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Morphological Adaptations by *Glehnia littoralis* to the Biomass and Heights of Peripheral Herbaceous Plants in Coastal Sand Dunes

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To clarify the effects of peripheral herbal plants on *Glehnia littoralis* growth in coastal sand dunes, the morphology of their aboveground portions was surveyed in five communities: *Carex kobomugi, Calystegia soldanella, Ischaemum anthephoroides, Oenothera biennis,* and *Elymus mollis*. Correlation coefficients (CC) were generally significant at the 1% level between community properties [total aboveground biomass (B) and height (H) of dominant species per unit area] and those of *G. littoralis* [leaf number (Nl), petiole angle (Anp), petiole length (Lp), petiole weight (Wp), Lp/Wp, Lp/weight of leaf blade (Wb), Wp/total weight (Wt), specific leaf area (SLA), stem length (Ls), and Ls/weight of stem (Ws)] The exceptions were among four pairings: B and Nl, B and Wt, H and Nl, and H and Wt. Of the two community properties, biomass had the greatest association with leaf properties while H was most closely related to those of the stems. Petiole angle increased along with leaf order, from 0° to 42° for the *C. kobomugi* community, from 5° to 55° for *Calystegia soldanella*, from 49° to 74° for *I. anthephoroides*, from 54° to 80° for *O. biennis*, and from 75° to 85° for *E. mollis*. In all communities, the properties of Wp, SLA, and Wb increased up to the third or fourth leaf, but then decreased; the exception was for Lp/Wp, which was the reverse. Leaf order of the largest one moved from first position to third as either B or H increased in a community.

Keywords: biomass, coastal sand dune, *Glehnia littoralis*, height, morphology, peripheral herbaceous plants

Coastal sand dune plants grow in harsh environments (Rozema et al., 1985; Moreno-Casaola and Espejel, 1986; Hesp, 1991; Costa et al., 1996). The main factors that can negatively affect their survival are unstable soil surfaces caused by erosion or sedimentation, direct and indirect salt influxes from seawater, deficient soil moisture and nutrient contents, and high air and soil temperatures (Chapman, 1964; Rozema et al., 1985). Bright sunlight is another harmful environmental factor (Fahn and Cutler, 1992), with complex effects on plant development, e.g., from rising air and soil temperatures, and an acceleration in soil water deficits (Chapman, 1964; Caldwell, 1985; Smith and Nobel, 1986; Hesp, 1991; Comstock and Ehleringer, 1992). To counteract and deflect such bright light, sand dune plants possess trichomes and a thick layer of wax on their leaf surfaces (Fahn and Cutler, 1992; Barbour et al., 1993).

Compared with those found on coastal sand dunes, inland plants grow under a lower light regime, which means the latter type must have various strategies for raising their photosynthetic potential, including changes in their morphology. This may involve the elongation of stems, internodes, and/or peduncles, so that leaves or flowers are located as high as possible (Daubenmire, 1974; Hart, 1988; Tilman, 1988; Grubb et al., 1996; Tsukaya et al., 2002; Kozuka et al., 2005). In a second strategy, the petioles elongate to elevate the positioning of the leaf blade (Niinemts et al., 2004b). Thirdly, leaf area density and specific leaf area (SLA) may increase so that photosynthetic potential is augmented (Cline, 1966; Grubb et al., 1996; Mitchell, 1998; Robinson and McCarthy, 1999; Casella and Ceulemans, 2002; Niinemts et al., 2004a; Simioni et al., 2004; Ali and Kikuzawa, 2005). In the fourth strategy, chlorophyll content increases (Meekins and McCarthy, 2000). In contrast, only two strategies are available for coastal sand dune plants -- either avoiding bright light or overcoming low light levels. Although the former option has been widely studied, little is known about the morphological adaptations required for survival under shade conditions (Tielbörger and Kadmon, 1997; Forseth et al., 2001).

Where density is high, each plant competes for nutrients, water, and light, but the particular plant response cannot always be explained by a single factor (Holmgren et al., 1997; Shumway, 2000; Forseth et al., 2001). Under low light intensity, stomatal conductance, water use efficiency, and nutrient status may not differ between perennial plants growing in a shrub canopy and those found in the open (Forseth et

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al., 2001). However, growth and flowering rates of plants growing under shrubs are reduced relative to those in the open. For communities composed of only herbaceous vegetation, each plant receives more sunlight than those under a shrub canopy. In this case, shading is not a negative factor, but intermingles with the more critical competition for water and nutrients (Kachi and Hirose, 1983; Tilman, 1988). Morphological changes due to environmental factors are important in studies of plant growth and population ecology, and enable researchers to examine how competition affects species succession within a coastal sand dune community (Olff et al., 1993).

