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Altitudinal variations in germination and growth responses of *Reynoutria japonica* populations on Mt Fuji to a controlled thermal environment

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The authors examined altitudinal variations in the thermal responses of seed germination and seedling growth in *Reynoutria japonica* (= *Polygonum cuspidatum*) under controlled environmental conditions. Seed populations were collected from different altitudes on Mt Fuji in Japan. The mean seed weight of the upland populations (above 1500 m) was significantly (1.5-fold) heavier than that of the lowland populations (below 1400 m). Under the lowest temperature regime of 15/10°C (day/night) the upland populations showed a significantly higher percentage and speed of germination than the lowland populations; this was not significant under higher temperature regimes. These results indicate that the germination traits of the upland populations on Mt Fuji are favorable for colonization in their cold habitats (low temperature and short growing season). Growth and shoot development were compared between the seedlings grown from seeds collected at altitudes of 700 and 2420 m. The upland seedlings showed a significantly larger biomass and leaf area than the lowland seedlings at 15°C, but there was no difference at 25°C. The difference in biomass at 15°C was attributed to the difference in seed weight. The upland seedlings produced a significantly larger number of branches with smaller and more numerous leaves at both 15°C and 25°C. These developmental traits of the upland seedlings were considered to represent the adaptation of the life form to upland environments. It was concluded that the *R. japonica* populations along an altitudinal gradient on Mt Fuji can be classified into two ecotypes, whose distribution border lies at an altitude of about 1400–1500 m. In this study, the seed weight and germination traits of two *R. japonica* seed populations collected in Chiba Prefecture were briefly compared with those of the lowland populations on Mt Fuji.

Key words: altitudinal gradient; development; germination; growth; *Reynoutria japonica*; thermal environment.

INTRODUCTION

In general, alpine and subalpine environments are characterized by low temperatures and high relative humidity, high wind speed and a short growing season (Masuzawa 1983; Bliss 1985; Körner & Diemer 1987; Friend *et al.* 1989). Most of the plant species originating from lowland regions cannot be easily acclimated to alpine regions, because the alpine environments are out of the climatic range in which the lowland species can germinate, grow and reproduce. In some lowland species, however, habitats are distributed over a wide altitudinal range. Altitudinally widespread species include typical rural plants *Plantago asiatica* (Shibata 1985), *Taraxacum officinale* (Oulton *et al.* 1979) and *Trifolium repens* (Mächler & Nösberger 1977). In general they inhabit disturbed bare land in alpine regions.

Temperature is an important environmental factor that limits the altitudinal distribution of plants. Altitudinally widespread species have been used to investigate the adaptive variations within a species to the thermal environment. Physiological properties, such as photosynthesis, of altitudinally widespread species reveal a wide range of optimum temperatures that enable them to widely colonize various altitudes of mountainous areas (Shibata

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1985). Altitudinally widespread species growing naturally in the upland areas acquire adaptive variations of germination, photosynthesis and growth form along the altitudinal gradient in these environments (Mooney 1963; McNaughton *et al.* 1974; Woodward 1975; Woodward & Pigott 1975). Such ecophysiological studies on the plants growing in mountainous areas are fewer in Japan as compared with other countries (Shibata 1985).

Reynoutria japonica (nomenclature follows Satake *et al.* 1982) is an altitudinally widespread species that originates from the lowland areas of the temperate regions of Japan (Shiosaka 1989). The upper limit of distribution on Mt Fuji (3776 m) corresponds to the timberline at 2500–2600 m in altitude (Masuzawa *et al.* 1991). *Reynoutria japonica* is a perennial, diecious herb. The adult female plants produce many seeds at the end of the growing season. The current-year seedlings of *R. japonica* in mountainous areas do not survive readily due to winter freezing. Maruta (1983) suggested that there is a critical amount of annual carbon production (critical size) in the subterranean parts in winter for survival over the freezing period. The present study examines intraspecific differences in seed weight, percentage and speed of seed germination, seedling growth and shoot development in *R. japonica* populations along an altitudinal gradient on Mt Fuji, and shows that upland populations adapt these properties to the severe conditions of the upland environments. In addition, the lowland populations on Mt Fuji are roughly compared with the low-altitude populations in Chiba Prefecture for seed weight and germination traits. These populations are different in horizontal distribution, there being a distance of about 120 km between the two locations.

