

Seasonal shifts in host usage in *Uroleucon gravicorne* (Homoptera: Aphididae) and implications for the evolution of host alternation in aphids

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ABSTRACT. 1. *Uroleucon gravicorne* (Patch) feeds on annual *Erigeron* species and on perennial *Solidago* species.

2. To test whether *Solidago* and *Erigeron* are analogous to winter and summer hosts of typical host-alternating aphids, reproductive performance, host preferences, and host associations were measured for *E.strigosus*, *S.junceae* and *S.nemoralis* during spring, summer and autumn.

3. Caged individuals can reproduce on both genera throughout the season, though colonies are rare on *Solidago* during summer.

4. Developmental rate, adult weight, and fecundity decline between May and August on all hosts; however, the drop is least on *E.strigosus*, intermediate on *S.nemoralis*, and greatest on *S.junceae*.

5. Throughout the season, reproductive performance is at least as great on *Erigeron* as on *Solidago*, the difference being least in spring.

6. Soluble nitrogen content shows the same seasonal trends as reproductive performance, declining in all hosts, but declining least in *E.strigosus*.

7. Preference tests and field records show that *U.gravicorne* moves from *Solidago* to *Erigeron* when the first alatae mature in late spring, feeds on *Erigeron* during the summer, and, in late summer, returns to *Solidago* where overwintering eggs are laid.

8. *Solidago* is not nutritionally superior during spring or autumn; its use during those seasons may result from the need for good oviposition sites.

Key words. Aphid, *Uroleucon*, host-alteration, herbivore, heteroecy, phenology.

Introduction

Seasonal shifts between host taxa are known for several insect groups (Claridge & Wilson, 1978; Melber *et al.*, 1981), but the superfamily Aphidoidea contains most examples. In the most familiar host-alternating (or heteroecious) life cycle, overwintering eggs and the first few spring generations occur on

a woody plant, the 'primary' host. A winged generation then migrates to plants which are usually herbaceous and taxonomically unrelated to the winter host. These summer hosts support a succession of alate-initiated colonies which give rise in fall to winged males and winged gynoparae (mothers of sexual females). These fly to winter hosts where wingless sexual females develop, mate, and deposit overwintering eggs.

Although host alternation characterizes only about 10% of modern aphid species (Eastop, 1972), it has been central in the

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evolution of their life cycles and host relations. A much greater proportion of species are apparently derived from heteroecious ancestors (Hille Ris Lambers, 1950), and the phenomenon has arisen multiple times in an array of aphid taxa. Furthermore, comparison of morphologies and life cycles of alternating and non-alternating taxa indicates that host alternation has been critical in the evolution of morph differentiation and host acquisition (Eastop, 1972, 1977; Hille Ris Lambers, 1966). A striking feature of aphid biology is the widespread occurrence of clonal polymorphism, in which genetically similar individuals may have very different structures and habits; almost all extreme examples of this phenomenon are associated with host alternation.

According to the most widely held theory, host alternation is an adaptation to seasonal fluctuations in phloem nutrient levels (Kennedy & Stroyan, 1959; Mordvilko, 1928). In perennials, these levels are high in spring when nitrogen is being mobilized for growth; once leaves are fully developed, phloem nutrient levels drop (Dixon, 1971; Mittler, 1953; Parry, 1979). Host alternating species escape this midsummer adversity by moving to herbaceous plants which are actively growing and thus more nutritious during summer. By itself, the complementary host growth theory implies that all phloem feeders should alternate hosts. An adequate theory for the evolution of host alternation should explain not only how the phenomenon originates and is maintained where it occurs, but also why it is more frequent in aphids than in other groups and, ideally, why it characterizes some aphids and is absent in others, including whole subfamilies, such as Drepanosiphinae and Callaphidinae.

Almost all studies of host alternation have been directed at a few highly specialized, obligately heteroecious members of one subfamily, the Aphidinae. Such studies are especially unlikely to increase our understanding of selective factors involved in the origin of heteroecy, particularly predisposing features in aphids. Here, we are more likely to benefit through attention to species which show more flexibility in seasonal shifts in host affinities. In this paper, I detail such a life cycle and consider its implications for theories

of host alternation in aphids and of plant–herbivore interactions in general.

The large genus *Uroleucon* Mordvilko is almost completely restricted to the plant family Compositae. Host alternation is unknown, and a typical species uses several plant species within a genus. *Uroleucon gravicorne* (Patch) is native to eastern North America and has a relatively wide host range, feeding on species of *Solidago* and *Erigeron* (Hottes & Frison, 1931; Leonard, 1936, 1963, 1964, 1967, 1968; Leonard & Bissell, 1970; Olive, 1963; Patch, 1919; Richards, 1972; personal observations). The contrasting phenologies of *Solidago* species (all perennial) and *Erigeron* species (annual) suggested that *U. gravicorne* might benefit from seasonal shifts between these genera. In this paper, I report investigations addressing the following questions:

Do relative qualities of hosts, as measured by aphid developmental time, adult size and fecundity, change seasonally?

