Growth of alligator weed (*Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae)) and population development of *Agasicles hygrophila* Selman & Vogt (Coleoptera: Chrysomelidae) in northern New Zealand

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Summary

Alligator weed (*Alternanthera philoxeroides*) is a problem aquatic weed in New Zealand. Little is known about the population ecology of its introduced biological control agents, *Agasicles hygrophila* and *Arcola malloi*. A study of alligator weed and *A. hygrophila* populations conducted at a Northland site in New Zealand found that alligator weed dry weights peaked in late January 1994 and late December 1994 and declined as a result of feeding by increasing populations of *A. hygrophila*. Aquatic alligator weed was present throughout the 1994 winter. Internal stem diameters probably did not limit *A. hygrophila* pupation, as the majority of stem diameters measured were above 1.21 mm, the width required for female pupation within the stem. Peak *A. hygrophila* populations occurred during February but the density of *A. hygrophila* was too low or the damage too late in the growing season to provide control, despite considerable defoliation. It was concluded that *A. hygrophila* is unlikely to cause a reduction in alligator weed in New Zealand even in conjunction with *Arcola malloi*. *A. hygrophila* was estimated to have a requirement of 277 degree days above the 13.3°C lower temperature development threshold to develop from egg to an ovipositional adult. Three generations of *A. hygrophila* were predicted to occur at Whatatiri in the 1994–95 season.

Introduction

Alligator weed, *Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae), a plant of South American origin, has become a problem in waterways and pastures in many parts of the world, including the southern USA, Puerto Rico, Burma, Thailand, Indonesia, India, China, Australia and New Zealand (Julien 1981, Julien *et al.* 1992). Alligator weed was first recorded in New Zealand in 1906 at Aratapu by the Northern Wairoa River (Cheeseman 1906). It is currently distributed from North Cape to the Waikato River in the North Island and appears to be spreading southwards, albeit at a slow rate (Stewart *et al.* 1995). Alligator weed grows in a range of ecosystems from almost arid conditions to swampy areas but it grows primarily as an emergent aquatic plant rooted in the substrate below shallow water (Julien 1995). In aquatic habitats, alligator weed forms large floating mats of interwoven hollow stems which extend over the surface of the water. Terrestrial plants can establish on very thick weed mats and this may accelerate succession and turn enclosed water bodies into swamps. Alligator weed is categorized as a 'National Surveillance Plant Pest' which means it is unlawful to knowingly propagate, distribute, spread or sell this plant in New Zealand (Vervoort and Hennessy 1996).

From 1960 to 1974 biological control agents for alligator weed control were selected from searches made in South America by the United States Department of Agriculture (Coulson 1977). Two of these, *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae) and *Arcola malloi* (Pastrana) (Lepidoptera: Pyralidae), were imported into Australia from the USA in 1976 (Julien 1981). An additional species, *Disonycha argentinensis* Jacoby (Coleoptera: Chrysomelidae), was imported into Australia from Brazil in 1979 (Julien and Chan 1992). Between 1981 and 1988 *A. hygrophila*, *A. malloi* and *D. argentinensis* were introduced into New Zealand from Australia (Roberts and Sutherland 1989), but *D. argentinensis* did not establish. *A. hygrophila* was introduced into Northland and Auckland in 1982 by the Entomology Division, Department of Scientific and Industrial Research (Roberts and Sutherland 1989). The beetle established and spread rapidly throughout Northland (Philip *et al.* 1988), however, there is limited quantitative information on its biology and effectiveness as a biological control agent.

Several years after its release *A. hygrophila* had failed to effectively control alligator weed in some areas (Roberts *et al.* 1984). Comparisons of climate data and temperature requirements of *A. hygrophila* (Stewart *et al.* 1995, 1996) suggested that temperatures in New Zealand were less than optimal for development, particularly in areas south of the Northland region. Port Waikato (Lat. 37°24'S Long. 174°43'E) is the southern-most limit of *A. hygrophila* distribution in this country (C. Stewart unpublished survey). The only site in New Zealand where *A. hygrophila* was known to be present each summer and autumn in sufficient numbers to cause visible damage and defoliation of alligator weed is at Whatatiri, Northland (Lat. 35°47'S Long. 174°04'E).

This study investigated the changes in temperature, the growth of alligator weed and the distribution and development of *A. hygrophila* populations in New Zealand. A further aim was to estimate the quantity of heat units available for *A. hygrophila* development in one season at Whatatiri.

Methods

Site description

The study was conducted on one of a number of man-made ponds at Whatatiri in the Whangarei District. The study site (approximately 1800 m²) was located at the western end of the southern-most pond which had the greatest area of aquatic alligator weed floating on its surface.

