THE PHYTOPHAGOUS INSECT COMMUNITY
ON THE VELD FIG,
FICUS BURTT-DAVYI HUTCH.

THESIS
Submitted in fulfilment of the
requirements for the Degree of
MASTER OF SCIENCE
of Rhodes University

by
SALLY JANE ROSS
January 1994

ACKNOWLEDGEMENTS

I owe many thanks to my supervisor, Dr Steve Compton, firstly for enticing me to South Africa to do a Masters degree, and secondly, for his constant enthusiasm, encouragement and humour, even whilst on the other side of the world. I am indebted to Prof. Pat Hulley for his invaluable support in Steve's absence, and for constructive comments on early drafts of this thesis. Martin Hill deserves a huge thankyou for valiantly ploughing through the final manuscript and making many helpful comments.

Thanks are also due to the following people: Sarah Radloff of the Mathematics Department, for her invaluable statistical advice and accompanying humour; Mr Cameron, senior groundsman of the 1820 Settler Botanical Garden, for allowing me to regularly crawl around under fig trees in the gardens; the Institute for Freshwater Research in the Geography Department, for allowing me access to their climatic data; and Gurutze Calvo Ugarteburu for peering at me through a theodolite for hours on end. A special thanks to Trillian for warding off the hordes of funny little men who hang out in the Botanical Gardens.

All of my friends - Costi-Poo, Gugie-pops, Willi-Jo, Marts, Dassie-Dave, Flopsy and the Hillbilly - deserve medals for putting up with my seemingly endless writing-up stage. An extra big thankyou to Costas for acting as a sounding board for ideas and for putting up with all of my wifflings, and to Gugu for keeping me sane in the last throws of the preparation. I am very grateful to my parents for their encouragement of my wanderlust and for their patience over the last year. Finally, it remains to thank the FRD and the William Waddell Trust Fund for financial assistance.

ABSTRACT

The quest for patterns in community organisation is a daunting task which may be made easier by concentrating on communities associated with a restricted range of resources and therefore of relative simplicity. Here, the phytophagous insect community on the African fig tree *Ficus burtt-davyi* Hutch. was studied in an attempt to gain some insight into the factors which influence the composition of insect herbivore communities at a very local level, on individual plants of one host species at a single location.

The tree's phenological patterns were determined, due to their relevance to herbivores, particularly those which are host-specific feeders. The trees exhibited inter-tree asynchrony and intra-tree synchrony in fruit crop initiation, whereas leaf production was synchronous both within and between trees.

Sixteen frequently occurring phytophagous insect species fed on the 123 *F. burtt-davyi* trees in the study area over a period of one year. Factors with the potential to influence the composition of this community were investigated at levels of the whole community (species richness), the guild, and the individual species. At each 'level' the effects of the measured factors on fluctuations in community composition were investigated, both over time (i.e. temporally) and spatially from tree to tree.

During the year the phytophage community was influenced largely by temperature, although rainfall and tree phenological changes did exert varying influences on the abundances of guilds and individual species. Tree to tree variation in species richness (and thus commensurately, in the frequencies of occurrence of guilds and individual species) was influenced primarily by tree architectural complexity. Architecturally more complex trees hosted a greater number of species, a relationship largely attributable to effects of passive sampling and within-tree microhabitat heterogeneity and/or the availability of living space. The distributions of the leaf and stem piercing species were strongly associated with the presence of ants and this relationship manifested itself within the community as a whole. The degree of isolation of trees had consequences for individual species and for overall species richness, with the numbers of species present decreasing as trees became more isolated.

A detailed analysis of guild distributional patterns revealed that the most important influential factors were those also evident at the level of the whole community and that species within guilds were, on the whole, no more similar to one another with respect to their habitat preferences than species from different guilds. The grouping of species into functional units therefore threw no additional light on the way in which this community is organised.

An analysis of possible interspecific interactions between all of the phytophagous species in the community revealed only positive associations, both between species within guilds and between those in different guilds. These were doubtless attributable to autocorrelation as a result of similar habitat preferences. Competition was therefore rejected as an organising force within the community.

TABLE OF CONTENTS

1 INTRODUCTION

The first approach to community ecology was made by Aristotle with his classification of animals according to their habitat. Theophrastus (372-288BC), a pupil of his, then described plant distributions in relation to altitude, and Plinius (23-79AD) produced a natural history book (Anderson and Kikkawa 1986).

Despite such early beginnings and the emergence of the term 'community' in the 1800's (Anderson and Kikkawa 1986), modern ecologists remain uncertain as to the precise nature of the latter (Drake 1990). Perceptions of the community vary from Cohen's (1989) broad 'whatever lives in a habitat (lake, forest, sea floor) that some ecologist wants to study', to Lawton and MacGarvin's (1986) more precise, yet still liberal 'an assemblage of co-occurring species with the potential to interact'. 'Co-occurring species' is a vague term which could encompass the insect borers living in a single tree branch or all species within an ecosystem. Where does one draw the line? In fact can one draw a line at all - are communities discrete entities? The answer seems to be 'no', but without sub-dividing ecosystems into manageable chunks we cannot hope to begin to understand them. Hence, Cohen's (1989) perception of a community is not as unrealistic as it at first seems.

This uncertainty with respect to the precise meaning of the word 'community' is symptomatic of the state of community ecology as a whole. In the early part of this century the debate as to the nature of the community came to a head (Roughgarden and Diamond 1986). Clements, taking a 'holistic' approach to ecology, perceived the climax community in a plant succession as a 'superorganism' arising as a result of directional and self-determining pathways

(Anderson and Kikkawa 1986; Clements 1936; Levin 1989; Roughgarden and Diamond 1986). In complete contrast, however, Gleason took an 'individualistic' approach, arguing that species assemblages arise simply as a result of random spread and establishment of organisms along environmental gradients. Hence, his boundaries were not as sharp and his species associations much less predictable than those of Clements' 'superorganism' concept (Anderson and Kikkawa 1986; Begon et al. 1987; Roughgarden 1989).

In the decades since these views were formulated many facets of community ecology have been widely explored (Cody 1989; Cody and Diamond 1975; Drake 1990; Koehl 1989; Levin 1989; Roughgarden 1989; Roughgarden and Diamond 1986; Tilman 1989). Currently, general opinion lies closest to Gleason's individualistic concept. Species assemblages, constituting a limited subset of all species in the species pool, are considered to result from interactions between species and their environment and to a lesser extent, from interactions between species within that environment. Among the latter are the processes of competition, predation, parasitism, commensalism, amensalism and mutualism. It is the degree to which these processes, particularly competition, play a role in community structuring, that is presently a cause of much controversy (Claridge 1987; Connell 1983; Diamond and Case 1986; Schoener 1983; Strong et al. 1984).

Competition between species for limited resources has been found to modify community membership in many systems, and certainly until the early 1980's was believed to be a major organising force in the majority of communities (Begon et al. 1987; Cody and Diamond 1975; Rathke 1976; Roughgarden 1989; Schoener 1982; Shorrocks et al. 1984; Strong 1984; Strong et al. 1984). Whilst partly due to the concentration on systems in which workers expected to find competition, this is most probably largely attributable to the fact that the majority of animal community studies have been directed at vertebrates, the group on which the classical framework of niche theory and resource partitioning has been based (Lawton and MacGarvin 1986; Schoener 1983). The members of such communities, however, are estimated to constitute a mere 4% of all living species (Strong et al. 1984) and as such are hardly a representative sample. In the last decade, insect communities have, however, attracted much, long overdue, attention: they constitute 57% of all living species in the world - 26% phytophagous species and 31% saprophagous and predacious species. Generally, in such communities competition has been found to play a less important role than in vertebrate communities and is therefore no longer perceived to be of over-riding significance in all groups.

Hence, one of the problems with the theory of community organisation is its global application to too great a diversity of communities comprising organisms with widely varying life cycles, generation times, and dispersal abilities, depending on differing resources in different geographical regions, and so on. One way of overcoming this difficulty is to concentrate on the food web and particularly the resource base of the community which, according to Price (1984, 1990), is most likely to be the critical organising influence as trophic systems are driven from below. Price (1984) proposes that other interactions such as competition, commensalism, mutualism, predation, and parasitism are most likely to be of secondary importance.

This is an appropriate point at which to direct our attention to one particular resource type and its associated community: plants and their phytophagous insects.

In their reviews of insect community organisation, Lawton and MacGarvin (1986) and Lawton (1984a) tackle the question of community structuring by considering the population dynamics of the component species. Generally, populations are regulated by density-dependent processes and perturbed by density-independent ones (Begon et al. 1987) and it is the form and relative magnitudes of both of these that determine community stability and predictability from year to year. How often does density-dependent population control occur though, and what form does it most commonly take in phytophagous insect communities?

The foregoing may be answered by examining the life tables and accompanying k-factor analyses of individual phytophagous insect species. Strong et al. (1984) composed a summary of 31 such tables of which as many as 30-50% showed no, or very weak density-dependence. This evidence, combined with that from the limited number of studies on whole phytophagous insect communities over a number of years (e.g. changing abundances of bracken-feeding insects over 10 years (Lawton 1984a, 1984b), and of grassland leafhoppers over 6 years (Waloff and Thompson 1980)) indicate that whilst herbivorous insect communities do not consist of randomly fluctuating populations, nor are they highly deterministic and predictable in structure (Lawton and MacGarvin 1986).

One can, however, gain some insight into the factors which limit community membership and hence confer some pattern on phytophagous insect communities by considering host plant and habitat influences on their phytophagous insects and the role played by interspecific interactions. Such aspects of the community organisation of phytophagous insects have been widely reviewed (Claridge 1986; Lawton 1984a, 1984b; Lawton and MacGarvin 1986; Lawton and Strong 1981; Price 1980; Southwood 1978; Strong 1984; Strong et al. 1984) and will now be discussed.

Host plant and habitat influences

Host plant and habitat influences manifest themselves both locally (i.e. at a particular site) and regionally (i.e. over the whole of a plant's range) and also within a short-term, ecological time scale and longer term, evolutionary time scale.

To date a wide range of host and habitat associated factors acting at varying scales have been identified as determinants of herbivore community composition: coevolutionary effects; host structural diversity; host range or area; taxonomic isolation; physical isolation; host density; effects of other neighbouring plant species; local abundance; leaf form; phytochemistry; and habitat topography (e.g. Banerjee 1981; Claridge 1987; Compton et al. 1989; Fowler 1985; Jones and Lawton 1991; Lawton 1984a, 1986; Lawton and Price 1979; Lawton and Strong 1981; Price 1990; Southwood 1978; Strong et al. 1977; Strong et al. 1984; Zwölfer 1986).

Coevolutionary effects

Coevolution, 'the reciprocal evolutionary change in interacting species', has often been used to explain the relationship between insect attack and the development of secondary defences by the host plant (Strong et al. 1984). This idea originated with Ehrlich and Raven (1964) and may be summarised as follows: some insect species evolve the ability to overcome plant phytotoxins and by feeding on such plants, reduce the fitness of the latter. As a result those plants containing the more noxious chemicals are selected for. Insects, in turn, become more tolerant and specialised, and so on (Strong et al 1984). Hence, coevolution provides a plausible mechanism to explain contemporary insect herbivore community structure, and indeed is supported by some evidence (e.g. Berenbauch 1983; Gilbert 1982). However, looking more closely, one finds many problems with this explanation (Lawton 1984a), 'the sustained, reciprocal and intense interactions ... necessary for coevolution (being) rare enough that the mainstream (of evolution) is not usually deflected' (Strong et al. 1984).

Host structural diversity

Often, the greater a host plant's structural diversity, the higher the richness (or number) of its associated insect herbivore species (Claridge 1987; Davis 1975; Fowler 1985; Janzen 1968; Lawton 1983, 1986; Lawton and Price 1979; Lawton and Schröder 1977; Leather 1986; Moran 1980; Strong and Levin 1979; Strong et al. 1984; Zwölfer 1986). The importance of host plant structural diversity was first suggested by Janzen (1968) although it wasn't until 1977 that Lawton and Schröder (1977) termed this latter, plant 'architecture'. They found herbivore species richness to decrease with decreasing structural diversity, from woody shrubs to perennial herbs to monocotyledons, a relationship often confirmed since (e.g. Lawton 1983; Strong and Levin 1979).

Two major plant attributes may contribute to this effect: size *per se* and the variety of plant parts (Lawton 1983). As in host plants with wide-ranging distributions, large plants may be encountered more frequently than smaller ones due to their greater 'apparency' (Feeny 1976) and hence may passively sample a larger subset of the insect species in the area. Additionally, via analogy with MacArthur and Wilson's (1967) theory of island biogeography, larger plants may have a lower herbivore extinction rate as they are able to support larger insect populations (Lawton 1986; Strong et al. 1984). The latter, however, assumes that herbivores are resource-limited with competition being a fundamental organising force in the community.

An increasing variety of plant parts, or microhabitat heterogeneity, offers a greater diversity of resources to herbivores: the number of microhabitats available for feeding, enemy avoidance, oviposition, overwintering, etc. increases and there are increasing possibilities for the zonation of herbivores within the multiple layers of differing microclimates in a large canopy (Lawton 1986; Strong et al. 1984; Zwölfer 1986).

Host range

Host geographical range can have a strong bearing on the number of phytophagous insect species feeding on a plant species, with numbers increasing as a host becomes more common and widespread (Cornell and Washburn 1979; Lawton and Price 1979; Lawton and Schröder 1977; Rey at al. 1981; Strong 1979). The potential explanations are exactly the same as those for plant architecture effects. As a host becomes more widespread, so it becomes more 'apparent' (Feeny 1976) to potential colonists, may encompass an increasing variety of habitats, and perhaps support larger insect populations, hence reducing extinction probabilities.

Taxonomic isolation

Taxonomic isolation of host plants may also have some effect on insect herbivore colonisation (Claridge 1987; Jaenike 1990; Strong et al. 1984), those with a larger number of close relatives often being colonised by a greater number of phytophagous insect species. This may be explained by the observation that insects are more likely to expand their host range to more closely related hosts than to more distantly related ones with widely different chemistries (Jaenike 1990). Such an effect has been found to account for small amounts of variation in several studies (Connor et al. 1980; Lawton and Schröder 1977; Moran and Southwood 1982), although the degree of herbivore species impoverishment on taxonomically isolated plants was usually small.

Physical isolation

MacArthur and Wilson's (1967) equilibrium theory of island biogeography predicts that physically isolated plants will host fewer herbivore species than those less isolated, due to lower immigration rates (Williamson 1981). In practice, however, this element of the island biogeography theory often breaks down when applied to plant-insect systems (e.g. Ward and Lakhani 1977). This may be due to the difficulty of identifying source areas of potential colonists, different herbivores colonising in different ways and therefore from varying maximum distances (Strong et al. 1984). However, this breakdown may not be attributable purely to such problems. For instance, the proportion of monophagous and polyphagous phytophages may be important, the larger the specialist component the greater the isolation effect and vice versa (Thomas 1990). The direct and indirect (herbivore-mediated) effects of isolation on the herbivores' predators and therefore on their prey must also be considered (Thomas 1989). Furthermore, some insect species show an indirect preference for isolated plants. Thompson and Price (1977), for example, found the number of parsnip webworms (*Depressaria pastinacella*: Lepidoptera) to be 50% higher on isolated plants than on those in dense stands, due to the increasing development of umbels suitable for oviposition as host plant density increased.

Host density and neighbour effects

The effects of host plant density and the diversity of surrounding vegetation are complex and often inseparable. Root (1973) proposed the 'resource concentration hypothesis' to explain the often observed decrease in herbivore diversity with increase in resource 'purity' (i.e. high host density and low neighbour diversity). Firstly, many herbivores, particularly specialist feeders, seem to be more likely to locate 'concentrated' hosts due to their greater 'apparency' (Feeny 1976; Holmes and Jepson-Innes 1989; Karban 1993a, 1993b; Rauscher 1981), both physically and chemically (for example, odours may be more concentrated: Ralph 1977). Secondly, and probably more importantly, once they have located dense, pure stands, specialist feeders are likely to stay there. Therefore, while generalists are more likely to move in and out to feed, reproduce, etc., a few specialists may attain greater relative densities in the simple environments (Root 1973; Ralph 1977). This in turn may cause biomass to become unevenly distributed between insect species and therefore diversity to decrease.

An alternative 'enemies hypothesis' proposes that more diverse habitats will harbour a more even distribution of biomass among herbivore species (and therefore, a greater species diversity) due to their supporting a wider variety of generalist predators and parasites sensitive to shifting prey populations (Root 1973).

Hence, the prediction is that less concentrated host plants will support a greater diversity and possibly number of species, than more concentrated hosts. However, such effects on species numbers are based on the assumption that herbivore densities are high enough for competition to be of importance. If the latter is not true (as is often the case in phytophagous insect communities: e.g. Strong et al. 1984) there is the possibility that the attraction of specialists to the dense, pure stands will simply swell the numbers of species, no competitive exclusion taking place and the more concentrated hosts supporting a greater number of species. However, there is as yet no direct empirical evidence of the effects of host plant density and the diversity of surrounding vegetation on species richness as opposed to on species diversity.

Foliage density

The above refers largely to host plant density relative to other plant species, but absolute foliage density can also be important. The results of work addressing this question are extremely varied, some herbivore species preferring high density hosts and others low density (e.g. lepidopterans: Thompson and Price 1977), whilst still others show no preference (Lawton and MacGarvin 1986; Strong et al. 1984). Hence, it is impossible to make simple generalisations as to the effect of absolute density on phytophagous insect species richness.

Habitat topography

Habitat topography affects insect distribution via interrupting air flow and hence producing sheltered zones where insects accumulate (Lewis 1969; Root 1973). Such topographical effects on community structure are poorly studied due to the difficulty of quantification: hills, rocks, buildings, and vegetation all alter air flow in distinctive ways and each insect species may react differently according to their mode of dispersal and size. Hence, one needs to understand air flow patterns around, over and through the various obstacles before predicting whether accumulation of insects on or avoidance by insects of the tree beyond will be encouraged.

Additional variables

The above are the most commonly studied patterns and effects, although there are numerous others which may be added to the list. Amongst these are the effects of local host abundance and leaf form. Plants that are less abundant within their geographic range might host fewer herbivore species than those which are more common, due to their lower 'apparency' and therefore degree of exposure (Neuvonen and Niemela 1981; Strong et al. 1984). Leaf form has also been found to have an effect on the number and identity of leaf-feeders, those plants with herbivore-unfriendly leaves (e.g. finely divided, spiny, hairy etc.) often hosting fewer species (Fowler and Lawton 1982; Lawton and Price 1979; Neuvonen and Niemela 1981).

Interspecific interactions

Returning to Strong et al.'s (1984) summary of life tables, one sees that of the density-dependent process affecting the life histories of the 31 insect species, natural enemies were dominant over intraspecific competition at a ratio of approximately 2:1. Given the apparent rarity of competition between members of the same species, its occurrence between more distantly related members of different species (interspecific competition) is even less likely. Many studies provide evidence of the total lack of importance of such interspecific competition (e.g. Lawton 1982, 1984a, 1984b; Root 1973; Strong 1982; for reviews see Connell 1983; Lawton and MacGarvin 1986; Schoener 1983; Strong 1984; Strong et al. 1984) and few reveal it's occurrence, which is often weak and usually involves only a few of the species in a community (McClure and Price 1975; Rathke 1976; Seifert and Seifert 1979; for reviews see Connell 1983; Lawton and MacGarvin 1986; Schoener 1983; Shorrocks et al. 1984; Strong et al. 1984). The implication is, therefore, that density-dependent regulatory processes in insect herbivore communities operate more often between trophic levels than within them.

Why should competition be so rare in such communities? There are several possibilities, one of which is that vagaries of the weather and/or natural enemies (predators and parasitoids) keep population densities below those at which competition would occur (Claridge 1987; Connell 1975; Lawton 1984a, 1984b; Lawton and MacGarvin 1986; Lawton and Strong 1981;

Schoener 1982). Hairston et al. (1960) argue that control by the weather is unlikely, and use the performance of introduced versus native herbivore species as evidence. Evidence for the significance of control by natural enemies is, however, plentiful. The life tables analysed by Strong et al. (1984) reveal that such factors are important density-dependent processes and cases of biological control give a further indication of the degree to which natural enemies can have an impact (Beddington et al. 1978; Strong 1982; also see Claridge 1987 for references and examples).

Further to the above, there are many examples of the occurrence of vacant niches in insect communities, revealed by the utilisation of parts of a host plant in one area of the world but not in another (e.g. gaps in niche utilisation by insects on bracken in England, Papua New Guinea, New Mexico, and Arizona - Lawton 1982, 1984b; and by herbivores on water hyacinth, soybean, grape vines, maize, cacao and sugarcane - see Lawton 1984b for references). This implies a shortage of potential colonisers at the different sites rather than a shortage of resources leading to competition (Lawton 1982; Lawton and MacGarvin 1986; Lawton and Strong 1981; Price 1980; Strong et al. 1984).

Additionally, Hairston et al. (1960) argue that the often observed abundance and general intactness of green plants indicates the availability of a food surplus to herbivores. Some have argued that this is due to a large degree to substantial parts of plants being rendered inedible due to physical and chemical defences (Ehrlich and Birch 1967; Feeny 1976; Murdoch 1966). This may be true to a certain extent, but as Hairston et al. (1960) comment, exceptions do occur when plants which are usually intact are temporarily destroyed during insect outbreaks, indicating that the herbivores are not normally limited by their food supply.

There remains one further possibility regarding competition to be considered. The fact that competition is rare in the present doesn't necessarily preclude it from having been important in the past, selection having favoured an avoidance of competition and thus a differentiation of niches (e.g Lawton 1984a; Lawton and MacGarvin 1986; Strong et al. 1984). Connell (1980) coined the term 'ghost of competition past' to describe this phenomenon. Such ideas are extremely difficult to test and hence remain largely unexplored. Strong et al. (1984) suggest that a plausible test of this hypothesis would be the comparison of insect herbivore communities which have evolved independently on the same host plant in different parts of the world. They propose that convergence of such communities under similar environmental conditions indicates a significant influence of competition in the past. However, such communities provide little evidence for convergence (Lawton 1978, 1982; Lawton and MacGarvin 1986; Strong et al. 1984). Furthermore, one might expect that if competition had been a potent organising force in the past, it would manifest itself to some degree in the present (Lawton 1984b). As already discussed, there is little evidence of it's importance in the present.

The evidence therefore points overwhelmingly towards a secondary role for competition as a structuring force in such communities. As Strong et al. (1984) conclude, the 'evidence says quite simply that although some species do compete, most species, most of the time, do not'. Instead, natural enemies usually dominate over competition in their regulatory role within insect herbivore communities, implying that such regulatory processes operate more often between trophic levels than within them. Until recently other types of interspecific interaction had been largely ignored. However, mutualisms, particularly those involving ants, may have profound effects on insect herbivore communities.

Ants can have extremely important and complex effects on phytophagous insect communities via their interactions (positive and negative) with other insects and the host plant (Table 1.1).

Table 1.1 A summary of the known effects of ants on phytophagous insect communities.

	ANT'S ACTIVITY	EFFECT ON PHYTOPHAGOUS INSECTS
ANTS TEND HONEYDEW-PRODUCING PHYTOPHAGOUS INSECTS, RECEIVING NUTRIENTS IN EXCHANGE	Place tended insects on most nutritious parts of plant.	+
	Prey on predators and parasites.	+
	Provide shelter to tended species in nests.	+
	Prey on tended species when numbers are high.	-
	Prey on non-tended species, decreasing biomass and possibly eliminating species from the community.	-
ANT-PLANT MUTUALISMS. ANTS RECEIVE FOOD AND/OR SHELTER	Usually attack phytophagous insects - degree of attack depends on reward i.e. food only or food and shelter.	-
	Rarely tend honeydew-producing insects.	+

Probably the most important effects of ants on general community structure occur via their predation of non-tended herbivores (Bach 1991; Mahdi and Whittaker 1993; Whittaker 1991) often after their attraction to extra-floral nectaries or honeydew-producing homopterans on thetree. In the latter case, while reducing numbers of some phytophages, they will increase numbers of homopterans. The total herbivore species richness may therefore be dependent on the balance between herbivore population increase via ant tending of homopterans and their decrease via predation. Conversely, ants may actually increase numbers of non-tended herbivores by removing general predators or disturbing parasitoid oviposition (Fritz 1983; Pierce and Elgar 1985; Whittaker 1991). Hence, the nature of the effects of ants on a herbivore community will depend on a complex balance of predatory and tending processes (Fritz 1983; Grant and Moran 1986; Whittaker 1991). Obviously, the extent to which an ant species affects community composition will depend to a large extent on its feeding habits (i.e. whether it is primarily a honeydew collector, active predator, scavenger, etc.), its size and possibly its diel activity rhythm.

Finally, relationships over three trophic levels (i.e. host plant, phytophage and predator) must be considered if communities are to be understood as fully as possible. Such relationships are extremely complex and variable (Leather and Walsh 1993; Strong et al. 1984). For instance, host plants may increase herbivore vulnerability to predators and parasitoids via phytochemical resistance and reduction of nitrogen levels and water content. Under such sub-optimal conditions herbivores will develop more slowly thus being exposed to predation for longer. On the other hand, this same scenario can work in reverse. The growth rate of the parasitoid populations may be more susceptible to the diminished growth rate of its host herbivore than the host herbivore is to the sub-optimal conditions of its host plant. The herbivore's vulnerability to parasitism will therefore be reduced. The intricacy of these systems makes generalisations difficult, at least until more research has been directed at them.

The above-mentioned variables can, to some degree, explain variation in community composition regardless of seasonal changes. However, trees do change seasonally: as young leaves flush, mature and finally senesce, their nutrient, defence and physical characteristics change (Basset 1991b; Coley 1980, 1983; Feeny 1970, 1976). Fruiting may also occur at intervals through the year. Whilst being directly affected by climatic factors, phytophagous insects also vary in their nutritional preferences, some becoming seasonal specialists and others remaining generalists. The behaviour and abundance of such generalists are, however, likely to alter seasonally. Hence, the widely noted seasonal changes in the structure of phytophagous insect communities (Basset 1991a; Price 1976; Strong et al. 1984).

Analysis of communities in order to establish which of the above factors influence their composition can be conducted at several levels (Terborgh and Robinson 1986). At one extreme, questions can be asked about the community as a whole; for instance, how is species number determined? At the other extreme, the individualistic responses of species to environmental factors and to other species can be investigated. Intermediate between the two lies the guild approach, the term 'guild' having been introduced by Root (1967) to describe a group of species exploiting the same class of environmental resource in a similar way. The grouping of species like this allows investigation at the functional level of organisation without reference to individual species responses. At each of these 'levels' (whole community, guild and individualistic) both seasonally (or temporally) and spatially varying factors will affect community composition.

This study is an attempt to gain some insight into the factors influencing the composition of a phytophagous insect community occurring on one host species at a single location in southern Africa. Hence, sources of between host-species and between-region variation are excluded to allow concentration on local effects.

The community under investigation is that of the phytophagous insects feeding on the veld fig, *Ficus burtt-davyi* Hutch. in Grahamstown. A fig species was chosen as many elements of the biology of these unique plants have been highly studied although such studies have rarely extended to the non-pollinating insect species. Of the four species of fig growing in the eastern Cape Province of South Africa (*Ficus sur* Forssk., *Ficus thonningii* Blume, *Ficus ingens* (Miq.) Miq., and *Ficus burtt-davyi* Hutch.) *F. burtt-davyi* is the most common and therefore was most suitable for this study.

Following on from this chapter, the thesis continues with a description of the host plant, study site and general methods employed throughout the study (chapter 2). A fairly detailed look at host plant phenology follows (chapter 3) as this will clearly have far-reaching effects on herbivore communities. The associated insect herbivores and their population dynamics are discussed in chapter 4.

Having introduced both the host and herbivore components of the system, attention is turned towards the factors with potential to influence the composition of the phytophagous insect community. Chapter 5 tackles the community as a whole, exploring environmental influences on herbivore species richness at both temporal (with time over the year) and spatial (between tree) scales. Following on from this, the same questions are approached from the perspective of the guild level (chapter 6). In an attempt to determine the degree to which individualistic species responses contribute to patterns at the guild level, chapter 7 commences with an investigation of the way in which the distribution patterns of the guilds arise, with particular reference to the two largest guilds (the leaf chewers and leaf and stem piercers). The chapter is completed with an analysis of the role of interspecific interactions within the community.

Chapter 8 concludes the thesis with a discussion of the significance of the results obtained throughout.

2 STUDY SYSTEM AND METHODS

STUDY SYSTEM

F. burtt-davyi, otherwise known as the veld fig, is one of about 105 African and 25 South African *Ficus* species and belongs to the species-rich subgenus Urostigma section Galoglychia (Berg 1990a). It occurs in a coastal strip about 60km wide, from George on the south coast of South Africa, north to Maputo in Mozambique (Fig. 2.1) (Berg 1990a; Van Greuning 1990; Von Breitenbach 1974). At the northern-most limit of it's range, *F. burtt-davyi* occurs mainly as a low, dense, sprawling shrub, bordering sand-dunes. Further south, however, in the coastal forests it grows as a tall shrub and, more often, a strangler. In the drier areas, which tend to be further inland, it occurs largely in rocky areas and grows as a rock-splitter or a soil-rooting shrub (Coates Palgrave 1984; Compton and Nefdt 1990; Van Greuning 1990).

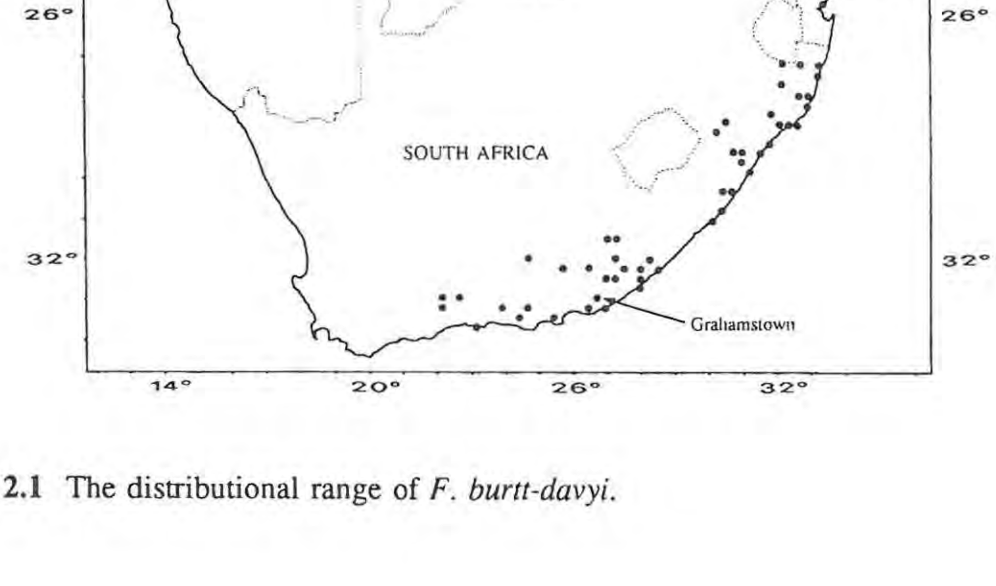


Figure 2.1 The distributional range of *F. burtt-davyi*.

The trees are smooth and pale-barked with leaves generally about 5-8cm long, elliptic to narrowly obovate, hairless, and arranged alternately. The green/red-tinged figs become yellowish when ripe, reaching a maximum of 15mm in diameter. They are smooth, covered in raised bumps, and occur in pairs in the leaf axils (Coates Palgrave 1984; Compton and Nefdt 1990; Van Greuning 1990).

In common with all other fig species, *F. burtt-davyi* produces latex, a milky, chemically complex, viscous secretion which is released from sites of tissue damage to provide chemical as well as physical protection against insect herbivores (Compton 1987, 1989; Dussourd and Denno 1991; Dussourd and Eisner 1987; Farrell et al. 1991; Williams 1991). Latex is contained under pressure within laticifers (living cells) distributed throughout the tree, often in association with the vascular tissues, and upon exposure to the air becomes sticky. As it hardens it may entrap the insects which caused the damage and/or gum up their mouth parts.

Each fig species is pollinated by an obligately host-specific species of agaonine wasp (Hymenoptera, Agaonidae, Agaoninae). The fig wasp larvae develop within the ovaries of flowers borne on the inner surface of an urn-shaped syconium which is accessed via a bract-covered ostiole. Upon hatching, the adult wasps mate, and the females then collect pollen and disperse in search of conspecific trees with receptive figs. *F. burtt-davyi* is monoecious and pollinated by *Elisabethiella baijnathi* Wiebes (Compton 1993).

The fruits of *F. burtt-davyi*, in common with other fig species, pass through five developmental stages (Galil and Eisikowich 1968). During the prefloral stage (A) the figs enlarge but remain small, green and hard, the ostiole being closed by scales. This stage is relatively long, Baijnath and Ramcharun (1988) having found it to last approximately 25 days. The female phase (B) follows, thus named as it is at this point that the female flowers are mature and the stigmas receptive. The ostiolar scales loosen to allow entry of the pollinating wasps and pollination occurs. This stage can be very brief (approximately two days) and the figs are still small, hard and green. In the following interfloral phase (C), lasting several weeks or even months, wasp larvae and seeds develop, the fruit increasing in size gradually but remaining hard and green. A short male phase (D) follows (lasting approximately four days) in which the mature anthers dehisce and the male wasps emerge from their galls, mate with the females still within their galls, and bore an exit tunnel through the syconial wall. Following the exit of the female wasps via this tunnel, the figs increase in size, soften and become yellow in colour. This is termed the postfloral stage (E).

STUDY SITE

This study was undertaken at a single site in Grahamstown in the eastern Cape Province of South Africa (33°22'S, 26°29'E) where I carried out an intensive sampling program over a one year period. Grahamstown is situated 60km inland from the south-east coast of South Africa (Fig. 2.1) at an altitude of 550m and although exposed to sporadic rainfall, (totalling 568mm in the study period) is frequently hot and dry. Daily temperature and rainfall measurements within the study period (Fig 2.2) were obtained from the Rhodes University weather station situated adjacent to the study area.

The study system comprised all of the *F. burtt-davyi* trees (123 individuals) grouped within an area of 0.2km^2 in the 1820 Settler Botanical Garden in Grahamstown. The nearest other large population of *F. burtt-davyi* is 1km away. The study area consists largely of locally

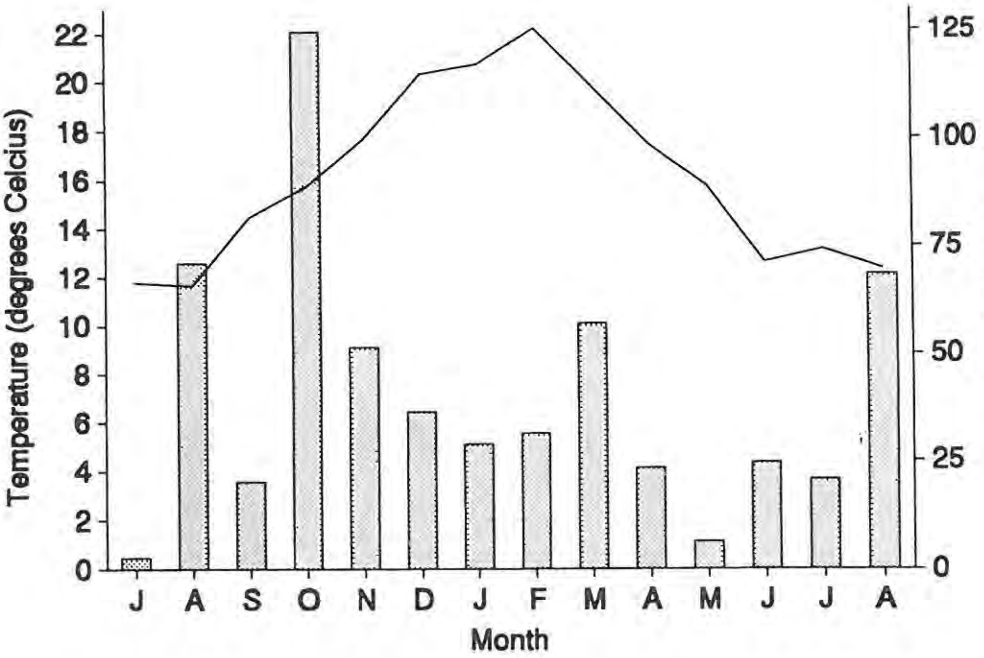


Figure 2.2 Mean monthly temperature (line) and total monthly rainfall (bars) for Grahamstown during the study period.

endemic false dry maccia type vegetation (Acocks 1975) interspersed with rocky outcrops, but also incorporates a small, relatively lush irrigated and managed region in which about 10% of the trees are growing (Figure 2.3).

