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INSECT PHENOLOGY MEDIATED BY HOST-PLANT WATER RELATIONS

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Abstract.—Water relations of host plants modify *Enchenopa binotata* life histories by mediating the termination of egg dormancy, thereby promoting synchronization of egg hatch. Dormant eggs must undergo dehydration and subsequent hydration to begin development. Dehydration of eggs is brought about in the field by declining water levels in branches during the fall and by prolonged cold. Hydration of eggs occurs when sap begins to rise in early spring. Since the ascent of sap occurs at different times in the six species of *Enchenopa* host plants, the phenology of egg hatch and adult maturation are allochronic. Shifts to novel host plants differing in phenology promote asynchrony of *Enchenopa* life histories among host-plant species. Thus, the host plant acts as an extrinsic disruptive factor that may promote genetic divergence and temporal reproductive isolation in *Enchenopa*.

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The major issue in the sympatric-speciation debate (Bush, 1975; Futuyma and Mayer, 1980; Jaenike, 1981) is whether mechanisms exist that are sufficiently disruptive to impede gene flow among populations. In terms of host-plant shifts by phytophagous insects, genetic traits associated with host recognition, mate selection, and survival are considered to precede or accompany the acquisition of a novel host. Continued selection pressures imposed by host plants then promote further divergence and reproductive isolation (Bush, 1975).

Alternatively, some characteristic of the host plant may be sufficiently disruptive to insect life histories to favor genetic divergence. If host-plant phenologies mediate insect life histories, phenological variation among host species could alter temporal relationships among sympatric populations of insects. Thus, if herbivore life histories are tightly coupled to host-plant phenologies, shifts to novel host species that differ in phenology could promote assortative mating, a prerequisite for sympatric divergence, along host-plant lines (Wood, 1980).

The *Enchenopa binotata* Say complex is a model system for testing the hypothesis that host-plant phenology can be sufficiently disruptive to act as an extrinsic barrier to gene flow. *Enchenopa binotata* is a complex of univoltine treehoppers (Homoptera: Membracidae) that utilizes six genera of deciduous trees in eastern North America. In the spring, egg hatch is synchronous on each host plant but is asynchronous among sympatric host-plant species even on a microgeographic scale (Wood and Guttman, 1982). When female *Enchenopa* are forced to oviposit on inappropriate hosts, eggs hatch in relation to the phenology of that host rather than the parent host plant (Wood and Guttman, 1983). Oviposition begins in late summer and continues through early fall. Eggs are inserted under the bark of branches in contact with the vascular tissue and are protected by egg froth throughout the winter (Wood and Patton, 1971). In the spring, a sign of egg maturation is a localized swelling of the bark in the area of the egg mass (Wood, pers. observ.). Egg hatch occurs in the spring, close to the time of flowering of *Juglans nigra* L., *Viburnum prunifolium* L., *Ptelea trifoliata* L., *Robinia pseudoacacia* L., and *Celastrus scandens* L. On *Cercis canadensis* L., eggs hatch after flowering, when vegetative growth begins. This and other evidence (Wood, 1980; Wood and Guttman, 1982) suggest that *Enchenopa* life histories are mediated by host-

plant phenology, rather than by a genetically determined developmental program cued by other environmental factors.

Eggs of many Homoptera absorb water and increase in volume prior to development (Claridge and Reynolds, 1972; Hinton, 1981). These eggs require an environmental source of water in liquid rather than vapor form for development (Hinton, 1981). Since *Enchenopa* eggs are in contact with the vascular tissue of the host, we postulate a relationship between egg hatch and host-plant water content as a possible mechanism linking host-plant and *Enchenopa* phenologies. First we investigated whether such a relationship exists by determining 1) whether *Enchenopa* eggs require water from host plants to hatch, 2) whether manipulation of host-plant water results in allochronic egg hatch, and 3) whether water content varies allochronically among six host-plant species of *Enchenopa*. Secondly, we examined factors that may promote the observed patterns of synchronized egg hatch within a single host-plant species. Specifically, we examined the effects of seasonality, temperature, branch water content, and plant dormancy on egg development.

