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Improving the estimation of landscape scale seed dispersal by integrating seedling recruitment

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Abstract

• **Context** Dispersal and recruitment play a critical role in determining the abundance and the spatial structure of regeneration.
• **Aim** In this study, we estimated landscape scale seed dispersal using the inverse modeling method by fitting seedling counts to seed tree location and fertility in the European silver fir *Abies alba* Miller.
• **Methods** Seed trees and seedlings from three age cohorts were counted in 30 plots on Mont Ventoux (southeastern France) at elevations from 995 to 1,605 m, where the following ecological variables were measured: elevation, slope, aspect, light availability, and tree density. We developed and fitted a dispersal model, including a new parameter,

recruitment rate, which depended both on the ecological characteristics of the plots and on seed production.

• **Results** Elevation was the factor that affected seedling recruitment the most, with an optimum value at around 1,200 m. Estimated *A. alba* seed dispersal distances were short (median values for the three cohorts, respectively, 16.4–13.2–19.6 m).

• **Discussion** We demonstrated that including the ecological characteristics of plots and post-dispersal recruitment processes realistically reduced estimates of seed dispersal distances which are otherwise grossly over-estimated using inverse modeling procedures.

Keywords Dispersal · Seedling · Recruitment rate · Inverse modeling · *Abies alba*

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1 Introduction

Among all the processes governing a plant's life cycle, dispersal and recruitment play a key role for population dynamics. Seed dispersal confers movement in space (Nathan and Muller-Landau 2000) and seedling recruitment (arrival of new individuals into a population or community) co-determines abundance and spatial structure of the regeneration (Wang and Smith 2002). The two processes together make colonization of new habitats possible and have attracted major interest in the context of climate change (Nathan et al. 2011). The spatial structure of recruited seedlings depends on many factors: adult fertility and location, seed dispersal, environmental characteristics of the site where seeds are deposited, spatial distribution of suitable microsites for regeneration, mortality, post-dispersal predation, and intra- and inter-specific competition (Sagnard et al. 2007). The relative importance of each of the processes

mentioned depends on the species' life-history traits (e.g., colonization ability, maturation age, etc.), tree density, seed predator populations, and the temporal fluctuations of climatic factors.

In the literature, two points of view are proposed for interpreting recruitment limitation (Clark et al. 2007). Some authors consider that seed dispersal is the limiting factor: populations are "recruitment limited" when there is a low and uncertain seed supply (Clark et al. 1999a; Wang and Smith 2002). Others propose that microsite distribution and environmental characteristics are the first determinants of recruitment (Beatty 1984). Therefore, most studies concerning seedling establishment focus either on seed dispersal or on microsite and environmental characteristics and comparatively fewer combined approaches have been reported. However, combined approaches clearly demonstrate that both factors play a significant role in recruitment limitation (LePage et al. 2000; Münzbergová and Herben 2005; Clark et al. 2007). Reliable estimates of seed dispersal and seedling recruitment are of critical importance for the analysis and modeling of population dynamics.

Both mechanistic and probabilistic approaches have been developed to model dispersal. While mechanistic models make it possible to include a realistic representation of processes such as seed abscission and turbulence (Soons and Bullock 2008), inverse modeling (IM) is of more immediate use for calibrating dispersal kernels from seed traps or seedlings plots (Clark et al. 1999b; Greene et al. 2004; Ribbens et al. 1994). Dispersal kernels estimated using IM from seed-trap data (seed counts) can be considered as a reference, as they only describe the most straightforward way that seeds travel from seed trees to ground (especially in the case of seeds that are dispersed via an abiotic vector, such as wind). However, such an approach is mainly adapted to the calibration of short-distance dispersal due to the difficulty in detecting rare events with small area seed traps. Replacing seed traps by regeneration plots (seedling counts) covering larger areas makes it possible to calibrate dispersal on greater spatial scales. However, these experiments do not directly provide seed dispersal estimates because the spatial structure of seedlings also integrates post-dispersal processes, such as germination and seedling recruitment. Significant variations in dispersal estimates can be observed because very strong demographic variation usually occurs at the very first stages of regeneration (Shibata and Nakashizuka 1995). To date, very few studies have taken recruitment limitations explicitly into consideration when modeling seed dispersal using seedling plot data (LePage et al. 2000).

The present study addresses the regeneration dynamics of the European silver fir (*Abies alba* Mill.) on Mont Ventoux, a mountain located in the south-east of France. Our objectives were (1) to determine the effect of seed supply and environmental variables (e.g., aspect, elevation, etc.) on silver fir

seedling density on Mont Ventoux, (2) to calibrate a "dispersal recruitment model" from seedling counts at the landscape scale which takes into account seedling recruitment. Results from this "dispersal recruitment model" (DRM) were compared with those of a "dispersal model" (DM) (without recruitment) and to those of a reference "seed dispersal model" (SM) published by Sagnard et al. (2007).

2 Material and method

2.1 Study site and species of interest

The experimental site is located on the northern slope of Mont Ventoux (44°11' N; 5°17' E) a 1,909-m-high limestone mountain located in south eastern France at the south-westernmost tip of the Alps. Climatic conditions vary from typically Mediterranean at low elevations to subalpine at high elevations.

Silver fir (*A. alba*) is a native European conifer and a keystone tree species distributed throughout temperate mountain forest ecosystems such as the Alps, at elevations between 300 and 1,800 m. It is a shade-tolerant species that forms mixed forests over a broad range of ecological conditions from the sub-Mediterranean to the upper montane altitudinal belts. On the northern slopes of Mont Ventoux, *A. alba* currently occupies a wide range of habitats from 1,000 to 1,650 m elevation. Silver fir forests form either pure stands or more generally mixed stands with beech (*Fagus sylvatica* L.) and pines (*Pinus uncinata* Ramond ex DC., *Pinus sylvestris* L., and *Pinus nigra* Arnold). Co-occurring species, such as Italian maple (*Acer opalus* Mill.), common whitebeam (*Sorbus aria* (L.) Crantz), and downy oak (*Quercus pubescens* Willd.), are also commonly present (Debussche et al. 1999). Native forests on Mont Ventoux result from a recent and rapid recolonization. By 1850, Mont Ventoux was almost entirely deforested due to excessive wood harvesting and over-grazing. Beech–fir forests were reduced to small patches in the most inaccessible parts of the mountain or in some reserved stands. Reforestation efforts undertaken from 1860 to the early twentieth century using mostly pine species made it possible for *A. alba* to rapidly recolonize planted pine forests (Debussche et al. 1999). This monoecious species produces female strobili (i.e., cones), located within the top third of the crown. Mature cones disarticulate in late summer and winged-seeds are dispersed by wind. However, primary dispersal occurs during several weeks or months due to seeds that are retained in the dense crowns of *Abies* trees. As far as we know, there is no significant secondary dispersal (by animals or on snow after seed release) after seeds reach soil.

