Intraleaf Distribution of Panonychus ulmi (Koch) (Acarina: Tetranychidae) on Dwarf Bamboo

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Seasonal and diel changes on leaf surface preferences by Sapporo populations of the European red mite, Panonychus ulmi (Koch), were studied throughout its life cycle on dwarf bamboo, Sasa senanensis (Franchet et Savatier). Mites overwintered as eggs, which hatched in May. Four or 5 generations were then produced, but by November, again only eggs were found. Non-diapause eggs, active immature stages and adult females were found predominantly on the uppersurface of the leaf, except during periods of low temperature or cloudy conditions. About half of the active stages that did populate the undersurface of the leaf were found predominantly near the leaf edge, but they were not able to feed on this surface. This fact suggests that the undersurface is a refuge from severe diurnal and nocturnal factors. Diapause eggs, quiescent stages and adult males were mainly found on the leaf undersurface.

The position of the active stages changed daily on the leaf surfaces: in the daytime they appeared on the uppersurface of the leaves, whereas at night they were found on the undersurface. These movements appear to be controlled by a complex interaction among light intensity, air temperature and relative humidity.

INTRODUCTION

Seasonal or diel changes of distribution on infested leaf surfaces in several spider mite species are well recognized (Blair and Groves, 1952; Shinkaji, 1959; Fott, 1963; Kato, 1972). Such changes appear to be caused by fluctuations of weather, illumination and temperature. The citrus red mite, Panonychus citri (McGregor), settles predominantly on the leaf undersurface during periods of low temperature (autumn to spring), whereas about half the individuals of active stages and eggs are found on the leaf uppersurface in summer (Shinkaji, 1959). Females of the European red mite, Panonychus ulmi (Koch), move to the leaf undersurface on days with rain, high winds and low temperature, but are found mainly on the leaf uppersurface on clement days (Fott, 1963).

Panonychus ulmi is a polyphagous species and is found on deciduous trees such as apple, peach, cherry, hawthorn and elm, and overwinters as diapause eggs (e.g., Blair and Groves, 1952). P. ulmi populations have also been recorded from dwarf bamboo, Sasa kurilensis Makino et Shibata, in the subalpine coniferous forest of Nagano Pref. in central Japan (Moriyama and Mori, 1977). This latter population occurs on leaves throughout the year and diapause eggs are laid along the midvein of undersurface of a leaf (Moriyama and Mori, 1977), unlike the eggs laid on apples which are deposited.
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on small branches and twigs (BLAIR and GROVES, 1952). The difference of oviposition sites between these populations may be attributed to the difference of the deciduous and evergreen nature of the host plants. However, it is unclear whether or not there are other differences between these mite populations.

The aim of the present study was to describe the seasonal and diel changes on intraleaf distribution of *P. ulmi* population on dwarf bamboo observed in the field throughout its life cycle.

**STUDY SITES AND METHODS**

**Study sites.** Observations were made in a forest on the campus of Hokkaido University, Sapporo (the campus site), and in a forest near Mt. Hakken at Misumai in Sapporo (the mountain site). The primary cover on both forest floors was dwarf bamboo, *Sasa senanensis* (FRANCHET et SAVATIER) with some herbs also present. The canopy consisted of deciduous broad-leaved trees. The mountain site was used only for the 1983 study of the diel change of infesting surfaces of active stages.

**Developmental stage, population density and intraleaf distribution.** The two leaf surfaces were divided into three parts: (1) from the midvein to the inner two parallel-veins, (2) from the leaf edge to the outer two parallel-veins, and (3) the intermediary part (Fig. 1A).

At the campus site, the developmental stages of the mite and the population densities of the mite and its predators were regularly observed on the 6 leaf segments using magnifying glasses (×10, ×20), on all leaves of 18–30 randomly selected culms of dwarf bamboo in three quadrats (5m × 5 m). The maximal number of leaves observed was 168 (including 111 new leaves) in 1983, and 156 (including 121 new leaves) in 1984. “New” leaves were those that opened in the early summer of the observation year, and “old” ones were those that had opened in previous years. The quadrats were situated where mite populations occurred in 1983 and the same positions were used throughout the study. The census was taken between 9:00 a.m. and 3:00 p.m. every ten days from April, 1983 to November, 1984, except for the snowy season from about December to mid-April and the period from mid-August to early September, 1984. The weather was always clear or a bit cloudy when observations were made.

Supplementary observations were made on July 31 and November 26, 1982, to examine the intraleaf distribution of eggs at the campus site. At that time, the two leaf surfaces were divided into two parts, i.e., axial 7 cm from the petiole, and the remainder (Fig. 1B).

