Eur. J. Entomol. **93**: 53–58, 1996
ISSN 1210–5759

Life history responses to host quality changes and competition in the Turkey-oak aphid, *Myzocallis boerneri* (Hemiptera: Sternorrhyncha: Callaphididae)

RICHARD SEQUEIRA and ANTHONY F.G. DIXON*

School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

Aphids, adult weight, competition, fat content, host quality, offspring size, *Myzocallis boerneri*

Abstract. Populations of tree-dwelling aphids are typically characterised by dramatic fluctuations in density within years. Seasonal changes in host plant quality and intraspecific competition are important factors in aphid population dynamics. The seasonal changes in life history traits under field conditions and the effects of high density on body size and reproductive potential of the Turkey-oak aphid, *M. boerneri* were investigated. Aphid body size is at its maximum in early spring, soon after bud burst, and declines progressively as the Turkey-oak foliage matures. The fat content of individuals, as a proportion of total body weight, remains constant throughout the season. By comparison, a small linear decline in the size of the soma results in an exponential decline in the size of the gonads. At small adult body sizes, embryo size (and implicitly birth weight) is conserved, presumably so that the survival of nymphs born in the summer is maximised.

INTRODUCTION

Aphids that live on deciduous trees show dramatic patterns of population fluctuation within years (Dixon, 1985a, 1990). Endowed with phenomenal reproductive capacities, aphids can achieve extremely high population densities during favourable times of the season. Periods of high density are usually followed by periods where density declines rapidly (Dixon, 1990). The widespread occurrence of this phenomenon in populations of various aphid species (Chambers et al., 1985; Dixon, 1977, 1985a,b, 1990) calls for a better understanding of the effects of intraspecifc competition on aphid life history functions.

Seasonal development of vegetation is an unavoidable constraint on the activities of aphids in temperate regions. Food quality and temperature vary greatly during the season. The complexity of aphid life cycles reflects the marked changes in the nutritional suitability of trees and shrubs (Dixon et al., 1993; Furuta, 1987). Tree foliage is a rich source of food for aphids during bud burst and early leaf development in the spring, and leaf senescence in the autumn. During the intervening summer months, the mature foliage is less favourable for aphid growth and development (Dixon, 1987; Dixon et al., 1993). Thus, seasonality is another major factor in aphid ecology, and it is important to determine how aphid life history components respond to seasonal fluctuations in host quality.

The aphid *Myzocallis boerneri* Stroyan is host specifc to Turkey-oak, *Quercus cerris*. Little is known about the life history responses (e.g., body size, reproductive potential, fat content, etc.) of this aphid to seasonal changes in nutritional suitability of the host tree and intraspecifc competition. In the spring of 1993, field and laboratory evaluations were initiated i) to determine seasonal changes in body size, reproductive biomass (gonads), fat

* Author for correspondence.

content and population density under field conditions, ii) to quantify the adverse effects of high densities on body size, and iii) to identify specific reproductive costs associated with a small body size.

MATERIAL AND METHODS

Biology of *M. boerneri*

Overwintering eggs laid on the twigs and branches hatch and produce the first generation of aphids at bud burst, usually around the end of April. All subsequent spring and summer generations are parthenogenetic. The appearance of sexual morphs (males and females) by the middle of October coincides with the beginning of leaf fall and marks the end of the aphid's seasonal cycle. All morphs except the sexual females are winged and show a strong propensity to fly when disturbed, especially on warm, sunny days. Adults can weigh up to 0.8 mg (wet weight) (Sequeira & Dixon, unpublished data). Population density increases rapidly to a peak in late spring and subsequently declines all throughout summer. A small recovery in numbers is usually observed in autumn, prior to leaf fall.