2.2 Experimental data

2.2.1 Regeneration plots

Seedlings were counted over 30 plots (20×20 m) installed in 2002 (Fig. 1). Each plot was divided in four subplots of 100 m². Plot locations were chosen in order to cover most of the variability of plant communities and environmental conditions (elevation, understory light, proximity to *A. alba* forest stands), following the classification of the French National Forest Service (ONF). Within-plot tree density variability and seed rain heterogeneity were taken into account by subdividing each plot into 4 square subplots of 100 m². Plots were sometimes pure silver fir stands but more generally mixed stands with beech (*F. sylvatica*) and pines (*P. uncinata*, *P. sylvestris*, and *P. nigra*, collectively referred to as pine).

- Seedlings inventory

Seedlings from three different cohorts were inventoried in each subplot in September 2008: (1) germinations of the year 2007, called “cohort 1”; (2) 2 to 5 years old seedlings, called “cohort 2,” that may originate from a maximum of four dispersal events (2002–2005); and (3) up to 30 cm high seedlings, called “cohort 3,” their age was based on a previous dendrochronological study. We estimated that this cohort may result from a maximum of 25 dispersal events. The values (mean, standard error, minimum, and maximum) of seedling number are described in Table 1.

- Biotic and abiotic variables

Elevation, slope, aspect, understory light, and tree density were determined for each subplot. Understory

light was determined during the summer 2008. At sunrise, one hemispherical photograph per subplot was taken below the canopy at 1 m above-ground height. A digital camera (CoolPix 950, Nikon Corporation, Tokyo, Japan) equipped with a fisheye lens was used. Photographs were then analyzed using the CANEYE software to calculate the transmitted light (both direct and diffuse) under the canopy (Davi et al. 2008). CANEYE makes it possible to interactively and concurrently classify a set of images exploiting the three colors. Once pixels were classified by the operator as sky or vegetation (leaves and branches), gap fraction was computed for 10° azimuth angle and 5° zenith angle sectors. The area considered was restricted to zenith angles lower than 60 μ° to prevent problems with a large fraction of mixed pixels. For each subplot, tree density (in square meters per hectare) was calculated per species (fir, beech, and pine) as the sum of basal area of trees measured at breast height at the end of year 2007. According to Dreyfus (2012) for the same study area, height growth of fir seedlings is strongly affected by asymmetric competition exerted by taller individuals of fir and beech together (in a pure or mixed canopy) while asymmetric competition by the pines (some species casting lighter shade) has no significant effect. Assuming a similar pattern for mortality induced by competition for light, with probably less transmitted light under fir and/or beech canopies than under pine canopies, we pooled fir and beech measurements, on the one hand, and the different pine species, on the other hand. Due to thinning, both canopy cover and tree density had strongly evolved since seedling birth date in cohort 3; thus, the transmitted light measured during the summer 2008 could not denote the

Fig. 1 Location of the regeneration plots (western part of Mont Ventoux north face). Circles indicate the regeneration plots. Dark grey areas represent silver fir forest stands (according to ONF data) where it is the main species (with high density in terms of basal area) and intermediate grey when it is the second and light grey when it is the third species (in proportion)

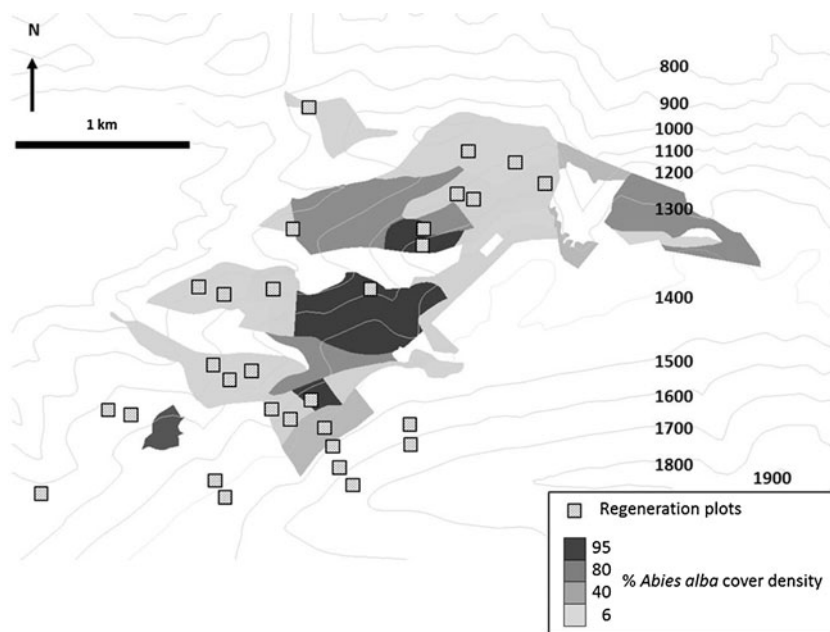


Table 1 Mean (Mean), standard error (SD), min value (Min), and max values (Max) of the environmental variables and seedling number on 100 m² (for the three cohorts) described on experimental plots

