



Title	Spatial patterns of oak (<i>Quercus crispula</i>) regeneration on scarification site around a conspecific overstory tree
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1 **Spatial patterns of oak (*Quercus crispula*) regeneration on scarification**
2 **site around a conspecific overstory tree**

3

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12

13 **Abstract**

14 Spatial patterns have been a major topic regarding natural regeneration of oak species, but the effects
15 may differ considerably in sites subjected to intense forestry practices, which greatly alter many aspects of
16 site conditions. We examined the hypothesis that the regeneration of oak (*Quercus crispula* Blume)
17 following scarification (displacement of inhibiting vegetation and surface soil using machinery) is enhanced
18 at a certain distance from a conspecific overstory tree, depending on the stage of development. We
19 conducted both field surveys in scarification sites with different stand ages (1-16 year-old) and a laboratory
20 seeding experiment to clarify factors contributing to its early establishment. The results demonstrate that
21 the spatial relationship between the regeneration of oak and the conspecific overstory tree at scarification
22 sites changes considerably among stages of the establishment. In the initial stage (0-1 years after the
23 scarification), a location beneath the crown provided favorable conditions, whereas at subsequent stages
24 (2-4 years), the distance-dependent effects were unclear, until eventually (8-16 years) a location outside
25 the crown became more favorable. The condition produced by the scarification was basically
26 competition-free and resource-rich, but it can also be harsh for acorns and small seedlings, imposing a
27 requirement for shading to moderate the environment in the initial stage. Such an effect of facilitation was
28 found also in the later (sapling) stage via the existence of neighbors of the other regenerated fast-growing
29 species. The current findings supported the effectivity of a shelter-wood system, in which the regeneration
30 starts from shaded condition followed by a gap status created by a successive felling. The area away from
31 the conspecific crown would have a potential if acorns are plentifully supplied (e.g. by direct seeding) and
32 they withstand the initial negative factors at the initial stage of development.

33

34 Key Words: natural regeneration; site preparation; demography; distance-dependency

35

36 1. Introduction

37 Alternative forestry regime with close-to-nature concept has attracted much attention in
38 recent years as a way of managing forests for both timber production and ecosystem
39 functioning (Kohm and Franklin 1997; Messier et al. 2013). It is often associated with natural
40 regeneration practices because the concept is largely compatible with natural conditions
41 and processes of the forest (Schütz 1999). However, regeneration sometimes fails at sites
42 where there are blocking factors for seed germination and/or seedling establishment (Royo
43 and Carson 2006). Therefore, the development of regeneration assistance practices has
44 been investigated in many regions. One such practice is scarification, which involves the
45 removal of understory vegetation together with surface soil by heavy machinery to expose
46 mineral soil as an appropriate seedbed (Yoshida et al. 2005; Prévost et al. 2010; Löff et al.
47 2012; Soto et al. 2015).

48 Scarification has been widely conducted in Hokkaido, northern Japan, since the 1970s.
49 The understory of forests in this region often contains thick coverage of dwarf bamboos,
50 which strongly inhibit the emergence and survival of seedlings (Noguchi and Yoshida 2004).
51 Therefore, it is believed that their removal will effectively enhance regeneration, and indeed
52 woody vegetation has successfully recovered in many cases (Yoshida et al. 2005). However,
53 most of the established stands have been dominated mostly by fast-growing species,
54 notably birches (*Betula platyphylla* var. *japonica*, *B. ermanii* Cham. and *B.*
55 *maximowicziana* Regel.) (Goto et al. 2010; Aoyama et al. 2011). Therefore, to further
56 expand the applicability of the practice, it is necessary to develop scarification technique that
57 allows the establishment of other species, particularly more shade-tolerant species.

58 Oak species generally have high economic and ecological value in temperate forests
59 (Johnson et al. 2009). The wood of the species is a valuable material particularly for
60 furniture, and its acorns are an important food resource for wildlife. *Quercus crispula* Blume

61 is one of the representative broadleaved tree species, with biggest size and longest lifespan
62 among broadleaved species, in Hokkaido (Sano 1997). Several previous reports have
63 presented the regeneration management of this oak species, but an appropriate silvicultural
64 practice widely applicable has not yet been established, leading to reductions in oak
65 resource in Japan.

66 Natural regeneration of oak species has recently been examined particularly with regard
67 to spatial patterns (Meiners and Martinkovic 2002; López-Barrera et al. 2006; Dickie et al.
68 2005; Yamazaki et al. 2009; Lhotka and Stringer 2013), because there are considerable
69 spatial variation in acorn dispersal and possible contributing factors, including soil, light,
70 herbivores, pathogens, mycorrhizae, and competitive vegetation. For instance, existence of
71 a conspecific overstory tree can positively affect the germination and growth conditions by
72 increasing the number of fallen acorns, mitigating intense light via its crown (Pulido and Díaz
73 2005; Urbieta et al. 2008; Löf and Birkedal 2009; Guo et al. 2011; Muhamed et al 2013), and
74 providing mycorrhizal fungi through its root system (Dickie et al. 2002; 2005; Jones et al.
75 2003). By contrast, the canopies or roots of conspecifics can be a source of specific
76 herbivores and pathogens (Wada et al., 2000; Scott and Matthew 2002; López-Barrera et
77 al 2006; Berkedel et al. 2010; McCarthy-Newmann and Kobe 2010), which decrease the
78 regeneration potential. Because scarification greatly alters the site conditions, these spatial
79 effects may differ according to their properties and intensity.

