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Density and population structure of the natural regeneration of Scots pine (*Pinus sylvestris* L.) in the High Ebro Basin (Northern Spain)

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Abstract – This paper presents the analysis of 11 natural regenerated stands in native Scots pine forests located in the High Ebro Basin (Northern Spain). The natural regeneration showed a continuous age distribution, early height differentiation and a high stability in the height position of seedlings. Total density and main crop (trees selected for future commercial harvest) density models were developed to study the relationship between natural regeneration and site variables. Soil sand content was an important ecological factor distinguishing two groups of plots. Hardwood and Ericaceae species competition were the main factors that explained total density but only in soils with low sand content. Intensive herbivore grazing was proposed to produce a strong reduction of viable seedlings. Thus, vegetation-control treatments and limitation of cattle grazing in regeneration areas are highly recommended in the native Scots pine forests of the High Ebro Basin.

natural regeneration / population structure / *Pinus sylvestris* / Mediterranean region / Spain

Résumé – **Densité et structure des peuplements de Pin sylvestre (*Pinus sylvestris* L.) régénérés naturellement dans le Haut-Bassin de l'Ebre (Nord de l'Espagne).** Dans cet article sont analysés 11 peuplements régénérés naturellement, situés dans les forêts autochtones de Pin sylvestre du Haut-Bassin de l'Ebre (Nord de l'Espagne). La régénération naturelle a été caractérisée par une distribution continue de l'âge, une différenciation en hauteur précoce et une stabilité dans les classes de hauteur des plantules. Des modèles ont été développés pour étudier les relations entre la densité de la régénération naturelle et les variables du site. La densité totale et la densité moyenne de la récolte (la densité d'arbres sélectionnés qui constitueront la récolte commerciale future) ont été étudiées. Le contenu en sable du sol s'est révélé un facteur écologique important, permettant de distinguer deux groupes de sites. La compétition entre le résineux, les feuillus et les espèces du genre Ericaceae a représenté le facteur principal qui expliquait la densité totale, mais seulement dans les sols peu sableux. Le pâturage intensif dû aux herbivores semble avoir produit une forte réduction des plantules viables. Par conséquent, les traitements pour contrôler la végétation adventice et la limitation du pâturage dans les zones de régénération sont très recommandés à l'intérieur des forêts autochtones de Pin sylvestre du Haut-Bassin de l'Ebre.

régénération naturelle / structure des peuplements / *Pinus sylvestris* / région Méditerranéenne / Espagne

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1. INTRODUCTION

The demand for natural landscapes, the multi-resource use of forests and the high cost of plantations focus European foresters' attention on natural regeneration [1, 2, 19, 24]. Works studying the population structure and the main factors affecting natural regeneration in Scots pine (*Pinus sylvestris* L.) are abundant in the literature. Most of them refer to boreal or Atlantic forests whereas studies in the Mediterranean or Atlantic-Mediterranean transition context are scarce. The climatic range is important because it influences the type and structure of soils, the composition of vegetal communities and the natural regeneration process. The climate affects the quantity and quality of seed crop [31] and determines the elongation of flower primordia [27], flowering phenology [20, 36] and pollen dispersal. The climatic factors are also important during germination and early development of seedlings. In Mediterranean forests, the summer length and climatic irregularity are the main causes of failure of natural regeneration, so that the combination of seed production and favourable climatic conditions for seedling establishment only occurs every 20–40 years [28, 33]. Other main factors that affect regeneration success are herbivory and interspecific competition. Herbivore grazing reduces population density and height growth up to 30%, and early growth losses are not made up with time [12]. Interspecific competition of vegetation groups like trees and shrubs [14], *Ericaceae* [17] and grasses [23] are reported to have different effects upon natural regeneration so they are studied independently in this paper.

The characteristics of natural regeneration of Scots pine in the southern limit of the distribution area for the species are poorly studied. Discussion of the important elements for natural regeneration density can be utilised to define the silviculture of Scots pine in Mediterranean areas where low-intensity forest management and in situ genetic resources conservation have increasing interest [16, 39]. The aim of this work was: (1) the analysis of population structure of natural regeneration, (2) the study of density of Scots pine seedlings in relation to site variables and (3) the construction of predictive models for natural regeneration density.

2. MATERIALS AND METHODS

2.1. Site description

The Scots pine forests studied were situated at 710–910 masl in High Ebro Basin (Northern Spain) covering 13 000 ha (*figure 1*). Silviculture in the area is based on natural regeneration following a shelterwood

system and silvicultural interventions are not frequent at early stages of development. A site preparation consisting in a light soil scarification was in common practice in the area from the 1950s to the 1980s and so affected all the stands older than 10 years. The climate shows both Atlantic and Mediterranean influences, with an annual average rainfall of 787 mm (123 mm in summer) and an average annual temperature of 11.2 °C, without pronounced droughts (*figure 1*). The high interannual variation of temperature and precipitation typical of Mediterranean climates is moderated by the Atlantic influence. The soils are calcareous cambisols evolving to luvisols in humid sites. The floristic community is composed of mixed Atlantic and Mediterranean elements. *Quercus faginea* Lamk. and *Fagus sylvatica* L. appear in soils with low sand content and some edaphic moisture, being substituted by *Quercus ilex* L. in xeric soils. In sites with a low pH, heather (*Daboecia cantabrica* (Hudson) C. Koch., *Calluna vulgaris* (L.) Hull., *Erica vagans* L. and *Erica cinerea* L.), gorse (*Ulex europaeus* L. and *Ulex gallii* L.) and fern (*Pteridium aquilinum* (L.) Kuch.) formations are frequent.

