POPULATION FLUCTUATIONS IN COMPLEX LIFE CYCLES: AN EXAMPLE FROM *PEMPHIGUS* APHIDS[1]

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Abstract. The population dynamics of organisms with complex life cycles are rarely examined due to the number of potentially interacting variables. Experimental manipulations of conditions and long-term data on abundances were used to investigate the bases of year-to-year fluctuations in population size in the aphid *Pemphigus betae,* which has a complex life cycle. Spring generations may live in leaf galls on cottonwood trees, whereas summer generations obligately inhabit roots of herbaceous *Rumex* and *Chenopodium* species.

Experimental manipulation of irrigation levels of root colonies in both field and garden experiments showed that soil moisture affects aphid survival and reproduction on roots. The importance of this single factor in governing population size is further supported by 6 yr of gall-density and weather data showing a strong relationship between gall abundance and the amount of rainfall the previous season. Censuses of autumn migrants arriving at cottonwoods during three of these years corroborate this.

Thus, weather affects success on summer hosts and consequently determines numbers of migrants returning to cottonwoods and gall abundances during the subsequent spring. This study demonstrates that conditions during one phase of a complex life cycle may largely determine the population size of future generations using alternate niches.

Key words: aphid; complex life cycles; density-independent control; host alternation; Pemphigus; population dynamics.

INTRODUCTION

Life cycles that involve switching between two or more discrete habitats, generally termed complex life cycles (Istock 1967, Wilbur 1980), have evolved in a wide variety of organisms. Examples include Amphibia, various host-alternating animal parasites, rust fungi, holometabolous insects with ecologically distinct adult and larval phases, and, the focus of this paper, certain groups of aphids that feed on discrete sets of host plants during different generations of the life cycle. Despite the abundance and taxonomically widespread distribution of such species, only a few studies have addressed the consequences of complex life cycles for population dynamics (Gill 1978, Wilbur 1980, Semlitsch 1983). In the case of host-alternating parasite species in particular, it is unclear how frequently conditions on one host govern abundance of parasite populations on alternate hosts.

Here we present results of studies on the factors governing population densities of the aphid *Pemphigus*

betae. This species divided its annual life cycle between cottonwood trees, where it inhabits leaf galls, and herbs, where it feeds on roots. Our preliminary field observations of root-infesting colonies of *P. betae* indicated that, in dry years, colonies are small and few survive on nonirrigated host plants by late summer. For example, on 22–24 May 1985, *P. betae* colonies were found on 78% of the 200 *Rumex* hosts examined in the zone of gall infestation in Utah study sites. On 15–17 August, only 5% of 60 *Rumex* examined at the same sites were infested, and these plants had few aphids (x^2[1 df] = 32.4, $P < .00001$). These preliminary field observations led us to hypothesize that dry soil in summer may impose a bottleneck on population size and that the severity of this bottleneck may determine infestation levels on the alternate hosts.

We addressed the following question: does weather, acting through effects on soil moisture levels, determine the success of root-feeding generations and thereby govern the subsequent abundance of galls on cottonwoods? Our approach combined experimental manipulation of conditions on the root host plants with analysis of long-term data on weather and densities on cottonwood hosts.

MATERIALS AND METHODS

Life cycle of Pemphigus betae in the Weber Canyon

Pemphigus betae has one of the most complex life cycles known for insects (Fig. 1). In spring, females hatch from overwintering eggs and initiate galls on leaves of narrowleaf cottonwood, *Populus angustifolia.* Inside these galls, they asexually produce up to 300 progeny (Whitham 1979). These develop into winged females that obligately migrate in early summer to species of *Rumex* and *Chenopodium.* Their progeny move underground and reproduce on roots through the growing season in a series of wingless, asexual generations. In autumn, root colonies produce a mixture of wingless females that remain over winter on roots, and winged migrants that fly to narrowleaf cottonwood, *Populus angustifolia.* Proportions of migrants in root colonies in autumn vary from 0 to >50% (Moran and Whitham 1988). Our work shows that 40% of this variation is due to a facultative response to crowding, with proportionately more migrants being produced in dense colonies. Upon arriving at the cottonwood hosts in autumn, migrants asexually produce the short-lived sexual forms that mate and deposit overwintering eggs in bark crevices, to complete the life cycle.

Experimental studies and censuses of life cycle stages were conducted from 1981 through 1986 along the Weber River in Weber and Davis Counties near Ogden, Utah.

