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The Biology and Herbivory Rates of *Novacastria nothofagi* Selman (Coleoptera: Chrysomelidae), a New Genus and Species on *Nothofagus moorei* in Australian Temperate Rain Forests

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Abstract

Novacastria nothofagi Selman, a new species and genus, is described and illustrated. A new key is produced to the genera related to *Calomela* Hope, incorporating *Novacastria*, gen. nov. The larvae feed exclusively on the young leaves of Antarctic beech, *Nothofagus moorei*, in Australian cool temperate rainforests. Larval emergence is synchronous with the simultaneous leaf flush of beech that occurs during spring (September–October). The larvae annually ate up to 50% of the new leaf flush over three years, and ignored old leaf material also present in the canopy. Despite this high rate of herbivory, beech canopies appear to tolerate what appears to be a pest outbreak.

Introduction

Novacastria nothofagi was first discovered during observations on leaf growth and mortality of the Antarctic beech *Nothofagus moorei* in the cool temperate rainforests of New England National Park, N.S.W.

This new genus and species is the first of the subfamily Chrysomelinae known to feed on *Nothofagus* spp. and is of considerable taxonomic significance, linking the paropsine genera with many of the non-paropsine genera of Australia. The beetles were collected on beech buds during autumn (March–April) 1980 as part of noctural beating samples for beech herbivores. The larvae were not observed until the following spring (September 1980), at which time they were reared in the laboratory and thereby related to the adults collected previously. The larvae feed exclusively on the young leaves of the Antarctic beech, resulting in severe defoliation of the new leaf flush. During subsequent years (1980–82) the biology of *N. nothofagi* in relation to its host plant, *Nothofagus moorei*, was recorded as part of long-term studies on the dynamics of the canopy in Australian rainforests (Lowman 1982).

Study Site

The site of original discovery and subsequent observations of *N. nothofagi* was at approximately 1400 m in New England National Park, located on the New England Plateau at the headwaters of the Bellinger and Macleay Rivers in central New South Wales. The park contains cool temperate rainforest in its cooler, moist, montane regions, intergrading into sclerophyll or subtropical rainforest vegetation on drier or lower elevation sites, respectively. The predominant bedrock is basalt and trachyte underlain by older Palaeozoic sedimentary layers.

The vegetation is dominated by Antarctic beech with a canopy of approximately 35 m height and 10·6 m depth. The understorey consists of sassafras *Doryphora sassafras*, mountain blueberry *Elaeocarpus holopetalus*, mountain laurel *Cryptocarya* sp.,

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possumwood *Quintinia sieberi*, tree-heath *Trochocarpa laurina* and several others. The area is classified as microphyll fern forest according to Webb (1959) and exhibits the features characteristic of cool temperate rainforest in Australia: single-species dominance of *Nothofagus*; two main canopy layers with the upper one rarely exceeding 30 m; absence of buttresses and lianas; and species with microphyll leaves. Additional information on the rainforest site is listed elsewhere (Lowman 1982).

N. moorei is an evergreen, monoecious tree of the family Fagaceae, distributed throughout cool temperate rainforest in New South Wales (Frances 1970; Floyd 1976). This includes the cool, moist montane regions in the headwaters of the Hastings, Macleay, Bellinger and Barrington Rivers and on the McPherson and Tweed Ranges. Antarctic beech grows to 30–40 m height with crooked, dark, moss-covered trunks, and tends to form single-species stands, dominating the upper canopy of the rainforest formation. The leaves are alternate, simple, elliptical, finely toothed, and very tough when mature.

Genus **Novacastria**, gen. nov. Selman

(Figs 1–15)

Type-species *Novacastria nothofagi*, sp. nov. Selman.

Diagnosis

Species of the genus *Novacastria* are chrysomelid beetles with the prothoracic coxal cavities open, antennae subincrassate, maxillary palps with apical segments securiform, elytra non-tuberculate with epipleura non-setate and not recessed by the downward extension of the elytra as in *Paropsis* Olivier, 1st visible abdominal sternite approximately 3 times as long as 2nd along the midline. Characterized by lacking a notopleural suture on the prothorax, and having appendiculate claws, the prosternum very broad, flat and parallel-sided, the anterior end not produced into a tooth, the posterior end broad and straight-edged.

The genus keyed out to the genus *Macelola* Selman in the key to the chrysomelid genera closely related to *Calomela* (Selman 1979). However, the new species differs from *Macelola* in having the claws appendiculate and the prosternum very broad, flat and parallel-sided. A new key is now published incorporating the new genus together with a description of both the adults and the larvae of the new species. Unfortunately nothing is known of the host plants or biology of the species of the genus *Macelola* (Selman 1975).

Novacastria nothofagi, sp. nov. Selman

(Figs 1–11)

Types

Holotype ♂, 'New England Nat. Park, N.S.W., ex. *Nothofagus moorei*. Collected M. Lowman Nov. 1980: *Novocastria nothofagi* sp. nov. Det. B. J. Selman 1981.' In Australian National Insect Collection, Canberra.

