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1 **Title:**

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

3

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7

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13

14 **Abstract:**

15 Stand regeneration is a crucial step in the management of many forests and its failure can
16 jeopardize future forest growth and production. Thus, adapting forestry practices to improve
17 seedling establishment is of prime importance to maintain sustainable forest management. In the
18 coastal dune forests of maritime pine in SW France, regeneration failure after clear-cutting has
19 greatly increased in the last decades. The aim of this study was to quantify the different stages
20 involved in the regeneration process (seed rain, germination, survival), and to assess the impact of
21 harvesting methods (partial cutting vs. clear-cutting) and of the use of direct seeding (seeding vs. no
22 seeding) on these stages. We established five trials located in areas with contrasting regeneration
23 statuses (of which two sites were in an area characterized by chronic regeneration failure), and we
24 investigated the effect of the harvesting method and the use of direct seeding in a factorial design.
25 We monitored the seed rain, germination and first-year survival for three years. Due to the transient
26 nature of the seed bank, we found that the seed rain of the previous year was the only possible
27 seed source for tree regeneration, and it increased with the proximity and size of surrounding
28 mature trees. Nonetheless, seed rain did not limit regeneration in these stands. In fact, germination
29 was the bottleneck stage of the regeneration process in all sites because it was short-lived and

30 consequently exposed to failure in case of unfavourable conditions. Once established, seedling
31 death was mainly due to summer drought. Clear-cutting without seeding resulted in severe
32 regeneration failures in 4 out of 5 sites, with the most severe in the failure area. Direct seeding
33 increased seedling emergence only in the first year, while partial cutting had a longer-lasting effect
34 by providing a regular seed supply over several years. Partial cutting also decreased biotic and
35 abiotic stresses through microhabitat modification under the tree canopy, resulting in a higher
36 number of germinations and greater seedling survival. This positive effect was more pronounced in
37 the two sites within the failure area, suggesting that conditions were more stressful in this part of the
38 forests. Consequently, we recommend avoiding clear-cutting in favour of partial cutting in all parts of
39 these forests, and ensuring the maintenance of sufficient forest cover to promote regeneration.
40 Direct seeding could be used in addition to partial cutting to maximize the chances of success, but
41 only in areas where natural regeneration is low.

42

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

45

46

47 **1. Introduction**

48 The renewal of forest stands is a key step in forest dynamics and for their sustainable
49 management. Natural regeneration is one way to do this and involves the stages of seed
50 production, seed dispersal, germination and seedling survival, each being influenced by many
51 interacting biotic and abiotic factors (Price et al., 2001; Kozłowski, 2002; Calama et al., 2017). The
52 establishment of a species results from the interactions between the quantity of available seeds and
53 the number of suitable microsites for regeneration (Harper, 1977; Schupp, 1995). The density of
54 seeds reaching the ground depends on the seed production, on the spatial arrangement and the
55 characteristics of the seed trees, and on the seed dispersal capacity (Greene et al., 1999; Viglas et
56 al., 2013; Montoro Girona et al., 2018). Then, seedling emergence and survival depends on
57 favourable local conditions such as soil moisture, soil temperature, or light (Harper, 1977;
58 Kozłowski, 2002). These ecological conditions vary widely, both spatially and over time (Beckage

59 and Clark, 2003; Gómez-Aparicio et al., 2005), and can be influenced by biotic interactions with
60 overstorey trees, herbaceous species or herbivore populations (Harmer, 2001; Wagner et al., 2011;
61 Lavoie et al., 2019). Consequently, regeneration failure can also depend on the local environmental
62 conditions.

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

88 stand density (Montoro Girona et al., 2016), and by supporting higher richness and greater
89 abundance of flora and fauna than clear-cuts (Fedrowitz et al., 2014). However, these positive
90 effects could be reduced in case of mortality of residual trees, as partially cut stands tend to be
91 more sensitive to disturbance (particularly windthrow) than unharvested stands (Montoro Girona et
92 al., 2019).

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

114 The aim of this study was to identify the processes involved in failures of natural
115 regeneration in the coastal forests of maritime pine, in interaction with silvicultural practices. For this
116 purpose, we established five stands located in areas with contrasting regeneration successes, and

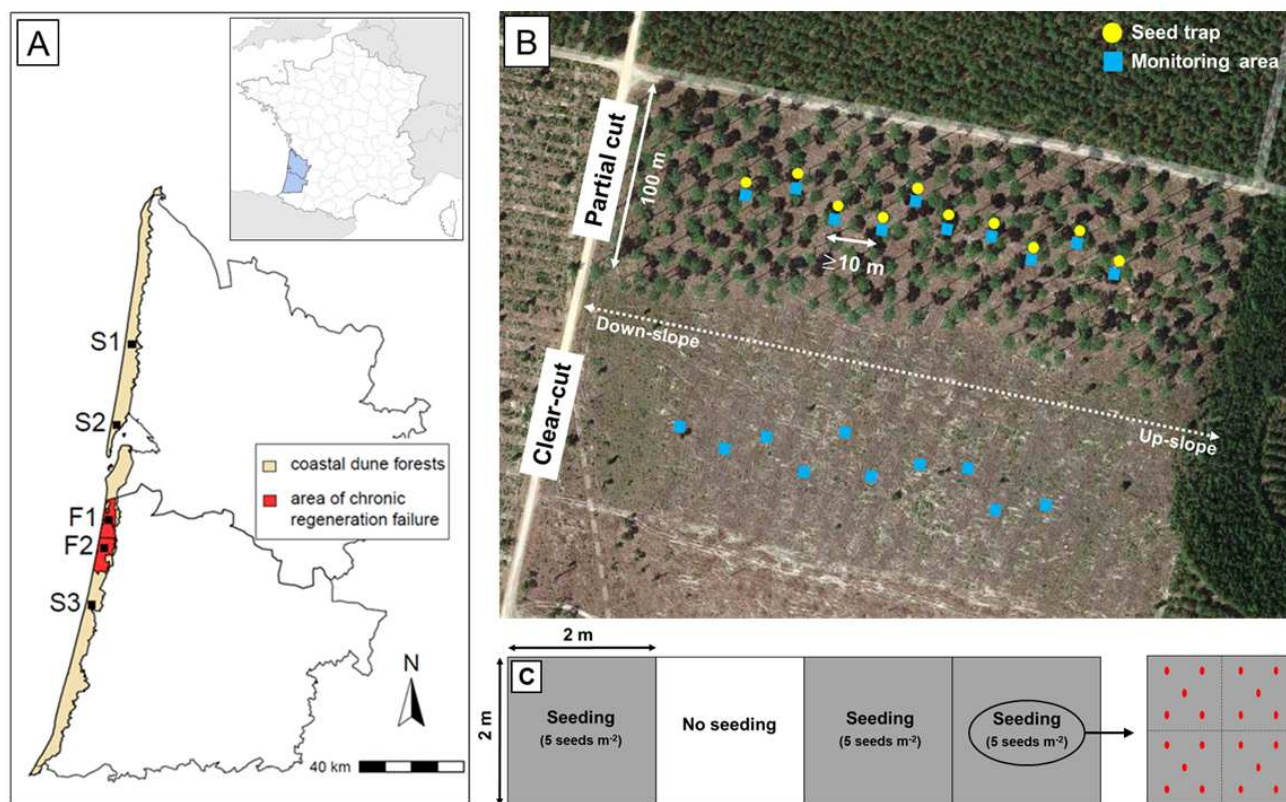
117 investigated the effect of the harvesting method (partial cutting compared to the usual clear-cutting)
118 and of the use of direct seeding (compared to the absence of seeding). We hypothesized that: i)
119 partial cutting could compensate for poor-regeneration years by supplying extra seeds each year,
120 and by increasing germination and seedling survival rates due to improved microclimatic conditions,
121 especially in the summer; ii) this positive effect would be more pronounced on sites within areas of
122 high regeneration failures, so that the threshold of 3,000 seedlings ha⁻¹ necessary for a successful
123 regeneration would be exceeded; and iii) direct seeding would improve the number of seedlings
124 regardless of the harvesting method, but it might be less useful than partial cutting that provides a
125 combination of seed supply and microhabitat amelioration. By improving our understanding of the
126 ecology of maritime pine regeneration, our findings should enable us to propose adequate
127 management strategies to ensure natural regeneration in these forests.

