Population dynamics of the chrysomelid leaf beetle *Chrysophtharta agricola* (Chapuis), a pest of *Eucalyptus nitens* plantations in Tasmania

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Abstract

The phenology of the southern eucalypt leaf beetle, Chrysophtharta agricola, *was assessed at three* Eucalyptus nitens *plantations in Tasmania: Florentine Valley, Frankford and Blue Gum Knob. Five branches were sampled from each of 20 trees at each site every two weeks for three summer seasons between November 1999 and March 2000, between October 2000 and March 2001, and at two of these sites between October 2001 and March 2002. On each occasion, the numbers of egg batches, larvae of each instar, and adults were recorded from each branch. Adults were collected and dissected in the laboratory to ascertain their reproductive maturity, mated status and sex ratio. Egg-to-final instar mortality was estimated, and natural enemies present in the plantations were recorded. Beetles first appeared in the field in mid to late October and laid eggs between early November and February. Overall, larval populations peaked in December, and egg-to-fourth instar mortality ranged from 85 to 100%. Newly emerged adults were present in plantations between January and March/April.*

Sex ratios of parent and new generation adults were rarely female biased. Peak defoliation scores coincided with late larval instars at Florentine Valley and with newly emerged adults at Frankford. Defoliation at Florentine Valley peaked at about 30% of current season's growth removed, while at Frankford the average peak defoliation represented about 50% of current season's growth removed. Spatial analyses indicated that C. agricola *life stages were randomly distributed throughout plantations.*

Introduction

Hardwood plantations (mostly *Eucalyptus* spp.) covered over 135 000 ha of land in Tasmania in 2001 (Wood *et al.* 2001). *Eucalyptus nitens* (Deane & Maiden) Maiden is currently the preferred plantation species at high altitude sites in Tasmania (Baker *et al.* 2002) because of its fast growth rate and cold tolerance. However, *E. nitens* is attacked by the eucalypt leaf beetles *Chrysophtharta bimaculata* (Olivier) and *C. agricola* (Chapuis) (Coleoptera: Chrysomelidae: Paropsini). *Chrysophtharta bimaculata* is a serious pest of *E. nitens* in adult-phase foliage (de Little 1989; Bashford 1993), while *C. agricola*

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adults feed preferentially on adult foliage of *E. nitens*, and the majority of oviposition (and hence, larval feeding) occurs on juvenile foliage (Lawrence *et al.* 2003; Nahrung and Allen 2003).

In the field, *C. agricola* adult beetles emerge from overwintering sites in October or November and lay eggs between November and March, usually completing one generation per season (Ramsden and Elek 1998). Eggs are laid in batches of 30–60 eggs (de Little 1979) and there are four larval instars (de Little 1979; Ramsden and Elek 1998). The final two instars cause the majority of defoliation by both *C. bimaculata* (Greaves 1966) and *C. agricola* (Nahrung 2004). The most vigorous feeding by adult paropsines occurs prior to overwintering, which may prevent foliage regrowth, leaving exposed shoots susceptible to damage by severe cold in winter (Elliott *et al.* 1993*;* Simmul and de Little 1999).

Knowledge of the phenology of insect pests may allow temporal prediction of attack and provide the potential for manipulation to assist control. For example, the biological insecticide *Bacillus thuringiensis* var. *tenebrionis* (Btt) is most effective against early instar larvae (Elek *et al.* 1998; Beveridge and Elek 2001); hence, a knowledge of the temporal appearance and duration of larvae in the field is required for effective application. Although laboratory-based studies by Ramsden and Elek (1998) and de Little and Madden (1975) have provided some details on the biology of *C. agricola*, there are no data on its population dynamics in the field. Here, we present the results of three seasons of field monitoring at two sites, and two seasons of field monitoring at one site for *C. agricola* life stages, abundance and natural enemies. We also estimate the feeding damage caused to new foliage in each field season. The aim of this study was to understand *C. agricola*'s population dynamics, including the duration of life stages in the field, natural mortality levels, the number of generations each year, and the onset of oviposition in the field.
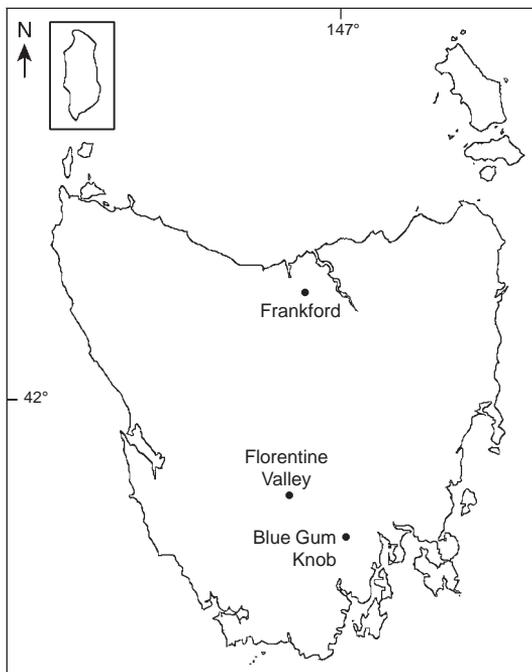

Figure 1. Approximate locations of three field sites in Tasmania sampled for Chrysophtharta agricola *between 1999 and 2002.*

Materials and methods

Phenology

We monitored three sites (Frankford, Blue Gum Knob, Florentine Valley: Figure 1) every two weeks between 1 November 1999 and 15 March 2000, 23 October 2000 and 19 March 2001, and at only two of these sites (Frankford and Florentine Valley) between 8 October 2001 and 18 March 2002. Hereafter, 'seasons' refers to these sampling periods (i.e. October/November to March), the duration of field activity by *C. agricola*.

On each sampling occasion, five branches in juvenile foliage from each of 20 randomly selected trees were examined for egg batches, larval instars and adults of *C. agricola*. On each occasion, trees within an area of about 3 ha were chosen by generating random number co-ordinates (*x,y*) that corresponded approximately with the number of metres along and into the plantation from one corner. The number of each larval instar

on each branch was counted and from this the average numbers of each life stage present per branch were calculated.

Site descriptions

Florentine Valley (42º38'S, 146º29'E) Elevation 400 m

Eucalyptus nitens was planted in 1996. Groundcover was predominantly grass and annual weeds. The section of the plantation we used (approximately 3.2 ha) was bordered by a road, native forest, older plantation trees and *Acacia* trees. Of the three sites monitored, this had the highest rainfall. Mean monthly rainfall between December 1999 and March 2002 was 96.7 ± s.e. 10.8 mm (range 24–241.3 mm). Mean maximum temperature from long-term Bureau of Meteorology data (40 yr) was 16.2°C; mean minimum was 5.2°C.

Blue Gum Knob (42º50'S, 146º53'E) Elevation 410 m

Eucalyptus nitens was planted in 1996 on a steep slope of ex *Pinus radiata* plantation. A gully, Lett Road, older *E. nitens* plantations and native forest regrowth border the section we monitored (approximately 2.9 ha). Groundcover comprised predominantly bracken and annual weeds, with some *P. radiata* regrowth. This site had the lowest rainfall between December 1999 and March 2002: mean monthly rainfall was 45.3 ± s.e. 6.2 mm (range 8.4–134.8 mm). This site had the highest average temperatures. Mean maximum temperature from long-term weather data (110 yr) was 17.4°C; mean minimum temperature was 6.7°C.

