

# Shoot Characteristics Affect Oviposition Preference of the Willow Spittlebug *Aphrophora pectoralis* (Homoptera: Aphrophoridae)

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**ABSTRACT** The relationships of shoot abscission, shoot toughness, and egg parasitism with shoot length were investigated in relation to oviposition preference by the willow spittlebug *Aphrophora pectoralis* Matsumura on *Salix miyabeana*, *S. sachalinensis*, and *S. integra*. Spittlebugs strongly preferred shoots >20 cm long even though this size class was a small proportion of all shoots. Oviposition increased with shoot length up to 40 cm but leveled off, or even decreased, on longer shoots. Shoot abscission rate decreased and toughness increased with increasing shoot length, but egg parasitism was not affected. Spittlebug oviposition preference is therefore likely to be affected by shoot abscission and shoot toughness.

**KEY WORDS** *Salix* species, shoot abscission, shoot toughness, egg parasitism, xylem sucker

OVIPOSITION PREFERENCE IS FUNDAMENTAL to understanding herbivore population dynamics (Ohgushi 1992, Price et al. 1995) and host plant selection (Thompson and Pellmyr 1991, Mayhew 1997). The patterns of herbivore attack on host plants have been explained by plant traits (e.g., age, growth rate, genotypes, resource quality, and chemical compounds) (Tahvanainen et al. 1985, Price et al. 1987a, Brodbeck et al. 1990, Woods et al. 1996, Craig et al. 1999, Dorn et al. 2001).

Recently, Price (1991) proposed the plant vigor hypothesis that herbivorous insects attack vigorous plants or plant modules more frequently than slower growing plants or plant modules. Many studies testing the plant vigor hypothesis have focused on galling insects (Price et al. 1995, Price et al. 1997). For example, the galling sawfly *Euura mucronata* Hartig exhibited a strong oviposition preference for longer, more vigorous shoots on which larval survival was high due to high food quality in rapidly growing shoots (Price et al. 1987b). However, little attention has been given to other herbivorous insects.

The spittlebug *Aphrophora pectoralis* Matsumura is a xylem-sucking insect uses *Salix* species as host plants (Komatsu 1997). Craig and Ohgushi (2002) demonstrated that ovipositing females of this species have a strong preference for long shoots and that oviposition preference is correlated with larval survival. These results suggest that larval survival is an important factor in determining oviposition preference of the spittlebug. However, the question of what plant traits determine the oviposition preference for long shoots remains unresolved. Willow shoots often drop off a

tree during winter. Because *A. pectoralis* eggs overwinter inside shoots, shoot abscission results in egg death. Spittlebug nymphs of *A. pectoralis* penetrate shoots with their stylets to feed, and feeding sites are restricted by stem tissue hardness in the spittlebug *Philaenus spumarius* L. (Hoffman and McEvoy 1986, McEvoy 1986). Therefore, shoot abscission and toughness may have significant roles in determining the oviposition preference for long shoots.

Natural enemies are another important factor determining oviposition preference of herbivorous insects (enemy-free space hypothesis, see Thompson 1988). For example, the mistletoe butterfly *Ogyris amaryllis* Hewitson has an oviposition preference for plants of the genus *Amyema* tended by ants, even though the plants are low quality for larvae (Atsatt 1981). This preference apparently evolved because the presence of ants on the plants decreases egg parasitism by a parasitoid, *Centrodora* sp. Although two egg parasitoids of the family Aphelinidae and Mymaridae were found in *A. pectoralis* (Craig and Ohgushi 2002), the effects of egg parasitism on oviposition preference have not been investigated.

The purpose of this study was to determine the effects of shoot toughness, shoot abscission, and egg parasitism on oviposition preference for long shoots in *A. pectoralis*. We investigated the relationship between shoot length and proportion of shoots in which spittlebug oviposition occurred, the effects of shoot length on shoot abscission and shoot toughness, and the relationship between shoot length and rate of egg parasitism.

