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Abstract. Shrubs persist in the understorey layer of forests throughout their lives, while tall trees remain there only during the juvenile stage and then grow into the canopy layer. Thus demographic parameters (recruitment-, mortality-, and growth-rates) of shrub species are expected to differ from those of tall tree species. We investigated aspects of the demography of four dominant deciduous-shrub species (*Viburnum furcatum, Lindera umbellata* var. *membranacea, Magnolia salicifolia*, and *Hydrangea paniculata*) in *Fagus crenata* forests at the beginning and at the end of a 7-yr period in a 1-ha permanent plot. For each species, the number of stems changed little (within ± 10%) during the study period, while total basal area increased markedly (11.7 - 33.8%), because (1) new stems continuously recruited by vegetative growth replaced the substantial number of dead stems, and (2) vegetative stems grew vigorously, probably due to nutrient support from parents. The results indicate that these four understorey shrub species have high ability to maintain their population size in the shaded forest understorey. While in each species more than half of the dead stems were standing dead, a substantial proportion of the dead stems (9.0-38.5%) showed signs of mechanical damage, such as stem breakage and suppression by fallen branches or trees. Snow pressure that resulted in decumbent stems was also an important mortality agent for *V. furcatum* (20.7%) and *L. umbellata* var. *membranacea* (5.6%). Probability of damage was constant across all DBH-classes for all study species. In each species, newly recruited stems and dead stems were spatially aggregated, largely due to habits of vegetative growth and mechanical damage, respectively. This study revealed that several demographic traits, resulting from recruitment by vegetative growth and death by mechanical damage, were shrub-species specific and markedly different from those of tall tree species.

Keywords: Death; *Fagus*; Growth rate; Recruitment; Size structure.

Nomenclature: Ohwi & Kitagawa (1983).

Abbreviation: RDGR = Relative diameter growth rate.

Introduction

The population dynamics of plant species can be described by demographic variables such as the recruitment-, mortality-, and growth-rates of individuals (Watkinson 1997). The balance among these variables has been found to regulate the dynamics and the structure of a population (Hara 1984; Kohyama & Hara 1989). In addition, evidence that both abiotic and biotic environmental factors influence the demography has resulted in a deeper understanding of the population dynamics of a plant species (Silvertown & Lovett Doust 1993). Since in tree species the environmental factors such as light conditions and natural enemies (e.g. herbivores and pathogens) affect demographic variables slowly and continuously over a long period of time, long-term periodic observations provide the only reliable way of uncovering general patterns in tree demography and estimating the long-term fates of tree populations (e.g. Condit 1995).

Most demographic studies in temperate forest communities have focused on the dynamics of the dominant tree species. These studies have revealed species-specific values for demographic variables and, hence, differences in these variables among co-occurring tree species within a forest. These differences have been considered as important features determining population structure and changing in species composition with time in forest communities (Whitney 1984; Nakashizuka 1991; Welden et al. 1991; Poulson & Platt 1996; Foré et al. 1997; Namikawa et al. 1997; Masaki et al. 1999). The studies of understorey shrub species performed so far have mostly focused on static population structure; age and size structures consisting of many small, young stems and a few larger, old stems have been described by a negative exponential model (Tappeiner 1971; Yamanaka & Tamai 1986; Kurmis & Sucoff 1988; Tamai & Tenpo 1990; Tappeiner et al. 1991; Staiter et al. 1997). Authors of studies of population dynamics by

matrix models (Huenneke & Marks 1987; Cipollini et al. 1994) have focused on the relative importance of demographic variables influencing the population dynamics, but not evaluated the environmental factors affecting these demographic variables.

Demographic variables are usually affected by several biotic and abiotic environmental factors. Factors relevant for shrub species are not expected to be the same as for the dominant tree species because understorey shrub species persist in the understorey layer throughout their lives, while tall tree species remain there only during the juvenile stage and then grow into the canopy layer. Consequently, understorey shrub species must be able to tolerate low irradiance, while tall tree species experience more favourable light conditions with increasing tree height (Yoda 1974; Yamada & Suzuki 1996; Seiwa 1999). Many shrub species in the forest understorey therefore usually regenerate not only by seedlings but also by vegetative growth (sprouting, layering, and fragmentation; Koop 1987; Wilson 1995; Peterson & Jones 1997). If stems derived from vegetative growth have potential for future growth and survival in the forest understorey, such growth can be considered to be one of the adaptive behaviours for understorey species to persist in the forest understorey. Understorey shrub species may also be at larger risk of becoming mechanically damaged than overstorey tall tree species, due to debris falling from the overstorey. On the other hand, they are more sheltered from direct damage by wind (Harcombe & Marks 1983). There is, though, considerable need for direct evidence with respect to what kind of environmental factors affect the demographic characteristics of understorey shrub species.