Frankford (41º20'S, 146º45'E) Elevation 240 m

Eucalyptus nitens was planted in 1996 following a pre-plant spray of glyphosate on degraded pasture land where a 1990 planting of *E. globulus* on the site had failed due to frost damage. *Eucalyptus nitens* seedlings were fertilised with 100 g of diammonium phosphate (B. Jordan, Gunns Ltd, pers. comm.). Groundcover was predominantly grass. The monitored site (approximately 3.2 ha) was traversed by two small streams and bordered by Barhams Road, older *E. nitens* trees and, from late 1999, new *E. nitens* seedlings on two sides. Mean monthly rainfall between December 1999 and March 2002 was 79.6 ± s.e. 9.5 mm (range 18.6–213.2 mm). Mean maximum temperature from long-term weather data (130 yr) was 16.9°C; mean minimum temperature was 4.6°C.

Adult reproductive development and sex ratios

Adult beetles were hand-collected from foliage on each sample date and either killed in the field in an ethyl acetate killing jar or placed individually into small plastic vials and taken to the laboratory where they were frozen. Adult sex was ascertained using differences in the first tarsal segment of the foreleg (Baly 1862; Steven 1973; de Little 1979). The generation to which adults belonged was determined using elytral colouration: overwintered parental (old) beetles were tesselated brown or grey (or black), while first-generation (new) beetles were dark grey with a bright red elytral rim (de Little 1979). Females were dissected and their reproductive status was assigned to one of three developmental classes: immature, intermediate and mature. Their mated status was determined by removing the spermatheca, squashing it on a microscope slide and checking for the presence of sperm under phase-contrast microscopy (x 400). Sex ratios were analysed for deviation from unity using a Chi-square contingency table (Bonferroni adjusted, $P < 0.002$). Cochran's test of linear trend was conducted on each season's data for each site to determine whether sex ratios altered over time. Only samples for which more than 10 individuals were collected were included in analyses. Newly emerged adults were divided into three developmental age classes (soft, medium and hard) based on the rigidity of their elytra, which was determined by compressing the elytra laterally between a pair of soft forceps. Reproductive development and mated status were compared between these age classes.

Mortality in the field

The population differential between egg and final instar larvae was calculated to estimate overall field mortality rates. Mortality between each developmental stage was estimated using the total of each life stage censused during each season. Per cent mortality was calculated as the number of each successive stage over the number of the previous stage.

Natural enemies

On each sample date, natural enemies currently or previously observed attacking any life stages of *C. agricola* within the plantations at Florentine Valley and Frankford were recorded. Natural enemies from each time period were identified to family or species. To examine any change in the species composition over time, the season was divided into early (October–November), mid (December–January) and late (February–March).

Damage caused by C. agricola *in the field*

The amount of damage to the current season's growth of each tree sampled on each occasion was awarded a score on a linear scale: zero (no damage), one (up to 20% foliage removed), two (~ 20–40% foliage removed), three (~ 40–60% foliage removed), four (~ 60–80% foliage removed) and five (> 80% defoliation). Scores were based on visual estimates of the area of crown foliage removed by *C. agricola* feeding. Only new foliage was scored because adults and larvae feed preferentially on young foliage (Nahrung *et al.* 2001; Nahrung and Allen 2003). Scores were averaged for each sample date (n = 20 per site per date), and peaks were related to life stages and populations present in the field at the time.

Foliage consumption

Using average eggs per day and longevity values obtained in laboratory experiments, larval foliage consumption estimates, mean

Table 1. Values and sources used to estimate the total volume of foliage consumed by one pair of Chrysophtharta agricola *adults and their offspring. (L1, L2, L3, L4 = first, second, third and fourth instars respectively; s = survivors)*

Estimate	Average	Source	Symbol
Adult longevity (days)	73	Mean of values in Nahrung & Allen (2003), Ramsden & Elek (1998) and unpublished data	Lo
Eggs/day	13	"	F
Female foliage consumption per day (mm²)	190	HFN, unpublished data	A
Male foliage consumption per day (mm²)	133	"	B
Mean foliage thickness (mm)	0.22	Nahrung *et al.* 2001	T
Mean egg – L1 mortality	0.667	This study	L1s
Mean L1 – L2 mortality	0.572	"	L2s
Mean L2 – L3 mortality	0.447	"	L3s
Mean L3 – L4 mortality	0.386	"	L4s
Mean L4 to adult mortality	0.803	G.R. Allen & V.S. Patel, unpublished data	Ps
L1 foliage consumption (mm³)	6.6	Nahrung (2004)	Z
L2 foliage consumption (mm³)	58.3	"	Y
L3 foliage consumption (mm³)	96.6	"	X
L4 foliage consumption (mm³)	185.9	"	W
Days feeding before overwintering	28	"	Q
Juvenile leaf (pairs 1–3) (mm³)	497.1	"	

stage-specific mortality estimates, and adult foliage consumption estimates (Table 1), we calculated the approximate volume of juvenile foliage consumed by each male–female pair of *C. agricola* and their resultant offspring over a field season. Symbols used below are explained in Table 1.

Surviving offspring from one pair was estimated by:

Eggs produced by one pair = Lo*F
Eggs surviving to L1 = Lo*F*(1 – L1s) = I
L1 surviving to L2 = I*(1 – L2s) = J
L2 surviving to L3 = J*(1 – L3s) = K
L3 surviving to L4 = K*(1 – L4s) = L
L4 surviving to adult = L*(1 – Ps) = M

Total foliage consumption (mm³) for one male and one female plus all surviving larval instars produced by one pair was then estimated by:

(A*T*Lo) + (B*T*Lo) + (I*Z) + (J*Y) + (K*X) + (L*W) + (M/2*A*T*Q) + (M/2*B*T*Q).

Spatial analysis of C. agricola *distribution within plantations*

An autoregressive spatial model was applied to spatial units of 10 m x 10 m to determine whether there was a spatial structure to the overall *C. agricola* distribution within plantations. Because trees sampled within plantations were randomly selected by generating random *x,y* coordinates, their approximate position could be matched (within the 100 m² plot) with the census of *C. agricola* life stages. Spatial analyses were conducted using the methods of Dutkowski *et al.* (2002). Data over the 1999–2000, 2000–2001 and 2001–2002 seasons were included in the models for Frankford and Florentine Valley. Counts for the number of egg batches, larvae and adults were square-root transformed and tested for spatial structure using a model that incorporated season, sample dates within seasons and trees within sample dates.

The standard model used the mixed model

$$\text{Distribution}_{ijkl} = \text{year}_i + \text{year}_i{*}\text{week}_j + \text{year}_i{*}\text{week}_l{*}\text{tree}_k + \text{Plot} + e_{ijkl}$$

where

i = year (or season),
j = week (or sample) within year,
k = tree within sample within year,
l = branch within sample within year, and
plot = the 10 m x 10 m spatial unit.

Year was treated as a fixed effect, and all other effects were treated as random. Variances were estimated using restricted maximum likelihood. Using the likelihood ratio test, this model was compared with one in which an extra, two-dimensional and separable first-order autoregressive (AR1) model was applied to the plots. Models were fitted using ASReml (Gilmour *et al.* 1999).

Results

General site comparisons

Frankford had the highest overall population size of *C. agricola* (eggs, larvae and adults censused) in 1999–2000 and especially in the 2000–2001 season, and Blue Gum Knob had the lowest. Because the population was so low at the Blue Gum Knob site, we discontinued monitoring there for the 2001–2002 season. In the 2001–2002 season, the Florentine Valley site had a large population, similar to the Frankford site (Figures 2, 3, 4).

