Host-plant mediated geographic variation in the life history of *Platycotis vittata* (Homoptera: Membracidae)

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Abstract. 1. The oak treehopper *Platycotis vittata* (Fabricius) is bivoltine throughout its range with discrete generations in the early spring and autumn. Females of both generations diapause.

2. Latitudinal variation in the timing of life history exists among four populations of *P. vittata* along the eastern coastal plain of the United States.

3. We disrupted synchronization between *P. vittata* life history and host-plant phenology in the springs of 1984 and 1985 by placing southern populations on northern trees with a different phenology. This caused some females to oviposit abnormally in late spring, without entering diapause. The offspring of these females had reduced reproductive success.

4. Winter diapause can be broken by providing females with a newly flushing tree with high levels of amino nitrogen in the sap. Females terminated winter diapause on trees breaking winter dormancy while females on trees still in winter dormancy did not, under identical photoperiod and temperature regimes.

5. The role of host-plant mediated life history variation as a process promoting intraspecific geographic differentiation in the arboreal sap-feeding guild is discussed.

Key words. Life history, plant phenology, sap-feeder, geographic variation, *Platycotis*, diapause, nitrogen, *Quercus*.

Introduction

Life histories of arboreal, sap-feeding insects are moulded by their intimate association with their host plant. At a microgeographic level, phenological and chemical variation in persistent host plants (trees) can shape the life histories and genetic structure of host-specialist homopteran species. For example, in aphids, growth

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and reproduction depend on levels of soluble nitrogen in phloem sap (Dixon, 1970), which is highest during spring flush and leaf senescence. These cyclic or seasonal changes in host-plant quality may promote aestivation or alternation of host plants (Dixon, 1977). Non-vagile scale insect genotypes have apparently adapted to particular *Pinus ponderosa* L. trees with a given array of chemical defences, while adjacent trees with different defences remain unexploited (Edmunds & Alstad, 1978).

In some univoltine treehoppers, life histories are mediated by host-plant phenology (Wood,

1980; Wood & Guttman, 1981, 1982, 1983; Wood, Olmstead & Guttman, 1990). This may promote race formation or reproductive isolation when shifts to novel host plants occur. If differences in insect life history effected by host-plant phenology can lead to local genetic divergence, then these same factors over the species' entire geographic range should promote considerable intraspecific variation. Since plant phenology varies latitudinally, host plant tracking by a specialist should promote latitudinal variation in insect life histories.

Evidence for latitudinal variation in insect seasonal cycles is extensive (see Tauber *et al.*, 1986, for a review). Diapause is the most significant synchronizing element in insect life cycles (Danilevsky, 1965; Tauber & Tauber, 1976) and most latitudinal variation has been explained by variation in diapause characters. Stimuli such as photoperiod and temperature are the most often cited mechanisms for diapause induction and termination (Beck, 1968; Masaki, 1980; Tauber & Tauber, 1981). Until recently, nutrition received little attention (Beck, 1968; Hodek, 1983), although recent studies demonstrated its role in modification of photoperiod effects (Usua, 1973; Istock *et al.*, 1975).

Here we test the hypothesis that subtle differences in insect life history, effected by host-plant phenology, can lead to considerable intraspecific geographic variation in life history. First we document latitudinal variation in the timing of life histories in four populations of the oak treehopper *Platycotis vittata* (Fabricius). Second, we examine the effect of disrupting the synchronization of insect life history from host-plant phenology on female reproductive success. This is done by transplanting cohorts from the southern populations to trees in a more northern location. Third, we examine the mechanism for diapause termination by placing cohorts from the same population on trees in different phenological stages under identical photoperiod and temperature regimes. Finally, seasonal changes in the availability of nutrients, a key element in this theory, are described.