Glehnia littoralis grows in a semi-rosette pattern on coastal sand dunes. Leaves on the lower stems develop along the soil surface and sclerophyllus (Lee, 1993). Most studies of this species have focused on either pharmacological properties (Seo and Ryu, 1976; Matsuura et al., 1996; Tu et al., 1999; Ishikawa et al., 2001; Ng et al., 2004) or allelopathy (Sato et al., 1996). Although distributed throughout the coastal sand dunes of Korea (Kim et al., 2005), little is known about its ecological properties (Lee et al., 1996; Park and Lee, 2000).

The aim of this research was to clarify the response of coastal sand dune plants to shading conditions by surveying the leaf and stem properties of *G. littoralis* in five communities where the dominant species differed in their biomass and heights. The growth parameters evaluated here included aboveground biomass and heights of the primary species in each community, plus petiole angles, lengths, and weights; leaf blade weights and areas; and stem lengths and weights for *G. littoralis*.

MATERIALS AND METHODS

The study area is located at Sindu-ri, Wonbukmyeon, Taean-gun, in the Chungnam Province of Korea (36° 50′-52′N, 127° 10′-13′E) (Fig. 1). This region abuts that of a nearby conservation area, 'Sindu Sand Dune', to the northeast. In the foredune, *Elymus mollis* and *Carex kobomugi* form pure or mixed stands, while various herbal species (*Calystegia soldanella*, *G. littoralis*, *Messerschmidia sibirica*, and *Lathyrus japonica* var. *aleuticus*) plus *Zoysia macrostachya* and two woody species (*Rosa rugosa* and *Vitex rotundifolia*) exist either in solitary or as small patches. At the rear of the foredune, *Imperata cylindrica* var. *koenigii*, *Ischaemum anthephoroides*, *Calamagrostis epigeios*, *Carex pumila*, *Artemisia capillaris, Oenothera biennis*, and *Agropyron tukushiense* form pure or mixed stands in small patches, depending on topographical conditions or the degree of human disturbance.

The field survey was accomplished on June 11, 2004, just before plants were beginning to flower. A total of 18 quadrats were located in five communities: *C. kobomugi*, *C. soldanella*, *O. biennis*, *I. anthephoroides*, and *E. mollis*, with each community name reflecting the species whose aboveground biomass was the largest in that quadrat. *G. littoralis* occurred as a single plant in 14 quadrats, with two growing in each of 3 quadrats, and 3 found in the final quadrat. Each quadrat was designed so this species would be located at the center. Because the total leaf coverage of *G. littoralis* was 25 to 40 cm, a quadrat of 50 × 50 cm was large enough to accommodate all the peripheral plants that affected its growth. Mean heights for *C. soldanella* (a liana), *L. japonica* var. *aleuticus* (semi-liana), and *I. anthephoroides* (a tussock species) were estimated in the field. Petiole angle (i.e., the angle between horizontal and the petiole) for *G. littoralis* was directly measured *in situ*. All plants within each quadrat were then cut down to the soil surface and transported to the laboratory. Samples of *G. littoralis* were divided into leaf and stem portions, and the leaves were further separated into petiole and blade. Stem and petiole lengths were measured, and the leaf blade was evaluated with a leaf area-measuring device (Delta-T Device, UK). All materials were oven-dried at 80°C for 48 h, then weighed on an analytical balance (Metler Toledo, Switzerland). After the heights of *C. kobomugi*, *O. biennis*, and *E. mollis* were recorded, these plants were oven-dried at 80°C for 48 h and weighed.

Factors were statistically analyzed for two groups: one for community, the other for *G. littoralis* only. The former included aboveground biomass (B) and mean height of the dominant species (H) in each quadrat, while the latter recorded the number of leaves (Nl), petiole angle (Anp), petiole length (Lp), petiole weight (Wp), Lp/Wp, Lp/weight of leaf blade (Wb), Wp/total weight (Wt), specific leaf area (SLA), stem length (Ls), and Ls/weight of stem (Ws). The formula for correlation coefficients was $y = A + Bx$. For the five communities, mean values for Anp, Lp, Wp, Lp/Wp, Wl, Al, SLA, and Wp/Wl were calculated as a function of leaf order within the individual plant. Factors that differed among their size values were converted into a relative value (%) for the largest plant.

