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Ecological Characteristics of a *Suaeda japonica* Population and the Effects of Early-Season Air Temperatures on Population Formation

Byeong Mee Min*
Department of Science Education, Dankook University, Seoul 140-714, Korea

A natural, tidal-flat population of *Suaeda japonica* was studied to determine how air temperatures early in the growing season affected population formation. Changes in germination rates, density, standing crop (amount of biomass aboveground), and plant heights and weights were monitored from February 1999 to September 2000. Seed germination occurred between mid-February and early May in 1999, and from mid-February to mid-April in 2000. The daily mean air temperature fluctuated below and over 0°C through the end of March in 1999 and until mid-March in 2000. Seedling losses due to freezing were greater in 1999 than in 2000. Densities in 1999 and 2000 were 790 and 2201 plants/m^2 in the early growing season, and 578 and 803 plants/m^2 later on, respectively. Therefore, the density and mortality of *S. japonica* was higher in 2000 than in 1999. Values of correlation were low between density and standing crop, but diverse between density and height. The variation in standing crops was remarkable but that of height was small among sites. Frequencies of size classes, based on height, followed normal distribution curves over time, but those based on weight were very great in the lower classes over the entire growing season.

Keywords: germination, seedling, standing crop, *Suaeda japonica*, tidal flat

Within the same area, a population composed of annual plant species will change its form or structure every year. Such a stand is perpetuated by seeds, and their production, dispersal, and germination rates are influenced by diverse factors (Harper, 1977), mainly light, soil water content, and temperature (Silvertown, 1982; Willis and Groves, 1991; Fenner, 1992). In the northern hemisphere, seed germination begins as air temperatures rise early in the growing season. Soil temperatures at the surface absorb sunlight more quickly than at greater depths (Roberts, 1979). Therefore, when all other environmental factors are suitable, those seeds in the upper soil layers are more likely to germinate earlier. However, if the resultant seedlings experience low temperatures, i.e., <0°C, they are more susceptible to death from freezing (Grime et al., 1981; Primack, 1987). Moreover, the greater the number of seeds that are located in those upper soil layers, the higher the rate of seedling mortality and, consequently, seedling densities decrease.

Under poor growing conditions, the density of the cohort population that is built up by germination will decline over time. Population mortality is influenced by physical and biological factors. If density is high and the environment is appropriate, this leads to intraspecific competition, one strong biological factor (Bertness and Shumway, 1993). However, if the environment is harsh, then physical factors will affect survival more than biological influences (Barbour, 1978; Olff et al., 1997). The intertidal flats are inundated periodically by seawater, a phenomenon that causes stress to vascular plant growth. This is an example of how population formation is determined instead by a physical factor (Bertness et al., 1992; Bertness and Shumway, 1993).

For marsh vegetation, the impact of tidal flooding on plant survival and/or growth is mainly caused by the high NaCl concentration of seawater, tidal silt deposition, tidal abrasion, and soil anoxia (Huckle et al., 2000). Vascular plants are also exposed to more severe environments in lower salt marshes than higher ones (Ungar, 1978, 1987; van der Valk, 1981; Bertness et al., 1992; Shumway and Bertness, 1992; Rand, 2000). Because plants are distributed only within their range of tolerance and because the number of species is limited in a low salt marsh, such vegetation can develop only by pure stands and zonation (Chapman, 1974; Snow and Vince, 1984). However, in high marshes, the lack of many physically

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*Corresponding author; fax +82-2-799-1431
e-mail bmeemin@hanmail.net

limiting factors leads to intraspecies or interspecies competition (Barbour, 1978; Rand, 2000). Competition for light is critical on such sites because plants are adapted to growth in full sunlight; if the density increases above a certain level, plant productivity decreases in a density-dependent manner (Jefferies et al., 1981).

Many studies have been conducted on the physiological and distributional properties of the *Suaeda* genus (Ihm and Lee, 1985; Ihm, 1987, 1989; Lee and Oh, 1989; Lee, 1990; Ihm et al., 2004). However, little research has been done on its population ecology. According to field surveys, intertidal-flat areas covered by *Suaeda japonica* change their population structure within only a small range, and nearly all of this species' seeds are located directly beneath their maternal plants, close to the soil and buried in surface (Min, 2005).

The aim of this study was to examine the effects of air temperature in the early growing season on *S. japonica* population formation, and to monitor changes in density-dependent properties (e.g., mortality rates, standing crop per unit area, and plant heights) over time for a natural population growing on an intertidal flat.

MATERIALS AND METHODS

The study area, described previously (Min, 2005), is located at Walgotdong, Shiheung city, Gyeonggi Province (36° 23′N, 126° 46′E). This site is relatively flat but small creeks cut off any pattern of vegetative continuity. *S. japonica* plants grow from the lowest to the middle elevations; other species, in order of their appearance as the elevation increases, include *Aster tripolium*, *Artemisia scoparia*, and *Phacerulus latifolius*. Although the vegetation is inundated for only 1 h during the spring tides, seawater always persists within the sediment in which the plant root systems are distributed, and the soil in this vegetated area is unaffected by fresh water.

Field surveys were carried out during two normal growing seasons, between February 1999 and September 2000. Seed germination rates were tallied from mid-February to mid-May of 1999, and from mid-February to mid-April of 2000. Outside of these two study periods, the occurrence of new seedlings was recorded by counting those removed weekly from three permanent quadrats (50×50 cm). A seedling was defined as a plant with two cotyledons 3 mm long; those that had died from freezing were tallied separately.