Alligator weed extended from the edges of the pond in large mats and the density and spatial distribution of the mats varied between the seasons and years. During winter months, flood waters from the Wairua River washed alligator weed and debris into the ponds. The pond was surrounded by stop banks which were covered in pasture and scrub species, including *Ulex europaeus* L., *Leptospermum scoparium* J.R. & G.Forst. and *Rubus fruticosus* L. There were other species of plants growing amongst the weed mat (Table 1), however, alligator weed was the dominant species present.

Air temperature and rainfall

Air temperatures were recorded using thermistor sensors and data loggers. The loggers were placed in small airtight plastic containers and each sensor (one sensor per data logger) was attached to an anchored polystyrene float, covered with a ventilated screen and placed 1–2 m from the pond edge, approximately 4 cm above the water surface in the alligator weed canopy. Air temperatures were recorded every 24 minutes for the period 15 November 1993 to 25 April 1995. From 15 November 1993 to 6 December 1994

readings were collected from one logger and from 7 December 1994 to 25 April 1995 readings were collected from two loggers. Due to seasonal flooding, data stored in logger one were destroyed on 13 to 27 December 1993, 27 May, 25 July to 6 August 1994 and 6 March to 4 April 1995. Readings were destroyed on logger two from 21 March to 4 April 1995. Rainfall measurements were obtained from the Wairua Falls (Station A54701) 3.25 km from the site. Daily rainfall readings were summed to produce weekly totals.

Alligator weed shoot and quadrat samples

Sampling was carried out by boat without disturbing the weed and at least 3 m from the bank to ensure only floating weed was assessed. Samples were taken over two years from November 1993 to April 1995. The sampling frequency varied during each season depending on insect activity and the season. During the first growing season (1993–94), samples were taken fortnightly. During the 1994 winter (May to October) samples were taken monthly. In the second growing season samples were taken fortnightly in spring and autumn and weekly during summer (January to March 1995). The number of insects per unit of shoot tissue and the standing crop or shoots of alligator weed per 0.1 m^2 were measured. The number of insects per m^2 were estimated from these data.

A shoot sample consisted of a randomly selected stem and its leaf tissue cut at water level. When each shoot sample was taken, the numbers of *A. hygrophila* adults, each larval instar and egg batches, were counted. In the laboratory, shoot length was measured and the numbers of eggs per batch were counted. Stems were cut open and the pre-pupae, pupae and teneral adults were counted. Leaves were then removed from the stems and leaf and stem tissue samples were individually dried to constant weight in a drying oven at 105°C.

Shoot samples were cut at water level from within a 0.1 m^2 circular quadrats, placed randomly on the weed mat within 50 cm of accessible edges. Shoots were counted per quadrat and total stem length (stems and flower stalks) was measured. Material from quadrats was dried to constant weight in a drying oven at 105°C.

The weed mat edge was divided into five sections, each approximately 30 m long, and 20 shoot samples and one 0.1 m^2 quadrat were randomly selected within 50 cm from the edge in each section on each sampling date. From December 1994 to April 1995 an additional sample of 10 shoots was collected from each of the five sections for stem diameter measurements on each sampling date.

Internal stem diameters were measured to determine if they were small enough to restrict the pupation of *A. hygrophila*. Measurements were taken (to the nearest 0.5 mm) at the midpoint of the internode falling within 80 cm of the apical node. If stems were less than 80 cm long, the uncut internode furthest away from the apical node was chosen for the stem diameter measurement. The presence of pupae in the internodes where internal diameters were measured was recorded.

Analysis of results

Data that were collected on a per shoot basis were converted to m^2 by combining data from individual shoot samples and the quadrats (number of shoots per quadrat). These provided overall estimates of the means for *A. hygrophila* densities, alligator weed dry weight, number of shoots and shoot length m^2. The variances were also pooled from the data for number of insects per shoot and standing crop and further pooled over time to give common variances for each parameter in each season. The standard errors were then calculated for each parameter and time using these pooled variances and the appropriate sample size using the SYSTAT statistical package (Wilkinson 1990).

Degree day (DD) calculations

Degree days were calculated from recorded temperatures, using a modified Simpson's Rule (Broughton and Ramsay 1979). Simpson's Rule is an integration method which calculates the area under the diurnal temperature curve and above the lower threshold temperature (Worner 1988). Where data were missing (11% of measurements), estimates from the Whangarei Airport (Station A54737, Lat. 35°46'S Long. 174° 22'E), 27 km from Whatatiri were inserted. The min-max method of Arnold (1960) was used to calculate DD from these data. This method was found to be reasonably accurate for data recorded at meteorological sites in northern New Zealand (Worner 1988).

The total DD requirement for *A. hygrophila* development from egg to adult was calculated by summing the DD values for each life stage. DD for each life stage were calculated as DD = 1/(slope of regression line). The slopes of the regression lines were taken from the linear regressions of development rate of *A. hygrophila* v. temperature in Stewart *et al.* (1999a).

