

# Leaf dynamics and insect herbivory in a *Eucalyptus camaldulensis* forest under moisture stress

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**Abstract** The influence of soil moisture content on leaf dynamics and insect herbivory was examined between September 1991 and March 1992 in a river red gum (*Eucalyptus camaldulensis*) forest in southern central New South Wales. Long-term observations of leaves were made in trees standing either within intermittently flooded waterways or at an average of 37.5 m from the edge of the waterways. The mean soil moisture content was significantly ( $P \leq 0.05$ ) greater in the waterways than in the non-flooded areas. Trees in the higher soil moisture regime produced significantly larger basal area increments and increased canopy leaf area. This increase in canopy leaf area was achieved, in part, through a significant increase in leaf longevity and mean leaf size. Although a greater number of leaves was initiated and abscised per shoot from the non-flooded trees, more leaves were collected from litter traps beneath the denser canopies of the flooded trees. Consumption of foliage by insects on the trees subjected to flooding compared to the non-flooded trees was not significantly different. However, the relative impact of insect herbivory was significantly greater on the non-flooded trees. Leaf chewing was the most common form of damage by insects, particularly Chrysomelidae and Curculionidae. No species was present in outbreak during this study. Leaf survival decreased as the per cent area eaten per leaf increased. In addition, irrespective of the level of herbivory, leaf abscission tended to be higher in *E. camaldulensis* under moisture deficit. The influence of soil moisture content on the balance between river red gum growth and insect herbivory is discussed.

**Key words:** *Eucalyptus camaldulensis*, flooding, insect herbivory, leaf dynamics, soil moisture.

## INTRODUCTION

The positive relationship between basal area increment and canopy leaf area has been demonstrated for several species of eucalypt (e.g. Attiwill 1962; Pook 1984b; Pereira *et al.* 1989). Canopy leaf area is a balance between the production, retention and loss of foliage (Pook 1984a). This balance is influenced by many factors including drought (Jacobs 1955; Pook 1984a, 1985, 1986) and insect damage through leaf consumption and the promotion of leaf abscission (e.g. Landsberg 1988; Lowman & Heatwole 1992; Abbott *et al.* 1993). Although a possible synergistic relationship between moisture deficit and insect herbivory on leaf abscission has been proposed, it has proven difficult to quantify (but see Cockfield & Potter 1986). Abbott *et al.* (1993) suggested that low rainfall and high levels of insect damage to leaves appeared to promote leaf abscission in *Eucalyptus marginata* Donn ex Sm. Similarly, Risley (1993) suggested that drought magnified the negative effect of herbivore damage on leaf

life span after examining the effect of artificial damage on the survival of leaves in dogwood (*Cornus florida* L.) and red maple (*Acer rubrum* L.). Also, any reduction in the rate of leaf production, growth and life span because of moisture stress (Kramer 1983) would result in an increase in the relative impact of herbivory, providing the consumption rate ( $\text{cm}^2$  per day) remained unaffected by drier conditions (Coley *et al.* 1985; Landsberg 1988).

The diversion of water from the Murray River for irrigation of agricultural crops (Bren 1988; Bacon *et al.* 1993a) has coincided with many trees in the Barmah-Millewa group of *Eucalyptus camaldulensis* Dehnh. (river red gum) forests exhibiting canopy symptoms typical of moisture stress in eucalypts (Ashton *et al.* 1975; Landsberg 1985; Pook 1985, 1986). Tree health and insect herbivory were investigated using long-term monitoring of leaves in the canopies of two sets of six mature *E. camaldulensis* that were subjected to either high or low soil moisture deficits.

The monthly census of leaf populations *in situ* over 7 months enabled us to assess the influence of soil moisture content on leaf dynamics and insect herbivory through

the assessment of leaf area gain, retention and loss in mature *E. camaldulensis*. In addition, we compared both the absolute and relative levels of insect herbivory on river red gums in the two groups. Finally, we sought to detect a synergistic relationship for leaf abscission between insect herbivory and moisture stress.

## METHODS

The experimental area was in Gulpa Island State Forest ( $35^{\circ}45'S$ ,  $145^{\circ}00'E$ , 5142 ha, 100 m a.s.l.) which forms part of a 70 000 ha managed river red gum forest on both sides of the Murray and Edward Rivers. The open sclerophyll forest is dominated by *E. camaldulensis* with a grassy understorey of *Vulpia/Bromus* spp. on the drier sites and semi-aquatic species such as *Eleocharis acuta* R.Br. and *Triglochin procera* R.Br. common in the flood prone areas (Bacon *et al.* 1993a). The forest is dissected by a series of shallow, ephemeral, natural waterways from which the flood waters spread. Three neighbouring plots, approximately  $100 \times 75$  m and carrying a mean stand basal area of  $17 \text{ m}^2 \text{ ha}^{-1}$  and a mean stocking of 187 stems  $\text{ha}^{-1}$ , were selected so that the lower edge of each plot was within one of the natural waterways. Intermittent inundation of these plots over a 2 year period was regulated by a series of small dams (Bacon *et al.* 1993a, b). Within each plot were two subplots ( $15 \times 75$  m), running approximately parallel to the channel. During flooding the first subplot was inundated while the second subplot was situated a mean distance of 37.5 m above the edge of the floodwater.

