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PHENOLOGY OF LEAF-FLUSHING AND MACROARTHROPOD ABUNDANCES IN CANOPIES OF *EUCALYPTUS* SAPLINGS

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ABSTRACT. Flushing of leaves and macroarthropod abundances were monitored in the canopies of five species of *Eucalyptus* saplings under different conditions and seasons. Leaf-flushing took place year round but was most prevalent during periods of high rainfall. Flushing was not synchronous among saplings even within a species. Saplings in open field conditions retained the young quality of new leaves longer than those in shaded woodlands. Arthropod numbers differed significantly among individual saplings and species of sapling, and with time and exposure. There were significant interactive effects. There were more arthropods on saplings in the sun than on those under a tree canopy. Values ranged from zero to over 20,000 insects on individual saplings at particular sampling times. Peaks of abundance were of short duration and were attributable to different species of insects at different sampling periods. Coleoptera, Hemiptera and Formicidae (ants) were the most common groups. Insect peaks were not consistently in concert with leaf flushes. Susceptibility to insect attack was influenced by whether or not a particular sapling flushed simultaneously with the occurrence of a peak of grazing insects. Canopies of saplings were more accessible to quantify temporal and spatial variation in insects than were mature trees.

INTRODUCTION

The abundance of arthropods on vegetation is affected by many factors including their diurnal periodicity (Heatwole *et al.* 1981), spatial preferences relative to vegetative structure (Crawley 1983, Lowman 1985), palatability of host plant in the case of herbivores (Rhoades & Cates 1976), specialization of herbivores (Fox & Morrow 1981) and distribution of predators. The numbers of plant-feeding insects borne by an individual sapling may have varying consequences. Moderate amounts of defoliation may stimulate plant growth (Jameson 1963, Lowman 1982) whereas severe defoliation may inhibit growth (Lowman & Heatwole 1987), lead to reduced reproductive capacity (Greaves 1967, Rockwood 1974), less wood production (Morrow & LaMarche 1978), lower photosynthetic rates (Hodgkinson 1974), individual mortality (Kulman 1971) and even ultimate changes in community composition (Fox & Morrow 1981).

On the New England tablelands of New South Wales a malady known as dieback occurs in which leaves die progressively from the tips of branches toward the bole, eventually leading to the death of the entire tree (Heatwole & Lowman 1986, Lowman & Heatwole 1993). One of the factors contributing to tree death appears to be extensive defoliation of canopies by insect herbivores (Nadolny 1983). As part of a long-term project on the impact of arthropods on eucalypt woodlands, the seasonal fluctuations of arthropod numbers on saplings were examined. This paper reports on the phenology of insect peaks and on the flushing of leaves in saplings.

MATERIALS AND METHODS

Canopies of eucalypt saplings were examined for abundance and diversity of macroarthropods and for phenological events, especially leafing. Species included: *Angophora floribunda* (Sm.) Sweet, *Eucalyptus melliodora* A. Cunn. ex Shau, *E. viminalis* Labill., *E. blakelyi* Maiden, and *E. caliginosa* Blakely et McKie, all of which are

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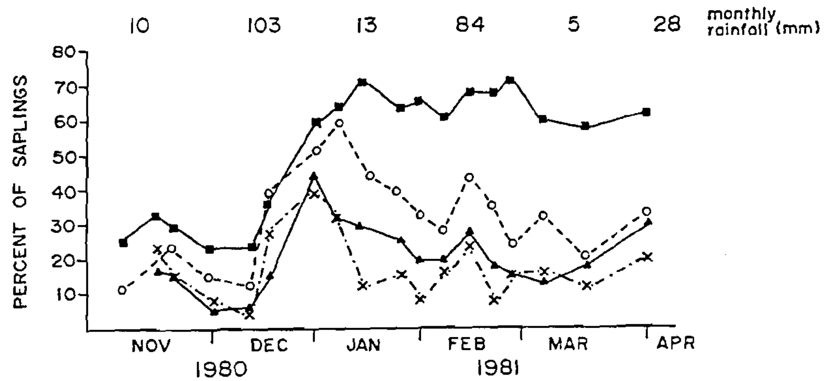

FIGURE 1. Temporal changes in proportion of saplings with new foliage and young foliage (see text). Symbols indicate proportion of saplings with new foliage since the previous sampling period in the open (triangles) and under the canopy (x's) and proportion with young foliage in the open (squares) and under the canopy (circles).

common in dry sclerophyll woodlands in the New England region of Australia. The study area was Eastwood State Forest, 15 km east of Armidale, New South Wales. A description of the vegetation and avifauna was provided by Ford and Bell (1981).

Fifteen saplings of each of the five species were selected for observation, ten in a sunny, open field adjacent to woodland and five in shaded woodland with tall, mature *Eucalyptus* trees overhead. All saplings were 1–3 m high, exhibited vigorous, apparently healthy growth, and were situated 0.5 km or less from each other. They were numbered with aluminum tags.

For each sapling at each observation period, the following data were recorded: (1) numbers and types of macroarthropods (identified to order, and, when possible, to family) on the entire canopy, (2) phenological events such as flowering, fruiting or leaf flushing, and (3) a rough estimate of leaf damage and any other relevant observations regarding sapling growth or insect-plant relationships. Voucher specimens were collected in vials containing 70% alcohol. When macroarthropods were too abundant for direct censusing, numbers on particular twigs or branches were counted and the results used to estimate total numbers for the whole sapling. Monitoring was conducted at fortnightly intervals from 5 November 1980 to 8 April 1981, a period spanning late spring, summer and autumn during a time of somewhat lower-than-normal rainfall. The 50-year annual mean precipitation was 792 mm whereas the respective annual rainfalls for 1980 and 1981 were 516 mm and 653 mm (Anonymous 1982).

The data were transformed to log + 1, and a repeated measures ANOVA was then conducted using the Statistical Analysis System (General Linear Models) (GLM/SAS) to assess sources of variation in arthropod numbers.

RESULTS

Leaf Flushing

The new season's leaves appeared lighter in color and were less rigid than older leaves. As long as the former maintained their identity, they were called young foliage regardless of how many observation periods they spanned. That portion of the foliage that had appeared since the previous sampling was called new foliage. New foliage provides an indication of the time of leaf flushing, and young foliage the accumulated recent growth.

At all times during the study there were at least some saplings producing new leaves (FIGURE 1). Although leafing phenology varied widely from sapling to sapling, even of the same species, there were peaks of leaf flushing during or following months that had high rainfall. There was a major flush in late December to early January with 40–45% of the saplings showing new foliage. Minor peaks of flushing occurred in November, mid-February and early April.

At any one time the amount of young foliage exceeded the new foliage and, therefore, there was an accumulation of young leaves produced over a longer period of time than the interval between samplings.

