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Interactive dynamics between wood-rotting fungi and ciid beetles

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INTERACTIVE DYNAMICS BETWEEN WOOD-ROTTING FUNGI AND CIID BEETLES

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The present study has shown that interactions between ciid beetles and fungal fruit bodies provide a valuable, experimentally accessible and yet relatively simple system for studying the evolutionary ecology of consumer-host relationships that complements more frequently studied systems such as plant-herbivore and host-parasitoid interactions. Previous studies of ciid-fungus interactions have been largely zoocentric, portraying the fungal component of the interactions as a passive non-interactive resource or habitat. By contrast, the present study demonstrated that fungal fruit bodies are not passive places of residence for fungivorous ciids, but dynamic, interactive contexts which both constrain and provide opportunities for the evolution of its inhabitants.

Field observations showed that ciid beetles exhibit strong preferences for their host fungi, and wind tunnel experiments showed that these beetles can discriminate between host and non-host species, as well as between different developmental stages of their host fungus solely on the basis of odour. Moreover, it was found that the developmental dynamics of fruit bodies of *Coriolus versicolor* **(L. ex Fr.) Quél.** drive the differential use of the resource by the beetles *Octotemnus glabriculus* **Gyllenhal** and *Cis boleti* **Scopoli** which differ in body size and breeding behaviour.

The predominant view that fungal fruit-bodies are no more than passive homes for fungivorous implies that infestation by ciids has no potential effects on the evolutionary fitness of host fungi. However, the present study showed evidence that such effects on fitness do indeed exist and are potentially very diverse in character.

Both *O. glabriculus* and *C. boleti* were found to have a negative effect on the reproductive potential of their host fungus *C. versicolor*. *Octotemnus glabriculus* caused significantly more damage than *C. boleti* but there were no synergistic effects through the joined trophic activities of both insects. The wide-ranging implications of these findings are discussed.

PREFACE

1. Fungi and insects

Fungi and insects participate in a wide range of vital processes for ecosystem ecology and evolution. Some fungi are primary decomposers contributing to nutrient cycling (Boddy & Watkinson 1995; Dighton 1995; Baldy et al. 1995; Niemela et al. 1995). Other fungi form mutualistic associations with algae, i.e. lichens, that pioneer the colonisation of exposed surfaces (Ott 1987; Sancho & Valladares 1993; Valladares & Sancho 1995; Schroeter & Sancho 1996; Grishin et al. 1996) or with higher plants, i.e. mycorrhizas, which facilitate the absorption of nutrients and therefore contribute toward primary production (Bolan 1991; Krapfenbauer et al. 1996; Johnson et al. 1997) and affect plant community structure (Theodose & Bowman 1997) and diversity (Ozinga et al. 1997). Fungi can also be parasites exerting negative selective pressure on plants (Diamond & Bird 1994; Takenaka 1995; Clay & Kover 1996) and animals (Osborne & Landa 1992; Cokendolpher 1993; Poinar & Poinar 1998). Insects can be detrivores that contribute to nutrient cycling by comminution of litter (Lee & Foster 1991; Faber et al. 1992; Schowalter 1992; Kaplin 1994), or herbivores or predators that impose selective pressure on their host plants (Andersen & Lonsdale 1990; Matches 1992; Tscharntke & Greiler 1995) or preys (Lebeck 1991; Feener & Brown 1997). Insects are also pollinators that facilitate sexual reproduction of higher plants (Vasudeva & Lokesha 1993; Batra 1995; Ducker & Knox 1985).

To understand fully the dynamics of these processes, it is necessary to know the effects of interactions of fungi and insects both with one another and with other organisms. Fungi and insects are two hyper-diverse taxa of living organisms (Colwell & Coddington 1994) and so, not surprisingly, they can interact with one another in a variety of ways. Such interactions range from complete dependence of entomophagous fungi on insects as food resource to complete dependence of fungivorous insects on fungi as food resource, with a vast spectrum in between (Wilding et al. 1989). There is evidence that fungivorous insects can affect mycorrhizal formation and functionality (Gehring & Whitham 1994; Gange & West 1994; Larsen & Jakobsen 1996a), the control or spread of root parasites (Lartey et al. 1994) and also can alter the dynamics of litter and wood decomposition (Hanlon & Aderson 1979; McGonigle 1995). Entomophagous fungi can affect insect populations including detrivores, herbivore, predators and pollinators. In more complex interactions phytopathogenic fungi can affect pollination dynamics by competing with flowers for visitors (Roy 1994) and endophytes, fungi living closely associated with photosynthetic tissues of most plants, can affect herbivory (Gange et al. 1994; Clay 1996; Faeth & Hammon 1997; Gehring & Whitham 1994).

The present study concentrates on the particular example of interactions between ciid beetles (Cucujoidae: Ciidae) and their host wood-rotting fungi in an effort to improve understanding of the evolutionary ecology of fungus-fungivore relationships. Chapter I presents a review of the literature on fungus-fungivore associations to put this study into context. Chapter II presents field and experimental evidence of the host preferences of ciid beetles. Chapter III uncovers the processes that enable coexistence of two beetle species in one host fungus. Chapter IV presents evidence on the impact that fungivory has on the reproductive potential of host fungi prior to an overall discussion and conclusions from this study in Chapter V.

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3. Acknowledgements

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CHAPTER I

THE EXTENT OF FUNGUS-FUNGIVORE INTERACTIONS

1. Fungivory

The nutrient value of fungal tissue for fungivores is comparable to that of plant tissues for herbivores (Martin 1992). Consumption of fungal tissues is, therefore, a strategy amply distributed among heterotrophic taxa, from amoebae to large mammals, e.g. deer and wild boar (Moore 1996). In mammals, fungivory appears to be a facultative or seasonal strategy. This aspect of fungivory will not be discussed further here: general reviews from which further insights can be gained are provided by Claridge & May (1995), Johnson (1996) and Tory et al. (1997). Instead, attention will be focused on fungivory by invertebrates, mainly collembolans, flies and beetles, with the aim of reviewing the literature from an integrational perspective, rather than to give an account of the diversity of the fungivorous fauna, in order to place the present study into the context of current understanding.

Plant-herbivore interactions and fungus-fungivore relationships can be seen as analogous systems (Bruns 1984; Hanski 1989) in which consumers exploit motionless living resources with potential negative consequences on the biological activities (growth and reproduction) of the latter. Nevertheless, there are marked disparities between the amount and character of work that has been done on these two kind of interactions. On the one hand, close relationships between some herbivores and their host plants have been know since at least Victorian times. More recently, thirty years of both empirical and theoretical investigations on plant-herbivore relationships have led to the accumulation of a large body of information in an effort to explain a variety of ecological and evolutionary patterns. These patterns include the frequency and intensity of herbivory and its variability; the impact of herbivory on the reproductive potential of plants; the distribution and effectiveness of defence mechanisms, both chemical and physical; the effects of plant characteristics such as apparency, phenology and life history on herbivory, as well as the co-variation of two or more of these factors (Crawley 1983; Dirzo 1984; Howe & Westley 1988; Karban & Baldwin 1997; Rosenthal & Janzen 1979, among others).

On the other hand, whilst fungus-fungivore associations have received sporadic attention for over 70 years, the emphasis has been almost entirely zoocentric, with the fungal component referred to only as the "food resource" or "habitat". This situation is analogous to that experienced at the beginning of the study of plant-herbivore associations (Harper 1986; Dirzo 1984). However, in the last fifteen years, appreciation of the role of fungi as a dynamic components of fungus-fungivore associations has increased, and the effects of fungivory on fungi are beginning to be better understood (e.g. Lartey et al. 1994; Newell 1984a; Newell 1984b; Wicklow & Yocom 1982).

Based on the growth properties of fungal tissues of higher fungi, two distinctive types of fungivory may be recognised; grazing on mycelium capable of indeterminate growth, and consumption of fully determined structures (e.g. fruiting bodies).

Process, patterns and mechanisms may differ between these two types of fungivory. Their study must, therefore, be complementary rather than alternative in order to fully understand the evolutionary ecology of fungus-fungivore interactions.

2. Grazing on mycelium

Mycelium may represent the largest proportion of fungal biomass for any given species of fungi (Frankland 1982). Mycelium grows as a space-filling entity that branches repeatedly with progressive reduction in the diameter of the branches (Rayner et al. 1994). Such characteristics make the mycelium a difficult resource to be exploited except in those areas where relatively large aggregates of hyphae are found. In soil, large aggregates of hyphae are formed by species of litter decomposer fungi in which fungal growth is not restricted to discrete resource units such as a single leaf, petiole, seed or twig. In these species, part of the mycelium is often organised into long aggregates (cords, rhizomorphs) that interconnect discrete units of resources forming a network (Rayner et al. 1985) on which fungivory may have significant effects. In the rhizosphere, root symbionts (parasites and mycorrhizal fungi) form mycelial aggregates around roots (Coleman & Crossley 1996) on which fungivory may not only have direct consequences on fungi but also have indirect consequences on their associated plants (Burdon 1987; Augspurger 1988). Other important associations occur between wood decomposer fungi and wood inhabiting insects which directly or indirectly exploit fungal mycelium as a food source.

Acari (mites), Collembola (springtails), Diptera (flies) and Coleoptera (beetles) are the main fungivorous taxa of arthropods grazing on fungal mycelium in soil

(McGonigle 1997). Additionally, nematodes are a major component of the fungivorous guild. Unpredictability in the composition of spatial and temporal assemblages of fungal communities (Frankland 1998) may imply that mycelium grazers are likely to be generalist rather than specialist from a taxonomic perspective but restricted to ecologically definable niches such as litter, rhizosphere or decaying wood. Specific interactions have, however, evolved in several taxa of insects (ants, termites, beetles, and wasps) that have mastered farming of their associated fungi (see sections 2.1.3 and 2.1.4).

Though few highly specialised associations have been described between mycelium grazers and their associated fungi, a large amount of experimental evidence shows that mycelium grazers are, in general, selective (Ananthakrishnan & Suresh 1983; Hedlund et al. 1995; Klironomos & Kendrick 1995; Larsen & Jakobsen 1996a; Larsen & Jakobsen 1996b; Newell 1984a; Newell 1984b; Walter & Lidquist 1989; Wicklow & Yocom 1982, see sections 2.1.1, 2.1.2 and 2.1.3 for details). Since grazing on fungal mycelium is not a random strategy, fungivory has the potential to affect fungal community structure (McGonigle 1997) just as herbivory has been shown to affect plant communities (see Crawley 1983).

Plant responses to herbivory vary between species and the context in which interactions take place, and range from positive to negative (Whitham & Maschinski 1991). By analogy, fungal responses to fungivory may be expected to vary from positive (Bengtsson et al. 1993; Hanlon & Anderson 1979; Hanlon 1981; Hedlund et al. 1991) to negative (Lartey et al. 1994; Newell 1984a; Newell 1984b; Wicklow & Yocom 1982) depending on the context, i.e. the circumstances of the fungivory (developmental stage of the fungus, environmental conditions, extent of damage, etc.) and species involved.

2. 1. Fungivory and fungal community structure

2. 1. 1. Litter decomposers

Evidence of the impact of fungivory on fungal community structure and diversity is only available for litter decomposer fungi (McGonigle 1997). These fungi illustrate the importance of fungivory in defining the context for the development of fungal community structure. On the one hand, fungivory may lead to co-dominance. The collembolan *Onychiurus latus* **Gisin** preferentially grazes on mycelium of *Marasmius androsaceus* **L ex Fr.** rather than on *Mycena galopus* **(Pers. ex Fr.) Kummer** (Newell 1984a). Field evidence showed that neither of these fungi exhibit dominance in natural communities but experimental work showed that *M. androsaceus* is a more aggressive competitor than *M. galopus*. Field co-dominance of these two fungi is mediated by the preference of *O. latus* to graze on the mycelium of the more aggressive fungus (Newell 1984a; Newell 1984b). On the other hand, fungivory may also lead to biased-dominance in fungal communities. Two fungal isolates (dark sterile 298 and basidiomycete 290) from aspen litter were co-dominant when inoculated together in microcosm experiments, showing equal colonising abilities. When mixed cultures were exposed to grazing by the collembolan *Onychiurus subtenuis* **Folsom**, however, the system was polarised by the suppression of the sterile dark 298 isolate. Further experimental evidence showed that the isolate basidiomycete

290 was unpalatable for *O. subtenuis* (Parkinson et al. 1979).

2. 1. 2. Root symbionts

Fungivore selectivity and response variability of root symbiont fungi to fungivory are likely to affect not only the structure of fungal communities but also that of plant communities. In the rhizosphere, roots of plants interact with both parasites and mycorrhizal fungi which potentially exert opposite effects on plant growth and reproduction (Augspurger 1988; Coleman & Crossley 1996). Preferences of fungivores for any one of these two types of fungi may have consequences on the growth and reproduction of individual plants, and on a large scale may have consequences for plant community structure (Burdon 1987; Augspurger 1988; Law 1988).

Evidence of the impact of fungivory on root parasites comes mainly from agricultural systems where the use of fungivorous Collembola has been attempted as biological control agents. Greenhouse experiments showed that mixed populations of the collembolans *Proisotoma minuta* **Tullberg** and *Onychiurus encarpatus* **Denis** significantly suppress root colonisation by *Rhizotonia solani* **Kühn** and also by the agent causing cotton seedling disease (Curl 1979). Furthermore, it has been shown that *P. minuta* has a strong preference for the root parasite *R. solani* rather than for mycoparasitic fungi such as *Trichoderma harzianum* **Reifai**, *Gliocladium virens* **Miller et al.** and *Laetisaria arvalis* **Burdsall**. Such collembolans preferences enhance the potential of biological control of mixed treatments (collembolans and mycoparasitic fungi) (Lartey et al. 1994).

Though greenhouse experiments have shown that fungivory has the potential to reduce colonisation by root parasites, open field systems offer a more complex scenario. The ample distribution of mycorrhizal associations in wild and cultivated plants (Harrison 1997) complicates the scenario for biological control of root parasites by using fungivorous collembolans. Just as collembolans have the potential to decrease root colonisation by parasites, collembolans can also affect mycorrhizal associations. Fpr instance, the fungivorous collembolan *Folsomia candida* **Willem** decreases mycorrhizal functionality between *Trifolium subterraneum* **L. cv. Mount Barker** and three arbuscular mycorrhizal fungi *Glomus calenodium* **(Nicol. & Gerd.) Trappe & Gerdeman**, *G. intraradices* **Schenck & Smith** *and G. invermaium* **Hall** (Larsen & Jakobsen 1996a). Fungivory on mycorrhizal fungi is not limited to collembolans and other taxa may affect plant-fungus mutualisms. The mycophagous amoebae *Saccamoeba* sp. and *Gephyramoeba* sp. reduce colonisation of pine roots by the ectomycorrhizal fungus *Rhizopogon luteolus* **Fr. & Nord.** (Chakrabotry et al. 1985).

2. 1. 3. Wood decomposers

Wood is a low quality resource due to extensive lignification, low contents of soluble sugars and mineral nutrients, and often high concentration of secondary compounds (e.g. tannins). Furthermore, wood is protected by bark which is suberised (i.e of a corky texture) and itself often contains secondary compounds such as tannins that may deter insect consumption (Swift & Boddy 1984). Only a limited number of specialised heterotrophs, mainly wood-rotting basidiomycetes (Swift & Boddy 1984) but also some ascomycetes, possess the necessary enzymatic repertoire for the primary exploitation of wood. Not surprisingly, insect colonisation of dead wood is generally preceded by primary decomposition by fungi.

A series of highly specialised associations has evolved between wood rotting fungi and insects. Wood wasps (Siricidae), bark and ambrosia beetles (Scolitydae and Platypodidae respectively) have mastered the propagation of their associated wood rotting fungi as a means by which they have indirect access to wood nutrients (Beaver 1989; Berryman 1989; Gilbertson 1984). Though, generally referred to as mutualistic associations, it is far from clear whether the "farming" behaviours of these insects confer any relative advantage to their associated fungi (Berryman 1989). The benefits that insects gain from their associations with fungi (food resource, conversion of tree metabolites into insect pheromones, widening of niche breadth by facilitating the exploitation of a large number of host tree species and host tree physiological conditions, stress alleviation by transformation of host tree secondary metabolites, etc.) are varied (Beaver 1989; Gilbertson 1984). On the other hand, the benefits on the fungal component are less diverse and understood, aside from the fact that in an ecological context, fungi associated with wood wasps, ambrosia and bark beetles may have the benefit of guaranteed propagation into competitor-free resources.

Most bark and ambrosia beetles are associated with fungi that are only known in their imperfect (anamorphic) state. This state refers to the lack of sexual reproduction and very diverse fungi are grouped based on this character into the subclass Deuteromycotina. The majority of fungi associated to bark and ambrosia beetles in which the sexual state is known belong to subclass Ascomycotina (see Baker 1963;

Batra 1967; Francke-Grosmann 1967; Kok 1979; Whitney 1982). Blue-stain fungi (*Ceratocystis*) are associated with bark beetles, but it is believed that many other genera are involved (Francke-Grosmann 1967). Ambrosia fungi appear to be more diverse. They include some species of *Ceratocystis*, (Francke-Grosmann 1967), yeast genera such as *Pichia* and *Hansenula* (Baker 1963; Bridges et al. 1984; Callaham & Shifrine 1960; Francke-Grosmann 1967; Gusteleva 1982; Whitney 1982), members of the hyphomycete genera *Fusarium*, *Cephalosporium* and *Ambrosiella*, and the filamentous hemiascomycete genus *Endomycopsis* (Beaver 1989).

All these fungi may not only have the benefit of effective dispersal (Beaver 1989) but selection of host trees by beetles may gain a positional advantage for their associated fungi, enabling them to become established where they would otherwise be rapidly out-competed by more aggressive primary decomposer fungi such as wood-rotting basidiomycetes. The dominance of ambrosia fungi in tunnels and chambers may be facilitated further by specific behaviours of inhabitant beetles (Beaver 1989), such as selective removal of fungal invaders or secretion of allelopathic chemicals.

Similar mutualistic benefits may occur in wood wasp-fungus associations. As far as is known, wood wasps are exclusively associated with fungi of the Stereaceae family (Gilbertson 1984) which are capable of independent living as members of the guild of primary decomposers (Baxter et al. 1995). There may, therefore, be scope for differential selection of certain genotypes of fungi by wood wasps to form partnerships and so gain the ecological benefits mentioned above. Whether these associations have an impact in ecological or evolutionary terms on fungal population or community structure is, however, an open question and more research is needed to address many other unanswered questions. For instance, what special characteristics (e.g. host tree preferences, growth rate, nutritive value, secondary metabolic production, etc.) are displayed by members of the Stereaceae family that facilitate their associations with wood wasps? How does intraspecific or interspecific variability affect these interactions? If variability has significant effects on the establishment of the interaction, is wood wasp-fungus association biased to specific genotypes or phenotypes of fungi?

A set of very poorly understood interactions between wood rotting fungi and fungivorous insects is that of Cecidomyidae fly larvae interacting with the mycelium of wood-rotting fungi in the sub-cortical layers of decomposing wood. Pioneering work on these interactions is currently being carried out at the University of Bath. Preliminary evidence shows that cecid larvae have preferences for certain species of fungi and therefore have the potential to affect community assemblages of their associated fungi. (C. Taylor unpublished).

Overall there is substantial information on the biology of wood-rotting fungus-insect associations. The emphasis of these studies has, however, been zoocentric and very little is know about the ecological and evolutionary consequences of these interactions on the fungal component.

2. 1. 4. Ants, termites and their fungus gardens

Highly specialised associations have emerged in ants (Attini) and termites (Macrotermitinae) that mastered farming of their associated fungi. These interactions have received recurrent attention (see Bass 1997; Bass & Cherrett 1996a; Bass & Cherrett 1996b; Cherrett et al 1989; Diniz et al 1998; Fisher et al 1996; Muller et al 1998; Muller & Wcislo 1998; North et al 1997; Pagnocca et al 1996a; Pagnocca 1996b; Wetterer 1998; Wood & Thomas 1988, among others) and so will only briefly be mentioned here.