Variable	Mean	SD	Min	Max
Elevation (m)	1,251.11	167.09	976	1,622
Slope (deg)	24.50	5.17	14	35
Fir–beech basal area (m ² /ha)	19.43	18.99	0	65.44
Pine basal area (m ² /ha)	21.56	16.67	6	68
Aspect (°)	330	15.43	288	297
Light (%)	15.50	6.44	7	53
Seedling density				
Cohort 1	122 122/year ^a	205.5	0	1,149
Cohort 2	30.2 7.5/year ^a	69.95	0	469
Cohort 3	32.31 1.3/year ^a	74.88	0	506

^aNumber of seedlings recruited per year according to the number of dispersal events cumulated per cohort

original light conditions of cohort 3. Hence, we only analyzed light effect on cohorts 1 and 2: for these cohorts, the plots were not thinned between seedlings establishment and light measurement. The number of expected seeds per subplot (seed supply) was estimated from a previously calibrated seed dispersal model (see below “Comparison with other dispersal curve”). Seed supply S at the subplot scale was computed as the sum of the estimated number of seeds for each m². The values (mean, standard error, minimum and maximum) of environmental variables are described in Table 1. Forest floor characteristics were assessed visually by determining rock, humus, litter, shrub, dead tree, and dicotyledonous percent recovery at the subplot scale.

2.2.2 Seed trees

Nine hundred seed trees (potentially producing seeds, i.e., over 15 cm in diameter at breast height (dbh)) were mapped within a 50-m radius around 24 of the 30 regeneration plots and their dbh was measured in cm (Fig. 1). Seed tree fertility depended on their dbh (see Appendix 1). The six remaining regeneration plots were located in very dense silver fir stands where we considered seed rain to be homogeneous in space. Considering that precise knowledge of tree location was not necessary, trees were not mapped. For these six plots, we positioned one tree every 100 m² (78 regularly spaced trees within a 50-m radius circle).

In order to take into account long distance seed trees (outside the 50-m radius circle of all the 30 plots), we positioned trees on a 10×10-m grid for the whole forest

where silver fir was present (ONF data) (Fig. 1). Fertility of each modeled tree was weighted by the percentage of *A. alba* cover given by the ONF for each forest management unit (see Appendix 1; Fig. 1). All available information was integrated into the open-source Geographic Information System GRASS (<http://grass.itc.it/>) which was used to generate modeled seed trees.

2.3 Models and analysis

2.3.1 Environmental effect on seedling density

The effect of seed supply and five environmental variables (elevation, slope, aspect, understory light, and tree density) on seedling density was analyzed using a General Linear Model (GLM) with a logarithmic link function (McCullagh and Nelder 1989) (Eq. 1).

$$N_{\text{obs}} = S_{\text{exp}} \times c_{\text{seed}} \times e^{(x_1 \times c_1 + x_2 \times c_2 + \dots + x_n \times c_n)} \quad (1)$$

Where N_{obs} is the number of observed seedlings; S_{exp} is the number of expected seeds per subplot (seed supply), calculated from a seed dispersal model (see below “Comparison with other dispersal curve”); x_1, x_2, \dots, x_n are environmental variables and c_{seed} and c_1, c_2, \dots, c_n are regression coefficients. The best fitting model was retained after analyses of deviance (minus twice the maximized log-likelihood) tables (χ^2 tests). For every environmental variable (x_n), a GLM was computed without x_n and residuals of the GLM were plotted against x_n to detect non-linear effect.

2.3.2 Dispersal modeling

Inverse modeling approach Dispersal curves were calibrated using the inverse modeling method (IM) developed by Ribbens et al. (1994). IM assumes that seedling density D_i in a subplot i is the overall sum over each adult j of the product of its fertility Fer_j by the dispersal kernel f which gives the probability that a seedling is “dispersed” at a distance r_{ij} from the tree (Eq. 2):

$$D_i = \sum_j \text{Fer}_j f(r_{ij}) \quad (2)$$

Individual seed tree fertility Fer_j was estimated from tree dbh and year, as described in Appendix 1.

Among all families of dispersal kernels we chose the 2Dt function (Eq. 3) described in Clark et al. (1999b).

$$f(r_{ij}) = \frac{P}{\pi u \left[1 + \frac{r_{ij}^2}{u} \right]^{p+1}} \quad (3)$$

These authors argued that this composite dispersal function was exponential in shape, but with a normally

distributed variable for the scale parameter. Hence, this more flexible kernel was adapted to better calibrate seed dispersal near and far from seed trees. The 2Dt model becomes a Gaussian function when the shape parameter p becomes large, and an exponential function when p tends towards zero (Clark et al. 1999b); u is a scaling parameter and r_{ij} is the distance between subplots center and seed tree location. An exponential power kernel was also tested; results were similar for the two younger cohorts but were unreasonable for the older cohort.

Dispersal recruitment model DRM explicitly includes a new recruitment rate parameter depending on both macro-environmental variables and seed supply. Recruitment rate is estimated separately using an iterative approach (see below “Parameter estimate”). To fit the function that predicts seedlings density (D_i) (number/100 m²), the overall equation becomes (Eq. 4):

$$D_i(r_{ij}) = \frac{p}{\pi u \left[1 + \frac{r_{ij}^2}{u}\right]^{p+1}} \cdot S \cdot \text{RR} \quad (4)$$

Where RR is the recruitment rate; S is the seed tree fertility, which is the number of cones multiplied by the number of seeds per cone (fixed at 253 in our model, see Appendix 1).

Parameter estimate RR was estimated as follows (Eq. 5):

$$\text{RR} = \frac{N_{\text{exp}}}{S_{\text{exp}}} \quad (5)$$

Where S_{exp} is the number of expected seeds per subplot (seed supply) (see below “Comparison with other dispersal curve”); N_{exp} is the expected number of seedlings depending on seed supply and environmental variables, estimated according to Eq. 1.

