

Influence of previous frost damage on tree growth and insect herbivory of *Eucalyptus globulus globulus*

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Abstract The plant stress hypothesis suggests that some herbivores favour stressed plants, whereas the plant vigour hypothesis proposes that other herbivores prefer vigorous plants. The effects of a prior stress, that of frost damage, were examined on the subsequent growth of *Eucalyptus globulus globulus* and on the response of insect herbivores. Frost damage affected tree growth by reducing new leaf area and increasing specific leaf area (SLA). However, herbivore abundance was not affected by prior frost damage. Two feeding trials using *Anoplognathus chloropyrus* and *Hyalarcta huebneri* and a morphometric study of *Ctenarytaina eucalypti* were conducted to assess the performance of herbivores on trees that had suffered more or less frost damage. Consumption by *A. chloropyrus* and *H. huebneri* was unaffected by foliage origin (damaged versus healthy). *Hyalarcta huebneri* grew faster when fed leaves from previously damaged trees, and *C. eucalypti* from previously damaged trees were larger than those from healthy trees. Enhanced insect performance on frost damaged plants may have resulted from the high specific leaf area (most likely thinner) leaves. The herbivore abundance data did not support the hypothesis that previously frost damaged plants are preferred by insects. However, increased growth of *H. huebneri* and larger body size of *C. eucalypti* on damaged trees indicates that previously stressed trees may produce leaves of higher nutritional value.

Key words: *Anoplognathus chloropyrus*, *Ctenarytaina eucalypti*, frost, *Hyalarcta huebneri*, insect–plant interactions, plant stress hypothesis, plant vigour hypothesis.

INTRODUCTION

The causes and consequences of plant stress are many and varied. Plant stress can be regarded as any unfavourable condition or substance that affects plant metabolism, growth or development (Lichtenthaler 1996). Plant stress and interactions with herbivores are not only ecologically interesting, but could also be economically important, especially if insect outbreaks reduce plant growth and/or cause seedling mortality. The present study examined the effects of a particular plant stress, that of frost damage, on the subsequent herbivory of *Eucalyptus globulus globulus*.

There are two main hypotheses as to how plant condition may affect herbivory. The plant stress hypothesis (White 1969, 1984) suggests that herbivores favour stressed plants, possibly because of increased tissue nitrogen availability. The plant vigour hypothesis (Price 1991) suggests that insects may favour vigorous plants by virtue of their rapidly growing and/or larger modules. These two hypotheses have often been discussed, and support has been found for both (see

reviews in Larsson 1989; Price 1991; Landsberg & Cork 1997; Koricheva *et al.* 1998).

The effects of plant stress on insect herbivory of *Eucalyptus* were first examined by White (1969) in a study of the effect of drought stress on psyllid outbreaks. White suggested that water stress was correlated with psyllid outbreaks on *Eucalyptus* species and hypothesized that stress increases the amount of nitrogenous compounds available to psyllids, thereby increasing their survival and reproduction (see Taylor 1997). Subsequent research has demonstrated that water stress can increase the total nitrogen and amino acid content of the leaves (e.g. *Eucalyptus camaldulensis*; Miles *et al.* 1982). However, moisture stress in *E. camaldulensis* has no effect on the rate of development of *Paropsis atomaria* larvae (Miles *et al.* 1982) or on the consumption of other herbivorous insects (Stone & Bacon 1995; but see Stone & Bacon 1994). Although other studies have shown that nitrogen is important in determining levels of insect herbivory on *Eucalyptus*, they have not examined the connection between plant stress and nitrogen per se (e.g. Fox & Macauley 1977; Ohmart *et al.* 1985). Notably, although there may be no difference in consumption of foliage by insects between stressed and healthy plants, the impact of herbivory may be

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greater on stressed plants, because of their reduced growth (Stone & Bacon 1995).

The present study examined a plant stress arising from frost-induced leaf loss. Frost damage to *Eucalyptus pauciflora* can result in photoinhibition, a delay in bud break, damage to young shoots and leaves and lower rates of stem growth (Ball *et al.* 1997). The impact is especially great if the frost is severe, if it occurs out of season, or if young plants are affected (King & Ball 1998). Even minor frosts can induce photoinhibition in eucalypts, and severe frost may cause tissue death and leaf senescence. Frost may be an important factor in determining the distribution of *Eucalyptus* species, especially in subalpine regions. Davidson and Reid (1985) found that rare, severe frosts caused changes in the dominance of five *Eucalyptus* species, according to their level of frost resistance. Likewise, Ball *et al.* (1991) found that the distribution of *E. pauciflora* seedlings was correlated with the occurrence and severity of cold-induced photoinhibition. Frost resistance can vary within a *Eucalyptus* species; for example, in a comparison of three genotypes of *Eucalyptus gunnii*, one had a higher intrinsic frost resistance than the other two genotypes (Leborgne *et al.* 1995). *Eucalyptus globulus globulus* is sensitive to frost and suffers severe damage at temperatures of approximately -6°C (Volker *et al.* 1994). Consequently, *E. g. globulus* is recommended as a plantation species only in frost free, low altitude sites (Beadle *et al.* 1996).

The young *E. g. globulus* trees used in the present study were severely damaged by an early winter frost. The stress due to the frost damage resulted in the mortality of many of the young trees and substantial leaf loss in the remaining trees. The frost damage resulted in variation in growth in the following summer, which provided an ideal opportunity to examine the effects of a previous stress on tree growth and subsequent insect herbivory. We predicted that insect herbivores would show a preference for and/or be more abundant on, trees that had suffered more severe previous frost damage.