Saplings in the open and under the canopy had similar patterns of leaf flushing. However, they differed in the length of time new foliage maintained its young appearance. After the major peak of flushing, a high proportion of saplings in the open (58–72%) maintained recognizably young foliage for the duration of the

TABLE 1. Results of a repeated measures ANOVA (GLM/SAS) on log (number of arthropods + 1) and log (number of arthropods exclusive of ants + 1) on 75 saplings of five species (ten saplings of each species in the open and five under the shade of the tree canopy) at 18 sampling periods during spring, summer and autumn.

Source of variation	F Value	Probability
ALL MACROARTHROPODS		
Among individual counts	$F_{1105} = 13.28$	P = 0.0001
Among samplings (time)	$F_{17,1105} = 2.91$	P = 0.0001
Among species of sapling	$F_{4,65} = 5.69$	P = 0.0005
Among individual saplings	$F_{65,1105} = 20.76$	P = 0.0001
Exposure (open versus shade)	$F_{1,65} = 40.00$	P = 0.0001
Species-time interaction	$F_{68,1105} = 1.69$	P = 0.0006
Exposure-time interaction	$F_{17.1105} = 1.94$	P = 0.0120
Species-exposure interaction	$F_{4,65} = 1.29$	P = 0.2844
Species-exposure-time interaction	$F_{65,1105} = 0.92$	P = 0.6626
MACROARTHROPODS (EXCLUDING ANTS)		
Among individual counts	$F_{1105} = 8.55$	P = 0.0001
Among samplings (time)	$F_{17,1105} = 2.29$	P = 0.0021
Among species of sapling	$F_{4,65} = 6.71$	P = 0.0001
Among individual saplings	$F_{65,1105} = 10.26$	P = 0.0001
Exposure (open versus shade)	$F_{1.65} = 51.50$	P = 0.0001
Species-time interaction	$F_{68,1105} = 1.38$	P = 0.0255
Exposure-time interaction	$F_{17,1105} = 2.56$	P = 0.0005
Species-exposure interaction	$F_{4.65} = 3.66$	P = 0.0095
Species-exposure-time interaction	$F_{68,1105} = 0.99$	P = 0.5095

study, even though less than 30% were flushing leaves. In the understory, leaves soon matured and lost their identity as young foliage.

The Macroarthropod Fauna

Most of the macroarthropods were not identified to species and, consequently, detailed treatment of the taxonomic composition was not carried out. However, an estimate of the number of species in the various major taxa was made. When it was uncertain whether similar morphotypes constituted one or more species, they were lumped, and the following estimates of species numbers therefore are conservative: beetles 52 species; ants 27; large to medium-sized bugs 26; psyllids, scales and galls (various taxa) 20; flies and mosquitoes 17; moths and butterflies (adults) 14; spiders 12; hymenopterans other than ants 5; dragonflies and damselflies 3; roaches 2; grasshoppers 2; neuropterans 1; and phasmids 1. There were undetermined numbers of species of small leafhoppers, small bugs and aphids. In addition, there were 19 different kinds of beetle and lepidopteran larvae which may or may not have been immatures of some of the same species as the observed adults of those groups. Thus, there were probably over 200 species of arthropods involved in the counts, and perhaps as many as 250. Microarthropods (e.g., mites) were not included in the study.

Temporal Fluctuations in Macroarthropod Abundance

Differences in arthropod abundance were assessed in terms of five factors: individual counts, time, species of sapling, individual sapling, and exposure (open versus under canopy). TABLE 1 summarizes the results of an analysis of variance performed for these factors for total arthropods and for total arthropods exclusive of ants. All categories had a highly significant effect upon the numbers of arthropods. All interactions were also significant, except for species-exposure for total arthropods and the three-way interaction of species-exposure-time both for total arthropods and total arthropods exclusive of ants. Thus, not only did the various individual counts differ from each other, but the numbers of total arthropods on saplings changed with time and varied among individual saplings, species of sapling, and between sapling canopies located in the sun compared with those under shade. Furthermore, the effect of exposure (sun versus shade) changed over time. These effects were highly significant (all P values <0.001 except for the exposure-time interaction for which P=0.012).

These results also held for arthropods exclusive of ants except that some P values were slightly higher (but still highly significant; all values were 0.025 or lower). In addition, there was one significant effect not noted for total ar-

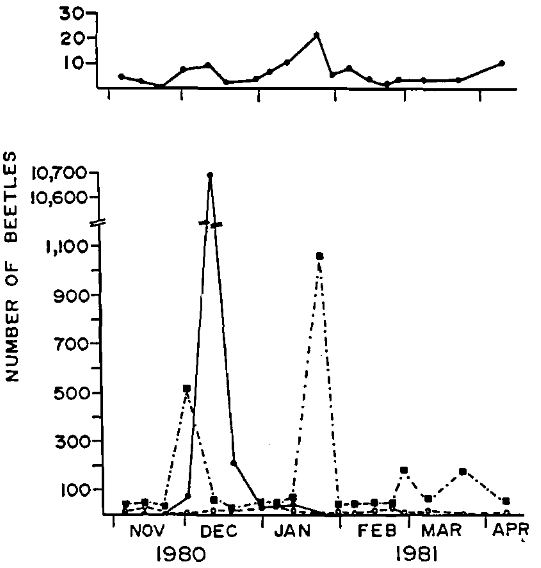

FIGURE 2. Temporal changes in numbers of beetles associated with saplings. Note differences in vertical scales. Upper: Curculionidae. Lower: Coccinellidae—circles and dashed line. Scarabaeidae—dots and solid line. Chrysomelidae (larvae plus adults)—squares and dot-dash line.

thropods: the various species of sapling were affected differently by exposure (P=0.0095).

The mean number of macroarthropods on the 75 saplings varied greatly during the study (FIGURES 2–8). There was extreme fluctuation in both the short term (fortnight-to-fortnight) and more extended (month-to-month) periods for individual saplings, with individual totals ranging from zero to over 20,000 for a particular sampling day.

One of the most striking features of temporal variation in arthropod numbers was that different taxa showed different seasonal patterns (FIGURES 2–4). Numbers of chrysomelids and weevils (Curculionidae) increased in late spring and peaked in early to mid-December (Australian summer), only to decline again and then peak a second time in January, with more minor fluctuations for the rest of the study (FIGURE 2). Two other abundant families had different patterns. The coccinellids showed relatively little fluctuation whereas the scarabs had one peak (December) rather than two.

