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Cone and seed production from stone pine (*Pinus pinea* L.) stands in Central Range (Spain)

Received: 11 October 2004 / Accepted: 21 September 2005
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Abstract Natural regeneration of stone pine (*Pinus pinea* L.) stands in the Central Range of Spain can be difficult to attain. The success of this regeneration is affected by factors such as the total amount of seed available, the short dispersal ability of the pinyon, the conditions required for germination, specific problems associated with the establishment, early survival of the seedlings due to severe summer heat and drought, competition for water and mineral resources and grazing damage. This study focuses on seed availability. The amount of available seeds depends on the number and size of the cones and the number of viable pinyons within the cones. In stone pine stands, both variables show great year to year variability. Both cone and seed production, for a given year, are also conditioned by the vigour and health of the tree, its size, the condition and attributes of the stand and the loss of seed through pests or predation. In this study, the main factors which influence cone and pinyon production are identified and a multivariate model to predict annual cone and viable seed production is developed. To consider the correlation among observations coming from the same tree, stand or year, random components are included in the model. The multivariate random structure allows for future calibration of the model for a given year from a small additional sample of observations. It is important to know the total amount of viable seed produced in a stand for a given year since regeneration cuttings for Stone pine should be concentrated in high crop years.

Keywords Seed production · Multivariate systems · Mixed model · Calibration

Communicated by Hans Pretzsch

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Introduction

The natural regeneration of forests constitutes one of the main objectives of silviculture. Temperate forests in Central and Northern Europe have been naturally regenerated for two centuries by following different silvicultural systems. However, the application of these well-known practices, especially the use of shelterwood systems to promote natural regeneration in Mediterranean forests, has generally failed. Several reasons for this lack of success have been suggested:

- (1) Most Mediterranean species show masting habits, which lead to long intervals between good seed crops. If a delay occurs between seed felling and a good crop year, it is probable that a layer of competing herbaceous plants will appear, covering the soil surface. This understory layer will make it difficult for seeds to reach the mineral soil and will obstruct the subsequent establishment of seedlings.
- (2) The seed of many Mediterranean species is too big for wind dispersal. This large seed size allows the seedling to survive after germination using its own reserves, but this means that regeneration is unlikely outside the area of influence under the crown of the seed tree. This factor, together with the low density of Mediterranean stands, will favour the presence of large gaps in the forest where regeneration seldom appears.
- (3) The main produce associated with several Mediterranean forests is obtained from standing trees: products such as cork, resin or fruits. Due to this fact, regeneration felling is usually delayed to the point where seed crops have significantly reduced in number or viability and the trees, which are more mature by that time, suffer greater damage.
- (4) The Mediterranean climate is characterized by a severe summer drought. This condition can even prevent the germination of spring-dispersed seeds. Summer drought is also the main cause of death in young plants.

- (5) The presence of livestock is quite common in Mediterranean forests. The impact of grazing on young plants can be so severe as to endanger the viability of seedling survival. Fire, another basic element in Mediterranean ecosystems, can also be a factor in the loss of young seedlings.

Stone pine (*Pinus pinea* L.) stands are not an exception to these general rules. A few studies have described the narrow optimal conditions required for the germination of seeds (Magini 1955) or for seedling establishment and survival (Masetti and Mencuccini 1991). Stone pine stands, compared to other Mediterranean forests, have a further limitation with respect to natural regeneration. The pinyon (pine nut), which is the edible seed of the Stone pine, is a widely used and highly appreciated food source. Stone pine cones are collected from natural stands, and the income derived from the managed exploitation of this product is often much larger than that associated with timber or firewood. The removal of cones from the forest is an activity which is not compatible with natural regeneration and as such should be regulated or even forbidden during the regeneration period.

The joint action of all these limiting factors has resulted in the continuous failure of natural regeneration in stone pine stands. As an alternative, the application of artificial regeneration by direct seedling after clear-cutting gaps or strips within the forest has been the most widely used method (Ximénez de Embún 1959).

The managers of stone pine forests cannot control factors such as the large pinyon size, the temperament of the species or the hot, dry conditions of the Mediterranean summers. But several things can still be done to help natural regeneration in these stands. For example, seed fellings should be concentrated in high seed crop years, cattle must be kept out of the forest during the regeneration period, cone collection should be forbidden at least during the first years after seed fellings and the stand rotation length should not be extended to a point where crop or seed viability is reduced. The selection of the year in which to start seed fellings, and consequently, to prohibit both livestock grazing and cone collection in the forest, is one of the main decisions to be taken by managers. This year must coincide with a good seed crop to ensure that a sufficient amount of viable seed reaches the soil before the invasion of competing species. Therefore, managers require effective tools to estimate seed production well in advance to plan their actions correctly.

Stone pine cone production, the amount of pinyons per cone and the viability of these pinyons are variables which show great between-year variability. Several recent studies have focused on predicting cone production from natural stone pine stands (Castellani 1989; García Güemes 1999; Cañadas 2000). These studies have been developed from an economic viewpoint, trying to estimate the average cone production, referred to as weight per hectare, for a given period. Between-year variability in stone pine cone production has seldom been discussed

(Gordo et al. 2000; Calama 2004). The study of seed production per cone was approached by Magini and Giannini (1971) and Montero et al. (2000), who give average values for pinyon contents and percentage of empty seeds as a function of stand attributes, such as site index, density or age. No references have been found which focus on between-year stone pine seed production.

The main aim of this study is to develop a model for predicting the total amount of cones and viable pinyons (for germination) produced in a stand for a given year. The model developed could provide a tool for forest managers to identify an adequate year to start seed fellings in order to regenerate stands, as well as to fix the length of the regeneration period or even, to permit commercial cone collection, albeit with some kind of limitation, in a specified year during the regeneration period.

Material

Study area

The stone pine (*P. pinea* L.) occupies more than 30,000 ha in the Central Range in Spain, of which 11,000 ha can be considered natural, pure, even aged stands of the species. Most of the important stands in the area are growing on the rocky granitic slopes, which define the valleys of the Alberche and Tietar rivers, occupying an altitudinal strip between 700 and 1,000 m. Below this limit, stone pine forms mixed stands with oaks (*Quercus ilex* L.), whilst on the upper limit of the strip, stone pine is replaced by resin pine (*Pinus pinaster* Ait.).

