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Combining partial cutting and direct seeding to overcome regeneration failures in dune forests.

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Abstract:

Stand regeneration is a crucial step in the management of many forests and its failure can jeopardize future forest growth and production. Thus, adapting forestry practices to improve seedling establishment is of prime importance to maintain sustainable forest management. In the coastal dune forests of maritime pine in SW France, regeneration failure after clear-cutting has greatly increased in the last decades. The aim of this study was to quantify the different stages involved in the regeneration process (seed rain, germination, survival), and to assess the impact of harvesting methods (partial cutting vs. clear-cutting) and of the use of direct seeding (seeding vs. no seeding) on these stages. We established five trials located in areas with contrasting regeneration statuses (of which two sites were in an area characterized by chronic regeneration failure), and we investigated the effect of the harvesting method and the use of direct seeding in a factorial design. We monitored the seed rain, germination and first-year survival for three years. Due to the transient nature of the seed bank, we found that the seed rain of the previous year was the only possible seed source for tree regeneration, and it increased with the proximity and size of surrounding mature trees. Nonetheless, seed rain did not limit regeneration in these stands. In fact, germination was the bottleneck stage of the regeneration process in all sites because it was short-lived and consequently exposed to failure in case of unfavourable conditions. Once established, seedling death was mainly due to summer drought. Clear-cutting without seeding resulted in severe regeneration failures in 4 out of 5 sites, with the most severe in the failure area. Direct seeding increased seedling emergence only in the first year, while partial cutting had a longer-lasting effect by providing a regular seed supply over several years. Partial cutting also decreased biotic and abiotic stresses through microhabitat modification under the tree canopy, resulting in a higher number of germinations and greater seedling survival. This positive effect was more pronounced in the two sites within the failure area, suggesting that conditions were more stressful in this part of the forests. Consequently, we recommend avoiding clear-cutting in favour of partial cutting in all parts of these forests, and ensuring the maintenance of sufficient forest cover to promote regeneration. Direct seeding could be used in addition to partial cutting to maximize the chances of success, but only in areas where natural regeneration is low.

Key words: Direct seeding, Drought, Forest management, Germination, Partial cutting, *Pinus pinaster*, Seed availability, Seedling survival, Tree regeneration.

1. Introduction

The renewal of forest stands is a key step in forest dynamics and for their sustainable management. Natural regeneration is one way to do this and involves the stages of seed production, seed dispersal, germination and seedling survival, each being influenced by many interacting biotic and abiotic factors (Price et al., 2001; Kozlowski, 2002; Calama et al., 2017). The establishment of a species results from the interactions between the quantity of available seeds and the number of suitable microsites for regeneration (Harper, 1977; Schupp, 1995). The density of seeds reaching the ground depends on the seed production, on the spatial arrangement and the characteristics of the seed trees, and on the seed dispersal capacity (Greene et al., 1999; Viglas et al., 2013; Montoro Girona et al., 2018). Then, seedling emergence and survival depends on favourable local conditions such as soil moisture, soil temperature, or light (Harper, 1977; Kozlowski, 2002). These ecological conditions vary widely, both spatially and over time (Beckage and Clark, 2003; Gómez-Aparicio et al., 2005), and can be influenced by biotic interactions with overstorey trees, herbaceous species or herbivore populations (Harmer, 2001; Wagner et al., 2011; Lavoie et al., 2019). Consequently, regeneration failure can also depend on the local environmental conditions.

Natural regeneration is frequently unsuccessful in temperate and Mediterranean managed forests (Calama et al., 2017; Dey et al., 2019), and could be increasingly threatened in the current context of global change in areas where droughts are expected to increase in frequency and intensity (IPCC, 2014). Thus, understanding the regeneration processes is very important in the adaptation of forest management practices to ensure the natural regeneration of stands. Forest harvesting, which is the starting point of the regeneration cycle, can be performed in two different ways in even-aged forests: i) clear-cutting, when all the trees are removed in a single harvesting operation and the new seedlings emerge from the soil seed bank. In the most difficult cases, natural regeneration can be assisted with a direct seeding using local seeds to overcome establishment limitations (Grossnickle and Ivetić, 2017); ii) partial cutting, when some of the mature trees are left unlogged in the stand to promote regeneration, and are harvested few years later, once regeneration is sufficient (Nyland, 2016). The degree of canopy closure induced by partial cuts can potentially influence several ecological processes and is therefore a key factor that can affect regeneration. First, the remaining trees can supply the viable soil seed bank for a few years to offset low seed availability for regeneration (Nyland, 2016). Second, forest cover can create more suitable conditions for seedling establishment by buffering microclimatic stresses (e.g. vapour pressure deficit, soil moisture or solar radiation) (Aussenac, 2000; Heithecker and Halpern, 2006). Partial cuts also modify light availability at the ground level and can influence the development of herbaceous and understorey species that may limit seedling establishment by competing for resources (Löf, 2000; Wagner et al., 2011). Finally, this habitat modification may also have an indirect impact on the behaviour of herbivores and therefore on the potential damage caused to seedlings (Reimoser and Gossow, 1996; Côté et al., 2004). In addition, partial cutting, which is increasingly used to ensure the sustainable management of many forests, can have other effects than promoting natural regeneration. Partial cutting also promote both economic and ecological features of mature stands, by increasing the radial growth of residual trees following the decrease in stand density (Montoro Girona et al., 2016), and by supporting higher richness and greater abundance of flora and fauna than clear-cuts (Fedrowitz et al., 2014). However, these positive effects could be reduced in case of mortality of residual trees, as partially cut stands tend to be more sensitive to disturbance (particularly windthrow) than unharvested stands (Montoro Girona et al., 2019).

Maritime pine (*Pinus pinaster* Aiton) is a widely distributed conifer in the Mediterranean basin and along the Atlantic coast of Western Europe, and is of high ecological, economic and social importance in its native area (Alía and Martín, 2003) and in countries where it has been introduced (mainly Australia, New-Zealand, and South Africa). The coastal forests of maritime pine in southwestern France cover about 100 000 ha (IFN, 2017). Natural regeneration following clear-cutting has been used traditionally for many decades for the renewal of these forests to fulfil their multifunctional role (i.e. wood production, soil erosion protection, preservation of biodiversity, recreation usage and aesthetic value) and to improve the conservation of genetic diversity and the capacity to adapt to global change. However, regeneration failures (i.e. less than 3000 seedlings ha^{-1} – or 0.3 m^{-2} – three years after harvest (Sardin, 2009)) have steadily increased in recent years, and persisted in spite of an additional supply of local seeds in some stands at the harvesting period. These failures were mainly observed in the central part of the coastal fringe occupied by dune forests (up to half of the regenerating stands may fail some years (Ouallet, 2012)), but this is beginning to spread to other areas, causing great concern among forest managers. In this type of ecosystem with freely draining sandy soils and regular severe summer drought, partial cutting is a method often used in other regions to renew pine forests, such as Spain (Calama et al., 2017). This method regularly results in sufficient seedling density in maritime pine forests (e.g. Rodríguez-García et al., 2010), but failures are also observed (e.g. González-Alday et al., 2009). This is because natural regeneration is highly dependent on site characteristics and on local climatic conditions, and is also variable between pine populations (Rodríguez-García et al., 2011b; Vergarechea et al., 2019).

The aim of this study was to identify the processes involved in failures of natural regeneration in the coastal forests of maritime pine, in interaction with silvicultural practices. For this purpose, we established five stands located in areas with contrasting regeneration successes, and investigated the effect of the harvesting method (partial cutting compared to the usual clear-cutting) and of the use of direct seeding (compared to the absence of seeding). We hypothesized that: i) partial cutting could compensate for poor-regeneration years by supplying extra seeds each year, and by increasing germination and seedling survival rates due to improved microclimatic conditions, especially in the summer; ii) this positive effect would be more pronounced on sites within areas of high regeneration failures, so that the threshold of 3,000 seedlings ha^{-1} necessary for a successful regeneration would be exceeded; and iii) direct seeding would improve the number of seedlings regardless of the harvesting method, but it might be less useful than partial cutting that provides a combination of seed supply and microhabitat amelioration. By improving our understanding of the ecology of maritime pine regeneration, our findings should enable us to propose adequate management strategies to ensure natural regeneration in these forests.