128 **2. Materials and methods**

129 **2.1. Study sites**

130 Our study combined experimentation (harvesting method and seeding as treatments, see
131 2.2.) and exploration on a regional scale, integrating a major regeneration failure area. Thus, we
132 established five trials along the coast in the maritime pine (*Pinus pinaster* Ait) sand dune forests of
133 SW France in areas with contrasting regeneration statuses (Fig. 1A): two of the sites were within
134 the area of chronic regeneration failure (hereafter referenced to as sites F1 and F2), while the three
135 other sites were in areas with frequent regeneration success (S1, S2 and S3). The lower number of
136 site in the failure area is explained by its geographically smaller area compared to the whole dune
137 forests (Fig. 1A). Stand area ranged from 7.4 to 11.5 ha and tree age ranged from 58 to 77 years
138 old (Table S1). The climate in the region is temperate oceanic. Average, minimum and maximum
139 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
140 °C for the four other sites (Table S1). Average annual precipitation ranged from 840 mm to 1007
141 mm (Table S1), with the wettest period in winter and the driest in July-August. All sites were chosen
142 on westerly facing slopes at about 2.5 km from the ocean, with an average slope of 10°. Soils are
143 young sandy soils (WRB classification: arenosols; USDA classification: entisols) mainly composed
144 of coarse sands (96–97%), are slightly acidic (topsoil values of pH = 4.5–5.0), and are extremely

145 poor in nutrients (Augusto et al., 2010). These soils have a low water holding capacity which,
146 combined with low summer rainfall, results in an extremely low soil moisture content and a high
147 water stress for seedlings in summer (Guignabert et al., 2020).



148
149 **Fig. 1:** A) Location of the five study sites. B) Aerial photography of S3 showing the two harvesting treatments,
150 and the distribution of the monitoring areas. C) Schematic of one monitoring area and of the seed
151 arrangement pattern.

152 2.2. Experimental design

153 Two silvicultural practices were tested factorially at each site in early 2015: i) the harvesting
154 method (usual clear-cut vs newly tested partial cut using the uniform shelterwood system), and ii)
155 the use of direct seeding (vs no seeding). To that end, each of the two harvesting methods was
156 carried out on half of all stands (Fig. 1B). Tree harvesting was performed mechanically with a feller-
157 buncher between January and March 2015. For the partial cut treatment, trees were chosen on the
158 basis of their vigour and appearance, and tree density after harvest was ~70 stems/ha in all sites.
159 The basal area after partial cutting was between 7.5 and 13.2 m² ha⁻¹ (Table S1). Other
160 management practices were carried out before logging in all experimental treatments: understory
161 vegetation was removed mechanically to limit post-logging competition and was combined with light
162 mechanical tillage to increase soil aeration and nutrient availability. Then, at each site, we

163 positioned ten monitoring areas in the centre of each harvesting treatment (Fig. 1B), each area
164 being split into four 4 m² quadrats (Fig. 1C). Three quadrats were sown with five seeds m⁻², which
165 corresponds to the quantity currently used by foresters in regeneration failure areas. Seeds were
166 sown following an identical pattern (Fig. 1C; ca. 0.5 cm deep) and came from cones collected from
167 stands of maritime pine located in the same forests. The fourth quadrat was unsown, and its
168 position was determined randomly. Finally, we installed a 1.5 m² seed trap one meter away of each
169 monitoring area in the partial cut treatment (Fig. 1C) to quantify the seed rain (10 seed traps per
170 site). Traps were wooden frames filled with high-density polyethylene mesh and with 25 cm high
171 edges in soft PVC, and were set up at about 25 cm above the ground (Fig. S1).

172 **2.3. Regeneration monitoring**

173 Seed rain was collected monthly in seed traps and counted from May to October in 2015,
174 2016 and 2017, then air-dried and stored at 4 °C. Seed weight and seed length were measured on
175 a random sample of 80 seeds per site of the 2015 seed rain, using a precision balance and a digital
176 calliper respectively. Since seed rain is known to be dependent on tree basal area and tree density
177 (Ruano et al., 2015b; Viglas et al., 2013), we measured the circumference of all trees within a 20 m
178 radius of each seed trap and their distance from the trap . Then, from these two variables we
179 calculated a seed source abundance index (SSAI) for each seed trap as follows: $SSAI =$
180 $\sum_{i=1}^n (TBA_i / d_i)$ with $TBA_i (m^2) = (c_i/100)^2 / 4\pi$ and where c (cm) is the circumference at 1.30 m
181 of tree i , TBA is the basal area of tree i (m²) and d the distance (m) of tree i from the seed trap. The
182 closer and bigger the tree, the more it contributes to the index value. The choice of a 20 m radius
183 circle around each seed trap was based on previous studies about the dispersal distance
184 corresponding to the majority of dispersed pine seeds (Juez et al., 2014; Ruano et al., 2015b).

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

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

197 **2.4. Complementary measurements**

198 *2.4.1. Soil seed bank*

199 Soil samples were collected from all sites to assess the soil seed bank, both in the clear-cut
200 and in the partial cut. This sampling was performed at the beginning of the experiment in April 2015,
201 after tree harvesting and before the beginning of the seed rain. A soil sample of 1/32 m² and 5 cm
202 deep was collected in the proximity of the four corners of each monitoring area, giving a total of 400
203 samples (5 sites x 2 harvesting methods x 10 monitoring areas x 4 samples) from a total surface
204 area of 12.5 m². Samples were then sieved using a 2 mm mesh and undamaged seeds were
205 counted and stored at 4 °C.