To survey the changes in density for the *S. japonica* population, three permanent quadrats (50×50 cm) were set up near the quadrat used for the germination survey, and plants were counted every two weeks, from mid-April to the end of September. Density (in m^2) was estimated from the sum of the three quadrats. To examine the relationship between density and plant size, a line was run from the highest to the lowest elevation, and the density classes were roughly divided into 10. At each site, a 20×20 cm quadrat was established, and the roots and shoots of all the plants were excavated. After the sediment was washed away in the laboratory, plant heights and oven-dry weights (85°C for 48 h) were separately measured. Density-dependent heights and weights were determined for each sampling time. Values for correlation coefficients between density and dry weight per unit area or density and mean height were calculated by the formula of $y = ax + b$. Plant sizes were divided into 31 classes, and the number in each was converted to a frequency for all sampled plants.

Air temperature data were based on the Monthly Weather Report (Korea Meteorological Administration, 1999, 2000) from measurements at the Incheon Meteorological Station (37° 29′N, 126° 38′E; 68.9 m above sea level). Because the mean and lowest daily air temperatures were never colder than 0°C from April to September in either 1999 or 2000, only air temperatures for February and March of those years were analyzed.

RESULTS AND DISCUSSION

Air Temperatures Early in the Growing Season and the Number of Seedlings Produced

Changes in the mean and lowest daily air temperatures were plotted from February to March for two consecutive years (Fig. 1). In 1999, monthly mean air temperatures were 0.5°C in February and 5.8°C in March. Daily mean air temperatures (MT) were above 4°C between the 16th and 17th and the 23rd and 26th of February, and from the 1st to the 5th, the 12th to the 20th, the 24th to the 28th, and after the 30th of March. Days when the lowest air temperatures (LT) were below 0°C included February 1st to 14th, 18th to 22nd, and 27th to 28th, as well as March 5th to 9th, 11th to 12th, 21st to 23rd, and 29th. Therefore, new plants were most at risk of freezing during six time periods.

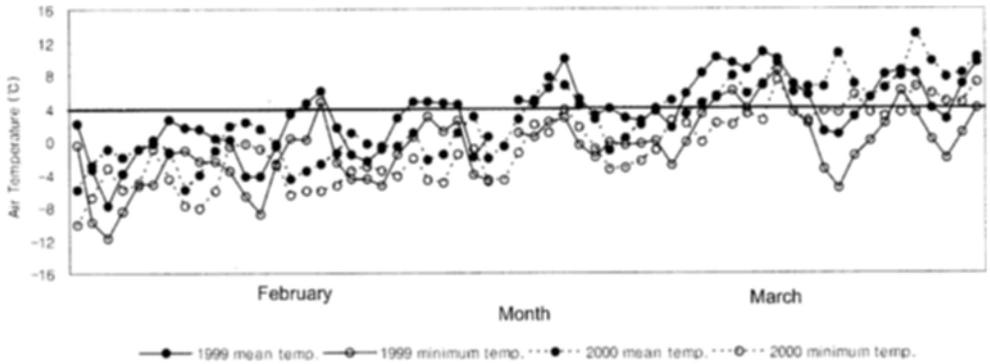


Figure 1. Maximum and minimum air temperatures at study area from February to March, in 1999 and 2000.

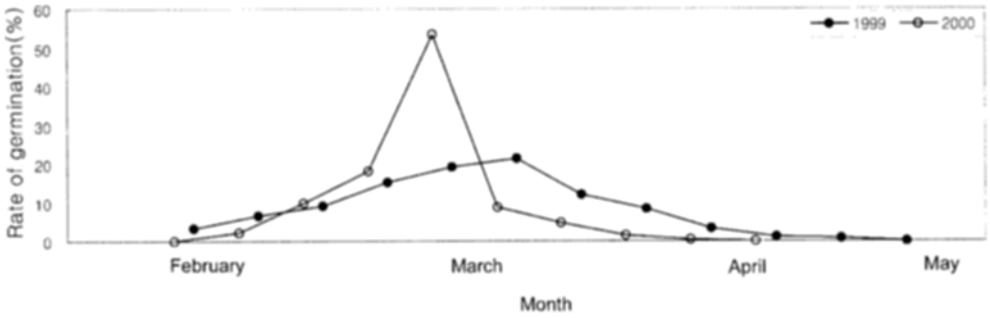


Figure 2. Germination rate of *S. japonica* seeds early in growing season.

In 2000, the monthly mean air temperatures were 0.0°C (February) and 6.0°C (March); MT periods included March 2nd to 5th, the 11th, and the 13th to the 31st; LT periods occurred February 1st to 29th and March 1st, the 6th to the 10th, and the 13th. Therefore, the Year 2000 had only two periods of freezing risk; during the last LT (March 13th), germinated seedlings were tolerant of a temperature of -0.1°C.

Although monthly mean temperatures for February and March were similar in 1999 and 2000, the last dates for LTs below 0°C varied, from as late as March 29th, 1999, to as early as March 13th in 2000. In addition, fluctuations in temperatures, from over 4°C (MT) to below 0°C (LT) were more frequent in 1999 than in 2000.