Both Attini and Macrotermitinae rely on the metabolic capabilities of their associated fungi to process plant material and deal with potential toxic compounds (Cherrett et al. 1989; Wood & Thomas 1989). As a consequence of their associations with fungi macrotermites are major contributors to plant detritus decomposition in tropical Africa. For instance, macrotermites consume 25% of the combined production of wood, grass and leaf litter in Southern Guinea whereas other termites only consume 7.5% (Wood & Thomas 1989). The Attini includes some of the most polyphagous taxa in the world but, it is in fact the associate fungi which metabolise the large diversity of plant tissues collected by ants. Arms races in these interactions are, therefore, likely to involve plants, fungi and ants since both the associated fungi and ants have the potential to respond to plant-defences (see Lapointe et al 1996). The impact of leaf-cutter ants is better know for their effects on tropical crops; annual losses to ants foraging activities are for many million dollars (Cherrett et al. 1989). The impact of Attini on natural vegetation is less clear and has been subjected to fewer studies, but some indications show that these ants may harvest 17% of the total leaf production in tropical forest (Cherrett et al. 1989).

Like those interactions between wood-rotting fungi and insects, benefits to the associated fungi of ants and termites are far from clear but in ecological terms may have similar advantages to those mentioned above.

3. Fungivory on fruiting bodies

Most basidiomycetes and some ascomycetes produce large, ordered hyphal aggregates (sporophores or fruiting bodies) specialised in spore production and dispersion. Sporophores are not only relatively large structures with a high density of hyphae but they are rich in nutrients compared to the mycelium, or substrate where the mycelium develops. It is known that a substantial translocation of nutrients takes place from the mycelium to the sporophores (Wessels 1994). For instance, it has been estimated for *Fomitopsis pinicola* **(Sow. ex Fr.) Karst.** that to supply a single fruiting body and its spores, for a single year, would require the translocation of all nitrogen stored in 0.2 m^3 of wood (Merrill & Cowling 1966).

Since sporophores are high-nutrient packs in relation to the substratum where the mycelium develops, consumption of sporophores by heterotrophic taxa is a strategy amply distributed (Hanski 1989). Sporophores are fully determined structures where visible effects of fungivory can readily be quantified. There are, however, no basic accounts on the frequency, intensity and distribution of fungivory on sporophores (Guevara unpublished).

Studies with fungivorous insects can be divided into two very distinctive categories. On the one hand, fruiting body (mainly Agaricales)-fungivore associations have been extensively used as model systems for various aspects of population and community biology, e.g. population structure (Charlesworth & Shorrocks 1980; Jaenike 1977;

Jaenike 1986; Jaenike 1988; Worthen 1989); genetic diversity (Ashe 1984; Jaenike 1986; Jaenike 1989 Whitlock 1992); competition (Grimaldi 1985; Grimaldi & Jaenike 1984; Shorrocks 1991; Shorrocks & Bingley 1994); predation (Worthen 1989; Worthen & Moore 1991; Worthen et al. 1995) and parasitism (Jaenike 1985; Montague & Jaenike 1985). On the other hand, fruiting bodies have been seen as novel sites for records of insects (Benick 1952; Rehfous 1955; Weiss 1920; Weiss & West 1920; Buxton & Barnes 1953; Buxton 1954; Roman 1970; Paviour-Smith 1960; Lawrence 1977; Hingley 1971; Crowson 1984; Buxton 1955).

Few studies have attempted to disentangle the fungal characteristics that may correlate with fungivorous preferences on fruiting bodies (Bruns 1984). Field and experimental evidence on this issue are presented in Chapter II.

It has been suggested that fungivory by invertebrates on sporophores is unlikely to have a significant effect on the reproductive potential of fungi (Courtney et al. 1990; Hanski 1989). This assertion is, however, premature. Given the zoocentric emphasis of studies with fungivorous invertebrates, such studies have concentrated their attention on dysfunctional and senescent sporophores (in which fungivorous populations are most apparent) rather than assessing consumption and its consequences on functional sporophores. It has been shown that fruiting bodies of basidiomycetes endure levels of consumption (10%-25%) equivalent to those commonly caused by herbivores on plants (Guevara, unpublished). Fungivory on sporophores may, therefore, have negative effects on the reproductive potential of fungi analogous to those observed in plant-herbivore interactions. This issue is presented in Chapter IV.

3. 1. Wood rotting fungi and ciid beetles

Ciid beetles (Cucujoidae: Ciidae) are the most common, if not the most conspicuous, arthropods inhabiting fruiting bodies of Aphyllophorales fungi (Lawrence 1973). Fruiting bodies of Aphyllophorales are relatively large, long lasting and vary in consistency from fleshy to woody or leathery (Webster 1980). In this habitat, ciid beetles are the best represented family and includes many more species than other common taxa such as tenebrionid beetles or tineid moths (Lawrence 1973).

Though the occurrence on and preferences of ciid beetles for Aphyllophorales fruiting bodies have long been realised (e.g. Weiss 1920; Weiss & West 1920; Donisthorpe 1935) there is little ecological information on these interactions. Studies with ciid beetles are almost entirely restricted to general surveys of insects inhabiting fungal fruiting bodies (Benick 1952; Rehfous 1955; Roman 1970; Donisthorpe 1935; Park 1931; Chagnon 1936; Donisthorpe 1931; Minch 1952; Pielou & Verma 1968). Some studies have concentrated on ciid beetles and their host preferences (Paviour-Smith 1960; Lawrence 1973). but in general fungi are considered little else than the 'food resource' or habitat. The dynamic roles of fungi in fungus-fungivore associations are illustrated in Chapter II and Chapter III and effects of fungivory on the reproductive potential of fungi are illustrated in Chapter IV.

4. Corollary

The study of fungivory has been approached from two distinctive perspectives. On the one hand, scattered studies of fungivory at the mycelium level have a fungocentric emphasis whereas, on the other hand, studies of fungivory on fully determined structures (fruiting bodies) are consumer biased.

In spite of the primary role of wood-rotting fungi in the processes of wood decomposition, very little is known of the effects that fungivores have on wood-rotting fungi. Effects of fungivory may not only have consequences at the population and community level of wood-rotting fungi but the dynamics of wood decomposition may be affected also.

Ciid beetles and their associated wood-rotting fungi offer a relative simple system in which to study the dynamics of fungus-fungivore interactions from an integrational perspective in which effects on both components can be assessed. Some advantages of this system are that wood-rotting fungi are common in local woodlands, wood-rotting fungi are easy to follow over time in field studies and some species are relatively easy to grow and propagate in the laboratory. Most ciid beetles are strict fungivores and both adults and larvae are entirely dependent on brackets of wood-rotting fungi.

CHAPTER II

CIID BEETLES BEHAVIOURAL RESPONSES TO HOST AND NON-HOST ODOUR COMPOUNDS

1. Summary

Most ciid beetles are strict fungivores specialised on fruiting bodies of wood-rotting fungi. Mechanisms of host selectivity are poorly understood but there is evidence that colonisation of fruiting bodies by ciid beetles is mediated by fungal odours. In this study the field distribution of ciid beetles, their behavioural responses to host and non-host odours in wind tunnel experiments and the odour profiles of host fungi were analysed. Field data showed that ciid beetles have preferences for their host fungi. Ciid beetles exhibited differential behavioural responses to odour compounds of host and non-host fungi in wind tunnel experiments. Host fungi closely associated with one or two species of ciid beetle showed characteristic odour profiles with a series of compounds not found in any of the other species analysed. Differences in odour composition among potential hosts suggest that odour compounds may play an important role in the evolution of host preferences in ciid beetles. Such processes are analogous to those observed in other interactions such as plant-herbivore, host-parasitoid and prey-predator associations.

2. Introduction

Most species of ciid beetles (Cucujoidea: Ciidae) are strictly fungivorous dependent on fruiting bodies of wood-rotting fungi (Lawrence 1973; Paviour-Smith 1960), though few species are more directly associated with dead wood, e.g. *Cis pygmaeus* **Marsham** in oak branches (Freude et al. 1967). There is a wide range of variability in the host preferences of the fungivorous ciids, with some species breeding in a large number of host species, e.g. *Cis bilamellatus* **Wood** (Paviour-Smith 1960); *Cis americanus* **Mannerheim** (Lawrence 1973) whereas other species are restricted to a small number of host species, e.g. *Cis boleti* **Scopoli**, *Octotemnus glabriculus* **Gyllenhal** *Cis nitidus* **Fabricius** (Benick 1952; Paviour-Smith 1960; Roman 1970); *Ceracis similis* **Ziegler** *Octotemnus levis* **Casey** (Lawrence 1973). The processes or factors that determine host preferences in ciid beetles are, however, unclear. Host hyphal structure (based on the different types of hyphae present in the fruiting bodies, see Cunningham 1947) has been proposed as the fungal characteristic that mediates host preferences of ciid beetles in Wytham Wood near Oxford, England (Paviour-Smith 1960). Though this hypothesis received further empirical support from a study in Southern France (Roman 1970), its validity has since been questioned, since one of the most common host species, *Ganoderma [applanatum] adspersum* **(Schulz) Donk**, was wrongly characterised by Paviour-Smith as having a dimitic hyphal system (brackets with two types of hyphae only:: generative and binding or structural hyphae), when in fact this species is characterised by a trimitic hyphal structure (brackets with three types of hyphae: generative, binding and skeletal hyphae). Being the trimitic structure charateristic of the alternative preference group in Paviour-Smith's scheme (Lawrence 1973). An alternative scheme with preference groups equivalent to those of Paviour-Smith (1960) but with a higher degree of complexity in the microstructural characteristics that delimit each group, was proposed instead by

Lawrence (1973).

Though it is plausible that the microstructural characteristics (consistency) of fruiting bodies may indeed restrict the utilisation of a number of potential host species by ciid beetles, this would only be possible after a colonising beetle had already landed on a potential host. The question is, therefore, how do ciid beetles locate their potential host species? The involvement of chemical cues in host or prey location is amply documented in analogous associations such as those between plants and herbivores (Gotoh et al. 1993; Kouloussis & Katsoyannos 1994; Mathieu et al. 1997; Zhang & McEvoy 1995), parasitoids and their hosts (Janssen et al. 1995a; Janssen et al. 1995b; Vanbaaren & Nenon 1996) and prey and predators (Hattingh & Samways 1995; Koveos et al. 1995; Downes & Shine 1998). There is also evidence of fungal odours mediating the preferences of mycelium-grazing collembolans (Hedlund et al. 1995). The hypothesis that fungal odours may be involved in host colonisation by ciid beetles was dismissed by Paviour-Smith (1960), who argued that ciid beetles exploit only "dead" and weathered fruiting bodies which (it was argued) are unlikely to release characteristic odour compounds. Lawrence (1973), on the other hand, suggested that host odours may play an important role at least in the initial colonisation of fruiting bodies by ciid beetles, and that thereafter further colonisation may be mediated by pheromones released by the beetles themselves.

The first experimental evidence that ciid beetles' colonisation of host fungi is mediated by fungal odours was obtained by Jonsson and co-workers (Jonsson et al. 1997). Based on field experiments they concluded that *Cis glabratus* **Mellie** relies only on fungal odours during colonisation. Furthermore, they established that *C. glabratus* only responds to odour compounds of their preferred host species (*Fomitopsis pinicola* **(Sow. ex Fr.) Karst**), and that in contrast with *Dorcatma robusta* **Strand** (Anobiidae), there is no evidence for the use of aggregation or sexual pheromones in *C. glabratus*.

In summary, there is variability among ciid beetle species in the range and specific identity of preferred host species (Lawrence 1973; Paviour-Smith 1960). There is also evidence that host colonisation may be mediated by host odours but not pheromones (Jonsson et al. 1997). These facts together suggest the existence of substantial variability in odour compounds among potential host species and differential behavioural responses of ciid beetles to odour compounds of host and non-host species.

In this study, I investigated the field distribution of ciid beetles on potential host species, and whether there is variability in odour compounds among potential host species. Experiments were also done to investigate whether ciid beetles exhibit differential behavioural responses when exposed to odours from host and non-host species under laboratory conditions, and the possible correlation of these behavioural responses with the field distribution was examined.

3. Materials and methods

3. 1. Field distribution

The distribution of ciid beetles among potential host species was studied in Bathwick Wood (ca. 2.5 ha), a deciduous woodland near Bath, England (Fig. 2.1). The study site was visited every 3 weeks from March 1995 to February 1997, on each visit, fallen trees, logs and stumps were checked for fruiting bodies of wood-rotting fungi. Samples from each

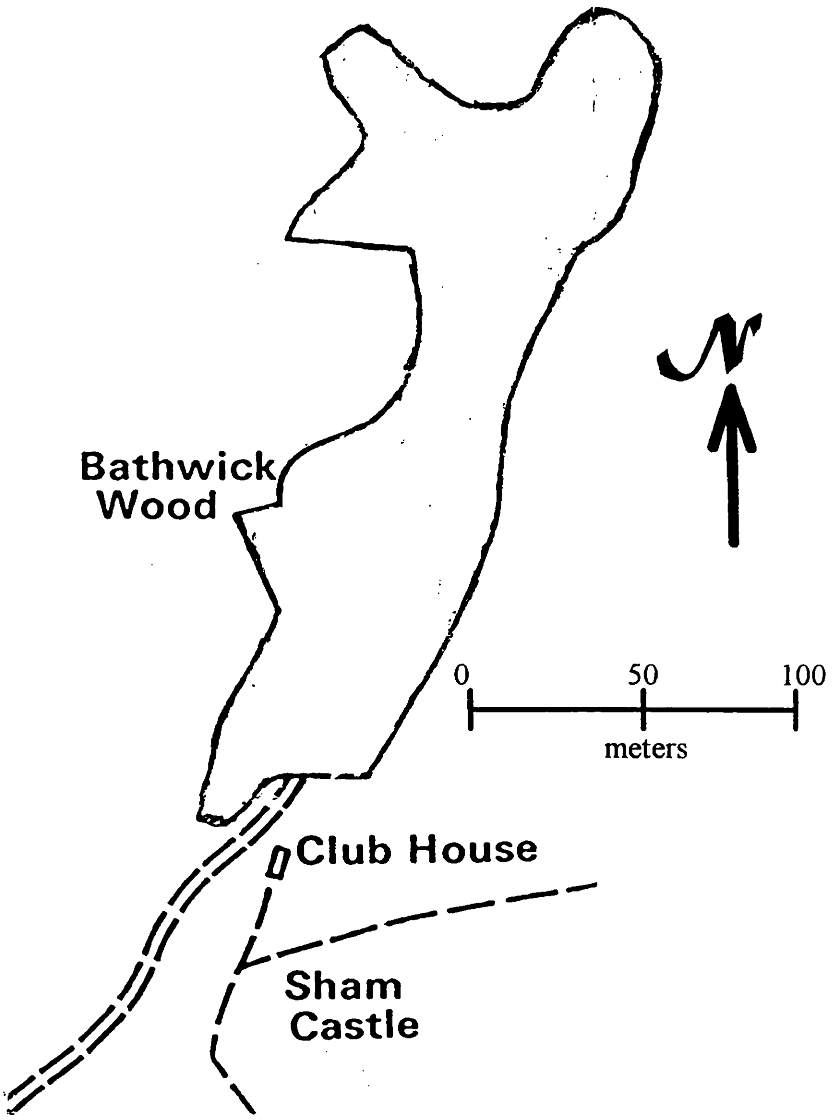

Figure 2.1 Bathwick Wood near Bath

genet (a cluster of fruiting bodies of the same genetic origin) were collected, dissected and ciid beetles counted and sorted by species.

3. 2. Extraction of odour compounds

Odour compounds of host fungi were collected by steam distillation. One-hundres and fifty grams of fresh and beetle-free brackets were crushed in liquid nitrogen and gently boiled in 200 ml of distilled water for 45 minutes while the volatile fraction was collected in a solvent trap containing 7 ml of dichloromethane placed in an ice bath to minimise evaporation. Fungal odour solutions collected in the solvent trap were stored at -20° C until needed for gas chromatography-mass spectrophotometry analysis (GC-MS) or behavioural experiments.

GC-MS analysis was performed in a Hewlett Packard 59970C MSD apparatus fitted with a DB5 column of 0.25 μm of internal diameter and 30 m long. The carrier gas was helium at a flow rate of 1 ml min^{-1} with initial oven temperature of 50° C increasing at a rate of 10° C per minute to a maximum temperature of 270° C.

3. 3. Orientation behaviour

The orientation behaviour of *O. glabriculus*, *C. boleti*, *C. nitidus* and *C. bilamellatus* toward odour compounds of potential host species was investigated in a wind tunnel. This was made entirely of glass (Fig. 2.2); air-flow was generated by placing the apparatus in the air intake of a laboratory fume cupboard. The experimental design was similar to that of Zhang and McEvoy (Zhang & McEvoy 1995) and included a circular experimental arena

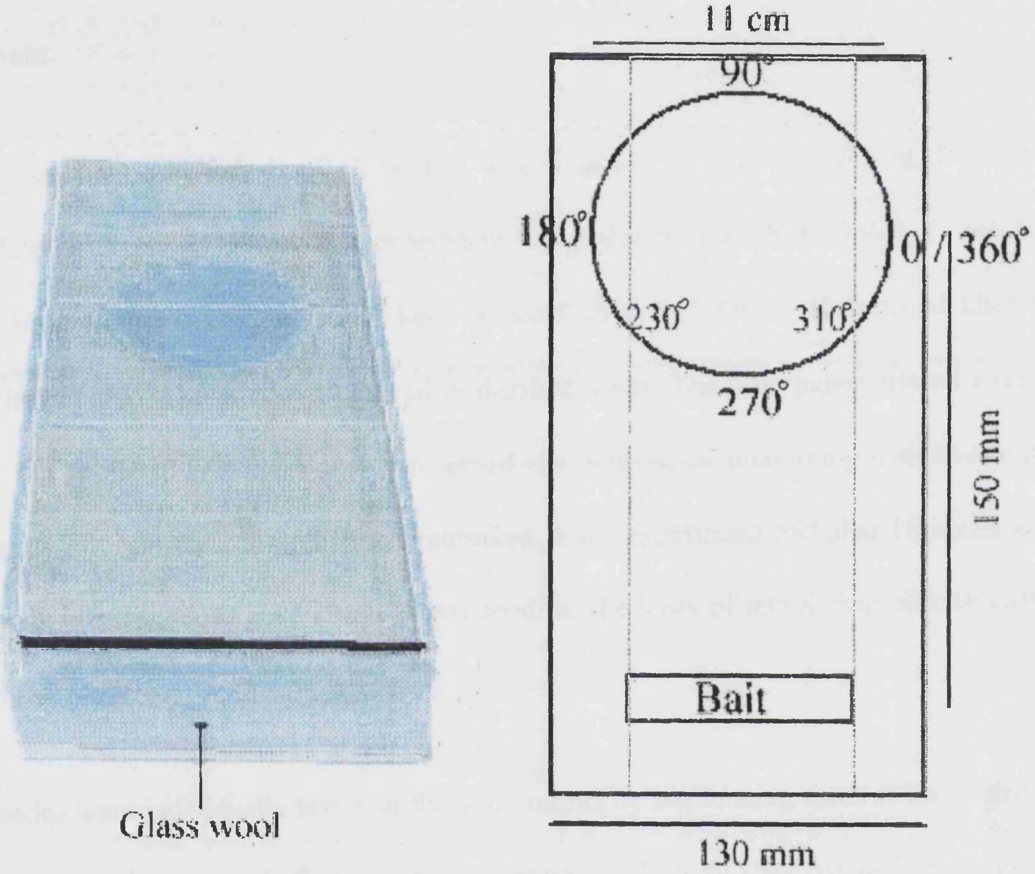

Figure 2.2 Wind tunnel

(110 mm in diameter) and a bait 150 mm up-wind. The bait consisted of pieces of fresh and beetle-free fruiting bodies or pieces of filter paper (60 mm x 10 mm) wetted with 200 µl of odour solution. When pieces of fruiting bodies were used, blank-baits served as controls whereas with odour solutions controls consisted of filter paper wetted with 200 µl of the solvent.