Materials and Methods

All experiments reported below were with *Enchenopa* eggs deposited in bittersweet (*C. scandens*) collected within 20 km of Newark, DE. The following technique was used to hydrate host-plant branches in all experiments. Glass tubes were attached to each end of small branch segments (32–250 mm in length) by wrapping joints with parafilm and coating them with wax. Branches were then suspended in a vertical position with wooden clothes pins attached to a rack in a walk-in environmental chamber (24°C, 12L: 12D photoperiod). Distilled water was added to the upper glass tube, which was checked several times a day to maintain water levels. Each branch was then examined daily for egg hatch, which could be determined by the presence of first-instar nymphs or embryonic membranes left by emerging nymphs.

Development time was expressed as the number of days from the time of collection or, in some experiments, from the day of hydration to egg hatch. Since the number of eggs per branch and the amount of parasitism varied among branches, observations of branches were terminated when 90–95% of viable eggs had hatched. Black eggs were not considered viable, since they were parasitized by *Polynema enchenopae* Girault (Hymenoptera: Mymaridae) or other parasitoids. Shriveled eggs or those that turned brown during the manipulations were also excluded, since prolonged observations (>150 days) indicated that they were inviable. To achieve a reasonable estimate of development time of *Enchenopa* for a given branch, branches with fewer than 10 eggs hatching were excluded from statistical analysis. In the Results, means are expressed with one standard error. A logarithmic transformation of egg development time (days) was performed to normalize data. Because of the unbalanced nature of the experiments (varying number of branches and number of eggs per branch), we used the Satterthwaite (1946) approximation to determine treatment effects on egg development time and to construct planned contrasts. Water content of branches was determined as the percentage of fresh weight of branches dried in an oven at 80°C for seven days.

Water Absorption by Eggs from Host-Plant Branches.—To determine whether *Enchenopa* eggs require water from the host plant to hatch, we collected branches with eggs on 7 March 1984 and immediately hydrated them or maintained them on moist paper towels under identical environmental conditions. We compared egg development time in the two groups by ANOVA using the GLM procedure in SAS (SAS Institute, 1982).

We also determined whether aqueous solutions can pass through *Enchenopa* egg membranes. Branches with eggs collected in January 1985 were bathed in aqueous nile-blue solution. After an hour, branches were rinsed with water to remove surface stain, and eggs were examined for the presence of stain.

Manipulation of Branch Water Content.—To quantify the effect of host-plant water content on *Enchenopa* egg hatch, we manipulated the timing of hydration of branches and compared development time

of eggs among treatment groups. Eight sets of branches were collected on 4 February 1985 and hydrated 0, 2, 3, 5, 7, 9, 11, and 13 days later. Branches that were not hydrated immediately were maintained on moist paper towels under identical environmental conditions. Development time was calculated as both the number of days to egg hatch from the day of collection and from the day of hydration. We assessed the effect of manipulating branch water content by comparing the development times of eggs on branches that were hydrated on different days using the GLM procedure of SAS (SAS Institute, 1982). Water content of branches at the time of hydration was determined in a separate set of branches maintained under the same conditions.

Variation Among Host Species in Water Content.—To determine whether the water content of the six *Enchenopa* host-plant species differs from each other we made weekly collections of branches from each host from 7 March to 16 May 1984. We collected branches at the same time of day from hosts growing within 18 m of each other in Newark, DE, to minimize environmental variation. From each of six host-plant species, we selected six branches that were appropriate *Enchenopa* oviposition sites (Wood, 1980). Branches were returned to the laboratory, where they were divided into 15 6-cm segments and analyzed for water content. A regression model for water content using sampling day and host plant (distinguished using indicator variables) as independent variables was used for analysis (the square and cube of sampling day were included). Interactions of sampling day, its square, and its cube with host plant were included so that we could test for differences between host plants in the constant, linear, quadratic, and cubic terms.