These valleys conform a mountainous area with an orography and relief characterized by a succession of hills and small valleys, with steep slopes defining an abrupt landscape. This typology of stands contrasts with the flat areas where the species typically occurs in other areas of the country (such as the Northern Plateau or Andalusia). The stone pine grows on poor soils, mainly composed of sands, with high presence of granite rocks in surface layers. The climate is genuine Mediterranean, defined by a long, hot, dry summer period (where mean monthly rainfall is about 10 mm) and more humid autumns and springs.

The complex orography of these stands has conditioned its management since ancient times. The difficulty for logging and extracting timber has led to stand production being mainly limited to pinyons and livestock. To favour individual cone production as well as the presence of pasture, stands have been maintained at low densities, reaching figures as low as 100 stems per hectare at older ages.

The application of shelterwood and selection systems to naturally regenerate these stands has traditionally failed as a result of cone collection each autumn and the continuous presence of livestock, especially goats, within the forests. The joint action of both factors has resulted

in a total absence of recently regenerated stands, conforming in some cases to a multi-aged structure (Montero et al. 2003) and, in many cases, open stands where only a few, very old pines make up the higher layer of the forest.

Data set

In 1996 a network of 49 experimental plots was installed in even-aged stone pine stands within the study area. It was intended that the criteria used for selecting the plots should include a balanced representation of all the possible age, site quality and density classes identified in the region. Plots were uniformly distributed across the study area (Fig. 1).

The plots were circular, of variable size, and comprised ten trees. For every tree, breast height diameter, total height, height to crown base and crown diameter were recorded at plot installation. The position of the trees was also noted with respect to the centre of the plot. The diameter increment over a 5-year period was recorded at plot installation and in 2001 for a sample of three to five trees per plot.

Between the year of installation and the present (8 years), cones have been collected every autumn from the five trees nearest to the centre of each plot. The cones cropped from each tree are classified as either 'healthy' or 'damaged'. Damaged cones are those attacked by *Dyorictria mendacella* Stgr. (Lepidoptera) and *Pissodes validirostris* Gyll. (Coleoptera). Healthy cones from each tree are counted and weighed. A sample of five healthy

cones per tree is separated and sent to a laboratory. These cones are oven-dried, and once they are opened, pinyons are extracted, counted and weighed. During the first 5 years (1996–2000), a sample of 100 pinyons per tree were separated, and these pinyons were cracked to obtain the nut ('white pinyon'). The number of empty pinyons in the sample (aborted seeds) was recorded and healthy, white pinyons were counted and weighed. A summary of the statistics for cone and pinyon data is shown in Table 1.

Methods

Selection of response and explanatory covariates

The main aim of this study is to develop a tool for estimating the total amount of sound seed, viable for germination, available for a given year from a specific tree. The total number of viable seeds produced by a tree is a non-observed variable that can be approached as a multiplication of observed variables:

$$Vs_{jk} \approx Nh_{jk} \cdot Np_{jk} \cdot (1 - Em_{jk}), \quad (1)$$

where Vs_{jk} is the number of viable seeds produced by the tree j during year k , Nh_{jk} the total number of healthy cones for tree j during year k , Np_{jk} the average number of pinyons per cone for tree j during year k , and Em_{jk} the rate of empty seeds in a sample of 100 pinyons for tree j during year k .

To solve this determination, we propose in a first step to develop single linear models for each one of the

Fig. 1 Location of study area and experimental plots

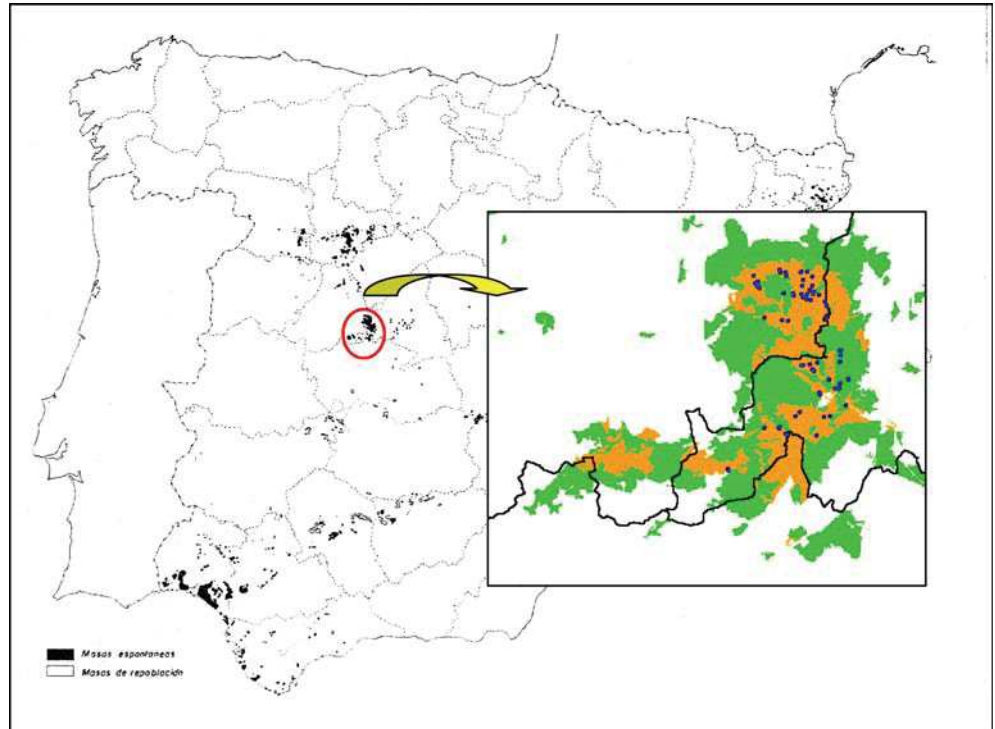


Table 1 Summary statistics for cone and seed variables (observed data)

	<i>Nh</i>	<i>Mw</i> (kg)	<i>Em</i>	<i>Np</i>
Average	16.31	0.308	0.095	83.72
Variance	1063.11	0.010	0.017	799.18
CV (%)	199.92	32.66	137.47	33.76
Min	0	0.029	0	2
Max	519	0.852	1	183
Years	8	8	5	8
<i>n</i>	1,896	1,379	895	1,359

where *Nh* is the number of healthy cones in a tree, *Mw* mean weight for the cones of a tree, *Em* rate of empty seeds, *Np* number of pinyons per cone, *CV* coefficient of variation, *Years* number of years sampled, *n* total number of data

response variables involving *Nh*, *Np* and *Em*. Preliminary models were fitted using ordinary least squares linear regression, selecting the covariates to be included in each model by applying a stepwise method, and considering collinearity among variables. The explanatory variables evaluated were either single tree, stand or crop attributes.