2.2. Measurements

The sample included 11 stands that represented the ecological variability of the study area (*table 1*). A wide range of altitude (750–900 masl), slope (8–45%) and overstorey basal area (1.20–16.80 m² ha⁻¹), and different soil types (from cambisols to luvisols) were sampled. Sampling within the stands was conducted systematically based on a random start (100 × 100 m grid). A total number of 80 plots were measured (*table 1*). The plots were circular with a fixed radius of 2.5 meters (19.6 m²). Age and total height were measured on all Scots pine seedlings with diameter at breast height (1.30 m) less than 75 mm. The age of the individuals was assessed by calculating the number of nodes. In some cases, there were not a clear differentiation of nodes and the seedlings were cut in order to estimate the age by ring counting. The seedlings were scored considering height position (dominant/codominant/intermediate/suppressed) and damage by grazing, stamping and pests (healthy/low damage/moderate damage/highly damaged). The term “main crop seedling”, that is the trees selected to become a component of a future commercial harvest, referred to those seedlings with the highest score in both variables (dominant and healthy). The Stocked Quadrats method, with quadrats size of 4.9 m², was used for stocking estimation. In this method, plots are divided in four quarters (the quadrats) and stocking is defined as the percentage of quadrats with at least one healthy and dominant seedling [26].

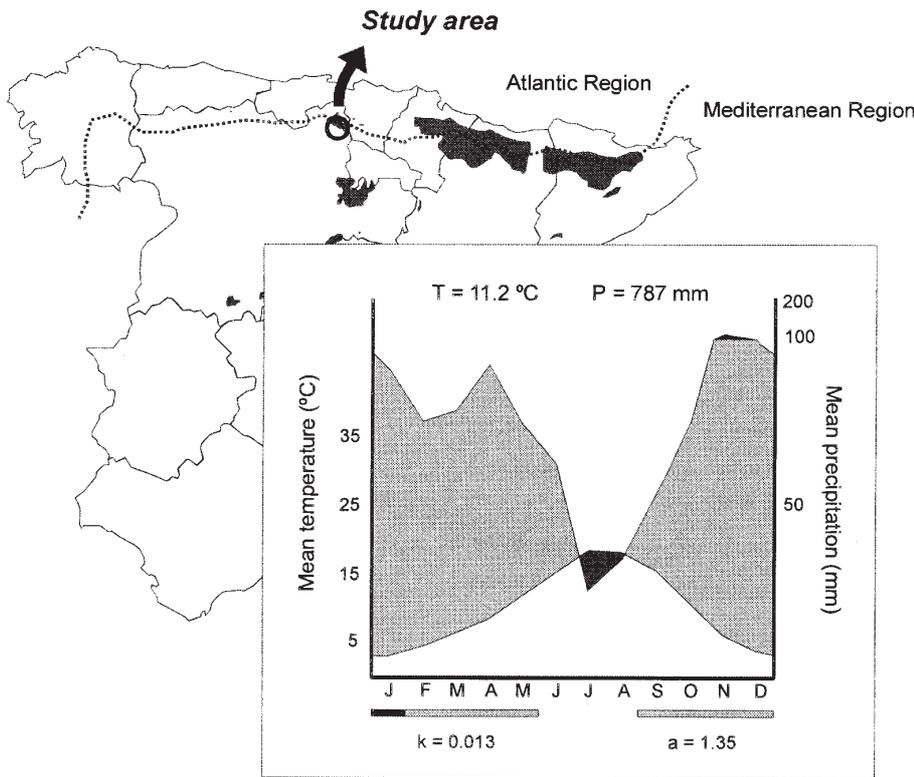


Figure 1. Walter-Lieth Climate Diagram and location map showing High Ebro Basin and its position related to the boundary between Atlantic and Mediterranean climates (dotted line) in Spain. The shadow area in the map indicates the native Northern Iberian distribution of Scots pine. Climate Diagram legend; dark shading: period of relative drought; light shading: period of relative humid season; T: annual average temperature; P: annual average rainfall; k: relative drought period/relative humid period ratio; a: period of relative drought in months.

Table I. Description of the stands.

