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Effects of surface disturbance and light level on seedling emergence in a Japanese secondary deciduous forest

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Abstract. The effects of soil surface disturbance and light level on seedling emergence were examined by creating experimental conditions differing in soil surface treatment and light level in a temperate deciduous broadleaved secondary forest in central Japan. The results of MANOVA showed that soil surface disturbance exerted a favourable influence upon the seedling emergence of many species. Effect of soil disturbance on total density and number of emerged species was greater than that of a high light level. The interaction between soil surface disturbance and light level revealed significant positive effects for seedling emergence, especially for small-seeded species. The relationship between the percentage of emerged seedlings and seed weight was significantly negative in the soil-surface disturbed and high light level condition, suggesting that minute-seeded species largely depend on both factors for seedling emergence. Both soil surface disturbance and high light level had a positive effect on the number of emerged species, suggesting that these factors contributed to species richness at the stage of seedling emergence.

Keywords: Artificial gap; Broadleaved forest; Gap light index; Seed weight; Soil surface; Species richness.

Nomenclature: Satake et al. (1989).

Abbreviations: PPFD = Photosynthetic Photon Flux Density; GLI = Gap Light Index; MANOVA = Multivariate Analysis of Variance.

Introduction

Gaps are openings created in the forest canopy (Watt 1947; Whitmore 1978), which often induce dynamic phenomena known as gap regeneration (Runkle 1981) or gap dynamics (van der Maarel 1988). Four major modes of gap formation are recognized: gaps formed by dead standing trees, branch-fall, stem-breakage, and uprooting. The different modes of gap formation have different effects on the gap environment and the species composition in a gap (Putz 1983; Putz et al. 1983; Schaetzl et al. 1989). Gaps by the former three modes mainly give rise to improvement of the light environment on the forest floor. The last mode, gaps formed by uprooting, brings about a severe disturbance on the forest floor in addition to the light improvement in the gap. As the soil mass adhering to the roots of uprooted gap makers is generally turned over, uprooting results in pit-mound microtopography. After uprooting, therefore, leaf litter is removed from the forest floor, and mineral soil is exposed, allowing the regeneration of small-seeded species (Hutnik 1952; Koroleff 1954; Putz 1983; Beatty & Stone 1985; Yamamoto 1988; Nakashizuka 1989; Kuuluvainen & Juntunen 1998).

Some experimental studies have tested the effects of gap environments on seedling emergence by artificially creating canopy gaps of different size (e.g. Thompson et al. 1998; Gray & Spies 1997) or by soil disturbance and the improvement of light conditions in natural forests (e.g. Osumi & Sakurai 1997; Yamamoto & Tsutsumi 1985) and in grassland (e.g. Lavorel et al. 1994; Bullock et al. 1995). Although these studies indicated that soil disturbance affected seedling emergence, the effects of light level and the interaction of the two factors have not been completely separated from those of soil disturbance. In addition, the effect of the two factors on species richness and diversity of all vascular plants has not been documented.

Suitable conditions for seedling emergence vary from species to species (e.g. Harper 1977). Seed weight has been investigated as a factor in seedling emergence. (e.g. Salisbury 1942; Baker 1972). Miles (1974) found that the canopy and ground layer both reduced establishment of seedlings. In field experiments using four biennial species, Gross & Werner (1982) demonstrated that two species which required bare ground in order to establish, had smaller mean seed sizes than two species which could germinate and survive in both bare ground and established vegetation. Winn (1985) showed that both seed size and microsite characteristics affected seedling emergence. To date, however, the effects of light levels and forest floor conditions have not been fully resolved.

In this study, we tested the effects of light level and soil disturbance together and separately. To do this, we created several artificial gaps of different sizes in a secondary forest and disturbed the soil surface. We addressed the following questions: 1. Do soil disturbance and light level affect seedling emergence both separately and together? 2. If so, do seedling emergence patterns correlate with seed weight? 3. Do soil disturbance and light level influence species richness and species diversity both separately and together at the emergence stage?