THE TREES

All fig trees in the study area were mapped (Fig. 2.4) using a theodolite and methods of radiation and traversing (Richie et al 1988).

ıre 2.3 The habitat types occupied by *F. burtt-davyi* in the 1820 Settler Botanical len, Grahamstown.

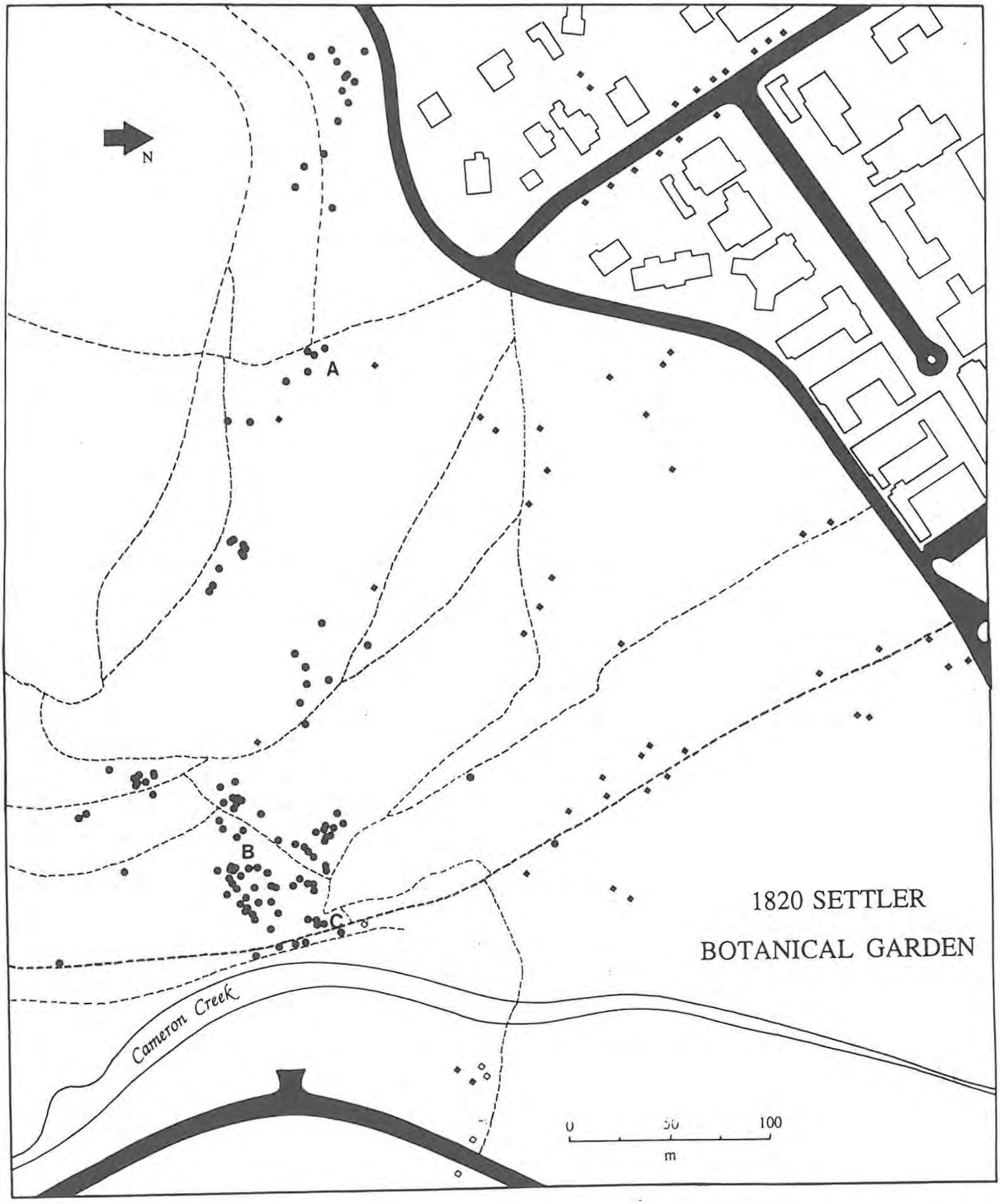


Figure 2.4 The study area showing the positions of all of the individual *F. burtt-davyi* (●), *F. thonningii* (◆), and *F. sur* (○) trees. A, B, and C indicate areas of the habitat types represented in Figures 2.3A, 2.3B, and 2.3C respectively.

The following physical characteristics of each tree were recorded:

(i) HEIGHT: from highest rooting point to top of crown.

(ii) TOTAL VOLUME: volume of canopy: height x greatest width x depth (at right angles to latter).

(iii) FOLIAGE VOLUME: volume of leafy branches only.

(iv) FOLIAGE DENSITY: foliage volume / total volume.

(v) MAXIMUM CROSS-SECTIONAL AREA OF CANOPY: length x breadth of the largest cross-section through the canopy.

(vi) STEM NUMBER: no. of stems at the last rooting point.

(vii) MAXIMUM STEM DIAMETER: measured 10cm beyond the last rooting point: *F. burtt-davyi* often grows on rock faces and along the ground, putting down roots at several points.

(viii) MAXIMUM AXIS NUMBER: The leaf axis, consisting of a series of nodes and internodes, is the basic structure of a plant's architecture (Jaeger and De Reffye 1992) and may be ordered according to its point of origin. Hence, the trunk, having grown directly from the seed of the plant, is an order one axis, the axes it bears, order two axes and so on, an order i axis being borne by an order i-1 axis. The maximum axis number of each tree was recorded.

(ix) INSOLATION: each tree was placed into one or more classes with respect to its exposure to the sun:

(a) full sun all day
(b) dappled sunlight all day
(c) shade all day
(d) mixed exposure to all three

Trees varied enormously in size and complexity (Appendix A) ranging from a 5cm tall individual in a rock crevice to an extensive, 6.5m high shrub (Figure 2.5).

SAMPLING PROCEDURE

Each of the 123 trees was visited at approximately three-weekly intervals (mean sample interval = 23.47 ± 2.67days) from 10.VII.91 to 12.VIII.92 on a total of 18 sample dates. On each sampling occasion the leaf and fruit phenologies of each tree were recorded, and every tree was searched thoroughly for the presence of phytophagous insect species. Where a tree was so large as to preclude a thorough survey, a maximum of 15 minutes was devoted to searching. It was established that all species were likely to be sampled in this time by producing a species recruitment curve following the exhaustive sampling of five of the largest trees (Fig. 2.6).

When fruit were present, any external fruit-feeding insects were recorded, and any obvious damage noted prior to destructive sampling. This latter was carried out at the interfloral and post-emergent stages. At the interfloral stage, if a crop consisted of more than 150 fruit, 50 figs were removed for dissection. However, with smaller crops a third of the figs were removed on the assumption that by the post-emergent sample date approximately a third of the fruit would have fallen or been consumed by frugivores. At the post-emergent sample date the remainder of the figs, to a maximum of 50, were removed for dissection. In the laboratory the fruit was split open to reveal the presence of internally feeding insects.

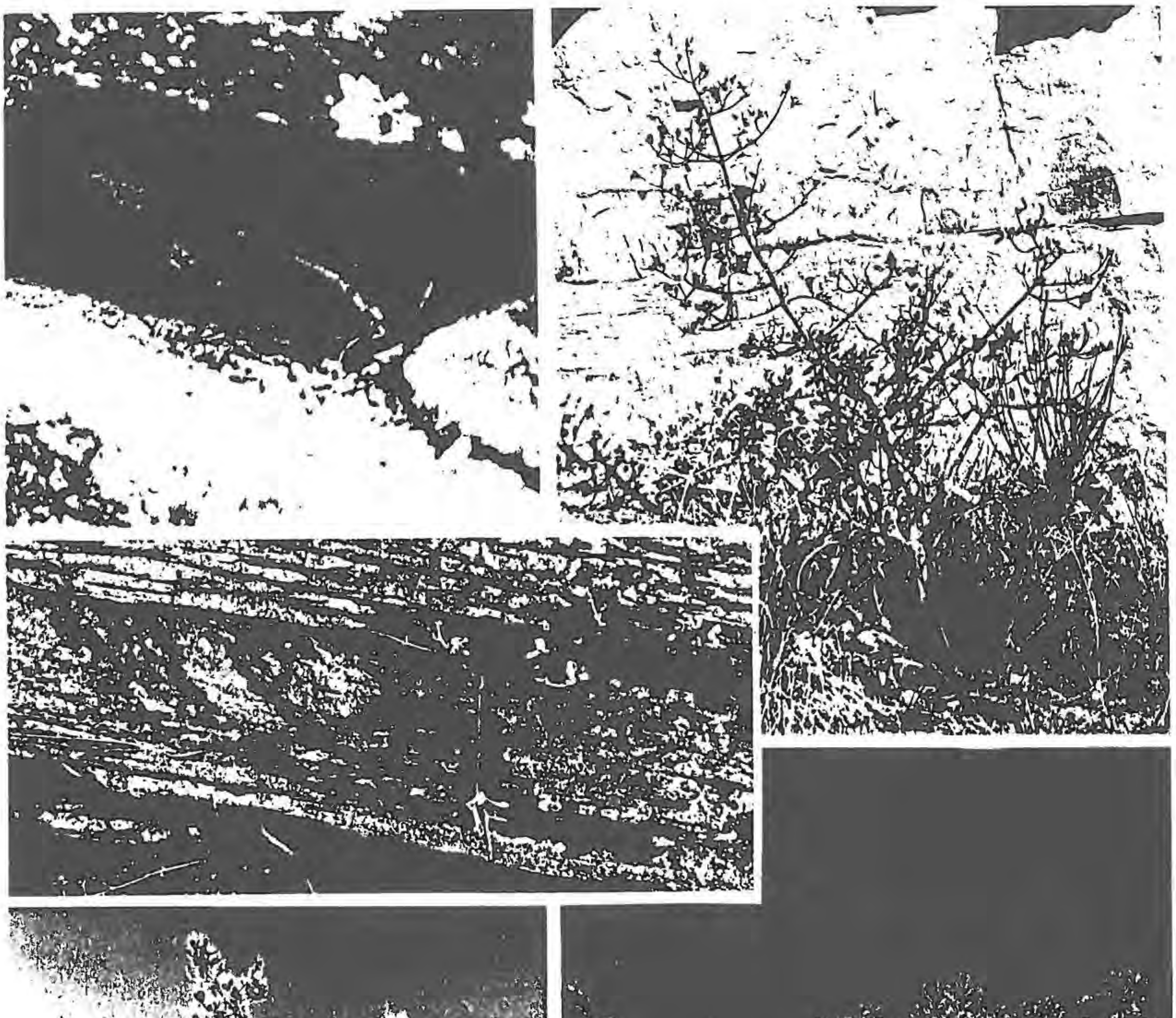


Figure 2.5 The variety of tree sizes and forms of *F. burtt-davyi* in the 1820 Settler Botanical Garden.

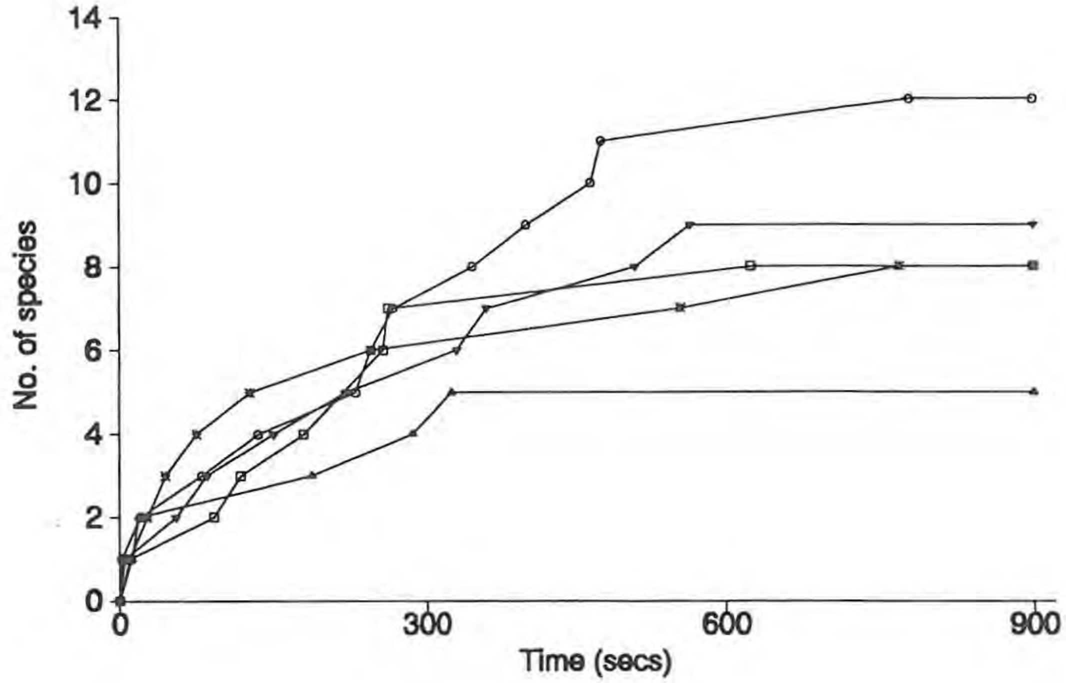


Figure 2.6 Species recruitment curves following the exhaustive sampling of 5 of the largest trees in the study area.

This chapter has provided general details of the study system and of methods relevant to all of the following chapters. More specific methodological details are provided in each chapter as necessary.

3 THE PHENOLOGY OF FRUIT AND LEAF PRODUCTION BY *F. BURTT-DAVYI*

INTRODUCTION

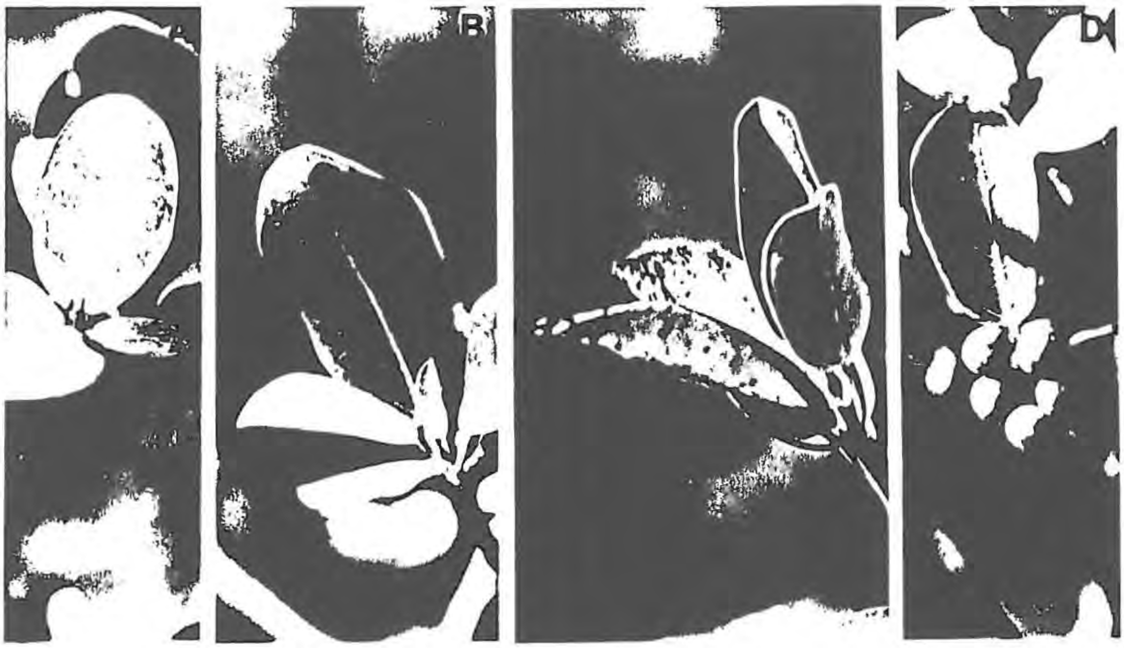
Phenological changes will clearly have profound effects on the insects feeding on plants, as phytophagous insects can have very specific preferences for leaf and fruit developmental stages (Aide 1993; Basset 1991a, 1991b; Claridge and Wilson 1976; Coley 1983; Feeny 1970; Strong et al. 1984) based on their varying nutrient contents, physical characteristics and levels of defense (Basset 1991b; Coley 1983; Mattson 1980; Strong et al. 1984). The distribution of these resources over space and time will therefore have considerable influence on the degree to which herbivores must migrate within and between hosts.

This chapter investigates the phenological patterns of *F. burtt-davyi* throughout the study period, and considers possible explanations for these patterns before discussing the implications for the phytophagous insects dependent on the trees.

METHODS

Leaf phenology

Leaves were classified as young (tender, partially enlarged and with a reddish tinge), mature (fully enlarged and green), or senescing (yellowing)(Fig. 3.1). Prior to leaf production, trees were classified as bare. Obviously, one or more of these leaf states could be present simultaneously on any one tree.



3.1 Phenological states of *F. burtt-davyi*. (A) young leaves, (B) mature leaves, (C)
ng leaves, (D) pollinated but pre-emergent figs (stage 2).

ationship between various climatic factors and the incidence of each of the three leaf
'as examined via Spearman Rank Correlation (STATGRAPHICS Proc. CORR). Those
: factors included were: maximum and minimum temperatures in the month preceding
ıple (MAXT and MINT); change in maximum and minimum temperatures from the
s month to this month (CHMAX and CHMIN); mean maximum and minimum
ıtures in the month preceding the sample (MNMAX and MNMIN); the change in mean
ım and minimum temperatures from the previous month to this month (CHMNMAX
MNMIN); and total rainfall in the month preceding the sample (RAIN). 'Month' refers
ır week period as opposed to a calendar month.

Fruit phenology

Trees were classified into one of five fruiting states: no fruit (0); all figs unpollinated (1); figs pollinated but wasps not yet emerging (2); some figs with wasps emerging (3); and figs from which all wasps have emerged (4). Crop size was estimated during stage 2. Trees were considered to be mature enough to bear fruit if they were larger than the smallest tree which bore fruit during the study (volume=$0.09m^3$).

The duration of each crop was calculated with the dates of initiation and completion estimated as being midway between consecutive sample dates in order to avoid gross underestimation. A Mann-Whitney U test (STATGRAPHICS Proc. WILCOX) was used to determine whether crops tended to be borne by larger as opposed to smaller trees. Relationships of tree size with cropping frequency and crop size were then investigated using Spearman's Rank Correlation Procedure (STATGRAPHICS Proc. CORR). Climatic effects (as for the leaf phenologies) on crop initiation and total number of fruiting trees were also investigated via Spearman's Rank Correlation Procedure.

RESULTS

Leaf phenology

F. burtt-davyi showed seasonal trends with respect to its leaf phenology (Fig. 3.2): the leaves senesced and fell in the autumn/early winter (March to July), new growth appearing largely between August and November, and mature leaves predominating throughout the summer.

Many of the different climatic factors were highly positively correlated (Table 3.1), making it difficult to separate the effects of minimum and maximum temperature changes. The

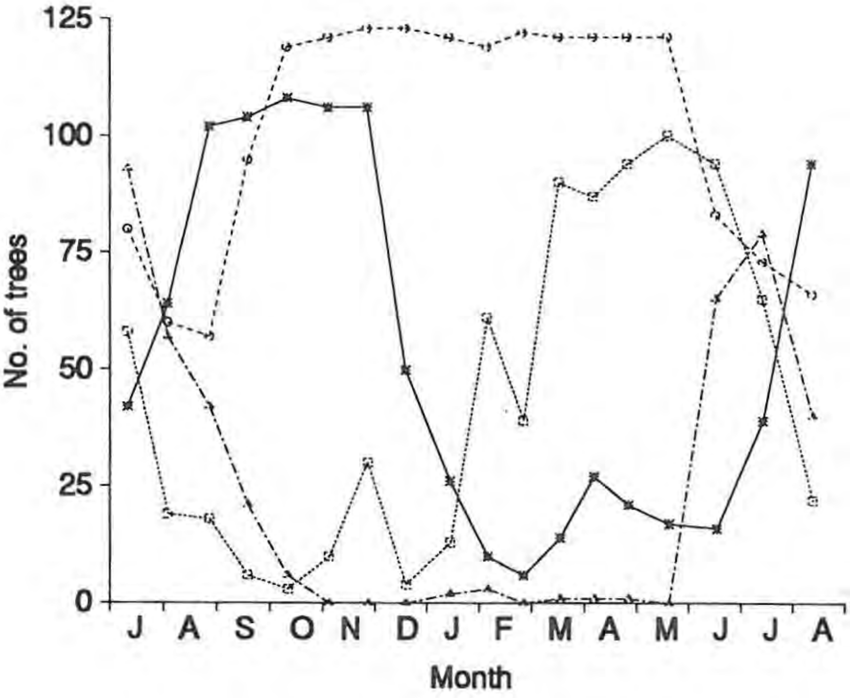


Figure 3.2 Temporal variation of leaf phenologies between July 1991 and August 1992. Curves represent numbers of trees bearing leaves of each phenological state: young (✳), mature (○), and senescing (□). △ represents trees without leaves.

correlation procedure indicated that young leaves became more scarce as mean monthly temperatures increased (Table 3.2). Rising temperatures (MAXT, MINT, MNMAX, MNMIN and CHMNMAX) promoted leaf maturation and leaf senescence followed temperature decreases (CHMAX and CHMNMIN). No relationships with rainfall were evident.

Fruit Phenology

Fifty-one of the 123 trees (representing 52% of the mature trees) fruited during the sample period, bearing a total of 84 crops (between one and three crops each), these varying in size from one to 20500 fruit (Table 3.3).

Table 3.1 Relationships between climatic factors: Spearman's correlation coefficients and their significance (* p<0.05, ** p<0.01, *** p<0.001). Climatic factors included are: maximum and minimum temperatures in the month preceding the sample (MAXT and MINT); change in maximum and minimum temperatures from the previous month to this month (CHMAX and CHMIN); mean maximum and minimum temperatures in the month preceding the sample (MNMAX and MNMIN); the change in mean maximum and minimum temperatures from the previous month to this month (CHMNMAX and CHMNMIN); and total rainfall in the month preceding the sample (RAIN).

	MAXT	CHMAX	MNMAX	CHMNMAX	MINT	CHMIN	MNMIN	CHMNMIN
CHMAX	0.4197	.	.	.	.	.	.	.
MNMAX	0.8308 ***	0.1366	.	.	.	.	.	.
CHMNMAX	0.6152 *	0.3430	0.5420 *	.	.	.	.	.
MINT	0.7680 **	0.2103	0.8660 ***	0.3399	.	.	.	.
CHMIN	0.1990	0.1560	0.2373	0.2306	0.4696	.	.	.
MNMIN	0.7815 **	0.1452	0.8922 ***	0.3605	0.9204 ***	0.1714	.	.
CHMNMIN	0.2094	0.3972	0.1950	0.1724	0.5198 *	0.6539 **	0.4010	.
RAIN	0.1132	0.3065	-0.0294	-0.1606	0.2471	0.0199	0.2917	0.5224 *

Although crops were more likely to be borne by larger trees ($Z=-6.8794$, $p=6.04\times10^{-12}$), neither crop number nor crop size increased with size of fruit-bearing trees ($r = 0.1571$, $p = 0.2666$ and $r = 0.1968$, $p = 0.1819$ respectively).

Crop duration varied greatly from 20.5 days to 212.5 days (Table 3.3) and within-crop overlap occurred only once. On average 79.5 days elapsed between the end of one crop and the beginning of the next, and 126.4 days elapsed between successive crop initiations (Table 3.3).

In contrast to the highly synchronous fruiting within individual trees, that between trees was

Table 3.2 Leaf phenology (young, mature and senescent leaves) - climate relationships indicated via Spearman's rank correlation coefficients. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Climatic factors included are: maximum and minimum temperatures in the month preceding the sample (MAXT and MINT); change in maximum and minimum temperatures from the previous month to this month (CHMAX and CHMIN); mean maximum and minimum temperatures in the month preceding the sample (MNMAX and MNMIN); the change in mean maximum and minimum temperatures from the previous month to this month (CHMNMAX and CHMNMIN); and total rainfall in the month preceding the sample (RAIN).

	YOUNG	MATURE	SENESCING
MAXT	-0.3725	0.7424**	0.0187
CHMAX	0.2166	0.2360	-0.5233*
MNMAX	-0.5854*	0.7513**	0.2230
CHMNMAX	-0.0424	0.4817*	-0.3399
MINT	-0.4015	0.7780**	0.0863
CHMIN	0.1426	0.1229	-0.3399
MNMIN	-0.4822*	0.8103***	0.1322
CHMNMIN	0.3626	0.3143	-0.6395**
RAIN	0.4130	0.2515	-0.2664

Table 3.3 A summary of the cropping statistics.

	N	MINIMUM	MAXIMUM	MEAN	STANDARD DEVIATION
CROP NO.	84	1.0	3.0	1.65	0.66
CROP SIZE	70	1.0	20500.0	1877.47	4464.95
CROP DURATION	64	20.5	212.5	77.11	47.69
INTERVAL BETWEEN INITIATIONS	24	24.0	374.0	126.40	71.76
INTERVAL BETWEEN END OF ONE CROP AND START OF THE NEXT	33	-24.0	280.5	79.50	91.31

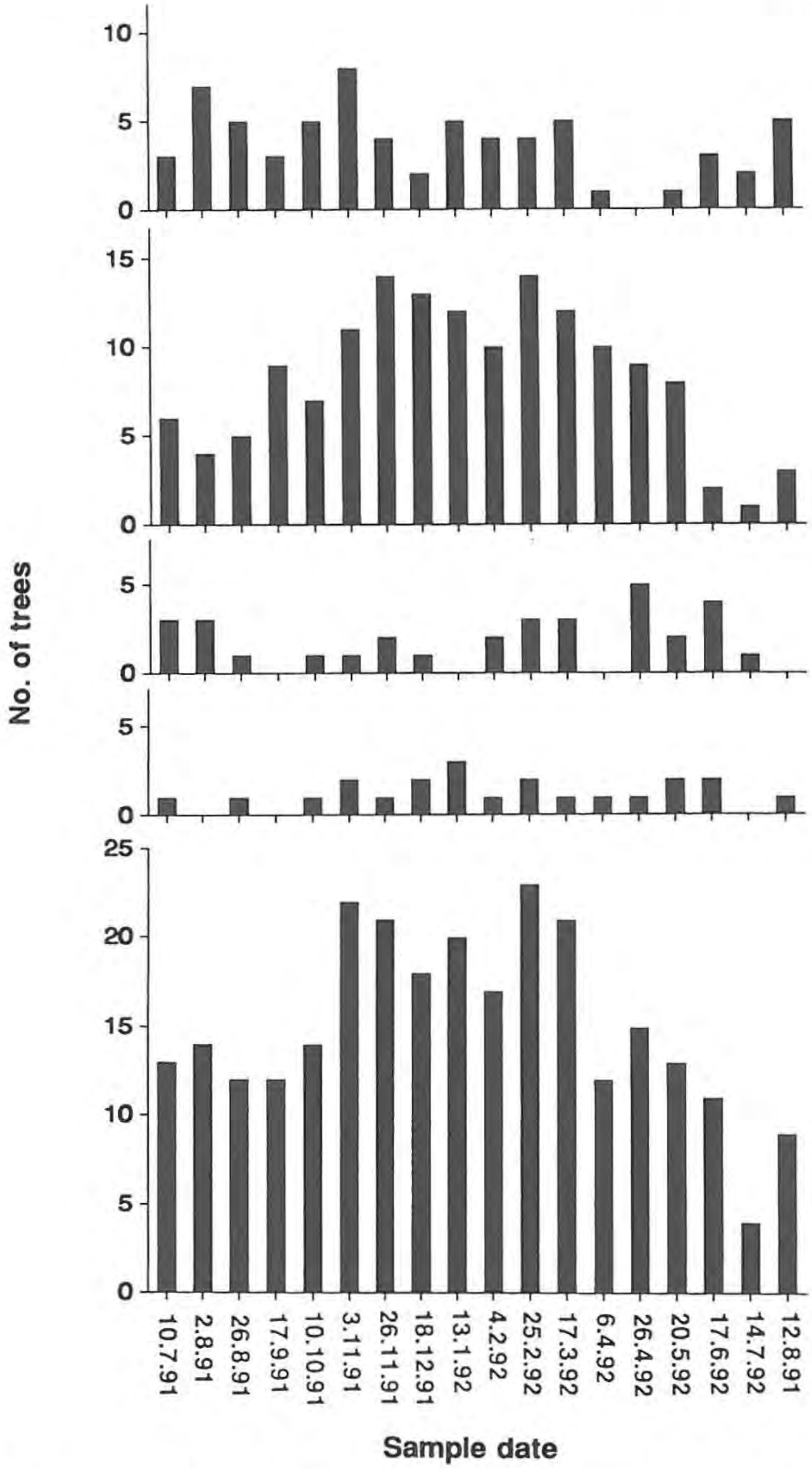


Figure 3.3 Temporal variation of fruiting phenology. Bars represent the number of trees bearing fruit of each of the following stages: (A) all figs unpollinated (stage 1), (B) all figs pollinated but wasps not yet emerged (stage 2), (C) some figs with wasps emerging (stage 3), (D) all figs with wasps having emerged (stage 4), and (E) the total number of trees in fruit.

Table 3.4 Fruit phenology - climate relationships indicated by Spearman's rank correlation coefficients. * $p < 0.05$, ** $p < 0.01$. Climatic factors included are: maximum and minimum temperatures in the month preceding the sample (MAXT and MINT); change in maximum and minimum temperatures from the previous month to this month (CHMAX and CHMIN); mean maximum and minimum temperatures in the month preceding the sample (MNMAX and MNMIN); the change in mean maximum and minimum temperatures from the previous month to this month (CHMNMAX and CHMNMIN); and total rainfall in the month preceding the sample (RAIN).

CLIMATIC VARIABLE	CROP INITIATION	TOTAL FRUIT
MAXT	0.4525	0.6356^{*}
CHMAX	0.4796	0.5522^{*}
MNMAX	0.1395	0.6138^{*}
CHMNMAX	0.5181^{*}	0.3975
MINT	0.6182^{*}	0.7818^{**}
CHMIN	0.6459^{**}	0.2120
MNMIN	0.5127^{*}	0.7356^{**}
CHMNMIN	0.6797^{**}	0.5335^{*}
RAIN	0.1395	0.3050

asynchronous, with fruit at all developmental stages occurring all year round. Numbers of trees bearing fruit peaked in the spring and late summer (Fig. 3.3) Spearman's rank correlations (Table 3.4) revealed that crop initiation was positively related to temperature and perhaps more-so to measurements of minimum than maximum temperature. The total number of trees in fruit was positively correlated with temperature in general. Rainfall was unimportant.

DISCUSSION

Leaf phenology

Few studies have addressed the question of patterns in leaf phenology of fig trees, but the general impression emerging from those that have, is one of extreme variability, both between species in the same region and within species in different regions (Corlett 1984, 1987; Milton 1991; Van Schaik 1986; Wharton et al. 1980). As may be expected in a seasonal environment, *F. burtt-davyi* is deciduous, trees losing their leaves for periods of three to nine weeks. *Ficus fistulosa* Reinw. was similarly found to undergo a two week deciduous period in the seasonal environment of Hong Kong, although in aseasonal Singapore, trees were never leafless and exchanged old leaves for new by flushing two to five times a year (Corlett 1987).

Other studies have revealed the occurrence of mixed patterns between different species within the same climatic area (Corlett 1984; Milton 1991). Milton (1991) studied four Neotropical figs occurring in a relatively aseasonal area. Two Urostigma species (*Ficus obtusifolia* H.B.K. and *Ficus costaricana* Liebm.) underwent complete changes of leaves at approximately eight month intervals whilst two Pharmacosycea (*Ficus yoponensis* Desv. and *Ficus insipida* Willd.) were evergreen. Corlett (1984), whilst working on the Urostigma species, *Ficus benjamina* Linn. and *Ficus microcarpa* Linn. in Singapore (aseasonal), also found mixed patterns of leaf production. *F. benjamina* exchanged all old leaves for new between zero and four times per tree per year over a period of seven to 20 days, also had general flushes of new leaves one to five times per tree per year, and leaf flushes localised to single branches. *F. microcarpa*, on the otherhand, produced new leaves mainly by localised flushing.

Two further groups of workers found evidence of patterns of an opposite nature to those expected when considering the seasonality of the environment. *F. sycomorus* Linn. in Namibia (Wharton et al. 1980) exhibited asynchronous leaf drop despite the seasonality of the environment, and some Sumatran figs displayed the deciduous habit despite their aseasonal surroundings (Van Schaik 1986).

Generally, one might expect leaf production in dry areas to be rainfall-limited and in more humid areas to be insolation and temperature-limited (Van Schaik 1986). Van Schaik (1986) found evidence in a Sumatran rainforest to support this, leaf emergence peaking during the dry seasons and being correlated with rising temperatures. Although not significantly related to leaf production by *F. burtt-davyi* in this study, rainfall did have a weak positive effect (Table 3.2: r=0.4130, p=0.09). As young leaves occur mainly in the spring their decrease in incidence with rising temperature doubtless reflects their absence from the trees in the summer months, rather than indicating their emergence in response to low temperatures. This was preceded by leaf senescence and fall, precipitated by decreasing temperature.

Fruit phenology

A maximum of approximately three crops per fig tree per year seems to be the norm in seasonal areas (Corlett 1987; Newton and Lomo 1979; see Berg 1990b for a review), whereas in aseasonal climates favourable for fig production all year round, the number of crops per tree tends to be greater (Corlett 1984, 1987), as many as seven crops being borne on *F. fistulosa* in Singapore in a year (Corlett 1987).

In addition to seasonality, tree size can affect the number of crops borne by individual fig trees, larger trees often tending to bear crops at shorter intervals due to their more rapid accumulation of reserves (Milton et al. 1982). This was the case in two Neotropical figs, *F. yoponensis* and *F. insipida* (Milton et al. 1982) and in some larger Panamanian strangler figs (Windsor et al. 1989). However, in the present study, although larger trees were more likely to bear fruit, there was no relationship between size of fruit-bearing trees and the number of crops borne.

Both this study, and that of Compton et al. (in press) on *F. burtt-davyi* in the Grahamstown area between 1985 and 1987, found crop duration to be extremely variable, although the shorter cropping times were attributable largely to tiny crops of less than 50 figs. These 'false fruitings' most probably help ensure the availability of at least some figs between major crops so facilitating pollinator survival. Although Corlett (1987)(*F. fistulosa*, Singapore - duration = 70-100 days), Newton and Lomo (1979)(*Ficus vogelii* (Miq.) Miq., Ghana - duration = 40-50 days), and Lambert and Marshall (1991)(Malaysian rainforest figs - most variable duration = 56-97 days) report far less variable development times, their studies were all conducted in less seasonal, more tropical environments, and the habitat conditions may have made the detection of very small crops difficult.

If the more variable crop durations and greater maximum development times of *F. burtt-davyi* in Grahamstown are attributable to the winter temperatures, one would expect crop duration to be longer in the winter months as noted by Bronstein and Patel (1992). They found the crop development time of *Ficus aurea* Nuttall, the Florida strangling fig, to be 50% longer in the winter, the C-phase (interfloral stage) being highly correlated with temperature. Unfortunately, it was not possible to compare differences between crop durations in the warmer versus the cooler months in this study, as the summer fell in the middle of the sample period, the winter therefore being split into two, and the longest crop durations during these periods thus potentially being half of what they would be if unsplit.

The overlap of fruit crops within a tree varies from fig species to species and from individual tree to tree. Corlett (1987), Lambert and Marshall (1991), Milton (1991), and Milton et al. (1982) all reported no overlap, intervals between crops varying from five to 22 months. On the other hand, Baijnath and Ramcharun (1983), Compton et al. (in press), Corlett (1987), Cornell (1984), and C. Zachariades (pers. comm.) all found varying degrees of overlap. For example, 71% of female crops of *F. fistulosa* in Singapore were initiated while figs from previous crops were still on the tree (Corlett 1987), and Baijnath and Ramcharun (1983) found young, mature and ripe syconia to all be borne simultaneously on *Ficus sycomorus* L. in South Africa. Baijnath and Ramcharun (1988) also noted extensive overlap to occur in *F. burtt-davyi* in the Durban area, this observation contrasting with my findings of no such overlap (except in one case) in *F. burtt-davyi* in Grahamstown. Additionally, Compton et al. (in press) found some overlap of *F. burtt-davyi* crops in Grahamstown, although only 2% of crops (over two years) overlapped sufficiently to allow self-pollination.

