Life history strategies of temperate liana *Hydrangea petiolaris* and its implications for the evolution of lianas

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Contents

Summary

Lianas (woody vines) have distinctive growth form in terms of parasitic climbing to host tree, and they are diversified throughout a plenty of taxa and genera, playing important roles in forest community. However, information of lianas' life history has been very limited. In this study thesis, we tried to make clear the lianas' life history from the two different view point; (1) resource allocation and allometry, and productive structure, and (2) demography and habitat preference.

In Chapter 2.1, allometric analysis of four *Hydrangea* species (*H. petiolaris, H. paniculata, H. macrophylla* var. *megacarpa*, and *H. hirta*) was conducted to test the hypothesis that the liana species (*H. petiolaris*) invests more in leaves and reproductive organs than the shrub species. Whole plants of the four species were sampled during the flowering seasons, and dry weights of each organ (leaves, trunks, roots and reproductive organs) were compared between *H. petiolaris* and the shrubs. *H. petiolaris* differed markedly from the three shrubs in terms of trunk and root allocations, while leaf allocation was not statistically different. The C/F ratios (the ratios of the dry weights of non-photosynthetic organs to photosynthetic ones) of the four species ranged from 9 to 12, and were not statistically different. These results did not support the hypothesis. The biomass of *H. petiolaris* was up to 100 times greater than those of the three shrubs. The growth form of *H. petiolaris* would

minimize allocation to supporting tissue and produce a large biomass. This advantage might therefore serve as a driving force for the evolution of lianas.

In Chapter 2.2, growth rate, growth speed, and productive structure of *H. petiolaris* were quantified. Cross-sectional disks of each main stem were obtained, and stem analysis was conducted. Whole plants with leaves and flowers were sampled, and productive structures were described. The juveniles of *H. petiolaris* in pre-climbing stage were sampled, and growth rate of the creeping length of stems to the number of cell layer at the base was quantified. The maximum elongation rate was approximately 1 m/year, and the maximum diameter growth was 0.5 cm/year. Leaves, trunks and reproductive organs were arranged from 2 to 6 m in heights. The number of cell layer of creeping juveniles ranged from 3 to 17. The growth rates of the juveniles ranged from 3 to 7 cm.

In Chapter 3.1, demography during early regeneration of *H. petiolaris* (from germination to seedling establishment) was clarified. Germination experiment was conducted on 7 different types of substrates to quantify the effect of substrates for seedlings emergence and survival of current year seedlings. Demography of natural seedlings (≥1 year old seedlings) was also monitored in coniferous forest and beech forest. The results were as follows; (1) germination rates and survival rates of current year seedlings were very low, and the values were significantly different among the substrates, (2) survival rates of natural seedlings (≥1 year old seedlings) were

relatively high, and the values were not significantly different among the substrates, (3) moss rich substrates and bare ground had significantly positive effect on the seedling establishment, and (4) relative areas of these substrates were not more than 4 %. Lateral shoot length of all natural seedlings was also measured, and the values were not more than 20 cm, suggested that it is necessary to establish around the root collar of host trees to climb on.

In Chapter 3.2, three dimensional light conditions were measured in coniferous forest in order to quantify the effect of light conditions to the distribution of *H. petiolaris*. Spatial heterogeneity of light condition was observed not only horizontally but also vertically. In 0.2 to 2 m in heights, the light conditions were homogenous and extremely dark in all areas, while in 4 to 8 m in heights, the horizontal heterogeneity was relatively high and bright patches caused by canopy gaps were observed. We also conducted concentric and cylindrical measurements of the light conditions around the host tree, *Cryptomeria japonica*. On the trunk surface, shaded by host tree and shrubs, the light conditions of forest floor and just below canopy (8 m in height) were very dark. Detaching 1 m in radius from the trunk surface, the shading by host's canopy was seldom observed, and it was suggested that the space between canopy layer and shrub layer provides preferable light condition for *H. petiolaris*. On the other hand, comparing the light condition between host trees and non-host trees, the mean values of host trees were greater than those of non-host

trees, and statistically differences were observed at some heights, suggested that the light conditions potentially controlled the distribution of *H. petiolaris*.

In chapter 2 and chapter 3, we succeeded to make clear the advantages and disadvantages of the distinctive life form of *H. petiolaris*. The species accorded huge biomass with minimum supporting tissues, resulting in huge biomass of reproductive organs. The advantages would be able to compensate the low probability of regeneration. Our size advantage hypothesis would be applicable to various root climbers.

Chapter 1

General introduction

In forest communities, lianas (woody vines) are generally recognized as special and/or distinctive plants compared to trees and shrubs. Their trunks are longer and more slender than those of the latter (Putz 1983, 1990), and they climb toward the crowns of tall trees by twining, clasping with tendrils or hooks, attaching to support surfaces by using adventitious roots or adhesive tendrils, or by leaning with the help of thorns or spines (Putz 1984; Putz & Holbrook 1991; Dewalt *et al.* 2000; Schnitzer & Bongers 2002). Some lianas display unusual growth patterns and dense growth via vegetative reproduction; hence, they are occasionally neglected when forest community dynamics are considered.

However, lianas usually appear in temperate and tropical forests throughout the world, and they comprise an abundant and diverse group of plants, particularly found in tropical forests (Gentry 1991; Appanah *et al.* 1992; Balfour & Bond 1993; Padaki & Parthasarathy 2000; Chittibabu & Parthasarathy 2001; Schnitzer & Carson 2001; Burnham 2002; Gerwing & Vidal 2002; Solórzano *et al.* 2002; Reddy & Parthasarathy 2003; Burnham 2004; Mascaro *et al.* 2004; Parthasarathy *et al.* 2004; Rice *et al.* 2004; Senbeta *et al.* 2005). In many tropical forests, lianas comprise ~25% of the woody stem density and species diversity (Muthuramkumar & Parthasarathy 2001;

Nabe-Nielsen 2001), and in liana-rich forests, they comprise 44% of all woody species (Pérez-Salicrup & Sork 2001). In terms of taxonomic composition, at least 133 families, or almost half of all vascular plant families, include a few climbing plants such as lianas, vines, epiphytes, and hemiepiphytes (Putz 1984; Gentry 1991); this suggests that the climbing habit has independently evolved in a diverse array of taxa (Gentry 1991; Schnitzer & Bongers 2002).

Further, lianas play a vital role in several aspects of forest dynamics. They enhance tree mortality and suppress tree growth (Dewalt *et al.* 2000; Pérez-Salicrup & Barker 2000; Schnitzer *et al.* 2000; Grauel & Putz 2004; Schnitzer *et al.* 2005); they also provide a valuable food source for animals and physically link trees together, thereby providing canopy-to-canopy access for arboreal animals (Gentry 1991; Schnitzer & Bongers 2002).

Thus, lianas are peculiar woody plants that comprise a group that is as abundant and diverse as the group comprising trees and shrubs; therefore, lianas have some advantages that drive the evolution of their life form. In addition, lianas also play an important role in forest dynamics, and these plants are very interesting research objects.

Although Charles Darwin conducted many studies on lianas in 19th century, lianas had been neglected as a scientific object until 1980 afterwards. Thus, at present, there is little information regarding their ecology, particularly their general biology (Putz

& Mooney 1991). The difficulty in collecting information on lianas is probably a result of the difficulty in studying these plants because of problems in distinguishing ramets from genets due to spreading vegetative reproduction and because of taxonomic uncertainties, including difficulties with regard to field identification (Caballé 1994; Schnitzer & Bongers 2002). In addition to these, another proposed problem is that the seedlings of most liana species have an upright stage and are therefore superficially indistinguishable from tree seedlings (Putz 1984).

For this thesis study, we selected the temperate liana *Hydrangea petiolaris*. *Hydrangea* is one of the interesting genera that occur in Japan, and it includes both lianas and self-supporting plants (In Japan, *Euonymus*, *Lonicera*, *Psychotria*, and *Rhus* are also include both liana and self-supporting plants). *Hydrangea* is widely distributed in cool temperate forests, and 2 or 3 species commonly occur in the same forest. Thus, we can clarify the life history strategies of lianas by comparing them with those of self-supporting plants within the same genus.

The goal of this thesis is to detect the advantages and/or disadvantages of the life form of the temperate liana *H. petiolaris* in order to discuss the evolution of lianas. First, we will address the characters of lianas growth form (Chapter 2). In Chapter 2.1, we make clear the differences in allocation patterns between lianas and self-supporting plants because lianas have long and slender trunks and this distinctive form would be important to understand their life history. We hypothesize

that lianas allocate less biomass to the supporting tissues because of the climbing habit. In other words, we hypothesize that lianas allocate more biomass to the leaves and/or reproductive organs than self-supporting plants do. In Chapter 2.2, we quantify the productive structure, growth rate, and growth speed of *H. petiolaris*. Next, we will quantitatively clarify the regeneration of lianas (Chapter 3). In Chapter 3.1, we will focus on demographic patterns during the pre-climbing stage, which comprises the stage of germination to that of attachment to host trees. Chapter 3.2 discusses the measurement of the three-dimensional light intensities in natural forests and their relationship with *H. petiolaris* distribution. Finally, we will summarize the results and discuss the evolution of the life form of lianas (Chapter 4).

Chapter 2

Section 1

Differences in the allocation patterns between liana and shrub *Hydrangea* species

Introduction

A liana has a distinctive growth form compared with trees and shrubs (Putz & Mooney 1991). The morphological difference between lianas and other woody species lies in the structure of the supporting tissues (trunks and roots). The trunks of lianas are more slender than those of other woody species because they use the structural support provided by the surrounding vegetation (Putz 1983). The growth rate in trunk diameter of lianas is also considerably slower than that of trees (Putz 1990). Moreover, compared with self-supporting plants, lianas may allocate a smaller proportion of biomass to roots because they only have to produce fine roots for nutrient absorption (Putz 1991). We can, therefore, hypothesize that the growth characteristics of lianas would contribute to an increase in investment in leaves and/or reproductive organs because the minimum investment in supporting tissues may compensate for the maximum investment in foliage and/or reproductive organs. Therefore, to clarify the advantages and disadvantages of the liana growth form, it is very important to test whether such a trade-off really occurs.

From an evolutionary viewpoint, the pattern of allocation to reproductive organs with reference to the growth form is an important indicator of fitness. Nevertheless, only a few studies have focused on the allocation to reproductive organs of lianas (During et al. 1994) and no studies have compared it with the allocation of self-supporting plants.

For a comparative study of allocation among species, phylogenetic constraints should be considered to avoid overstating the significance in hypothesis tests (Felsenstein 1985; Harvey & Pagel 1991; Silvertown & Dodd 1996). We should choose species from a genus in which both liana and other growth form species occur. In Japan, only a few genera include both lianas and self-supporting plants (*Euonymus*, *Hydrangea*, *Lonicera*, *Psychotria* and *Rhus*). In the present study, we chose *Hydrangea* because it is distributed widely in cool temperate forests and two or three species commonly occur in the same forest. Moreover, *Hydrangea* has strong morphological similarities among species, especially in flowers and seeds. These properties are useful to compare investments in reproductive organs among species.

In this study, we compared the allocation patterns among different growth forms, namely, three shrubs and one liana *Hydrangea* species. To elucidate size-dependency in the allocation patterns, we also compared the allometric relationships. We propose the following questions: (i) is there any difference in the allocation patterns between lianas and shrubs; and (ii) is there any allometric difference between lianas and

shrubs? Using the results of this study, we will discuss the implications for the evolution of lianas.

Materials and methods

Plant materials

Hydrangea petiolaris Sieb. et Zucc. is a deciduous liana that is distributed widely in cool temperate zones. *H. petiolaris* flowers from June to September and exhibits seed dispersal from late October to December. The seed is very small and dispersed by wind (Takahashi & Katsuyama 2000). Seed size is approximately 1.3 mm (Nakayama *et al.* 2000). Its seedling does not have upright stage, and it creeps until they start climbing (personal observation). *H. petiolaris* is categorized as a root climber that produces specialized adventitious roots that adhere to the supporting surface. It grows up to a height of 15–20 m (Takahashi & Katsuyama 2000). *Hydrangea petiolaris* has a relatively simple growth form that never expands horizontally by stolons or stoloniferous rhizomes.

　Hydrangea paniculata Sieb. et Zucc. is a deciduous shrub, the largest shrub among the Japanese *Hydrangea*. It has a wide distribution in cool temperate zones, almost overlapping that of *H. petiolaris*. It flowers from July to September, and the seed is dispersed by wind from October to December (Takahashi & Katsuyama 2000). Seed size is approximately 2.5 mm (Nakayama *et al.* 2000). Its growth form is similar to

canopy tree which has a main stem and monopodial shoot systems. Stem longevity of the species is more than 20 years and relatively long comparing with other *Hydrangea* shrubs (personal observation). It grows up to 2–5 m in height (Takahashi & Katsuyama 2000). Vegetative growth occurs when stems or branches pinned to the ground, adventitious roots are produced at the nodes and new stems grow upwards (Kanno and Seiwa 2004).

Hydrangea macrophylla var. *megacarpa* Ohwi is a medium-sized deciduous Japanese *Hydrangea* shrub. It is distributed in the Japanese coastal regions of Honshu, Hokkaido and Kyushu. It flowers from June to August and the seed is dispersed by wind from October to December (Takahashi & Katsuyama 2000). Seed size is approximately 0.9 mm (Nakayama *et al.* 2000). It grows up to 1–2 m in height (Takahashi & Katsuyama 2000). It sprouts prolifically at the ground surface, but it does not grow with rhizomes. It maintains the clump by quick turnover of stems (≤6 years; personal observation).

Hydrangea hirta Sieb. et Zucc. is the smallest deciduous Japanese *Hydrangea* shrub. It is distributed in the western part of Honshu. It flowers from June to July and exhibits seed dispersal from October to December. The seed is very small and dispersed by wind (Takahashi & Katsuyama 2000). Seed size is approximately 0.8 mm (Nakayama *et al.* 2000). It grows up to 1–1.5 m in height (Takahashi & Katsuyama 2000). It sprouts prolifically at the ground surface, but it does not grow

with rhizomes. It maintains the clump by stem turnover (≤8 years; Ishii and Takeda 1997).

Study sites

Plant samples were collected from the Niigata University Forest (NUF) located in the Osado mountains on Sado Island, Japan (38°12′N, 138°26′E) and from the Mikuni forest located on Mount Mikuni in Gunma Prefecture, Central Japan (36°45′N, 138°52′E). *Hydrangea petiolaris*, *H. paniculata* and *H. macrophylla* var. *megacarpa* are commonly distributed in the NUF, whereas only *H. hirta* is distributed in the Mikuni forest. Thus, we obtained samples of the former three species from the NUF and *H. hirta* from the Mikuni forest. Both study sites are in a cool temperate vegetation zone.