METHODS

Study site

The study site was located in pastoral land north of Canberra, ACT ($149^{\circ}02'49.9''\text{E}$, $35^{\circ}09'55.7''\text{S}$, altitude 615 m a.s.l.). Canberra has a mean annual rainfall of 600 mm and average daily maximum and minimum temperatures for winter of 11 and 1°C , respectively. The trees used were part of a larger study concerning resource abundance and herbivore response. The present study focused on 5 of the 20 existing plots at the site; each plot contained 25

E. g. globulus trees, with five trees from each of five different provenances. Seeds were obtained from the Australian Tree Seed Centre (Yarralumla, ACT) and the trees were planted in October 1998 as 6-month-old saplings with an inter-row spacing of 2.5 m. All trees were damaged to varying extents by a severe frost in late April 1999 (overnight minimum -4.9°C).

Study organisms

Tasmanian blue gum

The Tasmanian blue gum, *Eucalyptus* (subgenus *Symphyomyrtus*) *globulus* subspecies *globulus*, is endemic to south-eastern Australia with a taxonomically homogeneous core zone in eastern Tasmania (Dutkowski & Potts 1999). In combination with *Eucalyptus nitens* (which is predominantly planted in Tasmania; Tibbits 1986), *E. g. globulus* is the most widespread plantation pulpwood species throughout temperate Australia (more than 70 000 ha by 1996; Tibbits 1997). Plantations of *E. g. globulus* are usually established in areas with mild climates that are free of severe frosts (not below -6°C) and droughts (Eldridge *et al.* 1993).

Christmas beetles

The Christmas beetles, genus *Anoplognathus*, are endemic to Australia and Papua New Guinea and comprise approximately 39 species (Carne 1957, 1981). Adults of approximately 12 species have been recorded feeding on *Eucalyptus* (Carne 1957; Carne *et al.* 1974); however, the degree of host specificity warrants further examination (see Steinbauer & Wanjura 2001). Carne (1957) reported that immature leaves were completely consumed, whereas the tougher portions of mature leaves (i.e. the midrib) were left. Edwards *et al.* (1993) reported that differential resistance of some species of *Eucalyptus* to herbivory by Christmas beetles was correlated with the percentage of several individual terpene components, including 1,8-cineole. Christmas beetles can be considered generalist defoliators that choose between different trees based on their terpene compositions, whereas the amount of selected hosts consumed is determined by leaf toughness and secondary chemistry.

Case moth larvae

Case moths, the genus *Hyalarcta*, comprise two Australian species (Nielsen *et al.* 1996). *Hyalarcta huebneri* has been recorded from a number of eucalypt as well as non-eucalypt species (Heather 1975, 1976). Neonate psychid larvae reach their hosts via silken threads attached to the female's cocoon (Froggatt 1927). The ability to feed upon the first host reached

after dispersing from the natal tree suggests that leaf secondary chemistry may be comparatively unimportant to host specificity.

Blue gum psyllids

Genus *Ctenarytaina*, the blue gum psyllids, consist of approximately 25 species of non-lerp-forming psyllids (Taylor & Carver 1991). *Ctenarytaina eucalypti* is commonly recorded from *E. g. globulus* and *E. nitens* (Elliott *et al.* 1998); however, this insect may also be able to feed on other glaucous eucalypts within the *Symphyomyrtus* (Elliott & de Little 1985). Female *C. thysanura* differentiate between cultivars of *Boronia megastigma* on the basis of the 'hardness' of the terminal shoots (Mensah & Madden 1991); cultivars with tough and open shoots receive fewer eggs. These findings suggest that *C. eucalypti* should be most abundant in the terminal buds of eucalypts with the softest leaves and/or the most closed leaf arrangement.

Effect of prior frost damage on plant growth and herbivore abundance

To quantify the extent of frost damage to the plants, we conducted a survey of each living *E. g. globulus* tree in the five plots during 2 weeks in late November 1999. As the study was conducted several months after the frost damage had occurred, it was impossible to directly measure either the health of the trees before the frost, or the severity of the frost damage suffered by each tree. Instead, surrogate measures were used as indicators of pre-frost tree health and severity of prior frost damage. Basal stem diameter, a trait unaffected by frost damage, was used to indicate the health of each tree before the frost. We used the number of old (pre-frost) leaves remaining on each tree as an inverse indication of the severity of the frost damage suffered. Our assumption was that frost damage caused some leaf senescence and loss, the amount of which depended on the severity of damage. We also assumed that larger trees would have had both larger basal diameters and more leaves before the frost, thus the number of leaves that a tree retained after the frost (taking into account the basal diameter) reflected how much damage it suffered.

The aspects of tree growth measured to determine the recovery of the trees after the frost were the total number of new leaves produced, their average area and average specific leaf area (SLA). Specific leaf area is a measure of leaf thickness and/or density (Cunningham *et al.* 1999). Calculations were carried using three arbitrarily selected fully expanded new leaves from each tree.

To quantify herbivore abundance following frost damage, we counted the number of all herbivorous

insects on each tree. Large insects such as leafhoppers (Hemiptera), some larvae (Coleoptera and Lepidoptera) and beetles (Coleoptera) were counted individually. Small insects or life cycle stages that occurred in aggregations such as psyllids (Hemiptera), eggs (various families) and other larvae (Coleoptera and Lepidoptera) were recorded as the number of groups per tree. Herbivores were identified to at least order level and categorized according to feeding guild.

