Title	Spatial patterns of oak (Quercus crispula) regeneration on scarification site around a conspecific overstory tree
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Citation	Forest ecology and management, 393, 81-88 https://doi.org/10.1016/j.foreco.2017.03.011
Issue Date	2017-06-01
Doc URL	http://hdl.handle.net/2115/74846
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Type	article (author version)
File Information	Asada et al MS_final+TF.pdf

Spatial patterns of oak (*Quercus crispula*) regeneration on scarification site around a conspecific overstory tree

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Abstract

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

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

1. Introduction

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

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

Oak species generally have high economic and ecological value in temperate forests (Johnson et al. 2009). The wood of the species is a valuable material particularly for furniture, and its acorns are an important food resource for wildlife. *Quercus crispula* Blume is one of the representative broadleaved tree species, with biggest size and longest lifespan among broadleaved species, in Hokkaido (Sano 1997). Several previous reports have presented the regeneration management of this oak species, but an appropriate silvicultural practice widely applicable has not yet been established, leading to reductions in oak resource in Japan.

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

Therefore, the aim of this study was to find out whether or not locations more beneficial than others for early establishment of *Q. crispula* exist in scarification sites, and, if they exist, how locations may change with time. Although several previous studies have reported the efficacy of the scarification on oak regeneration (Miya and Koshika 2004; Harada et al. 2008), its spatial aspect (i.e. dependency on the distance from conspecific overstory tree) remain unclear. Scarification produces competition-free condition for seedlings at an initial stage, but effects of the many other factors and their temporal changes, in relation to the canopy-gap gradient, should also be considered. Thus, we examined the hypothesis that the regeneration of oak seedlings is enhanced at a certain distance from the nearest conspecific overstory tree, depending on the stage of development. For this purpose, we conducted: (1) a seeding experiment in the field to record the germination, survival, and growth of seedlings during the first growing season, together with the distance-dependency effects of possible contributing factors such as soil, light, herbivores, pathogens, mycorrhizae, and competitive vegetation; (2) retrospective surveys in existing older scarified sites to understand the growing conditions of oak seedlings in relation to the location of mature overstory tree; and (3) a laboratory experiment to clarify the effects of light and soil conditions on acorn germination, seedling growth, and survival. We use the results to propose appropriate practices for enhancing the regeneration of *Q. crispula* at scarification sites.

2. Materials and methods

2.1. Study sites

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

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

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

2.2. Year 1 post-scarification measurements

In the first year after scarification, we measured the early demography (germination, survival, and growth rates) of oak seedlings, together with several biotic and abiotic factors. The area that was scarified in autumn 2012 was designated as a study area (compartment 408 in UREF). We selected three scarified sites containing three patches for each, and established quadrats (1 m^2 area each) at the four distances outlined above.

In each quadrat, we took hemispherical photographs at a height of 0.15 m immediately following the scarification treatment using a digital camera with a fish-eye lens (Coolpix 950 and FC-E8, Nikon Co.). The amount of open sky was determined from these images. The acorns supplied in the first growing season were collected in a trap (50 × 50 cm opening) that was set beside each quadrat, and were counted. Soil fertility was measured in July and September 2013. We used an auger (4.5 cm diameter) to sample the surface soil (10 cm depth beneath the humus layer) with three replicates. We then oven-dried the samples (105°C, 48 h) and calculated their moisture content. We also determined the nitrogen concentration (mg/g) of subsamples (10 g) by extracting the soil nitrogen with 2-mol KCL and using an auto-analyzer (AACS-4, BL-TEC Co. Ltd., Osaka).

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

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

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

2.3. Year 2+ post-scarification measurements

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

In a 16-year-old site (compartment 321 in UREF) scarified in 1997, we determined the survival and height growth of naturally established oak saplings, together with the other tree species (mainly birches) in each distance class based on the measurements at age 8 years (Harada et al. 2008). All the oak saplings regenerated in the scarified area (0.34 ha) were identified and measured height in 2005. We again selected three patches to meet our criteria (i.e. size of the patch, existence of an oak tree and etc.), and re-measured saplings located in 7.5 m^2 quadrats set at each of four distance classes in 2013. The width (a direction perpendicular to the crown inside-outside) of the quadrat was extended to 7.5m to compensate the decrease in density.