80 Therefore, the aim of this study was to find out whether or not locations more beneficial
81 than others for early establishment of *Q. crispula* exist in scarification sites, and, if they exist,
82 how locations may change with time. Although several previous studies have reported the
83 efficacy of the scarification on oak regeneration (Miya and Koshika 2004; Harada et al.
84 2008), its spatial aspect (i.e. dependency on the distance from conspecific overstory tree)
85 remain unclear. Scarification produces competition-free condition for seedlings at an initial

86 stage, but effects of the many other factors and their temporal changes, in relation to the
87 canopy-gap gradient, should also be considered. Thus, we examined the hypothesis that
88 the regeneration of oak seedlings is enhanced at a certain distance from the nearest
89 conspecific overstory tree, depending on the stage of development. For this purpose, we
90 conducted: (1) a seeding experiment in the field to record the germination, survival, and
91 growth of seedlings during the first growing season, together with the distance-dependency
92 effects of possible contributing factors such as soil, light, herbivores, pathogens,
93 mycorrhizae, and competitive vegetation; (2) retrospective surveys in existing older scarified
94 sites to understand the growing conditions of oak seedlings in relation to the location of
95 mature overstory tree; and (3) a laboratory experiment to clarify the effects of light and soil
96 conditions on acorn germination, seedling growth, and survival. We use the results to
97 propose appropriate practices for enhancing the regeneration of *Q. crispula* at scarification
98 sites.

99

100 **2. Materials and methods**

101 **2.1. Study sites**

102 The field study was conducted in the Uryu Experimental Forest (UREF) of Hokkaido
103 University, which is located in the northern part of Hokkaido island, Japan (44°22'N,
104 142°12'E, 280 m a.s.l.). The climate there is characterized as cool-temperate, with a mean
105 annual temperature of 4.5°C and a mean annual precipitation of 1,298 mm (Uryu
106 Experimental Forest, unpublished). There is snow cover from November to May to a
107 maximum depth of ca. 200 cm. The dominant natural vegetation is conifer-broadleaved
108 mixed forest, which is widely distributed across the transition between the cool-temperate
109 and boreal vegetation zones in northeastern Asia. The major tree species in these forests
110 are *Abies sachalinensis* (Fr. Schm.), *Picea glehnii* Masters, *B. platyphylla* var. japonica, *B.*

111 *ermanii*, and *Q. crispula*, and the understory is densely covered with dwarf bamboo (*Sasa*
112 *senanensis* (Franchet et Savatier) Rehder and *S. kurilensis* (Ruprecht) Makino et Shibata).

113 We examined several scarification sites in UREF that contained different-aged stands.
114 The natural mixed forests in this region contain certain portion of non-wooded patches as a
115 result of some previous natural (windthrow) or artificial (partial cutting) disturbance. The
116 area of these patches ranged to a few hector, and maintained for a long-term by exclusive
117 dominance of dwarf bamboos (Noguchi and Yoshida 2005). We selected the non-wooded
118 patches, where scarified have been conducted, on flat topography (inclination < 3°) with c.a.
119 0.1 ha patch area, originated presumably by a historical strong wind in 1954 (Yoshida and
120 Noguchi 2009). The scarification treatment involved the removal of the root system of the
121 dwarf bamboos along with a portion of the surface soil (up to ca. 10 cm depth) using a
122 rake-dozer (D60P11, Komatsu, Ltd.). Some of the sites have essentially remained
123 untouched after the scarification, whereas others were artificially seeded with oak acorns.
124 (note: these sites are described in further detail below). The study design was identical
125 across all sites, using four distance classes from the crown of an overstory oak tree (ca. 50
126 cm diameter at breast height (dbh)), located at a southern border of the patch: inside the
127 crown, -2.5 m; beneath the crown edge, 0 m; outside the crown, +5 m; and +15 m; the latter
128 two were at least distant from all trees, not just the subject oak.

129 **2.2. Year 1 post-scarification measurements**

130 In the first year after scarification, we measured the early demography (germination,
131 survival, and growth rates) of oak seedlings, together with several biotic and abiotic factors.
132 The area that was scarified in autumn 2012 was designated as a study area (compartment
133 408 in UREF). We selected three scarified sites containing three patches for each, and
134 established quadrats (1 m² area each) at the four distances outlined above.

135 In each quadrat, we took hemispherical photographs at a height of 0.15 m immediately

136 following the scarification treatment using a digital camera with a fish-eye lens (Coolpix 950
137 and FC-E8, Nikon Co.). The amount of open sky was determined from these images. The
138 acorns supplied in the first growing season were collected in a trap (50 × 50 cm opening)
139 that was set beside each quadrat, and were counted. Soil fertility was measured in July and
140 September 2013. We used an auger (4.5 cm diameter) to sample the surface soil (10 cm
141 depth beneath the humus layer) with three replicates. We then oven-dried the samples
142 (105°C, 48 h) and calculated their moisture content. We also determined the nitrogen
143 concentration (mg/g) of subsamples (10 g) by extracting the soil nitrogen with 2-mol KCL
144 and using an auto-analyzer (AACS-4, BL-TEC Co. Ltd., Osaka).

