Chapter 6
Diversity of Herbaceous Plants in the Ooyamazawa Riparian Forest

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Abstract Various herbaceous plants grow in the forest floor of the Ooyamazawa riparian forest. The diversity of herbs is related to the complexity of the ground surface condition, which is formed by ground disturbances such as debris flow, landslides, and soil erosion. Most notably, micro-scale heterogeneity and disturbances have effects on the growth of herbs. Herbaceous plants may adapt to such ground conditions throughout their life cycle, i.e., during vegetative growth, vegetative reproduction, and sexual reproduction. We can observe a part of these ecological characteristics as functional groups. Furthermore, we will show the relationships between the ecological functional traits and their relation to vegetative reproduction and micro-disturbances in riparian areas.

Keywords *Chrysosplenium macrostemon* · *Deinanthe bifida* · *Elatostema umbellatum* var. *majus* · Forest floor plants · Ground disturbance · Rhizome type · Shoot elongation

6.1 Introduction

In mountain areas, slopes comprise several segments that are distinguished by changes in slope angle, which are termed as "breaks in slope" (Tamura 1969). Relatively active processes, such as soil erosion, landslides, and slope failures, occur more frequently on lower slope segments than on upper slopes and on ridge sites. Therefore, we can consider each segment as different habitats, which in turn have different types of vegetation established on it. In upper-stream mountain areas, the riparian forest corresponds to the forest on lower slope segments and on the valley bottom.

Generally, riparian forests have high species diversity. Herbaceous plants on the forest floor seem to largely contribute to the high species diversity (Kawanishi et al.

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2008). The variation pattern of species diversity among habitats reflects differences in species coexistence patterns. Tree species distributions are generally limited by various combinations of disturbances and resources (Loehle 2000), but these have the potential for rapid migration (Clark 1998). On the other hand, the distribution patterns of forest floor herbaceous plants are determined by the availability of suitable habitats under the forest, the likelihood of seed dispersal to these habitats, and the successful germination of seeds and their subsequent growth (Ehrlen and Eriksson 2000; Gilliam and Roberts 2003). Thus, the effect of a disturbance differs for trees and for understory plants. This means that in order to clarify the species diversity pattern and mechanisms of the whole forest, we must first recognize the community structure independently for each life form (Kawanishi et al. 2008).

6.2 Comparison of Species Richness Among Different Deciduous Forest Corresponding to Slope Segment

To recognize patterns of species diversity, we compared the species richness of riparian forest among different deciduous forests based on their slope segments. We classified the mountain slope segments as crest slope, upper side slope, lower side slope, and valley-bottom, according to the hill slope system of Tamura (1987) (Fig. 6.1).
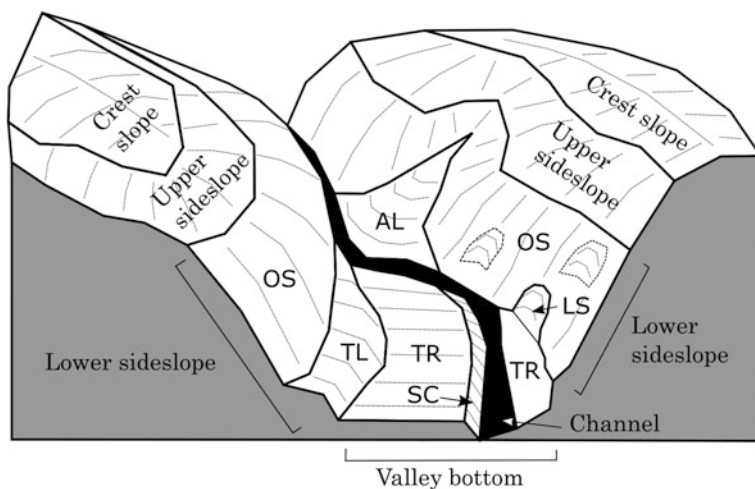

Fig. 6.1 Schematic diagram of landform types explained in this chapter (modified from diagram of Tamura 1987). Sub-small-scale landform types are shown as crest slope, upper side slope, lower side slope, and valley bottom, based on the hill slope system of Tamura (1987). Lower side slope and valley bottom are further sub-divided into micro-landform types (Kawanishi et al. 2004), i.e., terrace of debris flow (TR), alluvial fan (AL), terrace scarp (SC), new landslide site (LS), old landslide slope (OS), and talus (TL)

The valley vegetation of the Ooyamazawa river basin is a riparian forest that consists of *Fraxinus platypoda*, *Cercidiphyllum japonicum*, and *Pterocarya rhoifolia*, as was mentioned in a former chapter. On the other hand, *Fagus crenata– Fagus japonica* forests and *Tsuga sieboldii* forests are established on the upper side slopes and on the ridge, respectively (Maeda and Yoshioka 1952). Thus, species composition varies remarkably along the slope, and several forest types correspond to the micro-topography on the slope and in the watersheds (Kikuchi and Miura 1993; Sakai and Ohsawa 1994; Nagamatsu and Miura 1997). This structure of vegetation contributes in augmenting the plant species richness and diversity. In this chapter, we will discuss the distribution pattern of forest floor plants and how it relates to landforms, from the viewpoint of plant functional traits.

To recognize the pattern of species diversity, we attempted estimation using the hierarchical diversity model (Kawanishi et al. 2006). There are two levels, as follows: "*d*" is the sample quadrat diversity (Whittaker 1975), and "*D*" is the total diversity in a micro-landform unit. This hierarchical diversity model is a modified version of the model derived by Wagner et al. (2000).