2. Materials and methods

2.1. Study sites

Our study combined experimentation (harvesting method and seeding as treatments, see 2.2.) and exploration on a regional scale, integrating a major regeneration failure area. Thus, we established five trials along the coast in the maritime pine (*Pinus pinaster* Aït) sand dune forests of SW France in areas with contrasting regeneration statuses (Fig. 1A): two of the sites were within the area of chronic regeneration failure (hereafter referenced to as sites F1 and F2), while the three other sites were in areas with frequent regeneration success (S1, S2 and S3). The lower number of site in the failure area is explained by its geographically smaller area compared to the whole dune forests (Fig. 1A). Stand area ranged from 7.4 to 11.5 ha and tree age ranged from 58 to 77 years old (Table S1). The climate in the region is temperate oceanic. Average, minimum and maximum annual temperatures were 13.6 °C, 8.8 °C and 18.5 °C for S1 and about 14.1 °C, 9.3 °C and 19.2 °C for the four other sites (Table S1). Average annual precipitation ranged from 840 mm to 1007 mm (Table S1), with the wettest period in winter and the driest in July-August. All sites were chosen on westerly facing slopes at about 2.5 km from the ocean, with an average slope of 10°. Soils are young sandy soils (WRB classification: arenosols; USDA classification: entisols) mainly composed of coarse sands (96–97%), are slightly acidic (topsoil values of pH = 4.5–5.0), and are extremely poor in nutrients (Augusto et al., 2010). These soils have a low water holding capacity which, combined with low summer rainfall, results in an extremely low soil moisture content and a high water stress for seedlings in summer (Guignabert et al., 2020).

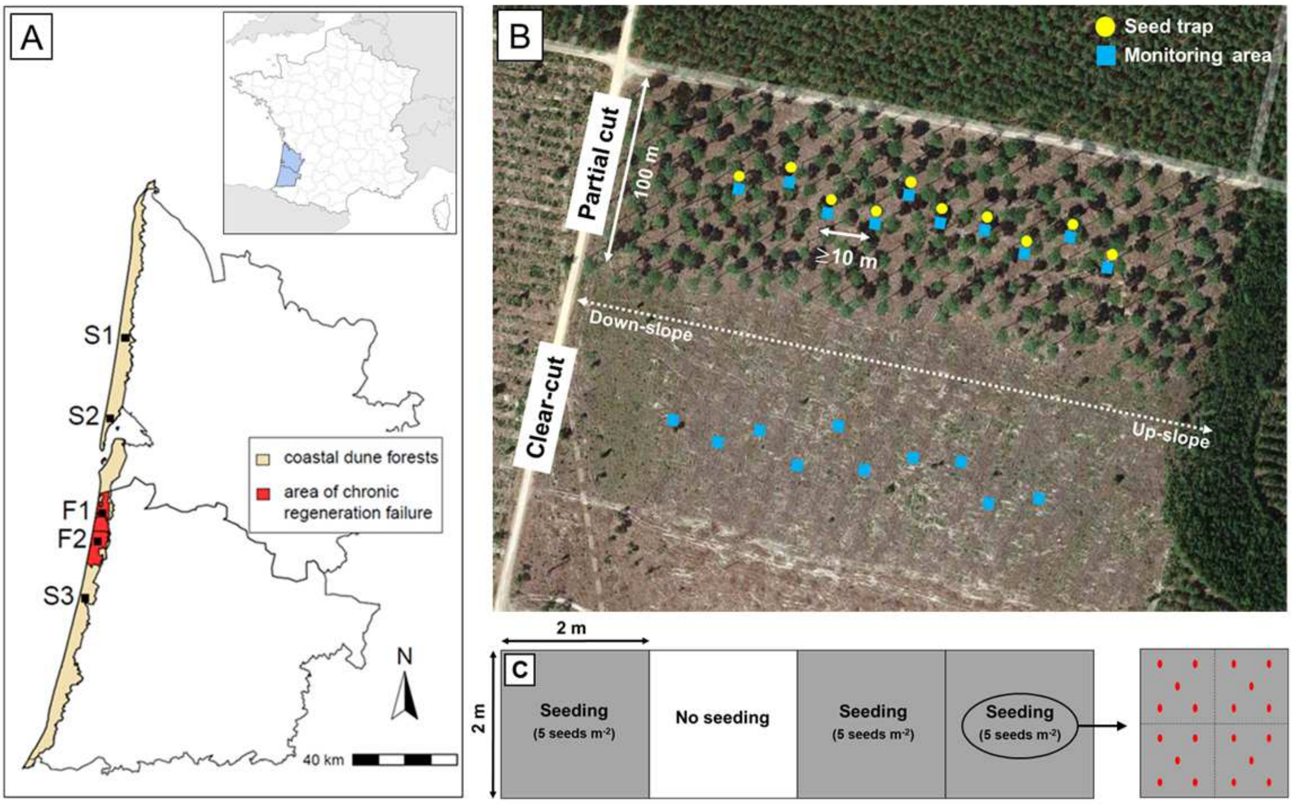

Fig. 1: A) Location of the five study sites. B) Aerial photography of S3 showing the two harvesting treatments, and the distribution of the monitoring areas. C) Schematic of one monitoring area and of the seed arrangement pattern.

2.2. Experimental design

Two silvicultural practices were tested factorially at each site in early 2015: i) the harvesting method (usual clear-cut vs newly tested partial cut using the uniform shelterwood system), and ii) the use of direct seeding (vs no seeding). To that end, each of the two harvesting methods was carried out on half of all stands (Fig. 1B). Tree harvesting was performed mechanically with a feller-buncher between January and March 2015. For the partial cut treatment, trees were chosen on the basis of their vigour and appearance, and tree density after harvest was ~70 stems/ha in all sites. The basal area after partial cutting was between 7.5 and 13.2 m^2 ha^{-1} (Table S1). Other management practices were carried out before logging in all experimental treatments: understorey vegetation was removed mechanically to limit post-logging competition and was combined with light mechanical tillage to increase soil aeration and nutrient availability. Then, at each site, we positioned ten monitoring areas in the centre of each harvesting treatment (Fig. 1B), each area being split into four 4 m^2 quadrats (Fig. 1C). Three quadrats were sown with five seeds m^{-2}, which corresponds to the quantity currently used by foresters in regeneration failure areas. Seeds were sown following an identical pattern (Fig. 1C; ca. 0.5 cm deep) and came from cones collected from stands of maritime pine located in the same forests. The fourth quadrat was unsown, and its position was determined randomly. Finally, we installed a 1.5 m^2 seed trap one meter away of each monitoring area in the partial cut treatment (Fig. 1C) to quantify the seed rain (10 seed traps per site). Traps were wooden frames filled with high-density polyethylene mesh and with 25 cm high edges in soft PVC, and were set up at about 25 cm above the ground (Fig. S1).

2.3. Regeneration monitoring

Seed rain was collected monthly in seed traps and counted from May to October in 2015, 2016 and 2017, then air-dried and stored at 4 °C. Seed weight and seed length were measured on a random sample of 80 seeds per site of the 2015 seed rain, using a precision balance and a digital calliper respectively. Since seed rain is known to be dependent on tree basal area and tree density (Ruano et al., 2015b; Viglas et al., 2013), we measured the circumference of all trees within a 20 m radius of each seed trap and their distance from the trap . Then, from these two variables we calculated a seed source abundance index (SSAI) for each seed trap as follows: $SSAI = \sum_{i=1}^{n}(TBA_i / d_i)$ with $TBA_i \ (m^2) = (c_i/100)^2/4\pi$ and where *c* (cm) is the circumference at 1.30 m of tree *i*, *TBA* is the basal area of tree *i* (m^2) and *d* the distance (m) of tree *i* from the seed trap. The closer and bigger the tree, the more it contributes to the index value. The choice of a 20 m radius circle around each seed trap was based on previous studies about the dispersal distance corresponding to the majority of dispersed pine seeds (Juez et al., 2014; Ruano et al., 2015b).

Seedling emergence and first-year survival were monitored each year from 2015 to 2017. Censuses were carried out monthly from May to October in 2015 and 2016, and only three censuses were made in 2017: in late March, before the germination peak; in mid-June, after the germination peak and before the drought period; and in late September, after the drought period. Cause of seedling death was recorded: drought, when the seedling turned from green to red/brown; or due to herbivores, when the seedling died after browsing by ungulates or rodents (see

Guignabert et al. (2020) for more details on the distinction). Non-lethal ungulate browsing events were also noted at each survey. For each monitoring year, the survival of seedlings that emerged in the spring was only surveyed until the end of that specific year, and not throughout the whole study. Thus, a final count of all living seedlings was performed in March 2018 to obtain an assessment of the regeneration density comparable to the density value defined by foresters as the threshold value necessary for a successful regeneration (i.e. 0.3 seedlings m^{-2}; Sardin, 2009).