206 *2.4.2. Seed germinative capacity*

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

219 2.4.3. Dendrometric features of partial cuts

220 The dendrometric features of a mature stand (e.g. basal area, canopy cover) are partly
221 related to the silviculture carried out during the forest rotation (e.g. thinning). We carried out this
222 additional study in winter 2018-2019 in other forest stands to find out whether the stand structure of
223 partial cuts might be a factor that should be integrated into the management considerations to
224 improve regeneration. It should be noted that this study was not carried out at our five experimental
225 sites, but at the scale of a large management canton. This area was located within the main failure
226 area (i.e. near F1 and F2), the only area where partial cuts had been implemented in the region so
227 far. We selected forest stands which had been harvested at least 3 years before (i.e. harvested in
228 winter 2013-14, 2014-15 and 2015-16), which represented 29 stands and 280 ha (stand average =
229 9.7 ha, min = 3.4 ha, max = 19.7 ha). For each stand, we measured: i) the seedling density, by
230 counting the number of seedlings in 80 plots of 6 m² positioned according to a systematic grid
231 pattern (all were summed and then reported as seedlings m⁻²); ii) the tree density by counting all
232 trees in the stand; iii) the basal area, estimated from the tree diameter. The diameter of each tree
233 (*d*, cm) was measured using a forest compensated calliper (i.e. graduated in 5 cm classes), the
234 method which is regularly used in silviculture to carry out inventories and provides a good estimate
235 of the basal area (Cordonnier et al., 2007). Stand basal area (*BA*) was then calculated for each
236 stand as: $BA (m^2/ha) = (\sum TBA)/stand\ area$, with $TBA (m^2) = \pi(d/100)^2/4$; iv) the forest cover,
237 which was estimated using the normalised difference vegetation index (NDVI) based on analysis of
238 multispectral images of the Pléiades satellite taken on 14 April 2018 and 03 September 2018, and
239 performed with ArcGIS. This variable, obtained in m², was then expressed as a percentage value by
240 dividing the value by the stand area; and v) the individual tree crown surface area (m² tree⁻¹), by
241 dividing the forest cover (m²) by the number of trees.

242 2.5. Data treatment and statistics

243 All statistical analyses were performed with R software version 3.5.2. (R Core Team, 2018).
244 Data regarding seed and seedling density (i.e. seed rain, soil seed bank, germination and final
245 seedling density) are expressed in number m⁻² and are continuous quantitative variables. Seedling
246 survival and browsing occurrence are binomial variables, while the different types of mortality are

247 expressed as a percentage. Assumption of normality and homoscedasticity were checked for all
248 models mentioned below, and the response variable was square root transformed when necessary.
249 Post-hoc Tukey pairwise multiple comparisons were carried out when we found that a multilevel
250 factor was significant.

251 *2.5.1. Seed rain and seed bank*

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

258 *2.5.2. Germination and seedling establishment*

259 Analyses regarding germination, survival, browsing occurrence and final seedling density
260 were performed following a two-step procedure: i) full analyses with the site, harvesting method and
261 seeding as explanatory factors, and all two- and three-way interactions; and ii) intra-site analyses of
262 harvesting method and seeding separately. A random intercept for each monitoring area was
263 included in all models to take into account the spatial dependence of the quadrats of the same
264 monitoring area. Germination, tested for each year separately, and final seedling density were
265 analysed using linear mixed models. Longitudinal analyses of seedling survival were performed on
266 the first cohort of emerged seedlings (i.e. cohort of May, which represents 75.4% of the seedlings in
267 2015) using Cox proportional hazard mixed models. We examined seedling survival only in 2015
268 because the number of seedlings in clear-cuts was too low to compare harvesting treatments and to
269 perform statistical tests for three out of five sites in 2016, and for all sites in 2017. Browsing
270 occurrence was tested with generalized linear mixed models for binary data with a logit link function.
271 The effects of the harvesting method on the distribution of causes of mortality (i.e. drought, rodents
272 or ungulates) were tested using chi-square tests between sites and within sites.

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

276 *2.5.3. Overall probability of recruitment*

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

- 280 i) Seed germinative capacity, estimated via our glasshouse test. .
- 281 ii) Germination, as the germination number divided by the viable seed rain (estimated by
282 combining total seed rain and seed germinative capacity) plus the viable seeds from direct
283 seeding. Since the germinations of a year resulted from the seed rain of the previous summer,
284 we used the seed rain data from 2014-2016 and germination data from 2015-2017. Seed rain
285 before harvest (i.e. 2014) was not measured in our study and was thus calculated from the
286 2015-2017 data by estimating the contribution of one tree to the seed rain (number of
287 seeds $\text{m}^{-2} \text{year}^{-1}$), and relating it to stand density before harvest.
- 288 iii) 1st year survival, as the number of living seedlings one year after emergence divided by the
289 germination number.
- 290 iv) 2nd/3rd year survival, as the number of seedlings counted three years after harvest divided by
291 the number of living seedlings at the end of each year. This represented the seedlings from
292 2015 that died in 2016 and 2017, and those from 2016 that died in 2017.

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

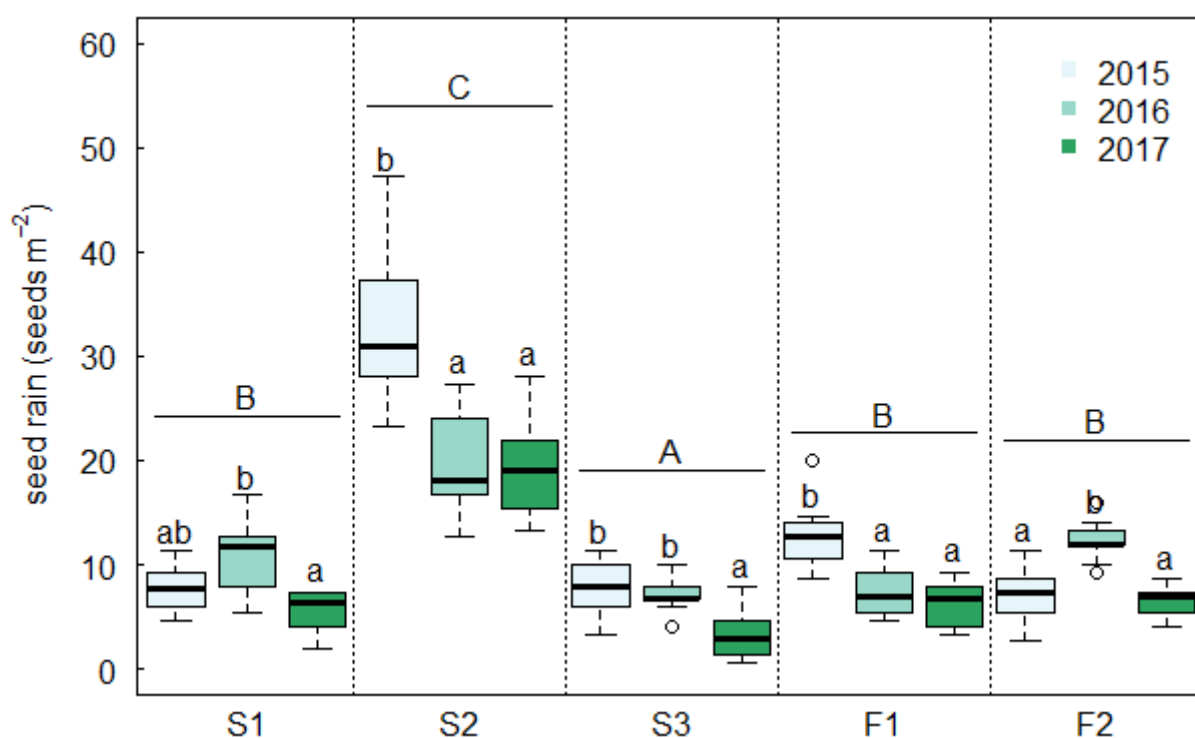
295 *2.5.4. Stand dendrometric features*