Stand number	Area (ha)	Number of plots	Overstorey basal area (m ² ha ⁻¹)	Altitude (masl)	Slope (%)	Aspect
1	4.30	5	4.30	800	8	S-W-N
2	7.25	8	11.30	885	8	W
3	5.90	6	3.40	750	21	N-E
4	5.20	5	6.12	760	33	N-E
5	11.42	12	3.05	840	9	S-W-N-E
6	4.25	5	1.20	850	36	N
7	8.59	9	1.79	760	11	W-N-E
8	5.03	5	3.00	800	45	S-W
9	6.07	6	1.58	810	15	N
10	8.72	9	1.70	900	24	S-W-N-E
11	10.11	10	16.80	875	16	S-E

The site variables measured were classified into physiographic data (altitude, slope and aspect), edaphic data (texture and thickness of the humus layer), vegetation data (cover and mean height of different vegetation groups), and forest management data (residual basal area, distance from the nearest seed source and soil preparation). The description of site variables is shown in *table II*. Soil was evaluated following a field categori-

cal method based on moistened samples collected at 20 cm depth [30]. Four sand content categories were differentiated: below 40%, between 40 and 65%, between 65 and 80% and higher than 80%. Some samples (18.75%) were also analysed in the laboratory in order to check the accuracy of field estimations. Cover of the different groups of plants was visually scored using schematic diagrams illustrating covers from 0 to 100%

Table II. Description of the site variables included in the regression models.

Variable	Type	Range	Classes	Description
<i>Physiographic data</i>				
ALT	Quantitative	700–900	–	Altitude above sea level (m).
SLO	%	0–90	–	Slope measured with a clisimeter located in the middle of the plot.
ASP	Binary	–	<i>asp1</i>	Exposition of the plot, a binary variable that indicates Northern exposition.
<i>Edaphic data</i>				
TEXT	Categorical	–	<i>text1</i>	Sand content of the soil following a field categorical method. Dummy variable for sand content higher than 80%.
			<i>text2</i>	Sand content of the soil following a field categorical method. Dummy variable for sand content between 65% and 80%.
			<i>text3</i>	Sand content of the soil following a field categorical method. Dummy variable for sand content between 40% and 65%.
THIC	Quantitative	0–9	–	Thickness of the humus layer (cm).
<i>Vegetation data</i>				
PC 1	Quantitative	–	–	⁽¹⁾ Principal Component 1. Related to cover and mean height of hardwood species.
PC 2	Quantitative	–	–	⁽¹⁾ Principal Component 2. Related to cover and mean height of <i>Ericaceae</i> plants.
PC 3	Quantitative	–	–	⁽¹⁾ Principal Component 3. Related to cover of grasses.
<i>Forest management data</i>				
BAS	Quantitative	0–31	–	Overstorey basal area (m ² ha ⁻¹).
DIST	Quantitative	1–80	–	Distance from the seed source (m).
PREP	Binary	–	<i>prep1</i>	Site preparation, a binary variable that indicates when site preparation has been made.
TIME	Quantitative	0–23	–	Time from the beginning of the regeneration process in each stand (years).

⁽¹⁾ See further explanation in the text.

(5% step) under different spatial patterns. Mean height of the different groups was measured as follows: for each group of species the plot was divided into portions each having roughly constant height, separate mean heights were obtained for each portion by measuring a sample of at least 10 individuals (when available), and the values were combined in a weighted mean [13]. The variable Time, defined as the number of years from the beginning of the regeneration process (known by management records), was used in order to know if density increased, decreased, or remained constant during the regeneration period.

2.3. Data analysis

The data analysis was conducted in two steps. The first step was the analysis of population structure of natural regeneration. Then, the selection and interpretation of the main factors that affected density and the construction of predictive models were made.

The population structure of each stand was analysed by means of total density, main crop density and stocking calculations. Pattern, height and age structure analysis were also performed. Pattern analysis was based on

Blackman's coefficient [13]. This test makes use of the equality of mean and variance of the Poisson distribution. If the ratio of variance to mean is less than one, a regular pattern is indicated, if greater than one, a clumped pattern. Deviations from a random spatial pattern were tested using the Student t-test. Height and age structure analysis was carried out comparing the mean height of seedlings belonging to consecutive age-classes. Student t-tests comparing consecutive age-classes were done for each stand following Schepper [37]. Only age-classes with more than five trees were included. In addition, box-and-whisker plots for total height and age distributions were plotted. The whole set of data (80 plots) was used in this first step.

Explanatory interpretation of factors affecting density of natural regeneration was made by multiple regression analysis, adjusting models between total density and main crop density, and the site variables in *table II*. Because vegetation variables were strongly correlated (Pearson's correlation coefficient higher than 0.75 in some cases), principal component analysis (PCA) was used to get a set of independent variables from these data. The number of factors retained in the PCA was determined using the factors/eigenvalues plot [15]. Three principal components, explaining a 69.24% of the total

variance, were included in the models. Principal Component 1 (PC 1) had a high correlation with cover (0.93) and mean height (0.91) of the hardwood species present in the study area (mainly *Quercus faginea*, *Quercus ilex* and *Fagus sylvatica*), Principal Component 2 (PC 2) was strongly correlated with the cover (0.88) and mean height (0.86) of plants of the *Ericaceae* group (*Daboecia cantabrica*, *Erica cinerea*, *Erica vagans* and *Calluna vulgaris*) and Principal Component 3 (PC 3) was correlated with the cover (0.95) of grasses present in each plot (mainly *Brachypodium phoenicoides* (L.) Roemer and Schultes, *Dactylis glomerata* L., *Holcus lanatus* L. and *Arrhenatherum elatius* (L.) Beauv.). Categorical variables with k classes were included in the models defining $(k - 1)$ dummy variables. Starting from the saturated model where the effect of continuous variables is allowed to vary across all categories, the significance of interactions was tested by gradually simplifying the model. Only the dummy variable *text1* (soil sand content higher than 80%) had a significant interaction both in the total density and main crop density models, thus suggesting different performance of the quantitative variables for plots with different sand content. There were not enough plots, only eight, in sites with high sand content to adjust any model, so they were dropped for further analysis. Once the plots that caused the interaction effect were dropped, the following linear model was constructed:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n + \varepsilon$$

