

Early Budding of *Acer palmatum* Caused by the Shade; Intra-specific Heterogeneity of the Host for the Maple Aphid

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1. Introduction

Inter- and intra-specific variation in host tree quality is commonly observed and many studies have revealed the effect of such variation on the ecology of insects (WRATTEN, 1974; JOURNET, 1980; MORAN, 1981; SUTTON, 1984; FURUTA *et al.*, 1984).

The maple aphid, *Periphyllus californiensis* Shinji, often hatches early in the spring before the budding of its hosts. Its growth does not begin until the buds begin to swell, so that not only premature mortality of the stem mothers but also the number of generations in the spring are influenced by the timing of bud burst (FURUTA *et al.*, 1984). Winged females in the 2nd generation emerging on early budding trees fly to late budding trees and there lay larvae at the same time as the stem mothers. The existence of early budding trees and dispersal of winged females contribute to a large aphid population on the late budding trees (FURUTA, 1987).

This aphid lays normal larvae on unfurling leaves or inflorescences and lays aestivating dimorphs on fully expanded leaves (HASHIMOTO & FURUTA, 1988; FURUTA, 1987). Most shoots of *A. palmatum* complete growth in about three weeks after the first emergence of leaves (FURUTA, 1987), and each tree provides the aphids with an abundance of good feeding material for the first two generations in the spring. When there is a large intra-specific variation in the time of budding, it causes prolongation of the period of food supply for the maple aphid, resulting in a broad heterogeneous distribution of favourable feeding materials in both time and space. This plays an important part in the dynamics of the aphid population. This paper reveals that (1) intra-specific variation in the time of budding of *Acer palmatum* is great enough to allow addition of another generation in the spring and (2) the variation is of ecological origin, caused by shade in the forest.

2. Materials and Methods

(1) Length of terminal buds of 5 branches about 2-3 m above the ground of 6 *A. palmatum* trees or the shoots extending from these buds was measured weekly in 1988 during the period from the end of February through early May in Tanashi Wood, the University Forest Experimental Station at Tanashi. One of the 6 trees (No. 1) is in a bamboo stand (Fig. 1) and the others (No. 2-6) are in a maple stand. The trees examined are 4-6 m in height.

At the time of bud measurement, the number of 1st instar larvae on tree No. 1 on the terminal 40 cm portion of the branches was noted. Phenology of the maple aphid was also recorded: first finding of the 2nd instar larvae, adult emergence of winged females in the 2nd generation and larviposition by the stem mothers or winged females.

The visible change of foliage color in the autumn was also observed in 1988. A color chart used for identifying color was divided into 24 hues (1-4: purplish red-reddish orange,

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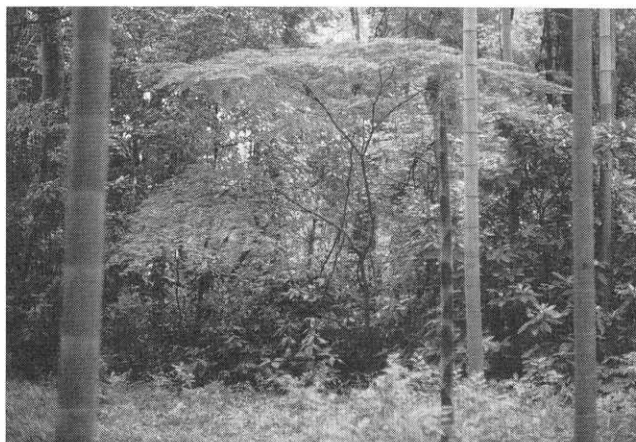


Fig. 1. No. 1 tree in the bamboo stand.

4-8: orange-yellow, 9-12: greenish yellow-green, 13-16: bluish green-greenish blue, 17-20: blue-violet, 21-24: purple-red purple) and into 9 tones (v: vivid, p: pale, lt: light, b: bright, dp: deep, dk: dark, ltg: light grayish, g: grayish, d: dull).