Daily rainfall data were obtained from Mathoura, 8 km south of the study site, while daily maximum and minimum temperatures were obtained from Deniliquin, 20 km north. Soil moisture content was monitored using neutron probes. Access tubes to 6 m depth were installed in the centre of each subplot (Bacon *et al.* 1993b). Soil samples were collected to calibrate neutron counts with soil water content. Neutron counts were measured over 15 s intervals with a CPN Hydroprobe Model 503DR (Martinez, CA 94553, USA). A measurement of soil moisture in the intermittently flooded subplots and non-flooded subplots was determined by averaging the soil water content ( $\text{g g}^{-1}$ ) from readings obtained at nine uniformly spaced depths (0.0–3.0 m) in each access tube. Readings were taken at nine intervals between September 1991 and March 1992.

### Foliage measurements

Two mature *E. camaldulensis*, of similar size and condition, within the flooded subplots of each plot and two similar trees in each of the three non-flooded subplots were selected in October 1990 (mean height = 22.2 m  $\pm$  0.9 (mean  $\pm$  1 SE); mean diameter at breast height (1.3 m) over bark (DBHOB) = 28.4 cm  $\pm$  3.7; total  $n = 12$ ). None of the selected crowns touched crowns of

neighbouring trees. Two leafy shoots, located at approximately mid-crown height, were selected from both the northern and southern aspects of each tree. Canopies were sampled using a hydraulic lift mounted on a trailer. Leaves were numbered sequentially from the shoot base upwards using a fine-point permanent water-proof marking pen. New leaves were marked each month. Actual leaf area was assessed by tracing the outline of each leaf, plus any non-photosynthesizing tissue present, onto translucent drafting paper. The non-photosynthesizing tissue included damage caused by sap-sucking, leaf mining and galling insects, fungal spots and natural senescence of old leaves. Potential leaf area was obtained from its estimated entire shape. Both actual and potential areas were measured with a digital planimeter (Planix 7, Tamaya). Areas were measured monthly from September 1991 to March 1992. Leaf area missing was expressed as the difference between the total potential leaf area and total actual leaf area as a proportion of the total potential area of all leaves in a sample (Landsberg 1989; Williams & Abbott 1991). Leaf abscission was calculated by using actual areas of leaves at the time previous to when they were recorded missing. Tree diameter (DBHOB) was recorded on 20 October 1990 and 18 July 1992.

To obtain additional information on leaf fall and leaf consumption by insects, three litter-collecting traps per treatment were placed under trees of similar appearance and adjacent to the monitored trees. The traps consisted of galvanized sheet-metal funnels with an upper diameter of 85 cm and a fine mesh collection bag tied to the base (Edwards *et al.* 1993). They were suspended between steel pickets at a height of 1.0 m at a random position beneath the tree canopy. Litter was collected over 30 days each month from September 1991 to March 1992. The litter contents were sorted into leaves, twigs, bark, fruiting material and insect frass. The frass consisted of solid insect excreta, very small regularly shaped fragments of leaf tissue (assumed to have derived from insect chewing) and very small buds. The sorted litter was dried at 65°C for 48 h and then weighed.

### Data analysis

All analyses used STATISTICAL ANALYSIS SYSTEM, versions 6.04 and 6.07 (SAS Institute Inc. 1989 & 1992). Preliminary analyses on sample leaf area, number of leaves per shoot and sample leaf area missing calculated from the labelled leaves showed there were no significant differences ( $P > 0.05$ ) between shoots within canopies, between trees within subplots and between plots. Samples were therefore pooled for comparisons between trees in the flooded subplots and trees in the non-flooded subplots. Means were derived by summing the measured values over all shoots sampled (e.g. no. leaves/shoot) and dividing by the number of shoots. Foliage trait and litter fall means were compared using either Student's *t*-test or Mann-Whitney *U*-test, depending on variance heterogeneity.

geneity of the sample populations. Standard data transformations (Steel & Torrie 1960) were used to normalize sample variances. Leaf survival was analysed using the PHREG procedure in SAS version 6.07 (SAS Institute Inc. 1992). This procedure performs regression analysis of survival data based on the Cox proportional hazards model (Cox 1972). Curves illustrating the proportion of leaves with designated levels of insect herbivory from flooded and non-flooded trees were compared using the Proc GLM procedure in SAS version 6.04.

## RESULTS

Rainfall during the 7 months was 96.4 mm, of which 58.8 mm fell in September. The average monthly maximum temperature during the period was 26°C and average minimum temperature 11.5°C. Inundation of the three natural waterways resulted in a significantly higher ( $t = 3.22$ ,  $df = 373$ ,  $P < 0.05$ ) mean monthly soil moisture content in the flooded subplots ( $0.099 \pm 0.006$   $g g^{-1}$ , mean  $\pm 1$  SE) compared to the non-flooded subplots ( $0.078 \pm 0.003$   $g g^{-1}$ ).