The value of *d* is affected by within-quadrat species richness, but not by the quantitative dominance of species; instead, it is based on the species–area relationship (cf. formulae 6.1):

$$d = \frac{S}{\log_{10} A} \tag{6.1}$$

where *S* is the number of species in a quadrat and *A* is the area of the quadrat. *D* (within-unit richness) shows the species richness per micro-landform, and was calculated as the total number of species in a micro-landform type (S_t) per total area (A_t, sum of the quadrat areas), such that:

$$D = \frac{S_t}{\log_{10} A_t} \tag{6.2}$$

Figure 6.2 is a case study of vegetation in the Ooyamazawa river basin (Kawanishi et al. 2006). Species richness (*d*, *D*) was shown in each landform, and each Raunkiaer's life type (dormancy type) was classified based on the position of the dormant bud. This type represents the difference between the woody plants (MM, M, N, Ch), perennial herbs (H, G), and annual herbs (Th). Originally, this type was used to show the relationship between global climate and vegetation; however, we can also use this spectrum for overstory trees and forest floor plants.

On mountain slopes in the Ooyamazawa basin, indexes *d* and *D* of trees were higher on the upper side slope and crest slope than on the valley bottom and lower side slope (Fig. 6.2, see Fig. 6.1 for positional relation of landform). In contrast, the *d* of forest floor plants (Ch, H, G, Th) was very high on the valley bottom and lower side slope. These results indicate that the effects of topographical factors on species diversity differ between forest floor plants and overstory trees.
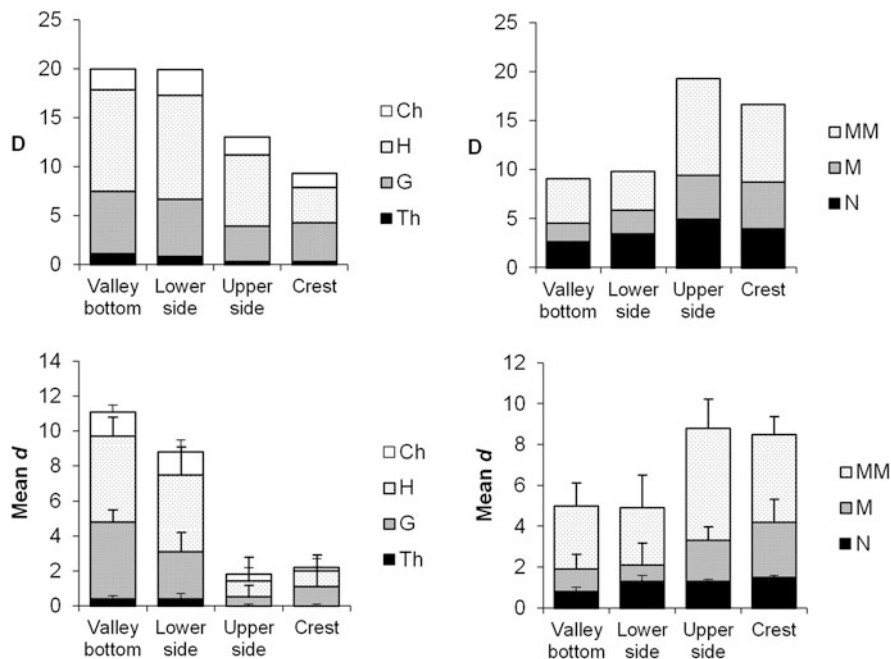
Fig. 6.2 Comparison of species richness for each life type among micro-landform types (Kawanishi et al. 2006). Indices *D* and means of index *d* are shown with standard deviations. Life types are Th: therophyte, G: geophyte, H: hemicryptophyte, Ch: chamaephyte, N: nanophanerophyte, M: microphanerophyte, and MM: megaphanerophyte

Why are overstory trees diverse in the upper slope areas? It would probably be related to the regeneration processes of trees, which depend on disturbances. For example, trees in beech forests on stable slopes generally regenerate in small canopy gaps when trees fall due to typhoons, etc. (Nakashizuka 1982, 1983, 1984). In addition, very few juvenile *Fagus crenata* are found in the beech forests on the Pacific Ocean side of Japan (including the Ooyamazawa river basin), although juveniles of many other species can be found (Shimano and Okitsu 1993, 1994). The regeneration processes in *Tsuga sieboldii* forests show similar patterns (Suzuki 1980). As a result, many small patches consisting of regenerate trees are allocated within a small area, producing a higher alpha diversity (d) for trees in the upper side slope and crest slope. In contrast, dominant trees on the valley bottom and lower side slope (e.g., *Pterocarya rhoifolia*, *Fraxinus platypoda*, and possibly *Cercidiphyllum japonicum*) generally regenerate simultaneously in the huge gaps created by rare, large disturbances (Sakio et al. 2002). Therefore, large disturbances would restrict the establishment of many deciduous trees that grow on the upper slope and would allow several trees to adapt to riparian disturbances. As a result, the index d for trees on the valley bottom and lower side slope is low. This tendency can be seen in other

riparian forests, such as on the floodplain forest (Aruga et al. 1996) and on the relatively stable riparian terrace forest (Suzuki et al. 2002).

In contrast, the mean *d* of herbaceous plants on the valley bottom and on the lower side slope is very high. This indicates that frequent disturbances increase the diversity of forest floor plants. The reason for this tendency is the absence of strong competitors, e.g., dwarf bamboo (*Sasamorpha borealis*), which were removed by frequent ground disturbances in a riparian area. Because light reaching the forest floor is very scarce in dense dwarf bamboo communities (Nakashizuka 1988), other herbs may not be able to grow. In addition, we can observe the land heterogeneity of disturbance sites (Sakio 1997; Sakio et al. 2002). This heterogeneity will contribute to the high diversity of micro-habitat types relating to ground surface condition, such as gravel size, content ration of organic matter, and water content. Therefore, the various ground disturbances may be responsible for the high beta-diversity of herbs in riparian forests. This will be discussed in the next section.

6.3 Relationships Between Landforms and Life Type Composition in the Forest Floor Vegetation

The forest floor vegetation varies among different habitats based on their landform, as stated above. Given these findings, we sought characteristics of herbaceous plants that confer adaptation to various habitats. In general, the likelihood of seed dispersal to various habitats, and the successful germination of seeds and their subsequent growth determine the distribution of herbaceous plants (e.g., Ehrlen and Eriksson 2000; Gilliam and Roberts 2003). In this study, we focus on growth propagation, and we aim to show that the habitat restriction of herbaceous plants in riparian forests is caused by differences in breeding.