METHODS

Seed collection

In this study, the term 'lowland' refers to the altitudinal zone below 1400 m and the term 'upland' to that above 1500 m.

Reynoutria japonica seeds were collected from 22 sites at different altitudes in the central region of the main island of Japan. Plants from which seeds were collected belonged to large plants in each collection site, because it was known that such plants had successfully established there. Of those collection sites, 22 sites from altitudes of 40 m, 240 m and above 500 m (up to 2420 m) were located on Mt Fuji (35°21′N, 138°44′E). The seed collections on Mt Fuji were carried out in early December 1989 and early November 1990 for the seed populations below 1400 m and in late October 1989 for the seed populations above 1500 m. Two other sites were located at 10 m in Sakura (35°43′N, 140°13′E) and at 270 m on Mt Kiyosumi (35°10′N, 140°10′E), Chiba Prefecture. The seed populations in Chiba were collected in early December 1990. The sites on Mt Fuji range from the basal region to the alpine region, and the sites in Chiba belong to the basal region.

Seeds collected from each site were air-dried at room temperature for about 2 weeks, and then the fresh weight per 100 seeds was determined (three replicates). Conveniently the fresh weight of seed refers to the weight of the fruit separated from the wing. The remaining seeds were stored in a refrigerator at 4°C until used for the experiments on germination and growth.

Seed germination

The lowland seed populations on Mt Fuji were stored in a refrigerator for 75 days, and the seed populations from the other altitudes all were stored for 95 days. Germination experiments were carried out using these seed populations that had been put in storage for different periods, and the results are grouped together.

Fifty seeds were placed on moist quartz sand in a 9 cm Petri dish and exposed to a temperature of 4°C for 10 days in the refrigerator, as the *R. japonica* seeds display embryo dormancy (Shibata & Arai 1970). The stratified seeds were germinated under three temperature regimes of 15/10, 25/20, 35/30°C (12 h day/12 h night) in temperature-controlled incubators. Two replicates were examined for each temperature regime. The germination experiment at 35/30°C could not be applied to seed populations from the altitudes of 40, 240 or 550 m on Mt Fuji, because of the lack of available seeds. The seeds were illuminated during the day time at a quantum irradiance of 150 μmol m^{-2} s^{-1} using white fluorescent tubes. Germination was surveyed every day until no further germination occurred for 3 days. Seeds were counted as germinating when the radicle emerged.

The quantitative evaluation of seed germination was based on two parameters, the final germination percentage and germination speed. The germination speed is defined as the reciprocal of the number of days until 50% of final germination percentage occurred.

Growth of seedlings

The growth responses of the seedlings to low and high temperatures were examined in two growth cabinets, at a day/night-constant temperature of either 15 or 25 °C, a mean relative humidity of 75 ± 5%, and a 12 h photoperiod. The illumination was provided at quantum irradiances of 200 ± 10 μmol m^{-2} s^{-1} for the first 10 days and thereafter at 420 ± 20 μmol m^{-2} s^{-1} using metal halide lamps.

Seeds collected at 700 m (lowland) and 2420 m (upland) on Mt Fuji were used for comparative experiments on seedling growth. Seeds were germinated on moist quartz sand in 9 cm Petri dishes. A 7 day old seedling was transplanted into a small cup (5 cm diameter, 6 cm deep) filled with fine gravel. Fifty-six seedlings for each altitude were arranged randomly in four containers (40 cm long, 50 cm wide, 15 cm deep), each supporting 28 plants. Seedlings were grown using a hydroponic culture system. The containers contained half-strength Hyponex solution (Hyponex Japan, 0.5 g L^{-1}). The nutrient solution was aerated continuously, renewed every week and adjusted to pH 5.5 with HCl every 2 days.

