Eur. J. Entomol. **98**: 177–182, 2001
ISSN 1210-5759

Effect of temperature on fecundity and development of the Giant Willow Aphid, *Tuberolachnus salignus* (Sternorrhyncha: Aphididae)

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Key words. Aphididae, Lachninae, *Tuberolachnus salignus*, developmental rate, threshold temperature, fecundity, survival, intrinsic rate of increase, willow, *Salix*, aphid, short rotation coppice

Abstract. This study investigates the thermal requirements, nymphal development rates and the fecundity of both alate and apterous adults of the giant willow aphid, *Tuberolachnus salignus* (Gmelin) at several temperatures. Nymphal development rate increased linearly with temperature. It was estimated that 196 ± 4 degree-days above a threshold temperature of 5.5 ± 0.3°C were required for apterae to complete development from birth to final ecdysis. The alate morph was significantly less fecund than the apterous morph and its fecundity did not vary with temperature. The apterous morph displayed highest fecundity at 20°C. Survival to reproduction was lower in the alate morph, but temperature had no effect on the proportion reproducing in either morph.

INTRODUCTION

The giant willow aphid, *Tuberolachnus salignus* (Gmelin) (Lachninae: Lachnini) is the largest of the over 120 species of aphid that feed on willows (*Salix spp.*). It has been identified as a potential pest of selected hybrid willows grown as short rotation coppice (SRC) for biomass production (Das, 1918; Sage, 1994). This species has an almost cosmopolitan distribution (Blackman & Eastop, 1994) and is present on SRC willow clones throughout the United Kingdom (A. Armstrong, pers. comm.).

Tuberolachnus salignus is apomictic (Blackman & Spence, 1996) and thus reproduces solely by parthenogenesis. It appears on willows in mid-summer and numbers can rise rapidly. Dense colonies often persist on the stems and branches of their host trees throughout autumn and, although numbers decline from November onwards, the species remains visibly present on the host until January or February. It is not known where, how or in what form these aphids spend the spring months. This study investigates the relationship between temperature and the development and fecundity of *T. salignus* on willow in the laboratory.

METHODS

The *T. salignus* clone used was originally collected from Roves Farm, Sevenhampton, Wiltshire (National Grid Reference: SU 210 888) and had been maintained in culture for three months. The aphids were raised on potted, growing willow trees (*Salix viminalis* "Q683") maintained at 15 ± 1°C and with a photoperiod of 16L : 8D. Nymphal development duration was estimated on the SRC willow hybrid "Q683" grown hydroponically in a 0.1% solution of "Miracle-Gro" (I.C.I. Garden Products, Haselmere, GU27 3JE) at four different temperatures (10±1, 15 ± 1, 20 ± 1 and 25 ± 1°C, ambient temperature) under conditions of controlled day length (16L : 8D). The proportion of adults reproducing, the number and mass of progeny, the duration of adult life and the intrinsic rate of natural increase (r_m) were estimated for apterae at 10, 20 and 25°C and for alatae at 10 and 20°C. Insufficient alatae were available to complete more than two treatments.

Nymphal development and survival

For each of 22 replicates per temperature, 4 young apterous adults were placed on an isolated cutting of the SRC willow clone "Q683" grown hydroponically (as above). Observations were made early morning, midday and late afternoon until the adults established and reproduced; this time was noted. When each twig hosted approximately 10 progeny the time was noted and the adults removed. The time at which the first and last progeny on each twig underwent ecdysis at each instar change was noted and newly moulted adults were removed. The last adult was left *in situ* and the time at which it began to reproduce recorded. To verify that this method did not bias the data towards slowly developing aphids, the duration of birth-adult of the first and last progeny on all twigs were compared using Student's t-test for paired samples and found to be not significantly different ($t = 1.3$, d.f. = 20, n.s.). The mean for each twig was used as data. Regression was used to analyse the influence of temperature on the rate of development (1/days) with standard errors of the parameters estimated according to Campbell et al. (1974). Survival was recorded daily and analysed using χ^2 tests for difference in proportions (Heath, 1995).