Do host preferences of colony-initiating winged forms change with season, and, if so, do they shift in directions that would optimize diet?

Do host associations of naturally occurring colonies show corresponding seasonal trends?

Does alate production change with host and season, and how does the observed pattern affect use of host taxa?

Do observed shifts in host quality result from changes in aphid requirements or in some intrinsic property of the plants, soluble nitrogen content for example?

Do factors other than nutritional quality promote seasonality in host usage and are these factors likely to be of general importance in host-alternating aphids?

Methods and Materials

Host plants

I selected three of *U. gravicorne*'s hosts, the annual *Erigeron stigosus* Muhl., and the perennials *Solidago juncea* Ait. and *S. nemoralis* Ait., for the study, carried out from 1978 to 1981 on the Edwin S. George Reserve (ESGR) in Livingston County, Michigan. These species, together with *E. annuus* (L.), appear to be the most commonly used hosts in the area. All three frequently grow together in old fields,

allowing field comparison of aphid performance with minimal differences in microhabitat. Among *Solidago* species, *S. juncea* and *S. nemoralis* contrast sharply in growth form and phenology. *S. juncea* flowers early (beginning in late July) and produces long rhizomes which may develop into rosettes or into flowering stems. *S. nemoralis* flowers approximately 4 weeks later and develops only a stout woody caudex from which flowering stems arise each year; consequently, lateral spreading of individual plant clones is minimal.

Seasonal changes in host favourability

Reproductive performance. Developmental time, adult weight, and fecundity were measured using cages constructed from 35 × 15 mm plastic Petri dishes. Edges were lined with foam rubber to form aphid proof seals on plant stems, and each cage half had a 2 cm diameter ventilation hole covered with fine mesh (40/cm) Lumite screening. Cages were held in place with plant ties and stakes. Most data were obtained using potted plants in a screenhouse (4.3 × 2.5 × 2.0 m) on the ESGR; thus, differences observed between hosts are probably due to differences in the plants and not in other aspects of the environment. Screenhouse conditions appeared to be within the range in which plants and aphids normally occur; this was supported by comparison of maximum and minimum temperatures recorded in the screenhouse and in two field sites. The phenologies, sizes and appearances of screenhouse plants were well within the ranges exhibited by naturally occurring plants in this area. Potted plants were obtained by transplanting rhizomes with developing shoots (*Solidago* spp.) and seedlings (*E. strigosus*) from the field soon after ground thaw in spring; plants were taken from old field and thin oak woodland sites within 5 km of the ESGR.

In addition to screenhouse data, reproductive performance was measured for a limited number of aphids caged on plants occurring naturally in two old field sites, 2.1 km apart on the ESGR.

Developmental time from birth to adulthood was measured by caging a reproductive aptera on a plant, checking the cage daily, and

removing her as soon as one or more nymphs had been deposited. Usually only 1 day, but occasionally 2 or 3 days, passed before a nymph was produced. As nymphs developed, cage position was adjusted to enable utilization of preferred feeding sites (the uppermost leaves or stem apices according to plant stage). Dates of moulting to adulthood and of first reproduction were recorded (± 24 h). Within 24 h of first reproduction and within 2 h of removal from the host, live adults were weighed on a Kahn electromicrobalance. Each cage gave one measure of developmental time and of weight: if the original mother produced more than one nymph within 24 h, I allowed all to develop to adulthood, and used the cage averages.

Developmental times were converted to a measure of day-degrees in order to compare performances of aphids not reared simultaneously. On this scale, each day is transformed to the difference between the average of the maximum and the minimum temperatures and 3.5°C, the approximate threshold temperature for *U. gramineae*'s development. This value was obtained by culturing *U. gramineae* in a controlled temperature chamber.

Fecundity and proportion of winged progeny were measured by allowing caged apterae to produce nymphs and transferring these mothers to successive cages before nymphs became adult (to avoid confusion between mothers and offspring). Nymphs were allowed to continue feeding until the youngest had reached the third instar (when wing pads permit recognition of alate morphs). They were then removed and numbers of each morph and instar recorded. Each estimate of fecundity required transferring the mother through four to six successive cages. Individual mothers were reared from birth on the host species on which fecundity was evaluated so that host effects on both nymphal and reproductive stages could influence fecundity. They were followed from the fourth instar to ensure that all progeny were counted.

Soluble nitrogen levels. During 1980 each plant species was sampled weekly from 1 May (time of egg hatch that year) to 25 October for determination of soluble nitrogen levels. Samples consisted of whatever part of the plant aphids fed upon: the uppermost leaves in early spring and the uppermost portion of

the stem during the remainder of the season. Samples were gathered at 10.00–11.00 hours each day, immediately dried (at 50°C), and stored in a freezer.

Prior to analysis, samples were ground in a Wiley mill and extracted in a solution of 2.5% trichloroacetic acid, 0.02% phenol and water for 7 h. Total nitrogen content of the extract was determined using a modified Kjeldahl technique (Derman *et al.*, 1978). Two to five samples of each plant species were analysed for each collection date; each was a mixture of many (> 25) plant stems.