The orientation behaviour of 20 beetles was recorded for each experiment. Beetles were isolated and starved before each experiment (*O. glabriculus* 4-5 h; *C. boleti, C. nitidus* and *C. bilamellatus* overnight) being kept on small pieces (5 mm x 10 mm) of filter paper (Whatman No. 1) wetted with 200 µl of distilled water. The filter paper offered a substrate for the beetle to rest upon and also served the purpose of minimising disturbance during manipulation in the course of the experiment. Each experiment included 10 males and ten female beetles whose gender was determined on the basis of morphological characteristics (Fig. 2.3)

Beetles were individually tested in the wind tunnel by introducing them at the centre of the experimental arena and allowing them to move freely until they reached the edge of the experimental arena (or until they failed to do so in 10 minutes). The position of those beetles that reached the edge of the experimental arena was marked, the beetle removed and a fresh beetle then introduced. Pilot experiments showed that ciid beetles do not follow paths previously walked by other individuals, therefore, it was not necessary to use a fresh piece of filter paper for each beetle tested.

Circular statistic procedures (Batschelet 1981) were used to analyse whether ciid beetles were significantly attracted toward fungal volatile components. In the present study the

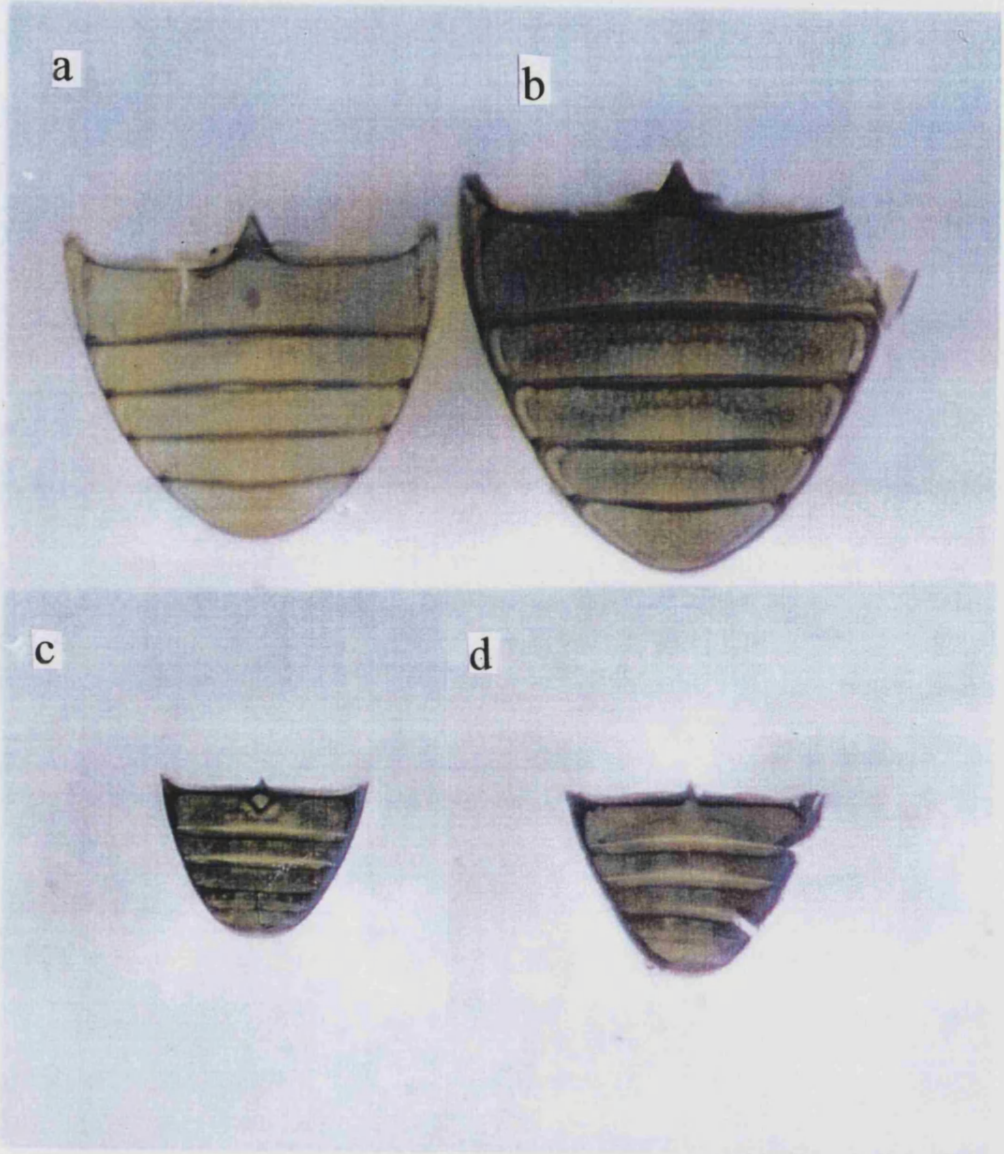

Figure 2.3 Sexual characteristics of ciid beetles on the first abdominal segment in ventral view. a) *Cis boleti* showing the circular fovea characteristic of *Cis* males and b) *C. boleti* female. c) *Octotemnus glabriculus* showing the triangular flap that projects over the first abdominal segment in males. d) *O. glabriculus* female

reference point (0° / 360°) was arbitrarily fixed at the positive end of the *X* axis of an imaginary Cartesian quadrant with origin at the centre of the experimental arena and the positive *Y* axis pointing down-wind; the angles were measured in counter-clock-wise direction (see Fig 2.2).

The Mardian-Watson-Wheeler test (Batschelet 1981 p. 104) was employed to investigate whether the orientation responses of each beetle species to the different baits differ between them. The null hypothesis for this test is that the observed sample distributions are derived from the same population and, therefore, there are not significant differences between them. A visual exploration of the plots of the distributions and the contribution of each sample towards the value of the statistic W were use to establish the nature of any observed difference. The Mardian-Watson-Wheeler test is a nonparametric analysis and the statistic W for the test is distributed as χ^2 with 2(k-1) degrees of freedom (Batschelet 1981 p. 104) where k is equal to the number of samples in the analysis.

4. Results

4. 1. Field distribution

A total of 277 samples of fruiting bodies of wood rotting fungi, including eight common and apparent potential host species for ciid beetles, were collected and dissected in the laboratory. *Coriolus versicolor* **(L. ex Fr.) Quél.** was the most commonly collected fungus with 74 records followed by *Hirneola auricula-judae* **(St. Amans) Bark.** (35 records), *Polyporus squamosus* **Huds. ex Fr.** (28 records), *Bjerkandera adusta* **(Willd. ex Fr.) Karst.** (27 records), *Pseudotrametes gibbosa* **(Pers. ex Pers.) Bond. & Sing.** (23 records), *Auricularia mesenterica* **(Dicks)**

Pers. (13 records), *Ganoderma adspersum* **[Schulz] Donk** (11 records) and *Piptoporus betulinus* **[Bull. ex Fr] Karst.** (6 records). The remaining 59 records came from fungi which were less commonly collected at the site with five or less records each (*Bjerkandera fumosa* **[Pers. ex Fr] Karst.**; *Stereum hirsutum* **[Willd. ex Fr] S. F.**; *Stereum rugosum* **[Pers. ex Fr] Fr.**; *Oxyporus populinus* **[Schum. ex Fr] Donk**; *Lycoperdon pyriforme* **Schaeff. ex Pers.**; *Daedaleopsis confragosa* **[Bolt. ex Fr] Schroet.**; *Flammulina velutipes* **[Curt. ex Fr] Karst.** and *Pleurotus* spp.).

The distribution of ciid beetles on potential host species was significantly different from a random distribution (Table 2.1). *Octotemnus glabriculus* and *C. boleti* showed strong preferences for *C. versicolor* and *P. gibbosa* fruiting bodies. *Cis nitidus* appeared to have a preference for *G. adspersum*. *Cis bilamellatus* did not show preferences for particular host species since it was found in large numbers in four of the common host species. Insufficient records of *Sulcacis affinis* **Gyllenhal** were available to allow any conclusion about its host preferences.

4. 2. Odour compounds in host fungi

GC-MS analysis revealed significant qualitative and quantitative variability of putative odour compounds among host fungi (Fig. 2.4). The peak eluted with a retention time of 7.558 minutes,identified as 1-octene-3-ol (Fig. 2.5), was common to all samples and was the only compound detected in *P. betulinus*. *Coriolus versicolor* and *G. adspersum* contained diverse odour compounds, many of which were detected in none of the other species analysed. Peaks with retention times of 15.546 minutes and 15.896 minutes were unique to *C. versicolor* and identified from the mass spectrometer data base as the sesquiterpenoids ar-curcumene (Fig. 2.6) and α-cedrene (Fig. 2.7) respectively. The identity of all other peaks could not be established.

Table 2.1 Frequency distribution of ciid beetles on potential host species. The table shows the number of records for each fungus and the number of records on which beetles were found. The G-test for independence (G=186.1; P<0.001; d.f.=24) was performed considering only those host species where at least 1 record of ciid beetle was found and frequencies of zero were effectively treated as 0.001 (Everitt 1977)

Fungus	Records	*O. glabriculus*	*C. boleti*	*C. bilamellatus*	*C. nitidus*	*S. affinis*
C. versicolor	74	64	49	2	0	0
P. gibbosa	23	13	17	0	0	4
B. adusta	27	0	2	7	0	1
P. betulinus	6	0	0	5	0	0
G. adspersum	11	0	0	0	9	0
P. squamosus	28	0	0	3	3	0
H. auricula-judae	35	0	0	0	2	0
Others	73	0	0	0	0	0

4. 3. Orientation behaviour

Ciid beetles showed differential behavioural responses when exposed to pieces of fruiting bodies of potential host species in wind tunnel experiments (Fig. 2.8 and Table 2.2).

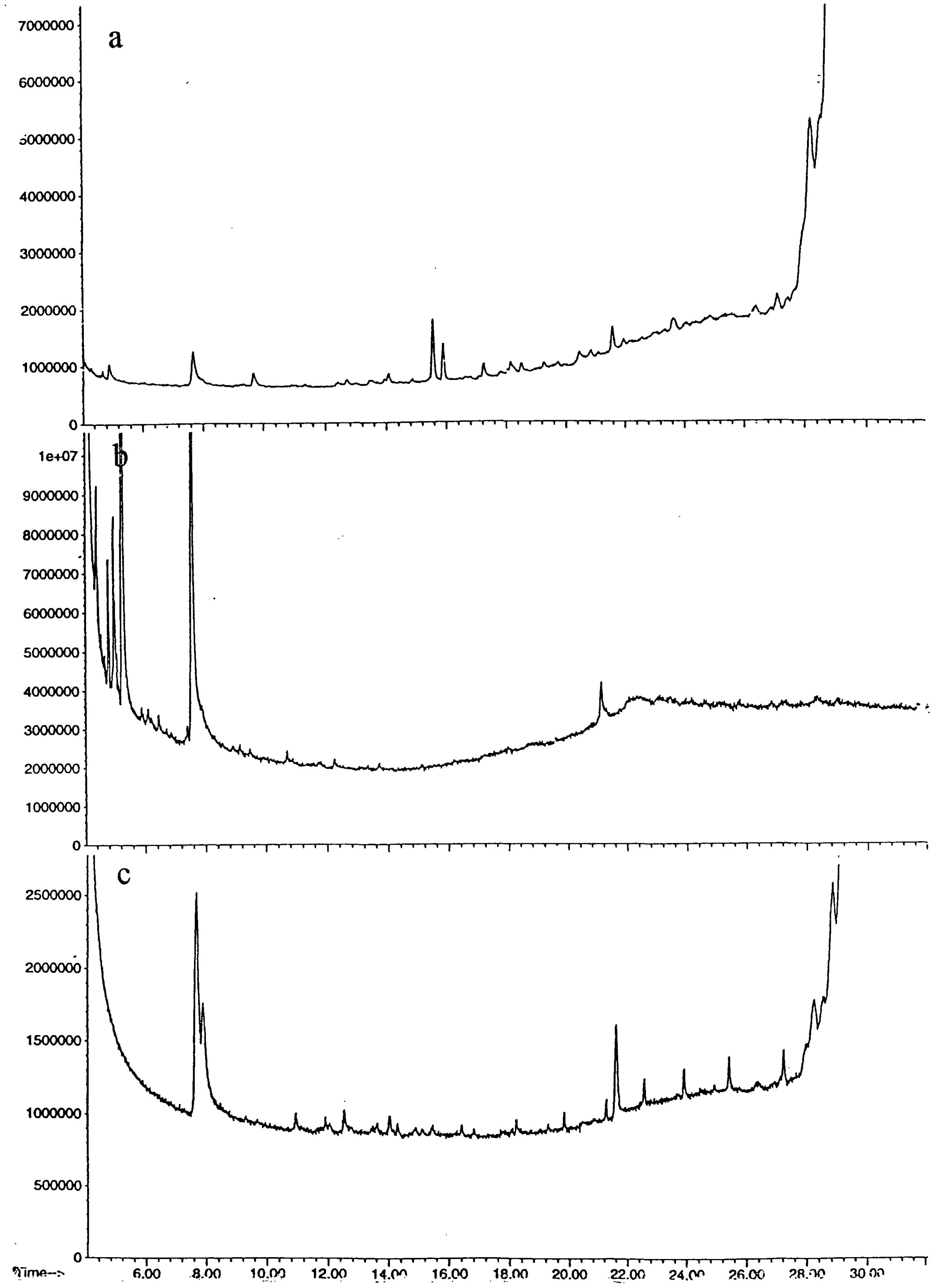

Figure 2.4 Chromatograms of odour compounds of a) *Coriolus versicolor*, b) *Ganoderma adspersum* and c) *Piptoporus betulinus*

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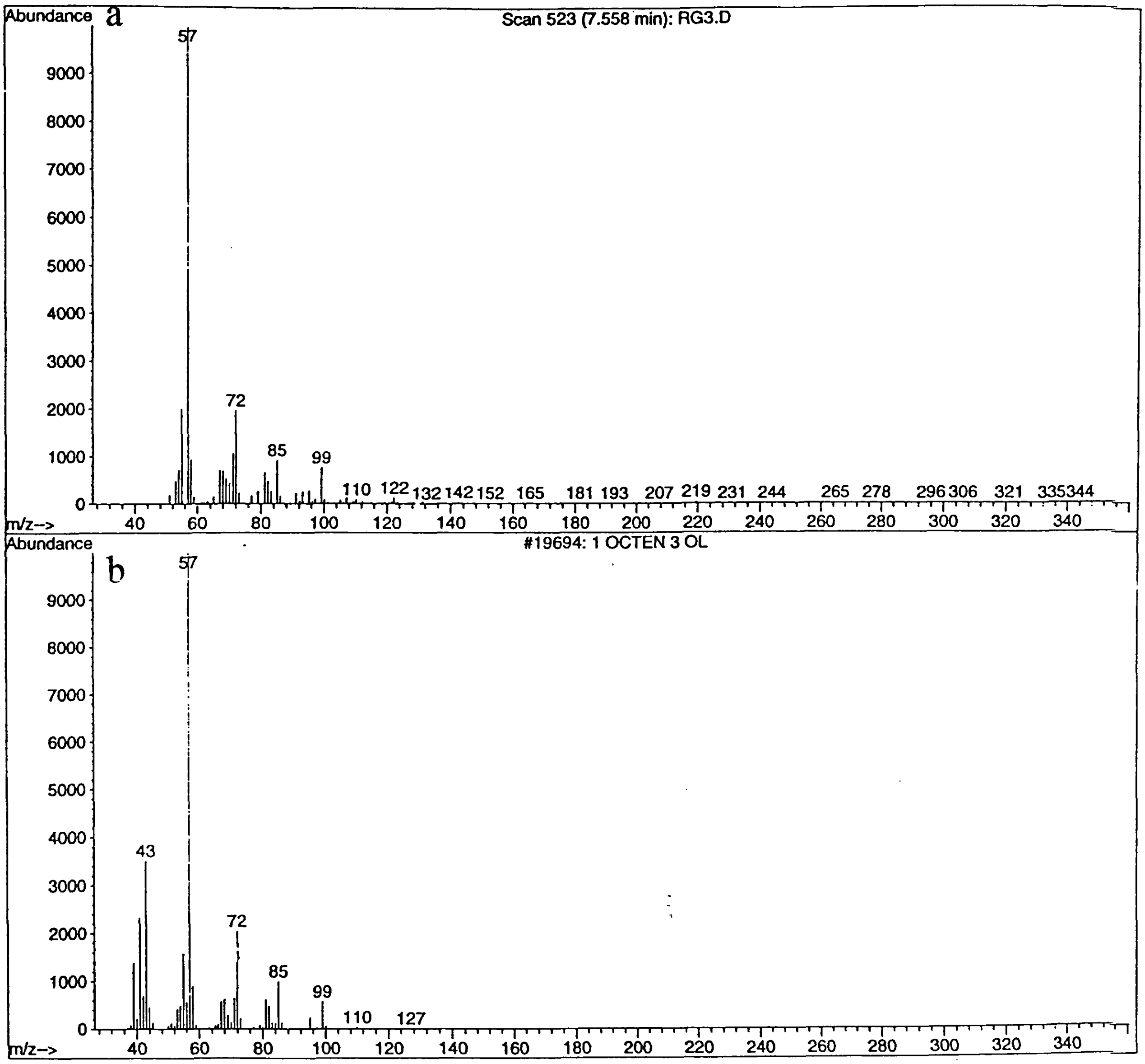

Figure 2.5 a) Mass spectrum of peak eluted with retention time of 7.558 minutes in all analysed samples. b) Library mass spectrum of 1-octen-3-ol

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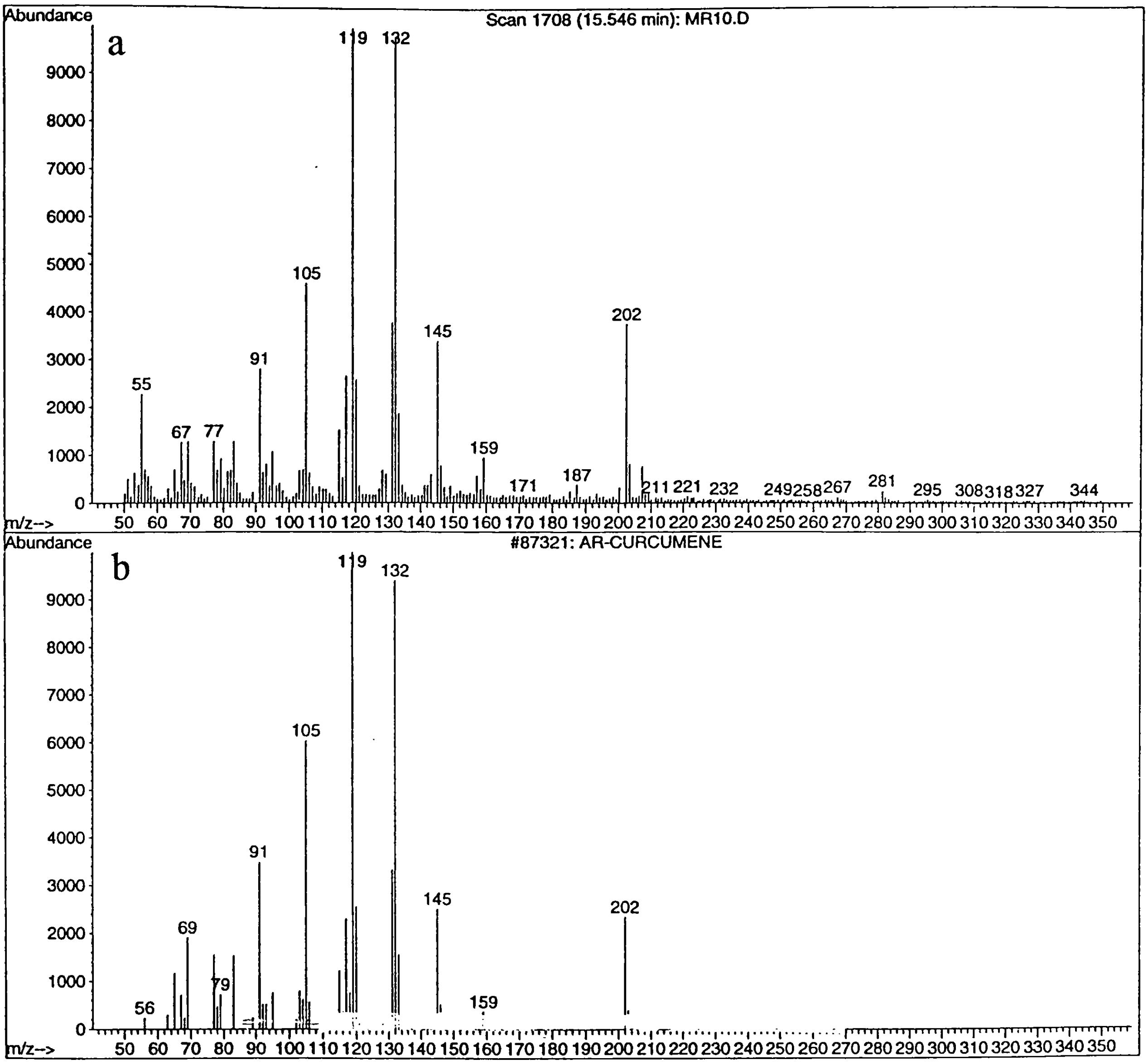