The dispersal curve parameters p and u were estimated by likelihood maximization. Assuming that observed number of seedlings O_i follows a Poisson distribution (Ribbens et al. 1994), the Poisson likelihood is estimated as follows (Eq. 6):

$$L(O_i, p, u) = \prod_{\text{subplot}=1}^{120} \frac{e^{-D_i} D_i^{O_i}}{O_i!} \quad (6)$$

Where O_i is the vector of the observed seedlings over the 120 plots; D_i is the expected number of seedlings in a subplot i calculated from the model. Median dispersal distance was then computed by numerical integration. Parameter estimation is achieved using an iterative process. In fact, parameter estimation of dispersal kernel (p and u) depends on RR (Eq. 4). But RR was itself estimated from the predicted seed supply which also depends on parameter p and

u . The seed supply (S_0), included in the first RR estimation (RR₁) was estimated from the seed dispersal model. Next, seed supply (S_i) was computed from the DRM calibrated with the estimated (RR _{i}) (Appendix 2). This procedure was repeated until of parameters p and u , converged.

Comparison with other dispersal curves Results from the DRM were compared with results obtained from: (a) a reference SM (seed trap experiments) adapted from Sagnard et al. (2007), using a 2Dt dispersal kernel (Eq. 3) rather than an exponential power dispersal kernel (data are the same as in Sagnard et al. 2007); (b) a DM that only depends on distance from seed trees and their size, without taking into account seedling recruitment. A supplementary parameter was estimated which consists in the number of recruited seedlings produced per seed tree (Fer). DM was computed based on the same data as for DRM, for the same three seedling cohorts. Pearson correlation coefficients between observed and predicted seedling numbers were computed for model validation.

Statistical tools Programs for computation of the dispersal modeling, GLM and spatial analyses were performed using the R statistical environment. The function *optim* of the package *stats* was used to estimate model parameters p and u .

3 Results

3.1 Effect of environmental variables on seedling density and recruitment rate

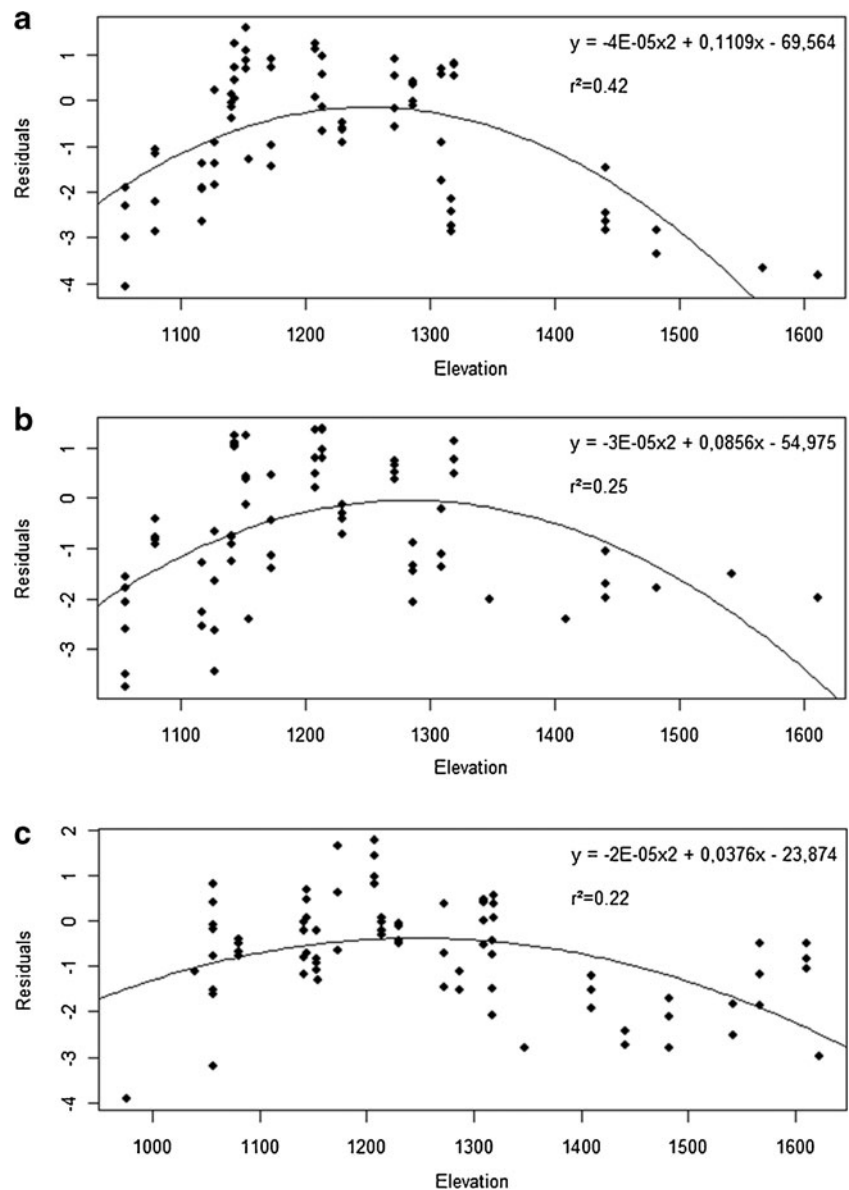
A non-linear relationship between elevation and seedling number was observed (Fig. 2). Consequently, elevation was transformed using a polynomial function of second order as follows (Eq. 7):

$$E' = a \cdot E^2 + b \cdot E + c \quad (7)$$

Where E is elevation; E' is the transformed elevation variable (E' is then included in Eq. 1); a, b and c are the parameters estimated from a least square analysis. Seedling density was the highest at 1,250 m for cohort 1, 1,285 m for cohort 2, and 1,250 m for cohort 3.

GLM coefficients, deviance, degree of freedom and variable significance are described in Table 2. Transformed elevation was the variable that most affected seedling density for cohorts 1 and 3, whereas cohort 2 density was most affected by slope. As expected, number of seeds was positively correlated with seedling density. The GLM coefficient for seed supply was equal to 0.204, 0.129, and 0.207 for the cohorts 1, 2, and 3 respectively. These values, much lower than one, showed that the number of emerged seedlings increased proportionally less than the number of dispersed

Fig. 2 Residuals of the GLM, that fits seedling numbers to environmental variables (except elevation), against elevation for cohorts 1 (**a**), 2 (**b**), and 3 (**c**). Circle observed values; line non-monotonous model fitted using Eq. 7



seeds on the subplots. Northern aspect was positively correlated with high seedling density although steep slopes had a negative impact on seedling density. Total transmitted light had no significant effect on cohort 1 density but had a negative impact on cohort 2. The higher the stand density (fir-beech and/or pine), the lower the quantity of seedlings. The recruitment rate ranged from 0.004 to 0.6 for cohort 1, from 0 to 0.08 for cohort 2, and from 0 to 0.054 for cohort 3.

