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Original article

Comparing volume growth in pure and mixed stands of *Pinus sylvestris* and *Quercus pyrenaica*

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Quercus pyrenaica

Abstract

• In Mediterranean forestry, it is important to improve knowledge about mixed stands dynamics, including their productivity. Previous studies have focused on the interactions between different species (competition, reduction of competition and facilitation) depending on site, species composition and structure.

• At the centre of this research are the possible differences between pure and mixed stands of *Pinus sylvestris* and *Quercus pyrenaica* in terms of density-growth relationships and volume growth per species.

• Using data from the second and third Spanish National Forest Inventory (606 plots), volume increment models for these species were fitted. Both species displayed a similar density-growth pattern for pure and mixed stands, with a maximum volume growth at maximum density. Volume increment per occupied area was also found to be greater in mixed stands as opposed to pure stands, suggesting a species interaction with reduced levels of competition in the former. However, the total volume growth was generally lower in mixed stands since the growth rate of oak is much lower.

• The results highlight the expedience of favouring *P. sylvestris-Q. pyrenaica* mixed stands with higher proportions of pine trees in order to gain the benefits of a more complex forest whilst retaining an acceptable level of wood production.

Mots-clés :
forêt mixte /
accroissement en volume /
relation densité-croissance /
***Pinus sylvestris* /**
Quercus pyrenaica

Résumé – Comparaison de la croissance en volume dans des peuplements purs et des peuplements mixtes de *Pinus sylvestris* et de *Quercus pyrenaica*.

• Dans la foresterie méditerranéenne, il est important d'améliorer les connaissances sur la dynamique des peuplements mixtes, y compris sur leur productivité. Des études antérieures ont mis l'accent sur les interactions entre espèces différentes (concurrence, réduction de la concurrence et facilitation), selon la station, la composition des essences et la structure.

• Cette recherche porte sur les différences possibles entre les peuplements purs et les peuplements mixtes de *Pinus sylvestris* et *Quercus pyrenaica* en termes de relation densité-croissance et croissance en volume par espèce.

• À partir des données du deuxième et du troisième Inventaire Forestier National Espagnol (606 placettes), des modèles d'accroissement en volume pour ces espèces ont été ajustés.

Les deux espèces ont affiché un modèle densité-croissance similaire pour les peuplements purs et les peuplements mixtes, avec un volume maximum de croissance à une densité maximale. L'accroissement de volume par zone occupée a également été trouvé plus important dans les peuplements mixtes plutôt que dans les peuplements purs, ce qui suggère une interaction entre espèces avec réduction des niveaux de concurrence dans celui-là. Toutefois, la croissance totale en volume a été généralement plus faible dans les peuplements mixtes puisque le taux de croissance du chêne est beaucoup plus faible.

• Les résultats soulignent l'opportunité de favoriser les peuplements mixtes *P. sylvestris-Q. pyrenaica* avec une proportion plus élevée de pins afin d'obtenir les avantages d'une forêt plus complexe, tout en conservant un niveau acceptable de production de bois.

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1. INTRODUCTION

In forestry, the importance of mixed stands has increased in recent decades due to the potential benefits which can be gained, such as increased production, greater diversity, improved nutrient cycling or reduced risk of biotic and abiotic damage (Cannell et al., 1992; Man and Lieffers, 1999). The question of potential productivity in mixed as opposed to pure stands has long been an area of interest in forest research (Assmann, 1970; Kelty, 1992) although there is a lack of general approaches for studying this topic.

According to ecological theory, there are three possible species interactions which take place in mixed stands, namely: competition, reduced competition and facilitation. The latter two result in greater productivity of mixtures (Kelty, 1992; Vandermeer 1989). In general, competition arises where the different species occupy the same niche. This frequently occurs when the species grow in the same canopy stratum and light is the most limiting resource (Assmann, 1970; Kelty, 1989; Linden and Agestam, 2003). A reduction in competition occurs when the different species use the above and below-ground resources in a different way because of differences in shade tolerance, phenology, leaf canopy or root system, or due to mycorrhizal linkages (Kelty, 1992; Man and Lieffers, 1999). Facilitation is generally associated with the increase in available nitrogen resulting from increased litter decomposition rates or due to the presence of nitrogen-fixing species (Kelty, 1992). Other possible forms of facilitation are the sheltering of one species by the other and the reduction of biotic and abiotic damage (Man and Lieffers, 1999).

To compare production levels between mixed stands and monospecific stands, one possibility is to relate the growth of the species in mixed stands to the area occupied by the respective species (Kennel, 1965). This approach has been used in studies at individual tree level to analyse the growing space efficiency or tree volume growth per unit of area, frequently through the crown projection area (Webster and Lorimer, 2003). Since the crowns may overlap or leave gaps in the canopy, the area available for each tree was defined by Kennel (1965) as the crown projection area, plus part of the adjacent gaps in the canopy, minus the overlaps with other crowns. When spatial information at tree level is not available, the species proportion by area (Prodan, 1959) can be used to assess the area occupied by each species at stand level, as it is frequently used in order to apply yield tables of pure stands to mixed species stands (Marschall, 1992; Speidel, 1972).

One aspect of mixed forest research that is largely neglected due to the lack of appropriate data is the density-growth relationship (Pretzsch, 2003). Wiedemann's hypothesis (Assmann, 1970, p. 231) or Langsaeter's plateau (Langsaeter, 1941) state that the volume increment does not vary over a wide range of densities. Results for different species growing in pure stands indicate that the density range, as well as the density at which volume increment is at a maximum, depend on species and site qualities (e.g. Assmann, 1970; Pretzsch, 2005). In the case of mixed stands, Pretzsch (2003) refers to the different growth-density patterns observed for mixed stands of Norway spruce and common beech in relation to pure stands. The former display greater elasticity of growth against a reduction in stand density.

Scots pine *(Pinus sylvestris* L.) and Pyrenean oak (*Quercus pyrenaica* Willd.) are two of the most important forest species in Spain not only for their widespread distribution (approximately 1 000 000 and 700 000 ha pure stands respectively) but also because of their ecological and socio-economic value. The two species form mixed stands where their natural ecological distributions overlap (colder and higher areas of oak distribution) and where Scots pine has been introduced into the natural distribution areas of the oak. In spite of the higher economic value of Scots pine wood, the advantages associated with the complexity and diversity of mixed stands mean that the latter are currently attracting greater levels of interest (Spanish Forest Plan, MMA, 2002). The ability of mixed stands to regenerate after a forest fire through both seed dispersal and resprouting is of particular interest. It is therefore important to improve our knowledge with regard to the dynamics of these stands, including the effect of composition on stand productivity.

