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Seedling establishment of deciduous trees in various topographic positions

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Abstract. We investigated the effect of topography-related environmental factors (i.e., ground-surface stability and soil moisture) on seedling establishment of 8 deciduous tree species. A field experiment was carried out using canopy species, which were classified into 3 groups based on the spatial distribution of adult trees (ridge, slope and valley). Demographic parameters were compared among species during the early stage of seedling establishment among 3 topographic positions in combination with gap and canopy conditions. The percentage of emerging seedlings tended to be lower on the ridge irrespective of the adult topographical distribution patterns. There was no clear trend in seedling emergence among the species groups classified by their spatial distribution. Seedling survival during 2 growing seasons was significantly different among species, topographic positions and light conditions. On the ridge, seedlings of the species dominating ridge tops had greater survival than those of other species, probably due to differences in demand for soil moisture. On the slope, frequent physical damage caused by surface material movement was observed and some species showed greater adaptability to the disturbed slope habitat. Survival of all seedlings was highest in the valley plots. Light conditions were the critical factor for seedling survival in some species. The results of this study suggest that topography creates diverse habitats for the establishment of tree seedlings. In addition to soil moisture, surface material movement may be a significant factor affecting seedling establishment.

Keywords: Erosion; Forest dynamics; Ground-surface disturbance; Seedling emergence; Seedling survival.

Nomenclature: Satake et al. (1981-1982, 1989); Iwatsuki (1992).

Introduction

Topographic variation in soil moisture, soil fertility gradients and landslide scars has been correlated with species composition of communities (Hack & Goodlett 1960; Tanaka 1985; Harrison et al. 1989; Kikuchi & Miura 1991; Basnet et al. 1992; Burns & Leathwick 1996; Tanouchi 1996). Recently, micro-scale ground-surface disturbances have been emphasized as a principal factor forming the vegetation pattern in hilly regions (Hunter & Parker 1993; Kikuchi & Miura 1993; Sakai & Ohsawa 1994). Hara et al. (1996) suggested that the difference in stability of the ground surface was likely to be the major cause of the observed differences in stand structure within a slope from the ridge to the valley bottom. Nevertheless, the mechanism of vegetation differentiation is still obscure, because studies usually only focus on static relationships between environmental measurements and the abundance or relative dominance of adults in each species.

In the life histories of trees, the most drastic population changes occur during seed and seedling stages (Harper 1977; Harcombe 1987). Thus, the population dynamics of forest tree species have been considered to be characterized mostly during these stages (e.g. Augspurger 1984; Streng et al. 1989; Schupp 1990; De Steven 1991; Jones et al. 1994; Shibata & Nakashizuka 1995; Seiwa 1998). Seedling dynamics across topographic positions might help clarify the role of the establishment process in topographic patterns. Tree seedling dynamics are affected by various environmental factors such as soil moisture (e.g. Potvin 1993; Ashton et al. 1995), micro-scale disturbance (Clark & Clark 1989; McCarthy & Facelli 1990; Kobayashi & Kamitani 2000), canopy cover (Streng et al. 1989; Titus 1990; Harrington 1991; Crow 1992; Titus & del Moral 1998; Denslow & Guzman 2000) and deep leaf litter layers (Clark & Clark 1989; Molofsky & Augspurger 1992;

Facelli 1994; Seiwa & Kikuzawa 1996; Seiwa 1997). Other biotic factors such as herbivores (Wada 1993; Ida & Nakagoshi 1996; Forget 1997; Seiwa 1998), fungal infection (Sahashi et al. 1994; Forget 1997; Seiwa 1998) and inter-species competition (Nakashizuka 1988; Callaway 1992) have also been reported to affect seedling demography.

Although these environmental factors sometimes vary according to topographic position (Tamura 1969; Conacher & Dalrymple 1977), little attention has been paid to the relationship between topography and seedling dynamics (but see Ashton et al. 1995). In this study, we investigated the effect of topography-related environmental factors, i.e. ground-surface stability and soil moisture, on seedling establishment of 8 deciduous canopy species in a field experiment. The study was conducted in a forest that has no clear 'seedling bank' of suppressed seedlings (Hirabuki et al. 1992). In this condition, natural seedling establishment after gap formation may be important for forest dynamics. In the field experiment, the effect of light conditions in artificial gaps or under closed canopies at different topographic positions on seedling establishment was also evaluated. Seeds were introduced to evaluate species establishment success after seed dispersal. We addressed 2 questions: 1. To what extent does seedling demography vary among species and topographic positions? 2. Which, if any, of the factors was correlated with differences in seedling survival among topographic positions?

Material and Methods

Study area and experimental design

This study was conducted in a broad-leaved deciduous forest in the Experimental Forest of Tohoku University in northeastern Japan (38° 48' N, 140° 45' E, 480–530 m a.s.l. see Fig. 1). Mean monthly temperature is

highest in August (23.0 °C) and lowest in January (−1.8 °C). Mean annual precipitation is 2140 mm and the maximum snow depth is 165 cm (Hirabuki et al. 1992). Brown forest soil covers the study area and the parent rock is tuff. Ca. 168 ha have been protected from human activities for more than 50 yr as a forest reserve.

The experimental site faces south (Fig. 1) and was established at 3 topographic positions (ridge, slope and valley positions) in combination with 2 light conditions (gap and canopy). The gap plots were created by cutting all trees, shrubs and understorey dwarf bamboo within a radius of 6 m in October 1995. A pair of gap and canopy plots was established within 100 m of each another in each of the 3 topographic positions. Three replicated plots were established for all combinations of topographic positions and light conditions, giving a total of 18 plots (Fig. 1). In each plot, 3 rectangular-frames (4.4 m × 0.7 m) were established and divided into 6 quadrats (0.4 m × 0.7 m), which were separated by 0.4-m wide strips between quadrats.