where y was the total density or main crop density depending on the model; x_1, x_2, \dots, x_n were the site variables; $\beta_0, \beta_1, \beta_2, \dots, \beta_n$ were the parameters to estimate; and ε was the experimental error. Linear models were estimated by weighted least-squares regression. This method does not alter the model structure and produces a near-constant variance of the residuals. The weighting factor was the inverse of the variance. Two thirds of the data (47 plots, after removing sandy plots) were used for the final model construction and one-third for its validation (25 plots).

The normality, linear independence and homogeneity of variance of the residuals were studied using the Shapiro-Wilk test, the normal probability plot and the residual values/predicted values plot. The variables were transformed, $x = (x + 0.5)^{0.5}$, to approach normality. This transformation is normally used with data that include many zero values [13, 38]. Percentage data were normalised using the logit transformation: $z = \log\{p/(1 - p)\}$. The logit transformation modifies a variable having a range 0 to 1 to a variable with no restrictions, similar to one that is normally distributed. Zero values were replaced with $25/n$ and 100-percent values with $100-$

$(25/n)$, where n was the sample size [4]. The atypical and influential points were detected by analysing the Studentized residuals and Cook's D , Dfbeta and Covratio values which measure the effect of an individual observation on the dependent variable, the regression coefficients and the variance-covariance matrix of the parameter estimates, respectively [32]. Validation of the models was done by studying the distribution, mean and variance of residuals of 25 plots not used in model construction. SAS® version 6.0 program was used for statistical analysis.

3. RESULTS

3.1. Population structure of natural regeneration

The mean total density was 0.51 ± 0.15 seedlings m^{-2} , with a minimum and maximum values of 0.13 and 0.93 seedlings m^{-2} , respectively (*table III*). Main crop density accounted for 46% of the total density. The stocking ranged from 18% in Stand 2 to 78% in Stand 7. Only 20% of plots had full stocking but 45% of plots were above 50% of stocking. The spatial pattern was clumped in all sites except in Stand 1, which showed a regular distribution.

The natural regeneration showed a nearly continuous age distribution (*figure 2*). There was a large difference between minimum and maximum individual tree age in each stand, with an uppermost range of 19 years (Stand 8) and 20 years (Stand 7). Although the upper stratum generally corresponded to the oldest seedlings, some new individuals had established during late stages of the regeneration phase. For instance, differences of 10 years between dominant trees could be found in Stand 9 (*figure 3*). However, there was a notable difference in mean height between consecutive age-classes (19 from 37 t-tests with $p < 0.05$) indicating a marked stability of the height position of seedlings. Within each age, the difference between the upper and the lower quartile for total height increased with age. In a particular and extreme case it was found a difference of 2 m in two seedlings that were both 13 years old (Stand 6).

3.2. Main factors affecting density of seedlings

The saturated models showed an interaction between soils with sand content higher than 80% (*text1*) and the other variables included in the models (*table IV*; only variables included in the final predictive models are shown). This result suggested a different pattern in soils with sand content above and below 80%. Field observations showed that the site preparation and the

Table III. Main characteristics and population structure parameters of natural regeneration in the study area.

Stand	Density (seedlings m ⁻²)	Main crop density	Mean age (years)	H _m (m)	Stocking (%)					Pattern
					0	25	50	75	100	
1	0.23 ± 0.12	0.12 ± 0.07	13.20 ± 2.09	1.94 ± 0.76	0	1	2	0	2	0.69 ^{ns}
2	0.13 ± 0.18	0.10 ± 0.13	1.43 ± 1.65	0.05 ± 0.05	4	2	2	0	0	1.84 ^{**}
3	0.28 ± 0.10	0.13 ± 0.56	8.00 ± 3.24	1.21 ± 0.50	1	1	0	3	1	2.06 ^{**}
4	0.59 ± 0.92	0.52 ± 0.89	4.50 ± 3.25	0.24 ± 0.16	1	1	2	0	1	2.63 ^{**}
5	0.50 ± 0.29	0.45 ± 0.29	1.44 ± 0.47	0.12 ± 0.03	2	0	3	3	4	4.31 ^{***}
6	0.41 ± 0.16	0.14 ± 0.12	10.40 ± 1.71	1.64 ± 0.49	0	0	2	3	0	2.76 ^{***}
7	0.69 ± 0.32	0.10 ± 0.10	12.07 ± 2.08	0.84 ± 0.29	0	0	3	2	4	4.44 ^{***}
8	0.33 ± 0.15	0.10 ± 0.10	10.00 ± 5.29	1.14 ± 0.64	1	0	2	2	0	6.27 ^{***}
9	0.23 ± 0.03	0.09 ± 0.04	18.50 ± 2.81	2.26 ± 0.53	0	1	2	3	0	1.74 [*]
10	0.93 ± 0.86	0.40 ± 0.45	3.83 ± 2.30	0.29 ± 0.21	3	0	1	3	2	7.03 ^{***}
11	0.82 ± 0.62	0.38 ± 0.31	3.60 ± 1.66	0.25 ± 0.14	3	1	2	1	3	10.49 ^{***}

H_m: Mean height; Stocking: Number of plots with 0, 25, 50, 75 and 100% stocking. Pattern: Blackman's coefficient and test of deviation from random distribution.