The annual precipitation and annual mean temperature recorded at the weather observatory nearest to the NUF are approximately 1500 mm and 14°C, respectively, (Aikawa 38°02′N, 138°14′E; elevation 6 m; Anonymous 1994–2003). The NUF has two forest types, a coniferous forest dominated by *Cryptomeria japonica* and a mixed deciduous broad-leaved forest dominated by *Quercus crispula* and *Pterocarya rhoifoia*. The annual precipitation and annual mean temperature recorded at the weather observatory nearest to the Mikuni Forest are approximately 1750 mm and 10°C, respectively, (Minakami 36°48′N, 139°00′E; elevation 531 m; Anonymous 1994–2003). The Mikuni forest is a mixed deciduous broad-leaved forest dominated by *Q. crispula*

and *Fagus japonica.*

Allocation and allometry

From 2001 to 2003, whole plants of the four species were sampled during the flowering seasons (from July to September). The samples, 5–18 individuals of each species (see Table 2.1.1), comprised mature individuals of various sizes. The mean heights were: 10 m for *H. petiolaris* (ranging from 8 to 14 m); 1.7 m for *H. paniculata* (1.4–2.1 m); 1.0 m for *H. macrophylla* var. *megacarpa* (0.7–1.6 m) and 0.9 m for *H. hirta* (0.6–1.4 m). The entire root system was excavated with a shovel and then cleaned. Most adventitious roots were sampled together with the trunks.

All samples were divided into leaves, trunks, roots and reproductive organs. In addition, the trunks of two individuals of *H. petiolaris* were divided into trunks and adventitious roots. Samples were dried in a ventilated oven (SANYO MOV–112(U), Tokyo, Japan) for 72 h at 60°C and the dry weight of leaves (M_L), trunks (M_T), roots (M_R) and reproductive organs (M_F) was measured. In addition, the dry weight of supporting tissues ($M_{Sup} = M_T + M_R$) and whole plants ($M_{Total} = M_L + M_T + M_R + M_F$) was calculated. Because the dry weights of the adventitious roots were very small (59 and 77 g), and the proportion to whole-plant weight was approximately 0.01, adventitious roots were treated as a part of the trunk.

Using these data, we calculated the proportions of the dry weight of each organ to

that of the whole plant, C/F ratios (the ratios of the dry weights of non-photosynthetic organs to those of photosynthetic ones, see Iwaki 1958; Hori *et al.* 1998) and top/root ratios ((M_L + M_T)/M_R). In this study, the C/F ratios were calculated as M_{Sup}/M_L.

The C/F ratio is generally used as an index of the relative proportion of dry matter loss by respiration to the net assimilation for herbaceous plants. In this study, however, we used it as an index of allocation pattern. We assumed that greater C/F ratios meant a higher proportion of supporting tissues, implying expensive production and/or maintenance costs.

The Steel multiple comparison test (Steel 1959) was used to check statistical differences, and the allometric relationship between the whole plant and each organ was calculated. To analyze allometric relationships, we followed the procedure of Niklas (1994a). Linear regression curves obtained by reduced major axis (RMA; Niklas 1994b; Sokal & Rohlf 1995) were established for log10-transformed data. The mathematical representation of these curves is $\log Y_2 = \beta + \alpha \log Y_1$, where Y_2 is the variable plotted against the ordinate, Y_1 is the variable plotted against the abscissa, β is the regression coefficient and α is the regression exponent. The extent to which the values of α differed among the species was evaluated on the basis of their 95% confidence intervals, L_1–L_2.

Results

Plant biomass

Plant size varied markedly among the four *Hydrangea* species (Table 2.1.1). The M_{Total} of *H. petiolaris* ranged from 1900 to 11 000 g, and the maximum value was up to 100-fold greater than the M_{Total} of the three shrubs. M_L and M_T of the four species showed the same trend as M_{Total}. The M_L of *H. petiolaris* ranged from 240 to 930 g, and the maximum value was up to 100-fold greater than the M_L of the three shrubs. The M_T of *H. petiolaris* ranged from 1500 to 9200 g, and the maximum value was up to 150-fold greater than the M_T of the three shrubs. The M_R of *H. petiolaris* ranged from 140 to 1100 g, and the maximum value was only up to 20-fold greater than the M_R of the three shrubs. Contrary to the trend for M_R, the M_F of *H. petiolaris* ranged from 20 to 720 g, and the maximum value was up to 700-fold greater than the M_F of the three shrubs.

Allocation patterns

Results of the allocation patterns among the four *Hydrangea* species are shown in Figure 2.1.1 and Table 2.1.2. Allocation ratios to trunk differed greatly between *H. petiolaris* and the three shrubs. M_T/M_{Total} of *H. petiolaris* was approximately 0.76, significantly greater than the values recorded for the three shrubs (P < 0.01). Allocation ratios to root also differed greatly between *H. petiolaris* and the three

shrubs. M_R/M_{Total} of *H. petiolaris* was approximately 0.11, significantly less than the values recorded for the three shrubs ($P < 0.01$). Moreover, the top/root ratio of *H. petiolaris* was approximately 8.9, significantly greater than the ratios of the three shrubs ($P < 0.01$). M_{Sup}/M_{Total} of *H. petiolaris* was approximately 86.3, which was not significantly different from the values recorded for *H. paniculata* and *H. macrophylla* var. *megacarpa* ($P > 0.05$), but significantly less than *H. hirta* ($P < 0.05$). Allocation ratios to leaves did not differ significantly among the four species. M_L/M_{Total} of *H. petiolaris* was approximately 0.1, which was not significantly different from the M_L/M_{Total} of the three shrubs ($P > 0.05$). The C/F ratio of *H. petiolaris* was approximately 9.5, which was not significantly different from the C/F ratio of the three shrubs ($P > 0.05$), although plant size and growth form differed considerably between *H. petiolaris* and the three shrubs. M_F/M_{Total} of *H. petiolaris* was 0.04, which was not significantly different from the M_F/M_{Total} of *H. paniculata* and *H. macrophylla* var. *megacarpa* ($P > 0.05$), but was significantly greater than *H. hirta* ($P < 0.01$).

Allometry

All allometric relationships between each organ and M_{Total} showed a size-dependent increase for all species (Fig. 2.1.2, Table 2.1.3). The regression exponent for M_T of *H. petiolaris* was 1.01 ± 0.03. Based on 95% confidence intervals for these RMA regression exponents, the values were not significantly different from the values of the three

shrubs (P > 0.05). The regression exponent for M_R of *H. petiolaris* was 1.19 ± 0.25, which was not significantly different from the values of the three shrubs (P > 0.05). The regression exponent for M_{Sup} of *H. petiolaris* was 1.00 ± 0.02, which was not significantly different from the values of the three shrubs (P > 0.05). The regression exponent for M_L of *H. petiolaris* was 0.85 ± 0.16, which was not significantly different from the values of the other three shrubs (P > 0.05). Although the regression exponents for M_F of *H. petiolaris* were not significantly different from those of the other three shrubs (P > 0.05), values varied widely among the species.

Characteristics of reproductive organs

The M_F of *H. petiolaris* was 9–700-fold greater than the M_F of the three shrubs (Table 2.1.1). The number of inflorescences of *H. petiolaris* was 10–20-fold greater than that recorded for the other three shrubs (Table 2.1.4). The maximum seed number per inflorescence was approximately 10 000 in all four species (Table 2.1.4). The highest reproductive organs of *H. petiolaris* were located at a height greater than 10 m, 7–11-fold higher than the height recorded for the three shrubs (Table 2.1.4).

Discussion

Our study quantified the common characteristics and distinctions between *H. petiolaris* and three *Hydrangea* shrubs. The three shrubs showed high similarities in

every parameter of allocations and allometries except for reproductive organs (Fig. 2.1.2, Table 2.1.3). Strictly to say, as we mentioned, growth form of *H. paniculata* is build-up type, similar to canopy tree, and other two shrubs are typical shrub that turnover their shoot with short interval. Nevertheless, the allocation parameters of the three shrubs are similar, suggesting that the phylogenetic constraints are exist in this genus. On the other hand, *H. petiolaris* showed markedly different trunk and root allocations from the shrubs, but showed similar C/F ratio and leaf allocation. Thus, the growth form difference between lianas and shrubs is reflected in allocation to trunk and root, but not to leaf. These results imply that there is a trade-off between trunk and root allocation, and that the total proportion of supporting tissue is not different among the four species. The C/F ratios of the four species were approximately 10. In general, the C/F ratio increases with plant size (Whittaker & Woodwell 1968; Givnish 1995). For example, the C/F ratios of deciduous canopy trees are not less than 49, while those of stunted trees at the timberline are approximately three (Larcher 2003). Thus, the C/F ratios of the four species were much less than those of trees, and we can conclude that the productive structures of all four *Hydrangea* species minimize allocation to supporting tissues.

However, the biomass of *H. petiolaris* was much greater than the biomass of the three shrubs, even though the productive structure was basically the same. Similar trends have been observed in the Western poison oak (*Toxicodendron diversilobum*),

which continually changes its growth form from shrub to vine. Gartner (1991) found that vines and shrubs of the same age grown in a garden showed approximately the same allocation ratios of leaves and stems. In the field, however, the vines were much taller (10–15 m in height) than the shrubs (4 m in height). From this, we can say that lianas are special growth forms that minimize allocation to supporting tissue, while also producing a large biomass.

The large M_F of *H. petiolaris* resulted from the large number of inflorescences, 10–20-fold greater than the number recorded for the three shrubs. The maximum seed number per inflorescence was similar among the four species (Table 2.1.4). Therefore, *H. petiolaris* could produce many more seeds than the three shrubs. Furthermore, because of the large plant size, the reproductive organs of *H. petiolaris* were located at a much higher position than those of the three shrubs. Inflorescence position is likely to affect the seed dispersal area directly because the seeds of *Hydrangea* species are typically wind dispersed. This suggests that *H. petiolaris* can disperse seeds to a much wider area than the three shrubs.

From the above factors, we can hypothesize that lianas have the potential to realize higher fitness than shrubs by way of their size advantage. The special growth form of lianas might be the only way to cope with minimized allocation to supporting tissues and a large biomass.

In this study, we analyzed the allometry and allocation of mature individuals.

However, some researchers have pointed out that juveniles of lianas tend to change their allocation rate drastically when they start climbing (Putz 1984; Sakai & Suzuki 1999). Comparative studies in various sizes from seedlings to mature individuals are needed to understand the differences in the allometry between lianas and shrubs in more detail.

Table 2.1.1 The dry weight of each organ and the whole plant of the four Phytolacca species

Species	M_t (g)		M_s (g)		M_r (g)		M_l (g)		M_{total} (g)	
	mean	stdev	mean	stdev	mean	stdev	mean	stdev	mean	stdev
H. pistulosa	6	293	952	169	7021	4187	969	675	1046	8625	1239
H. americana	5	353	168	821	150	1243	989	919	909	411	1282
H. macrophylla var. megasperma	18	5	46	153	1275	16	259	9	407	15	669
H. thyrsa	9	3	9	4813	123	11	61	9	354	49	101

M_t: leaves; M_s: stem and over organs; M_r: roots; M_l; over M_{total}; M_t + M_s + M_r + M_l; min: minimum; max: maximum

H. petiolaris

H. paniculata

H. macrophylla

var. megacarpa

H. hirta

Leaf

Reproductive organ

Trunk

Root

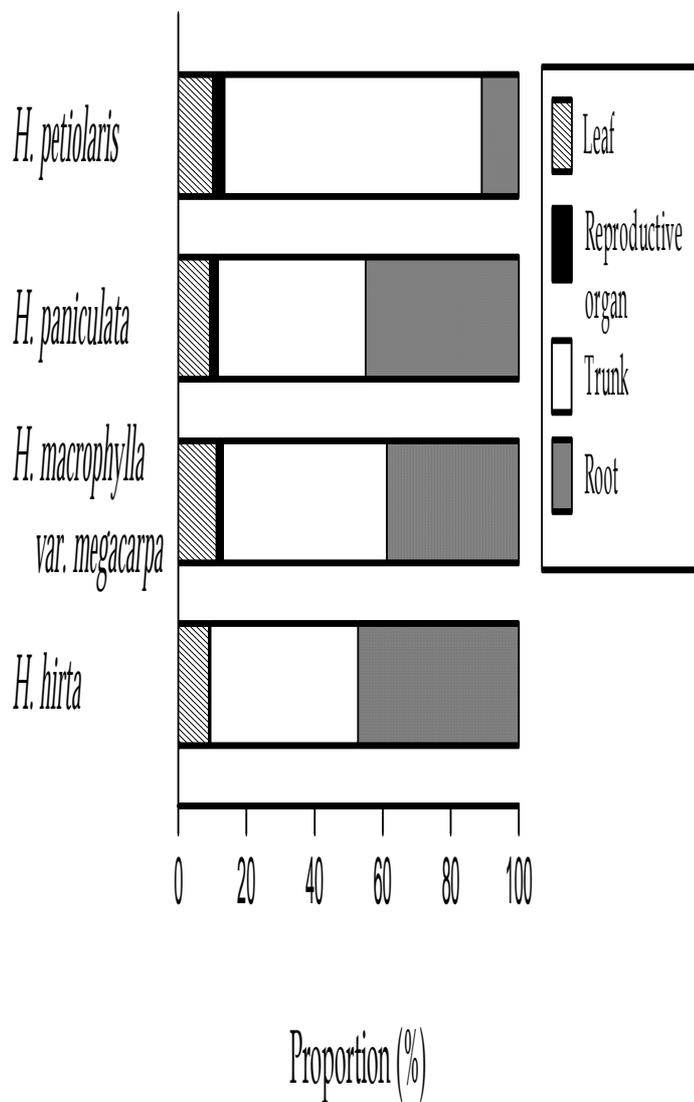0 20 40 60 80 100

Proportion (%)

Fig. 2.1.1. Proportions of the dry weights of each organ to the whole plant in the four *Hydrangea* species. The mean values of each species are shown.