(2) Effect of shade on the budding of maples was examined through a transplantation experiment in the field. In April 1988, five year old potted *A. palmatum* (20-30 cm in height) in the nursery were inspected and 30 trees with a bud length of 5-15 mm were chosen; 10 of these (Group I) were placed in a stand of bamboo and the other 20 (Groups II, III) were placed in the center of the nursery. Group I and II were kept where originally-positioned, but Group III was moved to the bamboo stand in mid-December 1988. In the spring of 1989, length of the terminal buds of the 30 trees was measured weekly from mid-February through early May. Weekly inspection was also made of the developmental stage of maple aphids on the trees as well as on the terminal 40 cm portion of 5-10 branches of 6 *A. palmatum* in Tanashi Wood and 2 *A. palmatum* in a small yard in Tokorozawa. The distance between Tanashi and Tokorozawa is 8 km and there is no remarkable difference in climatic condition. First findings of larviposition of stem mothers and winged females in the 2nd generation were recorded. The intensity of illumination was measured in mid-April and mid-June 1989. Illumination on the floor of the bamboo stand to the sunny place in the nursery was 7% in April and 2.0% in June.

The visible change of foliage color in the autumn was also observed in 1988.

(3) On 2 April 1989, 10 stem mothers just prior to beginning larviposition were captured from tree No. 1. They were released individually on another 10 potted *A. palmatum* which had been placed in the bamboo stand in April 1988. All the trees were kept in cages (2 mm mesh) and the larvae laid by the stem mothers were removed from the trees once every 5-7 days. In this way, the fecundity of stem mothers in the shade was measured.

3. Results

1) Phenology of the maples

Growth curves for the 5 examined buds or shoots of each tree followed a similar trend. Figure 2 shows the growth curves for the earliest and the latest budding trees in 1988. On the earliest (No. 1), the buds started visible growth in early March, young leaves emerged in early April and shoots ca. 20 cm long ceased growing at the end of April. On the other hand, on the latest budding tree (No. 2), visible growth of buds began in late March, young

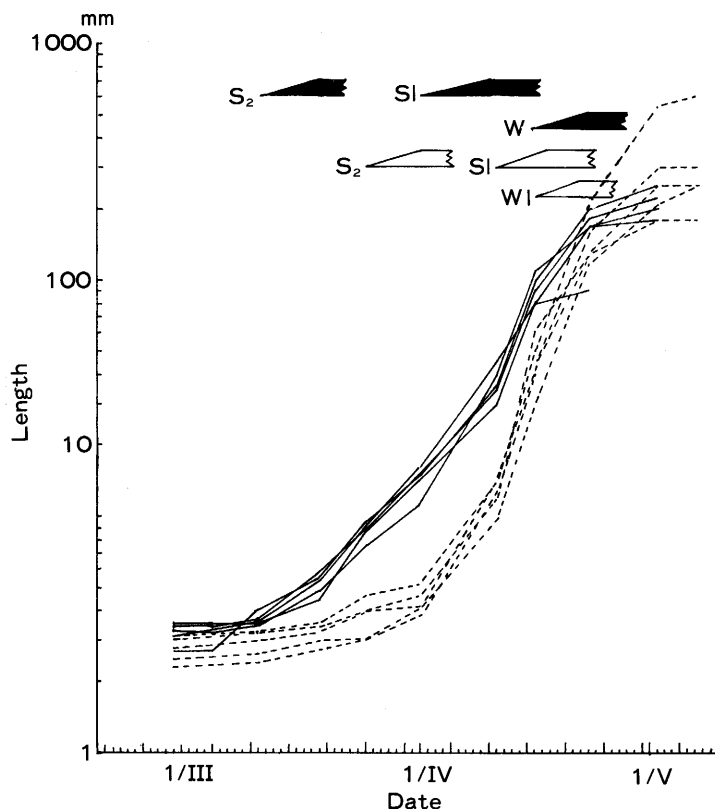


Fig. 2. Growth curves of the buds or shoots emerged from the buds of the two earliest and latest budding trees among the six trees observed and phenology of the maple aphid. S₂: 2nd instar of stem mother. SI: larviposition of stem mother. W: emergence of winged aphid. WI: larviposition of winged aphid.

