competition. The coefficient $\lambda_{2,1}$ associated with the competition index calculated for the neighbouring oaks of a pine focal tree was not significantly different from zero and does not appear in equation 2. This result suggests that the growth of pine is weakly influenced by oak. One may also notice that $\lambda_{i,i} < \lambda_{i,j}$, which means that intra-specific competition is higher than inter-specific for both species.

Table 2 here

2.3 Aggregating the individual-based model to obtain analytical results at stand level

The distance-dependent individual-based model mimics the dynamics of each tree, but for predictions at the stand level, simulations are necessary. To obtain analytical results at the stand level, we aggregated the individual model. This operation was hindered somewhat by the presence of local competition indices that introduce a spatial dependence; we therefore proceeded in two steps. We first applied the mean field approximation to obtain a distance-independent individual-based model (Levin and Pacala 1997; Dieckmann et al. 2000; Picard and Franc 2001). Secondly, we aggregated this distance-independent model into a model predicting the basal area increment of the whole stand. We call this aggregated model “the stand model”.

The mean field approximation is particularly well suited to simplify the spatial dependence in distance-dependent individual-based models. To apply this method to the model presented above (equations 1 and 2), we considered that the spatial pattern of trees was a point process realization. The mean field approximation assumes that all trees are affected in the same way by their neighbourhood. We can then replace the specific expression of a competition index for a given spatial pattern by its expected value across all possible outcomes of the point process. To calculate this expected value, we assumed that the point process is ergodic, which implies that the mean across several realizations equals the spatial average over one realization (Cressie 1993; Illian et al. 2008). Under this assumption, we replaced the average of a competition index by its spatial average calculated from all the trees in the stand. We thus obtained equations 3 and 4 which correspond to a distance-independent individual-based model:

$$\Delta r_{i,k,1} = \alpha_{k,1} + \beta_{k,1} girth_{i,k,1} + \lambda_{1,1} \left\langle N_{i,1,1} \right\rangle + \lambda_{1,2} \left\langle N_{i,1,2} \right\rangle \tag{3}$$

$$\Delta r_{i,k,2} = \alpha_2 + \beta_{k,2} girth_{i,k,2} + \lambda_{2,2} \left\langle G_{2,2} \right\rangle \tag{4}$$

where $\left\langle N_{1,1} \right\rangle$ and $\left\langle N_{1,2} \right\rangle$ are the spatial averages of the local density of oaks and pines for an oak focal tree, and $\left\langle G_{2,2} \right\rangle$ is the spatial average of the local basal area of pines for a pine focal tree. Under appropriate assumptions on the point process (homogenous and isotropic), the spatial averages of these indices can be related to Ripley's *K* function (Ripley 1977) and to the inter-type *K* function (Lotwick and Silverman 1982). In this way, we can link the growth to the spatial structure of the stand. Let us call $K_{1,2}$ the inter-type function between species 1 and 2. If 1 = 2, $K_{1,1}$ is known to be the Ripley's function for species 1. If d_2 is the density of species 2, $d_2\, K_{1,2}(r)$ is the expectation of the number of trees of species 2 found at a distance less than or equal to *r* from a randomly chosen tree of species 1. These functions are often used to test the null hypothesis of complete spatial randomness. For oak, we directly obtain the following relationships:

$$\left\langle N_{1,1}\right\rangle = \frac{N_1}{S}K_{1,1}(10)$$

$$\left\langle N_{1,2}\right\rangle = \frac{N_2}{S}K_{1,2}(10)$$

where N_1 and N_2 are the total number of oaks and the total number of pines in the stand, S is the plot area, $K_{1,1}(10)$ is the value of the Ripley's function at ten meters for the oak population, and $K_{1,2}(10)$ is the value of the inter-type function at ten meters for oak and pine populations. To simplify, we will call these variables $K_{1,1}$ and $K_{1,2}$ in the following sections. Equation 3 can now be written as follows:

$$\Delta r_{i,k,1} = \alpha_{k,1} + \beta_{k,1} girth_{i,k,1} + \lambda_{1,1}\frac{N_1}{S}K_{1,1} + \lambda_{1,2}\frac{N_2}{S}K_{1,2} \tag{5}$$

In the case of pine, we have to calculate the spatial average of the local basal area which implies taking into account the correlation between the individual basal area and the location of the trees. To simplify, we assumed that the individual basal area of a tree was independent of its location on the plot. We then calculated the average local basal area around a pine tree by multiplying the average individual basal area of a pine ($\overline{g}_2$) by the average local density of pines ($\left\langle N_{2,2}\right\rangle$). The average individual basal area of a pine is the ratio between the total basal area of pines in the stand and the total number of pines. The spatial average of the local basal area can thus be written as follows:

$$\left\langle G_{2,2}\right\rangle = \overline{g}_2\left\langle N_{2,2}\right\rangle = \frac{G_2}{N_2}\frac{N_2}{S}K_{2,2}(10) = \frac{G_2}{S}K_{2,2}(10)$$

where $K_{2,2}(10)$ is the value of the Ripley's function at ten meters for the pine population, called $K_{2,2}$ in the following sections. Equation 4 can now be written as follows:

$$\Delta r_{i,k,2} = \alpha_2 + \beta_{k,2} girth_{i,k,2} + \lambda_{2,2}\frac{G_2}{S}K_{2,2} \tag{6}$$

Equations 5 and 6 represent a distance-independent individual-based model resulting from the mean field approximation of equations 1 and 2. However, this model includes some spatial information on the populations through the Ripley functions at ten meters and the inter-type function at ten meters. These functions were calculated for the 9 plots from the observed spatial pattern of the trees (Table 3).

Table 3 here

We then proceeded to the second step and aggregated the individual-based model into a stand model. As all variables now characterize a plot, we can drop the k index without any risk of confusion. The principle of the aggregation is to sum the individual dynamics defined by equations 5 and 6. We chose basal area increment, denoted ΔG, to account for stand productivity. We did not choose volume increment, because volume requires data on tree height that were not available in our study. Next, we showed (see Appendix) that the stand model can be written as follows:

$$\begin{cases} \Delta G = \Delta G_1 + \Delta G_2 \\ \Delta G_1 = A(\gamma_1) N_1 + B(\gamma_1, \beta_1) N_1 \bar{r}_1 + C(\beta_1) G_1 \\ \Delta G_2 = A(\gamma_2) N_2 + B(\gamma_2, \beta_2) N_2 \bar{r}_2 + C(\beta_2) G_2 \end{cases} \tag{7}$$

where $\bar{r}_j$ is the mean tree radius for species *j*, functions *A*, *B* and *C* are defined by:

$$\begin{cases} A(\mu) = \pi\mu^2 \\ B(\mu, \nu) = 2\pi\mu(1 + 2\pi\nu) \\ C(\mu) = 4\pi\mu(1 + \pi\mu) \end{cases}$$

and:

$$\begin{cases} \gamma_1 = \alpha_1 + \lambda_{1,1} \dfrac{N_1}{S} K_{1,1} + \lambda_{1,2} \dfrac{N_2}{S} K_{1,2} \\ \gamma_2 = \alpha_2 + \lambda_{2,2} \dfrac{G_2}{S} K_{2,2} \end{cases}$$

Here, ΔG corresponds to the basal area increment of all trees alive in 2005. For this population of trees, no mortality or recruitment occurred during the study period 2000-2005. Thus, the growth process was sufficient to define the productivity of the population over the 6-year interval.