A number of studies concerning production in mixed stands of Scots pine in Northern and Central Europe have been conducted, the majority of which have centred on mixtures with Norway spruce, beech and birch (Assmann, 1970; Brown, 1992; Frivold and Frank, 2002; Linden and Agestam, 2003). However, none of the research carried out to date has focused on mixed stands of Scots pine and Mediterranean oak, such as *Quercus pyrenaica*. The objectives of this paper are to analyse the density-growth relationships in pure and mixed stands of *P. sylvestris* and *Q. pyrenaica* and to compare the growth of the species in pure and mixed stands with different compositions and stocking densities. This study used the species proportion by area (von Laer (cit. Prodan, 1959); Sterba, 1998) to define the composition of the mixture and to study the effect of composition on volume growth at stand level. In order to calculate the species proportion by area as well as the stocking degree, the maximum basal area according to Sterba (1987) was estimated for both species.

2. MATERIAL AND METHODS

2.1. Data

The study area covers the two main mountain areas in which mixed stands of *P. sylvestris* and *Q. pyrenaica* are present; the Central mountain range (Region 1) and the North-Iberic mountain range (Region 2) (Fig. 1). These areas represent two of the most important natural distribution areas of Scots pine in Spain, where it is also the main commercial species.

Data from the second and third Spanish National Forest Inventory (SNFI) were used for the purposes of the study. The SNFI is a systematic sample of permanent circular plots of variable radii distributed on a square grid of 1 km, with a measurement interval of 10 y (ICONA, 1990). The plots are composed of four sub-plots with radii of 5, 10, 15 and 25 meters, where trees with a diameter at breast height greater than 75, 125, 225 and 425 mm respectively, were measured. The data recorded for each sample tree are: azimuth, distance to the centre of the plot, species, diameter at breast height and total height. In this

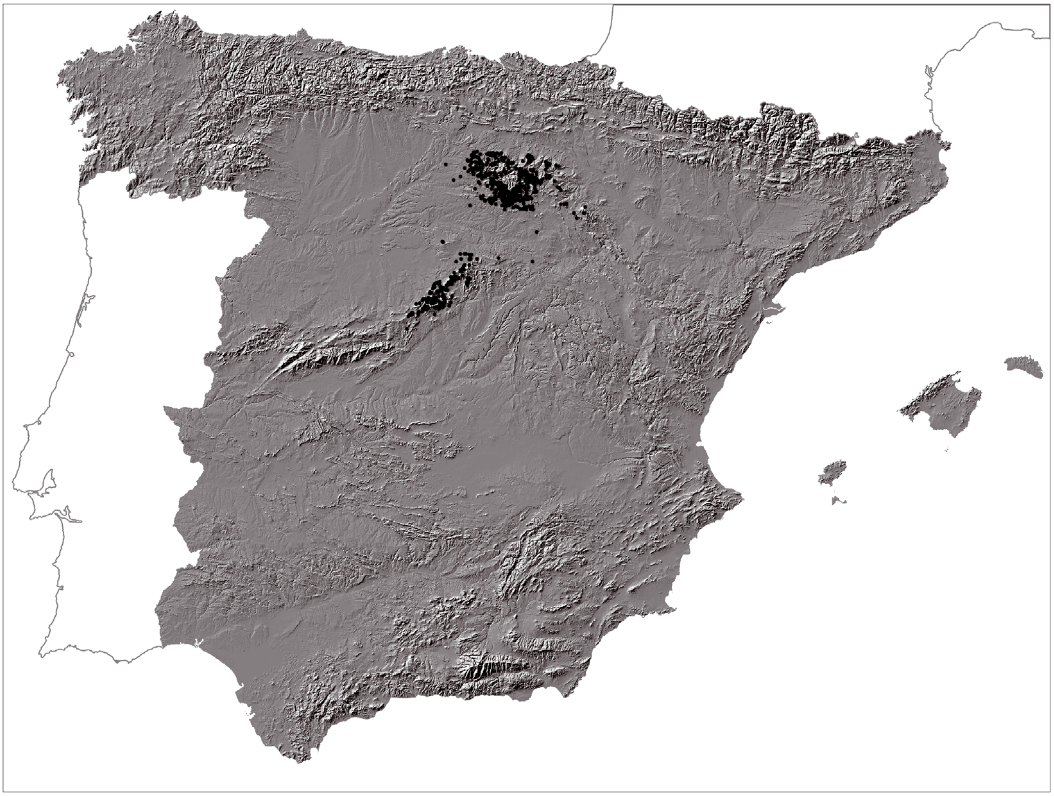

Figure 1. Plot locations in Spain.

study, tree stem volume over bark was estimated from tree diameter and height through the volume equations proposed in the Second SNFI. Stand variables were estimated using factors to expand subplots to a hectare and volume increment per plot was calculated by subtracting the volume at the Second SNFI from the volume at the Third SNFI and then adding the volume removed (natural mortality and felling) between the two observations. Since the moment in time at which the trees were either felled or died is unknown, the volume of these trees was estimated using the dbh and height of the Second SNFI. In order to avoid large errors, plots from which more than 5% of the stand basal area had been removed were not considered in the study.

Plots were selected according to the species composition, including pure stands of both *P. sylvestris* and *Q. pyrenaica* as well as mixed stands in which both species were present. The criteria for selecting mixed plots were: presence of both species; the proportion of both species (number of trees per hectare) being higher than 10% (MAPA, 1970); and the proportion of other species being lower than 10%. In order to estimate stand variables, trees of other conifer species were considered as pines and trees of other broadleaved species as oaks.

In the case of pure stands, a total of 730 plots from the Second SNFI for Scots pine and 581 for oak were selected to study the maximum basal area, rejecting those plots where the density was very low (due to factors such as grazing, recent felling, rocky areas etc.). From these plots, only 310 plots for Scots pine and 215 for oak were used to analyse the volume increment (data from the Second and Third SNFI). The other plots were rejected either due to the removal of more than 5% of the basal area in the period between the two inventories, the lack of re-measurement data or, in some cases, due to growth anomalies. The final number of mixed plots included in the analysis was 81 (Tabs. I–III).