The growth experiments were completed when the seedlings were 55 days old for the 15 °C treatment and 40 days old for the 25 °C treatment. Harvests were performed three times for the 15 °C plants and four times for the 25 °C plants during each growing period. Three or four seedlings were taken from each container at each harvest to obtain 14 seedlings. Stem length, number of branches, number of leaves and leaf area were determined. The harvested seedlings were dried at 80 °C for 3 days and then weighed.

Data analysis

Statistical analyses were applied only to the populations on Mt Fuji, because of the lack of data points for the Chiba populations. Homoscedasticity for data values between lowland and upland populations was tested previously using the Bartlett test. As a result mean values of seed weight, biomass, leaf area and developmental parameters of shoots in temperature treatment could be analyzed for significant difference with one-way ANOVA. Since there was no homoscedasticity for data values of germination parameters, nonparametric statistics (Wilcoxon test) were applied to the case. Significance levels of $P = 0.05$ were adopted.

RESULTS

Weight and germination of seeds

The seed fresh weight of *R. japonica* varied from 60 to 194 mg per 100 seeds (Fig. 1). The major change along the altitudinal gradient occurred around an altitude of 1400–1500 m. The mean seed fresh weight of 13 upland populations was significantly (1.5-fold) heavier than that of seven lowland populations on Mt Fuji (ANOVA: $F = 55.76$, $P < 0.001$). The seed weight of Chiba populations (10 and 270 m) was similar to the lowland populations on Mt Fuji.

The final germination percentage of *R. japonica* seeds showed high values of more than 60% in all

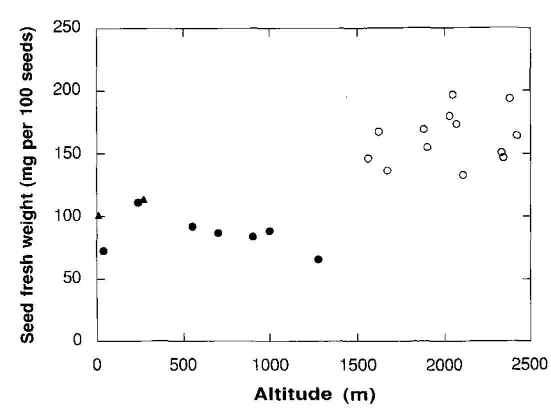

Fig. 1. Seed fresh weight of *R. japonica* along an altitudinal gradient. Values are means of three replicates (unit: 100 seeds). Symbols: (●), seven lowland seed populations below 1400 m in altitude on Mt Fuji; (▲), two seed populations in Chiba Prefecture; (○), 13 upland seed populations above 1500 m on Mt Fuji. For the seed populations on Mt Fuji, mean seed fresh weight significantly differs between lowland and upland, at $P < 0.001$ based on one-way analysis of variance.