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

301 **3. Results**

302 **3.1. Seed availability**

303 The number of seeds reaching the ground varied depending on the year and the site (both p
304 < 0.001 ; Fig. 2), with a different pattern of annual variation between sites (interaction $p < 0.001$). All
305 sites combined, seed rain averaged 11.1 ± 0.7 seeds m^{-2} year $^{-1}$, with a minimum of 6.1 ± 0.8 seeds
306 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
307 size and density of mature trees in the vicinity of the seed traps, as seed rain was positively related
308 to the seed source abundance index ($F_{(1,44)} = 9.59, p = 0.004$).



309 **Fig. 2:** Amount of seed rain for each site per year ($n = 10$ for each boxplot). Different uppercase letters
310 indicate significant differences between sites, whereas different lowercase letters indicate significant
311 differences between years within each site (post-hoc Tukey test).
312

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

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

319 119 ± 6.5 seeds m⁻², with the largest amount in S1 with 196.6 ± 1.6 seeds m⁻² and the lowest in F1
 320 with 79.6 ± 1.1 seeds m⁻².

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

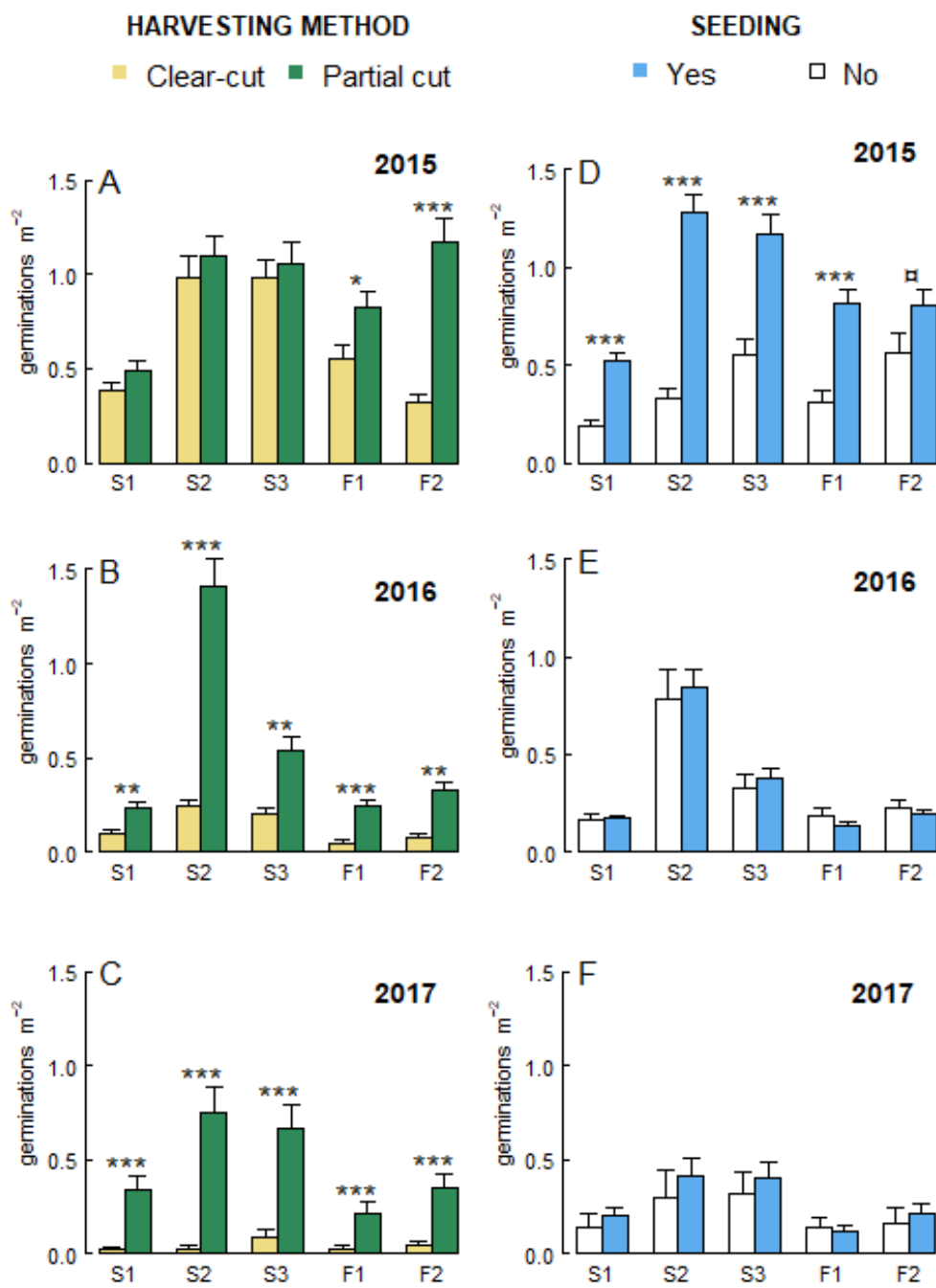
326 3.2. Germination

327 There was a significant site effect with, overall, a higher number of germinations in S2 and
 328 S3, and a fewer in S1 (Table 1; Fig. 3). The interactions “site x harvesting method” and “site x
 329 seeding” were also significant (Table 1), suggesting a major influence of site-specific conditions on
 330 germination. The harvesting method had a highly significant effect on germination each
 331 year (Table 1), with a higher number of germinations in partial cuts than in clear-cuts (Fig. 3). The
 332 average number of germinations in partial cuts was 0.93 seedlings m⁻² in 2015, and this decreased
 333 in the following two years (0.55 ± 0.06 seedlings m⁻² in 2016; 0.47 ± 0.09 seedlings m⁻² in 2017). In
 334 clear-cuts, the number of germinations decreased sharply between the first and the second year
 335 (0.65 ± 0.07 seedlings m⁻² in 2015; 0.14 ± 0.02 seedlings m⁻² in 2016), to reach nearly zero in the
 336 third year (0.04 ± 0.02 seedlings m⁻² in 2017). Interestingly, when we examined the results site by
 337 site, the positive effect of partial cuts was only observed in sites within the failure area in the first
 338 year (Fig. 2A) while it was observed in all sites in the second and third year (Fig. 2B-C). The use of
 339 direct seeding had a positive impact on germination only during the first year (Table 1; Fig. 2),
 340 where the average number of germinations was 0.92 ± 0.08 seedlings m⁻² in the seeded quadrats
 341 and 0.39 ± 0.07 seedlings m⁻² in the unseeded ones. This positive effect of seeding in the first year
 342 was observed in all sites (Fig. 2D).