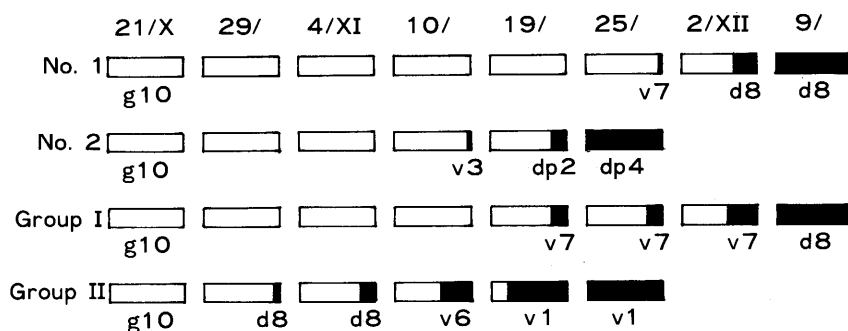


Fig. 3. Seasonal trends of the percentage of visible foliage color in the autumn (shown by black).

leaves emerged in mid-April and growth of shoots *ca.* 20 cm long ceased in early May. Thus great between-tree phenological difference was demonstrated.

The visible changes of foliage color of the earliest and latest budding trees are shown in Fig. 3. Color change and fall of leaves of the tree No. 2 began 2 weeks earlier than No. 1. The hue of No. 2 was reddish orange and that of No. 1 was yellow.

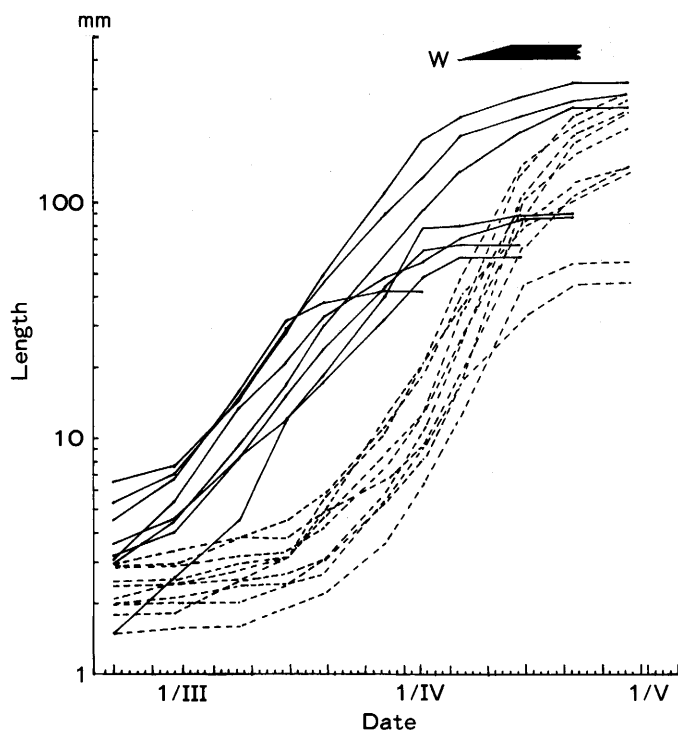


Fig. 4. Growth curves for the terminal buds or shoots emerging from the buds of the of trees in the bamboo stand (—) and in the nursery (----).

2) Transplantation experiment

Stem mothers hatched on 1 and 6 trees of Groups I and II, respectively, and none of the trees of Group III. The number of stem mothers on the tree of Group I was 27. In Group II, except two trees on which there were 189 or 29 aphids, 2–7 ($\bar{x}=4$) aphids were found at most. Growth curves for the buds and shoots of Groups I and II are shown in Fig. 4. When the first measurement was done many buds of Group I had already begun to swell, and though there is great between-tree variation in each group, the difference between groups is clearly shown. Trees of Group I exceeded 5 mm in bud length in early March and exceeded 30–60 mm in shoot length at the end of March. Shoot growth had slowed since about 2 April. In contrast, trees of Group II exceeded 5 mm in bud length at the end of March and 30–60 mm in shoot length in early April. Shoot growth slowed about 15 April. Thus, trees in the shade budded and put forth leaves several weeks earlier than those in the sunny location. Group III was intermediate between Groups I and II. Figure 5 shows the mean accumulated percentage of bud or shoot length which exceeded 20 cm. The shade in spring and also that the previous summer plays an important role in determining the time of budding. Figure 6 shows that there was no large difference in the number of leaves on the shoots of the two Groups I and II. Between node length of the shoots did not increase remarkably in the shade.

