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Shoot Growth and Distribution Pattern of *Carex kobomugi* in a Natural Stand

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To clarify the growth and distribution of *Carex kobomugi*, I surveyed the shoot heights and weights of a population growing in a sand dune at Sindu-ri, Wonbuk-myeon, Taean-gun, in Chungnam Province, Korea. During the growing season, size classes, based on leaf number and shoot heights, shifted, with those in the medium class moving to higher classes. Although the frequencies of those class characters showed a normal distribution curve throughout the season, the frequencies of each class based on shoot weight were evenly distributed in all size classifications. Coefficients of variation were 0.17 for leaf number, and 0.35 for leaf length and weight per plant. The maximum numbers of leaves were 8.16 ± 1.38 per plant for those that were non-flowering, but 2.66 ± 0.62 per plant for those that did flower. Non-flowering plants exhibited withered leaves by mid-September, while withering began in male plants by mid-May and by mid-July for females. At the end of the growing season, the lengths and weights of leaves from non-flowering plants were 47.8 ± 16.6 cm and 1773 ± 628 mg, respectively. When leaf order was considered, leaves increased in size along two-thirds of the ranking, then decreased. In a separate analysis, the growth of *Carex* plants was compared with those of *Elymus mollis* in the same sample quadrats. Biomass of the former accounted for only a small portion of the total biomass per unit area (*E. mollis* having a dry weight of >76.4 g m^{-2}), but under such competition, the leaf lengths and individual plant weights nonetheless increased for *Carex* as well.

Keywords: biomass, *Carex kobomugi*, dry weight, sand dune, seed

The extreme environment found in coastal sand dunes can limit plant growth (Rozema et al., 1985; Moreno-Casaola and Espejel, 1986; Hesp, 1991; Costa et al., 1996). Several factors are involved on such sites, including 1) the continuous influx of salt from seawater spray (Boyce, 1954; Barbour, 1978); 2) insufficient levels of water and minerals in the soil (Mooney, 1983; Pavlik, 1983; Olff et al., 1993; Ishikawa et al., 1995); 3) very strong sun light; 4) remarkable daily and annual fluctuations in soil temperature (Monson et al., 1983; Woodell, 1985); and 5) an unstable soil surface because of shifting sand (Maun, 1984; Moreno-Casaola, 1986; Zhang and Maun, 1990). To grow and reproduce in a coastal sand dune, plants must have adaptive mechanisms and a broad range of tolerances against these physical factors. One of the most important survival strategies is vegetative reproduction via rhizomes. Although sand dune species can produce many seeds, soil water deficits lead to low germination rates and the failure of ensuing plants to flower. Therefore, in such environments, annual plant species are rare and rhizomatous perennials are more widespread (Martinez et al., 1992; Davy and Fugueroa, 1993; Costa et al., 1996; Cordazzo and Davy, 1999).

Diverse microsites are formed by the influence of seawater and the degree of surface stability in coastal sand dunes. Such sites are composed of only a few species, whose community structures are simple, forming pure and sparse stands because those plants compete poorly with other plants or species, particularly for sunlight, and can be shaded out by more tolerant species when stand density is high (Taylor, 1989; Olff et al., 1993).

Carex kobomugi is a pioneer and dominant species of unstable coast sand dunes (Nobuhara, 1967; Nobuhara and Miyazaki, 1974; Sasaki, 1987; Ishikawa et al., 1995; Ishikawa and Kachi, 1998). Despite having a low seed germination rate (Ishikawa et al., 1993), this species effectively reproduces by its plentiful rhizomes, which adapt their growth to sand movements. I have previously reported shoot production from rhizomes as young as 5 years old (Min, 2004). With a guerilla-type growth pattern (Ishikawa and Kachi, 1998), this species can reproduce many shoots and widely propagate in a short time period even though it is generally inferior to phalanx-type plants in its ability to compete (Lovett Doust, 1981; Schmid and Harper, 1985; Bertness and Ellison, 1987). *C. kobomugi* exhibits three types of shoots: non-flowering, male-flowering, or female-flowering. To date, the factors that determine the sex of a particular shoot are unclear. Ecological studies of *C. kobomugi* populations have been conducted in Japan (Ishikawa and Kachi, 1998).