Seasonal changes in host preferences and usage

Host preference experiments. To evaluate host preferences, adult alatae were allowed to choose among intact plants in an outdoor screen enclosure (1 × 2 × 0.8 m). Plants were in pots buried up to shoot bases. Three groups of three pots were used, with one pot of each species per group. In each experiment thirty-five to forty-five alatae were released and left for 48 h; numbers choosing each stem were then recorded. Choice was scored only if an alata had committed herself to a host, as indicated by loss of ability to fly, abdomen enlargement, and, often, nymph deposition.

Patterns of field colonization. In 1981, I located all *U. grivicorne* colonies in each of three ESGR field sites, ranging in size from 162 to 222 m². Each contained all three plants, although *S. nemoralis* was most

common in all sites. Totals censused were 246 clones of *S. nemoralis*, forty-four reproductive stems and 128 leaf rosettes of *S. juncea*, and fifty-one individuals of *E. strigosus*. Every plant in each site was checked for aphids every third day during the periods 1 May to 10 July and 20 July to 30 August.

Literature records. To determine whether *U. grivicorne* shifts host with season over a wider geographic range, I pooled host data from the literature (Leonard, 1936, 1963, 1964, 1967, 1968; Leonard & Bissell, 1970; Olive, 1963; Patch, 1919), from the collection of the Illinois State Natural History Survey, and from the Canadian National Collection. Records were arranged by date and by host genus (*Solidago v. Erigeron*).

Results

Seasonal changes in host favourability

Reproductive performance. Relative favourabilities of hosts change markedly over the season (Figs. 1–4). All three plant species become less favourable during the interval between 1 May and 15 August; developmental times increase and fecundities and adult weights decrease during this period. However, quality declines much more in the *Solidago* species than in *E. strigosus*. In spring, developmental times are longest on *S. nemoralis*, intermediate on *S. juncea*, and shortest on *E. strigosus*; adult weights and fecundities rank in the order *S. juncea* > *E. strigosus* > *S. nemo-*

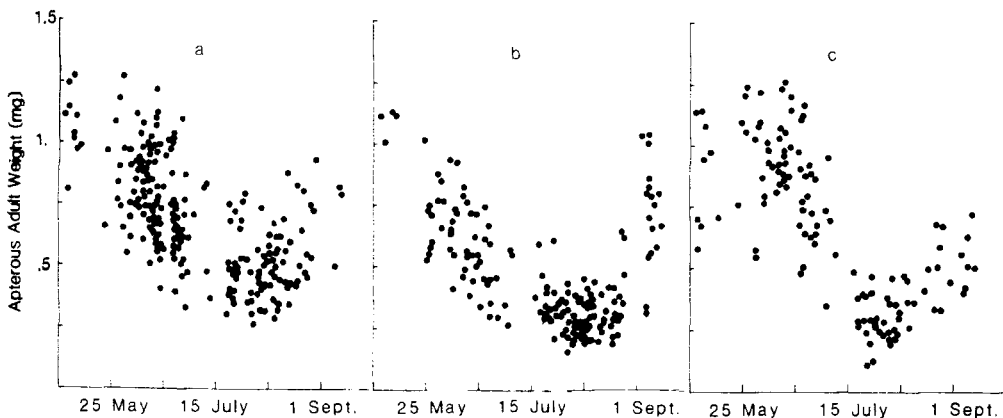


FIG. 1. Apterous adult weight versus time of season for *Uroleucon grivicorne*. Measures are for apterae reared on (a) *Erigeron strigosus*, (b) *Solidago nemoralis*, and (c) *Solidago juncea*. Aphids were reared on plants in a screenhouse and in the field.

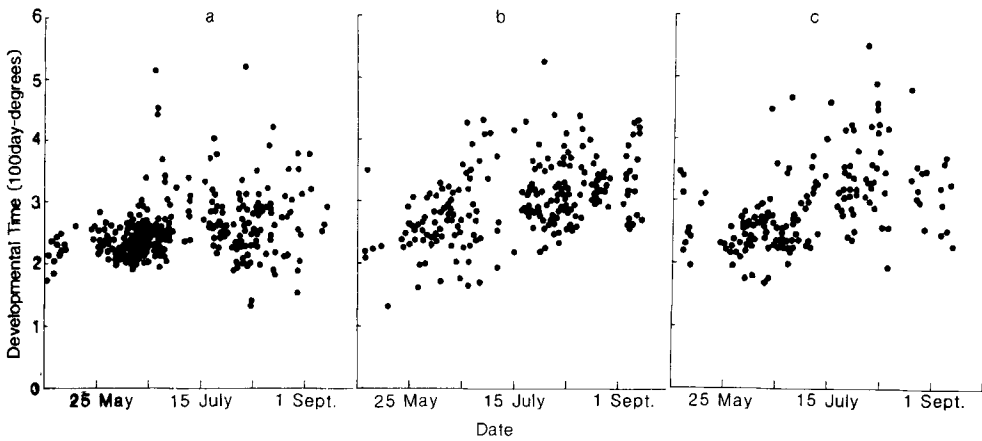


FIG. 2. Developmental time versus time of season for *Uroleucon gravicorne*. Measures are day-degrees from birth to adulthood for apterae reared on (a) *Erigeron strigosus*, (b) *Solidago nemoralis*, and (c) *Solidago juncea*. Aphids were reared on plants in a screenhouse and in the field.