To check for consistency, we compared the stand model to the individual-based model. We simulated the stand basal area increment over the 2000-2005 period for the 9 plots using both models, starting from the same initial state. We then calculated the mean absolute difference between the predictions of the two models for each species as follows:

$$E_s = \frac{1}{9}\sum_{k=1}^{9}\left|\Delta G_{k,s,IBM} - \Delta G_{k,s,SM}\right|$$

where E_s is the mean absolute difference between the two models for species *s*, $\Delta G_{k,s,IBM}$ is the stand basal area increment of species *s* predicted by the individual-based model for plot *k* and $\Delta G_{k,s,SM}$ is the stand basal area increment of species *s* predicted by the stand model for plot *k*. We also used a Wilcoxon signed rank test on $\Delta G_{k,s}$ to see if there was a significant difference between the two models.

2.4 Introducing the mixing proportion into the stand model

To determine the proportion of each species in a mixed stand, we must define a reference variable that quantifies its abundance in the stand. For example, one can choose the number of stems, but in this case, the small individuals of a species and the large ones of another species would have the same weight and this is generally not acceptable in forest ecosystems. To avoid such problems, it is preferable to choose variables that are related to the volume or biomass of populations (Pretzsch 2005). In this study, we used basal area which takes into account both the number and size of individuals. For a forest composed of two tree species, the proportion of a species *j* is defined as the ratio between the basal area of the species and the total basal area: $x_j = G_j / G$. In addition, we introduced the quadratic mean radius $\bar{r}_{G,j}$ so as to link the density of a species *j* to its basal area: $G_j = N_j \pi \bar{r}_{G,j}^2$. We chose the proportion of oak (x_1) to define the mixing proportion of the stand, noted *x*. The proportion of pine then is 1 – *x*.

With these new variables included, the stand model has 6 stand state variables: the total basal area *G*, the mixing proportion for oak *x*, the quadratic mean radius for oaks $\bar{r}_{G,1}$, the quadratic mean radius for pines $\bar{r}_{G,2}$, the mean radius for oaks $\bar{r}_1$, and the mean radius for pines $\bar{r}_2$. State variables are the minimum set of variables that are required to know the state of a forest stand. Every point (G, x, $\bar{r}_{G,1}$, $\bar{r}_{G,2}$, $\bar{r}_1$, $\bar{r}_2$) in $\mathbb{R}^{+6}$ potentially defines a forest stand. The mean radius can be seen as the first moment of the diameter distribution, whereas the quadratic mean radius corresponds to the non-centred second moment of the diameter distribution. For most statistical distributions, the variance is related to the mean, which means that $\bar{r}_{G,j}$ and $\bar{r}_j$ will generally be related. On the contrary, no relationship is a priori expected between x and the other 5 state variables. To check this, we tested the 9 plots to see if there was a significant correlation between x and any of the other state variables: all Pearson's correlation coefficients turned out to be non significantly different from zero.

The six state variables are complemented by 4 secondary variables that follow from them directly: the basal area of oaks $G_1 = xG$, the basal area of pines $G_2 = (1 - x)G$, the number of oaks $N_1 = xG/\left(\pi\bar{r}_{G,1}^2\right)$, and the number of pines $N_2 = (1-x)G/\left(\pi\bar{r}_{G,2}^2\right)$. The model also includes 10 parameters (α_1, α_2, β_1, β_2, $\lambda_{1,1}$, $\lambda_{1,2}$, $\lambda_{2,2}$, $K_{1,1}$, $K_{2,2}$, $K_{1,2}$) and 1 constant (the plot area S).

We introduced the mixing proportion x into equation 7 and we used the basal area and the quadratic mean radius to replace the density. The stand model can then be written as a function of the mixing proportion, the total basal area and the average dendrometric characteristics of each species:

$$\begin{cases} \Delta G = \Delta G_1 + \Delta G_2 \\ \Delta G_1 = A(\gamma_1)\dfrac{Gx}{\pi\bar{r}_{G,1}^2} + B(\gamma_1,\beta_1)\bar{r}_1\dfrac{Gx}{\pi\bar{r}_{G,1}^2} + C(\beta_1)Gx \\ \Delta G_2 = A(\gamma_2)\dfrac{G(1-x)}{\pi\bar{r}_{G,2}^2} + B(\gamma_2,\beta_2)\bar{r}_2\dfrac{G(1-x)}{\pi\bar{r}_{G,2}^2} + C(\beta_2)G(1-x) \end{cases} \tag{8}$$

with:

$$\begin{cases} \gamma_1 = \alpha_1 + \lambda_{1,1}\dfrac{1}{S}K_{1,1}\dfrac{Gx}{\pi\bar{r}_{G,1}^2} + \lambda_{1,2}\dfrac{1}{S}K_{1,2}\dfrac{G(1-x)}{\pi\bar{r}_{G,2}^2} \\ \gamma_2 = \alpha_2 + \lambda_{2,2}\dfrac{1}{S}K_{2,2}G(1-x) \end{cases}$$

Since a forest stand is characterized by 6 state variables, 6 dynamics equations are required to define its change over time. Equation 8 is equivalent to 2 independent equations for G and x. The dynamics equations for $\bar{r}_{G,1}$ and $\bar{r}_{G,2}$ follow from $\Delta N_1 = 0$ and $\Delta N_2 = 0$, since, as previously mentioned, the number of trees remained constant (no mortality, no recruitment). The dynamics equations for $\bar{r}_1$ and $\bar{r}_2$ can also be derived from the individual-based distance-dependent model (see Appendix) but we did not use them in the calculations described below.