Seasonal changes in life history traits

Field evaluations were initiated on a tree population in Earlham Park, Norwich, in 1993. From the first week of May, a group of newly moulted adult aphids from the tree population were collected each week and transferred to the laboratory where they were killed with fumes of ethyl acetate. The dead aphids were separated into two groups. Individuals from one group were dissected following the protocol of Brough et al. (1990), and the soma of each aphid separated from the gonads. The separated components were transferred to pre-weighed strips of aluminium foil, dried for 3 days at 40°C and weighed.

Aphids from the second group were dried individually at 40°C for 3 days and then subjected to a fat extraction procedure (Ito, 1986). Each dried aphid was submersed in 2 cc of a 2 : 1 mixture of chloroform and methanol. The solvent was changed three times, once every 24 hours. After the third solvent change, the aphids were again dried for 24 hours and weighed. Estimates of aphid population density were obtained at the time of sampling by counting the total number of aphids on 80 leaves (10 leaves selected at random from each of 8 fixed sampling points around the Turkey-oak tree).

Laboratory evaluations

A clonal population of *M. boerneri* was propagated in the laboratory from a single adult female. The laboratory population was maintained under controlled conditions (21°C and a 16 : 8 h photoperiod) on excised Turkey-oak leaf segments (approximately 7 cm x 4 cm) placed on nitrate-containing agar plates (3 g agar, 0.15 g NH_4NO_3 and 0.15 g of KNO_3 in 400 ml of tap water). A greenhouse population of *M. boerneri* was propagated by infesting potted 3–4 year-old Turkey-oak saplings. The infested saplings were maintained at approximately 25°C and natural photoperiod. Under these conditions, within about 2 months the greenhouse population consisted of very small adults. Adults from the greenhouse population were categorised as "small" whereas those from the laboratory population as "large".

Density effects on body size

The effects of high density on body size were investigated by rearing aphids under crowded or uncrowded conditions. Either 1 or 10 "large" adults were allowed to reproduce on a single leaf segment for 5 days after which the adults were removed and the nymphs allowed to reach maturity. Preliminary trials showed that this was the most effective protocol for rearing *M. boerneri* under crowded and uncrowded conditions. With 10 aphids reproducing continuously, the leaf segment is fully saturated with nymphs after 5 days whereas the leaf segment with 1 adult reproducing provides relatively benign developmental conditions. Dry weights of newly moulted F_1 adults from each treatment were obtained. Both treatments were replicated 5 times to obtain sufficiently large samples of adult aphids.

Recovery from small adult size

The time (in generations) required by aphids to recover from small body size was determined. Each of two groups of adult aphids, 15 "large" and 30 "small," were allowed to reproduce on one of two excised Turkey-oak leaf segments placed on nitrate-containing agar. From each group, 30 new-born nymphs were selected to constitute the "parental generation" and reared through 4 generations under identical physical conditions. Each generation was reared on a fresh leaf segment. In each offspring generation, the dry weights of newly moulted adults were obtained.

Reproductive costs of small size

The relationship between body size, embryo number and embryo size was determined. Newly moulted adults (not more than 24 hours old) from the "small" and "large" populations were anaesthetised with CO_2 and dissected under a binocular microscope. The number of embryos in each adult were counted and length of the three largest mature (sclerotised) embryos was obtained using an occular micrometer.

RESULTS

Seasonal changes of life history traits

Bud burst was observed in the last week of April. The Turkey-oak foliage matured within 6 weeks, in early June. Aphid density increased for 8 weeks and then declined steadily (Fig. 1a). Adult dry weight increased briefly during the early stages of leaf development and then decreased steadily for the duration of the trial (Fig. 1a). The relationship between somatic and gonadal biomass is exponential (Fig. 1b). At large sizes, a small reduction in somatic mass resulted in a large reduction in gonadal mass. The fat content of individuals did not change relative to body size over the season (Fig. 1c).

