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Effects of abiotic and biotic factors and stochasticity on tree regeneration in a temperate forest community[1]

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Abstract: How deterministic or stochastic is tree regeneration in a temperate forest? To answer this question, we analyzed the relative effects of abiotic and biotic factors on seed and seedling demography of tree species in an old-growth temperate forest, Ogawa Forest Reserve, Japan. The working hypothesis was that seed and seedling demography of trees would be controlled more deterministically in comparison with tropical forests and that the magnitude of deterministic effects of the abiotic and biotic factors would depend on regeneration traits relating to seed dispersal ability. We examined 5 abiotic factors (litter and humus cover, vegetation cover, light level, soil moisture, and relative elevation) and 2 species-specific biotic factors (distance from the nearest conspecific adult and density of conspecific seeds or seedlings) to quantify their contribution to the spatial variation in seedling emergence and survival for 18 principal tree species in the community. The results showed that conspecific seed density had a negative effect on seedling emergence for almost all species, as suggested by the Janzen–Connell model. On the other hand, various factors were detected for seedling survival of each species. We also found that regeneration traits relating to seed dispersal ability were significantly correlated with some of the abiotic factors. However, the 7 factors tested were less important than expected; seed and seedling demography appeared to be determined rather stochastically in this stable forest community. Even in a temperate forest, seed and seedling demography appeared to be rather stochastic, and niche partitioning among species during these stages was of limited importance.

Keywords: Janzen–Connell model, niche partitioning, Ogawa Forest Reserve, regeneration traits, seed and seedling demography, stochastic process.

Résumé : La régénération des arbres en forêt tempérée est-elle déterministe ou stochastique? Pour répondre à cette question, nous avons analysé les effets relatifs de facteurs abiotiques et biotiques sur la démographie des graines et des semis d'espèces arborées dans une vieille forêt tempérée, la réserve forestière d'Ogawa, au Japon. L'hypothèse de travail était que la démographie des graines et des semis des arbres serait régie de façon plus déterministe comparée avec les espèces des forêts tropicales et l'ampleur des effets déterministes des facteurs abiotiques et biotiques dépendrait des traits de régénération associés à la capacité de dispersion des graines. Nous avons examiné 5 facteurs abiotiques (la couverture de litière et d'humus, la couverture végétale, la quantité de lumière, l'humidité du sol et l'élévation relative) et 2 facteurs biotiques spécifiques aux espèces (la distance à l'adulte conspécifique le plus proche et la densité des graines ou semis conspécifiques) pour évaluer quantitativement leur contribution à la variation spatiale de l'émergence et de la survie des semis pour 18 espèces principales d'arbres dans la communauté. Les résultats ont montré que la densité de graines conspécifiques avait un effet négatif sur l'émergence des semis pour presque toutes les espèces, tel que suggéré par le modèle Janzen-Connell. D'autre part, différents facteurs influençant la survie des semis ont été détectés pour chaque espèce. Nous avons aussi constaté que les traits de régénération associés à la capacité de dispersion des graines étaient significativement corrélés avec certains des facteurs abiotiques. Cependant, les 7 facteurs évalués étaient moins importants que l'on s'attendait; la démographie des graines et des semis semblait être déterminée de façon stochastique dans cette communauté forestière stable. Ainsi, même dans une forêt tempérée, la démographie des graines et des semis semble être déterminée de façon plutôt stochastique et la différenciation des niches entre les espèces a une importance limitée durant ces stades de développement.

Mots-clés : démographie des graines et des semis, différenciation des niches, modèle Janzen-Connell, processus stochastique, réserve forestière d'Ogawa, traits de régénération.

Nomenclature: Satake *et al.*, 1989.

Introduction

Identifying the factors controlling regeneration of tree species is a key approach to understanding tree species coexistence in forest communities. Many researchers have shown that the regeneration of tree species is affected by various abiotic environmental factors (hereafter, abiotic factors) that define "regeneration niches" (Grubb, 1977; Silvertown *et al.*, 1999; Duncan & Armesto, 2003; Masaki *et al.*, 2005; 2007). In addition to the abiotic factors, species-specific biotic factors (hereafter, biotic factors) in relation to density or distant-dependent mortality (namely the Janzen–Connell model) are known to affect regeneration of many tree species, both in tropical forests (Clark & Clark, 1984; Harms *et al.*, 2000; Wright, 2002) and temperate forests (Shibata & Nakashizuka, 1995; Masaki & Nakashizuka, 2002). Effects of these abiotic and biotic factors have been extensively studied as examples of deterministic processes in seedling establishment.