Figure 2.6 a) Mass spectrum of peak eluted with retention time of 15.546 minutes from *Coriolus versicolor* odour solution. b) Library mass spectrum of ar-curcumene

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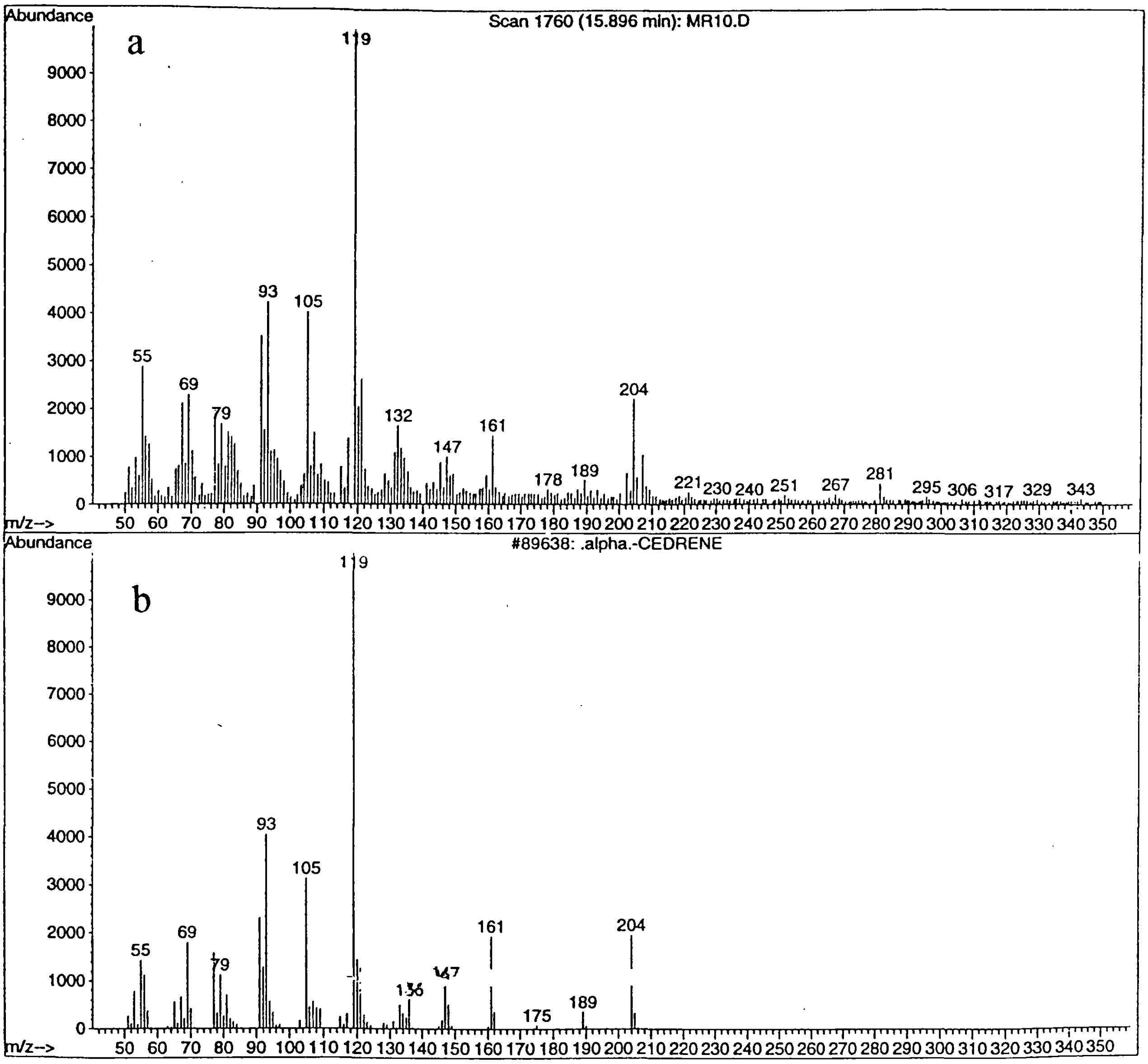

Figure 2.7 a) Mass spectrum of peak eluted with retention time of 15.896 minutes from *Coriolus versicolor* odour solution. b) Library mass spectrum of α-cedrene

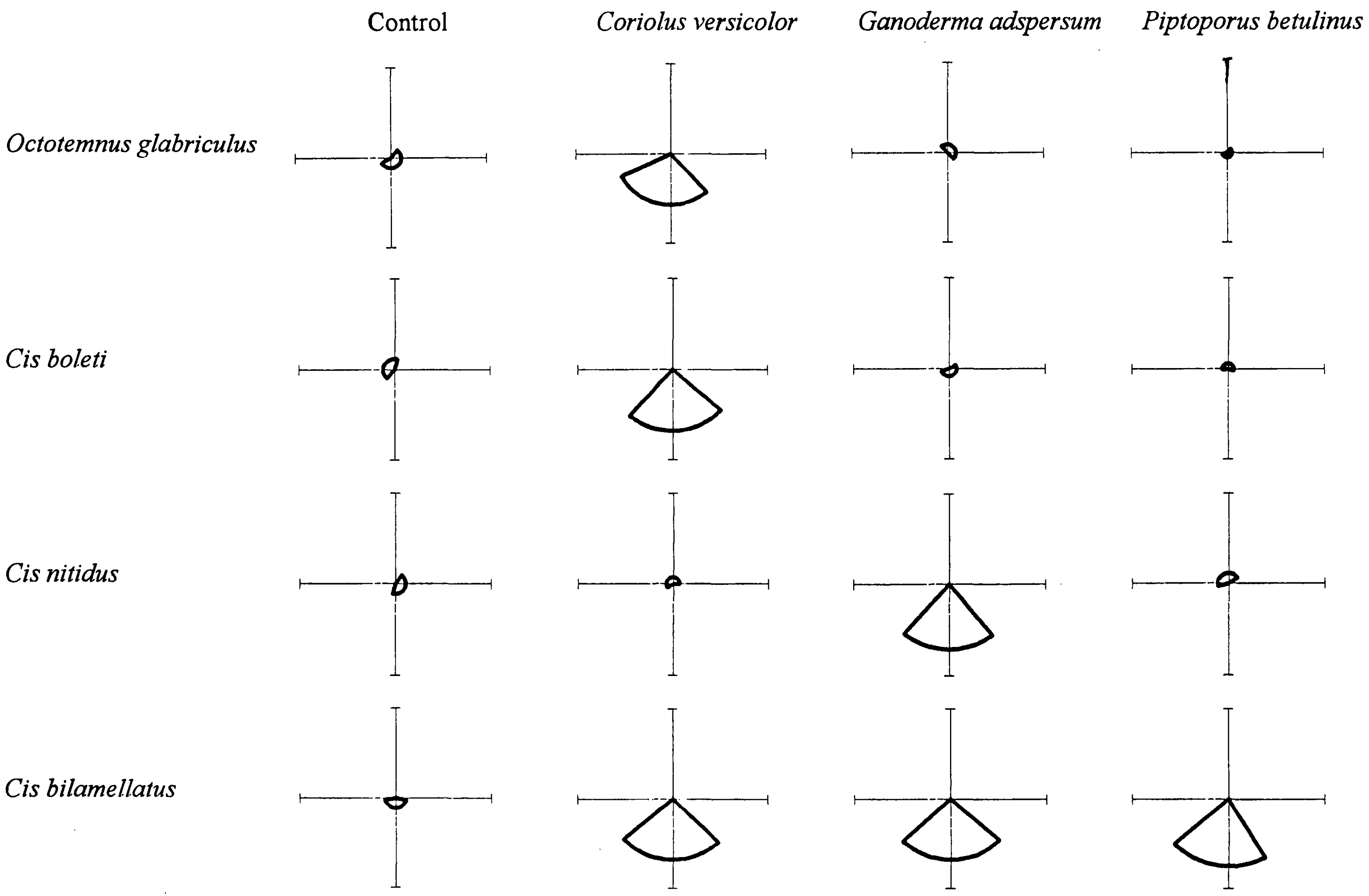

Figure 2.8 Ciid beetles behavioural responses to fruiting body sections.

Table 2.2. Numerical summary for the behavioural responses of ciid beetles to fungal fruit bodies. Φ= mean orientation response; S= standard deviation and r= strength of the response.

		C. bilamellatus	*C. nitidus*	*C. boleti*	*O. glabriculus*
Blank	Φ	267°	336°	153°	313°
	S	80°	79°	77°	100°
	r	0.11	0.11	0.12	0.06
C. versicolor	Φ	268°	107°	274°	259°
	S	47°	98°	45°	53°
	r	0.68	0.07	0.68	0.57
G. adspersum	Φ	271°	269°	296°	42°
	S	47°	40°	96°	89°
	r	0.68	0.71	0.08	0.09
P. betulinus	Φ	261°	115°	85°	305°
	S	39°	79°	101°	104°
	r	0.75	0.11	0.06	0.05

The Mardian-Watson-Wheeler test showed significant differences between the treatments for the four beetle species investigated (Table 2.3). The nature of the differences varied with the beetle species. It can be interpreted from Table 2.3 and Figure 2.8 that *Octotemnus glabriculus* and *C. boleti* were only attracted to *C. versicolor* fruit bodies whereas *C. nitidus* was only attracted to *G. adspersum*. *Cis bilamellatus* was attracted to all three fungi but not to the control.

Table 2.3 Summary for the Madian-Watson-Wheeler test for each beetle species exposed to fruit bodies of wood-rotting fungi. The table shows the values of $2(R^2/N)$ which are the components of the W statistic which is distributed as χ^2 with 2(k-1) degrees of freedom where k is equal to the number of samples analysed (Batschelet 1981 p.), For k=4 the critical values are $\alpha_{0.01}^{**}=16.8$ and $\alpha_{0.001}^{***}=22.5$. The highlighted values are those with the higher contribution towards the value of W in each test.

	O. glabriculus	*C. boleti*	*C. nitidus*	*C. bilamellatus*
Control	1.85	2.65	2.35	**22.47**
Coriolus versicolor	**10.86**	**12.91**	1.11	2.69
Ganoderma adspersum	2.87	1.73	**15.72**	1.87
Piptoporus betulinus	1.28	0.69	2.30	2.28
W	16.86^{**}	17.98^{**}	21.48^{**}	29.31^{***}

Behavioural responses observed when beetles were exposed to odour extracts from the solvent traps (Fig. 2.9, Table 2.4 and Table 2.5) were similar to and consistent with those observed when beetles where exposed to pieces of fruiting bodies.

4. 3. 1. Responses to different developmental stages of *Coriolus versicolor*

Field data showed that *O. glabriculus* and *C. boleti* are closely associated with brackets of *C. versicolor* and *P. gibbosa* (see section 4.1) and make differential use of *C. versicolor* by exploiting different developmental stages of the brackets (see Chapter III). *Octotemnus glabriculus* mainly exploits young brackets whereas *C. boleti* is dominant in mature brackets. Correspondingly, *O. glabriculus* and *C. boleti* responded differentially to odour compounds from young and mature brackets (Fig. 2.10, Table 2.6 and Table 2.7). *Octotemnus glabriculus* was attracted to both young and mature brackets whereas *C. boleti* was only attracted to mature ones. Neither of these beetles was attracted to the control [hazel wood (*Corylus avellana* L) colonised with mycelium of *C. versicolor* but lacking fruit bodies].

5. Discussion

Field records showed that ciid beetles are not randomly distributed among potential host species. The preferences of ciids for fungal hosts observed in the present study closely resemble those reported in previous studies in England (Paviour-Smith 1960), and in mainland Europe (Benick 1952; Rehfous 1955; Roman 1970). *Octotemnus glabriculus, C. boleti and C. nitidus* all appeared to have a restricted host range, whereas *C. bilamellatus*

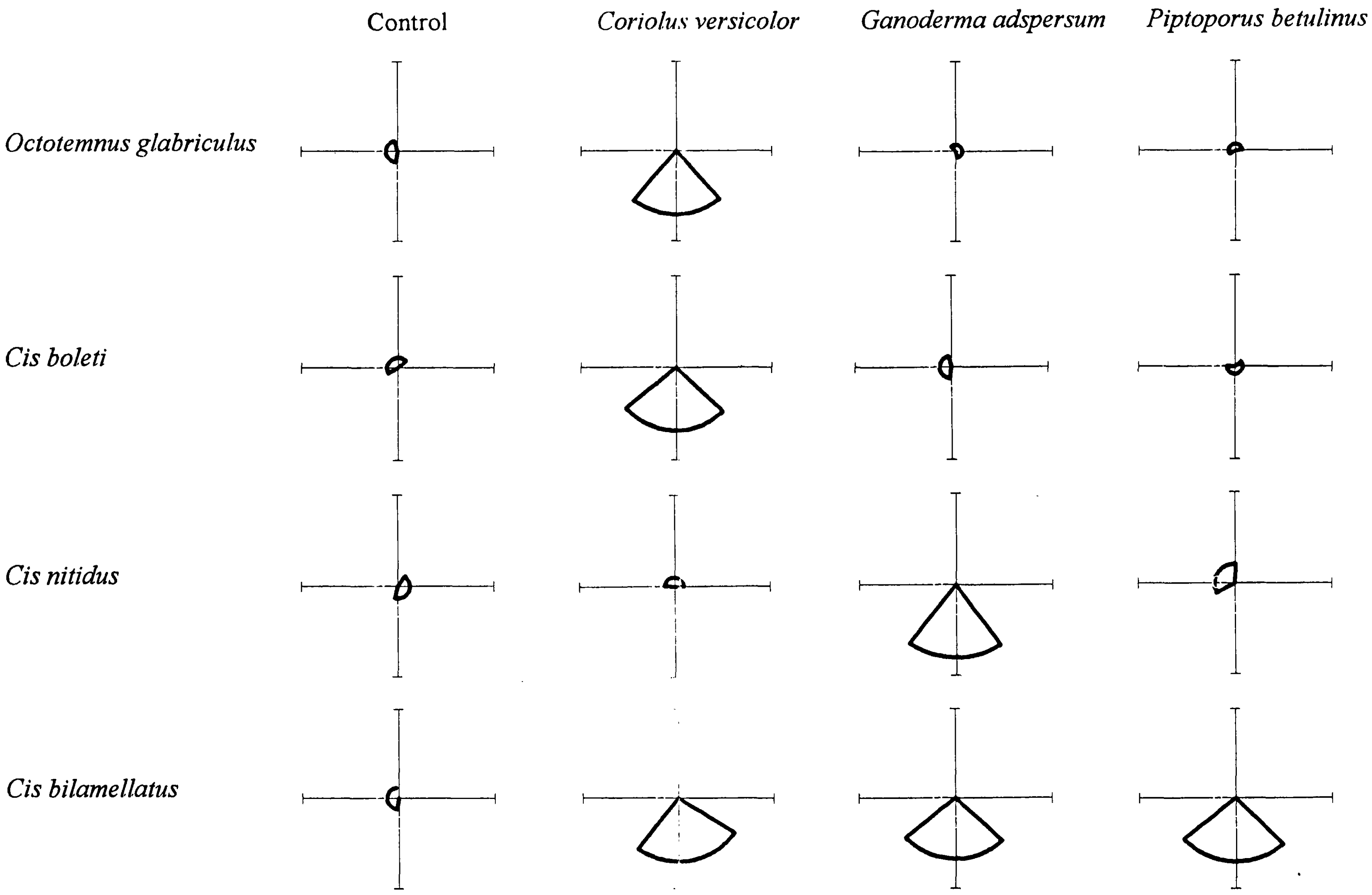

Figure 2.9 Ciid beetles behavioural responses to odour solutions.

Table 2.4. Numerical summary for the behavioural responses of ciid beetles to odour solutions. Φ= mean orientation response; S= standard deviation and r= strength of the response.

		C. bilamellatus	*C. nitidus*	*C. boleti*	*O. glabriculus*
Solvent	Φ	179°	332°	122°	180°
	S	76°	75°	81°	75°
	r	0.12	0.13	0.11	0.12
C. versicolor	Φ	280°	85°	274°	269°
	S	44°	84°	45°	38°
	r	0.70	0.10	0.68	0.70
G. adspersum	Φ	268°	267°	180°	21°
	S	48°	34°	76°	99°
	r	0.67	0.80	0.12	0.07
P. betulinus	Φ	264°	146°	281°	104°
	S	44°	57°	103°	99°
	r	0.70	0.21	0.08	0.07

Table 2.5 Summary for the Madian-Watson-Wheeler test for each beetle species exposed to odour solutions of wood-rotting fungi. The table shows the values of $2(R^2/N)$ that are the components of the W statistic which is distributed as χ^2 with 2(k-1) degrees of freedom where k is equal to the number of samples analysed (Batschelet 1981 p.), For k=4 the critical values are $\alpha_{0.01}^{**}=16.8$ and $\alpha_{0.001}^{***}=22.5$. The highlighted values are those with the higher contribution towards the value of W in each test.

	O. glabriculus	*C. boleti*	*C. nitidus*	*C. bilamellatus*
Control	3.32	2.75	2.01	**21.71**
Coriolus versicolor	**12.91**	**11.03**	1.71	1..34
Ganoderma adspersum	1.76	2.93	**14.98**	1.97
Piptoporus betulinus	1.98	1.24	2.3	1.75
W	19.97^{**}	17.95^{**}	21.10^{**}	26.77^{***}

appeared to have a wide range of host species.

In accordance with the observed field distributions, ciid beetles showed differential behavioural responses to odours of potential hosts. *Octotemnus glabriculus, C. boleti* and *C. nitidus* were significantly attracted only to odour compounds of their preferred host species (*C. versicolor* for the first two and *G. adspersum* for the latter) whereas *C. bilamellatus* was attracted to odour compounds of all three fungi tested.

