

Life Cycle of the Willow Leaf Beetle, *Plagiodera versicolora* (Coleoptera: Chrysomelidae) in Ishikari (Hokkaido, Japan)

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Abstract. Life cycle of the willow leaf beetle, *Plagiodera versicolora*, was studied at Ishikari (43°N, 141°E; Hokkaido, Japan). The field censuses of adults, egg clutches and pupae on the host-plant, *Salix sachalinensis*, in 1996 illustrated that *P. versicolora* showed bivoltine life cycle at Ishikari. The field census of adults in 1997 also illustrated the same dynamic pattern as bivoltine cycle. The overwintering-generation adults began to colonize on the host-plant trees from late May and laid egg clutches from early June. The first generation began to pupate from early July and emerged as adult from mid-July. The first-generation adults had oviposited from late July to end-August. The second generation pupated from mid-August and emerged as adult from late August. All adults disappeared from the host-plant trees by mid-September. In addition, a census on three willow species (*S. sachalinensis*, *S. miyabeana* and *S. integra*) was conducted in 1997. Both adults and egg clutches tended to be observed more on *S. sachalinensis* than on other species, though *S. sachalinensis* was not the most abundant willow species at Ishikari. This suggests that the bivoltine life cycle of *P. versicolora* is maintained on *S. sachalinensis*.

Key words: life cycle, Chrysomelidae, *Plagiodera versicolora*, willow, Hokkaido.

Introduction

To various degrees, all environments on earth change geographically. These environmental changes act as a major selective force shaping insect life cycles. Therefore, many insects occurring over wide geographical ranges show geographical variation in life cycles as a result of local adaptation (Tauber *et al.*, 1986; Danks, 1987). Often, several generations may be produced annually in the south, but only one near the northern limit of distribution. This variation in voltinism is because temperature shows clear latitudinal gradient.

Voltinism influences various insect traits (see Tauber *et al.*, 1986). In some multivoltine insects, for example, saw-toothed clinal variations in body size and developmental time have been reported (Masaki, 1973, 1978a, b, 1979; Kidokoro & Masaki, 1978; Masaki & Walker, 1987; Mousseau & Roff, 1989;

Ishihara, 1998; also see Tauber *et al.*, 1986). These clines reflect differences in voltinisms, resulting from local adaptations that prevent the wasteful production of an incomplete generation which cannot overwinter (Roff, 1980, 1983; Masaki & Walker, 1987; Tauber *et al.*, 1986). Furthermore, host-plant selection by herbivorous insects may influence their voltinisms, because rapid larval growth on high quality hosts may produce an additional generation (Scriber & Lederhose, 1992; Hunter & McNeil, 1997). This additional generation would change rates of population growth and potential rates of adaptation to a varying environment (Roff, 1983; Tauber *et al.*, 1986; Carrière *et al.*, 1995; Hunter & McNeil, 1997). Therefore, voltinism of an insect in a particular location should be an important information to clarify its local adaptation.

In the present study, we report the life cycle of the willow leaf beetle, *Plagiodera versicolora* Laicharting, and its preference for host-plant at Ishikari (Hokkaido, Japan). *P. versicolora* uses several willow species as host-plant and it shows multivoltine cycles (5-6 generations per year) in the Honshu island of Japan (see Kimoto & Takizawa, 1994). However, the life cycle in the Hokkaido island has not yet been reported in detail.

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Materials and Methods

The willow leaf beetle, *P. versicolora*, is known from wide areas over Asia, Europe and north Africa (Kimoto & Takizawa, 1994). In addition to this native distribution, *P. versicolora* has been introduced into north America since 1911 (Hood, 1940). Both adults and larvae feed on willow leaves. *P. versicolora* overwinters as adult diapause (Hood, 1940).

The study site in Ishikari (43°N, 141°E; Hokkaido, Japan) is located in a riverside of the Ishikari river. Six willow species (*Salix miyabeana* Seemen, *S. sachalinensis* Fr. Schm., *S. integra* Thunb., *S. subfragilis* Anders., *S. hultenii* Floderus and *S. pet-susu* Kimura) have been grown at the study site. Most adults and larvae of *P. versicolora* are found on *S. miyabeana*, *S. sachalinensis* and *S. integra*.

We took censuses of adults, egg clutches and pupae through season in 1996. We randomly selected 6 clones of *S. sachalinensis* and marked 44–146 one-year shoots of each clone on 27 May 1996. Adults, egg clutches and pupae on the marked shoots were counted at least once every several days from 28 May to 17 September. In 1997, similar survey was conducted from 18 May to 12 September on 15 clones on which 10–46 one-year shoots were marked, but egg clutches and pupae were not counted. The total numbers of the marked shoots were 557 in 1996 and 428 in 1997.