**Diel change of infested surfaces of active stages.** To determine the diel change of infested surfaces of active stages, groups of twenty leaves carrying active stages of *P. ulmi* were thinly coated on both surfaces with hair spray (TIARA®, hard type, Shiseido Co., Ltd., Tokyo) in the field, and observed under a dissecting microscope in the laboratory. The investigation was carried out every 1 to 4 hr on one or two days in summer during the 3-year period from 1983 to 1985. In 1983, the investigation was made at the mountain site, but in 1984 and 1985 it was made at the campus site. Temperature, relative humidity and illumination were recorded during observation. A dim red lamp was used at night to avoid disturbance of mite behaviour (cf. LEES, 1953).

**Survival of mites on the two leaf surfaces.** Adult females of *P. ulmi* were collected from the campus site on June 23, 1986, and were reared on leaf discs from the same
host in petri dishes (9 cm diam.) at 25±1°C and 15L-9D. Based on the author’s experience, an uppersurface was used for this leaf disc. In order to know whether or not active stages are able to survive on both surfaces of dwarf bamboo leaves, 10 or 20 larvae from a stock culture were introduced onto a disc of either a leaf uppersurface or undersurface, and the developmental stages and the number of live mites were recorded daily at 25°C and 15L-9D.
Similar experiments were carried out for adult females. After the emergence of females, they were singly reared on a disc (ca. 8 cm²) of either a leaf uppersurface or undersurface, and the number of eggs laid and the number of living females was recorded each day.

RESULTS

Developmental stage and population density

Figure 2 shows the seasonal changes in the abundance and stage structure of the P. ulmi population and the abundance of phytoseiid mites on dwarf bamboo leaves. The mite passed the winter in the egg stage on leaves, and most of the eggs hatched in early (1983) or late (1984) May. Four or 5 generations could be recognized before late October or early November.

Adults of the first generation of P. ulmi appeared in late May or early June (Fig. 2). The appearance time was well consistent with the opening of new leaves of the dwarf bamboo (Fig. 3A). Most of the adults dispersed to the new leaves and the rest remained on overwintered old leaves (Fig. 3B). After June or July, however, the old leaves were little used by the mites, until the laying of their diapause eggs in autumn (Fig. 3B). Thus evergreen leaves of dwarf bamboo assure the complete development of immature stages originating from diapause eggs in spring, and are again used as a deposition site for diapause eggs in autumn.

In 1983, the number of spider mites decreased after diapause eggs began to hatch in spring and remained at a low level thereafter, except during late autumn (Fig. 2). In 1984, on the other hand, after the spring population decrease occurred the density of the mites began to increase in June when the first generation females laid eggs, and reached a maximal density (85.2/leaf) in mid-July, after which the mites again rapidly

Fig. 3. Seasonal changes in (A) the number of leaves (relative to the maximum) of dwarf bamboo, and (B) the number of mites appearing on leaves of similar age at the campus site. Numerals in parentheses indicate the maximal number of leaves observed.
Table 1. Cumulative day-degrees above 10°C in Sapporo

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<td>1983</td>
<td>27 (15)</td>
<td>86 (25)</td>
<td>108 (29)</td>
<td>253 (31)</td>
<td>302 (31)</td>
<td>231 (30)</td>
<td>43 (15)</td>
<td>3 (2)</td>
<td>1,133</td>
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<td>1984</td>
<td>6 (3)</td>
<td>81 (16)</td>
<td>245 (30)</td>
<td>376 (31)</td>
<td>422 (31)</td>
<td>234 (30)</td>
<td>43 (17)</td>
<td>7 (4)</td>
<td>1,414</td>
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\(^a\) Modified from "Hokkaido no kisho" (Sapporo District Meteorological Observatory, ed.).
\(^b\) Numerals in parentheses indicate the number of days that were over 10°C.

decreased. The difference between years may be due to the difference in the amount of available heat for development. The cumulative total of temperatures above 10°C from May to October in 1984 was 1,401 day-degrees, which was 298 higher than that available in 1983 (Table 1).

Predators associated with the dwarf bamboo population were phytoseiid mites (Fig. 2), stigmatic and a small number of gall midges and thrips. The phytoseiid mites appeared from mid-May (1983) or mid-June (1984) to mid-October, and they did not overwinter on leaves. Their density was also lower in 1983 than in 1984. In 1984, the occurrence of phytoseiid mites followed that of *P. ulmi* with a time lag of 10 days, reaching a peak in late July (0.60/leaf), and then gradually decreasing.

*Intraleaf distribution of the mite*

The seasonal changes in the intraleaf distribution of each stage of *P. ulmi* were analysed in the six leaf divisions.