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

<i>df</i>	2015		2016		2017	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>

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



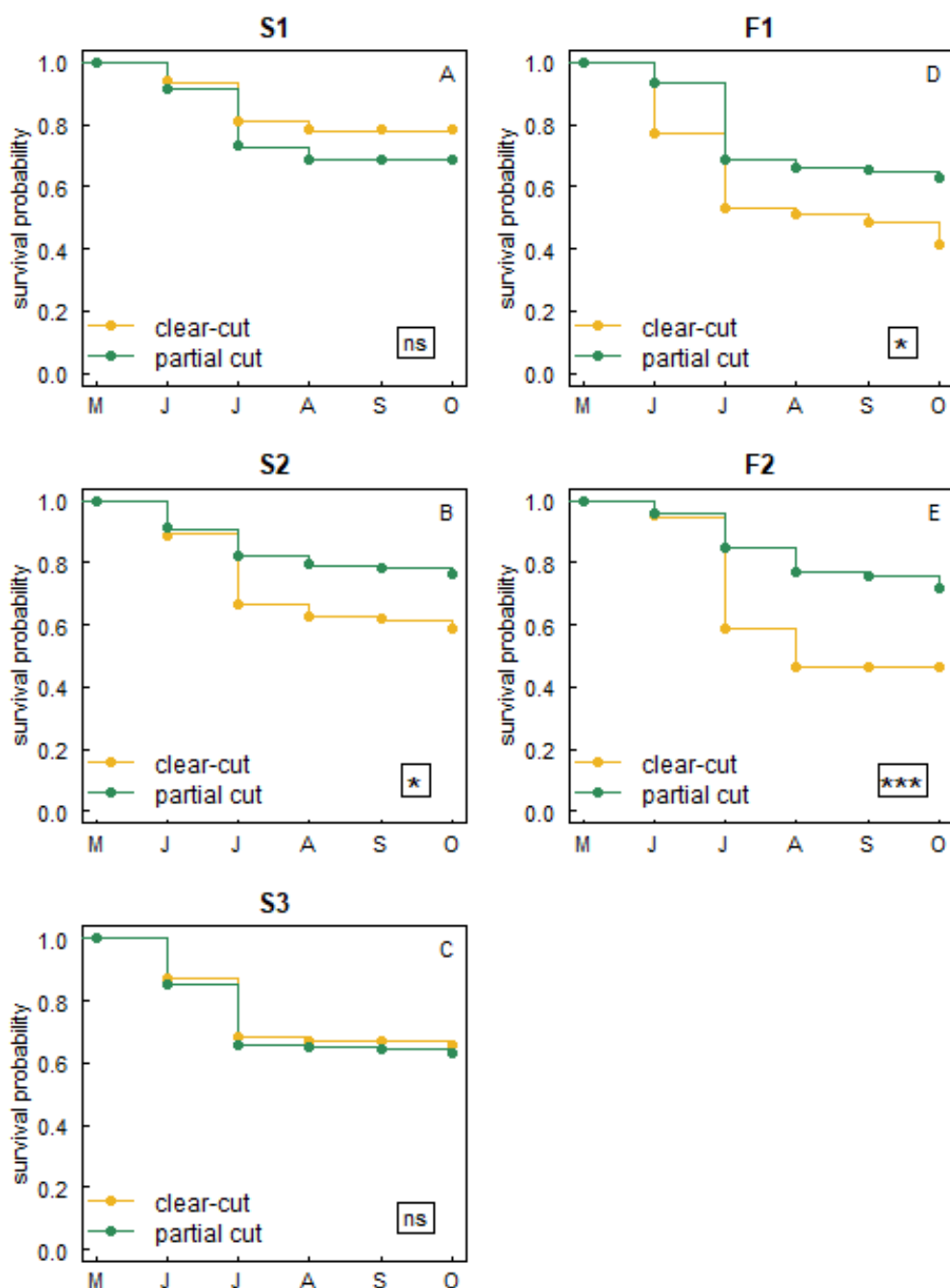
345

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

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

350 **3.3. Survival**

351 Seedling survival was influenced by the harvesting method ($\chi^2_{(1)} = 8.44$, $p = 0.004$), but not
352 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
353 positive impact on survival by decreasing mortality by 10.8% compared to clearcutting. On a site-by-
354 site basis, partial cutting had a positive effect on three out of five sites, including the two in the
355 failure area (mortality reduction of 17.5%, 21.5% and 25.6% for S2, F1 and F2 respectively; Fig. 4B-
356 D-E). In addition, F1 and F2 were the only two sites where clear-cut survival rate was lower than
357 50% (Fig. 4D-E).



358

359 **Fig. 4:** Seedling survival probability as a function of harvesting method in 2015, for each site separately.

360 Statistical significance between harvesting method is shown in the bottom right corner of each panel (Cox

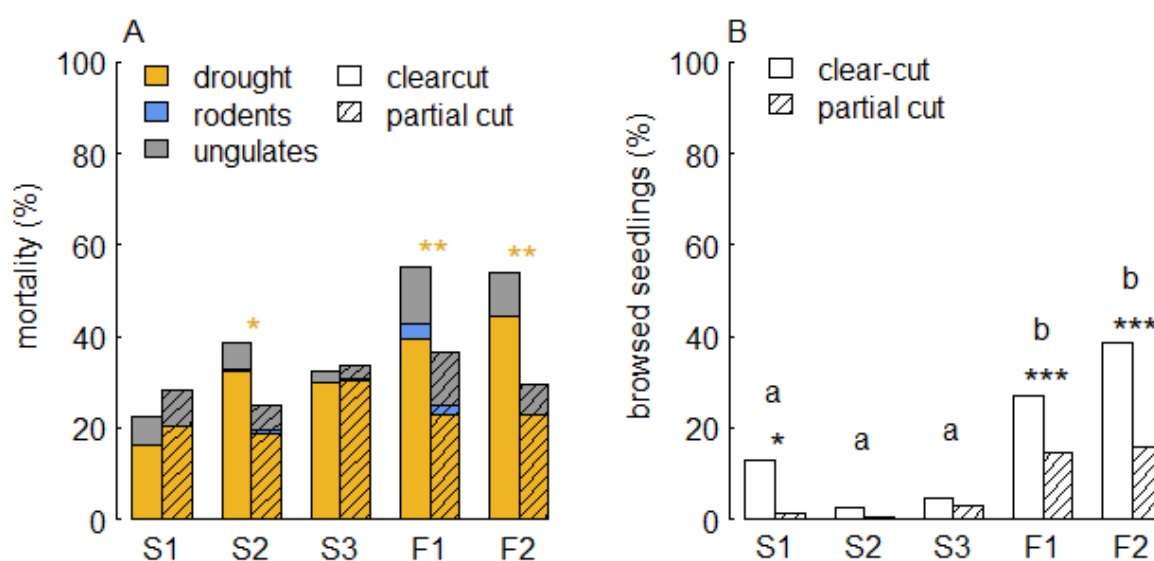
361 mixed models: *** $p < 0.001$; * $p < 0.05$; ns = non-significant).