The DD required to complete the pre-ovipositional period for adult females was estimated using the pre-ovipositional times at 20, 25 and 30°C (Stewart *et al.* 1999b). Linear regression was used to describe the development rate (1/days) v. temperature relationship. DD were estimated from the equation $y = 0.0373x\text{-}0.585$ ($R^2 = 60.2$). This gave an estimate of 27 DD for the pre-oviposition period and when added to the 250 DD calculated in Table 2, gave 277 DD required for development from egg to ovipositional female. This value was used to estimate the potential number of generations for *A. hygrophila* in the field.

The following calculations were made to estimate the earliest time that overwintered females would begin to lay eggs

Table 1. Plants found growing in the weed mat at Whatatiri.

Family	Plant name
Agavaceae	*Phormium tenax* J.R. & G.Forst.
Apiaceae	*Apium nodiflorum* (L.) Lag.
	Oenanthe pimpinelloides L.
Asteraceae	*Bidens frondosa* L.
	Cirsium vulgare (Savi) Ten.
	Conyza albida Spreng.
	Hypochoeris radicata L.
	Picris echioides L.
	Senecio esleri C.J.Webb
Cyperaceae	*Carex ovalis* Gooden.
	Cyperus eragrostis Lam.
Fabaceae	*Lotus pedunculatus* Cav.
Gramineae	*Glyceria maxima* (Hartm.) Holmb.
	Holcus lanatus L.
	Poa trivialis L.
Haloragaceae	*Myriophyllum aquaticum* (Velloso) Verdc.
Juncaceae	*Juncus ? articulatus* L.
	Juncus effusus L.
	Juncus ? gregiflorus L.
Onagraceae	*Ludwigia peploides* (Kunth) P.H.Raven
	Ludwigia palustris (L.) Elliott
Polygonaceae	*Polygonum ? capitatum* D.Don.
	Polygonum salicifolium Willd.
Rubiaceae	*Galium divaricatum* Lam.
Salviniaceae	*Azolla pinnata* R.Br.

Table 2. Estimated lower temperature development threshold (Stewart *et al.* 1999a) and degree day requirement for *Agasicles hygrophila*.

	Lower temperature development threshold (°C)	Degree days
Egg	12.91	53.6
1st instar	16.24	15.9
2nd instar	11.48	43.3
3rd instar	15.02	22.3
Pupa	12.58	114.7
Total		249.8

in the field. As *A. hygrophila* has no apparent winter diapause and no obvious biological fix point exists, an alternative approach was needed to estimate the DD available for *A. hygrophila* development in the field and to determine the number of generations possible.

In the 1994–95 season DD were calculated daily from 24 November 1994 to April 1995 using the estimated lower temperature development threshold (13.3°C) (Stewart *et al.* 1999a). To select the starting date for the first generation of eggs laid, the daily DD available were summed backwards from the first date a larva was seen in the field. Summing stopped on the date when the DD needed for development of the immature stage was reached. This date (24 November 1994) was recorded as the start date of the first generation of *A. hygrophila*. Daily DD were summed for subsequent generations and the date on which 277 DD was reached was recorded.

Results

Air temperature and rainfall

Weekly mean, minimum and maximum values for Whatatiri are shown in Figure 1. The mean weekly temperature ranged from 8.3–21.8°C during the study period. Mean weekly minimum temperature ranged from 0.1–16.1°C. Annual rainfall for 1994 measured close to the field site was 1010 mm. Greatest rainfall occurred during winter months (770 mm from May to October). Periods of high rainfall (177 mm in one week) led to flooding in April 1995.

Alligator weed shoots and quadrat samples

Floating aquatic alligator weed was present at Whatatiri throughout the study period. During the first growing season the mean number of shoots ranged from 578 ± 54.9 to 600 ± 60.6 m^{-2} from mid November through to early January (Figure 2). From then on the shoot density declined and was lowest in early April (124 shoots m^{-2}). Thereafter shoot density increased and peaked in the second growing season in late December (930 shoots m^{-2}). Shoot numbers fell to 196 shoots m^{-2} in late February 1995.

Shoot length peaked in late December at 209 ± 21.5 m m^{-2} in the first growing season, after which it declined to 10 m m^{-2} by late May (Figure 2). Shoot length steadily increased throughout the winter, with greatest growth occurring in spring and early summer (October to December). Length peaked in late December in the second growing season at 358 m m^{-2} and then declined to 16 m m^{-2} by late February.

When sampling began in mid November, plant growth had already commenced and total dry weight was estimated at 288 ± 107.5 g m^{-2} (Figure 3). Dry weight peaked at 405 ± 107.5 g m^{-2} in late January then decreased to 32 g m^{-2} by the beginning of March. During the winter months dry weight ranged from 25 to 81 g m^{-2} until the beginning of October. During the second growing season, dry weight began to increase rapidly from October reaching 646 ± 107.5 g m^{-2} in late December and declining to 44 g m^{-2} by late April. Total dry weight consisted of approximately equal amounts of leaves and stems throughout both seasons (Figure 3). Mean internal stem diameters ranged from 1.2-3.4 ± 0.34 mm.