*Eggs*

The eggs found from September to May were diapause eggs (Figs. 2 and 4A). These were always deposited on the leaf undersurface (Fig. 4A) and distributed both along the midvein and near the petiole (Table 2). Non-diapause eggs, however, were laid predominantly on the leaf uppersurface and were randomly distributed. An exception was noted in June and July, 1983, when the number of day-degrees above 10°C was about 120 less than that in each corresponding month of 1984 (Table 1): a large number of these non-diapause eggs were deposited on the leaf undersurface and occupied an area near the leaf edge. Thus the distribution of *P. ulmi* eggs on the leaf surfaces of dwarf bamboo was influenced by the nature of eggs, diapause or non-diapause, and by the cumulative day-degrees in the observed months.

*Adult females*

Adult females of *P. ulmi* were confined to the uppersurface of the leaf and were evenly distributed (Fig. 4B). A considerable number of individuals, however, occupied the leaf undersurface in late May and in early and mid-July, 1983, when the weather was a bit cloudy.

*Active immature stages*

Larvae and nymphs were distributed evenly on the leaf uppersurface, except for those individuals which hatched from diapause eggs and those in June and September (Fig. 4C). A considerable number of individuals found on the undersurface of the leaf occupied an area near the leaf edge.

*Quiescent stages*

The majority of the quiescent stages occurred on the leaf undersurface, and more than half of them settled along the leaf edge (Fig. 4D), which was slightly curled towards the undersurface. When a part of the leaf edge died, i.e., turned brown, no individuals
Fig. 4. A–E: seasonal changes of intraleaf distribution of each developmental stage of *P. ulmi* at the campus site. LDS means leaf undersurface, and LPS leaf uppersurface. Blank column: midvein, dark column: leaf edge, lined column: intermediary part. See also Figs. 1 and 4D.
settled there. Settling of the quiescent stages on the undersurface may reduce the risk of being washed off by rain.

**Adult males**

The density of adult males was very low and their distribution varied greatly with observation time. Their distribution on leaf surfaces was similar to that of the quiescent stages (Fig. 4E). This is because adult males search and guard the female teleiochrysalis by sitting on or close to her for mating just after emergence.

**Diel change of infested surfaces of active stages**

Figure 5 shows the daily change of the infested surfaces of active stages. The weather on the investigation days was fine, except on July 23–24, 1985, when it was rainy from 15:00 to 2:30. The number of individuals observed was 61.1 on the average, ranging from 27 to 161. The number of mites that appeared on the leaf uppersurface on each of the investigation days, except on the rainy days, was significantly greater in the daytime than at night ($p<0.005$, $t$ test). On July 23–24, 1985, when it was rainy after 15:00, however, the number of mites that occurred on the uppersurface of leaves from 16:00 to 19:00 was lower than that at the corresponding hour on July 24–25, 1985 ($p<0.05$, $\chi^2$ test). On these latter days the mites gradually moved from the leaf uppersurface to the leaf undersurface with decreased illumination, and vice versa (Fig. 5E).

Figure 6 shows the relationship between the percentage of the mites that appeared on the leaf uppersurface and the temperature or relative humidity, omitting the values from 16:00 to 19:00 on July 23–24, 1985. The correlation coefficient was high between the percentage and the temperature ($r=0.55$, $p<0.001$), and between the percentage and the relative humidity, ($r=-0.51$, $p<0.002$).

**Survival of mites on the two leaf surfaces**

On the uppersurface of leaves, 88% of the larvae survived and developed well to nymphal stages by the 4th day of inoculation (Fig. 7A), whereas on the undersurface, all individuals died within three days after inoculation (Fig. 7B). Thirty-nine out of 60 individuals introduced onto the undersurface starved to death and the rest drowned.

Adult females that were reared on the leaf uppersurface showed much higher survival rates and fecundities than those on the leaf undersurface (Fig. 7C, D). The results for females on the uppersurface well agree with the previous report on *P. ulmi* on dwarf bamboo (Gotoh, 1987). Adult females that were introduced onto the leaf undersurface did not survive more than 4 days after inoculation and they rarely oviposited (Fig. 7D). Their carcasses were shrivelled, except for 4 individuals which
Fig. 5. Diel change of infesting surfaces of active stages of P. ulmi. In 1983, the investigation was made at the mountain site (A), and in 1984 and 1985 at the campus site (B–E). LDS means leaf undersurface, and LPS leaf uppersurface. Hollow histograms indicate the number of individuals in the daytime, and dotted ones those at night. A: Aug. 3–4, 1983, B: Aug. 5–6, 1984, C: Aug. 7–8, 1984, D: July 23–24, 1983, E: July 24–25, 1985.

drowned, suggesting that they died of hunger. Thus it is almost impossible for a population of P. ulmi to develop, oviposit and feed on the undersurface of leaves of dwarf bamboo.

