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CAUSES OF LIFE HISTORY DIFFERENCES BETWEEN THE MORPHS OF *PEMPHIGUS POPULITRANSVERSUS*[1]

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Abstract.—The aphid *Pemphigus populitransversus* produces galls of two distinct morphs on cottonwood petioles. There are pronounced between-morph differences in both the number and maturity distribution of aphids within the galls. The progress of gall maturation was followed over the summer to determine whether these life history differences are explainable solely by the fact that galls of the "globular" morph are initiated some seven weeks later than those of the "elongate" morph or whether qualitative differences exist in the pattern of gall maturation. It was found that the *pattern* of maturation for the two morphs was similar, with globulars being always seven weeks behind. However, the *number* of nymphs and mature alates was about three times greater in globular galls.

Introduction

Pemphigus populitransversus Riley is a gall-forming aphid attacking leaves of cottonwoods, principally *Populus deltoides* Marshall and *P. sargentii* Dode. A nymphal stem mother hatches from a sexually produced egg in the spring and initiates a gall on a cottonwood petiole. The growing petiole tissue quickly encloses her in a capsule within which she parthenogenetically and viviparously produces nymphal fundatrigeniae which, as winged adults, leave the gall and fly to secondary hosts of the family Cruciferae.

In the study of a dimorphism of galls in this aphid Senner and Sokal (1974) found large differences in the numerical distribution of developmental stages in the two morphs. In fact, they noted that "the two samples can be differentiated on life history characteristics more clearly than on gall shape, the initial criterion for separation [into two morphs]" (p. 368). Galls of the "globular" morph contained fewer nymphs, most (98.1%) of which were in the smallest of three size classes. Galls of the "elongate" morph had about half their nymphs in the two largest size classes and had more alates (adult fundatrigeniae). Senner and Sokal hypothesized that "nymphs in the 'globular' galls . . . , although necessarily born sequentially, develop synchronously and . . . the bulk of alate production must be in the late fall. In the

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'elongate' sample . . . the nymphs seem to develop sequentially throughout the summer with alates presumably being produced continuously'' (p. 368).

Subsequently, Faith (1979a) discovered that the globular-elongate dimorphism was based on different times of gall initiation. Elongate galls are initiated in early May by stem mothers hatching from overwintering eggs. They are formed on the early flush of leaves (which are pre-formed in the bud) soon after bud-break. Globular galls are founded by stem mothers hatching some six weeks later from eggs that are laid in the spring. These galls are on the second, morphologically distinct, flush of leaves (Faith 1979a). The ranges of the two morphs seem to overlap essentially completely (Bird et al. 1979).

Faith (1979b) proposed that this difference in time of gall initiation provides a simple alternative to Senner and Sokal's explanation of the life history differences between the morphs. He showed that globular galls produced their first alates during the first days of August—again six weeks later than elongate galls attain this milestone. Perhaps globular galls are simply less mature, and at the time of collection of Senner and Sokal's original dimorphic sample (August 5, 1966 in West Point, Ga.) even the oldest nymphs were still small. The differences in the mean and variance of the distribution of life history stages should then disappear later on in the season.

It is the purpose of this paper to show that differences in gall age between the morphs can indeed account for the life history dimorphism discovered by Senner and Sokal. There is some evidence, however, that some developmental synchrony may exist in globular galls, but on a scale much smaller than Senner and Sokal originally envisaged.

Materials and Methods

Galls of *Pemphigus populitransversus* were collected at roughly weekly intervals from a midsized (approximately 15 cm dbh) eastern cottonwood tree (*Populus deltoides*) in Port Jefferson, L.I., N.Y. Five elongate galls were collected each time beginning on 13 June 1975 and ending on 7 September 1975. Five (occasionally six) globular galls were collected each time beginning on 31 July 1975, and ending on 4 October 1975. Galls could be assigned to one or the other morph unambiguously by noting whether they were on early or late leaves. Galls were immediately preserved in 70% ethanol. Later, each gall was opened and censused for the number of small, medium, and large sized nymphs, as well as the number of alates. Procedures were those of Senner and Sokal (1974).

Abbreviations and definitions of variables are listed in Table 1. Several empty or parasitized galls were eliminated from further study. Since Senner and Sokal coded the numbers of nymphs in each size category into 10 abun-

Table 1. Variables used in this study.