Water manipulation experiments

To examine the hypothesis that soil moisture levels affect aphid survival and reproduction in root colonies, we established an experimental garden plot in 1986 in which artificially established colonies were subjected to differing watering levels. This experiment included both of the major host plants of *P. betae* in the area, *Rumex crispus* and *Chenopodium album.* Also, we used two soil types, one almost pure sand and one loam, which differed in drainage characteristics. Seeds for experimental *Rumex* and *Chenopodium* hosts were collected from single maternal parents growing within the zone of gall censuses. Hosts were propagated in 4-L pots that were inserted in the soil in a fully exposed common garden on the banks of the Weber River in the zone where *P. betae* occurs naturally on both cottonwoods and roots. Plants were watered generously initially to allow establishment. On 15–18 June, each plant was inoculated with five adult *Pemphigus betae* obtained from roots of *Chenopodium* and *Rumex* growing at other sites in the Weber Canyon. To inoculate plants, soil immediately surrounding the stem and main root was loosened and aphids were deposited with a small paint brush. Following inoculations, high-water plants were watered thoroughly approximately every day using a sprinkler system. Low-water plants were also watered with a sprinkler system, but only enough to prevent wilting, every 5–8 d. Colonies were
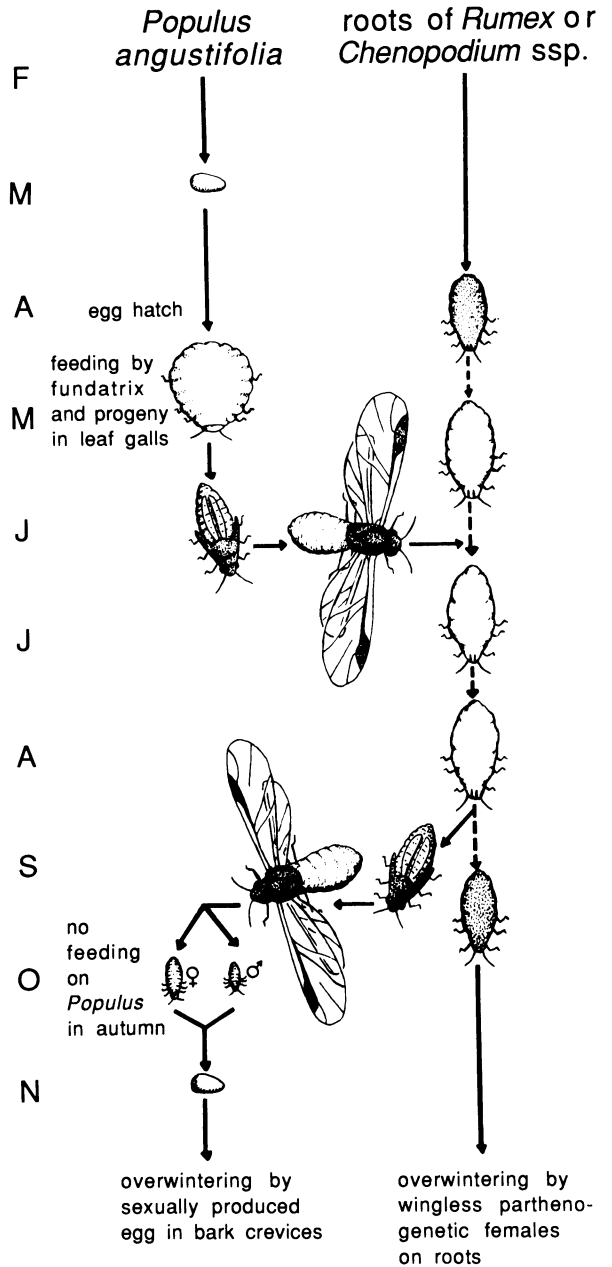

FIG. 1.   Life cycle of *Pemphigus betae* in the Weber Canyon, Utah.

harvested 20–22 August 1986, by crumbling pot contents, submerging them in 20-L buckets of water, and then counting floating aphids. Each of the eight water level × host plant taxon × soil type combinations was replicated 16 times, for a total of 128 plants. In 11 cases, initial establishment of plants or aphids failed, leaving a total of 117 colonies for statistical analysis.