Plot age is not recorded in the SNFI, hence site index, which is a useful variable for studying the density-growth relationship, could not be estimated. Despite this shortcoming, the SNFI provides data from a large number of plots covering a wide geographical distribution.

2.2. Potentially available stand area for a species in mixed species stands

According to von Laer (cit. Prodan, 1959), the area available for a species in a mixed stand, in this study termed "species proportion by area", can be calculated as

$$P_{\mathrm{i}} = \frac{\frac{G_{\mathrm{i}}}{G_{\max \mathrm{i}}}}{\sum_{\mathrm{i}} \frac{G_{\mathrm{i}}}{G_{\max \mathrm{i}}}} \tag{1}$$

where P_{i} is the area potentially available or species proportion by area for species i, G_{i} the observed basal area per hectare of species *i*, and G_{maxi} the maximum or potential basal area of species *i* (Tab. IV). The numerator is the area of a fully stocked pure stand of all the respective species needed to exhibit the observed basal area (G_{i}), and the denominator is the total area of fully stocked pure stands of all species together exhibiting G_{i} respectively (Sterba, 1998).

In order to use this approach to calculate the area occupied by a given species, the potential, i.e. the maximum basal area per hectare had to be determined for the two species under investigation.

Table I. Main stand variables of plots used to fit the equation (9) (data from 2nd SNFI). *N*- Natural stands; *P*- Plantation stands.

Species	Region	Origin	No. plots	Statistic	No. trees ha^{-1}	H_{dom} (m)	*Dg* (cm)	*G* (m^2 ha^{-1})
Pinus sylvestris	1	N	164	Mean	733	17.9	29.5	36.3
				std	657.5	4.7	9.7	12.3
				Min	129	8.2	10.9	16.9
				Max	5126	28.2	51.8	84.5
		P	98	Mean	1452	10.6	17.9	32.7
				std	659.3	2.9	4.6	11.2
				Min	349	5.9	9.7	15.2
				Max	3547	20.5	37.1	60.8
	2	N	304	Mean	755	16.4	27.9	35.9
				std	534.6	4.0	8.4	11.9
				Min	130	5.0	10.8	15.7
				Max	3530	27.8	51.5	76.5
		P	164	Mean	1379	11.5	19.3	31.8
				std	732.5	4.1	7.3	10.7
				Min	268	5.2	9.7	14.9
				Max	3756	22.7	40.8	59.8
Quercus pyrenaica	1		193	Mean	738	8.1	13.3	8.3
				std	759.8	2.5	6.0	7.4
				Min	78	3.6	7.6	0.6
				Max	4170	16.9	50.3	34.0
	2		388	Mean	862	8.7	14.7	12.2
				std	724.0	2.9	7.3	9.2
				Min	79	2.5	7.5	0.6
				Max	3756	17.4	51.8	45.9

Table II. Main stand variables of monospecies plots used to fit equation (13) (data from 2nd and 3rd SNFI). *N*- Natural stands; *P*- Plantation stands.

Species	Origin	No. plots	Statistic	No. Trees ha^{-1}	H_{dom} (m)	*G* (m^2 ha^{-1})	I_V (m^3 ha^{-1} y^{-1})	S^*
Pinus sylvestris	*N*	177	Mean	768	15.8	34.9	7.6	0.54
			std	540.9	4.3	12.1	4.6	0.17
			Min	129	5.0	16.0	0.2	0.27
			Max	2911	27.8	67.9	26.4	1.02
	P	133	Mean	1370	11.1	30.8	11.3	0.52
			std	686.8	3.9	11.5	4.3	0.17
			Min	310	5.2	14.9	1.5	0.29
			Max	3547	22.3	59.8	22.3	0.99
Quercus pyrenaica		215	Mean	931	9.5	13.4	2.4	0.36
			std	721.4	7.3	7.3	1.5	0.18
			Min	79	4.8	3.8	0.1	0.10
			Max	3675	17.4	40.2	8.4	1.09

* S is the stocking degree (G/G_{max}).

2.3. Maximum basal area in pure stands

Sterba (1987) developed a method to estimate the potential density based on the Competition Density Rule defined by Kira et al. (1959), the stand density index developed by Reineke (1933) and Assmann's theory of maximum basal area (Assmann, 1970). The Competition Density Rule, modified by Goulding (1970), relates the quadratic mean diameter to stand density and stand height through the equation:

$$Dg = 1/\left(a_0 H_{dom}^{a_1} N + b_0 H_{dom}^{b_1}\right) \quad (2)$$

where *Dg* is the quadratic mean diameter (cm), H_{dom} the dominant height (m), *N* the number of trees per hectare and a_i and b_i parameters to be obtained for each species. By calculating the basal area with the help of this relation and then setting the first derivative dG/dN to zero, the maximum basal area can be obtained:

$$N_{G\,max} = \frac{b_0}{a_0}(H_{dom}^{b_1-a_1}) \quad (3)$$

Table III. Main stand variables of mixed species plots by species and total, used to fit equation (13) (data from 2nd and 3rd SNFI). *N*- Natural stands; *P*- Plantation stands.

Species	Origin	N° plots	Statistic	No. trees ha^{-1}	H_{dom} (m)	G (m^2 ha^{-1})	I_V (m^3 ha^{-1} y^{-1})	A^*	P^*	I^*_{Vp} (m^3 ha^{-1} y^{-1})
Pinus sylvestris	*N*	39	Mean	569	13.3	17.4	4.6	0.28	0.63	7.9
			std	r 681.9	r 3.3	8.1	4.0	0.13	0.20	6.5
			Min	36	7.0	3.6	0.4	0.06	0.19	0.5
			Max	2915	19.3	38.8	19.4	0.61	0.96	22.4
	P	42	Mean	796	7.5	10.4	7.0	0.19	0.55	13.9
			std	447.4	2.7	6.8	4.1	0.11	0.21	7.8
			Min	36	4.0	1.9	0.5	0.04	0.19	1.8
			Max	1733	16.1	32.8	18.0	0.52	0.91	34.5
	Total	81	Mean	687	10.3	13.7	5.8	0.23	0.59	11.0
			std	580.1	4.2	8.2	4.2	0.13	0.21	7.8
			Min	36	4.0	1.9	0.4	0.04	0.19	0.5
			Max	2916	19.3	38.8	19.4	0.61	0.96	34.5
Quercus pyrenaica		81	Mean	496	8.6	6.2	1.3	0.17	0.41	3.9
			std	453.9	2.7	5.1	1.2	0.13	0.21	4.1
			Min	25	4.0	0.5	0.01	0.01	0.04	0.01
			Max	1974	15.8	23.6	4.9	0.59	0.81	16.7
P. sylvestris +*Q. pyrenaica*		81	Mean	1182		20.0	7.1	0.40		
			std	825.0		10.0	4.8	0.19		
			Min	71		4.0	0.8	0.10		
			Max	3813		46.1	21.3	0.94		