In contrast to deterministic processes, the importance of stochastic processes for tree community organization has been emphasized in the last decade. Two types of stochasticity in tree regeneration have been pointed out. The first is that every species is different in seed and seedling performance under different environmental conditions (*e.g.*, in variable-sized gaps), and a vacant site is not necessarily colonized by the best-adapted species due to dispersal limitation (Clark, Macklin & Wood, 1998; Brokaw & Busing, 2000; Muller-Landau *et al.*, 2002). The second is that all species in a community resemble each other, and a vacant site is occupied by the species that arrives first, which is known as the neutral theory (Hubbell, 2001). These arguments are based on the premise that seedling establishment is largely determined in a stochastic manner that facilitates coexistence of species in a forest community without any deterministic processes. However, actual regeneration in tree communities is known to be regulated by biotic and abiotic factors to a different degree depending on species (Brokaw & Busing, 2000; Nakashizuka, 2001). Furthermore, the assumption of neutral theory that all species are similar to each other has been controversial even in tropical forests (*e.g.*, Russo *et al.*, 2005; John *et al.*, 2007). Thus, to identify the relative importance of determinism *versus* stochasticity of tree species in various forest types and life stages is an issue of general interest to community ecology.

Temperate forest communities are expected to be more niche-determined (*i.e.*, deterministic) compared to tropical forests (Nakashizuka, 2001). This idea, however, has not yet been fully tested by actual demographic data of trees in a forest community. Furthermore, even if regeneration in a temperate forest is really regulated deterministically, few studies have been done to show whether the density- or distant-dependent biotic factors operate for the majority of the species within a community to facilitate species coexistence (as proposed by the Janzen–Connell model) or regeneration is affected more by abiotic factors. To understand the species coexistence mechanisms in temperate forests, we need to evaluate the commonness and relative importance of the deterministic (biotic and abiotic) and stochastic factors for each component tree species.

In this study, we analyzed comparative demography of seeds and seedlings in a temperate forest community to test the following working hypotheses. First, that the overall regeneration in the forest community is deterministically controlled. In this case, statistical models of seed and seedling survival constructed with abiotic and/or biotic factors as explanatory variables should depict the regeneration processes of the component tree species well. The alternative hypothesis is that the regeneration processes of temperate forest trees are stochastic, as proposed in tropical forests. Second, specific regeneration traits relating to seed dispersal ability are highly correlated with the relative importance of each biotic and abiotic factor and of deterministic *versus* stochastic processes. The seedlings of typical seed-rain type (Grime, 1979) species will be vulnerable to both biotic and abiotic environmental stresses (*e.g.*, deficiency of light and/ or soil moisture) because they produce many small seeds (de Chantal *et al.*, 2003; Yoshida *et al.*, 2005; Masaki *et al.*, 2007), and their regeneration will be more deterministic. Thus, we hypothesized that species of different seed dispersal ability will vary in influential factors, resulting in niche partitioning among species. The alternative hypothesis is that there will be no conspicuous difference in influential factors among species in a community.

We tested these hypotheses using a quantitative evaluation of seed and seedling demography for major species across multiple years over various site conditions within an old-growth temperate forest community (see Clark *et al.*, 1999; Wright *et al.*, 2005). We have monitored the spatio-temporal variation of seed fall, seedling emergence, and survival of 18 principal species in a temperate deciduous forest, the Ogawa Forest Reserve, for more than 12 y. Using this long-term quantitative data, we assessed the following specific questions: (1) To what extent can we predict seedling emergence and survival by statistical models incorporating the biotic and abiotic factors? (2) Are there any correlations between seed dispersal ability and the existence or non-existence of deterministic effects of biotic and abiotic factors?

Methods

STUDY SITE AND SPECIES

This study was conducted in a 6-ha permanent plot in the Ogawa Forest Reserve (OFR), located in the southern part of the Abukuma Mountains, central Japan (36º 56' N, 140º 35' E, elevation 610–660 m). This forest is an old-growth temperate deciduous forest. Canopy gap dynamics have been the main disturbance since the forest was designated as a reserve (Tanaka & Nakashizuka, 1997). The dominant canopy species are *Quercus serrata*, *Fagus japonica*, and *F. crenata* in descending order of basal area. Eighteen of the principal tree species, including these 3 dominant species, were chosen for the study (Table I). There is large variation of seed dispersal ability in this forest community because of large differences in seed size among tree species.

SEED AND SEEDLING DEMOGRAPHY

Seed fall, seedling emergence, and current-year seedling survival have been monitored (Figure 1) as described below. Seed fall data from 1987 to 1999 (12 y) and seedling census data from 1988 to 2001 (13 y) were used for this

TABLE I. Characteristics of 18 tree species studied in Ogawa Forest Reserve, Japan.

Family	Species	Abbreviations	Density (ha⁻¹)	Basal area (m²·ha⁻¹)	Seed weight (g)
Betulaceae	*Betula grossa*	BTG	6.5	0.58	0.0005
	Carpinus laxiflora	CRL	88.5	1.36	0.003
	Carpinus japonica	CRJ	11.3	0.28	0.005
	Carpinus cordata	CRC	84.8	0.68	0.008
	Carpinus tschonoskii	CRT	15.8	0.61	0.015
	Ostrya japonica	OSJ	12.0	0.83	0.006
Aceraceae	*Acer amoenum*	ACA	81.2	0.92	0.008
	Acer rufinerve	ACR	16.3	0.36	0.016
	Acer mono	ACM	29.5	0.89	0.023
Araliaceae	*Kalopanax pictus*	KAP	3.0	0.69	0.002
Rosaceae	*Prunus verecunda*	PRV	15.5	0.78	0.011
Cornaceae	*Swida controversa*	SWC	25.0	1.16	0.032
Styracaceae	*Styrax obassia*	STO	95.5	0.80	0.120
Fagaceae	*Fagus crenata*	FGC	18.8	2.77	0.109
	Fagus japonica	FGJ	113.8	6.66	0.121
	Quercus serrata	QRS	55.3	8.58	0.810
	Quercus crispula	QRC	9.5	1.20	1.600
	Castanea crenata	CSC	10.8	1.34	1.460
	Total of studied species		693.1	30.50	
	Total of all species in 6-ha plot		864.2	32.35	