Densities of *A. hygrophila* are shown in Figures 4–6. Adults were present in detectable numbers on alligator weed at Whatatiri from mid December to late June in the first season and were found from early December onwards during the second season (Figure 4). During the first season, the population started to increase in January and peaked at 156 ± 64.5 adults m^{-2} in early February. During the second season the population of adults started to increase in mid January and the first peak of 225 ± 64.5 m^{-2} occurred in late January.

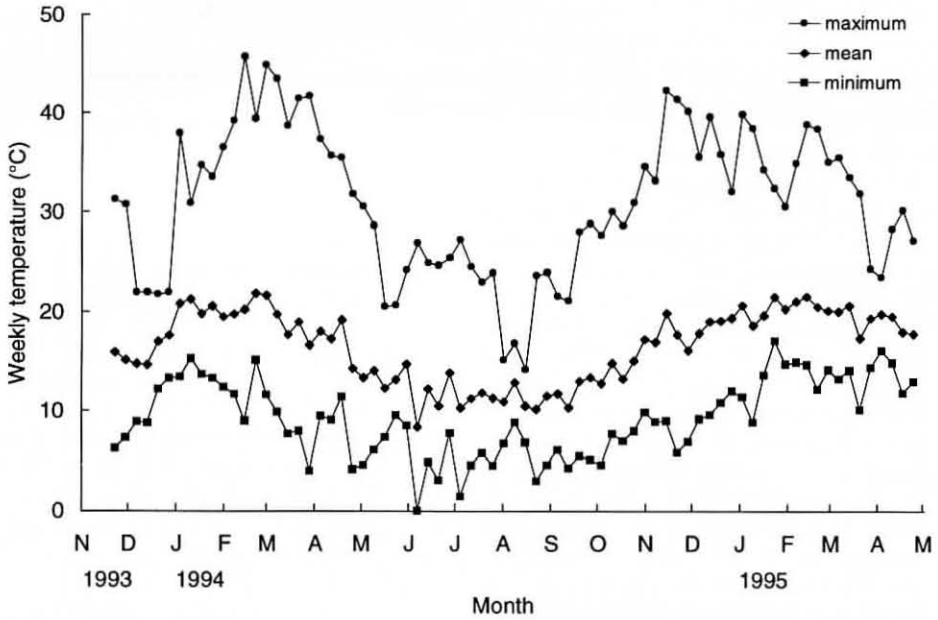

Figure 1. Mean, minimum and maximum weekly temperatures from temperature logger readings taken at Whatatiri from 15 November 1993 to 24 April 1995.

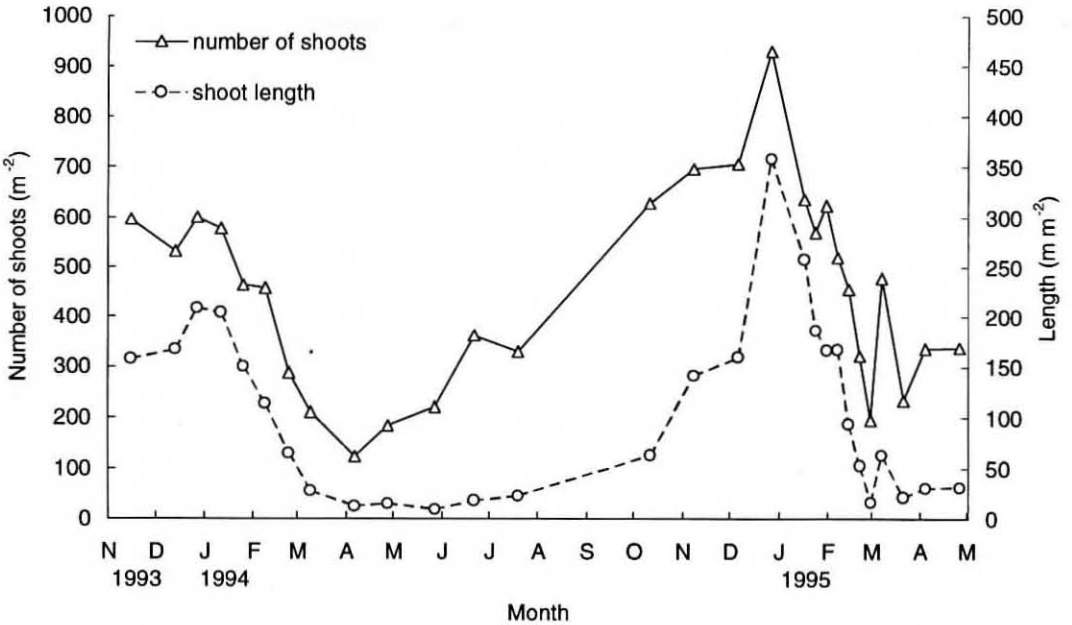

Figure 2. Number of shoots m^{-2} and stem length of *Alternanthera philoxeroides* at Whatatiri between 15 November 1993 and 26 April 1995.