## Materials and Methods

**Study Site.** The study site was located on a bank of the Ishikari River in Hokkaido, northern Japan (43°

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11', N, 141° 24', E) that has been disturbed by dyke building. Around the study area, six willow species, *S. miyabeana* Seemen, *S. sachalinensis* Fr. Schm., *S. integra* Thunb., *S. hultenii* Floderus, *S. subfragilis* Anders., and *S. pet-susu* Kimura, occur sympatrically (Ishihara et al. 1999). Our study included three of these: *S. miyabeana*, *S. sachalinensis*, and *S. integra*, all of which were abundant at the study site.

These three species of willows are widely distributed in Hokkaido and are dioecious, deciduous trees often occurring on riverbanks. *S. miyabeana* grows up to 7 m, *S. sachalinensis* up to 15 m, and *S. integra* up to 1.5 m and in Ishikari flower from mid-April to early May. After flowering, budbreak occurs in May, and leaf expansion and shoot elongation continue until mid-July. Most leaves become senescent by late October when new buds appear in leaf axils.

**Insect Life Cycle.** The spittlebug *A. pectoralis* is a xylem-sucking insect that utilizes Salicaceae as host plants (Komatsu 1997). It has a univoltine life cycle and overwinters in the egg stage. Overwintered eggs begin to hatch in early May, and nymphs produce spittle in which they live and feed. Adults begin to emerge in late June. Mating and oviposition occur from early August to mid-October. Females lay egg masses ( $\approx 10$  eggs per mass) inside the apex of current-year growing shoots. The apical region of the shoots, within which generally oviposition occurs, die within a week because of mechanical damage by the female's ovipositor.

In this study, we counted each oviposition scar as an egg mass. Although we did not compare the number of eggs per egg mass among three willow species, no significant difference was found in the length of oviposition scars (mm) (*S. miyabeana*:  $3.66 \pm 0.07$  [mean  $\pm$  SE],  $n = 40$ ; *S. sachalinensis*:  $3.57 \pm 0.06$ ,  $n = 40$ ; *S. integra*:  $3.67 \pm 0.06$ ,  $n = 40$ ; Kruskal-Wallis test;  $df = 2$ ,  $H = 1.1$ ,  $P = 0.59$ ). The number of eggs was highly correlated with the length of oviposition scars (Nozawa and Ohgushi 2002). This suggests that there was no difference in the number of eggs per egg mass among three willow species.

**Measurement of Shoot Characteristics.** In early May 1998, we randomly selected 117 shoots (1 yr old) from *S. miyabeana*, 107 from *S. sachalinensis*, and 96 from *S. integra*. In early September 1998, we measured the length of all current-year shoots on the selected one-year old shoots. In late September 1998, we recorded the number of current-year shoots with oviposition on each of the selected 1-yr-old shoots. To determine abscission rate of the current-year shoots during winter, we recorded the number of the current-year shoots in late April 1999. The abscission rate was obtained as the proportion of current-year shoots that had dropped off during winter.

To determine shoot toughness, we selected 35 current-year shoots from each willow species in early August 1999 when oviposition was occurring. We chose  $>20$  cm shoots on which most of oviposition scars were found. Shoot toughness was measured by texture analyzer TA-XT2 (Stable Micro Systems, London) with a needle penetrometer (model P/2N). We

recorded the pressure in Newtons (N) required for complete penetration in the apical region. Three measurements were made per shoot, and the average value was used as an index of shoot toughness.

**Egg Parasitism.** In the study area, one egg parasitoid of the family Aphelinidae and one of the Mymaridae were found (Craig and Ohgushi 2002). In early April 1999, we randomly collected 30 shoots (1 yr old) bearing eggs from *S. miyabeana*, 34 from *S. sachalinensis*, and 33 from *S. integra*. These shoots were kept individually in a small plastic case with moderate humidity. We recorded the number of emerged parasitoids and nymphs until late July. In early August, we dissected these shoots and counted immature parasitized and nonparasitized eggs. It is possible to distinguish between the parasitized and nonparasitized eggs, because parasitized eggs are black and brown in color and nonparasitized eggs are white. We calculated the rate of egg parasitism as the proportion of parasitized eggs to all eggs observed.

