論　文

Emergence-disappearance processes and mortality factors of current-year seedlings of *Abies firma* in a natural *Abies-Tsuga* forest, Wakayama

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モミ・ツガ天然林におけるモミ当年生実生の消長過程と死亡要因

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To clarify the demographical traits of current-year seedlings of *Abies firma*, we examined the emergence and survival processes of seedlings and mortality factors in a total of 213 seedling plots of 1 m^2 inside of a 0.96 ha plot in a natural *Abies-Tsuga* forest, Wakayama. Seedling emergence started in the middle of April, reached a peak in late April and declined thereafter. The causes of mortality changed seasonally; herbivory and damping-off prevailed from April to early July, while drought prevailed during summer. Emerged seedlings decreased with time and mortality rate reached 60 % of emerged seedlings at the beginning of December. From the multiple regression analysis, the distance from the nearest conspecific adult negatively affected seedling emergence, while the depth of litter (L) layer affected it positively. Vegetation cover of the ground-layer and the depth of litter (L) promoted the seedling survival rate. Slope angle had a slightly negative effect on seedling survival, although not significant.
Key words: *Abies-Tsuga* forest, *Abies firma*, seedlings, demography, mortality factors.

和歌山演習林のモミ・ツガ天然林において、モミ当年生実生のデモグラフィーを明らかにすることを目的に、0.96ha（80×120 m）のプロット内に213個の実生枠（1 m²）を設け実生の消長過程とその死亡要因を調べた。実生の発生は4月中旬から始まり、4月下旬にピークを迎えた後、急激に低下し、6月はじめには停止した。発生した実生は経時的に減少する傾向を示し、成長終了期の12月には死亡率は60％にも達した。死亡をもたらす原因は、動物による被食、菌類などの感染による立ち枯れ、乾燥などであったが、季節的にその度合いは異なっていた。斜面傾斜角度、相対光量子束密度、リター層の厚さ、繁殖成木からの距離、林床植物の被度といった要因を取り上げ、実生の発生と生残率について重回帰分析をおこなった。実生の発生にはリター層の厚さが正に、逆に繁殖成木からの距離が負にそれぞれ有意な影響を及ぼしていることが明らかとなった。生残率にはリター層の厚さと林床層植物の被度がそれぞれ正に有意な影響を、また有意ではなかったものの有意判定基準付近にあつた斜面の傾斜角度はわずかに負の影響を及ぼしていることが明らかとなった。
キーワード：モミ・ツガ天然林、モミ、実生、デモグラフィー、死亡要因

Introduction

The high mortality during the seedling stage is a general characteristic of tree population demography (Collins and Good, 1987, Shibata and Nakashizuka, 1995, Akashi, 1997). Identification of the factors that control germination, emergence, and survival rates in current-year seedlings is important to understand the regeneration pathways and plant population dynamics (Schupp, 1990, Eriksson and Ehrlen, 1992). Many studies have demonstrated that light availability, microtopography, substrate and vegetation cover of the ground-layer are major factors that affect the establishment and survival of seedlings (Kitajima and Augspurger, 1989, Facelli and Pickett, 1991, Jones et al., 1994, Shibata and Nakashizuka, 1995, Sakai et al., 1998, Seiwa, 1998).

Abies firma and *Tsuga sieboldii* generally form a forest zone between the cool temperate and warm temperate forests in western regions of Japan, especially on the Pacific Ocean side. *Abies firma*, which has a comparatively short seed masting cycle (ca. 2 years), forms seedling banks in the understory (Yuruki et al., 1987, Aragami, 1987), but details of the regeneration mechanism and the factors affecting the seedlings still remain unclear.

The forest floor that provides a bed for seedling emergence and subsequent survival is heterogeneous in time and space. Therefore, it is necessary to quantify and determine the factors affecting the emergence and survival

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of *Abies firma* seedlings. We used a total of 213 seedling plots along a continuous 0.96 ha to examine demographical traits, and to analyze the environmental factors that are involved in the process of emergence and early survival of this species.

Methods

Study area

The study was carried out in a natural *Abies firma-Tsuga sieboldii* forest that has been reserved for more than 70 years at Kyoto University Forest in Wakayama (30° 04'N, 135° 30'E). The area located in the eastern part of Wakayama Prefecture has a steep mountainous topography, with a slope angle varying from 25 to 45 degrees. The altitude ranges from 450 to 1200 meters above sea level. The mean annual temperature and annual precipitation are 12.4 °C and 2369 mm, respectively, including a small amount of snow (at the office of the Kyoto University forest in Wakayama, 550 m a. s. l.). The minimum and maximum daily temperature and daily precipitation during the study period in 1998 are shown in the Figure 1.