To find out how shrubs persist in the forest understorey, we investigated demographic variables and causes of death in four dominant deciduous broadleaved species (*Viburnum furcatum*, *Lindera umbellata* var. *membranacea*, *Magnolia salicifolia*, and *Hydrangea paniculata*), species which are commonly observed in the understorey of *Fagus crenata* forests (Hukusima et al. 1991). *V. furcatum* and *L. umbellata* var. *membranacea* occur in understoreys of mid- to late-successional stages, and *M. salicifolia* and *H. paniculata* occur in understoreys of a wide range of successional stages in *Fagus crenata* forests. The four shrub species studied are characterized by vigorous sprouting from buds at the base of their stems (Yamanaka & Tamai 1986; Hara 1990; H. Kanno & K. Seiwa unpubl.). These four species have greatly reduced fruit production under closed canopy compared with gaps (Hara et al. 1999; H. Kanno & K. Seiwa unpubl. data). In each species, stems over 2 cm in diameter at breast height (DBH) were measured at the beginning and at the end of a 7-yr interval in a 1-ha permanent plot. We aimed at answering the following questions: (1) what kind of biotic and abiotic environmental factors influence the demography of understorey shrub species? (2) to which extent do demographic variables explain the population dynamics of understorey shrub species?

Methods

Study site

The study was carried out in an old-growth *Fagus crenata* forest (780 m in altitude) on Mt. Kurikoma (38° 57' 29" N, 140° 47' 31" E and 1628 m in altitude) in Miyagi Prefecture, northeastern Japan. There is little evidence of human disturbance in the study area. The soil is brown forest soil, which has developed from the debris and the matrix originating from an old pyroclastic flow. The mean annual temperature and precipitation measured at the nearest meteorological station, Komanoyu (3.5 km east of the study site, 570 m in altitude; observation period, 1979-1990), are 8.2 °C and 2072 mm, respectively (Anon. 1993). Snow falls from November to April and normally reaches a depth of 2 m from January to March. The dominant canopy species are *Fagus crenata*, which may reach 25 m in height and age of ca. 250 yr (Hara et al. 1991), *Quercus mongolica* var. *grosseserrata* and *Magnolia obovata*. The most important co-dominating ground cover species are dwarf bamboos such as *Sasa palmata* and *S. kurilensis*, and evergreen shrubs such as *Ilex crenata* var. *paludosa* and *Cephalotaxus harringtonia* var. *nana*.

Field data

Field surveys were conducted twice, 1989 and 1996, in a 1-ha permanent plot (100 m × 100 m; < 6° slope), which was divided into 100 contiguous quadrats (10 m × 10 m). Emergence of large canopy gaps (ca. 250-500m^2) created by uprooted *F. crenata* were recorded at the present study site in 1984, 1985 and 1989 prior to the present study period (Hara et al. 1991), but they were not recorded during the study period. To obtain data for demographic variables for four dominant shrubs (*V. furcatum*, *L. umbellata* var. *membranacea*, *M. salicifolia*, and *H. paniculata*), all stems with DBH > 2 cm were marked in 1989, and censuses of the DBH of all the surviving stems and newly recruited stems with DBH > 2 cm was repeated in 1996. All recorded deaths were classified into: standing dead (dead stems which suffered no injuries), stem breakage (dead stems broken by large fallen branches or whole trees), stem

suppression (dead stems pressed to the ground by large fallen branches or whole trees), and stem decumbency (dead stems broken near the ground surface by snow pressure).