Not only is there a great deal of variation with respect to crop overlap, but also in the synchrony of intra-tree crop initiation. In this study *F. burtt-davyi*, as with most monoecious figs (Bronstein 1989), displayed a high degree of intra-tree synchrony, a pattern followed by *F. benjamina* in Singapore (Corlett 1984), *F. vogelii* in Ghana (Newton and Lomo 1979), tropical figs in Gabon (Gautier-Hion and Michaloud 1989) and *F. sycomorus* in Namibia (Wharton et al. 1980). Baijnath and Ramcharun (1988), however, found syconial initiation of *F. burtt-davyi* in the Durban area to be staggered over three to four weeks.

The latter is just one example of the ever-increasing number of recorded breakdowns in intra-tree synchrony. For example, Bronstein (1989) ascertained that an asynchronous fruiting pattern exists within *F. citrifolia* in Florida, and Bronstein and Patel (1992) found asynchronous flowering to occur in the Florida strangler, *F. aurea*, on 83% of sampling occasions.

When it comes to inter-tree fruiting patterns, however, there is a far greater degree of consistency, flowering asynchrony being exhibited by most fig species (Baijnath and Ramcharun 1983, 1988; Berg 1990b; Corlett 1984, 1987; Frank 1989; Janzen 1979; Gautier-Hion and Michaloud 1989; Lambert and Marshall 1991; Milton 1991; Milton et al. 1982; Newton and Lomo 1979; Van Schaik 1986; Wharton et al. 1980; Windsor et al. 1989) with very few exceptions (e.g. Corlett 1987).

The exceptions aside, why do most monoecious figs display inter-tree fruiting asynchrony? Typically, this fruiting pattern has been described as necessary to maximise the reproductive success of individual trees, random flowering throughout the year minimising the chances of flowering at the same time as conspecifics, and maximising the chances of wasp transfer between trees (Janzen 1979; Kjellberg and Maurice 1989; Milton et al. 1982; Windsor et al. 1989). However, truly random fruiting may be rare, occurring at irregular intervals and often at times when conditions would appear to be far from optimal (i.e. when many other plants within the ecosystem are not flowering). Milton (1991) proposes that maximisation of seed dispersal is of primary importance as it is of particular consequence in small-seeded species such as figs. Asynchronous fruiting will mean reduced competition for dispersers, and most importantly, Milton (1991) suggests, will improve the chances of an individual's seeds reaching the required germination conditions. However, such asynchrony may also be disadvantageous to the fig, increasing seed exposure to predators (Aide 1993).

With respect to intra-tree fruiting, both synchronous and asynchronous patterns have their advantages (Bronstein and Patel 1992; Janzen 1979). Synchronous fruiting will force pollinating wasps to disperse in search of receptive conspecifics so ensuring out-crossing. High pollinator mortality poses a problem here, however, particularly at low tree densities and in times of low fruiting frequencies within the population as a whole. Extinction of the pollinator population may be prevented at such times by asynchronous fruiting, so allowing self-pollination.

The degree to which self-pollination actually occurs in asynchronous fig crops is under some doubt, however. For instance, Bronstein and Patel (1992) found that although crop overlap occurred 83% of the time in *F. aurea*, sexual phases overlapped on only 5% of occasions. Similarly, although Corlett (1987) found huge crop overlap, only once was it sufficient to allow self-pollination. It would therefore seem that the staggering of fruit maturation may be of greater importance by lengthening the periods over which pollinators are released and hence increasing their chances of finding receptive figs on conspecifics (Baijnath and Ramcharun 1988).

Although the majority of monoecious figs exhibit inter-tree fruiting asynchrony, there are often certain times of year when more individuals are reproducing than at other times, particularly at more seasonal sites (Berg 1990b; Bronstein and Patel 1992; Baijnath and Ramcharun 1983; Corlett 1984; Lambert and Marshall 1991; Milton 1991; Wharton et al.

1980). The number of fruiting *F. burtt-davyi* trees in Grahamstown (this study; Compton et al., in press) peaked in spring and late summer/autumn as minimum temperatures increased. Similarly, in Durban numbers peaked in the warmer months (Baijnath and Ramcharun 1983). The lack of any link between rainfall and fruiting in this study comes as some surprise as one would expect optimum seedling survival, and hence fruiting frequency during wet periods. However, this lack most probably arises due to the fact that the study was carried out during a drought in which there were no marked wet periods.

Frank (1989) suggests that such population-wide flowering patterns can be explained by resource accumulation, plants flowering whenever they have acquired sufficient resources. Thus, in a seasonal environment, trees would accumulate resources seasonally and therefore flower in a partially synchronous manner. The optimal time for fruiting will therefore be controlled by factors such as temperature, light, water, availability of seed dispersers and predation (Frank 1989; Milton 1991; Windsor et al. 1989).

Consequences for the phytophagous insects

The foregoing outlines the phenological patterns exhibited by *F. burtt-davyi* and possible reasons for their existence, but what about the consequences for the insect herbivores dependent on the trees? The synchronous nature of leaf production within the tree population means that those herbivores having very specific feeding preferences with respect to leaf developmental stage or phloem translocation rate, will be restricted to relatively narrow windows of time in which to complete their development on *F. burtt-davyi*. Such herbivores may need to utilise alternative hosts in order to complete their life cycle, this requiring a well developed dispersal and host-finding ability.

The synchronous intra-tree fruit production creates the same problems for insect frugivores, which may have exceedingly narrow windows of time in which to complete their development, especially if they are restricted to a particular stage in the developmental cycle of the fruit. In the absence of diapause this necessitates moves onto other trees, although the asynchronous inter-tree fruiting pattern means that migration can, in theory, occur between conspecifics. In practise, however, this may not be so straightforward as trees producing fruit at the required stage of development may be far apart, posing detection and migration problems. The noted year-round availability of crops at all stages of development does, however, mean that fruit are constantly available to insect frugivores.

In conclusion, due to the phenology of *F. burtt-davyi*, not only the pollinating wasps face severe problems with respect to finding hosts at the correct stage of development, but also the insects feeding on the leaves and fruit.

4 THE PHYTOPHAGOUS INSECTS OF *F. BURTT-DAVYI* HUTCH.

During the year-long sampling period, 43 herbivorous insect species were found on the above ground parts of *F. burtt-davyi* in the study area (Table 4.1). These fell into seven feeding guilds: leaf chewers, leaf and stem piercers, leaf miners, leaf gallers, stem borers, fruit chewers, and fruit piercers (Table 4.1). This chapter provides brief descriptions of the biology of the 16 most frequently occurring phytophages. The dominant ant species present are also discussed.

The major phytophages were distinguished as ones occurring on more than 1% of the total number of samples taken over the year (2179), or in the case of fruit-feeders, in more than 1% of the samples of fruiting trees taken over the year (280). The Fig Tree Blue butterfly (*Myrina silenus ficedula* Trimen), despite occurring in only 0.6% of the samples, has been included here as it is a specialist fig-feeder.

Where details of host specificity are known they are discussed. However, phytophage feeding records on *Ficus* species and on woody plants in general in South Africa are few and far between. The majority of the 'non-major' phytophages are likely to be generalist feeders as they occurred so rarely on *F. burtt-davyi*, but in some cases the possibility that they are rare mono/oligophages cannot be ruled out.

Obviously, one year's data can provide no evidence relating to long term fluctuations of insect

Table 4.1 The phytophagous insects of *F. burtt-davyi* in the 1820 Settler Botanical Garden, Grahamstown. Arrangement is via feeding guild. Specimens of unidentified species have been lodged in the National Insect Collection, Pretoria.

FEEDING GUILD	FAMILY	SPECIES
LEAF CHEWERS	Buprestidae	*Sphenoptera* sp.
	Cerambycidae	*Prosopocera (Alphitopola)* sp.
	Chrysomelidae	*Cryptocephalus oneili* Jacoby
	Curculionidae	*Platycopes* sp.
	Choreutidae	*Brenthia* sp.
	Brachodidae	*Phycodes punctata* Walsingham
	Lycaenidae	*Myrina silenus ficedula* Trimen
	Sphingidae	*Pseudoclanis postica* (Walker)
	Hypsidae	*Aganais speciosa* (Drury)
LEAF MINERS	Nepticulidae	unidentified species
LEAF GALLERS	Cecidomyiidae	unidentified species
LEAF AND STEM PIERCERS	Coreidae	*Cletus* sp.
	Coreidae	*Gonocerus falactus* (Distant)
	Coreidae	*Anoplocnemis curvipes* (Fabricius)
	Scutelleridae	*Solenostethium liligerum* (Thunberg)
	Pentatomidae	*Atelocera natalensis* Stal
	Cicadellidae: Aphrodinae	unidentified species
	Cicadellidae	*Mgenia* sp.
	Cicadellidae	*Anstroagallia cuneata* (Cogan)
	Psyllidae	*Homotoma* sp.
	Aleyrodidae	*Acaudaleyrodes citri* (Priesner & Hosny)
	Aleyrodidae	unidentified species
	Aphididae	*Toxoptera aurantii* (Boyer de Fonscolombe)
	Margarodidae	*Icerya purchasi* Maskell
	Coccidae	*Ceroplastes* sp.
	Coccidae	*Coccus* sp.
	Coccidae	unidentified species
	Coccidae	unidentified species
	Coccidae	unidentified species
	Phlaeothripidae	*Gigantothrips caudatus* (Bagnall)
	ORDER: Thysanoptera	unidentified species
STEM BORERS	Curculionidae	*Diamerus* sp.

Table 4.1 *continued*

FEEDING GUILD	FAMILY	SPECIES
FRUIT CHEWERS	Scarabaeidae	*Leucocelis* sp.
	Scarabaeidae	*Genyodonta flavomaculata*
	Phoridae	(Fabricius) *Megaselia* sp.
	Drosophilidae	*Lissocephala* sp.
	Pyralidae	*Cirrhochrista convoluta* Hampson
	Pyralidae	unidentified species
FRUIT PIERCERS	Lygaeidae	*Dinomachus natalensis* Scudder
	Lygaeidae	*Lachnestes singalensis* (Dohrn)
	Lygaeidae	*Melanocoryphus amoenulus* Gerstaecker
	Lygaeidae	*Oxycarenus maculatus* Stal
	Lygaeidae	*Nysius* sp.

abundances and most insect populations fluctuate considerably from year to year (Root 1973; Solbreck 1991; Strong et al. 1984; Wolda 1992). Nonetheless, rare species do tend to remain rare and common species, common (Strong et al. 1984) and such a 'snap-shot' of the insect fauna on *F. burtt-davyi* is therefore likely to be at least qualitatively representative of the general situation on the tree in the study area.

LEAF CHEWERS

COLEOPTERA: BUPRESTIDAE: *Sphenoptera* sp.

One member of this large, essentially tropical group was recorded feeding in this study. The adult has metallic bronze forewings and body and the wedge-shape characteristic of the family. Adults feed by nibbling around the edges of the leaves so avoiding the main latex-supplying veins (Figure 4.1A). Once they have chewed a piece of leaf and the latex has welled up they move sideways to an ungummed-up area to nibble another piece of leaf before moving on again and so on. The result is a leaf with latex-filled corrugated edges.

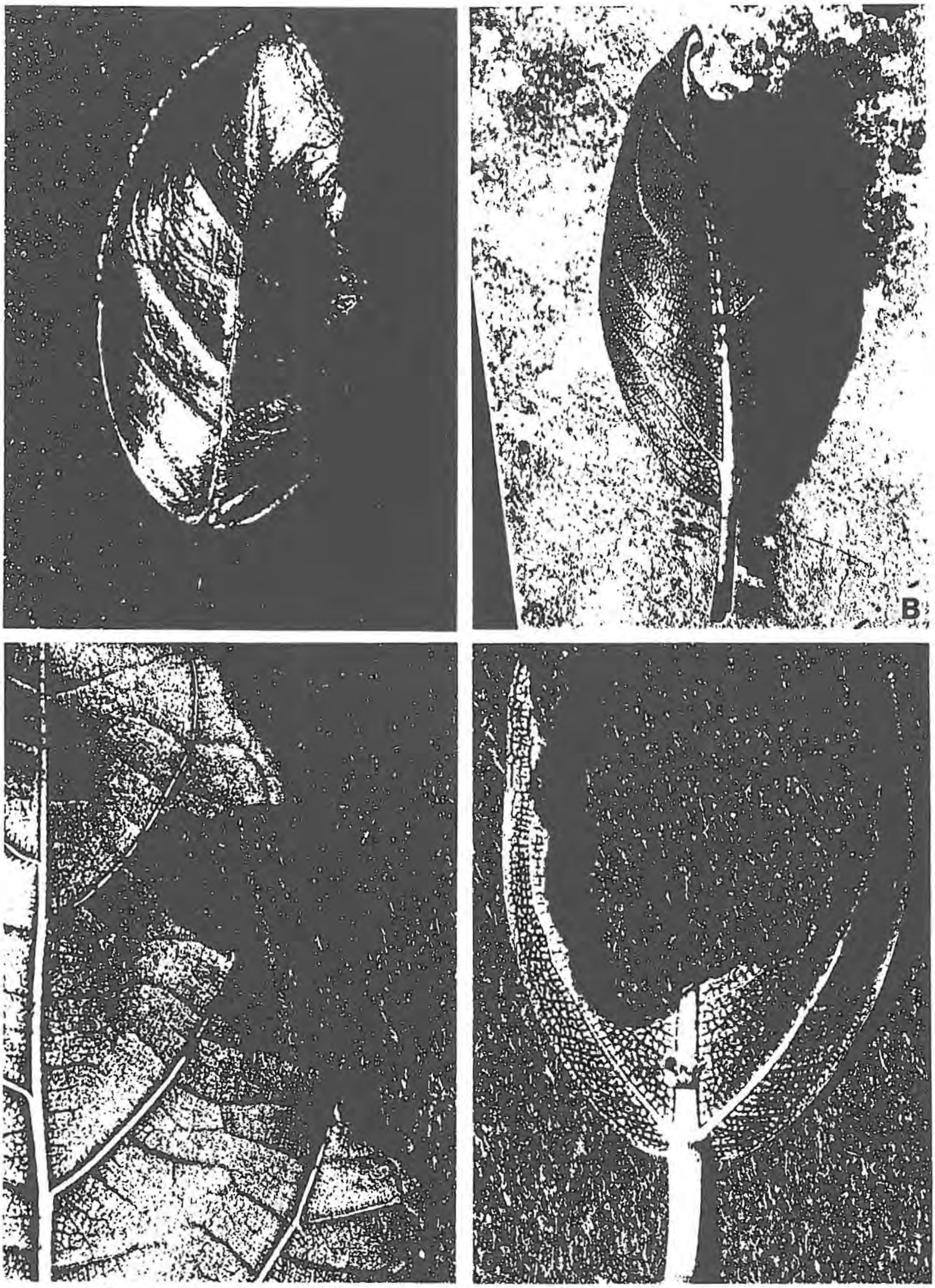


Figure 4.1 Damage patterns inflicted by the latex saboteurs on *F. burtt-davyi.* (A) *Sphenoptera* sp., (B) *Prosopocera* sp., (C) *A. speciosa* - early larval damage, (D) *A. speciosa* - final instar larval damage.

The adults are day-fliers and are most active during the warmest part of the day when they move very fast if disturbed. Their characteristic feeding damage was therefore seen more often than the insects themselves. Larvae of *Sphenoptera* species are recorded as wood borers, leaf miners, free-living root-feeders, or gallers (Richards and Davies 1977; Scholtz and Holm 1985). Larvae of the species under discussion were not, however, detected on *F. burtt-davyi*.

Damaged leaves were recorded from early October to mid-July (Figs 4.2 and 4.3A). However, the difficulty of determining the age of damage means that much of that recorded, especially in the later part of the season, will have been old. This is confirmed by the fact that adults were seen only between early October and early February, and fresh damage up to early April. Therefore, it would appear that the adults of this species are essentially spring to late-summer feeders, with the numbers of newly colonised trees peaking in late November.

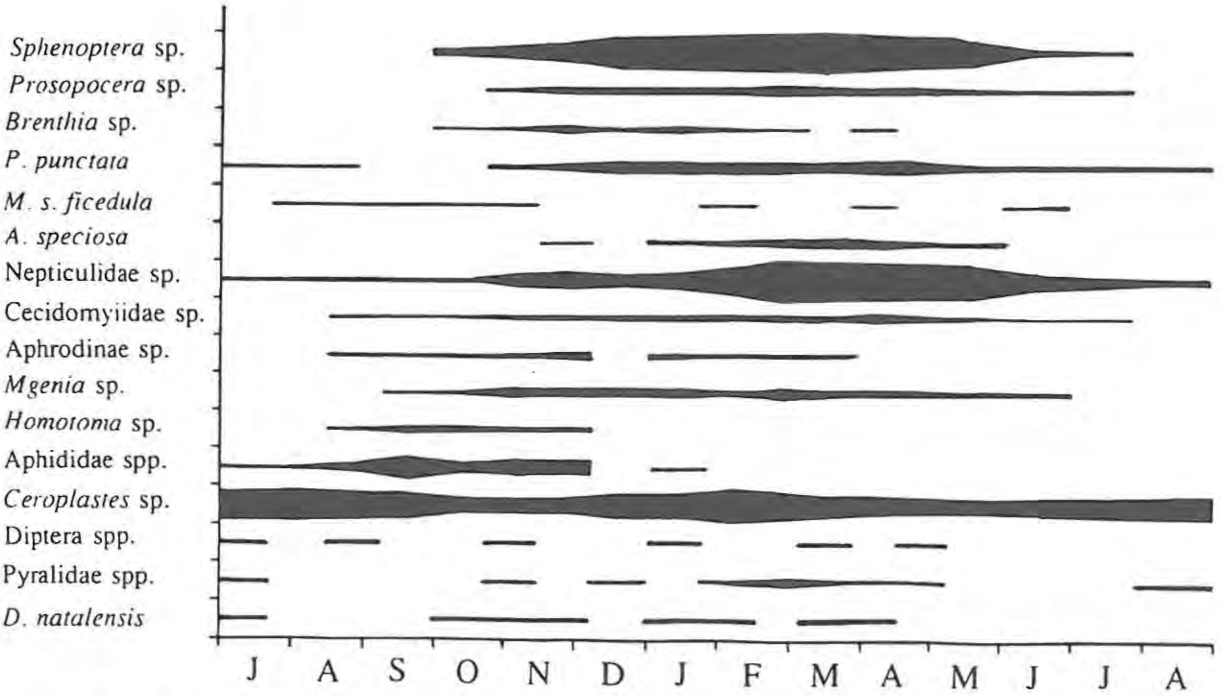


Figure 4.2 A summary of the patterns of colonisation by the 16 major phytophages over the year. Bar width gives an indication of the relative numbers of trees hosting each species at each sample date.

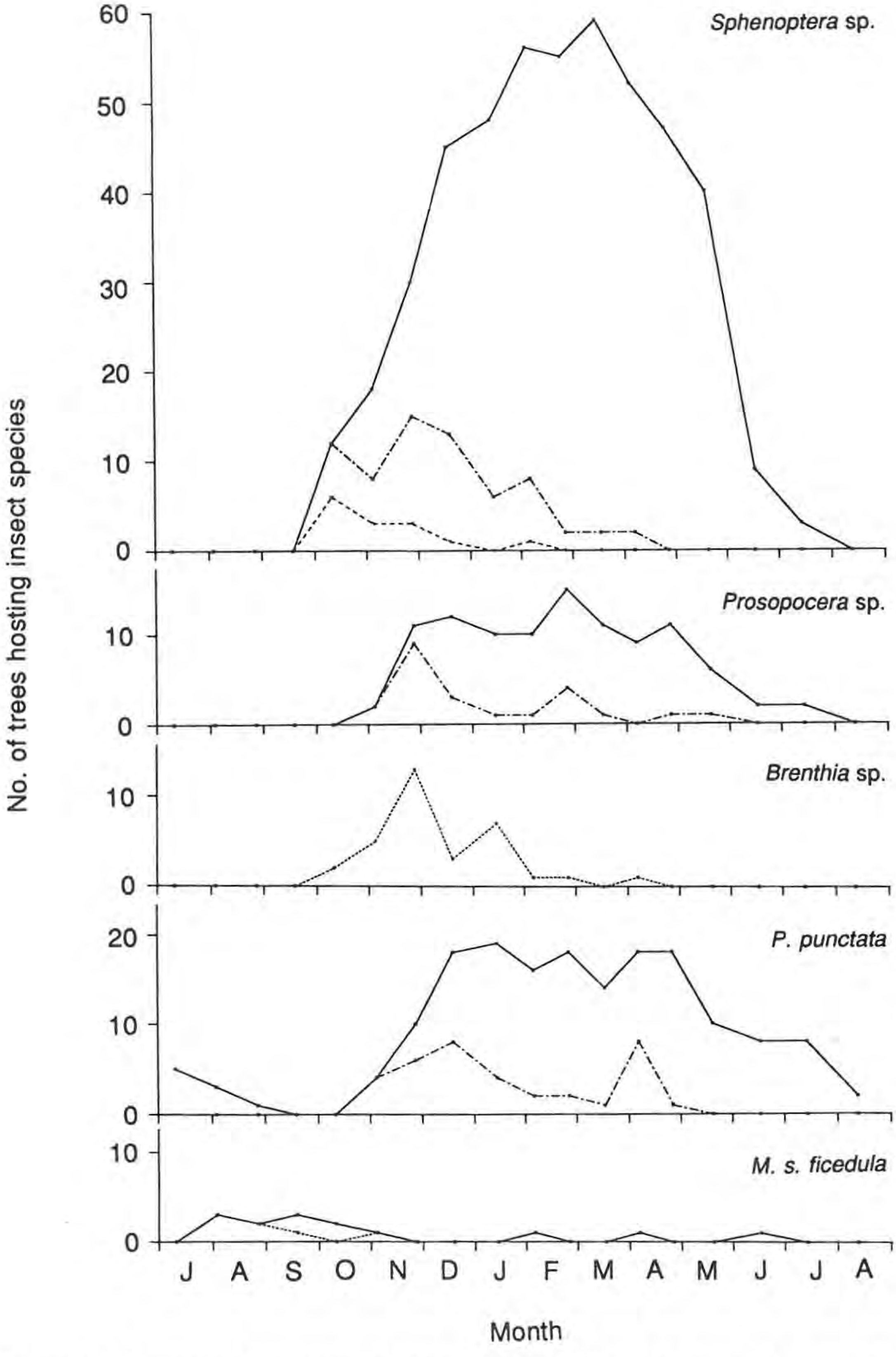


Figure 4.3 Seasonal fluctuations of the major phytophagous insects on *F. burtt-davyi.* Curves represent the number of trees on which insects of various life stages were found: —— represents the total number of records, –·–·– represents initial occurrences per tree only, ------ represents adults, and ······· represents larvae and nymphs.

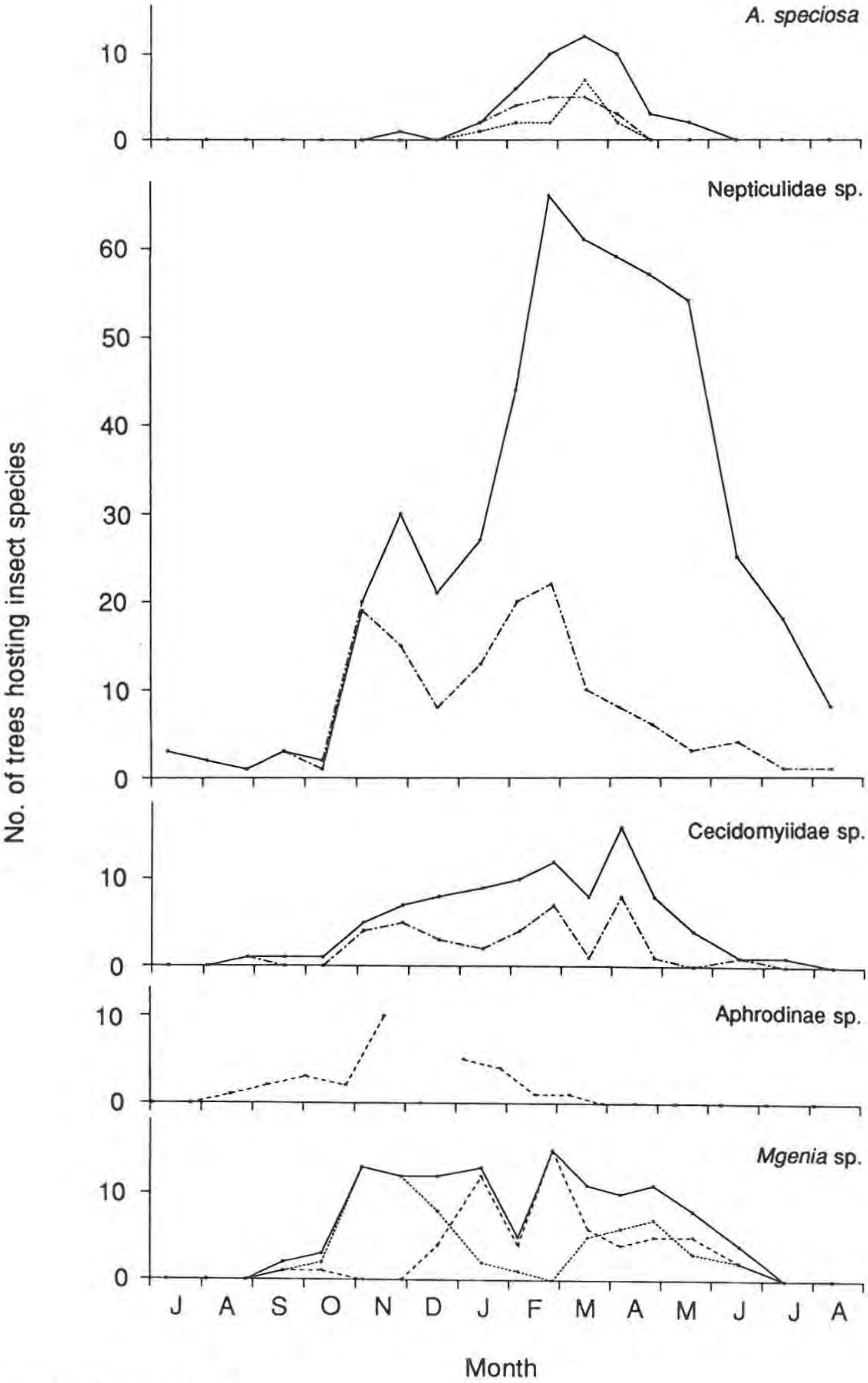


Figure 4.3 *continued*

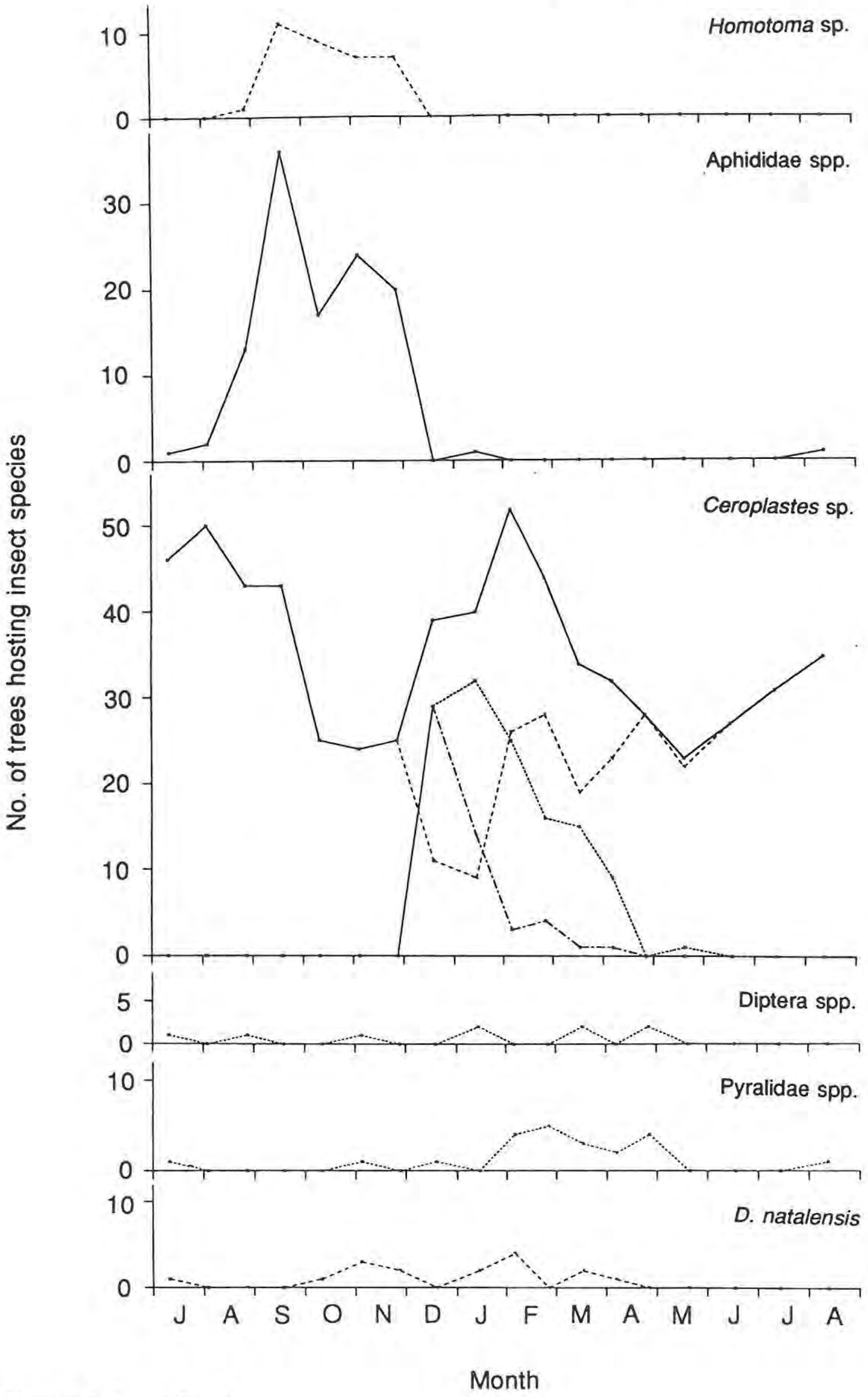


Figure 4.3 *continued*

COLEOPTERA: CERAMBYCIDAE: *Prosopocera* sp.

A single longhorn species of the genus *Prosopocera* was found on *F. burtt-davyi*. Most of the adults had silver-grey elytra patterned with darker grey, and grey-brown legs and antennae. The latter are approximately 1.3 times the body length, which is 8-9mm. There is a certain degree of colour variation, some individuals being browner than others.

Like the buprestid, this beetle has developed a method of latex avoidance (Figure 4.1B). It cuts off the latex supply to distal parts of the leaf by 'sabotaging' the midrib and side veins. It does this by closing its mandibles either side of the vein so making two puncture holes through which some of the latex drains. This process is repeated over and over again as the buprestid moves towards the leaf tip, sometimes stripping the epidermis from the vein as it goes. The latex supply broken, the beetle then feeds unhindered, either at the leaf tip or proximal to it where it makes holes in the leaf. Scholtz and Holm (1985) reported a similar kind of behaviour in a related genus, *Tragocephala*, although in this case it was to aid oviposition and larval feeding, with the adult females cutting a girdle around the branch prior to ovipositing beyond it. This action cuts off the sap supply, so improving conditions for larval development.

The majority of the records of *Prosopocera* sp. on *F. burtt-davyi* (Figs 4.2 and 4.3B) are based on the presence of the resulting characteristic feeding damage, as the adults were found on only one occasion, early in the morning. These were brought into the laboratory where their feeding behaviour was confirmed. As with the buprestid, the duration of the feeding period is likely to be exaggerated due to the impossibility of distinguishing between old and recent damage.

The larvae were not detected and probably feed on other host trees, although their specialised feeding behaviour suggests a close association with latex-producing plants. Cerambycid larvae most often bore into dead wood, although a few live in roots or the pith of herbaceous plants (Crawshay 1907; Richards and Davies 1977). They typically pupate in the wood, in the bark, or between the two.

The *Prosopocera* species found feeding on *F. burtt-davyi* appears to complete two life cycles per year, indicated by two peaks in damage initiation, one in late November and the second in late February, at the height of the summer (Fig. 4.3B). Richards and Davies (1977) found the speed at which the Cerambycid life cycle is completed to depend to a large extent on the supply of nutrients and moisture and Crawshay (1907) found temperature to have a marked influence. The time taken to complete the life cycle may be altered by months or even years by these factors, and the pattern seen in 1991/92 may therefore vary from year to year.

LEPIDOPTERA: CHOREUTIDAE: *Brenthia* sp.

One member of this family of micro-moths, *Brenthia* sp. was found during this study. This species has also been recorded on *F. sur* in the study area (C. Zachariades, pers. comm.). The adult has dark grey and orange-banded forewings, brown hindwings, and a wingspan of between 10 and 12mm. The larvae are pale green/yellow in colour with an orange and black head. They feed on the upper surfaces of younger leaves at the shoot tips where they roll the leaves slightly and spin a protective webbing which resembles the early stages of damage by *Phycodes punctata* Walsingham.

Details of the life cycle of *Brenthia* sp. are patchy, but field observations indicate that the period between the first appearance of the larvae and adult emergence spans a minimum of six weeks. In the laboratory, pupation was found to span a week to ten days. The larvae were present mainly in the spring to mid-summer, although they were found as late as the end of March (Figs 4.2 and 4.3C). Numbers reached a peak at the end of November when larvae were found on 13 of the 123 trees.

LEPIDOPTERA: BRACHODIDAE: *Phycodes punctata* Walsingham

P. punctata has previously been recorded feeding on *Ficus natalensis* Hochst. (Swain and Prinsloo 1986) in Natal, S. Africa, and a congeneric *Phycodes* species, on *F. sur* in the study area (C. Zachariades, pers. comm.).

The *P. puncata* adult is recognisable by its black-dotted, leaden grey forewings, dark brown hindwings and white body underside. The light green larva rasps the leaf surfaces at the shoot tips and as a protective measure, spins a webbing around the leaves thereby pulling them together and encasing itself within. The leaves gradually die and the larva moves along the branch, gradually increasing the extent of the tied bundle. By rearing field-collected larvae in the laboratory, it was established that the larval and pupal stages together span at least nine weeks.

P. punctata larvae were recorded for most of the year, with the exception of September (Figs 4.2 and 4.3D). Numbers started rising in the spring, reached a maximum in mid-January, and declined in the autumn. This pattern seems to correspond to rising and falling temperatures (Fig. 2.2, see Chapter 6 for confirmation). Two peaks in larval hatching occurred, in early summer and in late summer/autumn, these following shortly after peaks in rainfall and corresponding to young leaf flushes (Fig. 3.2). Autumn counts are probably slightly inflated due to the inclusion of some old damage no longer inhabited by larvae, as it was not always possible to distinguish between inhabited and deserted leaf bundles without their destruction.

LEPIDOPTERA: LYCAENIDAE: *Myrina silenus ficedula* Trimen

This species, the Fig Tree Blue Butterfly, feeds solely on *Ficus* species, *Ficus carica* L., *Ficus cordata* Thunb., *F. natalensis*, *F. sur* and *F. thonningii* having so far been identified as hosts (Clark and Dickson 1971, Migdoll 1987). *F. burtt-davyi* can now be added to this list.

The larvae were found feeding on the leaves and fruit of *F. burtt-davyi* throughout the year but always in very low numbers (Fig. 4.2 and 4.3E), the latter precluding the determination of any seasonal patterns. The numbers are probably slight underestimates due to the excellent camouflage of the larvae which are light green, brown and white in colour, the white areas resembling droplets of latex. Additionally, only one, or at the most two, larvae were found on a tree at any one time.

Many lycaenid larvae are associated with ants (Clark and Dickson 1971; Scholtz and Holm 1985) due to their secretion of a sugary fluid from a honey gland. C. Zachariades (pers. comm.) found *Pheidole megacephala* Fabricius tending *M. silenus ficedula* on *F. sur* trees in the study area, although on *F. burtt-davyi* there was no evidence of any such association.