2.4. Pot experiment

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

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

2.5. Statistical analyses

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

In addition, we analyzed the demography of oak saplings (survival and height increment during 8–16-year) at an individual-scale. The explanatory variables were sapling height and local crowding (i.e. sum of basal area of the neighbors, located within the surrounding 10 m^2 area) at the beginning of the period (i.e. 8-year-old). A binominal distribution (with a logit link function) was assumed for the survival model. For the height increment model, a normal distribution (with an identity link function) was assumed, and the initial diameter was used as an offset variable. The data from the three replications in the site were pooled and used.

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

3. Results

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

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

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

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

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

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

4. Discussion

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

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

In terms of the other factors measured, soil nutrients increased with increasing distance from the crown (Fig. 1c). Scarified soil generally exhibits higher nutrient levels than intact soil because of the decreased absorption by vegetation, and higher levels of microbial activity as a result of the increased soil surface temperatures via the more intense light (Ozawa et al. 2001). We suppose that such a rich soil condition might reduce the relative importance of mycorrhizal infection, which was revealed to be lower in seedlings at the distant locations from the conspecific tree (Fig. 3e) (cf. Dickie et al. 2002). In our pot experiment, both the soil and fungicide treatments appeared to have smaller effects on the survival and biomass production of seedlings than light levels did (Table 3), likely because of the soil nutrient availability being sufficiently high at the scarification site at least in an early stage of development.

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

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

Conclusion

Given a result of previous study which showed very few oak saplings in a natural stand (Takahashi et al. 2003), scarification can be a successful aiding practice for oak regeneration. Actually, the survival rate of regenerated oak seedlings and saplings reached more than 80 % in average throughout the study period (Fig. 3a, 4a, 5a). The temporal change in favorable location (i.e. inside the crown in the initial stage followed by outside in the subsequent stage) suggested that *Q. crispula* would fit to a shelter-wood system (Mattews 1989), in which the regeneration starts from shaded condition, followed by a gap status created by a successive felling of overstory trees. In actual, this system is applied for oak species in many regions (cf. Parker and Dey 2008; Povak et al. 2008). On the other hand, when the management targets existing gap area, supply of acorns to far outside the crown remains an issue; the current results demonstrated that secondary acorn dispersal by forest-dwelling rodents would be less important in scarified sites (Fig.2b,c), probably because of their low activity in open area (Hayashida and Igarashi 1995; Birkedal et al. 2010). Therefore, to utilize the advantage (i.e. higher survival) of the distant locations observed in the sapling stage (Fig. 5a), it is worth considering direct acorn seeding in the management (Löf and Birkedal 2009). It is imperative to shallowly bury acorns (Guo et al. 2011) to prevent desiccation. Based on the current results, it would be efficient to concentrate on the area away from the crown when sowing acorns and an abundant acorn supply would compensate for the low germination rate at an initial stage. Nevertheless, we have to acknowledge the possibility that, in a subsequent stage of stand development, dense neighbors might change into competitor (from facilitator) as such a change in the neighborhood effect has been observed in some species in scarification site (Harada et al. 2008). If it happens, we would need to consider thinning of the other species to enhance oak survival and growth. Future studies are required to develop more reliable approach in natural regeneration practice using scarification, with considering long-term forecasts for various factors.

Acknowledgements

We would like to thank two anonymous reviewers for their helpful comments and suggestions. We sincerely thank technical staff of the Uryu experimental forest, for their assistance in the field work, and members of the Nayoro laboratory for their valuable discussion for this study. We also thank M. Kobayashi for his assistance for the survey of mycorrhizal fungi, and to T. Watanabe and T. Inoue for their help to conduct soil chemical analyses. Thanks are extended to H. Shibata, K. Fukuzawa and M. Kobayashi for their critical reading of the manuscript. This study was supported by the research project fund from the Ministry of Education, Culture, Sports, Science and Technology of Japan (No. 23580194 and 26450187)

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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