362

363 Drought was the main cause of mortality (Fig. 5A). All sites combined, we observed a higher
 364 mortality due to drought in clear-cuts than in partial cuts ($\chi^2_{(4)} = 11.18$, $p < 0.001$). Within sites,
 365 partial cutting significantly reduced the percentage of drought-killed seedlings in S2 ($\chi^2_{(1)} = 7.39$, $p =$
 366 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,

367 except in F1 (Fig. 5A), and harvesting method had no influence on mortality caused by either type
 368 of herbivore.

369 Conversely to herbivory-killed seedlings, there was a strong effect of site ($\chi^2_{(4)} = 72.67, p <$
 370 0.001) and harvesting method ($\chi^2_{(1)} = 17.99, p < 0.001$) on the percentage of non-lethal browsed
 371 seedlings. Browsing was more frequent in clear-cuts and in the two sites within the failure area (Fig.
 372 5B). It was also on these two sites that the positive effect of partial cutting was the most
 373 pronounced, reducing the browsing occurrence by 12.6% in F1 and 22.5% in F2 (Fig. 5B).

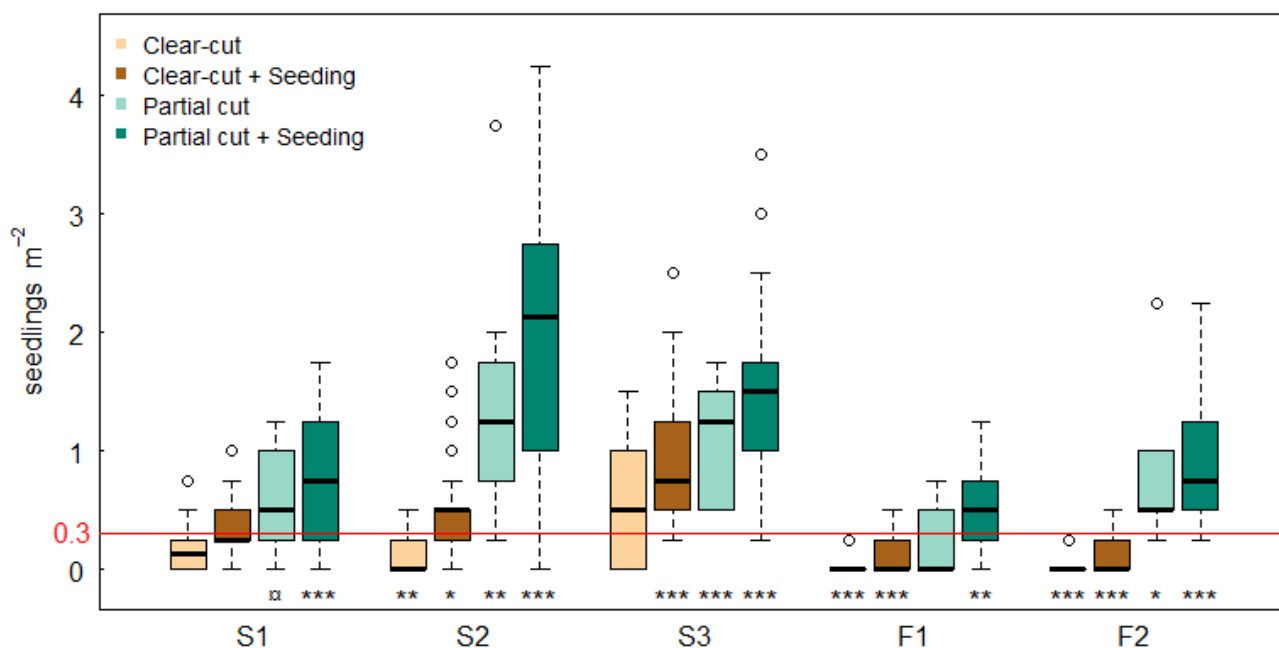


374 **Fig. 5:** A) Percentage mortality of each cause of death in 2015 according the site and harvesting method.
 375 Yellow asterisks indicate a significant difference in the distribution of drought-killed seedlings between the two
 376 harvesting method within a site (chi-square test: ** $p < 0.01$; * $p < 0.5$). B) Seedlings non-lethally browsed by
 377 ungulates in 2015 according to the site and the harvesting method. Different lowercase letters indicate
 378 significant differences between sites (post-hoc Tukey test). Asterisks indicate a significant difference in
 379 browsing occurrence between the two harvesting methods within a site (generalized linear mixed models: ***
 380 $p < 0.001$; * $p < 0.5$).
 381

382 3.4. Overall regeneration success

383 Three years after starting regeneration, seedling density was significantly higher in S2 and
 384 S3 compared to the three other sites ($F_{(4,90)} = 35.25, p < 0.001$). The harvesting method had a very
 385 significant effect on all the sites (Table S3) with a greater density of seedlings in partial cuts (Fig. 6),
 386 whereas the use of seeding had a significant positive effect only in three sites (S2, S3 and F1;
 387 Table S3). Interaction between harvesting method and seeding was not significant in all sites (Table
 388 S3), suggesting that these two practices had independent effects on seedling densities. Clear-

389 cutting without seeding did not result in a sufficient seedling density to secure regeneration in any
 390 site except for S3 (Fig. 6). Using direct seeding in addition to clear-cutting attained or exceeded the
 391 threshold of 0.3 seedlings m^{-2} for S1, S2 and S3, but was still largely insufficient for both sites in the
 392 failure area (Fig. 6). Partial cutting without seeding had a very positive effect, as it allowed four out
 393 of five sites to have a satisfactory regeneration, with F1 being around the predefined threshold (Fig.
 394 6). Adding seeds to partial cuts increased seedling density in all sites, allowing all of them to
 395 regenerate easily (Fig. 6).