3.2 Dispersal models

The estimated kernel parameters (p and u) are given in Table 3 for DRM, DM and SM. The reference SM dispersal curve showed a short median dispersal distance (Mdd) of 7 m. Shape parameter p equaled 1 and seed dispersal followed a Gaussian distribution (Fig. 3). We observed that the

shape parameter p was systematically greater by at least a factor of two for the dispersal curve computed using DRM rather than DM for all three cohorts (Table 3). Mdd was also systematically lower for DRM than for DM, and up to one order of magnitude for cohort 3 (Fig. 3). Overall, Mdd values calculated from the seed dispersal SM model were closer to DRM than to DM. Moreover, DM showed fatter tailed dispersal curves than DRM. Almost all seeds were dispersed within a radius of 30 m (from the seed tree) in the SM model (Table 3), which is consistent with the proportions estimated from DRM but much higher than values obtained from DM, especially for cohort 3. Similar results were observed for a radius of 100 m (Table 3). As for Mdd, the difference between DRM and DM was strongest for cohort 3. In conclusion, dispersal curves calibrated using DRM were more similar to our reference seed dispersal

Table 2 Effect of microhabitat characteristics on silver fir seedling density for each cohort

Cohort name	Variable	Coef	Deviance
Cohort 1	Elevation	1.167	4,457
	Aspect	0.014	1,413
	Fir-beech density	-0.015	221
	Seed	0.204	2,076
	Pine density	-0.013	330
	Slope	-0.013	265
Cohort 2	Slope	-0.138	1,756
	Elevation	0.913	423
	Fir-beech density	-0.018	482
	Aspect	0.005	136
	Seed	0.129	194
	Light	-3.838	21
Cohort 3	Pine density	-0.009	1
	Elevation	2.313	2,026
	Aspect	0.013	595
	Seed	0.207	774
	Slope	-0.048	213
	Pine density	0.014	198
	Fir-beech density	0.006	161

Generalized linear model coefficients are estimated using the Poisson regression model (link function: log) and $n=120$ sampling locations. *Coef* is the estimated coefficient of the environmental variables. Significance of variables was assessed by an analysis of deviance (Deviance; χ^2 test). The degree of freedom (*df*) is equal to 1 for all the variables, moreover the probability ($Pr(>|z|)$) is less than 0.001. Variables are ordered according to best fitting

curve SM than to dispersal curves calibrated using DM (Fig. 3). Last, in the case of DM, the number of seedlings produced per cone was 10.104, 0.569, and 0.042 for the

cohorts 1, 2, and 3, respectively. For cohort 1, the Pearson correlation coefficient between predicted and observed number of seedlings were similar for both models. For older cohorts (2 and 3), the Pearson correlation coefficient was greater for DRM than for DM (Table 3).

4 Discussion

4.1 Ecology of silver fir regeneration

Earlier studies found that seedling density depended both on ecological factors (elevation, slope, tree density and aspect) and on seed supply (LePage et al. 2000; Münzbergová and Herben 2005). We found similar results on Mont Ventoux.

However, all ecological factors were not equally important for seedling density. For cohorts 1 and 3, elevation was the factor that most affected silver fir seedling density which was maximum around 1,260 m. Elevation was the second factor that most affected seedling density for cohort 2. Growth of adult silver fir (Cailleret and Davi 2011; Carcaillet and Muller 2005) and rate of viable seed production (unpublished data) were also found to be optimal at an elevation of around 1,200 m on the northern side of Mont Ventoux.

Elevation can be seen as an integrative factor for temperature, precipitation and atmospheric humidity (Körner 2007). On Mont Ventoux, elevation and temperature are strongly correlated ($r^2=0.99$) with a temperature decrease of 0.7°C/100 mm. The relationship between elevation and both precipitation and atmospheric humidity is less clear. We suspect that mechanisms that affect seedling density at low and high elevations are different. At low elevations, the

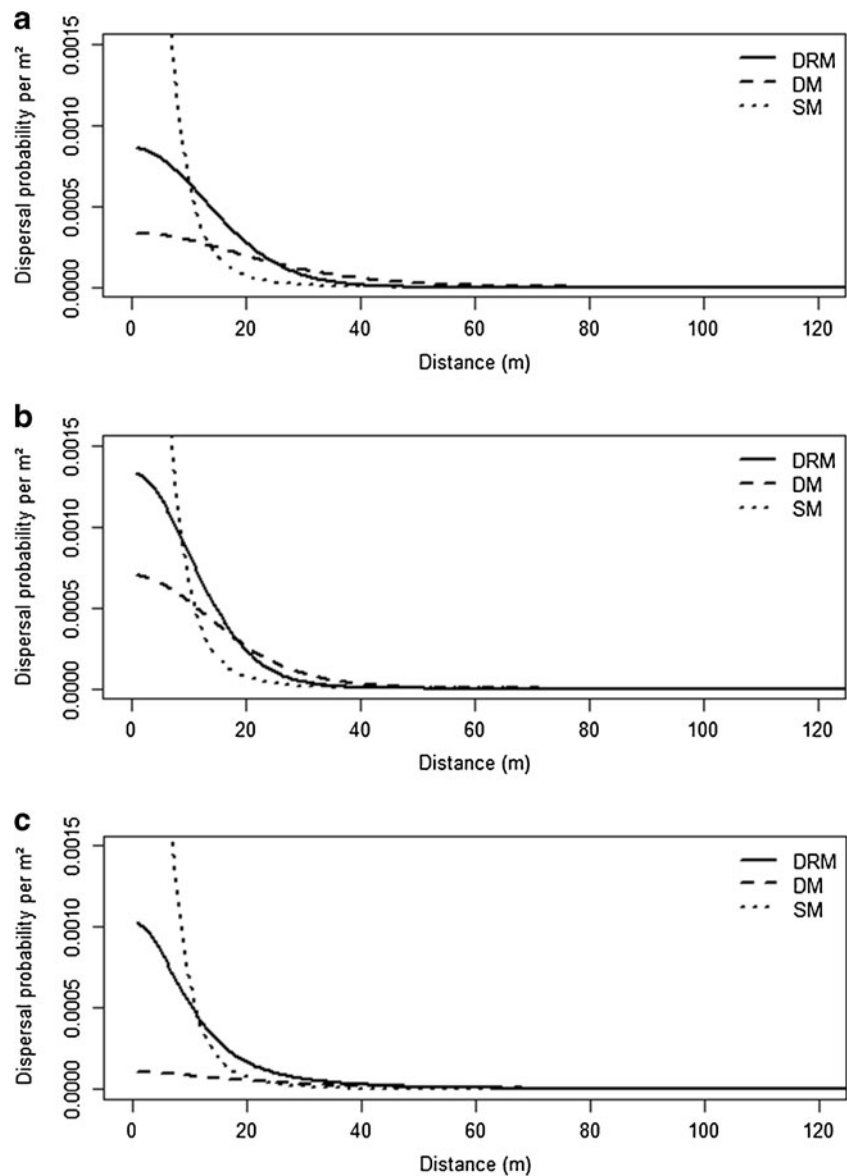
Table 3 Estimation and goodness-of-fit of dispersal model parameters