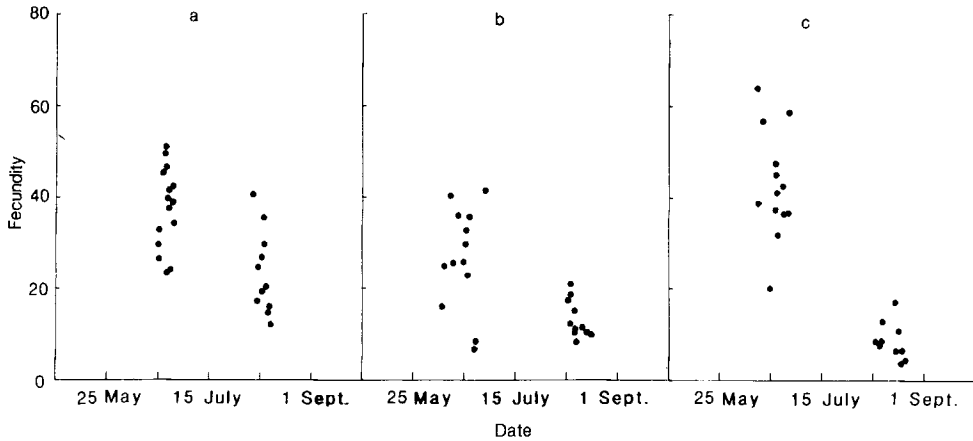


FIG. 3. Fecundity versus time of season for *Uroleucon gravicorne*. Values are numbers of nymphs produced during the first 400 day-degrees of adulthood for apterae caged in a screenhouse on (a) *Erigeron strigosus*, (b) *Solidago nemoralis*, and (c) *Solidago juncea*.

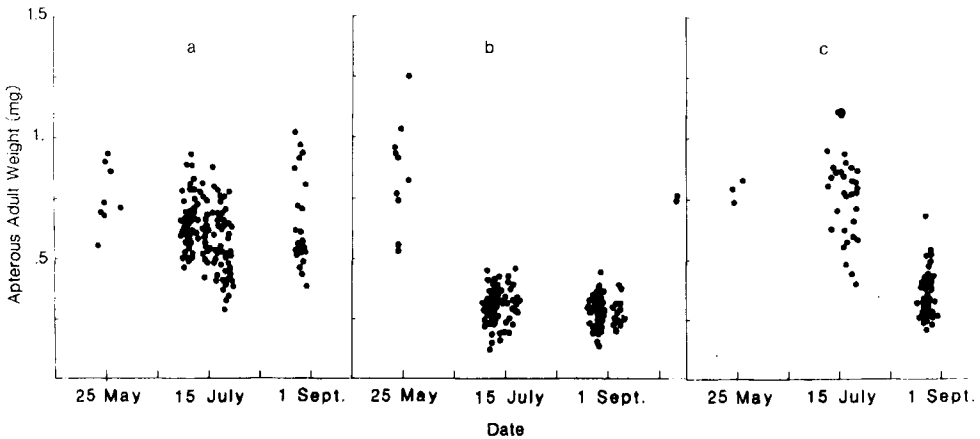


FIG. 4. Weights of field-collected *Uroleucon gravicorne* apterae collected from naturally occurring colonies on (a) *Erigeron strigosus*, (b) *Solidago nemoralis*, and (c) *Solidago juncea*.

TABLE 1. Reproductive performance of *Uroleucon gravicorne* by host and season.

Season	Host plant	Day-degrees to develop		Weight of adult apterae (mg)		No. of nymphs in 400 day-degrees	
		Mean	N	Mean	N	Mean	N
Spring	<i>E.strigosus</i>	239.0	105	0.86	92	37.7	15
	<i>S.nemoralis</i>	260.0	61	0.70	43	33.4	13
	<i>S.junceae</i>	252.7	62	0.94	47	43.1	13
	Anova, <i>P</i> <	0.001		0.001		0.002	
Summer	<i>E.strigosus</i>	267.3	154	0.56	115	36.1	8
	<i>S.nemoralis</i>	320.8	130	0.34	104	13.4	11
	<i>S.junceae</i>	317.1	92	0.50	65	8.6	10
	Anova, <i>P</i> <	0.0001		0.0001		0.001	
Autumn	<i>E.strigosus</i>	276.1	14	0.69	8	—	—
	<i>S.nemoralis</i>	337.5	28	0.65	22	—	—
	<i>S.junceae</i>	310.6	15	0.52	14	—	—
	Anova, <i>P</i> <	0.005		0.1		—	

TABLE 2. Slopes of regressions of developmental time, apterous adult weight, and fecundity on date, for the period 1 May to 15 August.