To determine whether the six host-plant species exhibit a decline in water content in the fall and winter, we collected branches in the same manner but once a month, beginning 10 September 1984. Initial and lowest water contents were compared using a Student's *t* test.

Synchronization of Egg Hatch Within a Single Host Species.—To determine seasonal effects on egg development time and whether a relationship between host plant and egg dormancy exists, we collected branches with eggs every 7–10 days from 30 October 1984 to 23 April 1985. Each branch was immediately hydrated and examined daily to determine the number of eggs that hatched and the date that bud break occurred. Bud break was operationally defined as occurring when buds had swollen to the point where emergent leaves were visible. Under our lab conditions, bud break and shoot development routinely occurred, indicating physiological activity within the cut branch segments. To determine whether such plant physiological activity affects egg development, we used ANCOVA, with date of branch collection as the covariate, egg development time (calculated from the day of collection) as the dependent variable, and date of bud break as the predictor variable.

We postulated that temperature and branch water content may mediate the synchronization of egg hatch. To examine the effects of extreme temperatures and dehydration, branches were collected on 28 December 1984 and assigned to one of four treatments. One set of branches was hydrated immediately and maintained at 24°C (12L:12D photoperiod); two sets of branches were maintained at either −2°C or 6°C in the dark; and the last set was maintained at 24°C (12L:12D) on moist paper towels. After five days, branches in the last three treatments were hydrated and maintained at 24°C (12L:12D). Egg development times were calculated from the day branches were collected, and these were compared by ANOVA.

Seasonal effects of branch dehydration on egg development time were determined for each of five sampling dates. We collected two sets of branches on each date. One set was immediately hydrated, and the other was maintained on moist paper towels for five days before hydration in the environmental chamber. Egg development times were calculated from the day of collection.

To determine whether plant dormancy and egg dormancy are coupled, *Enchenopa* females from bittersweet were collected from the field in September 1984 and allowed to oviposit on a bittersweet plant maintained at 24°C (12L:12D) to permit continued growth of the plant. After females died (in October), branches with eggs were regularly

examined for egg hatch. After 150 days, branches were removed from the host plant and examined under a dissecting microscope for evidence of egg hatch. Egg masses were counted, and the number of eggs was estimated by assuming that, on average, each egg mass contained nine eggs (Wood and Guttman, 1982).

RESULTS

Water Absorption by Eggs from Host-Plant Branches.—Eggs in branches that were immediately hydrated hatched 18.0 ± 0.2 (SE) days ($N = 263$) after they were collected, while those on branches maintained on moist paper towels showed no evidence of egg hatch after 16 days. Examination of eggs on these branches indicated no signs of development, such as the characteristic red eye spots of developing embryos, while the branches themselves were showing signs of dehydration, such as bark shrinkage. At this time, we attached glass tubes to these branches and hydrated them to determine whether eggs were viable and whether development depended on the presence of water. Eggs in these branches took 37.4 ± 0.7 days ($N = 23$) to develop. Thus, even though these eggs were maintained under identical temperature and photoperiod conditions, they required twice the development time of eggs from which water was not withheld.

When branches with eggs ($N \simeq 30$) were bathed in dye, many eggs were clearly stained, indicating that water-soluble dye moves through the egg shell. This result and the lack of development of eggs when exposed only to water vapor on moist paper towels suggest that *Enchenopa* eggs, like those of other Homoptera, absorb water (Hinton, 1981). Since the only water available in liquid form in the above experiment was that perfused through branches, we inferred that *Enchenopa* eggs absorb water from the host-plant branch.