Methods

Study organism. The distribution and biology of *Platycotis vittata* are unique for oak-inhabiting treehoppers. It is the only species that occurs in both the eastern and western United States. It has been reported on over thirty species of *Quercus* and occupies approximately 60% of the geographic range of its host plants (Fig. 1), suggesting a long historical association. *P. vittata* is presocial (T.K.W., pers. obs.), in that females remain with offspring until they become adults (Wood, 1976). Its life history is bivoltine throughout its range, with discrete generations in the early spring and autumn (Wood, 1976). The spring generation hatches around the time of bud break from eggs deposited in branches. The larvae feed gregariously and reach imaginal stage in 5–6 weeks. Newly-emerged adults are aposematically coloured (whitish-yellow with several red, longitudinal vittae) but later become cryptically coloured (brown to brownish-green). The spring generation females enter a summer diapause, in which feeding and mating, but not ovarian development, occur. They lay eggs in late summer, giving rise to an autumn generation. The adults mate before the onset of winter. The females enter an overwintering diapause, emerging in late winter to deposit eggs that give rise to the next spring generation. The seasonal timing of the two generations suggest they may track host-plant quality to ensure that sufficient resources are available for offspring (Wood *et al.*, 1984).
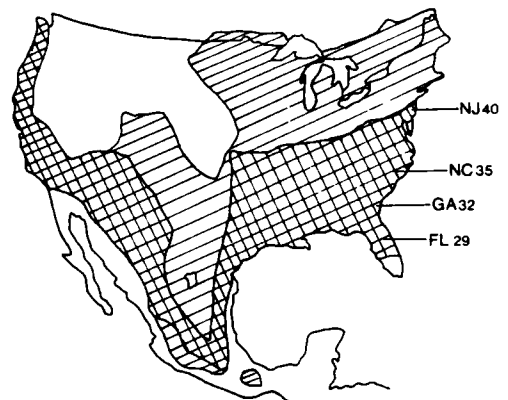

Fig. 1. Geographic distribution of *Platycotis vittata* in North America overlayed on the geographic distribution of its host plant, *Quercus*. Cross-hatching indicates areas of overlap between *Platycotis vittata* and *Quercus* distribution, while single-lined areas indicate where *Quercus* is present without *P. vittata*. Sites and site latitudes for the source populations are indicated.

Latitudinal variation in Platycotis vittata life history. As an indicator of seasonal variation in life history timing, the presence of teneral (newly eclosed) adults in both spring and autumn for each of four populations (Volusia Co., Florida, Savannah, Georgia, Lumberton Co., North Carolina and Burlington Co., New Jersey) (see Fig. 1) was determined from 178 museum specimens (tenerals have a distinct coloration and are easily distinguished) and the more than 3000 adults collected by both authors over a 4-year period. These four populations were used in subsequent experiments and for brevity we shall refer to them by their state of origin.

Disruption of synchrony between Quercus phenology and insect life history. Fifth instar nymphs and teneral adults were collected from Florida and New Jersey and transported to Newark, Delaware, in the spring of 1984. The host plants used for the experiment were grown in a 10 × 30 m clearing in the corner of a 14 ha woodlot on the campus of the University of Delaware. It contained two to five trees from each of seven species of oak (*Quercus alba* L., *Q.prinus* L., *Q.macrocarpa* Michx., *Q.rubra* L., *Q.phellos* L., *Q.coccinea* Muenchh. and *Q.velutina* Lam.) which had been transplanted as saplings in 1980. These trees varied in height from 2.5 to 4.5 m. *Platycotis vittata* aggregations occur naturally on trees of this size, and the insects could be observed easily. A single tree from each species except *Q.velutina* was used for the experiment. Twenty females and fifteen males from each population were placed on each tree in a polyester sleeve cage. Since each tree was a different species, a randomized complete block design was used with the individual trees as the blocking variable.

Due to latitudinal variation in adult eclosion, each population was placed on the experimental trees at a different time and consequently at a different stage of host plant phenology. Teneral adults were collected in Florida in early April and held in a glasshouse on oaks that were in full leaf until bud break occurred in Newark (20 April). Teneral adults were collected in New Jersey in late May−early June and were immediately placed on the experimental trees. Therefore, New Jersey adults were less than 1 week old when placed on the experimental trees while Florida adults were 3 weeks old. Florida adults were placed on the trees at bud break,

New Jersey adults 6 weeks after bud break.