**Statistical Procedures.** Chi-square goodness-of-fit analysis was used to determine whether distribution of spittlebug oviposition in the field was random with respect to shoot length (Zar 1999). The Spearman rank correlation was used to determine the relationship between shoot abscission rate and shoot length. Shoot toughness and egg parasitism among shoot length classes were compared using a Kruskal-Wallis test followed by nonparametric Tukey-type multiple comparisons for each of the three willow species (Zar 1999). Shoots were assigned to five classes according to length. When compared among willow species, data from all shoot length classes were pooled before analysis.

## Results

**Distribution Pattern of Spittlebug Oviposition.** In three willow species, 80% of shoots were  $<20$  cm (Fig. 1). Nevertheless spittlebug females strongly preferred ovipositing in long ( $>20$  cm) shoots (*S. miyabeana*:  $\chi^2 = 19.3$ ,  $df = 2$ ,  $P < 0.001$ ; *S. sachalinensis*:  $\chi^2 = 91.2$ ,  $df = 3$ ,  $P < 0.001$ ; *S. integra*:  $\chi^2 = 98.9$ ,  $df = 3$ ,  $P < 0.001$ ). The proportion of shoots with spittlebug eggs increased with shoot length up to 40 cm. However, the incidence of eggs decreased again on  $>40$  cm shoots in *S. miyabeana* and leveled off in *S. sachalinensis* and *S. integra*. Shoot abscission. Shoot abscission rate declined with increasing shoot length in three willow species (*S. miyabeana*:  $r_s = -0.93$ ,  $P = 0.05$ ; *S. sachalinensis*:  $r_s = -0.93$ ,  $P = 0.05$ ; *S. integra*:  $r_s = -0.93$ ,  $P = 0.05$ ; Fig. 2). More than 60% of  $<10$  cm shoots dropped off during winter, while no more than 30 cm shoots did.

**Shoot Toughness.** We found significant differences in shoot toughness among shoot length classes in the three willow species (*S. miyabeana*,  $H = 6.95$ ,  $df = 2$ ,  $P = 0.03$ ; *S. sachalinensis*,  $H = 7.4$ ,  $df = 2$ ,  $P = 0.02$ ; *S. integra*,  $H = 11.29$ ,  $df = 2$ ,  $P = 0.004$ ; Fig. 3). Shoot toughness of three willow species tends to increase with increasing shoot length. Shoot toughness (N) in *S. sachalinensis* was greater than *S. miyabeana* and *S.*

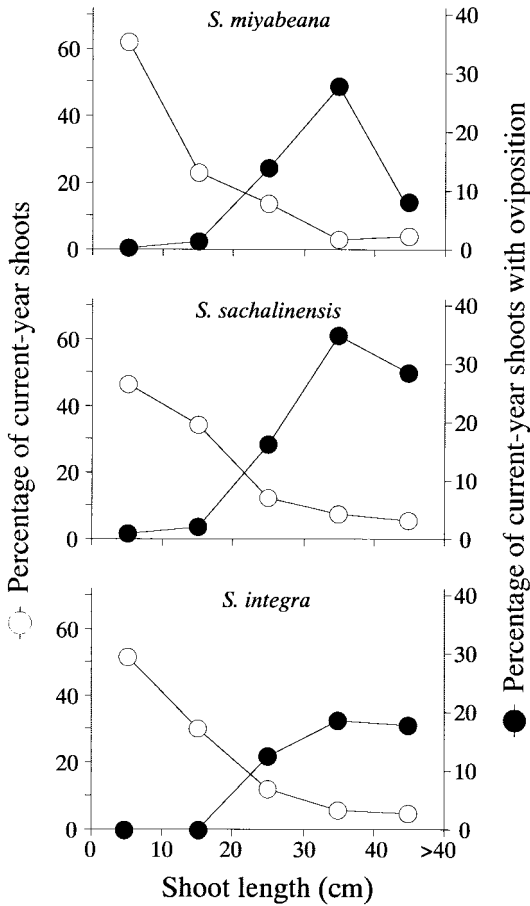


Fig. 1. Percentage of current-year shoots (open circle) and current-year shoots with oviposition (solid circle) in each shoot length class (*S. miyabeana*,  $n = 648$ , 19 for total shoots and oviposited shoots, respectively; *S. sachalinensis*,  $n = 659$ , 40; *S. integra*,  $n = 992$ , 35).

