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Leaf phenology, seasonal changes in leaf quality and herbivory pattern of *Sanguisorba tenuifolia* at different altitudes

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Abstract Leaf demography, seasonal changes in leaf quality and leaf-beetle herbivory of a herbaceous perennial plant, *Sanguisorba tenuifolia*, were compared between low- and high-elevation sites. Leaf nitrogen concentration was higher and leaf mass per area (LMA) was lower at the higher site than at the lower one. At the lower site, with a long growth period, plants produced many leaf cohorts and leaves emerged throughout the growing season. At the higher site, with a short growth period, however, leaf emergence was concentrated early in the growing season. The improvement of leaf quality and acceleration of leaf emergence at higher altitude are seen as adaptations to a short growing season. Results of a feeding trial suggested that leaf quality for the leaf-beetle *Galerucella grisescens* was higher at the higher site, but plants at the higher site showed less damage. Oviposition of *G. grisescens* was seasonal and unimodal at both altitudes, but the period of oviposition was shorter and its density lower at the higher site. The low temperature and short growth period at the higher site appear to reduce the activity of the leaf-beetles, resulting in a decrease in damage by herbivory, despite better leaf quality.

Key words Altitude · Phenology · Herbivory · Leaf quality · Oviposition

Introduction

Altitudinal change is accompanied by changes in temperature conditions. The length of the annual growing season for organisms decreases with elevation, and this is conspicuous in temperate and sub-arctic regions. Because sexually reproducing plants have to complete their life-cycles (leaf emergence, flowering and fruiting) rapidly when the growth period is short, leaf phenology at higher altitudes would be expected to differ from that at lower altitudes even within the same species (e.g. Kudo 1995). Diemer et al. (1992) found that forbs and grasses produced several leaf cohorts within a growth period at low altitudes, while most alpine species produced only one cohort. Thus plant leaf emergence patterns are expected to change according to differences in habitat.

Properties of individual leaves such as longevity, leaf mass per area (LMA), stomatal conductance, nitrogen content and photosynthetic activity also change along an altitudinal gradient (Woodward 1983, 1986; Körner et al. 1986, 1989; Friend et al. 1989; Diemer et al. 1992; Williams and Black 1993; Kudo 1996a; Sparks and Ehleringer 1997). Because plant growth and productivity are affected not only by physical environmental factors but also by biological factors such as herbivory (Louda 1984), changes in leaf traits may cause different relationships between plants and insects along an altitudinal gradient. Short photosynthetic period and low temperature at high altitudes result in lower productivity of plants. Thus, the defensive ability of plants may decrease with elevation, and leaf loss by herbivory might cause serious damage to plant growth at higher altitudes.

Temperature is the most important environmental factor affecting insect life-cycles (growth, reproduction, dormancy and migration). Insect life-cycle traits have evolved in response to seasonal temperature patterns in different habitats (Dingle 1986; Tauber et al. 1986). Decrease in temperature with elevation elongates the developmental period of insects, and also restricts their pre-mature period (Sota 1986) because the length of the growing season decreases with elevation. In addition, delay in snow-melt causes a delay in the emergence time of insects at high altitudes (Dingle et al. 1990). Changes in activity and life-cycle of herbivorous insects along an altitudinal gradient may cause different effects on host plants.

To understand plant-herbivore interactions under different conditions, therefore, it is important to know

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how each plant and insect respond to environmental factors specific to each habitat. In this study, I compare leaf demography, phenology and individual leaf traits of a plant species, and seasonal patterns of herbivory and oviposition of a herbivorous insect, at different altitudes, then evaluate leaf quality as a food resource for insects at both sites. Finally I discuss the effect of a change in temperature and growth period with altitude on the plant-herbivore interaction.