Table 2.1. Results of the Games-Howell multiple comparisons test (Q-value, α=0.05)

	H. pylori strains						
	N/Nmax	N/Ng-gu	N/Ng-sgu	N/Nj-gu	Ng/Ng-th	CF	Type strain
H. parainfluenza	0.859	0.235	0.004	0.004	0.635	0.859	0.004
H. muricolumoTluca and species	0.635	0.235	<0.004	<0.004	0.012	0.635	<0.004
H. ituro	0.012	0.004	<0.004	<0.004	0.004	0.635	<0.004

Significant differences are in bold. Significant values with effect sizes are shown. DNA means show no significant differences at P<0.05. Values with different superscripts in each column are significantly different.
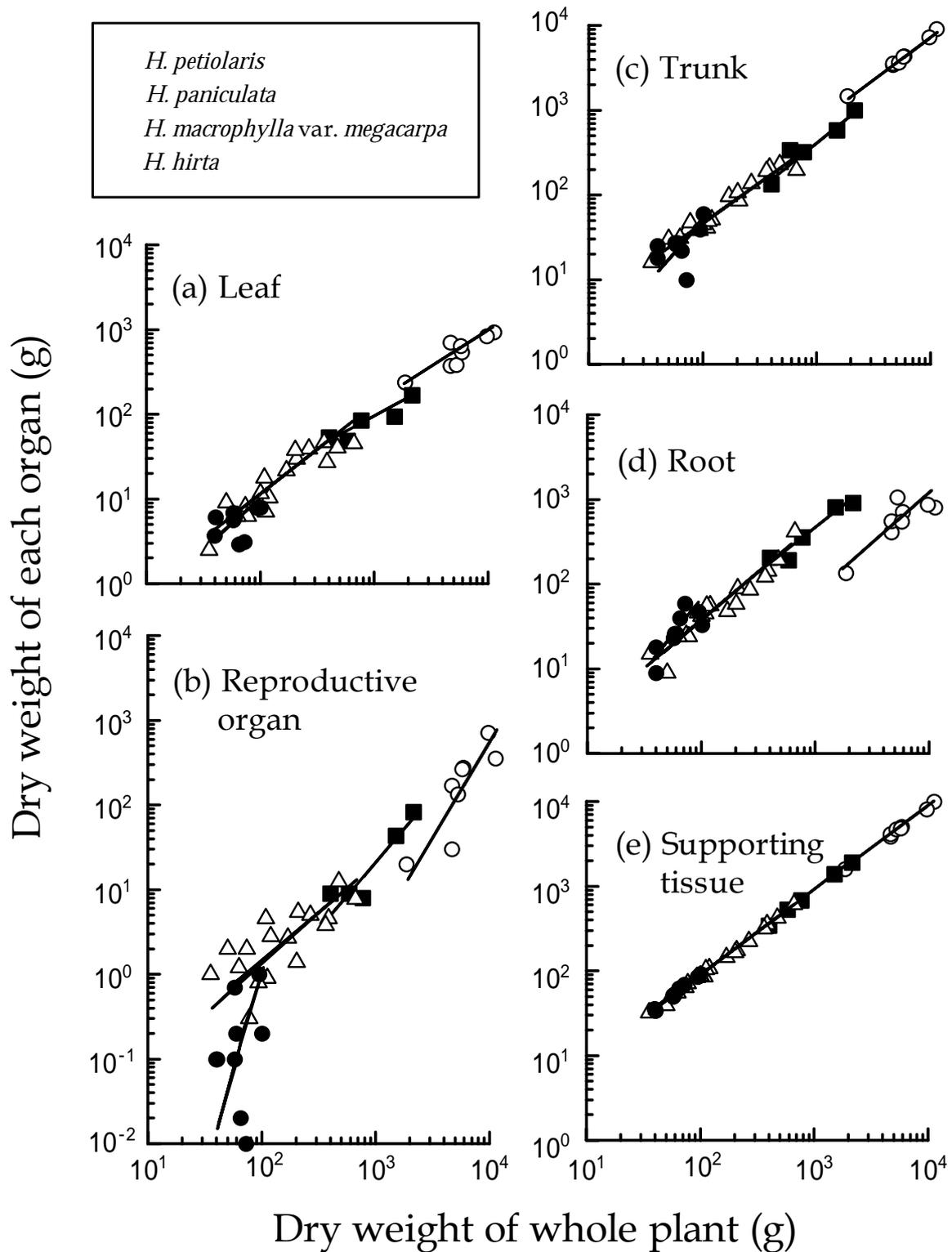
Fig. 2.1.2. Allometric relationships between the dry weight of the whole plant and the dry weight of each organ in the four *Hydrangea* species. (a) Leaf, (b) reproductive organ, (c) trunk, (d)root and (e) supporting tissue. Parameters for the regression curves are given in Table 2.1.3.

Table 2.1.3. Summary statistics of the reduced major axis regression analyses of log-transformed data from the four *Hydrangea* species.

Species	Y_1	Y_2	R^2	$\beta \pm SE$	$\alpha \pm SE$	L_1–L_2†
H. petiolaris	M_{Total}	M_L	0.886	-0.46 ± 0.60	0.85 ± 0.16	0.46–1.25
H. paniculata			0.921	-0.24 ± 0.48	0.73 ± 0.16	0.21–1.24
H. macrophylla var. *megacarpa*			0.920	-1.09 ± 0.23	1.05 ± 0.11	0.83–1.28
H. hirta			0.335	-1.41 ± 0.76	1.19 ± 0.42	0.19–2.19
H. petiolaris	M_{Total}	M_F	0.855	-6.28 ± 1.80	2.26 ± 0.48	1.09–3.44
H. paniculata			0.936	-3.40 ± 0.95	1.58 ± 0.32	0.56–2.60
H. macrophylla var. *megacarpa*			0.734	-2.14 ± 0.44	1.15 ± 0.20	0.74–1.57
H. hirta			0.146	-9.30 ± 3.15	4.69 ± 1.75	0.54–8.83
H. petiolaris	M_{Total}	M_T	0.997	-0.15 ± 0.13	1.01 ± 0.03	0.92–1.09
H. paniculata			0.962	-0.61 ± 0.50	1.08 ± 0.17	0.54–1.62
H. macrophylla var. *megacarpa*			0.976	-0.24 ± 0.12	0.96 ± 0.05	0.85–1.07
H. hirta			0.472	-1.34 ± 0.92	1.53 ± 0.51	0.32–2.73
H. petiolaris	M_{Total}	M_R	0.851	-1.69 ± 0.95	1.19 ± 0.25	0.56–1.81
H. paniculata			0.966	-0.56 ± 0.48	1.07 ± 0.16	0.56–1.58
H. macrophylla var. *megacarpa*			0.959	-0.72 ± 0.18	1.13 ± 0.08	0.96–1.30
H. hirta			0.787	-1.60 ± 0.71	1.70 ± 0.40	0.76–2.63
H. petiolaris	M_{Total}	M_{Sup}	0.999	-0.08 ± 0.08	1.00 ± 0.02	0.95–1.06
H. paniculata			0.999	-0.12 ± 0.06	1.02 ± 0.02	0.96–1.08
H. macrophylla var. *megacarpa*			0.998	-0.09 ± 0.04	1.01 ± 0.02	0.98–1.04
H. hirta			0.995	-0.16 ± 0.07	1.07 ± 0.04	0.97–1.16

†95% confidence intervals for α. Regression curves have the form $\log Y_2 = \beta + \alpha \log Y_1$. M_L, leaf; M_F, reproductive organ; M_T, trunk; M_R, root; M_{Total}, $M_L+M_F+M_T+M_R$; M_{Sup}, M_T+M_R.

Chapter 2

Section 2

Growth rate and productive structure of temperate liana *Hydrangea petiolaris*

Introduction

It is general assumption that growth form of terrestrial plants is regulated basically by allocation patterns and plant internal economy, and that the allocation parameters reflect the strategies of the plants to adjust surrounding environment. In Chapter 2.1, we quantified the differences of allocation parameters between the liana and shrub species, and the results revealed that allometry and allocation in *Hydrangea* were regulated by phylogenetic constraints, resulting in similar C/F ratios and reproductive allocations. Therefore, to clarify the advantage of lianas, we need to show how is the distinctive growth form realized under similar allocation rate.

In this study, we quantify productive structure, growth speed and growth rate, and discuss the development process of lianas growth form.

Materials and methods

Plant samples were collected from the Niigata University Forest (NUF; see Chapter 2.1). From 2001 to 2003, we sampled five mature individuals of *H. petiolaris* during

the flowering seasons in various forest stands (see Table 2.2.1). Cross-sectional disks

of each main stem at interval of 1 m from base to top were obtained for stem analysis.

The radial growth was measured along the major axis of the disk. The measurement

was conducted by using a microscope (NMR-D2XY; Nihon Kohki Seisakusho, Co.,

Ltd, Tokyo). From these data, we drew the growth curves of stem elongation and

diameter. We fir the growth data to logistic curve, and the equation was as follows;

$$Y = \frac{K}{1 + \exp^{a - r * X}}$$

where Y is stem elongation or diameter, K is the maximum growth, a is constant, r is

growth rate, and X is time.

For three of the five individuals, we sampled the whole plants including leaves

and flowers at each layer of 1 m from base to top. Most adventitious roots were

sampled together with the trunks. All samples were divided into leaves, trunks

(including adventitious roots), and reproductive organs. Samples were dried in a

ventilated oven (SANYO MOV-112(U)), Sanyo, Tokyo) for 72 h at 60°C and the dry

weight of leaves (M_L), trunks (M_T), and reproductive organs (M_F) was measured.

Using these data, we described the production structure diagram in each individual.

In September 2005, 19 juveniles of *H. petiolaris* in pre-climbing stage were sampled

in natural cedar forest in order to quantify the growth rate in the stage. We measured

the creeping length of stem (ranged from 4 to 108 cm) and obtained the disks at the

base. We counted the number of cell layer and adopted the value as cambial age because we could not distinguish late wood from early wood morphologically.

Results

Growth rates and production structures were very similar among the all samples. Growth curves of stem elongation fit logistic curves well ($R^2 \geq 0.978$). The stem elongation of *H. petiolaris* was accelerated when they reached 1 m in heights, and kept high growth rate (approximately 1 m/year) till it stopped at 8-10 m in heights (Fig. 2.2.1). Growth curves of diameter also fit logistic curves well ($R^2 \geq 0.910$). The diameter growth of *H. petiolaris* was accelerated when they reached 0.5 cm, and kept the constant growth (approximately 0.3 cm/year).

M_L of *H. petiolaris* was concentrated within a range from 2 to 6 m in heights in the three individuals (Fig. 2.2.2). M_T showed peak from 3 to 5 m in heights. Most part of M_F is distributed from 2 to 5 m in heights.

Stem length of creeping juveniles ranged from 4 to 108 cm, and the number of cell layer ranged from 3 to 17 (Fig. 2.2.3). Stem length per a cambial age of *H. petiolaris* seedling was varied among the individuals. The growth rates ranged 3 to 7 cm approximately.

Discussion

Stem analysis showed that the long and slender trunk of *H. petiolaris* was formed by quick elongation and minimized diameter growth. The maximum elongation rates were up to 1 m per a year, suggesting that *H. petiolaris* can get out of the limited light conditions of shrub layer. On the other hand, the maximum diameter growth rates were only 0.5 cm per a year (mean rates were 0.2 cm per a year). In the NUF, the diameter in the breast heights (DBH) of the largest *H. petiolaris* reaches 25 cm, suggesting that the longevity of *H. petiolaris* is more than 100 years. High elongation and low diameter growth have been observed in many lianas (Gartner 1991; Niklas 1994), implying common growth characters of lianas.

On the other hand, in juveniles in the pre-climbing stage, the maximum elongation rates were only 7 cm per a year, implying that the growth character of the species changes drastically when it start climbing. Diameter growth of juveniles was very little and annual ring could not be observed. If we assume that one cell layer is produced in a year, persistence of seedling bank may be approximately 15 years. This persistence would contribute the seedlings to wait till the improvement of light condition on forest floor or to extend the period for searching host trees.

Production structure of *H. petiolaris* was basically similar among three samples, although each site had different surrounding conditions. Leaves, trunks, and reproductive organs of *H. petiolaris* were concentrated from 2 to 6 m in heights. In

latter part of the thesis, we test whether this construction of *H. petiolaris* consistent

with the distribution of light conditions in the forest or not.

Table 2.2.1 Site description

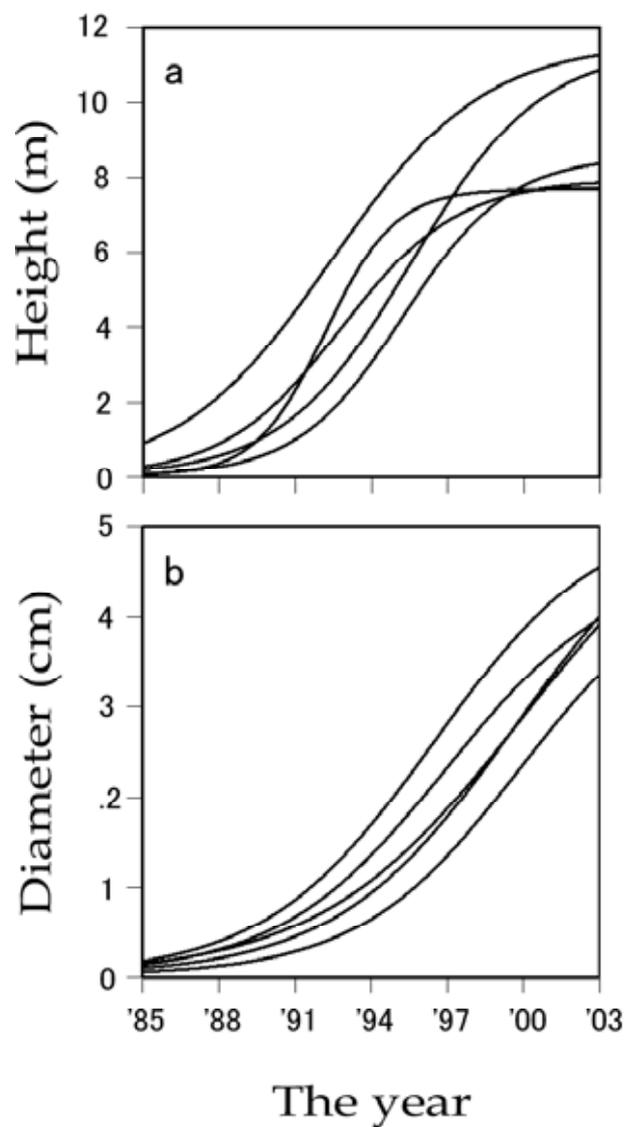| Site No.	Altitude (m)	Forest type	Seston analysis	Periphytical structure	Granulometrie of riparial zone
1	400	Artificial pasture forests			
2	650	Coniferous, deciduous broad-leaved mixed forests			
3	780	Coniferous, deciduous broad-leaved mixed forests			
4	800	Deciduous broad-leaved forests			
5	850	Deciduous broad-leaved forests			
6	880	Natural pasture forests			