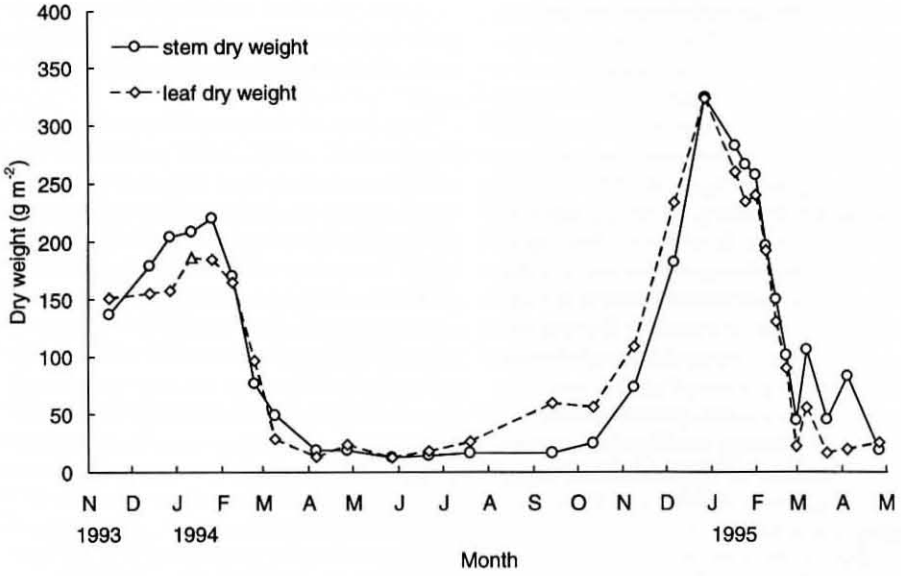

Figure 3. Dry weight (g m^{-2}) of *Alternanthera philoxeroides* at Whatatiri between 15 November 1993 and 26 April 1995.

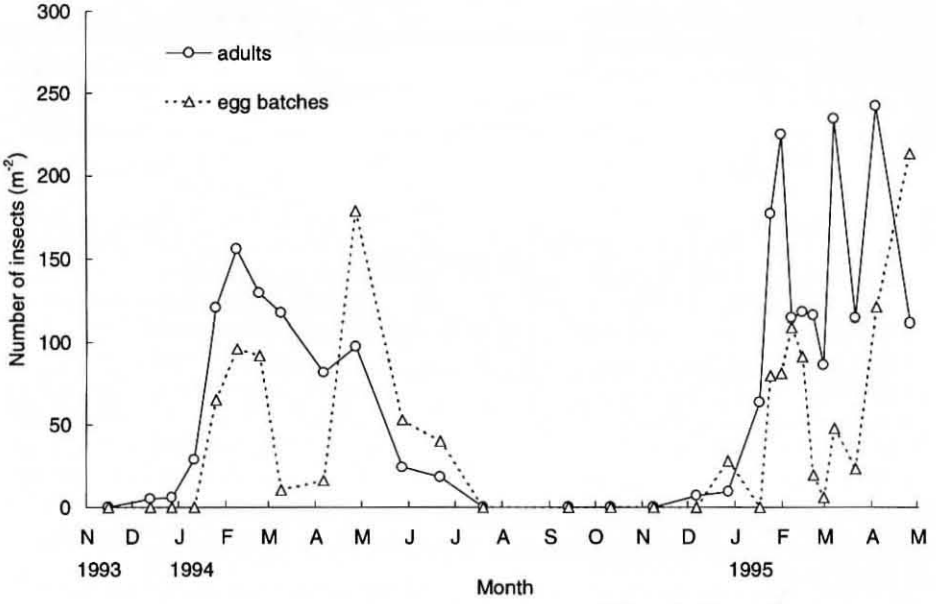

Figure 4. Seasonal occurrence of *Agasicles hygrophila* adults and egg batches at Whatatiri between 15 November 1993 and 26 April 1995.