Materials and methods

Study sites

Study sites were the Orochigahara mire (42°62′N, 141°40′E; 980 m above sea level, a.s.l.) as a high-altitude site and the Utonai mire (42°42′N, 141°41′E; 4 m a.s.l.) as a low-altitude site, in the central part of Hokkaido, northern Japan. The Orochigahara mire (hereafter the higher site) is a high-altitude moor located on the eastern side of Mt. Muine (peak 1461 m a.s.l.) and has established on a flat bed of volcanic ejecta (Tachibana et al. 1980). This mire is dominated by *Sphagnum* spp. and surrounded by a thicket of *Picea glehnii* Masters. Snow covers the ground from late October to May. *Sanguisorba tenuifolia* Fisch. predominated, and *Rhynchospora yasudana* Makino, *Carex omiana* Franch. et Savat., *C. michauxiana* Bökir. var. *asiatica* (Hult.) Ohwi, and *Geum pentapetalum* (Linn.) Makino were common. The higher site was never flooded during the growing season. The Utonai mire (hereafter the lower site) is a low-altitude moor that has developed on the Holocene tephras of Mt. Tarumae. *Rhynchospora alba* (Linn.) Vahl, *Phragmites australis* Trin and *Carex thunbergii* Steud. var. *appendiculata* (Trautv.) Ohwi predominated. The level of the water table usually fluctuated 6.5–21.0 cm below the ground surface, but the ground was sometimes flooded in September at the lower site. The total nitrogen content (organic plus inorganic matter) of peat was significantly higher at the lower site (2.51 ± 0.16%; mean ± SD) than the higher site (1.42 ± 0.44%) ($P < 0.001$; Mann-Whitney *U*-test). Air temperatures 30 cm above the soil surface were measured at 1-h intervals with automatic recording thermometers and thermistor sensors (KADEC-U, Kona System Co. Ltd., Sapporo) during the growing season at both sites in 1996. Daily mean air temperature through the growing season (mid-May to mid-October) was 16.4°C at the lower site, while that (mid-June to September) was 14.7°C at the higher site.

Plant material and herbivorous insects

Sanguisorba tenuifolia Fisch. (Rosaceae) is a herbaceous perennial plant, which is distributed in wet places in eastern Siberia and northeastern Asia (Ohwi and Kitagawa 1983). First shoot emergence starts in late spring, flowering begins in mid-August, and seed dispersal occurs around mid-September. Each adult shoot is composed of several radical leaves in a rosette. The radical leaves are imparipinnately compound and consist of 3–19 leaflets. The height of flower stalks is 100–160 cm at the lower site, and 60–120 cm at the higher site. There are some leaves on the flower stalk, but they are much smaller than radical leaves and shoots do not always have flower stalks. Therefore, only the properties of radical leaves were investigated in this study.

The main herbivorous insects on *S. tenuifolia* are leaf-beetles, *Galerucella grisescens* (Joannis) (Coleoptera: Chrysomelidae) which is distributed in China, Korea, Sakhalin, Siberia, Mongolia, Europe and Japan. This leaf-beetles oviposits egg masses on the abaxial side of leaves, pupates on leaves and overwinters as adults (Kimoto and Takizawa 1994). Both larvae and adults feed on leaves of *S. tenuifolia*.

Plants

Open places without any shading effects were selected for measurements at both sites. Three 0.5 × 0.5 m and three 1 × 1 m quadrats were set up at the beginning of the growing season in 1994 at the higher and the lower sites, respectively, differing in size because radical leaf density was higher at the higher site than at the lower site.

All shoots within each quadrat were identified by sticky markers. To obtain demographic records of radical leaves, times of leaf emergence and senescence were recorded at intervals of about 10 days during the first month, then at intervals of about 15 days in 1994, and at about a 10-day interval throughout the season in 1995. Basal diameters of petioles and lengths of mature radical leaves were measured for every shoot in each quadrat 1 month after leaf emergence. Leaf life-span and shoot properties were measured for radical leaves which had more than five leaflets because current seedlings have three leaflets and their mortalities were high.

At each census, about 100 newly emerged radical leaves were marked around the quadrats at both sites in 1995 as samples for measurement of leaf properties. They were referred to as 1st, 2nd, . . ., 10th cohort, respectively. Six radical leaves were taken from each cohort at about a 10-day interval. Sampling was conducted until all leaves were senescent for each cohort. For each leaf sampled, leaf area and dry weight (after 48 h at 70°C) were measured using a scanner connected to a personal computer (NIH Image ver. 1.49 software) and an electronic balance (R200D, Sartorius Co. Ltd., Tokyo), andLMA was calculated. Leaves were pooled and ground, and total nitrogen content was analysed by using a C-N analyzer (MT-1600, Yanaco Co. Ltd., Tokyo). Because expansion of radical leaves was almost complete within 1 month of emergence at both sites, maximum N content per unit leaf area was obtained for leaves over 1 month old. Resorption of leaf nitrogen was calculated as the difference between maximum and minimum nitrogen contents per unit leaf area.

Because there were significant correlations between the product of squared petiole diameter and leaf length and leaf dry weight ($r^2 = 0.673$, $P < 0.01$, $n = 150$ at the higher site; $r^2 = 0.680$, $P < 0.01$, $n = 350$ at the lower site), dry weight of radical leaves was estimated within quadrats by using these relationships, then total leaf mass per shoot was estimated.