Density effects on body size

High mortality of crowded nymphs was observed, especially during the later stages of development. By contrast, negligible mortality was observed among uncrowded nymphs. The cause of mortality in all cases was starvation after wandering off the leaf onto the agar. Body size (dry weight) differed between crowded and uncrowded individuals (ANOVA: d.f – 1.67; MS = 0.008; Error = 0.0003; F = 29.38; P < 0.0001). Crowded individuals were, on average, 30% smaller than their uncrowded counterparts.

Recovery from small adult size

The average weight of "large" mothers gradually drifted upwards between generations (Fig. 2). Differences in mean size between the different generations in the "large"

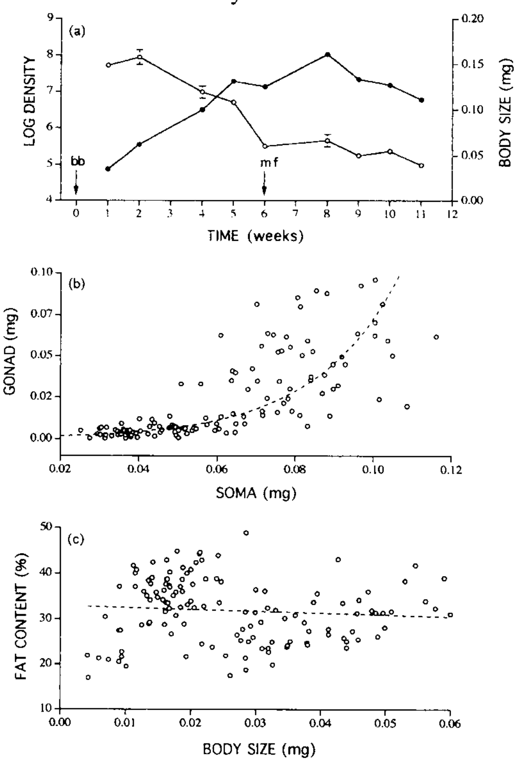

Fig. 1. The results of field evaluations of *M. boerneri* initiated in 1993. (a) Weekly changes in density (solid circles) and average body size (open circles); bb – bud burst, mf – mature Turkey-oak foliage. (b) The relationship between the size of soma and gonads of individual adults; the dashed line represents the least-squares fitted curve. (c) Fat content of individual adult females; the dashed line represents the least squares regression.

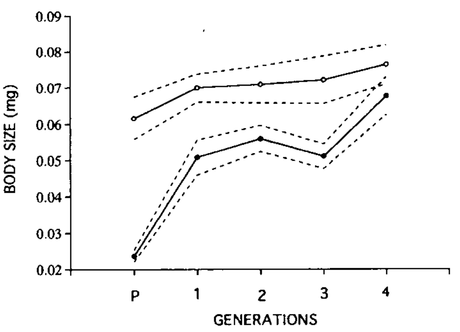

Fig. 2. The time in generations necessary for convergence between body sizes of "small" (solid circles) and "large" (open circles) aphids, starting with the parental generation (P). Dashed lines mark the 95% confidence region for the means.

group were statistically significant (ANOVA; df = 4.99; MS = 0.0007; F = 4.76; P = 0.002). The average weight of "small" mothers doubled in the first generation and then increased again between generations three and four (Fig. 2). At 21°C, generation time for both groups was approximately 12–14 days. Convergence in body size between the two groups required approximately 4 generations (Fig. 2).

Reproductive costs of small size

Indices of reproductive potential, viz., embryo number and size (length), show that a reduction in size is accompanied by a dramatic reduction in embryo number, i.e., reproductive potential. Small adults ranged in size (wet weight) from 0.031 to 0.071 mg. They contained no immature embryos and from 1 to 3 sclerotized embryos. The length of embryos from small adults ranged from 3 to 6 ocular micrometer (OM) divisions (1 OM division = 0.084 mm). Large adults weighed between 0.158 and 0.248 mg and contained from 3 to 7 sclerotized embryos in addition to numerous immature ones in various stages of development. The embryos from large adults were uniform in length (6 OM divisions). The total number of embryos ≥ 3 OM divisions (0.25 mm) in length in the large adults ranged from 9 to 17.