Chrysophtharta agricola was the predominant paropsine species at all sites, although *C. bimaculata* (Olivier), *C. variicollis* (Chapuis), *C. nobilitata* (Erichson), *Paropsis aegrota* Boisduval, *P. tasmanica* Baly, *P. porosa* Erichson, *P. charybdis* Stål, *P. delittlei* Selman, *Sterromela* sp. and *Trachymela* sp. were also found in the plantations.

Phenology

At Florentine Valley, egg numbers recorded in the field peaked between 20–29 November
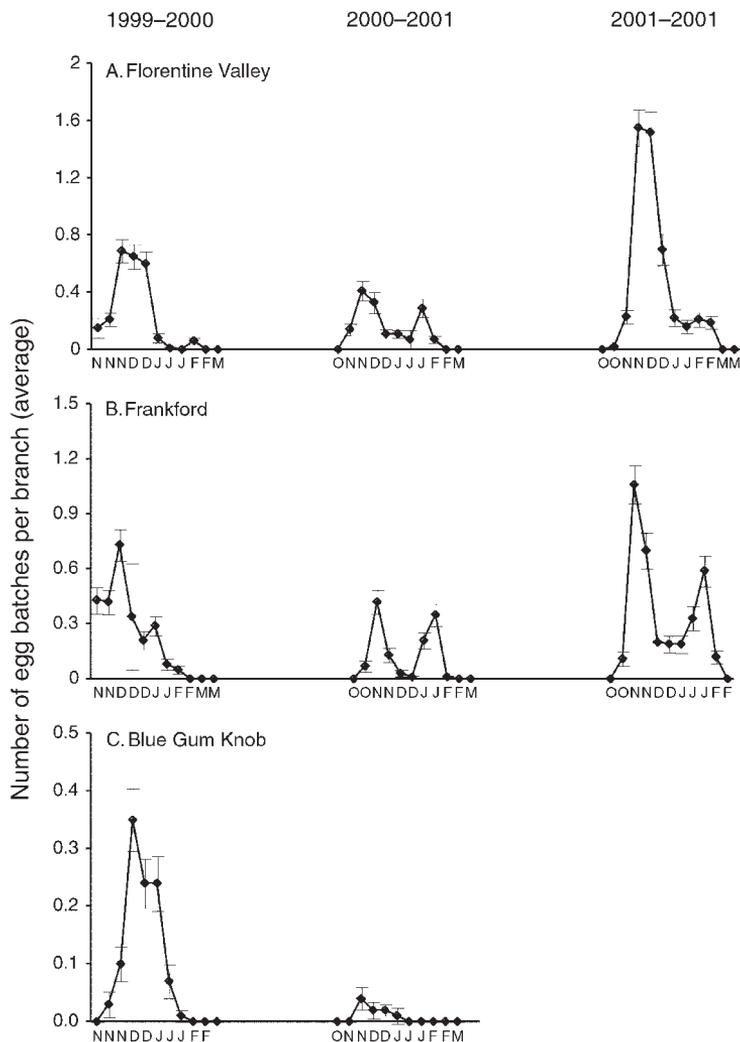
1999–2000   2000–2001   2001–2001

A. Florentine Valley

B. Frankford

C. Blue Gum Knob

Number of egg batches per branch (average)

Figure 2. Number of Chrysophtharta agricola *egg batches per branch (average ± s.e.) for each of three seasons at Florentine Valley (A), Frankford (B) and for two seasons at Blue Gum Knob (C). Note the variation in the scale of the y-axes.*

and ceased between 14–28 February in each season (Figure 2A). At Frankford, oviposition peaks were recorded in early December in the 1999–2000 season, in mid November in the 2000–2001 season, and in early November in the 2001–2002 season (Figure 2B). In the 2000–2001 and 2001–2002 seasons, adults newly emerged from pupation laid eggs, producing the second peaks in oviposition (Figure 2A, 2B). The 2000–2001 season was the only one at Florentine Valley in which newly emerged adults laid eggs. At Blue Gum Knob, the average number of egg batches per branch was less than half that recorded at Florentine Valley and Frankford, peaking in mid December in the 1999–2000 season and in November in the 2000–2001 season (Figure 2C).

First-instar larvae peaked in December at Florentine Valley in all three seasons, and the second to fourth instars peaked earlier in the 2000–2001 season than in the 1999–2000 and 2001–2002 seasons (Figure 3A). At Frankford, first and second instars peaked in late November to early December, third instars peaked in early to mid December,
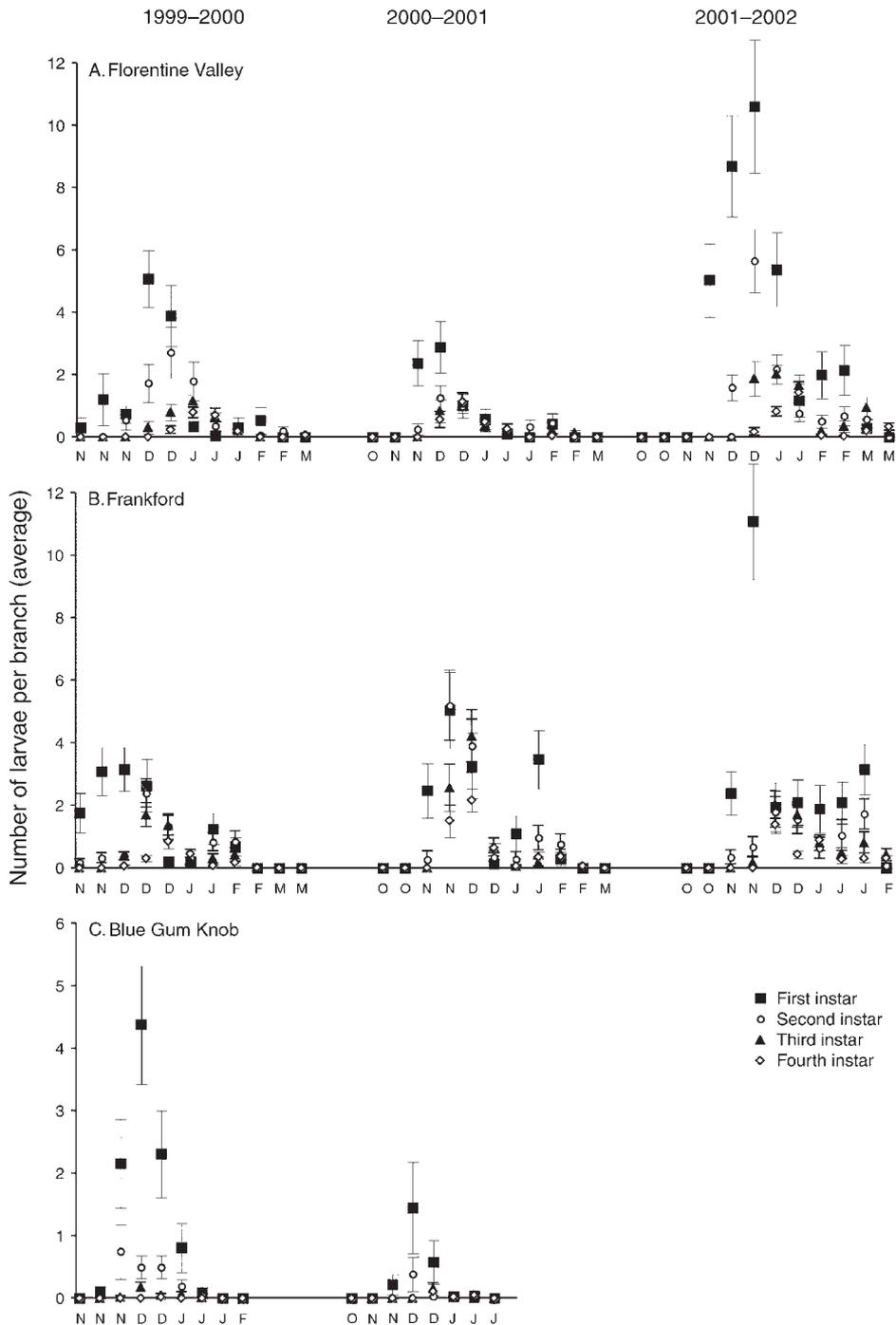
1999–2000   2000–2001   2001–2002

Figure 3. Number of Chrysophtharta agricola *larvae of each instar per branch (average ± s.e.) for each of three seasons at Florentine Valley (A), Frankford (B) and two seasons at Blue Gum Knob (C). Note the variation in the scale of the y-axes.*

and fourth instars in December in all three seasons (Figure 3B); the timing of all these peaks was earlier than at Florentine Valley.