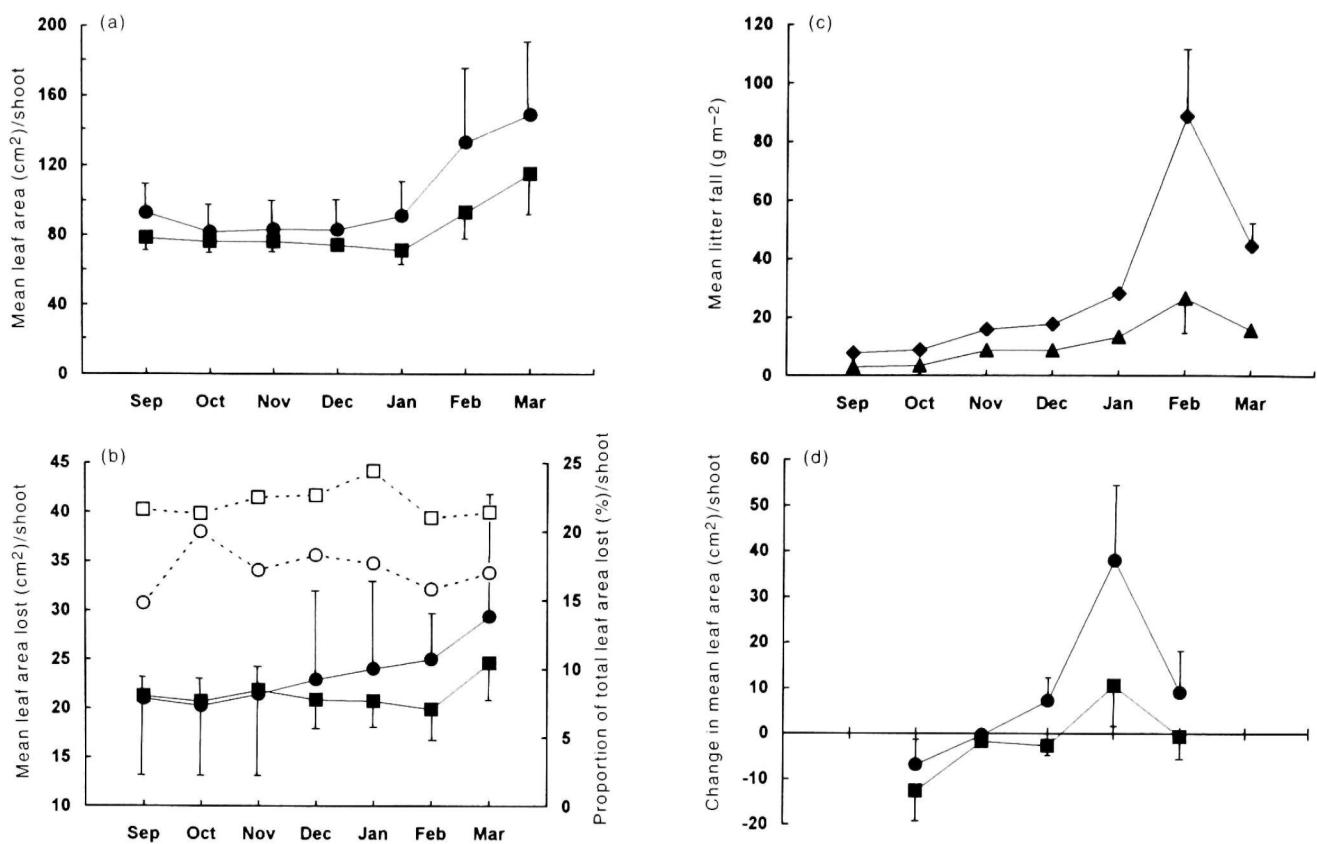
## Leaf production and growth

The initial mean number of leaves per shoot from the flooded subplots was  $9.6 \pm 0.83$  ( $n = 12$ ) and  $10.2 \pm 0.98$  ( $n = 12$ ) from the non-flooded subplots. Although the flooded trees had, on average, larger leaf areas and potential leaf areas per shoot per month than the non-flooded trees they were not significantly different ( $P > 0.05$ ) (Table 1, Fig. 1a). For both sets of trees, the largest monthly increase in leaf area per shoot occurred when the summer flush matured (Fig. 1a). Trees exposed to flooding carried significantly larger mean monthly leaves than trees in the non-flooded areas (Table 1, Mann-Whitney  $U$ -test,  $z = 3.09$ ,  $n_1 = 64$ ,  $n_2 = 71$ ,  $P = 0.002$ ). In addition, when only large ( $>5 m^2$ ) leaves were considered, the leaves from the flooded trees were significantly larger (Table 1, Mann-Whitney  $U$ -test,  $z = 2.45$ ,  $n_1 = 64$ ,  $n_2 = 71$ ,  $P = 0.014$ ). Differences in mean leaf size were due, in part, to a difference in the age composition of leaves. While the mean number of leaves per shoot per month was very similar between the two sets of trees (Table 1), the mean number of very young leaves (leaf area  $<1.0 m^2$ ) was significantly higher in the