Fecundity and longevity of apterous and alate virginoparae

For each of 22 replicates (apterae) or 30 replicates (alatae) per temperature a newly moulted adult was placed on a bare twig of the SRC willow clone "Q683". Alatae were induced by severe crowding of a laboratory culture at each temperature. Apterae came from the experiment above. Alatae were initially confined by a mesh-panelled 500 ml plastic bottle until establishment (1–2 days). For each replicate we recorded:

1. The time of final ecdysis
2. The mass of each individual at this time
3. The time at which reproduction commenced
4. The number of offspring born per day (removed on a daily basis)
5. The mass of five randomly selected offspring born on the 2nd day of reproduction

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6. The time at which reproduction ceased
7. The time of death

From these times the mean duration of the three adult life stages (pre-reproductive, reproductive and post-reproductive) were calculated. The intrinsic rate of natural increase (r_m) was calculated using the following formula (Wyatt & White, 1977):

$$r_m = \frac{0.74(\ln M_d)}{d}$$

where M_d is the number of nymphs produced over a period of time equal to that of the entire pre-reproductive period (d). This formula gives a good estimate of population growth rates in aphids (Leather & Dixon, 1984; Dixon et al., 1993). As no data were available on the duration of nymphal life for alatae, development prior to final ecdysis for this morph was assumed to take 20% longer than that of apterae. Whilst this assumption may not be accurate, the 20% increase is the average increase in development time required by alatae recorded in several studies (Mackay & Wellington, 1975; Dixon, 1998).

Survival between treatments was analysed using χ^2 tests for difference in proportions (Heath, 1995). All other comparisons were made by ANOVA with the least significant difference at 95% (LSD^{95}) used to determine differences (D) between specified treatments.

RESULTS

Nymphal development and survival

All progeny in this experiment developed into apterae. Developmental rate was positively and linearly related to rearing temperature over the range tested (Table 1) such that y = 0.0051x – 0.028 (r^2 = 0.969, ANOVA, F = 2681, d.f. 1,85, p < 0.001) (Fig. 1). Thus, for apterae, development from birth to final ecdysis required 196 ± 4 degree-days above a threshold temperature of 5.5 ± 0.3°C. Probability of survival (overall mean = 0.9, range 0.87–1) did not differ significantly between temperatures (χ^2 = 4.3, d.f.= 3, n.s.), nor between instars (χ^2 = 4.1, d.f. = 3, n.s.).

Longevity of apterous and alate virginoparae

Adult life span differed significantly between treatments (ANOVA, F = 29.11, d.f. = 4,93, P < 0.001) (Table 2). At 10°C the longevity of the morphs did not differ, but at 20°C the life span of alatae was shorter (LSD^{95} = 3.61, D = 23.91). Longevity of adult apterae did not differ between 10°C and 20°C, but decreased abruptly at 25°C