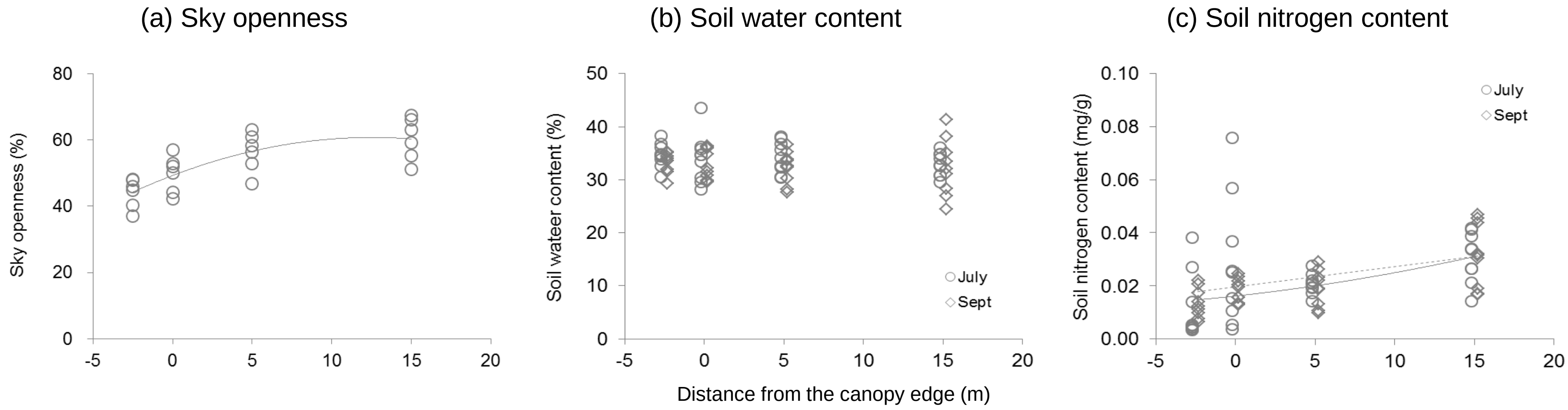

Fig.1. Distance-dependency of light and soil conditions in 0-1 year-old scarification sites. Fitted lines are shown when the generalized linear model selected the distance term(s)

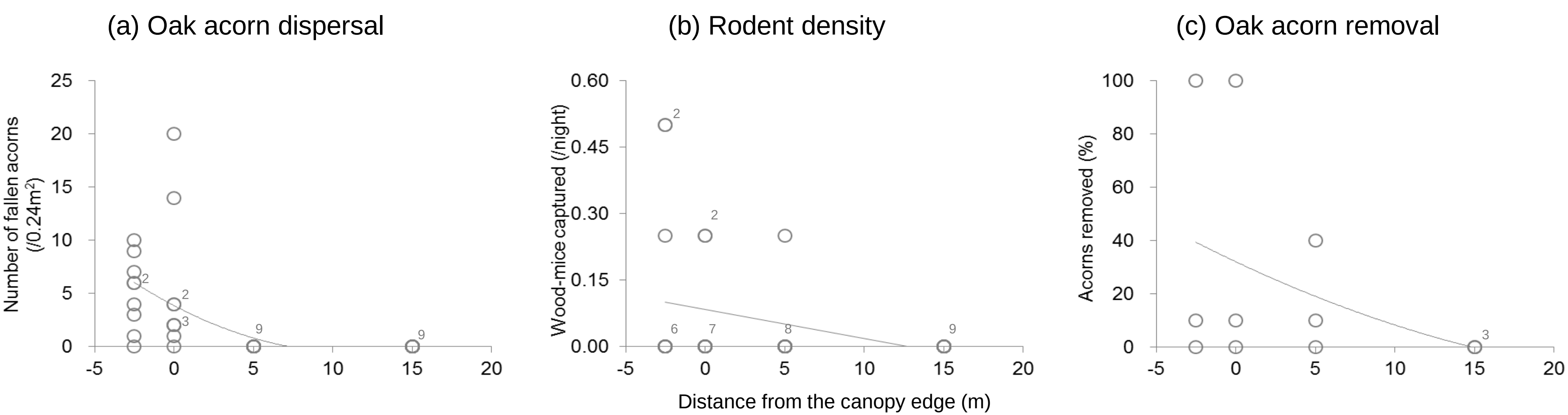

Fig.2. Distance-dependency of oak acorn dispersal and related issues in 0-1 year-old scarification sites. Numeric values in the plates indicate the number of overlapped points. Fitted lines are shown when the generalized linear model selected the distance term(s)