Table IV. Saturated models showing interaction effects between the dummy variable *text1* (soils with sand content higher than 80%) and the variables included in the final predictive models for total density and main crop density.

Model (<i>Adj-r</i> ²)	Variable	d.f.	Parameter estimate	Standard error	<i>t</i>
TOTAL DENSITY (0.3988)	CONSTANT	1	10.714	2.129	0.0388
	TIME	1	2.075	0.846	0.0181
	PC 1	1	-11.496	5.503	0.0424
	PC 2	1	-5.652	5.432	0.3037
	<i>Text1</i>	1	222.066	62.094	0.0008
	<i>Text1</i> * TIME	1	-16.589	7.991	0.0437
	<i>Text1</i> * PC 1	1	21.596	14.909	0.1544
	<i>Text1</i> * PC 2	1	30.224	44.077	0.4964
MAIN CROP DENSITY (0.4940)	CONSTANT	1	10.226	6.452	0.1203
	<i>Prep1</i>	1	27.576	8.380	0.0020
	PC 1	1	-5.980	4.983	0.2367
	PC 3	1	-10.602	6.236	0.0963
	<i>Text1</i>	1	74.384	19.194	0.0004
	<i>Text1</i> * <i>Prep1</i>	1	-36.834	35.294	0.3025
	<i>Text1</i> * PC 1	1	18.648	9.452	0.0550
	<i>Text1</i> * PC 3	1	13.327	22.279	0.5528

interspecific competition (both important in the plots with sand content below 80%) were apparently not affecting natural regeneration density in plots with high sand content. However, there were not enough plots in sites with sand content higher than 80% (only eight) to undertake the modelling of this group and, therefore, no conclusive results could be obtained. These plots were removed from the data set to allow the estimation of main effects in the final predictive models that are only valid for plots with sand content below 80% (table V).

The total density model, which accounted for 54% of the variation, included overstorey and understorey vegetation cover and mean height (PC1 and PC2, respectively) and the time from the beginning of the regeneration process. Total density of natural regeneration was positively correlated with the time from the beginning of the regeneration phase and negatively correlated with cover and mean height of hardwood and *Ericaceae* species. The magnitude of the correlation between each group of species and total density was similar, as shown by the parameter estimates. With respect to the main crop