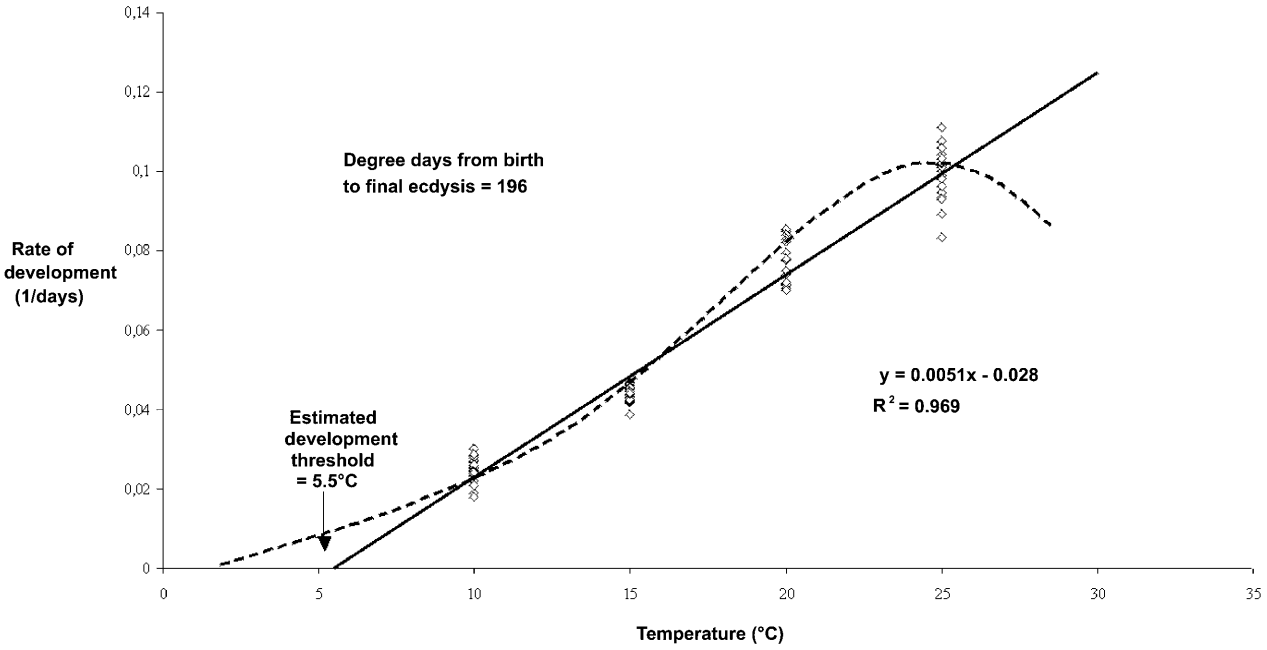

Fig. 1. Rate of development (1/days) from birth to final ecdysis of apterous *Tuberolachnus salignus* as a function of temperature (°C). ANOVA, F = 759, d.f. 127, p < 0.001. The broken line is a diagramatic representation of a speculative higher order regression.

TABLE 1. Mean duration, ± SE, in days of nymphal instars, total nymphal duration and rate of development (1/days) of *Tuberolachnus salignus* apterae reared at four different temperatures.

Duration in days	10°C	15°C	20°C	25°C
First instar	8.9 ± 0.2	5.2 ± 0.1	3.5 ± 0.2	2.0 ± 0.1
Second instar	8.3 ± 0.3	5.3 ± 0.1	2.6 ± 0.1	2.2 ± 0.1
Third instar	10.4 ± 0.2	5.4 ± 0.1	3.2 ± 0.2	2.9 ± 0.1
Fourth instar	12.9 ± 0.2	6.8 ± 0.1	3.7 ± 0.1	3.1 ± 0.1
Total nymphal duration	40.6 ± 0.9	22.8 ± 0.2	13.0 ± 0.2	10.1 ± 0.1
Rate of development	0.025 ± 0.001	0.044 ± 0.001	0.076 ± 0.001	0.099 ± 0.001

TABLE 2. Proportion of adults reproducing, intrinsic rate of natural increase (r_m), mean ± SE duration of adult life and the reproductive characteristics of apterae and alatae of *Tuberolachnus salignus* in relation to temperature.