Data analyses

To evaluate changes in size structure, differences in frequency distributions for DBH between 1989 and 1996 were analysed using Kolmogorov-Smirnov two sampling goodness-of-fit tests (Sokal & Rohlf 1995) for each shrub species. The 1989 and 1996 survey data were also used to calculate mortality and recruitment rates and rates of gain and loss in basal area for each shrub species by the following equations:

$$\text{Mortality rate (/yr)} = (N_d / N_l) / 7 \tag{1}$$

$$\text{Recruitment rate (/yr)} = (N_r / N_l) / 7 \tag{2}$$

$$\text{Rate of loss in basal area (/yr)} = (BA_d / BA_l) / 7 \tag{3}$$

$$\text{Rate of gain in basal area (/yr)} = ((BA_S + BA_r) / BA_l) / 7, \tag{4}$$

where N_d and N_r are the numbers of dead and recruited stems during the 7-yr period, respectively, and N_l is the number of living stems recorded in 1989. BA_d is the basal area in 1989 of the stems that died during the 7-yr period and BA_l that of stems alive in 1989. BA_S is the increase in basal area for stems surviving the 7-yr period, and BA_r is the basal area of the stems recruited in the 7-yr period, as recorded in 1996. Differences in mean mortality rate among the four shrub species were tested using G-tests (JMP statistical program; Anon. 1995). Differences in the distribution of deaths caused by standing dead, stem breakage + stem suppression, and stem decumbency were tested using G-tests among and within shrub species and among DBH-classes (2.1-2.5, 2.6-3.0, 3.1-3.5, and > 3.6 cm) for each shrub species. When an overall significant difference was found by G-tests, pairwise comparisons were performed and the significance level adjusted by the Bonferroni method: an overall adjusted p level of $\alpha = 0.05$ was at hand if at least one of the n tests resulted in a lower p value than α/n (Lehner 1996). Differences in mortality and recruitment rates among DBH classes were tested for each shrub species using χ^2-tests. Relationships between DBH in 1989 and the relative diameter growth rate (RDGR, year-1) were analysed for each species using Spearman's rank correlation tests (Sokal & Rohlf 1995).

To evaluate changes in the spatial structure of the four shrub species studied, the distributional patterns of stems alive both in 1989 and 1996 and stems recruited or dead during the study period were analysed by the I_δ-

index (Morisita 1959):

$$I_\delta = q \sum_{i=1}^{q} n_i(n_i - 1)/N(N - 1), \tag{5}$$

where q is the number of quadrats, n_i is the number of stems of the species in the i-th quadrat and N is the total number of stems in all quadrats. The index value equals 1.0 when the stems are randomly dispersed, is greater than 1.0 if the stems are aggregated, and less than 1.0 if the stems are evenly distributed or hyperdispersed. The significance of the departure of the I_δ-values from randomness was tested by using the F-statistic (Morisita 1959). The degree of spatial association between recruited and dead stems was analysed by calculating the ω-index (Iwao 1977), which varies from 1.0 for complete association, through 0 for independent occurrence, and to -1.0 for complete exclusion (Iwao 1977). The ω-index is calculated as:

$$\omega(+) = \frac{\gamma - \gamma(\text{ind})}{1 - \gamma(\text{ind})} \text{ for } \gamma \geq \gamma(\text{ind}) \tag{6}$$

or

$$\omega(-) = \frac{\gamma - \gamma(\text{ind})}{\gamma(\text{ind})} \text{ for } \gamma \leq \gamma(\text{ind}) \tag{7}$$

where

$$\gamma = \sqrt{\left(\frac{m_{dr}*}{m_r} \cdot \frac{m_{rd}*}{m_d}\right) \bigg/ \left(\frac{m_r*+1}{m_r} \cdot \frac{m_d*+1}{m_d}\right)} \tag{8}$$

and

$$\gamma(\text{ind}) = \frac{1}{\sqrt{\left(\frac{m_r*+1}{m_r} \cdot \frac{m_d*+1}{m_d}\right)}} \tag{9}$$

where m_r and m_r* are mean density and mean crowding of recruited stems, respectively, and m_d and m_d* are mean density and mean crowding of dead stems, respectively. In the equations, $m_{rd}*$ is mean crowding on recruited stems by dead stems and $m_{dr}*$ is mean crowding on dead stems by recruited stems. A 10 m × 10 m quadrat was used as the unit size for calculation of both the I_δ- and ω-indices. This quadrat size was considered to be reasonable after due consideration of size (i.e. maximum crown area and width of individual plant) of the four focal shrub species.