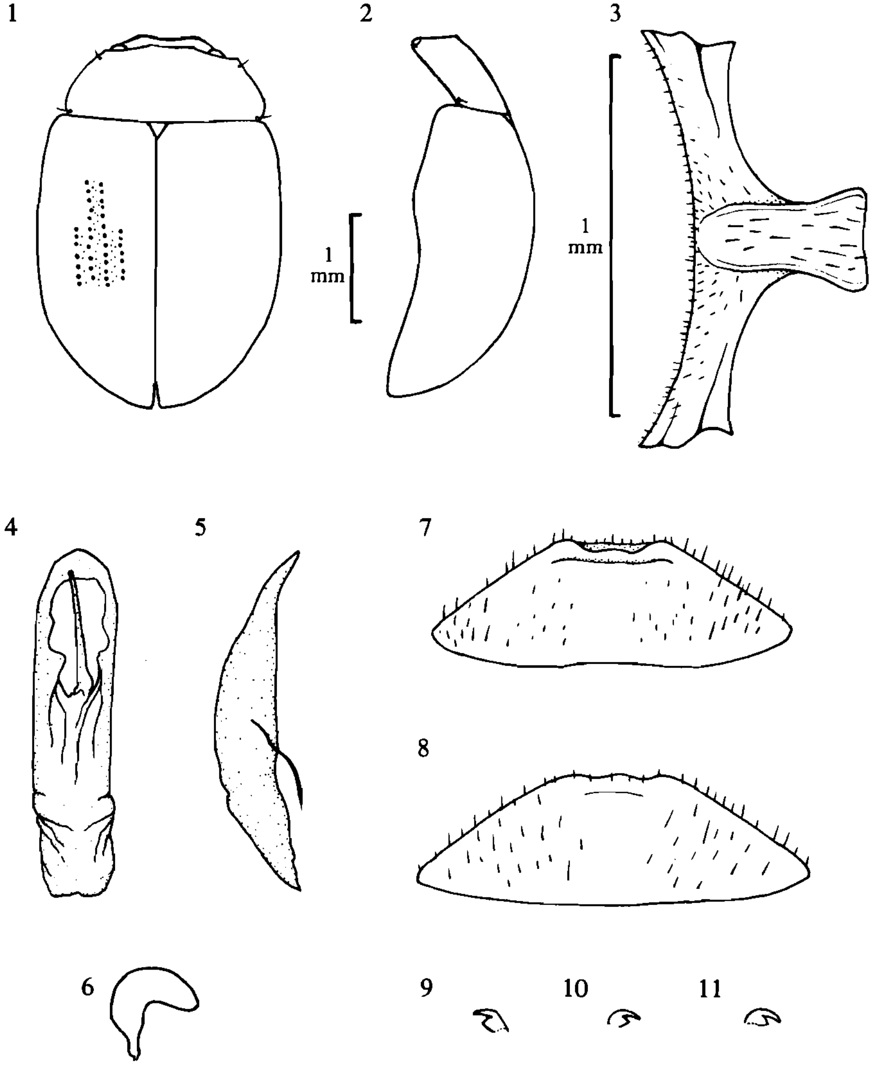
Paratypes: 1 ♂, 1 ♀, 4 sex undetermined, data as above, in Australian National Insect Collection, Canberra; 1 ♂, 1 ♀, in the author's reference collection; 2, sex undetermined, in British Museum (Natural History), London.

Adult

Length. 3·64±0·18 mm.

Colour. Unicolorous light to mid-brown when dead; eyes, tips, of mandibles, femora and 7 distal segments of antennae usually black or very dark brown; scutellum occasionally dark brown. When alive, body translucent mid-brown with greenish brown sheen on dorsal surface of elytra.