Odour compound profiles for each fungus differed. Significantly, those species closely

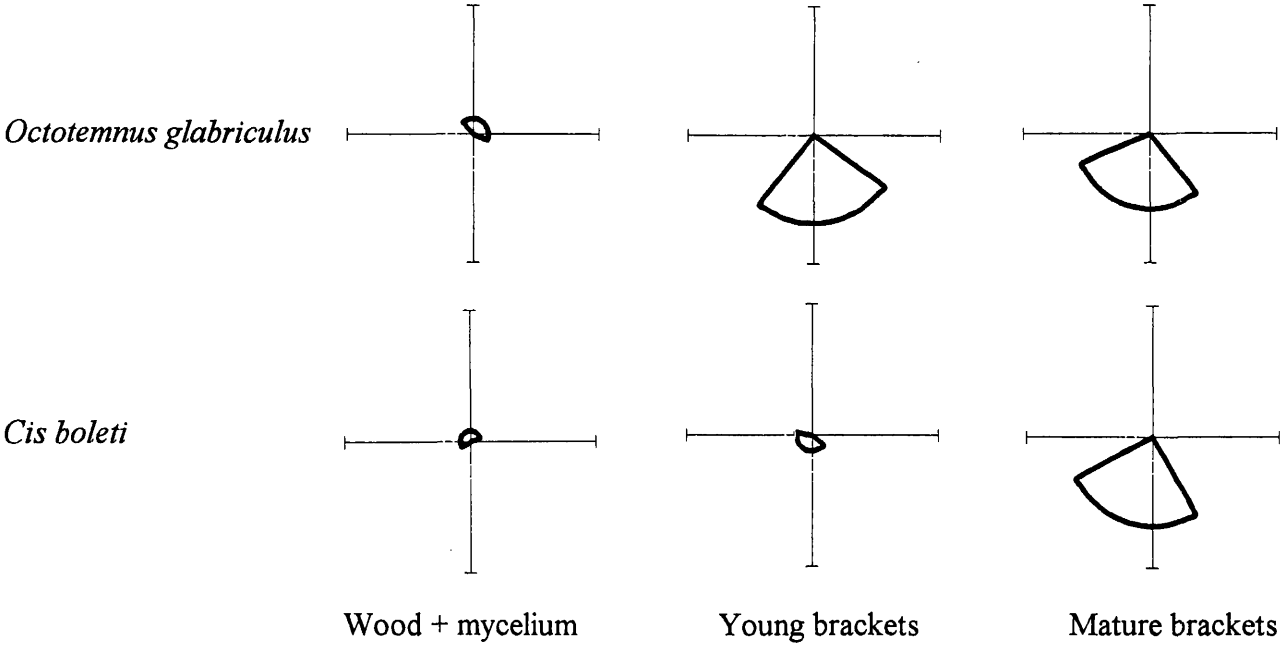

Figure 2.10 *Octotemnus glabriculus* and *Cis boleti* behavioural responses to fruiting body sections of different developmental stages.

Table 2.6 Numerical summary for the behavioural responses of *Octotemnus glabriculus* and *Cis boleti* toward brackets of *Coriolus versicolor* of different developmental stages. Φ= mean orientation response; S= standard deviation and r= strength of the response.

		C. boleti	*O. glabriculus*
Wood+mycelium	Φ	117°	56°
	S	96°	77°
	r	0.08	0.12
Young *C. versicolor*	Φ	245°	278°
	S	75°	47°
	r	0.12	0.68
Mature *C. versicolor*	Φ=	254°	256°
	S=	46°	53°
	r=	0.68	0.58

associated with a particular ciid beetle (*C. versicolor* with *O. glabriculus* and *C. boleti*, and *G. adspersum* with *C. nitidus*) were characterised by the presence of compounds absent from any of the other species analysed.

Table 2.7 Summary for the Madian-Watson-Wheeler test for each beetle species exposed to diffrent developmental stages of *C. versicolor* fruit bodies. The table shows the values of $2(R^2/N)$ that are the components of the W statistic which is distributed as χ^2 with 2(k-1) degrees of freedom where k is equal to the number of samples analysed (Batschelet 1981 p.). For k=3 the critical values are $\alpha_{0.01}^{**}=13.3$ and $\alpha_{0.001}^{***}=18.5$. The highlighted values are those with the higher contribution towards the value of W in each test.

	O. glabriculus	*C. boleti*
Control	**21.31**	2.48
Young bracket	1.94	3.45
Mature bracket	2.02	**9.65**
W	25.27^{***}	15.58^{**}

Overall, the data suggest that *O. glabriculus, C. boleti* and *C. nitidus* discriminate between their preferred host fungi on the basis of specific odour chemicals, whereas *C. bilamellatus* may use an odour compound common to many potentail hosts (such as 1-octene-3-ol) to locate host fruit bodies. Both male and female beetles were equally attracted to odour compounds of potential host fungi. This evidence suggests that ciid beetles do not make use of sexual pheromones during colonisation. This observation is supported by the field experimental findings of Jonsson and co-workers (Jonsson et al. 1997) who found no evidence of the use of pheromones by *C. glabratus* during colonisation of *F. pinicola* in Sweden.

Furthermore, *O. glabriculus* and *C. boleti* showed differential behavioural responses to odour compounds from different physiological stages of development of their host fungus *C. versicolor*. *Octotemnus glabriculus* was attracted to both young and mature fruiting bodies whereas *C. boleti* was only attracted to mature fruiting bodies. These differential behavioural responses are in accordance with the observed distribution of *O. glabriculus* and *C. boleti* in the field (see Chapter III).

Given the large amount of fungal material required for the extraction of volatile compounds by distillation, odour compounds from primordial fruit bodies were not collected. *In vivo* methods of collection of odour compounds may be necessary to obtain GC profiles for fruiting bodies in different developmental stages.

Overall, my data support the hypothesis that odour compounds have an important role in the colonisation of fruiting bodies of wood-rotting fungi by ciid beetles. Differences in odour composition among potential hosts suggest that these compounds may be the key to the evolution of host preferences in ciid beetles. Analogous observations have been made in many other systems, including plant-herbivore (Gotoh et al. 1993; Kouloussis & Katsoyannos 1994; Mathieu et al. 1997; Zhang & McEvoy 1995), host-parasitoid (Janssen et al 1995a; Janssen et al 1995b; Vanbaaren & Nenon 1996) and prey-predator (Hattingh &

Samways 1995; Koveos et al. 1995; Downes & Shine 1998) associations.

CHAPTER III

CONTEXTUAL DYNAMICS OF RESOURCE PARTITIONING BY FUNGIVOROUS BEETLES

1 Summary

The interaction between two fungivorous beetles and their host fungus is used to illustrate the concept that the dynamics of an expanding energetic context drive the differential use of the resource by its inhabitants through the attunement of their life histories to the rate of change of the system. Current competition appeared to have no significant effect on the interaction between the two fungivorous beetles, *Cis boleti* **Scopoli** and *Octotemnus glabriculus* **Gyllenhal**. Partitioning mediated by contextual dynamics is allied to the compression hypothesis in island biogeography theory that states that niches among successive colonist of an island are constrained by increasing territorial interactions. The former concept moves on from the latter in that processes are considered within a dynamically bounded rather than fixed frame of reference. The concept has potentially very wide application to all kinds of expanding (changing) systems, whether the expansion is independent of (as in the example presented in this chapter) or dependent on (as in many successional processes) the activities of the inhabitant organisms. It provides a means of understanding the auto-catalytic feedback processes that drive evolution in the direction of increased complexity, where competition can be seen as a consequence of the evolutionary process rather than as

the driving force *per se*.

2 Introduction

The obviation of competition through resource partitioning has been widely inferred as an evolutionary mechanism that enables co-existence of life forms potentially able to occupy the same ecological niche. Such partitioning is due to mechanisms that enable specialism in the acquisition of resources that vary in location and/or availability (MacArthur & Levins 1967).

The most common interpretation of partitioning is spatial, based on structural or behavioural mechanisms that maximise efficiency of resource capture in distinctive locations. An example occurs in bark beetles (*Ips*) that partition the branches of Norway spruce trees (*Picea abies* **(L.) Karst.**) on the basis of diameter, with small species (*Ips duplicatus* **Sahlb.**) occupying branches of small diameter at the top of tree and larger species (*Ips typographus* L.) restricted to thicker branches in the lower part of the tree (Schlyter & Anderbrant 1993). A second interpretation of partitioning is that of temporal partitioning based on behavioural or physiological mechanisms. Temporal partitioning allows the exploitation of resources available only at particular times (e.g. bees foraging for pollen at certain times of day; Stone et al. 1996) or of resources that are continually available, but which are found in environments that experience cyclic extreme climatic conditions (e.g. rodents feeding from bushes in arid zones; Abramsky et al. 1993)

Both spatial and temporal explanations of partitioning tend—as in many other aspects of evolutionary theory, including island biogeography theory and r-K-selection concepts (MacArthur & Wilson 1967; Pianka 1970)—to view events within a fixed frame of reference. Events within the boundaries of this frame may be dynamic, but the boundaries themselves do not shift, so that an inevitable "struggle for existence" in confined space/time ensues.

A different perspective is possible, however, when ecological and evolutionary processes are viewed within a frame of reference or "dynamic context" that expands and diversifies as a consequence of the assimilation and distribution of energy within a variably resistive boundary (Rayner 1997; Davidson et al. 1996). Such expandable domains are characteristic of all systems capable of growth through the increase in amount or activity of their contents, from single cells and their inhabitant organelles and molecules to animal territories, societies and ecosystems. Here, in a kind of evolutionary application of "Parkinson's law"—that work expands to fill the space/time available for its occupation—the expansion of the system itself creates opportunities for evolutionary innovation, i.e. diversification, rather than constraints (Rayner 1997). Often, as in many ecological successions, the expansion, due to energy input, of the system depends on the activities of its inhabitants, resulting in an auto-catalytic feedback process that makes selective cause and adaptive response difficult, or even unrealistic, to unravel. In other cases, as in the one I describe below, expansion may be independent of the inhabitants, making direct selective influence easier to discern. Expansion of the context, due to energy assimilation, will in itself impose differential selection on the growth and reproductive dynamics of the co-existing entities in ways that might be expected to amplify differences in their life histories. In principle, such selection may be analogous to that envisaged by the compression hypothesis (MacArthur & Wilson 1967) in island biogeography theory with the important difference that it results from the increasing scale of the system rather than progressive constraints due to territorial interactions within fixed boundaries.

To understand the accommodation and/or adaptation of life forms to expanding domains, it is important to take account both of their spatial and of their temporal dimensions, and to relate these to the rate of change of the system, i.e. to consider the relative trajectories of containers (contexts) and contents (inhabitants) rather than their specific location in space or time. This can be done by combining knowledge of spatial scales of organisation with knowledge of life histories, following principles similar to those of classical r-K-selection theory (Pianka 1970), but applying these principles in a dynamic context. Accordingly, a correspondence may be expected between the size and reproductive rate of inhabitants, and the scale and rate of expansion of their context.

Here I illustrate the possible application of spatiotemporal partitioning within a dynamic context by reference to a previously unresearched interaction between two fungivorous insects, *Cis boleti* Scopoli and *Octotemnus glabriculus* Gyllenhal, and the expanding fruit bodies ("brackets") of their host wood decay fungus, *Coriolus versicolor* (L. ex Fr.) Quél. Both beetles are entirely dependent on the brackets of their host fungus within which oviposition, larval feeding, pupation and adult emergence all take place. Brackets are formed from swelling primordia (1-5 mm diameter) which then grow from an expanding margin into semi-circular structures (7 -60 mm diameter).

3 Materials and methods

The study area was Bathwick Wood near Bath, UK a small (*ca.* 2.6 ha) deciduous woodland (see Chapter II) in which the host fungus *C. versicolor* is abundant and colonised by *O. glabriculus* and *C. boleti* at a high rate (Chapter II).

3.1 Field observations

Fifty-three genets (groups of brackets from a single genetic origin), as inferred from external morphology and paired cultures (Williams et al. 1981b) of *C. versicolor* were marked and followed from March 1995 to February 1997. Three randomly chosen brackets were collected every week from each genet for the two years. It is important to note that none of the genets was present (fruiting) for a period longer than 4 months but that the time period over which brackets from different genets were collected was two years. Brackets were dissected in the laboratory and ciid beetles identified and counted. The stage of development (larvae, pupa, teneral adult and mature adult) and sex of each beetle was recorded.

The developmental stages (actively expanding/ fully expanded) of 207 brackets were recorded. Ciid beetles in these brackets were sorted by species, counted and their distribution was investigated using the χ^2-test (Sokal & Rohlf 1981) This and all further statistical analysis were carried out in the GLIM 3.77 software (Baker 1987). The nature of the relation between the number of adult beetles of one species and those of the other species in those brackets where both species were found together was investigated using nonparametric correlation, Spearman procedure, in order to avoid assumptions on the normality of count data (Sokal & Rohlf 1981).

3.2 Field experiment

Laboratory-propagated fungi (Fig. 3.1) were introduced into the woodland in order to evaluate the colonisation preferences of *O. glabriculus* and *C. boleti*. Brackets of *C. versicolor* were propagated following the method of Williams and co-workers (Williams et al. 1981a) on small (~5 cm in diameter and ~4 cm high) logs of hazel wood. Three genets of *C. versicolor* with morphologically distinctive brackets (as observed in the woodland) were chosen. After 10 weeks of incubation to promote fruiting (Williams et al. 1981a), the propagated brackets were sorted into ten 'patches'. Each patch was made of 4 clones of each of the 3 genets (12 logs per patch). The ten patches were introduced into the woodland, at randomly chosen positions, on the first week of May 1996. The patches were observed for 24 weeks being checked as frequently as possible (at least three times per week). During each visit, the emergence of new primordia was recorded and brackets were scanned for evidence (*i.e.* tunnel openings or adult beetles) that colonisation had occurred. Colonised logs were removed and the brackets dissected in the laboratory. Taxonomic identity and sex of each of the colonists were recorded. It is important to point out that the date of emergence of propagated brackets could not be synchronised. The actual composition of each patch, in terms of the number and genetic origin of brackets at any time was not controlled. Patches therefore varied in size (number of brackets present) and the contribution of each genet at any time. For logistical reasons, the sampled logs were not replaced in the patches. One-way analysis of variance (Sokal & Rohlf 1981)) and

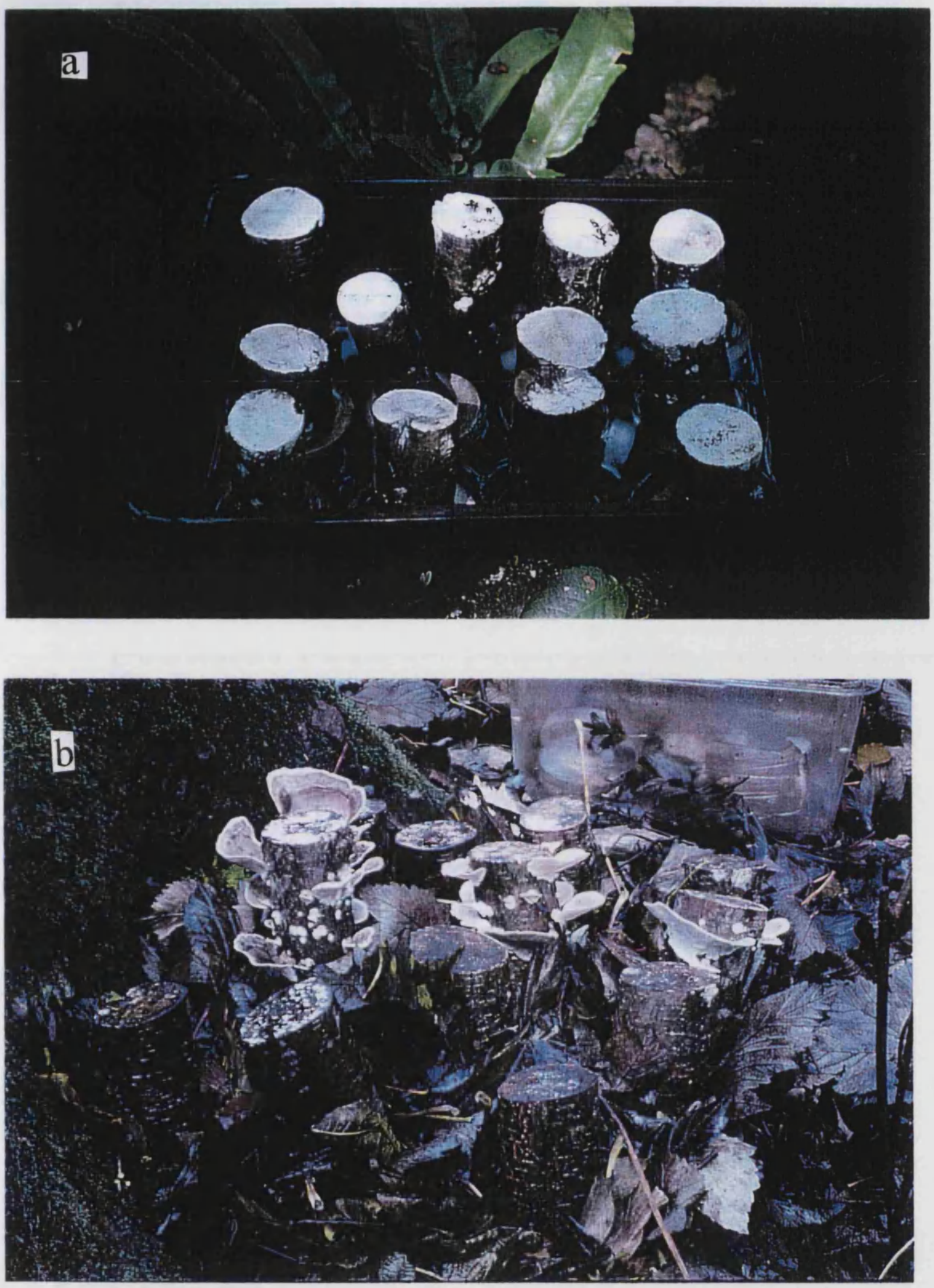

Figure 3.1 Propagation of *Coriolus versicolor* fruiting bodies. a) Hazel logs colonised by mycelium of *C. versicolor*. b) Fruiting bodies on hazel logs.

the Student-Newman-Kuels (SNK) procedure (Sokal & Rohlf 1969) were used to test whether the colonisation pattern of the two beetle species was biased by bracket age.

3.3 Female reproductive activity

Evidence of reproductive activity was obtained by dissecting 12 females from each species of beetle every week from 10 February 1997 to November 1997. The females for any week were randomly selected from three source patches allowing 4 females per patch. Females from the two species did not necessarily come from the same patches. It was recorded whether females had reduced ovaries or the ovaries were developed (Fig. 3.2). The developmental stage of source brackets was recorded.

4 RESULTS

4.1 Field observations

Genets of *C. versicolor* (Fig. 3.3a) were present all year round but with seasonal changes in abundance. The number of genets increased through the spring and summer. The highest availability of *C. versicolor* occurred in the autumn and declined through the winter to a minimum in early spring next year. This pattern was consistent in both years but the total number of genets was smaller in the second year.

The *C. versicolor* fruiting body resource was temporally partitioned between *O. glabriculus* (Fig. 3.3b) and *C. boleti* (Fig. 3.3c). The proportion of available genets

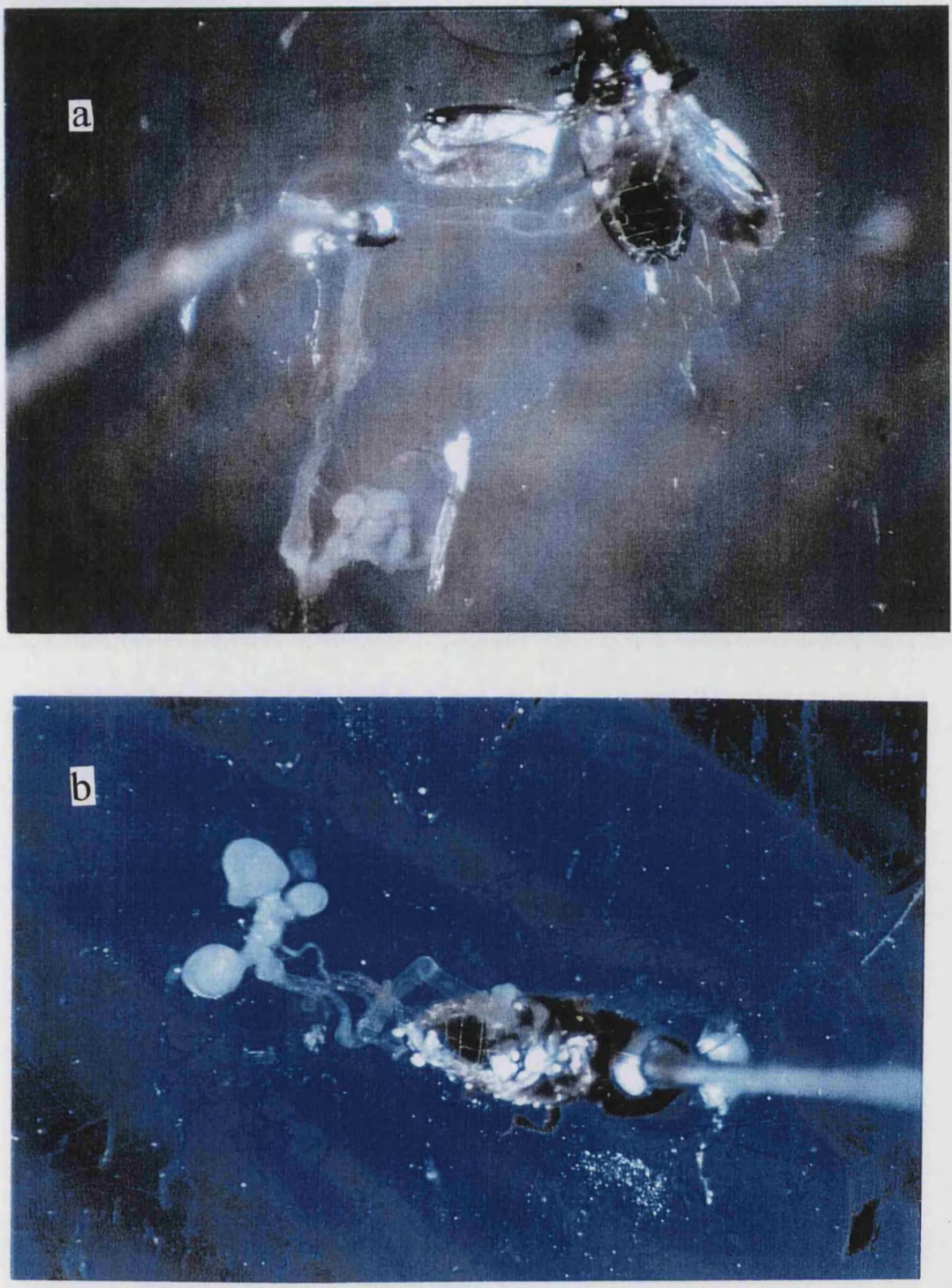

Figure 3.2. Dissected *Octotemnus glabriculus* females showing a) undeveloped and b) developed ovarioles.