Foliage period and leaf turnover per shoot were defined as the period from the emergence of the first leaf to the senescence of all leaves, and the ratio of the foliage period to the arithmetic mean life-span of individual leaves of a shoot, respectively. In total, 209 and 84 shoots were measured within a quadrat in 1994, and 197 and 104 shoots in 1995, at the higher and the lower sites, respectively.

Insects

Oviposition period and egg density of *G. grisescens* were measured in eight quadrats (1 × 1 m at the higher site, 3 × 3 m at the lower site) at each site, and the numbers of radical leaves and eggs of *G. grisescens* on leaves were counted at 1-week intervals in 1996.

Herbivory on radical leaves was investigated within the quadrats during each census in 1995. The degree of herbivory was classified into 11 levels based on loss area of radical leaf (A: none, B: 1–10, C: 11–20, . . ., K: 91–100% leaf loss).

Effects of leaf quality on growth of the leaf-beetles were compared between altitudes. Egg masses laid on *S. tenuifolia* leaves were sampled from the higher site 3 weeks after first leaf emergence. Larvae that hatched on the same day were reared individually in a plastic case with a wet filter paper in the laboratory at room temperature (*c.* 25°C). Each 50 larvae were fed 3-week-old *S. tenuifolia* leaves sampled from the higher and the lower site, because leaf quality, indicated by nitrogen concentration and LMA, tended to be stable about 3 weeks after leaf emergence. It was impossible to use insects from the lower site because there were very few eggs at the lower site at the time of sampling. Emergences were recorded every day, then adult weights were measured by an electronic balance (R200D, Sartorius Co. Ltd., Tokyo). The Mann-Whitney *U*-test was used to compare developmental periods from hatching to emergence and adult weights, and the *G*-test was used for survival rate from hatching to emergence.

Results

The plants

First leaf emergence occurred in mid-June at the higher site and in mid-May at the lower site in both 1994 and 1995 (Fig. 1). The foliage periods of *S. tenuifolia*, from the emergence of the first radical leaf to the senescence of all leaves, were 120 days in 1994 and 102 days in 1995 at the higher site, and 168 days and 175 days at the lower site, respectively. Recruitment of new leaves stopped about 40 days after the first emergence at the higher site, while it lasted around 110 days at the lower site. In total, four and ten cohorts of radical leaves appeared throughout the season at the higher and the lower site, respectively. Actual leaf number increased from the beginning of the growing season and attained a maximum around 1 month after first emergence at both sites in 1994 and 1995. At that time, it reached about 90% of total leaves produced during the season at the higher site, and at most 75% at the lower site. Leaf senescence occurred frequently in the middle of the season (July to early August) at the lower site, while it was concentrated at the end of growing season (late August to September) at the higher site.

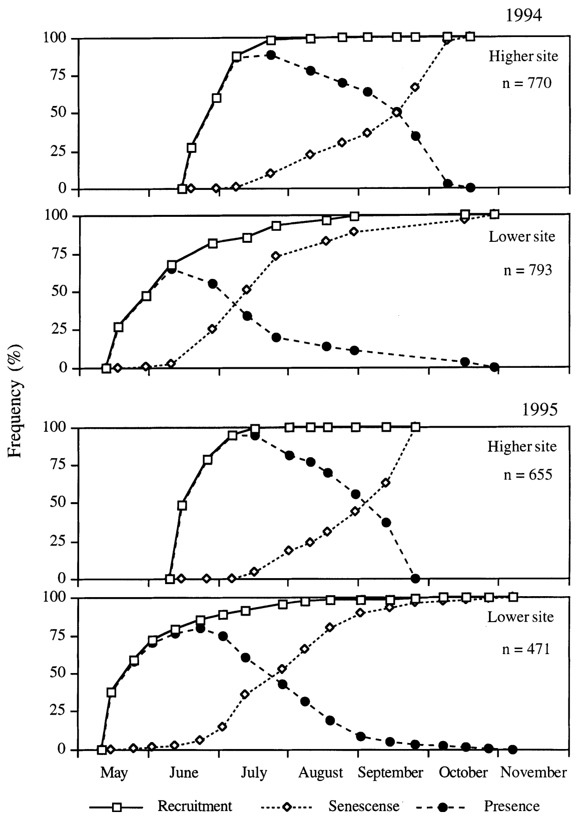
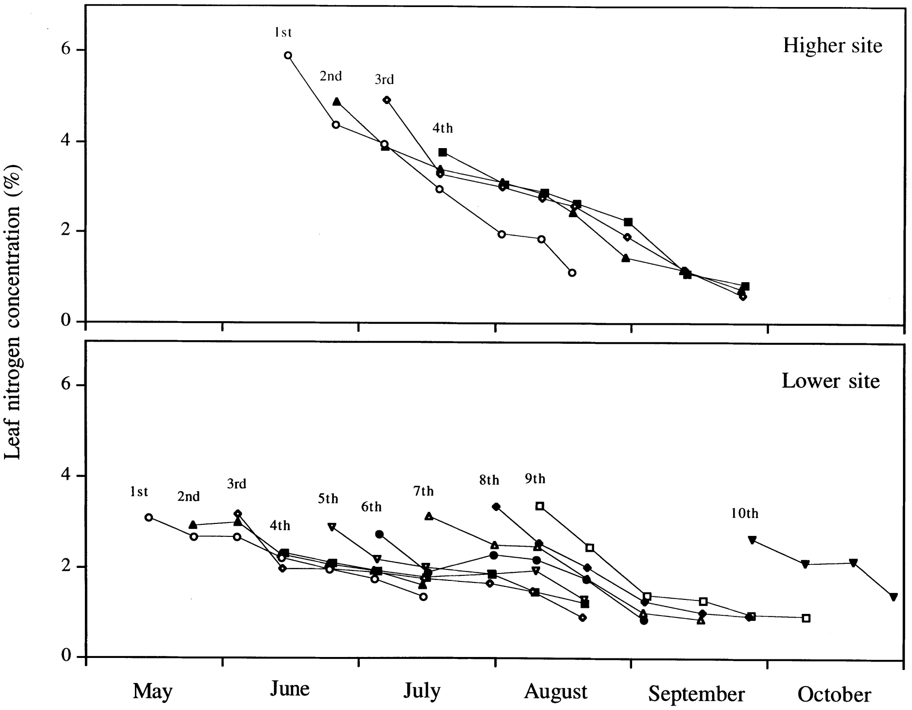