Manipulation of Branch Water Content.—If eggs require environmental water and that source is the host plant branch, then the manipulation of water in branches should result in allochronic egg hatch. When branches were collected from the field (4 February 1985 = day 0), they contained 44.37 ± 0.4% water ($N = 15$). Branches maintained on moist paper towels lost water through time ($y = 41.7 - 3.94x + 0.184x^2$, $R^2 = 0.772$, $d.f. = 82$, $P < 0.01$). As expected, manipulating the addition of water to host branches resulted in allochronic egg hatch ($F_{28, 1,449} = 62.19$, $P < 0.01$; Table 1), spreading egg hatch out, on average, over 32 days from the time of collection. When development time is calculated from the time branches are hydrated, the effect of timing of the addition of water is clear ($F_{28, 1,449} = 82.66$, $P < 0.01$; Table 1). The lack of significant differences in development time for the first three treatments indicates that development does not begin until eggs absorb water from the branch. The longer development times in the last two treatments suggest that branches must hydrate to some equilibrium point before eggs can absorb water (Table 1). Branches that were dehydrated for 9–13 days contained 19.62–23.19% water at the time of hydration. Eggs in these branches did not hatch after rehydration, and no branches broke bud, suggesting that this level of dehydration is lethal to both the eggs and the branches.

TABLE 1. Development time ($\bar{x}$ ± SE) of *Enchenopa* eggs on *Celastrus scandens* branches collected on 4 February 1985. Branches were hydrated on different days to manipulate water content. Means were compared using planned contrasts. Nonsignificant differences between means within columns are denoted by common superscript letters.

Days until hydration	Development time (days)		N
	Day 0 = day of collection	Day 0 = day of hydration	
0	$21.1^{a} \pm 0.1$	$21.1^{a,b} \pm 0.1$	349
2	$22.7^{b} \pm 0.1$	$20.7^{a,c} \pm 0.1$	397
3	$24.2^{c} \pm 0.1$	$21.2^{b,c} \pm 0.1$	458
5	$27.3^{d} \pm 0.2$	$23.3^{d} \pm 0.2$	192
7	$29.9^{e} \pm 0.5$	$24.9^{d} \pm 0.5$	82

Variation Among Host Species in Water Content.—Regression analyses indicated that all but *C. scandens* and *C. canadensis* differed significantly ($P < 0.05$) in one or more equation coefficients. Regression equations were derived for each host species and are given in Table 2. Weekly water contents for each host species are given in Table 3.

TABLE 2. Regression equations for water content (% arcsine-transformed) and time (in days) for each of six *Enchenopa* host plants collected from 7 March 1984 to 16 May 1984. E = Scientific notation for values in the regression equations. All regression equations were significant at $P < 0.05$.

Host plant	Regression equation
Juglans nigra	$y = 49.04 + 0.16x - 7.04E^{-4}x^2 - 2.99E^{-6}x^3$
Viburnum prunifolium	$y = 46.85 - 0.48x + 1.98E^{-2}x^2 - 1.79E^{-4}x^3$
Ptelea trifoliata	$y = 46.16 - 0.40x + 1.09E^{-2}x^2 - 4.76E^{-5}x^3$
Celastrus scandens	$y = 43.19 - 0.25x + 1.23E^{-2}x^2 - 8.73E^{-5}x^3$
Cercis canadensis	$y = 42.09 - 0.22x + 8.95E^{-3}x^2 - 6.73E^{-5}x^3$
Robinia pseudoacacia	$y = 36.08 + 1.06x - 1.09E^{-3}x^2 + 4.72E^{-5}x^3$

In the fall and winter, the percentage of water in the branches sampled dropped, but the time of lowest water content showed some variation among the six host species (Table 4).

Synchronization of Egg Hatch Within a Single Host Species.—There appear to be five distinct changes in development time throughout the fall–spring sampling period. Eggs collected through the end of November represent dormant eggs requiring 72–98 days to hatch (Table 5). This was followed by a transition stage through December, in which dormant and non-dormant eggs were present in the field. Average development times were shorter, but egg hatch was asynchronous (Table 5). Development time for eggs collected from 7 January to 4 February 1985 was significantly shorter and more synchronous than that of eggs collected earlier. Eggs collected from 13 February to 6 March 1985 took slightly less time to develop, and egg hatch was highly synchronous (Table 5), occurring shortly after bud break. After 14 March 1985, development times decreased continuously, indicating that development had begun in the field (Table 5).