The ridge plots (ridge) were located on a gentle (0–14°) ridge top with deep fine soils of sand or silt. The canopy tree layer was dominated by *Quercus serrata*, *Q. crispula* and *Fagus crenata*, and also included *Carpinus laxiflora*. In the understorey layer *Rhododendron obtusum* var. *kaempferi*, *Elliottia paniculata* and *Sasa palmata* were abundant. The slope plots (slope) were located on steep lower slopes (32–46°) near the valley bottom with a thin soil mixed with coarse gravel. The canopy layer was dominated by *Ulmus davidiana* var. *japonica* and *Magnolia obovata*. The understorey layer was sparse. The valley plots (valley) were located on a valley bottom (0–5°) with thick sandy soil. Canopy trees were *Alnus japonica*, *Ulmus davidiana* var. *japonica* and *Pterocarya rhoifolia*. The understorey layer was covered by tall herbs (e.g. *Aconitum japonicum*). Relationships between vegetation and topography near the study area are described in detail by Nagamatsu & Miura (1997).

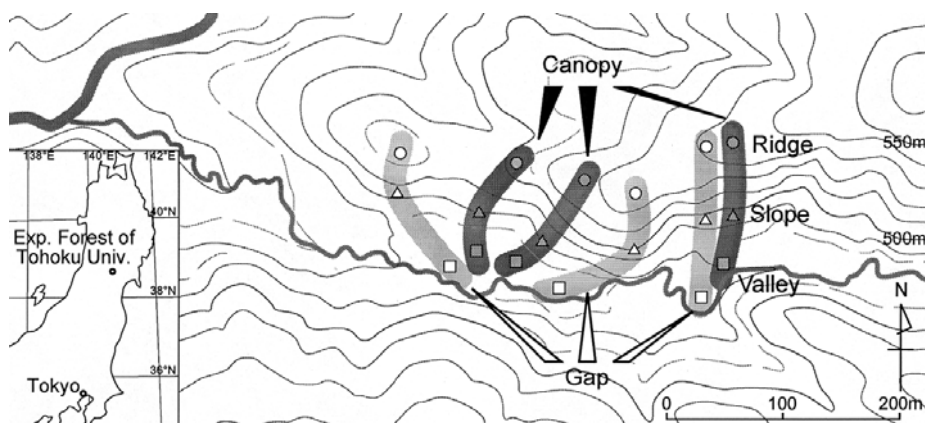


Fig. 1. Map of the study area. Pairs of gap and canopy plots on the ridge (○), slope (△) and valley (□) are arranged in 3 replicated plots. Gap plots were artificially created.

Tree species common in this forest were selected for the experiment: *Acer mono* var. *marmoratum* f. *dissectum* (Abbr. *Acer mono*), *Alnus hirsuta*, *A. japonica*, *Carpinus laxiflora*, *Quercus serrata*, *Q. crispula* and *Zelkova serrata*. The species studied were classified into 3 groups based on the spatial distribution of the adult trees along topographic positions in the study area using the vegetation data in Hirabuki et al. (1992). In the 25 stand data, species whose density was significantly higher on and around the ridge ($p < 0.05$, binomial test, see details in Hara et al. 1996) were classified into Group A (*Q. serrata*, *Q. crispula* and *C. laxiflora*; Table 1). Species whose density was higher on and around the lower slope and on the valley bottom became Group B (*Z. serrata* and *A. japonica*). Species that were not abundant and their density was not significantly different between the ridge and lower slope - valley bottom were Group C (*A. mono* and *A. hirsuta*). *Idesia polycarpa*, which does not occur naturally in the study area, was also subjected to the experiment because it was shown to have a distinctive distribution pattern in relation to topography (Group B) in a previous study conducted near this area (Nagamatsu & Miura 1997).

Seeds of each species (except *Q. serrata* and *Q. crispula*) were collected before and just after seed dispersal in 1995 from the deciduous broad-leaved forest in the reserve. Seeds (acorns) of *Q. serrata* and *Q. crispula* were collected in 1996, since these species produced no seeds in 1995. Seeds of *I. polycarpa* were collected at the Botanical Garden, Tohoku University (ca. 50 km south-east of the study area). Seeds having insect or fungal damage were discarded. Seeds were floated in water to eliminate non viable ones and were stored in a refrigerator (5 - 7°C) during winter.

Field experiment

To avoid severe seed predation by mammals during winter (Kikuzawa 1988; Seiwa & Kikuzawa 1996) and

seed drifting with melting snow all the seeds were sown in early spring, immediately after snow had melted. After sowing quadrats were covered by 0.5 cm × 0.5 cm mesh wire nets and buried to a depth of 5 cm to prevent seed removal by small mammals and jays.

Natural gaps, where seedling establishment actively occurs, are not only created by canopy disturbances but also by ground-level ones e.g. uprooting (Putz 1983; Nakashizuka 1989), slope failure (Hunter & Parker 1993) and flooding (Jones et al. 1994), which usually remove the A_0 horizon (including litter and humus). To simulate such natural conditions, we removed the A_0 horizon before sowing.

A known number of seeds (Table 1) of 6 species were sown in each quadrat in late April 1996 and in early May 1997 for *Q. serrata* and *Q. crispula* immediately after the snow had melted. Net-covers were removed after most of the seedlings had emerged (21 June 1996 for 6 species and 25 June 1997 for *Q. serrata* and *Q. crispula*). The number of seeds sown was determined by considering the seedling size of each species so as to reduce mutual shading among seedlings during the census. Control quadrats that received no experimental seed input had been established previously to monitor background seedling emergence, which was shown to be negligible.

Emergence and survivorship censuses were initiated on 1 May 1996 and were repeated at 2-wk intervals during the first growing season and monthly during the second season. Seedling emergence was defined as the appearance of cotyledons for 6 species or epicotyls for *Q. serrata* and *Q. crispula* above the soil surface. Naturally growing herbs were removed by hand during the study period to reduce the variation of inter-specific competition among plots. Thus the effects of neighbouring plants on seedling establishment among topographic positions were excluded. The causes of seedling mortality were classified into 4 categories: (1) herbivory, (2) withering, (3) physical damage and (4) unknown. Seedlings that died with symptoms such as a rotten stem or brownish body were diagnosed as (2). Seedlings whose roots were entirely exposed by soil erosion or killed by fallen branches or gravel were categorized as (3).