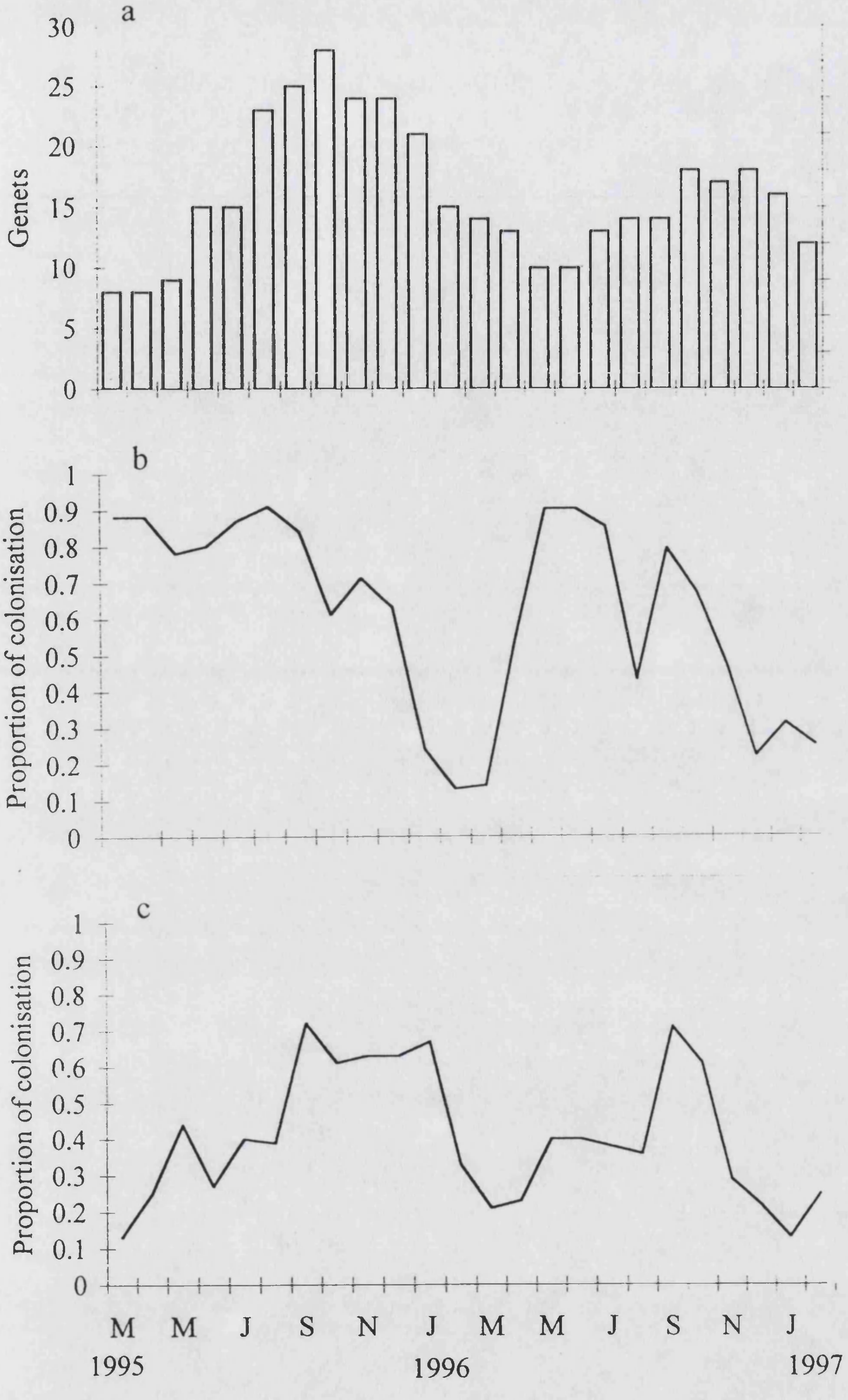

Figure 3.3. Temporal distribution of a) genets of *Coriolus versicolor* and the proportion of genets colonised by b) *Octotemnus glabriculus* and c) *Cis boleti*.

colonised by each of the fungivorous beetles changed over time. In spring and summer a higher proportion of genets was colonised by *O. glabriculus* (0.75-0.90) than that colonised by *C. boleti* (0.10-0.40). The proportion of genets colonised by *O. glabriculus* (0.20-0.60) declined through the autumn and was least in the winter (0.15-0.30). By contrast, the proportion of genets colonised by *C. boleti* increased through late summer and peaked in autumn (0.70). *C. boleti* remained abundant well into winter before declining by late-winter and early spring to its lowest levels (0.10). *O. glabriculus* was the sole colonist of 57% of the colonised brackets over the two year period whereas *C. boleti* was sole colonist of 31% of the colonised brackets. Only 12% of the colonised brackets were occupied by both beetles in apparent succession.

In addition to the temporal partitioning there was also a statistically significant bias (χ^2=69.3; P<0.001) in colonisation by the two beetles with respect to the developmental stages of the brackets (Fig. 3.4a). Young, actively expanding brackets, were almost exclusively colonised by *O. glabriculus* whereas *C. boleti* was restricted to and was the predominant species in fully expanded brackets.

4.2 Field experiment

The observed natural distribution patterns of *O. glabriculus* and *C. boleti* in brackets of different developmental stages of *C. versicolor* may have two possible explanations. First, *O. glabriculus* could breed earlier than *C. boleti* as a consequence of seasonal factors directly affecting its behaviour. In this case its occurrence in young brackets could simply result from the greater proportion of these brackets available for colonisation early in the year. Second, *O. glabriculus* could have a preference for

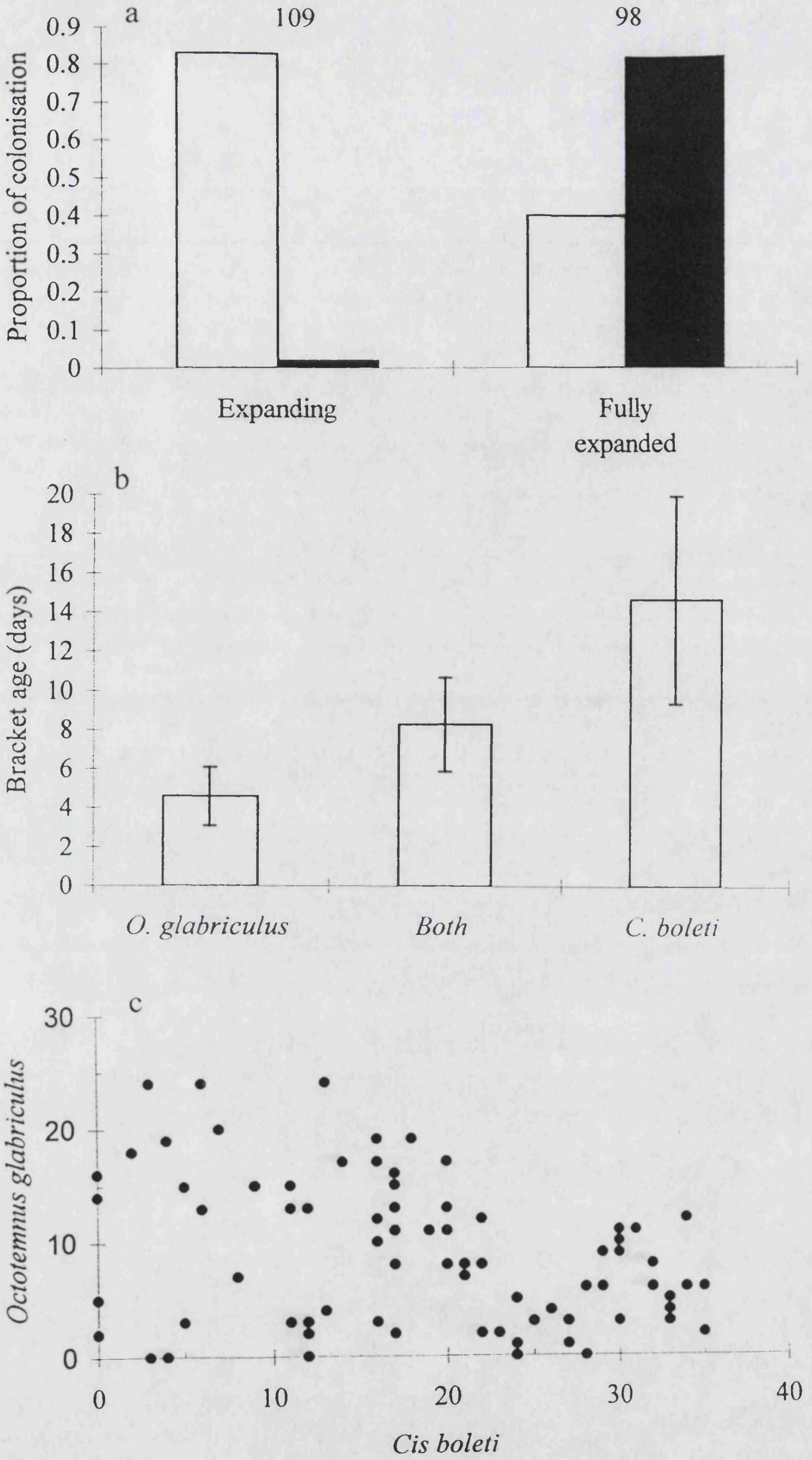

Figure 3.4. Developmental stages of brackets and ciid beetles distribution. a) Proportion of colonisation of naturally occurring brackets actively expanding and fully expanded by *Octotemnus glabriculus* (open bars) and *Cis boleti* (closed bars). b) Bracket age (mean ± standard deviation) of introduced resources in relation to the colonisation by *O. glabriculus* and *C. boleti*. c) Negative correlation between the number of adult individuals of *O. glabriculus* and *C. boleti* in fully expanded brackets.

young brackets, in which case the partitioning would be driven by the developmental and phenological dynamics of the host organism and hence only indirectly by purely seasonal factors.

These hypotheses were tested by investigating the colonisation behaviour of the two beetles on *C. versicolor* fruiting bodies propagated on sections of hazel (*Corylus avellana* L) in the laboratory (Williams et al. 1981a). The artificially propagated brackets were introduced into the woodland in summer, when the proportion of naturally occurring young brackets was low. *O. glabriculus* colonised 78 (80%) of the introduced fruiting logs whereas *C. boleti* colonised 54 (56%) of the introduced fruiting logs. Thirty-five (36%) of the introduced fruiting logs were colonised by both beetles. The observed high rate of colonisation of introduced logs by *O. glabriculus*, when the abundance of naturally occurring resources was low, suggests that the resource is limiting for this species. Moreover, there was a significant difference ($F_{2,94}=126.6$; $P<0.01$) between the ages of brackets colonised by each beetle species (Fig 3.4b). *O. glabriculus* was the only colonist in very young brackets (mean ± standard deviation 4.6 ± 1.5 days) whereas *C. boleti* was the only colonist in old brackets (14.7 ± 5.3 days) and those brackets colonised by both beetle species were middle-aged (8.3 ± 2.4 days). The SNK procedure showed significant differences in age ($P<0.01$) between those brackets colonised by *O. glabriculus* only and *C. boleti* only although neither of these differed significantly ($P>0.05$) from those brackets colonised by both beetles. Thus the observed distribution of the two beetle species in naturally occurring *C. versicolor* brackets closely reflects the experimentally observed colonisation behaviour of the beetles, which appears to be driven by preferential choice. In addition, the result suggests that the inevitable development of young brackets into old ones limits the available resource for *O. glabriculus*.

From both the field data (see Fig. 3.3a) and the field experiment (see Fig 3.4b) it is clear that adults of *O. glabriculus* occupy a broader range of developmental stages of *C. versicolor* fruiting bodies than *C. boleti*. There is, however, an element of competitive exclusion in fully expanded brackets. *O. glabriculus* is less commonly found coexisting with *C. boleti* in fully expanded brackets than in young fruiting bodies (Fig. 3.4a). Further evidence of competition is found in the significant negative correlation coefficient (R=-0.32; t=2.98; d.f.= 76; P<0.001) between the number of adult *C. boleti* and *O. glabriculus* within fully expanded brackets where *C. boleti* was the dominant species (Fig. 3.4c).

4.3 Female reproductive activity

There are also factors intrinsic to the beetles that operate to partition the *C. versicolor* bracket resource. The times of the year at which the two insects reproduce differ. Juvenile stages (larvae and teneral adults) of *O. glabriculus* (Fig. 3.5a) generally occurred only from spring to mid-summer, whereas those of *C. boleti* (Fig. 3.5b) were found from summer to mid-winter. The same pattern was evident regardless of whether the brackets were colonised by only one species or by both species. Neither occupancy by *O. glabriculus* to modify the niche and facilitate the proliferation of *C. boleti*, nor the suppression of *O. glabriculus* as a consequence of further niche modification (or direct competition) by *C. boleti* were therefore pre-requisites.

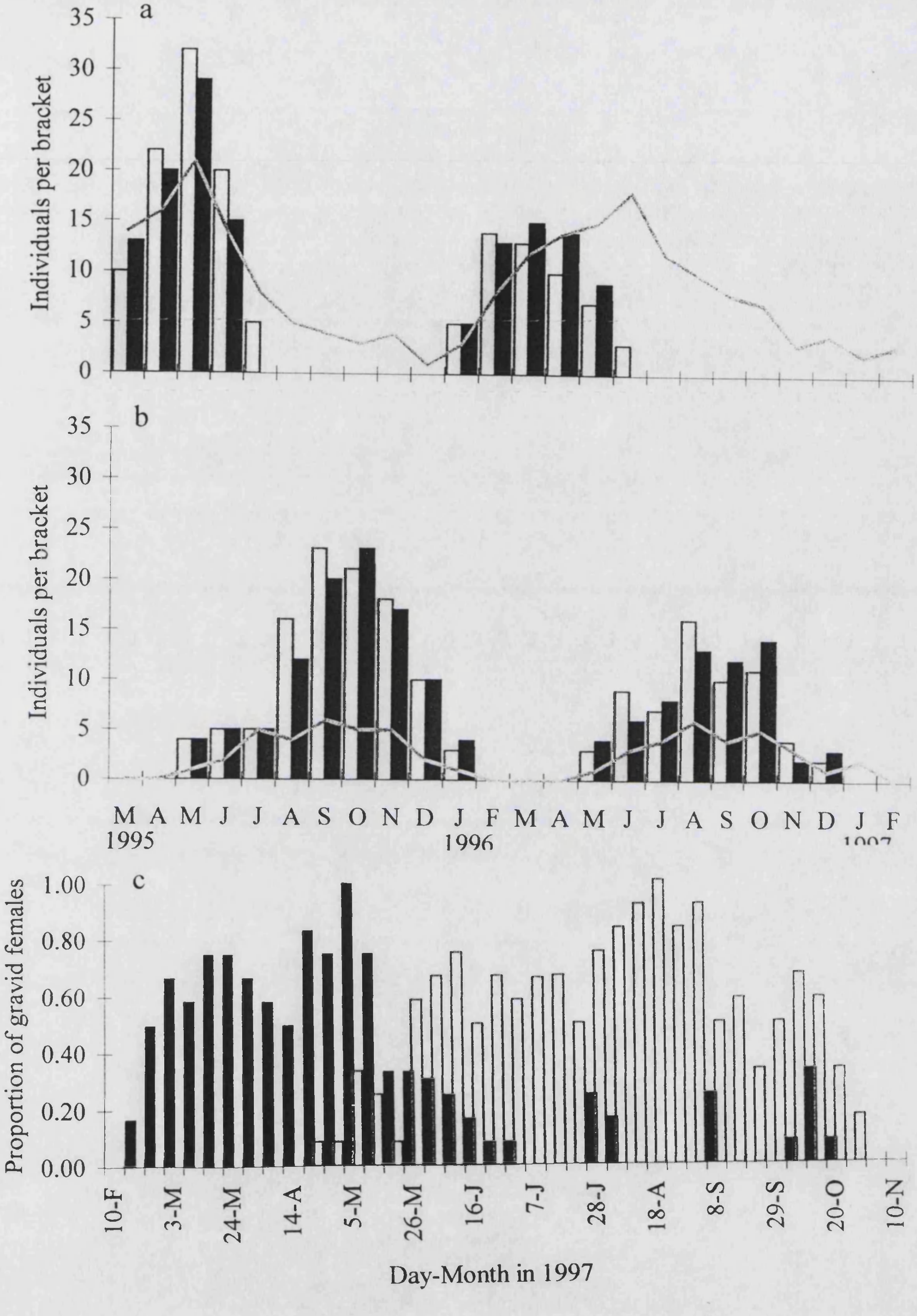

Figure 3.5. Reproductive period of ciid beetles. Average number of juvenile individuals of a) *Octotemnus glabriculus* and b) *Cis boleti* in brackets colonised by only one beetle species (open bars) and brackets where colonisation occurred by both beetle species in apparent succession (closed bars) and the number of conspecific adults (line). c) Weekly distribution of the proportion of females of *O. glabriculus* (close bars) and *C. boleti* (open bars) with matured ovarioles.

During 1997 the reproductive activity of both ciid species was monitored by dissecting female beetles and checking for enlarged ovarioles. The temporal frequency distribution of females with enlarged ovarioles confirms the separation of breeding seasons between the two beetles. Females of *O. glabriculus* matured eggs mainly from spring to mid summer whereas females of *C. boleti* matured eggs from summer to late autumn (Fig. 3.5c). Interesting exceptions were, however, observed when a low proportion of females of *O. glabriculus* matured eggs in late summer and early autumn. All these females were associated with young actively expanding brackets produced after sporadic wet spells. Interestingly, *O. glabriculus* females from older brackets did not mature eggs at these times.

5 DISCUSSION

Overall, the present data suggest that the active expansion of the host fungus is a key factor in the partitioning of *C. versicolor* fruiting bodies by the two beetles between different seasons. Current competition seems to play only a minor role since the breeding season of *O. glabriculus* is not extended when *C. boleti* fails to colonise brackets already occupied by the former, and *C. boleti* does not colonise young brackets that escape colonisation by *O. glabriculus* earlier in the year. Evidence both from field population data and also from a field colonisation experiment supports that *O. glabriculus* actively chooses young *C. versicolor* brackets whereas *C. boleti* chooses large, mature *C. versicolor* brackets. Further evidence of beetle choice of distinctive developmental stages of their host fungus has been obtained from behavioural studies in wind tunnel experiments (See Chapter II)

How the preference of *O. glabriculus* for young brackets originated —whether it was tuned by past competition (ghost of competition past) or precluded such competition in the first place— remains a moot point, as in many other examples of resource partitioning. Nevertheless the principle that partitioning of a resource by co-existing exploiters can arise from preferences for particular qualities of the resource which change as a consequence of intrinsic expansive dynamics remains unaltered.