Abbreviation	Definition
# SM NYM	The number of "small" nymphs in the gall, roughly those in the first or second instar.
# MD NYM	The number of "medium" nymphs in the gall, roughly those in the third, or penultimate, instar.
# LG NYM	The number of "large" nymphs in the gall, roughly those in the fourth, or ultimate, instar.
# ALATES	The number of adult fundatrigeniae in the gall.
G LH MN	By coding small, medium and large nymphs as 1, 2 and 3 respectively, the mean nymphal stage attained by all nymphs in the gall. Coded abundances of each stage were used.[1]
G LH VAR	By coding small, medium and large nymphs as 1, 2 and 3 respectively, the variance in nymphal stage attained by all nymphs in the gall. Coded abundances of each stage were used.[1]

[1] Abundances were coded into 10 classes following Senner and Sokal (1974): 0: 0 nymphs, 1: 1–10 nymphs, 2: 11–20, 3: 21–30, 4: 31–40, 5: 41–50, 6: 51–60, 7: 61–70, 8: 71–80, 9: 81 and greater.

dance classes, the mean developmental stage and its variance (G LH MN and G LH VAR respectively) were calculated for each gall using their coding scheme. I have reported the nymph abundances themselves as uncoded counts, however.

Results

The changes in variance in developmental stage attained (G LH VAR) over the season are plotted in Figure 1. During June the variance for elongate galls shows a sharp rise as the first nymphs mature. By July 1 a maximum variance (and mean) of the distribution is attained, and remains at that level until September (at which time the supply of elongate galls was exhausted). Alates are continually leaving the gall during this time, so the stable mean and variance represent a steady state distribution of developmental stages.

Globular galls progress along an essentially identical curve, save that it is *displaced* some 50 days later in the season. The initial rise is about as rapid as for elongates, and the same steady state is maintained from then on, at just the same level, until leaves drop in the autumn.

Figure 2 shows the progress of gall population size over the season, with each bar divided according to the numbers present for each developmental stage. The maximum population size of globulars is much greater than that of elongates. This maximum is attained more quickly (and lost more quickly)