This experiment (hereafter referred to as the transplant experiment) was expanded in 1985 to include populations from Georgia and North Carolina, in addition to those from Florida and New Jersey. In 1985, Georgia, North Carolina and New Jersey adults were less than 1 week old when placed on the trees, Florida adults were 3 weeks old. Florida and Georgia adults were placed on the trees at bud break, North Carolina adults 3 weeks post-bud break, and New Jersey adults 6 weeks post-bud break (see Fig. 2). The effect of this experimental manipulation was to present adults from North Carolina, Georgia and Florida with host plants in a different phenological stage than they would
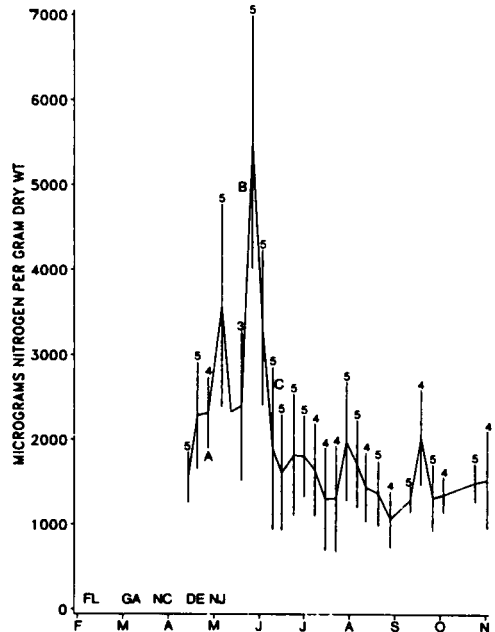

Fig. 2. Timetable of experimental manipulations in the transplant experiment. The symbols FL, GA, NC, DE and NJ correspond to the time of *Quercus* bud break in each of the respective populations. Cohorts from the Florida and Georgia populations were placed on the experimental trees at time 'A', North Carolina at time 'B' and New Jersey at time 'C'. The graph is a plot of the seasonal changes in soluble amino nitrogen of sap in *Quercus* stems, measured as micrograms per gram dry weight versus time. Vertical lines represent the standard error of the mean. The number above each line indicates sample size for that sample date.

normally encounter in their natural geographic location.

Life history data for spring generation females (day of oviposition, age at oviposition, clutch size) and their offspring (egg development time, per cent egg hatch, nymphal survival and development time and adult body weight) were recorded to determine the effect of disrupting host plant synchronization on female reproductive success. Per cent egg hatch and nymphal survival were arcsine transformed, while all other variables were natural log transformed prior to analysis. Latitudinal effects were analysed using PROC GLM (SAS Institute Inc., 1982).

Seasonal changes in availability of nutrients. Since water and nitrogen are the two nutrients most often cited as being limiting for phytophagous insects (Southwood, 1973), they were measured as an indication of overall hostplant nutritional quality. Two to three apical stems were collected weekly from 12 April to 27 October 1985 from five of the six trees species used in the transplant experiment. Stems were not collected from *Quercus macrocarpa* due to an insufficient amount of plant material. Due to the destructive nature of the sampling, the trees sampled were adjacent to, rather than the same trees that were used to rear the insects. Their close proximity to the experimental trees should have minimized differences between the trees sampled and the trees the insects were raised on.

The leaves were stripped, and the stems weighed. The stems were freeze-dried to a constant weight and per cent water content calculated. They were then extracted with 10 ml of 80% ethanol for 4 min in a mortar and pestle and washed with an additional 10 ml of 80% ethanol. Extract and residue were centrifuged at 3000 g for 10 min, the supernatant removed and the pellet reextracted twice. The combined supernatants were reduced with a rotovap, freeze-dried to dryness and partitioned with 8 ml each of chloroform and water. The aqueous fraction was filtered, buffered with 2 ml of pH 5.5 sodium acetate, and then assayed for soluble amino nitrogen using a ninhydrin reaction (Blackburn, 1968). Results were analysed for differences between sample dates using a repeated measures ANOVA, correcting for autocorrelation with the Greenhouse-Geiser method (BMDP, 1977).