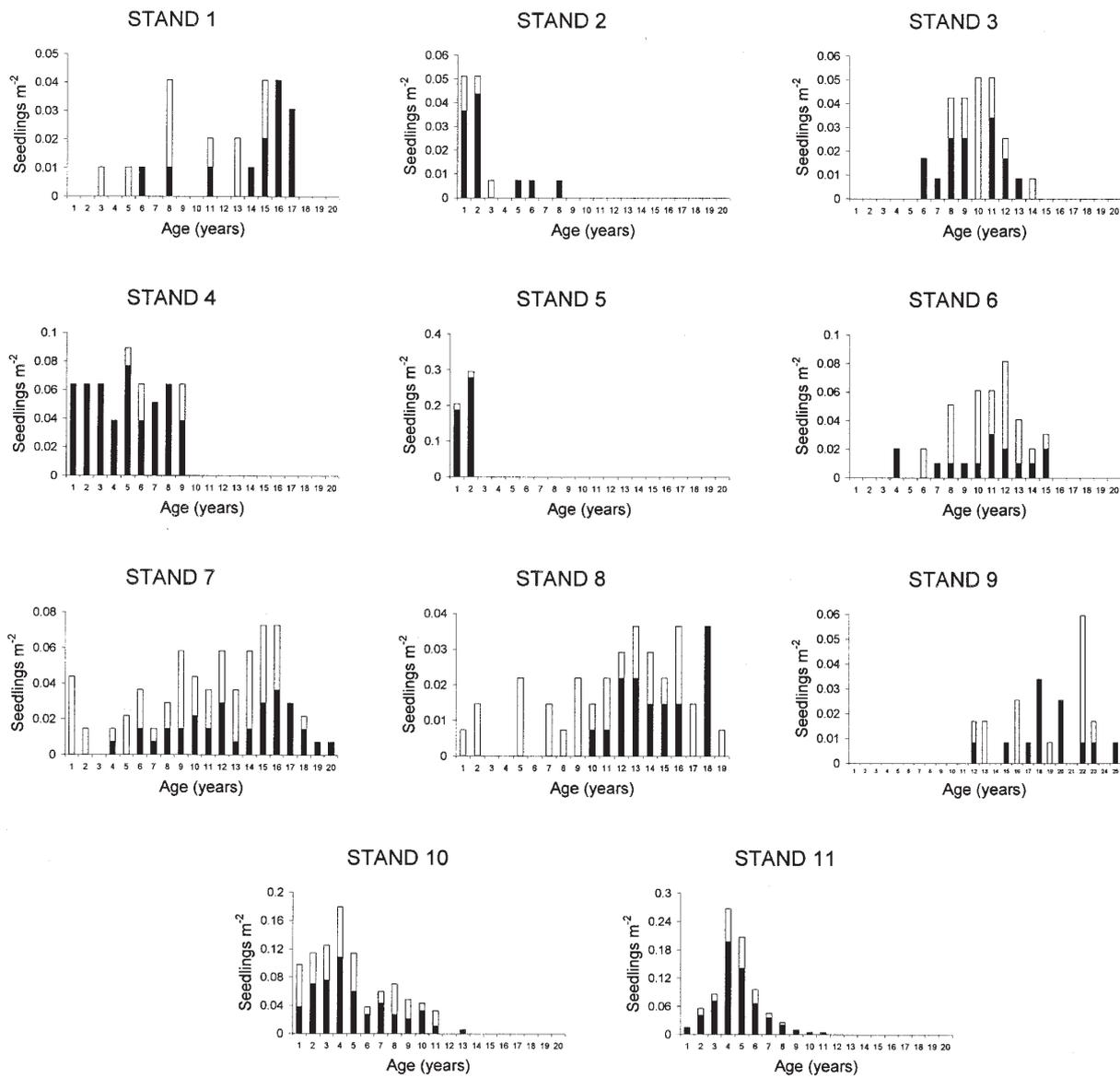


Figure 2. Age structure of 11 natural regenerated stands in the High Ebro Basin (Northern Spain). White bars indicate suppressed or injured seedlings.

density, the model showed a positive correlation between the establishment of successful seedlings and site preparation. In fact, holding constant the other factors (equal to the average in the study area), the model predicts an increase in the number of main crop seedlings from 0.03 to 1.30 seedlings m^{-2} when site preparation is made. On the contrary, grasses cover (PC 3) and cover and mean height of hardwood species (PC 1) were negatively correlated with the density of main crop seedlings.

The residual analysis of the final predictive models showed no violations of the assumptions (*figure 4*). Because atypical values were representative of the high ecological variability of the sampled area, they were not removed from the models. With respect to the validation analysis, the residuals showed a normal distribution both in the total density (Shapiro-Wilk's test = 0.98) and main crop density (Shapiro-Wilk's test = 0.93) models. The means of the residuals were 0.69 and 0.78 in the total