Fig. 2.2.1. Growth curves in (a) height and (b) diameter of *H. petiolaris*.Each line represents each individual.
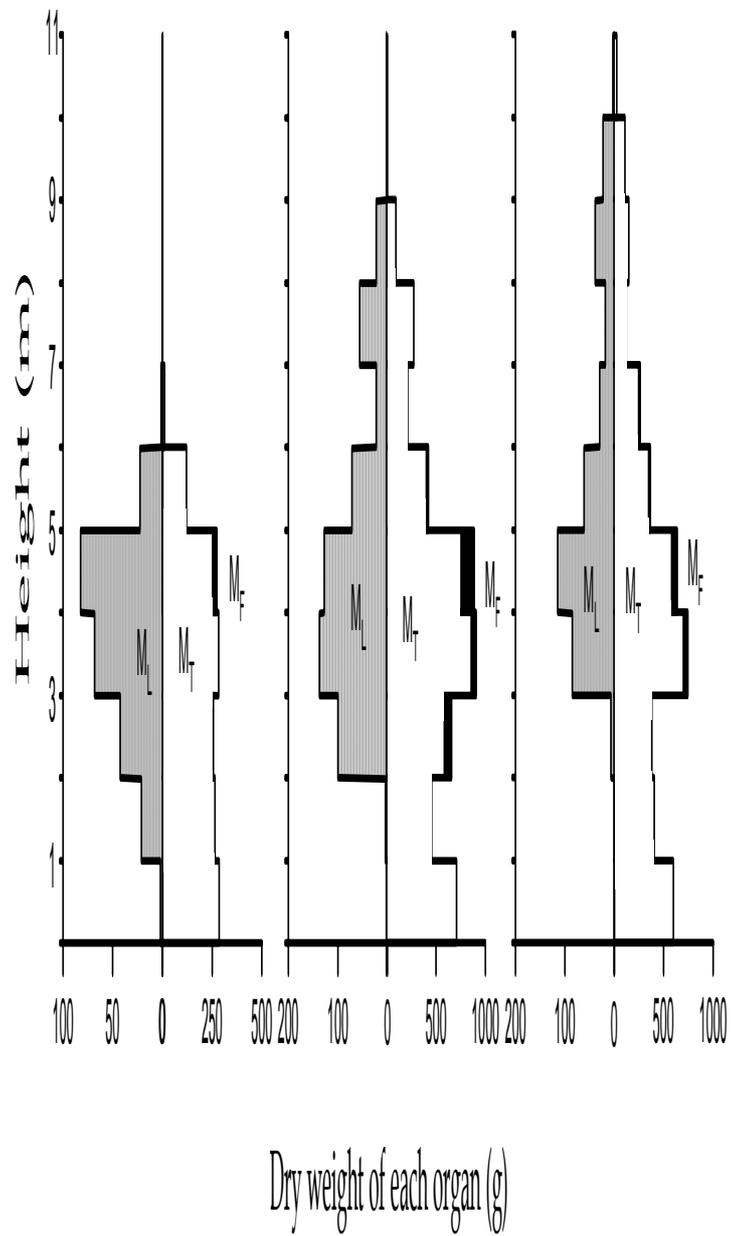
Fig. 2.2.2 Production structure diagram of *H. petiolaris*. W_L, dry weight of leaf; W_T, dry weight of trunk; W_F, dry weight of reproductive organ.
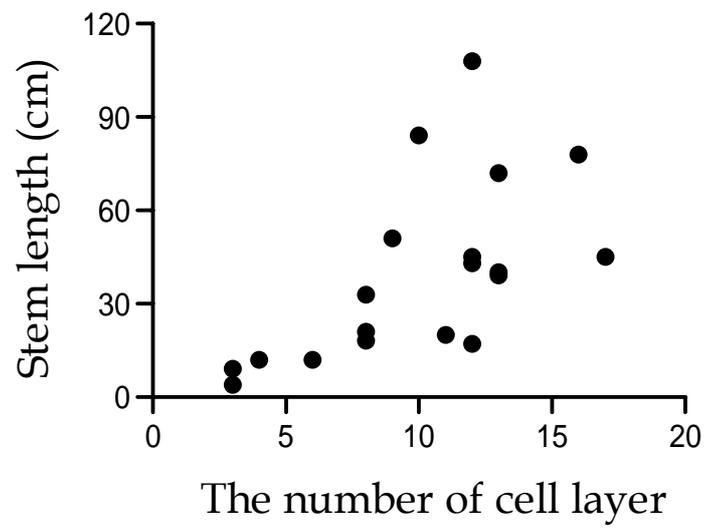
Fig. 2.2.3. Relationship between the number of cell layer and stem length of *H. petiolaris* seedling.

Chapter 3

Section 1

Seedling establishment and host preference of temperate liana *Hydrangea petiolaris* and its contribution to the regeneration

Introduction

The life history of lianas is different from that of trees and shrubs in that lianas climb on host trees. These plants possess various climbing mechanisms (Putz 1991), and each climbing mechanism favors specific host trees (Hegarty 1991; Teramura *et al.* 1991; Balfour & Bond 1993; Dillenburg *et al.* 1993; Chittibabu & Parthasarathy 2001; Muthuramkumar & Parthasarathy 2001; Nabe-Nielsen 2001). With regard to root climbers, some researchers have pointed out that they tend to climb on larger hosts (Nabe-Nielsen 2001) and relatively rough and hard bark (Talley *et al.* 1996a; Talley *et al.* 1996b; Carsten *et al.* 2002). This suggests that the distribution of lianas depends on the physical properties of the host trees.

Seedling establishment is another important aspect in the regeneration of lianas. It is noted that the early regeneration stage (from germination to seedling establishment) is one of the most critical steps in tree regeneration (Silvertown & Lovett-Doust 1993; Fenner 2000), and some studies have clarified that lianas have

high mortality rates during this stage (Nabe-Nielsen 2002; Sanches & Válio 2002; Gerwing 2004; Nabe-Nielsen 2004). In general, small-sized seedlings have higher mortality rates during the early regeneration stage (Fenner & Thompson 2005b), and regeneration success is influenced by the condition of microsites such as fallen logs, mosses, and bare ground (Takahashi 1994; Kameyama *et al.* 1999; Takahashi *et al.* 2000; Zamfir 2000; Sugita & Tani 2001; Narukawa *et al.* 2003; Castro *et al.* 2004; Mori *et al.* 2004; Hirayama & Sakimoto 2005). Moreover, the distance from the safe sites to the potential host trees may also influence the distribution of lianas as a consequence of climbing. Therefore, in order to clarify liana regeneration, demographic patterns of the early regeneration stage must be investigated.

However, studies on this topic are limited, although many studies have been conducted on host preferences, only a few have been performed to investigate the demographic patterns of the early regeneration stage. In this study, we selected a popular temperate liana, namely, *Hydrangea petiolaris*, and investigated its regeneration.

Through this paper, I would like to address the following questions: (1) What are the kind of substrates favorable for *H. petiolaris* regeneration? (2) What is the maximum distance that their seedlings can cover on the ground surface for attaching onto the host trees? (3) Does *H. petiolaris* prefer larger host trees over smaller ones? and (4) Do the differences in bark texture affect the distribution of *H. petiolaris*?

Materials and methods

Study sites

The study was conducted in the Niigata University Forest (NUF; 38°12′N, 138°26′E; 880 m a.s.l.) and the Kinpoku forest (KIN; 38°04″N, 138°19″E; 860 m a.s.l.), both of which are located in the Osado mountains on Sado Island, Niigata Prefecture, Japan. The NUF is a coniferous, deciduous broad-leaved mixed forest that is mainly occupied by the Japanese cedar (*Cryptmeria japonica*) and some deciduous broad-leaved trees (*Quercus crispula, Tilia japonica, and Pterocarya rhoifoia*). The KIN is a deciduous broad-leaved forest dominated by the *Fagus crenata* and *Q. crispula*. Both study sites are typical forests found in the cool temperate vegetation zone. The NUF study site (100 m × 100 m) was established in 2004 and the KIN study site (120 m × 80 m), in 2006.

The annual precipitation and annual mean temperature recorded at the weather observatory nearest to the NUF were approximately 1903 mm and 13.4°C (Hajikizaki: 38°19′N, 138°30′E; elevation, 58 m; Anonymous 2004–2005) and those for the KIN were approximately 1974 mm and 13.9ºC (Ryotsu: 38°04′N, 138°26′E; elevation, 2 m; Anonymous 2004–2005).

Experimental study of seedling establishment

A germination experiment was conducted to clarify the early regeneration of *H.*

petiolaris with special attention to the effect of substrates on seedling establishment.

In late October 2004, seeds of *H. petiolaris* were collected from 20 individuals in the

NUF. The seeds were weighed, and the relationship between the weight and the

number of seeds was calculated ($Y = 16057X$ where Y denotes the number of seeds

and X, the weight of the seeds (g); $R^2 = 0.999$).

A germination experiment was conducted on the west-facing slope (850 m a.s.l.) in

the NUF. We used two different forest stands and compared the respective results.

One was a coniferous stand dominated by *C. japonica* and the other, a deciduous

broad-leaved stand dominated by *Q. crispula* and *T. japonica*. The coniferous stand

had typical humid soils and a relatively dark forest floor, while the deciduous

broad-leaved stand had dry soils and a relatively light forest floor. However, *H.*

petiolaris showed frequent distribution on both the stands.

To investigate the effect of substrates on regeneration success, 15 places were

selected in each stand. We arranged them such that the each place included the

following 5 types of substrates within each 5 m × 5 m quadrate: litter (L), bare

ground (G), fallen logs (F), moss on fallen logs (M-F), and moss on the bottom part of

the trunk surface (M-T). G was made available by removing the litter in the 50 cm ×

50 cm quadrates, while the other conditions were used in their natural states. We set

each place on each G and M-T at two points (i.e. fungicide experiment and the

control) in order to investigate the effect of the pathogens; this is because many

studies have pointed out that the seeds of some species are susceptible to attack by fungi and bacteria (Fenner & Thompson 2005a). In this study, we selected the fungicide "Benomyl"(1-[(Butylamino) carbonyl-1H-benzimidazol-2-yl] carbamic acid methylester; DuPont Japan, Tokyo); it is one of the most popular fungicides for agriculture and is effective in protecting seeds from a broad range of fungal infections. The fungicide was diluted 600-fold and 100 ml was then sprayed on each substrate.

In early November 2004, the 15 cm × 15 cm quadrates were established for each substrate, and approximately 800 seeds (0.0500 g) were sown (n = 30 places × 7 substrates × 800 seeds = 168000 seeds). The sown seeds and substrates were covered by a nylon cloth, which is permeable by water and breathable, to prevent loss due to snow glide and strong winter winds. The nylon cloth was removed after the snowmelt. The number of seedlings that emerged was counted at approximate 10-day intervals from June to August, and 30-day intervals from September to October. In 2006, the number of seedlings was counted in June and October. The Steel-Dwass test, a nonparametric multiple comparison procedure, was used to compare the demographic parameters for each substrate. KyPlot 5.0 (Kyens Lab Inc.) was used to perform the statistical analysis.

Demographic patterns of natural seedlings

The demographic patterns of *H. petiolaris* seedlings were investigated in order to quantify the effect of the substrates on seedling establishment. A 40 m × 40 m plot was established within the 100 m × 100 m plot in the NUF and KIN. We further divided each plot into 256 subplots with dimensions of 2.5 m × 2.5 m. We defined a seedling as an individual that did not climb on hosts. In June 2005, all the seedlings in each of the subplot in the NUF were numbered using a small flag. We monitored their fate (alive, dead, and disappeared) from June 2005 to October 2006. In June 2006, all the seedlings in each subplot in the KIN were numbered, and their fate was recorded in October 2006. The lateral shoot length was measured in order to quantify their creeping effort because the seedlings continue creeping until they start climbing onto the host trees. Most seedlings began creeping on the forest floor in the mid-growing season of the second year (personal observation); hence, we defined the seedlings that did not creep as 1-year-old seedlings. Current-year seedlings were excluded from this study because these *H. petiolaris* seedlings could barely be distinguished from those of other *Hydrangea* species.

Substrates were categorized into the following 8 types: L, G, moss on bare ground (M-G), F, M-F, rock (R), moss on rock (M-R), and M-T. We recorded the substrate types for each seedling. The projected area of each substrate type was measured in each subplot.

We used the multiple regression model to clarify the effect of the substrate on the seedling establishment. Statistical analysis was performed using the JMP software (SAS Institute 2004).

The distribution of climbing stems and host preferences

We investigated the relationship between the location of *H. petiolaris* and properties of the potential host trees (size and bark) and the safe sites. All the *H. petiolaris* climbing stems (height ≥ 1.3 m) in the 100 m × 100 m plots in the NUF and KIN were numbered. We measured the diameter at breast height (DBH) and recorded their location. All the self-supporting plants (potential host trees; DBH ≥ 5 cm) were numbered, and their DBH and location were recorded.

We classified the bark texture of the all living stems as smooth, slightly rough, or rough, according to Campbell & Newbery (1993). The surface of the "slightly rough" stems consisted of small dimples, scales, or shallow fissures, while that of "rough" stems had large scales or fissures with an occasional tendency to flake. The number of climbing stems that broke and/or fell were recorded in order to quantify the effect of bark texture on the failure to climb.

We recorded the substrate types (classified earlier) that were within a radius of 20 cm from the base of the potential host trees (DBH ≥ 20 cm); this was performed because our field observations clarified that the *H. petiolaris* seedlings could creep on

the forest floor to a very limited distance, and they mainly used larger trees as hosts. The influence of safe sites on the distribution of climbing stems was analyzed using the chi-square test. In order to eliminate the effect of bark texture, each bark type was analyzed. The statistical analysis was performed using the JMP software (SAS Institute 2004).

Results

Seedling emergence and demographic patterns of the current-year seedlings

The germination experiment showed that the percentage of the seedlings that emerged significantly differed among the substrates, and it varied widely within each substrate (Table 3.1.1). In the deciduous broad-leaved stand, the maximum value in L was only 4.4%, whereas those in the other substrates ranged from 24.0% to 34.4%. In the coniferous stand, the maximum value in M-F was 21.3%, whereas in other substrates, this value did not exceed 16.0%.

The timing of seedling emergence varied among the substrates (Fig. 3.1.1). On G and F, seedlings emerged in mid-June and those on M-F and M-T emerged in mid-July. Compared to the other substrates, many seedlings in M-F and M-T survived till the end of the growing season.

The percentage of the current-year seedlings that survived till the end of the growing season significantly differed among the substrates, and a wide variation was

observed within each substrate (Table 3.1.1). In the broad-leaved stand, the maximum value was only 1.0% in G, whereas those in F and M-F, this value exceeded 60%. In the coniferous stand, the maximum value was 16.4% in G, whereas this value in other substrates ranged from 50% to 100%.