New seedlings numbered 3000 in 1999 and 3239 in 2000. The first year, seed germination began in mid-February and finished in early May, with the highest rate, 21.5%, occurring on March 21st (Fig. 2). In the second year, 2000, the germination period ran from mid-February to mid-April, peaking earlier, at 53.7%, on March 12th. Compared with Year 2000, germination in 1999 proceeded at a more uniform pace. During the latter, frequent fluctuations from LTs below 0°C to MTs above 4°C prolonged the time over which germination was possible. Normally, the ideal conditions require continuous temperatures above 0°C (LT) or 4°C (MT). This study, therefore, demonstrates that *Suaeda* seed is able to tolerate temperatures lower than 0°C. Germination in *Cynoglossum* is more favorable whenever a warmer spell follows a period of frosty weather (Boorman and Fuller, 1984).

Table 1. Mortality among *S. japonica* seedlings over the 1999 and 2000 growing seasons.

Day/month		Number of dead seedlings
1999	14/Feb	91
	21/Feb	183
	28/Feb	274
	07/Mar	463
	14/Mar	534
	21/Mar	377
	28/Mar	36
2000	12/Feb	3
	19/Feb	74
	26/Feb	321
	04/Mar	259
	11/Mar	294

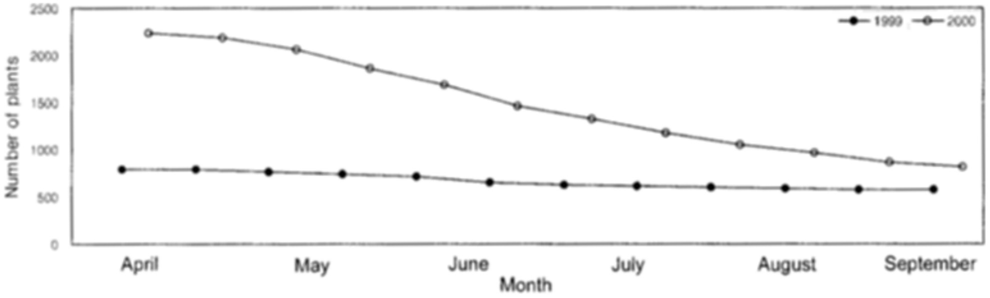


Figure 3. Change in *S. japonica* population density at permanent quadrat.

In contrast, seeds of *Salicornia europaea* agg. tend to germinate later in the year than do those of *Suaeda*, such that, by midsummer, the *Salicornia* seed bank is exhausted (Jefferies et al., 1981).

In 1999, the number of seedlings that died from freezing was 1958 out of 3000 plants (65.3%), compared with only 951 out of 3293 (28.9%) in 2000 (Table 1). This difference may have resulted because of the greater number of times during the 1999 germination period in which LT was below 0°C and MT was above 4°C. In this study, the minimum temperature that seedlings of *S. japonica* could tolerate was not surveyed. However, greater mortality was observed after new plants were exposed to -1.0°C LT. In previous research (Min, 2005), seeds of this species were reported to be distributed mainly near the soil surface, at a depth of 2 mm, suggesting that their shallow positioning made germination easier when air temperatures rose above 4°C.

Successful seedling recruitment depends on both the availability of seeds and the suitability of the post-dispersal environment for seedling emergence and growth (Harper, 1977). Some species also require a physical microsite and proper seed positioning in the soil for germination (Harper et al., 1965). In this study, the occurrence of low temperatures greatly affected population formation of the annual species *S. japonica*. Shallow placement of its seeds meant that germination occurred early in the growing season because the rate of increase in soil temperature was in inverse proportion to soil depth. This phenomenon, however, also increased the risk of new seedlings being exposed to low early-springtime temperatures in Korea that normally fluctuate from below to above 0°C. In this study area, the frost-free months are from May to October (Korea Meteorological Administration, 1990). However, germination of *S. japonica* begins in mid-February, so that the resultant seedlings often freeze. Therefore, the population of coastal vegetation near the Yellow Sea in Korea is thought to be unstable because cover by plants such as *Suaeda* sp. can change in its structure or location every year.

Changes in Density during the Growing Season

The decrease in density was relatively rapid early in the growing season but then began to taper over time (Fig. 3). For example, in 1999, plants found in the permanent quadrat on April 10 numbered 790 per m^2, then decreased slowly to 578 per m^2 by September 11. In 2000, densities were 2201 plants per m^2 (April 15), followed by an abrupt decline to 803 plants per m^2 on September 18. Considering that the seeds were dispersed unevenly, the number of resulting plants was similar to that counted in the quadrat

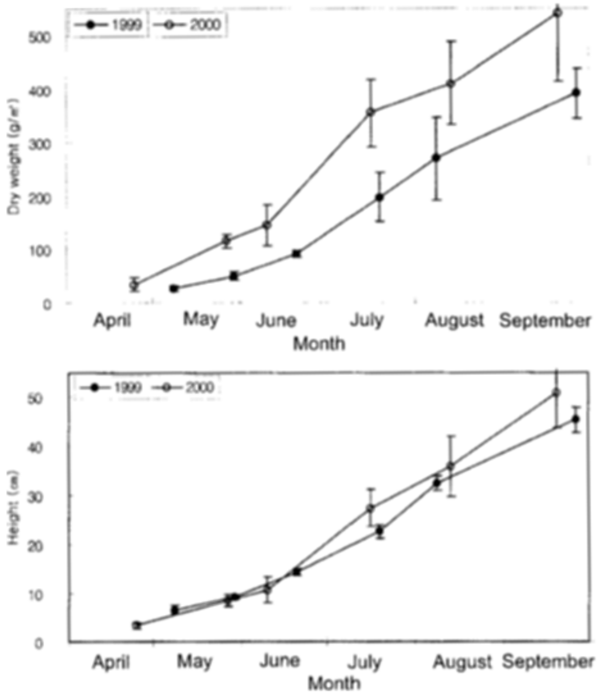


Figure 4. Changes in standing crop (upper) and plant height (lower) of *S. japonica* population during growing season.