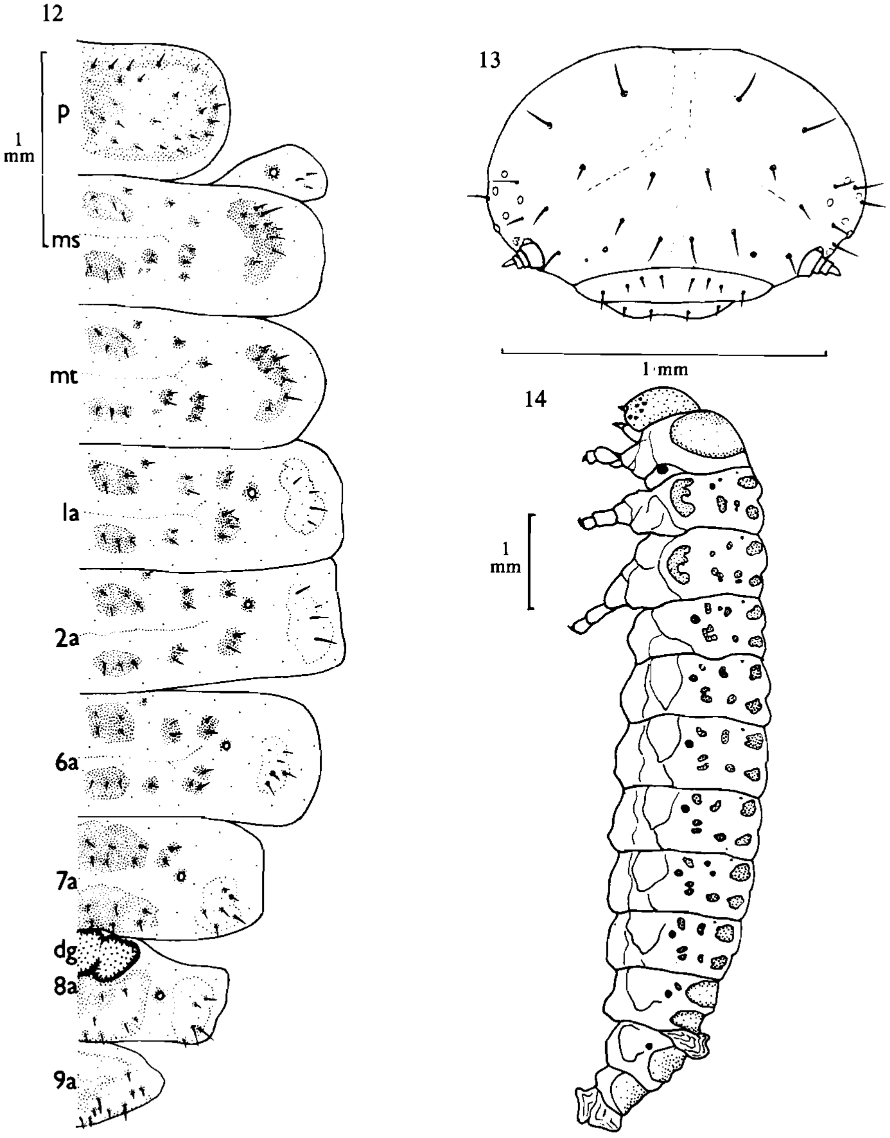
Head. Frons deeply and closely punctured, interstices coarsely shagreened, fronto-clypeal sutures distinct yet fine, front-clypeus 3 times as broad as long at the midline, the punctures large but indistinct, interstices coarsely shagreened, labrum strongly bilobed, eyes partly hidden by the pronotum, labial palps large and robust, distal segment securiform.



Figs 1–11. *Novacastria nothofagi*, sp. nov.: *1*, dorsal view; *2*, lateral view; *3*, prosternum; *4*, dorsal view of aedeagus; *5*, lateral view of aedeagus; *6*, spermathecae; *7*, male; *8*, female, fifth abdominal sternites; *9–11*, fore, mid and hind claws of male. Same scale for Figs 1 and 2; same scale for Figs 3–11.

Thorax. Pronotum 1·9 times as long as wide, each corner with a distinct seta; smooth and shiny, punctures small but distinct, especially along the lateral sides which have shallowly impressed foveae; prosternum (Fig. 3) very broad and flat, lateral margins raised, posterior edge almost straight, anterior edge straight but the central point slightly raised, surface smooth with sparse long curved setae, coxal cavities open.

Elytra. With 10 regular rows of punctures, punctures distinct (Fig. 1), interstices smooth and shiny with distinct micropunctures, lateral edges when viewed from the side produced downwards just behind the humerus (Fig. 2).



Figs 12–14. Larvae of *Novacastria nothofagi*, sp. nov. *13*, Arrangement of setae and tubercles on the dorsal surface of the final instar. *p*, pronotum; *ms*, mesothorax; *mt*, metathorax; *1–9 a*, abdominal segments, *dg*, dorsal defence glands. *14*, Front view of head. *15*, Lateral view of whole final-instar larva.

Legs. Tarsi with 2nd segment small, claws prominent and appendiculate (Figs 9–11).

Abdomen. 2nd–5th visible sternites heavily punctured with large punctures each bearing a small seta; shape of the posterior tip of the abdomen slightly different between the sexes (Figs 7, 8).

Genitalia. Male as in Figs 4, 5, aedeagus simple. Female as in Fig. 6, spermatheca stout and bent at 90°.

This, so far as is known, unique species is variable in the degree of darkening of the cuticle.