Fig. 1. Demographies of radical leaves at the higher and lower sites in 1994 and 1995. Recruitment and senescence of leaves are shown as cumulative percentages (*n* total number of radical leaves observed through a season)

Leaf nitrogen concentration was highest just after the leaf emergence within each cohort and decreased with age at both sites (Fig. 2). Reabsorption of leaf nitrogen was therefore higher at the higher site than that at the lower site (Table 1). LMA of the first leaf cohort was relatively stable through the foliage period, but that of other cohorts increased with leaf age at both sites (Fig. 3). The times of individual leaf cohorts lasted relative to the total length of the foliage period were 0.63, 0.89, 0.78, and 0.67 and 0.35, 0.30, 0.45, 0.39, 0.33, 0.34, 0.35, 0.33, 0.34, and 0.18 at the higher and the lower sites, respectively. Mean leaf N concentration of the first to third cohorts at the higher site (2.76 ± 1.42, $n = 144$) was higher than that of first to seventh cohorts at the lower site (2.00 ± 0.64, $n = 276$, $P < 0.0001$; Mann-Whitney *U*-test), and the mean LMA of the first to third cohorts at the higher site (5.08 ± 1.05, $n = 144$) was lower than that of first to seventh cohorts at the lower site (8.15 ± 1.46, $n = 276$, $P < 0.0001$; Mann-Whitney *U*-test). These cohorts (first to third and first to seventh, at the higher and the lower sites, respectively) accounted for more than 90% of total leaf recruitment at each site (Fig. 1).

Foliage period per shoot increased with shoot mass at the lower site, whereas an increase in foliage period terminated at about 100 days at the higher site (Fig. 4a). Radical leaf turnover per shoot increased with shoot mass at the lower site in both years (Fig. 4b). There was no significant relationship between leaf turnover and plant size at the higher site in 1994. There was a significant difference in the number of radical leaves per shoot between the higher (2.9 ± 1.1) and the lower (3.4 ± 1.4, $P < 0.01$; Mann-Whitney *U*-test) sites in 1994, but no difference in 1995 (2.7 ± 1.1 and 2.6 ± 1.2 at the higher and lower sites, respectively). Life-span of individual leaves was significantly longer at the higher site (80 ± 21 and 68 ± 20 days in 1994 and 1995, respectively) than at the lower site (50 ± 15 and 65 ± 19 days; $P < 0.001$, Mann-Whitney *U*-test). At the lower site, the leaf life-span of the first five cohorts (68 ± 18 days) was significantly longer ($P < 0.001$, Mann-Whitney *U*-test) than that of the later five cohorts (49 ± 15 days) which were produced after early July. These results indicate that plants at the higher site have rather stable foliage period irrespective of individual plant size, and produce leaves during a short time at the beginning of the growing season which are retained throughout the season (i.e. flush type), whereas plants at the lower site flexibly change the foliage period in accordance with plant size: larger plants extend the foliage period by producing several leaf cohorts and exchanging them (i.e. successive type).