LEPIDOPTERA: HYPSIDAE: *Aganais speciosa* (Drury)

A largely orange moth, this is one of about 18 similarly bright species of the family Hypsidae in South Africa (Pinhey 1975). The larva is also conspicuously coloured (possibly aposematically), being creamy-orange dorsally, black with orange spots laterally, and thickly covered with long hairs. Field observations revealed a larval development time of between nine and 14 weeks. The larvae were recorded feeding during the summer months between the end of November and mid-April, numbers peaking in mid-March as the temperature started to fall (Figs 4.2 and 4.3F).

Aganais speciosa (Drury) is another species to have developed a specialised feeding method in order to circumvent the latex defences of it's host plants (Figure 4.1C, D). Prior to feeding, the larger larvae chew through the midrib and/or the side veins on the underside of the leaf several times in order to cut off the latex flow to the areas beyond. They may then feed unhampered by the sticky latex. The young larvae, incapable of doing this, graze only on the surface of the leaf between the veins so avoiding the major suppliers of latex. Compton (1987, 1989) has previously noted this behaviour in *F. sur* as well as in *F. burtt-davyi*. The resultant distinctive feeding pattern was often all that was seen of this caterpillar.

LEAF MINERS

LEPIDOPTERA: NEPTICULIDAE: unidentified species

A single Nepticulid species was found during this investigation. Like the majority of the species in this family (Richards and Davies 1977) it mines the leaves in its larval form. The upper surface of the *F. burtt-davyi* leaf was mined, producing narrow galleries often terminating in a blotch. Pupation was not observed as it occurs away from the mines, and generally in the soil (Scholtz and Holm 1985). The adult, with a wing span of 3.0-4.0mm, has an ochreous-metallic band across the wing bases and dull, charcoal grey, tufted wing tips.

Species from the family Nepticulidae, like those from other leaf-mining families, tend to be highly host-specific (Hespenheide 1991).

This leaf miner was present throughout the year (Figs 4.2 and 4.3G) although only in very low numbers during the winter months when few trees had leaves (Fig. 3.2). There were two peaks in numbers during the year; one in late November and a second much larger one in late February, these corresponding to peaks in mine initiation (Fig. 4.3G). The second was twice the size of the first, despite the fact that the number of initiations were similar. It is possible that the life cycle could take a few months to complete, the later peak thus representing overlapping generations. However, this is not very likely, as microlepidopterans usually complete their life cycles in a matter of weeks (Pinhey 1975). The inclusion of increasing numbers of mines containing dead larvae, in the later counts would offer a more likely explanation.

LEAF GALLERS

DIPTERA: CECIDOMYIIDAE: unidentified species

One species of cecidomyiid gall midge was found. The adult is small in size (≈1.5mm long) and the larva galls the leaves, as is commonly the case in cecidomyiids (Richards and Davies 1977). The larva is bright red and the gall, a slightly raised circular area (of upto ≈8mm in diameter), most prominent on the upper surface of the leaf and often yellowing with age. Between one and 20 galls occurred on a single leaf (n=74 leaves, mean=4.73, sd=4.29).

Due to the great difficulty experienced with the rearing of the adults from the galls, very little can be ascertained with respect to life cycle details. However, a few successful laboratory rearings revealed that the larvae developed within the galls for at least three weeks.

Although the galler was present for most of the year, between late August and mid-July, it was found on only one tree from July to November 1991 and after May 1992. Peak numbers were reached in April as the temperatures decreased, when 16 trees were colonised (Figs 4.2 and 4.3H).

LEAF AND STEM PIERCERS

HEMIPTERA: CICADELLIDAE: unidentified species

One species of the subfamily Aphrodinae was found, probably representing an undescribed genus (M. Stiller, Biosystematics Division, PPRI, Pretoria, pers. comm.). It is a relatively slender species of 4.5 to 5.0mm in length and about 1.2mm in breadth. It has a brown/grey head and greyish, fine-veined wings covering a charcoal grey abdomen.

This species was present from late August to mid-March, peaking in the spring to early summer (Figs 4.2 and 4.3I). The missing data in mid-December (on the eighth sample date) is the result of a problem with identification.

HEMIPTERA: CICADELLIDAE: *Mgenia sp.*

This species is a robust plant hopper of 5.0-5.5mm in length and up to 2.0mm in breadth. It has a brown head and green abdomen covered by brown-patterned, thick-veined wings.

Nymphs and adults were present in spring, summer and autumn but absent in the winter months from mid-June to mid-September (Figs 4.2 and 4.3J). There were two generations in the year, peaks in nymph numbers being recorded in November and from March to April. As would be expected, the November maximum in nymph numbers was followed by a peak in adult numbers. However, the later peak was accompanied by a decline in adults until mid-July when none were found, indicating the probable overwintering of the second generation adults on another non-deciduous host.

In early February there was an unexpected fall in the numbers of this hopper, possibly attributable to the weather which, on the sample day, was unusual for the time of the year; overcast, drizzling and the maximum temperature 5°c lower than the previous day's. It is possible that this could have been responsible for the temporary sheltering of the hoppers.

HEMIPTERA: PSYLLIDAE: *Homotoma* sp.

A single psyllid species of the genus *Homotoma* was found on *F. burtt-davyi*. The nymphs feed in the leaf sheaths and were therefore not detected during routine surveys. The adults feed on the leaves and vary in colour from light brown to dark brown to red and are easily recognisable by a distinct brown strip along the costal margin of their otherwise transparent wings.

The adults were present only in spring between the end of August and the end of November and were recorded on between one and nine percent of trees on the five sample dates on which they were found (Figs 4.2 and 4.3K). Due to the lack of detection of the nymphs it was impossible to determine the number of generations occurring in this time. Within the psyllids the number of generations completed in a year varies greatly from a single generation, most common among temperate psyllids (Hodkinson 1974), to seven generations, occurring in some

South African psyllids, for example the citrus pest, *Trioza erytreae* (Del Guercio)(Annecke and Moran 1982). The psyllids as a whole, and particularly the nymphs, are very host specific (Scholtz and Holm 1985). *Homotoma* sp. was not found on the *F. sur* trees growing in the study area (C. Zachariades, pers. comm.).

HEMIPTERA: APHIDIDAE: *Toxoptera aurantii* Boyer de Fonscolombe

Although aphids were recorded on a relatively large proportion of the trees, individuals from only one tree were identified to species level (*Toxoptera aurantii* Boyer de Fonscolombe). Detailed analyses of the aphids present on *F. sur* trees in the study area, have revealed several species of aphid (including *T. aurantii*), with more than one species per tree sometimes being recorded at any one time (C. Zachariades, pers. comm.). It is therefore highly possible that more than one aphid species was present on *F. burtt-davyi*. However, because of the impossibility of separating the species visually in the field due to the considerable differences in appearance between morphs of the same species (Millar 1990), I have had to treat all records together as a single taxon. Alate black or green, and apterous black, green, yellow, or green/blue individuals were all recorded on the trees. They fed mostly on the stems and young shoots (the roots were not examined). Some aphids are also honeydew producers and as such attracted attendant ants (see later section of this chapter).

It appears that the aphids on *F. burtt-davyi* in the study area, whether one or more species, may alternate between hosts (i.e. are heteroecious) as testified by their presence on the trees only in the spring months (Figs 4.2 and 4.3L), the main infestation taking place over a three month period between the end of August and the end of November. Such host alternation within the aphids is relatively common, with the sexual phase of their cyclical parthenogenesis usually taking place in one season on one host, and the parthenogenetic phase occurring in a different season on a second host (Millar 1990). *T. aurantii*, however, is unusual in that it's life cycle seems to be anholocyclic, there being no sexual phase (Millar 1990). The number of trees hosting aphids was relatively high, reaching a maximum of 36 of the 123 (30%) trees in the study area.

HEMIPTERA: COCCIDAE: *Ceroplastes* sp.

During this study, five coccid species were recorded feeding on *F. burtt-davyi*, although only one, *Ceroplastes* sp., occurred commonly enough to be included in the quantitative analyses. The adult females of this wax scale are sedentary and are covered in a thick pinky-white wax covering. They have no marginal fringe, radiating processes or obvious plates. The adult females die as soon as hatching of the larvae is complete (Bodkin 1926). The first of the three larval instars are dull red/brown in colour and extremely mobile but soon become more conspicuous with the production of two white dorsal wax humps and 15 lateral wax processes. By this time they have settled on the upper surfaces of the leaves, mostly along the mid-rib and veins but at a later date, following the initial wax production, again migrate and this time settle on the shoots and branches. The wax processes and humps diminish in size and eventually disappear altogether, leaving the relatively smooth-bodied adult female. During his studies on the Palestinian wax scale, *Ceroplastes rusci*, L., Bodkin (1926) noted a similar developmental pattern, the initial period of sedentary behaviour lasting a month.

As a honeydew-producer, this phytophage was often tended by one or more ant species (see later section in this chapter).

There was one generation of this *Ceroplastes* species in the year, but two peaks in the total number of trees hosting it, one in early August and the other at the height of the summer, in early February (Figs 4.2 and 4.3M). There was also a further rise in numbers in August at the end of the sampling period. The August peaks are surprising and may reflect an artefact of sampling. By this time of year the scales are full-grown and the trees bare of leaves, with the result that single wax scales, previously difficult to detect, are far more visible. The number of host trees descends to a minimum between early October and late November due to adult mortality. However, numbers begin to rise again between late November and mid-December as young are produced. Hatching occurs mainly between mid-December and mid-January, although until early April occasional individuals continue to colonise a few new trees. The February peak is reached while there are still a large number of young around and as the early hatchlings begin to mature. High mortality, mainly amongst the young and less-so, among the more mature scales, is reflected in the decline from February to May.

FRUIT CHEWERS

DIPTERA: DROSOPHILIDAE: *Lissocephala* sp. and PHORIDAE: *Megaselia* sp.

One drosophilid species of the genus *Lissocephala* and one phorid species of the genus *Megaselia* was found in the fruit of *F. burtt-davyi*. The larvae of both species inhabited the figs at the same time and their very close resemblance to one another, combined with time constraints, allowed their identification only as dipterans whilst in the larval stage. As not all larvae were reared out, the identity of those on each tree are unfortunately not known. Therefore, details of the life cycles and seasonalities are not separable.

Members of the genus *Lissocephala*, together with those of the *Drosophila fima* group, are closely associated with figs in the tropical African region, many of the *Lissocephala* species having a narrow host-fig specificity (Lachaise et al. 1982). According to Lachaise et al. (1982) the adults oviposit in varying positions around the ostiole of the immature syconium. The first instar larvae, upon hatching, enter the fig via the ostiole at the same time as the pollinating wasps. The larvae develop within the syconium but outside the flowers until they reach the third instar when they leave the fig as the wasps emerge, and drop to the ground to pupate, thus avoiding destruction by frugivores. In this study the larvae were observed only in the post-emergent figs (those from which pollinating wasps had emerged). The pre-emergent fig sample was probably taken too early to reveal the first instar larvae.

One species of the large phorid genus, *Megaselia*, was found in this study. *Megaselia* sp. was also found only in post-emergent fruit. Whether this species actually feeds on fig material, wasp remains, or both, remains a mystery. Compton and Disney (1991), however, reported having seen the larvae entering vacated galls and the adults preying on fig wasps as they emerged. The larvae leave the figs prior to pupation and as the fruit ripens, so avoiding frugivores (Compton and Disney 1991). They pupate in the soil, the adults emerging after about two weeks. The latter must be relatively good dispersers as they must find another fig crop at the correct stage for oviposition. This task is somewhat simplified by the fact that the *Megaselia* species appear to be fairly generalist fig-feeders; Compton and Disney (1991) found five such species to feed on an average of 3.2 of a total of nine *Ficus* species. One of these was *F. burtt-davyi*, in the figs of which *Megaselia ficaria* Disney, *Megaselia parvorata* Disney, and *Megaselia vorata* Disney were found.

The two dipterans recorded in the figs of *F. burtt-davyi* were found in very few of the fig crops (3.2%) and at varying densities (maximum percentage of figs (of one crop) infested = 42%, minimum = 0.04%, mean = 0.17%, sd=0.15, n=50). Laboratory rearings showed the phorid to be by far the most abundant of the two. The larvae were found throughout most of the year, May and June excepted, no seasonal pattern being evident due to their low frequencies of occurrence (Figs 4.2 and 4.3N).

LEPIDOPTERA: PYRALIDAE: *Cirrhochrista convoluta* Hampson, and unidentified species

Two pyralid species were recorded during this investigation. It has been possible to identify only one of the two to species level; *Cirrhochrista convoluta* Hampson, which was also found in fruit of *F. sur* in the study area (C. Zachariades, pers. comm.). The adult is characterised by delicately brown-patterned forewings and body and brown-edged white hindwings. The unidentified species is smaller, with brown forewings, a body of varying shades, and paler hindwings.

The larvae of both species feed within the figs, hollowing them out. They feed mainly in figs at the interfloral stage of development (figs pollinated but with wasp progeny unemerged), although on one occasion they were found in wasp-emerged fruit and on another, in unpollinated fruit. The larvae tunnel from fig to fig leaving frass and debris behind them. The damage and the creamy-coloured, brown-headed larvae of the two species resemble one another very closely and as not all larvae were reared out to adulthood, the species could not be separated here.

Details of the life cycle are sparse. Partial rearings in the laboratory revealed a larval and pupation period of at least four weeks. The pyralids occurred at a fairly low frequency, being found on a maximum of five trees on any one sample date. They fed from the hottest months on into the autumn although individuals were found at the end of October and in mid-August (Figs 4.2 and 3.3O).

FRUIT PIERCERS

HEMIPTERA: LYGAEIDAE: *Dinomachus natalensis* Scudder

Five lygaeid species were found on *F. burtt-davyi* but only one of these, *Dinomachus natalensis* Scudder, was found frequently.

D. natalensis is one of nine South African members of the subfamily Heterogastrinae which almost all feed exclusively on fig seeds (Slater 1971, 1972). It has previously been recorded feeding on *F. natalensis* but was not found on *F. sur* in the study area (although one of its conspecifics was: C. Zachariades, pers. comm.). The adult is mottled brown/grey in colour, well camouflaged against the bark and extremely agile. During the year, it was found feeding on *F. burtt-davyi* figs at all stages of their development on the tree. The insects tended to aggregate around the bases of the fruit, feeding by inserting an elongated labium into the figs to reach the seeds.

D. natalensis occurred at a fairly low frequency, being found on a maximum of four trees at any one time and in total, on 12 of the 123 trees. As a result there is no obvious seasonal pattern to it's appearance (Figs 4.2 and 4.3P). Fruit availability was not a limiting factor as there were fruit crops available throughout the year, usually on ten trees or more (minimum = 5 trees).

ATTENDANT ANTS

HYMENOPTERA: FORMICIDAE: *Tetraponera* sp., *Crematogaster liengmei*(?) Forel, *Pheidole megacephala* (Fabricius), *Acantholepis capensis* Mayr

Four dominant ant species were recorded on *F. burtt-davyi* in the study area: Pseudomyrmecinae: *Tetraponera* sp.; Myrmecinae: *Crematogaster liengmei*(?) Forel and *Pheidole megacephala* (Fabricius); Formicinae: *Acantholepis capensis* Mayr (Fig. 4.4). *C. liengmei* occurred most frequently, followed by *A. capensis*, *P. megacephala* and *Tetraponera* sp. (on 12%, 7%, 5% and 0.9% of samples taken over the year respectively).

Way (1963) states that 'most ant species are omnivorous and combine predation or scavenging with the collecting of plant foods, of which honeydew is especially important'. Species do, however, differ with respect to their preferred food. In this study *C. liengmei* and *A. capensis* occurred 91.5% and 81.1% of the time respectively on trees supporting scale and/or aphid populations (Table 4.2). *P. megacephala* occurred 94% of the time on such trees although it was observed tending aphids on only 0.9% of these occasions (Table 4.2). These observations fit in with those of Arnold (1915-1924) who found species from all three genera to 'have a marked fondness for sugary substances', most being aphidicolous and/or coccidicolous. However, *P. megacephala*, whilst tending homopterans, has at the same time been observed to prey on other phytophages (Broekhuysen 1948: e.g. the tobacco slug larva in South Africa and the rice borer, fruit fly, and corn-leaf hopper in Hawaii), on predators and parasites of some noxious pests (Broekhuysen 1948) and on pollinating and non-pollinating fig wasps and their parasitoids (Compton and Robertson 1988). In areas where this ant is introduced, the balance of its diet tends to shift towards prey (Greenslade 1972). Similarly,

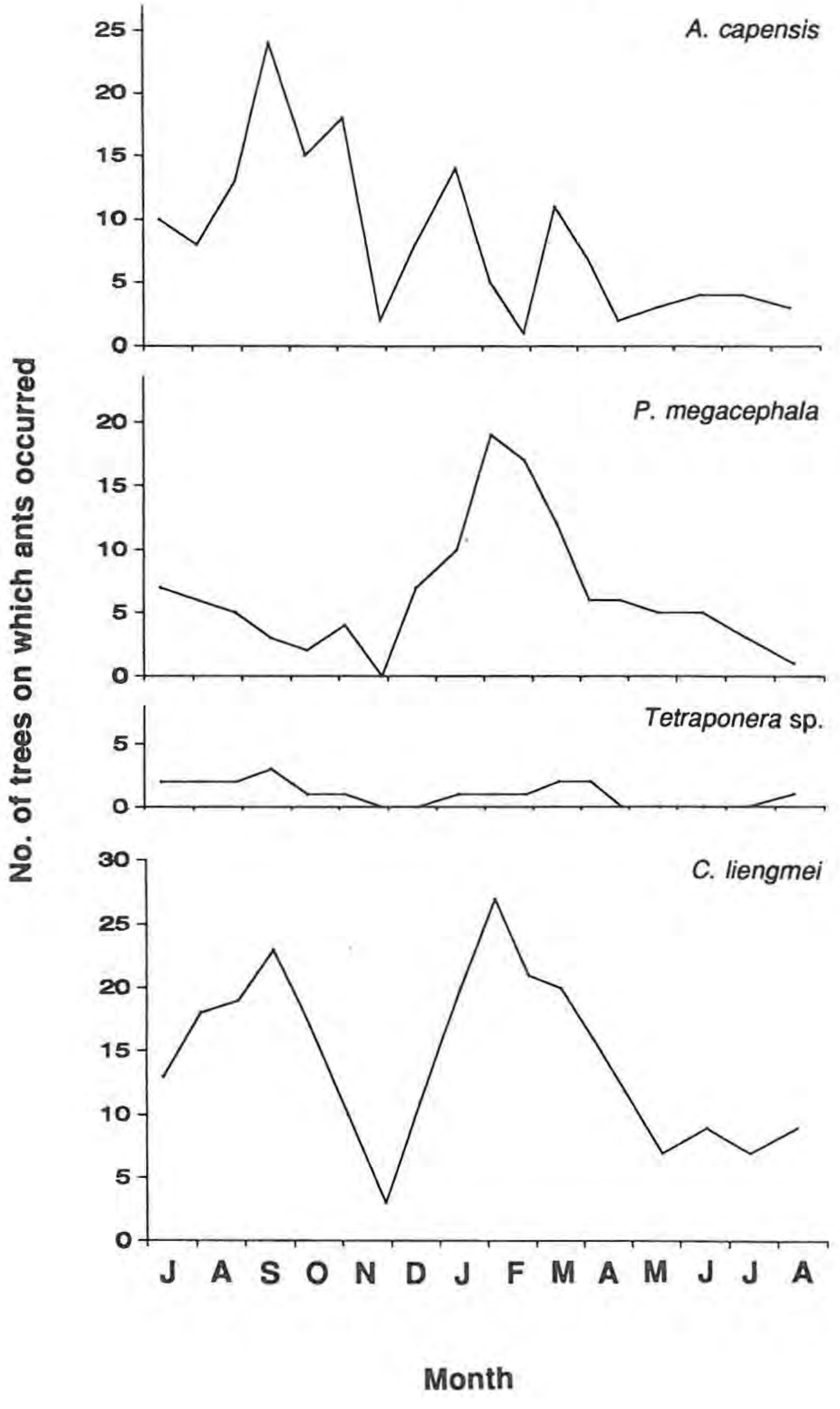


Figure 4.4 Seasonal fluctuations of the dominant ant species on *F. burtt-davyi*.

Table 4.2 The degree to which the ant species on *F. burtt-davyi* depend on homopteran-produced honeydew. The totals represent the number of samples on which ants of each species were found. The sub-totals indicate the numbers of these occasions on which each ant species co-occurred with scale insects, aphids, both of these, or neither of them.

ANT SPECIES	TREES SUPPORTING EACH ANT SPECIES PLUS:				
	SCALE INSECTS	APHIDS	SCALE INSECTS AND APHIDS	NEITHER	TOTAL
C. liengmei	204	16	16	22	258
A. capensis	87	23	10	28	148
P. megacephala	107	1	2	7	117
Tetraponera sp.	10	1	1	7	19

C. liengmei has been recorded as a predator of *Cactoblastis cactorum* (Berg) eggs in South Africa (Robertson 1988).

Only 63% of *Tetraponera* sp. individuals were observed to occur on trees supporting homopteran populations (Table 4.2) and only half of these actually appeared to be tending the homopterans. These observations imply that *Tetraponera* sp. relies to a greater degree on insect prey than on honeydew for food. Its fierce sting, large mandibles and pugnacity (Scholtz and Holm 1985; Wheeler 1922) add support to this hypothesis.

The number of trees on which *Tetraponera* sp. was found remained low all year round, whereas the number of trees foraged by *C. liengmei*, *A. capensis* and *P. megacephala* fluctuated greatly (Fig. 4.4). Numbers of *P. megacephala* were relatively low in the winter months, but rose after October in response to increasing numbers of *Ceroplastes* sp. Two peaks in numbers of *C. liengmei* occurred (Fig. 4.4). The first, in the spring, may indicate a response to the presence of honeydew-producing aphids, whereas the second may be linked to the high numbers of *Ceroplates* sp. *A. capensis* responds similarly to the winter aphid abundance, but not to the summer *Ceroplastes* sp. flush. In fact, during the latter, it's numbers plummet almost to zero, perhaps as a result of the rise in *P. megacephala* numbers.

Having described the constituents of the phytophagous insect community on *F. burtt-davyi*, the factors influencing community organisation at the level of the whole community, guild and individual species will now be investigated.

5 PHYTOPHAGOUS INSECT SPECIES RICHNESS - TEMPORAL AND SPATIAL RELATIONSHIPS.

INTRODUCTION

The term 'species richness' refers to the number of species co-occurring in ecological systems (Zwölfer 1986). It is one of two components of species diversity, a more complex measure of community structure incorporating estimates of the relative abundance of species (i.e. of common-ness and rarity).

Whittaker (1960) first noted that species diversity, which he termed γ-diversity, may be broken down into two components. The first of these, α-diversity, is the diversity of individual communities or particular habitat types and is also often described as local diversity (e.g. Harrison et al. 1992). The second component, termed β-diversity, relates to the amount by which the species composition changes from one of these communities or habitat types to another, i.e. the between habitat diversity (Cornell 1985) or turnover in species number (Harrison et al. 1992).

Cornell (1985) has classified herbivore species richness on the basis of Whittaker's (1960) components of diversity. He terms the number of species associated with a host plant population at a particular site, local herbivore species richness (equivalent to α-diversity), and the total number of associated herbivore species within the whole of a host plant's range, regional herbivore species richness (equivalent to γ-diversity).

Many factors combine to determine the species richness of phytophagous insect communities, some acting at the local level and others regionally. All play a part in the determination of the complexity of an ecosystem and hence have been widely studied and reviewed (Banerjee 1981; Claridge 1986, 1987; Compton et al. 1989; Fowler 1985; Jones and Lawton 1991; Lawton 1984a, 1984b, 1986; Lawton and MacGarvin 1986; Lawton and Price 1979; Lawton and Strong 1981; Price 1980, 1990; Southwood 1978; Strong 1984; Strong et al. 1977; Strong et al. 1984; Zwölfer 1986). Many were originally identified by analogy with the Equilibrium Theory of Island Biogeography (Janzen 1968, 1973; McArthur and Wilson 1967).

Of those factors outlined in Chapter 1 as being of potential importance to insect herbivore community composition, the following are of relevance when considering species richness within the herbivore community on a single host species at a single location: host plant size and structural diversity; tree isolation; host density and neighbour effects; habitat topography; ant-insect mutualisms; plant-herbivore-predator interactions; and lastly, seasonal changes.

The potential effects of these factors on phytophagous insect communities and the associated mechanisms by which they may arise were discussed in detail in Chapter 1. The consequences for species richness will be briefly reiterated here. Herbivore species richness has often been found to rise with increasing plant size and structural diversity (Claridge 1987; Davis 1975; Fowler 1985; Janzen 1968; Lawton 1983, 1986; Lawton and Price 1979; Lawton and Schröder 1977; Leather 1986; Moran 1980; Strong and Levin 1979; Strong et al 1984; Zwölfer 1986), and although not often seen to do so due to practical downfalls, it is also predicted to increase with decreasing degree of host plant isolation (MacArthur and Wilson 1967; Strong et al. 1984; Williamson 1981). Given that competition is usually not of fundamental importance in phytophagous insect communities (Chapter 1) it is possible that dense, 'pure' trees (i.e. those not surrounded by and intermingling with other plant species) may host a larger number of herbivore species than less dense, neighbour-diluted ones although to date there is no direct evidence for this. The effects of the topography of the surrounding habitat on species accumulation on hosts are unpredictable as they have as yet been little studied (Lewis 1969; Root 1973; Strong et al. 1984). Ant-insect mutualisms are likely to have mixed effects depending on the proportion of ant-tended phytophages within the community and on the feeding habits of the ants (Bach 1991; Fritz 1983; Grant and Moran 1986; Mahdi and Whittaker 1993; Pierce and Elgar 1985; Whittaker 1991), and plant-herbivore-predator interactions are relatively unpredictable in nature due to their complexity and lack of study to date (Leather and Walsh 1993; Strong et al. 1984).

The above factors are likely largely to affect spatial variation in species richness. The latter will, however, also vary temporally with climatic and host plant phenological changes (Basset 1991a; Price 1976; Strong et al. 1984).

Despite huge volumes of research on insect species richness predictors, these are most often aimed at explaining between species or genera differences and very rarely at the detailed scrutiny of one system centred around a single host species. This study is an attempt to achieve the latter and investigates differences in the species richness of the phytophagous insect community on individual trees of one species at a single location.

The chapter commences with a consideration of the temporal variation in herbivore species richness on *F. burtt-davyi* and continues with an analysis of the importance of plant architecture, microhabitat heterogeneity, tree isolation, foliage density, and the presence of ants, on the local between-tree variation in herbivore species richness on this fig species.

METHODS

General details of sampling methods and physical measurements are given in Chapter 2. Here, more specific methodological details are described.

Temporal variation

Phytophagous insect species richness was totalled for all trees at each sample date to give the total number of species feeding on *F. burtt-davyi* on each date. A Chi-square Goodness-of-fit Test (STATGRAPHICS Proc. CHISQ) was performed to test whether species richness varied (about a mean) with time.

Qualitative investigations of the temporal fluctuations of species richness with respect to climatic and phenological factors were supplemented by quantitative analyses. These latter involved the performance of a combination of All Possible Subset Regression (BMDP Proc. 9R, selection criterion ADJ R^2) and Stepwise Regression analyses (BMDP Proc. 2R, forward stepping) to determine the degree to which various climatic and phenological factors accounted for temporal variation in the distribution of herbivore species richness. Full details of these methods are given in Appendix 2. Climate was represented by seven independent variables: the maximum temperature during the week prior to and including the sample date (TMAX); the minimum temperature during this week (TMIN); the mean temperature during this week (TMEAN); total rainfall in the week prior to the sample date (RAIN1); total rainfall in the week two weeks prior to the sample date (RAIN2); total rainfall in the week three weeks prior to the sample date (RAIN3) and total rainfall in the month prior to the sample date (RAINM). Rainfall was measured over four different periods in order to try and detect time-lag effects (Basset 1991c). Changes in tree phenology were represented by seven independent variables: number of trees with young leaves (YLVS); with mature leaves (MLVS); bearing fruit (TOTFRUIT); bearing unpollinated figs (FRUIT1); bearing pollinated but pre-emergent figs (FRUIT2); bearing emergent figs (FRUIT3); and bearing post-emergent figs (FRUIT4).

During the preliminary analyses Shapiro-Wilk and Levene's tests (see Appendix 2) indicated that the data was normally distributed and homoscedascious. Therefore no transformation was necessary. Due to strong linear relationships between several of the independent variables (collinearity: see Appendix 2), two of these, the mean temperature in the week prior to the sample date (TMEAN) and the number of trees bearing post-emergent fruit (FRUIT4), were excluded from the analyses.

Spatial inter-tree variation

Cumulative insect herbivore species richness on each tree over the whole year was calculated. Variation of the species richness on each tree from the mean species richness per tree was investigated using a Chi-square Goodness-of-fit Test.

Tree architecture

An architectural rating was calculated for each tree based on six physical criteria representing tree size and architectural complexity: height (HT), canopy volume (VOL), largest cross-sectional area of the canopy (XAREA), maximum stem diameter (STDI), stem number

(STNO) and maximum number of axes (AXES). This was done largely to investigate effects of tree size, and coupled to this, microclimate diversity.

Cross-sectional area, being a two dimensional measurement, gives an indication of the maximum catchment area for insects. Measures of volume and height, however, whilst also describing the apparency of the tree, may additionally encompass microclimate heterogeneity and/or absolute 'living space'. Stem number and maximum axis number are most probably indirect estimates of tree size as opposed to contributing to habitat heterogeneity, as additional axes and stems will merely add further repeating units to the tree. Stem diameter, on the other hand, whilst potentially a measure of tree size and perhaps age, may also indicate the availability of a further resource, woody tissue.

The measurements of the above criteria are described in Chapter 2. The six physical measures were each divided up into 10 equal class intervals and trees scored from one to ten for each one. For each tree, scores were totalled across all six criteria to give the architectural rating. Prior to division into classes the data for volume, cross-sectional area and stem number were converted to logarithms to linearise their distributions.

Microhabitat heterogeneity

The presence of fruit on a tree adds a further resource and therefore increases the microhabitat heterogeneity of the tree. Two measures of fruiting were used: size of the largest crop borne by each tree (there may be a minimum size below which populations of fruit-feeders will not be sustained); and number of cropping events over the year, a crude indication of the seasonal spread and therefore 'apparency' (Feeny 1976) of fruiting.

A further potential contributor to microhabitat heterogeneity is the variety of insolation to which a tree is exposed. Phytophagous insects have varying preferences with respect to exposure to light so that the greater the number of insolation-defined microhabitats on a tree, the wider the range of species preferences that can be accommodated. Insolation was quantified by summing the number of sun/shade classes (1 to 4) to which a tree was exposed, the four classes being: full sun all day; dappled sunlight all day; mixed sun, shade and dappled; and shade all day.

Host density and neighbour effects

All of the *F. burtt-davyi* trees were associated to some degree with surrounding vegetation but quantification of the latter is extremely complex. Difficulties first arise when considering the question of physical concealment, colonisation by different herbivores being impeded to varying degrees by the same amount of intermingling/neighbouring vegetation. A similar problem arises when addressing the question of the degree to which surrounding vegetation may dilute chemical signals. These intricacies precluded quantification of neighbour effects in the limited time available. A crude estimate of tree foliage density, the effects of which are often inseparable from those of the surrounding vegetation, was however, possible.

The variable 'density' has most often been examined in agricultural systems where planting density may easily be manipulated (e.g. Root 1973). Here, though, the density index refers to the compactness of branching, and was established by estimating the volume occupied by the leafy branches only and dividing this by the total volume of the tree. Hence a compact tree will have a high density index and a rambling, well spread tree, a low one.

Tree isolation

The number of conspecifics within a 50m radius of each *F. burtt-davyi* tree was used as a measure of host tree isolation. Distance to the nearest immigrant source, a more direct estimation, was not employed due to the difficulty of the determination of likely colonist sources, each insect species having different requirements with respect to size of overwintering site and maximum distance over which dispersal is possible.

Ant presence

Finally, the variable 'ants' was quantified by calculating the number of sample dates on which ants (irrespective of species) were found on each tree, scores therefore lying between 0 and 18, the total number of sample dates.

Data analysis

The importance of the six measured potential determinants of spatially varying species richness (i.e. tree architectural complexity, insolation, tree isolation, foliage density, and ant presence) was evaluated using a combination of All Possible Subset and Stepwise Regression analyses as in the temporal analyses.

During the preliminary analyses, Shapiro-Wilk and Levene's tests (see Appendix 2) indicated a significant deviation of the spatial data from normality and homoscedasticity, so highlighting the need for transformation of the dependent variable, species richness per tree. Square-root and log (of richness+1) transformations of richness solved both problems of non-conformity and gave almost identical results. The results of the square-root transformation are given.

All Possible Subset and Stepwise Regressions were then performed on the six architectural variables to determine the relative contributions of each to the architecture-richness relationship. In order to ascertain the degree to which the positive relationships between all six variables and richness were due to differences in tree 'apparency' (Feeny 1976) versus varying habitat heterogeneity, analyses of covariance were performed. The contribution of tree apparency to the relationship was removed via designating maximum cross-sectional area (logarithmically transformed)(the 'purest' measure of apparency) the covariate.

Covariance analysis adjusts means for variability in the dependent variable attributable to one or more covariates prior to testing the equality of these means (BMDP Statistical Software Manual 1990; Rawlings 1988). The analyses were performed using BMDP Proc. 1V which allows the comparison of results of simple analyses of variance (i.e. prior to removal of the effects of covariates) with those of analyses of covariance. The program also tests the assumption that the regression lines for each group are parallel.

As preliminary results showed a positive relationship between ants and species richness, this aspect was investigated further by repeating the above regressions following the exclusion of all ant-tended herbivores from species numbers.

RESULTS

Temporal variation

Species richness varied significantly over the year (range=5 to 21 species, mean=13.22, chi-square=32.16, $p<0.05$). Numbers were generally highest in spring and summer although there was a good deal of variation between sample dates (between 14 and 21 species) even in these months (Fig 5.1) with species numbers falling dramatically at two points (mid-December and early February). On the first of these occasions, an unusually high maximum daily temperature (max. temp. = 38°C; mean monthly max. temp. for Dec. = 26.8°C) could have caused insects to take shelter away from the trees. However, there is no similar explanation for the fall on the second date. The final decline in species number, commencing in March, probably occurred in response to falling temperatures, leaf senescence and a fall in the number of fruiting trees (Fig 5.1). Species numbers reached a minimum in August when temperatures were at their lowest.

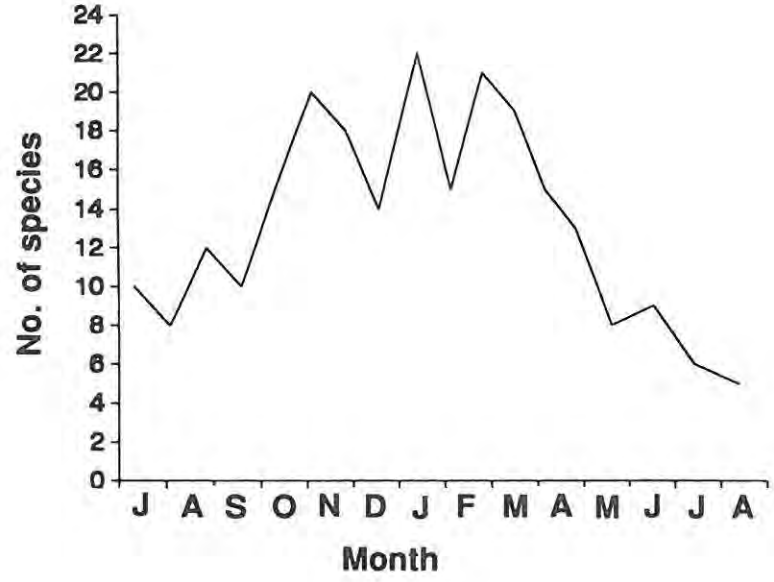


Figure 5.1 The variation of total herbivore species richness on the trees through the year (July 1991 to August 1992).

All Possible Subsets Regression and Stepwise Regression analyses confirmed the above qualitative results. A subset containing six of the 14 independent variables explained 82.09%

of the temporal variation in species richness (Table 5.1). Of these six variables, however, only two (the total number of trees in fruit and the minimum temperature in the week prior to the sample date) explained a significant amount of the variation. The Stepwise Regression Procedure identified the total number of trees in fruit to be of primary importance, and selected no other variables. Minimum weekly temperature was probably not selected due to its high correlation with the number of trees in fruit (r=0.7207, p=0.0030; see also Chapter 3 for temperature-phenology relationships). This idea was supported by the stepwise selection of minimum weekly temperature for entry into the regression equation (to explain 54.27% of the variation) following the removal of the fruiting variables from the analysis.