2.4. Complementary measurements

2.4.1. Soil seed bank

Soil samples were collected from all sites to assess the soil seed bank, both in the clear-cut and in the partial cut. This sampling was performed at the beginning of the experiment in April 2015, after tree harvesting and before the beginning of the seed rain. A soil sample of 1/32 m^2 and 5 cm deep was collected in the proximity of the four corners of each monitoring area, giving a total of 400 samples (5 sites x 2 harvesting methods x 10 monitoring areas x 4 samples) from a total surface area of 12.5 m^2. Samples were then sieved using a 2 mm mesh and undamaged seeds were counted and stored at 4 °C.

2.4.2. Seed germinative capacity

We carried out a glasshouse germination test in March/April 2017 to evaluate the germinative capacity of the seeds in the five sites. This test was performed using the three pools of potential seed sources: i) seed rain, using seeds collected from seed traps in summer 2016; ii) soil seed bank, using seeds collected from soil sampled in April 2016 following the same procedure described above; and iii) seeds used for direct seeding by the French National Forestry Office (seeds ref: "*PPA 303, dunes littorales de Gascogne*", collected in winter 2015-16). All seeds were stored at 4 °C in the same place between their collection and the test. We sowed 11 batches of 50 seeds in independent trays (50 x 30 cm) on March 15: five batches of soil seed bank and of seed rain (one per site), and one batch of seeds used for seeding. The soil used in all trays was collected from the F2 site and sieved to remove seeds potentially present in the collected soil. Trays were installed in a glasshouse at ambient temperature and watered every two days. New emergence was surveyed once a week for 8 weeks.

2.4.3. Dendrometric features of partial cuts

The dendrometric features of a mature stand (e.g. basal area, canopy cover) are partly related to the silviculture carried out during the forest rotation (e.g. thinning). We carried out this additional study in winter 2018-2019 in other forest stands to find out whether the stand structure of partial cuts might be a factor that should be integrated into the management considerations to improve regeneration. It should be noted that this study was not carried out at our five experimental sites, but at the scale of a large management canton. This area was located within the main failure area (i.e. near F1 and F2), the only area where partial cuts had been implemented in the region so far. We selected forest stands which had been harvested at least 3 years before (i.e. harvested in winter 2013-14, 2014-15 and 2015-16), which represented 29 stands and 280 ha (stand average = 9.7 ha, min = 3.4 ha, max = 19.7 ha). For each stand, we measured: i) the seedling density, by counting the number of seedlings in 80 plots of 6 m^2 positioned according to a systematic grid pattern (all were summed and then reported as seedlings m^{-2}); ii) the tree density by counting all trees in the stand; iii) the basal area, estimated from the tree diameter. The diameter of each tree (*d*, cm) was measured using a forest compensated calliper (i.e. graduated in 5 cm classes), the method which is regularly used in silviculture to carry out inventories and provides a good estimate of the basal area (Cordonnier et al., 2007). Stand basal area (*BA*) was then calculated for each stand as: $BA\ (m^2/ha) = (\sum TBA)/stand\ area$, with $TBA\ (m^2) = \pi(d/100)^2/4$; iv) the forest cover, which was estimated using the normalised difference vegetation index (NDVI) based on analysis of multispectral images of the Pléiades satellite taken on 14 April 2018 and 03 September 2018, and performed with ArcGIS. This variable, obtained in m^2, was then expressed as a percentage value by dividing the value by the stand area; and v) the individual tree crown surface area (m^2 tree^{-1}), by dividing the forest cover (m^2) by the number of trees.

2.5. Data treatment and statistics

All statistical analyses were performed with R software version 3.5.2. (R Core Team, 2018). Data regarding seed and seedling density (i.e. seed rain, soil seed bank, germination and final seedling density) are expressed in number m^{-2} and are continuous quantitative variables. Seedling survival and browsing occurrence are binomial variables, while the different types of mortality are expressed as a percentage. Assumption of normality and homoscedasticity were checked for all models mentioned below, and the response variable was square root transformed when necessary. Post-hoc Tukey pairwise multiple comparisons were carried out when we found that a multilevel factor was significant.

2.5.1. Seed rain and seed bank

We tested the effects of site and year on seed rain, the effects of site and harvesting method on soil seed bank, and the effect of site on seed morphology using analysis of variance. To investigate the influence of tree size and distance on seed rain, we performed linear mixed modelling with our seed source abundance index as an explanatory variable of the mean annual seed rain and the site as random effect. Differences in germinative capacity of the seeds between the three pools of seed sources and between sites were compared using chi-square tests.

2.5.2. Germination and seedling establishment

Analyses regarding germination, survival, browsing occurrence and final seedling density were performed following a two-step procedure: i) full analyses with the site, harvesting method and seeding as explanatory factors, and all two-and three-way interactions; and ii) intra-site analyses of harvesting method and seeding separately. A random intercept for each monitoring area was included in all models to take into account the spatial dependence of the quadrats of the same monitoring area. Germination, tested for each year separately, and final seedling density were analysed using linear mixed models. Longitudinal analyses of seedling survival were performed on the first cohort of emerged seedlings (i.e. cohort of May, which represents 75.4% of the seedlings in 2015) using Cox proportional hazard mixed models. We examined seedling survival only in 2015 because the number of seedlings in clear-cuts was too low to compare harvesting treatments and to perform statistical tests for three out of five sites in 2016, and for all sites in 2017. Browsing occurrence was tested with generalized linear mixed models for binary data with a logit link function. The effects of the harvesting method on the distribution of causes of mortality (i.e. drought, rodents or ungulates) were tested using chi-square tests between sites and within sites.

In addition, one-sample *t*-tests were used to determine whether the final seeding densities were significantly different from the regeneration success threshold for the four possible management scenarios (i.e. clear-cut, clear-cut + seeding, partial cut, partial cut + seeding).

2.5.3. Overall probability of recruitment

In order to identify the limiting stages of regeneration capacity, we calculated the transition probabilities of passing the successive stages of the regeneration process successfully, for each harvest treatment of each site. We estimated the following stages:

i) Seed germinative capacity, estimated via our glasshouse test. .

ii) Germination, as the germination number divided by the viable seed rain (estimated by combining total seed rain and seed germinative capacity) plus the viable seeds from direct seeding. Since the germinations of a year resulted from the seed rain of the previous summer, we used the seed rain data from 2014-2016 and germination data from 2015-2017. Seed rain before harvest (i.e. 2014) was not measured in our study and was thus calculated from the 2015-2017 data by estimating the contribution of one tree to the seed rain (number of seeds m^{-2} $year^{-1}$), and relating it to stand density before harvest.

iii) 1st year survival, as the number of living seedlings one year after emergence divided by the germination number.

iv) 2nd/3rd year survival, as the number of seedlings counted three years after harvest divided by the number of living seedlings at the end of each year. This represented the seedlings from 2015 that died in 2016 and 2017, and those from 2016 that died in 2017.

We finally calculated the overall probability of recruitment as the product of the successive probabilities.

2.5.4. Stand dendrometric features

Relationships between dendrometric features of partial cuts (tree density, basal area, forest cover, and tree crown surface – see Table S2 for descriptive statistics of these variables) and seedling density were prospected with linear regression. As the year of harvesting had no effect on seedling density (p = 0.33), these regressions were carried out using data from the 29 stands together.

3. Results

3.1. Seed availability

The number of seeds reaching the ground varied depending on the year and the site (both $p < 0.001$; Fig. 2), with a different pattern of annual variation between sites (interaction $p < 0.001$). All sites combined, seed rain averaged 11.1 ± 0.7 seeds m^{-2} year^{-1}, with a minimum of 6.1 ± 0.8 seeds m^{-2} year^{-1} in S3 and a maximum of 24 ± 2.3 seeds m^{-2} year^{-1} in S2. Seed rain was influenced by tree size and density of mature trees in the vicinity of the seed traps, as seed rain was positively related to the seed source abundance index ($F_{(1,44)} = 9.59$, $p = 0.004$).