study. In 1987, 221 seed traps with a surface area of 0.5 m² were placed at regular intervals in a 1.0-ha subplot in the centre of the 6-ha plot. Fallen seeds were identified and counted according to their condition (sound, immature, eaten by insects, or eaten by vertebrates) at each seed trap. In 1989, the subplot was extended to 1.2 ha and 42 extra seed traps were added. From 1993 to 1999, the number of traps in the subplot was reduced to 143. Adjacent to every trap, a 1-m² seedling quadrat was set. Newly emerged seedlings were tagged as current-year seedlings, and their survival condition was checked at the end of the growth season (mainly early October) every year. In 6 gaps that were newly formed from 1987 to 1993 around the subplot, we also placed a total of 66 sets of seed traps and quadrats. Detailed descriptions of the seed and seedling censuses were presented in Shibata and Nakashizuka (1995) and Tanaka (2002).

FACTORS TO EXPLAIN SEEDLING EMERGENCE AND SURVIVAL

To explain seedling emergence and survival, we surveyed 3 biotic factors and 5 abiotic factors in each seedling quadrat as follows. (1) Seed density: We estimated the seed density of each species from the number of sound seeds that had fallen into each seed trap. (2) Seedling density: Seedling density was calculated by counting the number of conspecific seedlings that had emerged in each quadrat. See the methods for details on both seed and seedling density. Seed density was put to the regression models of seedling emergence, and seedling density was put to those of seedling survival, mentioned below. (3) Distance from nearest conspecific adult: Individual size of adult trees was estimated by measurement of DBH at onset of fruiting for each species (Shibata & Tanaka, 2002), and all trees that had grown to adult size were mapped in the 6-ha plot. We then calculated the distance from the trunk of the nearest conspecific adult tree to each seedling quadrat. (4) Litter and humus cover, and (5) vegetation cover: In early April, just before the herbaceous vegetation emerged, a photograph of the forest floor was taken in each seedling quadrat to survey substrate condition. From the photograph, the proportion of litter and humus cover in a quadrat (denoted as coverage of

humus) was measured. In mid July, after the vegetation had emerged and covered the ground, photographs were taken again, and the proportion of vegetation cover was measured. This observation was made in 1989 and 2000. The value ranged from 0 to 99% for vegetation cover and from 2 to 100% for litter and humus. (6) Light level: Canopy openness was used as an index of light levels. Hemispherical canopy photographs were taken at a height of 1.0 m above the ground with a fish-eye lens in the season when the forest canopy was closed. The proportion of open canopy in each photograph was measured. This observation was made in 1988, 1990, and 2000. The index for diffuse light ranged from 0.2 to 8.6%. (7) Soil moisture: Mineral soil samples were collected beneath each seed trap 2 d after the last rainfall. Volumetric water content was calculated for every sample. This observation was done in 1992 and 2006. The value ranged from 6.5 to 39 g·100 cm⁻³. (8) Relative elevation: Since the slopes in the 1.2-ha subplot were relatively uniform and facing each other, relative elevation itself could be considered as an index of topographical position, with a gradient from valley to ridge. We classified the locations of the seedling quadrats into one of 4 categories (1: valley, 2: lower slope, 3: upper slope, and 4: ridge).

A detailed description of these surveys was given in Shibata and Nakashizuka (1995). The canopy dynamics of OFR has been relatively stable in the last decade (Tanaka & Nakashizuka, 1997). There have been no remarkable disturbances of the forest floor such as landslides in the study area, and the annual fluctuation of all of the 5 abiotics factors is not great.

ANALYSES

GENERALIZED LINEAR MODEL OF SEEDLING EMERGENCE AND SURVIVAL

To evaluate factors affecting seedling emergence, we calculated the probability of fallen seeds to emerge as seedlings using the following equation:

$$E/F = \exp(a + b_1 x_1 + b_2 x_2 + \ldots + b_n x_n + \text{error}) \quad [1]$$

where E is the number of emerged seedlings in each quadrat (1 m^2) as a dependent variable, and F is double the number of fallen seeds in the adjacent seed traps (0.5 m^2). The independent variables are $\{x_1, \ldots, x_n\}$, and $\{a, b_1, \ldots, b_n\}$ are unknown parameters. By transforming this equation, the number of seedlings in each quadrat was modeled (denoted as RMEmer) by the equation:

$$\log(E) = \log(F) + a + b_1 x_1 + b_2 x_2 + \ldots + b_n x_n + \text{error} \quad [2]$$