The characteristics of the life history of forest floor plants in Japan have been studied mainly in terms of reproductive ecology and seed ecology (e.g., Kawano 1975, 1985; Kawano and Nagai 1975). Generally, well-adapted to disturbances are annual herbs with short leaf lives and large growth amounts (Grime 2001). On the other hand, perennial herbs have various life history and life cycle characteristics that are related not only to environmental pressures or to interspecies competition, but also to their adaptation to disturbances (Kawano 1985). For example, some perennials have life history strategies equivalent to annual plants. Such plants are often called as "pseudo-annual plants". This includes *Cacalia delphiniifolia* (Fig. 6.3), *Cacalia tebakoensis*, *Senecio nikoensis*, and *Sanicula chinensis* (Numata and Asano 1969) which are interesting; however, there are still many unknown parts in their life history, so clarifying their significance is of great interest.

It is clear that the number of species capable of vegetative reproduction in the forest floor vegetation in the *Pterocarya rhoifolia* and *Fraxinus platypoda* forests is greater than that in the *Fagus crenata* and *Quercus crispula* forests (Oono 1996). Species that are early in making independent propagules from the mother individual

Fig. 6.3 Pseudo-annual
plants; *Cacalia
delphiniifolia*

by vegetative propagation are characteristically linked to the riparian *Fraxinus platypoda* forest. In general, the vegetative reproduction of herbaceous plants plays important roles in maintaining the population (Silvertown 1982; Grime 2001) and in recovering from damage caused by ground disturbance (Yano 1962). These indicate that the functional diversity of herbaceous plants greatly contributes to the species diversity of riparian vegetations. Therefore, I would like to describe the relationship between the life types of herbaceous plants and ground disturbances, with the aim of understanding the establishment of the forest floor vegetation in the riparian forests.

The habitat differentiation of herbs in the *Fraxinus playipoda* and *Pterocarya rhoifolia* forests is related to their vegetative reproduction characteristics (Kawanishi et al. 2004). In the Ooyamazawa basin, six landform types could be distinguished along the valley: debris flow terrace, alluvial fan, terrace scarp, new landslide site, old landslide slope, and talus (Fig. 6.1, Kawanishi et al. 2004). Forest floor plants were classified into 7 groups by cluster analysis, and we were able to identify three major groups (clusters A, B, D) (Table 6.1). Cluster A includes species belonging to spring ephemerals, storage rhizomes, and anti-vegetative reproduction. These species are perennial herbs and ferns with storage-type rhizomes, and they mainly grow on landforms such as debris flow terraces and alluvial fans where they are stable for long periods of time (Fig. 6.4, Kawanishi et al. 2004).

Spring ephemerals, such as *Corydalis lineariloba* (Fig. 6.5) and *Allium monanthum* (Fig. 6.6), have significantly greater concentrations of nitrogen and iron than other herbs (Muller 2003), which may relate to high anabolism. Storage organs have important roles in the effective distribution of carbohydrates and major

Table 6.1 Mean coverage (%) of species in each landform type with maximum coverage of species in parenthesis (Kawanishi et al. 2004, 2008)

Species name	GS	REP	MR	TR	AL	SC	LS	OS	TL
	Life type			Mean coverage (%)					