	Model	Estimated model parameters			Dispersal feature computed from model parameter			
		<i>p</i>	<i>U</i>	Fer	Mdd (m)	<i>p</i> 30m	<i>p</i> 100m	<i>r</i>
Cohort 1	DRM	13.24	4,884.31	253	16.4	0.894	0.999	0.67*
	DM	2.78	2,624.5	10.104	27.7	0.569	0.987	0.66*
Cohort 2	DRM	7.09	1,691.49	253	13.2	0.951	0.999	0.57*
	DM	4.84	2,193	0.569	18	0.81	0.999	0.44*
Cohort 3	DRM	0.64	197	253	19.6	0.666	0.92	0.72*
	DM	0.16	500	0.042	174	0.151	0.385	0.66*
Seed	SM	0.99	45	253	6.8	0.95	0.995	–

Fertility (Fer) is the number of seedlings (in the case of DM) or seed (in the case of DRM or SM) produced per cone. Note that the number of seeds per cone (in the case of DRM and SM) was fixed at 253, according to experimental data. Note also that *r* is the value of the Pearson correlation ($*p<0.001$) between the observed and predicted seedlings (log scale) in the regeneration stands

DM Dispersal Model, *DRM* Dispersal Recruitment Model, *SM* Seed Dispersal Model, *p* and *u* parameters of 2Dt dispersal kernels, *Mdd* median dispersal distance, calculated from the 2Dt kernel; *p* 30 m and *p* 100 m the cumulated probability of the dispersal curves observed at a distance of 30 and 100 m from a seed tree

Fig. 3 Dispersal curves calibrated on the 120 silver fir regeneration subplots (30 plots \times 4 subplots), for the cohorts 1 (**a**), 2 (**b**), and 3 (**c**). *DRM* dispersal recruitment model, *DM* dispersal model, *SM* seed model. These curves are 2Dt models linking the spatial distribution of seed trees with the spatial distribution of the seedlings. The values of the parameter p and u are: cohort 1—2.78 and 2,624 and 13.240 and 4,884.31, for DM and DRM, respectively. Cohort 2—4.8 and 2,193 and 7.09 and 1,691, for DM and DRM, respectively. Cohort 3—0.16 and 500 and 0.64 and 197, for DM and DRM, respectively. Seeds—0.99 and 45 for SM model



limiting factor is probably water supply (Carcaillet and Muller 2005). Silver fir is mainly found in mountainous regions characterized by their high humidity (Rolland et al. 1999). Tan and Bruckert (1992) confirmed this trend by showing that soil and atmospheric humidity were the two limiting variables conditioning regeneration survival. At high elevations, the limiting factor is most probably frost (Balcar and Kacálek 2008). Late frost at high elevation induces the death of young seedlings, hence limiting silver fir establishment. Seed rain also had a significant positive impact on seedling density, confirming the results of Sagnard et al. (2007). However, seedling density did not increase proportionally with seed supply (see Table 2 where the GLM regression coefficient between seed supply and seedling density was much lower than one), indicating that

seed supply saturates the seed's capacity to germinate. The other studied ecological factors were of lesser importance for seedling densities on Mont Ventoux. Silver fir is a drought intolerant species (Carcaillet and Muller 2005; Münzbergová and Herben 2005). Thus, steep slopes were unfavorable for seedling recruitment, probably because soil humidity decreases with slope steepness (Matthes and Larson 2006). A northern aspect, where relative atmospheric humidity is high, was favorable for silver fir establishment. High densities of adult trees had a negative impact on seedling densities (except for the old cohort, where pine density had a positive impact on seedling density) indicating that adult trees are in competition with seedlings for resources (particularly light and water). The variables assessed in our model were macro-environmental variables (e.g.,

elevation, slope, aspect, etc.). However, micro-environmental variables such as forest floor vegetation or forest floor recovery (rock, litter, deadwood recovery) are known to influence germination and seedling survival at a very local scale (1 m²). In our study, these micro-environmental variables had no significant effect at the subplot scale (100 m²) compared with macro-ecological variables, hence were not included in the analysis (detailed results of statistical tests not shown). In conclusion, the older the seedling cohort, the lower the recruitment rate, highlighting the impact of environment on seedling survival over time. This finding is confirmed by the number of seedlings recruited per year (Table 1) that ranges from 122 seedlings/year for the younger cohort to 1.3 seedlings/year for the older cohort.