Spatial inter-tree variation

Species richness was highly non-uniform among trees (Fig 5.2: range=0 to 15 species, mean=5.57, chi-square=308.88, p<0.0001).

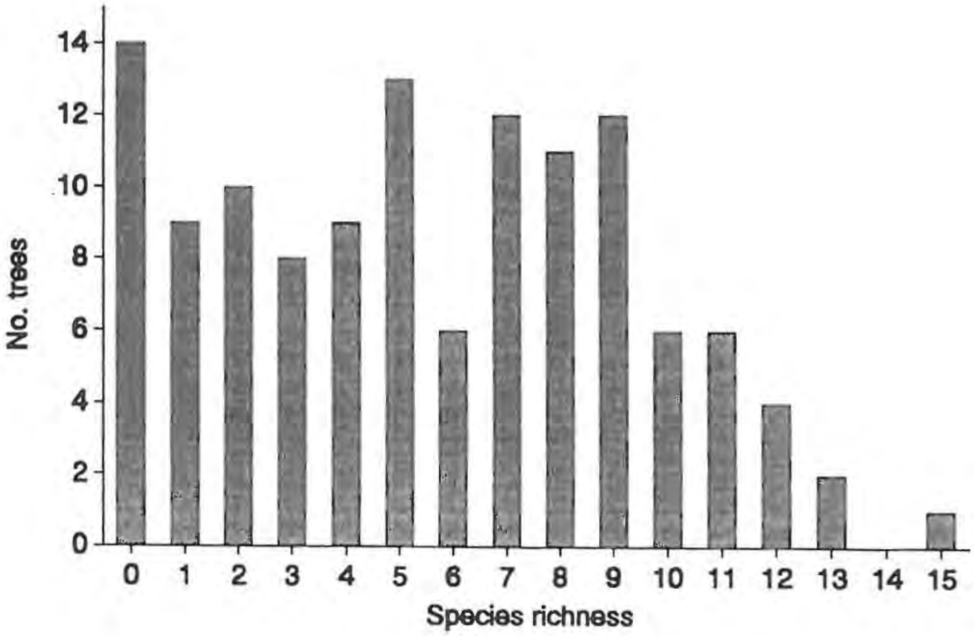


Figure 5.2 The variation of accumulated (over the study period) species richness among trees.

Table 5.1 Results following All Possible Subset and Stepwise Regression analyses. The independent variables are the total number of trees in fruit (TOTFRUIT), the number of trees bearing emergent figs (FRUIT3), the minimum temperature in the week prior to the sample date (TMIN), total rainfall in the month prior to the sample date (RAINM), total rainfall in the week prior to the sample date (RAIN1), and the number of trees bearinf pollinated but pre-emergent figs (FRUIT2). R, the multiple correlation coefficient, is a measure of the correlation between the dependent variable (square-root transformed richness) and its predicted value (BMDP Statistical Software Manual 1990). R^2, the coefficient of multiple determination, gives an estimate of the proportion of the variation explained by all independent variables in the equation. ADJ R^2 is an adjusted form of R^2, which allows for the misassumption that the variances and covariances in the normal equations are true values as opposed to estimates (Sokal and Rohlf 1981). The contribution of each variable to R^2 is the amount by which R^2 would be reduced if that variable were removed from the equation. The regression coefficient is a measure of the degree of association between an independent variable and the dependent variable. The t-statistic tests the hypothesis that the regression coefficient is zero. *** = $p<0.001$, ** = $p<0.01$, * = $p<0.05$, NS = not significant. [1] signifies the only variable to be selected by the Stepwise Regression analysis.

VARIABLE	ORDER OF ADDITION TO EQUATION	MULTIPLE			CONTRIBUTION TO R^2	REGRESSION COEFFICIENT	t-STAT.	2-TAIL SIG.
		R	R^2	ADJ R^2				
TOTFRUIT[1]	1	0.8850	0.7833	0.7697	0.1004	0.9768	3.09	**
FRUIT3	2	0.9028	0.8150	0.7904	0.0412	-1.0135	-1.98	NS
TMIN	3	0.9222	0.8505	0.8184	0.0515	0.4277	2.21	*
RAINM	4	0.9245	0.8547	0.8099	0.0281	0.0497	1.63	NS
RAIN1	5	0.9324	0.8693	0.8149	0.0294	-0.1087	-1.67	NS
FRUIT2	6	0.9403	0.8841	0.8209	0.0148	-0.5776	-1.19	NS

The All Possible Subsets Regression selected a 'best' subset containing four of the six variables: architecture, ants, isolation and insolation, which together explained 66.74% of the variation in square-root transformed richness (SQRT RICHNESS). Addition of the further three variables, density, maximum crop size and crop number, into the equation lowered this figure to 66.19% (Table 5.2). The stepwise procedure identified architecture and ants to be of primary importance, together accounting for 64.93% of the variation. Of this, 60.47% was attributable to plant architecture, the best explaining variable, and 4.46% to ants, added to the equation at the second step (Tables 5.2 and 5.3; Fig 5.3A & B). Insolation was added at the third and final step, increasing the coefficient of determination by 1.18% (Table 5.3A). The addition of further variables caused no significant improvements to the amount of variation explained.

Insolation and isolation both had very similar F-to-enter values (4.98 for insolation and 4.27 for isolation) at step three of the selection process, insolation being chosen by virtue of its slightly higher F-to-enter value. In a stepwise regression in which all variables were forced into the equation, isolation was added fourth and did not significantly improve the coefficient of determination (Table 5.2). However, in a further stepwise regression in which isolation was forced into the equation before insolation, its effects were significant (Table 5.3B), those of insolation, now entered fourth, becoming insignificant. Hence, insolation and isolation both contributed marginally significantly to the variation of species richness, although not together.

In summary, species richness rose most significantly with increasing architectural complexity and very much less strongly with increasing ant occurrence (Figs 5.3A & B). There was also a tendency for species numbers to rise with decreasing isolation (increasing numbers of trees

Table 5.2 Spatial between-tree analyses: multiple correlation coefficients, regression coefficients and their significance levels following the stepwise forcing of all 7 independent variables into the equation with square-root transformed richness. See Table 5.1 for explanations of the column headings.

VARIABLE	ORDER OF ADDITION TO EQUATION	MULTIPLE			CONTRIBUTION TO R^2	REGRESSION COEFFICIENT	t-STAT.	2-TAIL SIG.
		R	R^2	ADJ R^2				
Architecture	1	0.7798	0.6081	0.6047	0.2066	0.0770	8.42	***
Ants	2	0.8095	0.6553	0.6493	0.0224	0.0482	2.77	**
Insolation	3	0.8185	0.6699	0.6611	0.0114	-0.1819	-1.98	*
Isolation	4	0.8239	0.6789	0.6674	0.0033	0.0035	1.06	NS
Density	5	0.8251	0.6808	0.6664	0.0019	-0.1829	-0.81	NS
Crop no.	6	0.8259	0.6822	0.6648	0.0002	0.0330	0.28	NS
Crop size	7	0.8260	0.6823	0.6619	0.0001	0.0160	0.21	NS

Table 5.3 A: Final stepwise-selected subset of predictor variables. In the absence of the four excluded variables, regression coefficients and their significances alter slightly. B: The results following the substitution of isolation for insolation. See Table 5.1 for an explanation of the column headings.

	VARIABLE	ORDER OF ADDITION TO EQUATION	ADJ R^2	CONTRIBUTION TO R^2	REGRESSION COEFFICIENT	t-STAT.	2-TAIL SIG.
A	Architecture	1	0.6047	0.2524	0.0796	9.30	***
	Ants	2	0.6493	0.0373	0.0578	3.57	***
	Insolation	3	0.6611	0.0146	-0.1977	-2.23	*
	EQUATION: Sqrt richness = -2.082 + 0.0796arch + 0.0578ants - 0.1977inso						
B	Architecture	1	0.6047	0.3277	0.0696	10.56	***
	Ants	2	0.6493	0.0336	0.0557	3.38	***
	Isolation	3	0.6591	0.0126	0.0058	2.07	*
	EQUATION: Sqrt richness = -0.4048 + 0.0696arch + 0.0557ants + 0.0058iso						

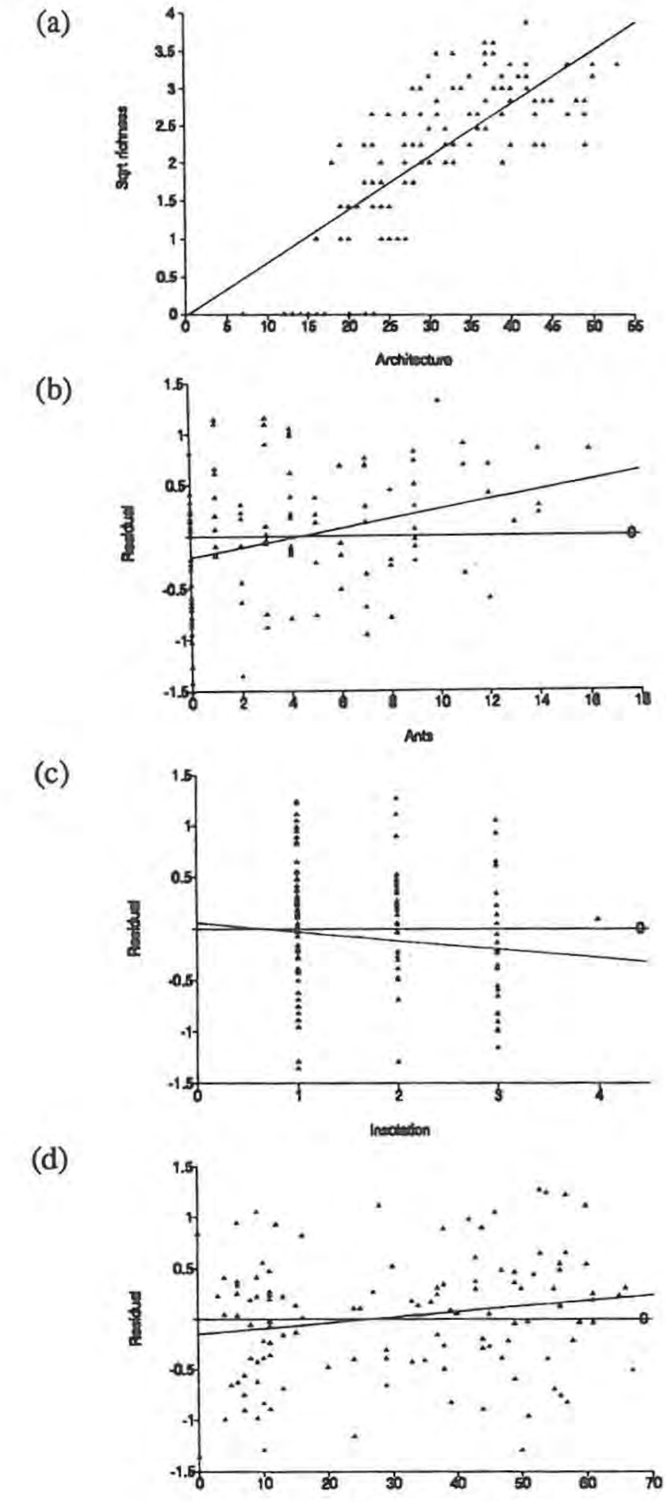


Figure 5.3 a) Correlation between tree architecture (architectural index) and sqrt richness: r=0.778, p<0.001 (eqn: y=-0.2912+0.0793x). b) Correlation between ant presence (the number of trees hosting ants) and the residuals from (a): r=0.301, p<0.001 (eqn: y=-0.1756+0.0473x). c) Correlation between insolation (the number of insolation classes to which the tree was exposed) and the residuals from (b): r=-0.165, p=0.071 (eqn: y=0.2092-0.1176x). d) Correlation between isolation (the number of conspecific trees within a 50m radius of the tree sampled) and the residuals from (b): r=0.192, p=0.035 (eqn: y=-0.1668+0.0057x).

within a 50m radius) and paradoxically, with a decreasing variety of insolation-defined micro-habitats (Figs 5.3C & D).

A breakdown of the architectural index into its constituents showed all six to be highly significantly correlated with species richness (SQRT RICHNESS) and with one another (Table 5.4). The stepwise procedure selected the variables in the following order: maximum cross-sectional area (LOG_XAREA), stem diameter (STDI), maximum number of axes (AXES), stem number (LOG_STNO), tree height (HT) and canopy volume (LOG_VOL). Maximum cross-sectional area (LOG_XAREA) alone accounted for 62.96% of the variation in species richness (SQRT RICHNESS). Following its entry into the equation only stem diameter added significantly to the coefficient of determination which, with all variables in the equation, reached 64.33% whereas with cross-sectional area and stem diameter alone, it reached 64.56%.

Table 5.4 Correlations between the architectural constituents and square-root transformed species richness (SQRT_RICH). All coefficients differ significantly from zero at p<0.001. Architectural constituents are: height (HT), canopy volume: logarithm-transformed (LOG_VOL), largest cross-sectional area of the canopy: logarithm-transformed (LOG_XA), maximum stem diameter (STDI), stem number: logarithm-transformed (LOG_ST) and maximum number of axes (AXES).

	LOG_XA	STDI	AXES	LOG_ST	HT	LOG_VOL
LOG_XA	-					
STDI	0.701	-				
AXES	0.581	0.720	-			
LOG_ST	0.642	0.401	0.305	-		
HT	0.703	0.795	0.539	0.510	-	
LOG_VOL	0.980	0.690	0.560	0.656	0.702	-
SQRT_RICH	0.795	0.655	0.567	0.459	0.635	0.780

Following the removal of the passive sampling (or apparency) effect via an analysis of covariance, the highly significant relationships of two of the five variables, stem number (LOG_STNO) and maximum number of axes (AXES), with species richness (SQRT RICHNESS) fell away, confirming the theory that these factors are merely alternative measures of tree size. The effects of canopy volume (LOG_VOL), tree height (HT) and stem diameter (STDI) remained significant, however. This would suggest that microclimate layering in larger trees provides scope for the zonation of herbivores. The relationship between stem diameter and species richness remained significant even after all size effects (LOG_XAREA, LOG_VOL and HT) had been removed. It therefore seems that stem diameter is not just a measure of tree size, but also reflects the availability of a further resource to herbivores, or some age-related effect.

Following the exclusion of ant-tended herbivores from the richness counts, ants no longer contributed significantly to the habitat-richness relationship (coefficient=0.0198, t=1.13, p=0.262 as opposed to a coefficient of 0.0482, t=2.77, p=0.007).

DISCUSSION

Temporal variation

Species richness peaked early in the growing season (November) in agreement with the idea that trees and woody shrubs can accumulate herbivore species rapidly due to their architecture being largely in place at the start of the season (Lawton 1978; Niemela and Haukioja 1982; Strong et al. 1984). This initial peaking also occurred at a time when both young and mature leaves were present on the trees (Fig 5.1). Thus, two major resource types as opposed to one were available to phytophages (Niemela and Haukioja 1982). However, the importance of the latter is questionable as numbers remain high later in the season when very few trees have young leaves. More likely to be of importance with respect to the availability of additional resources, was the total number of trees bearing fruit at this time.

Generally, in temperate areas insect activity reaches a minimum in the winter months, species either hibernating or migrating (Wolda 1988 and references therein). Hence, the emergence of the relationship between minimum weekly temperature and herbivore species richness was to be expected. As well as being influenced directly by temperature, insects were also affected indirectly via relationships between temperature and leaf and fruit phenologies of the trees (Chapter 3).

Further factors previously found to be of importance in the determination of seasonal variations in the frequencies of occurrence of herbivore species and in herbivore species richness are changes in chemical composition of the leaves through the year (Feeny 1970; Lawton 1978). Feeny's (1970) analysis of the effects of seasonal changes in oak leaves on winter moth caterpillar feeding, showed availability of nitrogen to be a limiting factor in larval development, and tannin content to inhibit larval growth. Increased leaf toughness later in the year also acted as a feeding deterrent. When looking at species richness on bracken, Lawton (1978) found the seasonal build-up in numbers to be related to some degree to the build-up of tannins and silicates and to decreases in the nutrient content of the leaves. Unfortunately, nothing is known at present about seasonal changes in fig tree chemistry although they do have a latex defence system (Compton 1987, 1989; Williams 1991).

Spatial inter-tree variation

The emergence of plant structural diversity as the dominant factor influencing herbivore species richness was not unexpected. Such a relationship was first revealed by Lawton and Schröder (1977) in their study of species richness on British plants. Here, geographic range explained the majority of the variation in richness of associated phytophagous insects, and plant type (perennial herbs - woody shrubs - weeds and other annuals - monocotyledons), or architecture accounted for a large part of the remainder. Strong and Levin (1979) confirmed these results shortly after, when looking into species richness of parasitic fungi on North American and British plants. These studies marked the beginning of a mass of similar work during the early 1980's aimed at explaining variation in phytophagous insect species richness. The majority of these bore testimony to the great importance of host architecture (e.g. Fowler 1985; Lawton 1986; Lawton and Price 1979; Moran 1980; Neuvonen and Niemela 1981)

To what degree, though, is this relationship attributable to the size component of architecture and to what degree to the complexity component? On *F. burtt-davyi* trees size emerged as the most important element in the architecture-richness relationship, in agreement with similar findings in studies dealing with richness determinants at such a scale (e.g. Fowler 1985, phytophagous insects on birch trees, saplings and seedlings; Lawton and Price 1979, agromyzids on umbellifers; Moran 1980, phytophagous insects on *Opuntia*). On the other hand, investigations encompassing a wider range of host plant types (e.g. trees, shrubs and monocotyledons) and therefore of degrees of complexity, have tended to find higher numbers of species area for area on more complex hosts (e.g. Lawton 1983, 1986, for reviews of architectural effects; Lawton and Schröder 1977, insects on British plants; Strong and Levin 1979, parasitic fungi on North American plant species and insects on British plant genera;

Strong et al. 1984, for a review). It would seem, therefore, that within the same species or closely related groups of species the differences in complexity are not significant enough to affect species richness.

Of the size variables, maximum cross-sectional area emerged above all others as important, indicating a strong passive sampling effect due to differences in tree apparency. However, there was an additional size effect on species richness (highlighted by the analysis of covariance), attributable either to differences in microhabitat heterogeneity and/or in the availability of living space. The larger the latter, the greater the size of the insect populations that can be supported and therefore the less the chance of extinction.

The microhabitat heterogeneity effect could explain the significance of the relationship of stem diameter with species richness once all size effects were removed, larger stem diameter signifying a greater degree of woody development and therefore the presence of an additional resource. This is somewhat unlikely though, firstly as the bark of *F. burtt-davyi* is very smooth so doesn't provide much in the way of fissures etc. for overwintering and shelter of non wood-borers, and secondly, because only one stem-borer occurring in very low numbers utilised the tree. Therefore, rises in species numbers did not reflect increasing numbers of wood-boring species. So, what could the explanation for the stem diameter-richness relationship be? The only obvious remaining alternative is that stem diameter is a measure of tree age and that there is some effect of the latter (perhaps a phytochemical one) on species accumulation. Plant age is difficult to quantify in natural systems and thus its effect on species saturation on individual plants has rarely been studied. Banerjee (1981), however, did look at the effects of the age of individual tea plants and found it to have a major effect on arthropod pest species accumulation until saturation was reached after 35 years. Hence, an age effect is not impossible although it would be very hard to confirm.

Although it appears that microclimate heterogeneity may have been responsible to some degree for differences in herbivore species richness, this effect is not attributable to the number of insolation-defined microhabitats as this was not related to an increase in species numbers. In fact the smaller the number of insolation-defined microhabitats, the larger the number of species, a relationship possibly attributable to the difficulty of defining insolation types. Alternatively, the majority of species may prefer one insolation type, in which case no relationship between the number of insolation classes and species richness would be expected.

Although positive, the relationships of crop size and number with species richness were not significant, despite their addition of a new food resource to the tree. This is most likely ascribable to the fact that only two 'major' fruit-feeding species were recorded, the potential for the swelling of species numbers by fruit presence therefore being minimal.

Hence, the architecture-richness relationship is largely attributable to tree size and within this, to apparency and perhaps microclimate heterogeneity and availability of living space. Tree age may also play a role in species accumulation although this was not confirmed directly.

Ant presence on trees emerged as a further important organising force. The positive relationship between ant presence and phytophage richness appears to be a simple one ascribable to ant-homopteran mutualisms. Due to the non-predatory nature of the dominant ant species (see chapter 4) on the trees, the positive nature of the relationship was not at all surprising. There could also have been some disturbance of parasitoids and general predators by the ants although if there was, the effect was not a strong one, as indicated by the non-significant relationship between numbers of non-tended phytophages and ant presence.

The emergence of isolation as a marginally significant organising force within the community is surprising given that this element of the island biogeography theory often breaks down when applied to plant-insect systems (Chapter 1). Perhaps the use of a measure of isolation not dependent on the arbitrary choosing of 'reservoir' size from which to measure colonisation distances helped. The relatively large proportion of specialised feeders (which are most likely to be affected by isolation: Strong et al. 1984) within the herbivore community may also be responsible to some degree for this relationship.

The lack of an effect of foliage density was not unexpected given that species' preferences can differ so widely and as the complex effects of diversity of surrounding vegetation could not be included in the analyses.

33.26% of the variation in species richness of individual *F. burtt-davyi* trees remained unexplained following the entry of tree architecture, ant presence, variety of insolation and tree isolation into the equation. This figure is surprisingly low considering the number of potential contributors which could not be measured here, and in the future could be reduced further by the addition of any of these to the equation: habitat topography; diversity of intermingling and surrounding vegetation; predator effects; and phytochemical changes.

Conclusions

The temporal variation of phytophagous insect species richness on *F. burtt-davyi* appeared to be largely governed by temperature and resource availability. Spatially, at the species richness level of organisation in this community, the dominant influencing factor was tree size, with phytophagous insects on *F. burtt-davyi* providing yet another example of the species-area effect. The latter was attributable largely to differences in tree 'apparency', to a lesser degree to microclimate heterogeneity and the availability of living space, and possibly in some way, to tree age. Ants played a secondary role by encouraging colonisation and survival of honeydew-producing homopterans, and the degree of tree isolation further influenced insect species richness to a small degree.

6 GUILD STRUCTURE OF THE PHYTOPHAGOUS INSECT COMMUNITY ON *F. BURTT-DAVYI*: HOW PREDICTABLE IS IT?

INTRODUCTION

The term 'guild' was coined relatively recently by Root (1967) to describe 'a group of species that exploits the same resource in a similar way'. This very broad definition allows a variety of interpretations, but essentially encompasses species which feed on the same resources, and occur together in the same microhabitats (Terborgh and Robinson 1986). Guild-level groupings usually occur at the 'foraging substrate' and 'foraging behaviour' levels (Terborgh and Robinson 1986). Hence, an insect feeding on leaves will be placed in a different guild to one utilising fruit (substrate level) and at the foraging behaviour level, leaf feeding insects may be sub-divided into leaf chewers, leaf piercers, leaf miners and leaf gallers.

The guild concept is a useful one as far as community ecology is concerned as it allows investigation of the functional structure of the system without reference to individualistic species responses (Root 1973). In other words it offers an intermediate level between that of the whole community and that of individual species responses, at which to search for patterns and causal factors.

In theory, those herbivorous insect species belonging to the same guild and therefore having common feeding and living habits will be influenced similarly by host and climatic factors affecting their common resource bases (Cornell and Kahn 1989). It is these similarities and the between guild differences which many community studies have examined in their quest for organisational rules (Basset 1991a, 1991c: Basset and Arthington 1992; Cornell and Kahn 1989; Moran and Southwood 1982; Southwood et al. 1982; Stork 1987; Strong et al. 1984).

As feeding habit and substrate are the primary determinants of guild membership, it follows that differential variation in nutrient, defence and physical characteristics of the different substrates (leaves, stems, fruit etc.) should play a fundamental role in differences in host selection by guilds. Nutrients are often limiting to insect herbivores (Basset 1991b; Mattson 1980; Strong et al. 1984) as nitrogen occurs in very low concentrations in plant tissue as compared to animal tissue, and the proportions of essential amino acids also vary between plant and animal proteins (Edwards and Wratten 1980; Mattson 1980; Strong et al. 1984). Evidence of the importance of nitrogen comes from the positive effects of host plant nitrogen content on insect growth rates, reproductive performance and survival (Edwards and Wratten 1980; Hill 1982; Strong et al. 1984). Similarly, water is often present in insufficient quantities and may limit nitrogen assimilation efficiency and nitrogen accumulation rate (Basset 1991b; Bultman and Faeth 1988; Faeth et al. 1981; Mattson 1980; Scriber 1977). Hence, as nitrogen and water levels fluctuate differentially within the feeding substrates the relative densities of the guilds dependent on them are likely to change.

Further physical attributes of importance to insect herbivores include leaf size, particularly important to leaf miners and gallers (Basset 1991b; Bultman and Faeth 1986; Faeth 1985), leaf fibre content (Basset 1991b), foliar phytochemistry (e.g. Compton 1987, 1989; Pennings and Paul 1992; Strong et al. 1984; Tallamy 1985), physical defences such as tough leaves and stems, trichomes, thorns, hooks etc. (e.g. Hulley 1988; Pennings and Paul 1992; Strong et al. 1984), and, for phloem feeders, translocation rate which is largely dependent on the magnitude of leaf production and plant vigour (Basset 1991b; Larsson 1985; White 1984). Most of the foregoing apply to the leaves, these being the most commonly utilised resource and therefore the most often studied. The above variables often change with leaf age, young leaves generally having higher nutrient concentrations and water contents whilst being less tough and fibrous (Basset 1991b; Coley 1983) and usually containing lower concentrations of secondary compounds (Coley 1983; Feeny 1970, 1976). These, of course, are general patterns to all of which there are exceptions.

In addition to the above, external factors may affect herbivores either directly, or indirectly via their effects on the host-plant. Such variables include insolation, which may alter leaf production, foliar nutrients, morphology and defence characteristics (Basset 1991b; Claridge 1986; Harrison 1987; Moore et al. 1988; White 1984), temperature and rainfall (Basset 1991c; Duviard and Pollet 1973; Moya-Raygoza et al. 1990; Wolda 1988), humidity (Basset 1991c), lunar phase (Basset 1991c), isolation, foliage density, ant presence and tree architecture (see chapter 5).

This chapter commences with a preliminary look at the phytophagous insect guilds found on *F. burtt-davyi* and their fluctuations in relative abundance through the year. Subsequently, guild frequency variations are investigated with respect to temporal and host related factors in an attempt to explain some of the patterns observed. This is accompanied by an analysis of guild-guild relationships.

METHODS

The phytophagous insects of *F. burtt-davyi* were assigned to seven guilds based on their modes of feeding (Chapter 4): ectophagous leaf chewers (LFCH), leaf and stem piercers - xylem, phloem and mesophyll (LFPI), leaf miners (MI), leaf gallers (GA), endophagous fruit chewers (FRCH), ectophagous fruit piercers (FRPI) and stem borers. The latter was represented by only two individuals of one species and was therefore excluded from the analyses.

The frequency of occurrence of each guild, as opposed to the number of species within a guild, was investigated as species numbers were very low. Frequencies of occurrence were calculated by summing occurrences of all 'major' species (see chapter 4) within a guild either per sample date (for the temporal analyses), or per tree (for the spatial data). Therefore, on a single sample date a species may have occurred a maximum of 123 'times' (i.e. on all 123 trees), and a guild containing six species for instance, a maximum of 123x6 'times'. Similarly, on a single tree over the whole sample period, a species may have occurred a maximum of 18 'times' (i.e. on all 18 sample dates), and a guild containing six species, a maximum of 18x6 'times'.

Additionally, the seasonal frequencies were converted into proportions to give an idea of temporal changes in the guild spectrum (i.e. of relative proportions of the different guilds in the community). Seasonal differences in the population ecologies of the component species mean that the guild spectrum and therefore the functional structure of the community are likely to change over time (Cornell and Kahn 1989).

Data Analysis

Temporal variation

Changes in the guild spectrum of the fauna over the sample period were examined using 2x18 contingency tables (STATGRAPHICS Proc. TABLE). Frequencies of occurrence of each guild were tested for uniformity over time against the sum of the frequencies of occurrence of the remaining guilds. A significant result indicates non-uniformity of a guild's proportion over the year.

The frequencies of occurrence of each guild at each sample date were analysed as a 6x18 contingency table (BMDP Proc. 4F) to test for overall seasonal differences among guild distributions. Expected values were examined in order to assess how well the distribution fitted that of the theoretical chi-square distribution (BMDP Statistical Software Manual 1990). A minimum value of 0.31 indicated a poor fit, and necessitated the combining of rows and columns where expected values were smaller than 1.0.

The influence of the same 14 climatic and phenological variables as used in chapter 5 was investigated here. All statistical details are described in full detail in Appendix 2.

Preliminary analyses indicated that logarithmic transformations of leaf miner (MI) and leaf galler (GA) frequencies (log(x+1)) and a square-root transformation of fruit chewer frequencies (FRCH)(sqrt (FRCH+1)) were necessary in order to achieve normality (Shapiro-Wilk test, BMDP Proc. 2D) and homoscedasticity (Levene's test, BMDP Proc. 7D) of the data.

The above analyses tested possible climatic and phenological effects on individual guild distributions over time, but what about inter-guild relationships? Do guild abundances fluctuate together, indicating preferences for the same times of year, or do such fluctuations complement one another, indicating differential influences of food quality or climatic factors? In an attempt to answer these questions and thus gain further clues to the factors influencing guild distributions, the strength and direction of correlations between pairs of guilds over time were evaluated.

Firstly, guild frequencies were correlated in pairwise combinations using the Spearman Rank Correlation procedure (STATGRAPHICS Proc. RANKCOR) for non-parametric data. Where positive correlations arose they indicated a certain degree of autocorrelation due to guilds being similarly influenced by the measured climatic and phenological factors, but may also have represented subsidiary correlations with other, unmeasured factors. If negative correlations had arisen they would have indicated the differential influence of food quality, habitat-related factors, or species interactions on guild representation.

In order to detect these subsidiary relationships, Spearman Rank Correlations were performed on pairs of residuals from the stepwise regressions. Where significant positive correlations remained, the possibility that they reflected the mutual correlation of each of the guilds concerned with a third guild was examined by pairwise partial correlation of the residuals (STATGRAPHICS Proc. PCORR). The latter holds variation of all other correlates (i.e. guilds) constant whilst examining inter-pair relationships.

Spatial between-tree variation

The frequencies of occurrence of each guild on each tree over the whole sampling period were analysed as a 6x123 contingency table (BMDP Proc. 4F) to test for between-tree differences. Columns and rows containing low expected values were amalgamated as for the temporal data.

The relative importance of ten potential determinants of spatial variation in guild distributions was evaluated using a combination of All Possible Subsets Regression and Stepwise Regression analyses (BMDP Procs. 9R and 2R respectively; see Appendix 2). The independent variables, tree architecture (ARCH), ant occurrence (ANTS), isolation (ISO), crop number (CROPNO), crop size (CROPSZ), and foliage density (DENSITY), as calculated in chapter 5, were used. Tree architectural complexity was not broken down into its constituent parts due to the strong correlations between all six (see chapter 5). An additional four independent variables, all measures of insolation, were added to the foregoing: exposure of at least part of the tree to full sunlight all day (SUN), to full shade all day (SHADE), to dappled sunlight all day (DAPPLED) and to a mixture of these (MIXED). For the fruit-feeding guilds, only those trees bearing fruit were included in the analyses and for the non fruit-feeders the independent variables, crop number (CROPNO) and maximum crop size (CROPSZ) were excluded.

Conditions of normality and homoscedasticity were satisfied for the regressions in which leaf chewer (LFCH), leaf miner (MI) and fruit piercer (FRPI) frequencies were dependent variables. However, transformations of leaf piercer (LFPI)(log(LFPI+1)) and fruit chewer (FRCH)(sqrt(FRCH)) frequencies were necessary in order to improve normality and similarity of variances. The residuals from the regression against leaf galler frequencies (GA), although homoscedacious, could not be normalised by any transformation and fruit chewer frequencies (FRCH) remained heteroscedacious despite transformation. Results for these latter two guilds must therefore be treated with caution.

Guild-guild relationships were investigated using Spearman's Rank Correlation procedure (STATGRAPHICS Proc. RANKCOR) as for the temporal data.

RESULTS

Of the phytophagous insect guilds, leaf and stem piercers occurred most frequently (Fig 6.1; Table 6.1) and had the largest host range (number of trees on which they occurred)(Table 6.1), although leaf chewers were almost as abundant and widespread. *Ceroplastes* sp. was the most prominent member of the piercers, accounting for 68% (641) of their occurrences and

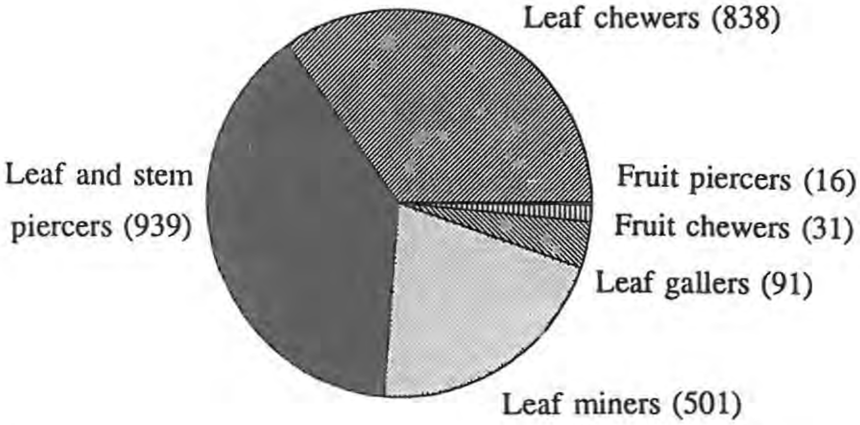


Figure 6.1 Total frequencies of occurrence of the six phytophage guilds, obtained by summing the frequencies of the 'major' species within each guild over the whole study period.

Table 6.1 Frequencies of occurrence and host ranges of guilds and their member species.

Guild	Species	Frequency of occurrence			Host range (no. trees)
		Number	Mean per sample	S.D.	
LEAF CHEWERS	*Sphenoptera* sp.	472	26.22	23.60	68
	P. punctata	172	9.56	7.06	32
	Cerambycidae sp.	101	5.61	5.39	19
	A. speciosa	46	2.56	4.06	19
	Choreutidae sp.	33	1.83	3.42	21
	M. s. ficedula	14	0.78	1.06	10
	Total	838	7.76	13.53	90
LEAF/ STEM PIERCERS	*Ceroplastes* sp.	641	35.61	9.34	83
	Mgenia sp.	119	6.61	5.55	57
	Aphididae spp.	114	6.39	10.85	54
	Homotoma sp.	35	1.94	3.70	22
	Aphrodinae sp.	29	1.61	2.59	26
	Total	939	10.43	14.62	101
LEAF MINERS	Nepticulidae sp.	501	27.83	23.29	91
LEAF GALLERS	Cecidomyiidae sp.	91	5.06	4.71	25
FRUIT CHEWERS	Pyralidae spp.	22	1.22	1.66	14
	Diptera spp.	9	0.50	0.79	8
	Total	31	0.86	1.33	19
FRUIT PIERCERS	*D. natalensis*	16	0.88	1.23	12

occurring on 67% of the 123 trees. The leaf hopper, *Mgenia* sp., and the Aphididae spp.occurred on 13% (119) and 12% (114) of occasions respectively (where an occasion refers to one tree on one sample date), and the *Homotoma* sp. and Aphrodinae sp., on 4% (35) and 3% (29) of occasions respectively. The species of this guild therefore fall into three groups with respect to their frequencies of occurrence.

Sphenoptera sp. was the most prominent species in the leaf chewing guild, accounting for 56% of the leaf chewers' occurrences and occurring on 55% of trees (Table 6.1). This figure is, to some degree, an over-estimate due to the reliance on leaf damage as an indicator of the presence of the species. However, with a frequency of occurrence of 472, it occurred at almost three times the frequency of *P. punctata*, the next most common species in the guild.

The leaf miner, Nepticulidae sp., occurred at a high frequency (501) and on 74% of the study trees. The latter makes it the most widespread species in the system. Although it's frequency of occurrence is the second highest of all species, it's abundance is probably somewhat exaggerated due to the recording of mines containing dead larvae and to the persistence of the mines following the exit of their inhabitant larvae.

The remaining three guilds occurred at relatively low frequencies ranging from 9 to 91, partly because they contained few species, and in the case of the fruit-feeders, also due to the restricted periods when food was available.