The aim of this study was to clarify the populational properties of *C. kobomugi*. Here, shoot frequencies were surveyed according to size class, and shoot growth patterns were defined based on sex and biomass per

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unit area in natural stands. A separate experiment involved comparing growth parameters between *Carex* and one of its competitors, *Elymus mollis*.

MATERIALS AND METHODS

Study area is located on a coastal sand dune that runs northeast to southwest at Sindu-ri, Wonbuk-myeon, Taean-gun, in Chungnam Province (36° 50′-52′N, 126° 10′-13′E; Min, 2004), Korea. Its length and width are 3.2 km × and 500 m, respectively. Mean annual precipitation and air temperature are 1232.1 mm and 11.7°C, respectively (Korea Meteorological Administration, 2001). The foredune, primary dune, and secondary dunes are successively formed from the shoreline. The foredune, 4 to 7 m high, spans 5 to 10 m at the high tide level. Sand influxes from the sea accumulate in the northeastern foredune but are eroded to the sea at the southwestern end. The primary dune is 100 to 150 m wide and up to 20 m tall. Both the foredune and the primary dune have steep slopes, and are unstable due to sand shifting near the shoreline, varying according to the microsite or season. In contrast, lower areas or those located far from the shoreline are well vegetated and stable because of the lack of sand movement. From the center point to the innermost region of this sand dune, *Pinus thunbergii* has been planted, and *Robinia pseudo-acacia* has become established by natural seed dispersal. Lowlands within the *P. thunbergii* forest form a flat or a wetland. This sand dune has been designated as a natural conservation area by the Cultural Heritage Administration. Although human disturbances are not as great as in the past, their impact continues at the periphery, where roads occur. There, non-native species, e.g., *Oenothera biennis*, grow vigorously. The main study site is located at the northeastern edge (36° 51′00″N, 126° 12′04″E) of this sand dune. *C. kobomugi* grows in a 300-m-wide band at the mean high-tide mark. Other sand dune species are found there as well, including *E. mollis*, *Ischaemum anthephoroides*, *Zoysia macrostachya*, *Carex pumila*, *Rosa rugosa*, *Lathyrus japonica* var. *aleuticus*, *Glehnia littoralis*, and *Calystegia soldanella*, plus the non-sand dune plants of *Imperata cylindrica* var. *koenigii*, *Agropyron tsukushiense* var. *transiens*, *Pueraria thunbergiana*, *O. biennis*, and *Artemisia capillaris*. These species, which can form either pure or mixed stands, show diverse coverage. The field survey presented here was conducted monthly on 1 × 1 m quadrats, from 13 April 2000 to 10 September 2001. Sampling sites were divided into two types, with separate objectives. In the pure stand, with five quadrats, the growth pattern of *C. kobomugi* was analyzed. In the mixed stand, the goal was to assess the effect of other plant species on the growth of *C. kobomugi*. This second type was sampled only once (10 September 2001) and eight sites were selected for examining plant heights and coverage by *E. mollis* and other species. For each sampling event, all the plants within a quadrat were cut and transported to the laboratory. Shoots of *C. kobomugi* were divided into non-flowering, male, or female plants, and their leaf numbers and lengths were recorded. The plant samples were then weighed after being oven-dried at 85°C for 48 h (Min, 2005). For the flowering plants, their leaves and sex organs were separated and weighed individually. In addition, leaf lengths and weights were surveyed according to leaf order on 19 July 2001, when the growth of *C. kobomugi* was nearly complete. Data for seed numbers and weights were obtained from all female plants on 3 September 2000.