Table 1. Dry weights of component species and heights of dominant species in 50 × 50 cm quadrat measured on June 11, 2004, at a sand dune of Shinduri.

Community	Dominant species		Other species		Total DW (g)
	DW (g)	Height (cm)	Scientific name	DW (g)	
CK 1	5.1	23.0	*Calystegia soldanella*	0.5	5.6
CK 2	12.8	24.4	*C. soldanella*	1.4	14.2
CK 3	16.6	27.9	*C. soldanella*	6.5	23.1
CK 4	18.1	29.3	*C. soldanella*	3.9	22.0
CK 5	31.5	25.5	*C. soldanella*	2.6	34.1
CS 1	10.3	5.0	*Carex kobomugi*	8.4	18.7
CS 2	10.1	5.0	*C. kobomugi*	8.3	18.4
IA 1	36.7	28.0	*C. soldanella*	4.8	45.8
			Zoysia macrostachya	4.3	
IA 2	59.9	40.0	*Elymus mollis*	7.8	101.5
			C. kobomugi	14.5	
			Lathyrus japonica var. *aleuticus*	19.3	
IA 3	77.7	45.0	*E. mollis*	4.2	110.6
			C. kobomugi	8.3	
			L. japonica var. *aleuticus*	20.4	
IA 4	107.7	53.0	*C. soldanella*	3.6	112.1
			Oenethera biennis	0.8	
OB 1	24.6	49.9	*E. mollis*	21.8	72.0
			C. kobomugi	1.7	
			L. japonica var. *aleuticus*	11.0	
			C. soldanella	1.9	
			A. tukushiense var. *transiens*	7.6	
OB 2	88.8	50.0	*E. mollis*	6.0	101.6
			C. kobomugi	1.6	
			L. japonica var. *aleuticus*	4.0	
			C. soldanella	1.2	
OB 3	52.3	52.8	*A. tukushiense* var. *transiens*	31.7	113.2
			C. kobomugi	27.8	
			L. japonica var. *aleuticus*	1.4	
EM 1	56.1	87.8	*C. kobomugi*	19.5	118.0
			C. soldanella	4.5	
			L. japonica var. *aleuticus*	37.9	
EM 2	70.5	96.5	*C. kobomugi*	13.8	132.9
			C. soldanella	2.7	
			L. japonica var. *aleuticus*	45.9	
EM 3	79.6	93.5	*C. kobomugi*	18.2	128.3
			C. soldanella	2.3	
			L. japonica var. *aleuticus*	28.2	
EM 4	242.6	96.9	*C. kobomugi*	6.9	250.0
			Messerschmidia sibirica	0.5	

CK, *C. kobomugi*; CS, *C. soldanella*; IA, *I. anthephoroides*; OB, *O. biennis*; EM, *E. mollis*.

RESULTS AND DISCUSSION

Height of Dominant Species and Biomass

The number of species in each of the 18 quadrats ranged from two to six (Table 1). In addition to the dominant species -- *C. kobomugi*, *C. soldanella*, *O. biennis*, *I. anthephoroides*, and *E. mollis* – the other four communities included 1) *L. japonica* var. *aleuticus* in *I. anthephoroides* (IA2 and 3), *O. biennis* (OB1, 2 and 3), and *E. mollis* (EM1, 2 and 3); 2) *Z. macrostachya* in *I. anthephoroides* (IA1); 3) *A. tukushiense* in *O. biennis* (OB1 and 3); and 4) *M. sibirica* in *E. mollis* (EM4). Species composition was similar within these five communities and, except for *O. biennis* and *Z. macrostachya*, all are commonly found in the coastal sand dunes of Korea (Lee and Chon, 1983; Kim et al., 2005).

Aboveground biomasses (B) ranged widely, from 22.3 g DW m^{-2} (Community CK1) to 1000.1 g DW m^{-2} (in EM4). The heights of dominant species (H) also varied broadly, from 5.0 cm (in CS1 and 2) to 96.9 cm (EM4). In Korean coastal sand dunes, biomass normally is between 86.72 to 817.96 g m^{-2} (Lee and Chon, 1983), so the range found in this study is larger than previously reported.