2.5 "Transgressive over-yielding" and optimum mixing proportion

Every value of the vector (G, x, $\bar{r}_{G,1}$, $\bar{r}_{G,2}$, $\bar{r}_1$, $\bar{r}_2$) defines a state of the forest stand. To determine the mixing proportion x that maximizes productivity, we considered (G, $\bar{r}_{G,1}$, $\bar{r}_{G,2}$, $\bar{r}_1$, $\bar{r}_2$) to be known variables, with x the only unknown state variable. This is equivalent to searching for the optimum in a subspace of the space of states. This approach is similar to "replacement series" experiments that compare pure and mixed stands while keeping the total density constant (Jolliffe 2000). With this condition, the basal area increment ΔG defined by equation 8 can be considered as a function of the mixing proportion x. By definition, there is "transgressive over-yielding" if x is such that $\Delta G(x) > \max\{\Delta G(0), \Delta G(1)\}$; in other words, $\Delta G(x)$ has a maximum value between 0 and 1. The optimum mixing proportion x_{max} then becomes the value of x where the derivative of $\Delta G(x)$ with respect to x is null, while ensuring that the derivative is positive for $x < x_{max}$ and negative for $x > x_{max}$.

A local sensitivity analysis was conducted to assess how x_{max} varied when one of the parameters was changed. As the different parameters were not expressed in the same units, we computed elasticities rather than sensitivities. The elasticity of x_{max} to that of the parameter p is defined as $\partial \ln(x_{max}) / \partial \ln(p)$.

3 Results

3.1 Difference between the individual-based model and the stand model

The predictions of the individual-based model and those of the stand model were very similar (Figure 2). The mean absolute difference between the two models for the 2000-2005 period was 0.051 m²/ha for oak (E_1) and 0.023 m²/ha for pine (E_2). This corresponds to a difference of 2.4% and 1.7% respectively between the two models.

Figure 2 here

However, the Wilcoxon signed rank test showed significant differences between the two models (for oak $V = 44$ and p-value = 0.00781; for pine $V = 45$ and p-value = 0.00390). The stand model gives values slightly lower than the individual model. However, despite these results, we considered that the difference between the two models was small enough to allow us to use the aggregated model to study the effect of mixing proportions on stand productivity.

3.2 Optimum mixing proportion formula

Since $\Delta G'(x) = \Delta G_1'(x) + \Delta G_2'(x)$, we calculated the derivative of the oak growth function and the derivative of the pine growth function separately. Let us pose $m_{1,s1} = 2(1+2\pi\beta_{s1})$, $m_{2,s1} = 4\pi\beta_{s1}(1+\pi\beta_{s1})$, $n_{1,s1} = \lambda_{s1,s1} K_{s1,s1}/S$, and $n_{2,s1} = \lambda_{s1,s2} K_{s1,s2}/S$, where $s1$ is one of the species and $s2$ the other one. For oaks we then obtained $\Delta G_1'(x) = a_1 x^2 + b_1 x + c_1$ with:

$$a_1 = \frac{3G^3}{\pi^2 \bar{r}_{G,1}^2}\left(\frac{n_{1,1}}{\bar{r}_{G,1}^2} - \frac{n_{2,1}}{\bar{r}_{G,2}^2}\right)^2$$

$$b_1 = \frac{2G^2}{\pi \bar{r}_{G,1}^2}\left(\frac{n_{1,1}}{\bar{r}_{G,1}^2} - \frac{n_{2,1}}{\bar{r}_{G,2}^2}\right)\left(2\alpha_1 + \frac{2Gn_{2,1}}{\pi \bar{r}_{G,2}^2} + \bar{r}_1 m_{1,1}\right)$$

$$c_1 = \frac{G}{\bar{r}_{G,1}^2}\left(\alpha_1 + \frac{Gn_{2,1}}{\pi \bar{r}_{G,2}^2}\right)\left(\alpha_1 + \frac{Gn_{2,1}}{\pi \bar{r}_{G,2}^2} + \bar{r}_1 m_{1,1}\right) + Gm_{2,1}$$

And for pines we obtained $\Delta G_2'(x) = a_2 x^2 + b_2 x + c_2$ with:

$$a_2 = -\frac{3{n_{1,2}}^2 G^3}{\bar{r}_{G,2}^2}$$

$$b_2 = \frac{2G^2 n_{1,2}}{\bar{r}_{G,2}^2}\left(2\alpha_2 + 3Gn_{1,2} + \bar{r}_2 m_{1,2}\right)$$

$$c_2 = -\frac{G}{\bar{r}_{G,2}^2}\left[\left(\alpha_2 + Gn_{1,2}\right)^2 + 2Gn_{1,2}\left(\alpha_2 + Gn_{1,2} + \bar{r}_2 m_{1,2}\right) + \bar{r}_2 m_{1,2}\alpha_2\right] - Gm_{2,2}$$

We can show (see Appendix) that the mixing proportion x_{max} corresponding to a maximum for the function $\Delta G(x)$ is the solution given by:

$$x_{max} = \frac{-b - \sqrt{b^2 - 4ac}}{2a} \qquad (9)$$

with $a = a_1 + a_2$, $b = b_1 + b_2$ and $c = c_1 + c_2$.

Thanks to model aggregation, we obtained an explicit expression for the optimum mixing proportion (x_{max}) as a function of the parameters of the stand model, the average dendrometric characteristics of each species, the total basal area and the spatial characteristics of the stand.

3.3 Mixing effect on stand productivity

For each plot, a mixing proportion between 0 and 1 was found that maximized the stand basal area increment. This mixing proportion varied between 38% and 74% depending on the plot (Figure 3).

Figure 3 here

The difference between the optimum mixing proportion (x_{max}) and the mixing proportion actually observed in the plots (x_{plot}) varied from 0 to 34% (Table 4). The productivity gain between these two proportions over the 6-year period was relatively low: 2.2% on average with a maximum of 9% (Table 4).

Table 4 here

Although the elasticities of x_{max} to the parameters of the model varied from one plot to another, a similar pattern was found across plots (Figure 4). The optimum mixing proportion x_{max} was the most sensitive to the oak parameters, then to the pine parameters, then to the inter-specific parameters. The parameters to which x_{max} was the most sensitive on average were $K_{1,1}$ and $\lambda_{1,1}$. For $K_{1,1}$ the elasticity is negative, meaning that an increase in $K_{1,1}$ brings a decrease in x_{max}. For $\lambda_{1,1}$ the elasticity is also negative but, as $\lambda_{1,1}$ is negative, it means that an increase in $\lambda_{1,1}$ brings an increase in x_{max}. The parameter to which x_{max} was the least sensitive on average was $K_{1,2}$, with a positive or negative sign that varied depending on the focal plot. From a quantitative point of view, a 1% increase in $K_{1,1}$ (or a 1% decrease in $\lambda_{1,1}$) led to a decrease in x_{max} of between 1 and 1.2% while a 1% increase in $K_{1,2}$ led to a variation in x_{max} of between 0 and 0.2% depending on the plots.