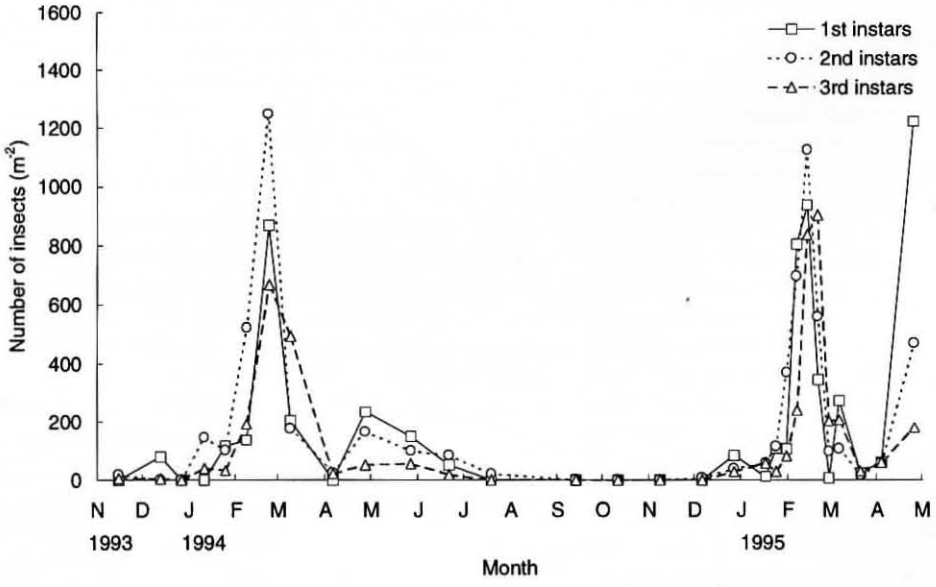

Figure 5. Seasonal occurrence of *Agasicles hygrophila* larval instars at Whatatiri between 15 November 1993 and 26 April 1995.

There were several equivalent peaks in March and April.

Egg batches were present in the first season from late January until early July (Figure 4). The number of egg batches peaked at 179 ± 43.2 batches m^{-2} during late April. Egg batches were present in the second season from late December, peaked at 109 ± 43.2 batches m^{-2} in early February and declined to six in late March, before rising again in April.

During the first growing season the numbers of the three larval instars all followed similar trends (Figure 5). First instars were present from mid December to mid June and second instars were present from mid November to mid July. Third instars were present from mid November to mid June. All instar numbers peaked in late February (870 ± 222.5, 1250 ± 224.9 and 668 ± 169.2 larvae m^{-2} for first, second and third instars respectively). Densities of first and second instars declined by the next sampling date in early March to 204 and 176 larvae m^{-2} respectively. The density of third instars declined to 21 m^{-2} by late April. Low levels of each instar were present during autumn until mid June (first and third instars) and mid July (second instars).

During the second season, second instar larvae were present from early December and first and third instars from late January (Figure 5). Maximum numbers of first (939 ± 222.5 larvae m^{-2}) and second (1126 ± 224.9) instars were reached in mid February whereas third instars peaked a week later (905 ± 169.2 larvae m^{-2}). The numbers declined sharply by the end of March to 23, 16 and 30 larvae m^{-2} for first, second and third instars respectively.

Prepupae were present in stems from early January to mid July in the first season and from late December to the end of the sampling period in late April in the second season (Figure 6). In the first season, pre-pupal densities increased from 64 m^{-2} in early January to 311 ± 91.1 in late February and then declined to levels ranging from 7 to 40 m^{-2} from April until mid July. During the second growing season, pre-pupal densities peaked at 474 ± 91.1 pre-pupae m^{-2} in mid February and then declined by mid March to levels between 9 and 74.

Pupae were present in the first growing season from early January until mid July and in the second season from early January until the end of sampling. In the first season, numbers peaked in mid February at 279 ± 75.0 pupae m^{-2}. The population decreased to 16 at the beginning of April and continued to levels of 6 to 29 pupae July. In the second growing season numbers peaked at 380 ± 75.0 pupae m^{-2} in mid February and then declined to a low level; by mid March only 10–19 pupae m^{-2} were present.

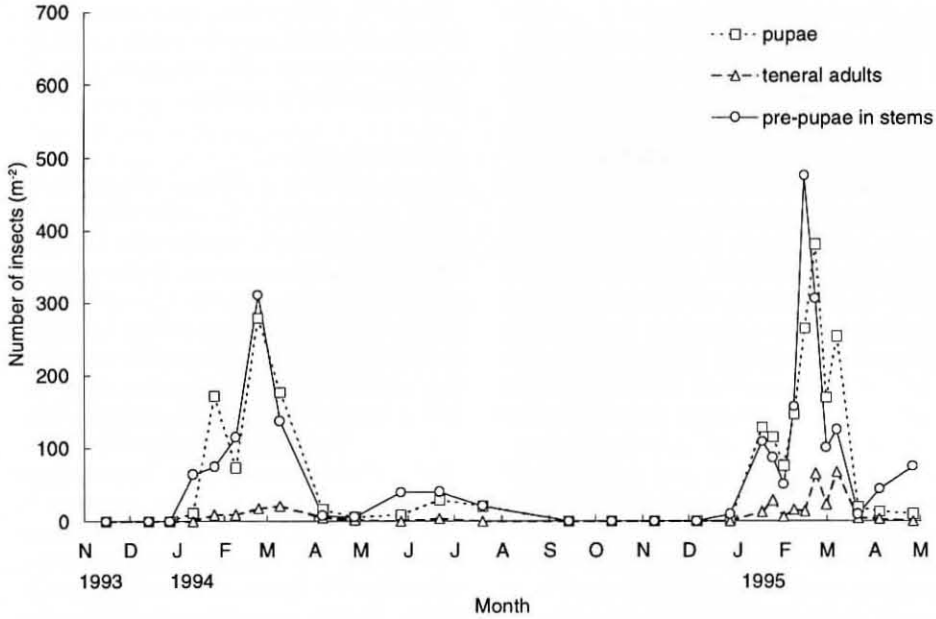

Figure 6. Seasonal occurrence of *Agasicles hygrophila* prepupae in stems, pupae and teneral adults at Whatatiri between 15 November 1993 and 26 April 1995.