Study site

We conducted this study in a temperate deciduous broadleaved secondary forest located in Kamikawa Village, Niigata Prefecture, central Japan (37° 33' N, 139° 3' E). The elevation of the study area is 450 m a.s.l. and slope inclinations range from 15° to 20°. The climate is classified as Japan Sea type with heavy snowfall (max. 4 m snow depth). The mean annual temperature is 11.7 °C and precipitation averages 2177 mm/yr at the closest meteorological station, Tsugawa (250 m a.s.l.).

The stand was around 50 yr old and had been without management since the 1940s. In the tree layer, *Fagus crenata, Quercus serrata,* and *Q. crispula* co-dominate. Mean tree diameter is ca. 20 cm DBH and mean height is 17 m. Other species include *Acanthopanax sciadophylloides*, *Acer mono*, *Cryptomeria japonica* and *Magnolia obovata*. On the forest floor, the woody species *Aucuba japonica* var. *borealis*, *Lindera umbellata* var. *membranacea* and *Clethra barvinervis*, and the herb species *Carex foliosissima* and *Mitchella undulata* are abundant.

Methods

Artificial gap creation

Between 1993 and 1996, we created eight artificial canopy gaps by felling one or several trees in a clump. We cut the felled trees into logs and brush wood, and removed the material from our quadrats. The gaps ranged from 30 - 380 m^2 in area. The size was calculated assuming gap shape to be an ellipse and then measuring the maximum diameter and the right-angled diameter at the mid-point of the maximum diameter. The edge of the gap was defined as the vertical projected edge of the canopy overhead. The range of gap sizes matches that of natural canopy gap creation, which produces gaps up to ca. 400 m^2 in climax *F. crenata* forests (Yamamoto 1989).

Field methods

Because we created the artificial gaps one to three years before the experiment started, buried viable seeds in the gaps might have already germinated. We therefore compared the floristic composition of buried viable seeds in the soil of the artificial gaps and of the closed canopy around the gaps.

We collected 60 soil samples (20 cm × 20 cm × 5 cm) each from artificial gaps and closed forest around the gaps site in early June 1997 after germination in the spring. There are buried viable seeds of almost all species and 80 % of that seed number in the top 5 cm of the soil (Nakagoshi 1981). Nakagoshi & Suzuki (1977) reported that total a soil volume of 20 l was sufficient for seed bank studies. Our soil samples were spread in barrels (30 cm × 50 cm × 5 cm) and placed in a greenhouse and kept moist. Emerged seedlings were observed and recorded once a week for approximately three months.

We prepared research quadrats differing in ground surface and canopy cover conditions in May 1997. In each gap and under the closed canopy around each gap, we established 10 quadrat pairs (1 m × 0.5 m each). A pair consisted of two quadrats, one with the soil surface disturbed and the other with it intact, placed side by side (Fig. 1). In the disturbed quadrats, we removed leaf litter and scarified the soil with hoes until the mineral soil layer was exposed (soil-disturbed treatment). We left the other quadrats in their natural state, which was usually covered with leaf litter (control). The total number of quadrat pairs was 160 (i.e. the total number of quadrats was 320). We randomly assigned these quadrat pairs in the gap and under the closed canopy, however avoiding the spots piled up with logs. Though these quadrat pairs are grouped by gap as they are, we used them as independent treatments, evaluating the light level in each quadrat. We therefore treated each quadrat pair as a separate observation.

In order to estimate the light level in the quadrats, we took a hemispherical photograph with a fish eye lens (Nikkor, 8 mm, F 2.8 S) at the centre of each quadrat pair, at a height of 1 m above the ground surface. The hemispherical photographs were transformed into computer data with an image scanner; photosynthetic photon flux density (PPFD) was estimated using the software HEMIPHOT (ter Steege 1993). We calculated the Gap Light Index (GLI; *sensu* Canham 1988) which was obtained from dividing the PPFD in each quadrat pair by that in open land as calculated by HEMIPHOT.