145 The population size of rodents, a major predator of acorns, was estimated in October
146 2013. We set a live trap alongside each quadrat for four nights and identified all trapped
147 rodents, following which we released them. At the same time, we also examined the rate at
148 which acorns were removed by rodents by placing average-sized acorns with a metal-tag
149 attached inside the quadrat and observing their presence/absence over the subsequent 4
150 days. Any absent acorns were located using a metal detector.

151 A seeding experiment was also initiated in September 2012. We collected acorns from
152 neighboring mature stands and regularly seeded the 30 × 30 cm area of the quadrats with
153 those of average size. We shallowly buried the acorns, and covered the quadrats with wire
154 mesh to prevent mammals or birds from feeding on them. The next spring (May 2013), we
155 recorded the germination rate of the acorns, and then subsequently noted the survival or
156 death of the seedlings, together with possible causes of death (disease, vertebrate herbivory,
157 invertebrate herbivory, withering, physical damage and unknown; refer to Yamazaki et al.
158 2009) once every 2 weeks. At that time, we also recorded whether the living seedling
159 experienced insect herbivory more than half of the total leaf area. A water-filled bowl (50 ×
160 50 cm) was also placed alongside each quadrat, and the number of fallen insects

161 (lepidopteran larvae) was counted each week.

162 All surviving seedlings were collected in November 2013, at the end of the first growing
163 season. We oven-dried these samples (78°C, 48 h), and individually measured their
164 above-ground and below-ground weights. We also examined the root-ends (312 per
165 seedling on average) of two average-sized seedlings per quadrat under a stereoscopic
166 microscope to identify the presence of mycorrhizal fungi.

167 **2.3. Year 2+ post-scarification measurements**

168 We also conducted censuses at older sites (2-3, 3-4, and 8-16 years post-treatment) to
169 clarify longer term establishment processes. The demography of seedlings was recorded in
170 the 2-year-old and 3-year-old sites (compartments 406 and 323 in UREF, respectively)
171 during the following one growing season. The scarification treatment at these sites has been
172 carried out in summer of 2010 and 2011, respectively. We selected three scarified patches
173 (ca. 0.1 ha area) with adjacent overstory oak trees (ca. 50cm dbh) for each, and established
174 1 m² quadrats at each of four distance classes. We then measured the height, basal
175 diameter, and percent leaf herbivory of oak seedlings in there. The seedling density of all
176 tree species ranged 8-36 /m², with scarce other vegetation, suggesting that the effects of
177 crowding on demography of oak seedlings was negligible in this stage of development.

178 In a 16-year-old site (compartment 321 in UREF) scarified in 1997, we determined the
179 survival and height growth of naturally established oak saplings, together with the other tree
180 species (mainly birches) in each distance class based on the measurements at age 8 years
181 (Harada et al. 2008). All the oak saplings regenerated in the scarified area (0.34 ha) were
182 identified and measured height in 2005. We again selected three patches to meet our
183 criteria (i.e. size of the patch, existence of an oak tree and etc.), and re-measured saplings
184 located in 7.5 m² quadrats set at each of four distance classes in 2013. The width (a
185 direction perpendicular to the crown inside-outside) of the quadrat was extended to 7.5m to

186 compensate the decrease in density.

187 **2.4. Pot experiment**

188 To support the field experiment, a pot seeding experiment was conducted during
189 September 2012 and November 2013 to examine the effects of light, soil, and fungicide
190 treatments on oak seedling germination, survival, and growth. We collected acorns from the
191 neighboring forests of the field experiment plots and selected those of average size. We
192 filled pots (10-cm diameter × 8-cm depth) with soil collected from areas adjacent to the
193 quadrats at each distance, and placed an acorn on the surface of each. The pots were
194 placed in a nursery field at the Nayoro Breeding Station of Hokkaido University (44°21'N,
195 142°27'E, 100 m a.s.l.).

196 In total, 144 pots were used (three light levels × four soil locations × two fungicide
197 treatments, with six replications). To examine the effect of light, we exposed the pots to three
198 light treatments by providing different levels of cover with mesh cloth: control (100%), 78%,
199 and 40% open. To avoid excessive desiccation, we irrigated the pots every 3 days and
200 examined the soil using the same methods as described above. We also examined the
201 effects of mycorrhizal or pathogenic fungi by spraying the soil in the pots with either a 0.01%
202 Tilt® emulsion (25% propiconazole; 9.81 ml) every 2 weeks during the growing season or an
203 equal weight of water (control). We recorded the germination of the acorns and the survival
204 of seedlings every 2 weeks during the growing season (May 2013 to October 2013), and
205 collected all surviving seedlings in November 2013, at the end of the first growing season.
206 We then oven-dried the samples (78°C, 48 h), and individually measured their
207 above-ground and below-ground weights.

208

209 2.5. Statistical analyses

210 We used generalized linear models for analyses in this study. First, we examined whether
211 or not the oak demographic parameters and possible contributing factors show
212 distance-dependency to a conspecific overstory tree in the 1-16 year-old sites. The squared
213 term of the distance was included as an explanatory variable in the model to consider the
214 possibility of a non-linear relationship. It was assumed that count data followed a Poisson
215 distribution (with a log link function), continuous variate data followed a normal distribution
216 (with an identity link function), and proportion data followed a binomial distribution (with a
217 logit link function). The data from the three sites with three replications for each were pooled
218 and used. Stepwise model selection based on the Akaike information criterion (AIC) was
219 used to select the variables to be retained in the final model.