* *A*, *P*, I_{Vp} according to Table IV.

Table IV. Calculation of the species proportion by area and volume increment of one species in mixed plots related to its occupied area.

Species	Basal area (*G*)	Maximum basal area (G_{max})	Area (*A*)	Species proportion by area (*P*)	Volume increment (I_V)	Volume increment related to *P* (I_{Vp})
1	G_1	G_{max1}	$A_1 = G_1/G_{max1}$	$P_1 = A_1/A$	I_{V1}	$I_{Vp1} = I_{V1}/P_1$
2	G_2	G_{max2}	$A_2 = G_2/G_{max2}$	$P_2 = A_2/A$	I_{V2}	$I_{Vp2} = I_{V2}/P_2$
Total (1+2)			$A = A_1 + A_2 = S$	1	I_V	

$$Dg_{G\,max} = \frac{H_{dom}^{-b_1}}{2 \cdot b_0} \tag{4}$$

and

$$G_{max} = \frac{\pi}{16\,000 \cdot a_0 \cdot b_0} \cdot H_{dom}^{-(a_1+b_1)} \tag{5}$$

N_{Gmax} and Dg_{Gmax} are the stem number and the quadratic mean diameter at maximum basal area, and G_{max} is the maximum basal area. Relating these expressions to Reineke's maximum stand density

$$N_{G\,max} = C \cdot Dg^{E} \tag{6}$$

the relationships between the parameters are:

$$C = \frac{b_0}{a_0}(2 \cdot b_0)^{E} \tag{7}$$

$$E = \frac{a_1}{b_1} - 1. \tag{8}$$

If the parameters C and E of the maximum stand density of Reineke are known for one species, the Competition Density Rule, and consequently the maximum basal area, can be fitted with the help of the following equation, which depends only on two parameters

$$Dg = 1/\left(\left(\frac{b_0}{C}\right)(2 \cdot b_0)^{E} \cdot H_{dom}^{a_1} N + b_0 H_{dom}^{a_1/(E+1)}\right) \tag{9}$$

For *P. sylvestris*, Reineke's maximum density was estimated from non-thinned permanent plots in the respective regions by Río et al. (2001), with the following result:

$$N_{max} = 403\,839.5 \cdot Dg^{-1.75}. \tag{10}$$

In the case of *Q. pyrenaica* there were insufficient permanent plots to accurately fit Reineke's maximum density relationship. Based on the SNFI plots and two thinning experiments with un-thinned permanent plots, and assuming the exponent stated by Reineke (1933) for most tree species ($E = -1.605$), the following equation, developed in a previous study (not published), was proposed:

$$N_{max} = 196\,512 \cdot Dg^{-1.605}. \tag{11}$$

The Competition Density Rule depending on two parameters (Eq. (9)) was fitted for both species using the pure stand data from the Second

SNFI (Tab. I) to estimate the maximum basal area for each species (G_{max}). This maximum basal area can be regarded as the potential density for a given stand height (Sterba, 1987).

The parameters b_0 and a_1 in equation (9) were estimated by non linear regression using the SAS "PROC NLIN" procedure (2004). In order to verify whether the maximum basal area differs between regions and stand origins, a comparison of models was made using the nonlinear residual sum of squares (Ratkowski, 1983). The full or complete model includes different parameters for each group, while the reduced model considers common parameters for all groups. The appropriate F-statistic is

$$F = \frac{(SSE_r - SSE_f)/(df_r - df_f)}{SSE_f/df_f} \quad (12)$$

where SSE_r and SSE_f are the sum of squared residuals of the reduced and full models, respectively; and df_r and df_f are the reduced and full model degrees of freedom. If the statistic F is greater than an F-distribution for degrees of freedom $v = df_r - df_f$ and $u = df_f$ a specific model for each group is needed.

2.4. Density-growth relationships in pure and mixed stands

2.4.1. *Volume increment*

The volume increments per hectare and year in each plot were used in pure stands to study density-growth relationships. In order to compare the volume growth of the species in pure and in mixed stands, the volume increment of each species observed in each mixed plot was divided by the species proportion by area, thus achieving an increment per hectare of the respective species, which can be compared to the growth in the pure stand with the same stocking degree (I_{Vp} in Tab. IV).

2.4.2. *Stocking degree*

The density-growth relationship was studied assuming that the maximum density for a given dominant height (H_{dom}) in a pure stand is represented by the estimated maximum basal area according to equation (5), where parameters a_0, a_1, b_0, b_1 vary with the species, origin of stands, and region and are estimated with the help of equation (9). In pure stands this G_{max} represents the maximum density ($S = 1$) and the stocking degree of plots is expressed as the ratio between the plot basal area per hectare and this maximum ($S = G/G_{max}$). In mixed stands the plot stocking degree is defined as the sum of the areas of fully stocked pure stands of both species together, A_1 and A_2, exhibiting G_1 and G_2, respectively (Tab. IV).

2.4.3. *Dominant height as a surrogate of age and site*

Volume growth for a given species and region depends on site quality and stand age as well as on stand density or stocking degree. When comparing volume growth in mixed and pure stands, it is important to consider these variables. As the SNFI offers neither age nor site index, the data sets cannot be split according to site quality and age, so a great variability in volume increments per stocking degree was found for each stand type.