We identified all of the current year's seedlings and recorded their numbers for each species in each quadrat in early July and again in the middle of September. Though the germination seasons differed among the

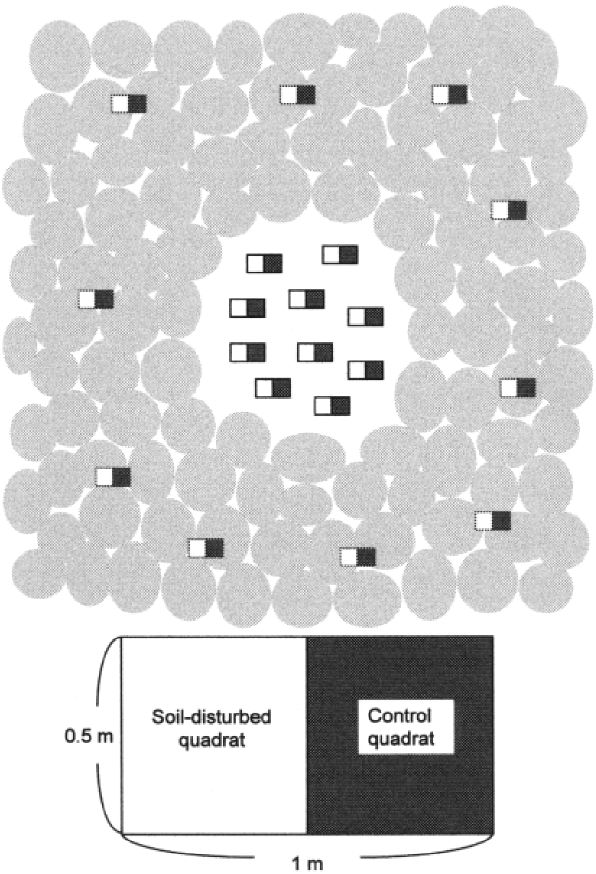

Fig. 1. Schematic diagram of a gap showing the 1 m × 0.5 m pair quadrats in the gap and under the closed canopy.

species, most species in this forest seemed to have finished their germination by early July, and mortality of the seedlings before July is usually very low (Kobayashi & Kamitani unpubl.). However, some species continued to germinate even after this point, so in our analyses, we employed the larger number from our two investigations as the emerged number of each species.

In order to correlate the germination traits to seed size, we collected ca. 10 seeds for each species in and around the study area, and dried and weighed them in the autumn of 1997. We could not obtain seeds for two species, *Carex foliosissima* and *Petasites japonicus*, of the 14 species treated in our analyses. Therefore, for *Carex foliosissima*, we employed data from the closely related species *Carex dolichostachya* (Nakagoshi 1985), and for *Petasites japonicus* we weighed the seed samples obtained from herbarium specimens (sample no. 185748) at the Faculty of Science of Niigata University.

Data analysis

To determine if the numbers of species and seedlings emerged from the soil samples were different between the gap and the closed canopy, we used the Mann-Whitney *U*-test. Also, we employed Kendall's τ-coefficient as an index of similarity in species composition between the gap and the closed canopy (Ghent 1963).

We distinguished two categories of soil surface treatment (disturbed/control) and of light level (higher/lower) and combined the two divisions to obtain four categories: disturbed/higher light level, disturbed/lower light level; control/higher light level, control/lower light level. Light level categories were based on mean GLI, as calculated for every quadrat pair, ranged from 1.0 to 59.3 %, with a mean of 12.5 %. Higher and lower light levels were defined as GLI ≥ 12.5% and GLI < 12.5%, respectively. Fig. 2 shows the distribution of quadrats with high and low light levels in gap- and closed canopy quadrats.

Using multivariate analysis of variance (MANOVA), we analysed the number of seedlings of the most abundant 14 species and the number of emerged seedling species as dependent variables, and the two factors, soil surface treatment and light level, as independent variables. As measures of species diversity and equitability for emerged seedlings, we used the Shannon-Wiener index (*H'*) and Pielou's index (*J'*), respectively; we based the calculation of these indices on the importance values based derived from the seedling numbers per species under the four conditions above. We also analysed the disproportionality of emergence to particular conditions in relation to the seed weight of the species, using correlation analyses. The seed weights were transformed into logarithmic data prior to statistical analysis. We used the SPSS statistical package (SPSS Inc. 1993) for the statistical tests.