The interval between bud break and egg hatch for branches collected through December was considerable, and there was no relationship between *Enchenopa* egg development time and the date of bud break (an indicator of plant physiological activity) (ANCOVA, $F_{6, 43} = 2.23$, $P > 0.05$). Asynchrony of hatch and the lack of a relationship with bud break at this time of the year suggest that eggs are dormant and that the termination of dormancy is not mediated by auxins or nutrients in plant sap. From January through the spring, the interval between egg hatch and bud break becomes shorter, and there is a significant relationship between *Enchenopa* development time and the timing of bud break (ANCOVA, $F_{9, 115} = 15.99$, $P < 0.05$). Thus, the relationship between plant phenology (bud

TABLE 3. Water content ($\bar{x} \pm$ SE) of 6 hosts of *Enchenopa* in 1984. Sample size was 15 with the exception of *Juglans nigra* on 12 March ($N = 11$).

	Water content (%)					
Date	*Juglans nigra*	*Viburnum prunifolium*	*Ptelea trifoliata*	*Celastrus scandens*	*Cercis canadensis*	*Robinia pseudoacacia*
12 March	47.8 ± 0.4	47.1 ± 1.4	45.9 ± 0.7	43.1 ± 0.2	41.9 ± 0.2	37.8 ± 0.4
19 March	51.1 ± 0.5	43.1 ± 0.3	44.1 ± 0.3	41.0 ± 1.8	40.2 ± 0.1	35.7 ± 1.4
26 March	52.4 ± 0.7	44.4 ± 0.4	41.6 ± 0.4	42.5 ± 0.3	41.4 ± 0.2	34.1 ± 1.7
2 April	54.8 ± 0.7	42.4 ± 0.2	40.3 ± 2.5	43.0 ± 0.2	41.7 ± 0.4	40.3 ± 0.6
9 April	47.7 ± 0.2	45.4 ± 0.2	45.5 ± 2.2	45.2 ± 0.3	41.2 ± 0.1	38.8 ± 0.4
16 April	53.6 ± 0.3	49.0 ± 0.4	44.1 ± 2.3	46.2 ± 0.4	42.6 ± 0.5	44.8 ± 0.5
24 April	56.2 ± 0.5	48.4 ± 0.5	45.8 ± 0.5	46.5 ± 0.4	42.8 ± 0.3	43.5 ± 0.4
30 April	55.2 ± 0.6	50.2 ± 0.2	46.5 ± 0.8	49.3 ± 0.6	46.1 ± 0.4	42.6 ± 0.5
2 May	54.1 ± 0.4	49.6 ± 1.1	45.9 ± 0.6	50.6 ± 0.4	45.3 ± 0.3	43.9 ± 0.6
7 May	56.1 ± 0.5	51.6 ± 0.5	48.5 ± 0.9	55.5 ± 0.5	47.5 ± 0.5	45.2 ± 0.4
9 May	55.2 ± 1.0	50.9 ± 2.0	54.2 ± 0.7	54.7 ± 0.5	46.4 ± 0.4	47.0 ± 0.5
14 May	55.9 ± 0.3	48.2 ± 0.6	53.5 ± 1.7	54.5 ± 0.5	47.6 ± 0.2	54.7 ± 0.8
21 May	55.2 ± 0.5	49.6 ± 1.3	55.1 ± 1.2	55.7 ± 0.4	47.3 ± 0.6	54.4 ± 1.0

TABLE 4. The changes in branch water content ($\bar{x} \pm$ SE) in each of six host plant species during the fall and winter of 1984–1985. Initial water contents were determined on 10 September 1984. Initial and lowest water contents differed significantly in all hosts ($P < 0.05$).