	Host plant	Slope	95% C.I. limits	N
Developmental time	<i>E.strigosus</i>	0.56	0.40, 0.88	132
	<i>S.nemoralis</i>	0.88	0.45, 1.31	103
	<i>S.junceae</i>	1.32	0.85, 1.79	109
Weight of apterous adult	<i>E.strigosus</i>	-0.0074	-0.0092, -0.0064	110
	<i>S.nemoralis</i>	-0.0079	-0.0087, -0.0060	71
	<i>S.junceae</i>	-0.0080	-0.0095, -0.0055	77
Fecundity	<i>E.strigosus</i>	-0.30	-0.45, -0.15	26
	<i>S.nemoralis</i>	-0.25	-0.38, -0.11	24
	<i>S.junceae</i>	-0.60	-0.73, -0.46	23

ralis (Table 1). In summer (20 June to 24 August), *E.strigosus* is far superior to either *Solidago* species in all three measures of performance (Table 1). Between 1 May and 15 August, the decline in reproductive performance is approximately linear and is least on *E.strigosus*, as indicated by all three measures (Table 2).

Although more variable, field measures of developmental times and adult weights show the same trends as data from greenhouse plants (Figs. 1 and 2). The higher variability, particularly pronounced in measures of developmental times, probably results from greater variability in microhabitat acting either directly on the aphids or indirectly through the physiological state of the plants. As a further check on the validity of inferring trends from cage experiments, I compared weights of adult apterae from naturally occurring colonies with weights of caged

individuals (Figs. 2 and 4). The latter were weighed within 24 h of first reproduction. Because ages of field collected adults varied and because weight generally increases after first reproduction (e.g. MacKay & Downer, 1979), field weights are expected to be greater; however, this difference is slight compared to those occurring between hosts and seasons. If one also compensates for time since birth, weights from field collections show the same trends as those of caged aphids: weights on *E.strigosus* decline only slightly, while those on *Solidago* species drop more sharply. In field and cage data, weights decline sooner on *S.nemoralis* than on *S.junceae*, though by mid-July both are equally low in quality, as indicated by long developmental times and low adult weights (Figs. 1-3).

The trend in adult weight results partly from seasonal differences in temperature rather than from changes in host properties.

However, host properties definitely influence adult size: aphids reared simultaneously on different hosts achieve different sizes (Table 1), and size declines much more on *S.nemoralis* and *S.juncea* than on *E.strigosus*. The autumn weight increase probably results from lower temperatures and not from improved host quality since it occurs on all hosts and since fecundities and developmental times do not similarly improve (Fig. 1, Table 1).

Soluble nitrogen. Soluble nitrogen content provides an independent index of seasonal changes in host properties. Admittedly, soluble nitrogen may not correspond with host quality, for several reasons (van Emden, 1969; van Emden & Bashford, 1969, 1971). Host species may differ in aspects of quality not related to nitrogen, in proportion of soluble nitrogen actually present in phloem sap, or in amino acid balances. Despite these drawbacks, seasonal changes in soluble nitrogen should reflect relative changes in quality among host species.

Soluble nitrogen declines in all hosts between spring egg hatch and mid-summer (1 May to 1 August) (Fig. 5). Both the extent of decline and even absolute levels correspond to the relative suitabilities of the plant species.

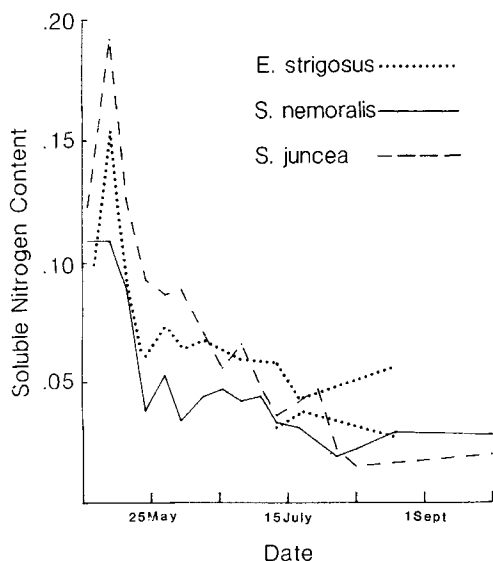


FIG. 5. Soluble nitrogen concentrations versus season in hosts of *Uroleucon grivicorne*. After 20 June, values for *Erigeron strigosus* are divided into stems with all heads open (lower line) and stems with one or more head unopened (upper line).

In May the ranking of soluble nitrogen levels is *S.juncea* > *E.strigosus* > *S.nemoralis*; in summer the ranking is *E.strigosus* > *S.nemoralis* > *S.juncea*. Between 1 May and 25 May, soluble nitrogen declines less rapidly in *S.juncea* than in *S.nemoralis*, remaining higher through most of June; similarly adult weight declines less rapidly on *S.juncea*. Overall decline in both aphid performance and soluble nitrogen is greater for *S.juncea* than for *S.nemoralis*. After mid-June, when *E.strigosus* begins to flower, I divided its stems into those with one or more heads not fully opened and those with all heads fully opened or beyond. Stems in earlier stages are preferred by alatae and have higher levels of soluble nitrogen (Fig. 5).