Schematic diagrams (Fig. 1) showed that *G. littoralis* was not shaded by peripheral plants in two communities (CK and CS), but was easily overgrown in three others (IA, OB, and EM). In particular, the leaves of *C. kobomugi* appeared bent, and differences arose between their lengths and heights (Min, 2004). Plants of *G. littoralis* were subjected to shading in two communities where liana species developed overhead or other plants grew nearby. In contrast, three communities where values for H and B were small did not decrease the level of light available to *G. littoralis*. Furthermore, because *I. anthephoroides* forms dense tussocks, *G. litorallis* was able to grow between those tussocks. Thus, the amount of light received by these *Glehnia* leaves varied according to location, with light intensity being more frequently interrupted when those leaves were close to the *I. anthephoroides* tussocks. Finally, growth of *G. littoralis* was better in the *O. biennis* and *E. mollis* communities, where its leaf development was equally affected by the dominant species.

Dry weights and heights for *G. littoralis* differed remarkably among plants, ranging from 3.07 to 18.55 g and from 9.5 to 48.8 cm, respectively (Table 2). Among the communities, mean petiole angles varied from 6.2° (CK1) to 90.0° (EM2). Specifically, leaves of plants in community CK1 mostly touched the soil surface, while those in EM2 were erect. No differences were seen among communities for leaf numbers, which ranged from 6 to 10. Four-year-old *G. littoralis* plants had four leaves, as had been estimated by Park and Lee (2000). Leaf areas and weights were from

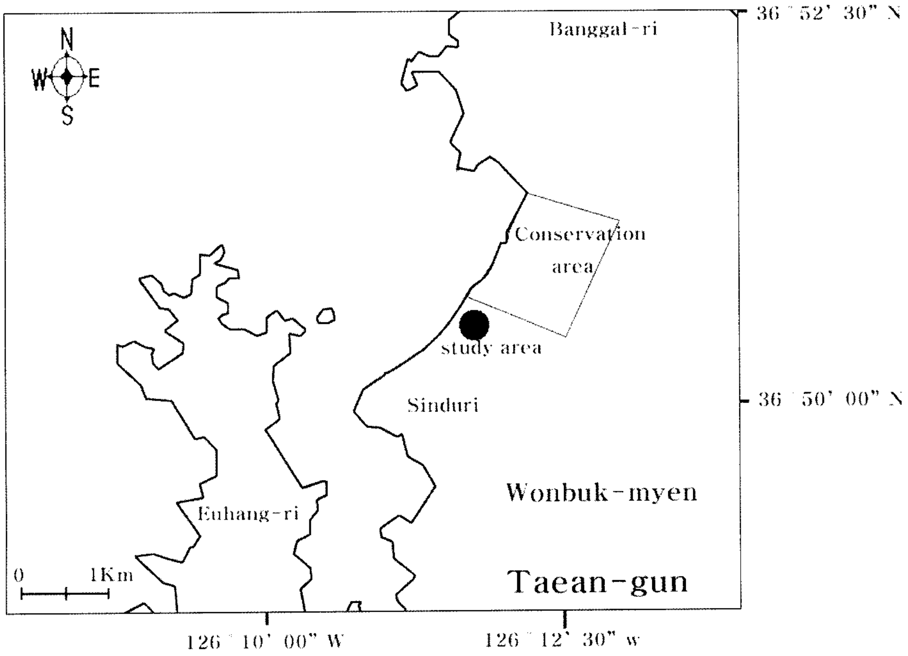

Figure 1. Map showing study area (● , study area).

Table 2. Leaf and stem properties of *G. littoralis* from each study community.

No.	Angle	Leaf blade				Petiole		Stem	
		No.	Area (cm^2)	DW (g)	SLA	Length (cm)	DW (g)	Length (cm)	DW (g)
CK 1	11.7	6	125.8	1.31	94.0	49.5	0.71	9.5	1.69
	6.3	8	160.4	1.90	82.1	59.0	0.73	9.7	1.86
CK 2	20.0	8	238.3	2.67	92.8	73.0	1.26	9.7	3.43
CK 3	26.7	9	294.7	3.65	81.2	83.5	1.12	12.6	5.32
CK 4	21.9	8	422.7	5.10	84.9	92.0	2.11	13.9	4.43
CK 5	22.5	8	174.8	2.05	86.8	54.5	0.66	6.7	2.66
CS 1	30.0	6	159.1	2.10	74.3	47.5	0.88	11.9	1.12
CS 2	19.4	8	374.8	4.46	78.3	77.5	1.88	10.9	4.13
IA 1	47.9	7	128.7	1.21	111.3	63.0	0.56	12.2	1.56
IA 2	80.7	7	194.3	1.86	106.6	90.0	1.02	22.7	2.06
IA 3	72.8	9	430.5	3.50	129.8	139.5	1.99	27.1	4.19
IA 4	62.5	8	333.0	3.34	97.6	73.5	1.22	18.8	2.90
OB 1	75.0	6	267.0	2.84	96.8	110.5	1.67	31.7	3.08
OB 2	64.4	8	243.7	2.24	107.9	121.0	1.32	32.5	1.74
OB 3	76.0	10	802.4	6.49	130.4	245.5	4.95	46.6	7.12
	77.5	8	364.9	2.61	136.1	144.0	1.66	36.5	3.34
EM 1	77.5	6	259.6	2.33	106.7	92.0	1.11	39.8	1.48
	73.0	6	178.8	1.52	111.0	87.0	0.86	35.7	0.69
	80.8	6	142.8	1.49	93.2	68.5	0.72	32.3	0.97
EM 2	90.0	5	240.9	1.78	136.0	70.0	1.25	34.5	1.70
EM 3	82.1	7	299.8	2.47	122.6	139.0	1.67	40.0	0.79
EM 4	77.8	10	681.7	4.51	148.6	198.0	2.68	48.8	3.43
	85.0	9	209.5	1.28	159.6	120.5	0.89	43.0	1.33