	Alatae		Apterae		
	10°C	20°C	10°C	20°C	25°C
Proportion reproducing	0.62	0.53	0.95	1	1
r_m	0.04 ± 0.001	0.13 ± 0.003	0.06 ± 0.001	0.19 ± 0.002	0.22 ± 0.004
Adult life (days)	39.2 ± 2.5	14.5 ± 1.2	42.2 ± 3.7	38.2 ± 1.3	18.3 ± 0.8
Adult mass (mg)	5.36 ± 0.21	5.09 ± 0.27	10.87 ± 0.34	11.62 ± 0.39	10.12 ± 0.26
Fecundity	33.5 ± 2.1	35.1 ± 1.9	51.3 ± 4.0	71.1 ± 2.4	43.4 ± 1.8
Nymphal mass (mg)	0.28 ± 0.01	0.33 ± 0.02	0.37 ± 0.01	0.37 ± 0.01	0.33 ± 0.01

(LSD^{95} = 7.96, D = 19.66). Two of the three components of adult longevity, namely the pre-reproductive and reproductive periods declined with increasing temperature (Fig. 2). The non-apparence of this trend in total longevity between 10°C and 20°C can be accounted for by an increase in the duration of the post-reproductive period at the intermediate temperature (10–20°C LSD^{95} = 5.12, D = 8.6, 20–25°C LSD^{95} = 2.92, D = 15.16) (Fig. 2). The relationship between adult mass and the proportion of adult life that occurred after reproduction was non-significant for apterae, for alatae the opposite was true with the two being positively associated (days = 4.13 mass – 9.89, ANOVA, F = 9.96, d.f. = 1,34, p < 0.005).

Adult survival

Survival patterns differed between the alate and apterous morphs [Figs 3a (apterae) and 3b (alatae)]. A significantly greater proportion of alatae (42%) died before reproducing than did apterae (2%) (χ^2 = 19.56, d.f. = 1, p < 0.001). This high proportion of alatae dying cannot be accounted for by a difference in mass at final ecdysis (mean mass of reproductives = 5.23 ± 0.17 mg, mean mass of non-reproductives = 5.15 ± 0.23 mg, t = 1.67, d.f. = 61, n.s.). Temperature had no influence (χ^2 = 0.097, d.f. = 1, n.s.) on the proportion of either morph reproducing (Table 2).

Fecundity

The intrinsic rate of natural increase (r_m) differed between treatments (ANOVA, F = 858, d.f. = 4,93, p < 0.001) (Table 2). Both morphs responded positively to temperature.

The number of nymphs produced (ANOVA, F = 33.24, d.f. = 4,93, p < 0.001) and the mass of new born nymphs (ANOVA, F = 11.14, d.f. = 4,93, p < 0.001) differed highly significantly between treatments. Rearing temperature did not affect the number of young produced by alatae, however the mass of their new-born nymphs was higher at 20°C than at 10°C (LSD^{95} = 0.038, D = 0.048).

Apterae produced heavier nymphs than alatae (10°C LSD^{95} = 0.029, D = 0.087, 20°C LSD^{95} = 0.040, D = 0.045), but responded differently to temperature over this range (Table 2). The mass of nymphs born to apterae did not change between 10°C and 20°C (LSD^{95} = 0.046, D =