RESULTS AND DISCUSSION

Frequency Distributions among Size Classes

Changes in leaf numbers, shoot heights and weights were recorded over one growing season for non-flowering plants of *C. kobomugi* (Fig. 1). Leaf numbers per shoot ranged from 1 to 5 (20 April) to 2 to 7 (11 May) to 3 to 15 (19 July). These frequencies followed a normal distribution curve early in the growing season, being positively skewed in April and May, but negatively skewed in July. Therefore, early leaf numbers tended to be similar on any given shoot, but later differed in their increase along the same shoot.

The frequency distribution of height classes showed a roughly normal distribution curve throughout the survey period. Ranges in height were narrower than those for leaf number, but the mode was located in a higher size class than found for leaf number. Moreover, the frequencies of higher size classes were more than those of the lower ones. The highest classes were obtained on 11 May, with a Class 4 then being achieved on July 19, indicating that several plants were conspicuously smaller or larger than the others.

The frequencies of per-shoot weight size classes generally showed normal distribution curves except for the data recorded from the 20 April sampling. Ranges for this parameter were extreme, i.e., 11 May measurements resulted in a variety of weights from Class 1 to Class 6, versus weights on 19 July ranging between Class 1 and Class 15. Therefore, the differences in growth among *C. kobomugi* plants increased conspicuously over the season. For example, the largest frequency class contained less than 20% of the total. Considering the fact that fewer new shoots were being produced after May, the growth rate of this species differed according to position along the shoot. Unfortunately, the main factors contributing to this phenomenon are unclear (Min, 2004).

Based on the three types of frequency distribution presented, one might conclude that development in plants of *C. kobomugi* is concentrated more in leaf