This *Abies-Tsuga* forest has more than 30 tree species per hectare. The density of trees (DBH ≥ 5 cm) and total basal area are 1460 stems and 79.01 m^2 /ha, respectively. The dominant canopy tree species are conifers *Abies firma* and *Tsuga sieboldii* occupying 29.1 and 22.8 m^2/ha of the basal area, respectively, which together represent more than 65% of the total basal area. Associated with them are broad-leaved species *Stewartia monadelpha*, *Quercus acuta*, and *Carpinus laxiflora*, occupying 4.8, 2.9 and 2.2 m^2/ha of basal area, respectively.

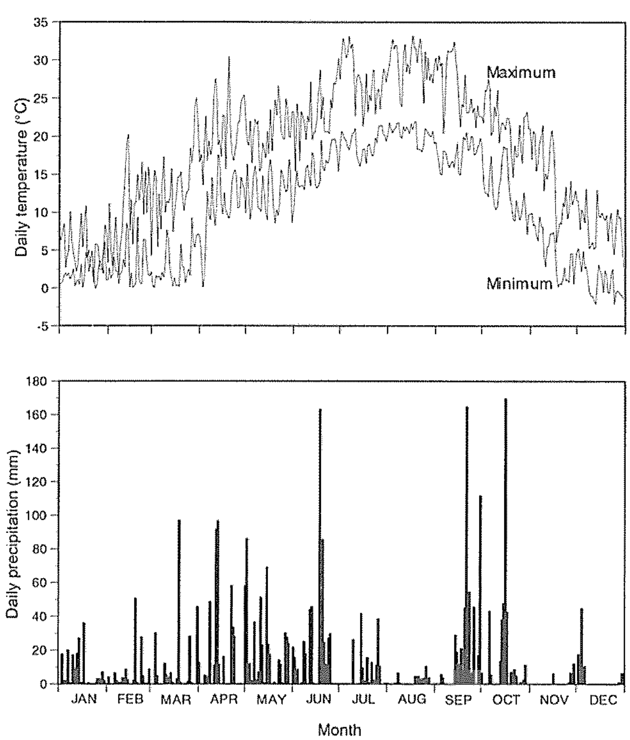

Figure 1. Minimum and maximum daily temperature and daily precipitation at Kyoto University Forest in Wakayama.

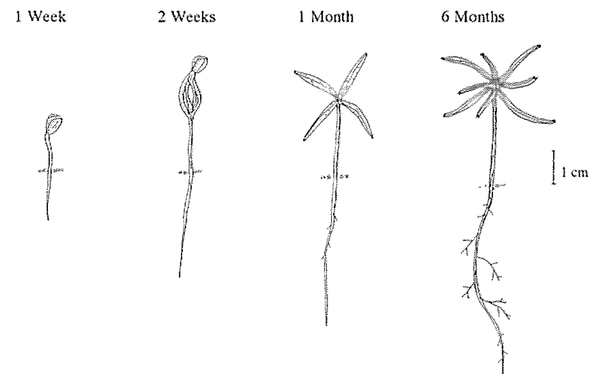

Figure 2. Morphology of current-year seedlings of *Abies firma*.

Seedling emergence and survival

One plot of 0.96 ha (80 × 120 m) (800 m a. s. l.) was established and divided into 96 grids of 10 × 10 m. The seedling plots of 1 m^2 were set at the center and corners of every grid. In addition, 21 seedling plots were set at the periphery giving a total of 213 plots. Newly emerged seedlings (Figure 2) were labeled. Seedling survival was followed by censuses from April to December in 1998. Censuses were carried out weekly from April to the beginning of June, every two weeks from the middle of June to September and once a month thereafter.

At every census date, we classified the mortality causes into the following 5 categories: herbivory for dead seedlings with cotyledons or hypocotyls eaten; damping-off for the dead seedlings with symptoms of rotten stem at the ground level caused by fungi which spread during the periods of high moisture on the soil surface; drought for seedlings still standing on the ground but with dried cotyledons; physical damage, for seedlings that were killed by micro-landslides (exposing the seedling root systems), rolling stones, or soil disturbance; and unknown for seedlings that disappeared from the plots. We grouped the mortality causes into about one month interval from April to September.