Results

Changes in population size with time

The total number of stems (DBH > 2 cm) of all species in the study plot in 1989 was 3154 (Table 1). *V. furcatum, L. umbellata* var. *membranacea, M. salicifolia*, and *H. paniculata* constituted 20.1%, 5.4%, 4.4%, and 2.0% of the total number of stems of all the species, respectively. From 1989 to 1996, there was little change in the number of stems (within ± 10%) for any of the four shrub species (Table 1), because their mortality rates were almost identical to their recruitment rates (Fig. 1A). Mean mortality rates differed significantly among the four shrub species (Fig. 1A, $G_3 = 103.75$, $n = 1006$, $p < 0.001$); the greatest mortality rate was observed in *L. umbellata* var. *membranacea*.

In contrast to the small changes in the number of stems, total basal area of the four shrub species increased markedly (11.7-33.8%) during the study period (Table 1), because loss rates were smaller than gain rates (Fig. 1B). Although the increase in total basal area was due both to growth of surviving as well as newly recruited stems, the relative contribution from these two groups differed among the four species; the proportion of the growth of newly recruited stems to the total gain was greatest for *L. umbellata* var. *membranacea* (72.5%), least for *M. salicifolia* (25.0%) and *H. paniculata* (21.9%), and intermediate for *V. furcatum* (51.1%). In overstorey trees, the total basal area changed little (Table 1) due to low frequency of gap formation during the study period.

Demographic parameters

For each shrub species, more than 50% of the stems in each size class at the initial survey had entered the next larger size at the second survey (7-yr after the first survey), and several stems even reached the size class above the next (Table 2). This rapid diameter growth was, in part, a result of a positive value of RDGR throughout the DBH-classes for all species (Fig. 2A), although RDGR decreased with increasing DBH_{1989} for *V. furcatum* ($n = 546$), *M. salicifolia* ($n = 112$), and *H. paniculata* ($n = 49$) (Fig. 2A, Spearman's r: $r_s < -0.127$, $p < 0.0087$). An exception was *L. umbellata* var. *membranacea*, which showed little change ($r_s = -0.072$, $n = 82$, $p = 0.521$).

Mortality rate differed only little among DBH-classes for each shrub species (Fig. 2B, χ^2 degrees of freedom-tests: *V. furcatum*, $\chi^2_3 = 4.41$, $n = 546$, $p = 0.22$; *L. umbellata* var. *membranacea*, $\chi^2_2 = 1.96$, $n = 171$, $p = 0.37$; *M. salicifolia*, $\chi^2_3 = 0.48$, $n = 140$, $p = 0.92$; *H. paniculata*, $\chi^2_4 = 4.58$, $n = 62$, $p = 0.33$). Recruitment rates of *V. furcatum* ($n = 785$), *M. salicifolia* ($n = 163$), and *H. paniculata* ($n = 78$) differed significantly among DBH-classes (Fig. 2C, $\chi^2_3 > 11.39$, $p < 0.01$), and were highest in the smallest DBH-class (< 2.5 cm). The exception was *L. umbellata* var. *membranacea* for which the difference was not significant ($\chi^2_2 = 4.67$, $n = 246$, $p = 0.096$).

Table 1. Changes in density and basal area of stems (DBH > 2 cm) for four dominant shrub species and the other woody species in the study plot (1-ha) during the 7-yr period from 1989 to 1996.

Species (Abbreviations)	Density (number of stems/ha)			Basal area ($\times 10^2$ cm² ha⁻¹)		
	1989	1996	Relative change (%)	1989	1996	Relative change (%)
Dominant shrub species						
Viburnum furcatum (Vf)	633	697	10.1	30.8	41.2	33.8
Lindera umbellata var. *membranacea* (Lm)	171	157	– 8.2	7.7	8.6	11.7
Magnolia salicifolia (Ms)	140	134	– 4.3	10.0	12.0	20.6
Hydrangea paniculata (Hp)	62	65	4.8	7.2	9.1	26.5
Other woody species						
Understory stems [a] (Understory)	1923	2045	6.3	255.4	330.4	29.4
Overstory stems [b] (Overstory)	225	218	– 3.1	3304.4	3363.9	1.8
Total	3154	3316	5.1	3615.4	3765.2	4.1