Summary statistics (Table 1) show that small adults are around 26% of the wet weight of large adults. The largest embryos from small mothers were 76% of the length of their counterparts from large mothers. On a per-unit weight basis, large adults have at least 37% more embryos than small adults.

TABLE 1. Summary statistics for wet weight (WW), length of largest embryo (EMBLEN) and number of embryos (EMBNO) greater than 0.252 mm (3 ocular micrometer divisions) of small and large mothers (n = 16 for both groups).

	Small			Large		
	WW	EMBLEN	EMBNO	WW	EMBLEN	EMBNO
mean	0.054	4.531	2	0.208	5.969	12.3
s.e.m.	0.003	0.244	0.183	0.005	0.031	0.544
c.v.	0.2	0.215	0.365	0.097	0.021	0.178
mean (c)[1]			37.12			59

[1] corrected mean, per unit weight of mother

DISCUSSION

The most logical outcome of competitive situations where individuals are scrambling for resources such as food is a reduction in body size. Changes in body size therefore provide a good surrogate measure of the intensity of competition provided that other factors such as food quality are kept constant. In aphids, intraspecific competition for resources is not difficult to demonstrate under laboratory conditions (Dixon & Wratten, 1971; Murdie, 1969a,b); individuals reared under crowded conditions are smaller than those reared under benign conditions, and a reduction in size generally results in lower reproductive potential (Dixon, 1985a,b; Dixon & Kindlmann, 1994; Leather & Dixon, 1984).

In contrast to the laboratory setting, scramble competition resulting in smaller individuals is difficult to demonstrate under field conditions. This is because nutrition and density tend to covary under field conditions. The decline in body size begins early in the season, much before density reaches a peak (Fig. 1a), and hence can be attributed partly to declining host quality. The generation-to-generation changes in gonadal biomass provide a good description of seasonal effects on reproductive potential. The soma to gonad ratio represents the aphid's commitment to reproduction and reflects the cumulative influence of developmental conditions throughout ontogeny.

The Turkey-oak aphid pays a heavy price for the seasonal changes in body size. First, at the level of the individual, a small reduction in size results in exponential decrease in reproductive potential (Fig. 1b). The second cost of a seasonal decline in body size is manifested at the population level. The loss of body size, and implicitly reproductive potential, is not quickly reversible (Fig. 2); at least 4 generations are required to recoup weight loss during the season. The steady loss of body size throughout most of spring and summer results in very small individuals at the end of summer. This is presumably the reason why *M. boerneri* population density does not recover in the autumn to the earlier spring levels (Dixon, 1990).

The reproductive strategy of callaphidids such as *M. boerneri* is complex. Assimilated energy is partitioned between the soma, gonads and storage (fat reserves). The fat content of individuals does not change during the season (Fig. lc) whereas the gonads get progressively smaller (c.f. Figs 1a, b). This means that the amount of fat is increasing relative to gonadal biomass as body size gets smaller during the season. In other words, although fat as a proportion of total body size remains constant, small adults have access to more fat reserves than large adults because the former have a smaller reproductive commitment.

Early in the season nutritional resources are directed toward maximising the reproductive rate. First-generation females (fundatrices) usually have a higher ovariole number (and implicitly a higher fecundity) than second and later generation females (Leather & Wellings, 1981; Wellings et al., 1980). This appears to be a genetically programmed feature of the life cycle of these aphids (Wellings et al., 1980).

Later in the season, when body size declines considerably, the reproductive strategy seems to be directed toward maximizing the "ecological competence" of the survivors rather than minimizing mortality. Small adults that achieve only 26% of the size of large adults nevertheless contain embryos that are, on average, 76% the length of their counterparts in large adults (Table 1). This suggests that embryo size, and implicitly birth weight, is conserved. Birth weight is correlated with the ability of new-born aphids to feed (Dixon, 1985a) and directly determines the survival of new-born nymphs.