The parameter $K_{1,1}$ indicates the degree of aggregation of oaks. When $K_{1,1}$ increases the oaks are more aggregated and this leads to an increase in intra-specific competition. $\lambda_{1,1}$ is the parameter that directly indicates the intensity of the intra-specific competition of oak because it is associated to the competition index calculated on oak competitors. Since $\lambda_{1,1}$ is negative, if this parameter decreases, it means that the intensity of the intra-specific competition increases. We can therefore conclude that the optimum mixing proportion depends mainly on the characteristics of the oak population and more particularly on parameters involved in the intra-specific competition of oak ($K_{1,1}$ and $\lambda_{1,1}$).

4 Discussion

4.1 Complementarity between species

Our results suggest a positive effect of mixture on the productivity of oak-pine stands (Figure 3). This result is consistent with those of Brown (1992) established for young oak-pine stands in an experimental design. Unlike Brown's study (1992), we showed that, for some mixing proportions, stand productivity reached a maximum; this indicates a situation of "transgressive overyielding" (Figure 3). The gain between optimum productivity and current productivity of the plots ranged from 0 to 9%. Our individual model was developed for mixing proportions varying between 28% and 59%. Within this range, we can have confidence in the stand model predictions. However, outside this range, and particularly for extreme mixing proportions, the behaviour of the stand model is not guaranteed and may give unrealistic predictions (see for example, plot D20 on Figure 3). The results obtained here assume that the relationships fitted on mixed stands can be extrapolated to pure stands.

The effect of mixture on productivity is based on two main assumptions: "niche complementarity" and "sampling effects" (Tilman et al. 2001). As we worked with only two species and a variable mixing proportion, the "niche complementarity" hypothesis is more likely to explain our findings. We studied a conifer-broadleaf forest with species having very contrasting traits for light interception. Consequently, the complementarity of the two species for the use of light is a strong hypothesis to explain a productivity increase in our mixed stands (Ishii et al. 2004; Ishii and Asano 2010). Common oak is able to grow in the different strata of the stand in contrast to Scots pine because oak is a more shade tolerant species than Scots pine (Niinemets and Valladares 2006). Moreover, in our model there was a non-significant influence of oaks on pines (equation 2) probably because the pines had a greater girth than oaks on average (Table 1). These two arguments may explain why a pure stand of pine could be less productive than a pine stand where oaks were able to colonize the lower strata. We also know that the light interception by the pine foliage is lower than the light interception by the oak foliage (Balandier et al. 2006; Sonohat et al. 2004). This may help to explain that in our oak model, the inter-specific competition was lower than the intra-specific competition (equation 1) which contributes to a higher productivity in mixtures than in pure stands of oak. The two species involved have different light requirements but also different root distribution patterns (Brown 1992). The complementarity in nutrient and water use could also contribute to a higher productivity in the mixture. The positive effect of mixture on stand productivity that we found could thus be explained by spatial segregations in the aerial and underground compartments. Our results concern the basal area productivity which does not include differences in wood density of both species (Pretzsch 2005). To go further in the study of the species complementarity, it would be interesting to estimate the effect of mixture on biomass productivity. Further research is also necessary to identify the ecological mechanisms that can explain the complementarity between these two species.

4.2 Over-yielding in mixed forests: a dynamic state

It is important to note that our models were developed from growth data corresponding to a given time period (2000-2005). It is likely that the parameters of these models change with time. For example, growth in juvenile Scots pine can be much faster than that of sessile oak (Brown 1992) and it is possible that the ratio between intra- and inter-specific competition changes over time for these species. This could explain why a situation of transgressive over-yielding could occur in mature stands and not in young stands. The impact of the temporal dimension on our results can also be seen through the optimum mixing proportion formula. Indeed, we calculated the optimum mixing proportion in the subspace of the state space defined by known values for (G, $\bar{r}_{G,1}$, $\bar{r}_{G,2}$, $\bar{r}_1$, $\bar{r}_2$). This means that x_{max} can be considered as a function of the state variables: $x_{max}(G, \overline{r}_{G,1}, \overline{r}_{G,2}, \overline{r}_1, \overline{r}_2)$. As all these quantities, including the mixing proportion itself, change with time, a pending question is whether

$$x(t) = x_{\max}\left(G(t), \overline{r}_{G,1}(t), \overline{r}_{G,2}(t), \overline{r}_1(t), \overline{r}_2(t)\right) \tag{10}$$

at a given time ensures that

$$x(t+\Delta t) = x_{\max}\left(G(t+\Delta t), \overline{r}_{G,1}(t+\Delta t), \overline{r}_{G,2}(t+\Delta t), \overline{r}_1(t+\Delta t), \overline{r}_2(t+\Delta t)\right)$$

at the subsequent time. There is actually no reason that this should be the case. This brings up two questions: (1) Are there any initial values for $(G, \overline{r}_{G,1}, \overline{r}_{G,2}, \overline{r}_1, \overline{r}_2)$ such that equation 10 would be verified at all times? (2) What type of silviculture - that is, an artificial modification of N_1 and N_2 - would make it possible to verify equation 10 starting from arbitrary values for $(G, \overline{r}_{G,1}, \overline{r}_{G,2}, \overline{r}_1, \overline{r}_2)$? The effect of mixture on stand productivity could be different for other periods not only quantitatively but also qualitatively. Including the time factor in our results will be the subject of future work.

4.3 Factors that influence the optimum mixing proportion

By simplifying and aggregating a distance-dependent individual-based model, we were able to express the productivity of the stand as a function of the stand characteristics, the model parameters and the mixing proportion (equation 8). Moreover, we have shown that it is possible to explicitly express the optimum mixing proportion as a function of the mean dendrometric characteristics of each species and the parameters of the individual model (equation 9). After applying the stand model to the 9 plots in the study, our results showed that there is some variability in the optimum value (Table 4). The optimum mixing proportion (x_{max}) ranged from 38% to 74% of oak depending on the plot. We can explain this variability among plots by studying the qualitative impact of the different factors on the optimum provided by the local sensitivity analysis (Figure 4). For example the elasticity of x_{max} to the spatial structure of oak (index $K_{1,1}$) was negative. It means that the less aggregated the oaks are, the fewer oaks there are within distance of 10 m on average, and consequently the more their growth is promoted. The optimum then moves towards a stand where oak is more represented. The same explanation can be used for pines and for the other factors. Finally, any change in a factor that promotes the productivity of a species moves the optimum towards a mixing proportion where the species is more represented. The local sensitivity analysis gave us also quantitative results. For a given set of dendrometric characteristics, the optimum mixing proportion was more sensitive to parameters involving oak - especially those concerning its intra-specific competition ($K_{1,1}$ et $\lambda_{1,1}$) - than to those involving pine (Figure 4). When the oak intra-specific competition increases, the optimum moves towards a stand with a higher proportion of pine. In other words, the more intra-specific competition decreases (decrease in $K_{1,1}$ or increase in $\lambda_{1,1}$), the more the optimum for productivity moves towards a pure stand of oak. Our plots had different spatial patterns (Table 3) because they probably experienced different ecological processes and different human actions (Ngo Bieng et al. 2006). As it has been recently shown for coexistence issues (see Hart and Marshall 2009), this spatial structure has a direct impact on the optimum mixing proportion by changing intra and inter-specific competition.