In addition, we took censuses of adults and egg clutches on different willow species in 1997. We randomly selected 11 clones of *S. miyabeana*, 22 clones of *S. sachalinensis* and 11 clones of *S. integra*, and marked 10–46 one-year shoots of each clone on 17 May. The total numbers of the marked shoots were 192 in *S. miyabeana*, 582 in *S. sachalinensis* and 106 in *S. integra*. Adults and egg clutches were counted at least once every several days from 17 May. These censuses were ended on 30 June for egg clutch and on 17 July for adult. In September 1997, 425 trees (clones) of willows were randomly selected at the study site and the abundance of each willow species was determined.

Results and Discussion

Fig. 1 illustrated that *P. versicolora* showed bivoltine life cycle at Ishikari, because the curves of adult numbers showed three peaks. However, generations were not completely separated each other. This is because *P. versicolora* has long adult longevity. We have confirmed that adults had survived for two months at 22°C, 16L–8D (unpublished data). The curve of adult number in 1997 also showed the same pattern as bivoltine cycle (Fig. 1b). However, the density of adults at the second peak in 1997 (6.3 per 100 one year shoots) was lower than in 1996 (10.2 per 100 one-year shoots).

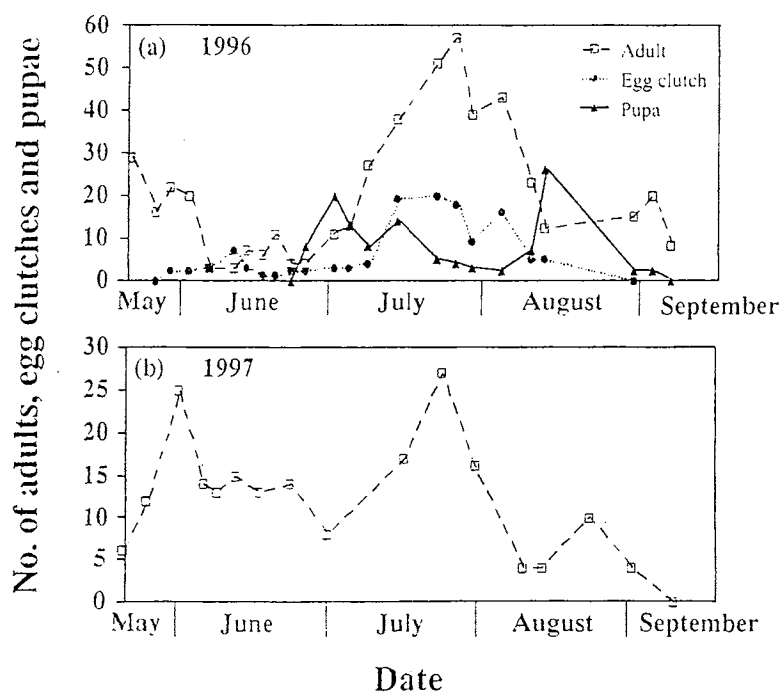


Fig. 1. Temporal changes in the numbers of adults, egg clutches and pupae observed on *S. sachalinensis* in (a) 1996 and (b) 1997 at Ishikari. The numbers of one-year shoots on which the census was conducted were 557 in 1996 and 428 in 1997.

The curves of egg clutch and pupae numbers in 1996 also supported its bivoltine cycle (Fig. 1a). The overwintering-generation adults began to colonize on the host-plant, *S. sachalinensis*, from late May. These adults began to lay egg clutches from early June. The first generation began to pupate from early July and emerged as adult from mid-July. The abrupt increase in the number of egg clutches from late July indicated that the first-generation adults began to oviposit (Fig. 1a). The oviposition by the first-generation adults ended before September. The second generation pupated from mid-August and emerged as adult from late August. However, the increase in the number of the second-generation adults was rather smaller than that for the pupae (Fig. 1a). This may be because the second-generation adults moved from the host-plant to their overwintering sites soon after emergence. The second-generation adults disappeared by mid-September. Hood (1940) and Stevens & McCauley (1989) reported that *P. versicolora* overwintered as adult diapause under the bark of willow trees.

Both adults and egg clutches tended to be found more on *S. sachalinensis* than on other willow species (Figs. 2, 3). The abundance of adults on *S. sachalinensis* was significantly greater than on *S. miyabeana* during the period of observation in 1997 (Fig. 2, Wilcoxon paired-sample test, $P < 0.05$) but not than on *S. integra* (Wilcoxon paired-sample test, $P > 0.05$). This was because in early June the numbers of adults on *S. integra* were greater than on *S. sachalinensis* (Fig. 2). However, the reason why the number of adults increased abruptly on *S. integra* remains unclear. The abundance of egg clutches on *S. sachalinensis* was significantly greater than on other two species

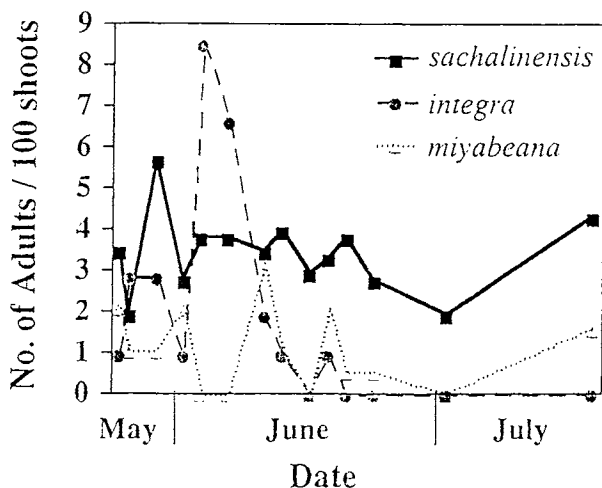


Fig. 2. Temporal changes in the numbers of adults per 100 one-year shoots on three willow species from 18 May to 17 July 1997 at Ishikari.