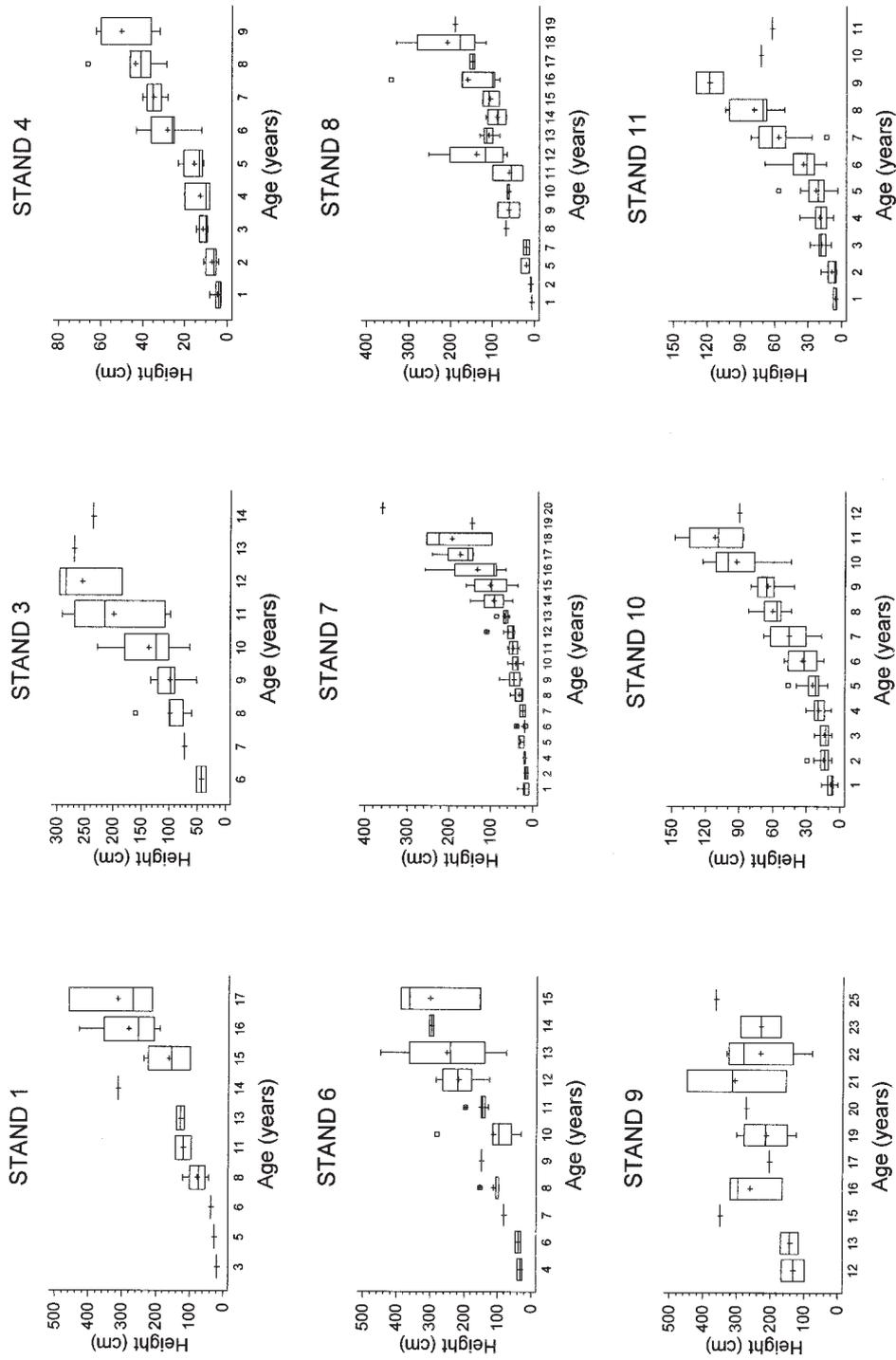


Figure 3. Box-and-Whisker Plots of the total height by age-class and stand. Stands with a mean age of less than two years have been excluded (Stands 2 and 5).

Table V. Weighted linear regression models for total density and main crop density.

Model (<i>Adj-r</i> ²)	Variable	d.f.	Parameter estimate	Standard error	<i>t</i>
TOTAL DENSITY (0.5378)	CONSTANT	1	14.012	8.154	0.0931
	TIME	1	2.738	0.699	0.0003
	PC 1	1	-11.831	2.120	0.0001
	PC 2	1	-9.512	4.408	0.0367
MAIN CROP DENSITY (0.5087)	CONSTANT	1	11.534	2.948	0.0003
	<i>Prep1</i>	1	20.912	4.284	0.0001
	PC 1	1	-5.136	1.475	0.0012
	PC 3	1	-8.877	2.164	0.0002

density and main crop density models, respectively, and not differed significantly from zero as shown by Student *t*-tests. In addition, the variances of the residuals were not different than the mean square errors of the models.

4. DISCUSSION

4.1. Population structure of natural regeneration

Multicohort stand dynamics were outlined by Oliver and Larson [29] for the single-species case, suggesting that the loss of vitality and death of shrubs and grasses due to the effect of minor disturbances allowed the establishment of new seedlings and produced nearly continuous age distributions. Complex stand structures and continuous age distributions due to episodic partial disturbances have been also found in mixed-species stands [9]. In contrast, in cases of severe disturbances, like a fire, the occupation of all the growing space in the first two-three years and the non viability of later settlers have been reported. For instance, Lust [25] indicated a regeneration period of only four years after a fire in a 600 ha Scots pine forest (High Campine, Belgium). A similar process to that described by Oliver and Larson [29] enhanced by the climatic irregularity of the area could produce the natural regeneration structure observed in the High Ebro Basin. A continuous series of climatic data (1951–1992; National Meteorological Agency, “Duero” Regional Centre) showed variation in climatic types from dry Mediterranean (during 7 years) to typical Atlantic (during 16 years) and a great variety of transitional types. Annual weather fluctuations have been reported as minor disturbances that are of great importance in the first stages of stand development [29]. The establishment of new seedlings in the stands may be caused by the loss of vitality and death of shrubs, grasses and other tree seedlings due to the effect of drought in dry years. The variation in height growth of Scots pine

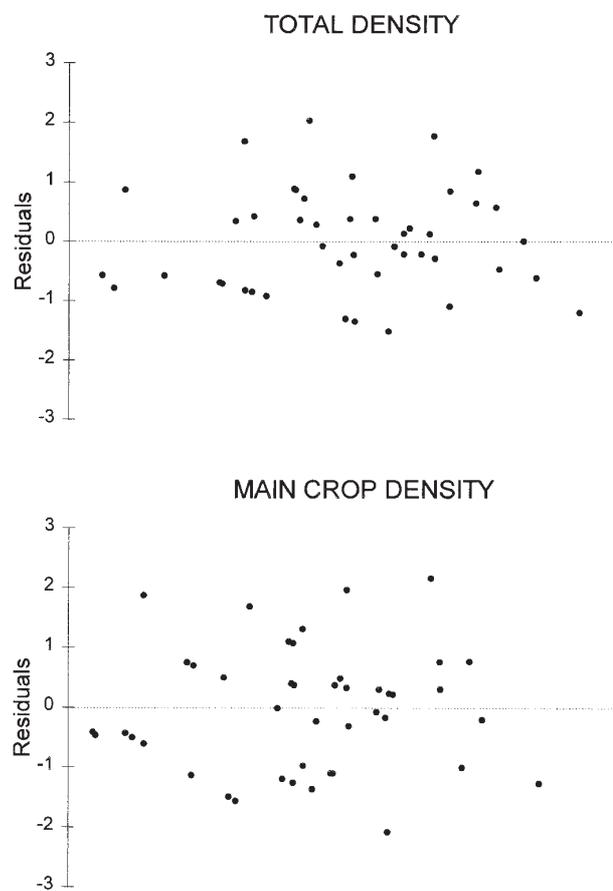


Figure 4. Residual values versus predicted values plot for total density and main crop density models.