4.2 Dispersal models and recruitment limitations

Silver fir seed dispersal occurs mostly at short distances from seed trees. The SM model showed that 95 % of dispersed seeds were found within a radius of 30 m and 99.5 % within a 100-m radius. The value of Mdd obtained for silver fir (7 m) is consistent with published values for anemochorous species. In *Abies magnifica* and *Abies concolor*, Mdd estimated from seed-trap data equals 26.7 and 8.83 m, respectively (Clark et al. 1999b). Moreover, estimation of seed dispersal curve from seedling plots (from DRM, Mdd ranges between 13.2 and 19.6 m) are in accordance with published values. In *Pinus strobus*, Mdd estimated from seedling plot experiments equals 15 m (Ribbens et al. 1994). In *Pinus halepensis*, Mdd estimated from seedling-plot data ranges from 10 to 13 m (Nathan et al. 2000). Finally, the study of Szymura et al. 2007 on the spatial pattern of natural regeneration in *A. alba* confirms our own results: seedlings were spaced at mean distances 5–25 m (and at maximum distance of 50 m) from the nearest seed tree.

Dispersal parameters computed from seedling-plot experiments differed when using the DM or the DRM, especially for the old cohort. Dispersal curves estimated using DRM were always closer to the reference SM curve for the three cohorts than the one estimated using DM, both in terms of Mdd and shape of the dispersal curve. When using DRM, Mdds were systematically shorter; this result was particularly obvious for the old cohort (>150 m for DM compared with 19.6 m for DRM). Using DRM, the tail of the dispersal curve also had a more similar shape to the tail of the reference seed dispersal curve (see Table 3 for values at 30 and 100 m). Moreover, DRM provided better seedling density predictions than DM for older cohorts which can be attributed to the effect of environmental variables on recruitment (see Pearson coefficient values in Table 3). Thus, and

considering that secondary dispersal in space is negligible in silver fir, DRM provides a much more realistic dispersal curve estimate than DM.

Distance dependent post-dispersal processes affecting seedling survival must be taken into consideration for dispersal curve estimation. If seedling recruitment is not taken into account (as in DM), dispersal curves calibrated from seedling counts become “artificially” fatter tailed. Among the factors affecting post-dispersal processes, competition may be the strongest in *A. alba*. Seedlings get less light under the crown of adult trees and have to share very local soil resources (water and nutrients) with them, leading to higher mortality rate for seedlings in the close vicinity of trees (Hofmeister et al. 2008). Allelopathy may also be strong in silver fir. Becker and Drapier (1985) reported that aqueous extracts of silver fir needles had toxic properties for their own seedlings, leading to lower seedling survival under seed trees. The Janzen–Connell hypothesis (Clark and Clark 1984) of greater seed and/or seedling predation near the seed trees could also explain why the peak of recruitment occurs at a certain distance from seed trees. However, although high intensity of browsing by roe deer or red deer has been reported in *A. alba*, there is no evidence that it results in such a spatial pattern in recruited seedlings (Motta 1996).

In DRM, recruitment rate integrates the lower seedling survival under seed trees. It thus makes it possible to infer seed density from seedling density and consequently to accurately estimate seed dispersal from seedling counts. In a similar approach, LePage et al. (2000) simultaneously quantified the effect of both seed source fecundity and distance, and substrate limitation for determining the spatial distribution and overall abundance of seedling recruitment in temperate forests. DRM differs from LePage et al.’s approach in two points: (1) variables included in the model are macro-environmental variables and (2) seed supply is included in the calculation of recruitment rate. Because DRM integrates seed dispersal limitations and macro-environmental factors that affect recruitment, it accurately estimates seed dispersal from seedling counts at landscape scale.

Another important point from our results concerns which type of cohort should be considered for dispersal estimates. The older cohort (which results from 25 dispersal events) should not be considered in DM. Its estimated dispersal curve diverges the most from the reference SM curve. This strong discrepancy (Mdd > 150 m against Mdd = 7 m) is probably due to the fact that the structure of the older cohort results from many mortality events, particularly near seed trees (allelopathy, competition, and density dependence). Thus, a dispersal curve estimated only from old cohort seedling counts (without taking into account recruitment)

is artificially elongated. In the case of DRM, this discrepancy is significantly reduced ($M_{dd}=19$ m). Nevertheless, the uncertainties on seed production, seed tree location and environmental variables over a period of 25 years remain high. Contrary to our expectations, the DRM dispersal curve of the 2 to 5 years old cohort was more similar to the reference seed dispersal curve SM than the dispersal curve of the 1 year old cohort was. As germination is the first step after seed dispersal, we had expected that a dispersal curve estimated from germination (cohort 1) would have been the most similar to the reference dispersal curve. One of the explanations could come from the existence of strong inter-annual variability of dispersal patterns (Sagnard et al. 2007). *A. alba* is an anemochorous species and Mont Ventoux is known to be very windy. If wind is high when cone disarticulation occurs, seeds are dispersed farther than when wind is weak or absent. As a consequence, seedling spatial patterns are more affected by dispersal when only a single year of dispersal is considered.

4.3 Importance of accurately calibrating dispersal

One interest of calibrating dispersal curves on seedlings rather than seeds lies in the fact that greater spatial scales can be investigated. Landscape scales such as the one in our study (up to several hundred hectares) can be assessed much more easily. At such spatial scales, inverse modeling is a useful methodology for estimating dispersal, especially when using flexible kernels such as 2Dt models (Clark et al. 1999b). Nevertheless, such an approach cannot model long distance dispersal very accurately. Yet long distance dispersal is of critical importance for understanding range movements, particularly under climate change (Cain et al. 2000; Nathan et al. 2011). Genetic analysis may be an interesting alternative approach, but could be limited when seed trees are numerous and/or unknown.

The originality of our approach is that it combines seed tree location and fertility (which control seed dispersal) and environmental conditions (which control recruitment) (LePage et al. 2000) within a single dispersal model. This model does not only provide a measure of seed movement, it also indicates where seeds can germinate and seedlings can establish (Cain et al. 2000; LePage et al. 2000). Our results show the importance of taking into account environmental variables driving the transition of seeds into recruited seedlings, in order to accurately calibrate dispersal curves. If dispersal curves are calibrated without taking into account the environmental characteristics of seedling reception site (via the recruitment rate), simulated colonization speed will be much higher than reality. As an example, the probability of dispersing a seed at a distance of 500 m (probability=0.67) using DM is equal to the probability

of dispersing a seed at a distance of 30 m using DRM (using data from the older cohort).