This concept is allied to the compression hypothesis in island biogeography theory (MacArthur & Wilson 1967) in which it is postulated that as a consequence of progressive colonisation by new species, niches tend to be compressed through increasingly territorial competition between inhabitants. The present example differs from this in that niches for occupants are constrained and opened by the expansion of a dynamically bounded system rather than simply constrained as a consequence of increasingly territorial interactions between colonists.

The simple system described here, illustrates and clarifies the potentially important roles of host (contextual) dynamics in resource partitioning and associated changes in life history traits in the emergence of co-existing systems. A recent study (Waltz & Whitham 1997) showed that plant development has the potential to affect arthropod community structure just as competition (Brown & Heske 1990), predation (Paine 1966) and plant genetics (Maddox & Root 1987; Fritz & Price 1988; Dickson & Whitham 1996) have been shown to do. In this light, there may be a case for re-interpretation of some examples of partitioning that have been regarded as purely spatial. For example the occurrence of different species of bark beetles on differentsized pine tree branches (Schlyter & Anderbrant 1993), referred to in the introduction to this chapter, can be interpreted not simply as an example of spatial partitioning, but as a consequence of the expansive dynamics of the host tree. As the tree grows, its branches increase in size, and there is a transition from young branches of small diameter at the top of the tree to mature thicker branches in the lower part of the tree.

The concept of partitioning mediated by contextual dynamics has potentially wide implications for all kinds of expanding system whether the expansion is independent of (as in the example here presented) or dependent on (as in many ecological successions such as the secondary succession of vegetation and avifauna in abandoned farmland, see MacArthur & Connel 1966) the activities of coexisting organisms. This provides a means of understanding the auto-catalytic feedback processes contributing to the emergence of complexity in such a way that competition arises as a consequence of the evolutionary process rather being the main driving force of evolutionary change. In the example here presented as well as in the secondary succession of vegetation and avifauna above referred, new niches for succeeding occupants are opened by the expansive dynamics of the context. Competition then may arise between succeeding and pre-established occupants as a consequence of the expansive dynamics of the context either exerted by pre-established occupants (ecological succession) or intrinsic to the context itself (fruiting bodies developmental dynamics) that facilitate the proliferation of succeeding occupants.

CHAPTER IV

FUNGIVORY ON *CORIOLUS VERSICOLOR* FRUITING BODIES BY CIID BEETLES: EFFECTS ON THE REPRODUCTIVE POTENTIAL OF THE HOST FUNGUS.

1. Summary

Ciid beetles are strict fungivores specialised on brackets of wood-rotting fungi. These insects are entirely dependent on their host fungi within which oviposition, larval feeding, pupation, emergence and adult feeding all take place. Though some species exploit dysfunctional brackets (in which spore production has ceased), others colonise functional brackets (i.e. expanding or actively producing spores) and therefore are likely to affect the reproductive potential of their host fungi. Two fungivorous ciid beetles, *Octotemnus glabriculus* Gyllenhal and *Cis boleti* Scopoli are specialised consumers of brackets of *Coriolus versicolor* (L. ex Fr.) Quél. These beetles colonise brackets of *C. versicolor* in apparent succession. *Octotemnus glabriculus* colonises young fruiting bodies whereas *C. boleti* colonises mature ones. It has been shown previously (see Chapter III) that this partitioning of the host fungal resource is in fact not a succession, but the consequence of the preferences of the two beetles for particular developmental stages of the host fungus.

The aim of the present study was to quantify the impact that these two beetles have on the reproductive potential of *C. versicolor* based on field and experimental data.

Both beetles were found to have a negative impact on the reproductive potential of *C. versicolor* but *O. glabriculus* caused significantly more damage than *C. boleti*. These results, together with previous evidence on the rates of colonisation of naturally occurring *C. versicolor* genets, suggest that both *O. glabriculus* and *C. boleti* have the potential to affect the population structure of *C. versicolor*.

2. Introduction

Fungi and insects are two hyper-diverse groups of living organisms (Colwell & Coddington 1994) which have come into trophic contact repeatedly through their evolutionary history. These interactions range from complete dependence of strict entomopathogenic fungi on insects as food resource, to complete dependence of strict fungivorous insects on fungi as food resource, with an ample spectrum in between (Wilding et al. 1989).

Among the antagonistic fungus-consumer relationships, the consumption of fruiting bodies of macrofungi by insects have received considerable attention, but these studies have concentrated on temperate drosophilids, largely with a zoocentric emphasis, dealing with aspects of population structure (Jaenike 1977; Jaenike 1986; Jaenike 1988; Worthen 1988; Worthen 1989); genetic diversity (Ashe 1984; Jaenike 1986; Jaenike 1989); competition (Grimaldi 1985; Grimaldi & Jaenike 1984; Shorrocks 1991; Shorrocks & Bingley 1994); predation (Worthen 1989; Worthen et al. 1995; Worthen & Moore 1991) and parasitism (Jaenike 1985; Montague & Jaenike 1985). Complementary studies on the effects of fungivory on the fungal component have been neglected by the dominant zoocentric viewpoint which considers the fungal partner simply as 'the resource'. This position is analogous to that observed in early studies of plant-herbivore interactions where plants were referred to only as 'the food source' (Dirzo 1984; Harper 1986).

Herbivory and fungivory can be seen as analogous relationships (Bruns 1984; Hanski 1989; Harper 1986) in which the trophic activities of consumers may have a negative impact on the biological activities (growth and reproduction) of plants and fungi respectively. There is, however, a marked contrast in the understanding of these two analogous trophic associations. On the one hand, the close associations between some phytophagous insects and their food plants have been recorded at least since Victorian times. More recently, a variety of ecological and evolutionary patterns have been described and documented during the last three decades, and a substantial theoretical framework attempts to explain those patterns and their variability. Such patterns include the frequency and intensity of herbivory; the impact of herbivory on the reproductive potential of plants; the distribution and effectiveness of defence mechanisms, both chemical and physical; the effects of plant characteristics such as apparency, phenology and life history on herbivory as well as the co-variation of two or more of these factors (Crawley 1983; Dirzo 1984; Howe & Westley 1988; Karban & Baldwin 1997; Rosenthal & Janzen 1979 among others). On the other hand, fungus (fruiting body)-fungivore interactions have not been described even at the basic level of patterns of consumption (i.e. frequency and intensity of fungivory and its spatio-temporal variability) (Guevara unpublished)

Ecological and evolutionary responses of fungi to fungivory would be comparable to plant responses to herbivory if the trophic activities of fungivores affect the reproductive potential of host fungi [i.e. when fungivory occurs before spores are discharged (Hanski 1989)]. In other words, from a fungocentric perspective, fungivory matters only while sporophores are functional (producing, maturating or discharging spores) rather than when they become dysfunctional and senescent. It has been suggested that fungivory by invertebrates on sporophores is unlikely to have a significant effect on the reproductive potential of fungi (Courtney et al. 1990; Hanski 1989). This assertion is, however, premature. Given the zoocentric emphasis of studies with fungivorous invertebrates, such studies have concentrated their attention on dysfunctional and senescent sporophores in which fungivorous populations are most apparent) rather than assessing consumption while fungi are still functional.

Wood-rotting fungi and their associated ciid beetles provide a system in which to explore the effects that fungivory on fruiting bodies may have on the reproductive potential of fungi. The system has the advantages that wood-rotting fungi are easy to manipulate and ciid beetles are highly specialised. In the present study, I explored the effects that two fungivorous ciid beetles, *O. glabriculus* and *C. boleti*, have on the reproductive potential of their host fungus, *C. versicolor*, based on field observation and experimental data.

3. Materials and methods

3. 1. Field observations

Field data were collected from a local woodland (Bathwick Wood) near Bath (see Chapter II). The extent to which ciid beetles occupy brackets of *C. versicolor* was investigated during 1995 and 1996. Thirty genets of *C. versicolor* were marked on first appearance of fruit bodies and changes in the number and specific identity of colonists were followed as the genets age by collecting randomly selected brackets of known age.

In 1998 sixty brackets of *C. versicolor* from 20 genets (3 brackets per genet) were collected. Functional hymenium surface (white coloured surface) and total hymenium surface, functional plus dysfunctional (yellowish) surface were, separately, copied onto transparency film (Fig. 4.1a). Then brackets were dissected and beetles were sorted by species and counted. Copied hymenium areas were scanned and then quantified using the NIH-Image software. The nonparametric Spearman correlation analysis (Sokal & Rohlf 1981) was used to explore relationships between the number of beetles and the percentage of functional reproductive surface.

3. 2. Experiments

Thirty pairs of logs with young brackets of *C. versicolor* were placed in split boxes, one pair per box. Each pair was propagated from the same genet with roughly equal numbers of brackets of the same size (Fig. 4.1b). The functional hymenium surfaces of all 30 pairs were copied and scanned as described above. One side of each box was maintained beetle-free as a control whereas in the other side beetles were added in order to simulate natural colonisation. All treatments were randomly assigned between the 30 boxes. Ten *O. glabriculus* were added to each of 20 boxes while 10 boxes were kept beetle-free. All 30 boxes were incubated for ten weeks in humid and temperate

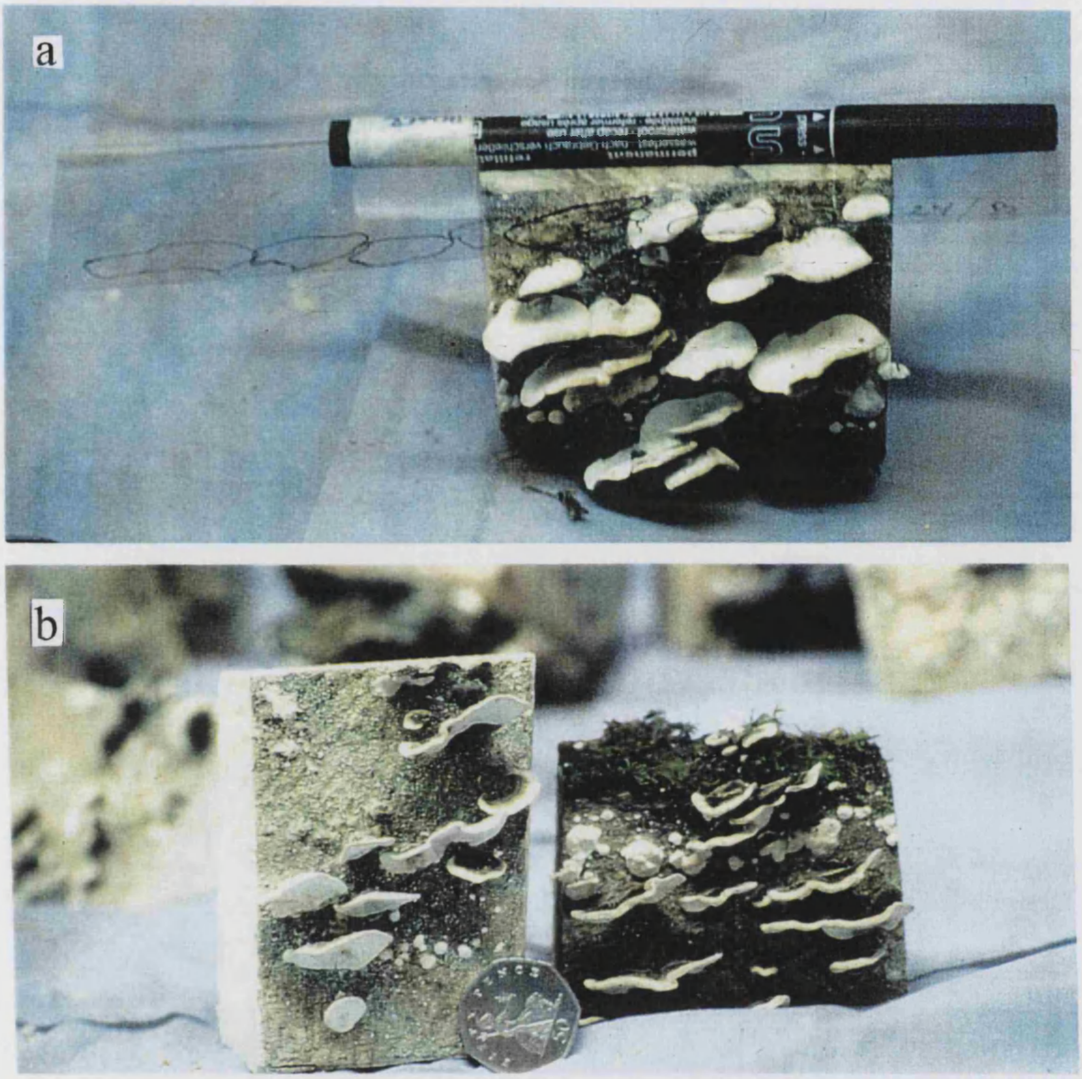

Figure 4.1 a) Hymenial surface of *Coriolus versicolor* copied onto transparency film. A long strip of transparency film was placed onto the hymenial surface of each fruit body, and the periphery of the functional mycelium was copied with a permanent marker. b) One of thirty pairs of logs with fruit bodies of *Coriolus versicolor*. Logs in a pair were colonised by the same genet of *C. versicolor* and they had approximately the same number of fruit bodies of approximately the same size.

conditions. Humidity was achieved by adding water to each box to a depth of 15 mm. and adding extra water every week to maintain this level. The incubator was set at 8° C (±3° C) and a photoperiod of 16 hours dark and 8 hours light. After 10 weeks, ten *C. boleti* were added to ten of the boxes that already contained *O. glabriculus* and to the ten that had no beetles. All 30 boxes were incubated for a further 10 weeks in the same conditions and the functional hymenial surface of all old and new brackets was then copied onto transparency film and scanned. The 30 boxes were then incubated for six weeks in dry conditions (with no water in the boxes) at 20° C (±3° C). Humid and temperate conditions were then re-established to promote fruiting during four weeks, and primordia produced were then counted.

The relationship between initial and final area of functional hymenium and the effects of fungivory were explored by using generalised linear models in the GLIM 3.77 software (Baker 1987). After the initial fitting that included in the predictive side of the model the three treatments and initial functional hymenial surface as a covariate, simplification was carried out until the simplest model was obtained. Effects of treatments on the number of newly produced primordia was investigated by one-way analysis of variance.

4. Results

4. 1. Field observations

Ciid beetles colonised a high proportion of the naturally occurring genets of *C. versicolor* all through the year with the exception of the late winter (Fig. 4.2a).

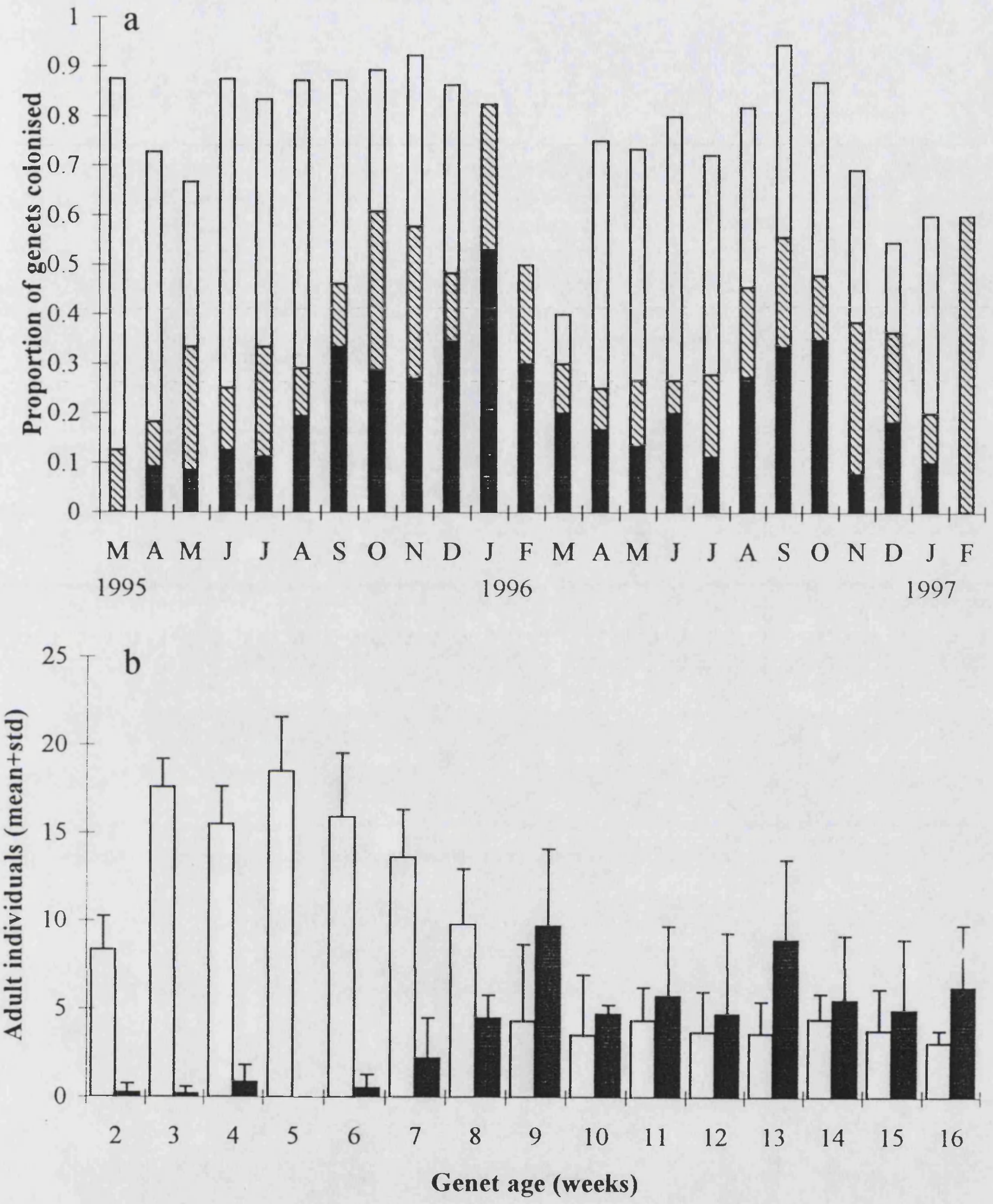

Figure 4.2 a) Frequency of colonisation of genets of *C. versicolor* by *C. boleti* (black section), *O. glabriculus* (open section) and both beetles (dashed section) over two years period. b) Number of adult individuals of *O. glabriculus* (open bars) and *C. boleti* (closed bars) in relation to genet age.

Octotemnus glabriculus colonised a high proportion of genets in the spring and early summer whereas *C. boleti* colonised a high proportion of genets from mid-summer to early winter.

The apparent seasonal partitioning of the *C. versicolor* bracket resource appeared to be mediated by the dynamic development (ageing) of the genets (Fig. 4.2b, see also Chapter III). A larger number of adult *O. glabriculus* was found in genets less than 7 weeks old whereas the number of adult beetles in genets 10^+ weeks old was smaller. By contrast, the number of adult *C. boleti* was large in genets 8^+ weeks old whereas the number of adults in genets less than 5 weeks olds was small (see Chapter III).

Octotemnus glabriculus colonised younger fruiting bodies than *C. boleti*. These results suggest that *O. glabriculus* could have a bigger impact on the reproductive potential of *C. versicolor* than *C. boleti*. Field data supported this hypothesis. The number of individuals of *C. boleti* per bracket showed no correlation with the percentage of dysfunctional hymenium surface (Fig. 4.3a) whereas the number of *O. glabriculus* showed a significant correlation ($R=0.77$; $t=10.63$; d.f.=76; $P<0.01$) with the percentage of dysfunctional hymenium surface (Fig. 4.3b).