Table 3. *Agasicles hygrophila* pupae (total of 67) found in *Alternanthera philoxeroides* stems (1250 stems sampled) of different internal diameter (±0.25 mm) as a percentage of total pupae found.

Stem diameter (mm)	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
% of total pupae	0	8.9	28.4	38.8	14.9	6.0	1.5	1.5

A total of 67 pupae were found in the 1250 stems sampled. Pupae were found in stems with diameters ranging from 1.0 to 4.0 mm (Table 3), with the largest percentage (38.8%) in stems with diameters of 2.0 mm.

Low numbers of teneral adults were found each year (Figure 6). In the first season they were found from late January to the end of April (2–17 adults m^{-2}) and in the second season they were found from early January to late March (3–64 adults m^{-2}).

Peak *A. hygrophila* populations occurred during February in 1994 and 1995. During the first growing season, all life stages peaked on the same sampling date except for eggs and adults which peaked a fortnight earlier. During the second season, clearer differences between the insect life stages were observed (possibly due to the increased frequency of sampling), however, the life stages still peaked within a short period between late January and mid February. Pre-pupal numbers peaked at the same time as second and third instars, which suggests these peaks resulted from different generations. It is probable that generations of *A. hygrophila* overlapped.

Degree Day (DD) estimates

Three generations were predicted at Whatatiri using DD accumulation (Table 4).

Discussion

Alligator weed and A. hygrophila populations

Aquatic alligator weed was present throughout the year and dry weights peaked in early summer in both seasons and declined as *A. hygrophila* populations began to build up. Julien *et al.* (1992) measured alligator weed in Australia throughout the 1977–78 season and found 368–656 stems m^{-2} fresh at water sites compared to 124–930 stems m^{-2} at Whatatiri. Dry weight per stem was heavier in Australia than at Whatatiri, 0.28–1.04 g compared to 0.08–0.88 g.

Julien *et al.* (1979) measured adult *A. hygrophila* densities over 100 m^{-2} in the first season after release in Australia and approximately 875 adults m^{-2} in the following season. The latter value is three and a half times higher than the highest record at Whatatiri and may be attributed to different environmental factors (e.g. nutrients and temperatures) which affected the *A. hygrophila* populations. At another site in Australia (Williamtown), in a drain with permanent water, a population of 155 adults, 674 pupae, 343 larvae and 88 egg batches m^{-2} was recorded in December 1978. One month later the population had declined to 31 adults, 100 pupae, 0 larvae and 15 egg batches m^{-2}. From both the Australian and this study it appears *A. hygrophila* populations fluctuate markedly in response to available food plant.

The decline in *A. hygrophila* numbers occurred after alligator weed dry weight declined (Figures 3–6). Alligator weed decline was attributed to damage caused by *A. hygrophila* and *A. malloi*. The increase in egg batches in autumn of both seasons (Figure 4) was caused by high numbers of fertile adults present and oviposition was probably stimulated by regrowth (Figure 2).

Alligator weed grew year round at Whatatiri and during the winter months it grew steadily in the absence of large *A. hygrophila* populations (and presumably *A. malloi*). While *A. hygrophila* was limited by low temperatures in winter (Stewart *et al.* 1999a, 1999b), alligator weed continued to grow giving it a competitive edge as the weed mats regenerated each spring. In Georges River (Sydney) the weed mats were destroyed by *A. hygrophila* (Julien *et al.* 1992); warm temperatures and good nutrition led to high *A. hygrophila* numbers which in turn allowed more damage and high alligator weed control.

There was sparse evidence from this study that *A. hygrophila* over-wintered as an adult. In the samples that were taken during winter, no life stages of *A. hygrophila* were found although individual adults were seen while sampling was done in July and October. Maddox (1968) suggested adults were the over-wintering stage and it is quite likely that adults overwintered at Whatatiri. Gangstad *et al.* (1975) found few *A. hygrophila* adults survived the winter months in Georgia and South Carolina in the USA, and feeding activity was not noticed until the following summer and autumn, a similar situation to that which occurred at Whatatiri.

In early April 1995 flooding washed large sections of alligator weed mat from the sampling area and this was replaced by alligator weed washed in from further upstream. Although the water levels rose over one metre above normal, the weed

Table 4. Estimated dates for *Agasicles hygrophila* females to reach their ovipositional stage for each generation using the 277 DD requirement (summing ended on 25 April 1995) at Whatatiri, Northland.