[a]Understory stems (15 cm ≥ DBH > 2 cm) included 25 tree, six shrub and two liana species (see Hara et al. 1991).
[b]Overstory stems (DBH > 15 cm) included 15 tree species (see Hara et al. 1991).
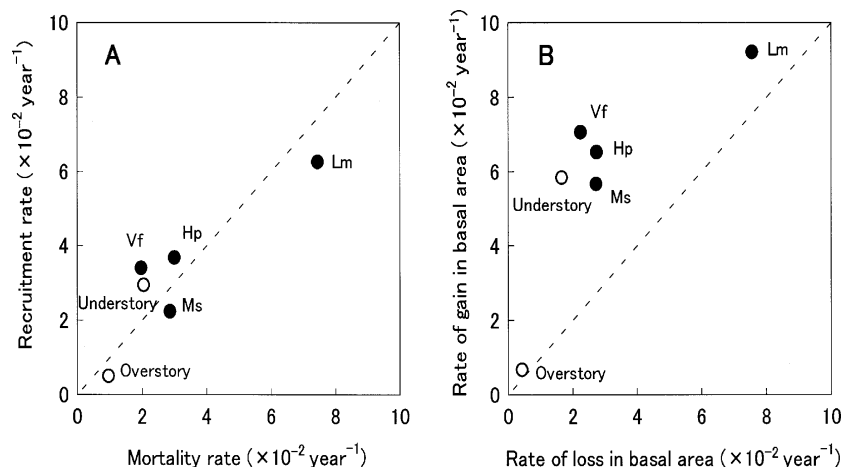
Fig. 1. Relationships between (**A**) recruitment and mortality rate and (**B**) rate of gain and loss of basal area for the four understory shrub species studied. Abbreviations of species names are given in Table 1.

Table 2. Transition matrix probabilities based on DBH-size classes for four dominant shrub species in the study plot (1-ha) during the 7-yr period from 1989 to 1996. Recruitment is not included in the transition matrices.

	DBH classes 1989			
DBH classes 1996	2.1 - 2.5	2.6 - 3.0	3.1 - 3.5	> 3.5
Viburnum furcatum				
2.1 - 2.5	0.43			
2.6 - 3.0	0.40	0.37		
3.1 - 3.5	0.09	0.44	0.24	
> 3.5	0.01	0.10	0.74	0.70
	2.1 - 2.5	> 2.5		
Lindera umbellata var. *membranacea*				
2.1 - 2.5	0.19			
> 2.5	0.31	0.37		
	2.1 - 2.5	2.6 - 3.0	3.1 - 3.5	> 3.5
Magnolia salicifolia				
2.1 - 2.5	0.18			
2.6 - 3.0	0.49	0.19		
3.1 - 3.5	0.07	0.27	0.20	
> 3.5	0.07	0.33	0.65	0.77