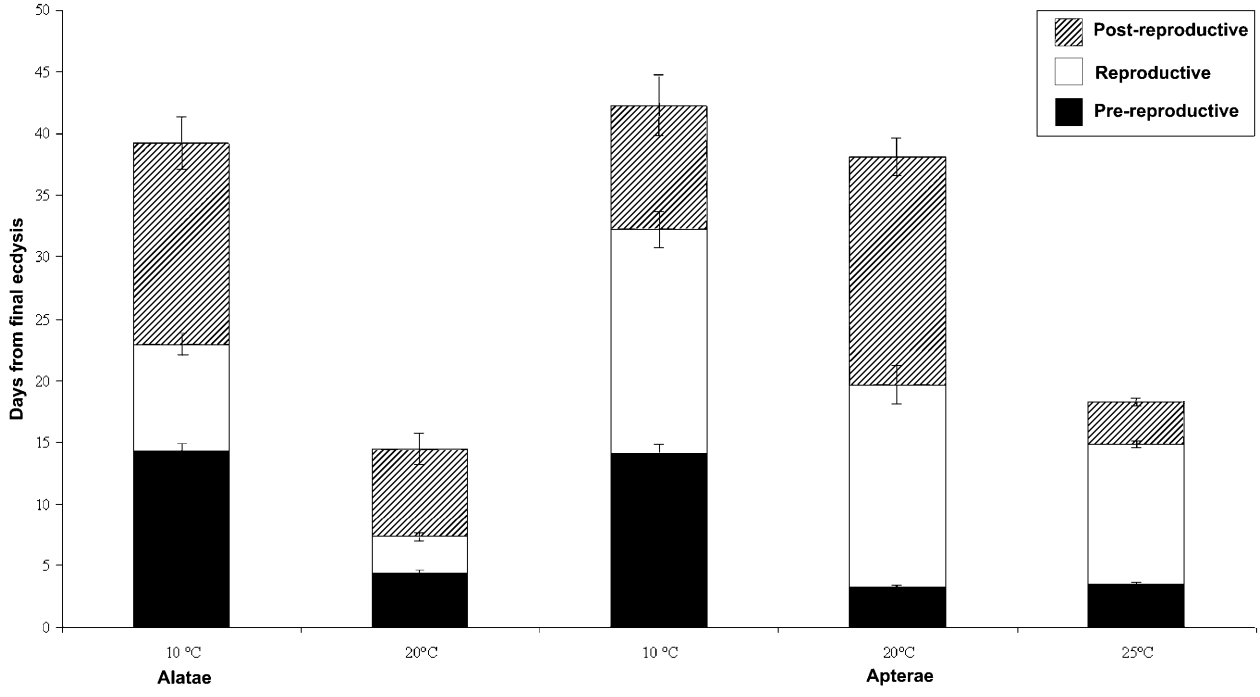

Fig. 2. Mean duration (± SE) of adult life stages of apterous and alate *Tuberolachnus salignus* at different temperatures.

0.005), but declined at 25°C (20–25°C LSD^{95} = 0.029, D = 0.058) (Table 2). The number of nymphs produced by apterae at 20°C was higher than at either 10°C or 25°C (LSD^{95} = 5.97, D = 20.29), which were not different to each other (LSD^{95} = 9.59, D = 0.45).

Fecundity schedules for the two morphs are presented in Figs 3c (apterae) and 3d (alatae). At the higher temperatures both morphs produced the majority of their young within seven days of commencing reproduction and the distributions were leptokurtic. At 10°C the pattern was different; alatae displayed a positive skew while apterae followed a platykurtic distribution thus spreading their reproductive investment more evenly across the whole reproductive period.

DISCUSSION

As with many other aphid species the rate of development from birth to adulthood is linearly related to temperature over the range of temperatures studied here (Leather & Dixon, 1984; Akey & Butler, 1989). The developmental threshold was calculated to be 5.5 ± 0.3°C, again similar to that measured in several temperate species of aphid (Campbell et al., 1974) and other insects (McDonald et al., 1998). However, studies of aphids that cover both higher and lower temperatures indicate that the relationship is non-linear at the extremes of aphid physiological tolerance (Barlow, 1962; Lamb & Mackay, 1988; Lamb, 1992). This pattern, which is very likely to hold true for *T. salignus*, is illustrated in Fig. 1. The continuing presence of active populations of this aphid in the field during the early months of the year indicates that not only do they have substantial cold tolerance, but also that the threshold temperature is likely to be below that which is suggested by this model.