Parameters were estimated by a Poisson regression model (see Masaki *et al.*, 2007). To estimate the general trend of seedling emergence, the total number of seedlings over the entire study period was used as E and average values of each factor were used as x_i. To evaluate the accuracy
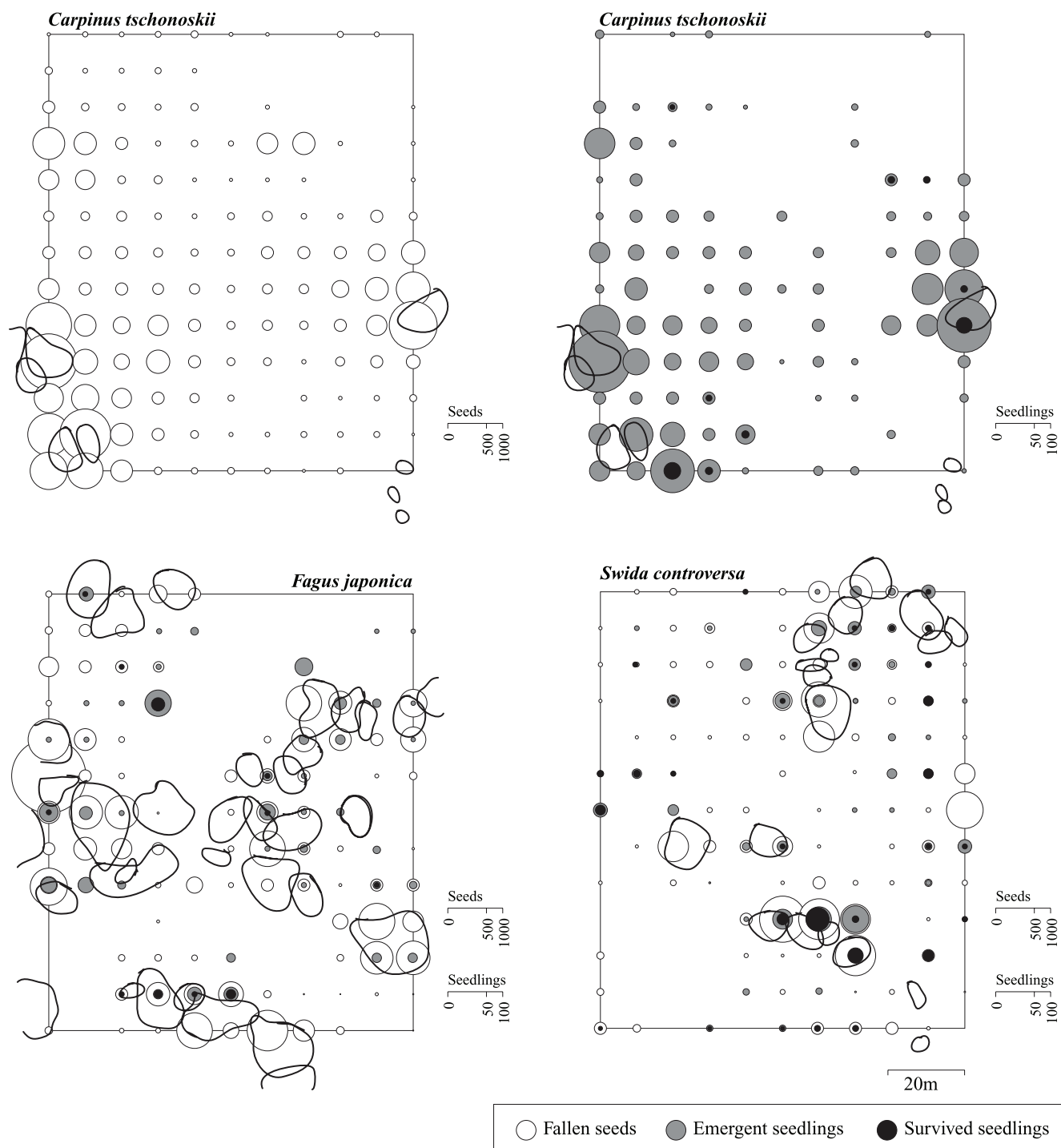

FIGURE 1. Examples of spatial pattern of seed fall, seedling emergence, and survival. Number of fallen seeds (white circles), emerged seedlings (grey circles), and survived seedlings (black circles) in the 1.2-ha plot is shown. The crowns of conspecific adult trees in and within 20 m of the boundary of the 1.2-ha plot are shown as outlines.

of fitting results, an index was calculated using residual deviance for the model (D) and for a model without any variables (D_0) with the equation, $(D_0 - D)/D_0$, denoted as the "coefficient of determination".