Adult aphids were preserved for subsequent determinations of size and fecundity. Sizes were obtained as body lengths of adult females, measured under a dissecting microscope. We obtained an index of fecun-

TABLE 1. (A) Aphid density in the eight treatments of the 1986 garden experiment testing the effects of soil moisture and soil type on *Pemphigus betae* densities. (B) ANOVA table.

A) Soil type	Host taxon	Watering level	
		High	Low
		$\log_{10}$ no. aphids per colony ($\bar{X} \pm$ SD)	
sand	*Rumex*	0.93 ± 0.74	0.54 ± 0.41
loam	*Rumex*	1.63 ± 0.42	0.41 ± 0.44
sand	*Chenopodium*	1.77 ± 0.55	1.13 ± 0.26
loam	*Chenopodium*	2.11 ± 0.50	1.68 ± 0.65

B) Source	df	ss	F	P
water level	1	16.0	64.6	<.0001
water level × host taxon	1	5.4	10.9	<.005
water level × soil type	1	19.5	39.3	<.0001
error	111	27.6		

dity by dissecting adult females and counting the number of embryos per female showing pigmented eyespots (an indicator of developmental stage). Body lengths and embryo numbers were obtained for colonies yielding four or more adult females.

In addition to the 1986 garden experiment, two field experiments involving manipulation of soil moisture were conducted, in different years and in sites differing in density of host plants. In 1985, 16 points, separated by at least 1.5 m, were selected and marked in a dense, *P. betae*–infested stand of *Chenopodium fremontii* near Ogden Bay Wildlife Area, Utah. Eight of these points, chosen randomly, were watered by slowly pouring 12 L of water every 3 d from 25 June until 5 September. Soil samples were then removed and aphids were counted by inspecting soil spread in trays. Due to the high density of the hosts, each sample contained roots from several plants. Numbers of aphids per 100 g dry soil were calculated. In 1986, a sprinkler system was used to water a relatively sparse stand of naturally occurring *C. album* at the garden site. From 1 July to late August, plants were (1) watered every 1–3 d, (2) watered approximately every 8 d or (3) not watered. On 28–29 August, 115 plants were censused by examining soil immediately surrounding the central taproots and counting numbers of *P. betae* per individual host.

Population censuses

Gall densities on *Populus angustifolia* were estimated for each year from 1981 through 1986. Using pole pruners, we haphazardly removed small branches from tree crowns and censused all leaves of the apical five shoots of each branch (the terminal plus four laterals). Since failed attempts to form galls leave characteristic leaf scars, we were able to census all individuals that had hatched on cottonwoods, whether or not they had successfully formed a gall. Galls, aborted galls, and total leaves were counted to yield estimates of attempt-

ed galls/1000 leaves. Yearly averages are from a minimum of 4600 leaves from the same set of ≈120 trees at three sites along a 7-km stretch of the Weber River.

Autumn migrants, which fly from root hosts to colonize cottonwoods, were censused during three autumns, from 1983 through 1985. We placed bands of 2 cm wide tape, coated with Tanglefoot, around tree trunks near the base of tree crowns. Migrants were trapped as they moved from their positions of alightment on the leaves to potential oviposition sites farther down the trunk. Censuses were conducted during the main flight periods, which last 4–6 wk during September and October. The same 30 trees, a subset of the trees censused for gall densities, were trapped during each census. Tanglefoot bands were placed in the same positions on individual tree trunks in all three years.

The relationship between yearly fluctuations in soil moisture and densities of aphids emigrating to cottonwoods was examined using linear regression analysis with rainfall as the independent variable and densities of the subsequent generation of fall migrants or galls as the dependent variables. We obtained rainfall data as the average total precipitation for the months of April through July from the United States Weather Service records for the Pioneer weather station in Ogden, Utah, the nearest weather station with reliable records. Data were obtained for the years 1980 through 1985, the 6 yr immediately preceding the seasons of gall censuses. We also obtained minimum temperature data, to determine whether variation in gall densities might result from differential overwintering mortality due to variation in severity of winter temperatures.

RESULTS

Water manipulation experiments

In the garden experiment, densities on the more heavily watered plants averaged over three times as great as those on less frequently watered plants, after 10 wk of differential watering (Table 1, Fig. 2a). For both hosts and both soils, increased watering had a strong positive effect on aphid reproduction. Watering regime showed significant interaction with host taxon and also with soil type, indicating that host and soil variables can moderate, though not eliminate, the impact of moisture on aphid reproduction (Table 1).