The effects of the frost on subsequent tree growth were assessed using general linear models. We examined the effects of both pre-frost tree health (as measured by stem diameter) and frost damage (as measured by the inverse number of old leaves remaining) on all measures of tree growth in the following season (number, area and SLA of new leaves). The effects of frost damage on herbivore abundance were assessed using a linear model that included all five plant variables. Two discrete variables, provenance and plot, were included in the analyses as random factors when statistically significant. Differences among provenances were also examined directly by using general linear models.

We used partial regression plots to illustrate relationships between two variables, each adjusted for the effects of all the other variables in the regression model. For example, the variable 'number of old leaves' was adjusted for stem diameter (pre-frost health), and plotted against the residuals of the dependent variable. This allowed us to assess the effect of each dependent variable on the independent variable while holding other variables constant. The relationships between all variables were summarized in a path diagram (see Discussion; for details on path analysis, see Mitchell 1993).

Chlorophyll fluorescence measurements were taken for each tree in February 2000 by using a Hansatech PEA Meter (King's Lynn, UK). The variable F_v/F_m was measured to determine if there was evidence of physiological stress in the new leaves (Ball *et al.* 1995). New leaves of 10 plants (collected in February 2000) were measured for total percentage nitrogen by Kjeldahl Nitrogen Analysis by using a Gerhardt Vapodest-5 apparatus for distillation and titration (Bonn, Germany). For the nitrogen analyses, we selected a subsample of trees, including the four trees used in the feeding trials.

Feeding trials and morphometric study

Four trees from the study site were selected for use in feeding trials to assess foliage quality for herbivores. The trees selected were from two provenances (Jeeralang North and Badgers Creek) and from two levels of prior frost damage (high and low).

Adult *A. chloropyrus* and larvae of *H. huebneri* were used in each feeding trial; 40 insects of each species were used. From each tree ($n = 4$), 20 fresh, weighed leaves were placed in 20 separate plastic vials with a moist plaster of Paris base (one leaf per vial). Ten of each of these vials received one insect each for the feeding trial and 10 vials remained without insects as controls. The insects were weighed, sexed, and randomly allocated to a vial. All vials were left at room temperature for either approximately 12 h (*A. chloropyrus*) or 48 h (*H. huebneri*) to allow the insects to feed. Insects were then removed from the vials, weighed and any mortality noted. Control leaves, remnant portions of trial leaves and insect frass were all dried at 40°C for 2 days and weighed (to the nearest 0.1 mg). Consumption and assimilation rates, frass production and approximate digestibility were calculated for both insect species (after Waldbauer 1968). Relative growth rate could be calculated only for *H. huebneri* larvae because adult *A. chloropyrus* are the ultimate developmental stage.

Ctenarytaina eucalypti were used to ascertain whether insect size varied according to host plant condition (Daly 1985; Padi & den Hollander 1996). Four growing tips infested with *C. eucalypti* were collected from each of the four trees used in the feeding trials. Ten adult female *C. eucalypti* and 10 late instar nymphs were selected from each tip and examined under a dissecting microscope. Measurements of body length (from head to base of ovipositor) and abdomen width (at widest point) were taken using an eye-piece graticule. Data from the feeding trials and the

morphometric study were assessed using ANOVA and Scheffé's post hoc tests.

RESULTS

Effect of frost on tree growth

The frost resulted in the mortality of 33.6% of the *E. g. globulus* at the site, although the five provenances were not uniform in their response (Table 1). An analysis of covariance demonstrated significant provenance effects on new growth that were independent of pre-frost tree health (F-ratio = 2.64, $P = 0.04$). Scheffé's post hoc tests indicated that trees from Jeeralang North grew significantly more after the frost than trees from Badgers Creek.

The number of new leaves produced in the season following the frost was influenced by basal stem diameter (a surrogate for pre-frost health), as well as provenance (Table 2, Fig. 1a). Bigger trees with larger basal stem diameters produced more new leaves postfrost than trees with smaller basal diameters. There was no significant correlation between the number of new leaves and the number of old leaves, that is, our indicator of frost damage (Table 2, Fig. 1b).

In contrast, both the area and SLA of the new leaves varied according to the number of old leaves remaining on a tree (Table 2, Fig. 1c-f). Trees that retained more of their old leaves (and were thus presumed less damaged) produced larger new leaves than did more

Table 1. Mortality of provenances of *Eucalyptus globulus globulus*

Seedlot	Provenance	No. trees alive in November 1999	Percentage mortality
16319	Jeeralang North, Vic.	20	20
16410	Badgers Creek, Tas.	14	44
16476	Geeveston, Tas.	15	40
17608	King Island, Tas.	19	24
18725	Otways National Park, Vic.	15	40
Totals		83	33.6

Table 2. Results of ANCOVA for the effects of stem diameter and number of old leaves on three postfrost growth variables (the number, size and SLA of new leaves)

	No. new leaves produced			Average area of new leaves			SLA of new leaves		
	d.f.	MS	P	d.f.	MS	P	d.f.	MS	P
No. old leaves (log)	1	514 873	0.140	1	1.113	0.030*	1	862.117	0.037*
Stem diameter	1	1 855 171	0.006*	1	0.367	0.207	1	10.0187	0.819
Provenance	4	1 296 997	0.001*	–	–	–	4	1215.850	0.0002*
Plot	–	–	–	4	0.634	0.033*	4	747.245	0.007*
Error	63	230 557		63	0.226		59	188.660	

*Significant result.

frost damaged trees (Fig. 1d). Trees that retained more old leaves also produced new leaves with a lower SLA (i.e. thicker leaves) than did trees with fewer old leaves (Fig. 1f).