125.8 cm^2 (CK1) to 802.4 cm^2 (OB3), and from 1.2 g (CK5) to 6.5 g (CK3), respectively. Values for SLA were 74.2 cm^2 g^{-1} (CS1) to 159.6 cm^2 g^{-1} (EM4). Thus, the thickest leaf was two times larger than the thinnest one. Furthermore, the SLA of *G. littoralis* was conspicuously smaller than that of *Symplocarpus renifolius*, a perennial herb growing under a closed canopy (301 to 499 cm^2 g^{-1}) (Min and Kang, 1994).

Relationship between Community Factors and Properties of *G. littoralis*

Correlation coefficients (CC) were not significant at the 5% level between B and two properties, Wt and Nl, of *G. littoralis*. However, except for those two properties, CCs between B and eight others were significant at the 1% level (Table 3). Therefore, I can conclude that plant size was not correlated with community. Petiole angle did change with increases in biomass, going from parallel with the soil surface to vertical (CC = 0.864). In contrast, leaf thickness was inversely proportional to biomass (CC = 0.868). Although the petioles lengthened with a biomass increase (CC = 0.770), they also became thinner (CC = 0.688). Petiole length against total weight also increased with biomass (CC = 0.877), such that more energy was allocated toward development of the petiole than the leaf blade (CC = 0.757). Finally, the stems elongated and became thinner as biomass increased (CCs = 0.893 and 0.694, respectively).

Although CCs between H and the properties of *G. littoralis* were similar to those reported with B, actual values generally were lower in the former comparisons. The three exceptions were between H and Lp/Wp (CC = 0.732), H and Ls (CC = 0.907), and H and Ls/Ws (CC = 0.877), the latter two being factors related to stem parameters. Thus, the length and slenderness of the stem were affected by height more than by the biomass of the dominant species.

Generally, sunlight infiltration is precluded as leaf angle increases. For example, the leaf tips of *Taraxacum officinale* turn up and peduncles lengthen in

Table 3. Correlation coefficients among properties of *G. littoralis*. (An, angle; W, weight; N, number; L, length; p, petiole; t, total; l, leaf; s, stem)

	H	Wt	SLA	Nl	Anp	Lp	Lp/Wp	Lp/Wt	Wp/Wl	Ls	Ls/Ws
B	0.862**	-0.329	0.868**	0.088	0.864**	0.770**	0.688**	0.877**	0.757**	0.893**	0.694**
H		-0.406	0.666**	-0.193	0.818**	0.687**	0.732**	0.854**	0.645**	0.907**	0.877**
Wt			-0.228	0.542**	-0.279	0.032	-0.720**	-0.628**	-0.271	-0.254	-0.534**
SLA				0.255	0.731**	0.780**	0.546**	0.777**	0.831**	0.743**	0.471*
Nl					-0.182	0.089	-0.118	-0.143	-0.087	-0.144	-0.373
Anp						0.819**	0.558**	0.764**	0.749**	0.916**	0.672**
Lp							0.251	0.675**	0.873**	0.853**	0.584**
Lp/Wp								0.800**	0.363	0.553**	0.651**
Lp/Wt									0.777**	0.819**	0.853**
Wp/Wl										0.791**	0.581**
Ls											0.772**

B, biomass in 50 × 50 cm quadrat; H, mean height of dominant species in 50 × 50 cm quadrat; *, significant at 5% level; **, significant at 1% level.