During winter, the mortality in the current-year seedlings was very high and the seedlings survived only on specific substrate types (Fig. 3.1.1 and Table 3.1.1). In the broad-leaved stand, seedlings were found to survive only on M-F; in the coniferous stand, this was observed only on L and M-F.

Pathogens did not affect seedling emergence (Fig. 3.1.1 and Table 3.1.1). The percentage of seedling emergence was not significantly different in G and M-T ($P > 0.05$; Steel-Dwass multiple comparison test).

Demographic patterns of seedlings of one year and above, and their creeping distances

The natural seedlings emerged on various substrates (Table 3.1.2). In both the NUF and KIN, litter covered over 90% of the ground surface, and each of the other substrates did not cover more than 2%. In the NUF, however, many natural seedlings were found on both L and M-F. In the KIN, many natural seedlings were found on G, M-G, and M-F, whereas they were barely found on L.

The multiple regression model demonstrated that substrates G, M-G, and M-F had a significantly positive effect on seedling establishment ($P < 0.05$; Table 3.1.3).

However, substrate L, on which the most number of natural seedlings appeared, was judged as non-ideal for establishment.

The percentage of the 1-year-old seedlings that survived was not high (Table 3.1.4). The values ranged from approximately 60% to 90% during the growing season in the NUF and KIN and were similar among all the substrates. During the winter season in the NUF, these values ranged from approximately 50% to 90%. Thus, the values throughout the year ranged from 30% to 40% in most substrates, whereas G and M-R demonstrated relatively high survival percentages.

The percentage of the old seedlings (≥ 2-year-old seedlings) that survived was high in all the substrates in both the plots; the values recorded were observed to be not less than 60% (Table 3.1.4).

The creeping distances of the seedlings were observed to be very short (Fig. 3.1.2). Over 90% of the total seedlings did not creep to a distance more than 20 cm on the forest floor, whereas some seedlings could creep to a distance up to 180 cm.

The distribution of climbing stems and host preference

H. petiolaris was found more frequently on larger trees than on smaller ones (Fig. 3.1.3). The larger the trees, the higher the percentage of tree climbing by *H. petiolaris.* The percentage reached 100% in deciduous broad-leaved trees, whereas in the case of coniferous trees, this value reached only 40% (*C. japonica*).

Substrates types observed around the potential host trees (DBH ≥ 20 cm) varied according to the host tree species (Table 3.1.5). In the NUF, several coniferous trees had L and M-T, whereas many deciduous broad-leaved trees had the above substrates and G. In the KIN, several deciduous broad-leaved trees among all species had L and G near their base, and M-T.

A significantly positive association was observed between the distribution of the climbing stems and the presence of safe sites (M-F, G, and M-G) close to the tree base in all the host species in the NUF and KIN ($P < 0.05$; Table 3.1.6; chi-square test).

Slightly rough and rough bark species were found in the NUF, while slightly rough and smooth bark species were found in the KIN (Table 3.1.7). *F. crenata* was categorized as having a smooth bark, while *Q. crispula*, *T. japonica*, and *P. rhoifolia* were categorized as having a slightly rough bark. *C. japonica* was categorized as rough bark. However, the proportion of broken and/or fallen stems among all climbing stems was not greater than 10% in any of the cases.

Discussion

The effect of substrates on seedling emergence and current-year seedling survival

Seedling emergence was observed to be affected by the substrate type. It was considerably less on L than on the other substrates in the broad-leaved-forest stand. In the coniferous stand, seedling emergence on L, G, and F was considerably less

than that on the others. The percentage of seedlings that emerged was not greater than 10% for these substrates, suggesting that seed death during germination is one of the major controlling factors involved in the regeneration of *H. petiolaris* with regard to these substrates.

Current-year seedling survival varied among the substrates. M-F showed relatively high survival rates in both the stands, and L displayed relatively high values only in the coniferous stand. In a span of one year, almost all seedlings in most substrates had died. However, many seedlings survived under two exceptional conditions, i.e., M-F in both the stands and L in the coniferous stand. This suggests that these substrates act as safe sites. It is generally known that M-F has a positive effect on seedling survival in the case of small seed species (Szewczyk & Szwagrzyk 1996; Narukawa & Yamamoto 2002; Parent *et al.* 2003; Simard *et al.* 2003; Motta *et al.* 2006) because it provides the favorable humid conditions (Cross 1981; Sohlberg & Bliss 1984, 1987; During & van Tooren 1990; Nilsson *et al.* 1996; Takahashi *et al.* 2000). On the other hand, the negative effect of L has often been observed on both seed germination and seedling establishment (Xiong & Nilsson 1999; Kitajima & Fenner 2000). Based on our field observation, canopy trees (*C. japonica*) often scatter their leaves as "leave-shoot complex", and they were homogeneously distributed on the forest floor. The leave-shoot complex has sufficient crevices for the small seedlings to access the ground surface. Thus, the roots of the seedlings were able to penetrate the

litter layer.

Seedling emergence on moss was delayed by a month when compared with other substrates. As a result, many seedlings survived on M-F and M-T till the end of the first growing season. The seedlings on these substrates might be able to avoid the drought till the beginning of the rainy season (from mid-June to mid-July). Further, the seedlings might also be tolerant to the drought after the end of the rainy season because the moss provides the required moisture (Sedia & Ehrenfeld 2003). Thus, in order to clarify the regeneration of *H. petiolaris*, a detailed investigation of delayed seedling emergence on their survival is necessary.

The effect of substrates on the distribution of natural seedlings and their survival

Natural seedlings were also observed to be concentrated on specific substrates. Several seedlings were found on M-F and L in the NUF (coniferous forest), and M-F, G, and M-G in the KIN (deciduous broad-leaved forest). This is partly consistent with the germination experiment, suggesting that the experiment by itself was capable of demonstrating the demographic patterns of seedling emergence and survival in intact conditions.

The inconsistency between the germination experiment and the distribution of natural seedlings was obvious in the case of G. In the former, G was made available by removing the litter, and almost all the seedlings were killed by burring with soils

and litterfalls (field observation). On the other hand, natural G (or M-G) usually lies under fallen logs and under the bent trunks of potential host trees in the chosen plots; many seedlings were found to survive in these conditions. In contrast to the artificial bare ground, these conditions are protected from litterfall, heavy rainfall, and severe drought. Thus, physical stability and humidity appear to be the cause of seedling concentration in these conditions. Many studies have shown that some controlling factors of seedling establishment are related to litterfall, e.g., burring (Cross 1981; Duchesneau & Morin 1999), physical damage (Simard *et al.* 2003; Gillman & Ogden 2005). Therefore, G and M-G would serve as safe sites in our plots.

L as a substrate did not have a positive effect on total seedling number. The seedling density on L was considerably less than that observed on the other substrates, although in the NUF, the number of seedlings was high on L. It has also been reported that in many *C. japonica* forests, L substrate has a negative effect on the seedling survival of small seed species (Maruyama & Kamitani 1986; Tomizawa & Maruyama 1993; Ota *et al.* 2002; Hirayama & Sakimoto 2005). Thus, the relatively high survival rates observed in the germination experiment in the coniferous stand may be a rare case.

From the facts mentioned above, we can conclude that M-F, G, and M-G are very important substrates that act as safe sites. They constitute only a small percent of the total area, implying that the seedling establishment of *H. petiolaris* is very limited.

Similar results have been observed in the *Hydrangea* shrub, *H. paniculata*, and establishment of them was limited on fallen logs and bare ground brought by uprooting of canopy tree (Kanno & Seiwa 2004). The success of seedling establishment is determined by the demographic patterns during the first year after seed dispersal because survival rates of older seedlings (≥1-year-old seedlings) were relatively high in all the substrates.

The distribution of climbing stems and host preferences

The creeping distance of the *H. petiolaris* seedlings was observed to be very short (≤20 cm in most individuals), implying that the most seedlings could not search for the host trees. The presence of the safe sites (M-F, G, and M-G) around the root collar of the canopy trees showed positive association with proportions of hosts to total trees (Table 3.1.6). This suggests that the requirement for climbing the host trees is the establishment of seedlings around the root collar of the potential host trees. However, we should pay attention to another possibility that the very limited number of seedling creep for more than 150 cm and succeed to attach host tree with very low probability. The longevity of the seedlings is probably more than 20 years (see Chapter 2.2), suggesting that this persistence would contribute to search host trees.

On the other hand, the type of bark texture did not affect the distribution of climbing stems in our plots because the mortality of these stems did not differ among

the bark texture types (Table 3.1.7). In general, host preferences have been understood based on the relationship between the climbing mechanisms and physical properties of the host trees (Putz & Mooney 1991). However, our study showed that the pre-climbing stage (from germination to reaching the host trees) was the key to understand the host preferences of *H. petiolaris.*

 H. petiolaris was observed to prefer deciduous broad-leaved trees over coniferous trees (*C. japonica*) for climbing. Our data suggests that the main reason for this would be the presence of G (Tables 3.1.5 and 3.1.6). Most deciduous broad-leaved trees had the substrate G around the root collar; however, the same was not observed with regard to the coniferous trees. In snowy regions, the trunks of deciduous broad-leaved trees are usually bent due to the snow pressure (Homma 1997). The bent trunks are likely to produce G by preventing litter from falling onto the ground surface. On the other hand, the shape of the trunk bottom of coniferous trees is relatively straight, and root collars are covered with litter. These differences in the shapes of the trunk bottoms are a result of the different ways in which wood formation occurs under conditions of severe disturbance or on a steep slope. Broad-leaved trees form tension wood at the upper sides of the slope and pull the trunk upright, while coniferous trees form compression wood at the lower sides and push the trunk upward (Mattheck 1991; Mattheck & Kubler 1997). As a logical consequence, safe sites are present more often around deciduous broad-leaved trees

than around coniferous ones.

H. petiolaris preferred larger trees over smaller trees for climbing. The phenomenon can be explained by the demographic patterns of the seedlings. They had a high mortality rate during seedling stage, implying that the seedlings require ample more time for successful climbing. Therefore, it is natural for older trees to have a higher percent of climbing by *H. petiolaris*.

Consequently, the requirement for regeneration of *H. petiolaris* is as follows: (1) seed dispersal only on specific substrates, i.e., M-F, G, and M-G; (2) seedling establishment close to potential host trees; (3) dominance of broad-leaved canopy trees; and (4) abiotic factors such as high slope inclination and/or heavy snowfall. The early regeneration stage was a critical step in the regeneration of *H. petiolaris*, and the distribution of *H. petiolaris* strongly depends on the potential host trees.

In this study, research was conducted in the forests in snowy region. However, *H. petiolaris* is also distributed in snow-poor region. In such region, the trunk of canopy trees is usually upright, implying that canopy trees do not provide enough safe sites around the root collar. Thus, high persistence of seedling bank and continuous stem elongation would be much more important than in snowy region.

Broad leaved tree stand   Coniferous tree stand

(a) Litter

(b-i) Bare ground

(b-ii) Bare ground with fungicide

(c) Fallen logs

(d) Moss on fallen logs

(e-i) Moss on bottom part of trunk surface

(e-ii) Moss on bottom part of trunk surface with fungicide
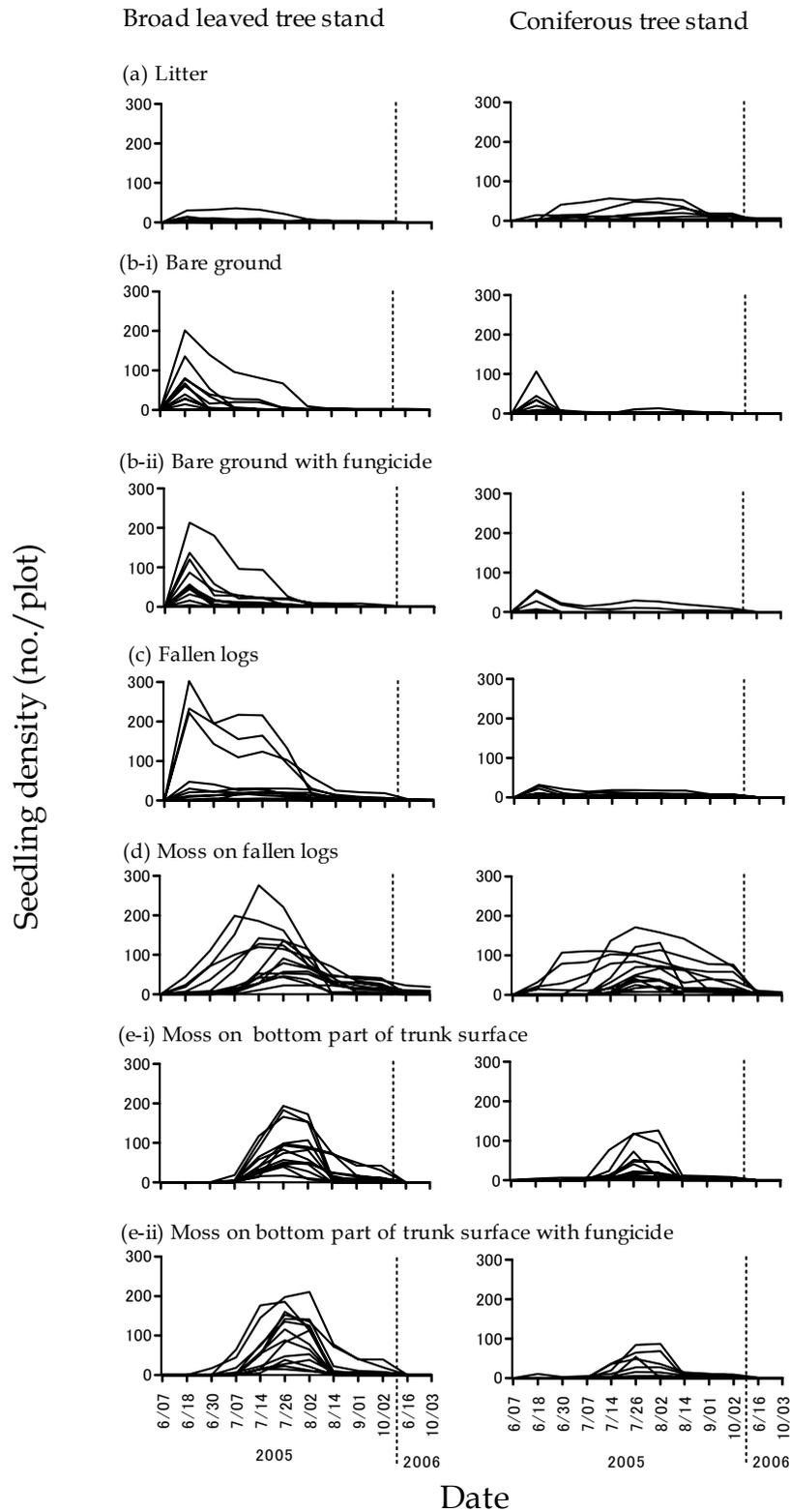
Seedling density (no./plot)

Date

Fig. 3.1.1. Change of seedling density from June 2005 to October 2006 in each substrate in the experiment study. Each line shows change of seedling density in each place (n = 15).