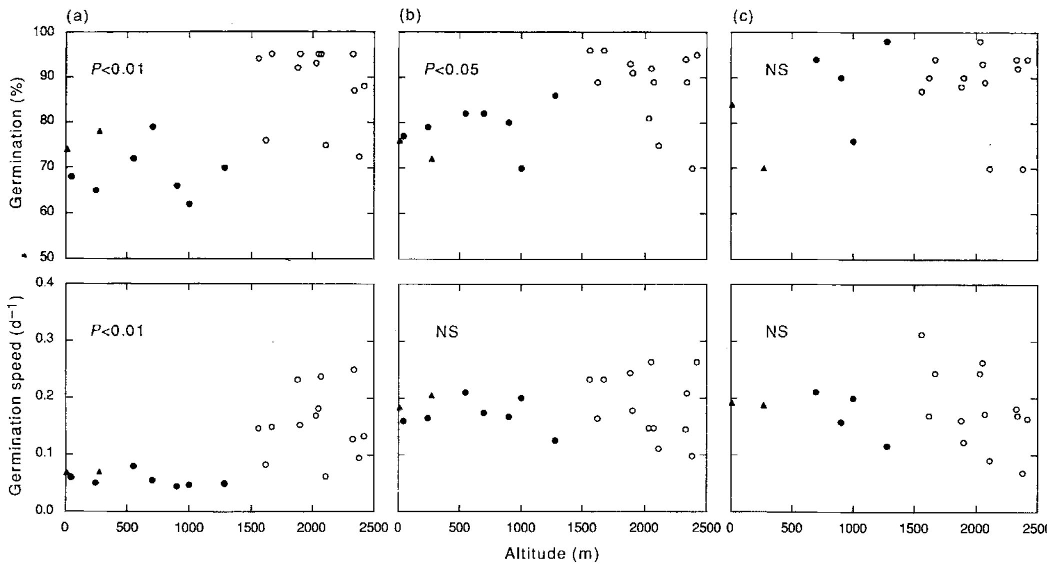

Fig. 2. Germination percentage and speed of *R. japonica* seeds from sites at different altitudes at (a) 15/10 °C, (b) 25/20 °C and (c) 35/30 °C. Values are mean of two replicates (unit: 50 seeds). Symbols: (●), seven lowland seed populations below 1400 m in altitude on Mt Fuji; (▲), two seed populations in Chiba Prefecture; (○), 13 upland seed populations above 1500 m on Mt Fuji. The percentage and speed of germination is statistically compared between lowland and upland populations on Mt Fuji in each temperature treatment using the Wilcoxon test. Signifcance levels are shown in figures; NS, not significant at $P = 0.05$.

the altitudes and temperature treatments (Fig. 2). For the Mt Fuji populations, the mean germination percentage of the upland populations at 15/10 and 25/20 °C was significantly higher than that of the lowland populations (Wilcoxon test: $W_0 = 31 \leqslant W_{7,13} = 41$, $P < 0.01$ for 15/10 °C; $W_0 = 43 \leqslant W_{7,13} = 48$, $P < 0.05$ for 25/20 °C). A significant difference in germination speed occurred only at 15/10 °C. The mean germination speed of the upland populations was significantly (2.5-fold) higher than that of the lowland populations (Wilcoxon test: $W_0 = 29 \leqslant W_{7,13} = 41$, $P < 0.01$). The germination speed of the upland populations was independent of the temperatures but showed a large variance. The germination percentage and speed of Chiba populations was similar to the lowland populations on Mt Fuji.

The major changes in the percentage and speed of germination along an altitudinal gradient on Mt Fuji were detected at an altitude of approximately 1400–1500 m as in the case of seed weight (Fig. 1).

Growth of seedlings

The effects of the temperature on plant biomass and total leaf area were compared between seedlings

Table 1. Developmental properties of shoots of *R. japonica* seedlings grown from seeds collected from sites at 700 and 2420 m altitudes on Mt Fuji at 15 and 25 °C

	15 °C (55 days)			25 °C (40 days)		
	700 m	2420 m	*P* level	700 m	2420 m	*P* level
Stem length (cm)	5.7 (2.3)	6.7 (1.1)	NS*	11.1 (2.6)	10.2 (2.3)	NS
No. branches	1.2 (1.2)	5.0 (1.4)	< 0.001	6.8 (1.9)	9.8 (1.1)	< 0.001
No. leaves	9.4 (3.5)	22.8 (5.5)	< 0.001	30.5 (4.2)	55.3 (8.6)	< 0.001
Area of leaf (cm^2)	12.7 (2.9)	7.9 (1.3)	< 0.001	8.8 (1.5)	4.6 (0.9)	< 0.001

Values are means and SD of 14 seedlings taken at 55 days for 15 °C and 40 days for 25 °C after germination. Statistical difference between altitudes is analyzed using one-way ANOVA. *NS: not significant at $P = 0.05$.