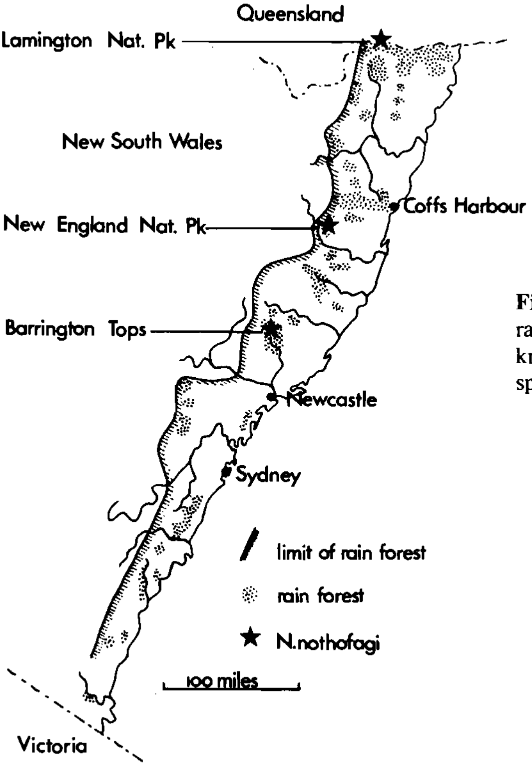


Fig. 15. Map showing the distribution of the rain forests of New South Wales and the known distribution of *Novacastria nothofagi*, sp. nov.

Larvae (Figs 12–14)

Length of final instar *c.* 7·4 mm, elongate, head and pronotum sclerotized and light brown. Meso- and metathorax and abdominal segments 1–7 with 2 rows of strongly sclerotized dorsal plates, slightly raised to form tubercles. Abdominal segments 1–6 with 12 dorsal plates between the spiracles. Between abdominal segments 7 and 8, a confluent pair of dorsal eversible glands. Abdominal segment 9 with anus surrounded by an eversible sucker. Setae well developed but not prominent. Head with 6 primary setae on vertex and 10 primary setae on frons (Fig. 13). Clypeus with 8 primary setae and labrum with 4 primary setae. Body segments with sclerites formed around the bases of the primary setae. Setal arrangement on the anterior sclerite nearest to mid-dorsal line of abdominal segments 1–6 clearly indicates that it is formed by the fusion of 2 adjacent anterior sclerites. Between abdominal segments 7 and 8, a pair of confluent dorsal eversible glands. Anus surrounded by an eversible sucker.

When alive, body a pale red or reddish green, the pronotum dark brown, the dorsal plates of the abdomen and meso- and metathorax forming a dark dorsolongitudinal line along the back, darkest at the anterior and posterior ends, the head a pale orange.

Pupa

Exarate, pale cream, setate. Posterior tip of abdomen with a single urogomphus. Pupation takes place in an earthen cell.

Distribution

Cool temperate rainforests of northern New South Wales (Fig. 15).

Taxonomic Position of Novacastria

The adult shows clear relationships with *Macelola* Selman in the key to the genera closely related to *Calomela* Hope (Selman 1979). Unfortunately, the larvae and pupae of *Macelola* are unknown. Both the larvae and the pupae of *Calomela* and *Novacastria* are very different, indicating that the presence or absence of a notopleural suture on the prothorax of the adult is a far more significant character than had previously been suspected. The elongate larvae of *Novacastria* have 12 dorsal sclerites between the spiracles of abdominal segments 1–6. This indicates that the larvae are similar to those of *Paropsisterna*, which also have 12 dorsal sclerites, and akin to those of *Paropsis* and some *Chrysophtharta*, which both have 14 dorsal sclerites. The larvae of *Novacastria* are clearly very different from those of *Calomela*, which are short with the anterior abdominal segments bloated, giving the larvae a humpbacked appearance. Also, the final-instar larva of *Calomela* has no setae or dorsal sclerite between the spiracles of abdominal segments 1–6, though the first-instar larva has 18 individual setae without sclerites around their bases or tubercles.

The pupae of *Novacastria* have a single posterior urogomphus. This contrasts with *Calomela*, where the pupae have a very well developed pair of urogomphi, and the paropsine genera like *Paropsisterna*, which have a pair fused at the base.

The immature stages therefore suggest that *Novacastria*, and probably the other genera in the key which lack a notopleural suture in the adult, should be placed in a separate tribal group from *Calomela* and the other genera which have a notopleural suture.

The arrangement of sclerites shows that both these groups and the paropsine generic complex are in the non-glanduliferous larval group of Kimoto (1962), though all possess exceptionally well developed dorsal defence glands between abdominal segments 7 and 8. If the tribal classification of Kimoto (1962) is used for the Australian genera, then *Calomela* and its related genera *Starycea* and *Carystea* are in his *Chrysolina* generic group; *Novacastria*, *Macelola*, *Platymela*, *Augomela*, *Parastarycea* and *Lamecola* are in his *Gonioctena* generic group. The two groups are separated on the characters of the pupae and larvae. The paropsine generic complex is intermediate between the two and almost certainly requires its own separate group.

Key to the Genera closely Related to *Calomela* Hope

This key to the adult beetles is a revision of that of Selman (1979).