220 In addition, we analyzed the demography of oak saplings (survival and height increment
221 during 8–16-year) at an individual-scale. The explanatory variables were sapling height and
222 local crowding (i.e. sum of basal area of the neighbors, located within the surrounding 10 m²
223 area) at the beginning of the period (i.e. 8-year-old). A binominal distribution (with a logit link
224 function) was assumed for the survival model. For the height increment model, a normal
225 distribution (with an identity link function) was assumed, and the initial diameter was used as
226 an offset variable. The data from the three replications in the site were pooled and used.

227 We further analyzed the data from the pot experiment to estimate the effects of light
228 (amount of open sky), soil fertility, and fungicide treatment on oak demography. It was
229 assumed that germination and survival followed a binomial distribution (with an identity link
230 function) and biomass followed a normal distribution. For the former two models, the number
231 at the beginning was considered as an offset variable. All statistical analyses were
232 performed in R version ver. 3.2.3 (R Core Team, 2016).

233

234

235 **3. Results**

236 Many of demographic and environmental parameters showed distance-dependency
237 around overstory oak tree (Table 1). The amount of open sky increased with increasing
238 distance from the crown (Fig. 1a). There was no relationship between the water content of
239 the soil and distance from the crown in July or September (Fig. 1b), whereas the nitrogen
240 concentration increased with increasing distance at all times (Fig. 1c).

241 Fallen acorns were not observed at distances >5 m from the crown (Fig. 2a). Furthermore,
242 the number of rodents captured (two species, *Apodemus speciosus* and *Myodes rufocanus*
243 *bedfordiae* were pooled) and the number of acorns removed by them were highest beneath
244 the crown, and tended to decrease with increasing distance (Fig. 2b, c). All of the acorns
245 removed by rodents were taken to intact (i.e. unscarified) ground that was covered with
246 dwarf bamboos, with no secondary dispersal to the scarified area.

247 In the field oak seeding experiment, the germination rate was 9.9% and the overall
248 survival rate during the first growing season was 89.8%. The germination rate was
249 negatively correlated with distance from the crown (Fig. 3a), whereas the survival rate
250 consistently averaged >70%, with no significant differences between distances (Fig. 3b).
251 Much of the observed mortality appeared to have been caused by drought (withering:
252 46.2%) and stem predation by rodents (vertebrate herbivory: 23.1%); the contributions of
253 the other mortality agents were minor (disease 7.7%, physical damage 5.2%, invertebrate
254 herbivory 2.6%). The proportion of oak seedlings exhibiting a leaf predation rate >50% was
255 also higher up to 5 m from the crown (Fig. 3c) and the number of fallen insects (lepidopteran
256 larvae) was more abundant beneath the crown (Fig. 3d). The proportion of oak seedlings
257 with mycorrhizal fungi also decreased with increasing distance (Fig. 3e).

258

259 At 2-3 and 3-4 year-old sites, the annual survival of oak seedlings was >80% across all
260 distances (Fig. 4a), and the height of seedlings did not change significantly with distance
261 from the crown (Fig. 4b). However, the proportion of seedlings with a leaf predation rate
262 >50% decreased with increasing distance (Fig. 4c).

263 By contrast, the survival of oak saplings during 8-16-year-old increased with increasing
264 distance from the crown (Fig. 5a). The growth analysis at an individual-scale revealed that
265 the survival of these saplings depended positively on their initial height (at age 8 years) and
266 the local crowding (sum of basal area of the neighbors in the surrounding 10 m² area),
267 whereas the height growth was not influenced by any factor (Table 2; Fig. 5b). The number
268 of saplings of other species (mostly birches, *Betula platyphylla* var. *japonica*) that
269 established following the scarification treatment also significantly increased with increasing
270 distance (Fig. 5c).

271 In the pot experiment, a germination rate of 13% and a first-year survival of 84% was
272 observed, which was similar to levels in the field. The germination rate decreased with light
273 condition (Table 3), whereas soil location and the fungicide treatment had no significant
274 effects. By contrast, survival was not influenced by any factor. The seedling biomass (both
275 above-ground and below-ground) at the end of the growing season decreased with light
276 condition (Table 3).

277

278 **4. Discussion**

279 Our findings clearly demonstrate that the spatial relationship between the regeneration of
280 *Q. crispula* and the conspecific overstory tree adjacent to scarification sites changes
281 considerably among stages of the early establishment. In the initial stage, a location
282 beneath the crown provided favorable conditions, whereas at subsequent stages, the
283 distance-dependent effects were unclear, until eventually a location outside the crown

284 showed higher survival of saplings.