|	2.1 - 2.5	2.6 - 3.0	3.1 - 3.5	3.6 - 4.0	4.1 - 4.5	> 4.5
Hydrangea paniculata						
2.1 - 2.5	0.17					
2.6 - 3.0	0.44	0.08				
3.1 - 3.5	0.11	0.25	0.20			
3.6 - 4.0	0.11	0.33	0.40	0.10		
4.1 - 4.5	0.06	0.17		0.10	0.14	
> 4.5				0.40	0.71	0.80
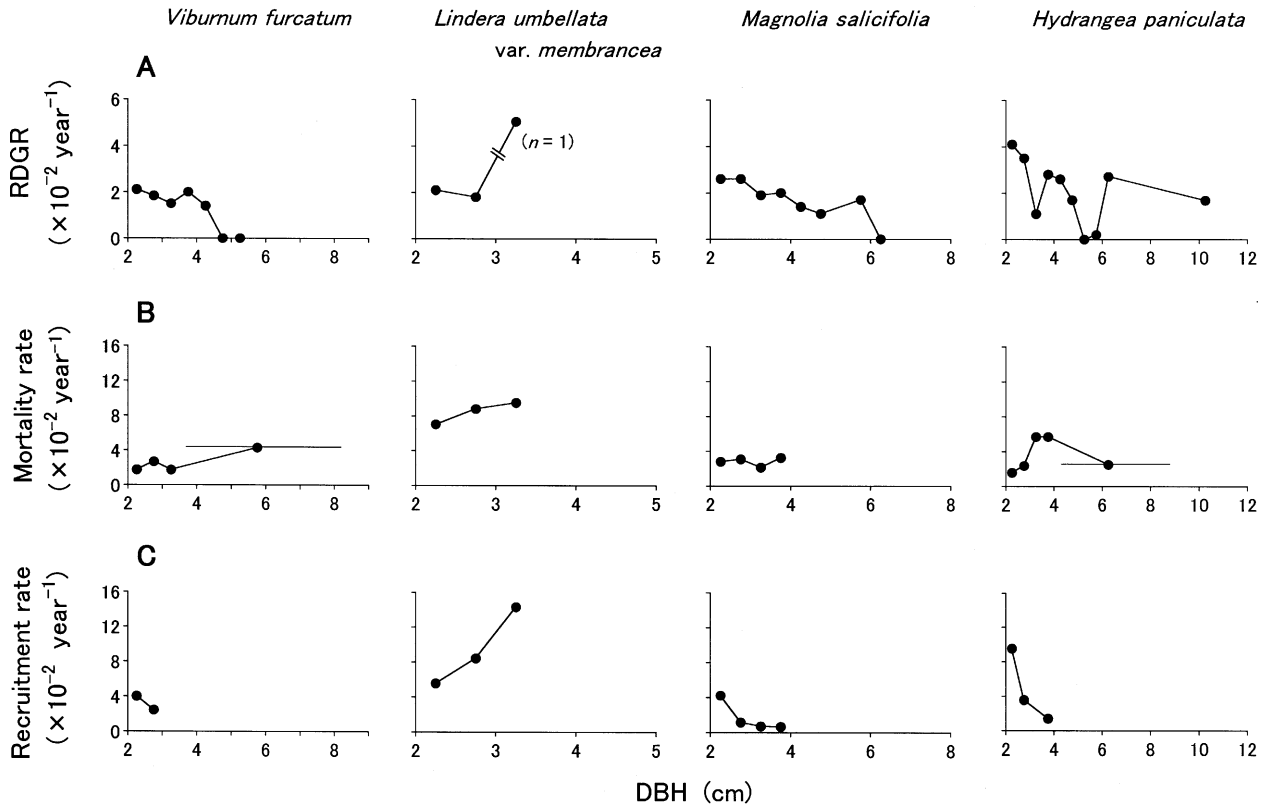
Fig. 2. Relationships between DBH in 1989 and (**A**) relative diameter growth rate (RDGR), (**B**) mortality rate and (**C**) recruitment rate for the four understorey shrub species studied. Bars represent the mean value for mortality rate across the range of DBH-classes in case of small sample numbers.

Changes in population structure with time

Although the frequency distribution for DBH for each of the shrub species was inversely J-shaped both in 1989 and 1996 (Fig. 3), the distributions in 1996 differed significantly from those in 1989 for *V. furcatum,* *L. umbellata* var. *membranacea,* and *M. salicifolia* (Kolmogorov-Smirnov test, $p < 0.028$), but not for *H. paniculata* ($p = 0.648$). For all species, the shape of the DBH distributions became more flat-topped (platykurtic), probably due to the higher RDGR of stems in the small size classes.
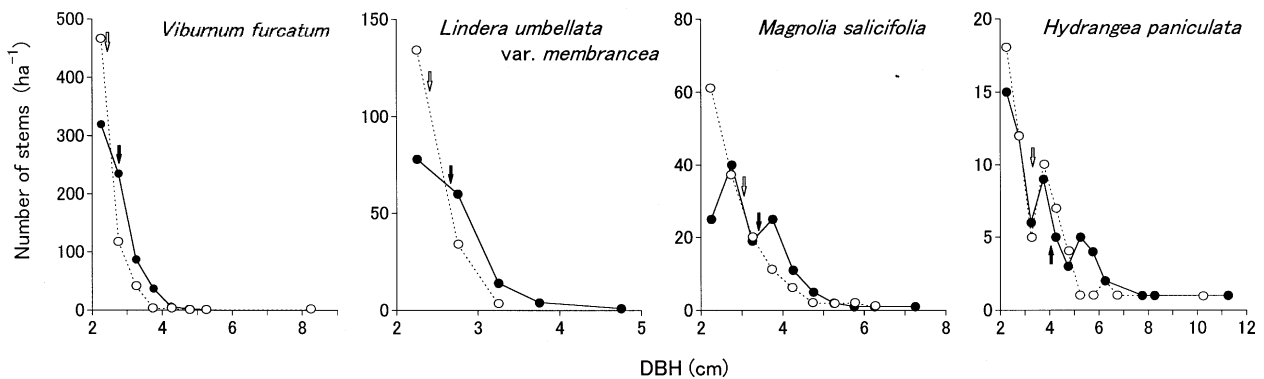
Fig. 3. Changes in the frequency distribution of stem diameter at breast height (DBH) for the four understorey shrub species studied (only stems with DBH > 2 cm included). White and black circles show the numbers of stems in each size class in 1989 and 1996, respectively. White and black arrows show mean DBH in 1989 and 1996, respectively.