Three types of RMEmer were constructed. The first model was the "biotic factors model". Independent variables were the 2 biotic factors, conspecific seed density and distance from the nearest conspecific adult. The second model was the "abiotic factors model". Independent variables were the 5 abiotic factors, litter and humus cover, vegetation cover, light level, soil moisture, and relative elevation. The coefficients of determination of these 2 models were compared to evaluate the contribution of the 2 biotic factors or the 5 abiotic factors to seedling emergence. The third model was the all-factors model, in which all 7 factors were independent variables. In the third model, the partial regression coefficient (denoted as PRC) by x_i was calculated to evaluate the degree of effect of each factor.

In the third model, we also examined annual variability in the accuracy of the model fitting and the response (positive or negative effect) to the factors. In this model, not only the total number of seedlings over the entire study period but also the number of seedlings in each year was used as E. However, several species in this study have a transient seed bank. To relate the cohort of seeds to that of seedlings, we determined the delayed germination year of each species from a time-series analysis between the number of fallen seeds and emerged seedlings. Then, depending on the delayed germination year, data on the seed density of the preceding 1 or 2 y was used as x_i. For other x_i, data for the nearest measurement year were used.

Seedling survival was analyzed with a logistic regression model (hereafter, RMSurv):

$$\text{logit}(\pi) = a + b_1 x_1 + b_2 x_2 + \ldots + b_n x_n + \text{error} \qquad [3]$$

where π is the dependent variable, probability of mortality of current-year seedlings. Independent variables, x_i, were the biotic factors conspecific seedling density and distance from the nearest conspecific adult and the 5 abiotic factors used in RMEmer. The combination of the 3 models compared was also the same as in RMEmer. The R software (R Development Core Team, 2008) was used for all the analyses.

INTERSPECIFIC VARIATION OF REGENERATION IN A COMMUNITY

To characterize interspecific variation of regeneration within a community, we made 2 types of correlation analyses. First, to examine whether the deterministic fate of seedling emergence was related to seed dispersal ability, coefficients of determination in the all-factors model of RMEmer (fitness of the model on seedling emergence) were correlated to 4 parameters: seed size, fecundity, seed shadow area, and survival ratio of current-year seedlings, described below. Then, to identify the factors closely related with seed dispersal ability, the PRC of each independent variable in the all-factors model of RMEmer (effect level of each factor on seedling emergence) was correlated with the 4 parameters. The same analyses were also done for RMSurv. The resulting coefficients of correlation were tested with respect to phylogenetic constraints using the independent contrasts

method (CAIC) (Purvis & Rambaut, 1995). The phylogeny of the species in this study came from Chase *et al.* (1993).

The 4 parameters of seed dispersal ability were used as indices of seed rain type, one of common regeneration traits. The parameters were defined and estimated for each species as follows. (1) Seed size: Dry weight of seed kernels. (2) Fecundity: Number of seeds produced per tree per year. Average sound seed fall density ($\text{ha}^{-1} \cdot \text{y}^{-1}$) in the 1.2-ha area was divided by the mean number of parent trees (seed-bearing trees) in this area during the observation period. Details were described in Tanaka *et al.* (1998). (3) Seed shadow area: Because our seed traps were regularly placed like a lattice (Figure 1), the sum of the number of seed traps that had more than a certain number of seeds was used as an index of seed shadow area. To estimate average seed shadow area for each species, the number of seed traps in which fallen sound seeds per year was more than 1 was divided by the number of adult trees in the 1.2-ha plot. (4) Survival ratio of current-year seedlings: The average number of survived current year seedlings ($\text{m}^{-2} \cdot \text{y}^{-1}$) was divided by the average number of emerged seedlings ($\text{m}^{-2} \cdot \text{y}^{-1}$) in the 1.2-ha plot.

Results

SUMMARY STATISTICS OF BIOTIC AND ABIOTIC MODELS

In the RMEmer, the coefficient of determination of the biotic factors model was greater than that of the abiotic factors model for most of the species (Figure 2). The values of coefficient ranged from 1% to 64% (average 23%) for the
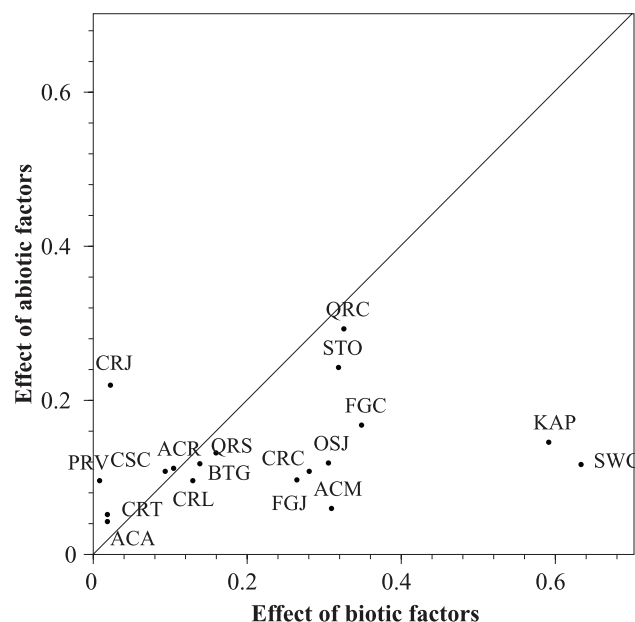

FIGURE 2. Relative importance of biotic factors *versus* abiotic factors for seedling emergence. Coefficient of determination of RMEmer (the multiple Poisson regression models of seedling emergence) for the biotic factors model is compared to that for the abiotic factors model. Independent variables of the biotic factors model are conspecific seed density and distance from the nearest conspecific adult for each species. Those of the abiotic factors model are litter and humus cover, vegetation cover, light level, soil moisture, and relative elevation. See text for a detailed explanation of the models' construction. Abbreviation of each species is the same as in Table I.

biotic factors model and from 4% to 29% (average 13%) for the abiotic factors model.