285 Scarification generally produces competition-free and resource rich condition on forest
286 understory (Ozawa et al. 2001; Löff et al. 2012). However, inversely, the condition can be
287 harsh for acorns and/or small seedlings, emerging a requirement to moderate the
288 environment (i.e. facilitation, Gómez-Aparicio et al. 2005; Resco de Dios et al. 2005; Jensen
289 et al. 2011). Actually, in our field seeding experiment, the environment beneath the crown
290 was beneficial for the acorn germination (Fig. 3a), and in the pot experiment, weaker light
291 levels led to higher levels of biomass production (Table 3), which would have positive
292 impacts on the subsequent survival and growth rate. In addition, the seedling deaths during
293 the first growing season were largely caused by withering, unlike the previous study in which
294 diseases were the major mortality agent in a natural forest (Yamazaki et al. 2009). These
295 findings are consistent with the results of previous studies regarding oak species in arid
296 region (Gómez-Aparicio 2005; Urbieta et al 2008; Muhamed et al. 2013), which found that a
297 high light-intensity and associated desiccation decreased the potential of regeneration.
298 Although the current study site is on a relatively humid location, the absence of crowns in
299 scarification site may provide an unsuitable environment for oak acorns and seedlings
300 particularly during drought conditions temporally occurred.

301 In terms of the other factors measured, soil nutrients increased with increasing distance
302 from the crown (Fig. 1c). Scarified soil generally exhibits higher nutrient levels than intact
303 soil because of the decreased absorption by vegetation, and higher levels of microbial
304 activity as a result of the increased soil surface temperatures via the more intense light
305 (Ozawa et al. 2001). We suppose that such a rich soil condition might reduce the relative
306 importance of mycorrhizal infection, which was revealed to be lower in seedlings at the
307 distant locations from the conspecific tree (Fig. 3e) (cf. Dickie et al. 2002). In our pot
308 experiment, both the soil and fungicide treatments appeared to have smaller effects on the

309 survival and biomass production of seedlings than light levels did (Table 3), likely because of
310 the soil nutrient availability being sufficiently high at the scarification site at least in an early
311 stage of development.

312 In the later stage of establishment, when saplings had grown up, survival outside the
313 crown became higher (Fig. 5a). Our analysis suggested this could be caused by facilitation
314 effect from neighbors, because the abundant regenerated trees had a large positive effect
315 on individual survival (Table 2). Such an effect have been reported for many tree species
316 grown in scarified sites (Resco de Dios et al. 2005; Harada et al. 2008), and the current
317 study revealed that this can continue to act in a 16-year-old stand for *Q. crispula*. The
318 advantage found in the distant area may also be related to cumulative effects of the relative
319 predation-free condition (Fig. 3c, 4c) provided by lesser density of herbivorous insects (Fig.
320 3d).

321 When interpreting the current results, it should be noted that annual variability in various
322 factors, such as climate, acorn production, the densities of rodents and herbivorous insects,
323 and their interactions, will also affect the spatial patterns of regeneration. For instance,
324 during a particularly dry year, the condition beneath the crown may become more important,
325 resulting in a higher regeneration density here. In addition, we should recognize that the
326 results were from only one forest in northern Hokkaido. We need additional studies in many
327 forests and regions to generalize the current findings.

328 **Conclusion**

329 Given a result of previous study which showed very few oak saplings in a natural stand
330 (Takahashi et al. 2003), scarification can be a successful aiding practice for oak
331 regeneration. Actually, the survival rate of regenerated oak seedlings and saplings reached
332 more than 80 % in average throughout the study period (Fig. 3a, 4a, 5a). The temporal
333 change in favorable location (i.e. inside the crown in the initial stage followed by outside in

334 the subsequent stage) suggested that *Q. crispula* would fit to a shelter-wood system
335 (Matthews 1989), in which the regeneration starts from shaded condition, followed by a gap
336 status created by a successive felling of overstory trees. In actual, this system is applied for
337 oak species in many regions (cf. Parker and Dey 2008; Povak et al. 2008). On the other
338 hand, when the management targets existing gap area, supply of acorns to far outside the
339 crown remains an issue; the current results demonstrated that secondary acorn dispersal by
340 forest-dwelling rodents would be less important in scarified sites (Fig.2b,c), probably
341 because of their low activity in open area (Hayashida and Igarashi 1995; Birkedal et al.
342 2010). Therefore, to utilize the advantage (i.e. higher survival) of the distant locations
343 observed in the sapling stage (Fig. 5a), it is worth considering direct acorn seeding in the
344 management (Löf and Birkedal 2009). It is imperative to shallowly bury acorns (Guo et al.
345 2011) to prevent desiccation. Based on the current results, it would be efficient to
346 concentrate on the area away from the crown when sowing acorns and an abundant acorn
347 supply would compensate for the low germination rate at an initial stage. Nevertheless, we
348 have to acknowledge the possibility that, in a subsequent stage of stand development,
349 dense neighbors might change into competitor (from facilitator) as such a change in the
350 neighborhood effect has been observed in some species in scarification site (Harada et al.
351 2008). If it happens, we would need to consider thinning of the other species to enhance oak
352 survival and growth. Future studies are required to develop more reliable approach in
353 natural regeneration practice using scarification, with considering long-term forecasts for
354 various factors.

355

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364

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Table 1. Summary of the generalized linear model examining the dependency on the distance from parent tree canopy in scarification sites.