The physical environment (canopy openness, material movement on ground surface and soil moisture) were monitored at each replicated plot. To estimate light conditions for emerged seedlings, hemispherical canopy photographs were taken at a height of 0.5m above the ground at the centre of each replicated plot with a fish eye camera (Nikon, F8 mm) on 21 July 1996. From the photographs, canopy openness in each replicated plot was calculated by the ratio of the open part of the canopy of the entire hemispherical area to the closed part. The material movement on the ground surface in each repli-

Table 1. The 8 deciduous tree species used in this experiment. Species dominant on the ridge were classified into Group A. Those dominant on the lower slope and valley bottom were Group B. Species whose density was not different among topographic positions were in Group C (see text for details).

Species	No. of seeds (m ⁻²) per plot	Seed dry weight (mg)	Distribution type
<i>Quercus serrata</i>	107	1833.3	A
<i>Quercus crispula</i>	107	3308.2	A
<i>Carpinus laxiflora</i>	3784	6.2	A
<i>Zelkova serrata</i>	107	14.6	B
<i>Idesia polycarpa</i>	1606	2.2	B
<i>Alnus japonica</i>	6120	3.4	B
<i>Acer mono</i>	2124	81.9	C
<i>Alnus hirsuta</i>	14 844	1.4	C

cated plot was estimated by the amount of sand, gravel and plant litter collected by surface-material traps (open-top boxes 50 cm × 20 cm × 25 cm in length, width and height, respectively). These boxes were embedded in the ground so that the top of each box was level with the ground surface. Three traps were randomly established for each replicated plot, and a total of 54 traps were established in this experiment. Material in each trap was collected every 3 months from May 1996 to November 1997. Materials were dried (105°C, 16 hr) and dry weight measured. To estimate soil moisture, we collected 3 samples of 100 cm³ soil from the upper 4 cm of the substratum for each replicated plot every month and every 2 months during the growing season (May to October) in 1996 and 1997, respectively. All samples were taken a few days after a sufficient rain. Soil water content (g) was to be 1500 kPa water retention (pF 4.2) by the centrifugation method (Anon. 1986).

Data analyses

Canopy openness, material movement and soil moisture were measured in all the replicated plots. The consistency of each factor within 3 replicated plots in 6 combinations of 3 topographic positions and 2 light conditions was checked using 1-way ANOVA. In canopy openness, consistency was estimated by Bartlett's test for homogeneity of variances since it had no repeated measurement in each replicated plot. Then, the effects of topographic position and light condition for 3 environmental factors were evaluated by 2-way ANOVA with replication based on the mean value of the 3 samples in each plot.

The effects of species, topographic position and light condition on the emergence ratio were analyzed by 3-way ANOVA after arcsine transformation (Sokal & Rohlf 1995). Then, the effects of topography-light combinations were examined in more detail in each species by 1-way ANOVA and multiple comparison tests (Tukey-Kramer test).

The seedling survival ratio at the end of each grow-

ing season were also analyzed by 3-way ANOVA after arcsine transformation (Sokal & Rohlf 1995) and the effects of species, topographic position and light condition were examined. Kaplan-Meier analysis, a non-parametric survival analysis, was conducted to evaluate the complex relationship between seedling survival curves and combination of topographic positions and light conditions in each species. Multiple comparisons were conducted in pairs of plots using the logrank test. Significance level was controlled by the Sequential Bonferroni test (Rice 1989). The computer software JMP (Anon. 1995) was used for these analyses.

Results

Environmental conditions

There was no significant difference in either material movement or soil moisture ($p > 0.05$; 1-way ANOVA) among the 3 replicated plots in each combination of topographic positions and light conditions. Neither was the variance of canopy openness in each plot significantly different ($p > 0.05$; Bartlett's test for homogeneity of variances). These results showed that the 3 replicated plots had similar environmental conditions in each combination of topographic position and light condition.

Canopy openness in a growing season was significantly greater in the gap than the canopy but not different among topographic positions (Table 2, Fig. 2a). The amount of material movement increased in the order of ridge, valley, slope under each light condition and was larger under the canopy than in the gap in each topographic position (Fig. 2b). Soil moisture throughout the 2 growing seasons differed among topographic positions, being highest on the valley and lowest on the ridge, but was not different between the gap and canopy conditions (Fig. 2c). There was no interaction between topography and light conditions in canopy openness, material movement and soil moisture (Table 2).

Table 2. Results of 2-way ANOVA for canopy openness, amount of material movement and soil moisture factors.

Source		d.f.	Mean square	F-value	p
Canopy openness	Topographic position	2	2.112	0.192	0.828
	Light condition	1	624.222	56.627	< 0.001
	Topographic position × light	2	9.757	0.885	0.438
Material movement	Topographic position	2	13.032	36.315	< 0.001
	Light condition	1	5.090	14.184	0.002
	Topographic position × light	2	0.266	0.741	0.477
Soil moisture	Topographic position	2	4372.003	302.897	< 0.001
	Light condition	1	1.402	0.097	0.755
	Topographic position × light	2	10.108	0.700	0.497