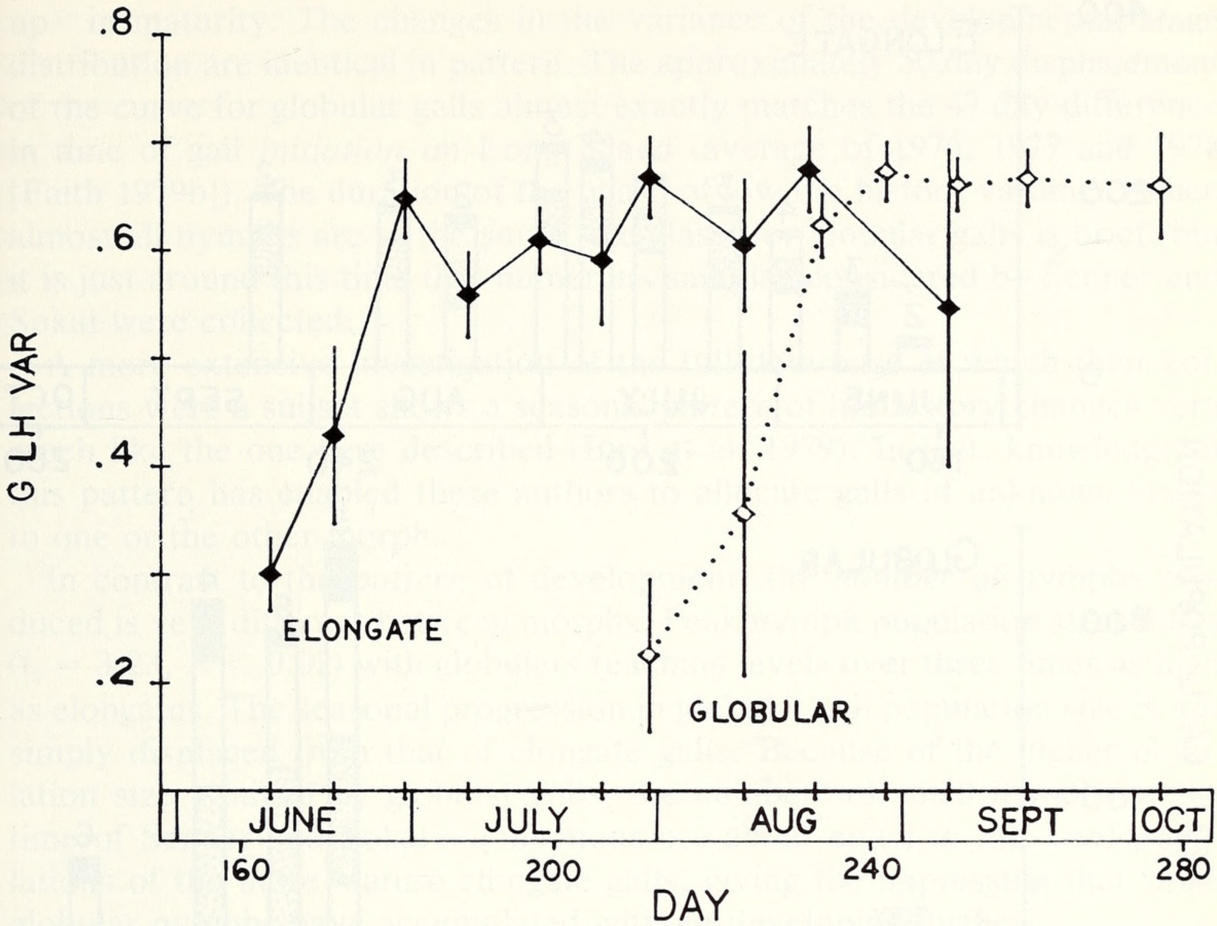

Fig. 1. Changes in life history variance (the variance of the distribution of maturities) in elongate galls (solid points) and globular galls (open points). Vertical bars indicate ± one standard error of the mean. Sample sizes may be obtained from Figure 2. Abscissa is number of days since January 1, 1975.

than in elongates. It should be noted that at the end of the initial, essentially "all small nymph" stage, globular galls have already attained about one third of their eventual peak population, whereas elongates have only reached about one seventh of their maximum at the analogous time. Furthermore, the initial phase of increase in life history variance is accompanied by rapid population size increase in elongates, but not so in globulars. Instead, the rapid increase in population just follows the attainment of the stable distribution of life history stages.

Discussion

At any given time until mid-August galls belonging to the globular morph will indeed have a very different distribution of developmental stages than those of the elongate morph, as noted by Senner and Sokal. These differences seem to be a consequence of the different ages of galls of the two morphs at any one time. They vanish in mid-August as globular galls "catch