Temporal variation

The proportions of all guilds changed significantly during the sample period (Table 6.2). Fruit chewers and piercers, however, were present in very low numbers and therefore proportions, and minimum expected values calculated during the analyses were less than one. This means that for these guilds the distribution of the chi-square statistic is not well approximated by the theoretical chi-square distribution (BMDP Statistical software Manual 1990), and the results of the test must therefore be treated cautiously.

Table 6.2 Test for uniformity of proportion of guild frequencies over the sample period (18 sampling occasions). A significant X^2 value indicates non-uniformity. [1] minimum expected value = 0.63, [2] minimum expected value = 0.31.

GUILD	CHI-SQUARE	DEGREES OF FREEDOM	2-TAIL SIG.
LEAF CHEWERS	204.93	17	<0.0000
LEAF/STEM PIERCERS	522.67	17	<0.0000
LEAF MINERS	145.77	17	<0.0000
LEAF GALLERS	22.75	17	0.1577
FRUIT CHEWERS	19.36[1]	17	0.3081
FRUIT PIERCERS	20.69[2]	17	0.2403

As the frequencies of occurrence of the four largest guilds fluctuated markedly over the year, the guild spectrum and functional structure of the phytophagous insect community also changed (Fig 6.2). In the winter and early spring (July to October) the leaf and stem piercers dominated. However, during the summer and autumn (November to early June) the proportions of leaf chewers, miners and gallers increased, with the leaf chewers taking over the dominant role (Fig 6.2).

Contingency tests indicated significant temporal differences (Chi-square = 564.68, df = 36,

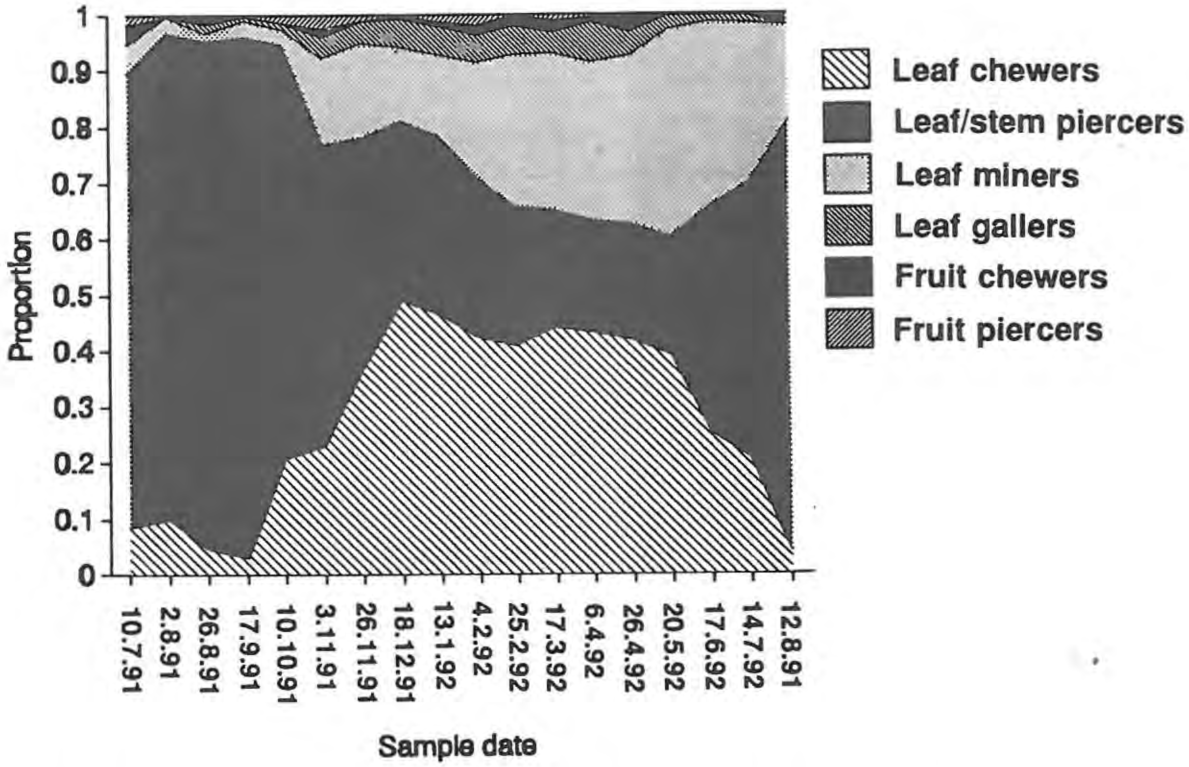


Figure 6.2 Variation of the guild spectrum with time, over the sampling period.

and stem piercing, leaf galling p = 0.000) in the distribution of absolute guild frequencies (Fig. 6.3). When all phytophages were considered, three variables (the number of trees bearing pollinated but pre-emergent figs (FRUIT2), the number of trees bearing young leaves (YLVS) and total rainfall in the week three weeks prior to the sample date (RAIN3)) explained 90.26% of the variation in frequency (Table 6.3). By forcing the entry of non-significant factors into the equation this figure reached a maximum of 94.30% (eight variables included in the equation), indicating that most of the temporal variation in total insect occurrence is accounted for by the climatological and phenological factors measured.

Changes in air temperature (maximum temperature in the week prior to and including the sample date (MAXT), minimum temperature in this week (MINT), and mean temperature in

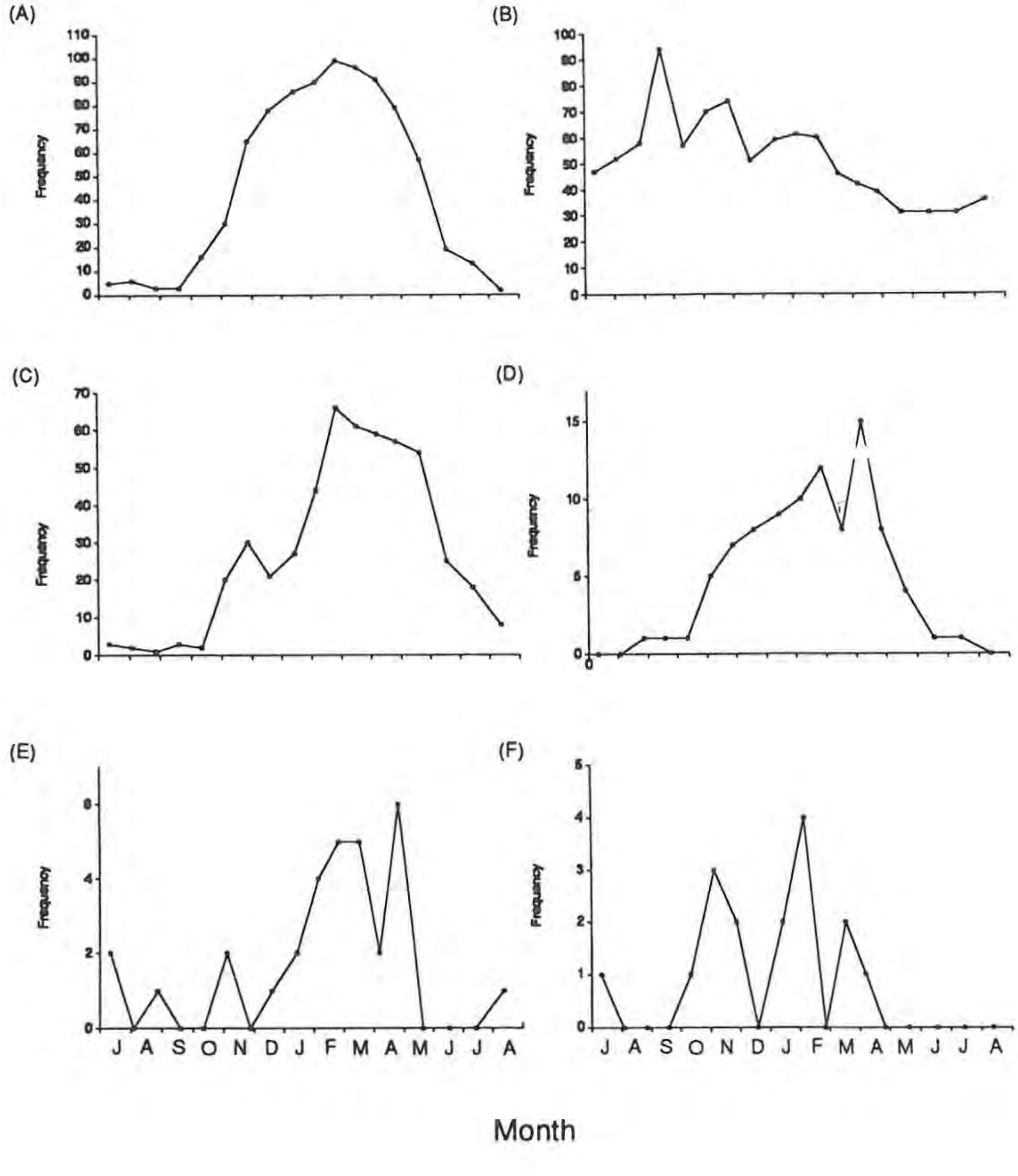


Figure 6.3 Temporal variation of the frequencies of occurrence of the six guilds: (A) leaf chewers, (B) leaf and stem piercers, (C) leaf miners, (D) leaf gallers, (E) fruit chewers, and (F) fruit piercers.

this week (MEANT)) explained substantial amounts of the variation in the leaf chewing, leaf and fruit chewing guilds (Table 6.3). The mean temperature in the week prior to the sample date (TMEAN), the sole significant determinant of leaf chewer frequency, explained a high proportion (80.44%) of the temporal variation in this guild. Leaf gallers and leaf and stem piercers were related rather to the maximum temperature during this week (TMAX), and fruit chewers to the minimum temperature (TMIN). Increasing minimum temperature in the week prior to the sample date (TMIN) seems to have had a negative effect on leaf galler numbers, a result inconsistent with the stronger positive influence of mean temperature during this week (TMEAN). This most probably arose as a result of the significantly positive correlation between mean weekly temperature (TMEAN) and minimum weekly temperature (TMIN). Because all temperature measures are highly correlated (r=0.6594 to 0.9706, p=0.0066 to 0.0001) the above differences must be treated with caution.

Rainfall was important in the determination of both leaf galler and miner distributions, on a monthly rather than a weekly scale, with guild frequencies rising as rainfall increased (Table 6.3).

Leaf phenology explained significant proportions of the temporal variation within the leaf piercing and mining guilds (Table 6.3). Leaf piercers favoured young leaves whilst leaf miners preferred mature leaves, and were negatively associated with young leaf presence.

Not surprisingly, the total number of trees in fruit, regardless of stage of development, was of significant importance in the determination of fruit piercer distribution. Fruit chewers, on the otherhand, were not correlated to fruit availability (Table 6.3).

The Spearman Rank Correlation procedure highlighted six (of 15) significant, positive correlations between pairs of guild frequencies (Table 6.4). However, when correlations were performed on pairs of regression residuals, only two significant correlations remained, those

Table 6.3 Stepwise regression analyses on factors influencing the temporal distribution of leaf chewers (LFCH), leaf and stem piercers (LFPI), leaf miners (MI), leaf gallers (GA), fruit chewers (FRCH) and fruit piercers (FRPI). Independent variables are: the maximum temperature during the week prior to and including the sample date (TMAX); the minimum temperature during this week (TMIN); the mean temperature during this week (TMEAN); total rainfall in the week prior to the sample date (RAIN1); total rainfall in the week two weeks prior to the sample date (RAIN2); total rainfall in the week three weeks prior to the sample date (RAIN3) and total rainfall in the month prior to the sample date (RAINM). Rainfall was measured over four different periods in order to try and detect time-lag effects (Basset 1991c). Changes in tree phenology were represented by seven independent variables: number of trees with young leaves (YLVS); with mature leaves (MLVS); bearing fruit (TOTFRT); bearing unpollinated figs (FRUIT1); bearing pollinated but pre-emergent figs (FRUIT2); bearing emergent figs (FRUIT3); and bearing post-emergent figs (FRUIT4). Upper figures are regression coefficients, their levels of significance indicated by * (***=$p<0.001$, **=$p<0.01$, *=$p<0,05$). Coefficients for those factors not explaining a significant amount of the variation and therefore not entering the equation are omitted and represented by -. Lower figures represent the contribution of a variable to R^2 (the coefficient of multiple determination), the amount by which R^2 would be reduced if that variable were removed from the equation. Superscript figures indicate the order in which variables entered the equation. Blank cells indicate variables excluded from the analyses. ADJ R^2 is an adjusted form of R^2, which allows for the misassumption that the variances and covariances in the normal equations are true values as opposed to estimates (Sokal and Rohlf 1981).

GUILD	INTERCEPT	TMAX	TMIN	TMEAN	RAIN1	RAIN2	RAIN3	RAINM	YLVS	MLVS	FRUIT1	FRUIT2	FRUIT3	FRUIT4	TOTFRT	ADJR^2
TOTAL	61.9080	-	-	-	-	-	1.2160^{*} 0.0265^{3}	-	-0.8750^{***} 0.2082^{2}	-	-	12.8644^{***} 0.5882^{1}	-	-	-	0.9026
LFCH	-70.8144	-	-	6.9665^{***} 0.8159^{1}	-	-	-	-	-	-						0.8044
LFPI	-14.3257	1.9584^{*} 0.2310^{2}	-	-	-	-	-	-	0.3938^{**} 0.5191^{1}	-						0.4561
MI	0.7326	-	-	-	-	-	-	0.0076^{**} 0.1072^{2}	-0.0114^{***} 0.3578^{1}	0.0079^{**} 0.1070^{3}						0.8230
GA	-1.4614	-	-0.0878^{*} 0.0525^{3}	0.1641^{***} 0.1751^{1}	-	-	-	0.0057^{**} 0.1130^{2}	-	-						0.8580
FRCH	-0.1296	-	0.1066^{**} 0.3640^{1}	-	-	-	-		-	-	-	-	-	-	-	0.3243
FRPI	0.8071	-	-	-	-	-	-		-	-	-	-	-	-	0.07189^{**} 0.4091^{1}	0.3721

Table 6.4 Pairwise correlations between temporally varying frequencies of guild occurrence: (a) Spearman correlations of guild frequencies; (b) Spearman correlations of residuals from stepwise regression models in table 6.3; (c) partial correlations of residuals. The guilds are: leaf chewers (LFCH), leaf and stem piercers (LFPI), leaf miners (MI), leaf gallers (GA), fruit chewers (FRCH) and fruit piercers (FRPI).

		LFCH	LFPI	MI	GA	FRCH
(a)	LFCH	-	-	-	-	-
n=18	LFPI	0.0817	-	-	-	-
	MI	0.8894^{***}	-0.1325	-	-	-
	GA	0.9273^{***}	0.2277	0.8166^{***}	-	-
	FRCH	0.6157^{*}	0.1021	0.5704^{*}	0.6092^{*}	-
	FRPI	0.4135	0.4598	0.2280	0.3940	0.3531
(b)	LFCH	-	-	-	-	-
n=18	LFPI	0.1063	-	-	-	-
	MI	0.3139	-0.2323	-	-	-
	GA	0.6656^{**}	0.1868	0.4946^{*}	-	-
	FRCH	0.4613	0.3664	-0.1621	0.2178	-
	FRPI	0.1043	0.2014	-0.1328	0.3202	-0.0062
(c)	LFCH	-	-	-	-	-
n=18	LFPI	-0.2176	-	-	-	-
	MI	0.0326	-0.1265	-	-	-
	GA	0.6293^{**}	0.2542	0.4635	-	-
	FRCH	0.2651	0.1703	-0.4292	0.2070	-
	FRPI	-0.0694	0.0981	-0.3294	0.3302	-0.2005

between leaf chewers and gallers and between leaf miners and gallers. Following the partial correlation procedure only the leaf chewer-galler relationship remained significant, suggesting a common cause, additional to those factors measured, for the temporal variation of these guilds.

Spatial between-tree variation

Spatially, guild distribution differed significantly (Chi-square = 295.41, df = 48, p = 0.000) between trees (i.e. guilds were not randomly distributed among trees).

Total phytophage abundance was positively influenced by tree architecture (ARCH), ant presence (ANTS), the incidence of full sunlight (SUN), and maximum crop size (CROPSZ), and negatively by the incidence of dappled sunlight (DAPPLED), all five variables accounting for a relatively high proportion (74.08%) of the variation among trees (Table 6.5). This figure could not be improved by forcing non-significant independent variables into the equation (seven variables entered: $ADJR^2=0.7478$).

The amount of variation in guild distribution explained by the measured factors varied widely from guild to guild, ranging from 72% for the leaf piercers to 8% for the leaf gallers (Table 6.5). Tree architecture emerged as an important distributional determinant among the leaf chewers, piercers, miners and gallers, all of which preferred more architecturally complex trees (Table 6.5).

It was only within the leaf and stem piercing guild that the presence of ants was significantly related to spatial distribution (Table 6.5). Here, not surprisingly, the ant relationship was of primary importance.

Table 6.5 Stepwise regression analyses on factors influencing the spatial distribution of leaf chewers (LFCH), leaf and stem piercers (LFPI), leaf miners (MI), leaf gallers (GA), fruit chewers (FRCH) and fruit piercers (FRPI). Independent variables are: tree architecture (ARCH), ant presence (ANTS), exposure of at least part of the tree to full sunlight all day (SUN), to full shade all day (SHADE), to dappled sunlight all day (DAPPLED) and to a mixture of these (MIXED), tree isolation (ISO), foliage density (DENSITY), crop number (CROPNO), and maximum crop size (CROPSZ). Upper figures are regression coefficients, their levels of significance indicated by * (***=$p<0.001$, **=$p<0.01$, *=$p<0,05$). Coefficients for those factors not explaining a significant amount of the variation and therefore not entering the equation are omitted and represented by -. Lower figures represent the contribution of a variable to R^2 (the coefficient of multiple determination), the amount by which R^2 would be reduced if that variable were removed from the equation. Superscript figures indicate the order in which variables entered the equation. Blank cells indicate variables excluded from the analyses. ADJ R^2 is an adjusted form of R^2, which allows for the misassumption that the variances and covariances in the normal equations are true values as opposed to estimates (Sokal and Rohlf 1981).

GUILD	INTERCEPT	ARCH	ANTS	SUN	SHADE	DAPPLED	MIXED	ISO	DENSITY	CROPNO	CROPSZ	ADJR^2
TOTAL	-10.6429	0.7401^{***} 0.1113^{1}	1.2289^{***} 0.0789^{2}	3.5233^{*} 0.0120^{5}	-	-4.0688^{*} 0.0130^{4}	-	-	-	-	1.7173^{**} 0.0186^{3}	0.7408
LFCH	-7.7060	0.3147^{***} 0.1962^{1}	-	4.0224^{***} 0.0772^{2}	-	-	-	0.0764^{**} 0.0561^{3}	-			0.4373
LFPI	-0.1197	0.0188^{***} 0.0789^{2}	0.0646^{***} 0.2383^{1}	0.1118^{*} 0.0119^{3}	-	-0.1181^{*} 0.0106^{4}	-	-	-			0.7224
MI	-2.4582	0.2038^{***} 0.3058^{1}	-	-	3.4983^{***} 0.0788^{2}	-	-	-	-			0.4512
GA	-0.1565	0.0618^{**} 0.0949^{1}	-	-	-	-	-	-	-			0.0872
FRCH	0.0064	-	-	-	-	-0.3392^{*} 0.0672^{2}	-	-	-	-	0.2698^{***} 0.2531^{1}	0.3433
FRPI	-0.7752	-	-	-	-	-	-	0.0150^{***} 0.2211^{2}	-	-	0.2585^{***} 0.2508^{1}	0.3884

The various classes of insolation explained differing amounts of the variation of leaf chewer (LFCH), leaf piercer (LFPI), leaf miner (MI) and fruit chewer (FRCH) distributions (Table 6.5). Constant exposure to the sun was of some importance to the leaf chewers and piercers, although in the latter case this variable only explained a very small amount (1.2%) of the variation. On the otherhand, trees exposed to constant shade were preferred by the leaf miners. Dappled sunlight was of significance within the leaf piercing and fruit chewing guilds, affecting the distribution of both negatively. This factor, however, only accounted for small proportions of the variation.

Tree isolation affected only leaf chewer and fruit piercer distribution, the less isolated a tree, the more likely its colonisation by these guilds (Table 6.5).

Lastly, crop size was the primary contributor to variation in the spatial distribution of the fruit chewers and fruit piercers (Table 6.5). Although crop number did not enter the equation for either of the fruit-feeders, this was due to its strong positive correlation with crop size (r=0.9510, p=0.000) rather than its insignificance as a distributional determinant. If crop size is excluded from the analyses, crop number enters the equation second in both cases. Therefore, although it does have some effect on tree choice by frugivores, this effect is masked by the stronger influence of crop size on distribution.

Twelve of the 15 Spearman Rank Correlations between guilds were significantly positive (Table 6.6), indicating that most guilds utilise the same kinds of trees. After removal of the effects of the measured habitat factors by investigating relationships between regression residuals, however, only one relationship remained significant: that between fruit chewers and

Table 6.6 Pairwise correlations between spatially varying frequencies of guild occurrences: (a) Spearman correlations of guild frequencies; (b) Spearman correlations of residuals from stepwise regression models in table 6.5; (c) partial correlations of residuals. In (b) and (c), n_1 refers to the number of cases in the majority of correlations, the exceptions being those involving the fruit-feeders, these having n_2 cases. The guilds are: leaf chewers (LFCH), leaf and stem piercers (LFPI), leaf miners (MI), leaf gallers (GA), fruit chewers (FRCH) and fruit piercers (FRPI).

		LFCH	LFPI	MI	GA	FRCH
(a)	LFCH	-	-	-	-	-
n=123	LFPI	0.5282***	-	-	-	-
	MI	0.4487^{***}	0.5023^{***}	-	-	-
	GA	0.2335^{**}	0.1659	0.3626^{***}	-	-
	FRCH	0.3013^{***}	0.2328^{*}	0.2237^{*}	0.1760	-
	FRPI	0.3390^{***}	0.2755^{**}	0.3648^{***}	0.1596	0.6460^{***}
(b)	LFCH	-	-	-	-	-
n_1=120	LFPI	0.0316	-	-	-	-
n_2=50	MI	0.1064	0.0596	-	-	-
	GA	0.0487	-0.0539	0.0830	-	-
	FRCH	0.1016	-0.0028	0.0685	0.2378	-
	FRPI	-0.0727	0.0676	-0.0608	0.0740	0.2857^{*}
(c)	LFCH	-	-	-	-	-
n_1=120	LFPI	0.0580	-	-	-	-
n_2=50	MI	0.1010	0.0584	-	-	-
	GA	-0.0952	0.0399	0.0898	-	-
	FRCH	0.0995	-0.0459	0.0803	0.2844	-
	FRPI	-0.0360	0.0289	-0.0892	0.1303	0.2557

fruit piercers. Following the partial correlation procedure, this relationship was no longer significant indicating that it arose due to the mutual correlation of these guilds with a third guild.

DISCUSSION

Temporal variation

The temporally varying factors, temperature, rainfall and leaf phenology, all played important roles in the determination of guild distribution over the year. Basset (1991c) classifies air temperature as a key governing factor of arthropod activity in temperate climates where it is more limiting than rainfall. Complementary to this, Wolda (1988) suggests that rainfall is more important in the tropics where seasonal changes in temperature are minimal. The insects on *F. burtt-davyi* in Grahamstown, like those in many other systems (e.g. Duviard and Pollet 1973; Moya-Raygoza et al. 1990), showed varying reactions to temperature and rainfall, four of the six guilds increasing in abundance with rising temperatures and two of them responding positively to increases in rainfall. This is understandable in an area where temperature shows substantial seasonal fluctuations, and where, during the study, rainfall was in short supply throughout the year (Chapter 2).

Only two of the four leaf-feeding guilds were influenced by leaf phenology. Leaf and stem piercers selected those trees with young leaves, in common with many herbivores which have been shown to feed selectively on such leaves (Aide 1993; Basset 1991a, 1991b; Coley 1983; Feeny 1970) due to their greater palatability. Additionally, Basset (1991b) found that the palatability of the Black Booyong (*Argyrodendron actinophyllum* Edlin) to phloem-feeders was increased by the higher translocation rate in the young shoots. Preferences for mature leaves (Basset 1991a - cicadellids and mesophyll feeders; Claridge and Wilson 1976 - typhlocybids; Strong et al. 1984 - polyphagous caterpillars) and cases of impartiality (e.g. Basset 1991b - chrysomelids and chewers in general), although far more rare have, however, also been noted. The leaf miners on *F. burtt-davyi*, with their preferences for mature leaves, are therefore not unique. This relationship is, however, likely to have arisen more as a result of an accumulation effect, with mature leaves being older and therefore having longer in which to be mined, than due to the selection of mature leaves in prefernece to young ones by the miner.

The fruit piercers fed on figs at all stages of their development (Chapter 4), hence their relationship solely with the total number of trees in fruit. On the otherhand, fruit chewers were most often detected in interfloral fruit (FRUIT2). Their numbers did not, however, fluctuate in relation to the number of trees bearing fruit at this stage. It can therefore only be assumed that such fruit crops were not in limited supply to the small numbers of these fruit-feeders.

The persistence of the positive leaf chewer-galler relationship implies that the shared susceptibility of these guilds to some unmeasured factor or factors affecting their common resource base (the leaf) is more important to their relative success over the year, than are their feeding habits which differ widely, the leaf chewers feeding externally and the leaf gallers, endophagously. Such a factor may be temporally changing nutritious status of the leaf (e.g. nutrient levels, toxin concentrations, toughness etc.).

Spatial between-tree variation

Most apparent, spatially (i.e. from tree to tree), is the strong effect of tree architecture on tree choice by the non fruit-feeding guilds, in three of which it was the dominant factor. Otherwise, there was a great deal of variation from guild to guild with respect to both the variables which emerged as being important and the total amount of variation they accounted for.

The emergence of ant presence as the dominant associative factor with leaf and stem piercer distribution was to be expected due to the mutualistic association between the honeydew-producing homopterans and tending ants (Chapters 4 and 5). However, whether the homopterans are attracted to trees with foraging ants on them, or vice versa, or whether they are mutually attractive, remains unknown.

The mixed response of guilds to insolation was to be expected given that changes in sunlight intensity result in conflicting selection pressures for herbivores (Bultman and Faeth 1988). Highly illuminated trees may be more attractive to herbivores due to their higher photosynthetic rate and therefore rate of nitrogen translocation (Basset 1991b) and/or to their higher sugar and starch levels (Bultman and Faeth 1988). White (1984) attributes elevated rates of nitrogen translocation in sun-leaves to their more rapid senescence (and therefore higher rate of nitrogen export) as a result of their exposure to sun at the hottest time of the day. Conversely, shading may confer changes beneficial to herbivores to leaves, such as increased leaf area, increased water content and reduced levels of toxic secondary compounds (Bultman and Faeth 1988; Claridge 1986). Shading may, of course, be directly beneficial to herbivores which may not be able to withstand the high temperatures associated with direct sunlight (e.g. the leaf miners which are immobile).

Preferences for sun-leaves have previously been noted in chrysomelids (Basset 1991b), aphids, coccids, sawflies, thrips, psyllids (White 1984: review) and leaf miners (Bultman and Faeth 1988; Faeth et al. 1981). Shade-leaves, on the other hand, offer a preferred food source to lepidopteran and coleopteran leaf miners (Bultman and Faeth 1988; Overgaard Nielson and Ejlersen 1988) and adult Coleoptera (Overgaard Nielson and Ejlersen 1988). It therefore seems that the response of phytophages to insolation is very varied, a result consistent with the mixed response seen in this study.

Investigation of nutritional differences between the leaves, stems and fruits of the trees was unfortunately beyond the scope of this study. Hence no conclusions as to the nutritionally based reasons for leaf chewers' and piercers' preferences for sun-trees and leaf miners' preferences for shade-trees may be drawn.

The preference of leaf chewers and fruit piercers for less isolated trees suggests a combination of restricted dispersal abilities and relatively specialised feeding behaviour within these groups. The former may well be true of the 'major' fruit piercer, *D. natalensis*, which was never seen to fly in this study, using running as a preferred means of escape. Slater (1971) reports similar behaviour for a congener, *Dinomachus marshalli* Distant. The large proportion of specialist latex-sabotaging insects within the leaf chewing guild, and the fig-specific feeding habits of the fruit piercing species may also have some bearing on the importance of the isolation effect to the tree by tree distribution of these guilds. Oligophagous species would be able to utilise other host species and therefore the degree of isolation of the *F. burtt-davyi* trees alone would be unimportant to them.

Obviously, the fundamental importance of fruiting attributes in the determination of frugivore distributions, meets expectations.

The emergence of tree architecture and ant presence as the two most important determinants of spatial variation in guild distribution corresponds to the results obtained with respect to the determinants of the variation of species richness. Insolation also played an important part in both cases.

A look at the guild-guild relationships, all of which were positive, revealed that despite their feeding on different parts of the plant and via different methods, the common preferences of guilds for certain habitat features outweighed the differences. The often substantial amounts of unexplained variation in guild distribution are most probably attributable to factors which were excluded from the analyses due to practical restrictions. These include variation in nutrient and defensive levels of leaves and in tree vigour and hence translocation rates.

Hence, guild distribution patterns have been revealed and to some extent explained, but how do they arise? Do the members of insect guilds share related habitat preferences? These questions will be addressed in the next chapter together with a look at the roles played by interspecific interactions in the community.

7 DO THE MEMBERS OF INSECT GUILDS SHARE RELATED HABITAT PREFERENCES?

INTRODUCTION

In chapter 6 it was established that the temporal and spatial distributions of the six feeding guilds found on *F. burtt-davyi* in Grahamstown could be explained to varying degrees by different subsets of the measured climatic, phenological and habitat factors. The question remains, however, as to how these patterns arise. Are there common habitat and temporal effects on species within a guild or do the patterns merely represent the sum of the distibution patterns of highly variable constituent species? Furthermore, are species within guilds more similar to one another than to those of other guilds with respect to their habitat preferences? In order to address these questions the two largest guilds (the leaf chewers and stem and leaf piercers) will be focussed on.

If one is to gain a full picture of the determinants of the observed patterns, an investigation of the interactions between components of the community is essential in addition to a study of the effects of the physical attributes. Therefore what role, if any, do interspecific interactions play within the phytophagous insect community feeding on *F. burtt-davyi*? Are the constituent species assembled independently of one another or are competition, mutualism and/or predation of some relevance here? As far as competition is concerned, if the species in a guild share similar habitat preferences they are likely to be aggregated together to a degree, therefore within the whole community they are the most likely to compete. Unfortunately, the role of predation cannot be evaluated since predators and parasitoids were not recorded in this study. The importance of interactions between all phytophagous insect species in the community will, however, be investigated.

METHODS

The factors influencing guild distribution patterns and those of their constituent species

In order to gain an initial impression of the ways in which guild patterns arose and of the similarity of species reactions to temporally (over the year) and spatially (from tree to tree) varying factors, linear regression models were produced for each of the 16 'major' herbivore species. Both temporal and spatial distribution patterns of each species were analysed with respect to the 'independent' variables used in chapters 5 and 6. Comparisons between those variables influencing guild temporal and spatial distributions (determined in chapter 6) and those influencing the distributions of their constituent species could then be made.

Stepwise Regression analyses (BMDP Proc. 2R, forward stepping; full details in Appendix 2) were applied to the frequencies of occurrence of the insect species, or transformations thereof, in order to produce the regression models. The temporal data for all species was approximately normally distributed and only that of *Mgenia* sp. failed to fulfil conditions of homoscedasticity (even following transformation). Hence all temporal data were untransformed. It was necessary to apply a variety of transformations to the spatial data, on the other hand, to achieve varying degrees of normality and homoscedasticity (Table 7.1). When no transformation resulted in a satisfactory degree of normality and/or homoscedasticity, that achieving the greatest degree of normality was implemented. As in chapter 5, fruiting variables were excluded from the regressions of non-fruit feeders, and only fruit-bearing trees were included in the analyses for fruit-feeders.

Table 7.1 The transformations performed on the spatial distributions of species abundances and their outcomes. + represents satisfaction of normal or homoscedacious conditions, and -, their non-satisfaction.

SPECIES	TRANSFORMATION	NORMAL	HOMOSCEDACIOUS
Sphenoptera sp.	-	+	+
Prosopocera sp.	sqrt(x)	-	+
Brenthia sp.	sqrt(x)	-	-
P. punctata	NO VARIABLES ENTERED INTO THE REGRESSION EQUATION		
M. s. ficedula	sqrt(x)	-	-
A. speciosa	-	-	+
Nepticulidae sp.	-	+	+
Cecidomyiidae sp.	-	-	+
Aphrodinae sp.	sqrt(x+1)	-	-
Mgenia sp.	sqrt(x)+sqrt(x+1)	+	+
Homotoma sp.	sqrt(x)	-	+
Aphididae spp.	sqrt(x)	-	+
Ceroplastes sp.	log(x+1)	-	-
Diptera sp.	log(x+1)	-	+
Pyralidae spp.	sqrt(x)	+	+
D. natalensis	-	+	+

The similarity of species with respect to the climatic and habitat factors influencing their distributions

The similarity of species' reactions to temporally and spatially varying factors was evaluated using two methods. The first of these involved the partial correlation (STATGRAPHICS Proc. PCORR) of both the temporal and spatial distributions of the frequencies of occurrence of pairs of all species in the study. In other words, correlations between pairs of species were investigated while holding relationships with the other 14 species constant. Hence, species effects on one another were removed and any positive correlations between species reflected similarities in the influences of temporal or habitat factors, and any negative correlations reflected opposing influences of such factors. As this procedure assumes normality (Bailey 1981), where relevant, the transformed data were used.

In order to gain an indication of the degree of similarity of the effects of temporally and spatially varying factors on species within guilds as opposed to those in different guilds, the numbers of positive correlations occurring between species within guilds were compared to the numbers occurring between species in different guilds with 2x2 Chi-square Contingency analyses (STATGRAPHICS Proc. TABLE).

The second method involved the comparison of the regression equations of the species within the two largest guilds (the leaf chewers and leaf and stem piercers), the only ones containing more than two species (Chapter 6). If species within guilds have more similar preferences with respect to their living conditions than those in different guilds, one would expect the regression equations of species within the same guild to differ to a lesser extent than those of species from different guilds.

As the numbers of species in the two guilds were not the same, a nested analysis of variance (the preferred method) could not be used to ascertain the above. The procedure, Linear Regression by Groups (BMDP Proc. 1R) which has no such restrictions was therefore used. This method fits multiple regression lines incorporating all variables and examines the equality of these lines across groups (species). It does so by assessing the degree to which the intercepts and slopes of the regression lines differ. Here, however, the method was modified to compare only the slopes of the regression lines, the similarities of intercepts being unimportant.

Subsequent to the linear regression analysis F-values were calculated to obtain a measure of the similarity of regression lines across groups. For both the temporal and spatial data the above analyses were performed three times to obtain F-values for comparisons between species within the leaf chewing guild, between species within the leaf and stem piercing guild, and between all species. If the regression lines of species within guilds are more similar than those of species in different guilds then the F-values for the within guild comparisons should have lower associated p-values than that representing the overall comparison.

Interspecific interactions

Interspecific interactions were investigated after removing the influences of temporal and habitat factors and the effects of mutual correlation with a third species, as discussed in chapter 6. Thus, partial correlations were performed on the residuals from the stepwise regression analyses which were applied to the distributions (temporal and spatial) of the frequencies of occurrence of each species in the initial analyses in this chapter.

RESULTS

The factors influencing guild distribution patterns and those of their constituent species

A preliminary comparison of those factors entering the individual species regressions with those entering the guild regressions revealed no obvious patterns of within guild similarities or otherwise (Tables 7.2 and 7.3). It did, however, give some indication as to how guild distribution patterns arose from those of constituent species. Not surprisingly, the dominant factors influencing guild distributions emerged as such due to their having similar influences on more than one of the constituent species.

Furthermore, at the spatial (between tree) scale in particular, it is clear that factors of lesser importance in the determination of guild distributions often emerged at this level due to the effect of a factor on only one species (particularly of the more commonly occurring species) in the guild. In other words, individual species preferences as well as those common to more than one species, often manifested themselves in the guild level analyses.

More often, though, factors of importance to the distribution of only one species in a guild were not expressed at the guild level. Additionally, in several cases within the temporal data, despite factors being of significance to more than one species within a guild, they did not manifest themselves at the guild level. Closer examination of the data reveals that in all three cases, relationships of the species with the factor concerned are of both a negative and positive nature, therefore cancelling one another out when combined.