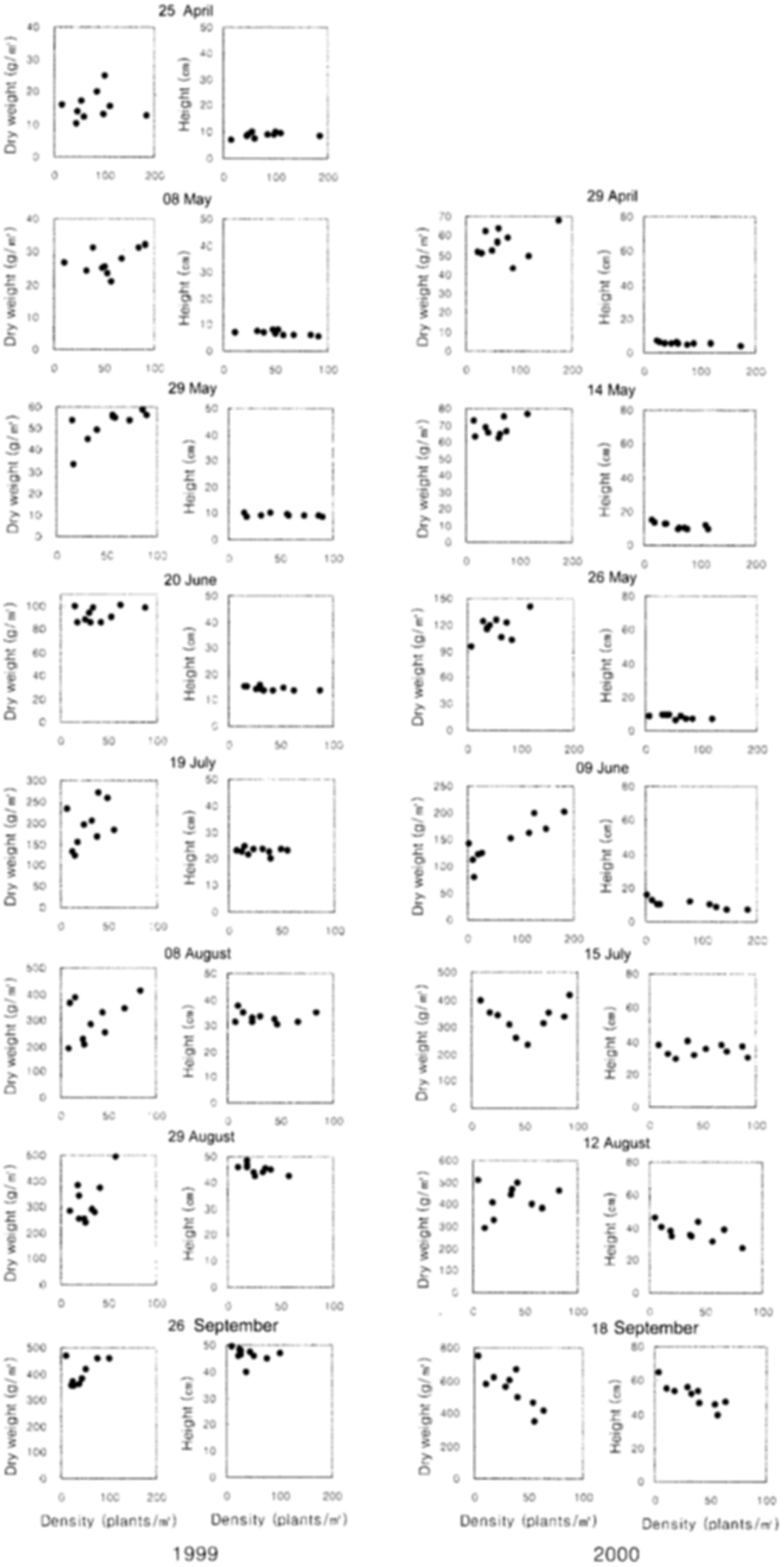


Figure 5. Relationship between density and standing crop, and between density and height over 1999 and 2000 growing seasons.

used to determine the germination rate, i.e., 75.8% (790/1042) in 1999 and 94.0% (2201/2342) in 2000, respectively, for counts in the density quadrat versus the germination quadrat. Survival rates for 1999 and 2000 were 73.2% and 36.5%, respectively, suggested that intraspecific competition was strong in proportion to density and that, regardless of the beginning tally, density at the end of the growing season was similar within the same environment. In general, density-dependent mortality was limited to areas with a very high number of plants, and occurred only in the early seedling stages (Augspurger and Kitajima, 1992). In contrast, mortality of *S. europaea* agg. which is an annual succulent halophyte of Chenopodiaceae, appears to be density-independent (Jefferies et al., 1981), as is that of *Vulpia fasciculata*, a sand dunes annual species (Watkinson and Harper, 1978). This discrepancy is believed to be related to dissimilarities in their maximum allowable densities rather than because of those two species' strategy.

Changes in Standing Crop and Height during the Growing Season

Changes in standing crop and plant heights also were monitored in 1999 and 2000 (Fig. 4). Both the amount of aboveground biomass and heights increased by the end of the growing season, with increments being most conspicuous in June and July. The standing crop for 2000 was 1.37 times greater than for 1999, i.e., 540.7±124.7 g DW m^{-2} versus 393.3± 47.6 g DW m^{-2}. This suggests that the growing environment was more favorable for *S. japonica* in 2000. Final mean heights were 45.4±2.5 cm (1999) and 50.8±7.1 cm (2000), with the difference in these data being less than that calculated for the final standing crops.