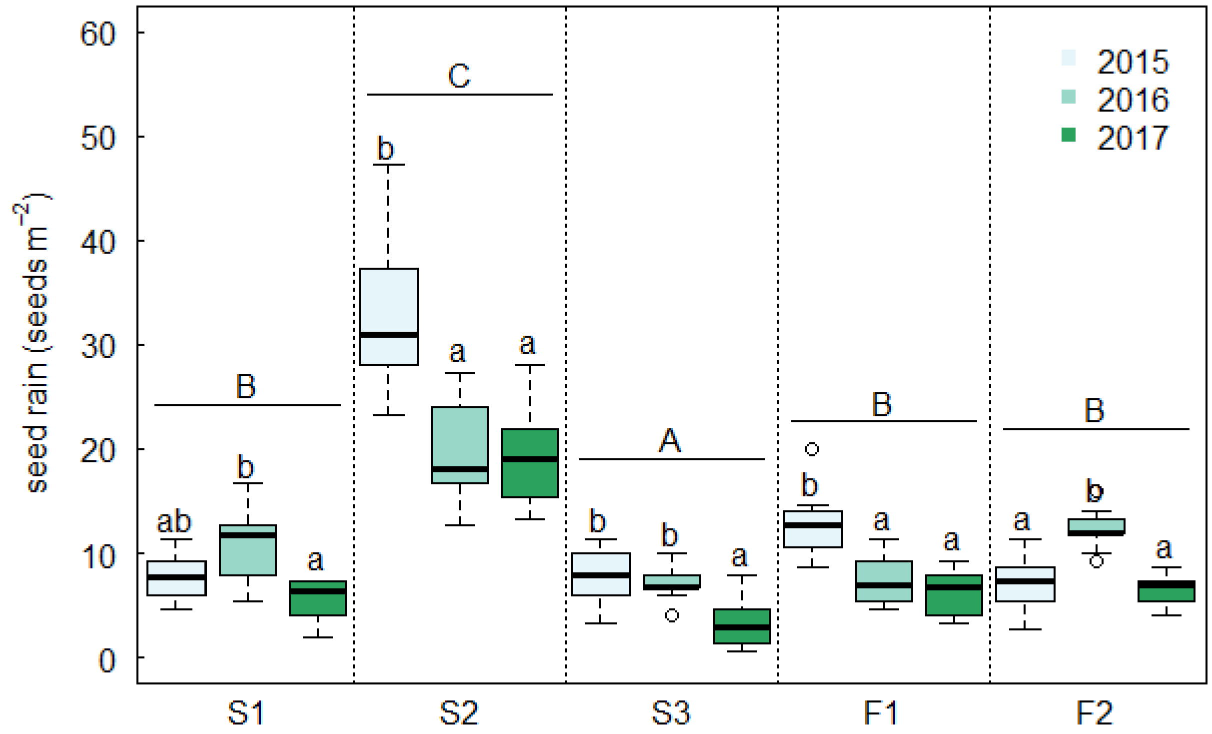

Fig. 2: Amount of seed rain for each site per year (n = 10 for each boxplot). Different uppercase letters indicate significant differences between sites, whereas different lowercase letters indicate significant differences between years within each site (post-hoc Tukey test).

Seed weight and seed length were significantly different between sites (Fig. S2). With an average weight ranging from 38.2 ± 1.6 mg (F2) to 47.3 ± 1.8 mg (S2), and an average length ranging from 7.28 ± 0.1 mm (F2) to 7.71 ± 0.1 mm (S2), the seeds from all sites were within the range of known values for maritime pine seeds in Atlantic and Mediterranean forests (Fig. S2).

The amount of seeds in the soil seed bank also varied according to the site ($p < 0.001$; Fig. S3), but not between clear-cut and partial cut areas ($p = 0.215$). The average number of seeds was

119 ± 6.5 seeds m^{-2}, with the largest amount in S1 with 196.6 ± 1.6 seeds m^{-2} and the lowest in F1 with 79.6 ± 1.1 seeds m^{-2}.

The germinative capacity of seeds showed very significant differences between the various seed pools ($\chi^2_{(2)} = 202.7$, $p < 0.001$; Fig. S4). The seeds used for the direct seeding had the highest germinative capacity (86%), followed by the seeds from the seed rain (26 to 32% depending on the site) and then the seed bank, of which no seeds from any stand germinated (Fig. S4). No difference in germinative capacity was observed between the seed rain of the five sites ($\chi^2_{(4)} = 0.57$, $p = 0.97$).

3.2. Germination

There was a significant site effect with, overall, a higher number of germinations in S2 and S3, and a fewer in S1 (Table 1; Fig. 3). The interactions “site x harvesting method” and “site x seeding” were also significant (Table 1), suggesting a major influence of site-specific conditions on germination. The harvesting method had a highly significant effect on germination each year (Table 1), with a higher number of germinations in partial cuts than in clear-cuts (Fig. 3). The average number of germinations in partial cuts was 0.93 seedlings m^{-2} in 2015, and this decreased in the following two years (0.55 ± 0.06 seedlings m^{-2} in 2016; 0.47 ± 0.09 seedlings m^{-2} in 2017). In clear-cuts, the number of germinations decreased sharply between the first and the second year (0.65 ± 0.07 seedlings m^{-2} in 2015; 0.14 ± 0.02 seedlings m^{-2} in 2016), to reach nearly zero in the third year (0.04 ± 0.02 seedlings m^{-2} in 2017). Interestingly, when we examined the results site by site, the positive effect of partial cuts was only observed in sites within the failure area in the first year (Fig. 2A) while it was observed in all sites in the second and third year (Fig. 2B-C). The use of direct seeding had a positive impact on germination only during the first year (Table 1; Fig. 2), where the average number of germinations was 0.92 ± 0.08 seedlings m^{-2} in the seeded quadrats and 0.39 ± 0.07 seedlings m^{-2} in the unseeded ones. This positive effect of seeding in the first year was observed in all sites (Fig. 2D).

Table 1: Results of the linear mixed models for the effects of site, harvesting method, seeding and their interactions on number of germinations for the three years. Significant effects ($p < 0.05$) are indicated in bold.

		2015		2016		2017	
	df	F	*p*	F	*p*	F	*p*

Site	4,90	13.09	**<0.001**	23.41	**<0.001**	8.89	**<0.001**
Harvesting Method	1,90	23.93	**<0.001**	106.58	**<0.001**	195.77	**<0.001**
Seeding	1,290	95.72	**<0.001**	0.02	0.884	2.75	0.099
Site x Harvesting	4,90	6.35	**<0.001**	7.95	**<0.001**	4.90	**0.001**
Site x Seeding	4,290	4.52	**0.002**	0.67	0.615	0.98	0.422
Harvesting x Seeding	1,290	0.11	0.741	0.31	0.577	0.38	0.540
Site x Harvesting x Seeding	4,290	0.05	0.994	1.08	0.367	0.80	0.523