Larval instar populations for Blue Gum Knob were lower than at Frankford and Florentine Valley (Figure 3C).
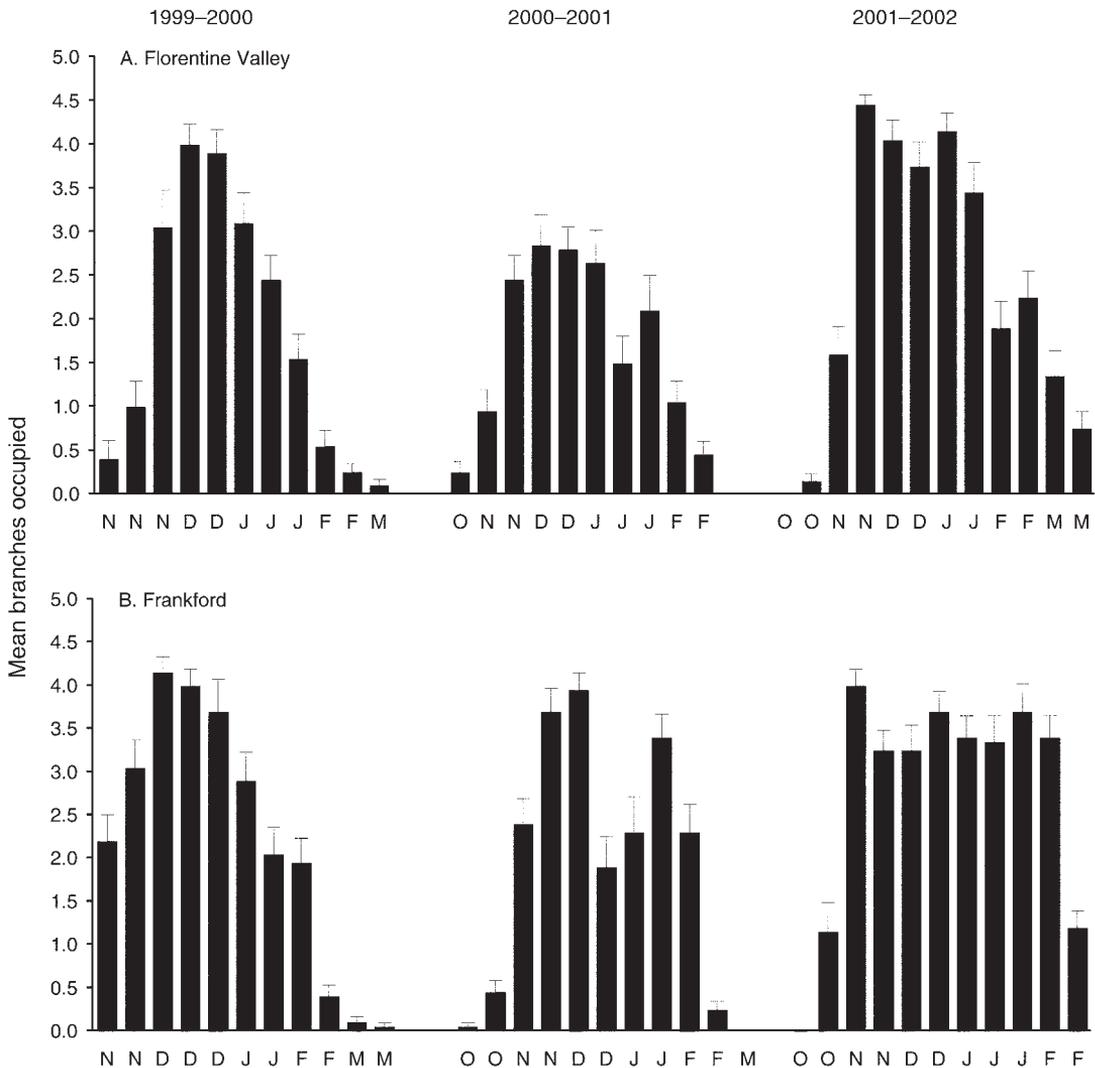
Figure 4. Number of branches occupied (average ± s.e.) by any developmental stage of Chrysophtharta agricola *per tree for each of three seasons at Florentine Valley (A) and Frankford (B).*

The average number of branches occupied with eggs, larvae or adult *C. agricola* per tree per sample peaked at Florentine Valley in coincidence with peak populations of first instars in the 1999–2000 season, first and second instars in the 2000–2001 season, and with eggs in the 2001–2002 season (Figure 4A). At Frankford (Figure 4B), the highest level of branch occupation in the 1999–2000 season coincided with the peak egg and first instar larvae. In the 2000–2001 season, the highest proportion of occupied branches occurred when the third and fourth instar larvae were highest: this was

also the season with the lowest egg and first instar mortality (Table 2). A second peak in branch occupancy occurred in the 2000–2001 and 2001–2002 seasons when newly emerged adults were laying eggs.