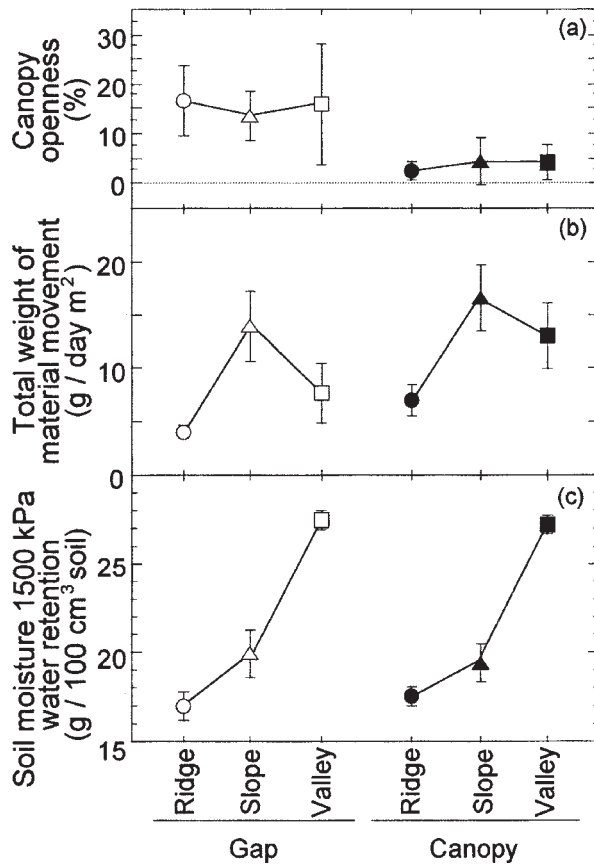


Fig. 2. Three environmental factors for each plot: (a) canopy openness after leaf expansion (June 1996), (b) amount of ground-surface material movement captured by traps and (c) soil moisture content. Data are means for 2 growing seasons in (b) and (c). Error bars in the figure indicate 95% confidence interval.

Seedling emergence

The ratio of seedling emergence ($100 \times$ number of emergence / number of seeds sown) was significantly different both among species and topographic positions, but not different with the light condition (Table 3). All 2-way and 3-way interactions were also significant.

Neither *Quercus serrata* nor *Quercus crispula* had any difference in seedling emergence among the 6 combinations of topographic positions and light conditions, and it was greater than in the other species in each combination (Fig. 3). In the other species studied, seedling emergence tended to be lowest on the ridge and highest on the valley under both gap and canopy conditions regardless of the species group. *Zelkova serrata* was an exception in that seedling emergence was higher on the slope under canopy conditions.

Table 3. Results of 3-way ANOVA on the ratio of seedling emergence ($100 \times$ number of emergence / number of seeds sown) of the 8 deciduous tree species.

Source	d.f.	Mean square	F-value	p
Species	7	1.873	188.298	< 0.001
Topographic position	2	0.426	21.410	< 0.001
Light condition	1	0.006	0.651	0.422
Spp. \times topo.	14	0.333	2.391	0.007
Spp. \times light	7	0.289	4.156	< 0.001
Topo. \times light	2	0.213	10.715	< 0.001
Species \times topo. \times light	14	0.473	3.398	< 0.001

Seedling survival

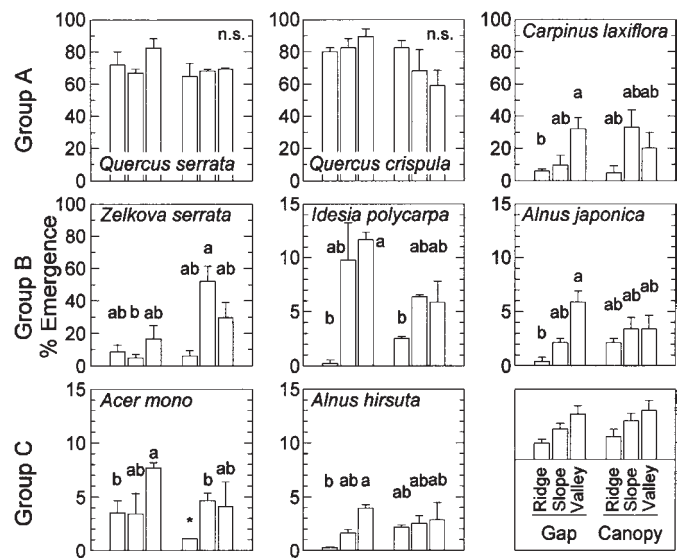
Seedling survival at the ends of both growing seasons was significantly different among species, topographic positions and between light conditions (Table 4). There were interactions among species, topography and light conditions in seedling survival curves (Table 4, Fig. 4).

In Group A species (*Quercus serrata*, *Q. crispula* and *Carpinus laxiflora*, which are dominant on the ridge) under both light conditions, seedling survival rates were same or higher on the ridge compared to the slope or valley (Fig. 4). By contrast, the Group B species (*Zelkova serrata*, *Idesia polycarpa* and *Alnus japonica*, which dominate the lower slope and valley bottom) had the lowest survival rates on the ridge compared to the slope and valley. Among Group C species (which are distributed from ridge to valley), the lowest survival rate for *Acer mono* was on the ridge, which was similar to that in the Group B species. In another Group C species, *Alnus hirsuta*, seedling survival rates on the ridge and the slope were not significantly different from each other.

Seedling survival rates were generally lower under canopy conditions than under gap conditions, particularly for *A. hirsuta*, *A. japonica* and *I. polycarpa* (Fig. 4). Exceptions were *Z. serrata* (Group B) and *A. mono* (Group C), in which the survival rates tended not to be different between gap and canopy conditions.

The cause of mortality could be detected for ca. 50% of the dead seedlings of each species in most plots (Fig. 5). *Q. serrata*, *Q. crispula* and *A. mono* seedlings were attacked by small mammals immediately after removal of the net covers; herbivory was the most prevalent cause of mortality. Withering was the second most common form of death for all species. Seedlings killed by physical damage were most frequent on the slope for most of the species studied. Exceptions were *Q. serrata* and *Q. crispula* under both gap and canopy conditions and both *Z. serrata* and *A. mono* in gap conditions, where death by physical damage was not observed on the slope.

Fig. 3. The ratio of seedling emergence ($100 \times$ number of emergence / number of seeds sown) of the 8 deciduous tree species. The species are grouped based on the distribution patterns of their adult trees; i.e., ridge, slope and valley, and widely distributed species for Groups A, B and C (see text). Each bar is the mean of 3 replicated plots for each species, light condition and topographic position. Error bars in the figure indicate 95% confidence interval. Also provided are statistical results of 1-way ANOVA for each species. Letters indicate groups showing significant difference ($p < 0.05$). *For *Acer mono*, a multiple comparison test for the ridge under canopy conditions could not be done due to lack of data.