One case presents a puzzle - the temporal distribution of the leaf and stem piercers is determined, to a degree, by maximum weekly temperature, whereas none of the constituent species distributions are similarly influenced. It is possible that this could have arisen due to an additive effect, with the non-significant relationships of maximum weekly temperature with the individual species having the same signs so that when the species were combined into the guild the relationship became large enough to be significant.

Table 7.2 A comparison between the importance of temporally varying factors in the determination of guild distributions and of constituent species distributions. The independent variables are: the maximum temperature during the week prior to and including the sample date (TMAX); the minimum temperature during this week (TMIN); the mean temperature during this week (TMEAN); total rainfall in the week prior to the sample date (RAIN1); total rainfall in the week two weeks prior to the sample date (RAIN2); total rainfall in the week three weeks prior to the sample date (RAIN3) and total rainfall in the month prior to the sample date (RAINM), number of trees with young leaves (YLVS); with mature leaves (MLVS); bearing fruit (TOTFRUIT); bearing unpollinated figs (FRUIT1); bearing pollinated but pre-emergent figs (FRUIT2); bearing emergent figs (FRUIT3); and bearing post-emergent figs (FRUIT4). Figures represent the order of entry of variables into the equation, and + and -, the nature of the factor's influence.

	TMAX	TMIN	TMEAN	RAIN1	RAIN2	RAIN3	RAINM	YLVS	MLVS	FRUIT1	FRUIT2	FRUIT3	FRUIT4	TOTFRUIT	ADJR^2
LFCH	.	.	1+	.	.	.	.	.	.	.	.	.	.	.	**0.8044**
Sphenoptera sp.	.	.	1+	.	.	.	.	.	.	.	.	.	.	.	0.8384
Prosopocera sp.	.	.	1+	.	.	.	.	.	.	.	.	.	.	.	0.7252
Brenthia sp.	.	.	.	2-	.	3-	1+	.	.	.	.	.	.	.	0.7458
P. punctata	1+	.	.	.	.	.	3+	2-	.	.	.	.	.	.	0.8183
M. s. ficedula	.	.	.	.	.	.	2-	1+	.	.	.	.	.	.	0.4381
A. speciosa	.	.	1+	.	.	.	.	.	.	.	.	.	.	.	0.3929
MI Nepticulidae sp.	.	.	.	.	.	.	2+	1-	3+	.	.	.	.	.	**0.8230**
GA Cecidomyiidae sp.	.	3-	1+	.	.	.	2+	.	.	.	.	.	.	.	**0.8580**
LFPI	2+	.	.	.	.	.	.	1+	.	.	.	.	.	.	**0.4561**
Aphrodinae sp.	.	.	.	2-	.	3-	1+	.	.	.	.	.	.	.	0.5086
Mgenia sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.7139
Homotoma sp.	.	.	.	.	.	.	3-	1+	2+	.	.	.	.	.	0.7666
Aphididae spp.	.	.	.	.	.	.	.	1+	.	.	.	.	.	.	0.6073
Ceroplastes sp.	.	.	.	.	1-	.	.	.	.	.	.	.	.	.	0.1680
FRCH	.	1+	.	.	.	.	.	.	.	.	.	.	.	.	**0.3243**
Diptera spp.	NO VARIABLES ENTERED INTO THE REGRESSION EQUATION														-
Pyralidae spp.	.	.	1+	.	.	.	.	.	.	.	.	.	.	.	0.3222
FRPI *D. natalensis*	.	.	.	.	.	.	.	.	.	.	.	.	.	1+	**0.3721**

Table 7.3 A comparison between the importance of spatially varying factors in the determination of guild distributions and of constituent species distributions. The independent variables are: tree architecture (ARCH), ant presence (ANTS), exposure of at least part of the tree to full sunlight all day (SUN), to full shade all day (SHADE), to dappled sunlight all day (DAPPLED) and to a mixture of these (MIXED), tree isolation (ISO), foliage density (DENSITY), crop number (CROPNO), and maximum crop size (CROPSZ).Figures represent the order of entry of variables into the equation, and + and -, the nature of the factor's influence.

	ARCH	ANTS	SUN	SHADE	DAPPLED	MIXED	ISO	DENSITY	CROPNO	CROPSZ	$ADJR^2$
LFCH	1+	.	2+	.	.	.	3+	.	.	.	**0.4373**
Sphenoptera sp.	1+	.	2+	.	.	.	3+	.	.	.	0.5691
Prosopocera sp.	1+	.	.	2+	.	.	.	.	.	.	0.1612
Brenthia sp.	1+	.	.	.	.	.	.	.	.	.	0.0745
P. punctata	NO VARIABLES ENTERED INTO REGRESSION EQUATION										-
M. s. ficedula	.	.	1+	.	.	.	.	.	.	.	0.0388
A. speciosa	.	1+	2-	.	.	.	.	.	.	.	0.0594
MI											
Nepticulidae sp.	1+	.	.	2+	.	.	.	.	.	.	**0.4512**
GA											
Cecidomyiidae sp.	1+	.	.	.	.	.	.	.	.	.	**0.0872**
LFPI	2+	1+	3+	.	4-	.	.	.	.	.	**0.7224**
Aphrodinae sp.	1+	.	.	.	.	.	.	.	.	.	0.0472
Mgenia sp.	1+	.	3+	.	2-	.	.	.	.	.	0.1541
Homotoma sp.	2+	1+	.	.	.	.	.	.	.	.	0.2462
Aphididae spp.	3+	1+	.	.	.	.	2+	.	.	.	0.2840
Ceroplastes sp.	2+	1+	.	.	.	.	.	.	.	.	0.6481
FRCH	.	.	.	.	2-	.	.	.	.	1+	**0.3433**
Diptera spp.	.	.	3+	2+	.	4+	.	.	.	1+	0.4088
Pyralidae spp.	.	.	.	.	1-	.	.	.	.	2+	0.1993
FRPI											
D. natalensis	.	.	.	.	.	.	2+	.	.	1+	**0.3884**

The similarity of species with respect to the climatic and habitat factors influencing their distributions

The partial correlations of the transformed raw data revealed marginally higher proportions of significantly positive correlations and lower proportions of significantly negative correlations between species within guilds than between species in different guilds at both the temporal and spatial scales (Tables 7.4 and 7.5). However, the differences were not significant (chi-square=0.7463, p=0.3876 for the temporal data, chi-square=0.2875, p=0.5918 for the spatial data) suggesting that species within guilds do not show more similar responses to temporal and habitat factors than do species in other guilds. The comparison of the species' regression lines confirmed this result. There was only one group in which the species regressions did not differ significantly from one another (Table 7.6): the group of regression equations representing the temporal distributions of the species within the leaf and stem piercing guild. Temporally, within the leaf chewing guild and spatially within both the leaf chewing and leaf and stem piercing guilds, species regressions differed as significantly as when all species were considered together ($p<0.000005$, Table 7.6). Therefore, although it would seem that leaf and stem piercing species are more similar to one another than to other species with respect to the temporally varying factors influencing their distributions, this does not seem to be a general trend among the guilds.

Table 7.4 Partial correlations between temporal distributions of the frequencies of occurrence of species pairs. Correlations of two species are investigated while holding relationships with the other 14 species constant. + indicates a significant positive correlation and -, a significant negative correlation. Bold lines denote areas of intra-guild relationships.

	Sphenoptera sp.	*Prosopocera* sp.	*Brenthia* sp.	*P. punctata*	*M. s. ficedula*	*A. speciosa*	Nepticulidae sp.	Cecidomyiidae sp.	Aphrodinae spp.	*Mgenia* sp.	*Homotoma* sp.	Aphididae spp.	*Ceroplastes* sp.	Diptera spp.	Pyralidae spp.
Prosopocera sp.	+														
Brenthia sp.															
P. punctata		+													
M. s. ficedula															
A. speciosa	+	-		+											
Nepticulidae sp.															
Cecidomyiidae sp.	+	-		+		-									
Aphrodinae spp.		+		-		+									
Mgenia sp.			+												
Homotoma sp.	+	-		+		-		-	+						
Aphididae spp.	-	+		-		+		+			+				
Ceroplastes sp.															
Diptera spp.	+	-		+		-		-	+		-	+			
Pyralidae spp.	-	+		-		+		+			+	-		+	
D. natalensis															

WITHIN GUILD CORRELATIONS:	POSITIVE	7/26 = 0.27
	NEGATIVE	2/26 = 0.08
BETWEEN GUILD CORRELATIONS:	POSITIVE	18/94 = 0.19
	NEGATIVE	15/94 = 0.16

CHI-SQUARE=0.7463, p=0.3876

Table 7.5 Partial correlations between transformed spatially varying distributions of the frequencies of occurrence of species pairs. Correlations of two species are investigated while holding relationships with the other 14 species constant. + indicates a significant positive correlation and -, a significant negative correlation. Bold lines denote areas of intra-guild relationships.

	Sphenoptera sp.	*Prosopocera* sp.	*Brenthia* sp.	*P. punctata*	*M. s. ficedula*	*A. speciosa*	Nepticulidae sp.	Cecidomyiidae sp.	Aphrodinae spp.	*Mgenia* sp.	*Homotoma* sp.	Aphididae spp.	*Ceroplastes* sp.	Diptera spp.	Pyralidae spp.
Prosopocera sp.	+														
Brenthia sp.	+														
P. punctata															
M. s. ficedula															
A. speciosa															
Nepticulidae sp.	+				-										
Cecidomyiidae sp.			+												
Aphrodinae spp.					+			+							
Mgenia sp.	+								+						
Homotoma sp.	+														
Aphididae spp.		+			+										
Ceroplastes sp.	+	-					+			+		+			
Diptera spp.															
Pyralidae spp.							+			+			-		
D. natalensis	+						-			-					+

WITHIN GUILD CORRELATIONS:	POSITIVE	5/26 = 0.19
	NEGATIVE	0/26 = 0.0
BETWEEN GUILD CORRELATIONS:	POSITIVE	14/94 = 0.15
	NEGATIVE	5/94 = 0.05

CHI-SQUARE=0.2875, p=0.5918

Table 7.6 The similarity of species regression lines within the leaf chewers (LFCH), leaf and stem piercers (LFPI), and both guilds combined (ALL) as determined by the F-test. F is calculated (see below) from SSR_2 (residual sum of squares within groups), SSR_3 (regression sum of squares over groups), n (number of cases in all groups combined), s (number of species) and k (number of independent variables). df represents the degrees of freedom and p, the probability that F differs from zero.

GUILD	SSR_2	SSR_3	n	s	k	F	df	p
TEMPORAL								
LFCH	1045.38	7541.02	108	6	10	6.6279	45, 48	<0.000005
LFPI	1472.42	3727.63	90	5	10	1.7018	36, 40	0.0516
ALL	2517.77	13454.41	198	11	10	4.2472	90, 88	<0.000005
SPATIAL								
LFCH	2309.66	3074.86	738	6	9	5.6653	40, 684	<0.000005
LFPI	215.08	251.34	615	5	9	3.0026	32, 570	<0.000005
ALL	2206.78	3380.66	1353	11	9	8.3382	80, 1254	<0.000005

Where: $F=[(SSR_3-SSR2)/(sk-s-k+1)] / [SSR_2/(N-SK)]$

Interspecific interactions

Partial correlation analysis of regression residuals revealed very few significant interspecific relationships (Table 7.7). All but one of the correlations were positive. As they do not represent mutualistic relationships they are most probably attributable to the effects of unmeasured variables given that common influences of spatially and temporally varying factors have already been shown to be responsible for a large number of positive interspecific correlations (Tables 7.4 and 7.5).

The negative correlation between *Brenthia* sp. and Pyralidae spp. occurred only temporally

Table 7.7 Partial regression analysis of regression residuals for both the temporal and spatial data for each species. + and - denote the nature of the relationship, and the attached figures refer to the regression coefficients (r) and their accompanying probability values (p).

	Sphenoptera sp.	*Prosopocera* sp.	*Brenthia* sp.	*P. punctata*	*M. s. ficedula*	*A. speciosa*	Nepticulidae sp.	Cecidomyiidae sp.	Aphrodinae spp.	*Mgenia* sp.	*Homotoma* sp.	Aphididae spp.	*Ceroplastes* sp.	Diptera spp.	Pyralidae spp.	*D. natalensis*
Sphenoptera sp.															TEMPORAL	
Prosopocera sp.																
Brenthia sp.	1+								1+						2-	
P. punctata								3+								
M. s. ficedula																
A. speciosa																
Nepticulidae sp.	2+															
Cecidomyiidae sp.																
Aphrodinae spp.					3+											
Mgenia sp.									4+							
Homotoma sp.																
Aphididae spp.					5+											
Ceroplastes sp.										6+						4+
Diptera spp.																
Pyralidae spp.										7+						
D. natalensis	SPATIAL															

Where:

TEMPORALLY: (1) $r=0.9211$, $p<0.01$; (2) $r=-0.8308$, $p<0.05$; (3) $r=0.9054$, $p<0.01$

SPATIALLY: (1) $r=0.2104$, $p<0.05$; (2) $r=0.2249$, $p<0.05$; (3) $r=0.2656$, $p<0.01$; (4) $r=0.2084$, $p<0.05$; (5) $r=0.3101$, $p<0.01$; (6) $r=0.2424$, $p<0.05$; (7) $r=0.3798$, $p<0.01$

and not spatially. This, in addition to the fact that the two species show no overlap in their resource requirements, *Brenthia* sp. feeding on and living in the young shoots and Pyralidae spp. within the fruit, eliminates competition as an explanation. Rather, this negative relationship most likely arises due to the fact that the occurrence of youngleaves and of fruit on the trees at the same time is rare, the temporal overlap of the species dependent on these resources therefore being unlikely.

DISCUSSION

The number of species involved in this study was very low compared to other systems investigated in the past. Root's (1973) study of the three phytophagous guilds on Collards (*Brassicae oleraceae*) in New York encompassed 94 species. Stork's (1987) investigation of the arthropod guild structure on 14 lowland rainforest tree species included approximately 3000 species in nine guilds. Similarly Cornell and Kahn (1989) analysed differences in the structure of four British arboreal insect phytophage guilds comprising 3035 species, and Claridge and Wilson (1982) looked into the species-area effect on 239 leaf mining species on British trees.

This present study, however, analysed the phytophages on only one tree species in a single temperate location and involved only 16 species divided among six guilds. All species are, to a certain degree, individualistic in their habitat preferences, and when species numbers per guild are low, individual species patterns, particularly of the more common species, are more likely to be portrayed at the functional, guild level. With large numbers of species in a guild, however, the patterns at this level of organisation are more likely to arise from similarities between species, with individual peculiarities being masked.

The comparison of species within guilds, whilst revealing certain common influential factors, also showed there to be differences. These differences were as great between species within guilds as between species in different guilds, implying a lack of strong organisational effects of variables at the guild level.

Obviously, looking for associations between species as a measure of interaction has its limitations. It will not take into account the complete absence of species from the community despite their presence in the species pool and their capability of establishing in isolation in the habitat when no other species are present. Nor will it detect the presence of species which depend on modification of the habitat by other species before they can establish (Greig-Smith 1986). Unfortunately, solving such problems was beyond the scope of this study so the above limitations must be kept in mind.

Although mutualistic interactions across trophic levels (ants - leaf/stem piercers) were seen to be of importance in chapters 5 and 6, they played no role within the phytophage trophic level. Furthermore, not surprisingly, there was no indication that interspecific competition played a role in structuring this community, either between species belonging to the same guild, or between those belonging to different guilds. Firstly, at such a gross scale of measurement as this (purely presence versus absence as opposed to actual abundances) only very strong relationships would have been detected. This was not an impossibility, however, as the ant-homoptern mutualisms were detected on the same basis. Secondly as discussed in Chapter 1, even at fine scales, competition has rarely been found to have a significant effect on the structure of herbivore communities (Claridge 1986; Law and Watkinson 1989; Lawton 1984a, 1984b; Lawton and MacGarvin 1986; Lawton and Strong 1981; Price 1980; Root 1973; Strong et al. 1984).

In conclusion, factors affecting the resources common to species within a guild, and affecting such species on the basis of their similar feeding methods, on the whole have no more of a common effect on these species than they do on species from different guilds. Furthermore, the species within the phytophagous insect community on *F. burtt-davyi* appear to be assembled independently of one another with interspecific interactions seeming to be of no importance.

8 DISCUSSION

> 'A theory explaining global patterns in community ecology is doomed to failure because the array of resources and the organisms that exploit them is so diverse...' (Price 1984).

Communities have been described as '...loosely ordered, complexly patterned, multiply determined' (Whittaker 1952), consisting of a '...confusing background of seemingly random noise' (Hopf and Brown 1986), and characterised by '...countless complex interactions and causal connections...' (Gauch 1982).

The daunting nature of community ecology leads one to ask whether a quest for patterns in community organisation can ever succeed, and if so, whether the patterns can subsequently be explained with any great success. However, despite the odds, such patterns are often revealed and explained to varying degrees by climatic, geographic and habitat-related factors, and interspecific interactions. One way to make this task more manageable is to decrease the scope of the study by concentrating on a reduced diversity of resources and therefore of associated organisms. This was the approach taken in this study which concentrated on the phytophagous insects feeding on a single host species.

In many respects the phytophagous insect community feeding on *F. burtt-davyi* was found to closely resemble other such communities: in the existence of a species-area relationship (in this case, largely attributable to increased passive sampling by larger, more apparent trees:

Chapter 5), a microhabitat heterogeneity effect on species numbers (Chapter 5), and with an apparent lack of interspecific competition (Chapter 7). However, other less commonly recorded relationships did emerge: namely those involving ants and tree isolation (Chapters 5, 6 and 7).

As tree architecture (a combination of tree size and microhabitat heterogeneity) strongly influences the species richness on each tree it presumably influences the subcomponents (species) of the community proportionately. Hence, the tendency for nine of the 16 individual insect species to occur more frequently on more complex trees (Chapter 7). Conversely, the elevation of species number with ant presence was found to be a manifestation of autecological ant-homopteran relationships (Chapters 5 and 7). That their effects were evident within the community as a whole was not surprising due to the wide occurrence of the ant-tended *Ceroplastes* sp. in particular (Chapter 6). Similarly, the isolation effect whereby greater numbers of species accumulated on less isolated hosts probably arose mainly as a result of the large component of specialised leaf-feeding latex saboteurs (Chapter 4). These are likely to be restricted to a maximum of three hosts in the study area, of which *F. burtt-davyi* is by far the most abundant. *F. sur* and *F. thonningii*, the only other native figs in the study area, are represented by approximately 10 and 42 individuals respectively (Fig. 2.4).

The importance of tree isolation to the distribution of leaf chewing insects was confirmed at the guild level of analysis (Chapter 6). It was also an important factor in the determination of the distribution of fruit piercing insects. Although this latter guild only comprised one species, *D. natalensis* is a fig-specific feeder (Chapter 4) and hence is also relatively specialised. In the study area it is likely only to feed on *F. burtt-davyi* as its proboscis is certainly too short to penetrate the figs and reach the seeds of *F. sur*, and probably also of *F. thonningii*. It also appears to be a poor disperser. Therefore it may well be that the latex defences and the unique structure of fig tree fruits lead to a higher proportion of specialist feeders than on many other host plants, thus increasing the importance of host tree isolation with respect to herbivore species accumulation on individual plants.

The primary importance of the effects of passive sampling and habitat heterogeneity on species number, and of factors (such as ant presence and tree isolation) affecting individual species distributions precisely fits Price's (1984) predictions for the insect communities on deciduous trees such as *F. burtt-davyi*. He classifies such trees as rapidly increasing (foliage) and pulsing (fruit) resources, and on the basis of their temporal fluctuations, predicts that of those factors of potential importance to insect herbivore communities (Chapter 1), the above are likely to be the most important determinants of their phytophagous insect community structure. Furthermore, as also predicted by Price, interspecific competition was rejected as an organising force in this community, lending support to the widely held view that phytophagous insect communities consist largely of independently assembled member species, the latter co-occurring due to similar influences of, and preferences for, temporal and habitat-related factors. Natural enemies are often proposed to be responsible for maintaining herbivore populations at densities below those at which competition becomes important. However, as is the case with the pollinator fig wasps of *F. burtt-davyi* (which suffer upto 95% mortality during dispersal: Compton and Robertson in prep.), high mortality due to the effects of abiotic factors during dispersal could be just as likely a controlling factor for those species which have to move between trees in order to maintain their populations.

Thus, the spatial tree to tree differences in community composition may be explained largely at the levels of individual species responses and species richness. At the guild level it was established that species within the same guild were no more similar to one another with respect to the variables influencing their spatial distributions than were species from different guilds. The responses of different species to habitat variables are therefore no less idiosynchratic when the insects are grouped into functional units. Thus, there appears to be a general lack of organisation based on guild membership, with studies at the guild level throwing no further light on the way in which this community is assembled on different trees.

Turning to variations in the structure of the community with time (temporal variation), it seems that effects at the guild level cannot be dismissed to such a great extent. Although within the leaf chewing guild, factors influencing species distributions were as different as those influencing the distributions of species in other guilds, species within the leaf and stem piercing guild did seem to have more in common with one another with respect to the factors influencing their distributions, than they had with species in other guilds.

Not surprisingly, at all levels of organisation within the community of herbivores on *F. burtt-davyi*, temperature was found to have the most significant and consistent effects. It was positively related to species richness both directly (Chapter 5) and indirectly, via its influence on tree fruiting patterns (Chapter 3), and to fluctuations in frequencies of occurrence of four of the six guilds (Chapter 6) and to six of the total 16 species (Chapter 7).

In contrast, the relationship between rainfall and the various components of the community was more varied. It had no effect on fluctuations in the number of species over the year

(Chapter 5), but positively influenced the temporal fluctuations of two of the guilds (Chapter 6), and showed mixed or no effects on individual species (Chapter 7).

Similarly, leaf phenology of the trees had no influence at the level of the whole community (Chapter 5), but did have important mixed influences at the guild (Chapter 6) and individual species levels (Chapter 7). Species richness and, for obvious reasons, the distributions of fruit piercing and chewing insects were related to the number of trees bearing fruit at any one time (Chapter 5). Thus, phenological effects were detectable within guilds and individual species but were not obvious at the level of the whole community.

It seems, therefore, that temporally varying factors may have been of more significance than spatially varying ones at the guild level of organisation. This is most likely due to the feeding substrate (leaves, stems and fruit), on which guild membership is partially dependent, changing more markedly over the year than it does from tree to tree. Additionally, climatic changes may influence guilds differentially on the basis of their feeding position.

Hence, distributional patterns within the phytophagous insect community were revealed and to some extent explained by the variables measured, and Lewin's (1983) warning of the danger of 'submerging important biological patterns in a statistical mirage', seemingly unfounded. However, there is always the danger that spurious relationships may have emerged due to chance, a potential problem with analyses involving numerous variables, some of which are interrelated. In order to try and allow for such effects I used more than one statistical method for each analysis (Chapters 5 and 6: Stepwise Regression Analysis and All Possible Subsets Regression Analysis; Chapter 7: Partial Correlation Analysis and Linear

Regression Analysis). In as much as the results were consistent between methods, one can feel more confident of their reliability.

In some of the regression analyses, conditions of normality and/or homoscedasticity were not satisfied by the data, even after transformation. Nonetheless, examination of the results obtained when regressing the same independent variables against varying transformations of one dependent variable, revealed that any disagreement (usually minor) between results occurred largely between the amount of variation explained by the different equations, rather than between the identity of the independent variables entering the equation. Hence, non-normality and/or heteroscedasticity of the data appears not to have such radical consequences after all.

The limitations of this study are probably attributable more to the data set itself than to its subsequent analysis. Firstly, the study was based only on a single year's data, so the year to year stability and predictability of the constituent populations and therefore of the community as a whole, remains unknown. Wolda (1988, 1992) emphasises that a year is a very brief window of time in such systems which often fluctuate greatly from one year to the next. There is therefore no way of knowing whether the patterns revealed in this study are repeated year after year, the observed community patterns therefore being predictable to a certain degree, or whether they were peculiar to the year of the study.

Secondly, due to time restrictions, the insects' degree of feeding specialisation was not fully documented. This is most likely to have bearing on the degree to which tree isolation is important as the larger the monophagous component of the community, the greater the effect of isolation is likely to be (Strong et al. 1984). As discussed above, the relatively high proportion of specialised latex saboteurs and the single specialist fruit piercer may well explain the importance of isolation in the structuring of this community. In order to gain a clear idea of the degree of feeding specialisation of all of the constituent species, more extensive sampling to include the two other native figs would be necessary, in conjunction with the execution of host preference tests for all of the phytophagous insects on all potential hosts in the study area.

Thirdly, other than the occasional opportunistic collection, predators and parasitoids were not sampled. Therefore, although competition was found not to be a determinant of community organisation, control by natural enemies, whilst being very likely, can only be proposed as one possible explanation for the maintenance of herbivore densities at levels below those at which competition would become important. Also unstudied were the suppressant effects of abiotic factors on the densities of those insects migrating between trees, their relative importance therefore being similarly unkown.

Hence, various improvements and additions can be recommended for future studies of the insect community feeding on *F. burtt-davyi*. Ideally, the sampling period should be extended to span a further two years at least, in order to gain an idea of the stability of the system. Further to this, more detailed knowledge of the insects' life histories, general biology, dispersal abilities, degree of dispersal-induced mortality and degree of feeding specialisation is essential to improve interpretation of the results. The proportion of specialist feeders within this community relative to other phytophage communities is of particular interest as it would give an indication of the importance of the fig latex defences in particular, to individual herbivores and the community as a whole.

Additionally, the presence/absence method of recording is relatively crude and could be improved by measuring insect abundances on each sampling occasion. This would improve the chances of detecting any very weak interspecific relationships that would not have been obvious at the presence/absence level, but may have consequences for the number of trees that could be studied. Finally, the extension of the sampling program to include natural enemies is essential in order to determine their role in the control of phytophagous insect populations.

Looking ahead, the scope of this work can also be expanded. The study was conducted at a single location and hence at very much a local level. With its relatively small distributional range, *F. burtt-davyi* is an ideal host on which to expand such a study to investigate the regional patterns in the composition of the community and the influence of regional factors on local community composition.

In conclusion, in spite of the limitations of this study, the indications are that within the phytophagous insect community on *F. burtt-davyi*, the idiosynchratic responses of individual species to the weather, host phenology and physical host attributes, the effects of host apparency, microhabitat heterogeneity and isolation on species accumulation, and mutualistic interactions between species at different trophic levels were responsible for determining the composition of the phytophagous insect community present on a particular tree at a particular time. The grouping of species into functional groups, or guilds, threw little further light on the organisation of this community. Furthermore, there was no indication that competitive interactions were important.

Therefore, this study joins the many other such studies of phytophagous insect community organisation in giving support to Lawton and Strong's (1981) suggestions with respect to a theory sufficient to explain limited membership within folivorous insect communities:

> '...we suggest that a theory that stresses that the autecological responses to weather, phenology and host chemistry of individual species of plants and insects, the effects of isolation, migration and habitat heterogeneity, geographical factors of interspecies associations, and the action of predators and parasitoids would usually be sufficient for folivorous insect communities...'

BIBLIOGRAPHY

Acocks, J.P.H. 1975. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa.

Aide, T.M. 1993. Patterns of leaf development and herbivory in a tropical understory community. Ecology **74**:455-466.

Anderson, D.J., and J. Kikkawa. 1986. Development of concepts. Pages 3-16 *in* Kikkawa, J. and D.J. Anderson, editors. Community ecology: pattern and process. Blackwell Scientific Publications, Oxford, England.

Annecke, D.P., and V.C. Moran. 1982. Insects and mites of cultivated plants in South Africa. Butterworths, Durban, South Africa.

Bach, C.E. 1991. Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*). Oecologia **87**:233-239.

Baijnath, H., and S. Ramcharun. 1983. Aspects of pollination and floral development in *Ficus capensis* Thunb. (Moraceae). Bothalia **14**:883-888.

Baijnath, H., and S. Ramcharun. 1988. Reproductive biology and chalcid symbiosis in *Ficus burtt-davyi* Hutch. (Moraceae). Pages 227-235 *in* Goldblatt, P. and P.P. Lowry, editors. Modern systematic studies in African botany. Allen Prees, Inc., Lawrence, Kansas, USA.

Bailey, N.T.J. 1981. Statistical methods in biology. Holder and Stoughton, London, England.

Banerjee, B. 1981. An analysis of the effect of latitude, age and area on the number of arthropod pest species of tea. Journal of Applied Ecology **18**:339-342.

Basset, Y. 1991a. Leaf production of an overstory rainforest tree and its effects on the temporal distribution of associated insect herbivores. Oecologia **88**:211-219.

Basset, Y. 1991b. Influence of leaf traits on the spatial distribution of insect herbivores associated with an overstorey rainforest tree. Oecologia **87**:388-393.

Basset, Y. 1991c. The seasonality of arboreal arthropods foraging within an Australian rainforest tree. Ecological Entomology **16**:265-278.

Basset, Y., and A.H. Arthington. 1992. The arthropod community of an Australian rainforest tree: abundance of component taxa, species richness and guild structure. Australian Journal of Ecology **17**:89-98.

Beddington, J.R., C.A. Free, and J.H. Lawton. 1978. Characteristics of successful natural enemies in models of biological control of insect pests. Nature **273**:513-519.

Begon, M., J.L. Harper, and C.R. Townsend. 1987. Ecology: individuals, populations and communities. Blackwell Scientific Publications, Oxford, England.

Berenbaum, M. 1983. Coumarins and caterpillars: A case for coevolution. Evolution **37**:163-179.

Berg, C.C. 1990a. Annotated check-list of the *Ficus* species of the African floristic region, with special reference and a key to the taxa of southern Africa. Kirkia **13**:253-291.

Berg, C.C. 1990b. Reproduction and evolution in *Ficus* (Moraceae): traits connected with the adequate rearing of pollinators. Memoirs of the New York Botanical Garden **55**:169-185.

Bernstein, I.H., C.P. Garbin, and G.K. Teng. 1988. Applied multivariate analysis. Springer-Verlag, New York, USA.

BMDP Statistical Software Manual. 1990. University of California Press, Berkeley, California, USA.

Bodkin, G.E. 1926. The Fig Wax Scale (*Ceroplastes rusci* L.) in Palestine. Bulletin of Entomological Research **17**:259-264.

Box, G.E.P., and D.R. Cox. 1964. Analysis of transformations. Journal of the Royal Statistical Society **26**:211-252.

Broekhuysen, G.J. 1948. The brown house ant (*Pheidole megacephala* Fabr.) in South Africa. Union of South Africa, Department of Agriculture Bulletin **266**:1-40.

Bronstein, J.L. 1989. A mutualism at the edge of its range. Experientia **45**:622-637.

Bronstein, J.L., and A. Patel. 1992. Causes and consequences of within-tree phenological patterns in the Florida strangling fig, *Ficus aurea* (Moraceae). American Journal of Botany **79**:41-48.

Bultman, T.L., and S.H. Faeth. 1986. Leaf size selection by leaf-mining insects on *Quercus emoryi* (Fagaceae). Oikos **46**:311-316.

Bultman, T.L., and S.H. Faeth. 1988. Abundance and mortality of leaf miners on artificially shaded Emory oak. Ecological Entomology **13**:131-142.

Claridge, D.W. 1986. The distribution of a typhlocybine leafhopper, *Ribautiana ulmi* (Homoptera: Cicadellidae) on a specimen wych elm tree. Ecological Entomology **11**:31-39.

Claridge, M.F. 1987. Insect assemblages - diversity, organisation, and evolution. Pages 141-162 *in* J.H.R. Gee and P.S. Giller, editors. Organisation of communities past and present. Symposia of the British Ecological Society #27. Blackwell Scientific Publications, London, England.

Claridge, M.F., and M.R. Wilson. 1976. Diversity and distribution patterns of some mesophyll-feeding leafhoppers of temporate woodland canopy. Ecological Entomology **1**:231-250.

Claridge, M.F., and M.R. Wilson. 1982. Insect herbivore guilds and species-area relationships: leafminers on British trees. Ecological Entomology **7**:19-30.

Clark, G.C., and C.G.C. Dickson. 1971. Life histories of the South African Lycaenid butterflies. Purnell, Cape Town, South Africa.

Clements, F.E. 1936. Nature and the structure of the climax. Journal of Ecology **24**:252-284.

Coates Palgrave, K. 1984. Trees of southern Africa. Struik, Cape Town, South Africa.

Cody, M.L. 1989. Discussion: structure and assembly of communities. Pages 227-241 *in* Roughgarden, J., R.M. May and S.A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Cody, M.L., and J.M. Diamond. 1975. Ecology and evolution of communities. Belknap, Cambridge, Massachusetts, USA.

Cohen, J.E. 1989. Food webs and community structure. Pages 181-202 *in* Roughgarden, J., R.M. May and S.A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Coley, P.D. 1980. Effects of leaf age and plant life history patterns on herbivory. Nature **284**:545-546.

Coley, P.D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecological Monographs **52**:209-233.

Compton, S.G. 1987. *Aganais speciosa* and *Danaus chrysippus* (Lepidoptera) sabotage the latex defences of their host plants. Ecological Entomology **12**:115-118.

Compton, S.G. 1989. Sabotage of latex defences by caterpillars feeding on fig trees. Suid Afrikaanse Tydskrif vir Wetenskap **85**:605-606.

Compton, S.G. 1993. One way to be a fig. African Entomology **1**:151-158.

Compton, S.G., and R.H.L. Disney. 1991. New species of *Megaselia* (Diptera: Phoridae) whose larvae live in fig syconia (Urticales: Moraceae), and adults prey on fig wasps (Hymenoptera: Agaonidae). Journal of Natural History **25**:203-219.

Compton, S.G., J.H. Lawton, and V.K. Rashbrook. 1989. Regional diversity, local community structure and vacant niches: the herbivorous arthropods of bracken in South Africa. Ecological Entomology **14**:365-373.

Compton, S.G., and R.J.C. Nefdt. 1990. The figs and fig wasps of *Ficus burtt-davyi*. Mitteilungen aus dem Institut für Allgemeine Botanik Hamburg **23a**:441-450.

Compton, S.G., J.-Y. Rasplus, and A.B. Ware. In press. African fig wasp parasitoid communities. *In* Hawkins, B.A. and W. Sheenan, editors. Parasitoid community ecology. Oxford University Press, Oxford, England.

Compton, S.G., and H.G. Robertson. 1991. Effects of ant-homopteran systems on fig-figwasp interactions. Pages 120-130 *in* Huxley, C.R. and D.F. Cutler, editors. Ant plant interactions. Oxford University Press, Oxford, England.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460-490 *in* Cody, M.L. and J.M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos **35**:131-138.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist **122**:661-696.

Connor, E.F., S.H. Faeth, D. Simberloff, and P.A. Opler. 1980. Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. Ecological Entomology **5**:205-211.

Corlett, R.T. 1984. The phenology of *Ficus benjamina* and *Ficus microcarpa* in Singapore. Journal of the Singapore National Academy of Science **13**:30-31.

Corlett, R.T. 1987. The phenology of *Ficus fistulosa* in Singapore. Biotropica **19**:122-124.

Cornell, H.V. 1984. Geographic texture of herbivore richness patterns on host plants. Bulletin of the Entomological Society of America **30**:6-15.

Cornell, H.V. 1985. Local and regional richness of cynipine gall wasps on Californian oaks. Ecology **66**:1247-1260.

Cornell, H.V., and D.M. Kahn. 1989. Guild structure in the British arboreal arthropods: is it stable and predictable? Journal of Animal Ecology **58**:1003-1020.

Cornell, H.V., and J.O. Washburn. 1979. Evolution of the richness-area correlation for cynipid gall wasps on oak trees: a comparison of two geographic areas. Evolution **33**:257-274.

Crawshay, G.A. 1907. The life history of *Tetropium gabrieli* Ws. = *T. fuscum* Sharp = *T. crawshayi* Sharp, etc. Transactions of the Entomological Society, London **1907**:183-212.

Davis, B.N.K. 1975. The colonization of isolated patches of nettles (*Urtica dioica* L.) by insects. Journal of Applied Ecology **12**:1-14.

Diamond, J., and T.J. Case. 1986. Community ecology. Harper and Row Publishers, New York, USA.

Drake, J.A. 1990. Communities as assembled structures: do rules govern pattern? Trends in Ecology and Evolution **5**:159-164.

Dussourd, D.E., and R.F. Denno. 1991. Deactivation of plant defence: correspondence between insect behaviour and secretory canal architecture. Ecology **72**:1383-1396.