Australian beetles of the subfamily Chrysomelinae with prothoracic coxal cavities open, antennae subincrassate, maxillary palps with apical segment securiform, elytra non-tuberculate with the epipleura non-setate and not recessed by the downward extension of the elytra as in *Paropsis*. 1st visible abdominal sternite *c.* 3 times as long as 2nd along the midline. 1

1. Notopleural suture present on the prothorax, posterior tip of prosternum distinctly bilobed 2
   No notopleural suture on the prothorax 4
2(1). Claws simple .... *Starycea* Selman
   Claws toothed 3
3(2). Claws with bifid teeth, many species with a single longitudinal green stripe on each elytron .... *Calomela* Hope
   Claws with appendiculate teeth .... *Carystea* Baly
4(1). Prosternum with posterior end truncate or only very slightly bilobed, the anterior end in some species produced into a distinct tooth, body elongated 5
   Prosternum with posterior end bilobed and anterior end not produced into a tooth 7
5(4). Prosternum with anterior end produced into a distinct tooth, antennal segments 5–11 greatly broadened, elytra iridescent .... *Platymela* Baly

Prosternum with anterior end only sometimes produced into a distinct tooth, especially in the male, antennal segments 5–11 not greatly broadened, elytra more convex in transverse section and never iridescent 6
6(5). Claws strongly bifid, prosternum not very broad and flat .... *Macelola* Selman
Claws strongly appendiculate, prosternum very broad and flat .... *Novacastria*, gen. nov.
7(4). Body globose 8
Body elongate 9
8(7). Prosternum broad and flat, without a central longitudinal ridge .... *Stethomela* Baly
Prosternum with a raised central longitudinal ridge, especially well developed at the anterior end .... *Augomela* Baly
9(7). Claws simple .... *Parastarycea* Selman
Claws appendiculate .... *Lamecola* Selman

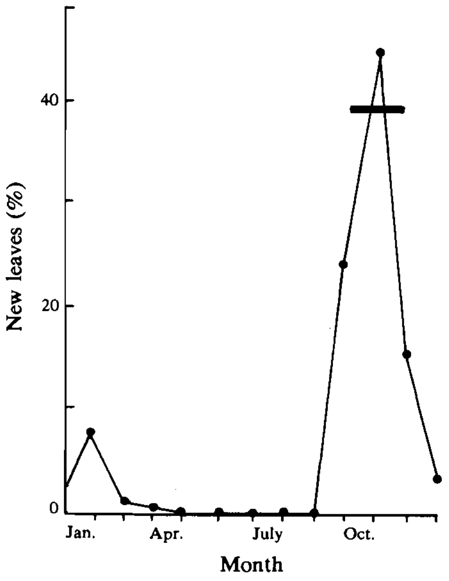


Fig. 16. Phenology of leaf emergence in *Nothofagus moorei* in New England National Park, N.S.W. Bar indicates duration of *N. nothofagi* larvae in the canopy. New leaves expressed as monthly percentage of annual total.

Life History of N. nothofagi *in relation to Phenology of the Host Plant*

N. moorei is distinctly seasonal in its pattern of leaf emergence, and the phenology of the beetle larvae appears to be synchronous with their host plant. Beech has one major annual leaf flush during early spring (September–October) (see Fig. 16), when 8–15 new beech leaves emerge per bud. Since the leaves live approximately 2 years (Lowman 1982), the spring leafing period represents an annual replacement of one-half the beech canopy.

In the present study, the larvae of *N. nothofagi* emerged during September–October, simultaneously with the budburst of beech (see Fig. 17). They fed on the terminal leaves of new beech shoots, and gradually progressed downward, consuming the older new leaves near the base of the shoot. In most cases, the terminal leaves were totally consumed or sometimes so riddled with holes that the remaining latticework segments of leaf tissue desiccated and died; the basal leaves were usually only partly eaten. The colour of the larvae changed slightly from red to red-green as they moved from the very young red leaves gradually down to feed on the slightly older and therefore greener leaves. The larvae fed for approximately 2 weeks while the young beech leaves were rapidly expanding, and then dropped to the ground where they metamorphosed in the leaf litter. Adults emerged in 8–14 days, just as the main leaf flush was completed. They were not major herbivores, although they occasionally removed very small portions of beech leaf tissue. They presumably mated and overwintered in the beech forests, although adult populations were never as conspicuous as the larval stages. Eggs were laid in beech buds several weeks before spring, hatching at budburst.

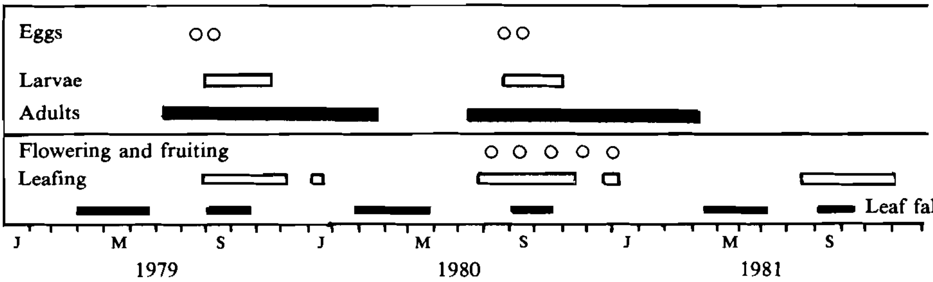


Fig. 17. Life cycle of *N. nothofagi* (upper) in relation to the phenology of its host tree, *Nothofagus moorei* (lower).