Response variable	Coefficient			AIC
	Intercept	distance	distance ²	
Year 0-1				
Sky openness	3.89	0.037	-0.002	-34.5
Soil water content July	-1.12	ns	ns	-56.1
Soil water content September	-1.08	ns	ns	-67.8
Soil fertility July	-4.18	0.043	ns	36.3
Soil fertility September	-4.29	0.143	-0.006	85.2
Acorn dispersal	2.60	-0.509	-0.233	774.3
Acorn removal	0.43	ns	0.045	85.7
Rodent density	-1.28	-0.255	ns	39.4
Acorn germination	-1.59	-0.053	ns	106.0
Survival of seedlings	1.92	ns	ns	30.7
Leaf predation > 50%	-0.77	ns	-0.015	40.0
Herbivorous insect density	0.51	-0.214	-0.066	69.0
Mycorrhizal infection	-0.83	-0.139	0.006	553.5
Year 2-3				
Survival of seedlings	2.54	ns	ns	49.4
Height of seedlings	3.42	ns	ns	7.3
Leaf predation > 50%	-1.77	-0.481	ns	25.5
Year 3-4				
Survival of seedlings	3.88	ns	ns	10.9
Height of seedlings	3.78	ns	ns	15.6
Leaf predation	-1.28	-0.073	ns	53.2
Year 8-16				
Survival of saplings	0.21	0.114	ns	41.7
Height of saplings	220.0	ns	ns	121.0
Local crowding	997.8	43.59	ns	193.9

The coefficients of the final selected model are shown (*ns* indicates the unselected variable). See text for detailed information

Table 2. Summary of the generalized linear model examining demography of individual saplings in the 16-year-old site.

Response variable	Coefficient			AIC
	Intercept	Initial height	Local crowding	
Survival of saplings	-1.490	0.039	0.001	74.2
Height of saplings	231.9	ns	ns	912.7

The survival during 8 years period (8 to 16-year-old) and the height at 16-year-old were examined. For the explanatory variables (Initial height and local crowding), the values at the beginning of the period (i.e. 8-year-old) were used. The coefficients of the final selected model are shown (*ns* indicates the unselected variable). See text for detailed information

Table 3. Summary of the generalized linear model examining demography of seedlings in the pot experiment.

Response variable	Coefficient				AIC
	Intercept	Light condition	Soil location	Fungicide	
Germination of acorns	-3.169	-0.036	ns	ns	104.2
Survival rate of seedlings	3.996	ns	ns	ns	18.6
Term-end biomass of seedlings	-0.035	-0.014	ns	ns	28.5

The coefficients of the final selected model are shown (*ns* indicates the unselected variable). See text for detailed information

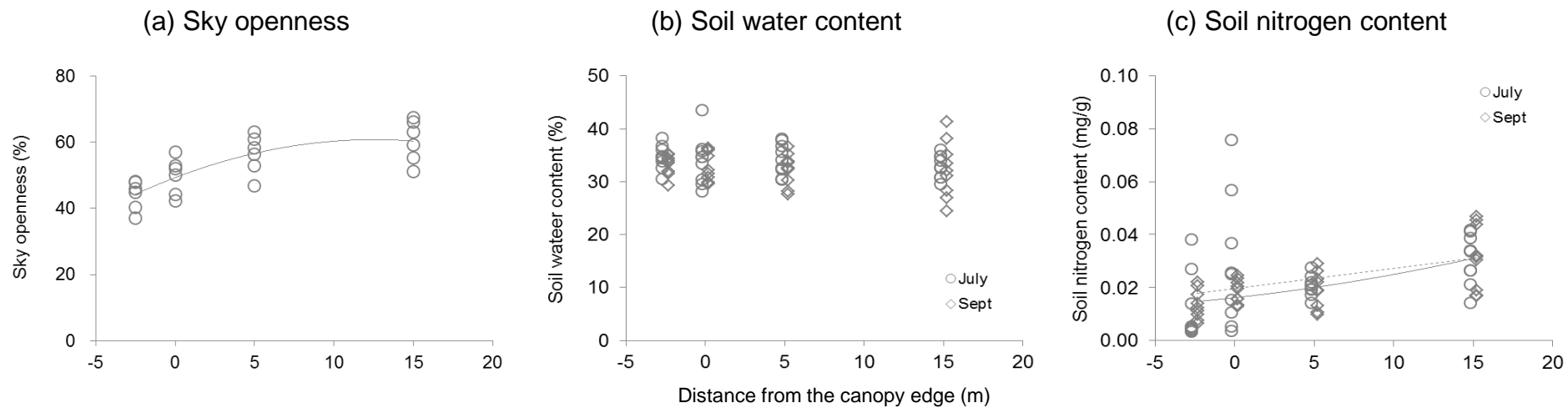


Fig.1. Distance-dependency of light and soil conditions in 0-1 year-old scarification sites. Fitted lines are shown when the generalized linear model selected the distance term(s)