The correspondence between soluble nitrogen and reproductive performance supports the view that observed host shifts are an adaptation for optimal utilization of hosts with different seasonal patterns of favourability. Possibly, some covarying factor, and not nitrogen availability itself, is the important variable in host quality.

Seasonal changes in host preferences and usage

The earliest winged forms overwhelmingly prefer *Erigeron* to either *Solidago* species (Fig. 6). As the season progresses, both *Solidago* species are chosen with increasing frequency, though *E.strigosus* is always chosen more often than either *Solidago* species during spring (Fig. 6). Experiments were performed through mid-August, after which time few alatae are produced and few colonies initiated in the field.

Early in the season, field observations agree with results of preference tests. Except for rare fundatrix-initiated colonies, *U.gravicorne* does not occur on *Erigeron* until late May when alatae begin to mature on *Solidago* and begin to appear on *Erigeron* (Fig. 7).

Field data and choice experiments from late summer show somewhat conflicting patterns. In field censuses, the shift to *Solidago* begins later (early August) and is more sudden than is suggested by results of host choice experiments (Figs. 6 and 7). Possibly, experimental conditions altered criteria by which alatae normally choose hosts. Also, sudden increases in numbers of alatae seeking hosts

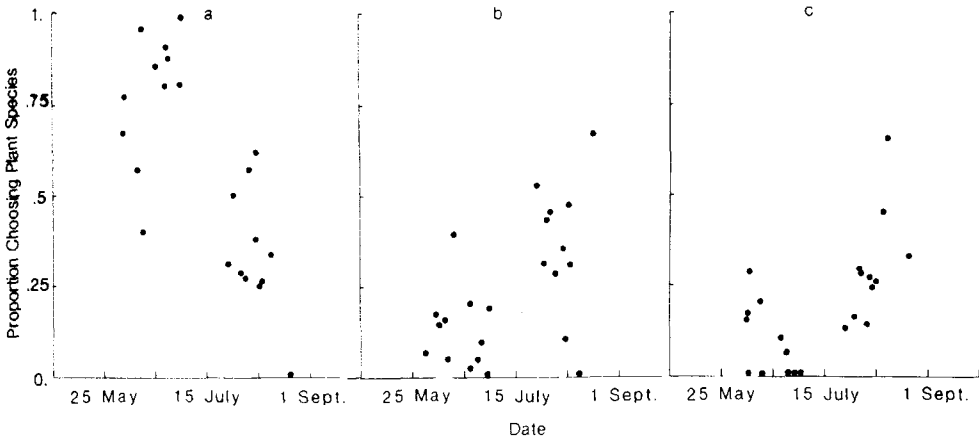


FIG. 6. Host preferences versus time of season for *Uroleucon gravicorne*. Points represent proportion of alatae in each choice experiment selecting (a) *Erigeron strigosus*, (b) *Solidago nemoralis*, and (c) *Solidago juncea*.

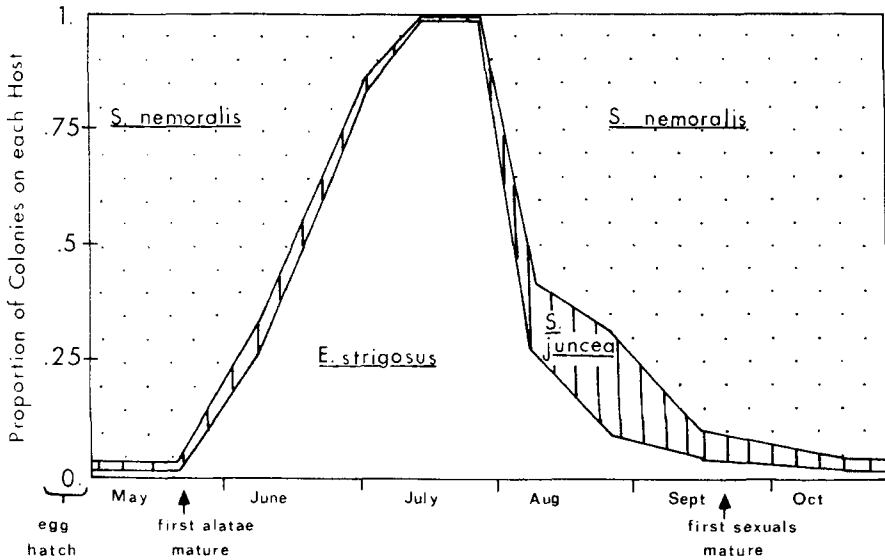


FIG. 7. Seasonal changes in proportions of *Uroleucon gravicorne* colonies on *Erigeron strigosus*, *Solidago nemoralis*, and *Solidago juncea* in three field sites in southern Michigan.

may give the appearance in the field of a discrete shift in preference towards *Solidago* even though preference for *Solidago* has been increasing over some time previously.