Observations of Larval Feeding Patterns

Feeding trials were conducted with the larvae to determine both age and species preference of leaf material, and to calculate daily rates of consumption. In all feeding trials, the following methods were employed.

Branches containing larvae were picked in the field and immediately brought into the laboratory where the trials commenced. Larvae were sorted into two age classes, week 1 and week 2, according to their size (greater than 5 mm were designated 'week 2') and to the age and position of leaves being consumed (older larvae, 'week 2', ate leaves that were almost fully expanded, greener, and located toward the base of a new shoot). Larvae were placed directly into individual petri dishes lined with moist filter paper and containing the leaf material required for a particular feeding trial.

Daily feeding rates were recorded by measuring the amounts of both original leaf area and leaf tissue remaining with an area meter (Lambda Instruments, model 300), and calculating the difference. Leaf area removal was usually expressed as percentage loss of an individual leaf. Although the absolute amounts of leaf tissue eaten varied according to leaf size, percentage values were used to express the data since they implied a proportion of photosynthetic area missing from the canopy, and were comparable within and among different-sized leaves, branches and trees. If a larva ate nothing, no data were recorded. Only entire leaves were presented as food choices.

Leaf Age Preferences

When presented with a choice between a young and an old beech leaf, the larvae consistently fed only upon the young leaf, and died if presented with mature leaves only. Consequently, only young leaf tissue was used in feeding trials.

Species Preference

Ten larvae of each age class were presented with a young leaf of *N. moorei*, and also a young leaf of either *Doryphora sassafras* or *Trochocarpa laurina*, two understorey species commonly associated with beech. The larvae consistently selected the beech, and if presented with only leaf material other than beech, ate nothing and died, confirming field observations which yielded no evidence of feeding by *N. nothofagi* on any other species co-occurring with beech.

Feeding Rates

Twenty larvae of each age class were each placed into a petri dish lined with moist filter paper containing one entire leaf that most closely resembled the colour and size of the leaf from which the larva had been removed. After 24 h, the area of leaf consumed was calculated, to obtain daily feeding rates for each age class.

The mean amounts consumed by 1-week-old and 2-week-old larvae are listed in Table 1. Young larvae (1 week old) ate approximately 0·31 cm^{-2} day^{-1}, and this rate subsequently increased to an average of 1·14 cm^{-2} day^{-1} for older larvae (2 weeks old). A mean rate for the two age classes, 0·73 cm^{-2} day^{-1}, was used in estimates of consumption per individual.

Table 1. Feeding rates of *N. nothofagi* larvae on young leaves of *N. moorei*

Results of 24-h trials, expressed per larva. Values for the dry weight of leaves given are ± standard errors

	1-week-old larvae	2-week-old larvae	Mean
No. of larvae	20	31	
Dry weight of leaves given	6·5±0·05	8·0±0·20	7·25
Leaves consumed			
Area (cm^2 day^{-1})	0·31	1·14	0·73
Dry weight (mg day^{-1})	2·20	9·12	5·66
Frass produced			
No. of particles per day	41·0	60·4	50·7
Dry weight (mg day^{-1})	0·13	0·53	0·53

Densities of Larvae in Relation to Availability of Food

The densities of larvae in the canopy were examined in relation to three factors: vertical distribution, temporal variability and spatial variability.

During September–October 1980, the numbers of new shoots, new leaves, and larvae per leaf were sampled over two periods at four different levels in the canopy. Twelve cubic metres were marked off around one beech tree in each of four canopy levels: 0–2 m, 2–4 m, 4–6 m, and 6–8 m (48 m^3 in total). Tapes and metres sticks were used to mark off each cubic area, and the corners were tagged with string. The 6–8-m zone was considered representative of the upper canopy, since it was exposed to direct sunlight. Each height interval was sampled by use of a ladder, and each cubic metre was censused for new shoots, new leaves per shoot, and larvae per leaf, the larvae at the onset of emergence and again later towards the completion of leaf flush.

Table 2 summarizes the results. Larval density was highest in the upper canopy, which also contained the greatest amount of available food (i.e. new leaves). Since the larvae are not very mobile, this suggests that the beetles may lay more eggs in the upper canopy buds.