Fig. 2 Seasonal changes in nitrogen concentration of each radical leaf cohort at the higher and lower sites in 1995. Many plants produced 4 leaf cohorts at the higher site, and 10 cohorts at the lower site during a season. Each point is the mean of six samples



The insects

G. grisescens was the only herbivorous insect observed to oviposit on leaves of *S. tenuifolia*, at both sites. Oviposition was observed from late May to mid July (about 6 weeks) at the lower site and from early to late June (about 3 weeks) at the higher site (Fig. 5). The total numbers of eggs throughout the oviposition period were counted at both sites. Next, the average numbers of radical leaves during the oviposition period were counted at a census in the eight quadrats. The density of eggs per radical leaf thus calculated was 3.51 and 0.77 at the lower and the higher sites, respectively. The growing period of *S. tenuifolia* was 172 and 111 days (average of 1994 and 1995) at the lower and the higher sites, respectively. Thus the densities of eggs per radical leaf per day were 0.0205 and 0.0069 at the lower and the higher sites, respectively. This indicates that the density of herbivores was higher at the lower site than at the higher site. The oviposition pattern was unimodal at both sites, indicating that both populations of this species had one generation per growing season. The number of eggs per egg mass was significantly smaller at the higher site (15.2 ± 5.5) than at the lower site (16.8 ± 5.8, $P < 0.01$; Mann-Whitney *U*-test).

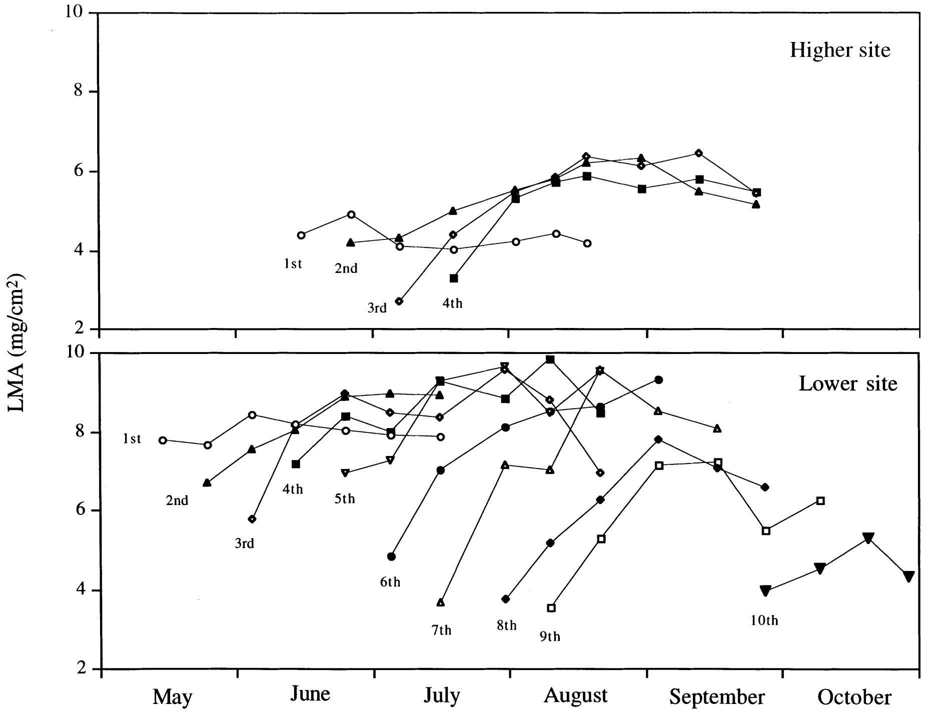
Table 1 Reabsorption of nitrogen for each leaf cohort. Reabsorption was calculated as the percentage difference between maximum and minimum nitrogen contents per unit leaf area (mg cm^{-2})

Cohort	Reabsorption (%)	
	Lower site	Higher site
1st	51.8	70.3
2nd	22.3	77.2
3rd	63.3	80.1
4th	35.8	72.2
5th	31.6	–
6th	56.7	–
7th	58.7	–
8th	50.4	–
9th	47.3	–
10th	43.3	–

Although leaf damage of *S. tenuifolia* by the leaf-beetles increased from the beginning to the middle of season at both sites, the degree of damage was much lower at the higher site than that at the lower site (Fig. 6). At the lower site, leaf damage was intensive in July when one-third of plants lost more than 30% of leaf area by herbivory. Herbivorous damage decreased after early August at the lower site because of a decline in defoliation by the leaf-beetles, senescence of old leaves, and recruitment of new leaves.