Factors controlling seedling emergence and survival

To investigate the factors involved in the emergence and survival rate of current-year seedlings of *Abies firma*, in each seedling plot we surveyed the percentage of photosynthetic photon flux density reaching the seedlings (% PPFD), slope angle, depth of litter (L) layer, distance from the nearest conspecific adult, and percentage of vegetation cover of the ground-layer.

We used a portable light meter (LI-250, LI-COR, Lincoln) to measure the percentage of PPFD. The sensor was placed 0.5 m above the ground over the seedling plot on a cloudy day in August of 1998. The values were converted to percent of PPFD by comparison with the values from a data logger mounted simultaneously in an adjacent open site. Slope angle was referred as the largest angle of the seedling plot measured with a protractor. The depth of litter (L) layer was measured by excavating a small soil profile. We measured the distance from the crown periphery of the nearest conspecific adult to the seedling plot. If the seedling plot was directly beneath the tree crown, the distance was registered as 0 m. We estimated the vegetation cover of the ground-layer by quantifying its presence in percentage in the seedling plot.

Statistical analysis

We performed multiple regression analysis to evaluate the effect of the factors involved in seedling emergence and survival. Dependent variables were number of emerged seedlings and survival rate. Independent variables were % of PPFD, slope angle, depth of litter (L) layer, distance from the nearest conspecific adult, and vegetation cover of the ground-layer. Since variables like the number of emerged seedlings, survival rate, the percentage of PPFD, and vegetation cover of the ground-layer are not normally distributed, we used the log-transformed form for the analysis.

Results

1. Emergence and survival processes

Emergence of current-year seedlings started in the middle of April and stopped at the beginning of June. The emergence rate reached a peak late in April and declined thereafter (Figure 3). A total of 1457 seedlings/213 m^2 emerged. The mean density of emerged seedlings was $6.8 \pm 5.5 / m^2$.

As in most tree species, the mortality of current-year seedlings after emergence was high in *Abies firma*. Survivorship curves of seedling cohorts decreased until October, and thereafter, the survival rate remained constant until December (Figure 4). At the beginning of December, the seedling survival rate was 40.8 %. The seedlings that emerged earlier had a higher final survival rate (Table 1).

Causes of seedling mortality showed a seasonal variation (Figure 5). Herbivory and damping-off were observed mainly during the first periods of the growing season. In contrast, drought was observed mainly from July to September when the amount of rainfall was small, and unknown causes of seedling disappearance were increased mainly in June during rainy season and September when typhoon No. 7 hit the area.

2. Factors affecting seedling emergence and survival rate

Expected factors affecting seedling dynamics fluctuated

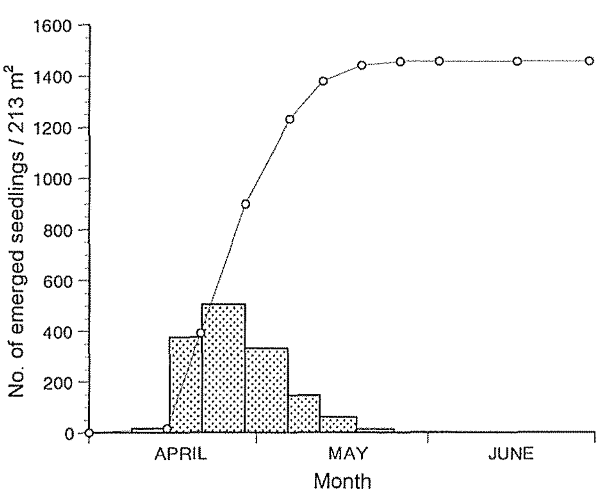

Figure 3. Accumulative numbers (open circle) and emergence of current-year seedlings of *Abies firma*.

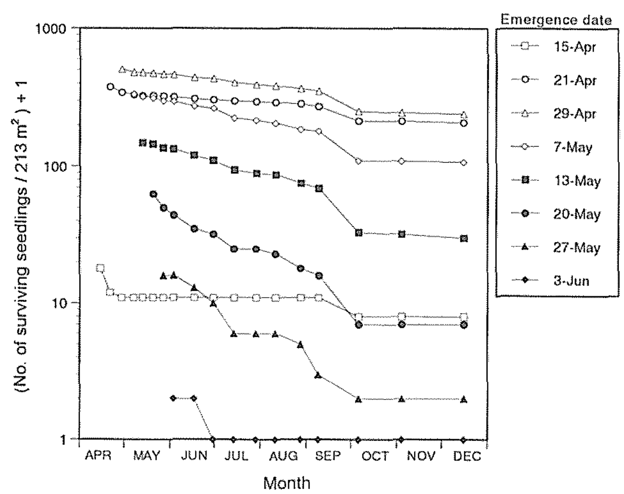

Figure 4. Survivorship curves of cohorts of current-year seedlings of *Abies firma* with different emergence dates. Numbers of surviving seedlings per 213 m^2 plus 1 are shown.