Synchronization of life history by host-plant tracking. To test if *P. vittata* synchronizes its life history by tracking host-plant quality, five 2 m *Quercus rubra* trees were kept in a cold, dark room for 1 month to accelerate winter dormancy, then placed in a glasshouse on 3 December 1985 under natural photoperiod. Three small cohorts of adult *P. vittata* (two or three males and three to five females) from each population were caged on these trees while two cohorts (five males and ten females) each from New Jersey and Florida were caged under identical conditions on red oaks naturally beginning winter dormancy. Cages were checked daily for oviposition. All trees were moved to a growth chamber on 10 January 1986 at 16:8 LD and a temperature of 27°C to stimulate plant growth.

Results

Latitudinal variation in life history

Considerable variation in *P. vittata* life history exists along a latitudinal transect in the eastern United States. The geographical extremes differ in eclosion times by 2 months in each generation. The occurrence of teneral adults decreases progressively with increasing latitude. Spring generation teneral adults appear in late March in Florida and in early June in New Jersey. Autumn generation tenerals appear in late September in New Jersey but not until late November in Florida. Georgia and North Carolina are intermediate between these two extremes. This overall pattern is consistent between years.

The latitudinal variation in *P. vittata* life history also exists when the synchrony between *Quercus* phenology and insect life history is disrupted (transplant experiment). Autumn generation nymphs became adults at the same time as if in their natural locality. Spring generation females from New Jersey oviposit earliest followed by North Carolina, Georgia and Florida females ($F=56.15$, $P<0.001$). New Jersey females were youngest at oviposition followed by North Carolina, Georgia and Florida females ($F=408.09$, $P<0.001$) (Table 1). New Jersey eggs hatched within the shortest time in the autumn, while Florida eggs developed slowest ($F=16.67$, $P<0.001$). There

Table 1. Latitudinal variation in life history traits for spring generation females from the transplant experiment. Oviposition and female age are, respectively, the day that females oviposited (day 1=the day the first diapausing female oviposited), and the female's age on that day. The units for clutch size are number of eggs per egg mass. Egg development is measured in days from oviposition to the beginning of egg hatch. The values are means plus or minus the standard error of the mean. Egg development and per cent egg hatch were calculated per egg mass. Numbers in parentheses are sample sizes. Significance values are *P=0.05, **P=0.01, ***P=0.001.

	New Jersey	North Carolina	Georgia	Florida	F	P
1985						
Oviposition	11.2±0.6 (76)	19.3±1.1 (46)	29.3±1.7 (35)	45.6±1.1 (44)	56.15	***
Female age	75.2±0.6 (76)	99.3±1.1 (46)	136.3±1.7 (35)	172.6±1.1 (44)	408.09	***
Clutch size	43.4±1.2 (72)	36.7±1.7 (41)	42.5±2.4 (33)	46.7±2.6 (44)	1.88	0.186
Egg development	15.7±0.4 (64)	17.3±0.7 (32)	18.1±1.0 (26)	24.5±0.9 (40)	16.67	***
Per cent hatch	96.5±0.9 (66)	95.4±1.6 (39)	97.0±1.7 (29)	93.4±2.2 (39)	3.15	0.058
1984						
Oviposition	7.1±0.6 (53)			35.4±0.8 (47)	97.77	***
Female age	66.1±0.6 (53)			163.4±0.8 (47)	1253.37	***
Clutch size	36.6±1.5 (53)			47.9±1.6 (47)	16.52	**
Egg development	13.0±0.3 (50)			27.0±0.9 (39)	87.23	***
Per cent hatch	88.5±1.8 (50)			96.3±1.3 (39)	15.77	*

was no difference between populations in clutch size (F=1.88, 0.15<P<0.20), per cent egg hatch (F=3.15, P=0.058), nymphal development (egg hatch to adult) (F=2.31, P=0.098), or adult female weight at eclosion (F=0.01, P>0.99), but nymphal survival was lower in the Florida population (F=3.33, P<0.01) (Table 2). In 1984 the results were identical except for larger clutch size (F=16.52, P<0.01) and higher per cent hatch (F=15.77, P<0.05) in the Florida popu-

lation (Table 1). There was no significant variation among trees in either year (Table 3).