The chlorophyll fluorescence data showed that the new leaves of all trees had a high photosynthetic efficiency. There was no correlation between F_v/F_m and frost damage (the number of old leaves; results not shown).

Effect of frost on herbivore abundance

There were insect herbivores on all the trees surveyed (mean \pm SE of 40.3 ± 4.1 herbivores per tree). The

most common insects (those found on more than 50% of the trees) were *C. eucalypti*, *Eurymela* spp. (leafhoppers), *Strepsicrates macropetana* larvae (leaf-tier) and *Gonipterus scutellatus* larvae (*Eucalyptus* snout beetle or weevil).

After allowing for the effects of subsequent tree growth (measured as total new leaf area), there were no effects of provenance on herbivore abundance (F-ratio = 1.33, $P = 0.27$). The number of herbivores on a tree was significantly correlated with stem diameter (our indicator of prefrost health; Table 3). Trees with larger stem diameters had fewer herbivores, as indicated by the partial regression plot (Fig. 2a). The amount of frost damage suffered by a tree, however, had no direct effect on herbivore abundance (Fig. 2b). Of all the

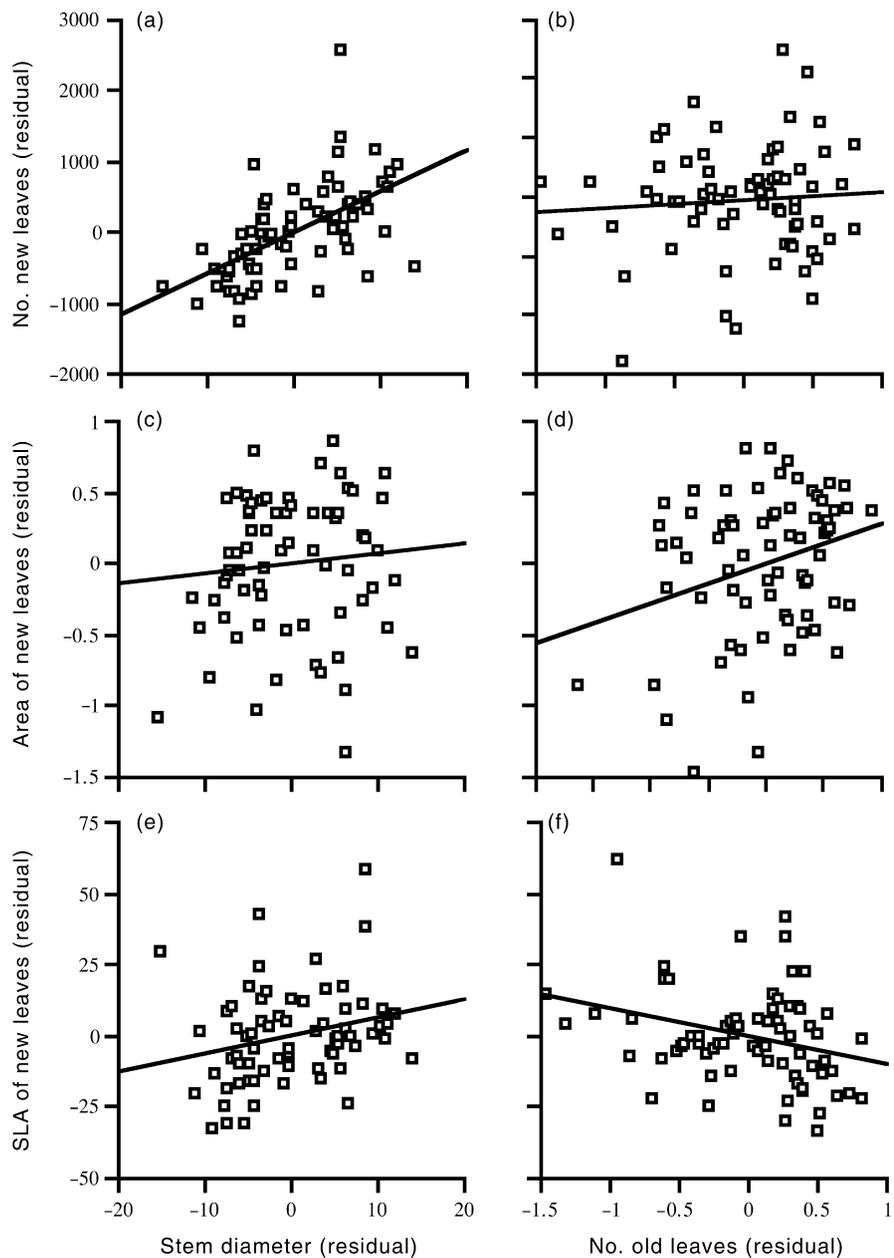


Fig. 1. Partial regression plots illustrating correlations between: the number of new leaves and (a) basal stem diameter and (b) the number of old leaves; area of new leaves and (c) basal stem diameter and (d) the number of old leaves; specific leaf area (SLA) and (e) basal stem diameter and (f) the number of old leaves. The plots illustrate the relationship between each independent variable and the dependent variable, holding other factors in the model constant.

variables measured, the number of new leaves explained the largest amount of variance in herbivore abundance. Trees that produced many new leaves were inhabited by more herbivores than those with fewer new leaves (Fig. 2c). The other two postfrost growth variables, namely the area and SLA of the new leaves, had no significant influence on herbivore abundance (Table 3, Fig. 2d-e).