The model proposed to explain *Nh_{jk}* shows the same structure as that proposed by Calama (2004) in his interregional growth and yield model for the species:

$$\log(Nh + 1) = \beta_{1,0} + \beta_{1,1}g + \beta_{1,2} \log(N) + \beta_{1,3}SI + e_1, \quad (2)$$

where *g*, *N* and *SI* are tree section (m²), stand density (stems/ha) and site index (m) respectively; *e₁* indicates residual error.

For both *Np* and *Em*, the variable with the greatest correlation was *Mw*, mean weight of cones for the tree in that year (kg). This relation indicates that the larger the cone, the greater the number of pinyons it contains, and that the smaller the cone, the lower the percentage of sound seeds. The number of pinyons within the cone was also highly correlated with the total number of cones, mainly indicating that in a good crop year, cones tend to be bigger and filled with a larger number of pinyons. This latter relation has also been found for several coniferous species, e.g. *Picea mariana* (Mill) BSP (Sirois 2000). The proposed preliminary models for both variables were:

$$Np = \beta_{3,0} + \beta_{3,1}Mw + \beta_{3,2} \log(Nh + 1) + e_3, \quad (3)$$

and

$$Em = \beta_{4,0} + \beta_{4,1}Mw + e_4. \quad (4)$$

Mw is a variable whose observation requires the collection of fully developed cones (in the autumn). To obtain prior estimates of this variable the following linear model was proposed:

$$Mw = \beta_{2,0} + \beta_{2,1}SI + e_2. \quad (5)$$

Univariate multilevel linear mixed models

The observed values for each response variable can be considered a sample of repeated observations taken in different years from trees located in experimental plots distributed within the study area. This hierarchical structure for the data indicates a possible lack of independence acting at three levels: observations coming from the same tree, observations coming from the same plot and observations taken in the same year. To avoid inference problems derived from this non-independent structure, a multilevel linear mixed model, including random components for the intercept of the model at tree within plot, plot and year level is proposed for each response variable. Let *y_{ηijk}* be the observation corresponding to the *η_{th}* response variable. The univariate multilevel mixed model for this variable is given by:

$$y_{\eta ijk} = \mathbf{x}_{\eta ijk}\beta_{\eta} + u_{\eta i} + v_{\eta ij} + w_{\eta k} + e_{\eta ijk},$$

where *x_{ηijk}* is the design vector for the *η_{th}* response variable associated with the *j_{th}* tree within the *i_{th}* plot measured during year *k*; *β_η* is the vector of fixed parameters for the *η_{th}* response variable; *u_{ηi}*, *v_{ηij}* and *w_{ηk}* are random components associated with the *η_{th}* response variable, common for the observations taken from the same plot, tree and year respectively; *e_{ηijk}* is a residual term of the error; *u_{ηi}*, *v_{ηij}*, *w_{ηk}* and *e_{ηijk}* show a univariate distribution with mean zero and variance *σ_{uη}²*, *σ_{vη}²*, *σ_{wη}²* and *σ_{eη}²*, respectively. Random components acting at different levels are assumed to be uncorrelated.

Multivariate multilevel linear mixed models

Linear models used to define the response variables can be written as a system of univariate multilevel mixed models:

$$\left. \begin{aligned} \log(Nh + 1)_{ijk} &= \beta_{1,0} + \beta_{1,1}g_{ijk} + \beta_{1,2} \log(N_i) \\ &\quad + \beta_{1,3}SI_i + u_{1i} + v_{1ij} + w_{1k} + e_{1ijk} \\ Mw_{ijk} &= \beta_{2,0} + \beta_{2,1}SI_i + u_{2i} + v_{2ij} + w_{2k} + e_{2ijk}, \\ Np_{ijk} &= \beta_{3,0} + \beta_{3,1}Mw_{ijk} + \beta_{3,2} \log(Nh + 1)_{ijk} \\ &\quad + u_{3i} + v_{3ij} + w_{3k} + e_{3ijk}, \\ Em_{ijk} &= \beta_{4,0} + \beta_{4,1}Mw_{ijk} + u_{4i} + v_{4ij} + w_{4k} + e_{4ijk}. \end{aligned} \right\} \quad (6)$$

The above functions define a simultaneous cone and pinyon yield system of equations, where endogenous variables, such as *log(Nh + 1)* or *Mw*, are used as response variables and predictors. Consequently, response variables can be correlated, indicating that an independent fit of each equation could lead to both bias and inconsistent parameter estimation (Borders 1989). To carry this out, a simultaneous fit of the

multivariate multilevel linear mixed system, following Goldstein (1995), was proposed:

(the vector 12×1 whose components are zeroes) and variance matrix $\mathbf{D}_{12}$. As correlation between random

$$\underbrace{\begin{pmatrix} \log(Nh+1)_{ijk} \\ Mw_{ijk} \\ Np_{ijk} \\ Em_{ijk} \end{pmatrix}}_{\mathbf{y}_{ijk}} = \underbrace{\begin{pmatrix} 1 & g_{ijk} & \log(N)_i & SI_i & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & SI_i & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & Mw_{ijk} & \log(Nh+1)_{ijk} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & Mw_{ijk} & 0 \end{pmatrix}}_{\mathbf{X}_{ijk}} \underbrace{\begin{pmatrix} \beta_{1,0} \\ \beta_{1,1} \\ \beta_{1,2} \\ \beta_{1,3} \\ \beta_{2,0} \\ \beta_{2,1} \\ \beta_{3,0} \\ \beta_{3,1} \\ \beta_{3,2} \\ \beta_{4,0} \\ \beta_{4,1} \end{pmatrix}}_{\boldsymbol{\beta}} + \underbrace{\begin{pmatrix} 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 \end{pmatrix}}_{\mathbf{Z}_{ijk}} \underbrace{\begin{pmatrix} u_{1i} \\ u_{2i} \\ u_{3i} \\ u_{4i} \\ v_{1ij} \\ v_{2ij} \\ v_{3ij} \\ v_{4ij} \\ w_{1k} \\ w_{2k} \\ w_{3k} \\ w_{4k} \end{pmatrix}}_{\mathbf{b}_{ijk}} + \underbrace{\begin{pmatrix} e_{1ijk} \\ e_{2ijk} \\ e_{3ijk} \\ e_{4ijk} \end{pmatrix}}_{\mathbf{e}_{ijk}}.$$

The above equations show the expression for a multivariate multilevel linear mixed model (Multivariate ML LMM) for a single observation. Multivariate ML LMM for n observations of the four response variables, taken on n_v trees located within n_u plots during n_w years can be expressed as follows:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{b} + \mathbf{e}, \quad (7)$$

where, in this case, $\mathbf{y}$ is a response $4n \times 1$ vector containing the observations for the response variables taken from the n_v analysed trees; $\mathbf{X}$ is a $4n \times 11$ design matrix including covariates and terms associated with fixed parameters, whose rows are vectors $\mathbf{x}_{ijk}$; $\boldsymbol{\beta}$ is the 11×1 vector of fixed parameters described previously; $\mathbf{Z}$ is a $4n \times 4$ ($n_u + n_v + n_w$) design matrix for the random components; $\mathbf{b}$ is a 4 ($n_u + n_v + n_w$) $\times 1$ vector containing the random components acting at tree, plot and year level; $\mathbf{e}$ is the $4n \times 1$ vector containing the residual error terms of the model.