In addition, both of the water manipulation experiments with naturally occurring colonies showed that plants given supplemental water supported significantly more aphids than did unwatered plants (1985 experiment, Mann-Whitney U: $U = 55$, $N = 16$, $P < .02$; 1986 experiment, Kruskal-Wallis: $\chi^2 = 12.9$, df = 2, $P < .0001$; Fig. 2b, c).

Higher numbers on plants that received more water resulted at least in part from enhanced growth and reproduction. Measurements of aphids from the garden experiment showed that aphids on watered plants were larger (Table 2). Furthermore, larger aphids were more
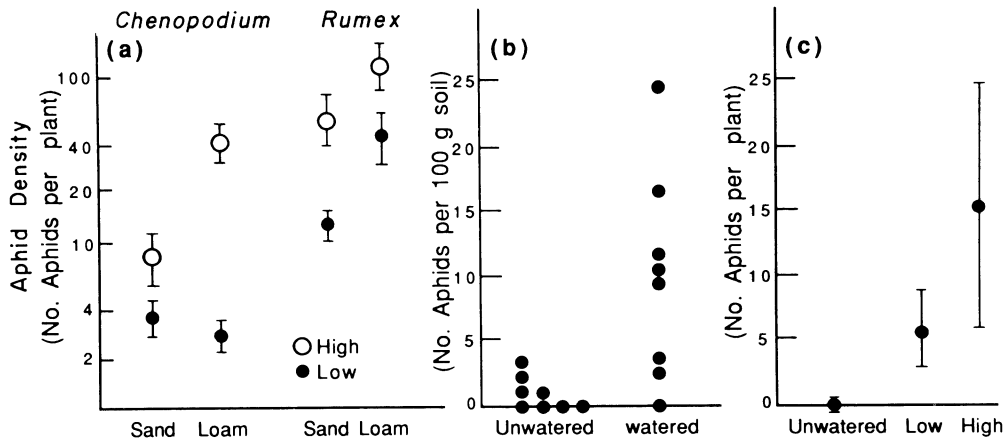
FIG. 2. Effects of experimentally varying soil moisture levels on densities of *Pemphigus betae* in root colonies. (a) 1986 garden experiment comparing effects of low and high watering levels on aphid densities with two host taxa and two soil types. Error bars represent standard errors of mean numbers of aphids per plant. (b) 1985 field experiment comparing densities on eight watered and eight unwatered sites in a dense stand of naturally occurring *Chenopodium fremontii*. (c) 1986 experiment comparing densities on individual naturally occurring *C. album* given three levels of water (none, low, and high). Error bars represent 95% confidence intervals of median numbers of aphids per plant.

fecund (linear regression of embryos per adult on log body length, adjusted $r^2 = 0.62$, $N = 221$, $P < .0001$). The mean numbers of embryos with eyespots in low- and high-water aphids were 5.9 and 9.0, respectively; thus, watering resulted in a 50% increase in fecundity.

Population censuses

Yearly censuses of galls and aborted galls showed that aphid populations fluctuated from a low of 7 attempted galls/1000 leaves in 1983 to a high of 218 attempted galls/1000 leaves in 1981. Because gall censuses reflect the entire colonizing population, including failed attempts, we were able to eliminate differential springtime performance on cottonwoods as a cause of these yearly fluctuations in population size. Also, densities showed no significant relationship to minimum temperatures during the preceding winter ($r^2 = 0.25$, $N = 6$, $P > .95$). With only 6 yr of census data, only very strong effects of winter temperatures would be expected to show significance, so we can conclude only

tentatively that low winter temperatures are not influencing *P. betae* population size.

To test the hypothesis that moisture levels affect success of root colonies on summer hosts and thereby determine the abundance of leaf-galling generations during the following spring, we determined if rainfall levels in one year can be used to forecast the subsequent year's gall densities. As predicted, aphid densities on cottonwood trees showed a significant positive relationship with precipitation during the previous growing season (regression of log-transformed aphid densities on precipitation, adjusted $r^2 = 0.69$, $P < .03$; Fig. 3). Thus, the observed year-to-year fluctuations of gall populations appear to be largely governed by variation in rainfall. This variation determines the severity of conditions on the summer hosts.

TABLE 2. (A) Body lengths (in millimetres) of adult female *Pemphigus betae* from colonies given different water levels and different host taxa (mean ± SD). (B) ANOVA table for effect of water level, host taxon, and individual host plant on body lengths.