Relationships among Standing Crop, Height, and Density

When the relationships among various growth parameters were analyzed, overall standing crop was found not to be proportionate to density (Fig. 5; Table 2), except for May 29, August 8 and 29 in 1999 as well as for June 9, 2000. However, standing crop was inversely proportionate to density on September 18. Differences in standing crop data among sites were great, and increased over time. In contrast, plant heights were either constant regardless of density, or were slightly decreased. This suggests that, in the case of high-density areas, the plants grew only upward, with just a few branches. When growing at lower densities, however, the plants showed more branching and less height growth. Therefore, intraspecific competition for sunlight increased in proportion to density, resulting in a more slender, less-branched morphology.

Table 2. Correlation coefficients between dry weight per unit area and density or between mean plant height and density in a *S. japonica* population during the 1999 and 2000 growing seasons.

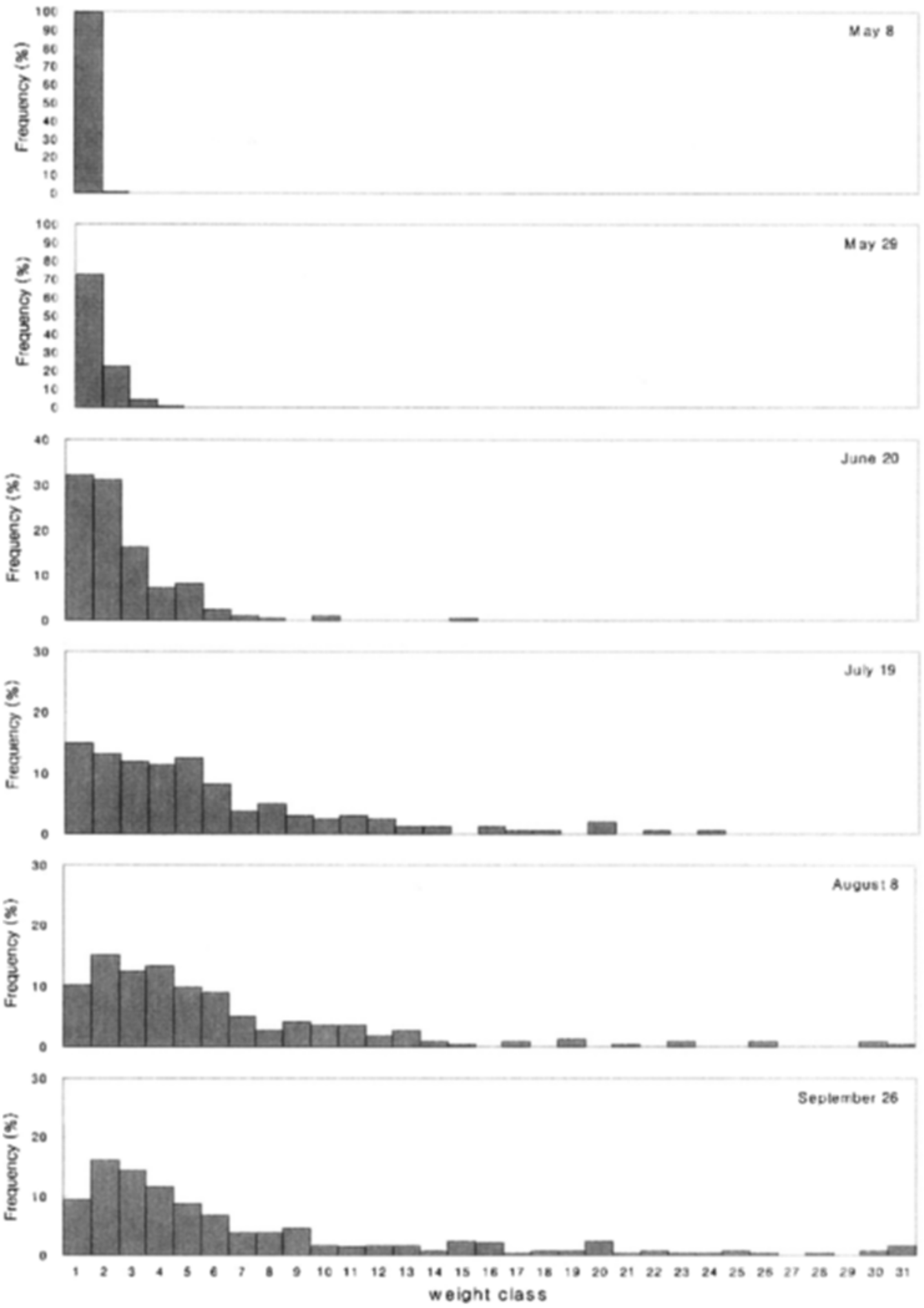
Day/month		Correlation Coefficient	
		Density-Dry weight	Density-Height
1999	25/Apr	0.0498	0.3529
	08/May	0.4266	-0.6081
	29/May	0.6189	-0.2684
	20/June	0.3767	-0.5356
	19/July	0.4330	-0.1499
	08/Aug	0.4530	-0.1603
	19/Aug	0.6130	-0.6234
	26/Sep	0.0195	-0.2225
2000	29/April	0.2992	-0.0178
	14/May	0.5867	-0.7122*
	26/May	0.5370	-0.7322*
	09/June	0.8718**	-0.8206**
	15/July	0.0669	-0.0248
	12/Aug	0.1839	-0.6542*
	18/Sep	-0.3280	-0.6540*

*, significant at 5% level; **, significant at 1% level.