In the feeding experiment, the developmental period of the leaf-beetles from hatching to emergence fed on leaves from the higher site was significantly shorter ($P < 0.01$, Mann-Whitney *U*-test) than those fed on leaves from the lower site (Fig. 7a). There was no significant difference in survival rate from hatching to emergence between leaf-beetles fed on leaves from the higher and lower sites ($P > 0.05$, *G*-test; Fig. 7b). Adults that ate leaves from the higher site were significantly heavier (4.5 ± 0.9 mg) than those that ate leaves from the lower site (3.6 ± 0.6 mg; $P < 0.01$, Mann-Whitney *U*-test; Fig. 7c). Thus leaves from the higher

Fig. 3 Seasonal changes in leaf mass per area (LMA) of each radical leaf cohort at the higher and lower sites in 1995. For details see Fig. 2

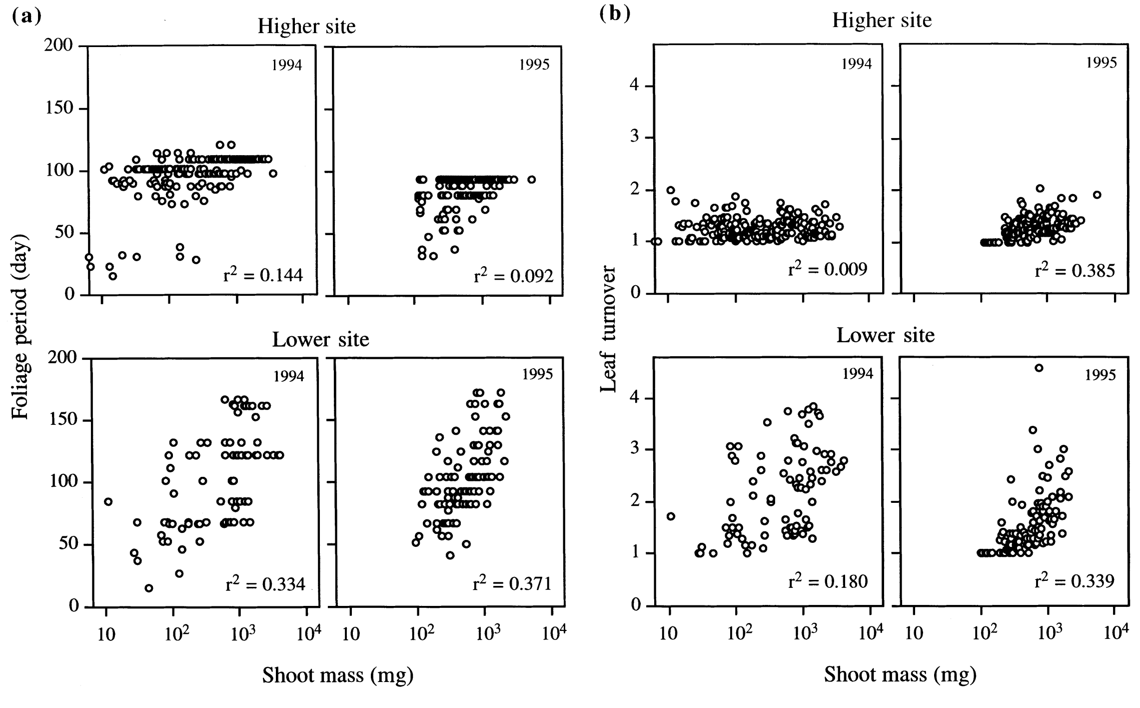


site, with high nitrogen concentrations, were a more suitable resource at least for the leaf-beetles at the higher site, although a feeding experiment on insects from the lower site was not conducted in this study.