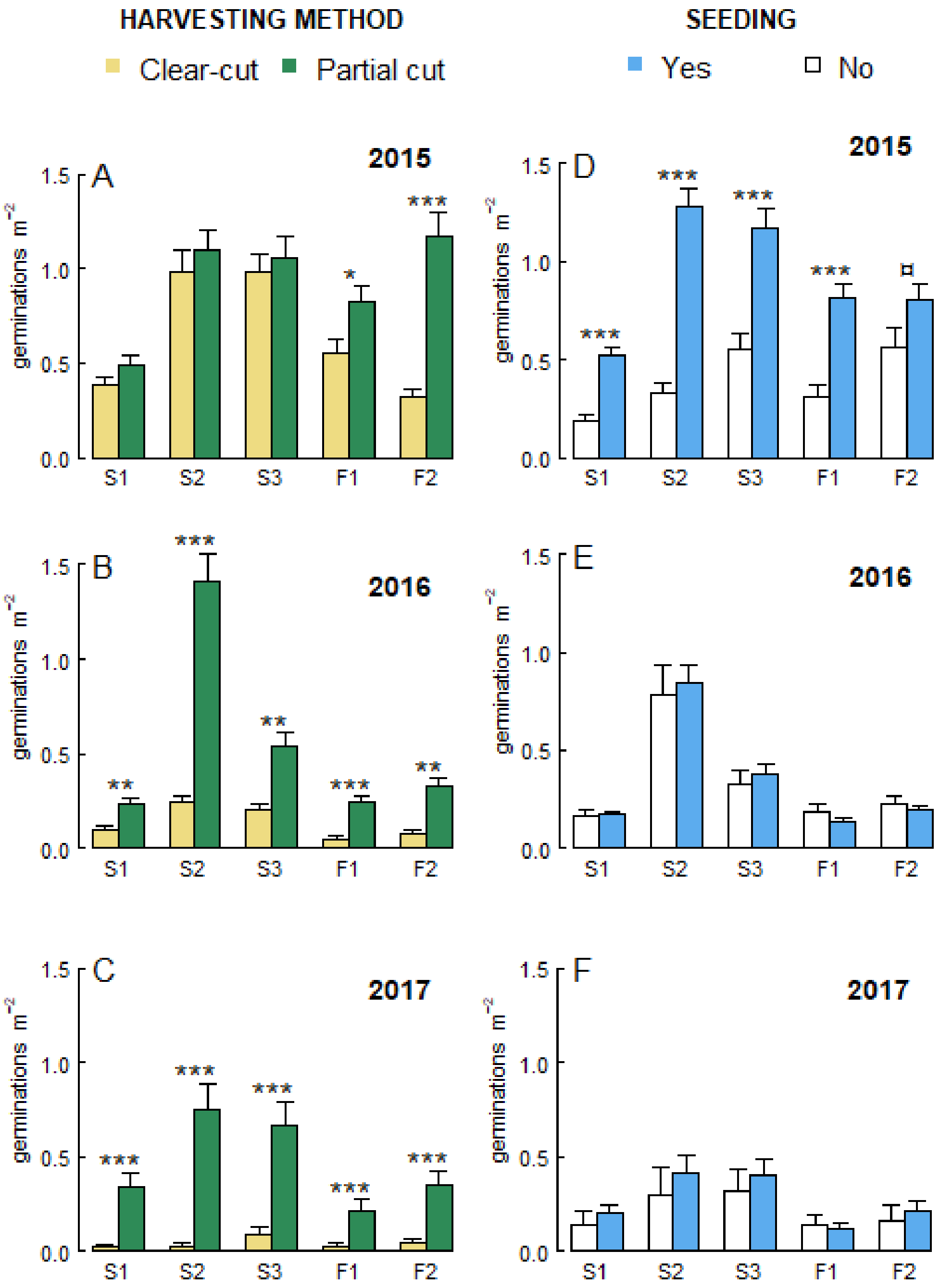

Fig. 3: Number of germinations m^{-2} observed for each site according to the harvesting method (A-B-C) and the presence of seeding (D-E-F). Panels A & D correspond to germinations from 2015, panels B & E to 2016,

and panels C & F to 2017. Asterisks indicate a significant difference between the two modalities within a site (linear mixed models: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ¤ $p < 0.1$).

3.3. Survival

Seedling survival was influenced by the harvesting method ($\chi^2_{(1)} = 8.44$, $p = 0.004$), but not by the site ($\chi^2_{(4)} = 8.48$, $p = 0.075$) or their interaction ($\chi^2_{(4)} = 9.16$, $p = 0.057$). Partial cutting had a positive impact on survival by decreasing mortality by 10.8% compared to clearcutting. On a site-by-site basis, partial cutting had a positive effect on three out of five sites, including the two in the failure area (mortality reduction of 17.5%, 21.5% and 25.6% for S2, F1 and F2 respectively; Fig. 4B-D-E). In addition, F1 and F2 were the only two sites where clear-cut survival rate was lower than 50% (Fig. 4D-E).

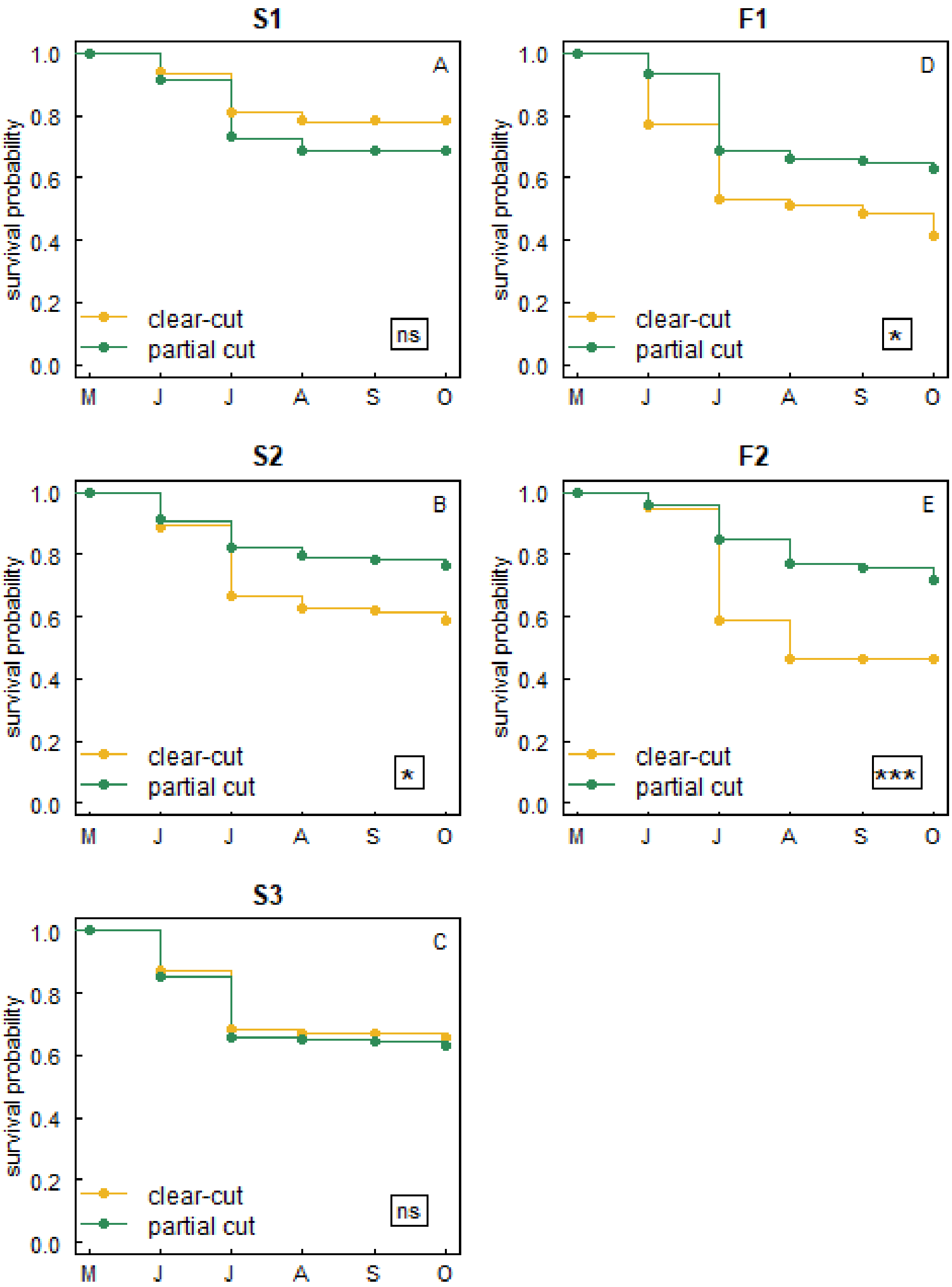

Fig. 4: Seedling survival probability as a function of harvesting method in 2015, for each site separately. Statistical significance between harvesting method is shown in the bottom right corner of each panel (Cox mixed models: *** $p < 0.001$; * $p < 0.05$; ns = non-significant).

Drought was the main cause of mortality (Fig. 5A). All sites combined, we observed a higher mortality due to drought in clear-cuts than in partial cuts ($\chi^2_{(4)} = 11.18$, $p < 0.001$). Within sites, partial cutting significantly reduced the percentage of drought-killed seedlings in S2 ($\chi^2_{(1)} = 7.39$, $p = 0.007$), F1 ($\chi^2_{(1)} = 6.28$, $p = 0.012$) and F2 ($\chi^2_{(1)} = 8.28$, $p = 0.004$; Fig. 5A). Seedling death by herbivores was mainly caused by ungulates, while damage caused by rodents was almost nil, except in F1 (Fig. 5A), and harvesting method had no influence on mortality caused by either type of herbivore.

Conversely to herbivory-killed seedlings, there was a strong effect of site ($\chi^2_{(4)} = 72.67$, $p <$ 0.001) and harvesting method ($\chi^2_{(1)} = 17.99$, $p < 0.001$) on the percentage of non-lethal browsed seedlings. Browsing was more frequent in clear-cuts and in the two sites within the failure area (Fig. 5B). It was also on these two sites that the positive effect of partial cutting was the most pronounced, reducing the browsing occurrence by 12.6% in F1 and 22.5% in F2 (Fig. 5B).