Table 3. Causes of death in the four dominant shrub species. Numerals show the number of dead stems in the study plot (1-ha) during the 7-yr period from 1989 to 1996. The proportions (%) are shown in parentheses.

Species	Standing dead	Stem breakage	Causes of death Stem suppression	Stem decumbency	Total
Viburnum furcatum	54 (62.2)	5 (4.6)	10 (11.5)	18 (20.7)	87
Lindera umbellata var. *membranacea*	76 (85.4)	5 (5.6)	3 (3.4)	5 (5.6)	89
Magnolia salicifolia	24 (85.8)	2 (7.1)	2 (7.1)	0 (0.0)	28
Hydrangea paniculata	8 (61.5)	5 (38.5)	0 (0.0)	0 (0.0)	13

Causes of death

The distribution of recorded causes of deaths differed significantly between all pairs of the four shrub species (Table 3, overall test: $G_6 = 28.59$, $n = 217$, $p < 0.0001$, Bonferroni-adjusted $p < 0.05$), except between *M. salicifolia* and *H. paniculata*. Standing dead accounted for the greatest proportion of deaths for all shrub species (Table 2, $G_2 > 14.30$, $p < 0.001$) and stem breakage was the second most common cause of death in the four species (Table 3). In *H. paniculata*, stem breakage accounted for 38.5% of the total dead stems. Fallen large branches or whole trees also suppressed and killed members of shrub species other than *H. paniculata*. Decumbent stems accounted for 20.7% and 5.6% of total dead stems in *V. furcatum* and *L. umbellata* var. *membranacea*, respectively. The proportion of each death-cause was constant across DBH-classes in three of the species (*L. umbellata* var. *membranacea*, $G_4 = 6.63$, $n = 89$, $p = 0.157$; *M. salicifolia*, $G_3 = 1.12$, $n = 28$, $p = 0.772$; *H. paniculata*, $G_3 = 2.22$, $n = 13$, $p = 0.529$). In *V. furcatum* ($G_6 = 22.19$, $n = 87$, $p = 0.0011$), the proportion of standing dead was highest in the smallest DBH-class (< 2.5 cm).

Spatial patterns of dead- and recruited stems

The I_δ-indices showed that living stems, both in 1989 and 1996, and dead as well as recruited stems during the study period, had clumped distribution for all four shrub species (Table 4). The dead stems were spatially independent of recruited stems in *V. furcatum*, *L. umbellata* var. membranacea, and *M. salicifolia* (because the ω-indices were close to zero; Table 4) but not in *H. paniculata*, in which the ω-index was negative, indicating negative relationships between dead and recruited stems.

Discussion

This study shows that the four studied understorey shrub species differ from tall tree species in important demographic traits. These differences are likely to be caused by the dissimilarity in environmental conditions faced by shrubs and herbs, since while the former persist in the forest understorey layer throughout their lives, the latter remain there only during the juvenile stage before growing into the canopy.

In this study, standing dead (accounting for more than 50% of recorded deaths), fallen debris, and snow pressure were the three major causes of death for the four shrub species studied. Similar results have been observed also for a tall tree species in a *Fagus-Magnolia* forest, southeast Texas, in which ca. 80% of the dead

Table 4. Spatial distributions of living-, dead- and recruited stems in the study plot (1-ha) during the 7-yr period from 1989 to 1996.

Species	Living 1989	1996	I_δ-index Dead	Recruited	ω-index Dead vs. Recruited
Viburnum furcatum	1.7 ***	1.7 ***	2.7 ***	2.1 ***	–0.13
Lindera umbellata var. *membranacea*	1.5 ***	1.8 ***	1.5 **	2.7 ***	0.14
Magnolia salicifolia	2.9 ***	2.7 ***	3.4 ***	3.2 **	0.27
Hydrangea paniculata	3.3 ***	2.5 ***	9.0 ***	5.8 ***	–0.52