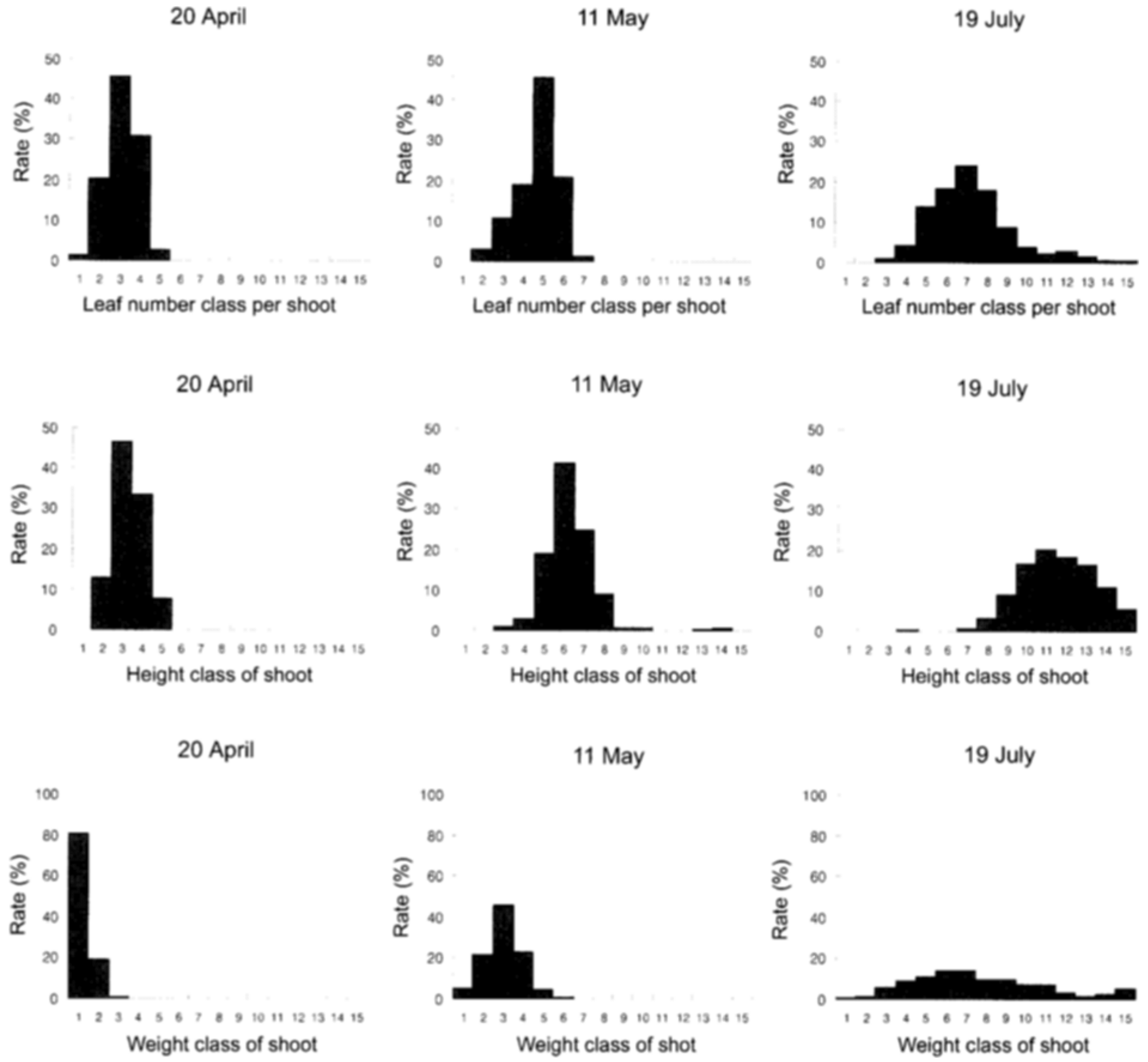

Figure 1. Frequency distribution of size classes for *C. kobomugi* population in 2000. At top: by leaf number – from 1 to 15 per plant. In center: by shoot height (mg) -- 1, 0.0-3.9; 2, 4.0-7.9; 3, 8.0-11.9; 4, 12.0-15.9; 5, 16.0-19.9; 6, 20.0-23.9; 7, 24.0-27.9; 8, 28.0-31.9; 9, 21.0-35.9; 10, 36.0-39.9; 11, 40.0-43.9; 12, 44.0-47.9; 13, 48.0-51.9; 14, 52.0-55.9; and 15, 56.0+. At bottom: by shoot weight (cm) -- 1, 0-199; 2, 200-399; 3, 400-599; 4, 600-799; 5, 800-999; 6, 1000-1199; 7, 1200-1399; 8, 1400-1599; 9, 1600-1799; 10, 1800-1999; 11, 2000-2199; 12, 2200-2399; 13, 2400-2599; 14, 2600-2799; and 15, 2800+.

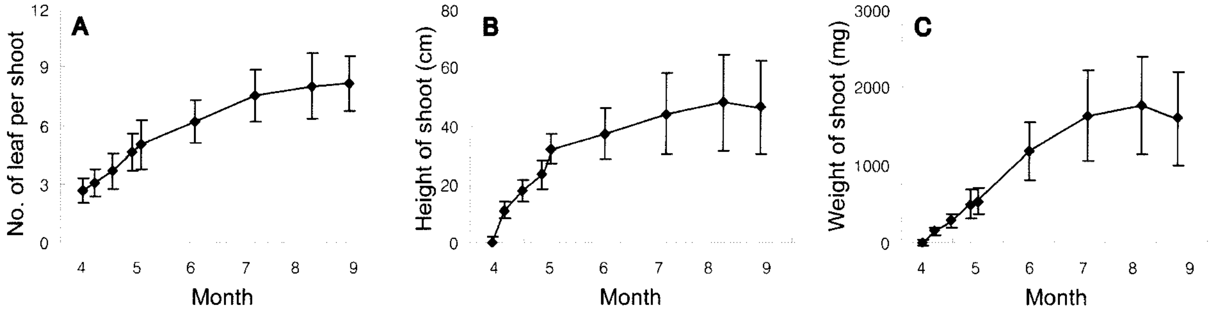

Figure 2. Seasonal changes in **A**, mean leaf number per shoot, **B**, mean shoot height, and **C**, mean shoot dry weight for non-flowering plants in *C. kobomugi* population in 2000.

length rather than leaf weight. This has previously been demonstrated in reports that sand dune plants require adequate sunlight to remain competitive with neighboring vegetation (Nobuhara and Miyazaki, 1974). Therefore, I believe that, because *C. kobomugi* must compete with peripheral species, its leaf morphology must be long and slender in order to capture the necessary light.