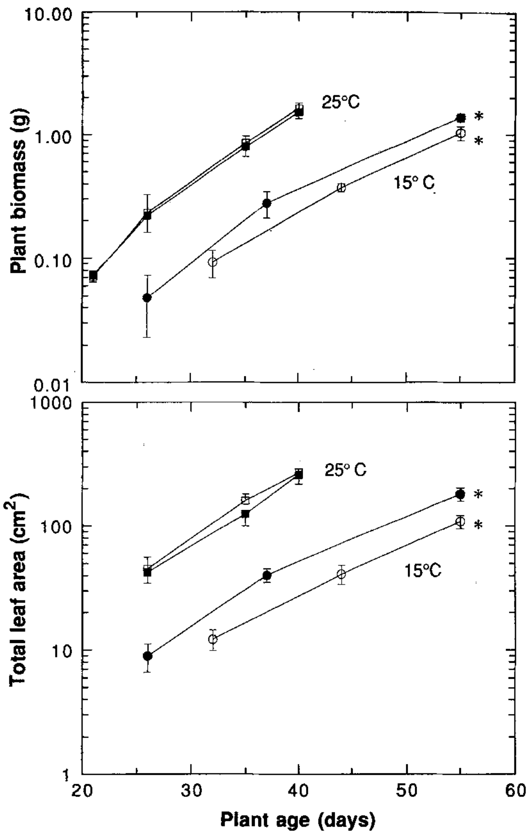

Fig. 3. Time course of plant biomass and total leaf area of *R. japonica* from sites at two altitudes at 15 and 25 °C. Symbols: (○), 700 m at 15 °C; (●), 2420 m at 15 °C; (□), 700 m at 25 °C; (■), 2420 m at 25 °C. Values are mean and SD (vertical bars, single sided for 25 °C) of 14 replicates. Statistical difference is analyzed between the final values at both altitudes using one-way analysis of variance: significant at $P < 0.001$ for 15 °C with asterisks; not significant at $P = 0.05$ for 25 °C.

grown from seeds collected at altitudes of 700 and 2420 m, which were selected as representatives of the lowland and upland areas (Fig. 3). Final plant biomass and leaf area at 15 °C were higher in the upland seedlings than in the lowland seedlings (ANOVA: $F = 56.26$, $P < 0.001$ for plant biomass; $F = 62.53$, $P < 0.001$ for total leaf area), whereas no differences in the biomass and leaf area between both seedlings were detected at 25 °C.

Shoot development

The difference in stem length between the lowland and upland seedlings was not significant (ANOVA: $P > 0.05$; Table 1). The upland seedlings produced a significantly larger number of branches than the lowland seedlings (ANOVA: $F = 80.01$, $P < 0.001$ for 15 °C; $F = 20.65$, $P < 0.001$ for 25 °C). The number of leaves was significantly larger in the upland seedlings than in the lowland seedlings (ANOVA: $F = 26.01$, $P < 0.001$ for 15 °C; $F = 60.21$, $P < 0.001$ for 25 °C). Moreover the leaves of the upland seedlings were significantly smaller than those of the lowland seedlings (ANOVA: $F = 18.07$, $P < 0.001$ for 15 °C; $F = 110.46$, $P < 0.001$ for 25 °C).

DISCUSSION

In *R. japonica* populations on Mt Fuji, the seed weight of the upland seed populations was 1.5-fold heavier than that of the lowland seed populations (Fig. 1). The increase in seed weight with altitude may be related to an environmental gradient. In general the seed size affects the initial growth of seedlings (Black 1959). Shiosaka (1989) reported that the amount of storage substrates in *R. japonica* seeds directly reflected the leaf area of the developed cotyledons. The dependence of plant growth on the size of storage organs increases with the shortening of the growing season (Yokoi 1967). The richness of reserve substances in large seeds enhances the survival rate of plants growing in habitats where environmental resources affecting matter production are limited (Grime & Jeffrey 1965; Wulff 1986). The upland *R. japonica* plants on Mt Fuji have to survive under severe environments, dryness (Maruta 1976), poor nutrients (Hirose & Tateno 1984) and low temperature (short growing season). Consequently, the increase in seed weight may make a positive contribution to the survival of *R. japonica* seedlings in the upland habitat on Mt Fuji.