**$P < 0.01$; ***$P < 0.001$.

individuals were standing dead (Harcombe & Marks 1983). On the other hand, in the shrub species studied by us, mechanical damage, such as stem breakage, stem suppression, and stem decumbency were also important causes of death (14.2 - 38.5% of dead stems). Furthermore, the probability of death caused by mechanical damage was independent of stem size for all four shrub species. This represents an important difference from that of tall tree species, in which the probability of death decreases with increasing size (e.g. Harcombe & Marks 1983; Weldon et al. 1991). In *V. furcatum*, for example, a large fallen branch of a canopy tree (*F. crenata*) simultaneously suppressed five stems of different sizes, including adult stems. This evidence thus indicates that large fallen branches and overtopping of whole trees are important causes of the size-independent death of shrub stems, and that they contributed to the aggregated distribution of the shrub species. These results also suggest that the probability of death due to large fallen branches or whole trees is closely related to frequency and extent of canopy gap formation. Another type of mechanical damage observed in this study was decumbent stems that were broken near the base and pressed to the ground by snow pressure. Since sprouting stems of shrub species usually grow rapidly instead of investing in mechanical toughness (Givnish 1995; Wilson 1995), they are vulnerable to damage by snow pressure. This study shows that rates of size independent mortality caused by mechanical damage differ among shrub species that persist in the forest understorey throughout their lives, dependent on their life form. Furthermore, it demonstrates that the probability of death is size-independent in shrub species but size-dependent in tall tree species (e.g. Platt et al. 1988; Nakashizuka 1991).

For the four shrub species studied, the density of living stems changed little and their total basal area increased markedly during the study period, although gap formation and local improvement of light supply to the understorey hardly occurred. Several studies analysing the population dynamics of forest understorey shrubs by matrix models also demonstrate population growth rates that are constant and (slightly) positive for long time periods (Huenneke & Marks 1987; Cipollini et al. 1994). It is also well known that shrubs usually recruit new stems by means of vegetative growth (e.g. Tappeiner 1971; Staiter et al. 1997), and that such stems receive substantial support by translocation of carbohydrates from the mother stem (Wilson 1995). This is likely to explain the positive values for RDGR of all species studied, even under shaded conditions, and also support the view that physiological integration enhance the shade tolerance and survivorship of shrub species in the forest understorey. Long-lived perennial herbs (e.g. Nault & Gagnon 1993) and even bryophytes (Økland 1995, 1997)

on the forest floor also show relatively stable population behaviour over several years due to their habit of vegetative growth. These observations suggests that production of new shoots by vegetative growth and at least a minimum of physiological integration is important for these understorey plants (shrubs, herbs, and bryophytes), because they must persist under low-light conditions in the forest understorey layer throughout their lives.

Spatially aggregated distributions of newly recruited stems as observed in this study demonstrate that vegetative growth of understorey shrub species is demographically important. In addition, we also found that the distribution of the recruited stems was independent of that of dead stems for all shrub species studied except *H. paniculata*. These distribution patterns indicate that replacement of a dead stem by a newly recruited stem in the same place is not giving the new stem an advantage. This is because gaps created by dead shrub stems cannot provide favourable light conditions for the growth of their own sprouted stems in a forest understorey, although canopy gaps created by fallen tall trees usually improve the light conditions for their newly sprouted stems (e.g. Koop 1987; Peters & Ohkubo 1990; Ohkubo et al. 1996; Sonoyama et al. 1997).

Although the four shrub species generally showed similar demographic traits (e.g. causes of death and stem recruitment by means of vegetative growth), both mortality rates and rates of gain in basal area were greater in *L. umbellata* var. *membranacea* than in the other three species. These differences are presumably due to the life span of stems of *L. umbellata* var. *membranacea*, which is the shortest among the four shrub species; maximum stem age of *L. umbellata* var. *membranacea* is about half (25 - 27 yr; Tamai & Tenmo 1990; H. Kanno et al. unpubl. data) that of *V. furcatum* (53 - 62 yr), *M. salicifolia* (54 yr), and *H. paniculata* (45 yr; Hara 1990; Honma 1996; H. Kanno & K. Seiwa unpubl. data).

Several environmental factors influencing the demographic traits of the shrub species, as shown in our study of long-term measurements, would also provide the strong potential benefits to understand the population dynamics of shrub species if those are incorporated into matrix model (see Rydgren et al. 1998). The present study showed that understorey shrub species have several adaptive habits that enable them to persist in the light-limited forest understorey (e.g. continuous stem recruitment by vegetative growth), although they are always exposed to a high probability of death by mechanical damage. Their ability to recover from mechanical damage by vegetative growth seems to be the most important adaptive habit for the four understorey shrub species studied.

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