Seasonal changes in availability of nutrients

Water content in the stems varies during the growing season (Fig. 3). It is significantly higher during the spring flush following bud break (F=9.71, P<0.01). Soluble amino nitrogen levels in the sap are also significantly higher during the

Table 2. Latitudinal variation in life history traits for autumn generation nymphs from the transplant experiment. Per cent survival was calculated for each host species since multiple-egg mass feeding aggregations were often formed. Nymphal development is measured as days from mean day of egg hatch on that host species to day of eclosion. Female weight is measured in milligrams. Numerical and significance values are as in Table 1.

	New Jersey	North Carolina	Georgia	Florida	F	P
1985						
Per cent survival	13.3±7.8 (6)	25.8±7.0 (6)	8.5±7.7 (6)	1.0±0.3 (6)	3.33	**
Development time	36.7±2.3 (89)	38.6±3.2 (164)	36.8±4.1 (118)	37.1±3.8 (10)	2.31	0.098
Female weight	27.3±0.7 (51)	34.5±0.8 (91)	24.2±1.4 (69)	29.1±2.3 (4)	0.01	0.991
1984						
Per cent survival	3.8±3.5 (6)			0.1±0.1 (6)	8.81	*
Development time	42.0±5.2 (65)			36.0±3.7 (2)	1.22	0.328
Female weight	24.9±6.0 (36)			29.7±4.5 (2)	0.78	0.544

Table 3. Variation among trees in life history traits from the transplant experiment.

	F	P
1985		
Oviposition	0.49	0.77
Female age	0.49	0.77
Clutch size	2.13	0.12
Egg development	1.65	0.21
Per cent hatch	1.23	0.35
Nymphal survival	1.60	0.22
Nymphal development	1.48	0.36
Female offspring weight	0.08	0.99
1984		
Oviposition	0.24	0.93
Female age	0.24	0.93
Clutch size	0.43	0.81
Egg development	1.20	0.42
Per cent hatch	3.88	0.08
Nymphal survival	1.99	0.23
Nymphal development	2.12	0.18
Female offspring weight	0.79	0.65
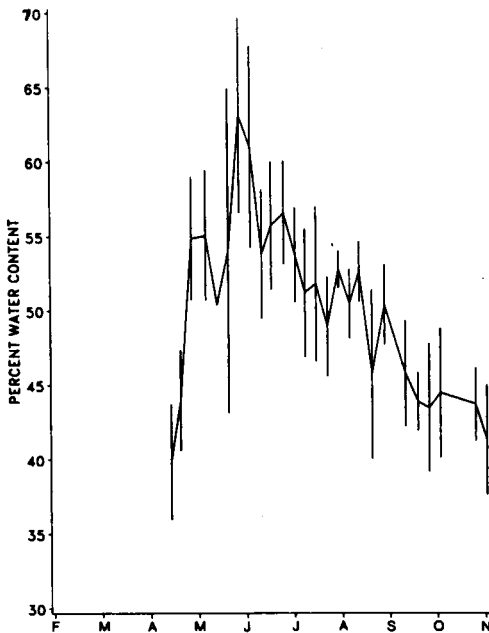
Fig. 3. Plot of seasonal changes in per cent water content in *Quercus* stems versus time. Vertical lines represent the standard error of the mean with a sample size of five trees per sample date.

spring flush ($F=9.55$, $P<0.01$) (Fig. 2). Neither water content nor soluble amino nitrogen show a peak in the autumn, when the autumn generation of *P. vittata* is developing.

Disruption of synchrony between Quercus phenology and insect life history

The transplant experiment involved manipulating the relationship between insect life history and host-plant phenology such that adults from Florida, Georgia and North Carolina experienced a different *Quercus* phenology than they would have in their natural environment. Four North Carolina and twenty-one Georgia females of the spring generation, exposed to the higher levels of soluble amino nitrogen (Fig. 2), oviposited in late May and early June without entering summer diapause (see Table 4). We shall call this 'abnormal' oviposition as opposed to oviposition in late summer after diapause, which we shall call 'normal'. Significantly more females from Georgia than North Carolina oviposited abnormally ($F=5.04$, $P<0.05$), but no Florida females oviposited abnormally.