The mathematical equations that we developed can also inform us about the conditions leading to a situation of over-yielding. For oak, the term $\left(\lambda_{1,1}K_{1,1}/\bar{r}_{G,1}^2 - \lambda_{1,2}K_{1,2}/\bar{r}_{G,2}^2\right)$ is a multiplicative factor for parameters a_1 and b_1 of the derivative of $\Delta G_1(x)$. Therefore, if $\lambda_{1,1}K_{1,1}/\bar{r}_{G,1}^2 = \lambda_{1,2}K_{1,2}/\bar{r}_{G,2}^2$ the relationship between oak productivity and the mixing proportion is a straight line which means that there would be no effect of mixture on oak productivity. In the special case where we have the same average size for both sub-populations ($\bar{r}_{G,1} = \bar{r}_{G,2}$), a random distribution of oaks and no spatial interaction between oak and pine ($K_{1,1} = K_{1,2} = \pi 10^2$), this condition corresponds to equality between intra-specific competition and inter-specific competition ($\lambda_{1,1} = \lambda_{1,2}$). The same result would have been achieved for pine if the parameter $\lambda_{2,1}$ had been different from zero when the individual model was fitted (section 2.2). This finding is consistent with a known theoretical result: for two species *A* and *B* growing in a mixture, if the effect of *A* on *B* is the same as that of *B* on *B* and if the effect of *B* on *A* is the same as that of *A* on *A*, then the productivity of a species in a mixture is the product of its proportion by its productivity in a pure stand (Harper 1977). In this case, the relationships between the productivity of species and the mixing proportion are straight lines (left side of Figure 1). However, our results also show that spatial structure and average size of sub-populations play a role in the conditions leading to over-yielding. This complements the results obtained from the Lokta-Volterra theoretical model of inter-specific competition (Loreau 2004). This means that, in the case of our two-species mixed forest, the condition "intra-specific competition greater than inter-specific competition" is not sufficient to ensure over-yielding.

5 Conclusion

Our results show that mixture has a positive effect on the productivity of oak-pine stands and that transgressive over-yielding can occur in these stands. These findings indicate good complementarity between these two species. Our modelling-based approach allowed us to express the optimum mixing proportion as a function of stand characteristics and parameters from a distance-dependent individual-based model. We showed that, for a given set of dendrometric characteristics, the optimum mixing proportion depends mainly on parameters involving the oak species, and especially those concerning its intra-specific competition. However, the mathematical equation for the optimum mixing proportion indicated that an intra-specific competition higher than inter-specific competition was not a sufficient condition to ensure over-yielding. We also showed how to use results obtained at the individual level to obtain results on the behaviour of the whole system. As part of the issue on productivity in mixed forests, this kind of approach can help us to better understand the link between productivity, stand characteristics and growth parameters of species.

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Tables

Table 1. Dendrometric characteristics of the plots. S = plot area; $\overline{r}_{G,1}$ = quadratic mean radius for oak; $\overline{r}_{G,2}$ = quadratic mean radius for pine; $\overline{r}_1$ = mean radius for oak; $\overline{r}_2$ = mean radius for pine; (sd) = standart deviation; N_1 = number of oaks per hectare; N_2 = number of pines per hectare; G_1 = oak basal area per hectare; G_2 = pine basal area per hectare.

Plot	S **(ha)**	$\overline{r}_{G,1}$ **(cm)**	$\overline{r}_{G,2}$ **(cm)**	$\overline{r}_1$ **(sd) (cm)**	$\overline{r}_2$ **(sd) (cm)**	N_1 **(trees.ha^{-1})**	N_2 **(trees.ha^{-1})**	G_1 **(m².ha^{-1})**	G_2 **(m².ha^{-1})**
D02	0.951	11.1	17.7	10.0 (4.9)	17.3 (3.5)	354.3	96.7	13.8	9.5
D108	0.800	8.5	16.9	8.0 (3.0)	16.7 (2.6)	353.8	231.3	8.1	20.8
D20	1.015	8.1	16.2	7.5 (3.0)	15.9 (3.1)	481.7	162.5	9.9	13.4
D27	0.625	8.2	17.7	7.3 (3.6)	17.3 (3.8)	396.8	128.0	8.3	12.6
D42	0.500	8.2	12.5	7.7 (2.8)	12.0 (3.5)	472.0	280.0	9.8	13.6
D49	0.994	8.7	15.2	8.0 (3.5)	14.8 (3.1)	493.0	237.4	11.8	17.2
D534	0.500	8.2	18.1	7.6 (3.0)	17.9 (3.1)	488.0	170.0	10.2	17.6
D563	0.500	12.3	16.2	11.4 (4.6)	16.1 (2.2)	242.0	212.0	11.4	17.4
D78	0.700	9.7	20.9	9.1 (3.2)	20.5 (4.1)	407.1	112.9	12.0	15.6

Table 2. Parameter estimates for the distance-dependent individual-based model (equations 1 and 2).

	Oak				**Pine**		
Plot	$\alpha_{k,1}$ **(mm)**	$\beta_{k,1}$ **(mm.cm^{-1})**	$\lambda_{1,1}$ **(mm)**	$\lambda_{1,2}$ **(mm)**	α_{2} **(mm)**	$\beta_{k,2}$ **(mm.cm^{-1})**	$\lambda_{2,2}$ **(mm.cm^{-2})**
D02	5.99	0.1026	-0.354	-0.242	4.60	0.0566	-0.000361
D108	12.08	0.0896	-0.354	-0.242	4.60	0.0620	-0.000361
D20	12.45	0.0427	-0.354	-0.242	4.60	0.0633	-0.000361
D27	12.73	0.0361	-0.354	-0.242	4.60	0.0512	-0.000361
D42	9.62	0.1633	-0.354	-0.242	4.60	0.0813	-0.000361
D49	13.01	0.0600	-0.354	-0.242	4.60	0.0511	-0.000361
D534	7.73	0.1357	-0.354	-0.242	4.60	0.0476	-0.000361
D563	6.00	0.1066	-0.354	-0.242	4.60	0.0491	-0.000361
D78	4.00	0.1766	-0.354	-0.242	4.60	0.0337	-0.000361

Table 3. Values of the Ripley's function for oak ($K_{1,1}$) and for pine ($K_{2,2}$), and values of the inter-type function ($K_{1,2}$) at a distance of 10 m in each plot. The 99% confidence limits under the null hypothesis are also given (upper and lower bounds). For the Ripley’s function, the null hypothesis corresponds to complete spatial randomness. For the inter-type function, the null hypothesis corresponds to population independence.