Table 3.1.1. Percentages of seedling emerged and survived in experimantal study. Minimum and maximum values are shown. Total number of the seedlings are shown in parentheses.

Stand	Substrate	Emergence (%)	Survival (%)		
			Oct. 05'	Jun. 06'	Oct. 06'
Broad leaved tree stand	L	$0-4.4^a$ (91)	$0-13.3^{ab}$ (4)	0 (0)	---
(n = 15 places)	G	$0.1-25.0^{ab}$ (734)	$0-1.0^a$ (2)	0-1.0 (2)	0-0.5 (1)
	G-fungicide	$0.5-26.5^b$ (914)	$0-4.6^a$ (4)	0 (0)	---
	F	$0-37.7^{ab}$ (927)	$0-100^{abc}$ (41)	0-10.0 (7)	0-10.0 (5)
	M-F	$2.9-34.4^b$ (1392)	$0-65.2^b$ (205)	0-15.5 (58)	0-15.5 (53)
	M-T	$2.1-24.0^b$ (1260)	$0-31.9^c$ (113)	0 (0)	---
	M-T-fungicide	$1.9-26.2^b$ (1470)	$0-26.7^{abc}$ (81)	0 (0)	---
Coniferous tree stand	L	$0-7.1^a$ (211)	$0-100^{ab}$ (62)	0-63.6 (13)	0-63.6 (13)
(n = 15 places)	G	$0-13.3^a$ (262)	$0-11.1^a$ (2)	0 (0)	---
	G-fungicide	$0-6.8^a$ (144)	$0-16.4^a$ (11)	0 (0)	---
	F	$0-3.6^a$ (132)	$0-50.0^{ab}$ (23)	0 (0)	---
	M-F	$0.9-21.3^b$ (970)	$0-87.5^b$ (332)	0-16.4 (33)	0-16.0 (18)
	M-T	$0.6-15.7^{ab}$ (537)	$0-60.0^{ab}$ (27)	0 (0)	---
	M-T-fungicide	$0-10.8^a$ (316)	$0-75.0^{ab}$ (23)	0-3.6 (1)	0-3.6 (1)

L, litter; G, bare ground; F, fallen logs; M, moss; T, bottom part of trunk surface. Values in the same row that do not differ significantly (P>0.05) are designated with the same superscript (Steel-Dwass multiple comparison test).

Table 3.1.2. Relative area of each substrate in the study plot (40m x 40m) and the number of natural seedlings on each substrate.

Substrate	NUF		KIN	
	Relative area (%)	No. of seedling	Relative area (%)	No. of seedling
L	92.8	569	91.4	49
G	0.3	33	1.7	317
M-G	0.2	85	0.4	271
F	0.1	62	2.2	92
M-F	2.0	462	1.7	346
R	---	---	0.3	4
M-R	0.01	7	0.9	75
M-T	0.8	95	0.1	37
Total		1313		1191

L, litter; G, bare ground; M, moss; F, fallen logs; R, rock; T, bottom part of trunk surface

Table 3.1.3. Effect of substrates to seedling establishement in the multiple regression model.

Substrate	NUF			KIN		
	Effect	*F*	p-level	Effect	*F*	p-level
L	⋯	2.388	n.s.	⋯	0.249	n.s.
G	+	15.295	<0.001	+	35.751	<0.001
M-G	+	4.700	0.031	+	5.209	0.023
F	⋯	0.834	n.s.	⋯	0.055	n.s.
M-F	+	50.788	<0.001	+	47.354	<0.001
R	⋯	⋯	⋯	⋯	0.005	n.s.
M-R	⋯	2.338	n.s.	⋯	0.093	n.s.
M-T	⋯	3.310	n.s.	⋯	0.116	n.s.

n.s., not significant (P>0.05); L, litter; G, bare ground; M, moss; F, fallen logs; R, rock; T, bottom part of trunk surface

Table 3.1.4. The number and survival percentages of natural seedlings on each substrate from 2005 to 2006 in NUF and KIN.

Seedling size	Substrate	Number NUF Jun. 05'	Oct. 05'	Jun. 06'	Oct. 06'	Number KIN Jun. 06'	Oct. 06'	Survival (%) NUF Jun. 05' to Oct. 05'	Oct. 05' to Jun. 06'	Jun. 06' to Oct. 06'	Survival (%) KIN Jun. 06' to Oct. 06'
1-year old seedlings	L	263	168	104	90	8	4	64	62	87	50
	G	21	18	16	16	166	124	86	89	100	75
	M-G	60	37	20	17	187	158	62	54	85	84
	F	28	18	11	11	43	35	64	61	100	81
	M-F	255	190	113	99	258	223	75	59	88	86
	R	0	0	0	0	1	0	0	0	0	0
	M-R	1	1	1	1	26	19	100	100	100	73
	M-T	53	37	19	19	23	22	70	51	100	96
	Total	681	469	284	253	712	585	69	61	89	82
Old seedlings (≥2 years old)	L	306	283	262	247	41	38	92	93	94	93
	G	12	12	12	12	151	146	100	100	100	97
	M-G	25	22	21	16	84	82	88	95	76	98
	F	34	34	33	29	49	45	100	97	88	92
	M-F	207	191	180	171	88	87	92	94	95	99
	R	0	0	0	0	3	2	0	0	0	67
	M-R	6	6	6	6	49	45	100	100	100	92
	M-T	42	34	30	29	14	14	81	88	97	100
	Total	632	582	544	510	479	459	92	93	94	96

L, litter; G, bare ground; M, moss; F, fallen logs; R, rock; T, bottom part of trunk surface
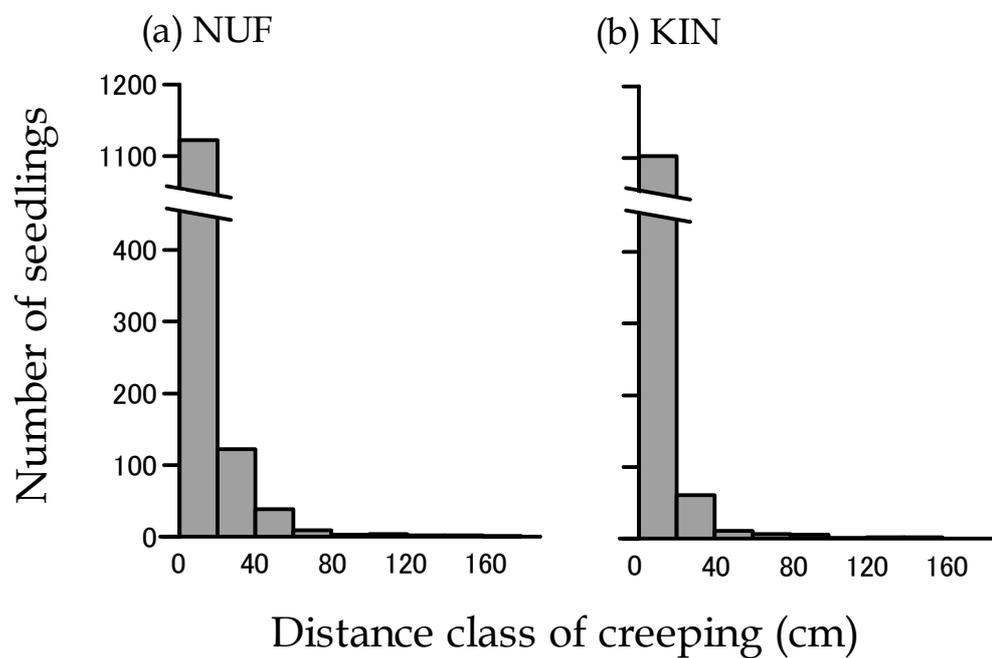
(a) NUF (b) KIN

Fig. 3.1.2. Diagrams of creeping distance class distribution of *H. petiolaris* seedlings in NUF and KIN.
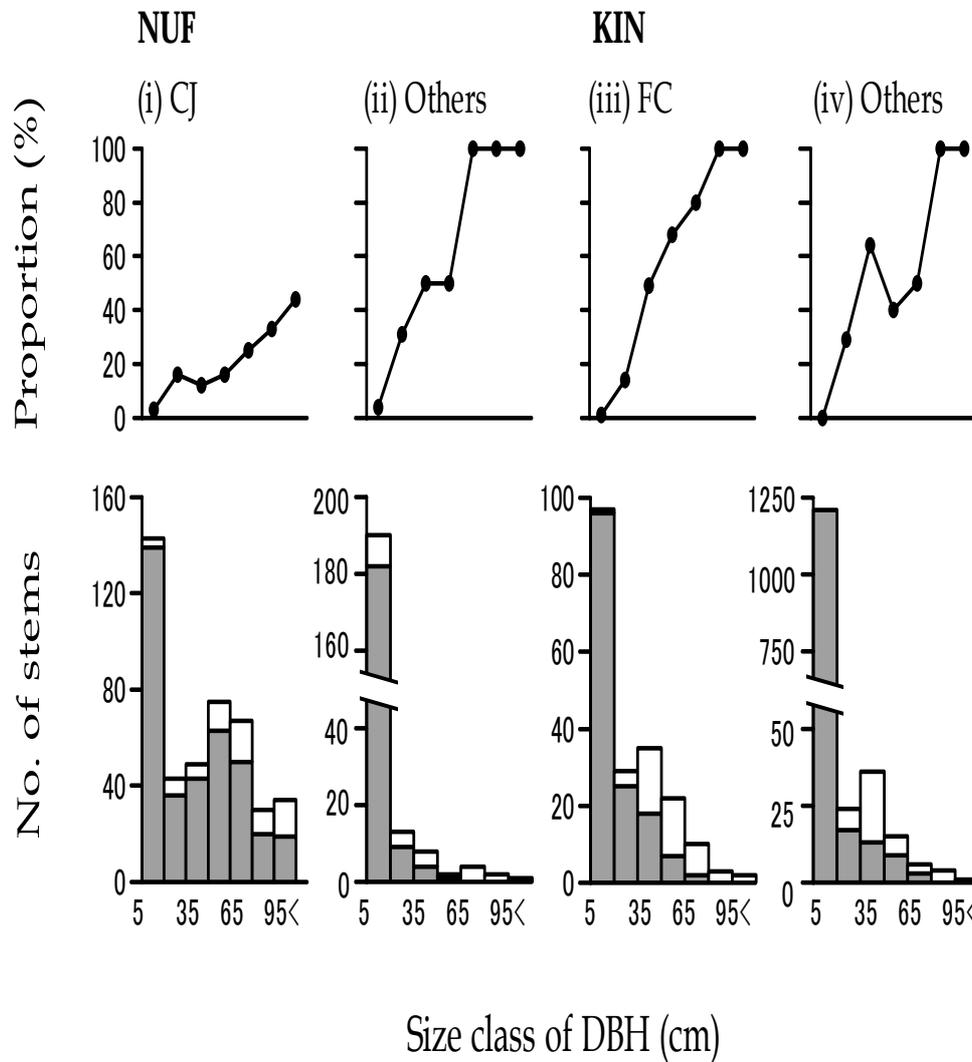
Fig. 3.1.3. Diagrams of DBH class distribution of potential host trees (DBH>5 cm) and proportions (%) of trees climbed by *H. petiolaris* to total trees in each DBH class. Solid bars show trees that were not climbed by *H. petiolaris,* and open bars show trees climbed by *H. petiolaris.*

Table 3.1.5. The probability (%) of the presence of each substrate within a radius 20cm of the base of trees (DBH≥20cm).

Plot	Species	L	G	M-G	F	M-F	R	M-R	M-T
NUF	*Cryptomeria japonica*								
	All trees (n = 299)	100	14.3	12.9	0	8.8	0	0	80.5
	Host trees (n = 67)	100	29.6	23.9	0	12.7	0	0	94.4
	Others (deciduous broad leaved trees)								
	All trees (n = 30)	100	66.7	26.7	0	3.3	0	0	86.7
	Host trees (n = 16)	100	75.0	31.3	0	6.3	0	0	87.5
KIN	*Fagus crenata*								
	All trees (n = 101)	100	93.1	53.1	0	1.0	0	0	65.3
	Host trees (n = 49)	100	95.9	58.4	0	2.0	0	0	73.5
	Others (deciduous broad leaved trees)								
	All trees (n = 82)	100	81.7	36.6	0	1.2	0	0	74.4
	Host trees (n = 45)	100	77.8	37.8	0	2.2	0	0	73.3

L, litter; G, bare ground; M, moss; F, fallen logs; R, rock; T, bottom part of trunk surface.

Table 3.1.6. The associations between the presence of safe site around root collar and the distribution of climbing stems using chi-square test.

Plot	Species (DBH≥20cm)	χ^2	df	P-value
NUF	*Cryptomeria japonica*	4.68	1	0.031
	Others	6.14	1	0.013
KIN	*Fagus crenata*	5.17	1	0.023
	Others	9.53	1	0.002

Table 3.1.7. The number of climbing stems that broke and/or fell and proportion of it to total climbing stems of *H. petiolaris* in each host tree in the NUF and the KIN.

Plot	Species	Bark texture	Climbing stems that broke and/or fell of *H. petiolaris*	
			Number	Proportion (%)
NUF	CJ	rough	15	7.7
	Others (TJ and PR)	slightly rough	5	6.7
KIN	*Fagus crenata*	smooth	14	9.2
	Others (QC and PR)	slightly rough	7	6.4

CJ, *Cryptomeria japonica*; TJ, *Tilia japonica*; PR, *Pterocarya rhoifolia;* FC, *Fagus crenata*; QC, *Quercus crispula*

Chapter 3

Section 2

Light environment of the habitat and its relationship with the distribution of *Hydrangea petiolaris*

Introduction

It is generally known that most lianas are abundant in canopy gaps and at forest edges (Putz 1984; Hegarty & Caballé 1991; Babweteera *et al.* 2000), and they are recognized as light-demanding plants. The climbing habit is regarded as an ecological strategy to gain access to preferable light conditions (den Dubbelden & Veburg 1996; Castellanos *et al.* 1999). However, compared to other lianas, root climbers tend not to dominate bright environments because their growth rates are lower than those of other lianas (Teramura *et al.* 1991) and because they cannot horizontally extend to additional adjacent host trees (Hegarty 1991; Putz & Holbrook 1991; Schnitzler & Heuzé 2006). Thus, the habitat of root climbers tends to be limited to regions just below and within the canopy of the host trees, and their growth, reproduction, and survival is directly affected by the host trees.