**Table 1.** Tree traits of mature *E. camaldulensis* measured in Gulpa Island S.F. Trees were situated either within an intermittently flooded waterway or an average 37.5 m from the edge of the waterway

Tree trait	Watering treatment	
	Flooded trees	Non-flooded trees
Mean monthly leaf area ( $cm^2$ /shoot)		
Actual leaf area*	$101.0 \pm 12.4^a$	$82.5 \pm 4.8^a$
Potential leaf area*	$130.4 \pm 15.2^a$	$114.1 \pm 6.6^a$
Mean monthly leaf size ( $cm^2$ )/shoot		
All leaves*	$11.9 \pm 9.6^a$	$9.3 \pm 0.5^b$
Leaves $>5.0 cm^2$ *	$17.5 \pm 0.8^a$	$14.5 \pm 0.3^b$
Mean monthly no. of leaves/shoot		
All leaves and buds*	$8.5 \pm 1.3^a$	$8.9 \pm 0.9^a$
Leaves and buds $<1.0 cm^2$ *	$1.8 \pm 0.2^a$	$2.6 \pm 0.3^b$
Leaves $\geq 1.0 cm^2$ *	$6.7 \pm 0.9^a$	$6.2 \pm 0.6^a$
Mean monthly no. of leaves shed/shoot		
All leaves and buds*	$5.5 \pm 1.0^a$	$6.9 \pm 0.9^b$
Leaves and buds $<1.0 cm^2$ *	$3.8 \pm 0.7^a$	$4.7 \pm 0.6^b$
Leaves $\geq 1.0 cm^2$ *	$1.7 \pm 0.3^a$	$2.2 \pm 0.4^a$
Mean monthly leaf area lost ( $cm^2$ )/shoot		
Total leaf area*	$38.1 \pm 5.1^a$	$44.4 \pm 3.7^a$
From insect chewing*	$23.3 \pm 3.3^a$	$21.3 \pm 0.9^a$
From leaf abscission*	$14.8 \pm 2.3^a$	$23.0 \pm 1.3^b$
Mean monthly leaf area lost/shoot as % of potential leaf area		
Total leaf area*	$33.3 \pm 3.1^a$	$40.1 \pm 3.0^b$
From insect chewing†	$17.3 \pm 1.4^a$	$22.1 \pm 1.0^b$
From leaf abscission*	$11.4 \pm 0.2^a$	$20.1 \pm 1.7^b$
Mean monthly necrotic leaf area/shoot		
Actual area ( $cm^2$ )*	$0.6 \pm 0.09^a$	$2.9 \pm 0.5^b$
As % of total leaf area*	$1.3 \pm 0.3^a$	$5.0 \pm 1.5^b$
Diameter increment† (DOBBH, cm)	$1.8 \pm 0.7^a$	$0.23 \pm 0.20^b$

Means in each row (mean  $\pm 1$  SE) followed by different letters are significantly different ( $P \leq 0.05$ ). Means were compared with either \*Mann-Whitney  $U$ -test or †Student's  $t$ -test depending on the heterogeneity of variances. Sample size consisted of two leafy shoots/canopy from six trees/treatment monitored *in situ* at monthly intervals, from September 1991 to March 1992. Tree diameter increment from 20 October 1990 to 18 July 1992.



**Fig. 1.** Seasonal changes in canopy traits of *Eucalyptus camaldulensis* (mean  $\pm$  1 SE) measured in Gulpa Island State Forest. (a) Actual mean leaf area ( $\text{cm}^2$ )/shoot on intermittently flooded trees (●) and on non-flooded trees (■). (b) Mean leaf area lost ( $\text{cm}^2$ )/shoot from insect chewing on flooded trees (●) and on non-flooded trees (■) and proportion of total leaf area lost (%)/shoot on flooded trees (○) and on non-flooded trees (□). Foliage variables were derived from shoot sample means rather than individual leaves: two shoots/canopy, six trees/treatment. (c) Litterfall means were derived after pooling the data from both the flooded and non-flooding treatments ( $n = 6$ ). (◆) All litter collected; (Δ) leaf litter. (d) Monthly incremental change (September to March) in mean leaf area ( $\text{cm}^2$ )/shoot on flooded trees (●) and on non-flooded trees (■). Bars represent  $\pm 1$  SE.

trees in the non-flooded subplots (Table 1, Mann-Whitney  $U$ -test,  $z = 2.03$ ,  $n_1 = 64$ ,  $n_2 = 71$ ,  $P = 0.042$ ). Leaves from both sets of trees reached maximum size in similar periods. Leaves initiated in November attained a maximum size in approximately 2.5 months while leaves initiated in January attained a maximum size after 1.8 months (for flooded trees,  $1.81 \pm 0.07$ ,  $n = 42$ ; for non-flooded trees,  $1.90 \pm 0.06$ ,  $n = 32$ ), with approximately 70% of their growth completed during the first 30 days.