Discussion

Seedling demography of the 8 tree species varied by topographic position. In the species whose adult trees dominate on and around the ridge (Group A; *Quercus serrata*, *Q. crispula* and *Carpinus laxiflora*) seedlings established successfully on the ridge in gaps due to greater seedling survival. Greater ratio of seedling emergence also contributed to establishment success of *Q. serrata* and *Q. crispula*. In contrast, establishment success of the other 5 species (Groups B and C) on the ridge was low. In these species, both emergence and survival rates were lower on the ridge than in the slope and valley. Although seed dispersal (which was not examined) may also be important, these results indicate that the seedling establishment process can contribute to species composition on the ridge.

Under field conditions, seedling emergence and survival are often inhibited by water deficit and litter accumulation (Molofsky & Augspurger 1992; Everham III et al. 1996; Seiwa & Kikuzawa 1996; Seiwa 1997). In the present study, seedling emergence (except for *Q. serrata* and *Q. crispula*) was lower on the ridge where soil moisture was lowest. These results suggest that soil moisture might be a factor affecting seedling emergence of 6 species along topographic positions. Ashton et al. (1995) suggested similar possible explanations for seedling distribution of *Shorea* species with the more drought tolerant on the ridge tops and the drought prone restricted to lower slopes and valleys. In our research seeds were buried in mineral soil, which might have provided the large *Quercus* seeds with better conditions for emergence and subsequent survival against drying (Seiwa & Kikuzawa 1996). In Group A species (abundant on the ridge) large seeds (acorns) of *Q. serrata* and

Q. crispula have substantial storage; thus seedlings of these species might emerge and grow in a wide range of topographies, including on ridge tops. High establishment success irrespective of topographic positions in other *Quercus* species was reported by Ashton & Larson (1996). Larger seed size represents investment in the seedlings and may expand the range of conditions for establishment. In *C. laxiflora*, seedling establishment on the ridge was due to greater seedling survival, similar results have also been reported by Shibata & Nakashizuka (1995).

Table 4. Results of 3-way ANOVA on the ratio of seedling survival at the end of the first growing season for 8 species (a) and at the end of the second growing season for 6 species (b).

a				
Source	d.f.	Mean Square	F-value	p
Species	7	744.574	3.555	0.002
Topographic position	2	1945.636	9.289	<0.001
Light condition	1	12619.021	60.250	<0.001
Spp. \times topogr.	14	810.159	3.868	<0.001
Spp. \times light	7	791.652	3.780	0.001
Topogr. \times light	2	1119.040	5.343	0.006
Spp. \times topo. \times light	14	355.741	1.698	0.067
b				
Source	d.f.	Mean Square	F-value	p
Species	5	1302.109	11.744	<0.001
Topographic position	2	1524.852	13.753	<0.001
Light condition	1	3581.872	32.306	<0.001
Spp. \times topogr.	10	458.121	4.132	<0.001
Spp. \times light	5	409.981	3.698	0.005
Topogr. \times light	2	480.980	4.338	0.017
Spp. \times topogr. \times light	10	117.885	1.063	0.403

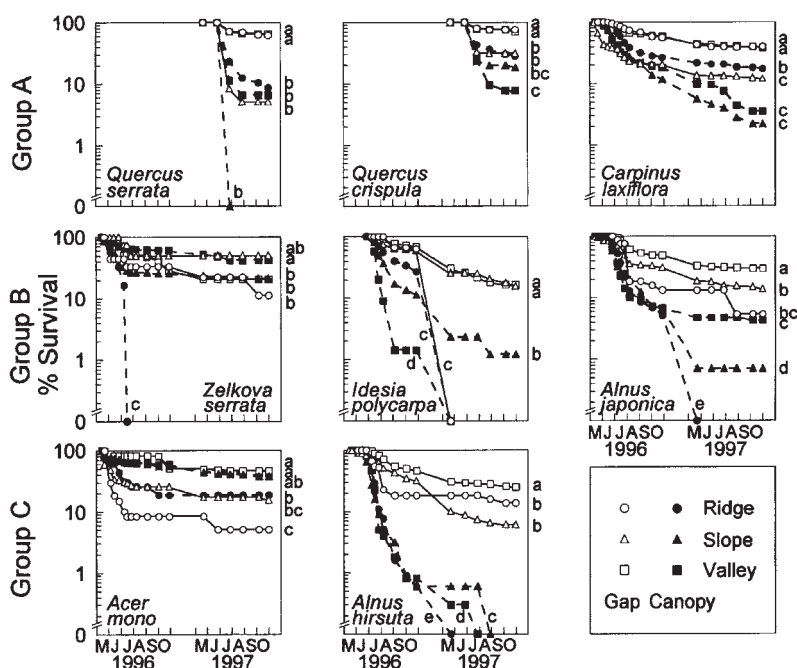


Fig. 4. Survivorship of 8 deciduous broad-leaved tree species from date of emergence (May 1 1996) to the end of the second growing season (Oct. 1997) on the ridge (O), slope (Δ) and valley (\square) plots. Unshaded and shaded symbols indicate gap and canopy plots, respectively. Survivorship is expressed as the mean of 3 replicated plots as a percentage of the seeds that emerged. Also provided are statistical results of a Sequential Bonferroni test after log rank test in each species. Letters indicate groups showing significant difference ($p < 0.05$).

Greater survival of *Q. serrata* and *Q. crispula* on the ridge partly resulted from comparatively low mortality from herbivory. Attacks by vertebrates and herbivores on seeds and seedlings have been considered an important factor affecting the population dynamics of trees (Shaw 1968; Jensen 1985; Kikuzawa 1988; Ida & Nakagoshi 1996).