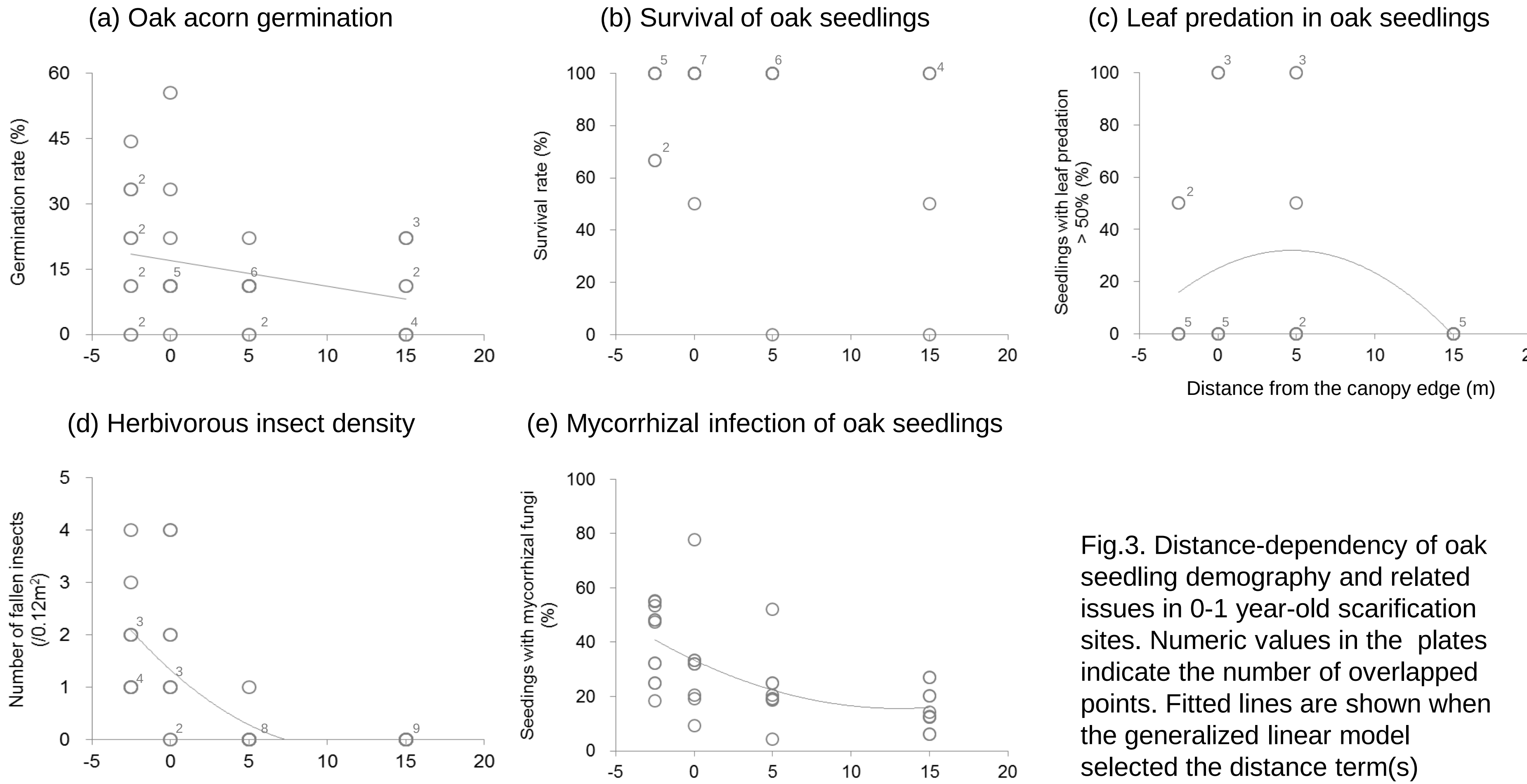

Fig.3. Distance-dependency of oak seedling demography and related issues in 0-1 year-old scarification sites. Numeric values in the plates indicate the number of overlapped points. Fitted lines are shown when the generalized linear model selected the distance term(s)