In RMSurv, however, the coefficient of determination of the biotic factors model was smaller than that of the abiotic factors model (Figure 3). The coefficient of determination of the model ranged from 0.1% to 21% (average 3%) for the biotic factors model and from 0.2% to 29% (average 7%) for the abiotic factors model.
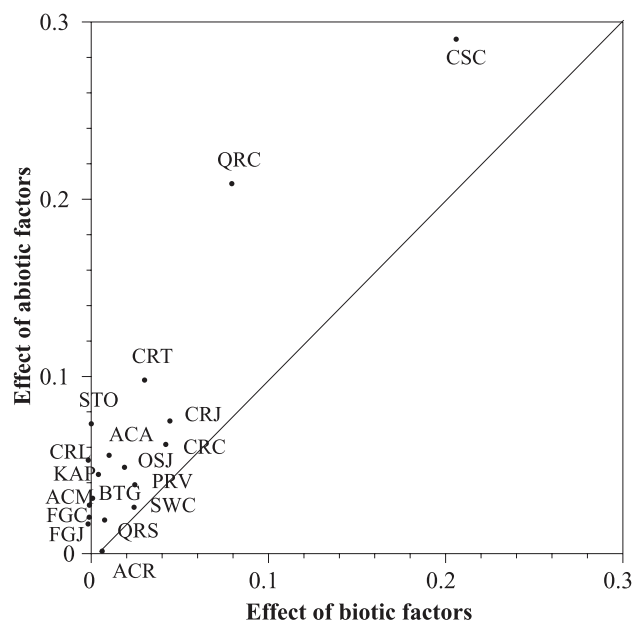

FIGURE 3. Relative importance of biotic *versus* abiotic factors for current year seedling survival. Coefficient of determination of RMSurv (the multiple logistic regression models of seedling survival) for the biotic factors model is compared to that for the abiotic factors model. Independent variables of the biotic factors model are conspecific seedling density and distance from the nearest conspecific adult for each species. Those of the abiotic factors model are the same as those for RMEmer. Abbreviation of each species is the same as in Table I.

SUMMARY STATISTICS OF ALL-FACTORS MODELS

In RMEmer, the coefficient of determination of the all-factors model ranged from 8% to 68% (average 32%) for the models in which the total number of seedlings over 12 y was regressed (Table II) and from 16% to 58% (average 32%) for the models in which the number of seedlings was regressed for each year. In RMSurv, this coefficient ranged from 1% to 46% (average 10%) for the former (Table III) and from 3% to 59% (average 17%) for the latter.

In the all-factors model of RMEmer, seed density had a significantly negative effect on seedling emergence for 15 of 18 species, and this trend was consistent among years for 13 species (Table II). Various abiotic factors were also significant, especially for the species of Betulaceae and Aceraceae. Whether the values of the parameters were positive or negative (*i.e.*, the sign of the parameters), however, was often inconsistent among years.

In RMSurv, on the other hand, seedling density had no significantly negative effect for any species but *Swida controversa* (Table III). Distance from the nearest conspecific adult had a positive effect for 4 of 18 species. Light level and litter and humus cover had a significantly negative effect for 10 and 7 species, respectively. Vegetation cover and relative elevation had significantly positive effects less frequently (4 and 8 species, respectively). The sign of the parameters was mostly consistent among years.

SEEDLING EMERGENCE AND SURVIVAL IN RELATION TO SEED DISPERSAL ABILITY

Two parameters of seed dispersal ability were related to the PRC of some of the factors estimated by RMEmer. Fecundity had a significantly positive relationship with the PRC of litter and humus cover ($r = 0.58$, $P < 0.05$). Seed shadow area also had marginally significant and positive relationships with litter and humus cover ($r = 0.47$, $P \approx 0.07$). These results mean that species with greater seed dispersal ability are more affected by local substrate composition

TABLE II. Factors affecting seedling emergence in the GLM. Plus (or minus) sign of estimated parameters and coefficient of determination of the multiple Poisson regression models (all-factors model) are shown. Parentheses indicate that the sign of the parameters varied among years. ($+++$, $---$: $P < 0.001$; $++$, $--$: $P < 0.01$; $+$, $-$: $P < 0.05$)