#### Leaf retention

Leaves remained longer on the trees exposed to flooding. One-third of the leaves labelled at the commencement of the study still remained after 7 months on the flooded trees while only a quarter of the original leaves were still present on the non-flooded trees. Regression analysis using the Cox proportional hazards model (Cox 1972) revealed that for leaves with a potential area greater than  $5.0 \text{ m}^2$ , non-flooded trees were significantly more likely to lose leaves than the flooded trees (likelihood ratio Chi-squared statistic = 8.55, df = 2,  $P = 0.014$ ). In this

analysis the covariant, total potential leaf area, was significant ( $P = 0.01$ ) and the resultant parameter estimate negative, indicating that leaf survival increased with increasing leaf size.

#### Leaf abscission and insect herbivory

On average, the trees monitored in the non-flooded areas shed significantly more leaves per shoot per month than the trees in the flooded areas (Table 1, Mann-Whitney  $U$ -test,  $z = -1.98$ ,  $n_1 = 70$ ,  $n_2 = 84$ ,  $P = 0.048$ ). While there was little difference in the number of mature leaves shed between the two sets of trees, a significantly higher number of very young leaves ( $\text{area} < 1.0 \text{ m}^2$ ) were shed prematurely from the non-flooded trees (Table 1, Mann-Whitney  $U$ -test,  $z = -1.99$ ,  $n_1 = 70$ ,  $n_2 = 84$ ,  $P = 0.046$ ). The total mean monthly actual area ( $\text{cm}^2$ ) lost per shoot through leaf abscission and insect herbivory was not significantly different between the two treatments (Table 1). However, when expressed as a percentage of total potential leaf area, trees in the non-flooded areas lost significantly more leaf tissue per shoot than trees in the

flooded areas (Table 1, Mann-Whitney  $U$ -test,  $z = -3.33$ ,  $n_1 = 70$ ,  $n_2 = 84$ ,  $P = 0.0009$ ). The mean total leaf area missing ( $\text{cm}^2$ )/shoot (i.e. leaf area lost through leaf shed plus insect herbivory) that had accumulated by March 1992 on the flooded trees was  $48.8 \pm 11.9\%$  compared with  $57.1 \pm 9.3\%$  on the unwatered trees ( $P > 0.05$ ).

Actual areas ( $\text{cm}^2$ ) of leaf tissue consumed by insects were not significantly different between the two watering treatments (Table 1). However, as a percentage of the total potential area, the relative impact of insect herbivory on leaves monitored in the non-flooded areas was significantly greater than in the flooded areas ( $t = -3.32$ ,  $n_1 = 64$ ,  $n_2 = 71$ ,  $P = 0.0015$ ). The seasonal accumulation of insect damage appeared to increase relatively slowly (Fig. 1b). In September, shoots from the flooded trees had a mean loss to herbivory of  $21.0 \pm 8.1 \text{ cm}^2$  (= 14.8% of total potential leaf area), which increased to  $29.3 \pm 12.7 \text{ cm}^2$  (= 17.0% of total potential area) by March (Fig. 1b). The seasonal fluctuation in the level of herbivory detected in the non-flooded trees was hardly discernible ( $21.27 \pm 2.3 \text{ cm}^2$  [= 21.6%] in September and  $24.6 \pm 3.19 \text{ cm}^2$  [= 21.4%] [ $P > 0.05$ ] in March [Fig. 1b]).

The relationship between leaf retention at various levels of insect herbivory may be a contributing factor to this apparent lack of accumulation of insect damage (Fig. 2). Although not significantly different at each of the nine levels of herbivory (5–80%) presented in Fig. 2, the mean proportion of leaves per shoot possessing areas missing greater than each designated level of herbivory was consistently higher in the flooded trees compared to the non-flooded trees. Thus not only did the labelled leaves on the non-flooded trees have a higher relative level of insect herbivory than leaves on the flooded trees (Fig. 1b), they also appeared to be less tolerant to insect damage (Fig. 2). The regression equations for Fig. 2 are as follows: for flooded trees,  $\ln(\% \text{ no. leaves}) = 4.140 - 0.056$

(% leaf area missing); and for non-flooded trees,  $\ln(\% \text{ no. leaves}) = 4.567 - 0.057$  (% leaf area missing). The model error  $df = 1211$ ,  $r^2 = 0.64$ , two equations are not significantly different ( $P = 0.53$ ).

The most common form of foliage damage was leaf chewing by insects, in particular, by beetle species of Chrysomelidae and Curculionidae. Leaf holes or damage caused by insect galling or curling were rare. Stone and Bacon (1994a) identified some of the diurnal insect species in *E. camaldulensis* canopies at the study site during the summer of 1991/1992. While relatively many species were observed no single insect species dominated during the study. Defoliation by arboreal vertebrates seemed minimal (Stone & Bacon 1994a).