Host records from the literature and from museum collections show roughly similar trends, suggesting that *U. gravicorne* shifts host throughout its range (Fig. 8). The paucity of records from *Solidago* in spring probably

results from *Solidago* being deserted before colonies are large and conspicuous to collectors. Recolonization of *Solidago* occurs in mid-August, as in ESGR field sites (Figs. 7 and 8). The main discrepancy results from seven collections on *Erigeron* in October: all were collected by Olive from *E. canadensis* in North Carolina, the southernmost area included in the records.

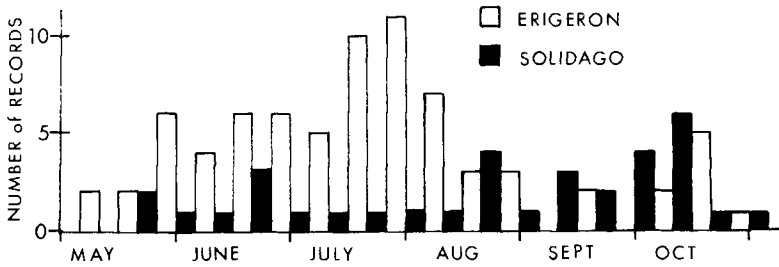


FIG. 8. Occurrence of *Uroleucon gravicorne* on *Erigeron* and *Solidago* according to season. Host records are taken from the literature and from museum collections (see text).

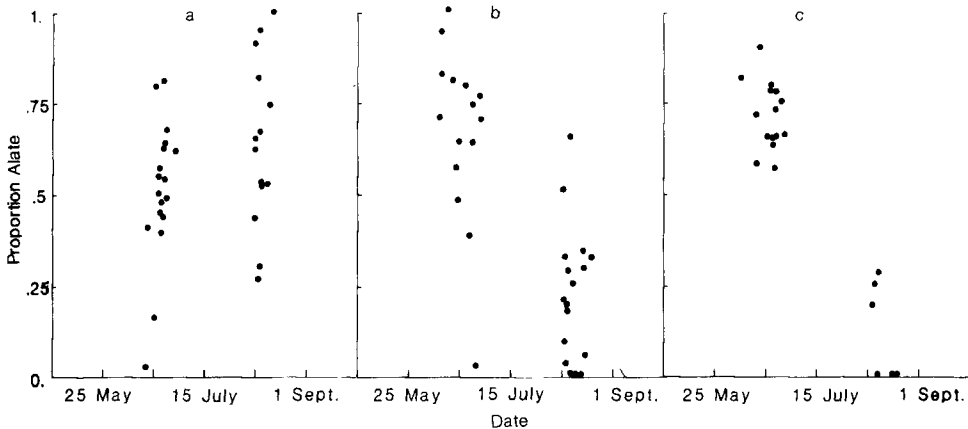


FIG. 9. Relative production of alate and apterous morphs versus time of season for *Uroleucon gravicorne* caged on (a) *Erigeron strigosus*, (b) *Solidago nemoralis*, and (c) *Solidago juncea*.

Morph production

On both *Solidago* species, winged forms predominate in the progeny produced before 15 July; thereafter, their proportions decrease greatly, especially on *S. juncea* (*S. nemoralis*: $R^2 = 0.50$, slope = 0.0068, $P < 0.0001$; *S. juncea*: $R^2 = 0.69$, slope = 0.0064, $P < 0.0001$; Fig. 9). On *E. strigosus* there is a slight and non-significant increase in proportion of winged progeny ($R^2 = 0.11$, slope = 0.0032, $P = 0.06$), with high variability among broods.

Discussion

As in typical host-alternating aphids, shifts in host preference in *U. gravicorne* appear to be 'programmed' and not simply the result of colonizing the best host available at the moment and remaining until it becomes crowded or less nutritious. In fact, trends in

host choice are approximately inversely related to trends in host quality. Thus, preference for and field colonization of *Solidago* increases during mid- to late summer when *E. strigosus* is superior (Fig. 6, Table 1). Actually, my measures of reproductive performance suggest that *Erigeron* is always superior to *S. nemoralis*, leaving unexplained colonization of *Solidago* in autumn and spring. Furthermore, both fundatrices and oviparae can and sometimes do live on *Erigeron* (Fig. 7, Table 1). In nature, host species may have differential effects not evident in the type of data I have presented; all stages in the herbivore's life cycle must be considered in order to understand relationships with host species.

One reason for use of *Solidago* may be that by 1 August many *E. strigosus* are beginning to senesce and will die before either new alatae or oviparae can be produced. More importantly, perennial hosts such as *Solidago* species may provide superior oviposition sites. First

instar fundatrices hatching from eggs laid on or near bases of *Solidago* stems will usually be near food, depending on the pattern of rhizome production; eggs on annuals will be near spring food supply only if other food-plants are growing nearby. Thus, avoidance of *Erigeron* in autumn may be part of a generalized ability to recognize and avoid senescent plants which will not live long enough to support development of sexuals, or it may be a more specific adaptation for putting autumn colonies (and thus oviparae and eggs) on host taxa more favourable for hatching fundatrices.