Results

Buried viable seed composition

Both the number of emerged species and the number of emerged seedlings per soil sample were not significantly different between the gap and the closed canopy (Table 1). The number of emerged species per sample was neither significantly different between the sites. Kendall's rank correlation analysis, an index of similarity of species composition, showed a significant correlation between the gaps and the closed canopy around the gaps ($\tau = 0.483$, $p = 0.004$). The similarity between seed banks in the forest and gap plots shows that the results on seedling emergence were probably not the result of differences in seed availability.

Table 1. Results of surveying seedling emergence for buried viable seeds in the gap and the closed canopy.

	Gap	Closed canopy	Probability
No. of soil samples	60	60	
No. of species emerged (per soil sample)	3.16 ± 2.14[a]	3.57 ± 2.47	0.325
Similarity in species composition (Kendall's τ)	0.483		0.004

[a] Mean and standard deviation.

Effects of soil surface disturbance and light level on seedlings

We recorded the seedling emergence of 29 woody and 25 herb species. There were three annual herb species from the *Asteraceae*: *Bidens frondosa*, *Erechtites hieracifolia* and *Crassocephalum crepidioides* – which do not usually occur in natural beech forests.

The surface-disturbance treatment significantly influenced the seedling emergence of almost all species (Table 2). For 12 species, the number of emerged seedlings was significantly higher in the soil-disturbed treatment. By contrast, the seedlings for only one species, *Acer amoenum* var. *matsumurae*, were more abundant in the control. The effect of soil surface disturbance on seedling emergence was higher than that of light level. For six species, the number of emerged seedlings was significantly higher under the higher light level. There was no species with significantly more seedlings under the lower light level.

The interaction of the two factors was important for five species that also responded significantly to the soil surface disturbance and the higher light level considered separately. *M. australis* was effected by both factors but not by the interaction of the two factors. *L. umbellata* var. *membranacea* showed a different result; the interaction of the two factors was significant, although neither single factor was effective alone.

Soil disturbance, light level and the interaction of the two factors significantly affected total density (Table 2). Although standard deviations were high, soil disturbance increased total density twenty-fold in the higher light conditions and twentyfive-fold in the lower light conditions. The higher light level increased total density three-fold in the soil disturbed conditions and four-fold in the control.

The number of emerged species per quadrat were positively influenced by both soil surface disturbance and light level, as well as by the interaction of the two factors (Table 2). Soil disturbance increased the number of species ten-fold in high light conditions and six-fold in low light conditions. Higher light increased the number of emerged species by a factor of about two-fold in both control and soil disturbed situations. Total number of species in the soil-disturbed quadrats with higher light level was highest in all cases. Thus, the species richness of the regenerated community was increased both by soil surface disturbance and by light improvement. Both H' (species diversity) and J' (equitability) were lower in the soil-disturbed treatment than in the control. In the soil-disturbed treatment, H' and J' were lower under higher light level than under lower light level. In the soil-disturbed quadrats with higher light level both indices had their minimum values.

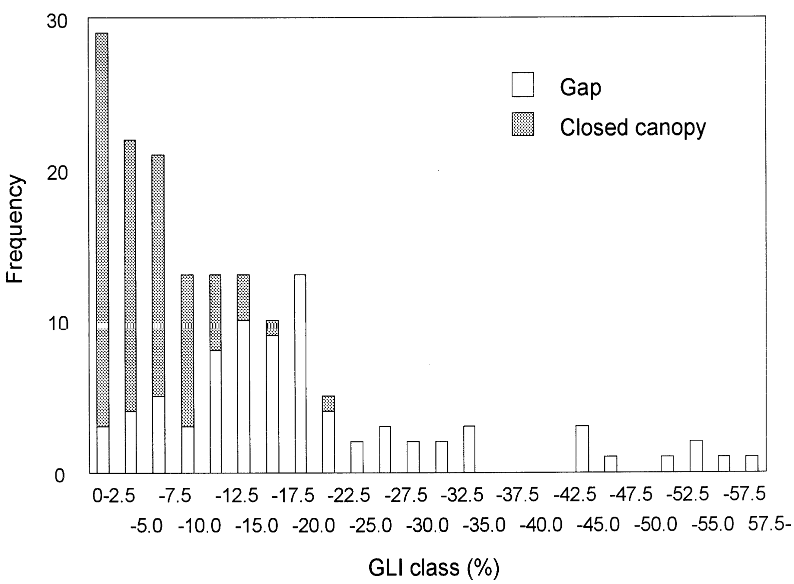

Fig. 2. Frequency distribution of GLI in the gaps and the closed canopy around the gaps.