Zelkova serrata and *Idesia polycarpa*, both Group B species (adults abundant on lower slope and valley bottom), had greater establishment success on the slope. Under canopies, emergence ratio of *Z. serrata* was not low and survival rate was intermediate compared to

under canopies on the ridge and valley. *Z. serrata* had a higher survival rate on the slope in gaps. In *I. polycarpa*, the emergence ratio tended to be high, and the survival rate was highest, in gaps. In contrast, the other 5 species had less establishment success on the slope compared to the other topographic positions. These results were consistent with the distribution patterns of adult trees of *Z. serrata* and *I. polycarpa*, which are sometimes dominant in frequently disturbed slope habitats (Sakai & Ohsawa 1994; Shimada 1994; Nagamatsu & Miura 1997). In this experiment, seedling mortality caused by physical damage was more frequent on the slope than in

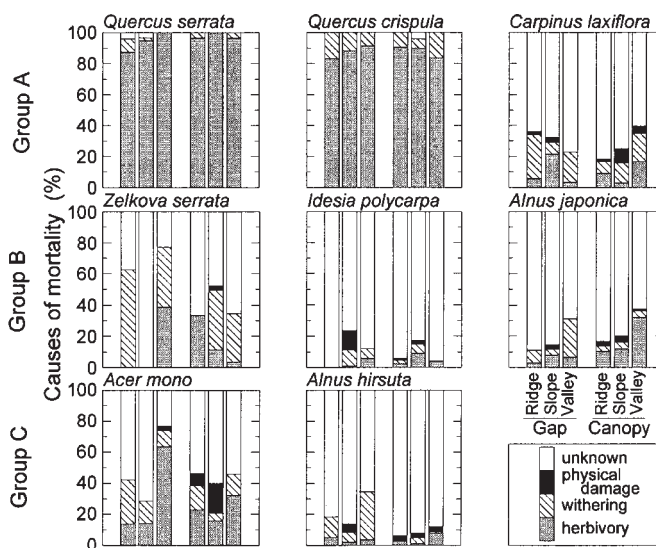


Fig. 5. Causal factors of seedling death for 8 deciduous tree species examined during 1 growing season for *Quercus serrata* and *Q. crispula* and 2 growing seasons for the remainder.

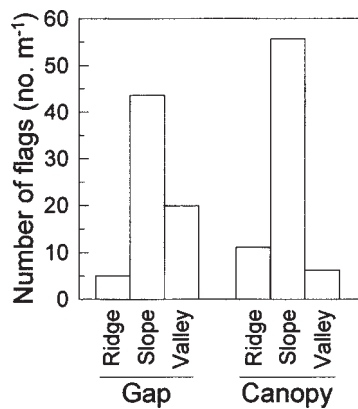


Fig. 6. Number of flags that disappeared during 2 growing seasons in each plot. Each bar is the total number of flags that disappeared in 3 replicated plots for all species.

the other topographic positions. This is also supported by the fact that the flags used for identification of individuals were lost most frequently on the slope ($p < 0.05$; χ^2 test, Fig. 6). These results indicate that physical damage caused by surface material movement could be an important factor which limits seedling establishment on hill slopes, in addition to other micro-disturbances such as litter fall, fallen logs and soil disturbance by vertebrates (Clark & Clark 1989; McCarthy & Facelli 1990; Shibata & Nakashizuka 1995). It is possible to assume that higher establishment successes of *Z. serrata* and *I. polycarpa* on the slope where physical damage was heavy, were due to their ability to adapt to physical damage, such as long horizontal roots in *Z. serrata* which would enhance its resistance to severe surface material flow (Nagamatsu, Seiwa & Sakai unpubl. data).

In the valley, seedlings of all 8 species established abundantly irrespective of their adult distribution. This suggests that a wide variety of tree species can grow on the valley bottom. The valley may represent a 'stressless' core of sites for seedling establishments based on the centrifugal organization idea (Keddy & MacLellan 1990), that all species can live under the optimum core habitat, but some survive at a more stressful peripheral habitat such as the ridge through greater tolerance to those conditions. Adult *Alnus japonica* and *Ulmus davidiana* var. *japonica* dominate the valley bottom in this area. According to the centrifugal organization idea (Keddy & MacLellan 1990) as in the valley, the optimum core habitat, competition intensity among seedlings is presumed to be higher than in stressful peripheral habitats (i.e. the ridge). Competition with herbaceous and shrub species (Nakashizuka 1988; Callaway 1992) may have an effect on seedling establishment success. In addition, resistance to fluvial disturbances is probably critical for species to grow successfully on the

valley bottom (Jones et al. 1994; Hupp & Osterkamp 1996). The frequency and intensity of floods and resulting sediment may influence the actual probability of seedling establishment.

The effects of light condition on seedling survival patterns were different among species. In *Alnus hirsuta*, *A. japonica* and *I. polycarpa*, seedling survival rates under canopies were much lower than those in gaps. They are 'light-demanding' early-successional species (Seiwa & Kikuzawa 1996; Sakai et al. 1997) and light conditions were a greater prior factor for seedling establishment success in these species than topographic position. In contrast, there was little effect of light conditions on seedling survival of *Z. serrata* and *Acer mono*, probably due to their greater shade-tolerance (e.g. Koike 1988) and/or shade avoidance (Seiwa 1998). Topographic position was a major factor in seedling survival for *Z. serrata* and *A. mono*. In *Q. serrata*, *Q. crispula* and *C. laxiflora* (Group A species) it seemed that both light conditions and topographic positions were the major factors affecting seedling survival. In these species, seedling establishment success was the highest on the ridge compared to other topographic positions under both light conditions. In addition, seedling survival rates on the ridge in Group A species were lower under canopies than in gaps.

The amount of material movement was heavier in the canopy plots than in the gap plots. The weights of plant litter were not different between the canopy and the gap plots ($p = 0.181$, 2-way ANOVA); however, the weights of gravel and sand were significantly different between these 2 light conditions ($p < 0.001$, 2-way ANOVA). The reason for this is obscure, but it may be due to a difference in the rain-induced erosion condition between the sites with and without canopy. Tsukamoto (1976) reported that a raindrop from a tree canopy is larger than one of throughfall and strikes the ground surface harder. Larger drops might increase material movement on the ground surface in the canopy plots. In studies on plant regeneration at disturbed sites, the effect of tree canopy was usually treated only as the indicator of their light condition (e.g. Hupp 1983 and this study); however, it may be worth considering that the tree canopy affected the amount of material movement and possibly also the seed-seedling dynamics through physical damage.