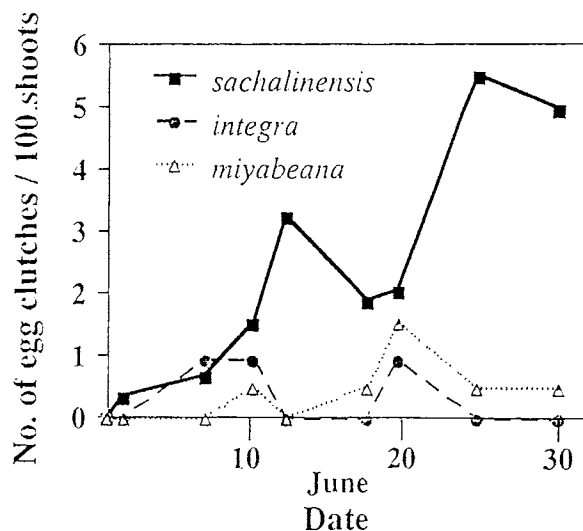


Fig. 3. Temporal changes in the numbers of egg clutches per 100 one-year shoots on three willow species from 18 May to 30 June 1997 at Ishikari.

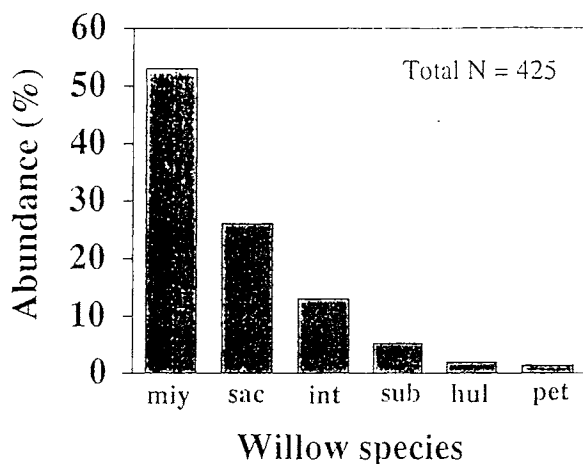


Fig. 4. Species composition of willows at Ishikari. miy: *S. miyabeana*, sac: *S. sachalinensis*, int: *S. integra*, sub: *S. subfragilis*, hul: *S. hultenii*, pet: *S. pet-susu*.

(Fig. 3, Wilcoxon paired-sample test, $P < 0.05$). In the abundance of either adults or egg clutches, there were no significant differences between *S. miyabeana* and *S. integra* (Wilcoxon paired-sample test, $P > 0.05$). Although adults laid egg clutches on *S. miyabeana* and *S. integra*, we could find only two pupae on *S. miyabeana* in mid July. However, the two pupae had been parasitized by the parasitoid fly, *Anthomyiopsis plagioderae* Mesnil, and the parasitoid wasp, *Schizonotus latus* Walker, respectively. This evidence suggests that most larval development and reproduction of *P. versicolora* might occur on *S. sachalinensis*.

However, *S. sachalinensis* was not the most abundant willow species at the Ishikari study site (Fig. 4). Despite that *S. miyabeana* is the most abundant species (Fig. 4), why were only a few egg clutches laid on

it? In the laboratory, larvae of *P. versicolora* can grow to the adult stage on both *S. miyabeana* and *S. integra* (unpublished data). However, in the field *P. versicolora* strongly prefers *S. sachalinensis* as host-plant to other willow species. It may be caused by the high quality of *S. sachalinensis* as food. The bivoltine cycle at Ishikari may be maintained by high growth rate on *S. sachalinensis*. If *P. versicolora* uses other willow species as host-plant, the bivoltine cycle may not be completed because of slow growth rates on them.

In addition to growth rate, predation pressure is an important factor for host-plant selection (Courtney, 1988; Thompson, 1988). We have not observed any *P. versicolora* larvae that could grow to the adult stage on *S. miyabeana* and *S. integra* in the field. This may be caused by the high predation pressures on *S. miyabeana* and *S. integra*. *P. versicolora* may avoid oviposition on such host-plant species.

We have just started to examine whether *S. sachalinensis* is the best host-plant for growth and survival of *P. versicolora*. Though host-plant selection by herbivorous insects may influence their voltinisms, only a few studies have focused on the relationship between host-plant range and insect voltinism (Scriber & Lederhouse, 1992; Hunter & McNeil, 1997). Such studies might reveal the evolutionary process of host-plant range in herbivorous insects.

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