seedlings has been suggested to be caused mostly by the spatial heterogeneity of the stand [21]. Differences in microsite variables affecting height growth could explain the possibility of promotion of later settlers to the

dominant stratum. Limited recruitment of tree seedlings due to low seed production or seed predation could also explain the observed population structure. Seed predation has important effects in the availability of seeds of *Pinus* species, being a key factor in small size populations [22]. As much as a 90% of pre-dispersal predation and a 61–96% of post-dispersal predation has been reported in relict stands of *Pinus sylvestris* in southeastern Spain [6]. However, seed availability does not seem a limiting factor in the High Ebro Basin where seed production is usually high and seed predation is reduced by the existence of other major food sources (e.g. *Fagus sylvatica*, *Quercus* spp).

The difference of height between consecutive age-classes indicates a high stability of the seedlings height positions. Ruha et al. [34] showed that the height positions are primarily established during the first 5–10 years at a mean height of less than 0.5–1 m and might be determined even by the height growth of the very first year. Early differentiation favours the natural selection of seedlings increasing the total yield at harvest time [14]. In the study area, the stability of the height positions is favoured by the heterogeneous pattern and the low-medium density of trees. In contrast, in high density stands of 6 to 15-year-old Scots pine, Ganther [11] observed trees moving from one height class to another. The early height differentiation and the stability of height positions allow an early selection of trees in the study area. In precommercial thinning, the height position of a tree could be used as an important criterion in the selection of the remaining trees.

4.2. Main factors affecting density of seedlings

Limited recruitment of seedlings in forest species due to interspecific competition is well-stated in the literature. The climatic conditions of the study area are suitable for the establishment of hardwood species (mainly *Q. faginea* and *F. sylvatica*). Schepper [37] showed constant growing rates for Scots pine in comparison with exponential growing rates for initial stages of oak species. This causes a clear initial competitive disadvantage for pine regeneration and poorly stocked stands as in the study area. The competition from broad-leaved species also seems to be the main limiting factor for Scots pine recruitment in Northern Italy [5]. The models assign a relevant role to the presence of *Ericaceae* in the natural regeneration success. Inhibition of germination of red clover by phenolic compounds from the aerial parts and roots of *Erica vagans*, *Calluna vulgaris* and *Daboecia cantabrica* has been reported in laboratory assays [3]. Other plants with potential allelopathic effects on Scots pine regeneration – like *Vaccinium myr-*

tillus or *Pteridium aquilinum* – are not likely to be of importance in the area because they have inhibitory compounds which are relatively more soluble than those from *Ericaceae* species [17] or their stocking is low in the study area. Lust [25], studying natural regeneration after a fire, pointed out the importance of physiographic factors (aspect, slope). In our study, physiographic factors were not significant probably due to a greater importance of interspecific competition and the absence of large disturbances [29, 40]. On the other hand, Scandinavian authors reported the importance of neighbouring seed-producing stands for regeneration success [2, 35, 41]. The extreme temperatures of Northern Europe limit Scots pine's flowering and cone production [18], whereas in High Ebro Basin seed production is usually abundant.

The grass layer is a physical barrier preventing fallen seeds from contacting the mineral soil. It also means a strong competition with settled seedlings. For instance, a 16% of height growth reduction has been observed in *Pinus taeda* with grass seeding of *Festuca arundinacea* applied at a rate of 2.8 g m⁻² [10]. Competition intensity with herbaceous vegetation is likely to increase in environments with low water availability [7]. In the study area, tree seedling success may be strongly influenced by competition for water during dry years. In addition, livestock and herbaceous plants are in close interrelation. Continuous cattle grazing changes the floristic community producing a dense pasture enriched with palatable species where cattle tend to concentrate. A strong reduction of main crop seedlings due to herbivores grazing and stamping in forest regeneration areas is common in the High Ebro Basin. In these cases, injured plants are frequent and the density of main crop seedlings is reduced. Cattle pressure produces reductions of growth, vigour and quality of wood in the Scots pine seedlings. Gong et al. [12] reported that in native pinewoods at Glen Tanar, Aberdeenshire (Scotland), the dominant seedlings, defined as the tallest 10 percent of seedlings in each plot, when aged 12 (61.5 cm height) were 22 cm higher in fenced than in unfenced plots. Slow-growing Scots pine plants are less able to compensate for biomass losses and, therefore, they have less chances to survive when attacked [8]. In consequence, damage is more detrimental in poor sites, thus increasing regeneration difficulties. Fencing seems to be, in the long term, the only reliable way of securing the development of natural regeneration in these areas.

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