		Plot								
***K* (m²)**		**D02**	**D108**	**D20**	**D27**	**D42**	**D49**	**D534**	**D563**	**D78**
$K_{1,1}$	Observed	349.4	330.8	350.7	346.0	346.0	328.4	312.9	304.9	333.8
	Upper	338.4	337.4	327.4	338.1	336.8	328.9	336.1	359.3	336.3
	Lower	293.1	293.5	298.6	293.5	293.8	300.4	293.6	277.3	292.3
$K_{2,2}$	Observed	444.3	321.4	404.0	504.8	323.3	381.5	364.9	321.0	378.2
	Upper	392.2	349.5	356.2	389.5	352.9	349.3	386.7	364.7	391.7
	Lower	245.0	283.6	277.0	250.8	280.9	287.7	259.6	269.7	248.9
$K_{1,2}$	Observed	281.9	294.3	291.1	308.0	316.2	311.7	343.9	308.8	304.7
	Upper	376.4	342.4	349.9	449.2	341.1	331.0	342.2	339.1	365.1
	Lower	255.7	289.3	275.3	206.9	291.8	287.6	286.7	296.1	278.8

Table 4. Optimum mixing proportion (x_{max}) and observed mixing proportion (x_{plot}) for each plot; $\Delta G(x_{max})$ = stand basal area increment for $x = x_{max}$; $\Delta G(x_{plot})$ = stand basal area increment for $x = x_{plot}$; Gain = relative difference between $\Delta G(x_{max})$ and $\Delta G(x_{plot})$.

Plot	**x_{max} (%)**	**$\Delta G(x_{max})$ (m²/ha/an)**	**$x_{plot.}$ (%)**	**$\Delta G(x_{plot})$ (m²/ha/an)**	**Gain (%)**
D02	59.3	0.477	59.2	0.477	0.00
D108	43.1	0.591	28.0	0.561	4.91
D20	37.5	0.555	42.6	0.552	0.61
D27	46.5	0.295	39.8	0.292	0.96
D42	45.7	0.374	41.9	0.373	0.21
D49	46.2	0.647	40.8	0.642	0.64
D534	40.8	0.291	36.7	0.290	0.40
D563	73.6	0.320	39.6	0.291	9.05
D78	57.3	0.401	43.6	0.387	3.41

Figure captions

Figure 1. The three main types of productivity response for a mixed stand composed of two species A and B according to the mixing proportion (adapted from Harper, 1977). Total density is assumed to be constant for the different mixing proportions. On the left, mixture has no effect on stand productivity: productivity of mixed stands is equivalent to the juxtaposition of pure stands. In the middle, mixture has a negative effect on stand productivity: productivity of mixed stands is lower than the productivity expected in juxtaposed pure stands. On the right, mixture has a positive effect on stand productivity: productivity of mixed stands is higher than the productivity expected in juxtaposed pure stands.

Figure 2. Comparison between the distance-dependent individual-based model and the stand model for oak (a) and pine (b) and for the 9 plots. Basal Area Increment = stand basal area increment predicted by the models over the 2000-2005 period. Individual model: distance-dependent individual-based model (equations 1 and 2). Stand model: stand model obtained by aggregation of the individual model (equation 7).

Figure 3. Stand productivity according to the mixing proportion for the 9 plots and for each species. The solid curve represents total stand productivity. The curve with black dots represents pine productivity. The curve with white dots represents oak productivity. The dashed vertical line represents the mixing proportion observed in the plot (x_{plot}). The solid vertical line represents the optimum mixing proportion (x_{max}).

Figure 4. Elasticiticies of x_{max} to the 10 parameters of the stand model for each plot. The bars show the absolute values of the elasticities, the sign of the elasticities being written on top of each bar.