Table 1. Number of emerged and surviving seedlings and their survival rate at different emergence dates. Numbers of seedlings per 213 × $1m^2$ plots are shown.

	Emergence date							
	April 15	April 21	April 29	May 7	May 13	May 20	May 27	June 3
No. of emerged seedlings	17	376	506	333	147	62	15	1
No. of surviving seedlings*	7	207	239	106	29	6	1	0
Survival rate(%)	41.2	55.1	47.7	31.8	19.7	9.7	6.7	0

*counted in December

Table 2. Mean and range of slope angle, %PPFD, depth of L layer, distance from conspecific adult, and vegetation cover in the study plot

Variable	Mean ± 1SD	Range
Slope angle (degree)	26.8 ± 7.8	42.0 - 3.0
PPFD* (%)	2.7 ± 1.5	11.5 - 0.7
Depth of L layer (cm)	1.2 ± 0.5	3.0 - 0.3
Distance from conspecific adult (m)	2.7 ± 2.7	12.9 - 0
Vegetation cover (%)	7.6 ± 9.8	77.0 - 0

*photosynthetic photon flux density

with the seedling plot (Table 2). Generally the topography was steep and the understory was dim. The vegetation cover of ground layer was low in general but the range was large. The number of emerged and surviving seedlings of *Abies firma* varied with the seedling plot respectively (Figure 6). The results of the analysis revealed that the depth of litter (L) layer had a significant positive effect on the number of emerged seedlings ($P<0.020$), while the distance from the nearest conspecific adult tree had a significant negative effect ($P<0.021$) (Table 3). These results suggest that the availability of dispersed seeds of *Abies firma* decreases with increasing the distance from adult trees.

The multiple regression model showed that vegetation cover of the ground layer ($P<0.0002$) and depth of litter (L) layer ($P<0.024$) had significant effects on the final survival rate of current-year seedlings, while the effect of slope angle was marginal ($P<0.057$) (Table 3). Contrary to our expectation, vegetation cover of the ground layer had a significant positive relation with survival rate. The slope angle had a marginal negative effect on seedling survival although not significant, which may indicate that the process related to micro-topography affected the seedling establishment of this species to some extent.

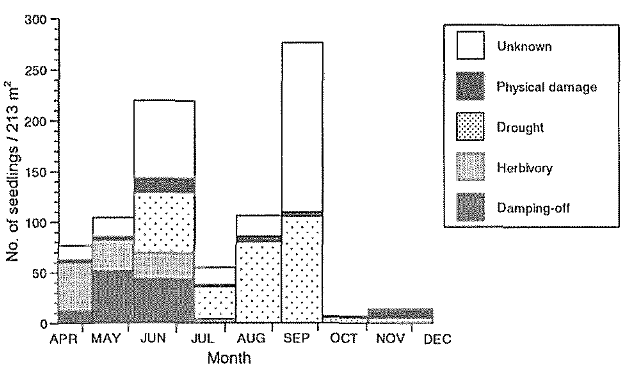

Figure 5. Causes of mortality of current-year seedlings of *Abies firma*.

Discussion

High seedling mortality is a general characteristic of most tree species. In this study, a high mortality of current-year seedlings of *Abies firma* was observed during the growing season and killed up to 60 % of the emerged seedlings. Comparable results for *Abies firma* have been reported in Kyushu (Aragami, 1987) and Shikoku (Ichikawa and Ogino, 1986, Sakai et al., 1998) regions. From demographical studies of tree seedlings, seasonal and site characteristics factors have been pointed out as factors causing seedling mortality.