Visible color change and fall of leaves of Group II began 2–3 weeks earlier than Group I (Fig. 3). The hue of Group II was purplish red and that of Group I was yellow. Thus it was ascertained that trees in the shade began to change foliage color later than those in the sun and the hue became yellow.

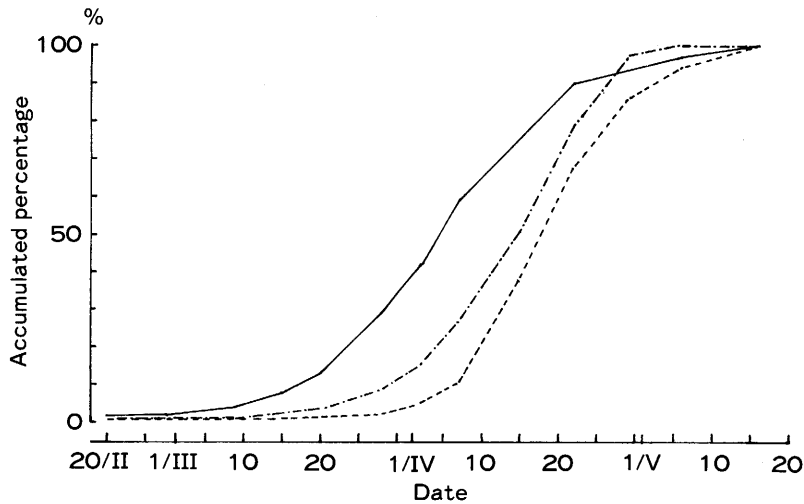


Fig. 5. Mean accumulated percentage of the length (exceeding 20 cm) to the maximum length of the shoot at each observation. Groups I (—), II (---) and III (····).

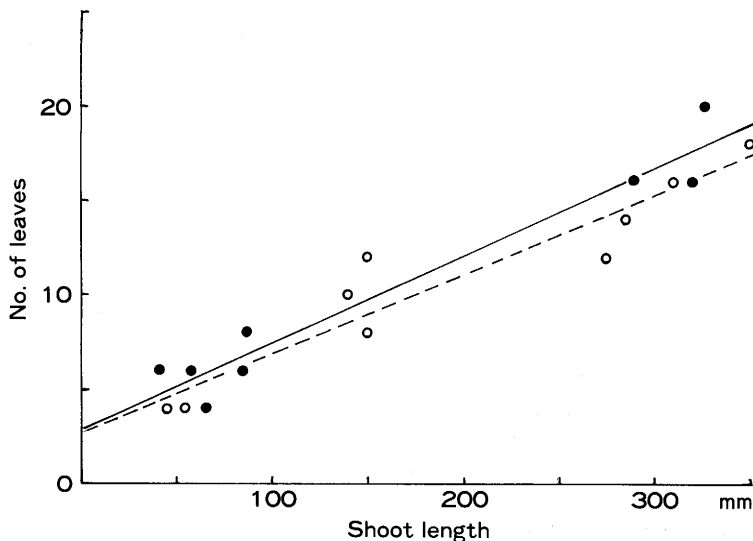


Fig. 6. The number of leaves on each shoot of Groups I (●) and II (○).

3) Phenology of the maple aphid

1988: Hatching of the larvae began during the period from 23 to 29 February. Figure 7 shows the number of 1st instar larvae and the percentage at each observation to the highest number of 1st instar larvae that year. Though the percentage itself does not indicate the accumulated percentage of the larvae hatched, the figure does reveal that most larvae had hatched by 20 March when most buds reached 5 mm in length.