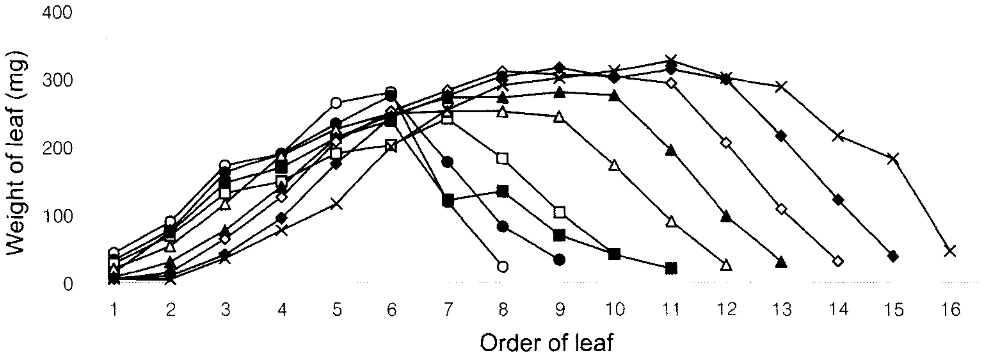

Figure 3. Relationship between leaf dry weight (mg) and leaf ranking for flowering plants in *C. kobomugi* population on 19 July 2001 (n = 20).

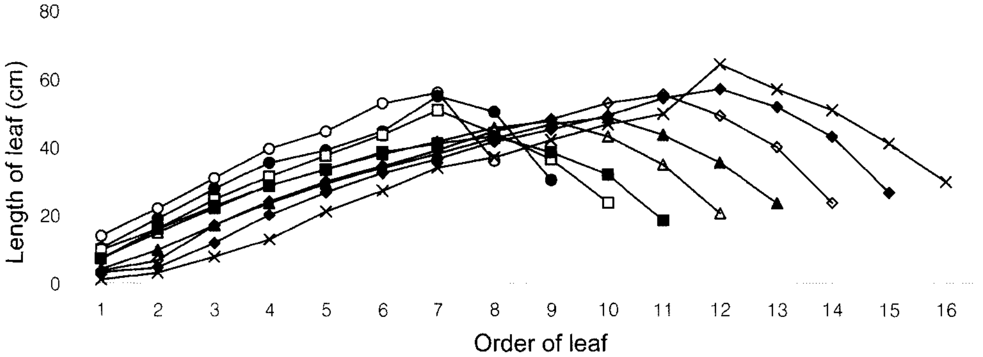

Figure 4. Relationship between leaf length (mg) and leaf ranking for non-flowering plants in *C. kobomugi* population on 19 July 2001 (n = 20).

Shoot Growth along the Sexes

Changes in leaf numbers and shoot heights and weights were also determined for non-flowering *Carex* plants (Fig. 2). Leaf numbers per shoot increased from 2.66 ± 0.62 (13 April) to 8.16 ± 1.38 (19 July). Thereafter, the net leaf increment was 0.64 per shoot, demonstrating that most of the leaf development occurred before then.

Leaves increased in length to 47.9 ± 16.6 cm on 10 September, with the most development occurring up until 16 May, followed by a slower growth rate. Standard deviations were small early in the growing season but then became greater.

Per-shoot leaf weights increased sharply until 20 August, reaching a maximum of 1773 ± 628 mg. The standard deviation for this parameter was similar to that calculated for shoot height. Leaf withering was observed in the field on 19 July.