Adult reproductive development and sex ratios

Sex ratios were generally 1:1 in both generations (Figures 5, 6). For Florentine Valley site, Cochran's test of linear trend showed that in the 1999–2000 and 2001–2002 seasons, sex ratios became more skewed to female-bias as the season progressed
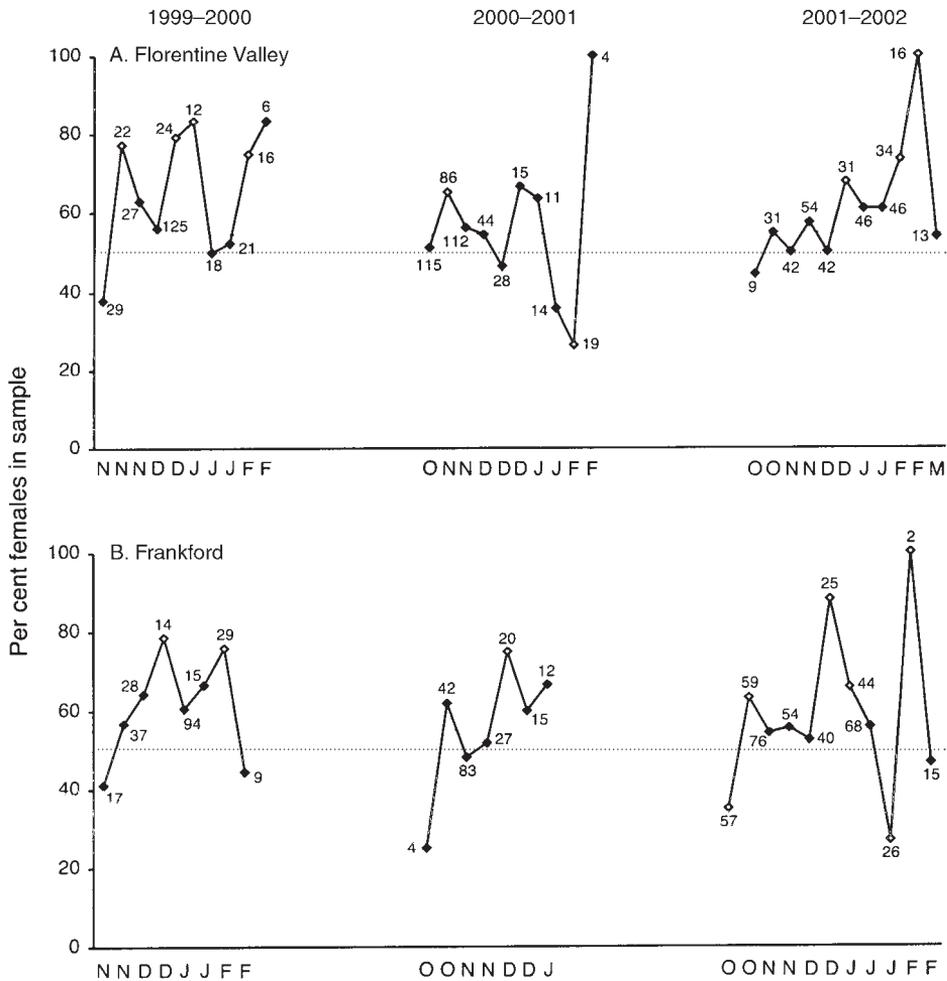
Figure 5. Percentage of female parent (old) Chrysophtharta agricola *adults hand-collected from foliage for each of three seasons at Florentine Valley (A) and Frankford (B). Open symbols denote samples for which the sex ratio differed significantly from unity (Chi-square analysis,* P < 0.05*). Numbers at each data point indicate the total sample size for each (samples < 10 were not included in analyses). Dotted line represents 1:1 sex ratio.*

($\chi^2_8 = 18.7$, $P = 0.02$; $\chi^2_{10} = 19.2$, $P = 0.04$, respectively) but remained approximately normal during the 2000–2001 season ($\chi^2_8 = 8.6$, $P = 0.38$). At Frankford, sex ratios were stable in the 1999–2000 and 2000–2001 seasons ($\chi^2_6 = 7.8$, $P = 0.25$, $\chi^2_5 = 6.4$; $P = 0.27$, respectively) but tended towards female-bias in the 2001–2002 season ($\chi^2_9 = 32.4$, $P < 0.001$). The sex ratios of new generation adults were usually 1:1 (Figure 6).

Overlap in adult generations (i.e. parent beetles and their adult offspring were present simultaneously in the field) occurred at Florentine Valley for 6–8 weeks in each season, and at Frankford for 4–10 weeks each season. Mating occurred between the parental and offspring generations (Nahrung and Allen, unpublished data).

All parent (old) females dissected from either site in all summers were reproductively mature ($n = 1168$), but only in the 2000–2001 season did first-generation (new) adults attain reproductive maturity before over-wintering at both Frankford and Florentine Valley. In the 2001–2002 season, new adults underwent reproductive development and laid eggs only at Frankford. No 'soft' females from either site in any year had mated or
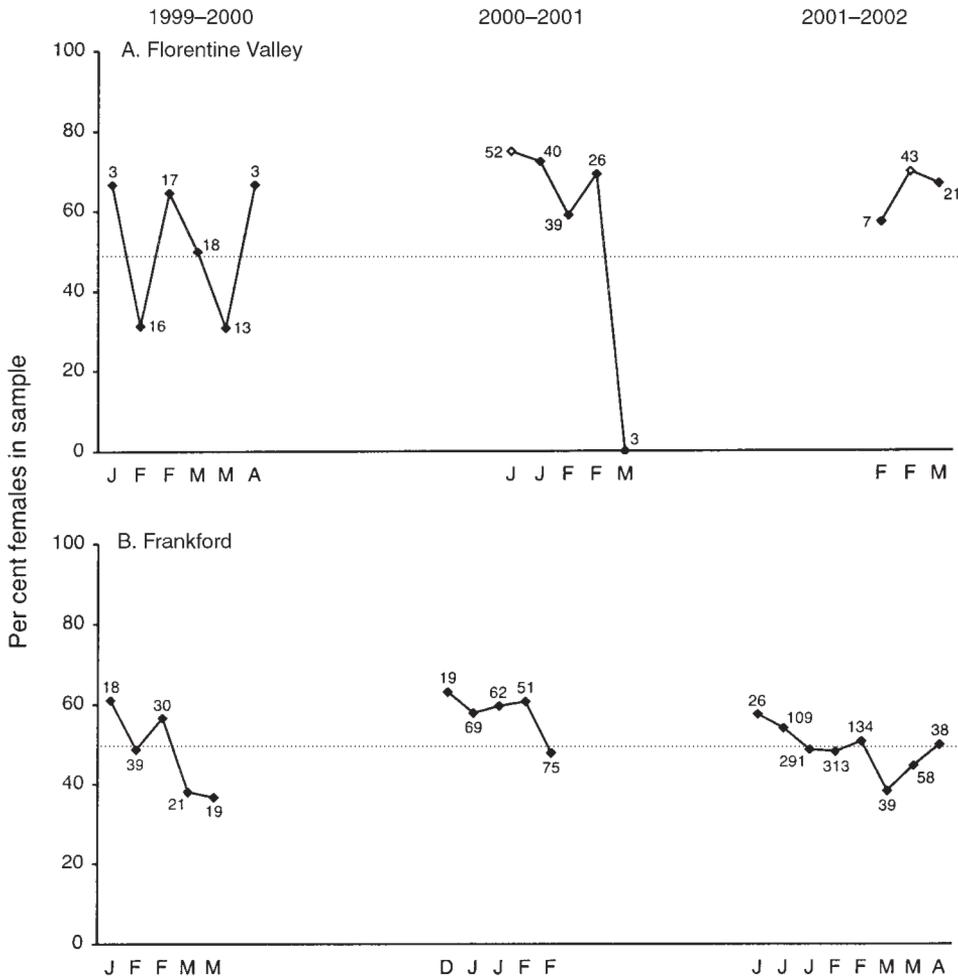
Figure 6. Percentage of female first-generation (new) Chrysophtharta agricola *adults hand-collected from foliage for each of three seasons at Florentine Valley (A) and Frankford (B). Open symbols denote samples for which the sex ratio differed significantly from unity (Chi-square analysis,* P < 0.05*). Numbers for sample points indicate the total sample size for each. Dotted line indicates 1:1 sex ratio.*

undergone any reproductive development (*n* = 297). The proportions of new adults with 'soft', 'medium' and 'hard' elytra in the 2000–2001 and 2001–2002 seasons at Frankford and Florentine Valley show the development of teneral adults after emergence from pupation (Figure 7). The proportion of parental generation females that had mated was high at the start of each collection period and quickly rose to 100% (Figure 8). First-generation females that had mated remained less than 50% in each summer and declined as the season progressed (Figure 8).

Mortality in the field

Estimated mortality at each immature life stage from egg to L4 varied (Table 2). The highest mortality levels were recorded between eggs and first instars at Florentine Valley and Frankford in each season. At Blue Gum Knob, however, mortality was highest during the first or second larval instars. These data do not reflect emergence of larval parasitoids because they usually do not emerge until the fourth instar or later (A.D. Rice, pers. comm.).