Although larvae usually exhibit a sedentary feeding behaviour, they may progress along the shoot and occasionally to adjacent shoots as they consume one leaf and move to another. There were two general patterns of larval movement that affected their distribution during the spring infestation. First, within one shoot, the larvae gradually descended from the apical leaves to the basal leaves of the shoot; they exhausted the supply of very young leaves at the shoot tip and thus moved slowly down to slightly older, less succulent tissue. This tendency to feed first on the apical leaves appeared to be an obligate preference, since 1-week-old larvae died in feeding trials when presented with only basal (i.e. slightly older) leaves rather than the apical (i.e. younger) leaves upon which they normally fed. The increasing toughness of beech leaves with age may make them increasingly resistant to the mouthparts of the very young larvae.

Because of this tendency to begin feeding at the shoot apex, the terminal leaves tended to be the most heavily, if not totally, defoliated; whereas the basal leaves of some shoots escaped defoliation altogether.

The second shift of larval distribution involved spatial mobility on a seasonal basis throughout the levels of canopy in relation to the shoot phenology. Since beech budburst exhibits a slight time lag progressively from the upper to lower canopy, the highest concentrations of larvae may be expected to shift in accordance with food availability. To test this, one-way analyses of variance were performed on the number of larvae at different canopy heights at three different dates (see Table 3). The results indicated that there were significant differences in the distribution of larvae on a temporal scale. At the onset of budburst in the upper canopy (late September), there were significantly more larvae in the upper heights. Once leaf emergence had occurred throughout the entire canopy (10 October), there were still significantly more larvae in the upper canopy, presumably since food availability there was also greatest (see Table 2). At the end of the season of leaf emergence (26 October), however, there were more larvae in the lower canopy where young leaves were still available.

Table 2. Distribution of new leaves and shoots between levels of the canopy of *N. moorei*, and distribution of larvae of *N. nothofagi*

Values are means from two days of peak feeding activity, 30 September and 10 October 1980; numbers of new shoots and of larvae per leaf are ± standard errors

Canopy ht (m)	No. of new shoots per m^3	No. of new leaves per shoot	Total No. of new leaves	No. of larvae Per leaf	No. of larvae Per m^3
0–2	4·0±2·0	6·5	26·0	1·37±0·13	35·6
2–4	13·9±2·1	6·7	93·3	1·40±0·20	130·6
4–6	20·9±1·4	7·3	151·5	1·56±0·14	236·3
6–8	32·5±3·7	9·6	279·5	2·49±0·92	697·1
Mean	17·8	7·3	137·6	1·71	274·9
Total per m^2 ground	71·3		550·3		1099·6

Table 3. Shifts in larval density at different canopy heights of *N. moorei* as a reflection of the changes in leafing phenology throughout the tree over time

Heights ranked in ascending order by Student–Newman–Keuls test; superscripts indicate heights which were statistically similar on the same day

Date	Degrees of freedom	Heights				*F*	Significance
30 Sept.	3, 92	1 m^A	3 m^{AB}	6 m^{BC}	8 m^C	3·70	$P<0·01$
10 Oct.	3, 96	1 m^A	3 m^A	6 m^A	8 m	7·39	$P<0·001$
26 Oct.	3, 96	8 m	6 m^A	3 m^A	1 m^A	7·24	$P<0·001$

The Effects of Larvae upon the Host Tree

Defoliation was compared in three trees within each of three sites by measuring proportions of leaf area missing at the end of the 1980 growing season. Since the branches were marked and each leaf numbered it was also possible to estimate loss due to complete leaf removal. The amounts missing, expressed as percentage of total leaf area, may represent a slight overestimate of herbivory by *N. nothofagi*, since other phytophagous insects were occasionally observed. But the beetle larvae contributed approximately 95% of the loss.

Table 4 shows the mean proportions removed from the 1980 new-leaf flush, with an overall grazing loss of 32·06%. There is considerable variability both among trees and between sites, indicating that larval distribution is patchy. It is evident from this limited survey, however, that *N. nothofagi* larvae in spring cause a high loss of potential photosynthetic tissue from beech canopies.

The relationship between a herbivore, the quantity of its food supply and the proportion removed has been quantified as: $X=(N\times F\times 100)/M$, where X is the percentage loss of foliage, N is the numbers of insects, F is the average amount of food, in grams, consumed during the lifetime of an individual herbivore, and M is the biomass, in grams, of foliage in the canopy [from Rudnev (1935) in Rafes (1968)]. For beech: $X=32\%$ foliage loss; $F=0·08$ g consumed during the lifetime of a larva; $M=548$ g foliage biomass in the canopy*; so N is estimated as 219·2 larvae per square metre ground surface.