Structure for variance–covariance matrices

Vector $\mathbf{b}_{ijk}$ for a single multivariate observation $\mathbf{y}_{ijk}$ is distributed under a multivariate normal, with mean $\mathbf{0}_{12}$

components corresponding to different hierarchical levels is supposed to be negligible, $\mathbf{D}_{12}$ is a 12×12 block diagonal matrix composed of three 4×4 submatrices $\mathbf{D}_u$, $\mathbf{D}_v$ and $\mathbf{D}_w$, which define random between plot, within plot and between year variability. $\mathbf{D}_u$, $\mathbf{D}_v$ and $\mathbf{D}_w$ can show several structures, depending on the different covariance parameters considered. Comparisons among different variance structures were made on the basis of two times log likelihood ($-2LL$), level of significance for fixed effects and variance components and biological sense for the covariance parameters.

In fitting the multivariate ML model, $\mathbf{D}_u$, $\mathbf{D}_v$ and $\mathbf{D}_w$ were considered common for every plot, tree and year analysed. Under the common assumption of independence between random components corresponding to different subjects, the variance matrix for the random variability associated with the multiple observations vector $\mathbf{y}$ is a block diagonal matrix $\mathbf{D}$, comprising as many matrices $\mathbf{D}_u$, $\mathbf{D}_v$ and $\mathbf{D}_w$ as plots (n_u), trees (n_v) and years (n_w), respectively, considered in the sample.

Vector $\mathbf{e}_{ijk}$ includes residual error terms for the multivariate observation $\mathbf{y}_{ijk}$, and it is distributed following

a multivariate normal with mean $\mathbf{0}_4$ and variance matrix $\mathbf{R}_4$. Correlation between residual terms corresponding to different response variables is considered to be negligible. $\mathbf{R}_4$ is then proposed as a diagonal matrix with components $\sigma_{e\eta}^2$. In fitting the model from a multiple multivariate observation (e.g. n observations from the four dimensional variable), and considering independence between residual terms from different subjects, $\mathbf{R}$ is $4n \times 4n$ diagonal matrices with diagonal components $\sigma_{e\eta}^2$ (with η : 1–4).

Fit and estimation of the multivariate multilevel linear mixed model

In fitting a multivariate ML LMM, our interest focuses on obtaining estimates for the fixed parameters of the model, β ; for the components of $\mathbf{D}$ and $\mathbf{R}$; and individual predictions for the components of vector $\mathbf{b}$ specific for each plot, tree and year. Multivariate ML LMM was fitted using the SAS procedure MIXED (Little et al. 1996; Singer 1998). A simultaneous fit was carried out by multiplying each term of the model by a dummy index variable f_η whose value is 1 if the component is included in the equation for the η th response variable and 0 if not. The model implemented can be described as:

$$\begin{pmatrix} f_1\mathbf{y} \\ f_2\mathbf{y} \\ f_3\mathbf{y} \\ f_4\mathbf{y} \end{pmatrix} = \begin{pmatrix} f_1\mathbf{X} \\ f_2\mathbf{X} \\ f_3\mathbf{X} \\ f_4\mathbf{X} \end{pmatrix} \beta + \begin{pmatrix} f_1\mathbf{Z} \\ f_2\mathbf{Z} \\ f_3\mathbf{Z} \\ f_4\mathbf{Z} \end{pmatrix} \mathbf{b} + \begin{pmatrix} f_1\mathbf{e} \\ f_2\mathbf{e} \\ f_3\mathbf{e} \\ f_4\mathbf{e} \end{pmatrix}, \quad (8)$$

where $\mathbf{y}$, $\mathbf{X}$, $\mathbf{Z}$, β and $\mathbf{b}$ are as previously stated. Appendix 1 shows the basic structure for the developed SAS program. This model is solved as a univariate ML LMM (Singer 1998; Hall and Bailey 2001). To take into account significant deviation from multivariate normal distribution, the components of matrices $\mathbf{D}$ and $\mathbf{R}$ were estimated using the MIVQUE0 method (Rao and Kleffe 1988). Estimates of the variance matrices are defined as $\hat{\mathbf{D}}$ and $\hat{\mathbf{R}}$. An estimate for the variance–covariance matrix of the observations is given by:

$$\hat{\mathbf{V}} = \mathbf{Z}\hat{\mathbf{D}}\mathbf{Z}^T + \hat{\mathbf{R}} \quad (9)$$

Fixed parameters vector β was estimated using generalized least squares (GLS) techniques:

$$\hat{\beta} = (\mathbf{X}^T \hat{\mathbf{V}}^{-1} \mathbf{X})^{-1} \mathbf{X}^T \hat{\mathbf{V}}^{-1} \mathbf{y} \quad (10)$$

Finally, the empirical best linear unbiased predictor (EBLUP) for the vector $\mathbf{b}$, including the random components specific for each plot, tree and year analysed was predicted using:

$$\hat{\mathbf{b}} = \hat{\mathbf{D}}\mathbf{Z}^T \hat{\mathbf{V}}^{-1} (\mathbf{y} - \mathbf{X}\hat{\beta}). \quad (11)$$

In fitting the fixed parameters of the model, variance components, random terms and residual variances were obtained for each response vector. To reduce computational effort and help convergence of the routines, it is necessary to make the scale of the response variables and residual variance terms as homogenous as possible. To do this, the following transformations of the response variable were proposed:

$$\text{Ln} = \log(Nh + 1)/10,$$

$$Np100 = Np/100.$$

Results

Fitting multivariate multilevel linear mixed model

Among the different evaluated variance–covariance structures for matrices of random components, we finally considered a diagonal (type VC) structure for $\mathbf{D}_u$, $\mathbf{D}_v$ and a complete structure (type UN) for $\mathbf{D}_w$. The best results, in terms of $-2LL$, were obtained considering type VC for the three matrices, but as significant correlations between random terms for different response variables at the same year level were identified, we included these covariation terms within the model.