Species name	GS	REP	MR	TR	AL	SC	LS	OS	TL
Cluster A									
Scopolia japonica	sm	rhi	rs	8.1 (40)$^+$	7.4 (40)$^+$	2.1 (20)$^-$	1.6 (10)$^-$	3.2 (30)$^-$	9.5 (50)$^+$
Corydalis lineariloba	sp	tub	rr	7.0 (20)$^+$	9.0 (20)$^+$	4.3 (20)	1.7 (10)$^-$	3.6 (15)$^-$	3.0 (15)$^-$
Spuriopimpinella nikoensis	f	av	rs	1.5 (5)	5.5 (10)$^+$	2.2 (10)	0.5 (7)$^-$	0.6 (7)$^-$	1.4 (10)
Aconitum sanyoense	f	tub	rr	2.2 (15)$^+$	5.0 (30)$^+$	2.4 (20)$^+$	0.5 (10)$^-$	0.2 (3)$^-$	0.3 (7)$^-$
Veratrum grandiflorum	sm	rhi	rs	1.2 (10)	7.0 (20)$^+$	0.3 (5)$^-$	0.1 (2)$^-$	1.1 (20)$^-$	0.0 (0.1)$^-$
Mitella pauciflora	f	rhi	rc	4.5 (20)$^+$	2.4 (10)$^+$	0.4 (3)$^-$	0.7 (5)$^-$	0.4 (7)$^-$	0.4 (3)$^-$
Dryopteris crassirhizoma	f	av	rs	3.0 (10)$^+$	1.2 (10)	0.6 (5)$^-$	0.4 (5)$^-$	0.5 (10)$^-$	1.0 (10)
Cornopteris crenulato-serrulata	f	rhi	rc	2.4 (7)$^+$	1.9 (5)$^+$	0.3 (2)$^-$	0.5 (5)$^-$	0.3 (10)$^-$	0.4 (3)$^-$
Adoxa moschatellina	sm	rhi	rr	2.8 (10)$^+$	2.3 (15)$^+$	0.5 (2)$^-$	0.1 (2)$^-$	0.3 (5)$^-$	2.9 (15)$^+$
Allium monanthum	sp	tub	rr	3.1 (20)$^+$	0.5 (3)$^-$	0.7 (2)$^-$	0.7 (5)$^-$	0.7 (10)$^-$	1.3 (10)
Asarum caulescens	f	run	rc	2.4 (20)$^+$	0.9 (5)	0.9 (5)	0.3 (4)$^-$	1.3 (20)	0.2 (2)$^-$
Cacalia yatabei	f	rhi	rr	1.2 (15)$^+$	0.6 (2)	0.5 (7)	0.5 (10)	0.3 (3)$^-$	0.2 (3)$^-$
Polystichum tripteron	f	av	rs	1.4 (7)$^+$	0.1 (2)$^-$	0.7 (7)	0.4 (5)	0.0 (1)$^-$	0.8 (7)
Chrysosplenium ramosum	f	run	rr	1.0 (7)$^+$	0$^-$	0.4 (10)	0.4 (3)	0.3 (3)	0$^-$
Polystichum ovato-paleaceum	f	av	rs	0.4 (5)	0.1 (3)$^-$	0.6 (5)$^+$	0.8 (7)$^+$	0.2 (3)	0.1 (1)$^-$
Diplazium squamigerum	f	rhi	rc	1.6 (20)$^+$	0.2 (5)	0.2 (5)	0.0 (0.1)$^-$	0.3 (5)	0.2 (2)$^-$
Cluster B									
Chrysosplenium macrostemon	f	run	rr	0.6 (5)$^-$	0.1 (3)$^-$	1.0 (10)$^-$	4.5 (30)$^+$	3.8 (50)$^+$	0.1 (1)$^-$
Elatostema japonicum var. *majus*	f	bul/rhi	rc	0.2 (3)$^-$	0.0 (0.1)$^-$	3.6 (20)$^+$	5.2 (20)$^+$	2.0 (25)	0.0 (1)$^-$
Veronica miqueliana	f	rhi	rc	0.0 (1)$^-$	0.1 (2)$^-$	1.0 (7)$^+$	2.0 (10)$^+$	0.8 (7)	0.0 (0.1)$^-$
Persicaria debilis	f	th	rr	0.0 (0.1)$^-$	0$^-$	0.4 (7)	2.3 (10)$^+$	0.9 (10)$^+$	0.0 (0.1)$^-$
Cacalia farfaraefolia	f	rhi	rr	0.0 (1)$^-$	0.1 (1)$^-$	1.6 (7)$^+$	0.7 (3)	0.4 (5)	0.2 (5)$^-$
Laportea bulbifera	f	tub/bul	rr	0.8 (7)$^-$	0.5 (3)$^-$	1.3 (5)	2.6 (10)$^+$	1.4 (7)	2.5 (7)$^+$
Stellaria sessiliflora	f	run	rc	0.1 (3)$^-$	1.1 (20)	0.5 (7)	1.0 (7)	0.8 (5)	1.5 (5)$^+$
Impatiens noli-tangere	f	th	rr	0.6 (7)	0.0 (0.1)$^-$	0.7 (3)	1.2 (5)$^+$	0.4 (5)$^-$	1.7 (7)$^+$
Laportea macrostachya	f	rhi	rs	1.0 (10)	0.3 (3)$^-$	0.1 (2)$^-$	0.8 (3)	1.1 (7)	3.9 (20)$^+$
Deinanthe bifida	f	rhi	rs	0.2 (3)$^-$	0$^-$	0.3 (3)$^-$	2.1 (10)$^+$	2.5 (20)$^+$	0.4 (5)$^-$
Meehania urticifolia	f	run	rc	1.0 (5)	0.8 (3)	0.4 (3)$^-$	0.5 (5)	0.6 (5)	1.5 (7)$^+$
Dryopteris polylepis	f	av	rs	1.1 (7)$^+$	0.0 (0.1)$^-$	0.2 (3)$^-$	0.6 (3)	1.0 (5)$^+$	1.3 (5)$^+$
Cluster C									
Galium paradoxum	f	rhi	rr	0.2 (5)	0$^-$	0.1 (1)	0.8 (7)$^+$	0.0 (0.1)$^-$	0.8 (7)$^+$
Cluster D									
Hydrangea macrophylla var. *acuminata*	f	rhi	rc	0.2 (3)$^-$	0$^-$	3.0 (40)$^+$	1.3 (7)$^+$	0.4 (5)$^-$	0.5 (5)
Chrysosplenium album var. *stamineum*	f	run	rr	0$^-$	0$^-$	1.5 (7)$^+$	1.0 (7)$^+$	0.0 (2)$^-$	1.3 (20)$^+$
Astilbe thunbergii	f	rhi	rs	0$^-$	0$^-$	1.0 (10)$^+$	0.8 (10)$^+$	0.0 (0.1)$^-$	0.0 (0.1)$^-$
Cacalia delphiniifolia	f	rhi	rr	0.0 (1)$^-$	0.3 (7)	0.6 (7)$^+$	0.4 (5)	0.4 (3)	0.0 (0.1)$^-$
Cluster E									
Chrysosplenium echinus	f	run	rr	0.6 (7)$^+$	0.9 (10)$^+$	0.2 (2)$^-$	0.9 (15)$^+$	0$^-$	0.2 (3)
Cluster F									
Chrysosplenium pilosum var. *sphaerospermum*	f	run	rr	0.2 (7)$^-$	0.1 (3)$^-$	6.3 (30)$^+$	5.5 (25)$^+$	0.9 (15)$^-$	0.7 (15)$^-$
Cluster G									
Urtica laetevirens	f	rhi	rc	0.0 (1)$^-$	0.0 (0.1)$^-$	0.0 (0.1)$^-$	1.3 (20)$^+$	0.5 (15)	0.7 (10)$^+$

(continued)

nutrients in the plant body (e.g., Mooney and Billings 1961; Kimura 1970), and substances reserved in rhizomes sustain these species. Therefore, the distribution of these species would be restricted by breaks in the persistence of the storage organs. The rich organic matter in the soil of stable habitats, such as debris flow terraces and alluvial fans, may contribute to the maintenance of these plants (Fig. 6.4).