shaded areas, while leaves develop in contact with the soil surface and peduncles are shorter in open areas (Hart, 1988). Shading can also cause the lengthening of stems and internodes (Daubenmire, 1974; de Kroon and Hutchings, 1995). All these morphological strategies enable plants to compete with each other for light or avoid shading (Tilman, 1988; Tsukaya et al., 2002; Kozuka et al., 2005). In coastal sand dunes, competition for light results in the succession of plant communities. When their density or biomass increases within an area, tall plants have an advantage, so that succession progresses from shorter to taller vegetation (Olff et al., 1993). In shaded areas, plants allocate more energy to the development of stems than other organs, or change their stem structures to receive as much light as possible (Grubb et al., 1996). When many leaves are produced in the same location, *Populus* cannot successfully use all the available light, so this species expends more energy in petiole development rather than in leaf blades, thereby lengthening those petioles (Niinemts et al., 2004b). However, this diminished leaf area also decreases photosynthetic efficiency (Niinemts et al., 2004b; Kozuka et al., 2005).

In woody plants, SLA is inversely proportional to the light intensity received, such that leaves are generally larger in the lower layer or in shaded areas compared with their morphology higher up in the plant or on more open sites (Cline, 1966; Yun and Elwynn, 1986; Grubb et al., 1996; Mitchell, 1998; Robinson and McCarthy, 1999; Casella and Ceulemans, 2002; Simioni et al., 2004; Ali and Kikuzawa, 2005). In herbs, SLA increases when shaded by other plants or objects (Nobel, 1991; Erikmeier and Schussler, 1993); SLA also changes in parallel with recipient light intensity, thus broadening the tolerance range of an individual plant (Wang et al., 2004). A decline in the amount of available light also increases chlorophyll content and leaf area (Meekins and McCarthy, 2000; Niinemts et al., 2004a). However, in coastal sand dunes, the exceedingly bright sunlight is harmful to vegetative growth, causing plants to change their leaf orientation in order to lessen and diminish the impact of direct light radiated on the leaf surface (Hesp, 1991).

Based on the results described here, as well as those reported previously, the physiological properties of *G. littoralis* can be summarized in as three points. First, the leaves of this species have adapted to cope with bright sunlight. Second, this species is able to modify its morphology, i.e., through increased height or biomass, when competing with other nearby plants. Third, the main adaptive strategies of *G. littoralis* to high light intensities include changes in the length and angle of petioles, plus thickening of the leaves and the production of longer stems. Likewise, this species is able to respond to shaded conditions by decreasing various growth parameters, in the following order: stem length, petiole angle, petiole length as a percentage of total plant weight, leaf thickness, petiole weight in proportion to leaf weight, stem thickness, petiole length, and petiole thickness.

Except for Wt and Ni (both related to aboveground plant growth), the CCs between community and properties of *G. littoralis* were largely significant at the 1% level. Thus, plant size was not correlated with the adaptive response of plants. Of all the values deter-