Chrysomelid larvae were present throughout the study as sedentary feeders and did not fluctuate much with time, whereas the adults emerged in late summer and were only counted in field sampling when sunny conditions prevailed and young leaves were present. Chrysomelid adults also

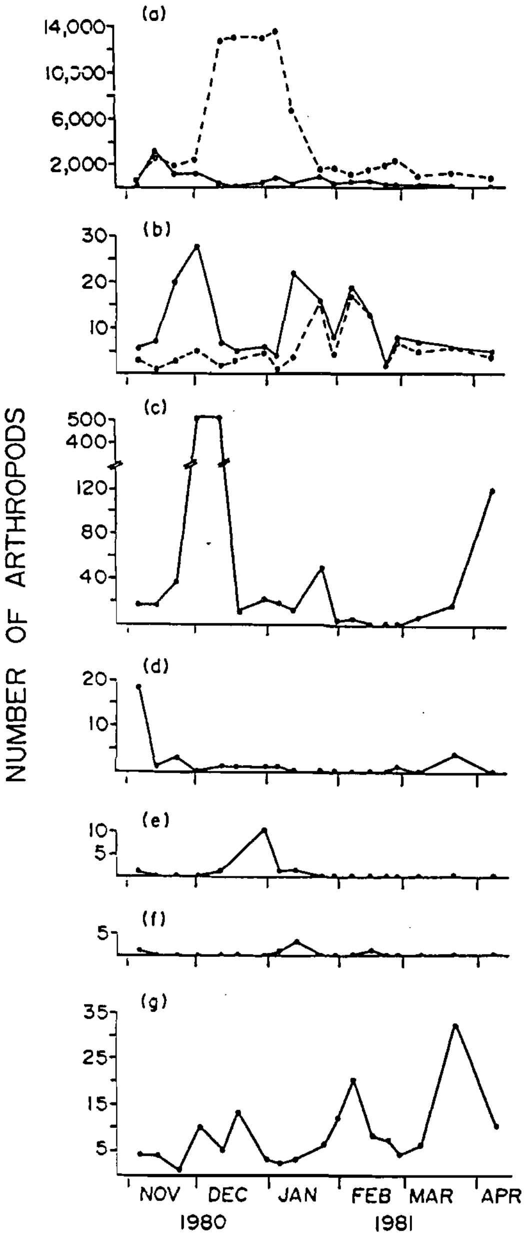

FIGURE 3. Temporal changes in numbers of individuals of various arthopod taxa found on saplings. Note differences in vertical scales.

(a) Psyllids plus scale insects (circles and dashed lines) and aphids plus leafhoppers (dots and solid line).
(b) Lepidoptera. Herbivorous larvae—circles and dashed line. Adults plus larvae—dots and solid line.
(c) Diptera
(d) Blattodea
(e) Orthoptera
(f) Phasmatodea
(g) Arachnida (spiders)

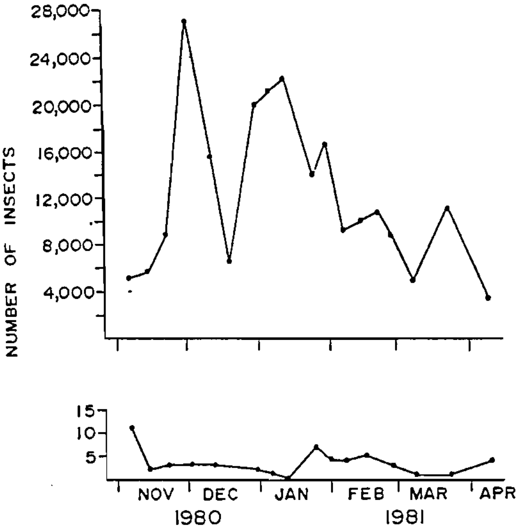

FIGURE 4. Temporal changes in numbers of individuals of ants (upper) and other Hymenoptera (lower) associated with saplings. Note differences in vertical scales.

swarm in the foliage of adult eucalypts in late summer (Lowman and Heatwole 1992).

Because of their different behaviors, scales (sedentary) were graphed separately from aphids and leaf hoppers (mobile). The two groups displayed different temporal patterns. The former fluctuated but generally declined from November onward, whereas the latter reached a peak in early December and maintained high numbers until January when there was a decline (FIGURE 3a).

The Diptera showed peaks of abundance on saplings in November-December and again in April but relatively low numbers otherwise (FIGURE 3c).

Numbers of ants fluctuated widely throughout the entire study, sometimes reaching values in excess of 20,000 individuals for the 75 saplings (FIGURE 4).

Arthropods of groups other than those discussed above, were represented by very few individuals at all seasons, the maximum value for any group being less than 35 individuals for the 75 saplings and values often only 0–1 (FIGURES 3, 4); in the Lepidoptera (FIGURE 3b), a late November to early December peak occurred, and two subsequent ones in January and February. The spiders (FIGURE 3g) had low numbers in spring and early summer, followed by two peaks, one in February and one in March.

It was deemed ecologically more important to carry out analyses on the basis of trophic position rather than taxon, and subsequent treatment is on a trophic basis. There were two major peaks in chewing insects, one in December and another in January (FIGURE 5). Because most of the chewing insects were beetles, the pattern for this trophic category resembles the composite one for beetles (FIGURE 2). The first peak in chewing insects consisted mainly of chrysomelid and scarab beetles. The latter were represented primarily by two species of Christmas beetles, *Anoplognathus porosus* (Dalman) and *A. hirsutus* Burm., which together accounted for over 11,000 individuals on 12 December 1980. The second peak was almost entirely chrysomelids.

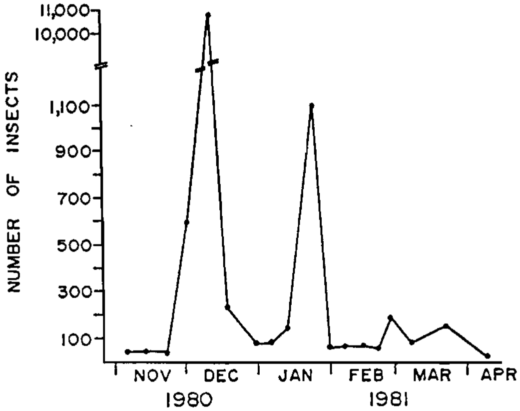

FIGURE 5. Temporal changes in numbers of individuals of chewing insects associated with saplings.

The peaks of abundance of arthropods on the saplings did not seem related to the time of flushing of new foliage. For example, the first peak of chrysomelids occurred at about the lowest point of leaf flushing, when few saplings had young foliage (FIGURES 1, 2). The second peak of chrysomelid abundance also missed any flushing peak although a high proportion of saplings did have young foliage at that time. Similarly, scarab abundance was already declining at the time saplings began to flush leaves (FIGURES 1, 2). Taking all chewing insects collectively, the first peak of abundance occurred at a low point of flushing and of young foliage whereas the second one missed peak flushing but did coincide with the period of sustained high incidence of young foliage (FIGURES 1, 5). The relationship of phenology and arthropod loads of individual saplings is discussed below.