A)	Host taxon	High water	Low water
	Rumex	2.07 ± 0.35	1.69 ± 0.31
	Chenopodium	1.87 ± 0.29	1.60 ± 0.228

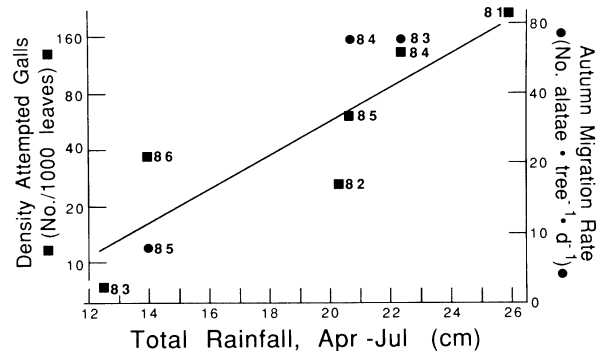| B)	Source	df	ss	F	P
	water level	1	6.31	100.9	<.0001
	host taxon	1	0.14	2.3	>.1
	water level × host taxon	1	1.47	23.5	<.0001
	individual host plant	93	16.5	2.8	<.0001

FIG. 3. The dependence on precipitation during the previous growing season of numbers of autumn alatae and densities of attempted galls for *Pemphigus betae* in the Weber Canyon, Utah. The equation for the relationship, with ±1 SE of the slope and intercept in brackets, is $GD = -0.0491$ [±0.511] + 0.0898 [±0.0258] × RF, where $GD =$ log gall density and $RF =$ rainfall for the preceding year.

Censuses of autumn migrants colonizing cottonwoods further corroborate the proposed role of soil moisture in *P. betae* population dynamics. Colonizers were significantly fewer during 1985, a dry year, than during 1983 and 1984, which shared higher rainfall totals and higher numbers of colonizing alatae (ANOVA: $F_{2,10} = 6.0$, $P < .02$; Fig. 3).

DISCUSSION

The physiological mechanisms through which soil moisture affects success of root-feeding generations are not known. Low moisture may negatively affect aphids by causing a decline in host plant quality and/or by causing the aphids become dehydrated due to their close contact with a dry soil environment. At least some effect of host nutritional quality is suggested by the depressed size and fecundity of aphids feeding in dry soil.

Large root colonies produce more autumn migrants that will fly to cottonwoods. This increase is both a direct outcome of greater numbers and a consequence of density dependence in the rate of migrant production (Moran and Whitham 1988). In our watering experiments, in dry years only colonies in irrigated sites reached densities high enough to produce any migrants (Fig. 2). Irrigation of agricultural crops tends to buffer root colonies against the vagaries of weather and dampen population fluctuations. Most of the lower part of the Weber Canyon, where our gall censuses were conducted, is too steep and rocky for farming, so root colonies are dependent on natural rainfall for successful reproduction and production of fall migrants. In other nearby canyons, where the summer hosts occur as weeds in irrigated agricultural fields, aphid abundance appears to be relatively high and constant among years. In fact, an early study of *P. betae* infestations in irrigated sugar beet fields showed that irrigated fields supported very high rates of increase, both on the beets and on *C. album* occurring as weeds in the same fields (Parker 1915).

Such a direct and simple effect of weather on population size has not been found in aerially feeding aphids, perhaps because natural enemies play a major role in population dynamics (Dixon 1985). Weather can affect the impact of aphid predators and parasitoids (e.g., Force and Messenger 1964, Hodek et al. 1965). The resulting relationship between abiotic factors and aphid abundance is thus expected to be complex whenever natural enemies are important. Root-feeding aphids suffer relatively low levels of predation and parasitism (Bodenheimer and Swirski 1952). The only such enemy encountered in *P. betae* root colonies was a predaceous chloropid fly larva, *Choropisca glabra* Meig. (Parker 1918), which was restricted to a small proportion of colonies in irrigated sites. Thus, a subterranean existence appears to afford sanctuary from most potential enemies and may simplify the effect of weather on abundance.

Our previous and ongoing work shows that genetic and developmental susceptibility traits of cottonwood are important determinants of *P. betae* spatial distributions (Whitham 1983, Kearsley and Whitham 1988, Moran and Whitham 1988). However, this study shows that weather, acting through effects on soil moisture, is responsible for year-to-year population fluctuations. This finding implies that complexity in the life cycle and biotic relationships of a species need not be accompanied by correspondingly complex population dynamics.

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