*integra* (*S. miyabeana*,  $4.56 \pm 0.31$  [mean  $\pm$  SE],  $n = 35$ ; *S. sachalinensis*,  $6.54 \pm 0.42$ ,  $n = 35$ ; *S. integra*,  $5.69 \pm 0.30$ ,  $n = 35$ ;  $H = 14.29$ ,  $df = 2$ ,  $P = 0.0008$ ).

**Egg Parasitism.** In *S. miyabeana* and *S. sachalinensis*, there were no significant differences in egg parasitism among shoot length classes (*S. miyabeana*,  $H = 3.52$ ,  $df = 4$ ,  $P = 0.48$ ; *S. sachalinensis*,  $H = 6.87$ ,  $df = 4$ ,  $P = 0.14$ ; Fig. 4). In *S. integra*, egg parasitism in 20–40 cm shoots was significantly higher than those in other shoot length classes ( $H = 10.10$ ,  $df = 4$ ,  $P = 0.04$ ; Fig. 4). No significant differences were found in egg parasitism among willow species (*S. miyabeana*,  $17.1 \pm 1.8$  [mean  $\pm$  SE],  $n = 30$ ; *S. sachalinensis*,  $14.9 \pm 2.0$ ,  $n = 34$ ; *S. integra*,  $20.2 \pm 2.9$ ,  $n = 33$ ;  $H = 14.9 \pm 2.0$ ,  $df = 2$ ,  $P = 0.34$ ).

### Discussion

We found that females of *A. pectoralis* exhibited a strong oviposition preference for long shoots in three

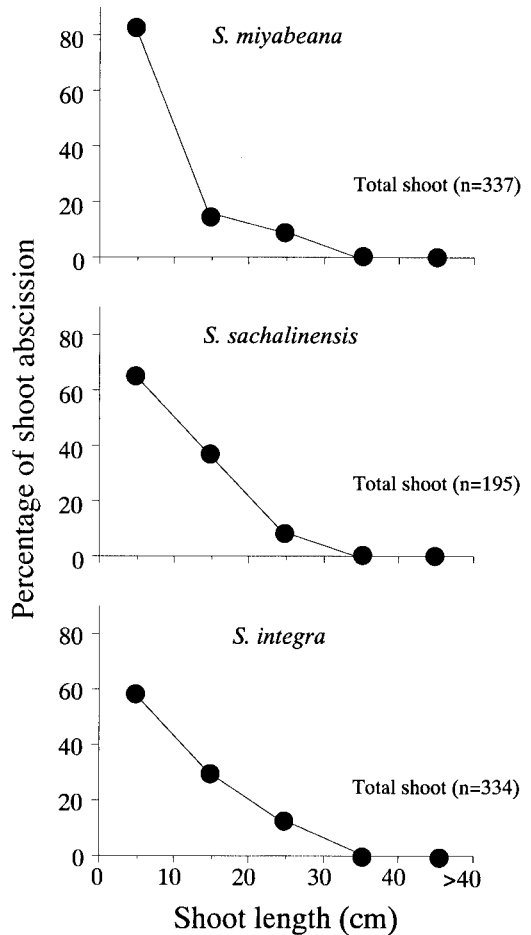


Fig. 2. Percentage of shoot abscission during winter in each shoot length class.

willow species. Although 80% of shoots were <20 cm, the percentage of shoots that received oviposition was highest in 30–40 cm shoots, which were only 6% of all shoots. However, oviposition rate leveled off or even decreased in the longest (>40 cm) shoots. Shoot abscission rate decreased consistently as shoot length increased in all three willow species. In contrast, shoot toughness increased as shoot length increased. Egg parasitism was not related to shoot length in three willows, though the percentage of parasitized eggs in 20–40 cm shoots of *S. integra* was significantly higher than those in other shoot length classes.