Discussion

Leaf quality of *S. tenuifolia* differed between altitudes: plants at the higher site had leaves with higher nitrogen contents and lower LMA than plants at the lower site. Some previous studies have shown that leaf nitrogen concentration and/or photosynthetic rates of deciduous plants tend to increase at high altitudes among and within species (Körner et al. 1986; Körner 1989; Friend

Fig. 4 a Relationships between the estimated shoot mass and foliage period per shoot, and **b** radical leaf turnover per shoot at the higher and lower sites in 1994 and 1995 (r^2 coefficient of determination)



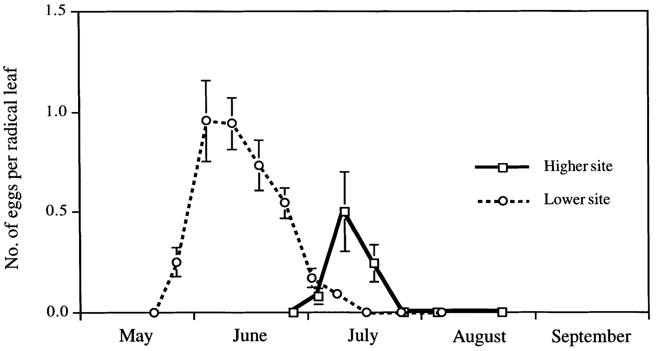


Fig. 5 Seasonal changes in egg density of *Galerucella grisescens* per radical leaf at the higher and the lower site in 1996. Means ± SE of eight quadrats are shown

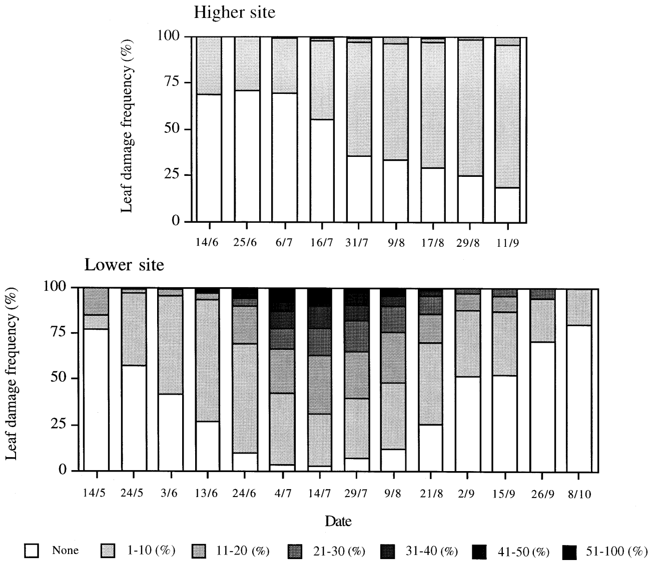


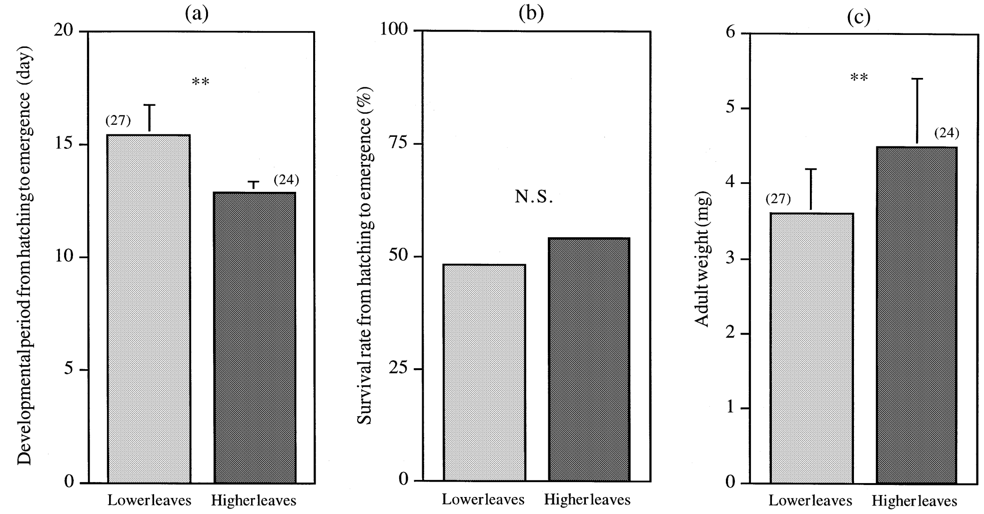
Fig. 6 Grazing damage to radical leaves by herbivores at each census time. Frequencies represent the ratio of the number of radical leaves for each degree of grazing damage to the number of radical leaves present within quadrats at each census time at the higher and lower sites in 1995

et al. 1989; Kudo 1996a). It has also been reported that LMA of some deciduous species decreased with elevation, accompanied by decreases in the foliage period of plants (Kudo 1996a; but see also Körner 1989). The increase in leaf nitrogen and decrease in LMA may help to maintain positive photosynthetic carbon gain when the growth period is short (Kudo 1996a), because the length of the growing season at the higher site was 2 months shorter than at the lower site. In spite of high initial nitrogen investment, final leaf nitrogen was lower and reabsorption of leaf nitrogen was higher at the higher site. This may be a mechanism to utilize nitrogen effectively under conditions of low nutrient availability (Pugnaire and Chapin 1993).