Variation in Macroarthropod Abundances among Species of Saplings

Eucalyptus caliginosa had far more arthropods present overall than any other species (66% of the total individuals) with the remainder similar to each other (5.7–11.8%) (FIGURE 6). The ranking in decreasing order of total insect numbers

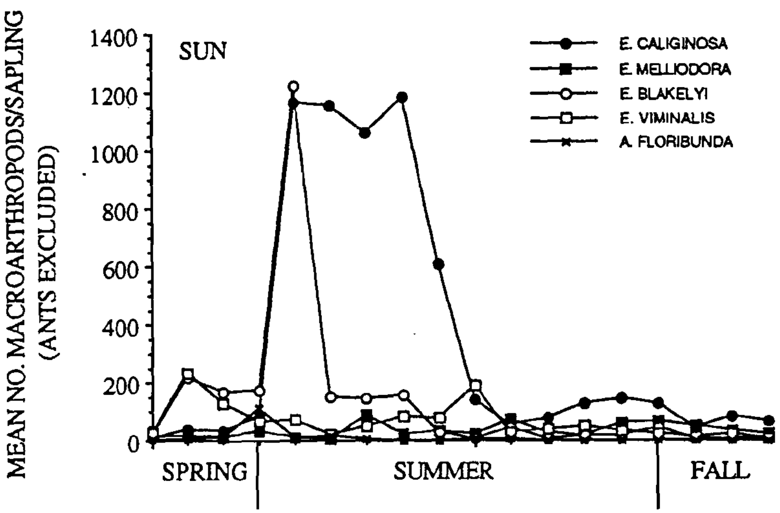

FIGURE 6. Seasonal changes in abundance of macroarthropods (exclusive of ants) on saplings of different species located in the sun.

was *E. caliginosa, E. blakelyi, E. viminalis, E. melliodora,* and *A. floribunda.* This same ranking and general relationship occurred for sucking insects, for all herbivores combined, and for all arthropods exclusive of ants. For nectarivores, predators, omnivores and ants, *E. caliginosa* saplings still had the highest numbers of arthropods (40–73%) of any species, and the hierarchy of the remaining species varied only slightly. However, the results were quite different for chewing insects (and for the component categories of scarabs and total beetles) and miscellaneous arthropods. These were most abundant on *E. blakelyi* (55–93%) with the next greatest numbers on *E. viminalis* (5–18%) and small numbers in varying order on the remaining species.

Chrysomelids differed from either of the above two patterns in that the greatest proportion of adults was on *E. melliodora* and *E. viminalis* (42%) and most of the larvae (85%) were on *E. viminalis.*

In summary, *E. caliginosa* tended to have the greatest numbers of insects generally and for most trophic and taxonomic categories, except for those that grazed on leaves. Of the latter, the chrysomelids were most abundant on *E. viminalis* and *E. blakelyi* and the scarabs on *E. blakelyi.*

Variation in Macroarthropod Abundance among Individual Saplings

For illustrative purposes two saplings out of the 15 for each species were selected and the temporal patterns of change in total arthropod abundance portrayed in FIGURE 7. Even these few examples show that there were great differences in arthropod burden among individual saplings even of the same species. Peaks on one sapling seldom coincided with those on nearby conspecifics. Nearly simultaneous peaks on different saplings were often caused by different taxa of arthropods.

Eucalyptus caliginosa sapling no. 6 (FIGURE 7c) had only one large peak and that was due primarily to ants. *E. caliginosa* no. 2 (FIGURE 7d) had a slightly later peak (early January), due both to large numbers of scale insects as well as to ants. A second and even larger peak in February was due almost entirely to ants and occurred at a time that *E. caliginosa* no. 6 had its lowest number of arthropods. Thus, on the same date one sapling had its highest numbers of associated arthropods and another of the same species nearby had its lowest.

Two *E. blakelyi* saplings both had early summer peaks; however, one was due to ants (no. 21; FIGURE 7f) and the other was due to Christmas beetles (no. 23; FIGURE 7e). The latter sapling had an abundance of new leaves at the second sampling period (mid-November) when there were few insects on it. By the second week in December, an outbreak of approximately 10,000 Christmas beetles (FIGURE 5) had destroyed 90% of the foliage (new and old); a week later almost no foliage remained and insect levels had returned to slightly over 100. No new growth appeared on this sapling until late January although other saplings had new foliage during the intervening time; in early February it had a new leaf flush. There was nearly complete survival of this canopy during the subsequent two sampling periods and no