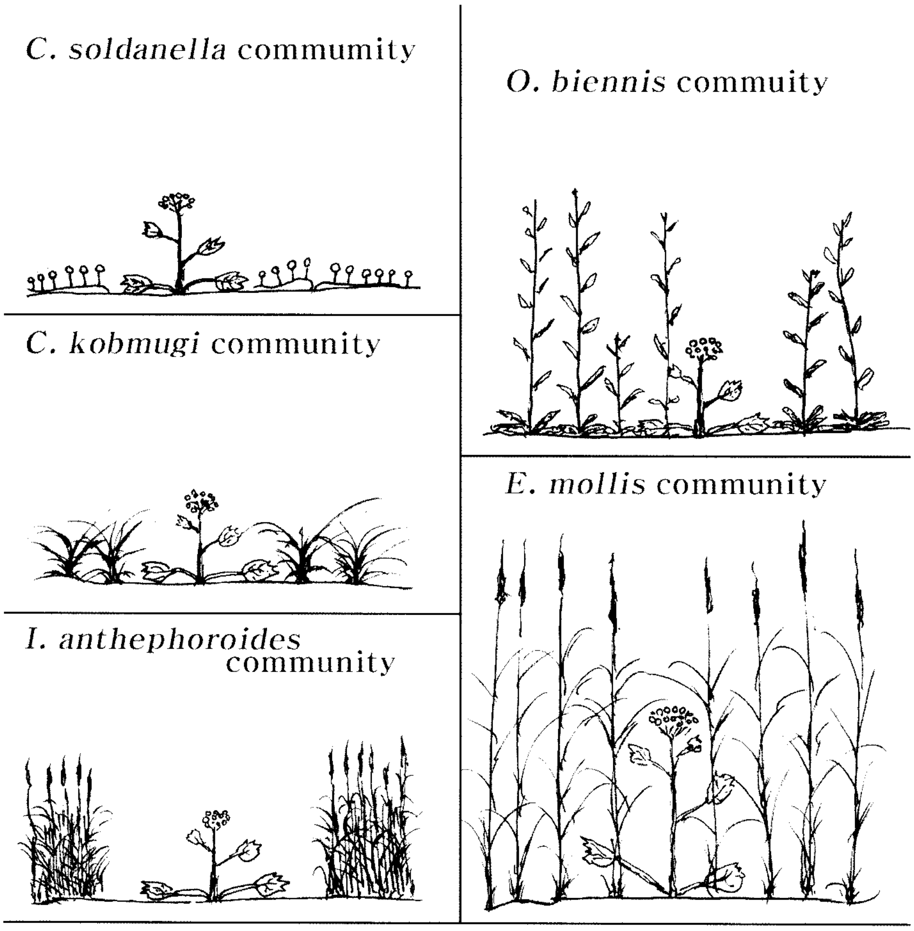

Figure 2. Schematic diagram of *G. littoralis* and other plants in 5 communities.

mined here, the CC between Anp and Ls was the greatest (0.916). CC values were >0.8 between SLA and Wp/Wl, Anp and Lp, Lp and Wp/Wl, Lp and Ls, Lp/Wp and Lp/Wt, Lp/Wt and Ls, and Lp/Wt and Ls/Ws. Therefore, the effects of shading are thought to be interrelated among the properties of each organ. For example, petiole angles and stem lengths might be good indicators of this shading effect. Mean CC values for each pairing decreased in the order of Lp/Wt, Wp/Wl, Ls, Anp, SLA, Lp, Ls/Ws, and Lp/Wp. Therefore, these data demonstrate that petiole length as a percentage of total weight (CC = 0.781) is the most suitable indicator of plant response to shading.

Changes of Properties along the Leaf Order in Each Community

Petiole angles of *G. littoralis* increased with leaf order in five communities (Fig. 2). For example, the respective angles for leaf Numbers 1 and 8 were 0° and 42° in the *C. kobomugi* community; 5° and 55°, *C. soldanella*; 49° and 74°, *I. anthephoroides*; 54° and 80°, *O. biennis*; and 75° and 85° for *E. mollis*. Furthermore, leaves that emerged from underground early in the growing season may have been affected by surrounding plants as well as by those leaves that formed on the upper stem, whereas the petiole angle of the last leaf might have been determined by the height or biomass of neighboring plants. This phenomenon should be investigated further.

The petiole angle for the upper leaves on short *G. littoralis* plants was relatively large. Two hypotheses are proposed to explain how petiole angle is designed to cope in adverse environments. Such morphology might enable the plant either to avoid strong sunlight (small angle values, more erect leaves) or else protect itself against heat from the soil surface (large angle values, more horizontal leaves). If the former theory were the main factor, then it would be false that an increase in that angle farther up on the stem would allow for the reception of more sunlight, thus improving the heights of other plants or the total biomass