On the other hand, the other two species groups (B and D) characteristically comprised annual plants (such as *Impatiens noli-tangere*, Fig. 6.7 and *Persicaria debilis*, Fig. 6.8), perennials with bulbils (e.g., *Elatostema umbellatum* var. *majus*., Fig. 6.9, *Laportea bulbifera*, Fig. 6.10), and plants with replacement rhizomes (e.g., *Chrysosplenium macrostemon*, Fig. 6.11, *Cacalia delphiniifolia* Sieb. et Zucc., Fig. 6.3, *Cacalia farfaraefolia* Sieb. et Zucc., means pseudo-annual). These species are dominant in locations where small annual disturbances occur frequently, like a sandbar along the stream and a new landslide site with unstable soils (Table 6.1). Generally, annual plants are adapted to unstable sites that experience continual or annual disturbances (Silvertown 1982). These aforementioned perennials would also be adapted to unstable habitats, because their life cycle is advantageous in maintaining populations that are subjected to soil disturbance, such as annual plants. These results indicate that the distribution pattern of herbaceous plants making up the forest floor vegetation is related to the attributes of their storage organs and to their vegetative reproduction properties.

6.4 How Do the Herbaceous Plants React to Micro-Ground Disturbance?

6.4.1 Three Different Perennial Plants

Whether or not a plant group can be maintained when the plant body is damaged by surface disturbance is expected to be related to the vegetative breeding style. Practically, how can the population of herb species be restricted by ground disturbance? There are new landslide sites in the foot part of the slope along the Ooyamazawa stream. In the newly collapsed site, the spring water from the pipe, which is thought to be the trigger of collapse, and the influence of the surface flow, which occurs at the time of rain because of steep inclination, are strong (Fig. 6.12). Therefore, the soil of the ground surface will move frequently over one year. Herbs growing in such a location must be largely influenced by how they can maintain their
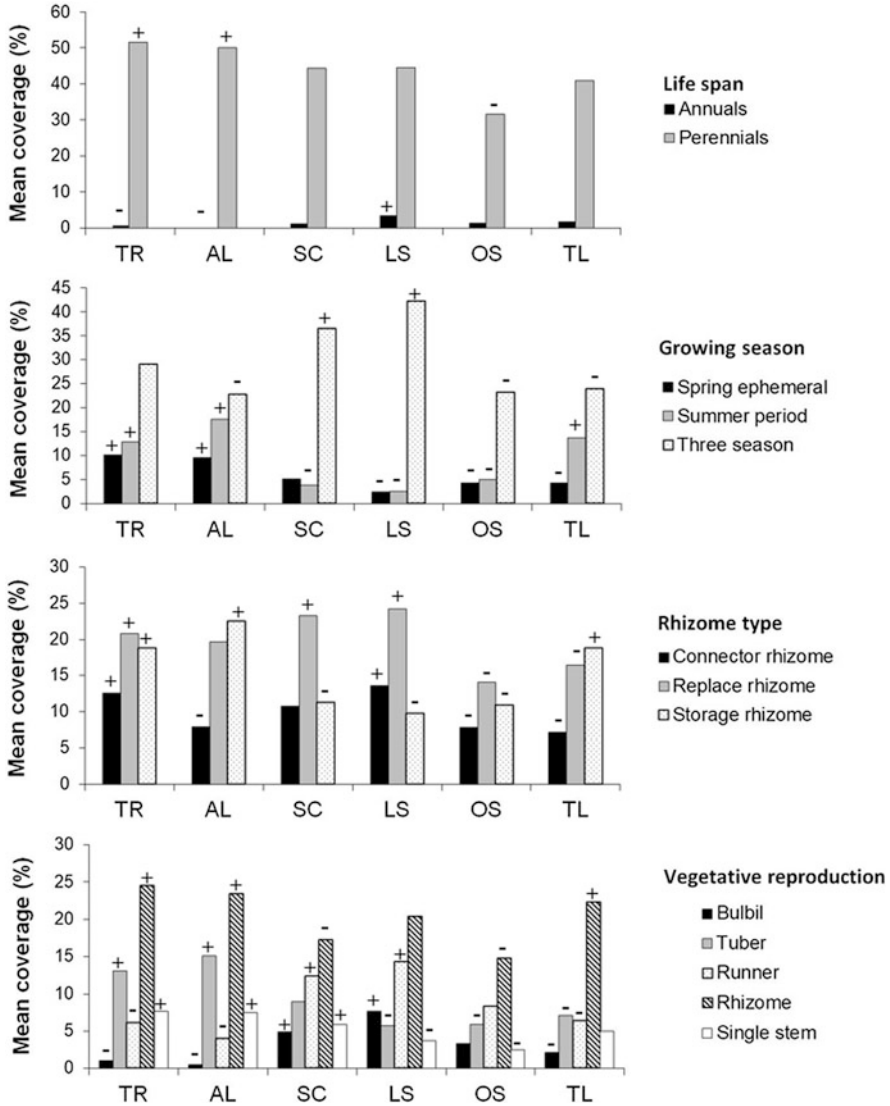
Fig. 6.4 Comparison of the mean coverage (%) of different life type groups in each geomorphic type (original data from Kawanishi et al. 2004). Mean coverages are shown and marked as desirable (+) or undesirable (−) sites, based on the χ^2 test ($P < 0.001$). See Fig. 6.1 for landform type abbreviations (TR, AL, SC, LS, OS, TL)

population, thanks to their resistance to this high frequency of disturbance. How does the life cycle of each species relate to disturbance?

Chrysosplenium macrostemon, *Elatostema japonicum* var. *majus*, and *Deinanthe bifida* are the major forest floor vegetation constituent species of the *Fraxinus playipoda* and *Pterocarya rhoifolia* forests, which are established on the Pacific

Fig. 6.5 *Corydalis lineariloba*

Fig. 6.6 *Allium monanthum*

side. These three species tend to appear on relatively unstable, small, collapsed terrains (Kawanishi et al. 2004); however, each has unique propagation characteristics.

   Chrysosplenium macrostemon is a small perennial plant that breeds at the creeping stem on the ground surface (Fig. 6.13). The mother plant body dies after the new clone plant is formed at the apical bud and/or axillary bud of the creeping stem at the end of the growing season. This life cycle of *Chrysosplenium* resembles that of a pseudo-annual plant. On the other hand, *Elatostema japonicum var. majus* is a

Fig. 6.7 *Impatiens noli-tangere*

Fig. 6.8 *Persicaria debilis*

deciduous perennial that does not lose the main rhizome, but instead forms a bulbil in the node of the aerial stem and separates the vegetative propagation body every year (Fig. 6.14). On the other hand, *Deinanthe bifida* grows exclusively by underground stem: new underground shoots and old shoots are connected, and no vegetative propagation material to separate these is created (Fig. 6.15). Since these species are distributed in the most unstable collapsed places on the slope, this serves as a good reference to identify the relationship between propagation style and reaction to disturbance.