The importance of timing oviposition to coincide with the availability of nutrients should become apparent by examining the reproductive success of the females which oviposited abnormally. Females that oviposited abnormally had larger clutch sizes than females that oviposited normally (Georgia: $F=10.46$, $P<0.01$; North Carolina: $F=23.92$, $P<0.01$) (Table 4). Nymphal development was faster for the offspring of abnormal Georgia females ($F=9.64$, $P<0.05$), but there was no difference within the North Carolina population ($F=0.92$). None of the other life history parameters were significantly different (Table 4).

However, the reproductive success of their offspring was dramatically different. None of the offspring of North Carolina females that oviposited abnormally survived to reproduce, while only 31% of the female offspring of abnormal Georgia females oviposited in late August and September (Table 4). A random sample of the offspring of Georgia and North Carolina females that oviposited normally were collected in mid-November and mated. These females oviposited on newly flushing trees in the glasshouse. They had a higher per cent oviposition, clutch size and per cent egg hatch

Table 4. Costs of abnormal oviposition on female and offspring reproductive success. Numerical and significance values are as in Tables 1 and 2.

	North Carolina				Georgia			
	Abnormal	Normal	F	P	Abnormal	Normal	F	P
Eggs								
Female age	65.1±6.4 (4)	109.3±7.3 (46)	16.54	*	47.5±3.9 (21)	135.6±6.6 (35)	111.51	***
Clutch size	59.4±5.8 (4)	36.7±4.1 (41)	23.92	**	62.5±4.8 (21)	43.3±4.0 (33)	10.46	**
Development time	14.5±1.6 (4)	17.3±2.0 (32)	0.92	0.43	16.4±1.3 (17)	18.9±1.6 (26)	9.64	*
Per cent hatch	98.5±4.4 (4)	95.4±4.2 (39)	0.57	0.51	96.2±2.7 (20)	98.4±2.7 (29)	1.49	0.29
Nymphs								
Per cent survival	9.0±0.9 (3)	20.1±7.4 (6)	1.66	0.29	10.6±6.3 (6)	1.5±4.4 (6)	2.81	0.17
Development time	46.1±3.2 (21)	39.0±1.3 (164)	N/A		34.8±2.6 (134)	49.0±1.3 (118)	8.95	0.21
Offspring (females)								
Adult weight	No obs.	34.5±0.8 (91)	N/A		21.4±1.5 (83)	24.2±1.4 (69)	0.28	0.65
Per cent oviposition	No obs.	100.0±0.0 (16)	N/A		31.0±1.9 (6)	87.5±5.7 (6)	11.22	*
Clutch size	No obs.	50.0±2.7 (16)	N/A		29.0±2.4 (26)	47.5±3.3 (14)	20.78	***
Nymphal survival	No obs.	2.9±0.8 (6)	N/A		0.0±0.0 (6)	2.3±1.1 (6)	4.37	0.06

No obs. indicates no observations were available since no offspring of 'abnormal' North Carolina females survived to reproduce. N/A indicates that no statistical test was performed. For North Carolina nymphal development time, this was due to insufficient sample size (number of trees with nymphs surviving to adulthood).

than did the female offspring of Georgia females that oviposited abnormally (Table 4).

Synchronization of life history by host-plant tracking

Thirty-three of the forty-eight females placed on the red oaks that had their winter dormancy accelerated oviposited in the glasshouse under natural photoperiod, while none of the females on the trees in normal winter dormancy oviposited. Oviposition occurred from 16 December 1985 to 21 January 1986. Most ovipositional activity occurred prior to moving the trees to the growth chamber on 10 January. All five 'accelerated' trees broke bud between 21 and 23 January, while the control trees broke bud between 10 and 15 March. Females terminated winter diapause on trees breaking winter dormancy while females on trees still in winter dormancy did not, under identical photoperiod and temperature regimes.