The selected structure assumes correlation between random components for a given year, indicating that systematic deviations for response variables detected in a given year are correlated (e.g. mean weight of cones and number of empty pinyons). Covariation structure between random year components for different response variables will allow us to explain contemporaneous correlation between response variables and to calibrate the model for a given response variable using measurements of another variable taken in the same year.

Results after fitting model (4) under the variance–covariance structure proposed are shown below. The fixed parameter associated with site index (SI) in the model for Ln was identified as nonsignificant, and subsequently it has been removed from the equation. All other fixed parameters, variance components and the main part of the covariance components included are significant.

$$\text{Ln}_{ijk} = 0.2641 + 0.6492g_{ijk} - 0.0310 \log(N_i) + u_{1i} + v_{1ij} + w_{1k} + e_{1ijk},$$

$$Mw_{ijk} = 0.1301 + 0.01199 \text{ SI}_i + u_{2i} + v_{2ij} + w_{2k} + e_{2ijk},$$

$$Np100_{ijk} = 0.3068 + 1.3448Mw_{ijk} + 0.4142 \text{ Ln}_{ijk} + u_{3i} + v_{3ij} + w_{3k} + e_{3ijk},$$

$$Em_{ijk} = 0.2368 - 0.4151Mw_{ijk} + u_{4i} + v_{4ij} + w_{4k} + e_{4ijk},$$

With

natural regeneration carried out by Massetti and Mencuccini (1991) in a stone pine forest in Toscana

$$\begin{pmatrix} u_{1i} \\ u_{2i} \\ u_{3i} \\ u_{4i} \end{pmatrix} \approx N \left[\begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \mathbf{D}_u = \begin{pmatrix} 0.003614 & 0 & 0 & 0 \\ 0 & 0.000891 & 0 & 0 \\ 0 & 0 & 0.001871 & 0 \\ 0 & 0 & 0 & 0.000729 \end{pmatrix} \right],$$

$$\begin{pmatrix} v_{1ij} \\ v_{2ij} \\ v_{3ij} \\ v_{4ij} \end{pmatrix} \approx N \left[\begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \mathbf{D}_v = \begin{pmatrix} 0.001825 & 0 & 0 & 0 \\ 0 & 0.000953 & 0 & 0 \\ 0 & 0 & 0.007355 & 0 \\ 0 & 0 & 0 & 0.000658 \end{pmatrix} \right],$$

$$\begin{pmatrix} w_{1k} \\ w_{2k} \\ w_{3k} \\ w_{4k} \end{pmatrix} \approx N \left[\begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \mathbf{D}_w = \begin{pmatrix} 0.004312 & 0.001001 & 0.004390 & -0.00297 \\ 0.001001 & 0.003253 & 0.000820 & -0.00110 \\ 0.004390 & 0.000820 & 0.013300 & -0.00181 \\ -0.00297 & -0.00110 & -0.00181 & 0.002334 \end{pmatrix} \right].$$

Finally, the distribution for the residual error terms associated with a single multivariate observation is given by:

(Italy) were used to determine the total amount of sound seed necessary to obtain a single seedling per standing tree, located out of the area shaded by the crown,

$$\begin{pmatrix} e_{1ijk} \\ e_{2ijk} \\ e_{3ijk} \\ e_{4ijk} \end{pmatrix} \approx N \left[\begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \mathbf{R}_4 = \begin{pmatrix} 0.01063 & 0 & 0 & 0 \\ 0 & 0.00427 & 0 & 0 \\ 0 & 0 & 0.02769 & 0 \\ 0 & 0 & 0 & 0.01308 \end{pmatrix} \right].$$

The use of a ML mixed model allows us to identify and divide the total variability detected for each response variable in different sources. The fixed effects model, defining the expected unconditional mean response, explains this variability in part. Systematic random variability is associated with among plot, among tree within plot and among year variability, as well as a non-explained term for residual variance. Figure 2 shows the percentage of total variability explained by the different effects for the response variables analysed.

Application of the model

The aim of this study is to predict the number of sound seeds that a single tree can produce in a given year. We are interested not only in the expected mean value for the tree crop, but also in its confidence interval, since it will allow the estimation of the probability for a given crop.

Since no regeneration studies have been developed within the study area, results from the experiment on

surviving at least a 2-year period after germination. From that study, we consider that only 3% of the seed disseminated falls out of the area of crown influence. The percentage of seed germination outside the shaded area is about 10%. Finally, only 30% of the seedlings survive after a 2-year period. Taking into account these figures, to obtain a single surviving seedling, the number of sound seeds available per tree would need to be:

$$\frac{1}{0.03 \times 0.1 \times 0.3} = 1111 \text{ sound seeds per tree.}$$

Due to the economic losses associated with the interruption of cone collection and grazing activities during the regeneration period, together with the appearance of intolerant herbal species in the first spring after regeneration fellings, cuttings must be programmed to start in a year with a high probability for a crop of sound seed greater than 1,111.

As an example of how the model developed can help managers to decide when to start regeneration fellings, we will consider a single tree, located in a plot within the study area but not used in the fit of the model. Tree and plot characteristics are the following:

Tree	Plot	dbh (cm)	g (m ²)	SI (m)	N (stems/ha)
2810301	28103	47.6	0.178	17.70	228

Case a: no previous or additional observations are available

In this case, only the observed exogenous variables for tree 2810301 are available. Some of the variables on the right hand side of the model, such as Ln and M_w , must be previously estimated as endogenous variables from the observed exogenous variables, and then used to make predictions about Np_{100} and Em .

Since no additional observations are available, it is not possible to make predictions about the random components included in the model. Estimated values for the response variables are then given by the expected unconditional mean value:

$$\hat{y}_{ijk} = E(y_{ijk}) = E(X_{ijk}\beta + Z_{ijk}b_{ijk} + e_{ijk}) = X_{ijk}\beta.$$

Cone production

The predicted mean value is given by:

$$\hat{Ln}_{ijk} = 0.2641 + 0.6492g_{ijk} - 0.0310\log(N_i) = 0.21151.$$

The confidence interval for the prediction was calculated assuming that fixed parameters are estimated without error. In this case, prediction variance is given by:

$$\begin{aligned} \text{Var}(\hat{Ln}_{ijk} - Ln_{ijk}) &= \sigma_{2u1}^2 + \sigma_{2v1}^2 + \sigma_{2w1}^2 + \sigma_{2e1}^2 \\ &= 0.003614 + 0.001825 + 0.004312 \\ &\quad + 0.01063 \\ &= 0.020381. \end{aligned}$$

The standard error for a single observation is then $\sqrt{\text{Var}(\hat{Ln} - Ln)} = 0.1427$, and approximate confidence interval for a probability $(1-\alpha)$ is:

$$0.21151 \pm t_{\alpha/2} 0.1427,$$

where $t_{\alpha/2}$ indicates the value for a t distribution with a probability $1-\alpha/2$.