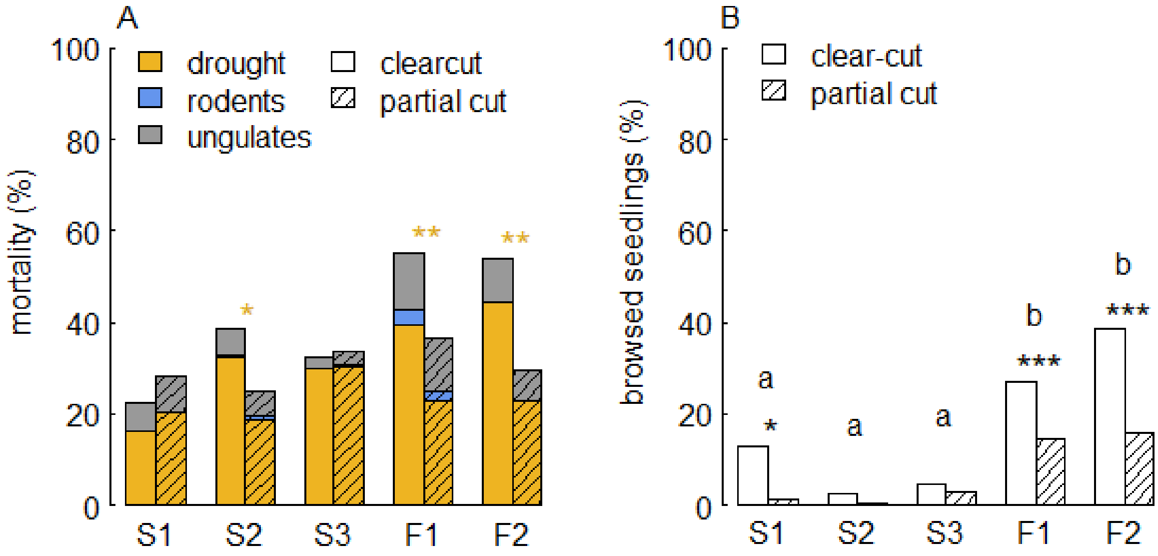

Fig. 5: A) Percentage mortality of each cause of death in 2015 according the site and harvesting method. Yellow asterisks indicate a significant difference in the distribution of drought-killed seedlings between the two harvesting method within a site (chi-square test: ** $p < 0.01$; * $p < 0.5$). B) Seedlings non-lethally browsed by ungulates in 2015 according to the site and the harvesting method. Different lowercase letters indicate significant differences between sites (post-hoc Tukey test). Asterisks indicate a significant difference in browsing occurrence between the two harvesting methods within a site (generalized linear mixed models: *** $p < 0.001$; * $p < 0.5$).

3.4. Overall regeneration success

Three years after starting regeneration, seedling density was significantly higher in S2 and S3 compared to the three other sites ($F_{(4,90)} = 35.25$, p < 0.001). The harvesting method had a very significant effect on all the sites (Table S3) with a greater density of seedlings in partial cuts (Fig. 6), whereas the use of seeding had a significant positive effect only in three sites (S2, S3 and F1; Table S3). Interaction between harvesting method and seeding was not significant in all sites (Table S3), suggesting that these two practices had independent effects on seedling densities. Clear-cutting without seeding did not result in a sufficient seedling density to secure regeneration in any site except for S3 (Fig. 6). Using direct seeding in addition to clear-cutting attained or exceeded the threshold of 0.3 seedlings m^{-2} for S1, S2 and S3, but was still largely insufficient for both sites in the failure area (Fig. 6). Partial cutting without seeding had a very positive effect, as it allowed four out of five sites to have a satisfactory regeneration, with F1 being around the predefined threshold (Fig. 6). Adding seeds to partial cuts increased seedling density in all sites, allowing all of them to regenerate easily (Fig. 6).

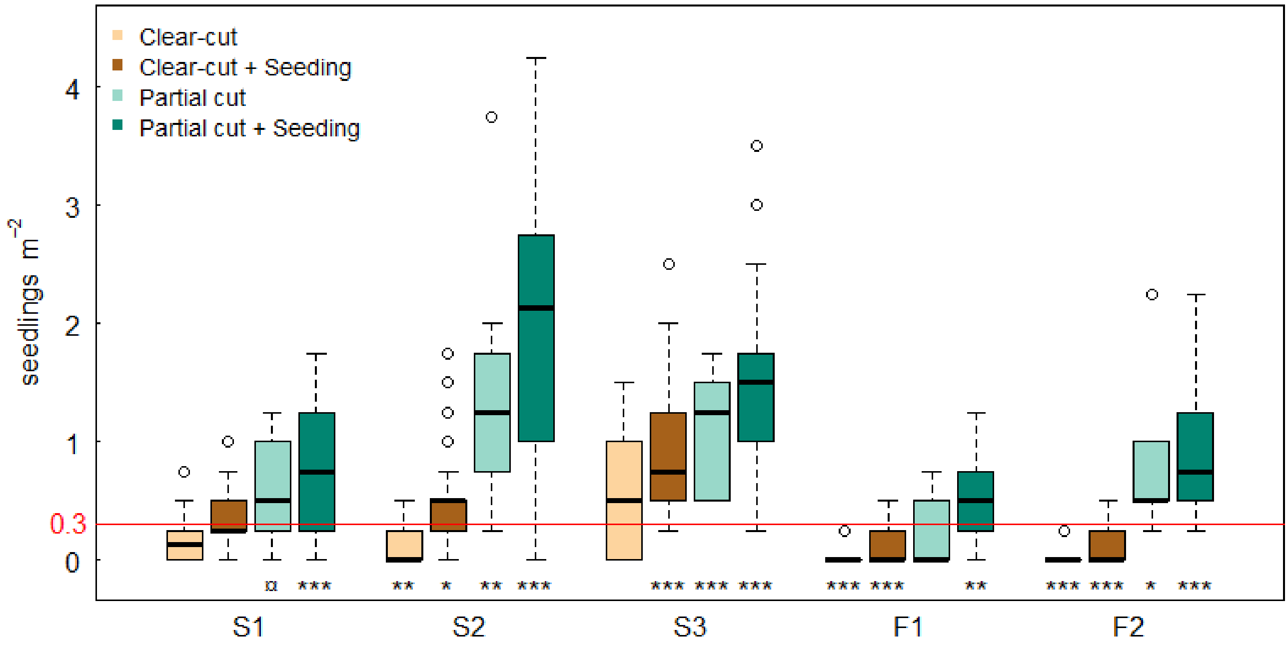

Fig. 6: Seedling density in March 2018 in each site (i.e. three years after harvest) as a function of the four modalities of the harvesting method x seeding treatment combination. The red line represents the threshold of 0.3 seedlings m^{-2} indicating sufficient regeneration. Asterisks indicate a significant difference from the threshold values (one sample *t*-test: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ¤ $p < 0.1$).

In addition, results from the regional survey of the 29 stands harvested with partial cuts showed that seedling density was not related to stand density (Fig. 7A) or basal area (Fig. 7B). Conversely, stands with a higher forest cover (Fig. 7C) or with trees with well-developed crowns (Fig. 7D) were associated with a more abundant regeneration.

In terms of recruitment probability, we observed strong differences between sites with a minimal overall probability of 0.7% in F1 and a maximum probability of 3.4% in S3. The probability of finding a seedling three years after seed dispersal was higher in partial cuts than in clear-cuts in all sites because of higher germination and greater survival (Table 2). Between all stages, the transition from viable seed rain to germination showed the lowest probability in all sites (Table 2). Sites in failure areas showed the lowest recruitment probability in clear-cuts because of the lowest level of survival, while lowest probabilities of germination were observed in S1 (Table 2). Overall, the probability of final recruitment was between 0.4% and 3.1% in clear-cuts and between 0.9% and 3.6% in partial cuts.