Dussourd, D.E., and T. Eisner. 1987. Vein-cutting behaviour: insect counterploy to the latex defence of plants. Science **237**:898-901.

Duviard, D., and A. Pollet. 1973. Spatial and seasonal distribution of Diptera, Homoptera, and Hymenoptera in a moist shrub savanna. Oikos **24**:42-57.

Edwards, P.J., and S.D. Wratten. 1980. Ecology of insect-plant interactions. Studies in Biology no. 21. Edward Arnold, London, England.

Ehrlich, P.R., and L.C. Birch. 1967. The "balance of nature" and "population control". American Naturalist **101**:97-107.

Ehrlich, P.R., and P.H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution **18**:586.

Faeth, S.H. 1985. Host leaf selection by leaf miners: interactions among three trophic levels. Ecology **66**:870-875.

Faeth, S.H., S. Mopper, and D. Simberloff. 1981. Abundances and diversity of leaf-mining insects on three oak host species: effects of host-plant phenology and nitrogen content of leaves. Oikos **37**:238-251.

Farrell, B.D., D.E. Dussourd, and C. Mitter. 1991. Escalation of plant defence: do latex and resin canals spur plant diversification? American Naturalist **138**:881-900.

Feeny, P.P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology **15**:565-581.

Feeny, P.P. 1976. Plant apparency and chemical defence. Recent Advances in Phytochemistry **10**:1-40.

Fowler, S.V. 1985. Differences in insect species richness and faunal composition of birch seedlings, saplings and trees: the importance of plant architecture. Ecological Entomology **10**:159-169.

Fowler, S.V., and J.H. Lawton. 1982. The effects of host-plant distribution and local abundance on the species richness of agromyzid flies attacking British umbellifers. Ecological Entomology **7**:257-265.

Frank, S.A. 1989. Ecological and evolutionary dynamics of fig communities. Experientia **45**:674-680.

Fritz, R.S. 1983. Ant protection of a host plant's defoliator: consequence of an ant-membracid mutualism. Ecology **64**: 789-797.

Galil, J., and D. Eisikowich. 1968. Flowering cycles and fruit types of *Ficus sycomorus* in Israel. New Phytologist **67**:745-758.

Gauch, H.J. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, England.

Gautier-Hion, A., and G. Michaloud. 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. Ecology **70**:1826-1833.

Gilbert, L.E. 1982. The coevolution of a butterfly and a vine. Scientific American **247**::102-107.

Grant, S., and V.C Moran. 1986. The effects of foraging ants on arboreal insect herbivores in an undisturbed woodland savanna. Ecological Entomology **11**:83-93.

Greenslade, P.J.M. 1972. Comparative ecology of four tropical ant species. Insectes Sociaux **19**:195-212.

Greig-Smith, P. 1986. Chaos or order - organisation. Pages 19-29 *in* Kikkawa, J. and D.J. Anderson, editors. Community ecology: pattern and process. Blackwell Scientific Publications, Oxford, England.

Hairston, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control and competition. American Naturalist **44**:421-425.

Harrison, S. 1987. Treefall gaps versus forest understory as environments for a defoliating moth on a tropical forest shrub. Oecologia **72**:65-68.

Harrison, S., S.J. Ross, and J.H. Lawton. 1992. Beta diversity on geographic gradients in Britain. Journal of Animal Ecology **61**:151-158.

Hespenheide, H.A. 1991. Bionomics of leaf-mining insects. Annual Review of Entomology **36**:535-560.

Hill, R.L. 1982. Seasonal patterns of phytophage activity on gorse (*Ulex europaeus*), and host plant quality. Pages 237-242 *in* Proceedings of the 5th International Symposium on Insect-Plant Relationships, Wageningen.

Hodkinson, I.D. 1974. The biology of the Psylloidea (Homoptera): a review. Bulletin of Entomological Research **64**:325-339.

Holmes, R.D., and K. Jepson-Innes. 1989. A neighbourhood analysis of herbivory in *Bouteloua gracilis*. Ecology **70**:971-976.

Hopf, F.A., and J.H. Brown. 1986. The bull's-eye method for testing randomness in ecological communities. Ecology **67**:1139-1155.

Hulley, P.E. 1988. Caterpillar attacks plant mechanical defence by mowing trichomes before feeding. Ecological Entomology **13**:239-241.

Jaeger, M.,and P.H. De Reffye. 1992. Basic concepts of computer simulation of plant growth. Journal of Bioscience **17**:275-291.

Jaenike, J. 1990. Host specialisation in phytophagous insects. Annual Review of Ecology and Systematics **21**:243-273.

Janzen, D.H. 1968. Host plants as islands in evolutionary and contemporary time. American Naturalist **102**:592-595.

Janzen, D.H. 1973. Host plants as islands. II. Competition in evolutionary and contemporary time. American Naturalist **107**:786-790.

Janzen, D.H. 1979. How to be a fig. Annual Review of Ecology and Systematics **10**:13-51.

Jones, C.G., and J.H. Lawton. 1991. Plant chemistry and insect species richness of British umbellifers. Journal of Animal Ecology **60**:767-777.

Karban, R. 1993a. Induced resistance and plant density of a native shrub, *Gossypium thurberi*, affect its herbivores. Ecology **74**:1-8.

Karban, R. 1993b. Costs and benefits of induced resistance and plant density for a native shrub, *Gossypium thurberi*. Ecology **74**:9-19.

Kjellberg, F., and S. Maurice. 1989. Seasonality in the reproductive phenology of *Ficus*: Its evolution and consequences. Experientia **45**:653-660.

Koehl, M.A.R. 1989. Discussion: from individuals to populations. Pages 39-53 *in* Roughgarden, J., R.M. May and S.A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Lachaise, D., L. Tsacas, and G. Couturier. 1982. The Drosophilidae associated with tropical African figs. Evolution **36**:141-151.

Lambert, F.R., and A.G. Marshall. 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. Journal of Ecology **79**:793-809.

Larsson, S. 1985. Seasonal changes in the within-crown distribution of the aphid *Cinara pini* on Scots pine. Oikos **45**:217-222.

Law, R., and A.R. Watkinson. 1989. Competition. Pages 243-284 *in* Cherrett, J.M., editor. Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwell Scientific Publications, Oxford, England.

Lawton, J.H. 1978. Host-plant influences on insect diversity: the effects of space and time. Symposium of the Royal Entomological Society, London **9**:105-125.

Lawton, J.H. 1982. Vacant niches and unsaturated communities: a comparison of bracken herbivores at two sites on two continents. Journal of Animal Ecology **51**:573-595.

Lawton, J.H. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology **28**:23-39.

Lawton, J.H. 1984a. Herbivore community organisation: general models and specific tests with phytophagous insects. Pages 329-352 *in* Price, P.W., C.N. Slobodchikoff and W.S. Gaud, editors. A new ecology. Novel approaches to interactive systems. John Wiley and sons, New York, USA.

Lawton, J.H. 1984b. Non-competitive populations, non-convergent communities, and vacant niches: the herbivores of bracken. Pages 67-95 *in* Strong, D.R., D. Simberloff, L.G. Abele and A.B. Thistle, editors. Princeton University Press, Princeton, New Jersey, USA.

Lawton, J.H. 1986. Surface availability and insect community structure: the effects of architecture and fractal dimension of plants. Pages 317-331 *in* Juniper, B.E. and T.R.E. Southwood, editors. Insects and the plant surface. Edward Arnold Ltd., London, England.

Lawton, J.H., H. Cornell, W. Dritschilo, and S.D. Hendrix. 1981. Species as islands: comments on a paper by Kuris et al. American Naturalist **117**:623-627.

Lawton, J.H., and M. MacGarvin. 1986. The organisation of herbivore communities. Pages 163-186 *in* Kikkawa, J. and D.J. Anderson, editors. Community ecology: pattern and process. Blackwell Scientific Publications, Victoria, Australia.

Lawton, J.H., and P.W. Price. 1979. Species richness of parasites on hosts: agromyzid flies on the British Umbelliferae. Journal of Animal Ecology **48**:619-637.

Lawton, J.H., and D. Schröder. 1977. Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. Nature **265**:137-140.

Lawton, J.H., and D.R. Strong. 1981. Community patterns and competition in folivorous insects. The American Naturalist **118**:317-338.

Leather, S.R. 1986. Insect species richness of the British Rosaceae: the importance of host range, plant architecture, age of establishment, taxonomic isolation and species-area relationships. Journal of Animal Ecology **55**:841-860.

Leather, S.R., and P.J. Walsh. 1993. Sub-lethal plant defences: the paradox remains. Oecologia **93**:153-155.

Levin, S.A. 1989. Challenges in the development of a theory of community and ecosystem structure and function. Pages 242-255 *in* Roughgarden, J., R.M. May and S.A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Lewin, R. 1983. Santa Rosalia was a goat. Science **221**:636-639.

Lewis, T. 1969. Factors affecting primary patterns of infestation. Annals of Applied Biology **63**:315-344.

MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Mahdi, T., and J.B. Whittaker. 1993. Do birch trees (*Betula pendula*) grow better if foraged by wood ants? Journal of Animal Ecology **62**:101-116.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics **11**:119-161.

McClure, M.S., and P.W. Price. 1975. Competition among sympatric *Erythroneura* leaf hoppers (Homoptera: Cicadellidae) on American sycomore. Ecology **56**: 1388-1397.

Migdoll, I. 1987. Field guide to the butterflies of southern Africa. Struik, Cape Town, South Africa.

Millar, I.M. 1990. The aphids (Homoptera: Aphidoidea) of South Africa. An identification guide. Entomology Memoir **78**. Department of Agricultural Development, Pretoria, South Africa.

Milton, K. 1991. Leaf change and fruit production in six Neotropical Moraceae species. Journal of Ecology **79**:1-26.

Milton, K., D.M. Windsor, D.W. Morrison, and M.A. Estribi. 1982. Fruiting phenologies of two Neotropical *Ficus* species. Ecology **63**:752-762.

Moore, L.V., J.H. Myers, and R. Eng. 1988. Western tent caterpillars prefer the sunny side of the tree, but why? Oikos **51**:321-326.

Moran, V.C. 1980. Interactions between phytophagous insects and their *Opuntia* hosts. Ecological Entomology **5**:153-164.

Moran, V.C., and T.R.E. Southwood. 1982. The guild composition of arthropod communities in trees. Journal of Animal Ecology **51**:289-306.

Moya-Raygoza, G., V. Bedoy V., and E. Santana C. 1990. Seasonal patterns of insect abundance in natural patches of *Zea diploperennis*. Maydica **35**:177-182.

Murdoch, W.W. 1966. Community structure, population control, and competition - a critique. American Naturalist **100**:219-226.

Neuvonen, S., and P. Niemela. 1981. Species richness of macrolepidoptera on Finnish deciduous trees and shrubs. Oecologia **51**:364-370.

Newton, L.E., and A. Lomo. 1979. The pollination of *Ficus vogelii* in Ghana. Botanical Journal of the Linnean Society **78**:21-30.

Niemela, P., and E. Haukioja. 1982. Seasonal patterns in species richness of herbivores: macrolepidopteran larvae on Finnish deciduous trees. Ecological Entomology **7**:169-175.

Overgaard Nielson, B., and A. Ejlersen. 1977. The distribution pattern of herbivory in a beech canopy. Ecological Entomology **2**:293-299.

Pennings, S.C., and V.J. Paul. 1992. Effect of plant toughness, calcification, and chemistry on herbivory by *Dolabella auricularia*. Ecology **73**:1606-1619.

Pierce, N.E., and M.A. Elgar. 1985. The influence of ants on host plant selection by *Jalmenus evagoras*, a myrmecophilous lycaenid butterfly. Behavioural Ecology and Sociobiology **16**:209-222.

Pinhey, E.C.G. 1975. Moths of southern Africa. Tafelberg, Cape Town, South Africa.

Price, P.W. 1976. Colonisation of crops by arthropods: non-equilibrium communities in soybean fields. Environmental Entomology **5**:605-611.

Price, P.W. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton, New Jersey, USA.

Price, P.W. 1984. Alternative paradigms in community ecology. Pages 353-383 *in* Price, P.W., C.N. Slobodchikoff and W.S. Gaud, editors. A new ecology. Novel approaches to interactive systems. John Wiley and sons, New York, USA.

Price, P.W. 1990. Host populations as resources defining parasite community organisation. Pages 21-40 *in* Esch, G.W., A.O. Bush and J.M. Aho, editors. Parasite communities: patterns and processes. Chapman and Hall, London, England.

Ralph, C.P. 1977. Effect of host plant density on populations of a specialised seed sucking bug, *Oncopeltus fasciatus*. Ecology **58**:799-809.

Rathke, B.J. 1976. Competition and coexistence within a guild of herbivorous insects. Ecology **57**:76-87.

Rausher, M.D. 1981. The effect of native vegetation on the susceptibility of *Aristolochia reticulata* (Aristolochiaceae) to herbivore attack. Ecology **62**:1187-1195.

Rawlings, J.O. 1988. Applied regression analysis: a research tool. Brooks/Cole Publishing Company, California, USA.

Rey, J.R., E.D. McCoy, and D.R. Strong. 1981. Herbivore pests, habitat islands, and the species-area relationship. American Naturalist **117**:611-622.

Richards, O.W., and R.G. Davies. 1977. Imm's general textbook of entomology. Volume 2: classification and biology. Chapman and Hall, London, England.

Ritchie, W., M. Wood, R. Wright, and D. Tait. 1988. Surveying and mapping for field scientists. Longman, Harlow, England.

Robertson, H.G. 1988. Spatial and temporal patterns of predation by ants on eggs of *Cactoblastis cactorum*. Ecological Entomology **13**:207-214.

Root, R.B. 1967. The niche exploitation patterns of the Blue-gray Gnatcatcher. Ecological Monographs **37**:317-350.

Root, R.B. 1973. Organisation of plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs **43**:95-124.

Roughgarden, J. 1989. The structure and assembly of communities. Pages 203-226 *in* Roughgarden, J., R.M. May and S.A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Roughgarden, J., and J. Diamond. 1986. Overview: the role of species interactions in community ecology. Pages 333-343 *in* Diamond, J. and T.J. Case, editors. Community ecology. Harper and Row Publishers, New York, USA.

Schoener, T.W. 1982. The controversy over interspecific competition. American Scientist **70**:586-595.

Schoener, T.W. 1983. Field experiments on interspecific competition. American Naturalist **122**:240-285.

Scholtz, C.H., and E. Holm. 1985. Insects of southern Africa. Butterworths, Durban, South Africa.

Scriber, J.M. 1977. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). Oecologia **28**:269-287.

Seifert, R.P., and F.H. Seifert. 1976. A community matrix analysis of *Heliconia* insect communities. American Naturalist **110**:461-483.

Shorrocks, B., J. Rosewell, K. Edwards, and W. Atkinson. 1984. Interspecific competition is not a major organising force in many insect communities. Nature **310**:310-312.

Slater, J.A. 1971. The biology and immature stages of South African Heterogastrinae, with the description of two new species (Hemiptera: Lygaeidae). Annals of the Natal Museum **20**:443-465.

Slater, J.A. 1972. Lygaeid bugs (Hemiptera: Lygaeidae) as seed predators of figs. Biotropica **4**:145-151.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research. Freeman and co., New York, USA.

Solbreck, C. 1991. Unusual weather and insect population dynamics: Lygaeus equestris during an extinction and recovery period. Oikos **60**:343-350.

Southwood, T.R.E. 1978. The components of diversity. Pages 19-40 *in* Mound, L.A. and N. Waloff, editors. Diversity of insect faunas. Symposia of the Royal Entomological Society of London **9**. Blackwell Scientific Publications, Oxford, England.

Southwood, T.R.E., V.C. Moran, and C.E.J. Kennedy. 1982. The richness, abundance and biomass of the arthropod communities on trees. Journal of Animal Ecology **51**:635-649.

Stork, N.E. 1987. Guild structure of arthropods from Bornean rain forest trees. Ecological Entomology **12**:69-80.

Strong, D.R. 1979. Biogeographic dynamics of insect-host plant communities. Annual Review of Entomology **24**:89-119.

Strong, D.R. 1982. Harmonious coexistence of hispine beetles on *Heliconia* in experimental and natural communities. Ecology **63**:1039-1049.

Strong, D.R. 1984. Exorcising the ghost of competition past: phytophagous insects. Pages 28-41 *in* Strong, D.R., D. Simberloff, L.G. Abele and A.B. Thistle, editors. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, USA.

Strong, D.R., J.H. Lawton, and T.R.E. Southwood. 1984. Insects on plants. Commmunity patterns and mechanisms. Blackwell Scientific Publications, Oxford, England.

Strong, D.R., and D.A. Levin. 1979. Species richness of plant parasites and growth form of their hosts. The American Naturalist **114**:1-22.

Strong, D.R., E.D. McCoy, and J.R. Rey. 1977. Time and the number of herbivore species: the pests of sugarcane. Ecology **58**:167-175.

Swain, V.M., and G.L. Prinsloo. 1986. A list of phytophagous insects and mites on forest trees and shrubs in South Africa. Department of Agriculture and Water Supply. Entomological Memoir **66**:1-91.

Tallamy, D.W. 1985. Squash beetle feeding behaviour: an adaptation against induced cucurbit defences. Ecology **66**:1574-1579.

Terborgh, J., and S. Robinson. 1986. Guilds and their utility in ecology. Pages 65-90 *in* J. Kikkawa and D.J. Anderson, editors. Community ecology: pattern and process. Blackwell Scientific Publications, Victoria, Australia.

Thomas, C.D. 1989. Predator-herbivore interactions and the escape of isolated plants from phytophagous insects. Oikos **55**:291-298.

Thomas, C.D. 1990. Herbivore diets, herbivore colonisation, and the escape hypothesis. Ecology **71**:610-615.

Thompson, J.N., and P.W. Price. 1977. Plant plasticity, phenology and herbivore dispersion: wild parsnip and the parsnip webworm. Ecology **58**:1112-1119.

Tilman, D. 1989. Discussion: population dynamics and species interactions. Pages 89-100 *in* Roughgarden, J., R.M. May and S.A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Van Greuning, J.V. 1990. A synopsis of the genus *Ficus* (Moraceae) in southern Africa. South African Journal of Botany **56**:599-630.

Van Schaik, C.P. 1986. Phenological changes in a Sumatran rain forest. Journal of Tropical Ecology **2**:327-347.

Von Breitenbach, J. 1974. The wild figs of southern Africa. Trees....in South Africa, Journal of the Tree Society of South Africa **26**:58-80.

Waloff, N., and P. Thompson. 1980. Census data of populations of some leafhoppers (Auckenorrhyncha, Homoptera) of acid grassland. Journal of Animal Ecology **49**:395-416.

Ward, L.K., and K.H. Lakhani. 1977. The conservation of juniper: the fauna of food-plant island sites in southern England. Journal of Applied Ecology **14**:121-135.

Way, M.J. 1963. Mutualism between ants and honeydew-producing Homoptera. Annual Review of Entomology **8**:307-344.

Wharton, R.A., J.W. Tilson, and R.L. Tilson. 1980. Asynchrony in a wild population of *Ficus sycomorus* L. South African Journal of Science **76**:478-480.

Wheeler, W.M. 1922. Ants on the American Museum Congo expedition. A contribution to the myrmecology of Africa. Bulletin of the American Museum of Natural History **45**:1-256.

White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia **63**: 90-105.

Whittaker, J.B. 1991. Effects of ants on temperate woodland trees. Pages 67-79 *in* Cutler, D.F. and C.R. Huxley, editors. Interactions between ants and plants. Oxford University Press, Oxford, England.

Whittaker, R.H. 1952. A study of summer foliage insect communities in the Great Smokey Mountains. Ecological Monographs **22**:1-44.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs **30**:279-338.

Williams, C.E. 1990. Host plant latex and the feeding behaviour of *Chrysochus auratus* (Coleoptera: Chrysomelidae). The Coleopterists Bulletin **45**:195-196.

Williamson, M.H. 1981. Island populations. Oxford University Press, Oxford, England.

Windsor, D.M., D.W. Morrison, M.A. Estribi, and B. de Leon. 1989. Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panama. Experientia **45**:647-653.

Wolda, H. 1988. Insect seasonality: why? Annual Review of Ecology and Systematics **19**:1-18.

Wolda, H. 1992. Trends in abundance of tropical forest insects. Oecologia **89**:47-52.

Zwölfer, H. 1986. Species richness, species packing, and evolution in insect-plant systems. Ecological Studies **61**:301-319.

APPENDICES

APPENDIX 1 Physical attributes of the *F. burtt-davyi* trees in the study area. The measured variables are tree height (m)(HT), canopy volume (m^3)(TOTVOL), foliage volume (m^3)(FOLVOL), foliage density (DENSITY), maximum cross-sectional area of the canopy (m^2)(XAREA), stem number (STNO), maximum stem diameter (cm)(STDI), maximum axis number (AXES), number of conspecifics within a 50m radius (ISO), insolation - at least part of the tree exposed to full sun all day (SUN), to shade all day (SHD), to dappled sunlight all day (DAP), and mixed exposure to all three (MIX).

TREE	HT	TOTVOL	FOLVOL	DENSITY	XAREA	STNO	STDI	AXES	ISO	SUN	SHD	DAP	MIX
1	1.75	2.19	0.3	0.136986	0.75	1	14.5	6	4	1	0	0	0
2	2.5	75	31.5	0.42	21	15	22	7	10	1	0	1	0
3	1	0.75	0.56	0.746667	0.75	2	8.5	5	11	1	0	0	0
4	0.25	0.0062	0.0031	0.5	0.05	2	9	4	11	1	0	0	1
5	0.55	0.044	0.014	0.318182	0.1	1	5	4	13	1	0	0	0
6	1.25	1.56	0.78	0.5	1.16	5	7	4	11	1	0	0	0
7	0.25	0.0038	0.0026	0.684211	0.04	1	1	3	11	0	0	1	0
8	1.5	3	1.125	0.375	1.5	3	16	6	11	1	0	1	0
9	3	63	27	0.428571	18	23	25	7	10	1	0	1	1
10	1.25	2.73	1	0.3663	1	4	11	5	10	0	0	0	1
11	1.25	5.16	3.25	0.629845	4.5	6	23.5	5	9	1	0	0	0
12	1	5	3.12	0.624	2.5	6	16.5	8	11	1	0	1	1
13	1	2	2	1	2	8	21	7	9	1	0	0	1
14	1.5	9	3.05	0.338889	4.75	5	28	7	4	1	0	0	1
15	3	270	110	0.407407	22	74	23	7	4	1	0	1	1
16	0.75	0.38	0.09	0.236842	0.3	5	6.5	5	6	1	0	0	1
17	0.5	0.05	0.03	0.6	0.16	1	6	5	6	1	0	0	0
18	3.25	20.11	11.25	0.559423	6	10	22	6	6	1	0	1	1
19	1	0.19	0.03	0.157895	0.28	6	5.5	5	6	1	0	0	1
20	3	41.25	5.25	0.127273	5.25	7	22.5	8	5	0	1	1	1
21	0.5	0.03	0.01	0.333333	0.09	2	5	4	6	0	0	0	1
22	3	10.5	3	0.285714	3	5	28	6	8	1	0	1	1
23	3	18.56	9	0.484914	6	25	18.5	6	8	1	0	1	1

Appendix 1 *continued*

TREE	HT	TOTVOL	FOLVOL	DENSITY	XAREA	STNO	STDI	AXES	ISO	SUN	SHD	DAP	MIX
24	0.5	0.02	0.03	1.5	0.15	3	1.5	3	8	1	0	0	0
25	0.5	0.06	0.06	1	0.16	11	1.5	3	9	1	0	0	0
26	0.4	0.042	0.027	0.642857	0.09	6	4	3	10	1	0	0	0
27	0.8	0.29	0.21	0.724138	0.38	16	4	4	10	1	0	0	1
28	3.25	16.25	6.81	0.419077	5.5	3	21.5	5	9	1	0	1	1
29	0.15	0.00075	0.00075	1	0	1	1	1	9	1	0	0	0
30	3	36	7.44	0.206667	7.94	19	18.5	7	9	1	0	1	1
31	0.3	0.11	0.11	1	0.43	1	8	5	11	0	0	0	1
32	1.25	2.34	1.25	0.534188	1.25	11	6.5	4	12	1	0	1	1
33	1	0.38	0.11	0.289474	0.3	2	6.5	5	7	0	0	0	1
34	3.5	136.5	86.62	0.634579	15.3	14	38.5	8	7	1	0	1	1
35	3	126	116.38	0.923651	19.2	42	28.5	7	7	1	0	1	1
36	2.25	11.25	3.75	0.333333	3	17	11	4	13	1	0	1	1
37	0.55	0.011	0.011	1	*	*	*	*	9	0	1	0	0
38	0.6	0.045	0.06	1.333333	0.06	1	5	4	24	1	0	1	1
39	1	0.625	0.08	0.128	0.3	4	5.5	5	6	0	0	1	0
40	2.25	30.38	7.81	0.257077	6	10	23	6	34	0	1	1	0
41	1	0.56	0.36	0.642857	0.6	5	5.5	3	38	0	1	1	0
42	0.75	0.94	0.15	0.159574	0.5	4	10.5	5	52	1	0	1	0
43	0.75	0.16	0.03	0.1875	0.09	2	4.5	4	47	0	0	0	1
44	2.3	5.75	0.34	0.05913	1.5	3	14.5	5	47	1	0	0	1
45	0.6	0.14	0.054	0.385714	0.18	5	3	4	50	1	0	0	0
46	2	0.38	0.041	0.107895	0.33	3	6.5	4	43	1	0	1	1
47	0.25	2.11	0.19	0.090047	0.75	1	15	5	44	1	0	0	1
48	2	64	8	0.125	4	8	29	6	45	1	0	1	1
49	3	48.75	15	0.307692	7.5	7	26	7	29	1	0	1	1
50	0.25	0.89	0.17	0.191011	0.88	4	11	5	11	0	1	0	1

Appendix 1 *continued*

TREE	HT	TOTVOL	FOLVOL	DENSITY	XAREA	STNO	STDI	AXES	ISO	SUN	SHD	DAP	MIX
51	3.25	28.44	3.88	0.136428	3.25	3	15.5	5	11	1	0	1	1
52	1.25	3.75	1.38	0.368	3	5	15.5	6	16	1	0	0	0
53	2.25	1.69	0.28	0.16568	0.63	2	15	4	16	1	0	0	0
54	2.75	49.5	9	0.181818	6	20	17.5	5	15	1	0	1	1
55	2.75	68.75	36	0.523636	10	11	32	7	15	1	0	1	1
56	0.8	0.5	0.1	0.2	0.5	5	4.5	4	24	0	0	0	1
57	0.5	0.0025	0.0025	1	0.05	1	3.5	2	24	0	0	0	1
58	1.5	4.5	0.97	0.215556	1.62	10	7.5	4	20	1	0	1	0
59	1	1.38	0.75	0.543478	1.5	1	13.5	5	28	0	0	0	1
60	4.25	17	1.31	0.077059	1.05	3	23	6	13	1	0	0	1
61	2.75	33	0.935	0.028333	2.35	5	23	5	49	1	0	0	1
62	3	72	3.93	0.054583	5.7	7	27	5	55	1	0	0	0
63	1.25	1.95	0.35	0.179487	0.7	6	9.5	5	53	1	0	0	1
64	1	182.25	6	0.032922	6	1	45.5	8	49	1	0	0	1
65	0.2	0.001	0.00025	0.25	0	1	3	4	56	0	0	0	1
66	0.1	0.00025	0.00012	0.48	0	1	3.5	*	56	0	0	0	1
67	0.05	0.000062	0.00014	2.258065	0	2	2.5	3	55	0	0	0	1
68	0.75	0.045	0.0017	0.037778	0.02	1	7	7	56	0	0	0	1
69	2	0.6	0.166	0.276667	0.46	1	19.5	7	56	1	0	0	0
70	2	4	0.972	0.243	1.66	2	15	7	54	1	0	0	0
71	2.5	0.5	0.15	0.3	0.38	4	17	6	53	1	0	0	0
72	2	2.25	0.09	0.04	0.36	1	14	8	56	0	0	0	1
73	1	5.62	2.25	0.400356	3	10	16.5	7	61	0	0	1	1
74	3	47.25	2.81	0.059471	3.75	10	18	8	65	0	0	0	1
75	2	10.5	1.88	0.179048	1.5	4	25.5	7	56	1	0	0	0
76	0.3	0.084	0.0038	0.045238	0.04	1	6.5	6	61	0	0	0	1
77	0.15	0.016	0.0045	0.28125	0.04	1	7.5	7	61	0	0	0	1

Appendix 1 *continued*

TREE	HT	TOTVOL	FOLVOL	DENSITY	XAREA	STNO	STDI	AXES	ISO	SUN	SHD	DAP	MIX
78	1.25	2.73	0.75	0.274725	1	10	12.5	7	67	1	0	0	0
79	2.25	6.75	0.36	0.053333	1.21	4	21.5	5	59	1	0	0	1
80	1	1.125	0.09	0.08	0.25	6	8	4	60	1	0	0	1
81	5	180	5.16	0.028667	8.5	9	55	8	57	1	0	1	1
82	4	192	2.56	0.013333	4.12	1	39.5	7	58	1	0	1	1
83	4.5	126	9.88	0.078413	11.8	7	40	8	54	1	0	1	1
84	5	165	5.45	0.03303	8.56	6	38	8	49	1	0	1	1
85	1.5	7.5	0.75	0.1	1.5	15	24	6	40	1	0	0	1
86	0.2	0.001	0.001	1	0.02	1	1	3	39	0	0	0	1
87	0.25	0.02	0.0056	0.28	0.04	3	5.5	4	37	0	0	0	1
88	2	48	4	0.083333	6	14	25	7	29	1	0	0	1
89	1.5	4.5	0.68	0.151111	1.12	6	13.5	5	30	1	0	1	0
90	0.2	0.008	0.0002	0.025	0.04	3	1	3	25	1	0	0	0
91	1	0.09	0.0056	0.062222	0	2	6	2	27	0	0	0	1
92	3	9	0.84	0.093333	1.12	3	35	7	33	1	0	0	1
93	0.2	0.004	0.004	1	*	*	*	*	37	0	0	0	1
94	0.5	0.125	0.055	0.44	0.28	5	4	2	37	0	0	0	1
95	3	18	1.5	0.083333	2	7	26.5	6	37	1	0	0	0
96	2.5	5	0.38	0.076	0.75	2	12.5	5	36	1	0	0	0
97	1.5	1.688	0.036	0.021327	0.18	1	9	3	0	0	0	0	1
98	3.25	4.062	1.69	0.416051	2.25	3	16.5	4	0	0	0	0	1
99	1	1.875	0.018	0.0096	0.11	4	5.5	4	33	0	0	0	1
100	1.75	14.22	2.25	0.158228	3	3	14.5	5	35	0	0	0	1
101	3	13.5	9	0.666667	6	2	13.5	5	3	0	0	0	1
102	2.25	16.875	12	0.711111	6	5	21	7	38	0	1	1	0
103	3.5	61.25	3.22	0.052571	6.62	15	20.5	5	38	0	1	0	1
104	4	70	5.66	0.080857	9.62	20	30.5	7	29	0	1	1	1

Appendix 1 *continued*

TREE	HT	TOTVOL	FOLVOL	DENSITY	XAREA	STNO	STDI	AXES	ISO	SUN	SHD	DAP	MIX
105	0.2	0.262	0.012	0.045802	0.1	1	7	3	38	0	0	0	1
106	1	0.375	0.089	0.237333	0.26	1	7	4	44	1	0	0	0
107	0.5	0.125	0.041	0.328	0.16	2	7.5		43	0	0	0	1
108	3.5	243.75	12	0.049231	6	20	27.5	9	39	1	1	1	1
109	0.5	0.281	0.05	0.177936	0.25	1	10.5	6	45	1	0	0	0
110	1	1.5	0.123	0.082	0.63	4	8	6	48	0	0	0	1
111	1	1	0.001	0.001	0.02	2	8	6	50	0	0	1	1
112	0.75	0.015	0.00025	0.016667	0	1	7.5	5	51	1	0	0	0
113	1	2.25	0.4	0.177778	1.35	2	15	6	42	1	0	0	0
114	0.5	0.06	0.0058	0.096667	0.08	1	8	7	43	0	0	0	1
115	0.25	0.00125	0.000001	0.0008	0	1	4	2	44	0	0	0	1
116	1.5	0.015	0.000002	0.000133	0	2	12.5	5	44	0	0	0	1
117	1	1.25	0.08	0.064	0.2	2	11	6	51	0	1	0	0
118	2.5	17.5	1	0.057143	4	5	17	7	46	1	0	0	0
119	0.75	2.25	0.016	0.007111	0.14	2	18.5	10	49	0	1	0	0
120	2	15	2	0.133333	4	8	22	6	66	0	0	0	1
121	1.5	2.25	0.05	0.022222	0.25	1	18	6	60	1	0	0	0
122	2.5	30	1.83	0.061	4.28	3	25.5	7	57	1	1	0	1
123	1	0.3	0.018	0.06	0.09	2	6	4	57	1	0	0	0

APPENDIX 2 Regression Analysis

Regression analyses are used to determine the relative importance of various independent variables in explaining the variability of a dependent variable. Two methods were used in combination throughout the data analyses in this study: All Possible Subsets Regression (BMDP Proc. 9R, selection criterion ADJ R^2) and Stepwise Regression (BMDP Proc. 2R, forward stepping). The former procedure estimates regression equations for selected 'best' subsets of independent variables which explain as much of the variation of the dependent variable as possible i.e. which give the highest adjusted coefficient of multiple determination (ADJ R^2) (Sokal and Rohlf 1981). In order to maximise ADJ R^2, however, this method often selects variables which, although they improve the amount of variation accounted for, do so by an insignificant amount. To eliminate these variables and to confirm the results obtained from the All Possible Subsets Regression, a Stepwise Regression was also performed.

An All Possible Subsets Regression was used in conjunction with the Stepwise Regression as the latter can rely to too large a degree on chance (Bernstein et al 1988). The selection procedure is very sensitive to small and often insignificant differences between the variables' effects on R^2 and can therefore accentuate the differences between them. The advantage of the All Possible Subsets Regression is that it allows an examination of the ADJ R^2 of all variable combinations.

A forward-stepping Stepwise Regression selects one independent variable at a time to enter into the multiple linear regression equation until the addition of further variables produces no appreciable increase in R^2. The order in which variables are included is determined by evaluation of the increments in R^2 attributable to the addition of each variable at each successive step. That resulting in the greatest increment is entered into the equation (Sokal and Rohlf 1981). BMDP Proc. 2R bases its selection on a computation of an 'F-to-enter' value corresponding to a test of the significance of the increment in R^2 due to the addition of a new variable. That variable with the largest F-to-enter value at each step is added to the equation.

Normality and homoscedasticity

The residuals, the differences between the values predicted by the fitted regression equation and the observed values, were analysed following the regression analyses. This enabled the detection of problems with the model or data. Common problems relate to failure of the basic assumptions that the observations are independently normally distributed with common variances (homoscedacious) (Box and Cox 1964; Rawlings 1988). The Shapiro-Wilk test for normality (BMDP 2D; Rawlings 1988) and Levene's test for equality of variances (BMDP 7D) were applied to the residuals. Problems may arise with the normality test due to it's assumption of independence, the residuals being non-independent. In such cases the accuracy of the test is dependent on sample size and number of independent variables, accuracy increasing with increasing sample size and decreasing with increasing number of independent variables. Simulation studies have shown that for n=40 and eight independent variables the approximation is accurate (Rawlings 1988). Hence, the 123 cases and seven independent variables used in the spatial analyses are more than adequate. For the 18 cases and 14 independent variables used in the temporal analyses, however, the approximation will be less accurate and the results of the Shapiro-Wilk test for normality must therefore be treated with caution.

Outliers and collinear relationships

Further problems with such data sets may arise due to outliers and linear relationships between independent variables (collinearity) (Rawlings 1988). An outlier is defined by Rawlings (1988) as 'an observation which in some sense is inconsistent with the rest of the observations in the data set'. If sufficiently outlying, they may have far reaching effects on the model. Residuals were examined for the presence of outliers by looking at their 'distance' from the overall mean, those more than three standard deviations away from the latter being considered to be significantly outlying (BMDP Statistical Software Manual 1990). If two or more independent variables are highly correlated, the computations become inaccurate and important variables may be replaced by those of lower importance. BMDP Proc. 2R examines data for collinearity prior to performing the regression analysis and excludes variables that are too highly related from the analyses.