Mean weight for cone

$$\hat{M}_{w_{ijk}} = 0.1301 + 0.01199 SI_i = 0.3423 \text{ kg},$$

$$\text{Var}(\hat{M}_w - M_w) = \sigma_{u2}^2 + \sigma_{v2}^2 + \sigma_{w2}^2 + \sigma_{e2}^2 = 0.009367,$$

$$\text{Std Err}(\hat{M}_w) = 0.0967.$$

Number of pinyons per cone

$$\hat{N}p_{100ijk} : 0.3068 + 1.3448 \hat{M}_{w_{ijk}} + 0.4142 \hat{Ln}_{ijk} = 0.8547.$$

In this case, the prediction variance takes into account the error associated with the use of non-observed, but estimated variables as predictors, such as $\hat{M}_w$ and $\hat{Ln}$:

$$\begin{aligned} \text{Var}(\hat{N}p_{100} - Np_{100}) &= \sigma_{u3}^2 + \sigma_{v3}^2 + \sigma_{w3}^2 + \sigma_{e3}^2 \\ &\quad + \beta_{3,1}^2 \text{Var}(\hat{M}_w - M_w) \\ &\quad + \beta_{3,2}^2 \text{Var}(\hat{Ln} - Ln) = 0.07065, \end{aligned}$$

$$\text{Std Err}(\hat{N}p_{100}) = 0.2658.$$

Rate of empty pinyons

$$\hat{Em}_{ijk} = 0.2368 - 0.4151 ijk = 0.0947,$$

$$\begin{aligned} \text{Var}(\hat{Em} - Em) &= \sigma_{u4}^2 + \sigma_{v4}^2 + \sigma_{w4}^2 + \sigma_{e4}^2 \\ &\quad + \beta_{4,12} \text{Var}(\hat{M}_w - M_w) = 0.01842. \end{aligned}$$

$$\text{Standard Error}(\hat{Em}) = 0.1357$$

Total number of available viable seeds

To estimate the total number of viable seeds $\hat{V}$ s for the subject tree, we used Eq. 1. The expected values considered were $\hat{N}p_{100}$ (0.8547) and $\hat{Em}$ (0.0947). From this, we calculated the expected number of sound seeds per cone $\hat{S}c$:

$$\hat{S}c = 100 \cdot \hat{N}p_{100} (1 - \hat{Em}) = 77.38.$$

To obtain 1,111 sound seeds from the subject tree we then require $Nh = 1,111/77.38 = 14.35$ cones. If we transform Nh into Ln :

$$Ln = \log(14.35 + 1)/100 = 0.2731.$$

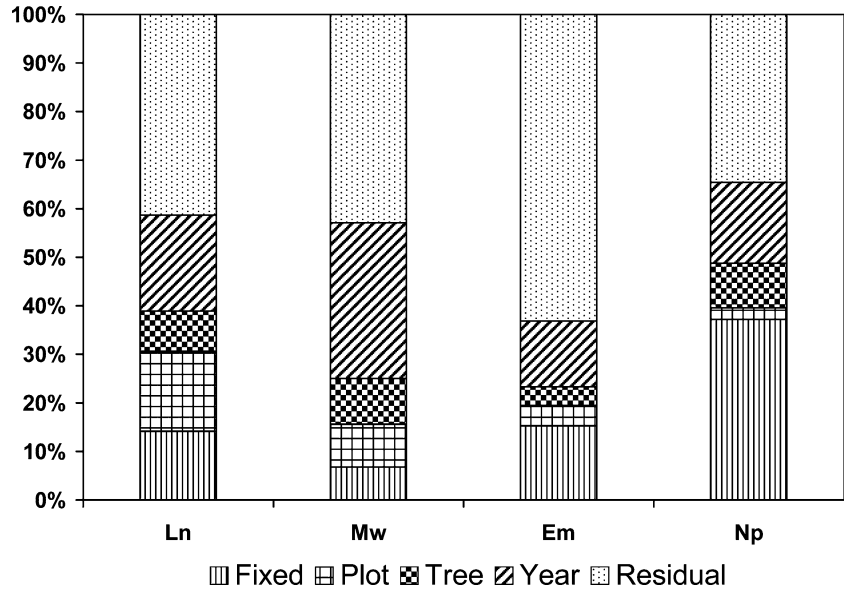
Taking into account the confidence interval for Ln , the probability of the predicted value for $\hat{Ln}$ being equal or larger than 0.2731 or, the probability of a crop larger than 1,111 sound seeds, is 0.3336. Under these conditions we can conclude that a tree the size of the subject tree, growing in a stand with similar conditions, will only produce a crop larger than 1,111 sound pinyons in 33.36% of years.

Case b: additional simultaneous observations of endogenous variables are available

Let us suppose that during the summer, a visual estimation has been made of the total number of cones available in two trees within the same plot. Additional data from these trees are as follows:

Tree	Plot	dbh (cm)	g (m ²)	SI (m)	N (stem/ha)	Nh	Ln
2810305	28103	36.4	0.1041	17.70	228	13	0.2639
2810311	28103	51.4	0.2079	17.70	228	51	0.3951

Fig. 2 Percentage of variability explained by the fixed part of the model, random components and residual non-explained variability, for the four response variables included in the multivariate model