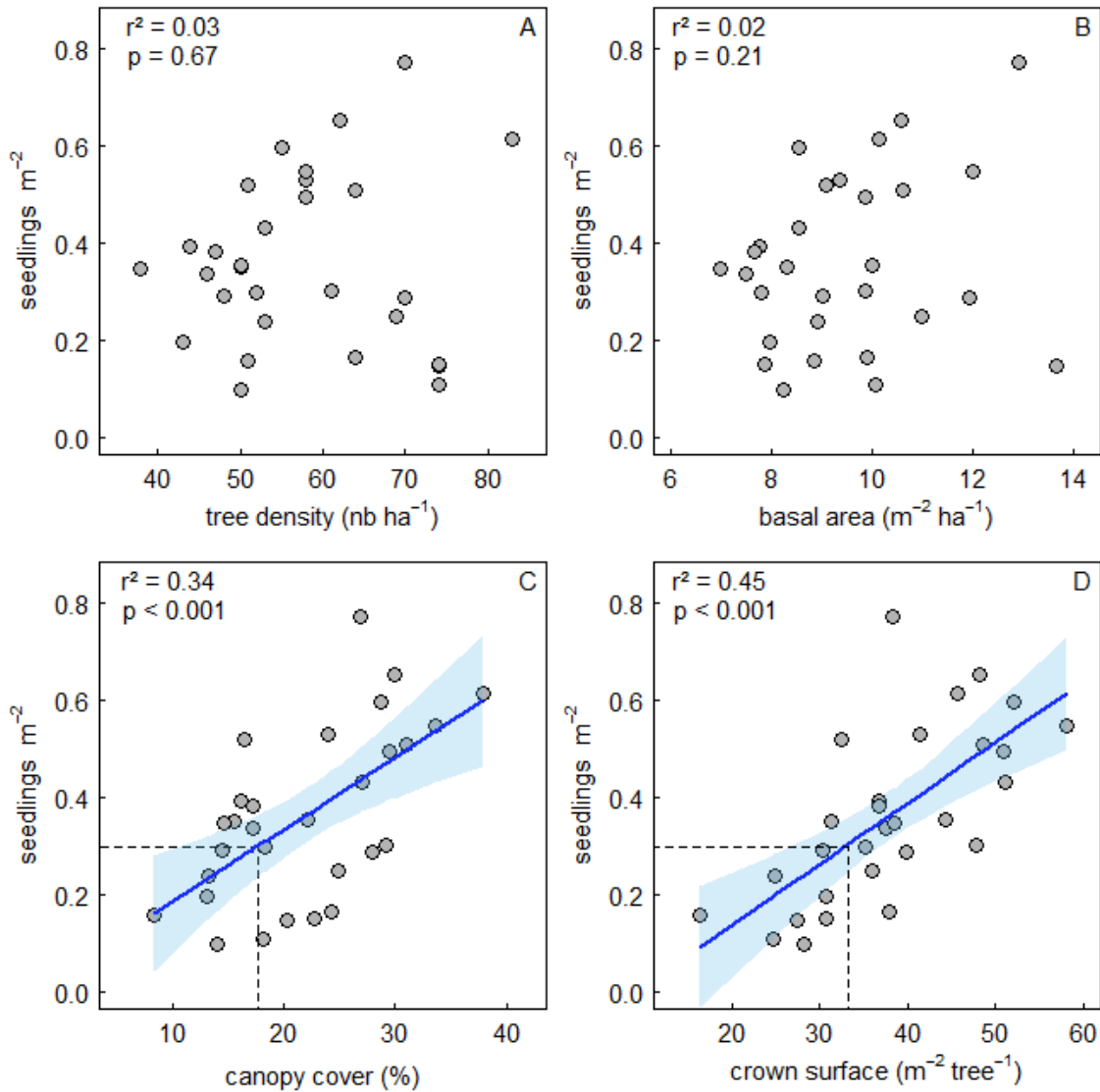


396
 397 **Fig. 6:** Seedling density in March 2018 in each site (i.e. three years after harvest) as a function of the four
 398 modalities of the harvesting method x seeding treatment combination. The red line represents the threshold of
 399 0.3 seedlings m^{-2} indicating sufficient regeneration. Asterisks indicate a significant difference from the
 400 threshold values (one sample *t*-test: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; \square $p < 0.1$).

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

405 In terms of recruitment probability, we observed strong differences between sites with a
 406 minimal overall probability of 0.7% in F1 and a maximum probability of 3.4% in S3. The probability
 407 of finding a seedling three years after seed dispersal was higher in partial cuts than in clear-cuts in
 408 all sites because of higher germination and greater survival (Table 2). Between all stages, the

409 transition from viable seed rain to germination showed the lowest probability in all sites (Table 2).
 410 Sites in failure areas showed the lowest recruitment probability in clear-cuts because of the lowest
 411 level of survival, while lowest probabilities of germination were observed in S1 (Table 2). Overall,
 412 the probability of final recruitment was between 0.4% and 3.1% in clear-cuts and between 0.9% and
 413 3.6% in partial cuts.



414
 415 **Fig. 7:** Influence of dendrometric characteristics of partial cuts on seedling density. A) tree density; B) basal
 416 area; C) forest cover; and D) tree crown surface area. *P*-values and *r*² of the regressions are shown in the top
 417 left corner. Blue lines represent significant regressions, with the 95% confidence intervals in light blue. The
 418 dashed line represents the threshold of 0.3 seedlings m⁻² indicating sufficient regeneration.

419 **Table 2:** Stage-specific transition probabilities leading to the recruitment of *Pinus pinaster* seedlings,
 420 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
1 st year survival	0.707	0.678	0.537	0.690	0.681	0.688	0.465	0.631	0.438	0.632
2 nd /3 rd year survival	0.891	0.965	0.771	0.885	0.981	0.961	0.693	0.709	0.822	0.834
Overall probability 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

421

422 **4. Discussion**

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

430 **4.1. Influence of forestry practices on seed availability**

431 Seed rain showed large spatial and temporal variations but did not appear to be a limiting
 432 factor in our context, as the two failure sites did not differ from the others and as S3, with the lowest
 433 seed rain, was one of the sites with the highest number of germinations and with the greatest
 434 regeneration three years after harvest. Two recent studies on maritime pine stands suggesting that
 435 neither seed production nor seed dispersal are limiting factors for regeneration showed similar
 436 results, with 7–24 seeds m⁻² (Ruano et al., 2015b) and 7–15 seeds m⁻² (Juez et al., 2014).
 437 However, it will be important to pay attention to these issues in the future as extreme climatic
 438 conditions are expected to increase and could lead to a decrease in seed production (Mutke et al.,