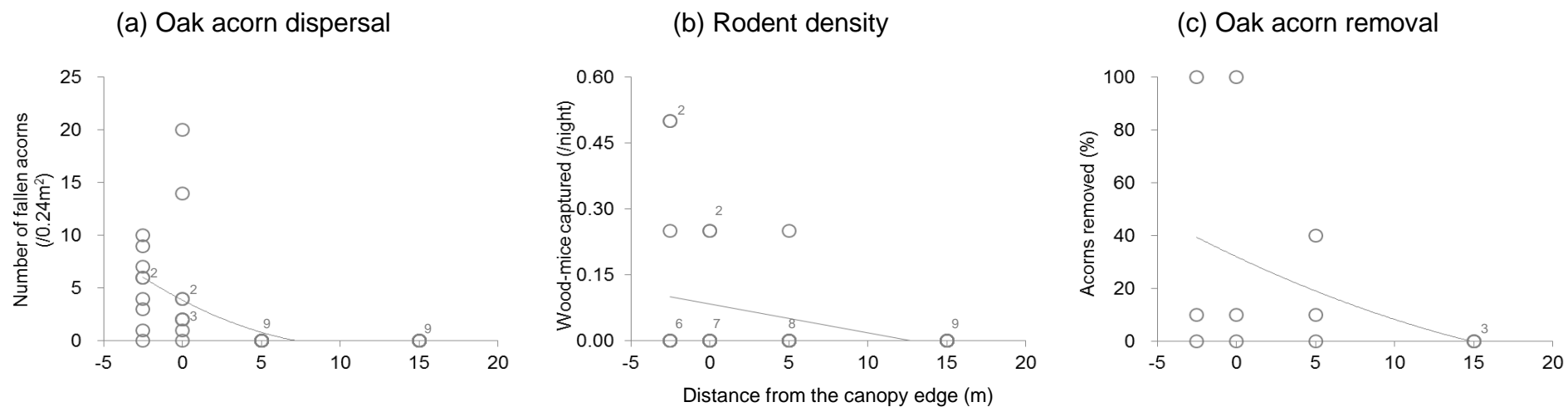
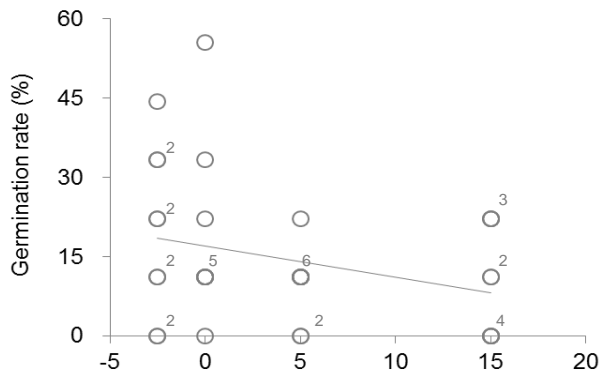
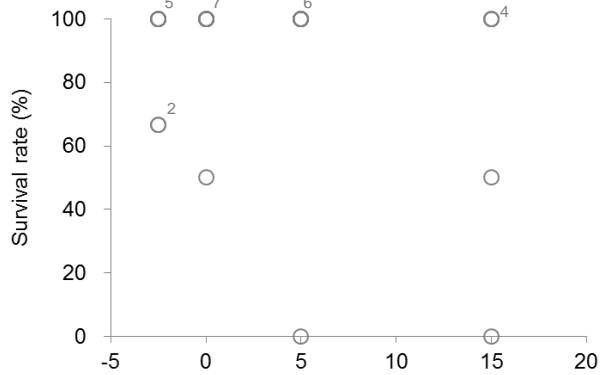


Fig.2. Distance-dependency of oak acorn dispersal and related issues in 0-1 year-old scarification sites. Numeric values in the plates indicate the number of overlapped points. Fitted lines are shown when the generalized linear model selected the distance term(s)

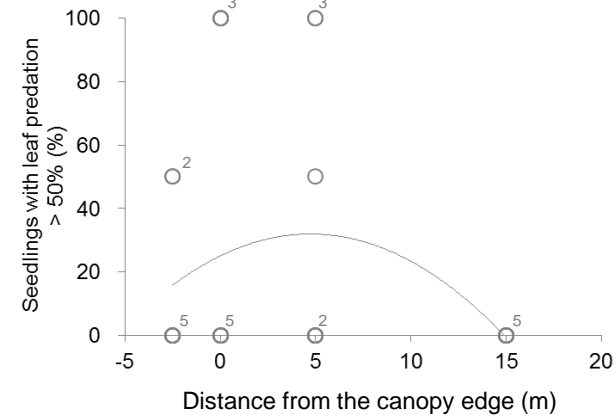
(a) Oak acorn germination



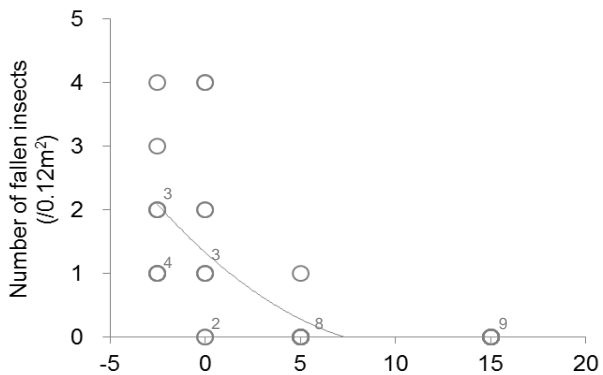
(b) Survival of oak seedlings



(c) Leaf predation in oak seedlings



(d) Herbivorous insect density



(e) Mycorrhizal infection of oak seedlings

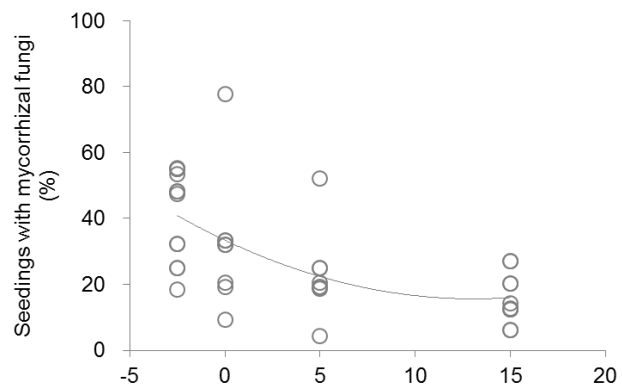


Fig.3. Distance-dependency of oak seedling demography and related issues in 0-1 year-old scarification sites. Numeric values in the plates indicate the number of overlapped points. Fitted lines are shown when the generalized linear model selected the distance term(s)