Since two additional observations of endogenous variable Nh are available, it is possible to make predictions about the EBLUPs for the random components associated with Ln specific for plot 28103 (u_1), trees 2810305 and 2810311 (v_{11} and v_{12}) and measurement year (w_1). Due to the correlation identified between random year components for the different response variables, it is also possible to make predictions about the random year components associated with mean cone weight (w_2), number of pinyons (w_3) and rate of empty pinyons (w_4). The vector of predicted random components $\hat{\mathbf{b}}$ is calculated as:

$$\hat{\mathbf{b}} = [\hat{u}_1, \hat{v}_{11}, \hat{v}_{12}, \hat{w}_1, \hat{w}_2, \hat{w}_3, \hat{w}_4]^T = \hat{\mathbf{D}}\mathbf{Z}^T\hat{\mathbf{V}}^{-1}(\mathbf{y} - \mathbf{X}\hat{\beta}).$$

where $\hat{\mathbf{D}}$ is the 7×7 block diagonal matrix including variance components associated with the terms of $\hat{\mathbf{b}}$, $\mathbf{Z}$ is the 8×7 design matrix whose rows are the vectors $\mathbf{z}_{ijk}$ associated with the additional observations of the response variable, $\hat{\mathbf{V}} = \mathbf{Z}^T\hat{\mathbf{D}}\mathbf{Z} + \hat{\mathbf{R}}$, with $\hat{\mathbf{R}}$ a 8×8 block diagonal matrix including the residual variances for the additional observations, and $(\mathbf{y} - \mathbf{X}\hat{\beta})$ is a 8×1 vector including the residuals between the observed and the expected unconditional values of the response variables for the additional sample of trees. Since no observations have been made for Mw, Np and Em, the observed values for these variables equal the expected values.

Under these conditions:

$$\hat{\mathbf{b}} = [0.03803, 0.00488, 0.01431, 0.02867, 0.00235, 0.02025, -0.02018]^T.$$

To make predictions for the subject tree, only the values for random plot and year components were considered, since the random tree components predicted were specific for other trees. Estimated values for the response variables are then given by the conditional expectation for the predicted random variables:

$$\begin{aligned}\hat{y}_{ijk} &= E(y_{ijk}|\hat{\mathbf{b}}) = E(\mathbf{X}_{ijk}\beta + \mathbf{Z}_{ijk}\hat{\mathbf{b}}_{ijk} + \mathbf{e}_{ijk}) \\ &= \mathbf{X}_{ijk}\beta + \mathbf{Z}_{ijk}\hat{\mathbf{b}}_{ijk}.\end{aligned}$$

Cone production

$$\hat{Ln}_{ijk} = 0.21151 + \hat{u}_1 + \hat{w}_1 = 0.27829.$$

To estimate variance prediction in this case, we only consider the variance associated with random tree and residual components σ^2_{v1} and σ^2_{e1} together with the variance of the error associated with the prediction of $\hat{u}_1$ and $\hat{w}_1$ (Vonesh and Chinchilli 1997, p. 363):

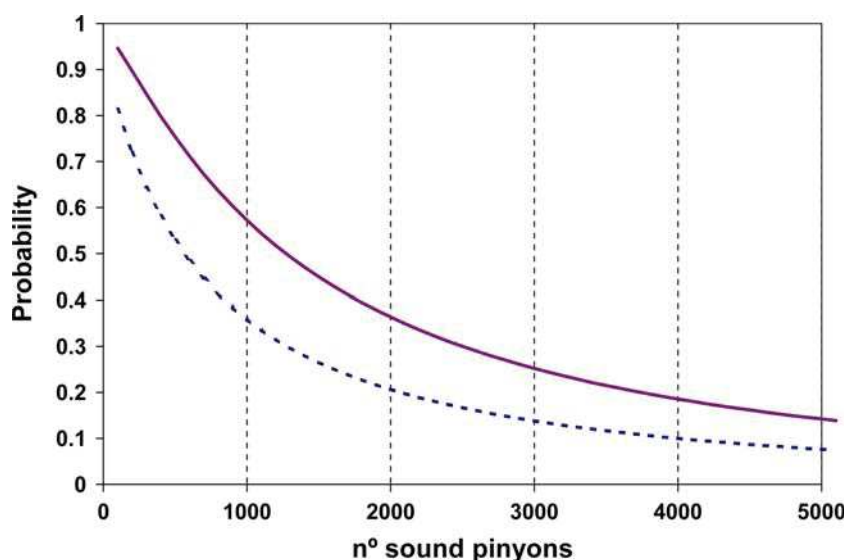
$$\begin{aligned}\text{Var}(\hat{Ln}_{ijk} - Ln_{ijk}) &= \mathbf{z}_{ijk}^T[\mathbf{Z}^T\hat{\mathbf{R}}^{-1}\mathbf{Z} + \hat{\mathbf{D}}^{-1}]\mathbf{z}_{ijk} + \sigma_{v1}^2 \\ &+ \sigma_{e1}^2 = 0.002891 + 0.001825 \\ &+ 0.01063 = 0.015346.\end{aligned}$$

The standard error for a single observation is then 0.1238, which means a reduction of 13.24% in standard error of prediction when compared with the fixed effects response. The approximate confidence interval for a probability $(1-\alpha)$ is then given by $0.2782 \pm t_{\alpha/2}0.1238$.

For simplicity, we only include the expected conditional mean value (after including random year components) and confidence interval with probability $(1-\alpha)$ for the rest of the response variables analysed, operating as in the previous cases: Mean cone weight: $0.3446 \pm t_{\alpha/2}0.0858$. Number of pinyons per cone: $0.9058 \pm t_{\alpha/2}0.2523$. Rate of empty pinyons: $0.0735 \pm t_{\alpha/2}0.1316$.

To estimate the total number of viable seeds produced by the tree in this year, the total number of viable seeds per cone is again considered a fixed figure, calculated using the expected value for the number of

Fig. 3 Sound seed crop probability curves for tree 2810301 under fixed effects model (*dotted line*) and conditional random components model including plot and year random components (*continuous line*)



pinyons per cone and the rate of sound seeds in a sample of pinyons. In this case $\hat{S}c$ equals 83.91, which means that only 13.23 healthy cones are required to obtain 1,111 sound seeds. This quantity is smaller than that estimated previously, since the availability beforehand of information resulted in larger estimates for the number of pinyons per cone and the percentage of viable seeds. Transforming the number of healthy cones into variable Ln , we obtain $\log(13.23 + 1)/10 = 0.2656$.

Taking into account the confidence interval for Ln under the conditions defined for this year, the probability of $\hat{Ln}$ being equal to or greater than 0.2656 or the probability of a crop greater than 1,111 sound seeds from the tree this year, is 0.5403.

In the previous paragraphs, we have shown how the model works to estimate conditional or unconditional crop values as well as the probability of a crop being larger than that deemed as satisfactory for attaining natural regeneration. The model developed is so flexible as to obtain conditional or unconditional estimates of probability for any given crop value. In this way, Fig. 3 shows the probability for expected unconditional (fixed effects) and conditional (including random plot and year components predicted from the additional subsample used before) values for the crop, ranging between zero and 5,000 sound seeds per year for the subject tree.