439 2005; Ruano et al., 2015b). In our context, the main problem seems to be seed storage and
440 conservation in the belowground seed bank until germination, which is a highly variable stage
441 between provenances and populations of this species (Wahid and Bounoua, 2013; Calvo et al.,
442 2016). In particular, the Atlantic provenance, which includes our coastal forests (de la Mata et al.,
443 2012), showed the lowest germination rates in response to drought (Nuñez Paniagua et al., 2013).
444 Here, we observed a probability of germination of only 4–18%, a fairly low percentage compared to
445 other studies on maritime pine in situ (13–62%; Ruano et al., 2015a) or under controlled conditions
446 (14–27%; Cruz et al., 2019). As seed weight was similar in our study and previous ones, this low
447 germination rate is more likely to be explained by: high post-dispersal predation by many different
448 organisms (Ruano et al., 2015a), the presence of a litter layer and harvest debris acting as a
449 physical barrier preventing seeds from reaching the soil (Facelli and Pickett, 1991), or a very poor
450 conservation of seed germinative capacity in the soil (Kozłowski, 2002). Indeed, the number of
451 germinations in 2015 was slightly over one seedling m⁻² at the most, while the soil seed bank was
452 high, with an average of 119 seeds m⁻². Although pine species form only a short-lived soil seed
453 bank with an expected minor role for regeneration (Izhaki et al., 2000), such quantities of seeds in
454 the soil is not surprising with regard to other pine forests, where 150 and 187 seeds m⁻² were
455 reported for *P. pinaster* and *P. halepensis* stands respectively (Daskalakou and Thanos, 1996; Luis-
456 Calabuig et al., 2002). However, most seeds in the belowground seed bank are not viable, as
457 shown by two studies on Aleppo pine: Izhaki et al. (2000) found that the density of germinable pine
458 seeds was 0.83 seeds m⁻², while Daskalakou and Thanos (1996) showed that only 8 to 18% of the
459 seeds stored in the soil were sound. Our glasshouse test of germination capacity correspond to
460 those results, showing that only seeds from the seed rain of the previous summer could contribute
461 to germination in the following spring, while those stored in the seed bank were not viable for
462 germination. Moreover, the significant decrease in number of germinations in clear-cuts between
463 the first and second year, and then near-zero in the third year confirmed that seeds do not remain
464 viable for more than a year in the soil in most cases. Finally, although seeds from direct seeding
465 had a germination capacity of 86%, their effect on germination was only observed in the first year.
466 This confirms the short life span of the soil seed bank, and that the regeneration of maritime pine
467 depends almost exclusively upon the seed rain falling during the year before harvest.

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

480 **4.2. Influence of partial cutting on microhabitat**

481 Our results showed a positive effect of partial cuts, both for germination and survival stages.
482 However, the outcome of partial cutting is affected by local site conditions (Rodríguez-García et al.,
483 2010), and this was also observed in our study, with large variations between the five sites. Effect of
484 partial cutting was significantly positive in two sites for germination (F1 and F2) and three sites for
485 survival (S2, F1 and F2). The similar differences in germination found in S1, S2 and S3, which also
486 had very different survival rates, and the fact that S2 was similar to F1 and F2 for survival but not
487 germination, suggests that the mechanisms of canopy-induced effects are different depending on
488 the stage of regeneration considered. In general, the positive effects of partial cutting increased
489 gradually with the increase of forest cover, as demonstrated in our regional survey (Fig. 7).

490 However, the influence of partial cutting on the microhabitat can only be discussed for the
491 first year of the study for two reasons: i) germination in 2015 was linked to the seed rain in 2014
492 (before exploitation and so were similar in the two harvest modalities), and differences observed
493 that year were therefore mainly due to the influence of harvesting method and not related to seed
494 availability. In contrast, the role of microhabitat on germination became indistinguishable in the
495 second and third years because differences in germination were essentially the consequence of an

496 additional seed supply by seed-trees; and ii) we could not perform statistical analyses regarding
497 seedling survival as the number of seedlings was too low in clear-cuts in the second and third
498 years.

499 *4.2.1. Influence on germination*

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

524 foraging activity increases with the volume of coarse woody debris on the stand (Puig-Gironès et
525 al., 2020), this may explain the lower number of germinations in clear-cuts where woody debris was
526 more abundant.

527 *4.2.2. Influence on seedling survival*

528 Summer drought was the main cause of mortality in all sites, and was reduced by partial
529 cuts in three sites (S2, F1 and F2). This is in agreement with previous studies on maritime pine that
530 demonstrated enhancement of seedling recruitment beneath conspecific mature trees where
531 canopy cover buffered abiotic stresses (Ruano et al., 2009; Rodríguez-García et al., 2011a, 2011b).
532 The positive impact of canopy cover on survival would mainly be characterized by a decrease in
533 vapour pressure deficit, as demonstrated on oak seedlings in the same coastal forests (Muhamed
534 et al., 2013), where higher vapour pressure deficit increased seedling transpiration demand and
535 seedling sensitivity to drought (Will et al., 2013). Even if we did not have accurate microclimate
536 measurements in each harvesting method x site locations, we observed that S1 had lower
537 temperatures and S3 had higher precipitation. Consequently, they should both have a lower aridity
538 level than the other three sites especially in summer (Ouallet, 2012). This may explain why the
539 effect of partial cutting was positive only in S2, F1 and F2. It is also important to mention that the
540 summer of 2015 was an average summer, while the summer of 2016 was the driest of the last
541 decade, particularly the July-August period (precipitation: 94-110 mm in 2015 vs. 15-26 mm in
542 2016). We were unable to compare survival during that year because we lacked seedlings in clear-
543 cuts. However, survival in partial cuts in 2016 was between 42% and 76% (Fig. S5), whereas in
544 comparison with another study carried out in the same year in a clear-cut within the failure area,
545 only 10% of seedlings survived (Fig. S5; Guignabert et al., 2020). This suggests that the benefit of
546 partial cutting is even more positive during an extremely dry summer. This drier summer in 2016
547 also showed that mortality after the first year could be high as well (up to 30% in F1) although it
548 remained lower than the first summer mortality. In this previous study, we also found that
549 understory vegetation could facilitate seedling establishment at intermediate water stress and that
550 damage by deer and rodents, which were quite important, could be modulated by shrub presence
551 (Guignabert et al., 2020). Therefore, further studies investigated the effect of partial cutting on

552 seedling establishment should consider these biotic interactions, as overstorey canopy may modify
553 the outcome of plant-plant interactions (Rodríguez-García et al., 2011a).

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

569 **4.3. Conclusion and management implications**

570 Overall, seedling density in all sites three years after harvest was higher in partial cuts than
571 clear-cuts, and was higher in seeded than unseeded plots (but only significant in three sites). These
572 practices influenced the whole regeneration process by various mechanisms discussed in the
573 foregoing paragraphs, validating our three initial hypotheses. Indeed, partial cutting had a positive
574 effect in the long term by providing seeds each year, and by reducing biotic and abiotic stresses,
575 which improved germination and survival (hyp. 1). This positive effect was actually more
576 pronounced in the failure area, as the only two sites where partial cutting had an impact on both
577 germination and survival were within this area (hyp. 2). Lastly, direct seeding had a positive impact
578 on germination, but seedling density was always higher in partial cuts than in clear-cuts + seeding,
579 which makes its use less beneficial (hyp. 3). Thus, sufficient regeneration can be achieved in all

580 stands by using these two practices appropriately. Their effects are independent, thus enabling us
581 to propose a revision of silvicultural practices currently applied in these forests, while additional
582 research with longer-term monitoring and more replications, particularly in the area of chronic
583 regeneration, should be pursued to optimize these management recommendations.

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

603

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614

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