Taking into account only those leaves known to have lost tissue by insect chewing during the 7 month period, the mean monthly incremental rate of leaf area lost was  $10.5 \pm 1.37\%$  in the watered trees and  $12.5 \pm 1.54\%$  in the unwatered trees. In addition, Fig. 2 shows that less than 10% of the monitored leaves ever had a level of insect herbivory greater than 50%. Based on these two facts, we assumed that the event of a leaf being completely consumed by insects between observations was rare and that leaves went missing through abscission, either prematurely or by natural senescence. Thus it was possible to separate the relative impacts of insect herbivory (leaf chewing) and leaf abscission.

The area lost to leaf abscission per shoot (based on the difference between total leaf area missing and consumption of leaves by insects) followed the same pattern as the number of leaves shed per shoot (Table 1, Mann-Whitney  $U$ -test,  $z = -3.9$ ,  $n_1 = 70$ ,  $n_2 = 84$ ,  $P = 0.0001$ ). Likewise, leaf area lost per shoot through abscission as a proportion of total potential leaf area is significantly greater in the non-flooded areas than in flooded areas (Table 1, Mann-Whitney  $U$ -test,  $z = -3.8$ ,  $n_1 = 70$ ,  $n_2 = 84$ ,  $P = 0.0001$ ). Within treatments, insect herbivory and leaf abscission contributed similarly to total leaf loss in the non-flooded subplots (48% vs 52%,  $P > 0.05$ ). However, on the monitored shoots from the flooded trees, the relative impact of insect herbivory was significantly greater, contributing on average 61% to total leaf loss compared to 39% from leaf abscission ( $t = 2.4$ ,  $df = 138$ ,  $P = 0.02$ ).

Photosynthesizing tissue lost by sap-sucking and leaf-mining insects or fungal spots was recorded as necrotic tissue. Significantly less leaf area ( $\text{cm}^2$ ) per shoot per month was recorded as necrotic tissue on the flooded trees than on the non-flooded trees (Table 1, Mann-Whitney  $U$ -test,  $z = -3.95$ ,  $n_1 = 64$ ,  $n_2 = 71$ ,  $P = 0.0001$ ). Similarly, the mean monthly proportion of necrotic tissue per shoot was significantly different between the two sets of trees (Table 1, Mann-Whitney  $U$ -test,  $z = -3.3$ ,  $n_1 = 64$ ,  $n_2 = 71$ ,  $P = 0.0009$ ).

The mean monthly litter fall collected from the flooded subplots was  $28.1 \pm 6.3$  and  $21.3 \pm 4.0 \text{ gm}^{-2}$  from the non-flooded subplots ( $t = 1.70$ ,  $df = 31$ ,  $P = 0.07$ ). The

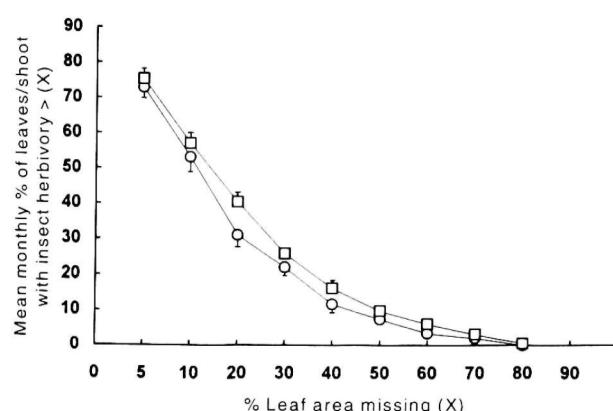


Fig. 2. The mean monthly percentage of *Eucalyptus camaldulensis* leaves per shoot suffering greater than designated levels of insect herbivory (% leaf area missing). (□) Flooded trees; (○) non-flooded trees; bars represent  $\pm 1$  SE.

**Table 2.** Mean monthly litterfall ( $\text{g m}^{-2}$ ) of *E. camaldulensis* in Gulpa Island State Forest from September 1991 to March 1992. Litter traps were located in one of three intermittently flooded waterways or at an average of 37.5 m from the edge of the three waterways

Component	Litterfall (oven dried $\text{g m}^{-2}$ )	
	Flooded trees (n = 12)	Non-flooded trees (n = 21)
Leaves*	13.02 ± 2.94 <sup>a</sup> (46.2)	6.84 ± 0.80 <sup>b</sup> (32.5)
Twigs*	4.26 ± 1.44 <sup>a</sup> (15.2)	4.63 ± 1.04 <sup>a</sup> (21.8)
Bark†	8.24 ± 3.53 <sup>a</sup> (29.3)	8.55 ± 3.39 <sup>a</sup> (40.2)
Reproductive parts†	1.31 ± 0.70 <sup>a</sup> (4.65)	0.43 ± 0.23 <sup>b</sup> (2.01)
Insect frass*	1.31 ± 0.17 <sup>a</sup> (4.65)	0.83 ± 0.13 <sup>b</sup> (3.91)