The intraspecific differences in the thermal responses of germination percentage are larger under low temperature rather than under high temperature conditions (Shibata 1981, 1985). In the case of *R. japonica* on Mt Fuji, lower temperatures depressed the germination percentage of the lowland populations, but did not affect that of the upland populations (Fig. 2). The differences in the thermal requirement between the lowland and upland populations become even larger below 10 °C: at 6 °C the upland seeds from altitudes above

1500 m on Mt Fuji show a high germination percentage of more than 50% (J. Suzuki, unpubl. data). This result is in accordance with the field observation by Masuzawa *et al.* (1991), who observed the germinated plants at the timberline on Mt Fuji in early spring, when the mean daily temperature is about 10 °C. The high-percentage germination under low temperatures leads to sufficient recruitment of seedlings and a resulting increase in the number of surviving seedlings (Symonides 1983a,b). The germination percentage, however, may not play a significant role in the colonization of *R. japonica* in the upland areas, because *R. japonica* plants that produce many seeds seem to be able to recruit a sufficient number of seedlings at the observed germination percentage.

A more important factor for colonization in the upland areas is germination speed (Sayers & Ward 1966; Washitani & Kabaya 1988). Alpine and subalpine plants initiate germination as soon as the thermal environment becomes favorable (Bliss 1985). In the present study, the upland populations exhibited a 2.5-fold higher germination speed than the lowland populations at 15/10 °C (Fig. 2). The ability to germinate in early spring compensates for the shortened growing season and it therefore guarantees the successful establishment of *R. japonica* seedlings in the upland areas on Mt Fuji. Furthermore the rapid germination, and also large seed size, allows the high-altitude seedlings to develop an adequate root system to withstand water stress during the drought period (July) after the rainy season on Mt Fuji (Maruta 1976).

Geographical variations in the morphological and physiological characteristics within a species have been reported in many species (McWilliams *et al.* 1968; Thomposon 1970; Baker 1972; Beppu & Takimoto 1981; Yamanishi & Fukunaga 1983). The present study, even if rough, attempted to compare the variations between the lowland populations on Mt Fuji and in Chiba which were distributed in horizontally-different, local regions, being about 120 km apart across Tokyo Bay. These populations would seem to be identical in both seed weight and germination traits, though this has not been statistically tested (Figs. 1 and 2). This can probably be attributed to the similarity of their growing environments. The mean annual temperatures (1951–78) in Sakura and on Mt Kiyosumi, where the two Chiba populations are located, are 14.7 °C and about 13.5 °C, respectively (Japan Meteorological Agency 1982). The mean annual temperatures are between 9.0 °C at Tarobo (1954–61, 1300 m in altitude) and 15.8 °C at Yoshiwara (1951–78, 60 m) on Mt Fuji (Fujiwara 1971; Japan Meteorological Agency 1982). The mean annual precipitations also are similar. In further investigations the authors intend to explore the morphological and physiological variations in *R. japonica* populations over a wider geographical range of distribution.

The current-year seedlings of *R. japonica* on Mt Fuji require a critical amount of annual carbon production to survive over the freezing period, and seedlings with a biomass below 10 mg could not survive the winter at altitudes of either 1400 or 2500 m (Maruta 1983). In addition, Maruta (1983) compared the relative growth rate (3 July to 5 September) of the current-year seedlings growing at 1400 and 2500 m altitude on Mt Fuji, and found no significant difference between them. These findings indicate the possibility that a growth strategy in response to thermal changes with altitude is necessary for the survival of *R. japonica* seedlings in mountainous areas in winter (Mooney 1963; Shiosaka 1989). Indeed, this possibility seems to be supported by the evidence that at the low temperature of 15 °C, seedlings grown from the upland seeds exhibited significantly larger plant biomass than those grown from the lowland seeds (Fig. 3). However, mean relative growth rate, or the slope of time course of plant biomass on a log scale, is almost similar for both seedlings. This implies that the difference in plant biomass at 15 °C is derived from the difference in initial seed weight. Such an effect of seed size disappears when plants experience a warmer environment.

The upland populations of *R. japonica* on Mt Fuji seem to adapt the developmental properties of their shoots to the upland-specific environment (Table 1). The windy environment in the upland areas restricts the altitudinal distribution of plants, especially trees (Rochow 1970; Meinzer *et al.* 1985). The upland seedlings of *R. japonica* produced a significantly larger number of branches with smaller and more numerous leaves than the lowland seedlings. The branching pattern can be functionally compared with the prostrate type of growth form observed in many alpine plants (Turesson 1925, 1930; Clausen *et al.* 1940). Moreover small leaves may be able to avoid damage from high wind velocity. Billings and Mooney (1968) reported that windswept ridges in the Arctic are often covered with small-leaved dwarf rosette plants, whose characteristics allow them not only to withstand winter cold and wind without a snow cover but also to tolerate the drought of summer. The characteristics of shoot development in the *R. japonica* populations on the uplands on Mt Fuji may be genetically fixed, because they persisted at both 15 and 25 °C.