Figures

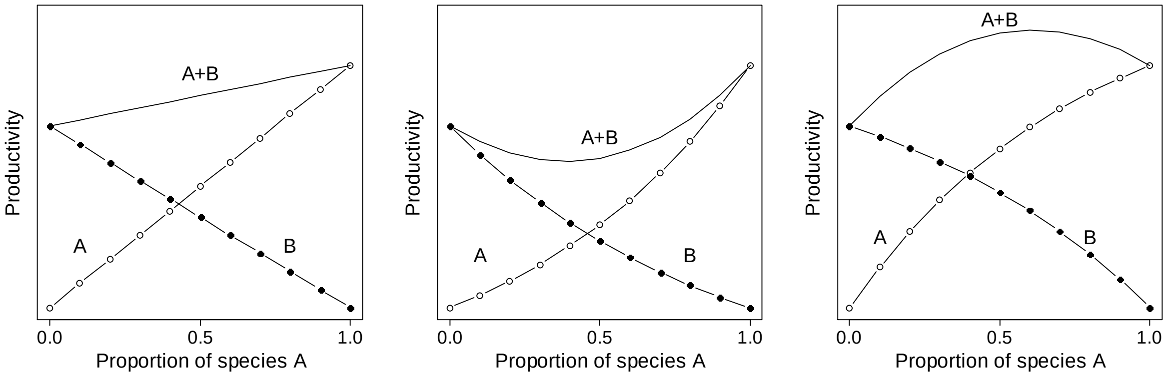

Figure 1

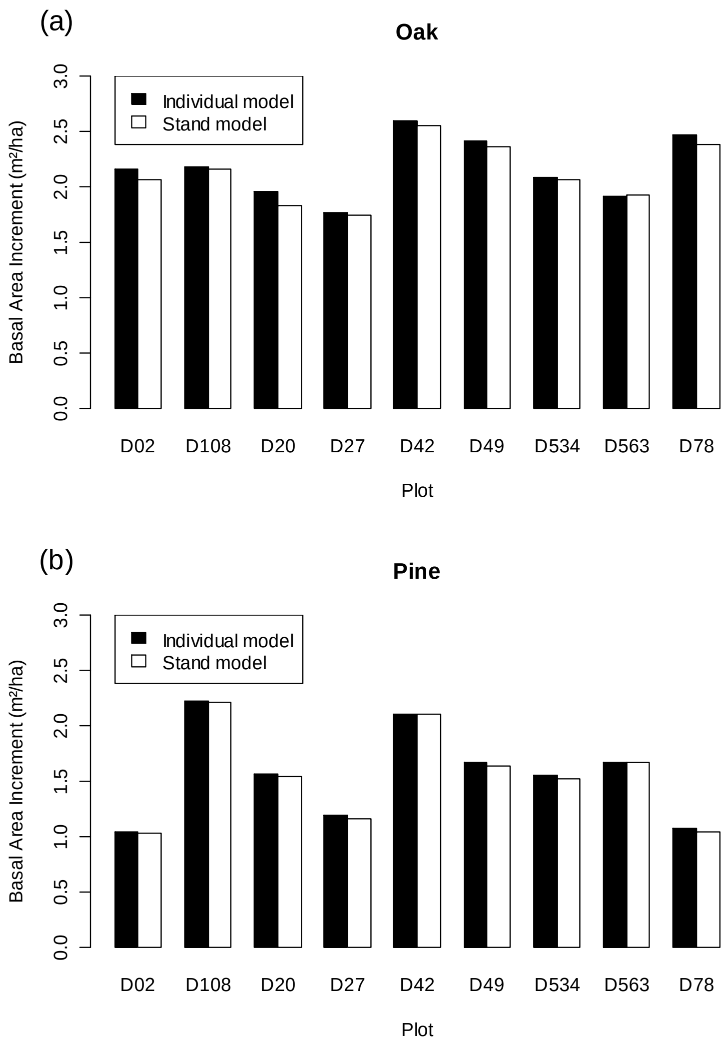
(a)
Oak
Individual model
Stand model
Basal Area Increment (m²/ha)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
D02
D108
D20
D27
D42
D49
D534
D563
D78
Plot
(b)
Pine
Individual model
Stand model
Basal Area Increment (m²/ha)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
D02
D108
D20
D27
D42
D49
D534
D563
D78
Plot

Figure 2

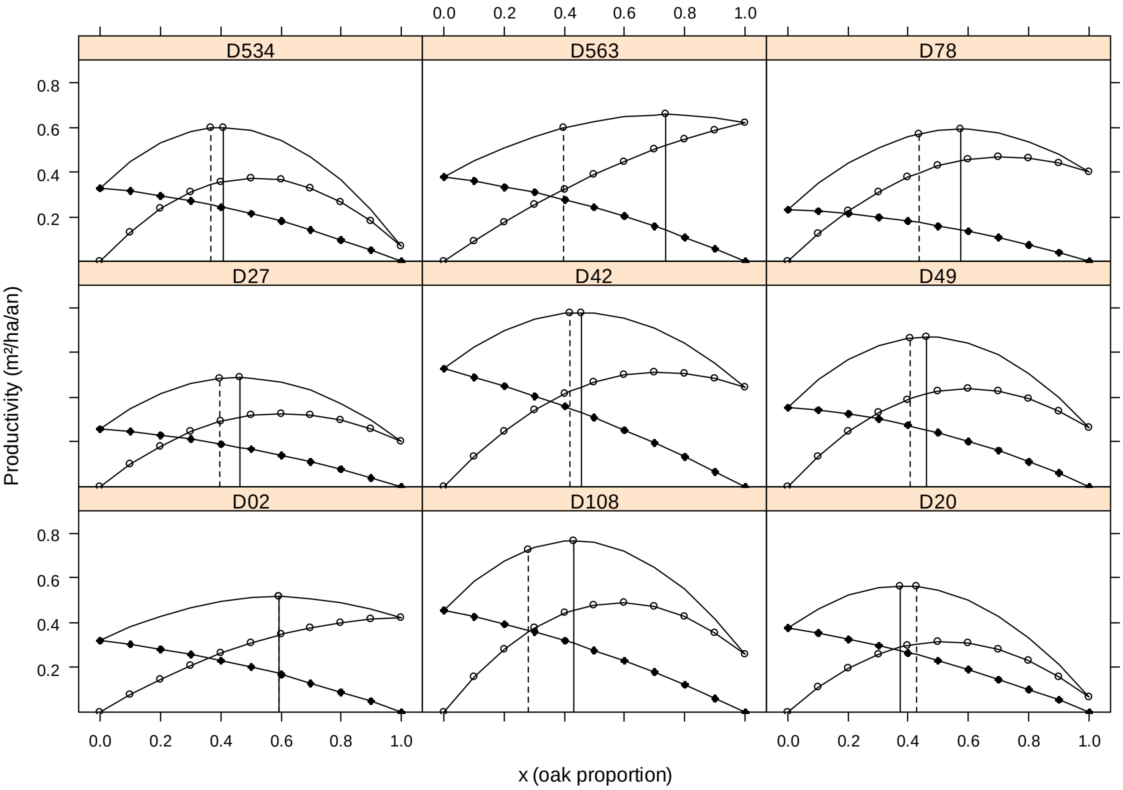
D534
D563
D78
D27
D42
D49
D02
D108
D20
Productivity (m²/ha/an)
x (oak proportion)
0.0
0.2
0.4
0.6
0.8
1.0

Figure 3

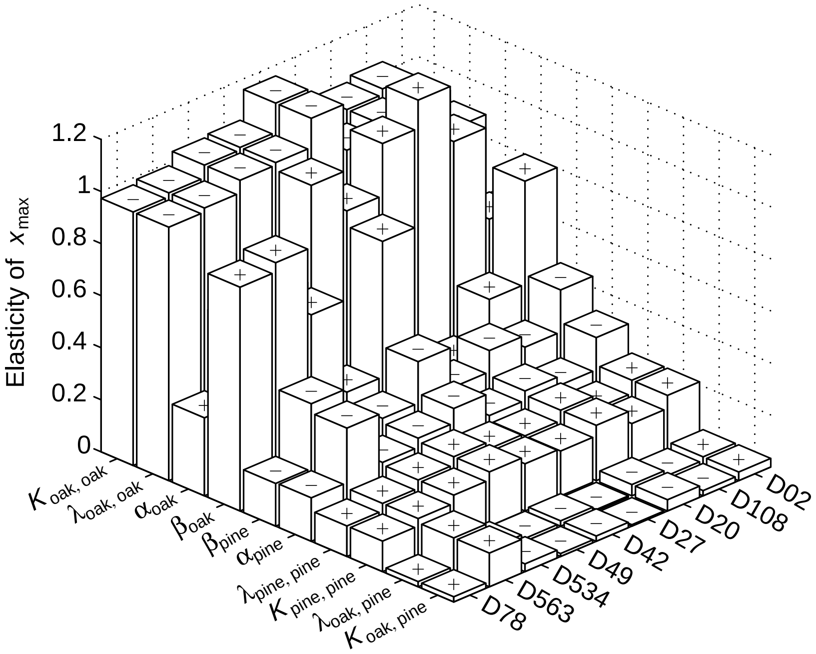
Elasticity of x_{max}
1.2
1
0.8
0.6
0.4
0.2
0
$K_{oak, oak}$
$\lambda_{oak, oak}$
α_{oak}
β_{oak}
β_{pine}
α_{pine}
$\lambda_{pine, pine}$
$K_{pine, pine}$
$\lambda_{oak, pine}$
$K_{oak, pine}$
D02
D108
D20
D27
D42
D49
D534
D563
D78
+
−