Discussion

Directional variation in life history timing along a latitudinal gradient may lead to differentiation in genotype or phenotype frequencies. Simple cline models suggest that differences in gene frequencies can evolve along a smooth environmental gradient, in spite of continuous gene flow, if dispersal distance is small (Endler, 1977). The length of the growing season increases clinally from north to south, causing concomitant variation in *Quercus* phenology. Synchronization of *P. vittata* life history with host-plant phenology promotes latitudinal variation in *P. vittata*'s phenology. This variation results in a 3–4-month difference in summer diapause duration between extremes of the latitudinal transect. Summer diapause duration is shortest, but winter diapause longest, in New Jersey. Latitudinal variation in timing of diapause termination may result in asynchronous insect phenologies among populations possibly leading to host race formation and speciation (Tauber & Tauber, 1981).

Egg hatch and nymphal development in the spring corresponds to spring flush in *Quercus*, when water and nitrogen levels in the sap are highest. There is a large cost to asynchrony between *P. vittata* life history and *Quercus*

phenology. The Georgia and North Carolina females in the transplant experiment that did not enter summer diapause, deposited eggs when oviposition in these populations normally does not occur. There were no negative effects on their offspring compared to offspring of females which did diapause, probably because the levels of soluble amino nitrogen available during both groups' nymphal development were comparable.

However, there were large differences in the reproductive success of the female offspring. The abnormal spring oviposition apparently decoupled *P. vittata* life history phenology from the phenology of the host plant, preventing the female offspring from accumulating sufficient energy for reproduction and resulting in greatly reduced fitness. This very strongly suggests that synchronized timing of life histories with host phenology is critical in determining reproductive success.

Since proper timing of oviposition is critical to reproductive success, a reliable mechanism for determining when to oviposit is needed. *Platycotis vittata* feed on the phloem sap for hours at a time, providing the opportunity to closely track changes in host-plant quality as cues for diapause induction and termination. Although we know of no previous studies that directly measure seasonal variation in water and nitrogen content in *Quercus* stems, the pattern of high levels in the spring with a decline throughout the summer is supported by studies of other north temperate deciduous tree species both for nitrogen (Mittler, 1958; Thomas, 1927) and water content (Gibbs, 1939). The evidence provided from the glasshouse experiment suggests that changes in host-plant nutrition can cue winter diapause termination in *P. vittata* although an interaction between host-plant nutrition and photoperiod cannot be ruled out.

Induction of summer diapause also appears to be cued by host-plant nutrition. The Georgia and North Carolina females displayed bimodal egg laying, ovipositing under two different photoperiod and temperature regimes. While some Georgia and North Carolina females oviposited early, during the spring peak in host-plant nutrition, none of the Florida females did. The Florida females were already 3 weeks old when exposed to the high nitrogen levels of the flushing trees. They had been maintained for those 3 weeks on trees in full leaf in the glass-

house. These trees presumably were in a similar phenological state to the Florida trees. This suggests that there may be a critical period during which a female either begins ovarian development or delays it by entering diapause. This decision may be determined by host-plant quality.

This study has demonstrated latitudinal variation in the life history of *Platycotis vittata*. The variation appears to be the result of synchronization of life history with the phenology of the host-plant. These results raise several questions regarding the *Platycotis–Quercus* system and interactions between arboreal, sap-feeding insects and their host-plants in general. How frequently do such interactions display the latitudinal variation in life history that exists in *Platycotis vittata*? Can such latitudinal variation provide barriers to gene flow as Endler's models suggest? Will this lead to geographic differentiation between populations in morphological or physiological traits, or even to genetic divergence? The answers to these questions are unknown. Preliminary evidence suggests that morphological differences do exist between populations of *Platycotis vittata*, but it is unclear whether there are genetic differences. Further research needs to be done to determine whether the process described here is important in promoting intraspecific geographic differentiation in the arboreal, sap-feeding insect guild.

Acknowledgments

References

Beck, S.D. (1968) *Insect Photoperiodism*. Academic Press, New York.

Blackburn, S. (1968) *Amino Acid Determination: Methods and Techniques*. Marcel Dekker, New York.

BMDP (1977) University of California Press, Berkeley.

Danilevsky, A.S. (1965) *Photoperiodism and Seasonal Development of Insects*. (English translation). Oliver and Boyd, London.

Dixon, A.F.G. (1970) Quality and availability of food for a sycamore aphid population. *Animal Populations in Relation to their Food Resources* (ed. by A. Watson), pp. 272–287. Blackwell Scientific Publications, Oxford.