The number of degree-days required for nymphal development is high for an aphid (Campbell et al., 1974). Body size may offer some explanation of this as *T. salignus* is one of the largest aphid species recorded and feeds on phloem elements located below the bark. This long duration could also be a reflection of an adaptation to poor food quality. The species appears in the field in mid-summer, a time at which trees are considered to be nutritionally poor hosts (Dixon, 1998) and during which heteroecious aphids reside on their secondary herbaceous hosts. *Tuberolachnus salignus* also persists long after the host tree has shed its leaves and become largely photosynthetically inactive. With a major proportion of its temporal distribution occurring on what are considered physiologically unsuitable hosts a long development time would be expected (Llewellyn et al., 1974). Additionally, Llewellyn et al. (1974) found no relationship between the concentration of amino acids in the phloem and *T.*

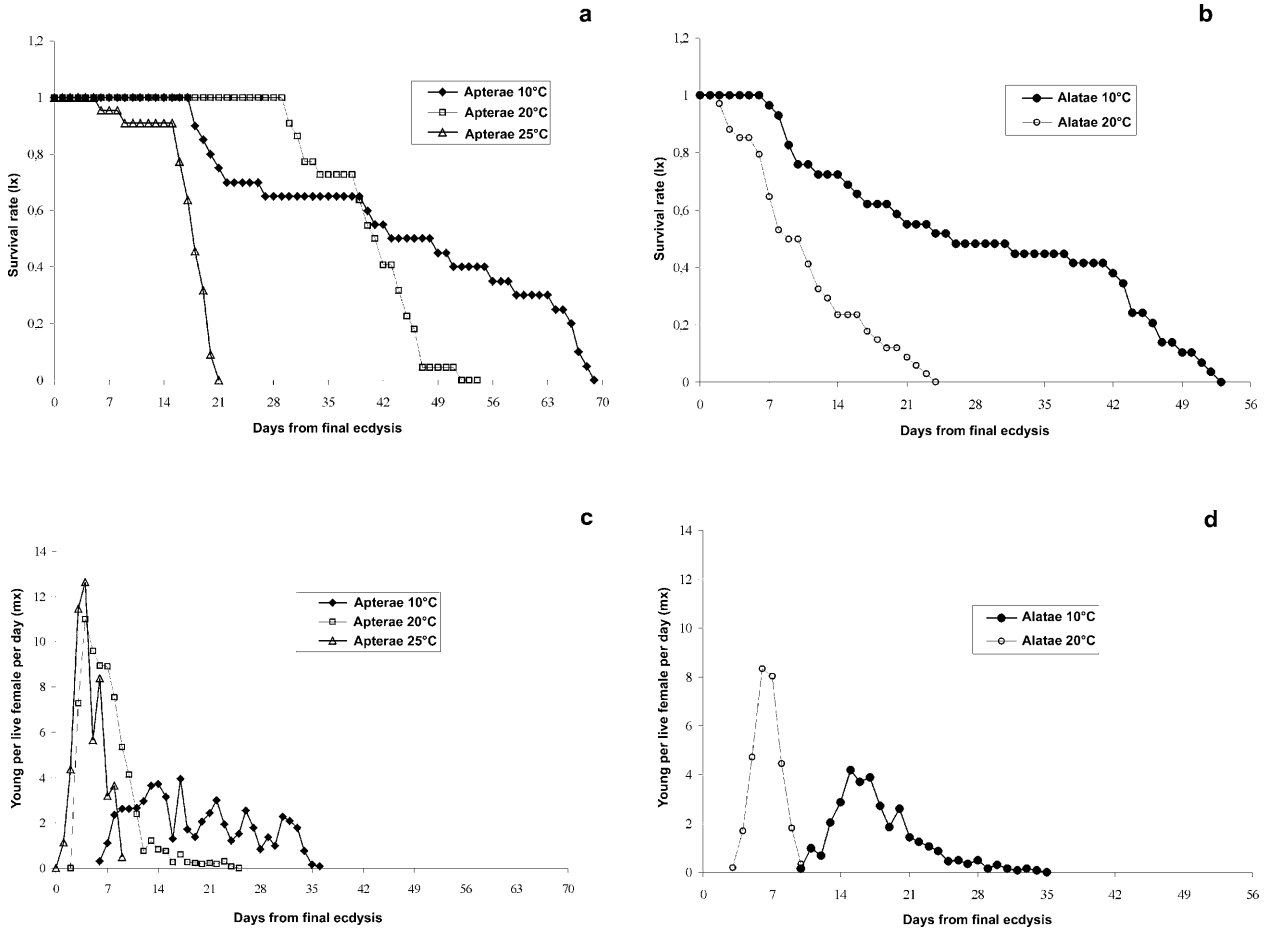

Fig. 3: a,b – survival rates of adult apterous and alate *Tuberolachnus salignus* at different temperatures; c,d – post-final ecdysis fecundity schedules of apterous and alate *Tuberolachnus salignus* at different temperatures.

salignus growth rate. This is in contrast to another large aggregative stem-feeding aphid species, *Cinara pini* (L.), which varies its growth rate substantially in response to seasonal changes in host plant quality (Kidd et al., 1990). It is thus also possible that *T. salignus* has traded the ability to respond to the increase in food quality induced by increased nutrient translocation during autumnal senescence, for the ability to subsist on poor quality nutrition. This trade-off in which tolerance of poor nutrient conditions comes at the expense of the ability to respond to fertilisation is well known in plants (Chapin, 1980; Crawley, 1986).

Interestingly, although there was no influence of temperature on within morph pre-reproductive mortality, a significantly greater proportion of alatae died than apterae between final ecdysis and reproduction. Wing production is known to be linked to a reduction in fecundity in several other aphid species (Banks & Macaulay, 1964; Mackay & Wellington, 1975; Newton & Dixon, 1990; Dixon, 1998) and indeed in this study apterae were more fecund and gave birth to larger young than alatae. It appears here however, that in addition to a decreased reproductive output being alate also bears a cost in terms of survival to reproduction. This