Fig. 6.9 *Elatostema umbellatum* var. *majus*

Fig. 6.10 *Laportea bulbifera*

From this point of view, we considered the mechanism of habitat selection of forest floor plants, focusing on the reactivity of individuals to disturbance. Firstly, we observed the fine-scale movement of the ground surface at the collapsed site. Secondly, leaf morphology, relating the shoot elongation and the reaction of the damaged individuals, was clarified. Finally, we considered the relationship between micro-disturbances and life types.

Fig. 6.11 Chrysosplenium macrostemon

Fig. 6.12 The trace of small piping phenomenon where underground water has spring out

6.4.2 Micro-disturbance on Small Landslide Site in Lower Side Slope

Because the new landslide site is the most unstable part of the slope, this site is suited for studying the tolerance of herbs to disturbances. So, we established an investigation plot on a small cliff part of the top and on the foot of a new landslide scar (Fig. 6.16). On this slope, there is clear knick line (convex break line) at the boundary of the upper valley side slope, and a small cliff, which is seen as a

Fig. 6.13 Whole plant
body of *Chrysosplenium
macrostemon*

Fig. 6.14 Whole plant
body of *Elatostema
japonicum* var. *majus*

Fig. 6.15 The flower and whole plant body of *Deinanthe bifida*

Fig. 6.16 Small landslide on the lower side slope

newly collapsed land in the new period that was made on the foot of slope. The survey plot was then set up in this newly collapsed site. *Chrysosplenium macrostemon*, *Elatostema japonicum* var. *majus*, and *Deinanthe bifida* are distributed in such unstable slopes, and involve slope failures among the riparian forests, as mentioned above. We can easily observe that the ramet of these herbs had damages, including breakage of stems, burial, dropout, etc. These may due to micro-disturbances such as erosion of the surface accompanying piping as well as fine slippage.

6.4.3 Stem Elongation and Leaf Formation Pattern of Three Herbs

Elongation of the stem and the leaf formation in differently sized individuals are shown in Figs. 6.17, 6.18, and 6.19 for *Chrysosplenium macrostemon*, *Elatostema japonicum* var. *majus*, and *Deinanthe bifida*, respectively.

Figure 6.17 shows the shoot elongation and the leaves of *C. macrostemon* for small size (Cm-s), large size (Cm-l), and damaged (stem break) ramet (Cm-d). Regardless of the size of ramet, they begin extending the shoot from the overwinter rosette in early May, and they continue to grow until the beginning of September. Leaves (opposite phyllotaxis) were gradually attached at each node and corresponded with plant growth. For the large ramet, its side branches extended. The shoots stopped stem growth and leaf formation after winter rosette leaves formed on the shoot apex or on the lateral bud around late August. The rosette leaves of the previous year disappeared by the middle of June, and current leaves developed until the end of the observation at the end of October. With regard to the damaged ramet, though the stem had been broken in August, the stem tip of broken shoot continued to grow, formed foliage leaves, and subsequently formed overwinter rosette leaves. At the base of broken shoot, the elongation of the side branches improved slightly.

Shoot elongation and larvae of *D. bifida* are shown in Fig. 6.18 for the non-damaged small size (Db-s), medium size (Db-m), and the damaged large size shoot (Db-d). The schematic figure showing the rhizomes and the position of the above-ground shoots (Db-d) are also represented. The ground stems of *D. bifida* developed from the beginning of May and made two of three pairs of leaves until late June. On the other hand, the damaged shoot had relatively large dichotomous rhizomes (Fig. 6.18, Db-d), and the above-ground stems of this ramet started to grow from the tips of the thick rhizome in spring. Usually, although some preliminary buds had formed at the rhizomes of *D. bifida*, these buds do not elongate under safe conditions. However, when the above stem is damaged like that of shoot 1 (Fig. 6.18), preliminary sprouts begin to elongate at the branch of rhizome. Moreover, the preliminary sprouts (shoot 1-1) at the foot of damaged stem extended
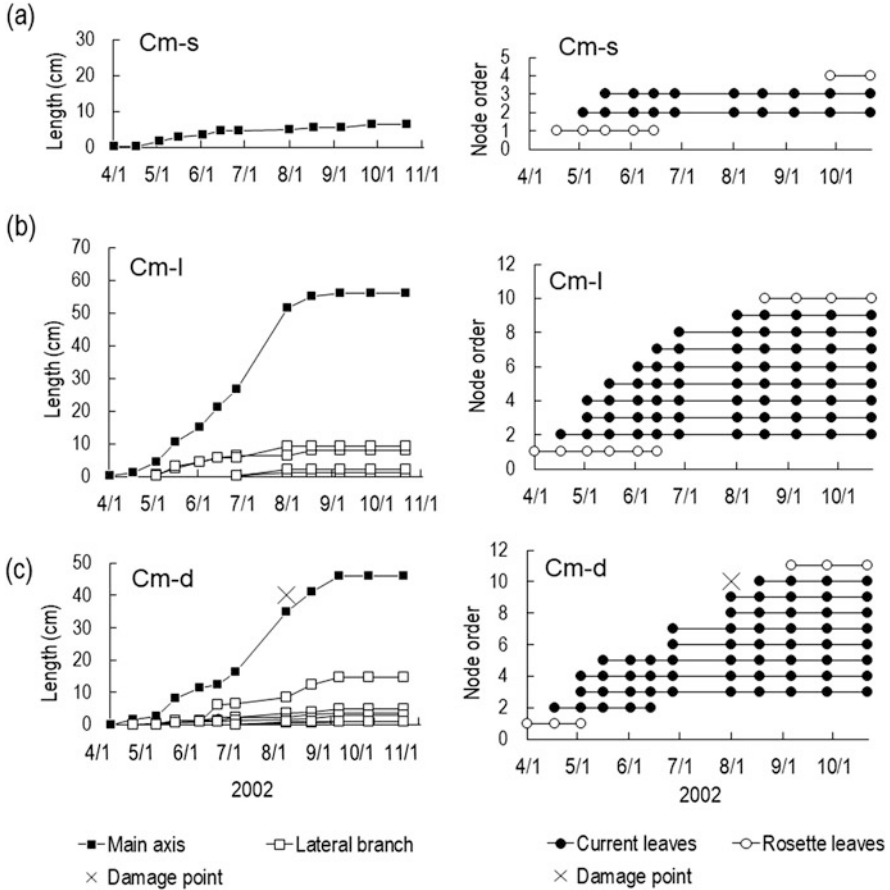
Fig. 6.17 Seasonal changes in the length of current shoots (left) and leaf survival states in each node on the main axis (right) of *Chrysosplenium macrostemon*. Small (Cm-s) and large (Cm-l) were shown as undamaged stems among growing seasons. The main axis of the shoot of the Cm-d individual was damaged (with a broken stem) in August. The survey was conducted in 2003