Only a few studies have been conducted to clarify the three-dimensional light conditions in the habitat of lianas (Castellanos *et al.* 1999), and the relationship between these light conditions and the distribution of lianas has not been studied. In

Chapter 3.1, we clarified that the root climber *H. petiolaris* preferred deciduous broad-leaved trees as hosts rather than coniferous trees, suggesting that the distribution of *H. petiolaris* is controlled by the light distribution in the forest.

In this section, we discuss the fine-scale measurement of the three-dimensional light conditions in forests, and we clarify the relationship between these conditions and *H. petiolaris* distribution. Moreover, in Chapter 2.2, we quantified that leaves, trunks, and reproductive organs of *H. petiolaris* were concentrated from 2 to 6 m in heights. Thus, we check the relationship between light conditions and construction of *H. petiolaris*.

Materials and methods

Study sites

The measurement of light condition was conducted in a 100 × 100 m plot in Niigata University Forest (NUF; see Chapter 3.1). The canopy height in this forest is approximately 15–20 m, and the height of the lowest branches is approximately 6–7 m. *Viburnum furcatum, Lindera umbellata* var. *membranacea,* and *H. macrophylla* var. *megacarpa* dominate the shrub layer.

Study methods

The three-dimensional light conditions were measured with 2 different spatial scales

to quantify the spatial heterogeneity of the light conditions in the forest. In October 2006, we simultaneously measured photosynthetically active photon flux density (PPFD) with quantum sensors (S-LIA-M003; Onset Computer Corporation, Massachusetts, USA) and a data-logger (HOBO Micro Station, Onset Computer Corporation, Massachusetts, USA) in the forest and at an open site near the forest (control) on cloudy days (maximum PPFD of control < 500 µmol photons m^{-2} s^{-1}). From the results, we calculated the relative PPFD (rPPFD; ratio of the PPFD in the forest to that in the open site). We measured the PPFD at 5 heights (0.2, 2, 4, 6, and 8 m) in a 10-m grid (5 × 121 = 605 points) using the prove cylinder method (Sumida 1993). At the heights from 2 to 8 m, the light condition was measured by attaching the quantum sensor to the top of measuring rods (FT-12, Senshin Industry Co., Ltd., Osaka, Japan).

We measured the micro-scale light condition around the canopy tree *Cryptomeria japonica*. In order to measure the PPFD under optimum conditions, we selected 3 individual trees whose branches extended evenly for maximum light exposure and on which no lianas had climbed. We conducted concentric and cylindrical measurements of the light conditions, i.e., 12 exposure × 4 radii (0, 1, 2, and 3 m from the trunk surface) × 5 heights (0.2, 2, 4, 6, and 8 m) = 240 points per tree.

For both the forest and the canopy trees, the differences in the rPPFD among the heights were examined using the Tukey-Kramer honestly significant difference

(HSD) test. From the results, we could contour map the light condirions in the forest. We estimated the rPPFD of each tree (diameter at breast height (DBH) ≥ 20 cm) from the contour map. In order to clarify the relationships among the tree species (broad-leaved trees and coniferous trees) and that between the host trees and light conditions, the rPPFD values were compared among the trees (broad-leaved trees, coniferous trees, all trees, and host trees) by using the Tukey-Kramer HSD test.

Results

Spatial heterogeneity of the light conditions in the forest

The differences of light conditions were found horizontally and vertically (Fig. 3.2.1). At heights of 4, 6, and 8 m, bright and dark patches were clearly observed, and their positions at these 3 heights were very similar. The highest rPPFD values ranged from 0.61 to 0.77, while the lowest values ranged from 0.004 to 0.01. On the other hand, at heights of 0.2 and 2 m, the light condition was very weak and was horizontally homogenous. The highest rPPFD values did not exceed 0.28, and the canopy gaps observed at heights of 4, 6, and 8 m seemed irrelevant to the light conditions of the forest floor.

In the forest, the rPPFD values differed significantly among the heights (Fig. 3.2.2). The mean rPPFD increased continuously with height, while ranges from minimum to maximum value of rPPFD in each height were discontinuously varied. The values at

0.2 m ranged from 0.01 to 0.13 and were significantly less than those at other heights ($P < 0.05$). The values at 8 m ranged from 0.01 to 0.77 and were significantly greater than those at 0.2, 2, and 4 m ($P < 0.05$). At heights of 2, 4, and 6 m, the rPPFD values did not differ significantly ($P > 0.05$).

Micro-scale heterogeneity of the light conditions around the host trees

The micro-scale light conditions around the host trees varied concentrically and cylindrically (Fig. 3.2.3). At all heights, the rPPFD values increased with the distance from the trunk surface. The rPPFD values were similar on all sides of the trunks of all trees, except one (No. 2) at a height of 8 m.

When we pooled the rPPFD data collected under all exposure conditions, a vertical difference was clearly observed. Close to the trunk surface, the highest rPPFD values were observed at heights of 2 and/or 4 m, and the values at 0.2 and 8 m were significantly lower than those at 2 and 4 m ($P < 0.05$).

At a 1-m radial distance from the trunk surface, the lowest rPPFD value was observed at a height of 0.2 m ($P < 0.05$). At heights of 2, 4, 6, and 8 m, the rPPFD did not differ significantly ($P > 0.05$).

At a 2-m radial distance from the trunk surface, the lowest rPPFD value was observed at a height of 0.2 m ($P < 0.05$). The rPPFD values did not differ significantly among the heights of 2, 4, 6, and 8 m ($P > 0.05$).

At a 3-m radial distance from the trunk surface, the lowest rPPFD value was observed at a height of 0.2 m (P < 0.05). The rPPFD values did not differ significantly among the heights of 2, 4, 6, and 8 m (P > 0.05); the rPPFD value was the maximum for an individual tree (No. 2) at 8 m (mean rPPFD, 0.21).

Effect of light condition on the distribution of H. petiolaris

The light condition partly affected the distribution of *H. petiolaris* (Table 3.2.1). With regard to both tree types (broad-leaved trees and coniferous trees) at heights of 2 and 6 m, the rPPFD values for the host trees were significantly greater than those for the non-host trees (P < 0.05). At 0.2, 4, and 8 m, the rPPFD values did not differ significantly (P > 0.05), although the mean rPPFD values for the host trees were greater than those for the non-host trees.

With regard to the coniferous trees at a height of 6 m, the rPPFD values for the host trees were significantly greater than those for the non-host trees (P < 0.05). At heights of 0.2, 4, and 8 m, the rPPFD values did not differ significantly (P > 0.05), although the mean rPPFD values for the host trees were greater than those for the non-host trees.

With regard to the broad-leaved trees, the rPPFD values did not differ significantly between the host and non-host trees at all heights (P > 0.05), although the mean rPPFD values for the host trees were greater than those for the non-host trees.

Discussion

Our results showed spatial heterogeneity of light condition not only horizontally but also vertically. In terms of the light condition and patchiness, we can categorize the forest layer depend upon light conditions as follows: "shrub layer" (from 0.2 to 2 m) and "sub-canopy layer" (from 4 to 8 m). In the "sub-canopy layer," the horizontal heterogeneity of the light conditions was relatively high, and bright patches caused by canopy gaps were observed. In all areas of the "shrub layer," however, the light conditions were homogenous and extremely dark. This suggests that the growth and survival of *H. petiolaris* is controlled by the severe light conditions in the shrub layer. Juvenile *H. petiolaris* plants have to grow to a height of 2 m in order to escape the limitations imposed by light. It is generally known that shade provided by surrounding vegetation such as shrubs and/or dwarf bamboos is one of the main causes of seedling mortality (Nakashizuka & Numata 1982; Fenner & Thompson 2005). Lianas usually have a higher growth rate than self-supporting plants (French 1977; Putz 1984; Bell *et al.* 1988; Gartner 1991; Givnish 1995; Mulkey *et al.* 1996), suggesting that they have the potential to avoid the extremely dark conditions in the shrub layer. Thus, we suspect that *H. petiolaris* has relatively low mortality rates under limited light.

In the micro-scale measurement, the influence of shade due to the host canopy was clearly observed on the trunk surface at a height of 8 m. Thus, on the trunk surface,

preferable light conditions for *H. petiolaris* are distributed within spaces between canopy layer and shrub layer (from 4 to 6 m, in this study). In addition, our data showed that at a radial distance of 1 m or more from the trunk surface, the influence of shade due to the host canopy was seldom observed. These results are entirely consistent with the construction of *H. petiolaris* (see Chapter 2.2), implying that *H. petiolaris* make the utmost use of preferable light conditions between canopy layer and shrub layer.

On the other hand, from the viewpoint of temporal stability, we can state that the trunk surface of a host tree is a relatively stable habitat for lianas because self-supporting trees cannot invade these specific spaces. Therefore, these spaces would be a customized habitat preferred by *H. petiolaris*.

The light conditions partly affected the distribution of *H. petiolaris*. In all species, the mean rPPFD values for the host trees were greater than those for the non-host trees, and at some heights, statistically significant differences in the rPPFD values were observed between the host and non-host trees. This suggests that the light conditions in the sub-canopy layer potentially control the distribution of *H. petiolaris*. Our study site is a well-matured forest that is dominated by approximately 300- to 500-year-old *C. japonica* trees, and the forest canopy is relatively sparse and bright. Thus, the influence of limited light on the distribution of *H. petiolaris* may be clearly revealed in an immature forest or a coppice forest that has a high density of canopy

trees.

Our field observations show that *H. petiolaris* plants in canopy gaps and at forest edges usually have many more inflorescences than those inside the forest. Therefore, whether or not the heterogeneity of three-dimensional light conditions determines the reproductive efforts of *H. petiolaris* would be worth examining in the future.
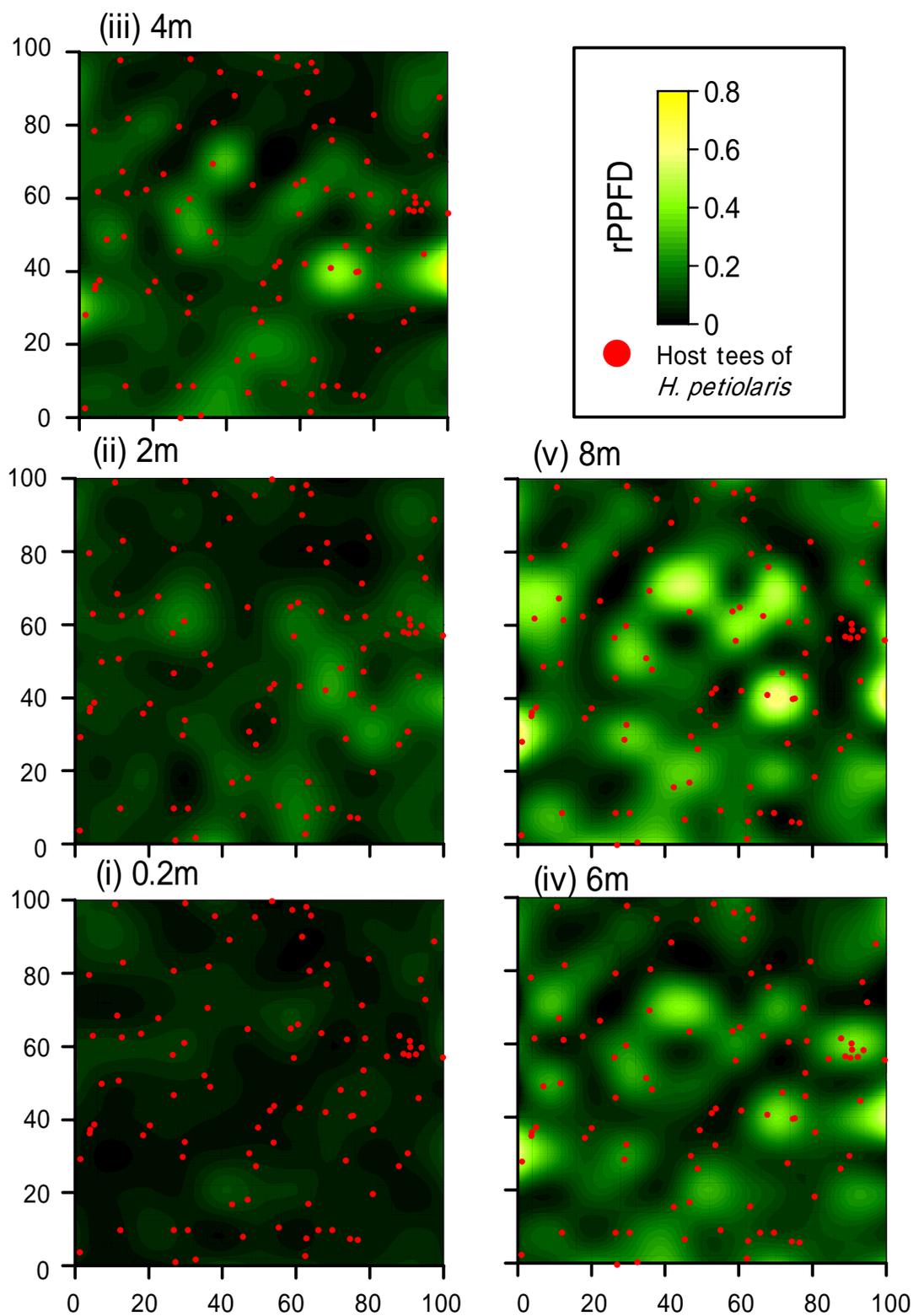
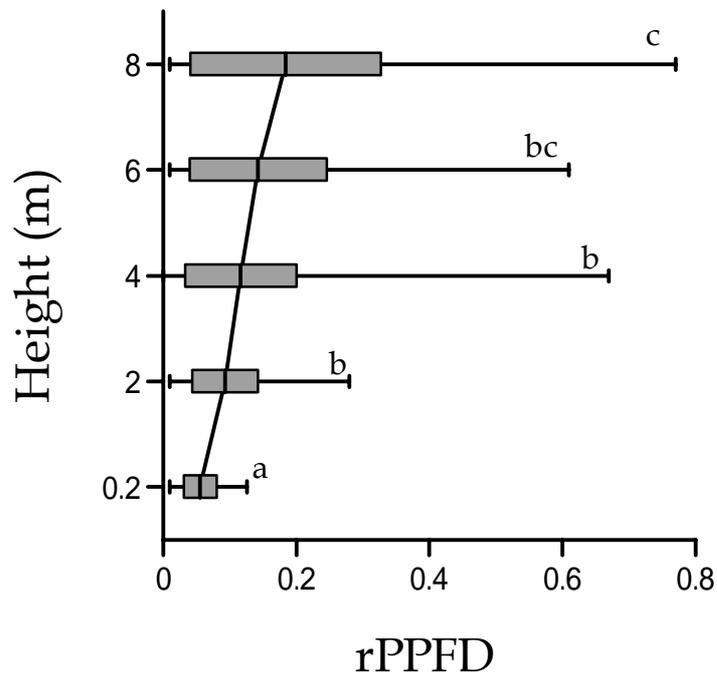Fig. 3.2.1. Contour map of light condition in each height in 100 m x 100 m plot. A circle shows location of host trees of *H. petiolaris* (DBH≥5 cm).