The coefficients of variation (standard deviation/mean) were 0.17 for leaf number, and 0.35 for both leaf length and weight, and were comparable in each size class.

In general, the photosynthetic efficiency of *C. kobomugi* is half as much in August as it is in April, enabling these plants to tolerate higher air temperatures (Ishikawa et al., 1990, 1996). Aboveground biomass in this species averages 1.4 to 1.5 g in June and 1.5 to 1.9 g in August (Ishikawa and Kachi, 1998). Here, *Carex* growth was very slow in August and September, and individual shoot weights ranged from 1.1 to 1.8 g, results consistent with those previous reports.

In non-flowering plants, leaf weight was compared with its order along the shoot (Fig. 3), with weight increasing up to the half ranking, then decreasing. That is, the fewer the number of leaves on a shoot, the heavier the first leaf was. Two theories were considered to explain the size of the first leaf: either its development is inhibited earlier in the season, or else air temperatures are higher later on, slowing its growth. Generally, leaves that were produced earlier grew more slowly and died earlier. Overall, any increase or decrease in leaf length as a function of its ranking was similar to the trend found with leaf weight (Fig. 4), although the ranking of the longest leaf was lower than the heaviest one. This might have been because leaves that developed later in the season concentrated their growth in length rather than mass.

In flowering plants, leaves numbered 2.66 ± 0.61 per shoot on 13 April, the same as for non-flowering *Carex*, but withering decreased those numbers later on (Fig. 5A). Leaf lengths increased to 13.0 ± 1.9 cm on 11 May, then either remained constant or else slightly increased. Male spikes had consistent leaf lengths later on, while those of the female lengthened as they matured. Shoot weights were constant until 15 June, then increased up to 20 August, as reflected by the dif-

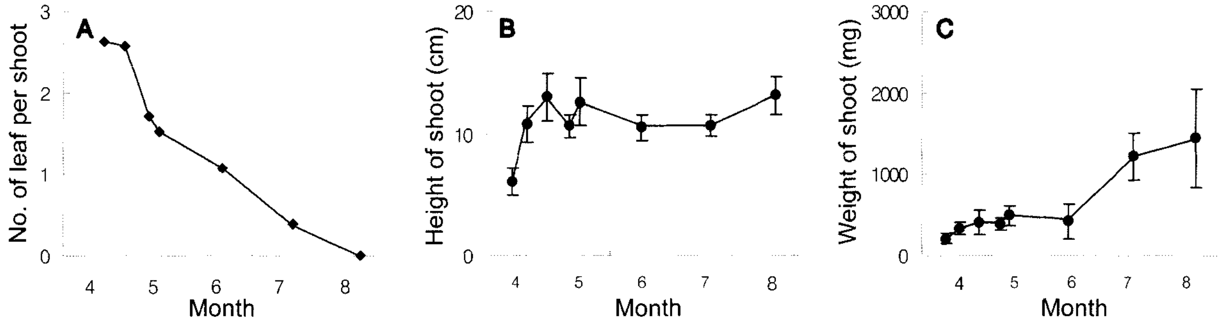

Figure 5. Seasonal changes in mean leaf number per shoot (**A**), mean shoot height (**B**), and mean shoot dry weight (**C**), for flowering plants in *C. kobomugi* population in 2000.