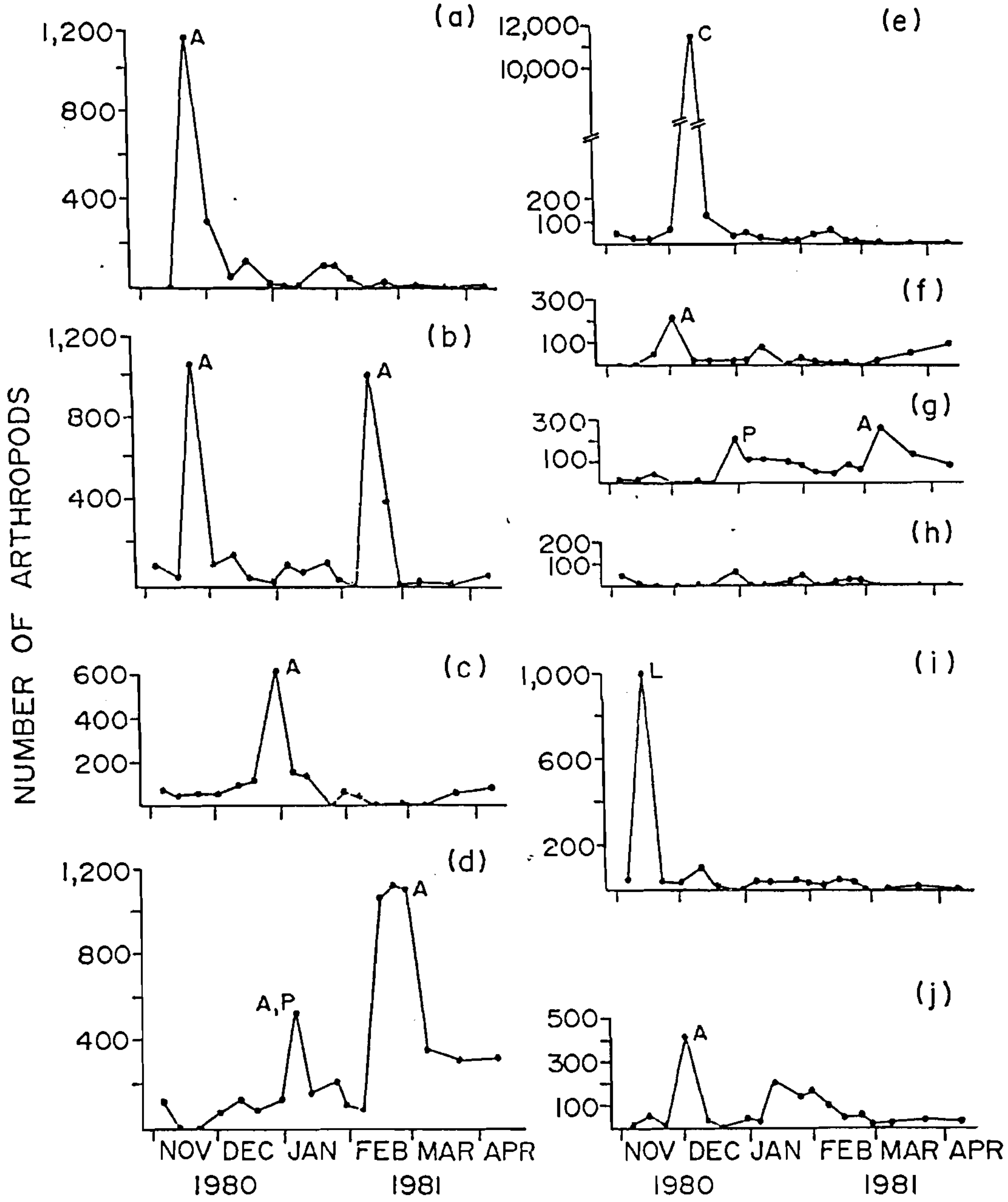

FIGURE 7. Selected examples of temporal changes in patterns of abundance responsible for major peaks indicated near tip of peak.

A = Ants; P = psyllids; C = Christmas Beetles (*Anoplognathus:* Scarabaeidae); L = leafhoppers.

(a) = *A. floribunda* sapling no. 44. (b) = *A. floribunda* no. 41. (c) = *E. caliginosa* No. 6. (d) = *E. caliginosa* no. 2. (e) = *E. blakelyi* no. 23. (f) = *E. blakelyi* no. 21. (g) = *E. melliodora* no. 13. (h) = *E. melliodora* no. 11. (i) = *E. viminalis* no. 35. (j) = *E. viminalis* no. 31.

extensive damage occurred during the remainder of the study. Thus, one major leaf flush of this sapling was nearly completely destroyed by grazing insects during a period of peak abundance, but its second major flush occurred just after a second peak of chewing insects (compare FIGURES 5 and 7) and that foliage escaped serious insect attack.

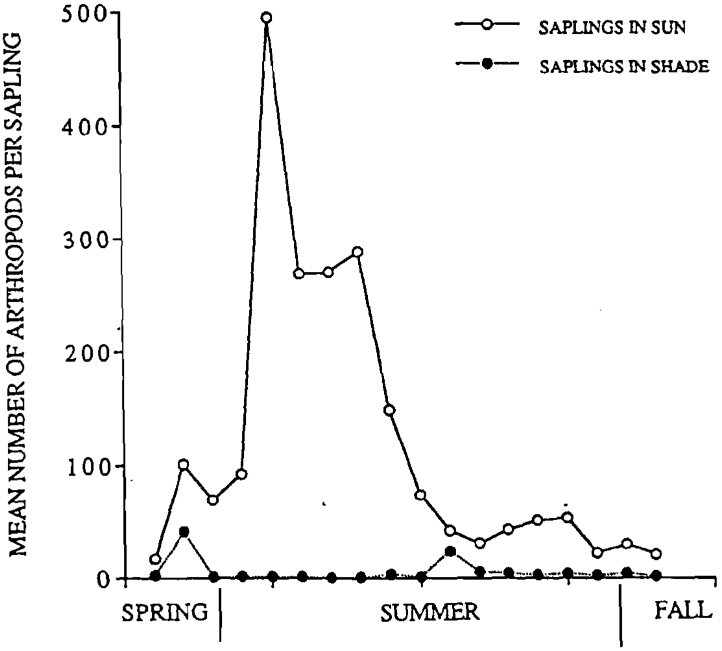

FIGURE 8. Comparison of temporal changes in abundances of arthropods on saplings located in the sun and those under the shade of a canopy.

On *E. melliodora* no. 13 (FIGURE 7g) there were two peaks, one in late January due to psyllids and the other in March due to ants. Numbers of arthropods were continuously low on *E. melliodora* no. 11 (FIGURE 7h).

Eucalyptus viminalis no. 35 (FIGURE 7i) had a November peak of leafhoppers which was lacking on *Eucalyptus viminalis* no. 31 (FIGURE 7j). The latter, however, had a peak of ants in early December which the former lacked.

The two *Angophora* saplings selected as examples (nos. 44 and 41) both had simultaneous peaks in November due to ants. A second peak of ants in February on no. 41 (FIGURE 7b) did not occur on no. 44 (FIGURE 7a). Indeed the latter had its lowest numbers of associated arthropods at that time. The simultaneous occurrence of the early peaks of ants on both saplings may have been coincidental as it did not occur at that time on other *Angophora* saplings.

Clearly, each individual sapling has its own pattern of abundances of associated arthropods. Most peaks in arthropod numbers consisted of aggregation of individuals of particular species, not of all arthropods in general.

Differences Between Saplings in the Open and Under a Canopy

Arthropods were consistently more abundant on saplings in the open than on those located under the canopy of the woodland (FIGURE 8). This may have resulted from direct responses of the arthropods to microclimatic differences between the two situations. However, leaves were recognizable as new foliage longer in the open than under the canopy (FIGURE 1). If new foliage is more palatable than old foliage (Lowman & Box 1983) and if palatability declines in concert with the visual characteristics identifying foliage as new, then it is possible that in the open new eucalypt foliage retains its maximum attractiveness to herbivorous insects longer than it does under the canopy. Differences in insect numbers in the two places might, therefore, reflect responses of herbivorous insects to leaf quality. This hypothesis requires testing.

Trophic Structure

Although most insects were not identified to species, many could be assigned to a broad trophic category by morphology of the mouthparts, on the basis of known food habits of the higher taxonomic category to which they belonged, or from direct observations of feeding in the field. The categories used were omnivores, predators, herbivores, and miscellaneous (mostly unknown). The herbivores were further divided into chewing insects, sucking insects and nectarivores.