Table 2. The effects of soil surface disturbance and light level on seedling emergence analysed by MANOVA. Seedling density for the most abundant 14 species and number of emerged species are given.

Species	Density (per quadrat)[1]				MANOVA[2]		
	Dh	Dl	Ch	Cl	T	L	T × L
Acer amoenum var. *matsumurae*	0.02 ± 0.13[3]	0.01 ± 0.10	0.06 ± 0.25	0.05 ± 0.22	*	ns	ns
Actinidia arguta	0.23 ± 0.53	0.33 ± 0.81	0.06 ± 0.31	0.04 ± 0.25	**	ns	ns
Aralia elata	0.58 ± 1.45	0.56 ± 1.08	0.02 ± 0.13	0	***	ns	ns
Betula grossa	0.37 ± 0.66	0.33 ± 0.86	0	0.02 ± 0.13	***	ns	ns
Callicarpa japonica	0.42 ± 0.78	0.36 ± 0.68	0.03 ± 0.18	0	***	ns	ns
Carex foliosissima	13.16 ± 28.48	4.06 ± 8.23	0.13 ± 0.59	0.02 ± 0.14	***	**	**
Clethra barvinervis	6.61 ± 11.20	1.61 ± 4.57	0.13 ± 0.66	0.03 ± 0.30	***	***	***
Erechtites hieracifolia	0.35 ± 0.73	0.11 ± 0.35	0.06 ± 0.25	0	***	***	*
Lindera umbellata var. *membranacea*	0.05 ± 0.22	0.14 ± 0.38	0.08 ± 0.33	0.03 ± 0.17	ns	ns	*
Morus australis	0.11 ± 0.32	0.02 ± 0.14	0.02 ± 0.13	0	**	**	ns
Petasites japonicus	0.15 ± 0.47	0.03 ± 0.17	0	0	***	*	*
Stachyurus praecox	0.95 ± 1.24	0.68 ± 1.19	0	0.01 ± 0.10	***	ns	ns
Vitis coignetiae	0.35 ± 1.12	0.23 ± 0.82	0.06 ± 0.25	0.03 ± 0.17	**	ns	ns
Weigela hortensis	2.74 ± 6.70	0.49 ± 1.54	0.02 ± 0.13	0.01 ± 0.10	***	**	**
Total density (per quadrat)	30.56 ± 34.87	9.78 ± 12.62	1.55 ± 2.51	0.38 ± 0.79	***	***	***
Number of species (per quadrat)	5.66 ± 3.10	3.58 ± 2.50	0.97 ± 1.43	0.35 ± 0.73	***	***	**
Total number of species	47	32	27	21			
Number of quadrats	62	98	62	98			
H' (Shannon-Wiener index)	2.10	2.16	2.86	2.86			
J' (Pielou's index)	0.55	0.62	0.87	0.94			

[1]D: Soil surface disturbance; C: control, h: higher light level, l: lower light level; [2]T: treatment of soil surface, L: light level; [3]Mean and standard deviation. *, ** and *** indicate significance levels of < 0.05, < 0.01 and < 0.001, respectively; ns = non significant.