Dixon, A.F.G. (1977) Aphid ecology: life cycles, polymorphism and population regulation. *Annual Review of Ecology and Systematics*, 8, 329–353.

Edmunds, G.F. & Alstad, D.N. (1978) Coevolution in insect herbivores and conifers. *Science*, 199, 941–945.

Endler, J.A. (1977) *Geographic Variation, Speciation and Clines*. Princeton University Press.

Gibbs, R.D. (1939) Studies in tree physiology. I. General introduction: water contents of certain Canadian trees. *Canadian Journal of Research*, 17, 460–482.

Hodek, I. (1983) Role of environmental factors and endogenous mechanisms in the seasonality of reproduction in insects diapausing as adults. *Diapause and Life Cycle Strategies in Insects* (ed. by V. K. Brown and I. Hodek), pp. 9–34. Junk, The Hague.

Istock, C., Wasserman, S.S. & Zimmer, H. (1975) Ecology and evolution of the pitcher-plant mosquito. 1. Population dynamics and responses to food and population density. *Evolution*, 29, 296–312.

Masaki, S. (1980) Summer diapause. *Annual Review of Entomology*, 25, 1–25.

Mittler, T.E. (1958) Studies on the feeding and nutrition of *Tuberolacnus salignus*. II. The nitrogen and sugar composition of ingested phloem sap and excreted honeydew. *Journal of Experimental Biology*, 35, 74–84.

SAS (1982) *SAS User's Guide*. SAS Institute Inc., NC.

Southwood, T.R.E. (1973) The insect/plant relationship — an evolutionary perspective *Insect/Plant Relationships* (ed. by H. F. van Emden), pp. 3—30. Royal Entomological Society London Symposium No. 6, London.

Tauber, C.A. & Tauber, M.J. (1981) Insect seasonal cycles: Genetics and evolution. *Annual Review of Ecology and Systematics*, **12**, 281—308.

Tauber, M.J. & Tauber, C.A. (1976) Insect seasonality: diapause maintenance, termination and post-diapause development. *Annual Review of Entomology*, **21**, 81—107.

Tauber, M.J., Tauber, C.A. & Masaki, S. (1986) *Seasonal Adaptations of Insects*. Oxford University Press.

Thomas, W. (1927) Nitrogenous metabolism of *Pyrus malus*. III. The partition of nitrogen in leaves, one- and two-year branch growth and non-bearing spurs throughout a year's cycle. *Plant Physiology*, **2**, 109—137.

Usua, E.J. (1973) Induction of diapause in the maize stemborer *Busseola fusca*. *Entomologia Experimentalis et Applicata*, **16**, 322—328.

Wood, T.K. (1976) Biology and presocial behavior of *Platycotis vittata* (Fabricius) (Homoptera: Membracidae). *Annals of the Entomological Society of America*, **69**, 807—811.

Wood, T.K. (1980) Divergence in the *Enchenopa binotata* Say complex (Homotera: Membracidae) effected by host plant adaptation. *Evolution*, **34**, 147—160.

Wood, T.K. & Guttman, S.I. (1981) The role of host plants in the speciation of treehoppers: an example from the *Enchenopa binotata* complex. *Insect Life History Patterns: Habitat and Geographic Variation* (ed. by R. F. Denno and H. Dingle), pp. 39—54. Springer-Verlag, New York.

Wood, T.K. & Guttman, S.I. (1982) Ecological and behavioral basis for reproductive isolation in the sympatric *Enchenopa binotata* complex (Homoptera: Membracidae). *Evolution*, **36**, 233—242.

Wood, T.K. & Guttman, S.I. (1983) *Enchenopa binotata* complex: sympatric speciation? *Science*, **220**, 310—312.

Wood, T.K., Guttman, S.I. & Taylor, M.C. (1984) Mating behavior of *Platycotis vittata* (Fabricius) (Homoptera: Membracidae). *American Midland Naturalist*, **112**, 305—313.

Wood, T.K., Olmstead, K.L. & Guttman, S.I. (1990) Insect phenology mediated by host-plant water relations. *Evolution* (in press).