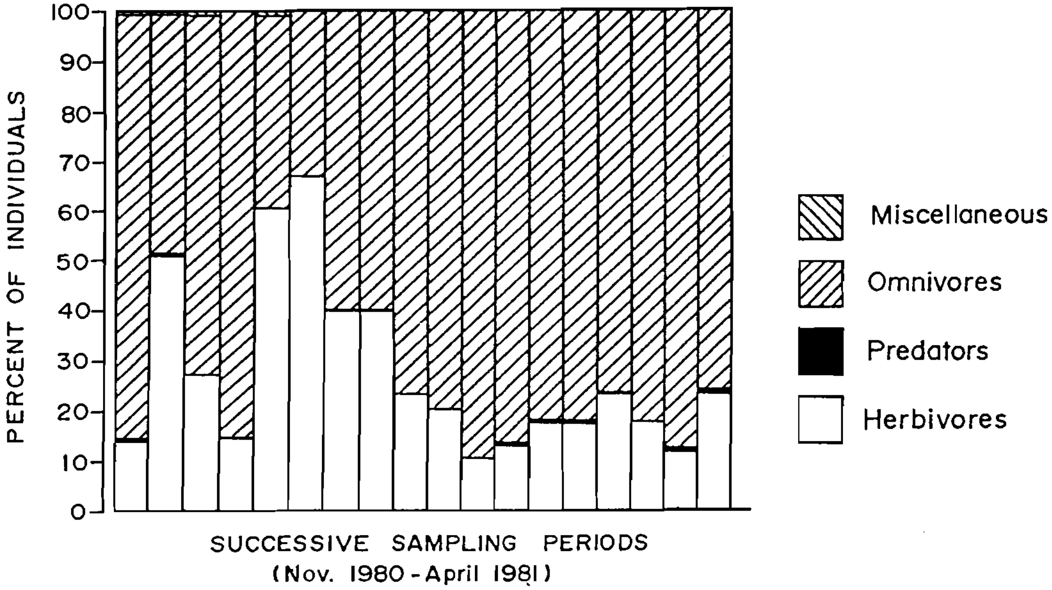

FIGURE 9. Trophic structure of the arthropods associated with saplings.

When all arthropods were included, most of the individuals were either omnivores or herbivores with the relative proportions fluctuating temporally from a preponderance of one to a preponderance of the other. All other trophic categories collectively accounted for only a small proportion of the total number of individuals (FIGURE 9).

These results were heavily weighted by ants which accounted for almost all of the omnivorous individuals. The representation by ants varied greatly and may have been weather-dependent. Consequently, the data were re-analyzed excluding ants. When that was done, the proportion of the total numbers of arthropods on the saplings that were herbivores consistently exceeded 95% (FIGURE 10). Thus, it appears that there is always a high proportion of herbivores associated with the saplings, supplemented by large, but variable numbers of ants.

In order to ascertain whether there were seasonal changes in the overall relative proportions of feeding types within the herbivores, that trophic category was analyzed separately. Sucking herbivores maintained numerical dominance throughout the study, but their relative proportions changed (FIGURE 11). Most of the time they accounted for 90% or more of the herbivorous individuals.

There were several occasions on which there was a departure from this situation. Usually chewing insects accounted for 15% or fewer of the herbivores, but in mid-December and late January these values leaped to over 40% and over 30%, respectively. These shifts in trophic structure reflect the peaks in abundances of beetles (FIGURE 2), and like those peaks, do not coincide with major flushes of leaves on the saplings. In early December and again in late January, nectarivores reached an unusually high proportion (about 10%); these were not coincident with any of the six times that flowers occurred on individual saplings and must have been related to events elsewhere in the community.

Although sucking insects dominated the herbivorous trophic category numerically, they were not necessarily more important to the sapling than were grazing insects. Psyllids, scales, aphids and leafhoppers are all small, whereas scarabs and chrysomelids are much larger. The latter groups may have contributed a greater biomass, at least on occasions, than did the sucking insects.

It should be noted that the trophic structures presented here refer only to that segment of the arthropod assemblage associated with the shoots of saplings. Trophic structure for the assemblage as a whole, and including arthropods underground, or associated with other plants, may be quite different.

DISCUSSION

The present finding that chrysomelid and curculionid beetles were among the dominant chewing herbivores is shared by other studies on Australian eucalypts. Stone and Bacon (1995) identified chewing insects, particularly Chryso-

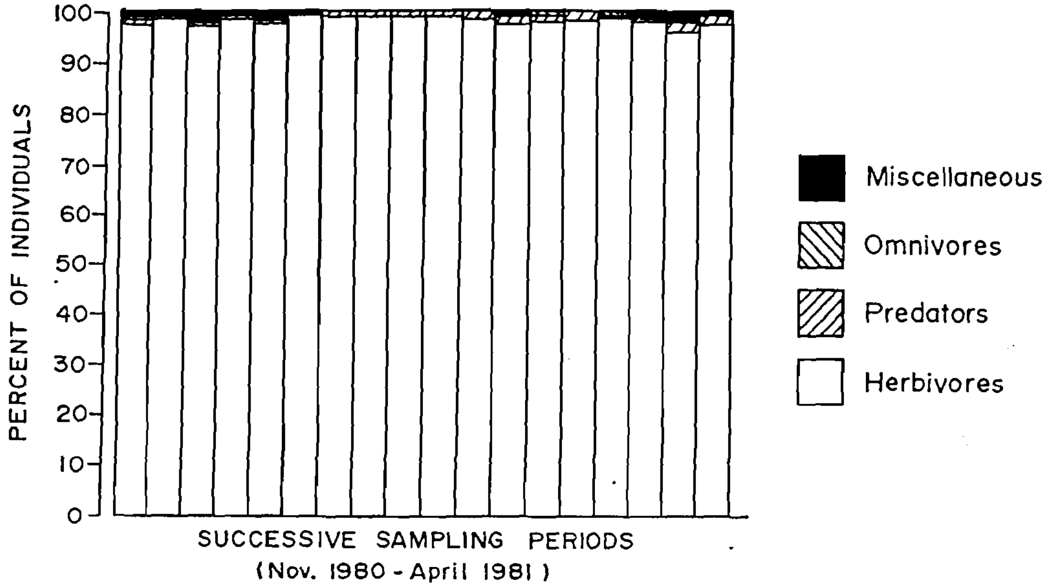

FIGURE 10. Trophic structure of arthropods, excluding ants, associated with saplings.

melidae and Curculionidae, as the source of most foliage damage in *Eucalyptus camaldulensis*.

It has been noted that dieback of eucalypts on the New England Tableland of Australia is more severe on isolated trees or patches of trees in the open than it is in woodlands (Heatwole & Lowman 1986). The present finding that leaves in the open maintain their new appearance, and perhaps their attractiveness to insects, longer than those under the shade of a canopy may provide a partial explanation.