Similarly, in other heteroecious aphids, return to the winter host may benefit not the morphs actually possessing adaptations for locating and feeding on these plants in autumn, but rather the first few descendant spring generations. Certainly in Eriosomatinae, any advantage of complementary host growth patterns is enjoyed by spring generations; the winter host is not used at all for food in autumn, by either sexuparae (which fly to the winter host) or their non-feeding sexual offspring. In the aphidine *Rhopalosiphum padi* L. as well, gynoparae and oviparae, the morphs which feed on bird cherry (*Prunus padus* L.) in autumn, show very low reproductive rates, averaging fewer than two nymphs per gynopara and less than one egg per ovipara (Leather, 1980). The many gynoparae which fail to locate hosts further increase the cost of moving in autumn. However, oviposition on bird cherry provides fundatrices with easily located, high quality food, enabling very high reproductive rates in spring (Leather & Dixon, 1981). Examples from other herbivorous insect groups suggest that oviposition preferences, adaptations for placing progeny in favourable circumstances, may often outweigh benefits of immediate optimization of diet (Claridge & Wilson, 1978; Claridge *et al.*, 1977).

Why is *S. juncea* utilized less than *S. nemoralis* during spring, despite its apparent nutritional superiority? Both are perennials and begin to grow at the same time in spring; in this regard they are similar from the point of view of hatching fundatrices. The earlier flowering and senescence of *S. juncea* may prevent its utilization in spring; as in *E. strigosus*, most stems are dead before maturation of oviparae. Late summer alatae do colonize

both *Solidago* species (Figs. 6 and 7). On *S. nemoralis*, these colonies always produce sexuals and overwintering eggs, whereas *S. juncea* stems drying out before mid-September are deserted without production of sexuals – through the production of alatae.

Feeding is possible though rare on *Solidago* in mid-summer. *R. padi* cannot reproduce on its winter host in mid-summer (Dixon, 1971), while *Aphis fabae* Scop. can and does if natural enemies are removed, permitting persistence of spring colonies (Way & Banks, 1968). Natural enemies are not common in spring on *Solidago* but may still be responsible for eliminating persistent *U. grivicorne* colonies.

In most host-alternating aphids, the summer host is more recently acquired (Eastop, 1977). *U. grivicorne* probably fed originally only on *Solidago*, since its closest relatives [*U. cadens* Moran, *U. caligatum* (Richards) and *U. tissoti* (Boudreaux)] are restricted to *Solidago*. Other *Lambersius* species do feed on *Erigeron*, e.g. *U. erigeronensis* (Thomas) and *U. macgillivrayae* (Olive) but are less closely related to *U. grivicorne* (Moran, 1982).

Similarity between seasonal host shifts in *U. grivicorne* and in other aphids is clearly due to convergence, and host alternation has evolved multiple times in aphids (Eastop, 1972, 1977; Hille Ris Lambers, 1950, 1979). The phenomenon is rare in other herbivorous insects suggesting that some features of aphids cause host alternation to evolve frequently.

Among properties predisposing aphids to host alternation is the large number of generations per year, made possible by parthenogenesis and telescoping of generations. This promotes movement between individual plants in two ways. First, colonies fill plants quickly and thus must disperse to new plants for continued expansion. Second, lineages (in this case clones) go through many adult, and thus potentially winged (dispersive), stages. If aphids are already forced to move between host individuals, then shifts between host taxa are less costly and can evolve more easily.

Also important, though not unique to aphids, is the predictability of fluctuations in host quality. Most of aphid evolution has taken place in temperate areas where primary determinants of food plant quality are the

regular cycles in phloem nutrient content arising from yearly growth cycles.

These two hypothesized predisposing characteristics are attractive in that they apply to aphids but not to most herbivorous insects. However, they fail to explain host alternation in the aphidoid family Adelgidae which is oviparous, thus lacking telescoping of generations and which alternates between conifers in 2 year rather than 1 year cycles. Possibly, the extension to 2 years (also found in Hormaphidinae and Fordinae, see Eastop, 1977) evolved secondarily. Still, by themselves, the factors suggested also fail to explain other recurring features of heteroecious life cycles, particularly why summer generations are less host specific and why summer hosts are almost always more recently acquired. In other words, why have monophagous aphids on herbaceous taxa not sometimes acquired perennials as winter hosts? The most promising hypothesis is that the high level of specialization of fundatrices has caused selection to favour lineages which utilize newly abundant, favourable plants in summer but which return to the ancestral host for production of sexual females (Mordvilko, 1928; Kennedy & Stroyan, 1959).

In *U.gravicornis*, however, all morphs including fundatrices could reproduce as well or better on *Erigeron*. Thus, neither of the two major hypotheses for host alternation is applicable; host shifts can be attributed neither to overspecialization of certain morphs (so that the ancestral host is retained despite superiority of the newer host) nor to simple maximization of nutrient intake (so that both hosts are retained because each is nutritionally superior at some time of the season). I have argued that fundatrices hatching on *S.nemoralis* are more likely to locate food; this benefit to retaining the winter host may be widespread in heteroecious aphids, given the typical growth forms of winter and summer hosts. These results for *U.gravicornis* add to accumulating evidence that patterns of host usage by herbivorous insects can be understood only by considering ecological factors other than nutritional quality.

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