to about 5 cm past the damaged point. Other preliminary buds (shoot 2-1, 2-2) did not elongate.

Shoot elongation and leaf formation of E. *japonicum* var. *majus* are shown in Fig. 6.19. Non-damaged small (Ej-s), large (Ej-l) size shoot, and the damaged large size shoot (Ej-d) are shown as an example. Starting from early May, the ground stem of *E. japonicum* var. *majus* was growing alternate leaves while extending its shoot. Shoot elongation and leaf formation were almost finished in early August. The individuals shown in the figure formed a bulbil at the sixth node from the beginning of September. In damaged individuals (Ej-d), all stems had been buried by soil debris, making it impossible to accurately observe their reaction to the damage.
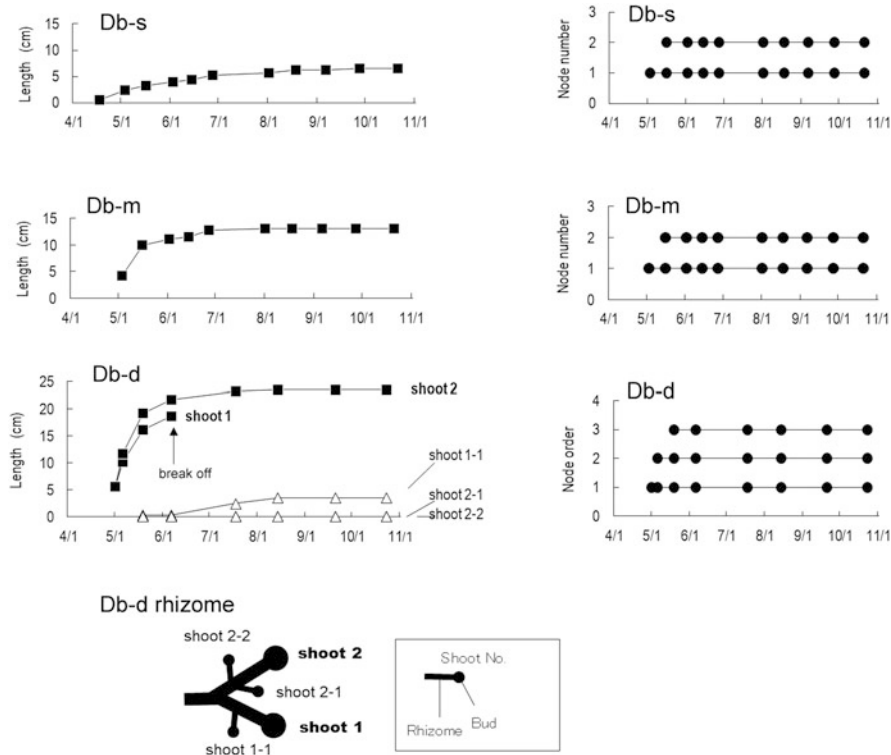
Fig. 6.18 Seasonal changes in the length of current shoots (left) and leaf survival states in each node on the main axis (right) of *Deinanthe bifida*. Small (Db-s) and medium (Db-m) size stems were shown as undamaged among growing seasons. The main stem of the shoot of the Db-d individual was damaged (stem was broken off) in June (Db-d). The survey was conducted in 2003. Rhizome pattern diagrams of damaged individuals (Db-d) are also shown. The survey was conducted in 2003

6.4.4 Adaptation to Micro-disturbance

In *C. macrostemon,* the shoots elongate until late summer, and as such, shoots can attach more leaves, which is similar to a long shoot. Shoots positively induce adventitious roots, after which stems will easily take root even if disturbances do not occur. In addition, the shoots could grow even if a stem had been broken or buried. These characteristics indicate that each shoot branch can be a ramet that is independent from the individual root even during the early seasons. Therefore, even if the plant body is damaged by ground disturbances, they can grow and form a vegetative propagation body, such as an overwintering rosette. Thus, it is possible to form vegetative propagules at the tip of each shoot and disperse the ramets every year.