We have also shown that silver fir has weak dispersal capacities. Its impressive colonization dynamics over the last 150 years owe probably much more to seed supply and microsite availability than to long distance dispersal. Therefore, in the context of climate change, the question “Will silver fir migrate fast enough to keep pace with its ecological niche?” remains wide open.

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Appendix 1

(1) Cone production: cone production was estimated from a fertility model calibrated by Pichot et al. (2006)¹ on 280 silver fir trees over 4 years in the same area (2002 to 2005):

$$N_{\text{cones}} = A \times (C - 100)^{0.25} - 2.84 \times A - 25.68$$

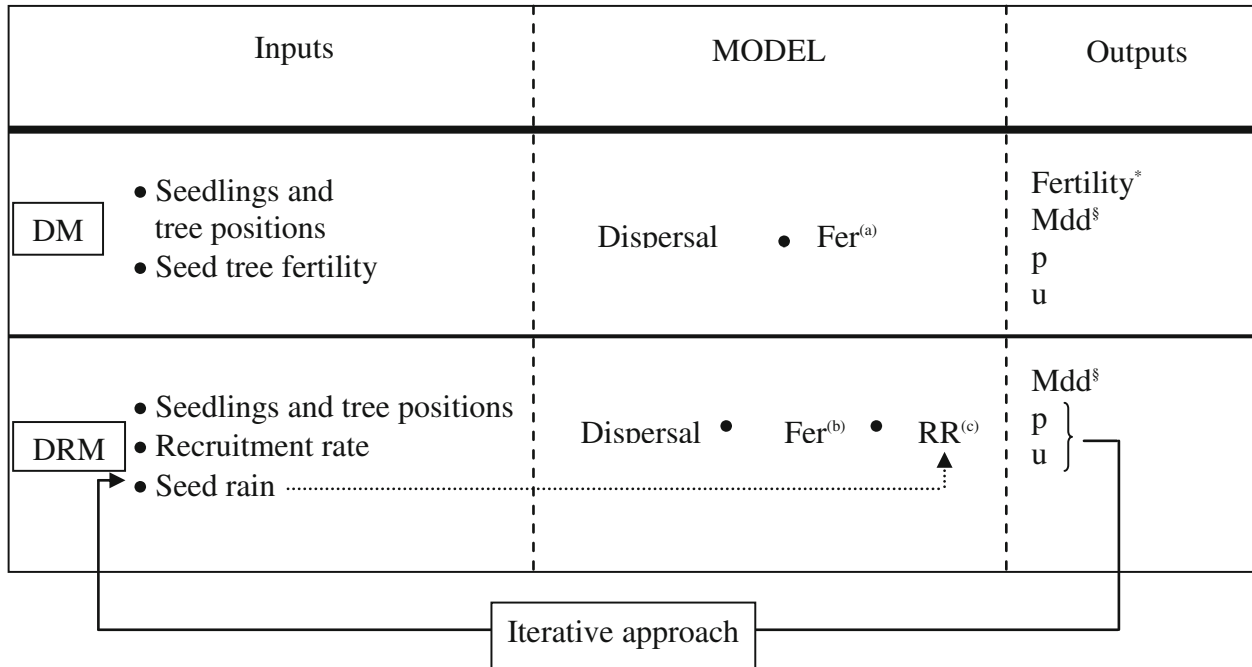
Where N_{cones} is the number of cones; C the circumference of the stem (mm) at breast height and A is a year effect (A ranges from 16 to 30).

For modeled seed trees, cone production was assigned to 40 for a seed crop year, which corresponds to the mean number of cones observed for adult trees. This value was balanced by the percentage of silver fir cover (given by the French National Forest Service). The number of seeds per cone was considered to be constant and set to the average value of 253 estimated by dissection of 153 cones (collected from 53 seed trees on Mont Ventoux).

(2) Accounting for several dispersal events: a dispersal event was applied every year through a seed production depending on climate and growth condition of previous years. For cohort 1 (germinations born in 2007), we calculated one year of dispersal applying a mean value of year effect ($A=23$). Because only 4 years of dispersal were cumulated for cohort 2 (2002–2005) we considered that seed tree diameters remained unchanged. For these 4 years, we used the random year effect calculated for the same years. For modeled seed trees, the mean number of cones was set to 160 (4 years \times 40 cones). Cohort 3 was considered to result from 25 dispersal events (1977 to 2002), during which average diameter of seed trees and then cone production increased. In order to take into account the evolution of seed tree production over this period, diameter evolution from 2002 to 1977 was simulated using allometric relations calibrated for this species (Dreyfus, unpublished data). Cone production of the dense silver fir stands (modeled seed trees) was assumed to be constant (1,000 cones=25 years \times 40 cones/year).

¹Pichot, C., C. Bastien, F. Courbet, B. Demesur-Musch, P. Dreyfus, B. Fady, N. Frascaria-Lacoste, S. Gerber, F. Lefèvre, M. E. Morand-Prieur, S. Oddou, E. Teissier Du Cros, A. Valadon. 2006. Déterminants et conséquences de la qualité génétique des graines et des semis lors de la phase initiale de régénération naturelle des peuplements forestiers. Actes du BRG 6:277–297.

Appendix 2



Dispersal model: DM

Dispersal recruitment model: DRM

^(a) Effective seed tree fertility (diameter)

^(b) Number of seeds

^(c) Recruitment rate (depending on seed supply and environmental variables)

* Number of seedlings produced by one tree

§ Median distance dispersal

p: Shape parameter of 2Dt dispersal kernel

u: Scale parameter of 2Dt dispersal kernel

Inputs and outputs of dispersal and dispersal recruitment models. An iterative approach is only computed for the DRM, in order to take into account the dependence between RR the seed rain.

The RR depends on environmental variables and seed supply (S_n). Seed supply (S_{n+1}) is computed again at each step with the estimated parameters p and u , until they become stable.

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