It is clear that there was considerable seasonal fluctuation in numbers of macroarthropods associated with eucalypt saplings. Such changes could result from one or a combination of the following influences: (1) natural increase or decrease resulting from reproduction and mortality

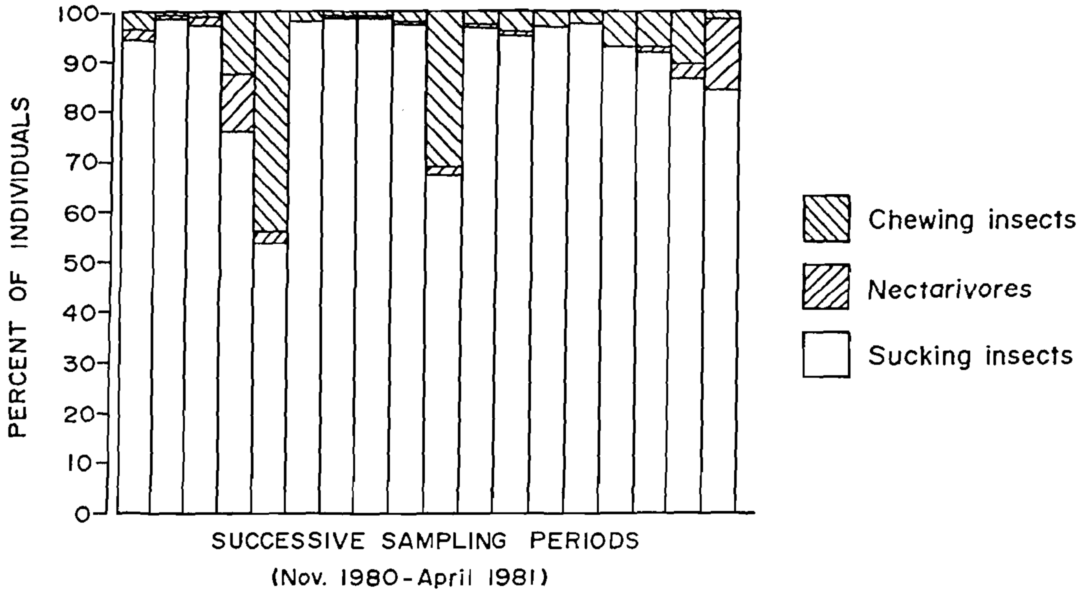

FIGURE 11. Trophic structure of herbivorous arthropods associated with saplings.

in the populations resident on the sapling, (2) immigration and emigration of animals between the saplings and other sites in the area, (3) changes in activity levels of animals that were not resident on the saplings but visited them in varying numbers, and (4) physiological changes within the saplings over time (particularly leaf and stem toxicity and nutrient content) depending on immediate or seasonal weather conditions.

Ants were almost certainly of type three above and they showed very great short-term changes in numbers associated with the saplings. All of the species nested in the ground and foraged widely including upon saplings. Heatwole *et al.* (1981) showed that the numbers of ants foraging on vegetation were directly related to the weather on particular observation days. Also, some ants reduce or cease foraging activity outside of the nest when they have adequate stored food reserves (Whitford & Ettershank 1975, Whitford 1976). These factors may have been operating in the present study as well.

The various species of eucalypt saplings differed markedly in the number of arthropods they harbored. They ranked (from highest to lowest numbers of arthropods): *E. caliginosa, E. blakelyi, E. viminalis, E. melliodora,* and *A. floribunda.* The eucalypts in the New England area were not all equally susceptible to dieback (see Heatwole & Lowman 1986). *Eucalyptus nova-anglica* was the most susceptible and the first to be affected. The second phase claimed three additional species, two of which were included in the present study (*E. blakelyi* and *E. melliodora*). Unfortunately, data are not available for sufficient species to ascertain whether susceptibility to dieback bears a consistent relationship to insect burden.

Saplings of other taxa of trees also exhibit marked interspecific differences in insect burden. For example, among five species of understory euphorbiaceous saplings in Papua-New Guinea, the density of ants varied 20-fold and the density of herbivores varied three-fold (Whalen & Mackay 1988).

Numbers of associated arthropods may reflect interspecific differences in foliar nutrient levels. Foliage of some eucalypt species in eastern Australia have higher nitrogen and phosphorus levels than do those in Western Australia, and also have greater abundance and diversity of arthropods (Majer *et al.* 1992).

Strong fliers are highly mobile and can move from one sapling to another or between saplings and other habitats. Also, like ants, their visits may be weather-dependent. It is almost certain that one or both of these effects were operating in the case of the Lepidoptera and Diptera as in both cases the peak numbers of adults on the saplings exceeded the preceding numbers of larvae on the same saplings. Thus, adults must have flown in from elsewhere. Immigration and emigration must also be considered a possibility for beetles and for hymenopterans other than ants as well as for some of the groups represented by few individuals. Some mobile animals may briefly visit a sapling and then move on, only to be replaced by other conspecific individuals. Thus, numbers at a spot-count may be much lower than the total number of individuals visiting over the course of the day. Such a situation probably occurred with respect to parasitoid hymenopterans.

The more sedentary groups such as the Hemiptera and Arachnida are less subject to large, short-term fluctuations of the second or third types, especially the psyllids and scales. Thus, their numbers are more likely to be strongly influenced by factors affecting demographic changes of resident populations.

Variation in insect numbers among saplings may also be a consequence of physiological changes within plant tissues. For young saplings, the production of photosynthetic tissue represents a great investment, especially since the leaves are long-lived (Lowman & Heatwole 1992). Eucalypts, like many other plants, have evolved characteristics that provide effective defense of their leaves. Different physical, chemical, nutritive, temporal, and spatial attributes have been examined for leaves in recent literature in an attempt to explain differences in insect herbivory among tree canopies.

Leaf tissue may accumulate chemical substances that are unpalatable to herbivores, e.g., toxins or digestion-reducing substances (Chapman 1974, Cates & Rhoades 1977, Lowman & Box 1983). In some cases, leaves can mobilize these substances rapidly to sites of insect attack (Carroll & Hoffman 1980). It has been suggested that plants may indirectly deter herbivores with leaves of low nutritive quality that renders them less desirable (Onuf 1978, Lansberg & Wylie 1983), and stresses on eucalypts (e.g., decreased water availability and soil fertility) cause a reduction in foliar quality (Landsberg 1990c) that makes the leaves less attractive to herbivores. However, Landsberg and Gillieson (1995) found no support for a relationship between high herbivory and either high plant stress or low-resource environments in eucalypt associations. Grazing itself may even induce greater, rather than lesser, palatability of leaves. For example, Landsberg (1990a) found that *Eucalyptus blakeleyi* suffering from dieback had higher nitrogen content and was more heavily grazed by insects than were healthy trees. This was probably a direct response to grazing as artificially clipping leaves to simulate grazing induced higher nitrogen content and greater herbivory rates in the regrowth (Landsberg 1990b). Clearly, the interaction of grazing and foliar nutrient content is complex and subject to sources of variation.

The numbers of arthropods on saplings were much higher on saplings in the open than under the canopy. This may be related to differences in maturation rate, since foliage on shaded saplings lost the appearance of "new" foliage faster than did those in the sun. This in turn may reflect differences in nutrient levels and attractiveness to grazing insects. Majer *et al.* (1992) showed that young eucalypt leaves had higher nutrient content than did older leaves and that nutrient levels were higher in foliage of the canopy than of the subcanopy. Given the differences in apparent maturation rate between leaves in the open and those under the canopy in the present study, a comparison of their leaf chemistries would be of interest.

From the point of view of the saplings, the important consideration is the change in numbers of associated arthropods and how those arthropods behave trophically, rather than whether the changes are caused by immigration-emigration, natality-mortality, weather-dependent activity, leaf quality or some other factor.