When adult females were transferred to the leaf undersurface every other day after the 3rd day of emergence, daily egg production decreased considerably (about 2–4 eggs; Fig. 7E), in comparison with females reared only on the leaf uppersurface (Gotoh, 1987). The oviposition rate went down drastically when females were placed on the leaf undersurface, and this decrease was not completely recovered even if they were later moved to the uppersurface. Such alternation of females from one surface to the other, however, nonetheless resulted in better daily egg production and survival rate than that of females reared solely on the leaf undersurface.

DISCUSSION

The P. ulmi population on dwarf bamboo produced 4 or 5 generations a year with a peak of population density in July, 1984. This is similar to the P. ulmi populations
Fig. 6. Relationship between the percentage of individuals that appeared on the leaf uppersurface and temperature (left), and between that percentage and relative humidity (right).

Fig. 7. Survival of immature stages and adult females, and oviposition rates of adult females on the uppersurface and undersurface of dwarf bamboo leaves at 25°C and 15L:9D. LDS means leaf undersurface, and LPS leaf uppersurface. L: larva, PC: protochrysalis, PN: protonymph, DC: deutochrysalis, DN: deutonymph. Numerals on bars indicate the daily egg production per female on the leaf uppersurface (n=21), cited from Gotoh (1987).

on apple in Essex, UK (Blair and Groves, 1952), in Hirosaki (Hukushima, 1956) and Sapporo (Mori, 1961), Japan, and in British Columbia, Canada (Downing and Moillet, 1967), except for the overwintering sites. The dwarf bamboo population overwintered on leaves as diapause eggs, whereas the apple population did so on branches and twigs as mentioned earlier. The reason for this is that the evergreen leaves of dwarf bamboo, unlike apple, guarantee a place for overwintering (cf. Fig. 3).

The present study showed that the leaf surfaces chosen by P. ulmi varied not only seasonally and daily, but also had an effect on the developmental stages. Non-diapause eggs, active immature stages and adult females occupied predominantly the uppersurface of the leaf, whereas diapause eggs, quiescent stages and adult males were found on the undersurface. The preference of occupied sites found in the dwarf bamboo population is more conspicuous than those observed on the apple and peach populations of P. ulmi and the citrus population of P. citri. Adult females of P. ulmi on apple and peach were found primarily on the leaf undersurface (Blair and Groves, 1952) or the uppersurface (Foott, 1963), and other stages were found on the undersurface. In the citrus population, every stage, except for adult males who appeared only on the undersurface, was evenly divided on both surfaces in summer, but most of them appeared
on the undersurface in other seasons (SHINKAJI, 1959). These differences in distribution seem to be due to the differences in feeding surfaces. The apple and peach populations of *P. ulmi* and the citrus population of *P. citri* are able to utilize both surfaces of their host leaves as feeding sites (e.g., BLAIR and GROVES, 1952), but the *P. ulmi* population on dwarf bamboo was unable to feed on the undersurface of these leaves (Fig. 7).

FOOTT (1963) reported that adult females of *P. ulmi* on apple moved from the uppersurface of the leaf to the undersurface when air temperatures were less than 63.5–70.0°F (ca. 17–21°C). Although adult females of *P. ulmi* on dwarf bamboo are mainly found on the leaf uppersurface in the daytime, they deposited diapause eggs solely on the undersurface in autumn. Furthermore, non-diapause eggs and active immature stages tended to be found on the undersurface of leaves in spring and early summer, especially in 1983 when the total day-degrees were less than those in 1984. This suggests that undersurface of leaves is preferred for both the oviposition sites chosen by females and the settling sites of immatures under low temperatures.

Active immature stages found on the undersurfaces of dwarf bamboo leaves obviously occupied the sites nearest the leaf edge (Fig. 4C), though they could not feed on this surface. It is, therefore, likely that these stages move frequently from the under- to the uppersurface to feed, and the undersurface is their refuge from severe environmental factors such as dew and high winds.

Such diel changes in occupied surfaces by active stages have been reported for *P. ulmi* (BLAIR and GROVES, 1952; FOOTT, 1963) and *P. citri* (KATO, 1972), but have not previously been examined throughout an entire day. In the present study, active stages located predominantly on the uppersurface of leaves in the daytime, whereas they settled on the undersurface at night and on rainy days. Furthermore, on July 24–25, 1985, when there was scarcely any fluctuation in temperature and relative humidity, the active stages moved from the uppersurface to the undersurface as illumination decreased, and vice versa (cf. Fig. 5E). This fact suggests that the diel change of occupied surfaces of the mites may be controlled largely by illumination. When high temperature and low relative humidity prevailed, mites were apt to occupy the leaf uppersurface, suggesting that these factors also influence diel change. To elucidate more precisely the influence of these factors, however, requires further investigations under controlled conditions.

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