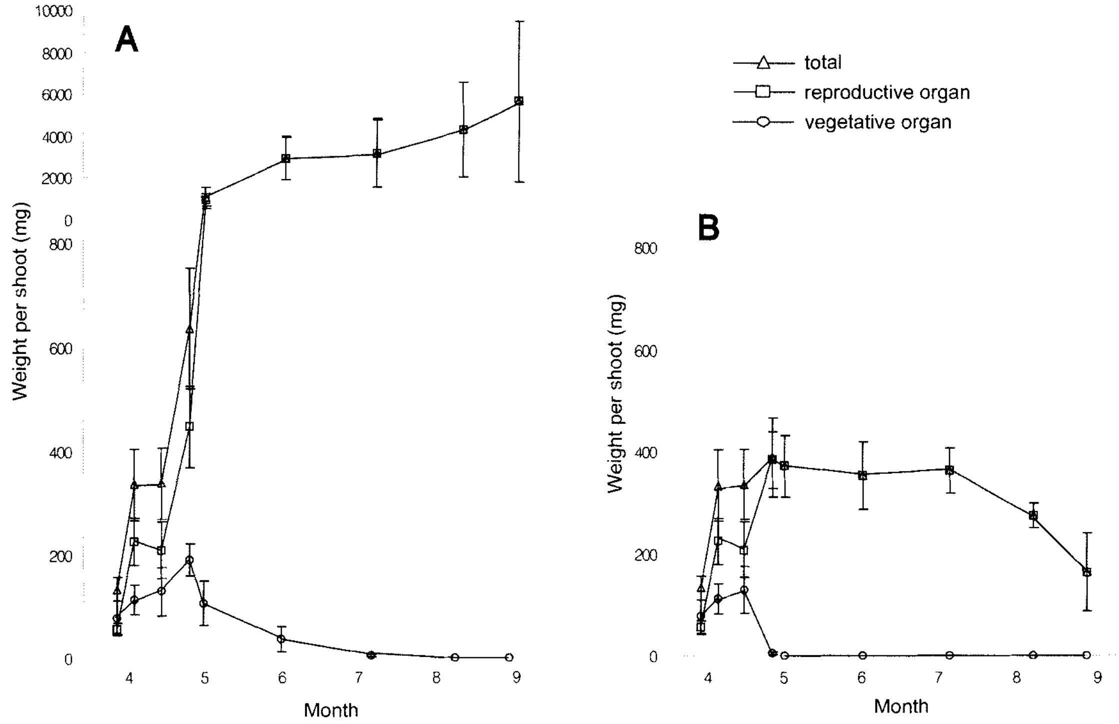

Figure 6. Seasonal changes in biomass for each organ from flowering plants (**A**, female; **B**, male) in *C. kobomugi* population in 2000.

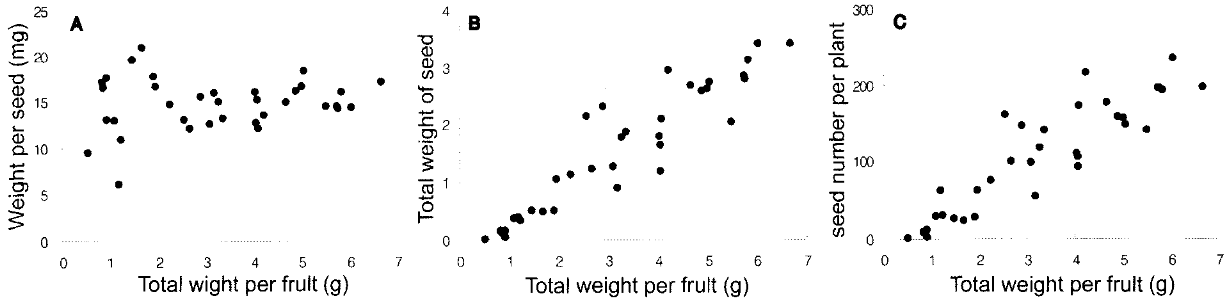

Figure 7. Relationships between total fruit weight and **A**, weight per seed; **B**, total seed weight; and **C**, number of seed per plant, on 3 September 2000.

ferences already described between male and female shoots (Fig. 6).

For the female shoot, leaf weights abruptly increased up to 11 May before decreasing more gradually. For the male shoot, its leaves began to wither on 11 May. Its spike reached a maximum weight of 129 ± 47 mg on 30 April, then decreased to where it remained in a withered state after 11 May. Likewise, the weight of their sex organs differed conspicuously between the male and female shoots.

Seed Production

The number and total weight of the seeds, and the

Table 1. Aboveground biomass, density, and mean height and weight per plant for *C. kobomugi* and *E. mollis*, measured on 10 September 2001.