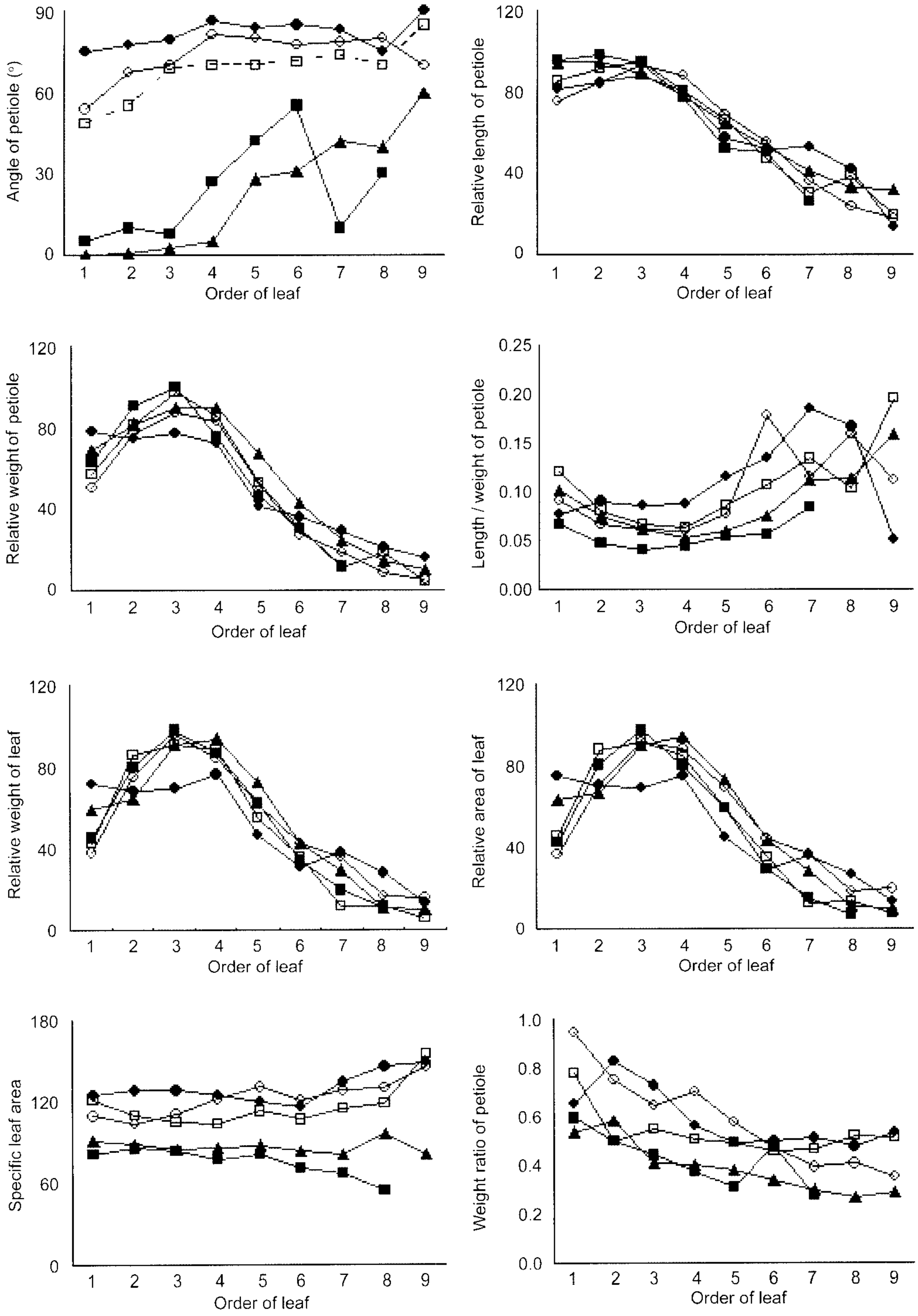

Figure 3. The changes of leaf properties along leaf order in a plant of *G. littoralis* in the 5 communities.

from a community. If the latter theory were the main factor, the leaves in closest contact with the soil surface would experience enormous thermal exposure. In fact, Chapman (1964) has reported that, compared with other environments, soil-surface temperatures in sand dunes can be as high as 60°C (Chapman, 1964). Therefore, of these two hypotheses, the latter is the more probable. Data from the Seosan Meteorological Station (Korea Meteorological Administration, 1991) show that the average surface temperatures in April and May, when leaves are emerging on the lower stems, are 12.9°C and 19.4°C, respectively.

Although the maximum surface temperature at this particular study site may have been higher than that, it is believed that heat from the soil surface could not seriously affect leaf growth. Nevertheless, this theme is worthy of further research.

The order of the longest petiole-containing leaf differed according to community, being Number 2 in the *C. kobomugi* and *C. soldanella* communities, but Number 3 in those of *I. anthephoroides, O. biennis*, and *E. mollis*. Petiole weight increased from the first to the third leaf, but then decreased from the fourth leaf, except for the *E. mollis* community. The third leaf was conspicuously larger than the others in the *C. soldanella* and *I. anthephoroides* communities, but in the *E. mollis* community, this property successively decreased from the first leaf. The ratio of petiole length to weight, which indicates petiole thickness, increased with leaf order in the *E. mollis* community. In the others, this ratio decreased from the first to the third or fourth leaf but then increased from the fourth or fifth leaf. Thus, the trend of this property was the opposite of that for petiole length. In the future, it would be worth studying the process of *G. littoralis* growth in the *E. mollis* community, a site with tall plants and large biomass.

In all except the *E. mollis* community, both area and weight of the leaf blades increased to the third or fourth leaf, then declined from the fourth or the fifth leaf, possibly because more energy was being allocated for the development of reproductive organs. SLA changed irregularly in accord with leaf order, perhaps because of the status of light intensity at the time of leaf formation. This, too, should be further investigated.

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