Generation	Immature indicator
1	6 January 1995
2	13 February 1995
3	27 March 1995
Excess DD	159

was probably never submerged as population levels were not obviously affected. It is unlikely that many *A. hygrophila* were washed into the ponds because the new alligator weed had minimal insect damage. The results obtained at Whatatiri were contrary to those expected, based on the literature reports which stated *A. hygrophila* can be adversely affected by flooding (e.g. Coulson 1977).

Maddox and Hambric (1970, 1971) suggested *A. hygrophila* populations were limited by nutrient deficient alligator weed with tough, fibrous epidermal tissue and the absence of hollow internodes. This would prevent the completion of the life cycle due to the lack of pupation niches and the authors suggested larvae could not enter the stems at all. Vogt *et al.* (1979) indicated that pronotal width (1.21 mm in females and 1.07 mm in males) determined the minimum internal stem diameter in which pupation could occur. If stems were too narrow, the pre-pupae may have enlarged them by chewing, but not ingesting, the internal pithy walls (Vogt *et al.* 1979). This may have happened with 9% of stems at Whatatiri that had internal diameters <1.21 mm and which held pupae. The greatest proportion of pupae (91%) were found in stems with internal diameters which exceeded 1.25 mm (1.5 ± 0.25 mm) (Table 3). Therefore the development of most pupae was not restricted by stem diameter at Whatatiri because mean internal stem diameters were above 1.5 mm except in early March 1995 when alligator weed had suffered defoliation.

Vogt *et al.* (1992) considered that *A. hygrophila* populations in the United States were overlapping, however, they were not measured. In this study no clear peaks allowed discrimination of generations.

Degree days and development

The DD analysis suggests that at any site where less than 554 DD are accumulated (allowing two generations), *A. hygrophila* populations are unlikely to be large enough to defoliate alligator weed. In this study, one method of determining the number of generations were used. Exactly when DD summing should begin is difficult to determine and will vary between years. The method used assumed the first immature *A. hygrophila* life stage seen belonged to the first generation. DD were counted backwards to predict when eggs were laid, thus giving the start date. There are disadvantages when using this method, as accuracy may be affected by the length of the time intervals between sampling dates and ability to detect individuals in a small population. Where sampling intervals are long (>3 weeks) it is possible to miss a generation, especially during the spring when alligator weed is rapidly growing and insect numbers are low. These predictions suggest three generations per growing season at Whatatiri.

Population numbers of *A. hygrophila* were low at the beginning of spring and this was probably due to high mortality for all life stages during winter due to low temperatures. The lower temperature development thresholds for *A. hygrophila* life stages ranged from 11 to 16°C (Table 1); temperatures that are commonly experienced during winter at Whatatiri (Figure 1). Results from laboratory experiments (Stewart *et al.* 1999a) showed there was high mortality (94%) of immature stages reared at 15°C. No eggs that were incubated at 10°C hatched. It is therefore unlikely that egg laying and development for *A. hygrophila* will occur during winter.

Clearly *A. hygrophila* persists from one season to the next. However, there is little information on over-wintering survival or fecundity of the survivors. A previous study (Stewart *et al.* 1999a) indicated that the number of frosts at a given location may influence its suitability for *A. hygrophila* development. Egg viability was reduced after adults were chilled overnight. This suggests the over-wintering ability of *A. hygrophila* would be reduced in areas which have similar low temperatures and frosts.

Two generations of *A. hygrophila* at Whatatiri were sufficient to provide defoliation but not alligator weed control. At Whatatiri, despite predictions for control, temperatures limit *A. hygrophila* population increase until it is too late in the growing season and they also limit the size of the population needed to provide control. The work at Whatatiri was conducted some years after release when field populations of the insect were well established compared with Australian data that included the first summer peak of *A. hygrophila* after its release (during the previous autumn) and the second summer peak. *A. hygrophila* numbers were three times higher than those at Whatatiri and resulted in permanent reduction of aquatic mats on Georges River (Julien *et al.* 1979). Considering that Whatatiri is a most favourable site in New Zealand for *A. hygrophila*, it is unlikely that this beetle will provide control of alligator weed in New Zealand even in conjunction with *A. malloi*.

Stewart *et al.* (1995) predicted that *A. hygrophila* could only control alligator weed from Auckland to Northland and in several coastal areas in the North Island where optimum temperatures for the insect are only sustained for a short period of time (Stewart *et al.* 1999a, New Zealand Meteorological Service 1983). This study shows that the low winter temperatures (<15°C) in winter limits over winter survival and prevents significant population increase before mid-summer, even at the most suitable site, Whatatiri. This suggests that earlier predictions were wrong, although the weed may be actually defoliated in north of New Zealand, overall weed reduction is unlikely.

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