Figure 4

Appendix

Aggregating the distance-independent individual-based model

Given a distance-independent individual-based model:

$$\Delta r_{i,j} = \gamma_j + \beta_j girth_{i,j} \tag{11}$$

where $\Delta r_{i,j}$ is the radial increment of a tree i belonging to a species j between time t and time $t+\Delta t$, $girth_{i,j}$ is the girth at time t for a tree i. Starting from equation 11, we can develop a stand model for species j using an aggregation approach. The stand can be defined with three aggregated variables for each species: the number of trees N_j, the mean radius $\overline{r}_j$ and the basal area G_j. The dynamic equations of these variables must be defined using equation 11. Since we assume that there is neither mortality nor recruitment between t and $t+\Delta t$, we have $\Delta N_j = 0$. The mean radius is defined as follows:

$$\overline{r}_j(t) = \frac{1}{N_j}\sum_{i=1}^{N_j} r_{i,j}$$

where $\overline{r}_j(t)$ is the mean radius at time t. The mean radius increment can thus be written as a function of the individual radial increments:

$$\Delta\overline{r}_j = \overline{r}_j(t+\Delta t) - \overline{r}_j(t) = \frac{1}{N_j}\sum_{i=1}^{N_j} r_{i,j}(t+\Delta t) - \frac{1}{N_j}\sum_{i=1}^{N_j} r_{i,j}(t) = \frac{1}{N_j}\sum_{i=1}^{N_j}\Delta r_{i,j}$$

It follows from equation 11 that:

$$\sum_{i=1}^{N_j}\Delta r_{i,j} = \gamma_j N_j + 2\pi\beta_j N_j \overline{r}_j$$

And the mean radius increment is given by:

$$\Delta\overline{r}_j = \gamma_j + 2\pi\beta_j\overline{r}_j$$

Similarly, ΔG_j can be written as a function of the individual basal area increments ($\Delta g_{i,j}$):

$$\Delta G_j = G(t+\Delta t) - G(t) = \sum_{i=1}^{i=N_j} g_{i,j}(t+\Delta t) - \sum_{i=1}^{i=N_j} g_{i,j}(t) = \sum_{i=1}^{i=N_j}\Delta g_{i,j}$$

where $g_{i,j}$ is the basal area of a tree i and $\Delta g_{i,j} = g_{i,j}(t+\Delta t) - g_{i,j}(t)$. Since $g_{i,j}(t) = \pi\left(r_{i,j}(t)\right)^2$ we can write $g_{i,j}(t+\Delta t)$ as a function of $r_{i,j}(t)$, $r_{i,j}(t+\Delta t)$ and $\Delta r_{i,j}$:

$$g_{i,j}(t+\Delta t) = \pi\left(r_{i,j}(t+\Delta t)\right)^2 = \pi\left(r_{i,j}(t) + \Delta r_{i,j}\right)^2 = \pi\left(\left(r_{i,j}(t)\right)^2 + 2r_{i,j}(t)\Delta r_{i,j} + \left(\Delta r_{i,j}\right)^2\right)$$

Therefore:

$$\Delta g_{i,j} = 2\pi r_{i,j}(t)\Delta r_{i,j} + \pi\left(\Delta r_{i,j}\right)^2$$

It follows from equation 11 that:

$$r_{i,j}(t)\Delta r_{i,j} = \gamma_j r_{i,j}(t) + \beta_j 2\pi\left(r_{i,j}(t)\right)^2 = \gamma_j r_{i,j}(t) + \beta_j 2 g_{i,j}(t)$$

and

$$\left(\Delta r_{i,j}\right)^2 = \gamma_j^{\,2} + \gamma_j\beta_j 4\pi r_{i,j}(t) + \beta_j^{\,2} 4\pi^2\left(r_{i,j}(t)\right)^2 = \gamma_j^{\,2} + \gamma_j\beta_j 4\pi r_{i,j}(t) + \beta_j^{\,2} 4\pi g_{i,j}(t)$$

We can now express the individual basal area increment as a function of $r_{i,j}(t)$, $g_{i,j}(t)$ and the parameters of equation 11:

$$\Delta g_{i,j} = \pi\gamma_j^{\,2} + 2\pi\gamma_j\left(1 + 2\pi\beta_j\right) r_{i,j}(t) + 4\pi\beta_j\left(1 + \pi\beta_j\right) g_{i,j}(t)$$

Since $\sum_{i=1}^{N_j} 1 = N_j$, $\sum_{i=1}^{N_j} r_{i,j} = N_j \overline{r}_j(t)$ and $\sum_{i=1}^{N_j} g_{i,j} = G_j(t)$, we can sum the individual basal area increments to obtain the stand basal area increment:

$$\Delta G_j = \pi\gamma_j^{\,2} N_j + 2\pi\gamma_j\left(1 + 2\pi\beta_j\right) N_j \overline{r}_j + 4\pi\beta_j\left(1 + \pi\beta_j\right) G_j$$

Therefore, the system of equations for the stand model is:

$$\begin{cases} \Delta G_j = \pi\gamma_j^{\,2} N_j + 2\pi\gamma_j\left(1 + 2\pi\beta_j\right) N_j \overline{r}_j + 4\pi\beta_j\left(1 + \pi\beta_j\right) G_j \\ \Delta\overline{r}_j = \gamma_j + 2\pi\beta_j \overline{r}_j \\ \Delta N_j = 0 \end{cases}$$

Optimum mixing proportion

Since $\Delta G'(x)$ is a polynomial equation of the second degree, its roots are:

$$x_1 = \frac{-b - \sqrt{b^2 - 4ac}}{2a} \text{ and } x_2 = \frac{-b + \sqrt{b^2 - 4ac}}{2a}$$

The table below shows that for the nine plots, a is always positive so the function $\Delta G'(x)$ is convex. It is negative between x_1 and x_2 and positive for $x < x_1$ et $x > x_2$. x_1 is thus a maximum for the function $\Delta G(x)$.

Coefficients and roots of $\Delta G'(x)$ for the 9 plots.

Plot	***a***	***b***	***c***	x_1	x_2
D02	1493	-64785	37871	0.593	43
D108	14688	-168693	69966	0.431	11
D20	15403	-172769	62590	0.375	11
D27	6466	-83284	37311	0.465	12
D42	5225	-74980	33143	0.457	14
D49	13152	-185208	82799	0.462	14
D534	9357	-102027	40109	0.408	10
D563	268	-31239	22837	0.736	116
D78	5457	-95660	52986	0.573	17