Figures in parenthesis are percentages of the total. Means in each row (mean ± 1 SE) followed by different letters are significantly different ( $P \leq 0.05$ ). Comparison of means tested with either a \*Student's *t*-test or †Mann-Whitney *U*-test depending on heterogeneity of variances.

most common component of the litter fall was leaves (Table 2 and Fig. 1c). The traps beneath the flooded tree canopies collected twice as much leaf material as traps beneath the non-flooded trees. The trees subjected to flooding also dropped significantly more insect frass and reproductive parts (buds and fruits). Peak litter falls in both treatments occurred during February (Fig. 1c), corresponding to the maturation of the summer flush (Fig. 1a).

#### Net tree growth

Figure 1d compares the net incremental change in mean leaf area per shoot between the two groups of trees. Although not significantly different the consistent trend illustrated in Fig. 1d is supported by the significant increase in basal area growth in the flooded trees compared to the non-flooded trees (Table 1). The watered trees grew approximately eight times faster, in terms of trunk diameter increment between October 1990 and July 1992 ( $t = 2.23$ , df = 10,  $P = 0.049$ ).

## DISCUSSION

### Moisture stress and leaf dynamics in *E. camaldulensis*

As expected, the periodically flooded areas had significantly higher soil moisture levels than the non-flooded areas. The difference in canopy leaf dynamics of trees exposed to the flooding corresponded with a significantly

larger mean basal area increment compared to trees sited, on average, 37.5 m above the edge of the flooded waterways. Similar enhancement in productivity was observed by Heinrich (1990) after artificial flooding of *E. camaldulensis*. The flooded trees showed an increase in canopy leaf area through a significant increase in leaf retention and mean leaf size. This influence of moisture status on leaf size in *E. camaldulensis* was also detected after a single discrete sampling of foliage at the study site in March 1992 (Stone & Bacon 1994b). In this study, because both sets of permanently labelled leaves took similar times to attain maximum leaf size and the leaves were significantly larger on the flooded trees, the rate of leaf expansion from initiation to maturity differed between the two watering treatments.

The higher density of shoots per canopy in the flooded trees (Stone & Bacon 1994b) and the competitive growth patterns of maturing leaves in eucalypts (Jacobs 1955; Pook 1984a) explains why significantly more leaves were collected in litter traps under these trees. The higher turnover of canopy foliage in the well-watered eucalypts is indicative of vigorous growth (Jacobs 1955; Specht & Brouwer 1975; Pook 1984a). However, although the flooded trees shed more leaves on a canopy basis than the non-flooded trees, on an individual shoot basis, the reverse occurred. Significantly more leaves abscised per shoot from the non-flooded trees. The similarity in mean number of leaves per shoot between the flooded and non-flooded trees and the significant reduction in leaf retention on the non-flooded trees suggests that these trees had a higher rate of leaf initiation. This was supported by the higher monthly mean proportion of leaf buds per shoot (leaf area  $< 1.0 \text{ m}^2$ ) of the non-flooded trees. We assume that the higher level of leaf initiation followed by increased abscission per shoot would incur higher metabolic costs, relative to the density of canopy shoots (Landsberg 1988). This result, however, differed from a study of *E. maculata* Hook. in Kiola State Forest, near Batemans Bay, in which there was a marked depression in new leaf production concurrent with a severe drought in the latter half of 1980 (Pook 1984a). Similarly, *Eucalyptus blakelyi*, near Canberra, stopped producing any new growth during severe drought in the 1982/83 summer (Landsberg 1985). The soil moisture content in the non-flooded subplots, although suboptimal for *E. camaldulensis*, was possibly not as extreme or as stressful as for the species studied by Landsberg (1985) and Pook (1984a, 1985, 1986).

### Moisture stress and insect herbivory on *E. camaldulensis*

Although the flooded trees lost significantly more leaf mass per canopy through litter fall and insect frass and slightly more leaf area through insect herbivory per shoot, the impact of these losses was lessened by vigorous canopy growth. As a proportion of total leaf area, trees at

the non-flooded sites experienced significantly higher levels of both types of leaf loss. The positive relationship between foliage consumption and the collection of frass falling from canopies has been demonstrated with other eucalypt species (Ohmart *et al.* 1983; Edwards *et al.* 1993). Among the non-flooded trees, the leaf area lost ( $\text{cm}^2$ ) to abscission and insect herbivory was similar. However, the mean leaf area/shoot lost to insect herbivory was significantly greater than that lost through leaf abscission in the flooded trees. Overall the level of insect herbivory in both the flooded and non-flooded trees is relatively high compared to other eucalypt forests (Stone & Bacon 1994a and references therein).