Table 2. Estimated seasonal mortality (% loss) at each immature life stage of Chrysophtharta agricola *in the field at three sites. (L1 = first instar, L2 = second instar, L3 = third instar, L4 = fourth instar)*

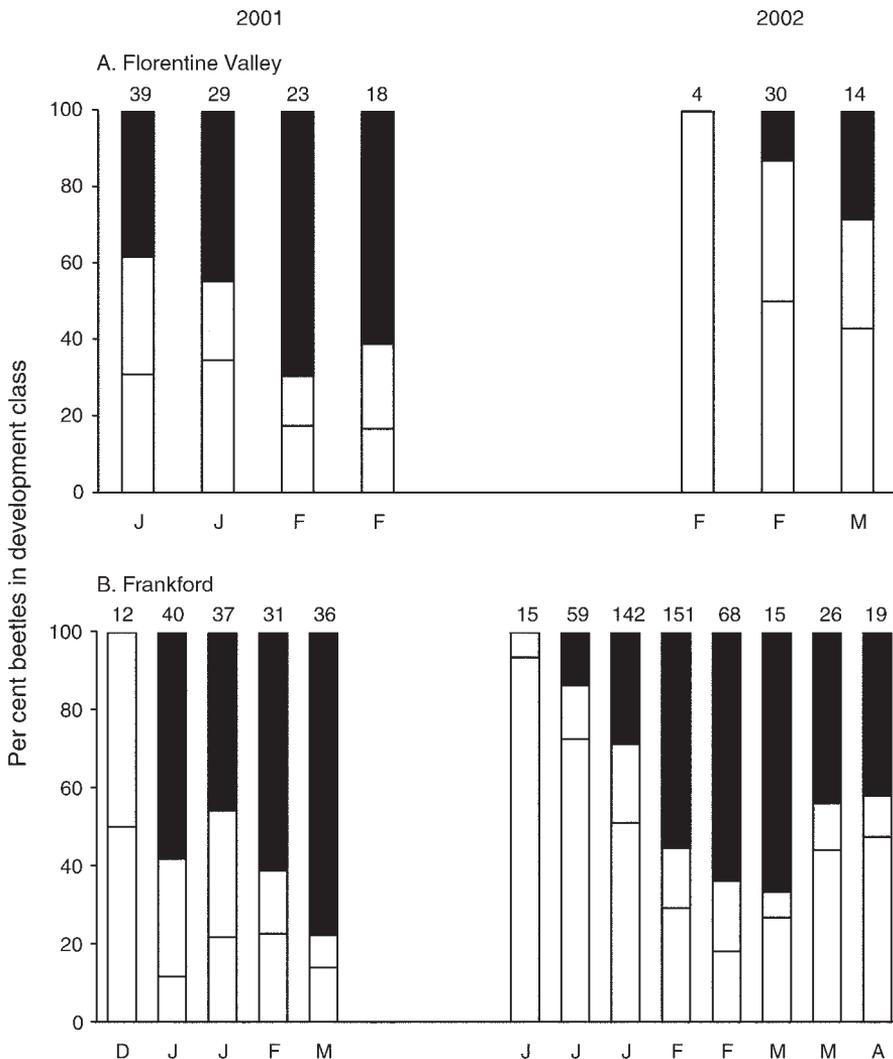| Life stage	Florentine Valley			Frankford			Blue Gum Knob	
	99–00	00–01	01–02	99–00	00–01	01–02	99–00	00–01
Egg to L1	83.2	83.8	75.5	82.9	57.1	76.4	68.4	14.1
L1 – L2	38.6	49.5	66.1	49.9	25.9	68.2	79.8	79.3
L2 – L3	59.2	26.9	39.9	33.0	30.8	18.8	84.4	64.5
L3 – L4	36.8	9.5	57.9	56.1	36.2	43.4	35.5	-
Overall mortality for egg – L4	**97.3**	**94.6**	**97.9**	**97.5**	**85.9**	**96.5**	**99.9**	**93.3**

Figure 7. Percentage of newly emerged adult Chrysophtharta agricola *collected that were in each of three developmental classes from Florentine Valley (A) and Frankford (B). Developmental classes were soft (□), medium (▣) and hard (■), and were based on the rigidity of elytra that hardened as a function of age. Numbers above each column indicate sample size.*
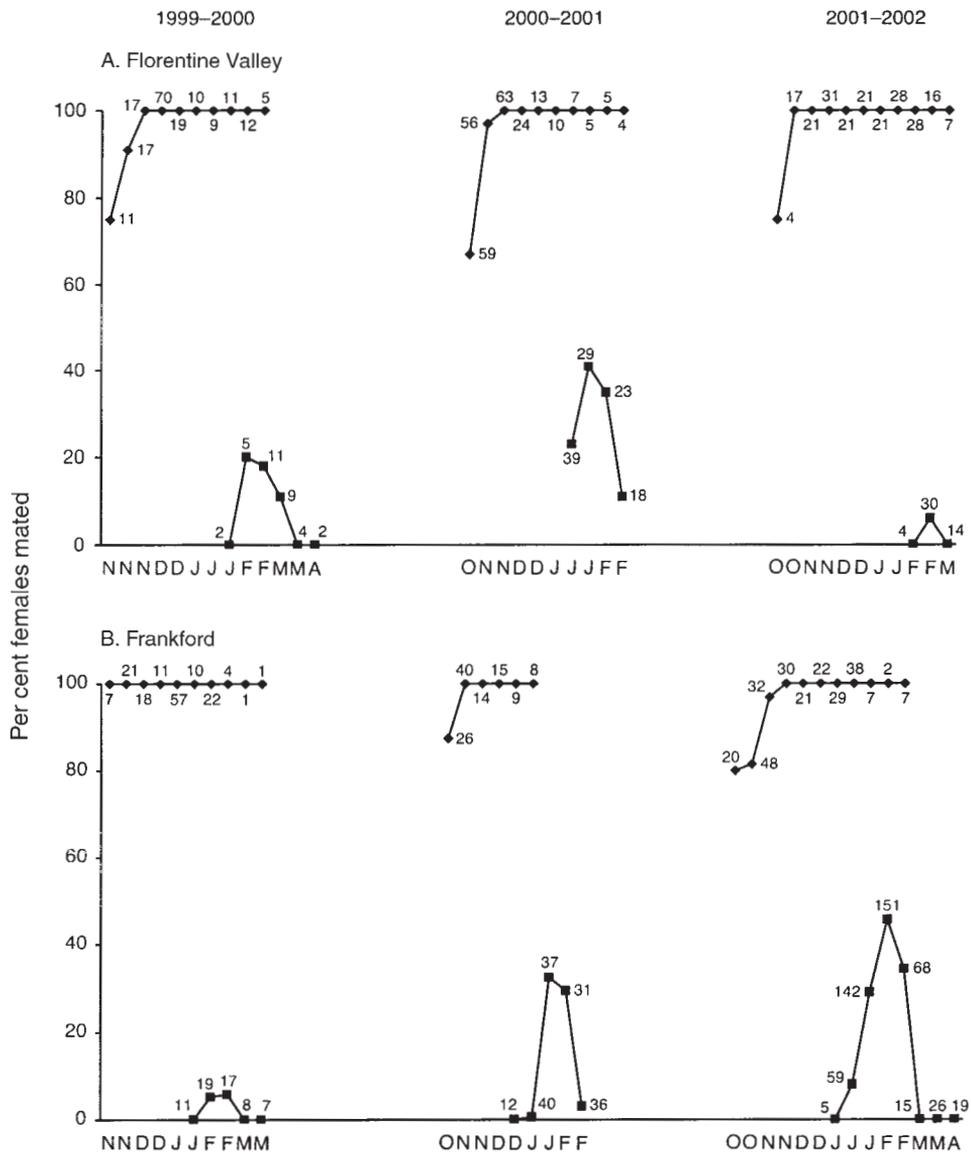
1999–2000   2000–2001   2001–2002