Changes in Plant Size during the Growing Season

Out of the 31 designated weight classes, all plants were placed in the smallest class early in the season, but a few moved into the larger ones over time during both 1999 and 2000. However, frequencies were always high within the lower classes for the total season (Fig. 6, 7). Therefore, weight usually did not increase in most plants. Nevertheless, some of the smaller plants grew vigorously such that the largest plant weighed 40 times more than the smallest. The frequency pattern of 2000 converged more in the lower classes than did that of 1999 at the end of the growing season. Therefore, because density in 2000 was higher than in 1999, plant weights were inversely proportionate to density.

For the height classes, the maximum frequency shifted from the lower to the higher classes over time in each growing season (Fig. 8, 9). The patterns of fre-

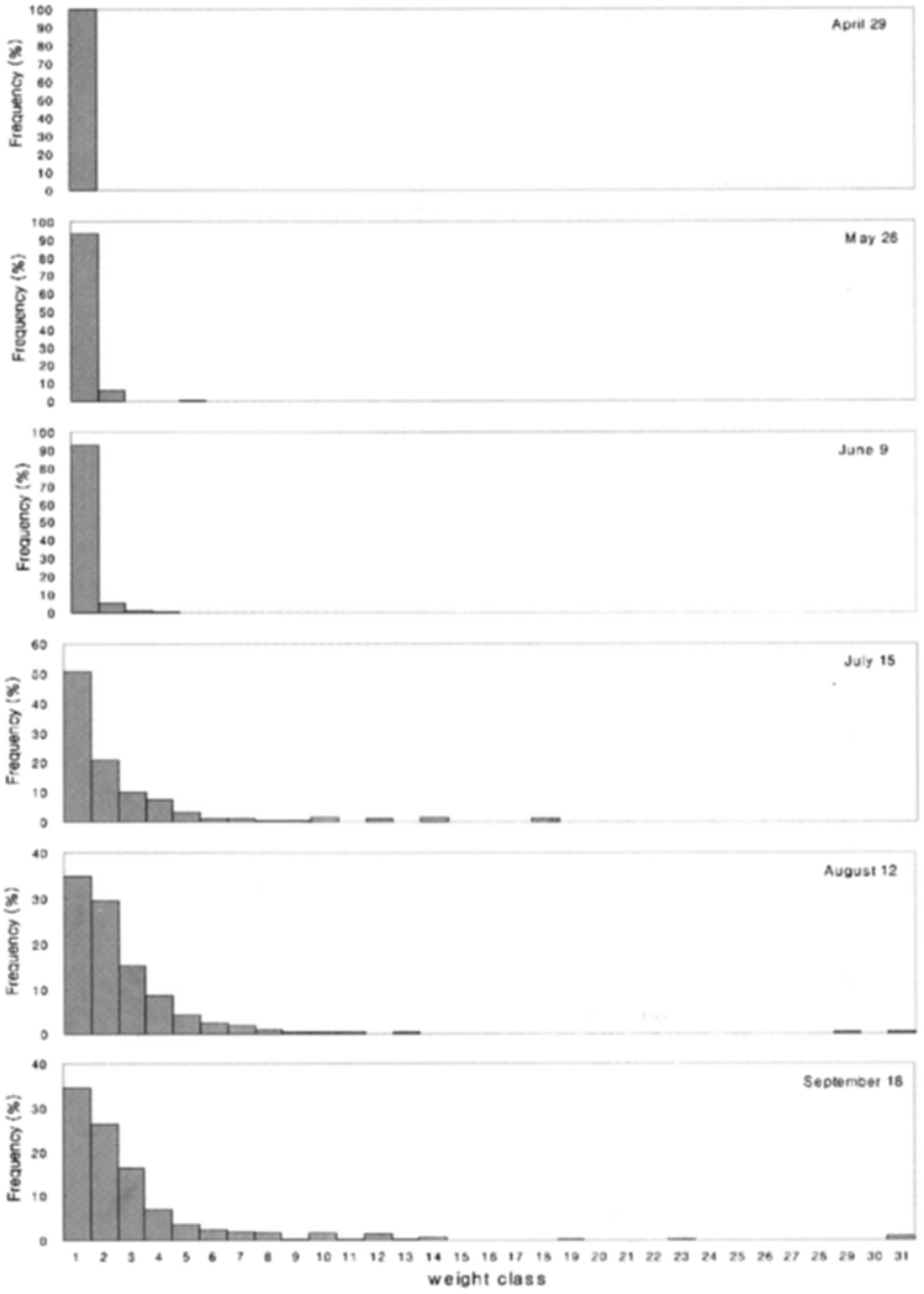


1	~0.199	5	0.800~0.999	9	1.600~1.799	13	2.400~2.599	17	3.200~3.399	21	4.000~4.199	25	4.800~4.999	29	5.600~5.799
2	0.200~0.399	6	1.000~1.199	10	1.800~1.999	14	2.600~2.799	18	3.400~3.599	22	4.200~4.399	26	5.000~5.199	30	5.800~5.999
3	0.400~0.599	7	1.200~1.399	11	2.000~2.199	15	2.800~2.999	19	3.600~3.799	23	4.400~4.599	27	5.200~5.399	31	6.000~
4	0.600~0.799	8	1.400~1.599	12	2.200~2.399	16	3.000~3.199	20	3.800~3.999	24	4.600~4.799	28	5.400~5.599		(unit: g)

Figure 6. Weight class distribution of *S. japonica* population in 1999.

quency distribution generally showed normal curves; 2000 was more irregular than 1999. The largest plant was 3.2 times taller than the smallest one.