This study illustrated that oviposition preference of the spittlebug is most likely affected by shoot abscission. It is adaptive for females to avoid laying in short shoots because of the high abscission rate of short shoots. As *A. pectoralis* eggs overwinter in the shoots, when females oviposit in short shoots, eggs are subjected to heavy mortality due to shoot abscission. This effect of shoot abscission on oviposition preference has also been shown in the galling sawfly *Euura lasiolepis* Smith, which has an oviposition preference for

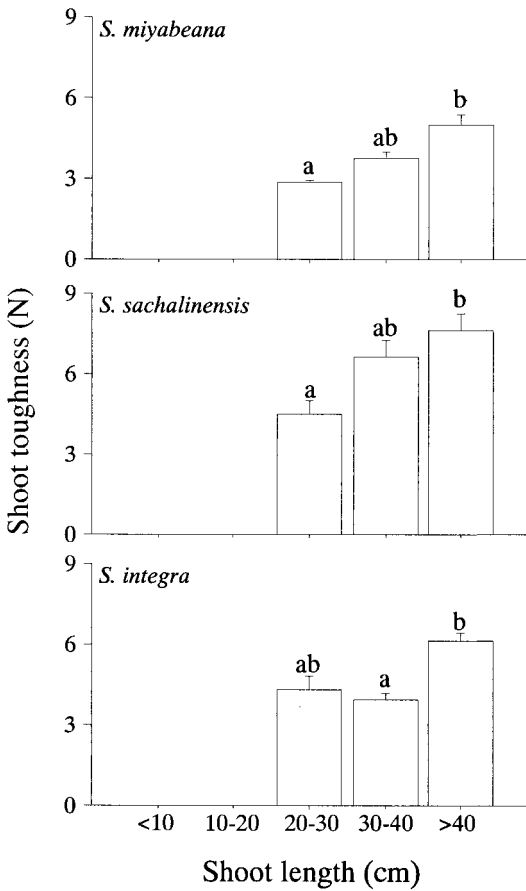


Fig. 3. Shoot toughness at apical region in each shoot length class. Mean and SE are presented ( $n = 35$  for each willow species). Mean values with different letters are significantly different at 5% level in each willow species.

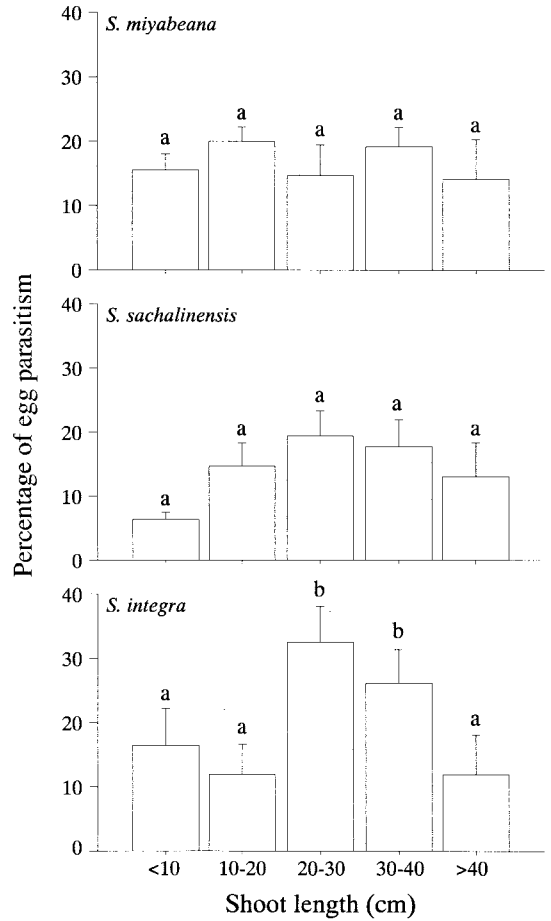


Fig. 4. Egg parasitism by the two parasitic wasps in each shoot length class. Mean and SE are presented (*S. miyabeana*,  $n = 30$ ; *S. sachalinensis*,  $n = 34$ ; *S. integra*,  $n = 33$ ). Mean values with different letters are significantly different at 5% level in each willow species.

long shoots (Craig et al. 1989). Oviposition preference of the sawfly for long shoots reduces the risk of larval mortality due to shoot abscission. Similarly, ovipositing females of the leafminer *Stilbosis quadricostatella* Chambers chose individual trees of the oak *Quercus geminata* Small with low rates of leaf abscission (Stiling et al. 1991).