The topographic position is a critical factor for seedling establishment for 8 temperate tree species. In addition to soil moisture, material movement on ground surface may also be a significant factor affecting this process. The most intense mortality in plants often occurs at the juvenile stage (Harper 1977; Harcombe 1987). The processes which shape future species composition may, therefore, operate strongly on seedling

establishment process although the differential rates of mortality and growth after the seedling establishment will also influence species composition and forest structure. On ridge tops, it seems reasonable to suppose that species composition may be largely determined by the seedling establishment process. There is no clear 'seedling bank' of suppressed seedlings in this forest (Hirabuki et al. 1992). Although the results of this study are not linked directly to the present forest dynamics in the study area, they suggest that topography creates diverse habitats for the establishment of tree seedlings and affects further forest structure. These topographic variation should help maintain a greater biological diversity in forest composition and their dynamics in the local forest community.

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References

- Anon. (Japanese Society of Soil Science and Plant Nutrition) (ed.) 1986. *Dojyo hyojun bunseki-sokutei hou*. Hakuyushya, Tokyo, JP. (In Japanese.)
- Anon. 1995. *JMP user's guide version 3.1 of JMP*. SAS Institute, Cary, N.C.
- Ashton, M.S. & Larson, B.C. 1996. Germination and seedling growth of *Quercus* (section *Erythrobalanus*) across openings in a mixed-deciduous forest of southern New England, USA. *For. Ecol. Manage.* 80: 81-94.
- Ashton, P.M.S., Gunatilleke, C.V.S. & Gunatilleke, I.A.U.N. 1995. Seedling survival and growth of four *Shorea* species in a Sri Lankan rainforest. *J. Trop. Ecol.* 11: 263-279.
- Augspurger, C.K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65: 1705-1712.
- Basnet, K., Likens, G.E., Scatena, F.N. & Lugo, A.E. 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. *J. Trop. Ecol.* 8: 47-55.
- Burns, B.R. & Leathwick, J.R. 1996. Vegetation-environment relationships at Waipoua Forest, Northland, New Zealand. *N. Z. J. Bot.* 34: 79-92.
- Callaway, R.M. 1992. Effects of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology* 73: 2118-2128.
- Clark, D.B. & Clark, D.A. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. *Oikos* 55: 225-230.
- Conacher, A.J. & Dalrymple, J.B. 1977. The nine unit landsurface model: an approach to pedogeomorphic research. *Geoderma* 18: 1-154.
- Crow, T.R. 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. *Oecologia* 91: 192-200.
- De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. *Ecology* 72: 1066-1075.
- Denslow, J.S. & Guzman, G.S. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *J. Veg. Sci.* 11: 201-212.
- Everham III, E.M., Myster, R.W. & Van De Genachte, E. 1996. Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *Am. J. Bot.* 83: 1063-1068.
- Facelli, J.M. 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* 75: 1727-1735.
- Forget, P.-M. 1997. Effect of microhabitat on seed fate and seedling performance in two rodent-dispersed tree species in rain forest in French Guiana. *J. Ecol.* 85: 693-703.
- Hack, J.T. & Goodlett, J.C. 1960. Geomorphology and forest ecology of a mountain region in the Central Appalachians. *Geol. Surv. Prof. Paper* 347: 1-66.
- Hara, T., Hirata, K., Fujiwara, M. & Oono, K. 1996. Vegetation structure in relation to micro-landform in an evergreen broad-leaved forest on Amami Ohshima Island, south-west Japan. *Ecol. Res.* 11: 325-337.
- Harcombe, P.A. 1987. Tree life tables: simple birth, growth, and death data encapsulate life histories and ecological roles. *BioScience* 37: 558-568.
- Harper, J.L. 1977. *Population biology of plants*. Academic Press, London, UK.
- Harrington, G.N. 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology* 72: 1138-1149.
- Harrison, E.A., McIntyre, B.M. & Dueser, R.D. 1989. Community dynamics and topographic controls on forest pattern in Shenandoah National Park, Virginia. *Bull. Torrey Bot. Club* 116: 1-14.
- Hirabuki, Y., Takehara, A. & Iizumi, S. 1992. The vegetation in the Ippitsuyama-Tashiro Natural Conservation Area, Miyagi Prefecture. In: Anon. (ed.) *The scientific report of the Ippitsuyama-Tashiro Natural Conservation Area, Miyagi Prefecture*, pp. 33-78. Miyagi Prefecture, Sendai, JP. (In Japanese.)
- Hunter, J.C. & Parker, V.T. 1993. The disturbance regime of an old-growth forest in coastal California. *J. Veg. Sci.* 4: 19-24.
- Hupp, C.R. 1983. Seedling establishment on a landslide site. *Castanea* 48: 89-98.
- Hupp, C.R. & Osterkamp, W.R. 1996. Riparian vegetation and fluvial geomorphic processes. *Geomorphology* 14: 277-295.
- Ida, H. & Nakagoshi, N. 1996. Gnawing damage by rodents to the seedlings of *Fagus crenata* and *Quercus mongolica* var. *grosseserrata* in a temperate *Sasa* grassland-deciduous forest series in southwestern Japan. *Ecol. Res.* 11: 97-103.
- Iwatsuki, K. 1992. *Ferns and fern allies of Japan*. Heibonsha, Tokyo, JP. (In Japanese.)
- Jensen, T.S. 1985. Seed-seed predator interactions of Euro-