Dominant height expresses a compound effect of site quality and age and is frequently used instead of age and site index to estimate stand yield and growth (e.g. Assmann (1970) when defining his general yield level, or Abetz (1975) in his thinning guidelines). In this study, dominant height has been included in growth-density relationships to reduce the variability of data and to compare pure and mixed stands.

2.4.4. *Models*

The density-growth relationships were studied through a model in which volume increment of one species is the dependent variable and dominant height, stocking degree, and species proportion by area the independent variables.

$$I_V = a_0 + a_1 \cdot f(H_{dom}) + a_2 \cdot f(S) + a_3 \cdot f(P) + \varepsilon \quad (13)$$

where I_V is the volume increment per hectare and year (m^3 h^{-1} y^{-1}), H_{dom} is the dominant height (m), S is the stocking degree, and P is the species proportion by area. Firstly, a quadratic relationship on S was tested to detect whether there was a maximum volume increment below the maximum stocking degree or if the maximum increment occurred with maximum density. As the latter option was found for all types of stands (by species, origin and composition), other functions were also tested (linear and logarithmic), as well as the interactions between variables.

This model was fitted to different data sets: natural and plantation Scots pine, region 1 and 2. In order to facilitate the comparison among data sets, the inclusion of dummy variables for each data set or the validity of a unique, reduced model was studied using the F-test in the same way as in the fit of the competition density rule. All fits were made via linear regression using the SAS software and basic hypotheses of linear regression were checked. If residuals showed the presence of heteroscedasticity, the dependent variable was transformed to correct it. A significance level of $p < 0.05$ was used throughout the study.

3. RESULTS

3.1. Maximum basal area in pure stands

The competition density rule depending on two parameters (Eq. (9)) was fitted to the Scots pine data, splitting the plots according to regions and origins. The comparisons between regions and origins indicated that different models were needed for natural and plantation stands, but that data from both regions could be combined in one model (Tab. V). In all the fits presented, the parameter estimates were statistically significant (Tab. VI).

Using the coefficients a_1 and b_0 found (Tab. VI), the equations for maximum basal area are

$$\text{Natural Scots pine } G_{max} = 36.82 \cdot H_{dom}^{0.2061} \quad (14)$$

$$\text{Plantation Scots pine } G_{max} = 33.41 \cdot H_{dom}^{0.2347}. \quad (15)$$

The estimated maximum basal area of natural Scots pine stands is slightly higher than that of plantation stands for the

Table V. Comparison of models for different data sets using the non-linear sum of squares (F) for equation (9).

Species	Data	Comparison	F	p
Pinus sylvestris	Region 1	Natural vs. Plantation	5.81	0.0034
	Region 2	Natural vs. Plantation	4.43	0.0124
	Natural	Region 1 vs. Region 2	2.63	0.0730
	Plantation	Region 1 vs. Region 2	1.03	0.3594
	Both regions	Natural vs. Plantation	9.26	0.0001
Quercus pyrenaica	All	Region 1 and Region 2	3.18	0.0425

Table VI. Fit-statistics and parameter estimates (standard errors in parenthesis) for equation (9). N is the number of plots, se the standard error of the estimate of the quadratic mean diameter, *dg* (cm).

Species	Data	N	se	R^2	a_1	b_0
Pinus sylvestris	Natural	468	4.345	0.761	0.6183 (0.0302)	0.2763 (0.0320)
	Plantation	262	2.397	0.863	0.7048 (0.0231)	0.4081 (0.0320)
Quercus pyrenaica	Region1	193	4.533	0.440	0.6109 (0.0544)	0.5385 (0.1051)
	Region 2	388	5.831	0.369	0.5428 (0.0434)	0.3847 (0.0612)

same height, the differences decrease as dominant height increases.

For *Quercus pyrenaica* the comparison between regions showed that different models are required for region 1 and 2 (Tab. V). The parameter estimates and model statistics for both regions are presented in Table VI. The maximum basal area expressions for both regions are

$$\text{Oak in region 1 } G_{max} = 15.13 \cdot H_{dom}^{0.3988} \quad (16)$$

$$\text{Oak in region2 } G_{max} = 16.46 \cdot H_{dom}^{0.3543}. \quad (17)$$

For low dominant heights the maximum basal area of region 1 is slightly lower than for region 2, while for higher dominant heights the basal area is higher for region 1.

3.2. Density-growth relationships in pure and mixed stands for *Pinus sylvestris*

Scots pine presented higher volume increments in plantation stands than in natural ones in both pure and mixed stands (Tabs. II and III). Thus, the inclusion in equation (13) of a dummy variable representing the stand origin was investigated, as well as possible interactions with the other variables. The quadratic relationship on S did not prove statistically significant. The final model for pure Scots pine stands is

$$\sqrt{I_V} = a_0 + a_1 \cdot \ln(H_{dom}) + a_2 \cdot \ln(S) + a_3 \cdot P + a_4 \cdot OR \quad (18)$$

where I_V is the volume increment ($m^3\ h^{-1}\ y^{-1}$) for pure stands (I_V in Tab. II) and the volume increment related to the area occupied by the species in mixed stands (I_{Vp} in Tab. III); H_{dom} the dominant height (m); S the stocking degree; P the species proportion by area; OR a dummy variable for stand origin that is 1 for plantation stands and 0 for natural ones; and a_i estimated parameters (Tab. VII).

This model for Scots pine stands reveals a negative relationship between volume increment and dominant height, whereas the relationship between volume increment and stocking degree was found to be positive. In the latter case, the maximum volume increment is obtained for the maximum stocking degree ($S = 1$) (Fig. 2). The selected model does not include the interaction between stocking degree and species proportion by area, so the same relationships between volume growth and stocking degree can be assumed for both pure and mixed stands. However, the variability of data is very high (Tab. VII) and the number of plots with high densities ($S > 0.8$) is scarce, particularly in mixed stands, so this relationship is not well covered by high density plots. The 'species proportion by area' parameter (P) reveals a decrease in volume increment as the species proportion increases, indicating the lowest volume increment in pure stands (Fig. 2).