Table 3. Results of ANCOVA for the effects of stem diameter, number of old leaves and the three postfrost growth variables on herbivore abundance

	Total herbivores per plant (log)		
	d.f.	MS	P
No. old leaves (log)	1	0.071	0.391
Stem diameter	1	0.423	0.038*
No. new leaves	1	3.846	<0.0001*
New leaf size	1	0.121	0.261
New leaf SLA	1	0.044	0.500
Error	64	0.094	

SLA, specific leaf area. *Significant result.

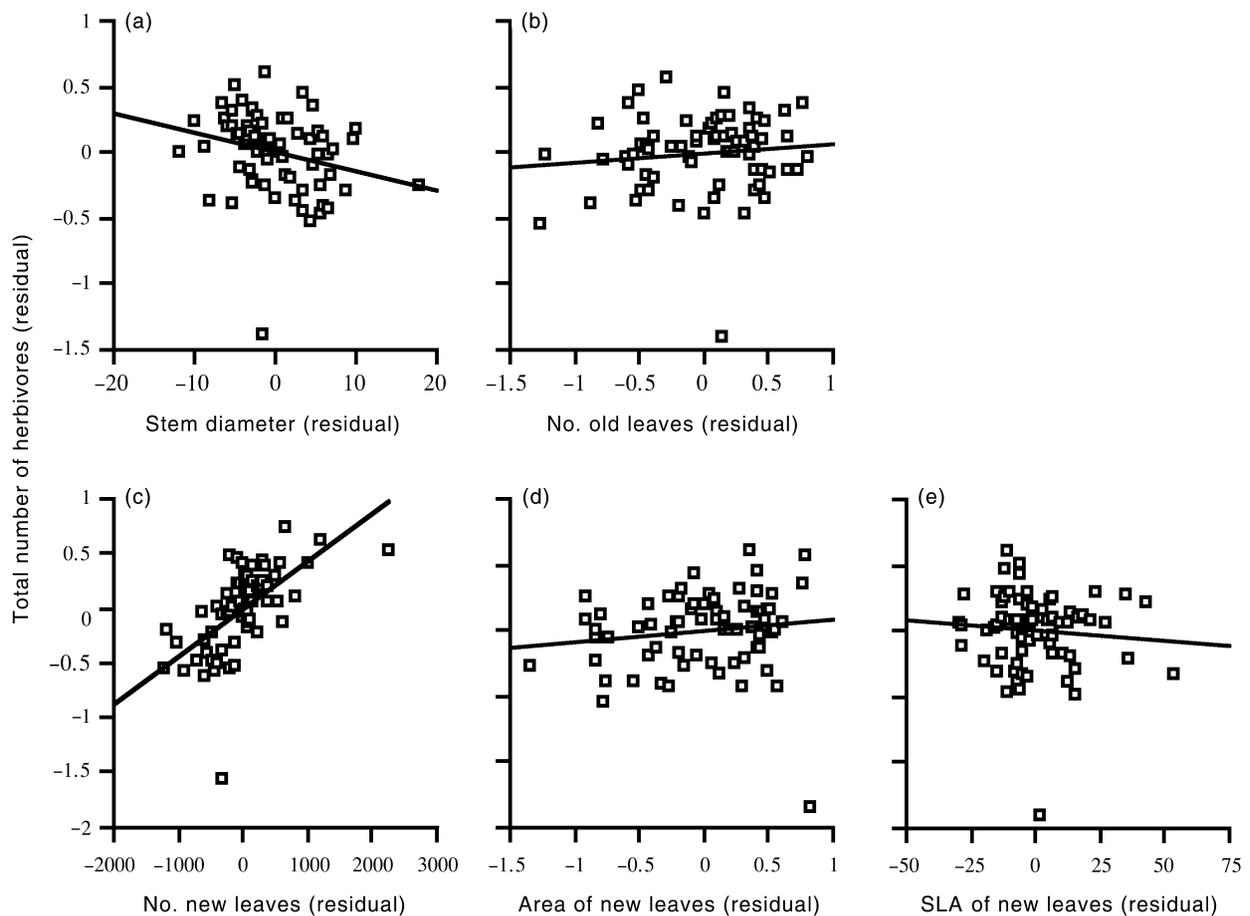


Fig. 2. Partial regression plots illustrating correlations between the total number of herbivores and (a) basal stem diameter; (b) the number of old leaves; (c) the number of new leaves; (d) the average area of the new leaves; (e) the specific leaf area (SLA) of the new leaves.

Feeding trials and morphometric study

No consistent differences in consumption were found for insects feeding on leaves produced by trees that had suffered more or less frost damage; however, *C. eucalypti* and larvae of *H. huebneri* tended to perform better on leaves produced by trees that had been more damaged.