For both treatments, leaf retention decreased as the percentage leaf area removed by insects increased. This relationship has been demonstrated in a wide range of plant species (e.g. Lowman 1982; Lam & Dudgeon 1985; Risley 1993). In this study, however, *E. camaldulensis* appeared to be very sensitive to insect herbivory when compared to the levels of damage per leaf tolerated by other eucalypt species (e.g. Abbott *et al.* 1993; Lowman & Heatwole 1992). High levels of herbivory per leaf were rare in both sets of trees, with fewer than 10% of leaves having greater than 50% leaf area missing. In addition, the significantly lower retention rate of leaves on trees in the lower soil moisture regime probably contributed to the apparent lack of seasonal accumulation of insect damage. These leaves seemed to be more prone to abscission at any particular level of herbivory (Fig. 2) when compared to leaves from the flooded trees. This

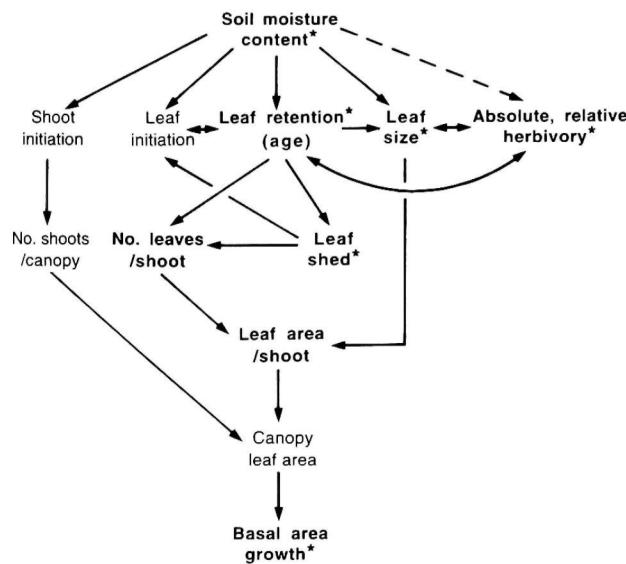
supports the proposition of a synergistic relationship between tree moisture stress and insect herbivory in terms of leaf abscission. A similar phenomenon was suggested by Abbott *et al.* (1993) for *E. marginata* Don ex Sm. while Cockfield and Potter (1986) observed an interaction between feeding damage by a scale insect and water stress on leaf abscission of *Euonymus fortunei*.

The mean rate of herbivory (tissue consumed/unit time as opposed to mean level, tissue consumed/unit leaf area) was only slightly higher on shoots monitored in the non-flooded trees. A shortcoming of our study was that each leaf was not assigned to an age category (*sensu* Lowman 1985; Landsberg 1988, 1990) when their areas were measured. Alternatively, this shortcoming could have been avoided if the study had continued for a further 12 months (i.e. for a period covering the natural senescence of leaves initiated in the spring of 1991). Thus, although the smaller mean size of leaves on trees in the lower soil moisture regime would have contributed to a higher rate of consumption, knowledge of the proportion of different leaf age cohorts is required before a more complete interpretation of consumption rates between watering treatments can be made (Coley 1980; Raupp & Denno 1983; Landsberg 1988; Larsson & Ohmart 1988; Ernest 1989; Ohmart 1991; Sand-Jensen & Jacobsen 1994).

## **Balance between moisture availability, canopy production and insect herbivory**

Figure 3 summarizes the processes, identified in this study and from the literature, by which soil moisture content influences the balance between foliage production, retention and loss and levels of insect herbivory. This balance, in turn, directly influences canopy leaf area and hence basal area growth. In order to interpret the impact of defoliation on this balance we determined both the absolute and relative levels of insect herbivory. The relative position of insect herbivory between the two flooding treatments changed depending on whether herbivory was expressed as an absolute or relative term (Fig. 1b).

Our results suggest that although well-watered *E. camaldulensis* may sustain high absolute levels of insect herbivory, vigorously growing dense canopies reduce the relative impact of insect herbivory. However, two models, the resource-availability model of plant anti-herbivore defence (Coley *et al.* 1985), and the plant vigour hypothesis (Price 1991), predict that high levels of resource are conducive to high levels of damage from opportunistic herbivores. Therefore, a question arising from this study is how insect populations would respond to the presence of sustained high levels of resource resulting from improved watering (see Landsberg & Ohmart 1989; Larsson & Ohmart 1989; Ohmart 1991; Price 1991 for general discussions on this theme). Would the trees



**Fig. 3.** A conceptual model illustrating the influence of soil moisture on the balance between foliage production and insect herbivory on *Eucalyptus camaldulensis* in Gulpa Island State Forest. Variables measured in this study are in bold. Asterisk denotes a significant difference ( $P < 0.05$ ) between the two flooding treatments; dashed line applies to insect herbivores that have part of their life history in contact with the ground.

'outgrow' any increase in herbivory or would certain insect populations 'outgrow' canopy production? Further work is required to determine whether the abundance and composition of herbivorous insects will change after long-term alleviation of moisture stress. Answers to this question are desirable before the establishment of irrigated plantations of *E. camaldulensis* and other species.

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