1. Seasonal dynamics

Emergence of current-year seedlings of *Abies firma* continued for 2 months. However, seedlings emerged earlier showed a tendency to have higher final survival rates (Table 1). In this *Abies-Tsuga* forest, the time of seedling emergence almost corresponds with the early time of leaf flushing of canopy trees, which lasted for about 2 months (G. Angeles-Pérez, unpublished data). Understory plants utilize light penetrating before leaf flushing in the canopy layer in early spring (Seiwa, 1998). Our result could be attributed to the higher light availability before completing leaf flushing in the canopy layer. Similar results have been

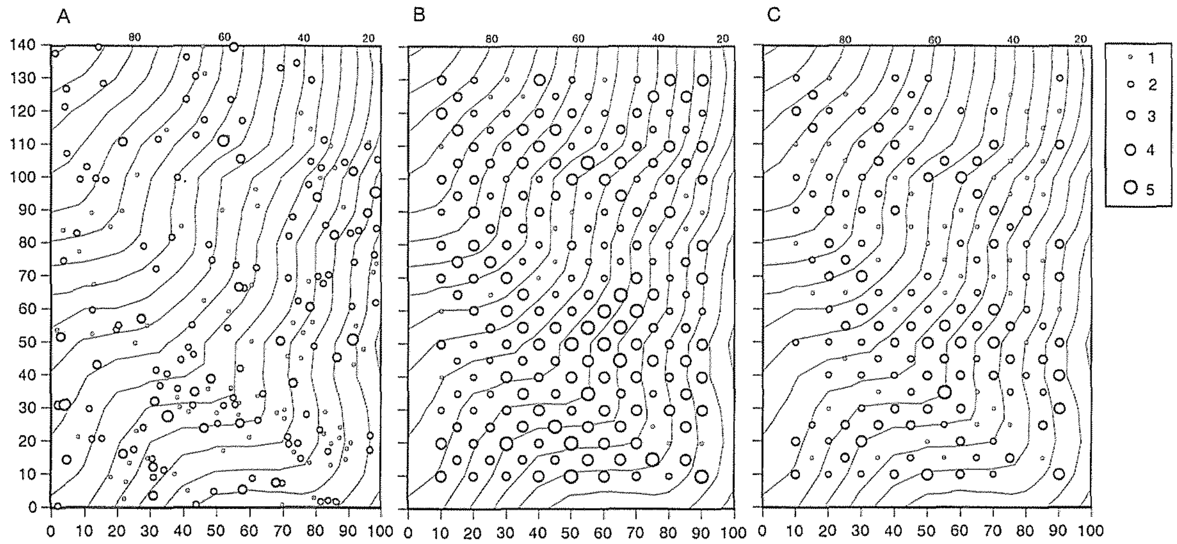

Figure 6. Spatial distribution of A) adult trees, B) number of emerged seedlings, and C) number of surviving seedlings of *Abies firma*.
A: Adult trees, 1: 20≤dbh<40, 2: 40≤dbh<60, 3: 60≤dbh<80, 4: dbh≥80. (unit : cm)
B: Emerged seedlings per 1 m^2, 1: 1-2, 2: 3-4, 3: 5-8, 4: 9-16, 5: >16.
C: Surviving seedlings per 1 m^2, 1: 1-2, 2: 3-4, 3: 5-8, 4: 9-16, 5: >16.

found in *Carpinus* spp. (Shibata and Nakashizuka, 1995) and *Acer mono* (Seiwa, 1998) in Japan, and deciduous tree species in a floodplain forest (Jones et al., 1994) in USA.

The causes of mortality changed seasonally (Figure 5). Several studies concerning the causes of mortality of tree seedlings have been conducted for *Chamaecyparis obtusa* (Yamamoto and Tsutsumi, 1980), *Cryptomeria japonica* (Tamai et al., 1985, Muroyama and Tamai, 1986), *Pinus densiflora* (Kikuchi et al., 1996) and *Fagus crenata* (Sahashi et al., 1994) in Japan, and *Tachigalia versicolor* (Kitajima and Augspurger, 1989) in the tropics. Herbivory and damping-off predominating in early periods of the first growing season were commonly important causes. However, drought that was one of the dominant mortality causes in our study was not important in others, except for *Chamaecyparis obtusa* (Yamamoto and Tsutsumi, 1980). Thus drought may be a species-specific and/or site-specific cause.

2. Spatial seedling performance

From various plant demographical studies, canopy cover, the amount of litter, substrate, microtopography and vegetation cover of the ground-layer have been considered important for seedling establishment and survival. In this study, we assessed the slope angle, % of PPFD, depth of litter (L) layer, distance from the nearest conspecific adult, and vegetation cover of the ground-layer as affecting factors.