Phenology of the maple aphid differed considerably among the trees (Fig. 2). Second instar larvae appeared at about the time buds reached 5 mm in length, and those on the early budding trees (black) appeared 2 weeks earlier than those on the latest budding (white) tree. Larviposition of the stem mothers was first found when the shoots reached

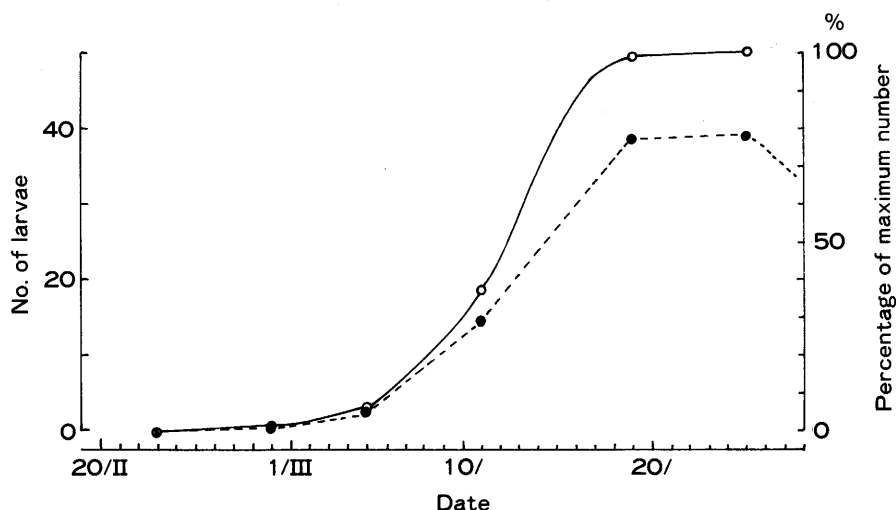


Fig. 7. The number (●) of 1st instar stem mothers of *Periphyllus californiensis* per branch (40 cm) of No. 1 tree and the percentage (○) of the larvae found to the maximum number found.

a length of 30–60 mm. The larviposition of the stem mothers on the earliest budding tree began a week earlier than that on the latest budding tree. Both the adult emergence of the winged females and their larviposition were recognized on 23 April. On the latest budding tree, some winged females laid larvae at the same time as the stem mothers. Thus, the intra-specific variation in the time of budding is great enough to permit addition of another generation.

1989: First larviposition of stem mothers was found on 28 March (2 trees in Tanashi; 1 in Group I), 2 April (2 Tanashi), 7 April (2 Tanashi; 1 Tokorozawa; 3 in Group II) and 15 April (3 Group II). Thus, the time of larviposition differed greatly among trees of the same species, though there was no great difference in climatic conditions except illumination.

Larviposition by winged females arriving from other trees was first found on 14–15 April on 2 out of 6 trees in Tanashi and 1 tree in Tokorozawa. Winged aphids laid larvae at the same time as stem mothers on the same tree. On some *A. palmatum* trees, aphid populations were thus established by both stem mothers and winged females, and on one tree the population was founded by winged females alone.

4) Fecundity of the stem mothers in the shade

All stem mothers placed on the floor of the bamboo stand laid larvae but the fecundity could only be estimated in 4 out of 10, since an accurate count of the number laid by other individuals was not possible. The number of larvae laid by the 4 stem mothers 44–53 ($\bar{x} \pm s = 49.2 \pm 3.9$), larger than that (35.7 ± 12.9) seen on potted trees brought from a sunny location into a thermostatic chamber by HASHIMOTO and FURUTA (1988). Though the fecundity of stem mothers differ according to the host condition, shaded trees may be beneficial for stem mother fecundity.

4. Discussion

Maples have a high adaptability to the shade (KOIKE, 1986, 1987a) and seedlings appear and grow in the shade on the forest floor. Budding begins early, autumnal color change and leaf fall occur late and the leaves become yellow, though they turn red in a sunny place.

When anthocyan is synthesized leaves turn red, however, when there is insufficient light, anthocyan is not synthesized and leaves become yellow which is the color of carotinoids in them (Koike, 1987b). It is therefore quite reasonable that leaves in the shade do not become red.