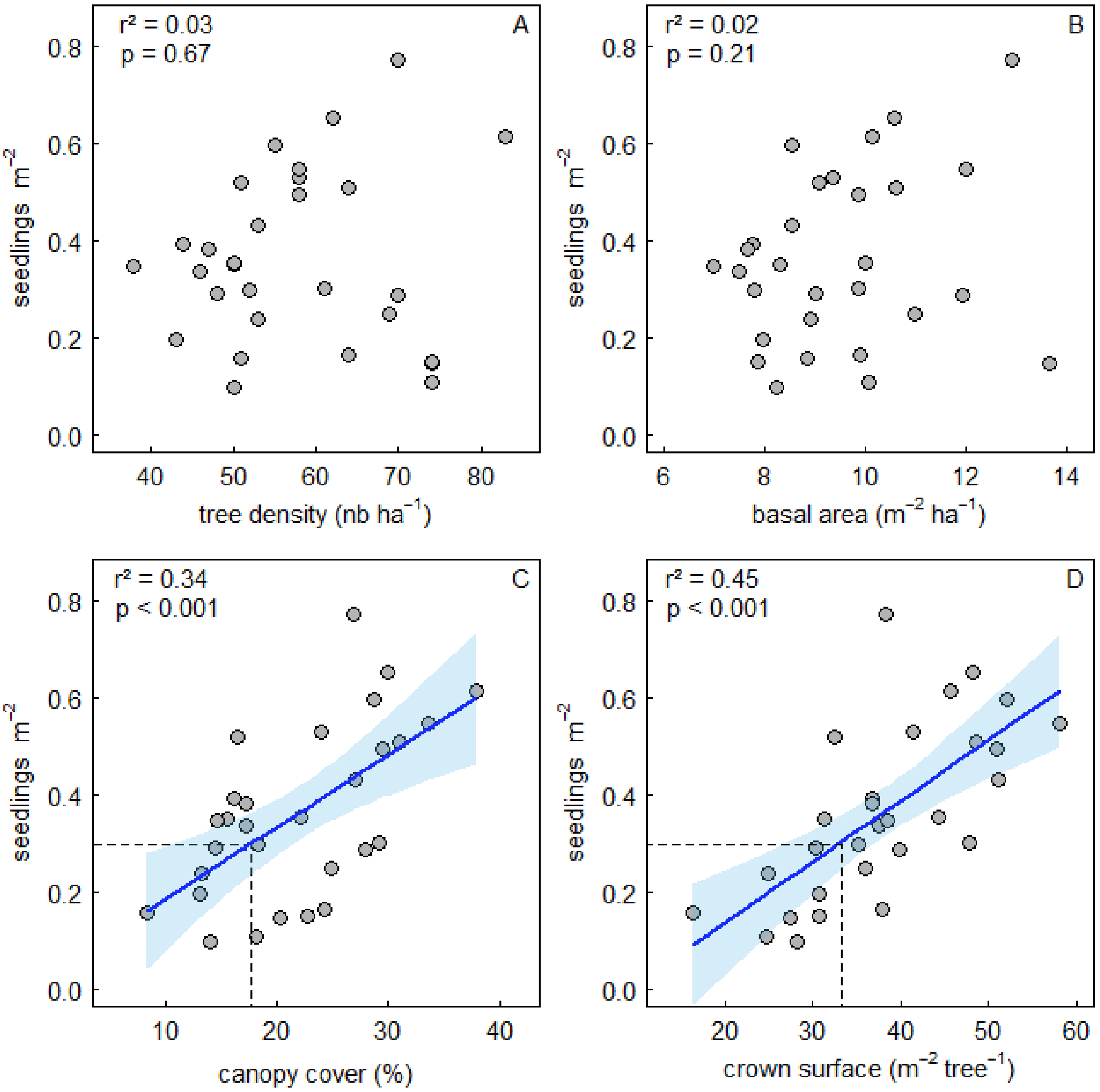

Fig. 7: Influence of dendrometric characteristics of partial cuts on seedling density. A) tree density; B) basal area; C) forest cover; and D) tree crown surface area. *P*-values and r^2 of the regressions are shown in the top left corner. Blue lines represent significant regressions, with the 95% confidence intervals in light blue. The dashed line represents the threshold of 0.3 seedlings m^{-2} indicating sufficient regeneration.

Table 2: Stage-specific transition probabilities leading to the recruitment of *Pinus pinaster* seedlings, according to the site and harvesting method.

Stage	S1		S2		S3		F1		F2	
	Clear-cut	Partial cut	Clear-cut	Partial cut	Clear-cut	Partial cut	Clear-cut	Partial cut	Clear-cut	Partial cut
Seed germinative capacity	0.300	0.300	0.320	0.320	0.300	0.300	0.260	0.260	0.320	0.320
Germination	0.036	0.053	0.042	0.073	0.154	0.182	0.055	0.079	0.037	0.114
1st year survival	0.707	0.678	0.537	0.690	0.681	0.688	0.465	0.631	0.438	0.632
2nd/3rd year survival	0.891	0.965	0.771	0.885	0.981	0.961	0.693	0.709	0.822	0.834
Overall probabilty of recruitment for a given seed	0.007	0.010	0.006	0.014	0.031	0.036	0.005	0.009	0.004	0.019

4. Discussion

Partial cutting and direct seeding, the two practices evaluated as alternatives to clearcutting, had a positive effect on regeneration in these dune forests. However, their effects on each stage showed site-specific differences, suggesting the importance of local factors on the success of the regeneration process (Rodríguez-García et al., 2010, 2011b). These two practices have two main axes of influence on the regeneration process: the increase of seed availability, improving seed rain and germination; and the modification of microhabitat beneath the tree canopy, affecting both germination and survival.

4.1. Influence of forestry practices on seed availability

Seed rain showed large spatial and temporal variations but did not appear to be a limiting factor in our context, as the two failure sites did not differ from the others and as S3, with the lowest seed rain, was one of the sites with the highest number of germinations and with the greatest regeneration three years after harvest. Two recent studies on maritime pine stands suggesting that neither seed production nor seed dispersal are limiting factors for regeneration showed similar results, with 7–24 seeds m^{-2} (Ruano et al., 2015b) and 7–15 seeds m^{-2} (Juez et al., 2014). However, it will be important to pay attention to these issues in the future as extreme climatic conditions are expected to increase and could lead to a decrease in seed production (Mutke et al., 2005; Ruano et al., 2015b). In our context, the main problem seems to be seed storage and conservation in the belowground seed bank until germination, which is a highly variable stage between provenances and populations of this species (Wahid and Bounoua, 2013; Calvo et al., 2016). In particular, the Atlantic provenance, which includes our coastal forests (de la Mata et al., 2012), showed the lowest germination rates in response to drought (Nuñez Paniagua et al., 2013). Here, we observed a probability of germination of only 4–18%, a fairly low percentage compared to other studies on maritime pine in situ (13–62%; Ruano et al., 2015a) or under controlled conditions (14–27%; Cruz et al., 2019). As seed weight was similar in our study and previous ones, this low germination rate is more likely to be explained by: high post-dispersal predation by many different organisms (Ruano et al., 2015a), the presence of a litter layer and harvest debris acting as a physical barrier preventing seeds from reaching the soil (Facelli and Pickett, 1991), or a very poor conservation of seed germinative capacity in the soil (Kozlowski, 2002). Indeed, the number of germinations in 2015 was slightly over one seedling m^{-2} at the most, while the soil seed bank was high, with an average of 119 seeds m^{-2}. Although pine species form only a short-lived soil seed bank with an expected minor role for regeneration (Izhaki et al., 2000), such quantities of seeds in the soil is not surprising with regard to other pine forests, where 150 and 187 seeds m^{-2} were reported for *P. pinaster* and *P. halepensis* stands respectively (Daskalakou and Thanos, 1996; Luis-Calabuig et al., 2002). However, most seeds in the belowground seed bank are not viable, as shown by two studies on Aleppo pine: Izhaki et al. (2000) found that the density of germinable pine seeds was 0.83 seeds m^{-2}, while Daskalakou and Thanos (1996) showed that only 8 to 18% of the seeds stored in the soil were sound. Our glasshouse test of germination capacity correspond to those results, showing that only seeds from the seed rain of the previous summer could contribute to germination in the following spring, while those stored in the seed bank were not viable for germination. Moreover, the significant decrease in number of germinations in clear-cuts between the first and second year, and then near-zero in the third year confirmed that seeds do not remain viable for more than a year in the soil in most cases. Finally, although seeds from direct seeding had a germination capacity of 86%, their effect on germination was only observed in the first year. This confirms the short life span of the soil seed bank, and that the regeneration of maritime pine depends almost exclusively upon the seed rain falling during the year before harvest.

Partial cutting and direct seeding were therefore two effective practices to increase seed stocks and improve germination. Direct seeding had an instantaneous impact by significantly increasing the number of germinations on all sites, up to 4-fold greater than in the unseeded plots, but only in the first year. This strong impact can be explained by their higher germination capacity as a result of a prior selection during which only the heaviest –and hence those most likely to be viable– seeds were selected. It can also be explained by the shorter time spent in the soil by these seeds, as seed rain occurred in summer while direct seeding was done in winter, and was therefore less vulnerable to predation or detrimental environmental conditions. However, the effect of seeding in our study was probably overestimated because seeds were sown manually one-by-one and were thus incorporated into the soil under better conditions, in contrast to the broadcast seeding practiced by foresters. Conversely to seeding, partial cutting had a longer-lasting effect with a regular yearly seed supply, leading to higher germination in all sites in the second and third years.