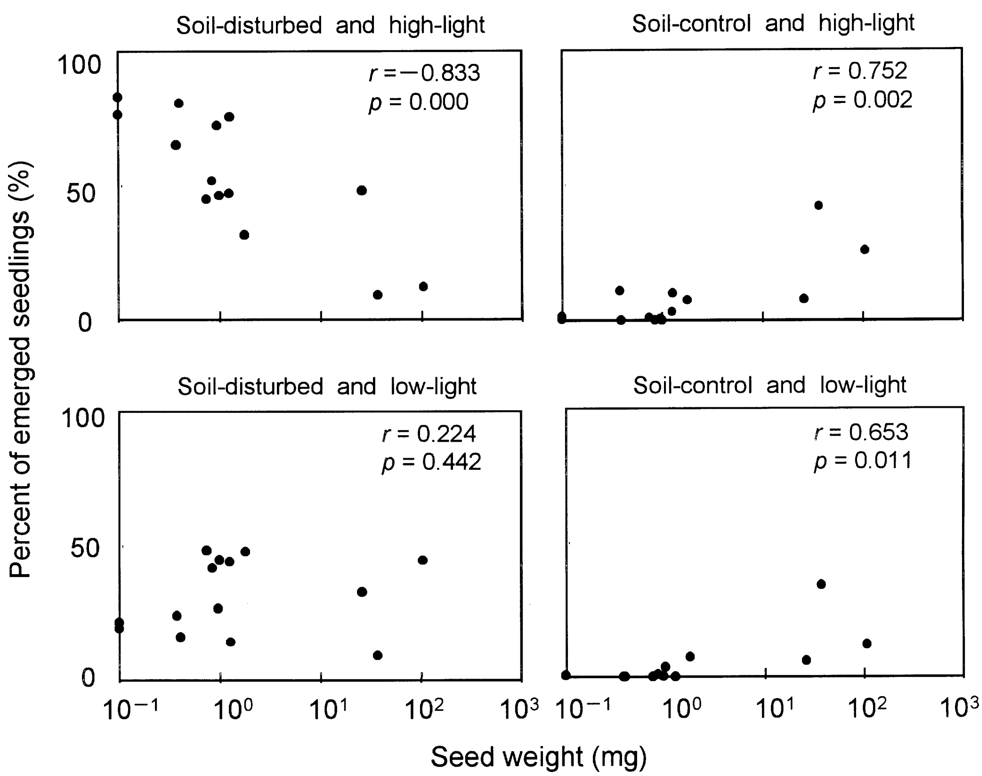

Fig. 3. Relationships between emergence pattern of seedlings and seed weight for the 14 abundant species following from Table 2 based on their occurrence in 320 quadrats. Emergence for each condition was related to total emergence and correlated to seed weight (logarithmic scale). Pearson's correlation coefficient (r) and probability (p) are indicated.

Table 3. Groups of species and their seed weight and growth form for the 14 abundant species according to the MANOVA results (Table 2). **A.** Species affected positively by both soil surface disturbance and light level and the interaction of the two factors. **B.** Species affected positively by soil surface disturbance. **C.** Species not affected.

	Seed weight (mg)	Growth form
Group A		
Petasites japonicus	0.05	Herb
Weigela hortensis	0.10	Shrub
Clethra barvinervis	0.10	Shrub
Erechtites hieracifolia	0.38	Herb
Carex foliosissima	0.96 [1]	Herb
Morus australis[2]	1.28	Tree
Group B		
Aralia elata	0.75	Shrub
Stachyurus praecox	0.85	Shrub
Betula grossa	1.00	Tree
Callicarpa japonica	1.26	Shrub
Actinidia arguta	1.79	Vine
Vitis coignetiae	26.07	Vine
Group C		
Acer amoenum var. *matsumurae*	37.05	Tree
Lindera umbellata var. *membranacea*	105.93	Shrub

[1]Data for closely related species; [2]effected by both factors but not by their interaction.

The relationship between the percentage of emerged seedlings and seed weight under different conditions

In the soil-disturbed treatment, the percent of emerged seedlings had a significant negative correlation with seed weight under the higher light condition ($r = -0.833$; $p = 0.000$) (Fig. 3). However, the correlation was not significant in the disturbed soil under the lower light level. Without soil surface disturbance, the percent of emerged seedlings correlated positively to seed weight, irrespective of light conditions.