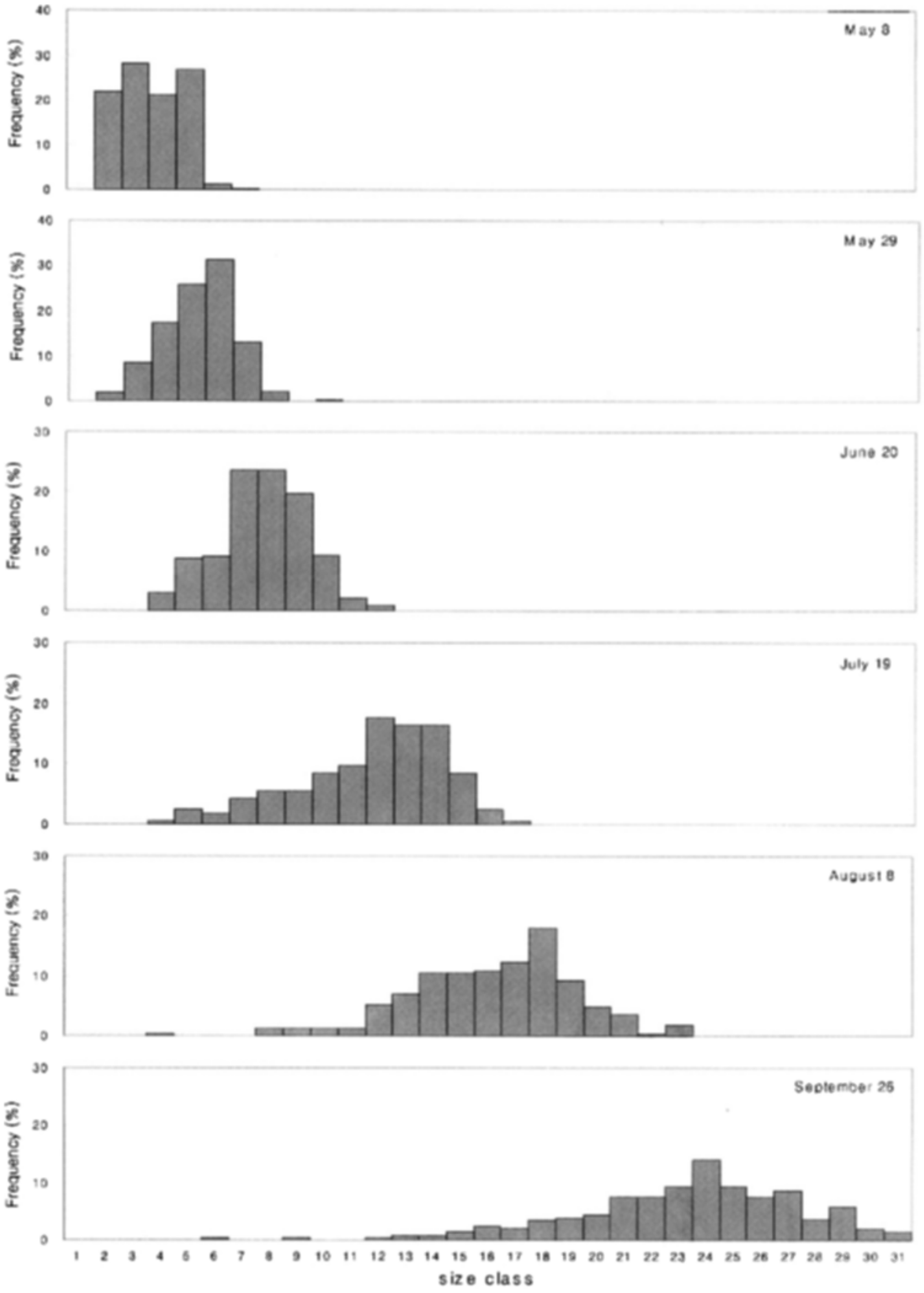
When the standing crop unit area and mean heights were integrated with density, and changes in size class frequency were compared over time, the



1 ~0.199	5 0.800~0.999	9 1.600~1.799	13 2.400~2.599	17 3.200~3.399	21 4.000~4.199	25 4.800~4.999	29 5.600~5.799
2 0.200~0.399	6 1.000~1.199	10 1.800~1.999	14 2.600~2.799	18 3.400~3.599	22 4.200~4.399	26 5.000~5.199	30 5.800~5.999
3 0.400~0.599	7 1.200~1.399	11 2.000~2.199	15 2.800~2.999	19 3.600~3.799	23 4.400~4.599	27 5.200~5.399	31 6.000~
4 0.600~0.799	8 1.400~1.599	12 2.200~2.399	16 3.000~3.199	20 3.800~3.999	24 4.600~4.799	28 5.400~5.599	(unit: g)

Figure 7. Weight class distribution of *S. japonica* population in 2000.

growth of *S. japonica* plants was found to be density-dependent, i.e., weight increases were inversely proportionate to density over the season. However, plant height was density-independent. This demonstrates



1	~1.9	5	8.0~9.9	9	16.0~17.9	13	24.0~25.9	17	32.0~33.9	21	40.0~41.9	25	48.0~49.9	29	56.0~57.9
2	2.0~3.9	6	10.0~11.9	10	18.0~19.9	14	26.0~27.9	18	34.0~35.9	22	42.0~43.9	26	50.0~51.9	30	58.0~59.9
3	4.0~5.9	7	12.0~13.9	11	20.0~21.9	15	28.0~29.9	19	36.0~37.9	23	44.0~45.9	27	52.0~53.9	31	60.0~
4	6.0~7.9	8	14.0~15.9	12	22.0~23.9	16	30.0~31.9	20	38.0~39.9	24	46.0~47.9	28	54.0~55.9		(unit: cm)

Figure 8. Height class distribution of *S. japonica* population in 1999.

that plants invested more energy in branching under low-density conditions versus stem development when growing on a high-density site, thereby enabling them to compete strongly with other plants for sunlight.