Host	Water content (%)		t	$d.f.$
	Initial	Lowest (month)		
Juglans nigra	51.4 ± 1.1	47.4 ± 1.1 (January)	6.6	26
Viburnum prunifolium	52.2 ± 2.3	42.4 ± 7.9 (January)	4.5	28
Ptelea trifoliata	49.9 ± 3.7	42.3 ± 1.3 (November)	7.2	28
Celastrus scandens	56.6 ± 5.0	41.4 ± 1.1 (November)	11.1	28
Cercis canadensis	41.5 ± 1.0	40.3 ± 1.0 (September)	3.1	28
Robinia pseudoacacia	46.7 ± 1.7	38.1 ± 1.2 (February)	15.4	28

break) and *Enchenopa* egg development only holds when bud and egg dormancy are simultaneously terminated.

In December, we collected branches to test the effects of dehydration and cold temperatures on egg dormancy (eggs are dormant through December). Branches hydrated on the day of collection contained more water (44.24 ± 0.64%) than those hydrated five days later (32.34 ± 0.97%) but otherwise maintained under identical conditions (Table 6). The effect of dehydration on these dormant eggs was a reduction in development time of more than 50% (Table 6). Branches exposed to cold temperatures did not become dehydrated: water content of branches at the time of hydration for the 6°C treatments was 43.38 ± 0.72% and that for branches in the −2°C treatment was 41.63 ± 1.18%. Eggs in these branches hatched 46–48 days after hydration, a reduction in development time of about 25% compared to eggs in branches that had been hydrated and kept at warm temperature (Table 6). Thus, both cold temperatures and dehydration influence egg dormancy.

Cold temperatures and branch dehydration may also function to synchronize egg hatch in the field. Branches in the dehydration treatments (hydrated five days after collection) contained significantly lower amounts of water ($\bar{x} = 31.06\%$, SE = 0.7%, $N = 50$) at the time of hydration than those branches that were hydrated immediately ($\bar{x} = 45.18\%$, SE = 0.3% water, $N = 69$; $t = 20.31$, $d.f. = 117$, $P < 0.001$). Eggs in dehydrated branches collected from 28 December 1984 to 7 January 1985 had faster development times (Table 7) than eggs in branches that were hydrated immediately.

TABLE 5. The development time ($\bar{x} \pm$ SE) of *Enchenopa* eggs on *Celastrus scandens* branches collected from 30 October 1984 through 10 April 1985. ANOVA indicated a significant effect of collection date on development time ($F_{[242, 11,255]} = 570.89$, $P < 0.01$). All means differed significantly, except those with common superscript letters (planned contrasts by Satterthwaite approximation, $P < 0.01$).

Collection date	N	Development time (days)
30 October	140	90.2 ± 1.3
11 November	136	77.2[a] ± 1.7
21 November	94	97.7 ± 2.1
7 December	24	56.0[a] ± 6.9
21 December	193	62.9 ± 2.2
28 December	124	74.7 ± 2.6
7 January	115	26.7 ± 1.1
14 January	234	22.6 ± 0.5
23 January	352	21.6 ± 0.2
29 January	873	23.4[b] ± 0.2
4 February	349	21.1[b] ± 0.2
13 February	847	19.1[b] ± 0.1
20 February	830	19.4 ± 0.1
27 February	636	17.9 ± 0.1
3 March	456	17.3 ± 0.1
14 March	1,229	15.7 ± 0.0
20 March	699	14.9 ± 0.1
27 March	1,287	14.0 ± 0.0
3 April	978	11.8 ± 0.0
10 April	1,599	10.2 ± 0.0

TABLE 6. The development time ($\bar{x} \pm$ SE) of *Enchenopa* eggs collected on 28 December 1984 from *Celastrus scandens*.

Manipulation		N	Development time (days)
Day branch hydrated	Temperature (°C)		
0	24	124	74.7 ± 2.6
5	24	83	29.2 ± 1.1
5	6	143	45.9 ± 2.0
5	−2	166	47.7 ± 2.0

TABLE 7. Development time ($\bar{x} \pm$ SE) of *Enchenopa* eggs in *Celastrus scandens* branches collected 28 December 1984 through 27 February 1985.