The life history of *C. macrostemon* resembles pseudo-annual plants, as is described above. The characteristics of the habitats of pseudo-annuals in forests
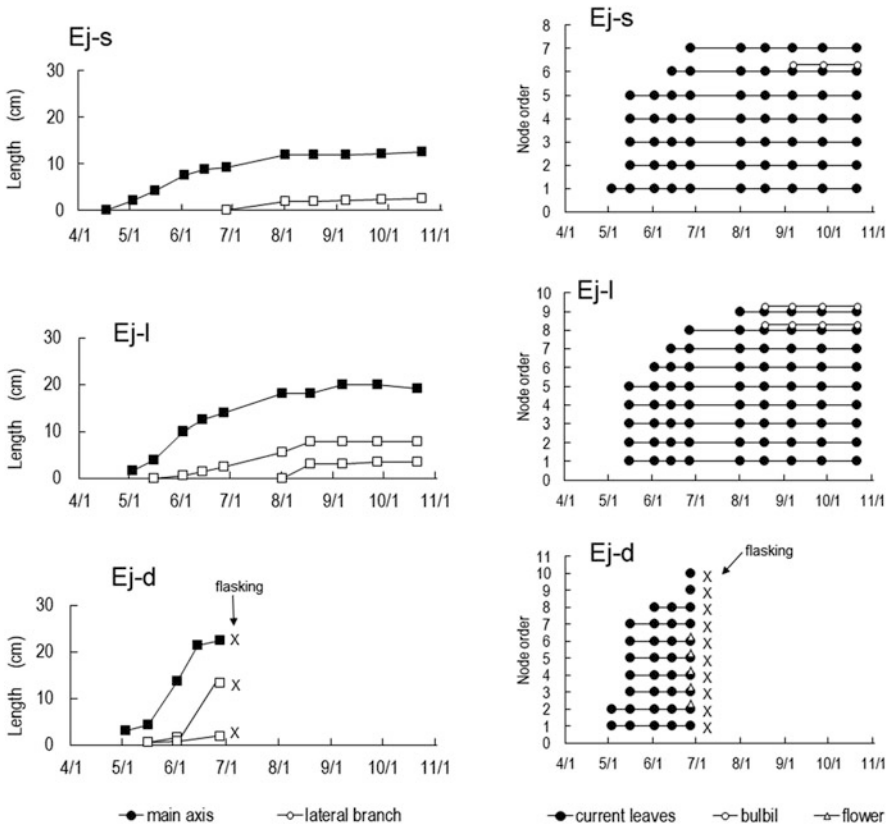
Fig. 6.19 Seasonal changes in the length of current shoots (left) and leaf survival states in each node of the main axis (right) of *Elatostema umbellatum* var. *majus*. Non-damaged small (Ej-s), large (Ej-l) size, and the damaged large size shoot (Ej-d) are shown. The survey was conducted in 2003

are that they are stable or somewhat unstable and experience no disturbance (Kawano 1985). In contrast, annuals, biennials, and perennials (making bulbil) tend to habit unstable sites with regular disturbances (Kawano 1985). This tendency is also shown in studies that compare different ecosystems (Svensson et al. 2013).

Coastal plants are examples of adaptation to permanent disturbance in unstable habitats. Coastal plants such as *Wedelia prostrata* with long horizontal stems (runner) and *Carex kobomugi* that extend long rhizomes underground are able to survive the strict beach environment (Yano 1962). This is because they can establish adventitious roots from the nodes on the runner or on the rhizome even if the above-ground shoots are buried by sand sedimentation or if the rhizomes are cut by wind erosion. This indicates the advantage of clonal plants in unstable sites. The life history of *C. macrostemon*, which involves generating adventitious roots while growing the creeping stems, may be adaptive on unstable slopes along the mountain stream where the ground surface moves finely.

Chrysosplenium plants grow mainly in unstable riparian areas along the mountain stream (Wakabayashi 2001), and several species distribute sympatrically in one region (Fukamachi et al. 2014). Fukamachi et al. (2014) clarified habitat environments and the overlap of the distribution of the *Chrysosplenium* species and pointed out that the micro-environment may contribute to coexistence. The mechanism of coexistence is not yet clear; thus, I would like to research the relationship between the shoot elongation pattern of each species and the slight variability of ground surface. On the other hand, shoot elongation and leaf formation of *D. bifida* start in spring, and are almost completed by early summer (Fig. 6.17), after which stems and leaves will no longer form. Because of this, the plant ends up having only 2–3 pairs of leaves. In general, the rhizome typically has a stouter stem than a stolon. Its old portion decays, separating the ramet into two new ramets when the rotting reaches a branch junction (Bell and Bryan 2008); *D. bifida* typically has these types of rhizome. The rhizome is relatively thick, stout, and has a lot of strong adventitious roots, with few that are branched. These growth patterns (i.e., simultaneous expansion of the leaf in spring) and morphology will indicate that they may primarily utilize the storage material of the rhizomes during new leaf formation. When shoots are damaged, preliminary sprouts of the rhizomes start to grow. Therefore, it is highly possible that the storage material of the rhizome is also needed in the growth of new preparative stems and leaves as recovery from the disturbance. Based on this fact, it is seen that *D. bifida* has an anabolic system that stores its annual assimilation products in rhizomes as much as possible.

E. umbellatum var. *majus* grows shoots until midsummer and gradually exhibits leaves. Both the shoot extension and the foliation are stopped and completed in the middle of August when the bulbil begins to form. From this time, the assimilation products seem to be also used for the formation of bulbils and storage of rhizomes. Unfortunately, we could not observe the reaction of damaged ramet was not clear. But we could observe the preliminary buds in the underground stem. Some preliminary sprouts may grow up from the bud in rhizomes if the upper shoot was damaged or lost.

And then, perennials having bulbil (such as *Laportea bulbifera*, *Sedum bulbiferum*, *Dioscorea bulbifera*, and *Lilium lancifolium*) grow on relatively unstable habitat (Kawano 1985). Bulbil of *E. umbellatum* var. *majus* also may have important role to maintain the population on unstable slope.

As described above, the elongation and development characteristics of shoots of these three species were different, and were thought to be closely related to the method of vegetative propagation. Reactivity to damage is determined by shoot growth, vegetative propagation characteristics, and how much storage of assimilation products has been done. In this book, we introduced only three species studied by the authors, but the life type of herbaceous plants constituting forest floor vegetation is diverse, and the life cycle and life history of most species are unknown. As introduced in Chap. 8, most of the current Japanese forests are affected by deer, and there are many areas where forest floor vegetation is declining. In order to examine its conservation and restoration, it is desirable to elucidate the mechanism by which species diversity of forest floor plants is maintained. For that purpose, we will need to advance more research on forest floor herbs.

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