3.3. Density-growth relationships in pure and mixed stands for *Quercus pyrenaica*

The model obtained for *Q. pyrenaica* also includes the logarithm of the dominant height and the logarithm of the stocking degree (Eq. (19)), although in this case the sign of the parameter for the dominant height is positive (Tab. VII), indicating a higher volume increment as dominant height increases (Fig. 3). The interaction between the species proportion by area (P) and the logarithm of dominant height was found to be significant, indicating lower volume increments as the species proportion by area increases, with a larger effect for higher dominant heights (Fig. 3). The maximum volume increment was also found at the maximum stocking degree (the inclusion of a quadratic term on S was not statistically

Table VII. Fit statistics and parameter estimates (standard errors in parenthesis) of the equations (18), (19). *N* and *se* as in Table VI.

Species	*N*	*se*	R^2_{adj}	Intercept a_0	$\ln(H_{dom})$ a_1	$\ln(S)$ a_2	*P*	$P \cdot \ln(H_{dom})$ a_3	*OR* a_4
Pinus sylvestris	391	0.734	0.374	6.755 (0.418)	–0.909 (0.136)	1.278 (0.114)	–0.833 (0.208)	–	0.424 (0.0911)
Quercus pyrenaica	296	0.612	0.172	0.414 (0.349)	0.892 (0.160)	0.186 (0.077)	–	–0.331 (0.061)	–

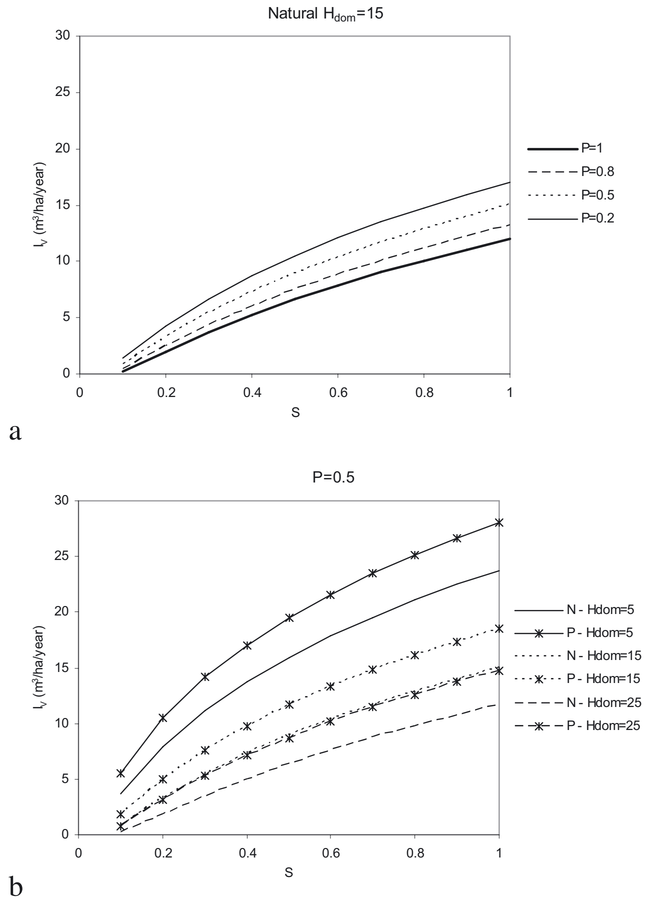

Figure 2. Volume increment of Scots pine (I_V) over stocking degree (S) according to equation (18): (a) varying species proportion by area (P) for a dominant height (H_{dom}) of 15 m; (b) varying origin (N-natural; P-plantation) and H_{dom} for $P = 0.5$; when $P < 1$, I_V is the volume increment of the species related to its occupied area, I_{Vp} in Table IV.

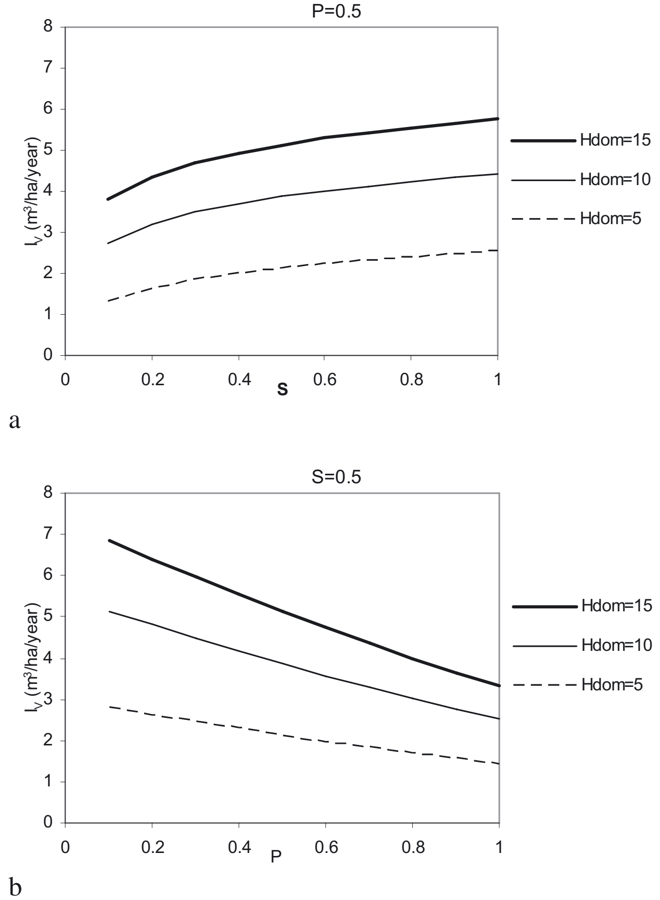

Figure 3. Volume increment of *Quercus pyrenaica* according to equation (19): (a) varying the stocking degree (S) and dominant height (H_{dom}) for a species proportion by area (P) of 0.5; (b) varying P and H_{dom} for $S = 0.5$; when $P < 1$, I_V is the volume increment of the species related to its occupied area, I_{Vp} in Table IV.

significant). As in the model for Scots pine, the interaction between stocking degree and species proportion by area did not prove statistically significant. The final model is

$$\sqrt{I_V} = a_0 + a_1 \cdot \ln(H_{dom}) + a_2 \cdot \ln(S) + a_3 \cdot P \cdot \ln(H_{dom}). \quad (19)$$

The F-test indicated the validity of one common model for both regions (results not shown). The variability explained by this model is smaller than for Scots pine (Tab. VII).