The present study suggests that the *R. japonica* populations along an altitudinal gradient on Mt Fuji can be divided into two ecotypes whose distribution border lies at an altitude of about 1400–1500 m.

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REFERENCES

BAKER H. G. (1972) Seed weight in relation to environmental conditions in California. *Ecology* 53: 997–1010.

BEPPU T. & TAKIMOTO A. (1981) Growth of various ecotypes of *Lemna paucicostata* in Japan under various temperature conditions, and their wintering forms. *Bot. Mag. Tokyo* 94: 107–14.

BILLINGS W. D. & MOONEY H. A. (1968) The ecology of arctic and alpine plants. *Biol. Rev.* 43: 481–529.

BLACK J. N. (1959) Seed size in herbage legumes. *Herbage Abst.* 29: 235–41.

BLISS L. C. (1985) Alpine. In: *Physiological Ecology of North American Plant Communities* (ed. B. Chabot & H. A. Mooney) pp. 44–65. Chapman and Hall, New York.

CLAUSEN J., KECK D. D. & HIESEY W. M. (1940) Experimental studies on the nature of species. I. The effect of varied environments on western North American plants. *Carnegie Institution of Washington Publication* 520: 1–452.

FRIEND A. D., WOODWARD F. I. & SWITSUR V. R. (1989) Field measurements of photosynthesis, stomatal conductance, leaf nitrogen and d^{13}C along altitudinal gradients in Scotland. *Funct. Ecol.* 3 117–22.

FUJIWARA I. (1971) The climate and weather of Mt Fuji. In: *The Report of Comprehensive Scientific Investigation*, pp. 211–345. Fuji Kyuko, Tokyo (in Japanese with English summary).

GRIME J. P. & JEFFREY D. W. (1965) Seedling establishment in vertical gradients of sunlight. *J. Ecol.* 53: 621–42.

HIROSE T. & TATENO M. (1984) Soil nitrogen patterns induced by colonization of *Polygonum cuspidatum* on Mt Fuji. *Oecologia* 61: 218–23.

JAPAN METEOROLOGICAL AGENCY (1982) *The Monthly Normals of Temperature and Precipitation at Climatological Stations in Japan (1951-1978).* The Japan Meteorological Agency, Tokyo (in Japanese).

KÖRNER CH. & DIEMER M. (1987) *In situ* photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. *Funct. Ecol.* 1: 179–94.

MÄCHLER F. & NÖSBERGER J. (1977) Effect of light intensity and temperature on apparent photosynthesis of altitudinal ecotypes of *Trifolium repens* L. *Oecologia* 31: 73–8.

MARUTA E. (1976) Seedling establishment of *Polygonum cuspidatum* on Mt Fuji. *Jpn. J. Ecol.* 26: 101–5.

MARUTA E. (1983) Growth and survival of current-year seedlings of *Polygonum cuspidatum* at the upper distribution limit on Mt Fuji. *Oecologia* 60: 316–20.

MASUZAWA T. (1983) An ecological study of microclimate at timberline on Mt Fuji. II. Air temperature, relative humidity and light condition. *Rep. Fac. Sci. Shizuoka Univ.* 17: 91–9.

MASUZAWA T., NISHITANI S., SUZUKI J., KIBE T. & AIHARA E. (1991) Seasonal changes in the soil temperature over a three-year period at the timberline on Mt Fuji. *Rep. Fac. Sci. Shizuoka Univ.* 25: 69–78.

MCNAUGHTON S. J., CAMPBELL R. S., FREYER R. A., MYLROIE J. E. & RODLAND K. D. (1974) Photosynthetic properties and root chilling responses of altitudinal ecotypes of *Typha latifolia* L. *Ecology* 55: 168–72.