The 14 species analysed in this study were divided into three groups according the their responses to soil surface disturbance and light level (Table 3). Group A consists of the species whose seedlings were positively influenced by both the surface disturbance and the higher light level; they are also effected positively by the interaction of the two factors except for *Morus australis*. Group A species were herbs and most had small seeds. Group B consisted of species whose seedlings were positively influenced by the soil-disturbed treatment, but not by the higher light level. These species had also light seeds, but heavier than those of Group A. Group C includes the two woody species with heavy seeds.

Discussion

Soil surface disturbance exerted a positive influence upon seedling emergence of all species except *A. amoenum* var. *matsumurae* and *L. umbellata* var. *membranacea*, two species with the largest seeds in this study. The occurrence of a litter layer prevents seeds from reaching the soil surface and reduces germination and seedling establishment (Koroleff 1954; Miles 1974; Hamrick & Lee 1987). Soil surface disturbance, therefore, is an important factor for seedling emergence in small-seeded species: e.g. *Betula papyrifera* (Hutnik 1952, 1954; Kinnaird 1974; Marquis 1965), *B. alleghaniensis* (Marquis 1965), *Chamaecyparis lawsoniana* (Zobel 1980), *C. obtusa* (Yamamoto & Tsutsumi 1985; Yamamoto 1988), *B. platyphylla* var. *japonica* (Morita 1995) and *B. maximowicziana* (Osumi & Sakurai 1997).

The effect of a higher light level, in combination with soil surface disturbance, was also positive for several species with small seeds. The higher light level as such, however, was not as conspicuous as that of soil surface disturbance, and tended not to act independently (cf. Kneeshaw et al. 1998). This suggests that the effect of soil surface disturbance is larger and that a high light level is of secondary importance, i.e. it affects seedlings emerged after disturbance.

Seed weight and microsite determined the seedling emergence pattern. The significant negative correlation between the percent of emerged seedlings and seed weight suggested that minute-seeded species depend for their seedling emergence on both soil surface disturbance and high light level. Miles (1974) examined the relationship between seed weight and seedling establishment under conditions with the canopy removed and the soil bared, but there was no correlation. The inconsistent results may be due to differences in the seed weight range treated in his and our studies; in our forest experiments we treated a wider range of seed weights (0.05 - 105.93 mg) than he did (0.09 - 9.37 mg). Our results were rather consistent with previous experimental studies which revealed that both seed mass and microsite characteristics affect seedling emergence. Winn (1985) showed that large seeds had a higher percentage emergence and also that litter and herbaceous cover inhibited seedling emergence in woodland habitats. Reader & Buck (1991) also showed the potential seedling establishment was directly related to seed mass of 13 species on experimentally created mounds in an abandoned pasture.

The positive correlation between seed weight and seedling emergence when the soil surface was not disturbed suggested that species with large seeds are more dependent on high light conditions rather than on soil disturbance for their emergence. Large seeds are advantageous having sufficient energy storage to enable the seed to germinate (Salisbury 1942). Also, large seeds have less stringent requirements for their emergence than small seeds (Winn 1985).

Nakashizuka (1989) reported that both species richness and species diversity (H' and J') of seedlings were higher in sites with soil disturbance, such as mounds and fallen boles by uprooting, than in sites without soil disturbance in a temperate old-growth forest. In our study, the indices of species diversity of emerged seedlings, H' and J', were not positively influenced by either soil surface disturbance or high light level, though the number of species per quadrat was affected by the two factors combined. This result is explained by the extreme dominance of a few species. In particular, *C. foliosissima* and *C. barvinervis* had a large number of seedlings which emerged in the soil-disturbed treatment. On the other hand, the sites without soil disturbance did not have such extreme dominants, and thus the equitability (J') and Shannon-Wiener indices (H') were higher than in the disturbed sites.

Abe et al. (1995) suggested that differentiation of the regeneration niche contributes to the maintenance of species diversity in an old-growth temperate deciduous forest. In the present study, species richness increased both by gap creation and by soil disturbance, because species with a large number of small seeds (Mizui 1991; Salisbury 1942) which do not usually emerge under dark conditions and on a stable forest floor, were encouraged to germinate. Though the survival and competitive results of these species after seedling establishment is not clear, we can conclude that differentiation of the regeneration niche with different types of disturbances contributes to species richness, at least at the emergence stage.

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