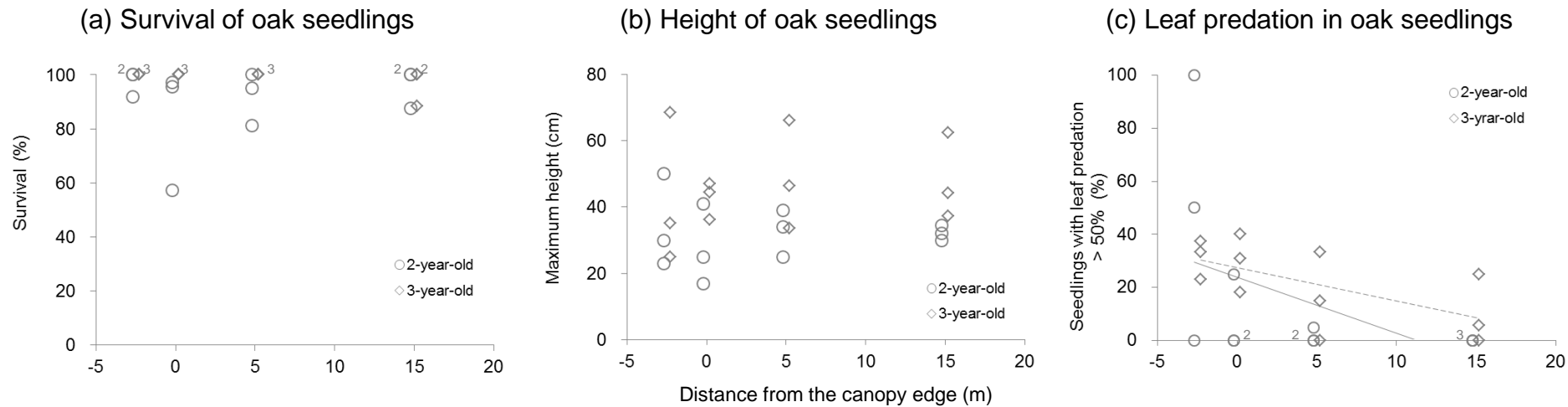


Fig.4. Distance-dependency of oak seedling demography and related issues in 2-3 and 3-4 year-old scarification sites. Numeric values in the plates indicate the number of overlapped points. Fitted lines are shown when the generalized linear model selected the distance term(s)

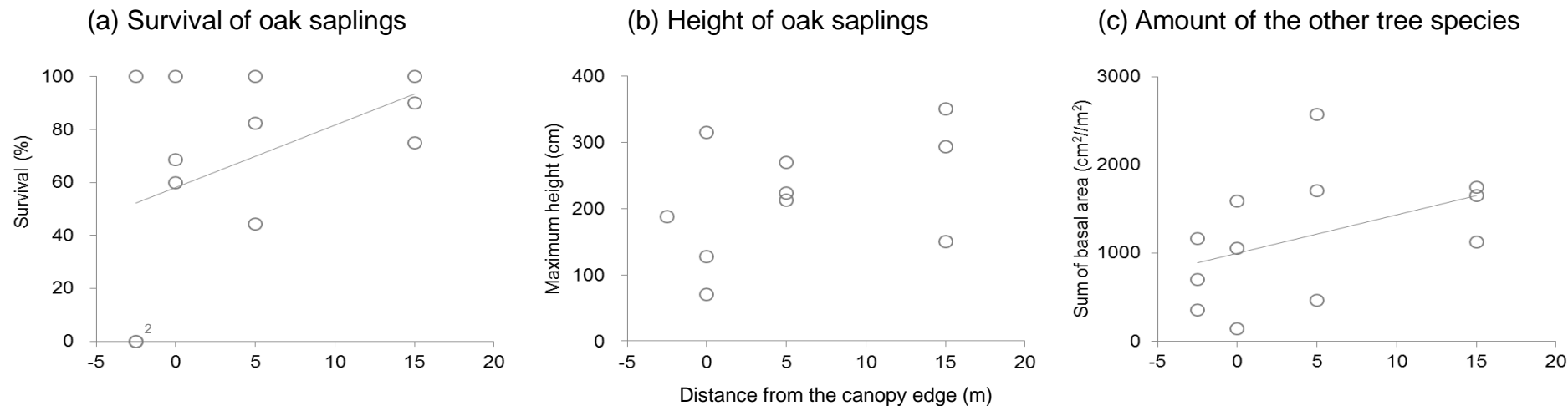


Fig.5. Distance-dependency of oak sapling demography and a related issue in 16 year-old scarification sites. Numeric values in the plates indicate the number of overlapped points. Fitted lines are shown when the generalized linear model selected the distance term(s)