4.2. Influence of partial cutting on microhabitat

Our results showed a positive effect of partial cuts, both for germination and survival stages. However, the outcome of partial cutting is affected by local site conditions (Rodríguez-García et al., 2010), and this was also observed in our study, with large variations between the five sites. Effect of partial cutting was significantly positive in two sites for germination (F1 and F2) and three sites for survival (S2, F1 and F2). The similar differences in germination found in S1, S2 and S3, which also had very different survival rates, and the fact that S2 was similar to F1 and F2 for survival but not germination, suggests that the mechanisms of canopy-induced effects are different depending on the stage of regeneration considered. In general, the positive effects of partial cutting increased gradually with the increase of forest cover, as demonstrated in our regional survey (Fig. 7).

However, the influence of partial cutting on the microhabitat can only be discussed for the first year of the study for two reasons: i) germination in 2015 was linked to the seed rain in 2014 (before exploitation and so were similar in the two harvest modalities), and differences observed that year were therefore mainly due to the influence of harvesting method and not related to seed availability. In contrast, the role of microhabitat on germination became indistinguishable in the second and third years because differences in germination were essentially the consequence of an additional seed supply by seed-trees; and ii) we could not perform statistical analyses regarding seedling survival as the number of seedlings was too low in clear-cuts in the second and third years.

4.2.1. Influence on germination

Soil moisture and soil temperature, which are closely related to the light reaching the forest floor, are the main drivers of germination and could be affected by forest canopy structure (Aussenac, 2000; Castro et al., 2005). In our study, the effect of canopy cover had a strong impact in the two sites within the failure area, as well as a slightly positive effect in the other three sites, as confirmed by the greater probability of germination in partial cuts than in clear-cuts for all sites. This suggests that partial cutting induced slightly more suitable conditions for germination in all sites, and that another factor was involved at this stage within the failure area which was reduced by the presence of a canopy. Canopy mitigation of light intensity in partial cuts was similar in the five stands (Guignabert et al., 2018). This could explain the slight positive effect on all sites because it was the only factor similarly impacted by the partial cutting in all sites. This positive effect was more likely to be due to a decrease in soil temperature than an increase in soil moisture, since the effects of harvesting method were identical in the driest site and the wettest site (see S2 and S3 in Table S1). However, soil moisture was probably a primordial factor for germination in our forests because the site with the highest amount of precipitation (S3) was by far the one with the highest probability of germination. Thus, we may not have preserved enough forest cover in the experimental partial cuts to have a real impact on soil moisture, because the regional sandy soils do not hold enough water, or to maintain a low light intensity as pine forests usually have low LAI values (Gonzalez et al., 2013). Further studies are therefore needed to investigate the role of light and water availability on the germination process to better understand the canopy-induced effects on seedling emergence. The large difference in the number of germinations between the two harvesting methods in the failure area is intriguing and could be the result of a biotic component rather than improved microclimate, such as rodent seed predation. Indeed, rodent seed predation is one of the main bottlenecks in some Spanish pine stands (Ruano et al., 2015a), and a former study has already shown higher rodent damage in this area of our coastal forests (GEREA, 1990). As rodent foraging activity increases with the volume of coarse woody debris on the stand (Puig-Gironès et al., 2020), this may explain the lower number of germinations in clear-cuts where woody debris was more abundant.

4.2.2. Influence on seedling survival

Summer drought was the main cause of mortality in all sites, and was reduced by partial cuts in three sites (S2, F1 and F2). This is in agreement with previous studies on maritime pine that demonstrated enhancement of seedling recruitment beneath conspecific mature trees where canopy cover buffered abiotic stresses (Ruano et al., 2009; Rodríguez-García et al., 2011a, 2011b). The positive impact of canopy cover on survival would mainly be characterized by a decrease in vapour pressure deficit, as demonstrated on oak seedlings in the same coastal forests (Muhamed et al., 2013), where higher vapour pressure deficit increased seedling transpiration demand and seedling sensitivity to drought (Will et al., 2013). Even if we did not have accurate microclimate measurements in each harvesting method x site locations, we observed that S1 had lower temperatures and S3 had higher precipitation. Consequently, they should both have a lower aridity level than the other three sites especially in summer (Ouallet, 2012). This may explain why the effect of partial cutting was positive only in S2, F1 and F2. It is also important to mention that the summer of 2015 was an average summer, while the summer of 2016 was the driest of the last decade, particularly the July-August period (precipitation: 94-110 mm in 2015 vs. 15-26 mm in 2016). We were unable to compare survival during that year because we lacked seedlings in clear-cuts. However, survival in partial cuts in 2016 was between 42% and 76% (Fig. S5), whereas in comparison with another study carried out in the same year in a clear-cut within the failure area, only 10% of seedlings survived (Fig. S5; Guignabert et al., 2020). This suggests that the benefit of partial cutting is even more positive during an extremely dry summer. This drier summer in 2016 also showed that mortality after the first year could be high as well (up to 30% in F1) although it remained lower than the first summer mortality. In this previous study, we also found that understorey vegetation could facilitate seedling establishment at intermediate water stress and that damage by deer and rodents, which were quite important, could be modulated by shrub presence (Guignabert et al., 2020). Therefore, further studies investigated the effect of partial cutting on seedling establishment should consider these biotic interactions, as overstorey canopy may modify the outcome of plant-plant interactions (Rodríguez-García et al., 2011a).

At a larger scale than the seed-seedling microsite, harvesting method also affects habitat and therefore the behaviour of ungulate and rodent species (Reimoser and Gossow, 1996; Fisher and Wilkinson, 2005). Browsing by herbivores can kill seedlings or reduce height growth leading to recruitment failure of tree species or to poorly shaped trees, thus reducing their commercial value (Côté et al., 2004). In our study, ungulate browsing on pine seedlings was higher at both sites in the failure area, and higher in clear-cuts than in partial cuts. Post-harvest development of herbaceous vegetation is greater in clear-cuts than partial cuts because of differences in light intensity, increasing food supplies for ungulates. This results in higher risk of browsing damage in clear-cuts than partial cuts (Reimoser and Gossow, 1996), a risk that is more severe in areas with high ungulate abundance (Tremblay et al., 2007). This was potentially the case for the sites within the failure area, because they were located within a military area where hunting is controlled and lower in comparison to other parts of the coastal forests (Guignabert, 2018). In addition, it has been shown that rodents could have a negative impact on seedling survival in a recently clear-cut stand in the failure area (Guignabert et al., 2020), but this seems not systematic as it was rarely observed in the five sites of the present study.

4.3. Conclusion and management implications

Overall, seedling density in all sites three years after harvest was higher in partial cuts than clear-cuts, and was higher in seeded than unseeded plots (but only significant in three sites). These practices influenced the whole regeneration process by various mechanisms discussed in the foregoing paragraphs, validating our three initial hypotheses. Indeed, partial cutting had a positive effect in the long term by providing seeds each year, and by reducing biotic and abiotic stresses, which improved germination and survival (hyp. 1). This positive effect was actually more pronounced in the failure area, as the only two sites where partial cutting had an impact on both germination and survival were within this area (hyp. 2). Lastly, direct seeding had a positive impact on germination, but seedling density was always higher in partial cuts than in clear-cuts + seeding, which makes its use less beneficial (hyp. 3). Thus, sufficient regeneration can be achieved in all stands by using these two practices appropriately. Their effects are independent, thus enabling us to propose a revision of silvicultural practices currently applied in these forests, while additional research with longer-term monitoring and more replications, particularly in the area of chronic regeneration, should be pursued to optimize these management recommendations.

Clear-cutting without seeding led to severe regeneration failure in 4 out of 5 sites, the last one being around the threshold limit. Applying direct seeding enabled only two sites to significantly exceed the required seedling density. Consequently, the practice of clear-cutting currently used in these forests should be avoided, even with the addition of direct seeding. Indeed, seeding had an immediate effect and if the harvesting followed a poor year of seed production or if the spring and/or summer following harvest was very dry, regeneration would not be sufficient resulting in a silvicultural stalemate in the stand, making forest renewal impossible. In contrast, partial cutting had a strong positive impact on all sites and should be the method preferred here, as already performed in the Iberian peninsula in the same type of pine forests with sandy soils and severe summer drought (Calama et al., 2017). The forest cover and to a lesser extent the basal area should be considered when carrying out partial cutting, which should not be based on a specific tree density. The forest cover retained for partial cutting should be at least 18%, preferably with trees with well-developed crowns (>33 m^2). In areas of regeneration failures where the canopy effects are important for both germination and survival, leaving a denser forest cover (around 30%) would be better. Even if the basal area had no effects on the final seedling density, it was positively related to a higher seed rain. Thus, keeping trees with high diameter and great vigour is also recommended as they are a good indicator of higher cone production (Bravo et al., 2017), and should be distributed as homogeneously as possible throughout the stand. In addition, partial cutting could be combined with a direct seeding to maximize the chances of success, but only in failure areas.

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