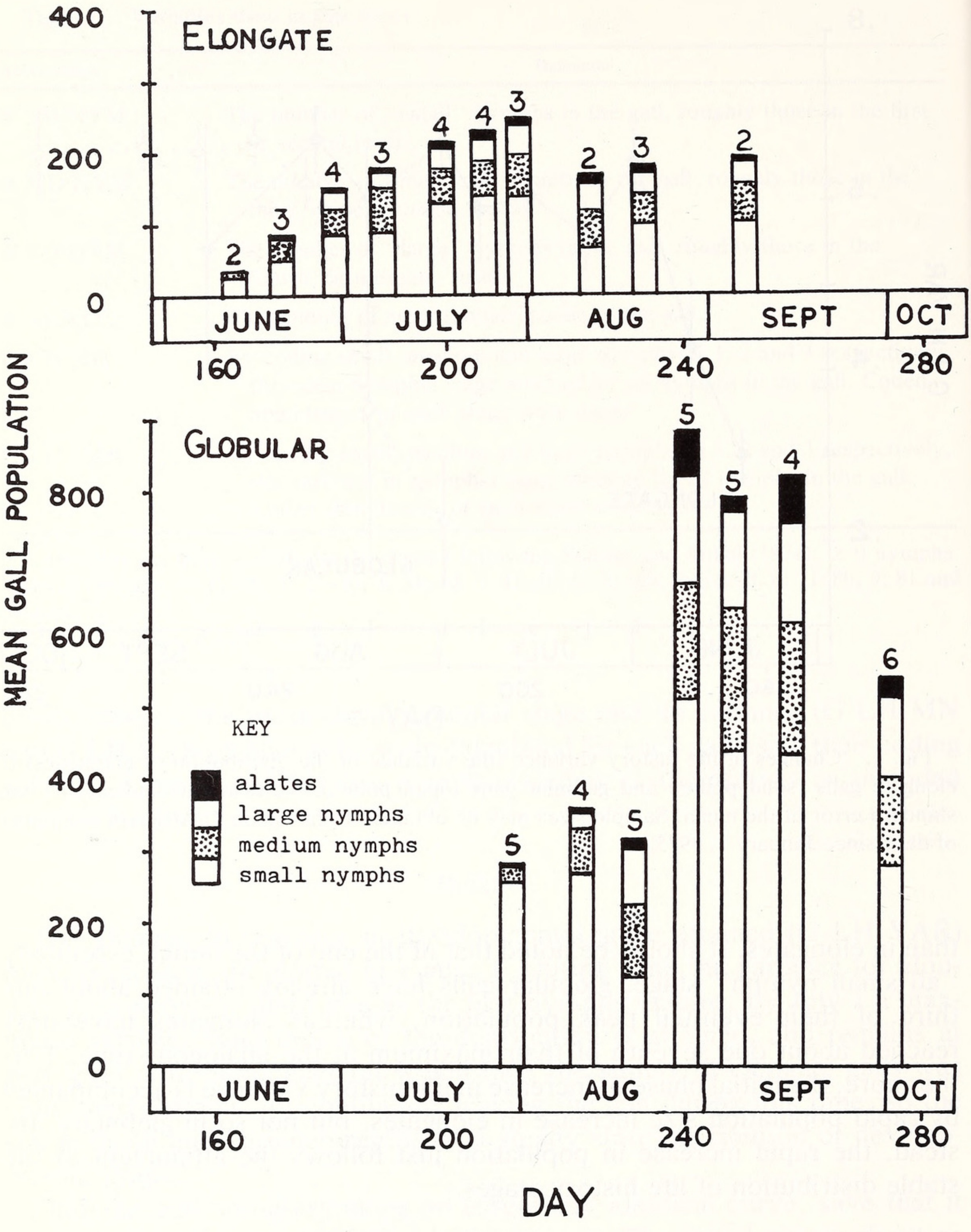

Fig. 2. Changes in mean gall population size for elongate (top) and globular (bottom) galls. Each bar is divided into segments proportional to the numbers of small, medium, and large nymphs, and alates. The sample sizes are shown above each bar. Abscissa is the same as Figure 1.

up'' in maturity. The changes in the variance of the developmental stage distribution are identical in pattern. The approximately 50 day displacement of the curve for globular galls almost exactly matches the 47 day difference in time of gall *initiation* on Long Island (average of 1976, 1977 and 1978 [Faith 1979b]). The duration of the phase of low life history variance (when almost all nymphs are in the small size class) for globular galls is brief, but it is just around this time that numerous samples considered by Senner and Sokal were collected.

A more extensive investigation of the full data base of which their collections were a subset shows a seasonal pattern of life history changes very much like the one here described (Bird et al. 1979). In fact, knowledge of this pattern has enabled these authors to allocate galls of unknown status to one or the other morph.

In contrast to the *pattern* of development, the *number* of nymphs produced is very different between morphs. Peak nymph population sizes differ ($t_s = 3.23$, $P < 0.02$) with globulars reaching levels over three times as high as elongates. The seasonal progression in globular gall population size is *not* simply displaced from that of elongate galls. Because of the higher population size attained by globular galls, the numbers of small nymphs at the time of Senner and Sokal's collections are about equal to the *total* populations of the more mature elongate galls, giving the impression that small globular nymphs have accumulated without developing further.

A closer look at Figures 1 and 2 reveals some support for a much smaller scaled version of the "developmental synchrony" hypothesis in globular galls, spanning some two weeks in August instead of the whole season. In these galls the phase of rapid increase in life history variance happens without an appreciable increase in the number of nymphs in the gall, as though a large initial cohort begins to mature before many new small nymphs are produced. Elongate galls, in contrast, show a gradual rise in number of nymphs during their phase of life history variance increase.

In conclusion, an investigation of the progress of maturation of globular and elongate galls of *Pemphigus populitransversus* shows that the between-morph differences in maturity distribution of the nymphs can be ascribed largely to their different ages at any point in time. A large scale qualitative difference in the progress of maturation, such as that hypothesized by Senner and Sokal, is not found. However, some differences independent of gall age are found; these are peak population size and its rate of attainment.

Whether the life history differences between morphs can be considered to be adaptations to different circumstances is difficult to say. Certainly the existence of the globular morph enables exploitation of a new resource, namely the late flush of leaves, which seems to be unexploited by other *Pemphigus* species. Stem mothers seem to have no limit to the numbers of nymphs they can produce. Unborn nymphs may still be found in stem mothers taken from galls on abscised leaves in the autumn. However, the fecundity of stem mothers should be influenced by genetic and environmental factors. The greater fecundity and consequent higher population size of globular galls may be a phenotypic response to maturation in the warmer climate of mid-summer or to nutritive or anatomical differences between the early and late flushes of leaves. Faith (1979a) has shown strong association of population size with measurements of the leaves both within and between morphs.

Acknowledgments

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