A. Florentine Valley

Per cent females mated

B. Frankford

Figure 8. Percentage of parent generation (♦) and first generation (■) Chrysophtharta agricola *females that had mated throughout each of three field seasons at Florentine Valley (A) and Frankford (B). Numbers beside each data point denote the number of females in the sample.*

Natural enemies

Many natural enemies were observed attacking *C. agricola* in plantations for the duration of the field season (Table 3): nematodes, egg parasitoids and European wasps were least common. Adult and larval Neuroptera and syrphid flies, and adult asilid flies were also observed within plantations but were not seen consuming any life stages of *C. agricola*. We were unsuccessful in rearing syrphid larvae on *C. agricola* eggs or larvae in the laboratory (data not presented). Syrphid and asilid flies and Neuroptera are recorded as predating other chrysomelid beetle eggs and larvae (Cox 1996). Adult *C. agricola* infected with pathogenic fungi *Beauvaria bassiana* and *Entomophthora* sp. were also recorded during this study.

Table 3. Natural enemies observed attacking Chrysophtharta agricola *in the field at Florentine Valley (FLO) and Frankford (FRA) throughout three field seasons 1999–2000, 2000–2001, 2001–2002 (early season, October– November; mid season, December–January, late season = February–March; +, species present; –, species not observed).*

| Natural enemies		Site	Early 99–00	Early 00–01	Early 01–02	Mid 99–00	Mid 00–01	Mid 01–02	Late 99–00	Late 00–01	Late 01–02
Egg/larval predators											
Coccinellidae	*Cleobora mellyi* (Mulsant)	FLO	+	+	+	+	+	+	+	+	+
		FRA	–	+	+	+	+	+	+	+	+
	Harmonia conformis (Boisduval)	FLO	+	+	+	+	+	+	+	+	+
		FRA	–	+	+	+	+	+	+	+	+
Cantharidae	*Chauliognathus lugubris* (F.)	FLO	+	+	+	–	+	+	–	+	+
		FRA	+	+	+	+	+	+	–	–	+
Miridae	undescribed sp.	FLO	+	+	+	+	+	+	+	+	+
		FRA	+	–	+	+	+	+	+	+	+
Spiders		FLO	+	+	+	+	+	+	+	+	+
		FRA	–	+	+	+	+	+	+	+	+
Pentatomidae		FLO	–	–	+	–	–	+	–	–	–
		FRA	–	–	–	–	+	–	–	–	+
Vespidae	*Vespula germanica* F.	FLO	–	–	–	–	–	–	+	–	–
		FRA	–	–	–	–	–	–	+	+	–
Reduviidae		FLO	–	–	–	+	–	–	+	–	–
		FRA	–	–	–	+	+	–	+	+	–
Larval parasitoids											
Tachinidae	Tachinid sp. 1	FLO	+	+	+	+	+	+	+	+	+
		FRA	+	+	+	+	+	+	+	+	+
	Paropsivora sp.	FLO	+	+	+	+	+	+	+	+	+
		FRA	+	+	+	+	+	+	+	+	+
Braconidae	*Eadya paropsidis*	FLO	+	+	+	+	+	+	+	+	+
		FRA	+	+	+	+	+	+	+	+	+
Egg parasitoids											
	Enoggera nassaui	FLO	–	–	–	–	–	–	–	–	–
		FRA	–	–	–	–	+	+	–	–	–
Adult parasites											
Nematodes*		FLO	–	–	–	–	–	–	+	+	–
		FRA	–	–	–	–	–	–	–	–	–
Podapolipidae		FLO	+	+	+	+	+	+	+	+	+
		FRA	+	+	+	+	+	+	+	+	+
Erythraeidae	*Leptus* sp.	FLO	+	+	+	+	+	+	+	+	+
		FRA	–	–	+	–	–	+	+	–	–

* Assessed by dissection
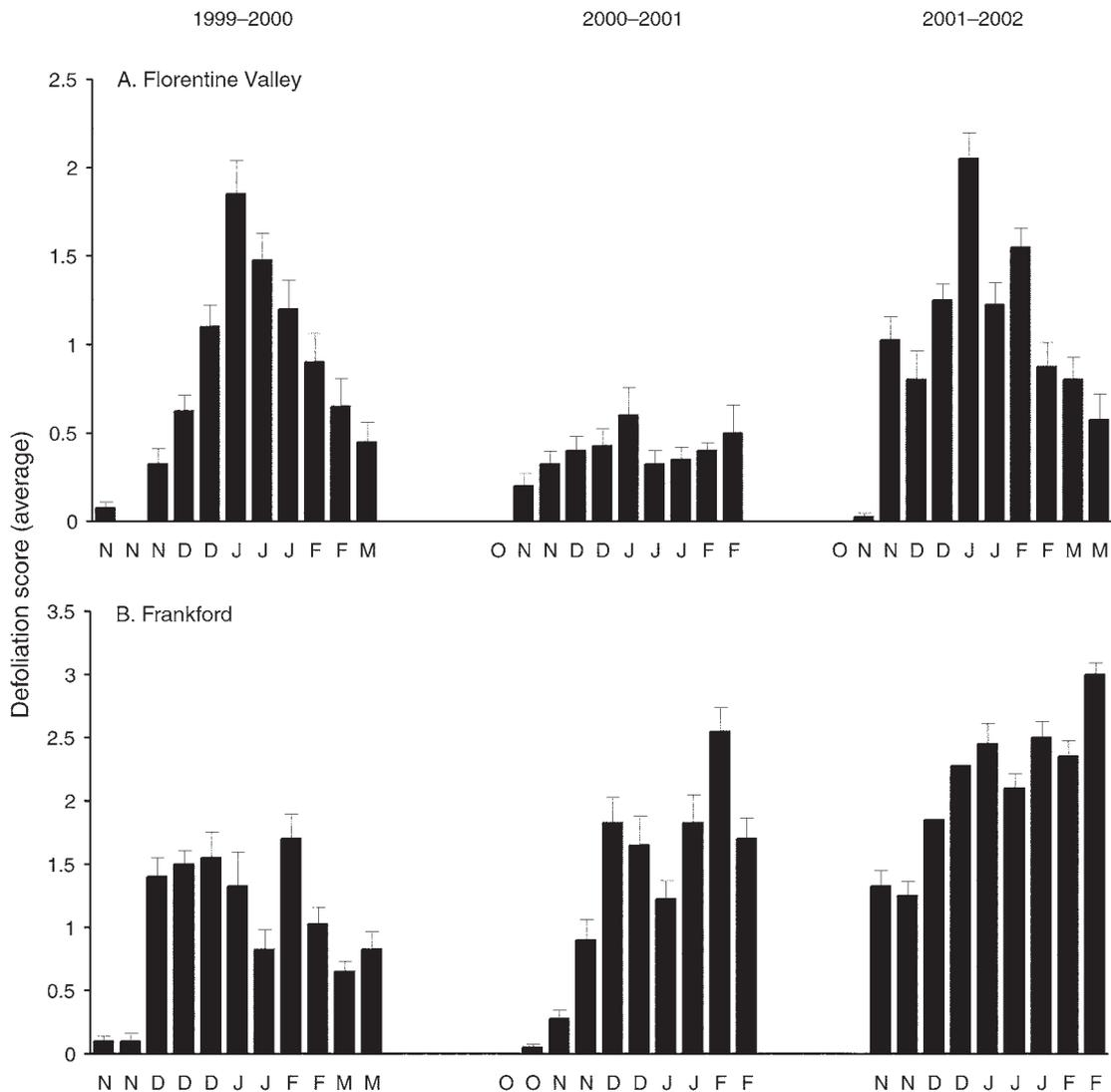
Figure 9. Defoliation scores (average + s.e.) of feeding damage by Chrysophtharta agricola *over three field seasons at Florentine Valley (A) and Frankford (B).*