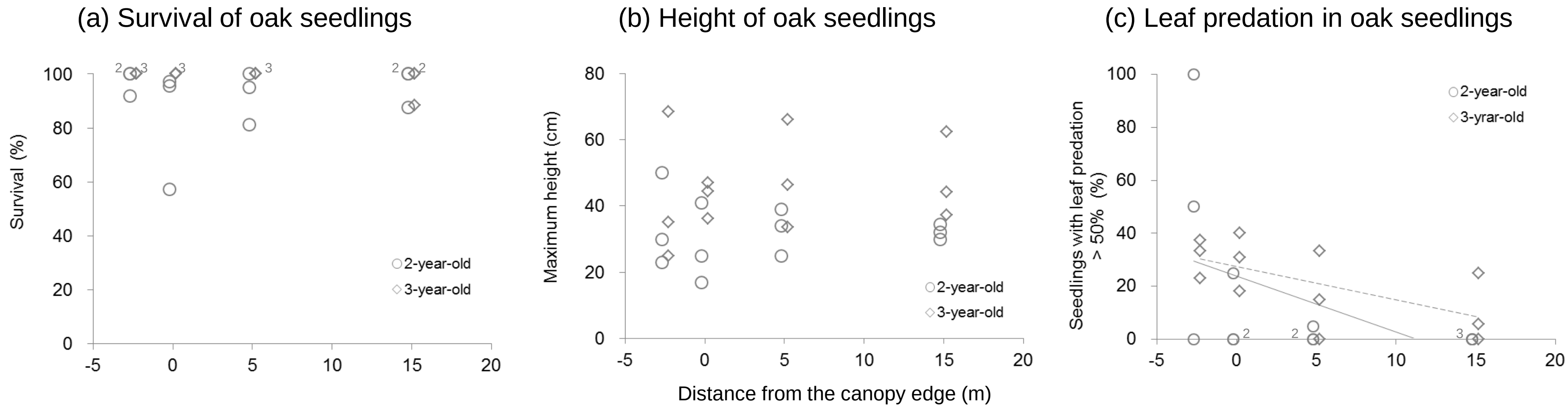

Fig.4. Distance-dependency of oak seedling demography and related issues in 2-3 and 3-4 year-old scarification sites. Numeric values in the plates indicate the number of overlapped points. Fitted lines are shown when the generalized linear model selected the distance term(s)

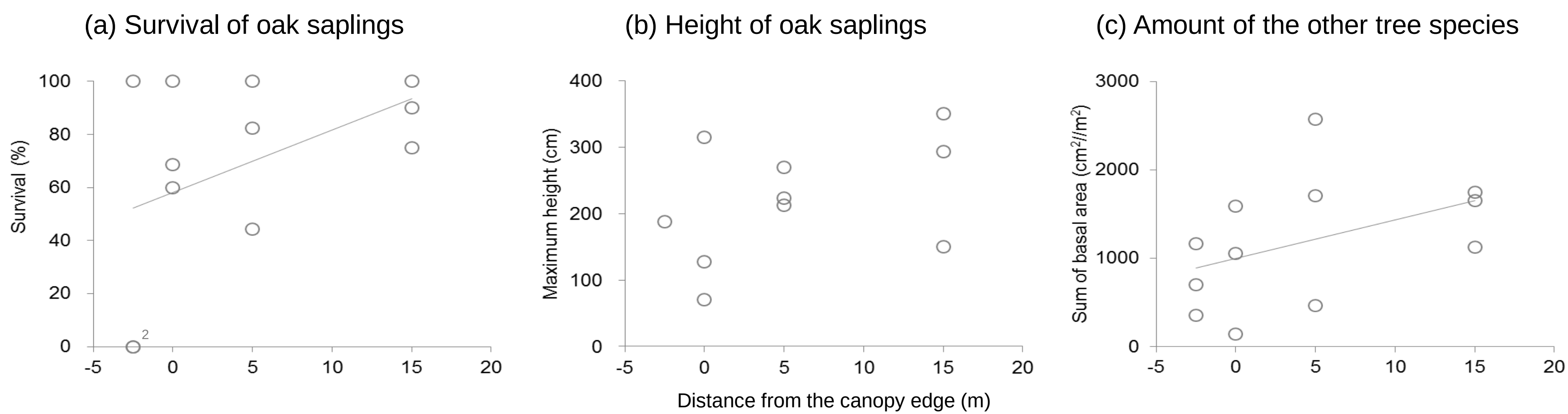

Fig.5. Distance-dependency of oak sapling demography and a related issue in 16 year-old scarification sites. Numeric values in the plates indicate the number of overlapped points. Fitted lines are shown when the generalized linear model selected the distance term(s)