Though early budding and late defoliation seem advantageous for photosynthesis, trees in the sun put forth leaves late and shed them early. A possible explanation for this may be the cold in early spring and early winter which has a adverse effect on trees in a sunny locations, but information remains too sparse to be certain.

In the forest, maples are usually mixed with other deciduous trees and occupy not only the upper story but also the middle- or under-story. As the maple aphid infests both young and old trees, the distribution of its host is usually highly heterogeneous in the forest.

Heterogeneous distribution of the host is not restricted to space only. As described, trees in the shade put forth leaves several weeks earlier than trees in sunny places. Leaves on lower branches of a high tree must also put forth leaves early. Thus the distribution of favorable feeding materials for maple aphid heterogeneous in time also. Successful utilization of this host heterogeneously distributed both in time and space is only possible when the aphid lays eggs on early budding trees, adjusts its life history to the phenology of the host and disperses among the trees.

Aestivating dimorphs suffer high and density-independent mortality (FURUTA, 1985). Therefore, the duration in an aestivating dimorph state is a factor determining total mortality of this stage. On shaded trees on which aestivating dimorphs must spend a longer period few seem to survive. Unless winged aphids fly from late budding trees and lay oviparous females, no eggs are deposited there. As most winged aphids lay larvae on trees whose foliage is orange-yellow and only a few lay larvae on those which are red (FURUTA, 1986), winged aphids in the autumn tend to lay larvae on shaded trees.

The maple aphid hatches early in the spring before the budding of its host. Because the amount of soluble nitrogen in leaves decreases rapidly (HASHIMOTO and FURUTA, 1988), the aphids are able to utilize each host tree only for several weeks. On early budding trees stem mothers and the larvae they lay take about 3 weeks and 2 weeks, respectively, to complete their development from 2nd instar to first larviposition. In a thermostatic chamber winged aphids completed their development in 10 days at 17°C (FURUTA *et al.*, 1984). Though some shoots of *A. palmatum* continue growing and putting forth leaves for about a month, 90% of the buds of high maples send out leaves 6–8 days after the first leaf emergence (FURUTA, 1987). The aphid population showed poor development in a year when larviposition by stem mothers began 10 days after the first appearance of leaves (FURUTA, 1987). If the stem mother hatches after budding of the host, its larvae will fail to find sufficient food to fully develop. The stem mother must therefore develop as soon as the buds begin to swell. The budding time of maple trees, however, differs not only among species but also among trees of the same species in relation to site conditions. In this situation, hatching of the stem mother before budding assures that the larvae will have adequate food.

Stem mothers often suffer starvation and high mortality during their 1st instar period (FURUTA *et al.*, 1984). The dispersal of winged females from early budding trees to late budding trees therefore has two functions: First, to find suitable material on which to lay their larvae, and second to compensate for the high mortality of stem mothers on late budding trees. Shoots of late budding trees grow a little faster than those of early budding trees once growth begins (Figs. 2 and 4). However, winged aphids lay larvae faster than stem mothers and can utilize late budding trees; stem mothers and winged females lay 50% of their larvae in 3–4 days and 1–2 days, and complete the laying within 8–10 days and 3–4 days, respectively (FURUTA, 1987).

Summary

Maples which have passed a summer in the shade put forth leaves early and shed leaves late. Their autumnal color becomes yellow though that of the trees in the sun become red. Winged maple aphids emerging on shaded *A. palmatum* fly to late budding *A. palmatum* and lay larvae at the same time as the stem mothers. Thus intra-specific variation of the phenology of maples caused by site conditions is great enough to allow addition of another generation for the maple aphid. In the autumn most winged aphids lay larvae mostly on trees of yellow leaves, *i.e.* on shaded trees. Thus, stem mothers overwinter on shaded trees every year.