pattern has been noted before (Mackay & Wellington, 1975) and has been associated with difficulties in final ecdysis for winged individuals. At 20°C alatae have a longer pre-reproductive period than apterae; this is explained by both a restless phase when dispersal is attempted and to the time required for the autolysis of wing muscles which liberates resources for reproduction (Johnson, 1958; Dixon, 1976). This difference remains, but is less apparent at 10°C.

At all temperatures examined the post-reproductive life of both morphs comprised a significant proportion of the aphid life span. Wratten (1977) and Dixon & Wratten (1971) suggest that aggregative aphids, such as *T. salignus*, confer a benefit on their clonal siblings by improving the nutritional quality of the host by increasing "sink" characteristics. Kidd & Tozer (1985), however, could find or suggest no benefit in a long post-reproductive life for apterous *Cinara pinea*. Although the feeding rate of *T. salignus* does decline in the post-reproductive stage (Llewellyn et al., 1974) it has been shown (Peel & Ho, 1970) that an increase in colony size led to a marked above-linear increase in mass transport of assimilate from the leaves. In alatae, for which post reproductive life is strongly linked to the adult mass, the feeding benefit conferred to offspring by the continuing presence of the parent may be sufficient to postulate that the long post-reproductive life seen here is of adaptive significance to alatae, but selectively neutral to apterae.

The giant willow aphid is unusual in many ways: its size, longevity, the lack of sexual morphs and the large dorsal projection set it apart from most other aphids. The lack of sexual reproduction and thus the inability to produce overwintering eggs, indicates that, in spite of the high day-degree requirement of the species, ambient temperature is very important to its ability to achieve high populations. This may partially explain why the aphid continues to reproduce during the summer months when trees are relatively poor hosts, in marked contrast to other tree aphids (Dixon, 1998). As this species will become of increasing applied interest to SRC biomass producers, a greater knowledge of its biology and ecology will be required.

ACKNOWLEDGEMENTS. We wish to thank R. Sage, ETSU and the Game Conservancy Trust for their support of this work and R.J. Lamb for his constructive comments on the manuscript.

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Received May 15, 2000; accepted August 30, 2000