Damage caused by C. agricola *in the field*

At Florentine Valley, peak defoliation scores coincided with the peak of third and fourth larval instars in each season (Figure 9A), and occurred within a week of each other in each season. The average peak defoliation represented about 30% of the current season's growth removed in each season (range = 0–50%). At Frankford, defoliation scores were generally higher and peaked later in the season than those at Florentine Valley,

coinciding with first-generation adult feeding (Figure 9B). Average peak defoliation at Frankford represented about 50% of the current season's growth removed (range = 10–90%). On branches that had been severely defoliated, larvae and newly emerged adults fed on soft green stems.

Foliage consumption

Each male–female pair of *C. agricola* adults and their resultant lifetime offspring

(adjusted for stage-specific mortality) were estimated to consume approximately 40 cm³ of juvenile *E. nitens* foliage, equivalent to about 80 average juvenile *E. nitens* leaves (pairs 1–3).

Spatial analysis of C. agricola *distribution within plantations*

Chrysophtharta agricola life stages were randomly distributed between 10 m x 10 m plots within plantations, with no evidence of spatial clumping, patchiness, or 'edge effects'. The lack of a significant log-likelihood increase (Frankford: eggs 0.84, larvae 0, adults 0.65; Florentine Valley: adults 0.82), or no convergence (Florentine Valley eggs and larvae) indicates that the pattern of variation of distribution showed no spatial structure at the scale tested.

Discussion

Chrysophtharta agricola adults are active in plantations between mid to late October and March (Ramsden and Elek 1998; this study) and overwinter in leaf litter between late February and October. Egg numbers generally peaked in the field in mid to late November, and the highest field mortality occurred during the egg and first instar stages (see also Nahrung *et al.* 2001). de Little *et al.* (1990) reported similarly high total field mortality for the immature stages of *C. bimaculata*, with the highest field mortality during the egg stage. For *C. agricola,* egg and early instar predation by ladybirds, mirids, cantharids and spiders was high, but mortality was also highest during the first instar stage in the absence of natural enemies for *C. agricola* (see Ramsden and Elek 1998; Nahrung *et al.* 2001), as for *C. bimaculata* (Baker *et al.* 2002).

In addition to natural enemies, plant attributes contribute to larval mortality. For example, leaf toughness affects the survival of early instar paropsine larvae (Steven 1973; Ohmart *et al.* 1987; Larsson and Ohmart 1988; Howlett 2000) and likewise affects

the establishment of *C. agricola* (Nahrung *et al.* 2001). Manna, a saccharine secretion exuded rapidly in response to damage, is produced by *Eucalyptus nitens* (Steinbauer 1996). Feeding by *C. agricola* can result in its production (HFN, pers. obs.). The exudate forms crystalline nodules at the site of damage and inhibits larval access to the feeding site, and mires young larvae, resulting in death. Manna is a carbohydrate source utilised by natural enemies (Steinbauer 1996), and the larval parasitoids of *C. agricola* feed on it in the field and laboratory (A.D. Rice, pers. comm.; HFN, pers. obs.), although whether the presence of manna increases attack on *C. agricola* by natural enemies is unknown.

Oviposition by newly emerged adults is dependent upon the photoperiod on the date they emerge from pupation (Nahrung 2003), and development time to emergence from pupation is dependent upon the temperatures experienced by immature stages (see Nahrung *et al.*, in press). This is illustrated clearly in a comparison between seasonal development at the Florentine Valley site: in the 2000–2001 season, second to fourth instar larval peaks each occurred earlier than in the other two monitored seasons, and this was the only year in which newly emerged adults laid eggs.

Dissections of adult beetles showed that females mate soon after emergence from overwintering and carry sperm in their spermatheca for the entire field season. This study showed overlap of parental and new generation adults of at least 4–10 weeks. Sex ratios were equal. In the laboratory, males and females had equivalent longevity (Nahrung and Allen 2003), and males persisted throughout the field season.

The spatial distribution of *C. agricola* within plantations was found to be random between 10 m x 10 m plots. Thus, in designing a monitoring protocol for this species, any trees still in juvenile foliage can be monitored with an equivalent chance of finding *C. agricola* life stages, at least in plantations

with high populations such as those studied here. The monitored *C. agricola* populations at Frankford and Florentine Valley were very high. Sites that have lower *C. agricola* abundance could exhibit patchiness in spatial distribution if females do not move far from oviposition sites. Spatial patchiness of *C. agricola* in plantations may also depend on the adult-juvenile foliage phase of trees because eggs and larvae are more common on juvenile foliage than on adult foliage (Nahrung and Allen 2003). Only juvenile foliage was sampled in these surveys and this may have influenced the apparent homogeneity of intra-plantation distribution. Furthermore, the spatial resolution obtained using 100 m² plots may not have been adequate to detect patchiness within plantations. Factors that affect the intra-plant distribution of adults, eggs and larvae on trees are discussed by Nahrung and Allen (2003) and Nahrung *et al.* (2001).

The highest number of branches occupied usually coincided with egg to second instar peak abundance, and reflects the high mortality rates of these developmental stages. An exception was during the 2000–2001 season at Frankford, when branch occupation was highest during third and fourth larval instar peaks. This season experienced the lowest mortality of egg and early instars, and lowest overall mortality, although there was no difference in natural enemy species composition compared with other seasons. However, natural enemy abundance was not assessed.

The high field mortality rates presented here are similar to those for *C. bimaculata*: de Little *et al.* (1990) found a cumulative 95–97% egg–larval mortality attributable to natural enemies. However, *C. agricola* and *C. bimaculata* population levels in plantations and beetles' high fecundity mean that even 3–5% survival can result in severe tree defoliation. Long-term measurements of the effect of defoliation on juvenile phase *E. nitens* need to be conducted to determine the effect of

C. agricola feeding on growth rate and wood quality. Elek (1997) reported a significant loss of growth and wood volume over two years in three-year-old *E. nitens* trees from which greater than 50% of current season's foliage had been removed.

Defoliation scores peaked at Florentine Valley coincident with the peak of third and fourth instar larvae in the 1999–2000 and 2001–2002 seasons, while in the 2000–2001 season, and in each season at Frankford, the highest defoliation occurred when newly emerged adult numbers were highest. Feeding by new adults is likely to have a large impact on tree growth because damage later in the season may prevent foliage regrowth, leaving exposed shoots susceptible to damage by severe cold in winter (Elliott *et al.* 1993; Elek 1997). Higher levels of defoliation also occurred during seasons in which newly emerged adults laid eggs, because of feeding from the resultant larvae (Figure 9).

Feeding estimates reported here of 80 juvenile leaves consumed by the surviving lifetime offspring and adult feeding of one adult pair over the field season might allow prediction of seasonal foliage loss if adult populations and leaf production can be estimated. The amount of foliage required for male and female *C. agricola* to build up sufficient fat body for overwintering needs to be quantified more accurately to predict the effects of defoliation, especially as late-season (pre-overwintering) feeding is more likely to impact on tree growth (Elliott *et al.* 1993; Elek 1997).

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