Consumption rates by *A. chloropyrus* did not differ when given leaves from either severely or moderately damaged trees (Fig. 3). Consumption differed between the two provenances of *E. g. globulus*; beetles consumed more leaf matter from the Jeeralang North provenance trees. There were also no significant differences in consumption by larvae of *H. huebneri* between leaves according to level of prior frost damage (Fig. 4a). However, larvae that fed on leaves from more frost damaged trees grew faster (Fig. 4b). Larvae of *H. huebneri* consumed more and grew faster on the Jeeralang North provenance. This absence of differences in consumption (in both *A. chloropyrus* and *H. huebneri*) when given leaves of differing degrees of prior damage may suggest

that frost does not affect subsequent defoliation by these insects.

The morphometric data for *C. eucalypti* suggest that psyllid adults and nymphs, which were collected from trees that had suffered high levels of previous frost damage, had longer body lengths than those from trees that suffered less damage (Fig. 5a,b). Provenance differences were also significant: *C. eucalypti* from the Badgers Creek provenance were longer than those from the Jeeralang North provenance. There were no differences in abdominal widths for psyllids from trees with differing frost histories or provenances (results not shown).

The Kjeldahl analysis also showed no correlations between percentage leaf nitrogen and either provenance or the number of old leaves (results not shown). However, the growth differences of *H. huebneri* larvae, combined with the larger size of *C. eucalypti*, seem to suggest that these insects perform better when fed on new leaves produced by previously frost-stressed plants.

DISCUSSION

A prior stress, caused by a severe frost, affected the production of new growth by *E. g. globulus*, but not the abundance of herbivores. Trees more severely damaged by the previous frost produced smaller and

thinner new leaves than healthier trees; however, the total number of new leaves that a tree produced was not influenced by prior frost damage. The abundance of insect herbivores on a tree was affected mainly by the number of new leaves and thus was not detectably influenced by previous frost damage. These relationships are summarized in a path diagram that illustrates

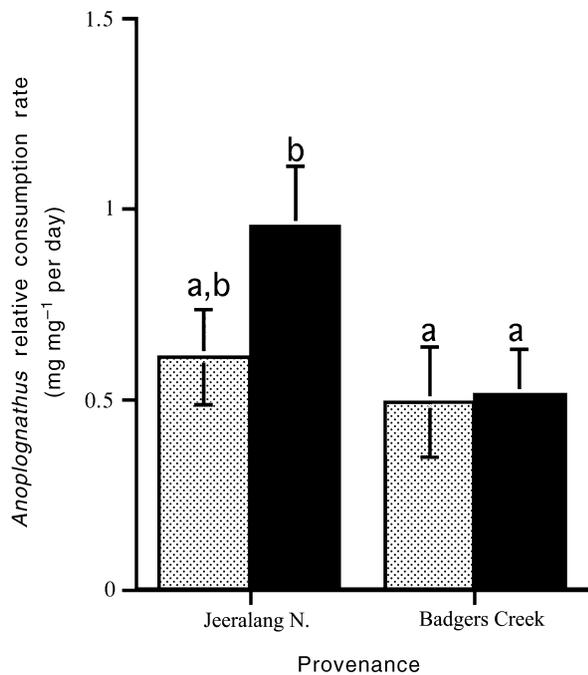


Fig. 3. Consumption by *Anoplognathus chloropyrus* (mean ± SE) of leaves of each provenance and frost damage level. (▨), High damage; (■), low damage. Different letters indicate significant differences according to Scheffé's post hoc tests. Frost damage $P = 0.20$; provenance $P = 0.05$; interaction $P = 0.25$.