It is notable that in *S. tenuifolia* there are differences not only in individual leaf traits but also in the leaf emergence pattern of shoots between the altitudes. Foliage period per shoot of *S. tenuifolia* increased with shoot mass at the lower site, whereas the period of foliage extension stopped at around 100 days at the higher site (Fig. 4a) because of the limitation of the growth period. The ratio of average leaf life-span to the foliage period was 0.29 in 1994 and 0.37 in 1995 at the lower site. At the higher site, however, it was 0.66 and 0.67, respectively. When the growth period is short, the flush emergence habit is considered to be advantageous in order to utilize the entire growing period effectively (Kikuzawa 1995).

Decrease in air temperature with elevation influenced the activity and phenology of insects. The oviposition period of the leaf-beetles (*G. grisescens*) at the higher site was shorter than at the lower site (Fig. 5). Overwintered leaf-beetles appeared 1 month later at the higher site than at the lower site due to late leaf emergence caused by late snow disappearance. Thus, not only lower temperature but also delay of snow-melt time affected phenology of the leaf-beetles at higher altitude. A similar phenomenon has been observed in a grasshopper, *Melanoplus sanguinipes*, which appeared later at a high altitude because of later snow-melt time (Dingle et al.

Fig. 7 a Developmental period, **b** survival rate from hatching to emergence, and **c** adult weight of *Galerucella grisescens* fed on leaves sampled from the higher and lower sites at room temperature (**$P < 0.01$, Mann-Whitney *U*-test; *N.S.* not significant, *G*-test). *Sample sizes* are shown in parentheses (*vertical bars* SD)



1990). Because lower temperature makes developmental period of this leaf-beetle longer (Toda and Yano 1993) and it has to overwinter as an adult, oviposition is limited to a shorter period at the beginning of growing season at the higher site (Fig. 1).

Leaf nitrogen is an important factor determining food quality for herbivorous insects. It has been shown that feeding on high-nitrogen leaves resulted in higher rates of development (Mattson 1980; McClure 1980; Scriber and Slansky 1981; Karowe and Martin 1989), high production of progeny (McClure 1980), and high survival of nymphs (McClure 1980) or larvae (Karowe and Martin 1989). Although production of high-nitrogen leaves is important to achieve high photosynthetic rates (Field and Mooney 1986; Reich et al. 1992), leaf nitrogen concentration may be negatively correlated with LMA or leaf toughness (Coley 1983; Reich et al. 1992) especially in deciduous plants. Generally leaf nitrogen concentration decreases (Mattson 1980; Schroeder and Malmer 1980; Scriber and Slansky 1981; Schultz et al. 1982; Coley 1983; Jonasson 1989; Mauffette and Oechel 1989; Hunter and Lechowicz 1992; Kudo 1996b), and cellulose content (Coley 1983; Mauffette and Oechel 1989), leaf toughness (Schultz et al. 1982; Coley 1983) and LMA (Gratani 1996; Kudo 1996b) increase with leaf age. Thus it is considered that as the physical strength of leaves increases, leaf quality as foods for herbivores decreases with leaf age. It is known that *Bemisia argentifolii* (Homoptera: Aleyrodidae) can discriminate leaf age and lays eggs on young leaves with high nitrogen concentrations (Bentz et al. 1995). Under the same temperature conditions, the larvae of *G. grisescens* fed on leaves from the higher site grew faster (Fig. 7a) and were heavier as adults than those fed leaves from the lower site (Fig. 7b). This result partly supports the idea that the leaf quality at the higher site is better for the leaf-beetles, although it is possible that production of secondary nitrogen compounds to prevent herbivorous damage results in the higher leaf nitrogen concentration at higher site, and that the leaf beetles evolve adaptations to the plants, that is "coevolve" (Futuyma 1983). Although production of low-LMA and high-nitrogen leaves should lower leaf defensive ability, herbivore pressure remained at low levels at the higher site, due to lower temperature and shorter growing season. Thus plants with low defensive ability at the higher site could be free from serious damage by the leaf-beetles.

In summary, the phenology, quality and quantity of leaves vary widely within and among habitats throughout a season even within the same species. The variation observed between different altitudes was a result of responses of plants to changes in growing season length, and temperature directly affects the activity and life-cycles of herbivorous insects. This study has demonstrated that production of leaves of high quality for herbivores did not always result in high herbivory attack. Plant-herbivore interaction varies along this environmental gradient.

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