	Biotic factors		Abiotic factors					Coefficient of determination
	Seed density	Distance	Litter and humus	Vegetation	Light	Soil moisture	Relative elevation	
Betula grossa	$---$	$--$	$---$		$(+)$	$(---)$	$(---)$	0.22
Carpinus laxiflora	$(---)$	$(-)$	$---$	$+++$	$---$	$+++$	$(+++)$	0.29
Carpinus japonica	$(--)$			$(---)$	$---$		$+++$	0.24
Carpinus cordata	$---$	$---$	$(-)$				$(---)$	0.35
Carpinus tschonoskii	$---$		$---$	$+++$		$+++$	$---$	0.10
Ostrya japonica	$---$		$-$	$(++)$	$++$		$+++$	0.39
Acer amoenum	$---$		$-$	$(+++)$	$---$			0.08
Acer rufinerve	$---$	$---$	$---$	$++$		$-$		0.19
Acer mono	$---$		$(+++)$	$(-)$	$(---)$	$(+++)$	$(--)$	0.36
Kalopanax pictus						$-$		0.64
Prunus verecunda						$+$	$+$	0.11
Swida controversa	$---$	$---$	$(+++)$		$---$	$(+++)$	$+++$	0.68
Styrax obassia	$---$	$-$		$-$				0.39
Fagus crenata	$---$			$++$			$---$	0.48
Fagus japonica	$---$	$+++$				$---$	$---$	0.36
Quercus serrata	$---$	$---$	$(++)$				$(+++)$	0.28
Quercus crispula								0.38
Castanea crenata	$--$				$-$			0.20

during the seedling emergence process. However, these 2 parameters had no significant correlation with the coefficient of determination of RMEmer. The other 2 parameters, seed size and survival ratio of current year seedlings, did not have a significant correlation with either the PRC of each factor or the coefficient of determination in RMEmer.

At the seedling survival stage, the survival ratio of current-year seedlings had a positive relationship with the PRC of seedling density ($r = 0.83$, $P < 0.001$) and light level ($r = 0.77$, $P < 0.01$). This parameter also had a positive correlation with the coefficient of determination of RMSurv ($r = 0.64$, $P < 0.01$). Besides this, fecundity had a marginally negative correlation with the coefficient of determination of RMSurv ($r = –0.54$, $P < 0.1$), suggesting that less fecund species tend to have a more stochastic seedling demography.

Discussion

Temperate forest communities are expected to be more niche-determined than determined by chance compared to tropical forests (Brokaw & Busing, 2000; Nakashizuka, 2001). However, the regression models of both seedling emergence and survival in this study showed low values of the coefficients of determination (Tables II and III). Also, the models on seedling emergence showed inconsistent effects of abiotic factors among years (Table II). These results suggest that the deterministic factors tested in this study can explain only a small part of seed and seedling demography. At least for the seed and seedling stages, there appeared to be no conspicuous differences among species in terms of dependency on biotic and abiotic factors, and niche partitioning among the species at these regeneration stages was not obvious. Neutral theory was proposed at first to explain the maintenance of abundant species richness in tropical forests (Hubbell, 2001), but a similar mechanism might also operate in temperate forests.

This result is partly attributable to the small spatial variation in abiotic factors in this forest. The topography is mostly gentle, and extremely wet sites such as swamp or xeric sites such as thin ridge are not found in the study forest. The frequency of chance events such as new large canopy-gap creation has been low for the past several decades (Tanaka & Nakashizuka, 1997). Thus, the abiotic environmental conditions in this forest are not very spatially heterogeneous. Such abiotic environmental conditions could result in the narrow range of responses of seeds and seedlings. This may have led to the low importance of the deterministic factors in contributing to the variable regeneration patterns in comparison to stochasticity in this stable forest. While several deterministic factors were found to have significant effects on both seedling emergence and survival, such effects are expected to be almost negligible and not affect species assembly substantially unless environmental variation becomes greater. If rare and large disturbances (e.g., landslides, forest fire, large gap creation) expand the range of environmental gradients, abiotic factors may have substantial weight for niche partitioning among species (D. Nagamatsu, Y. Kominami & T. Manabe, unpubl. data). That the relative importance of niche partitioning depends on rare disturbance events is an issue to be tested in the future to confirm the generality of the results of this study.

While significant effects of abiotic factors were limited, the effects of biotic factors were more common and variable among the regeneration stages. At seedling emergence, the contribution of biotic factors was generally large (Figure 2). A negative effect of seed density was common among most of the species (Table II). Such negative density-dependent effects might result from seed predation or species-specific fungal attack at the post-seed-dispersal stage (Tanaka, 1995; Masaki et al., 1998). On the other hand, for survival of current-year seedlings, the effects of biotic factors (i.e., negative effect of seedling density) were generally weak (Figure 3), but a positive effect of distance from a conspecific adult occurred for several species (Table III). Thus, these biotic factors mostly operating