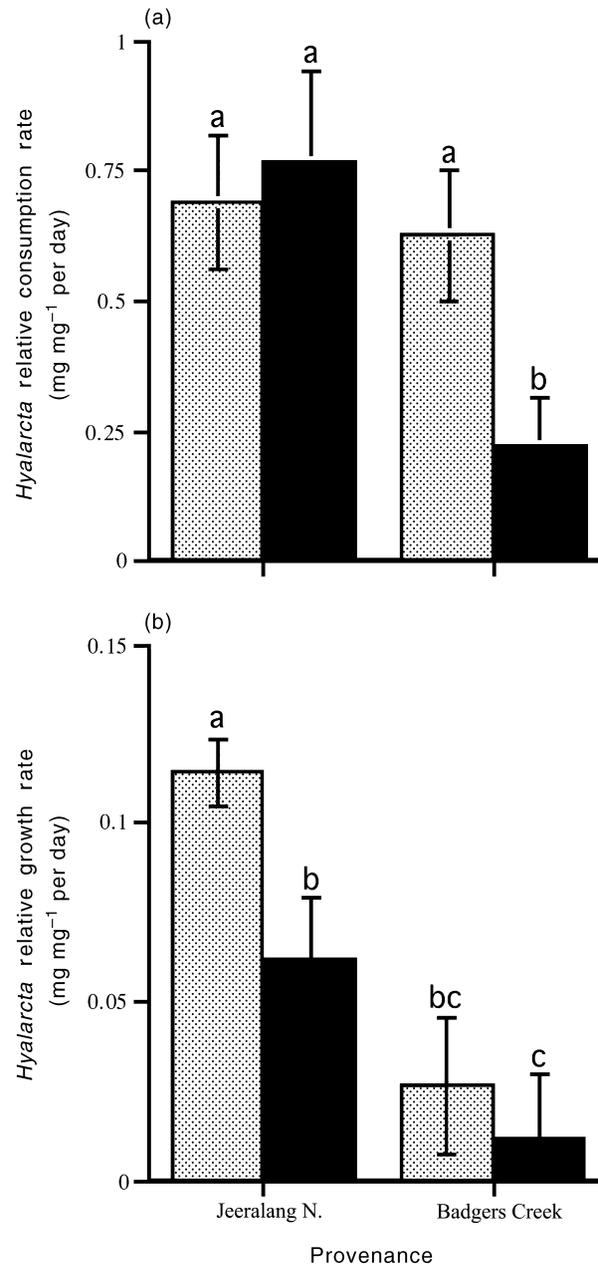


Fig. 4. Performance of *Hyalarcta huebneri*. (a) Consumption rate (mean ± SE) and (b) growth rate when fed leaves of each provenance and frost damage level. (▨), High damage; (■), low damage. Different letters above the bars indicate significant differences according to Scheffé's post hoc tests. (a) Frost damage $P = 0.17$; provenance $P = 0.02$; interaction $P = 0.06$; (b) frost damage $P = 0.05$; provenance $P = 0.0005$; interaction $P = 0.31$.

the relative effects of the variables we considered (Fig. 6).

The diagram distinguishes between the pre-frost vigour of the plants (basal stem diameter) and the severity of the frost damage to those plants (inverse number of old leaves), and indicates their relative influ-

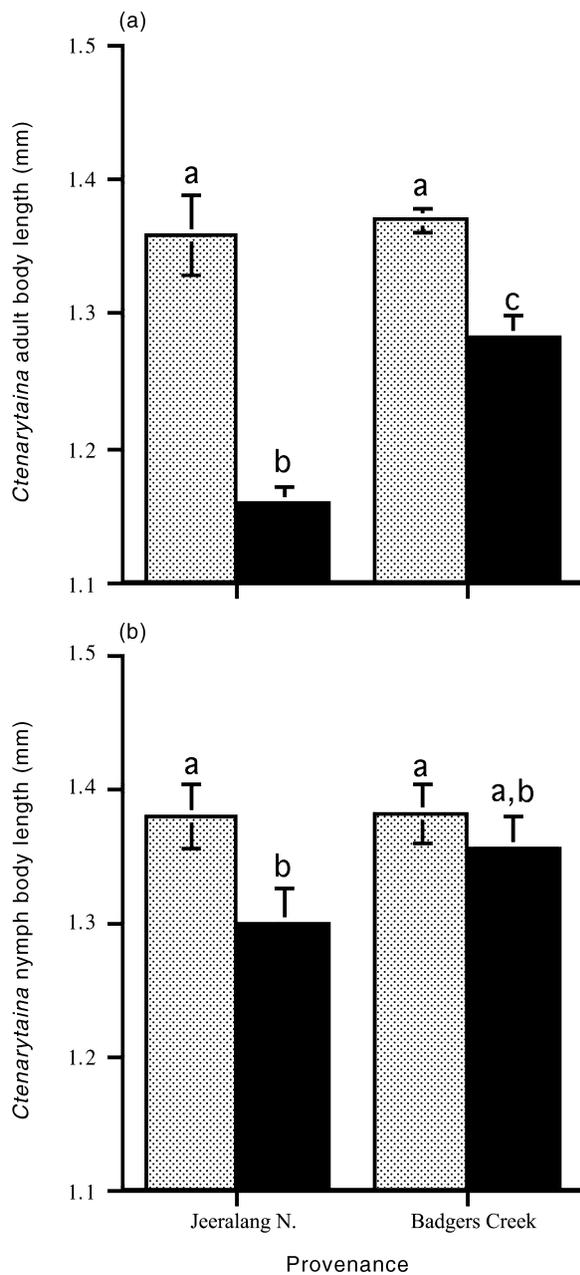


Fig. 5. Size of *Ctenarytaina eucalypti*. (a) Adult and (b) nymphal body lengths (mean \pm SE) for each provenance and frost damage level. (▨), High damage; (■), low damage. Different letters above the bars indicate significant differences according to Scheffé's post hoc tests. (a) frost damage $P < 0.0001$; provenance $P = 0.0007$; interaction $P = 0.005$; (b) frost damage $P = 0.0007$; provenance $P < 0.0001$; interaction $P < 0.0001$.

ences on three aspects of new plant growth (number, area and SLA of the new leaves). The diagram shows that two of the measured factors significantly influenced herbivore abundance: the basal stem diameter and the number of new leaves. Prefrost plant growth can affect herbivore abundance either directly (negative influence) or indirectly via the influence of basal diameter on the number of new leaves (strong positive influence). The negative direct path may indicate that, for a given number of new leaves, bigger plants are less susceptible to herbivores. Notably, frost damage did not influence herbivore abundance either directly or indirectly via other paths.

We have shown that the stress associated with frost damage does affect the growth response of the trees. We predicted a corresponding response in herbivore abundance but did not detect such a pattern. Studies that have examined the effects of plant stress on entire communities of herbivores have found that while plant stress is often important, the responses vary between different herbivore species and feeding guilds (Waring & Price 1990; Koricheva *et al.* 1998; Schowalter *et al.* 1999). Unfortunately, the guild sample sizes in the present study were too small to analyse with any statistical power. Hence, we are not able to comment on the responses of particular feeding guilds to previous tree damage.