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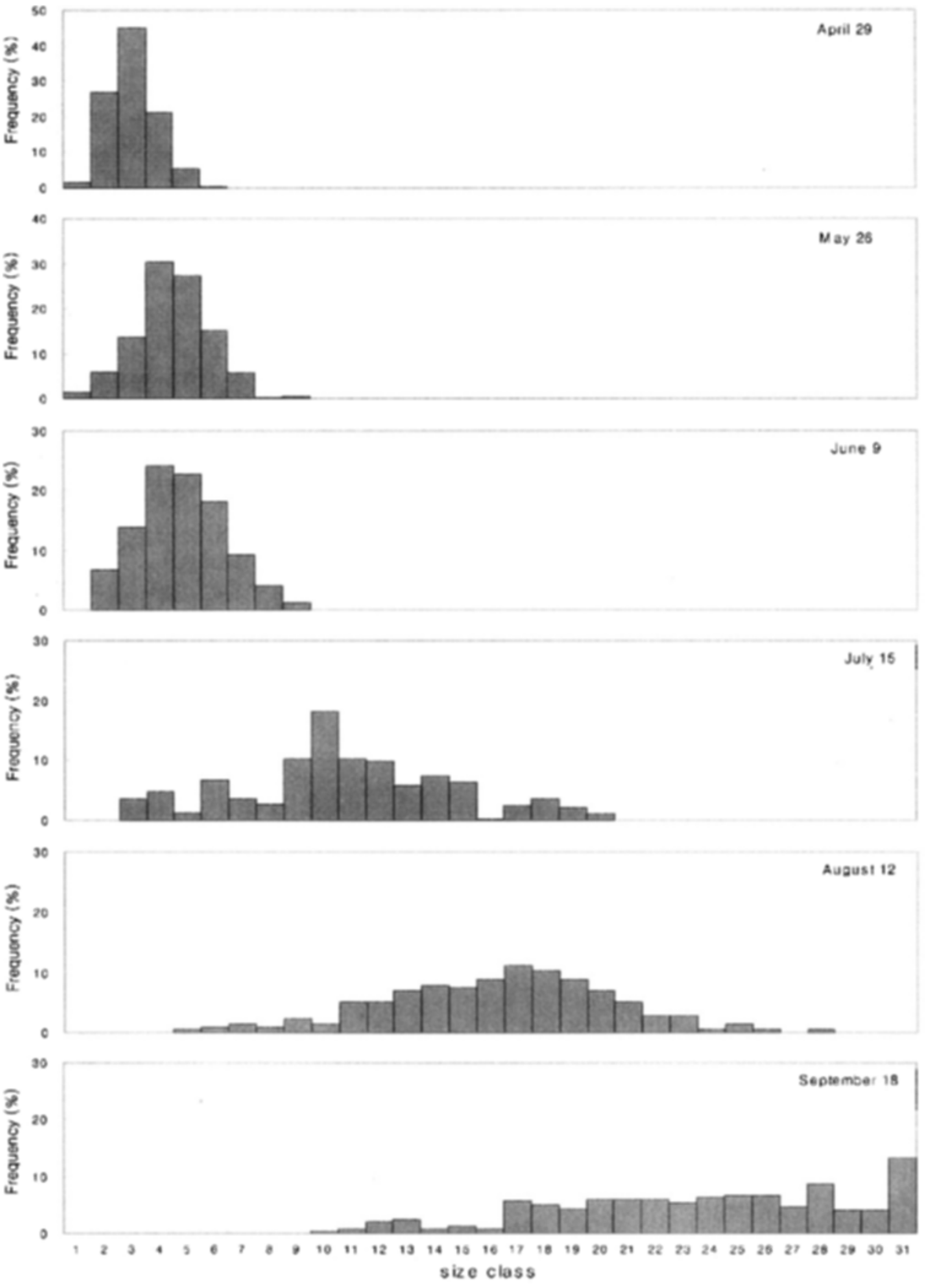

1	~1.9	5	8.0~9.9	9	16.0~17.9	13	24.0~25.9	17	32.0~33.9	21	40.0~41.9	25	48.0~49.9	29	56.0~57.9
2	2.0~3.9	6	10.0~11.9	10	18.0~19.9	14	26.0~27.9	18	34.0~35.9	22	42.0~43.9	26	50.0~51.9	30	58.0~59.9
3	4.0~5.9	7	12.0~13.9	11	20.0~21.9	15	28.0~29.9	19	36.0~37.9	23	44.0~45.9	27	52.0~53.9	31	60.0~
4	6.0~7.9	8	14.0~15.9	12	22.0~23.9	16	30.0~31.9	20	38.0~39.9	24	46.0~47.9	28	54.0~55.9		(unit: cm)

Figure 9. Height class distribution of *S. japonica* population in 2000.

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