ACKNOWLEDGEMENTS. The authors are indebted to V. Jarošík and J. Thacker for useful comments on earlier drafts of the manuscript. R.S. was supported by a N.E.R.C. research grant (GR3/8026) to A.F.G.D.

REFERENCES

BROUGH C.N., DIXON A.F.G. & KINDLMANN P. 1990: Pattern of growth and fat content of somatic and gonadal tissues of virginoparae of the vetch aphid, Megoura viciae Buckton. *Entomol. Exp. Appl.* **56**: 269–275.

CHAMBERS R.J., WELLINGS P.W. & DIXON A.F.G. 1985: Sycamore aphid numbers and population density II. Some processes. *J. Anim. Ecol.* **54**: 425–442.

DIXON A.F.G. 1977: Aphid ecology: life cycles, polymorphism and population regulation. *Annu. Rev. Ecol. Syst.* **8**: 329–353.

LEATHER S.R. & WELLINGS P.W. 1981: Ovariole number and fecundity in aphids. *Entomol. Exp. Appl.* **30**: 128–133.

LEATHER S.R. & DIXON A.F.G. 1984: Aphid growth and reproductive rates. *Entomol. Exp. Appl.* **35**: 137–140.

DIXON A.F.G. 1985a: *Aphid Ecology*. Blackie, Glasgow, 157 pp.

DIXON A.F.G. 1985b: Structure of aphid populations. *Annu. Rev. Entomol.* **30**: 155–174.

DIXON A.F.G. 1987: Seasonal development in aphids. In Minks A.K. & Harrewijn P. (eds): *Aphids, their Biology, Natural Enemies and Control (World Crop Pests, Vol. 2 B)*. Elsevier, Amsterdam, pp. 315–320.

DIXON A.F.G. 1990: Population dynamics and abundance of deciduous tree-dwelling aphids. In Watt A.D., Leather S.R., Hunter M.D. & Kidd N.A.C. (eds): *Population Dynamics of Forest Insects*. Intercept, Andover, pp. 11–23.

DIXON A.F.G. & KINDLMANN P. 1994: Optimum body size in aphids. *Ecol. Entomol.* **19**: 121–126.

DIXON A.F.G. & WRATTEN S.D. 1971: Laboratory studies on aggregation, size and fecundity in the black bean aphid, Aphis fabae Scop. *Bull. Entomol. Res.* **61**: 97–111.

DIXON A.F.G., WELLINGS P.W., CARTER C. & NICHOLS J.F.A. 1993: The role of food quality and competition in shaping the seasonal cycle in the reproductive activity of the sycamore aphid. *Oecologia* **95**: 89–92.

FURUTA K. 1987: Amounts of favourable feeding materials in spring for the maple aphid, Periphyllus californiensis Shinji, estimated from the phenological relations between the aphid and host trees. *J. Appl. Entomol.* **104**: 144–157.

ITO K. 1986: Starvation longevity and lipid accumulation in non-diapausing and diapausing adults of the coreid bug Cletus punctiger. *Entomol. Exp. Appl.* **40**: 281–284.

MURDIE G. 1969a: Some causes of size variation in the pea aphid, Acyrthosiphon pisum Harris. *Trans. R. Entomol. Soc. Lond.* **121**: 423–442.

MURDIE G. 1969b: The biological consequences of decreased size caused by crowding or rearing temperatures in apterae of the pea aphid, Acyrthosiphon pisum Harris. *Trans. R. Entomol. Soc. Lond.* **121**: 443–455.

WELLINGS P.W., LEATHER S.R. & DIXON A.F.G. 1980: Seasonal variation in reproductive potential: a programmed feature of aphid life cycles. *J. Anim. Ecol.* **49**: 975–985.

Received April 11, 1995; accepted May 5, 1995