Table 4. Variability in herbivory rates among branches, trees and sites for *N. moorei* during the growing season of 1980

The loss of leaf area per branch calculated from 8–15 leaves, of both the current and previous year's leaf flushes. Mean leaf size, 13·6±0·03 cm^2

Site No.	Tree No.	Leaf area loss (%) from branch No. 1	2	3	Mean
1	1	74·17	18·33	21·88	38·09
	2	42·00	36·24	46·08	41·44
	3	52·00	45·83	5·68	34·56
2	1	60·07	8·69	12·42	27·06
	2	56·89	11·20	50·89	39·66
	3	47·33	66·83	40·10	51·42
3	1	17·40	25·17	9·54	17·37
	2	1·33	11·00	32·48	14·94
	3	29·56	25·56	19·82	23·98
Mean for site 1					38·03
Mean for site 2					39·38
Mean for site 3					18·76
Mean for all sites					32·06

This result appears too small in view of the 1100 individuals per cubic metre counted in the canopy at times of peak larval density (see Table 2). However, the number which survive to inflict damage during their entire potential life span damage is much lower, and was estimated by counts of larvae falling to the gound to metamorphose. Numbers of larvae falling into 1-m^2 litter traps ranged from 0 to 618, with an average of 215 larvae per square metre of ground, which is comparable to the 219·2 estimated.

Discussion

Herbivory rates in natural plant communities lie within the range of 3–15% leaf area removed, e.g. in hardwood forests (Bray 1961, 1964; Reichle *et al.* 1973; Nielson 1981) and neotropical rainforests (Odum and Ruiz-Reyes 1970). Much higher rates, of 20–75%, have been reported in Australian *Eucalyptus* forests (Morrow 1977*a*, 1977*b*; Journet 1981), rates of up to 30% in Australian coral cay vegetation (Heatwole *et al.* 1981), and of 32% in Australian cool temperate beech forests as reported here. These higher rates raise interesting questions about the interaction of predators and insect herbivores in Australian forests. Chrysomelid beetles are major herbivores in both the eucalypt and beech forests, yet Coleoptera appear less important in the dynamics of neotropical foliage (Elton 1973;

* Based on annual beech leaf fall measurements and leaf longevity of 2 years (i.e. half the beech canopy is shed annually) (Lowman 1982).

Langenheim, personal communication). Cool temperate rainforests in New South Wales are unique in that *N. moorei* creates a monospecific canopy that would appear to provide a very extensive food supply to *N. nothofagi*; however, the synchronous leafing phenology results in an ephemeral availability of young leaves.

As the larvae mature and move down the branch to feed upon slightly older leaves, they occasionally leave portions of young leaves uneaten. These fragments (usually less than 10% of original leaf area) subsequently desiccate and absciss. The herbivory rates measured in this study may, therefore, slightly overestimate the absolute amounts eaten by insects. Conversely, some new leaves may have been totally eaten before being marked on the branch, thereby resulting in a slight underestimate of grazing losses. These two sampling artefacts, with contrasting consequences, may cancel any sampling error.

Several attributes of the plant may act as defences against leaf-eating herbivores. In beech, these defences appear to vary between leaf tissue of different ages, since the larvae exhibited obligate preference for young leaves despite the abundance of old tissue. The old leaves had both great physical toughness and high toxicity (approximately 10·5 mg tannic acid per 100 mg dry weight) (Lowman and Box 1983). The young leaves were extremely soft and had approximately half the tannic acid content of adult leaves (5·5 mg per 100 mg dry weight). This level, though comparatively high, was nonetheless not effective in preventing attack by *N. nothofagi*. Nitrogen levels may also vary between ages of leaf tissue (White 1978), although these analyses are still under way.

Beech canopies also exhibit temporal defence mechanisms, by providing an unapparent food supply for larvae (Feeny 1976). The young beech leaves, with their synchronous and rapid spring leaf flush, represent a very ephemeral food supply, albeit plentiful when available. Such an abundance of food for only a short duration may create predator satiation, so that some of the new leaves 'escape' to maturity.

Some sections of beech canopy appeared to escape attack because of the sedentary nature of the larvae. In the beech canopy, the larvae eat steadily down along the beech branches but sometimes never reach the basal leaves, which thus survived to maturity. On a small scale, occasional branches are often left totally unattacked, and individual trees and sites within the cool temperate tableland receive variable amounts of damage (see Table 4).

On a large scale, the patchy distribution of Australian rainforest trees, due to both environmental (edaphic, climatic) factors and human interference (logging, farming) means that pockets of rainforest are geographically isolated, and some may escape attack by insects. Large discontinuities in distribution have not proved effective in isolating beech trees from *N. nothofagi*, however, since the beetles were found at Barrington Tops and Lamington National Parks, which respectively represent the southern and northern extent of *N. moorei*.

Local variability in plant–herbivore relationships has been noted in terms of host specificity (Fox and Morrow 1981), but not in terms of the variability in overall rates of herbivory at different spatial scales: within canopies, between trees, or among sites. The beech–beetle relationship illustrates these types of local spatial variability in herbivory rates, and also variability with respect to factors such as leaf age, time, and canopy level. Despite the patchy distribution of young beech leaves both in space and in time, the larvae severely deplete the annual new leaf flush, their emergence closely synchronizing with the leaf flush and resulting in the removal of 32% of the leaf area.

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