Of most obvious importance to the saplings were chewing insects (FIGURE 5). They were abundant at the beginning of the study but soon dropped to rather low levels and fluctuated at levels below 1,100 individuals for the rest of the study. However, minor damage to leaves (up to 10%) was frequent and occasionally moderate (up to 60%) damage occurred. Some individual saplings showed brief, albeit severe, infestations and sustained heavy damage (over 60%).

Sucking insects are also potentially deleterious to the saplings. On particular saplings, psyllids briefly showed high numbers (FIGURES 3, 7).

Thus, for the herbivorous insects as a group, or by either chewing or sucking categories individually, there were seasonal fluctuations, and within those, the history of individual trees varied, some having few herbivores at any time, others having large numbers of either grazing or sucking ones for brief periods, but never having chronically high populations. The phenology of herbivores was different for each individual tree, peaks among individual saplings seldom coinciding. Thus, there was an 'outbreak' of a species of herbivore on one sapling at one time followed by similar events involving a different or perhaps the same herbivore at another time on a different sapling. These momentary buildups and declines did not seem to be related consistently to an individual sapling's leafing phenology. It may be that once herbivores have settled on an abundant food source they ignore nearby ones that might develop (such as a slightly later-leafing sapling) until after the amount or quality of their immediate resource has declined.

The decline of herbivore peaks did not seem to result from the attraction of predators. Peaks in herbivores were not followed by, or coincident with, peaks in predators for any sapling.

The overall ratio of herbivorous individuals (combining chewing, sucking and nectar-feeding types) to predatory individuals (including entomophagous parasites) ranged from 15:1 to 437:1 and averaged 140:1.

Thus, at all times on all saplings, insect herbivores were in much greater abundance than were insect predators; the numbers of the latter probably were never sufficiently high to decrease markedly the herbivore population. Most herbivore peaks were rather transient, suggesting immigration of large numbers of individuals to a particular sapling in new leaf, feeding on it and then moving on. Such an ephemeral occupancy of a site provided insufficient time for local buildup of predators on that sapling through increased natality, and there were never any large numbers of migrant predators. This pattern of shifting herbivory would have two advantages to the herbivores: (1) It allows them to seek out the best food sources of the moment (e.g. new leaves), and, as new, high-quality resources appear, to exploit them rather than utilize those which have become inferior through age or buildup of grazing-induced toxins. It is possible that the greater numbers of arthropods in the open than under the canopy may reflect such a response. (2) It allows the herbivores to move on before demographic responses by local, sedentary predator populations have time to take place. Since mobile insect predators are either too few, or are not attracted quickly enough to temporary local concentrations of herbivores, they probably do not exert effective control over them. The more sedentary herbivores perhaps are more subject to predatory control.

As omnivores, ants may function as predators on some occasions, serve as scavengers on others, or follow other trophic pursuits at still other times. They show large, temporary peaks of abundance on particular saplings. Because ants can mobilize large numbers in a short time and alter their feeding habits, the hypothesis was advanced that they might be attracted to particularly abundant, temporary food sources. Exclusion of ants from some euphorbiaceous saplings in Papua-New Guinea resulted in an elevation in the number of herbivores present and in greater levels of damage to leaves (Whalen & Mackay

1988). However, exclusion of ants from mature and new foliage of *Eucalyptus incrassata* in Australia did not affect rates of herbivory (Mackay 1991). In the present study, the question was asked whether ants were attracted to concentrations of herbivorous insects upon which they preyed during peak periods. This was not the case. In no case did any ant peak coincide with that of a chewing herbivore, or follow close behind it. There was a positive relationship between some ants and sucking herbivores, but not as predators; rather, ants may have protected populations of aphids and eurymelids which they tended for their secretions. Sucking insects did not show such rapid or pronounced changes in numbers as did grazing herbivores; however, ant peaks were not related consistently to changes in populations of sucking herbivores. Mackay (1991) found that exclusion of ants from tending eurymelid bugs on *Eucalyptus incrassata* saplings caused a decline in the bug populations.

Great temporal and spatial variability in numbers of arthropods in the canopy seems to be a common feature of eucalypts. Recher *et al.* (1996) found that arthropods were more abundant on trees in eastern Australia than in Western Australia and that different seasonal patterns were exhibited in the two places, with seasonal variability greater in the west. In eastern eucalypt forests proportionately more taxa peaked in spring and summer and declined to a minimum in winter. In western forests some taxa had autumn, spring, or even winter peaks, while others had summer or winter minima. Year to year variation in arthropod numbers could be as great as that between seasons, indicating the need for long-term studies. However, correlation of arthropod abundances with environmental factors were detected in their study. They found that some herbivorous groups responded to time of leaf production, whereas decomposers and fungus feeders responded to moisture, and predators/parasites to food supply.

Dispersion of food resources in time and/or space may influence arthropod abundances. Spacing of plants may minimize mortality from herbivory or drought (Feeny 1970). Species that are patchy in distribution may be more difficult to locate and may escape pest outbreaks (Janzen 1968). The variable leafing patterns among the 75 saplings, despite their close geographic proximity and taxonomic similarities, may represent a temporal defense through irregularity; the supply of young leaves was patchy and unpredictable throughout summer months.

The leaf flush of individual saplings may escape insect peaks altogether (e.g. *E. melliodora*, sapling no. 11; FIGURE 7h). However, in general the insects on eucalypt saplings may lead to reduction of plant growth as manipulative experiments with insecticides have shown (Lowman & Heatwole 1987). There was no sapling mortality during the present study.

In conclusion, there was considerable variation in the phenology of leaf flushing among individual saplings, even of the same species at the same site. Grazing insects aggregated on only one or a few individual saplings and ignored others close by. Thus, time and amplitude of peaks of insect numbers varied greatly among saplings. Some saplings escaped intense attack by grazing insects if they leafed when no herbivorous species were abundant, or if they flushed just after another nearby tree had leafed out and attracted available insects. Other saplings hosted dense populations of herbivores.

In view of such variability of arthropods during times of leaf flushing, and the lack of coincidence in peak insect numbers on different saplings, mean values (even when accompanied by standard errors) for a large number of saplings do not accurately characterize the seasonality of herbivores. One must examine a series of case histories with a view to observing the various patterns of herbivory that take place.

It is perhaps more important to understand the dynamic nature of the interaction than to obtain an estimate of the average number of insects on the saplings at different times. Any temporal, spatial or interspecific comparisons must take into account that each sapling may have a different history in terms of number of leaf flushes, number and amplitude of peaks of herbivores, and species of insects involved in those peaks. Williams (1990) similarly emphasized that for eucalypts a comparative assessment of levels of herbivory using mean values may not adequately reflect actual field processes. Haukioja *et al.* (1994), after comparing herbivory on birches and eucalypts, predicted that the most useful syntheses of herbivore-plant interactions will be those based more on a specific knowledge of plants and herbivores and an understanding of their adaptations and interactions than on constructs arising from general theoretical assumptions.

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