The feeding assays show no differences in herbivore consumption of new leaves produced by trees that had sustained more or less damage. However, the assays suggest that leaves of stressed trees may be nutritionally superior to leaves of healthy trees for these herbivores. *Hyalarcta huebneri* larvae fed on leaves from previously damaged trees grew more rapidly than larvae fed leaves from previously less damaged trees, although they did not consume more. Similarly, *C. eucalypti* feeding on previously damaged trees were longer than those on healthy trees. Both these findings might indicate that previously damaged trees provide tissues that are of higher nutritional value. Enhanced insect performance, when the insects are fed leaves from previously damaged trees versus those from healthy trees, may be attributable to differences in leaf thickness. High SLA leaves are likely to be thinner and perhaps easier to chew (for mandibulate insects such as *H. huebneri*) or pierce (for sucking insects such as *C. eucalypti*). Herbivores are known to perform better when feeding on thinner leaves, although this response can also be the result of other leaf traits such as leaf water and nitrogen content (Ayres 1987; Stamp & Bowers 1990; Matsuki & MacLean 1994). Nonetheless, differences in leaf thickness did not result in higher insect abundance in the field.

The feeding trials demonstrated that the consumption and performance of *A. chloropyrus* and *H. huebneri* differed according to the eucalypt provenance from which the leaves were obtained. It is possible that

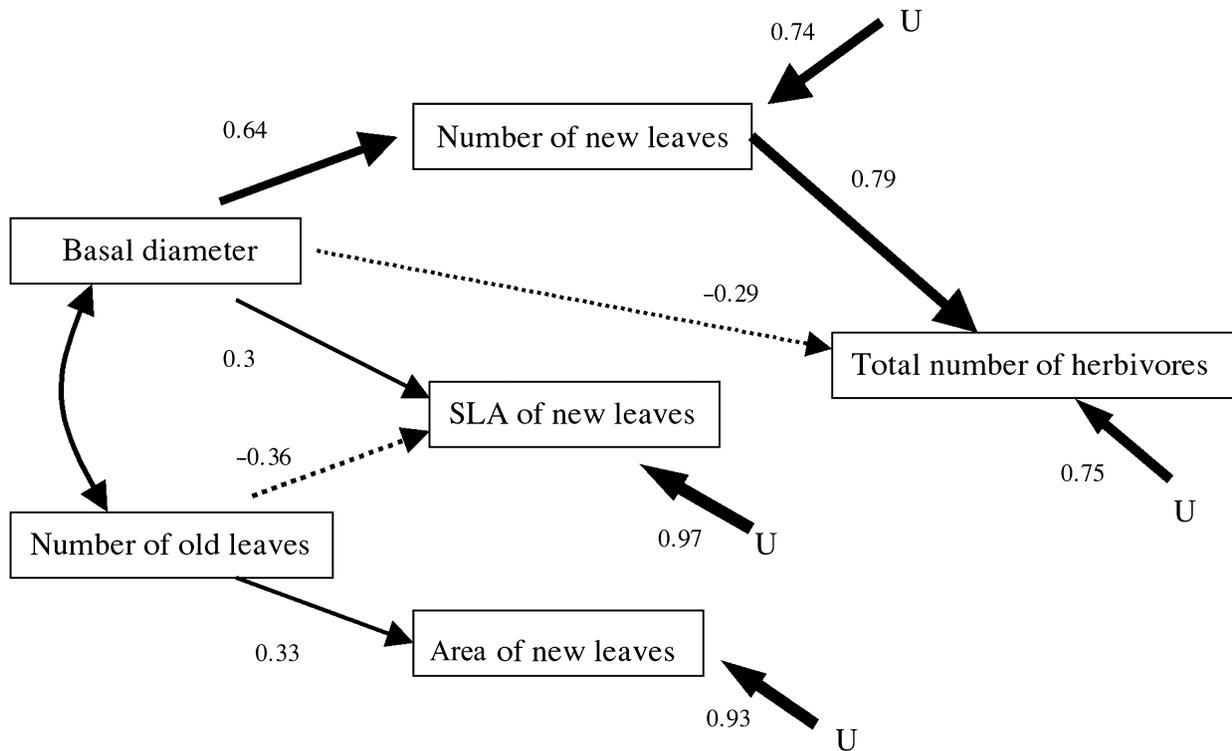


Fig. 6. Path diagram showing the relative strengths of the relationships between variables. Path coefficients are derived from the coefficients of the multiple regression analyses and the thickness of the arrows reflects the strengths of the paths. Dotted arrows indicate a negative relationship and the ‘U’ paths indicate the effects of unknown causes on the model. The following non-significant paths were not included in the diagram: number of old leaves to number of new leaves and number of herbivores; basal diameter to area of new leaves; specific leaf area (SLA) and area of new leaves to number of herbivores.

consumption by these species differed because of the variance in the terpenoid profiles of the leaves (Edwards *et al.* 1993) as these compounds are known to affect the feeding behaviour of Christmas beetles (M. Matsuki, pers. comm.).

Our prediction was that herbivore abundance would be positively influenced by the degree of frost damage suffered by the host plants. The data from the present study suggest otherwise, that herbivore abundance is most influenced by factors that are unaffected by plant stress. The trees we studied appear to be exhibiting some form of ‘postfrost damage syndrome’ characterized by the production of smaller, thinner new leaves (a response that shows some similarities to dieback, as described by Landsberg 1990a,b,c). As a result of producing such regrowth, these trees may be nutritionally superior for certain insects (e.g. *H. huebneri* and *C. eucalypti*), although they do not appear to attract more insects.

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