Quadrat	*C. kobomugi*					*E. mollis*			Other plants (g/m^2)	Total weight (g/m^2)
	Flower	Density ($plants/m^2$)	Height (cm)	Weight (mg/plant)	Weight (g/m^2)	Density ($plants/m^2$)	Height (m^2)	Weight (g/m^2)		
1	○	36	14.3	702	199	52	86.1	206	29	412
	×	97	46.8	1,786						
2	○	30	18.9	2,796	132	44	78.9	138	9	279
	×	21	49.0	2,270						
3	○	0	-	-	136	35	83.1	120	27	283
	×	79	44.4	1,935						
4	○	33	11.3	550	165	29	72.0	76	17	259
	×	87	46.0	1,690						
5	○	38	16.6	1,945	156	20	83.3	26	30	212
	×	77	40.9	1,066						
6	○	26	19.1	2,378	173	14	78.0	14	51	238
	×	99	41.0	1,123						
7	○	43	13.5	1,042	129	-	-	-	29	158
	×	82	41.5	1,027						
8	○	2	11.4	790	131	-	-	-	20	151
	×	121	42.0	1,079						

weight per seed from a single plant are shown in Figure 7. Spikes contained between 0 and 236 seeds. Regardless of how prolific seed production was, however, individual seed weighed 15 ± 1 mg. Although one could surmise that *C. kobomugi* produces viable seeds, albeit not in great quantity, their rate of germination is very low (Yamamoto, 1964), being close to 0% for intact seed in the field (Ishikawa et al., 1993). Therefore, new recruits of *C. kobomugi* are few (Ishikawa et al., 1990).

Effects of Peripheral Plants on *C. kobomugi* Growth

Total biomass and plant heights were compared between *C. kobomugi* and *E. mollis* (Table 1). Two other species were identified in the sample quadrats -- *C. soldanella* and *L. japonica* var. *aleuticus* -- but these were lianas so their heights were similar to that of the *Carex* plants. Total dry weights ranged from 151 to 412 g m^{-2}, of which the biomass of *C. kobomugi* accounted for only 129 to 199 g m^{-2}. Therefore, the difference in total dry weight among all quadrats was larger than that for *C. kobomugi* only. The densities of *C. kobomugi* and *E. mollis* were 51 to 133 plants m^{-2} and 14 to 52 plants m^{-2}, respectively, and no correlation was found between their densities. Plants of *E. mollis* were taller (72.0 to 86.1 cm versus 40.8 to 49.0 cm), such that on sites where both species grew together, *C. kobomugi* was shaded by *E. mollis*. Individual plants of *C. kobomugi* weighed 1066 to 2270 mg. In the sampling area where the biomass of *E. mollis* was >76 g m^{-2}, leaf lengths and plant weights for *C. kobomugi* were conspicuously increased. In contrast, for plots where plants of *E. mollis* were small or where other species also were growing, those values for parameters measured from *C. kobomugi* were small and similar to the other species. Two conclusions may be inferred from those data: 1) *C. kobomugi* grows well when shaded by other, taller plants; and 2) *C. kobomugi*, with its longer leaves, can compete successfully with peripheral plants for sunlight.

Furthermore, because *C. kobomugi* can produce many rhizomes when competition is less, this species can grow vigorously at the edge of the mean high-tide level where other plants cannot survive (Ishikawa and Kachi, 1998). However, Ishikawa and Kachi (1998) have also shown that, in areas that contain competitors such as *I. cylindrica* var. *koenigii*, the growth rate of *C. kobomugi* is noticeably lower during the main growing season (from April to June). In that case, although *C. kobomugi* produces many buds, the number of rhizomes that arise from those buds is small. Nevertheless, in the study presented here, *Carex* shoots grew well in the shade. This demonstrates that further research is needed in coastal sand dunes, where the competition for light can induce succession and where taller plants become more easily established (Olff et al., 1993).

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