3.4. Growth comparisons in pure and mixed stands

Using the fitted models (Eq. (18) and (19)) to estimate the volume increments of both species growing in mixed stands, the effect of composition on total volume increment can be studied as in a replacement series (Kelty, 1992). Calculations were performed separately for both origins and with values near the observed means of the SNFI mixed stands in order to simulate conditions similar to those reflected in the real data.

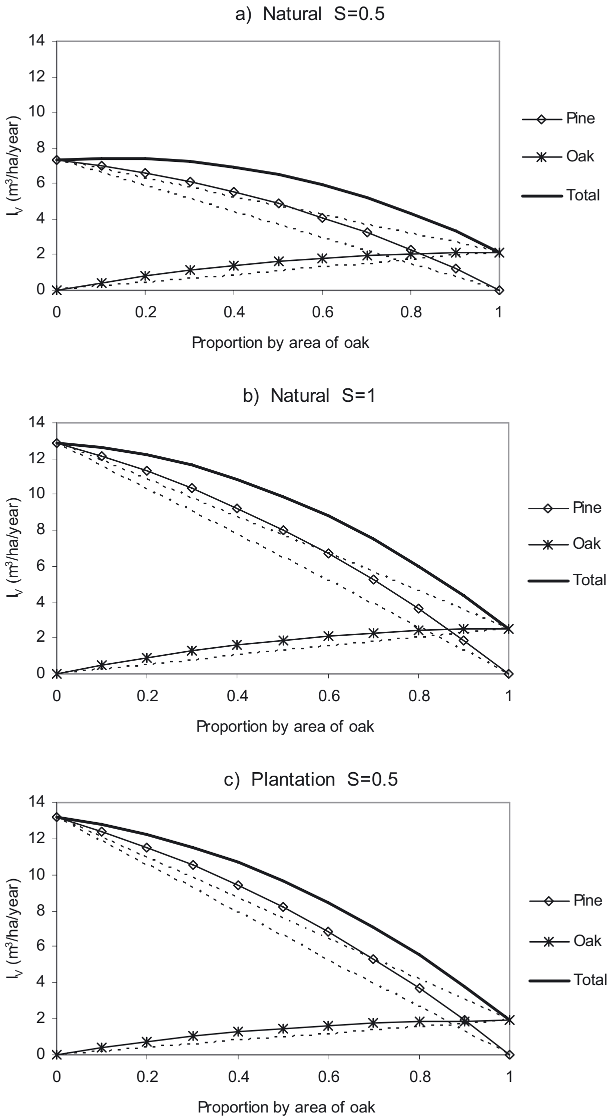

Figure 4. Total and by species estimated volume increment in mixed stands over species composition (expressed as proportion by area of oak): (a) Scots pine is natural, the stocking degree (S) is 0.5 and the dominant heights (H_{dom}) of Scots pine and oak are 13 and 8 m respectively; (b) similar to (a) but with $S = 1$; and (c) Scots pine was planted, $S = 0.5$. and H_{dom} of Scots pine and oak are 7.5 and 7 m respectively. Dashed lines reflect the expected volume increment (total and by species) if there were not reduction of competition in mixed stands, that is the volume increment of each species is proportional to the species proportion by area.

For pine and oak with dominant heights of 13 m and 8 m, respectively, and a stocking degree of 0.5 (Fig. 4a), the maximum total increment was found for an oak proportion of 0.1, although this increment is only slightly higher (0.12 $\mathrm{m^3\ ha^{-1} y^{-1}}$) than that of pure Scots pine stands. If similar dominant heights are introduced while increasing the stocking degree to 1 (Fig. 4b), the total growth is maximum for the pure stand. A similar pattern is found for mean conditions in mixed stands where Scots pine was planted (Fig. 4c).

For each species as well as for the total stand, the estimated volume increments in the three examples were higher than those which would be expected if intra and inter-specific interactions were equivalent (dashed lines in Fig. 4), indicating a reduction in competition in mixed stands.

The relative increments (*RI*) (Eq. (20)), defined as the ratio between volume increment in mixed stands and its corresponding volume increment in pure stands (similar to relative yield defined in Kelty (1982)), was calculated for different stocking degrees and for the mean dominant heights of natural and plantation mixed plots (Fig. 5).

$$RI(\text{species1}) = \frac{I_{V_1}\text{in mixtures}}{I_{V_1}\text{ in pure plots}}. \qquad (20)$$

The *RI* was always higher than the expected *RI* if intra and inter-specific interactions were equivalent (*RI* equal to the species proportion), increasing with a higher stocking degree.

4. DISCUSSION

A maximum basal area derived from the competition density rule was used in this study to estimate the stocking degree. The adjustment of this rule by fixing the two parameters related to the maximum density of Reineke seems to be a good method for estimating potential densities, since it gives the maximum density line previously fitted which is especially important when this line has been accurately fitted with non-thinned permanent plots, whilst also allowing the maximum basal area for each dominant height to be estimated (Sterba, 1987).

Differences in estimated maximum basal areas depending on Scots pine origins were larger for low dominant heights, probably due to the different dominant height growth patterns at young ages of natural and plantation stands, with higher increments in plantation forests (Río et al., 2006). The same dominant height indicates a different development stage for each origin, and consequently, different maximum basal areas. The differences found for oak growing in the two studied regions may be caused by the high variability found in stand typologies in *Q. pyrenaica* forests (Roig et al., 2007), ranging from open woodlands to very dense stands with stagnating-increment.