Collection date	Hydration date			
	Day of collection		Five days after collection	
	N	Development time (days)	*N*	Development time (days)
28 December	124	74.7 ± 2.6	83	29.2 ± 1.1
7 January	115	26.7 ± 1.1	174	23.1 ± 0.5
29 January	873	23.4 ± 0.2	467	22.1 ± 0.1
4 February	349	21.1 ± 0.1	208	23.3 ± 0.2

Eggs collected on 29 January 1985 had similar development times, whether or not branches were air dried prior to hydration. After egg dormancy ended in the field, the effect of further branch dehydration increased egg development time (4 February) or was lethal (27 February).

On actively growing host plants, only 0.68% of the 1,458 eggs deposited hatched after 150 days. In contrast, during the same period, eggs on dormant hosts in the field developed rapidly when brought into the laboratory. The most striking effect of the inhibition of plant dormancy on egg masses is that 48.14% were partially or entirely overgrown by bark callus tissue. Thus, plant dormancy appears to be critical to the termination of egg dormancy and viability.

DISCUSSION

The experiments presented here demonstrate that the termination of dormancy of *Enchenopa* eggs is related to changes in the water content of host-plant branches. The decline in water content of branches in the fall and winter apparently dehydrates *Enchenopa* eggs to some uniform state. When the sap begins to ascend in the spring, eggs uniformly absorb water and begin to develop as a function of ambient temperature. Such a mechanism provides very tight tracking of essential nutrient resources in the host plant and provides a basis for the synchronization of life histories on a given host-plant species. Amino acids and carbohydrates are associated with the movement of water in plants (Scriber and Slansky, 1981). Thus, eggs that track changes in water content in the spring appear to hatch at a time when there are sufficient nutrients available to support nymphal development. In many trees, concentrations of amino acids in plant sap reach their highest levels shortly after bud break and decline as the growing season progresses. Thus, hatching too early or too late may dramatically affect nymphal development, survival, adult body size, mate selection, and fecundity (Dixon, 1977; Lawton and McNeill, 1979; Mattson, 1980; Scriber and Slansky, 1981; Slansky, 1982; Wood and Guttman, 1982).

In addition to the above life-history consequences, insertion of eggs into woody deciduous hosts by univoltine insects (such as *Enchenopa*) may promote synchronization of dispersal and mating. *Enchenopa* males are relatively short-lived compared to females, and females mate only once. Therefore, mating is related to the maximum availability of males and occurs within a restricted temporal window (Wood and Guttman, 1982). The ultimate effect of host-plant phenology is on the temporal sequence of mating. Consequently, host-plant phenology may determine whether populations on different host species are panmictic.

Enchenopa on each of its six host-plant species exhibit life-history and morphological variation related to specific hosts. Reproductive isolation in this complex of species appears to be based on allochronic life histories that correspond to differences in host-plant phenologies (Wood, 1980; Wood and Guttman, 1982, 1983). Wood (1980) suggested that speciation in this complex could occur in sympatry through shifts to host plants differing in phenology. In this model, the most critical point is that slight temporal shifts in *Enchenopa* life history promote assortative mating along host-plant lines. The basis for these temporal life-history shifts was postulated to be the timing of egg hatch to some aspect of

plant phenology. Since water uptake varies among host plants in the spring and since allochronic egg hatch can be experimentally induced, it is clear that host-plant phenology can alter *Enchenopa* life histories. Temporal disruption of life histories appears to be a potential factor promoting assortative mating and, ultimately, genetic divergence in these insect herbivores. In temperate regions in particular, phytophagous insect species that insert water-absorbing eggs into plant tissues of deciduous trees and subsequently shift to a novel host with a different phenology would appear to be potential candidates for genetic divergence. Here, we have demonstrated a plant-related mechanism to disrupt life histories. Whether slight temporal changes in insect phenologies actually promote assortative mating along host-plant lines remains to be tested empirically.

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