TABLE III. Factors affecting seedling survival in the GLM. Plus (or minus) sign of estimated parameters and coefficient of determination of the multiple logistic regression models (all-factors model) are shown. Parentheses indicate that the sign of the parameters varied among years. ($+++$, $---$: $P < 0.001$; $++$, $--$: $P < 0.01$; $+$, $-$: $P < 0.05$)

| | Biotic factors | | Abiotic factors | | | | | |
	Seedling density	Distance	Litter and humus	Vegetation	Light	Soil moisture	Relative elevation	Coefficient of determination
Betula grossa							+	0.04
Carpinus laxiflora			--	+++	(---)	(---)	+++	0.05
Carpinus japonica								0.12
Carpinus cordata		+			---			0.09
Carpinus tschonoskii			---	++	---		++	0.13
Ostrya japonica		+				+	++	0.09
Acer amoenum		+++	---	+++	---			0.07
Acer rufinerve		–						0.01
Acer mono			–	+++	---		+++	0.03
Kalopanax pictus					---			0.06
Prunus verecunda	+							0.08
Swida controversa	–	+++	---		---		+	0.06
Styrax obassia					---		+++	0.09
Fagus crenata								0.02
Fagus japonica							+++	0.02
Quercus serrata	+++		---		(--)			0.03
Quercus crispula			–					0.31
Castanea crenata	++				--			0.46

at the seed-to-seedling stage may have the potential to contribute to the replacement of species in a community, partly supporting the Janzen–Connell model as a coexistence mechanism in this temperate forest community.

Significant effects of abiotic factors were detected at both the seedling emergence and the survival stages, but also in a variable manner among the regeneration stages. At the emergence stage, the effects of these factors were inconsistent among years (Table II), and the contribution of demographic variation was not large (Figure 2). In other words, the same factor showed both positive and negative effects on seedling emergence depending on the year. Although the cause of this variation is still unclear, what is obvious is that demography at the seedling emergence stage is unpredictable in terms of abiotic environments. At the seedling survival stage, the effects of the abiotic factors were consistent among years (Table III), and their contribution was generally larger for most of the species (Figure 3). However, the significant effects of the factors did not meet with our expectations. For instance, the effect of light was negative, and that of vegetation was positive (Table III). We still do not have any explanation for these unexpected results. Further study on the effects of the abiotic environment is needed.

Large variation in seed dispersal ability among species on the order of 10^5 for seed size, 10^4 for fecundity, and 10^2 for seed shadow area (Shibata & Tanaka, 2002; Tanaka & Kominami, 2002) may result in large variation in dependence on abiotic factors at the regeneration stages. Our expectation is that seed-rain–type species with high seed dispersal ability, which increases the probability of reaching safe-sites, that is, a favourable environment for germination and establishment (Howe & Smallwood, 1982; Willson, 1992), tend to have small and vulnerable seedlings (Nakashizuka *et al*., 1995) and should be strongly regulated by abiotic factors during various stages of regeneration. The results of this study partly support this prediction, especially for species of Betulaceae (Table II), a typical seed-rain species (Shibata & Nakashizuka, 1995; Yoshida *et al*., 2005). At the seedling emergence stage, seed dispersal ability is still significantly correlated with PRC (effect level) of litter and humus cover after phylogenetic constraints were considered. However, the coefficients of determination of RMEmer were not correlated significantly with any of parameters relating to seed dispersal. Furthermore, the survival ratio of current year seedlings, which has a trade-off relationship with seed dispersal ability (T. Nakashizuka, unpubl. data), had a significantly positive relationship with the coefficient of determination of RMSurv. This suggests that species of greater dispersal ability (*i.e*., seed-rain type) tend to be rather less regulated by deterministic factors at the seedling stage. From these results, we think that the species with different seed dispersal traits do not simply partition their niches via deterministic abiotic factors at the seed and seedling stages.

In conclusion, most of the results in this study suggested that seed and seedling demography of trees was only slightly determined by the factors tested in this forest. Generally, the initial stages of life history are considered to be the most vulnerable to environmental stresses, and performance of the species is likely to be differentiated at these stages. However, there were no conspicuous differences in seed and seedling demography among species in terms of response to abiotic environmental variation in this temperate forest, just as postulated in neutral theory for tropical forests. This may suggest that the fundamental mechanism of forest dynamics and maintenance of species richness is similar between tropical and temperate forests. However, the topographic niche segregation among the adult tree species of the studied forest reported by Masaki *et al*. (1992) strongly suggests variation in seed and seedling demography among species. Several reasons are likely to explain this discordance. First, the current forest structure still reflects large disturbances of the past (Masaki *et al*., 1992). At present, this forest has become mature and relatively stable. This may be a reason why the current rules of seed and seedling demography as prescribed by the present environmental variation fail to explain the present distributional patterns of trees. Second, unmeasured factors may be critical to an explanation of spatial variation of seed and seedling demography. For example, spatial variation in the composition of ectomycorrhizal fungi (*e.g*., Peay *et al*., 2010) may have deterministic effects on seed and seedling fate. Other possible unknown factors also need to be explored. Third, growth and survival at later stages of life history can differ among species (*e.g*., Tanaka *et al.*, 2008). To test these other possibilities and to develop a more general theory of species coexistence in forests, comparative systematic study of tree life history using unified methods for both temperate and tropical forests will be necessary.

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