The distance from a conspecific adult had a negative effect on seedling emergence (Table 3). Seeds of *Abies firma* are dispersed by wind. The mean distance from the nearest

Table 3. Multiple regression analyses of emerged seedlings and survival rate

	Variable	Coeff	SE	Std coeff.	*P*	SS	Total *F*	r^2
Emerged seedling	Slope angle	-0.003	0.003	-0.070	0.337			
	%PPFD (log)	0.170	0.122	0.099	0.165			
	Depth of L layer	0.144	0.061	0.216	**0.020**			
	Distance from conspecific adult	-0.021	0.009	-0.158	**0.021**			
	Vegetation cover (log)	-0.043	0.048	-0.063	0.369			
	Constant	0.641	0.132	0.000	0.000			
	Model				0.005	2.348	3.249	0.088
Survival rate	Slope angle	-0.011	0.006	-0.134	0.057			
	%PPFD (log)	0.378	0.215	0.120	0.081			
	Depth of L layer	0.246	0.108	0.203	**0.024**			
	Distance from conspecific adult	-0.012	0.016	-0.050	0.453			
	Vegetation cover (log)	0.321	0.084	0.258	**0.000**			
	Constant	1.170	0.233	0.000	0.000			
	Model				0.000	13.106	5.830	0.147

conspecific adult was comparatively short (2.7±2.7 m). Therefore, the result may indicate that the seed dispersal strategy of *Abies firma* is insufficient because of its large seed size of 40 mg (Japan Tree Breeding Association, 1981). On the other hand, the depth of litter (L) layer had a positive effect on seedling emergence. Facelli and Pickett (1991) pointed out that litter has the property to improve moisture availability in the soil. Broncano et al. (1998) reported that large seeded species require high levels of soil moisture for germination. *Abies firma* seedlings originated from large seed stock may easily grow up through the litter (L) layer with long hypocotyl. Thus the result suggests that maintaining high soil moisture by litter cover is critical for germination of *Abies firma*.

Some studies have revealed that vegetation cover has a negative effect on seedling survival by increasing the above and belowground competition (Facelli and Picket, 1991, Shibata and Nakashizuka, 1995). However, in this study, vegetation cover had a significant positive effect. Maguire and Forman (1983) emphasized the effect of understory herbs and shrubs on the seedlings of tree species, and reported that whether the effect is positive or negative depends not only on the species involved but also on the surrounding physical conditions. The forest where our study was carried out has a steep topography and sparse understory vegetation (Table 2). Consequently, an increase in vegetation cover of the ground layer could diminish soil movement giving more stability for seedling establishment, even though the effect of slope angle was marginal due to high variability. Tsujita et al. (1986) mentioned that in an *Abies-Tsuga* forest in Shikoku, movement of soil elements along slopes is very heavy. The soil and litter movement along slopes is particularly pronounced at the time of intense rainfall (Tsukamoto, 1991).

The seedling survival rate increased with the depth of the litter (L) layer (Table 3). The substrate is considered to affect seedling survival by modifying water availability in the soil. For example, the presence of a thick litter layer prevents excessive evaporation from the soil surface (Gray and Spies, 1997). However, the root system of the seedlings must penetrate the litter layer to reach the mineral soil where the soil moisture is more stable. Current-year seedlings of *Abies firma* had a root length of 4.7 cm 6 months after emergence (Figure 2), while mean depth of L layer was 1.2 cm (Table 2). The large seed size of this species could permit the development of deep rooting system, which enabled seedlings to uptake water from the stable soil layers.

Conclusion

Our results differ to some extent from those observed in previous studies. Previously, light availability was emphasized to be one of the most important factors affecting seedling establishment. However, in this study, % of PPFD did not affect the seedling survival rate of *Abies firma*. The large seed size of this species (large amount of seed reserves) is considered to have permitted seedlings to survive independently of light conditions. On the other hand, understory vegetation cover of the ground-layer positively affected seedling performance. The steep topography in the region, the high rainfall during rainy season and typhoon attack, could increase soil movement along the slope. Nevertheless, the presence of vegetation cover could stabilize the ground and prevent soil erosion, which has been considered to damage small current-year seedlings.

The Kii peninsula including Wakayama prefecture is characterized by both large precipitation, brought by rainy season and typhoon attack, and steep topography. This study showed that such topography and intensive rainfall are important factors for seedling establishment in this region.

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