Discussion

Multivariate ML LMMs allow the simultaneous fit of correlated functions including random components acting at different levels. Estimation of the total amount of viable seed produced by a tree in a given year is approached by identifying the number and mean weight of cones, number of seeds per cone and

percentage of viable seeds. These variables are correlated among each other, since they share explanatory covariates or some act as predictor covariates for the others. On the other hand, these variables show different levels of variability associated with the hierarchical units where observations are taken. Due to these conditions, the implementation of the model as a multivariate ML LMM seems feasible. The use of multivariate ML mixed models in forest science is very recent (Fang et al. 2001; Hall and Clutter 2004; Zhang and Borders 2004).

The covariates explaining the number of cones are the same as those proposed previously by several authors (Gordo et al. 2001; Cañadas 2000). Although site index was removed after simultaneous fit, the remaining variables indicate that the biggest trees in the lowest density stands produce larger cone crops. The percentage of variability explained by the fixed part of the model is about 15%, a rate that seems quite low, although it is similar to that obtained by Calama (2004). Year and plot random components explain jointly almost 40% of variability; therefore, by including these effects in predictions, estimates are significantly improved.

The mean weight of cones is a variable mainly related to site conditions, although the fixed part of the model only explains less than 10% of total variability. The mean weight of cones is largely related to weather conditions during the spring immediately before the cones mature. This can be reflected in the high level of variability, nearly 40%, explained by year components. In any case, mean weight is the response variable which shows the smallest dispersion (coefficient of variation is 32.26%), so average values can be considered good indicators of the real observed value.

The number of pinyons per cone and the percentage of empty seeds are variables mainly explained by

the mean weight of cones, and they are largely correlated. Larger cones contain more pinyons and a higher percentage of sound seeds. Correlation between sound seeds and total number of seeds has been identified in several forest studies since Bramlett and Hutchinson (1964). For both response variables, the main part of non-explained systematic variability is again associated with year level, as was also stated by Sirois (2000).

Given the importance of systematic variability explained by random year components, it was quite important to identify covariance parameters acting at this level. The random year component for empty seeds shows high negative correlation with the rest of the variables, indicating that in years when the rate of empty seeds is greater, the total number of cones, mean weight of cones and total number of pinyons per cone are smaller. The main reasons for this causal relation could be climatic conditions or factors affecting the rate of self-fertilization. Positive correlations between random year components associated with the number of cones, number of pinyons per cone and mean weight of the cones were also identified.

The estimation of variance components allows us to predict EBLUPs for random components using additional measurements of the response variables. Since we have identified significant correlations between random components corresponding to different variables, it is possible to make predictions for the random year component using additional observations for a correlated variable. The inclusion of random plot and year effects, predicted from a small sample of observations, improves the precision and reduces the uncertainty of the estimates. By including more trees, plots and years of observation in the sample, random components would be predicted more efficiently. Observations taken for a single tree in different stands for a given year will give us a good prediction of the EBLUP for the components of that year. On the other hand, by repeating measurements for several trees from a single stand, we will obtain efficient predictions for the random plot component.

The developed model has shown its utility in helping to decide when to start regeneration fellings in a given stand. Results at tree level can be easily extended to stand level by using inventory data for diameters or diameter distribution of the stand. In this case, the decision to start cutting can be assumed if, for example, more than 50% of the trees within the stand show crop probabilities greater than 60%. Another possible use of the model would be to decide whether or not to allow commercial cone collection during a regeneration period in a year when the estimated cone crop is unlikely to be large enough to ensure the total amount of seeds required. As cones are easily observable during the spring before they

mature, decisions and actions can be adopted with sufficient anticipation, since both cuttings and cone collection are carried out during the following winter. Finally, by using the expected unconditional fixed effects model it is also possible to determine, for example, the return period for a given crop, or the number of crops larger than a given quantity during a regeneration period of a given length. Under the proposed conditions for dispersal, germination and establishment defined for an area different from the study area, we can confirm that seed production is a limiting factor for regeneration. It is necessary to improve our knowledge of the specific conditions for regeneration and seedling survival in stone pine stands in the Central Range of Spain, which will allow us to estimate more adequately the total number of sound seeds necessary to ensure regeneration.

Acknowledgements The authors wish to thank the helpful comments from two anonymous reviewers, whose remarks and indications significantly improved the original manuscript.

Appendix 1

Fitting multivariate multilevel linear mixed models using SAS procedure MIXED

Let us suppose we are interested in fitting a multivariate ML LMM including three response variables x_1 , x_2 and x_3 observed from n individuals identified at two hierarchical levels, named levelA and levelB. Two evaluated independent variables are defined as y_1 and y_2 . In the first step, we create a database (named 'fit' in the basic program) including three times the variables coming from each individual, and creating three new dummy variables, f_1 , f_2 and f_3 , where f_i equals 1 for the i th repetition and zero in the rest of cases. The database then includes $3n$ rows with the following structure:

Individual	levelA	levelB	x_1	x_2	x_3	y_1	y_2	f_1	f_2	f_3
a	1	1	x_{1a}	x_{2a}	x_{3a}	y_{1a}	y_{2a}	1	0	0
a	1	1	x_{1a}	x_{2a}	x_{3a}	y_{1a}	y_{2a}	0	1	0
a	1	1	x_{1a}	x_{2a}	x_{3a}	y_{1a}	y_{2a}	0	0	1

To make a simultaneous fit, the following SAS basic program is then used. Additional explanatory commentaries are included within the program between /* */:

```

data fit;
input individual x1 x2 x3 levelA levelB y1 y2 f1 f2 f3;
run;

data fit; set fit;

    response = f1*x1 + f2*x2 + f3*x3;

    /* Variable "response" then equals x1 for the first repetition, x2
    for the second, etc. */

data fit; set fit;

    f1y1 = f1*y1;
    f2y1 = f2*y1;
    f3y1 = f3*y1;
    f1y2 = f1*y2;
    f2y2 = f2*y2;
    f3y2 = f3*y2;

run;

proc mixed data=fit;
class levelA levelB;
model response = f1 f1y1 f1y2 f2 f2y1 f2y2 f3 f3y1 f3y2 / noint;

random f1 f2 f3 f4/ subject=levelA type=un;
random f1 f2 f3 f4/ subject=levelB type=un;

/* In this program only the intercepts f1, f2 and f3 of the models
are supposed to vary randomly among units within a given level */
/* "type=un" indicate a complete variance-covariance structure for
random components associated with that level*/

run;

```

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