Fig. 3.2.2. Range of rPPFD in each height in the forest. Each bar represents the mean values±SD. Horizontal bars show the range from minimum values to maximum values. A mean value of each bar are linked by a line. Values that do not differ significantly ($P > 0.05$) are designated with the same superscript (Tukey-Klamer's HSD test).
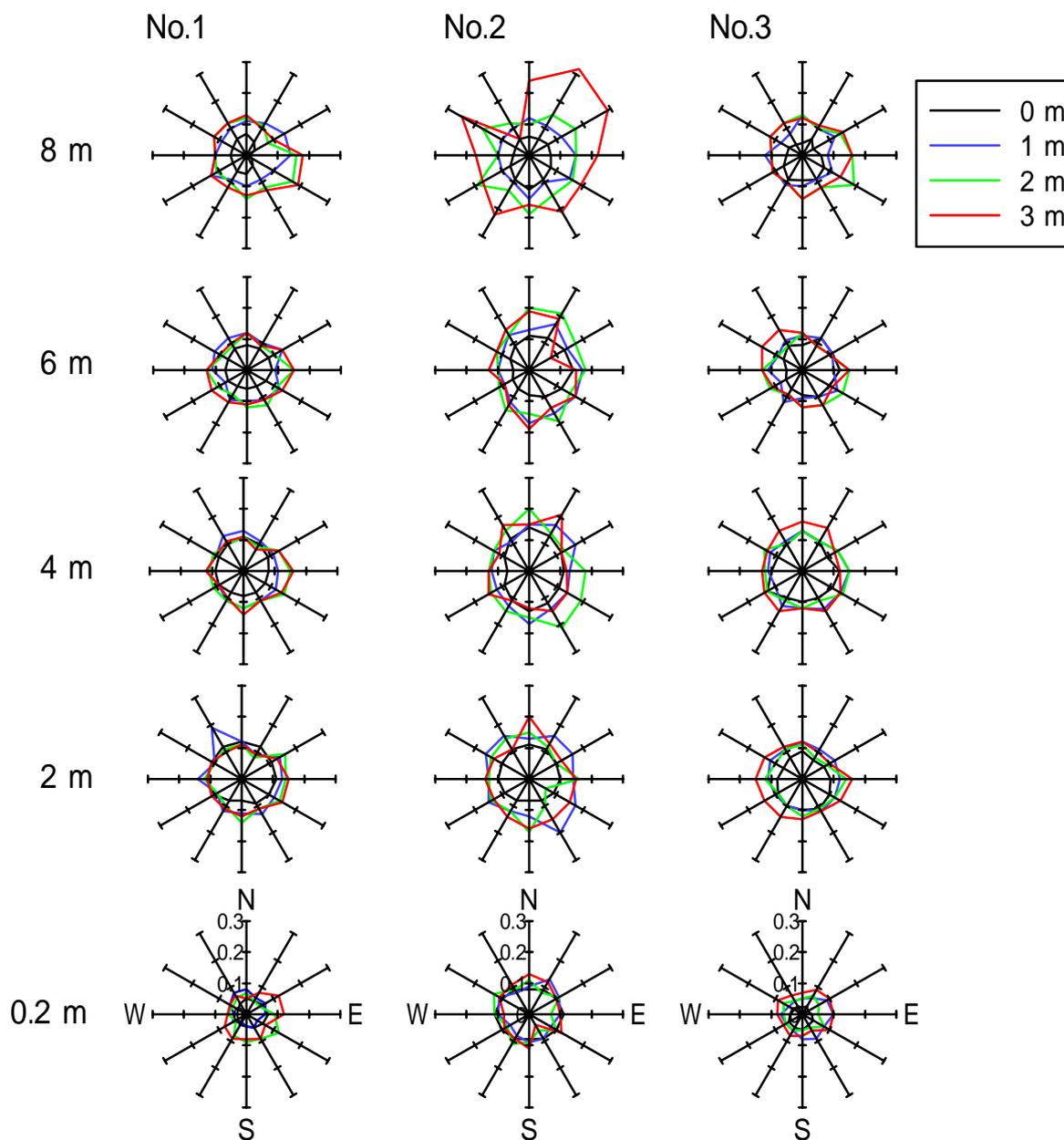
Fig. 3.2.3. Light condition in each height around *Cryptomeria japonica*. Each line shows rPPFD. The difference of color show the difference of radial distance from trunk surface.
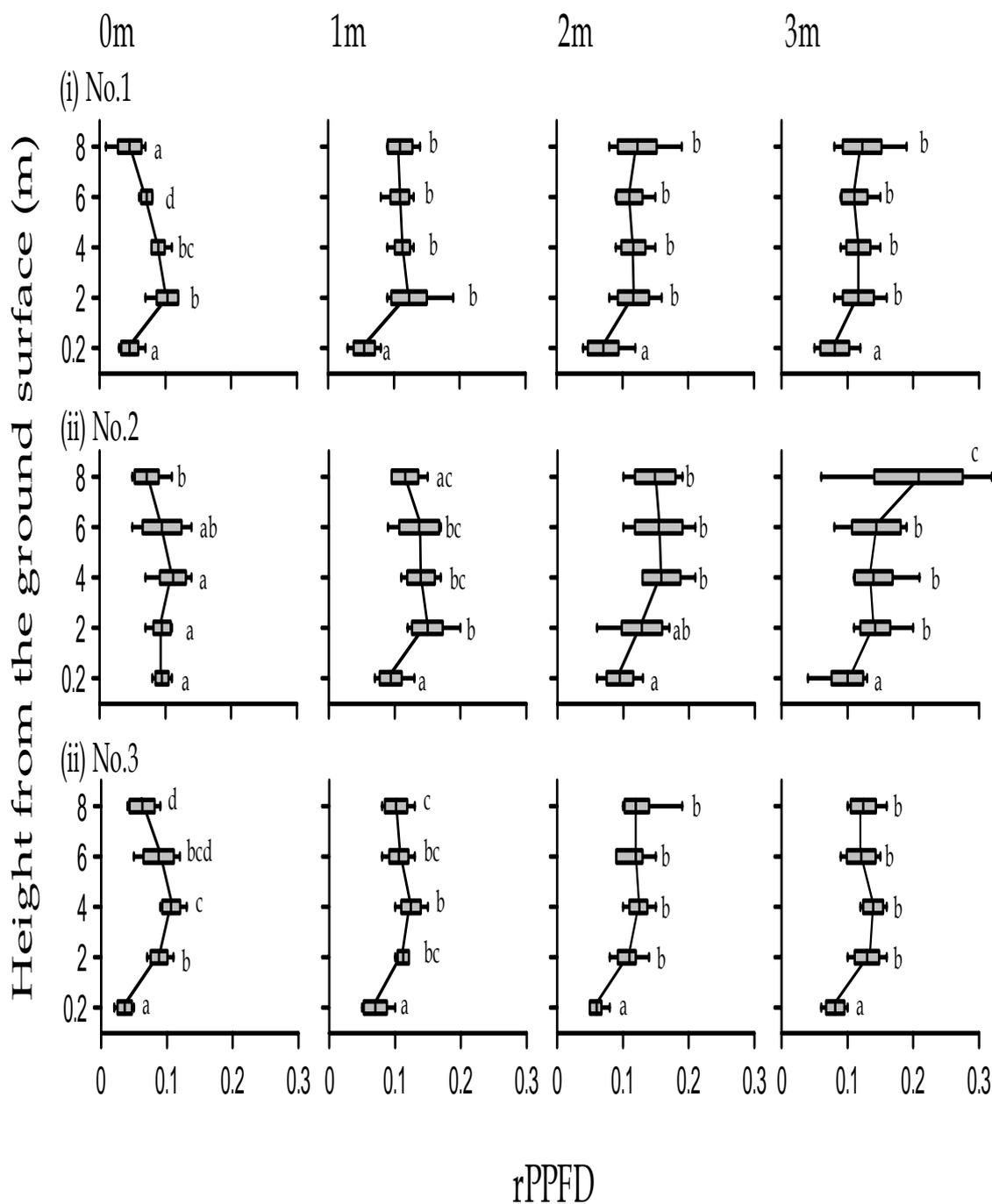
Fig. 3.2.4. The range of rPPFD in each height in each radial distance from trunk surface. Each bar reprezents the mean values±SD. Horizontal bars range from minimu to maximum values. A mean value of each bar are linked by a line. Values in the same row that do not differ significantly (P>0.05) are designated with the same superscript (Tukey-Klamer's HSD test).

Table 3.2.1 The aPPFD in each tree species in each height. Mean values (±SD) are shown.

	aPPFD in each height				
	0.2 m	2 m	4 m	6 m	8 m
All trees (broad-leaved trees and coniferous trees)					
Non-host trees (n = 36)	0.069±0.065^a	0.089±0.086^b	0.110±0.107^c	0.137±0.107^d	0.164±0.169^e
Host trees (n = 13)	0.069±0.072^a	0.075±0.074^a	0.125±0.115^b	0.164±0.063^c	0.179±0.108^c
Coniferous trees					
Non-host trees (n = 22)	0.069±0.065^a	0.089±0.085^b	0.110±0.107^c	0.134±0.107^d	0.164±0.169^e
Host trees (n = 7)	0.069±0.065^a	0.089±0.069^ab	0.122±0.067^b	0.164±0.065^c	0.167±0.111^c
Broad-leaved trees					
Non-host trees (n = 14)	0.069±0.070^a	0.120±0.167^bc	0.094±0.065^ab	0.159±0.107^cd	0.169±0.167^d
Host trees (n = 6)	0.069±0.065^a	0.145±0.167^b	0.141±0.108^b	0.160±0.065^ab	0.205±0.167^c

Values in the same row that do not differ significantly (P>0.05) are designated with the same superscript (Tukey-Kramer's HSD test)

Chapter 4

General discussion

In this thesis, we succeeded to make clear the advantages and disadvantages of the distinctive life form of this species.

Allometry was very similar between the liana and shrubs in the genus *Hydrangea*. It is generally known that shrub allocates less biomass to supporting tissues and more biomass to leaves and/or reproductive organs compared with tree (Whittaker & Woodwell 1968; Givnish 1995; Larcher 2003). This suggests that shrub can minimize production and/or maintenance costs of supporting tissues. On the other hand, the leaves and/or reproductive biomass of shrub are considerable small as a consequence of small plant sizes. However, lianas had similar allometry to shrub accompanied with huge amount of leaves and reproductive organs as a consequence of climbing; hence the special growth form of lianas would be only way to accord huge biomass with minimum supporting tissues.

In Japan, other two genera also include both lianas and shrubs within the same taxa; *Euonymus* and *Psychotria*. Each genus composed of a huge root climber and some shrubs like a *Hydrangea*, and the huge root climbers are supposed to have size advantage comparing to the shrub species, as we clarified in *Hydrangea*. Therefore, our size advantage hypothesis is applicable to various lianas and it is worth while

checking in near future.

On the other hand, the demography of *H. petiolaris* in the early regeneration stage was strongly subjected to phylogenetic constraints of the genus *Hydrangea*. *Hydrangea* species have specific reproductive characters such as very small seed size, anemochory and so on. These characters limited the safe sites of *H. petiolaris* resulting in regeneration with very low probability. Therefore, a large number of seeds may be necessary for the regeneration of *Hydrangea* species, and we can consider that the size advantage of *H. petiolaris* would compensate with the low probability of regeneration.

Two root climbers mentioned above, *E. fortunei* and *P. serpens*, have very different reproductive characters compared with *H. petiolaris*. They are evergreen broad-leaved lianas, and their seed dispersal types are endozoochory. The seed sizes range from 0.14 to 0.26 g per 10 seeds (Nakayama *et al.* 2000) , and the values are 250 to 500 times greater than that of *H. petiolaris* (ca. 0.060 g/1000 seeds; see Chapter 2). Thus, the regeneration strategies and controlling factors would vary among the root climbers, even though the size advantage hypothesis is to be adopted to all of them. And, considering those factors, we would like to emphasize that the following four criterions are very important to understand the diversity of regeneration strategy of root climbers systematically; (1) safe sites, (2) the survival probability in the early regeneration stage, (3) the searching process for the host trees, and (4) host

preferences.

Synthesizing all results mentioned above, we can summarize the life history of *H. petiolaris* as follows;

(1) *Early regeneration stage (from germination to seedling establishment)*

A lot of very small seeds are dispersed by wind, and germinate. Most current year seedlings are to be killed during the first winter. Limited number of seedlings survive on the small specific substrates such as moss on fallen logs, bare ground, and moss on bare ground.

(2) *Creeping stage (from seedling establishment to attaching host trees)*

The seedlings start creeping from second year with very low growth rate. The seedlings around root collar of host trees start climbing on the host trees without creeping, while others survive as a seedling bank, and search host trees for a long time. In snowy region, most of deciduous broad-leaved trees have safe sites around their root collar.

(3) *Climbing stage (juvenile)*

When the juvenile starts climbing successfully, the elongation speed is accelerated drastically. Diameter growth of climbing stems is very slow. The stem grows up to approximately 10 m in heights, just below the canopy layer, and leaves, trunks and reproductive organs are arranged from 2 to 6 m in heights.

(4) *Flowering stage (seed production/dispersal)*

Producing millions of seeds, adult individuals disperse them much wider areas than other *Hydrangea* shrubs. The longevity of adult *H. petiolaris* is more than 100 years, and the values are much longer than other *Hydrangea* shrubs.

We have succeeded to clarify quantitatively the life history strategies of lianas by using the temperate root climber *Hydrangea petiolaris* as a model plant. This thesis is first attempt that have quantified the complete life history of lianas. However, it might be difficult to generalize some part of our results to all lianas because life history of *Hydrangea* species is regulated by phylogenetic constraints. Comparative studies in various genera are needed in the future.

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