In this study, we did not investigate the possibility of nutritional differences among shoot length classes. However, nitrogen concentration may have an important effect on the larval performances of herbivorous insects, such as survival rate, growth rate, and fecundity (Scriber and Slansky 1981). In particular, xylem sap has low concentration in nitrogen compared with other plant tissues (Mattson 1980), and some xylem feeders use plant quality as a cue to plant choice (Prestidge and McNeill 1983, Brodbeck et al. 1990, Thompson 1994, Rossi et al. 1996). For example, the oligophagous xylem-feeding leafhopper *Carneiocephala floridana* Ball prefers the salt-marsh cord grass, *Spartina alterniflora* Loiseleur-Deslongchamps, with higher nitrogen content (Rossi and Strong 1991).

Similarly, some studies have documented that chemical compounds also have an important impact on the oviposition preference of herbivorous insects (Zucker 1982, Rowell-Rahier 1984, Tahvanainen et al. 1985, Kolehmainen et al. 1995). For example, a shoot galling sawfly *Euura amerinae* Linnaeus, which has an oviposition preference for long shoots, recognizes shoot size by the concentration of phenolic glucoside, which increases with shoot length (Kolehmainen et al. 1995). Also, a leaf-galling aphid *Pemphigus betae* Doane that prefers larger leaf for oviposition may recognize leaf size by phenolic concentrations that decrease with leaf size (Zucker 1982).

Although some galling insects have an oviposition preference for the longest (most vigorous) shoots (Price et al. 1995, Price et al. 1997), *A. pectoralis* did not prefer the longest shoots. This may be explained by the fact that shoot toughness increases with shoot length. Toughness of plant tissues often has negative effects on herbivorous insects (Hoffman and McEvoy 1986,

Craig et al. 1990, Scheirs et al. 2001). For example, feeding sites of the meadow spittlebug *Philaenus spumarius* nymphs were restricted to the apexes of the stems of pearly everlasting *Anaphalis margaritacea* Benth & Hook. Because stem toughness increases with distance from the apical region, the nymphs could not penetrate the lower parts of stems with their stylets (Hoffman and McEvoy 1986).

In *S. miyabeana*, oviposition preference declined dramatically in >40 cm shoots with increased shoot toughness. However, despite the increased toughness of *S. sachalinensis* compared with the other two willow species, oviposition preference for >40 cm shoots did not decline. Egg mass density on *S. sachalinensis* was significantly higher than on *S. miyabeana* or *S. integra* (Craig and Ohgushi 2002), suggesting that there are unknown benefits (e.g., higher resource quality, escaping from natural enemies) from ovipositing in *S. sachalinensis* shoots that may partially compensate for the negative effect of shoot toughness of the longer shoots.

Natural enemies can also affect oviposition preference in herbivorous insects (Atsatt 1981, Thompson 1988, Ohsaki and Sato 1994, Yamaga and Ohgushi 1999). For example, Ohsaki and Sato (1994) studied a butterfly *Pieris napi japonica* Shirozu that oviposits on *Arabis* plants with low quality for larvae performance in terms of survival rate, development time, and pupal mass. Since these plants grow mainly under other weeds throughout the growing season, parasitoids have difficulty in finding the butterfly larvae on the host plants. Thus, the butterfly may oviposit on these plants to avoid attack by specialist parasitoids, despite the poor food quality available to larvae.

However, the two egg parasitoids of the spittlebug were unlikely to affect oviposition preference, because egg parasitism was not a function of shoot size. Although in *S. integra* egg parasitism was significantly higher in the 20–40 cm class compared with other shoot length classes, ovipositing females did not avoid these shoots. Therefore, egg parasitism may not affect oviposition preference on *S. integra* or the two other willow species examined. Why egg parasitism was higher in 20–40 cm shoots remains unclear.

Previous studies have documented that some herbivorous insects (especially galling insects) have an oviposition preference for vigorous plants and plant modules (Price 1991). This study indicates that *A. pectoralis* also has an oviposition preference for long shoots and the preference is affected by shoot abscission and shoot toughness. However, *A. pectoralis* did not prefer the longest (most vigorous) shoots, and such a pattern has not reported in galling insects. Therefore, this result suggests that we should investigate whether the plant vigor hypothesis explains patterns of oviposition preference in other guilds of insect herbivores (Kimberling et al. 1990).

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