Key words: phenology, maple, budding, aphid, shade

References

- FURUTA, K. (1985): Spatial distribution and mortality of aestivating dimorphs of the maple aphid, *Periphyllus californiensis* Shinji (Homoptera, Aphididae). *Z. ang. Ent.* **100**, 256-264.
- FURUTA, K. (1986): Host preference and population dynamics in an autumnal population of the maple aphid, *Periphyllus californiensis* Shinji (Homoptera, Aphididae). *J. Appl. Ent.* **102**: 93-100.
- FURUTA, K. (1987): Amounts of favourable feeding materials in spring for the maple aphid, *Periphyllus californiensis* Shinji, estimated from the phenological relations between the aphid and host trees. *J. Appl. Ent.* **104**: 144-157.
- FURUTA, K., H. HASHIMOTO and N. IWAMOTO (1984): The effect of budding and flowering of maple trees on the development of the maple aphid, *Periphyllus californiensis* Shinji (Homoptera, Aphididae) population. *Z. ang. Ent.* **98**: 437-444.
- HASHIMOTO, H. and K. FURUTA (1988): Reproduction of maple aphid (*Periphyllus californiensis*) in spring in relation to phenology of host tree. *Jpn. J. Appl. Ent. Zool.* **32**: 169-175.
- JOURNET, A. R. P. (1980): Intraspecific variation in food plant favourability to phytophagous insect: Psyllids on *Eucalyptus blakelyi* M. *Ecological Entom.* **5**: 249-261.
- KOIKE, T. (1986): Photosynthetic response to light intensity of deciduous broad-leaved tree seedling raised under various artificial shade. *Environ. Control in Biol.* **24**: 51-58.
- KOIKE, T. (1987a): Photosynthesis and expansion in leaves of early, mid and late successional tree species, birch, ash, and maple. *Photosynthetica* **21**: 503-508.
- KOIKE, T. (1987b): Rakuyo koyo-ju no kaiyo to koyo no sikata. *Hoppo-Ringyo* **39**: 322-325.
- MORAN, N. (1981): Intraspecific variability in herbivore performance and host quality: a field study of *Uroleucon caligatum* (Homoptera: Aphididae) and its *Solidago* hosts (asteraceae). *Ecological Entom.* **6**: 301-306.
- SUTTON, R. D. (1974): The effect of host plant flowering on the distribution and growth of hawthorn psyllids (Homoptera: Psylloidea). *J. Anim. Ecol.* **53**: 37-50.
- WRATTEN, S. D. (1974): Aggregation in the birch aphid *Euceraaphis punctipennis* (Zett.) in relation to food quality. *J. Anim. Ecol.* **43**: 191-198.

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被陰によるイロハモミジの早期開芽

——モミジニタイケアブラムシの寄生の種内不均質性——

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要 旨

イロハモミジの春の開葉時期には個体により大きな差がある。この差が環境条件，すなわち被害によってひきおこされることを実験的に確かめ，アブラムシの生息環境としての影響を考察した。

鉢植のイロハモミジの若い苗木の中から同じ程度の芽の伸びを示すものを1988年4月に選出し，竹林の林床と日あたりのよい苗畑にただちに移したものの，12月まで苗畑に放置したのち竹林に移したもののについて1989年春の生物季節を観察した。その結果，被陰によって芽と新梢の伸長は著しく早まることが確認された。なお，1988年秋の紅葉と落葉の時間には遅れが生じ，苗畑のカエデの葉は赤く紅葉したが，竹林のカエデは黄色く変色した。

芽と新梢の伸長が早まることにより，被陰下のカエデ上のモミジニタイケアブラムシは早く発育を開始し，そこで羽化した有翅成虫は伸長の遅い同種のカエデ上に飛来し，そのうえで発育した幹母と同時に産仔した。このことによりアブラムシは春に1世代多く経過することができるとともに，森林に存在するカエデを有効に利用することになる。また，被陰下のカエデは秋に黄色に変色するが，秋の有翅虫は黄色い葉上で産仔する傾向があるので，有翅虫が飛来して有性世代虫を産下するのに適している。このことは春に被陰下のカエデで幹母が早く発育を開始することを確実にする効果がある。日陰や日あたりという環境の多様性はアブラムシの生息空間を時間的に多様なものとしている。

キーワード： カエデ，生物季節，アブラムシ，日陰，生息場所