- pean beech, *Fagus sylvatica* and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos* 44: 149-156.
- Jones, R.H., Sharitz, R.R., Dixon, P.M., Segal, D.S. & Schneider, R.L. 1994. Woody plant regeneration in four floodplain forests. *Ecol. Monogr.* 64: 345-367.
- Keddy, P.A. & MacLellan, P. 1990. Centrifugal organization in forests. *Oikos* 59: 75-84.
- Kikuchi, T. & Miura, O. 1991. Differentiation in vegetation related to micro-scale landforms with special reference to the lower sideslope. *Ecol. Rev.* 22: 61-70.
- Kikuchi, T. & Miura, O. 1993. Vegetation patterns in relation to micro-scale landforms in hilly land regions. *Vegetatio* 106: 147-154.
- Kikuzawa, K. 1988. Dispersal of *Quercus mongolica* acorns in a broadleaved deciduous forest 1. Disappearance. *For. Ecol. Manage.* 25: 1-8.
- Kobayashi, M. & Kamitani, T. 2000. Effects of surface disturbance and light level on seedling emergence in a Japanese secondary deciduous forest. *J. Veg. Sci.* 11: 93-100.
- Koike, T. 1988. Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. *Plant Species Biol.* 3: 77-87.
- McCarthy, B.C. & Facelli, J.M. 1990. Microdisturbances in oldfields and forests: implications for woody seedling establishment. *Oikos* 58: 55-60.
- Molofsky, J. & Augspurger, C.K. 1992. The effects of leaf litter on early seedling establishment in a tropical forest. *Ecology* 73: 68-77.
- Nagamatsu, D. & Miura, O. 1997. Soil disturbance regime in relation to micro-scale landform and its effects on vegetation structure in a hilly area in Japan. *Plant Ecol.* 133: 191-200.
- Nakashizuka, T. 1988. Regeneration of beech (*Fagus crenata*) after the simultaneous death of undergrowing dwarf bamboo (*Sasa kurilensis*). *Ecol. Res.* 3: 21-35.
- Nakashizuka, T. 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. *Ecology* 70: 1273-1278.
- Potvin, M.A. 1993. Establishment of native grass seedlings along a topographic/moisture gradient in the Nebraska sandhills. *Am. Midl. Nat.* 130: 248-261.
- Putz, F.E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64: 1069-1074.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.
- Sahashi, N., Kubono, T. & Shoji, T. 1994. Temporal occurrence of dead seedlings of Japanese beech and associated fungi. *J. Jpn. For. Soc.* 76: 338-345.
- Sakai, A. & Ohsawa, M. 1994. Topographical pattern of the forest vegetation on a river basin in a warm-temperate hilly region, central Japan. *Ecol. Res.* 9: 269-280.
- Sakai, A., Sakai, S. & Akiyama, F. 1997. Do sprouting tree species on erosion-prone sites carry large reserves of resources? *Ann. Bot.* 79: 625-630.
- Satake, Y., Hara, H., Watari, S. & Tominari, T. (eds.) 1989. *Wild flowers of Japan. Woody plants. I, II.* Heibonsha, Tokyo, JP. (In Japanese.)
- Satake, Y., Ohwi, J., Kitamura, S., Watari, S. & Tominari, T. (eds.) 1981-1982. *Wild flowers of Japan. Herbaceous plants (including dwarf shrubs). I-III.* Heibonsha, Tokyo, JP. (In Japanese.)
- Schupp, E. W. 1990. Annual variation in seedfall, postdispersal predation, and recruitment of a neotropical tree. *Ecology* 71: 504-515.
- Seiwa, K. 1997. Variable regeneration behaviour of *Ulmus davidiana* var. *japonica* in response to disturbance regime for risk spreading. *Seed Sci. Res.* 7: 195-207.
- Seiwa, K. 1998. Advantages of early germination for growth and survival of seedlings of *Acer mono* under different overstorey phenologies in deciduous broad-leaved forests. *J. Ecol.* 86: 219-228.
- Seiwa, K. & Kikuzawa, K. 1996. Importance of seed size for the establishment of seedlings of five deciduous broad-leaved tree species. *Vegetatio* 123: 51-64.
- Shaw, M.W. 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in north Wales. II. Acorn losses and germination under field conditions. *J. Ecol.* 56: 647-660.
- Shibata, M. & Nakashizuka, T. 1995. Seed and seedling demography of four co-occurring *Carpinus* species in a temperate deciduous forest. *Ecology* 76: 1099-1108.
- Shimada, K. 1994. Topographical distribution of five pioneer tree species and significance of their tree forms in natural forests on Mt Takao, central Japan. *Jpn. J. Ecol.* 44: 293-304. (In Japanese with English summary.)
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry*. 3rd ed. Freeman, New York, NY, US.
- Streng, D.R., Glitzenstein, J.S. & Harcombe, P.A. 1989. Woody seedling dynamics in an east Texas floodplain forest. *Ecol. Monogr.* 59: 177-204.
- Tamura, T. 1969. A series of micro-landform units composing valley-heads in the hills near Sendai. *Sci. Rep. Tohoku Univ. 7. Ser. (Geogr.)*. 19: 111-127.
- Tanaka, N. 1985. Patchy structure of a temperate mixed forest and topography in the Chichibu mountains, Japan. *Jpn. J. Ecol.* 35: 153-167.
- Tanouchi, H. 1996. Survival and growth of two coexisting evergreen oak species after germination under different light conditions. *Int. J. Plant Sci.* 154: 516-522.
- Titus, J.H. 1990. Microtopography and woody plant regeneration in a hardwood floodplain swamp in Florida. *Bull. Torrey Bot. Club* 117: 429-437.
- Titus, J.H. & del Moral, R. 1998. Seedling establishment in different microsites on Mount St. Helens, Washington, USA. *Plant Ecol.* 134: 13-26.
- Tsukamoto, Y. 1976. Forest canopy and rain drop erosion. *Jpn. J. For. Environ.* 17: 5-9. (In Japanese.)
- Wada, N. 1993. Dwarf bamboos affect the regeneration of zoochorous trees by providing habitats to acorn-feeding rodents. *Oecologia* 94: 403-407.

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