Patterns found for density-growth relationships in Scots pine indicate a maximum volume growth for maximum density (Fig. 2), a similar pattern to that found for pure Scots pine stands in the same regions based on thinned permanent plots (Río et al., 2008), as well as for other areas in which Scots pine populations are found (Mäkinen and Isomäki, 2004). Regarding mixed stands, as the volume increment for both species growing in mixtures increases with the stocking degree, the sum follows the same pattern, although there are few plots at high densities. Pretzsch (2003) reported a saturation relationship between growth and density in mixed stands of Norway spruce-beech, with similar growth for medium and high densities and lower increment losses than in pure stands when density was reduced. The higher relative volume increments in mixed stands found in our study (Fig. 5), even where the

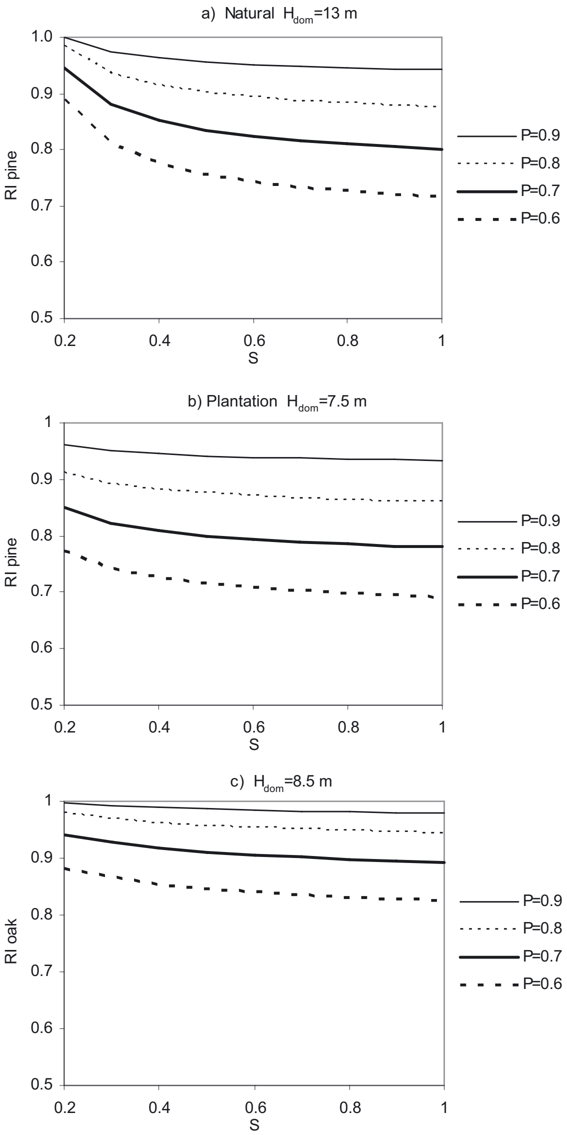

Figure 5. Estimated relative increment (Eq. (20)) of Scots pine (*RI* pine) and oak (*RI* oak) in mixed stands with different species proportions by area (*P*) for different stocking degrees (*S*): (a) natural Scots pine with dominant height of 13 m; (b) Plantation Scots pine with dominant height of 7.5 m; and (c) oak with dominant height of 8.5 m.

stocking degree was lower, suggests a greater level of elasticity in mixed stands where the stocking degree is reduced.

The different behaviour of dominant height in density-growth models for both species can be explained by the compound effect expressed by dominant height. For Scots pine it seems to indicate the development stage (lower growth in more developed stands), while for oak it seems to indicate mainly site quality (positively related to volume increment). The effect of the species proportion by area in both models indicates better use of an occupied area whenever the competition comes from the other species, i.e. a reduction of competition in mixed stands. The higher volume increments in plantation stands may be due to the lack of older plantation forests since most of the reforestations were carried out during the second half of the 20 century (Gil and Prada, 1993).

The low variability explained by the growth-density models may be due to the lack of age and site index information and to the characteristics of the SNFI data, in which measurement errors are frequent. The height measurements are usually even more inaccurate for broadleaved trees, explaining the poorer results for oak. Nevertheless, similar variabilities were obtained by Pretzsch (2005) in density-growth models developed for pure stands which included site index and diameter as covariates and which were based on long-term experimental plots.

Both studied species showed higher volume increments per hectare in mixed stands than in the respective monospecies stands. Similar results were found for mixtures of Scots pine with Norway spruce, alder and oak (Brown, 1992; Linden and Agestam, 2003). However, Frivold and Frank (2002) were not able to report a positive mixture effect where Scots pine grows alongside birch, probably because of the similar volume growth patterns of both species.

Despite the fact that the growth rate of each component species is higher in mixed than in pure stands, the total volume increment in mixed stands is generally lower than in pure Scots pine stands with a similar stocking degree. This fact is explained by the much higher productivity of one species in pure stands (Kelty, 1992). In the case of *P. sylvestris* and *Q. pyrenaica*, the differences in volume growth are very large; hence the reduction in area available to the Scots pine is not compensated by the increased growth of both species in mixed stands. Other studies concerned with mixed stands in which Scots pine are present reported a larger total production in comparison to pure stands for mixtures with Norway spruce and beech (Assmann, 1970; Brown, 1992; Linden and Agestam, 2003), although lower production was found where the mixture included oak and alder (Brown, 1992) because of the much smaller yield of these species.

Among the possible causes of a reduction in competition in mixed stands (Kelty, 1992; Man and Lieffers, 1999), the reduction in crown competition is probably one the main factors in stand compositions such as that considered in the present study. *P. sylvestris* and *Q. pyrenaica* present different shade tolerance and height growth patterns (Ruíz de la Torre, 1979), so mixed stands are frequently stratified with an overstory canopy of pine and an understory of oak (more shade tolerant and lower height growth). However, the influence of other factors should also be considered since the aforementioned stratification is not so patent for planted as opposed to natural stands of Scots pine (Tab. III).

There is evidence of differences in phenology and in the physiological responses of both species, although few studies have been developed in mixed stands (Inclan et al., 2007; Rodríguez-Calcerrada et al., 2008). A reduction in root competition might also occur in this mixture because of differences in the secondary roots, which are large and oblique in pine whereas oak develops stolons and abundant horizontal roots (Ruíz de la Torre, 1979). It is also likely that the deciduous leaves of the oak have a positive effect on nutrient cycling (facilitation) (Kelty, 1992), although previous studies concerning nutritional interactions in mixed forests revealed differing responses depending on species and environmental factors (Rothe and Binkley, 2001). Therefore, further research into the ecology of mixed stands with this composition are required.

5. CONCLUSIONS

The results of this study help to further our knowledge with regard to mixed stands of *P. sylvestris* and *Q. pyrenaica* and thus contribute towards achieving the objective of sustainable forest management in such stands. Although mixed stands are less productive than stands of pure Scots pine, the reduction in pine volume increment in mixed stands is lower than the corresponding reduction in occupied area. Therefore, by retaining or including a proportion of oak at around 20–30% per area, certain benefits associated with more complex forests could be gained without bringing about a great loss in pine wood production.

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