MCWILLIAMS E. L., LANDERS R. Q. & MAHLSTEDE J. P. (1968) Variation in seed weight and germination in populations of *Amaranthus retroflexus* L. *Ecology* 49: 290–96.

MEINZER F. C., GOLDSTEIN G. H. & RUNDEL P. W. (1985) Morphological changes along an altitude gradient and their consequences for an Andean giant rosette plant. *Oecologia* 65: 278–83.

MOONEY H. A. (1963) Physiological ecology of coastal, subalpine, and alpine populations of *Polygonum bistortoides*. *Ecology* 44: 812–16.

OULTON K., WILLIAMS G. J. III & MAY D. S. (1979) Ribulose-1,5-bisphosphate carboxylase from altitudinal populations of *Taraxacum officinale*. *Photosynthetica* 13: 15–20.

ROCHOW T. F. (1970) Ecological investigations of *Thlaspi alpestre* L. along an elevational gradient in the central Rocky Mountains. *Ecology* 51: 649–56.

SATAKE Y., OHWI J., KITAMURA S., WATARI S. & TOMINARI T. (1982) *Wild Flowers of Japan. Herbaceous Plants II.* Heibonsha, Tokyo (in Japanese).

SAYERS R. L. & WARD R. T. (1966) Germination responses in alpine species. *Bot. Gaz.* 127: 11–16.

SHIBATA O. (1981) Physiological and ecological studies in environmental adaptation of plants. I. Germination behavior of weed seeds collected from different altitudes. *J. Fac. Sci. Shinshu Univ.* 16: 97–106.

SHIBATA O. (1985) *Altitudinal Botany.* Uchida Rokakuho Publishing, Tokyo (in Japanese).

SHIBATA O. & ARAI T. (1970) Seed germination in *Polygonum reynoutria* Makino grown at different altitudes. *Jpn. J. Ecol.* 20: 9–13 (in Japanese with English summary).

SHIOSAKA H. (1989) Species biology of *Polygonum cuspidatum* from different altitudinal habitats. MSc thesis Shinshu University (in Japanese).

SYMONIDES E. (1983a) Population size regulation as a result of intra-population interactions. II. Effect of density on the survival of individuals of *Erophila verna* (L.) C.A.M. *Ekol. Polska* 31: 839–81.

SYMONIDES E. (1983b) Population size regulation as a result of intra-population interactions. III. Effect of density on the growth rate, morphological diversity and fecundity of *Erophila verna* (L.) C.A.M. individuals. *Ekol. Polska* 31: 883–912.

THOMPSON P. A. (1970) Characterization of the germination response to temperature of species and ecotypes. *Nature* 225: 827–31.

TURESSON G. (1925) The plant species in relation to habitat and climate. *Hereditas* 6: 147–236.

TURESSON G. (1930) The selective effect of climate upon the plant species. *Hereditas* 14: 99–152.

WASHITANI I. & KABAYA H. (1988) Germination responses to temperature responsible for the seedling emergence seasonality of *Primura siebolidii* E. Morren in its natural habitat. *Ecol. Res.* 3: 9–20.

WOODWARD F. I. (1975) The climatic control of the altitudinal distribution of *Sedum rosea* (L.). Scop. and *S. telephium* L. II. The analysis of plant growth in controlled environments. *New Phytol.* 74: 335–48.

WOODWARD F. I. & PIGOTT C. D. (1975) The climatic control of the altitudinal distributions of *Sedum rosea* (L.) Scop. and *S. telephium* L. I. Field observations. *New Phytol.* 74: 323–34.

WULFF R. D. (1986) Seed size variation in *Desmodium paniculatum* II. Effects on seedling growth and physiological performance. *J. Ecol.* 74: 99–114.

YAMANISHI H. & FUKUNAGA N. (1983) Ecotypic differentiation of *Plantago asiatica* L. in Japan islands. *Jpn. J. Ecol.* 33: 473–80.

YOKOI Y. (1967) Ecological consideration on the transformation of matter in higher plants—Especially on the seedling formation from reserve substances. *Biol. Sci.* (Tokyo) 18: 148–54 (in Japanese with English summary).