4. 2. Experiments

Experimental evidence showed that *C. boleti* had a significant impact on the reproductive potential of *C. versicolor* (Fig. 4.4a), causing a reduction of 31% in functional hymenial surface compared to controls. *Octotemnus glabriculus* had an even stronger impact, causing a reduction of 53% in functional hymenium surface compared

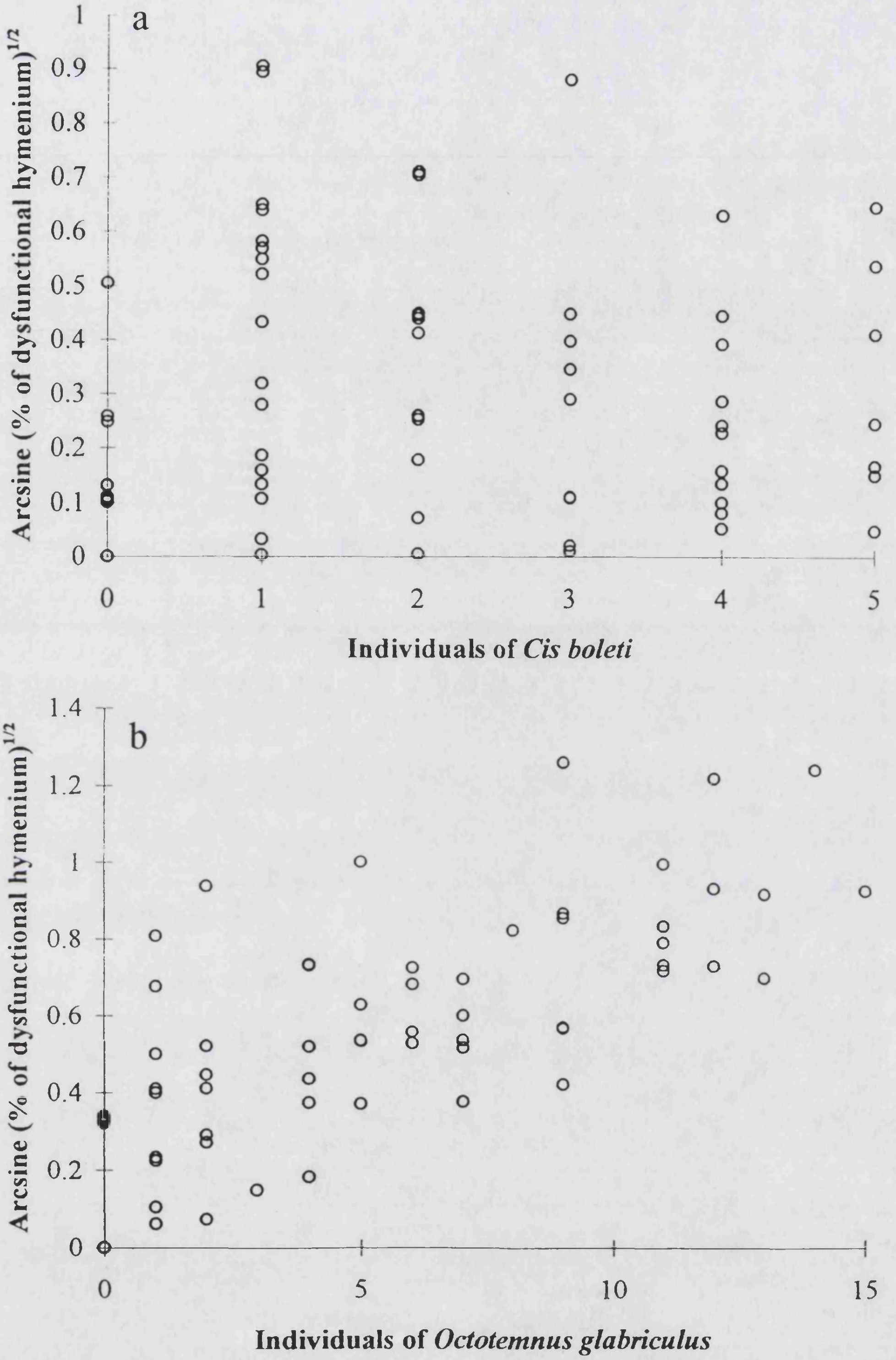

Figure 4.3 Spearman correlation between the percentage of dysfunctional hymenium surface and individual numbers of a) *Cis boleti* (R=0.19; t=1.8; P>0.05) and b) *Octotemnus glabriculus* (R=0.77; t=10.63; P<0.001).

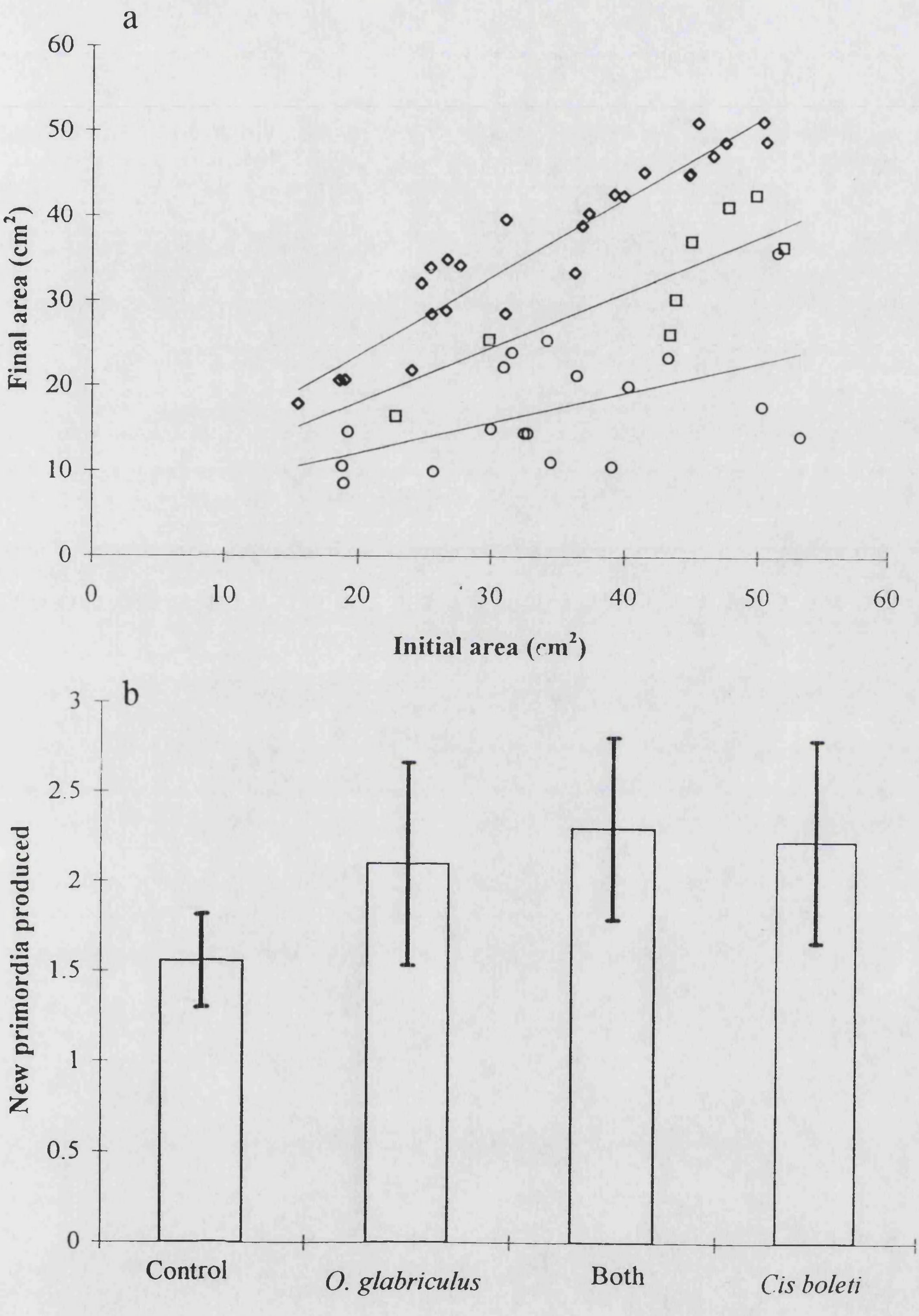

Figure 4.4 Effects of fungivory on a) the area of functional hymenium of *Coriolus versicolor* by *Cis boleti* (squares) that caused a reduction of 31% and *Octotemnus glabriculus* alone and *Cis boleti* plus *Octotemnus glabriculus* (circles) which caused a reduction of 57% compared to controls (diamonds). b) Effects of fungivory on the production of new primordia of *C. versicolor*.

to controls. When both beetles were added there was a reduction of 64% in functional hymenium surface compared to controls, but this latter reduction was not significantly different from that caused by *O. glabriculus* alone.

Longer term effects on the reproductive potential of *C. versicolor* ,i.e. production of new primordia, were not statistically different between treatments (P>0.05). Genets of *Coriolus versicolor* exposed to fungivory tended, however, to produce more new brackets than controls (Fig. 4.4b).

5. Discussion

A salient aspect of this study was the detection of a significant reduction in the reproductive potential of *C. versicolor* by the trophic activity of *O. glabriculus* and *C. boleti*. This reduction is comparable to that observed in analogous plant-herbivore relationships (see Crawley 1983; Dirzo 1984; Howe & Westley 1988; Rosenthal & Janzen 1979).

Field data showed that the number of *O. glabriculus* individuals per bracket correlated with the percentage of dysfunctional hymenium surface whereas the number of *C. boleti* individuals per bracket did not correlate with the percentage of dysfunctional hymenium.

Experimental evidence, however, showed that both beetles have a significant negative impact on the reproductive potential of *C. versicolor; O. glabriculus* caused more extensive damage than *C. boleti*. Fungivory by both beetles in succession did not cause further significant reduction in the reproductive potential of *C. versicolor* than that caused by *O. glabriculus* alone. This later observation is supported by field data where the number of *C. boleti* individuals did not show significant correlation with the percentage of dysfunctional hymenium.

Octotemnus glabriculus caused more extensive damage than *C. boleti*. Field data showed that the number of individual *O. glabriculus* per bracket was higher than the number of *C. boleti*. Experimental data showed that equal numbers of individuals of both beetles have significant different effects on the reproductive potential of *C. versicolor*. This observation suggests that damage caused by *O. glabriculus* on young (actively expanding) brackets is magnified as brackets expand resulting in a greater long-term reduction in reproductive potential. Analogous effects occur in plant-herbivore interactions where damage inflicted on actively expanding areas of a leaf (the base close to the petiole) result in magnified damage after full growth is achieved (Coleman & Leonard 1995).

Overall, this study shows that ciid beetles have the potential to reduce the reproductive potential of their host fungi. Such effects are analogous to those observed in plant-herbivore interactions. (Crawley 1983; Dirzo 1984; Howe & Westley 1988; Rosenthal & Janzen 1979). Fungivory by ciid beetles on wood-rotting fungi offer a system for observation, experimentation and testing of theories from which the evolutionary ecology of wood-rotting fungi can be better understood.

CHAPTER V

DISCUSSION

1. Discussion

The main achievement of the present study has been the demonstration that fungal fruit bodies are not passive places of residence for fungivorous ciid beetles, but dynamic, interactive contexts which both constrain and provide opportunities for their inhabitants. At the same time, it has become clear that these fruit body-ciid interactions provide a valuable, experimentally accessible and yet relatively simple system for studying the evolutionary ecology of consumer-host relationships. This system complements other more intensively studied systems such as plant-herbivore and host-parasitoid interactions, which have been widely interpreted in terms of attack-defence mechanisms based on underlying assumptions about the effects of consumption on fitness, or from the perspective of parasitoid fitness in terms of optimisation theory and competition.

The commonly upheld notion that fruit bodies are no more than passive homes (Hanski 1989; Courtney et al. 1990) implies that there is no interaction between the parties and therefore, no potential reciprocal effects on their evolutionary fitness. The present study provides clear evidence that such interactions do indeed exist and that they are potentially very diverse in character and have wide-ranging implications.

The concept of partitioning mediated by contextual dynamics, exemplified by the partitioning of *Coriolus versicolor* **(L. ex Fr.) Quél.** fruit bodies by *Octotemnus glabriculus* **Gyllenhal** and *Cis boleti* **Scopoli** which I have shown to be mediated by the state of development of the resource, is allied to the proposition from the compression hypothesis in island biogeography theory (MacArthur & Wilson 1967) that niches are compressed as a consequence of increasing competitive interactions between colonists. However, the contextual dynamic concept differs from the compression hypothesis in that the boundaries of the context (island) expand as a consequence of its intrinsic developmental dynamics. Consequently, niches are both constrained and opened up creating opportunities for potential occupants.

This phenomenon is not restricted to the example presented in this study but is expected to be of wide occurrence in host-inhabitant interactions such as host-parasitoid associations. For instance, two congeneric and sympatric parasitoid wasps, *Cotesia glomerata* **L** (Hymenoptera: Braconidae) and *C. rubecula* **Marshall**, make differential use of larval stages of their host species of Pieridea (Lepidoptera). *Cotesia rubecula* more readily attacks early first instars of *Pieris brassicae* **L** and *P. napi* **L** whereas *C. glomerata* shows a higher degree of parasitism of older instars of both host species. The oviposition behaviour of *C. glomerata* and *C. rubecula* is at least partially determined by host defensive behaviours which increase in intensity with advancing age (Brodeur et al. 1996). Such defence responses are not only restricted to the more aggressive physical responses from older larvae to parasitoid handling during oviposition, but also include maturation of the host immune system by means of which older larvae have a greater chance to encapsulate the parasitoid eggs (Brodeur & Vet 1995). Similar age-dependent interactions have been observed in other host-parasitoid systems. *Anisopteromalus calandre* **Howard** (Hymenoptera: Pteromolidae) shows a higher degree of parasitism on young larvae of the Anigoumois grain moth, *Sitotroga cerealla* **Oliveir**, and the maize weevil, *Sitophilus zaemais* **Motschulsky**, than on older larvae (Smith et al. 1995). *Trichogramma pretiosum* **Riley**, has a preference for young eggs (<72 hours) over old eggs of *Diatraea grandiosella* **Dyar** (Calvin et al. 1997). Further examples of the effects of host age on parasitoid preferences are presented in Awadalla (1996); Harvey et al. (1998); Miura & Kobayashi (1998); Olaye et al. (1997) Ruberson & Kring (1995); Simmons & Zuk (1994); Tillman (1994), among many others. The emphasis in the interpretation of such phenomenon has been parasitoid-centred, i.e. fitness in terms of optimisation theory (clutch size) and competition, rather than from the view of interactive dynamic systems which facilitate the emergence of complexity.

Since systems such as those discussed above are fully interactive, it can be concluded that ageing of living beings not only affects consumer preferences, but also affects host (or resource) responses to attack. In plant-herbivore relationships, plant responses to herbivory have been shown to vary with the time (age or developmental stage of the plant) of herbivory. For instance, *Melampyrum pratense* **L** and *M. silvaticum* **L** show distinctive responses to early season and late season herbivory. When herbivory occurs in the early season both species compensate by producing more flowers and fruits in which the proportion of aborted seeds does not differ from the proportion of aborted seeds in herbivore-free plants. In contrast, plants that suffer late season herbivory do not produce more flowers but the percentage of aborted seeds per fruit is significantly lower than the proportion of aborted seeds in herbivory-free plants (Lehtila & Syrjanen 1995). Similar responses have been observed in *Gentianella campestris* **Fullanous** (Gentianaceae) which overcompensates for mid season herbivory but not to early season or late season herbivory (Lennartsson et al. 1998). Compensatory growth as a response to herbivory in *G. campestris* appears to be limited by insufficient reserves early in the season and by meristem differentiation late in the season (Lennartsson et al. 1998).

Partitioning mediated by contextual dynamics not only applies to those systems in which the dynamics of the context (host) are independent of the inhabitants (like the example presented in Chapter III and the host-parasitoid interactions referred to above) but it also applies to those systems where the activities of the inhabitants drive the dynamics of the context, as applies to many ecological successions. In these systems the dynamics of the interactions tend to be both cause and consequence of partitioning. The implications of the concept of partitioning mediated by contextual dynamics are, therefore, wide-ranging for our overall understanding of how complex systems have evolved and continue to evolve. Since the experimental study of most ecological successions can present considerable logistic complications (including space, time and complexity), the study of relatively simple systems that can be experimentally manipulated offers an opportunity to unravel some of the processes, mechanisms and consequences that may occur in the evolution of more complex systems.

A key factor for the stability of partitioning mediated by contextual dynamics is that the occupants of the context must be at the right place at the right time. In other words, for the example presented in the present study, the occupants have to be able to discriminate between different developmental stages of the context or host. Evidence presented in Chapter II showed that ciid beetles can make use of fungal odours to differentiate between developmental stages of their host fungus. Although, as previously discussed, fungal odours may be key factors in the evolution of host preferences in ciid beetles, the question of how the coupling between host odours and the chemo-sensorial system and/or behaviour of ciid beetles evolved is an open question. Is the use of chemical cues a cause or a consequence of ciids' preferences? The same question also applies to other interactions in which occupants of a developing host assess the age or size of their potential host on the basis of signals other than direct contact. An example of this is provided by the parasitic wasp *C. glomerata* which discriminates between young and old larval instars of *P. brassicae* without contacting the caterpillars (Mattiacci & Dicke 1995).

On the basis that hosts undergo a continuous increase in size during development, it is likely that the main constraint faced by occupants of such hosts is space, which would be limited in immature hosts because of their small size. In the case of the example provided in the present study, fruit bodies of *C. versicolor* grow from ball-shaped primordia (1-7 mm in diameter) into fully expanded semicircular brackets (10-80 mm in diameter). Clearly, primordia and young fruit-bodies do not physically suit *C. boleti* (4-5 mm long) which is, therefore, restricted to older (normally larger) fruit bodies. On the other hand, *O. glabriculus* is a small beetle (2-3 mm long) that fits physically into large primordia and young fruit bodies and may only be restricted from older fruit bodies by competition with *C. boleti*, as suggested by the field data discussed in Chapter III. If this is the case, it is easy to see how physical constraints in the case of *C. boleti* and competitive exclusion of *O. glabriculus* by *C. boleti* might contribute to the partitioning of the expanding fruit body resource. In this way, the fine tuning between the chemo-sensorial system and/or beetle behaviours and characteristic odours from different developmental stages of the host fungus might evolve as a consequence of partitioning mediated by contextual dynamics and such coupling would in turn reinforce the partitioning.

From the present study and other current investigations at Bath it is now clear that some ciid beetles have strong preferences for particular host species [e.g. *O. glabriculus* and *C. boleti* prefer *C. versicolor*; *Cis nitidus* **Fabricius** prefers *Ganoderma adspersum* **(Schulz) Donk** (Chapter II), *Cis festivus* **Panzer** prefers species of *Stereum* (G. M. Orledge Unpublished)] whereas other ciid species are more generalist (e.g. *Cis bilamellatus* which is found in a wide range of wood-rotting fungi). I have shown in Chapter II through the use of wind tunnel experiments, that ciid beetles can discriminate between host and non-host fungi using odour compounds as the only cue. However, as mentioned above, the question of whether the tuning between the chemo-sensorial system and/or beetle behaviour and fungal odour compounds is a cause or a consequence of the preferences remains to be answered. The simplest hypothesis would suggest that the coupling between host odours and the chemo-sensorial system and/or beetle behaviours evolved from trial and error on palatable and unpalatable, harmless and toxic potential host species and has in turn reinforced the associations between ciid beetles and eatable hosts.

Though palatability/non-palatability and toxicity of fruit bodies of wood-rotting fungi may be ancestral to their interactions with ciid beetles, it is clear that ciid beetles affect the reproductive potential of their host fungi. The fruit body's characteristics of some species may, therefore, have evolved as defence mechanisms against fungivory in an analogous fashion to the widely discussed attack-defence mechanisms in plant-herbivore interactions (Crawley 1983; Dirzo 1984; Howe & Westley 1988; Rosenthal & Janzen 1979, among others).

Coriolus versicolor is a perennial fungus in logs or stumps of deciduous trees on which it fruits intermittently for several years. The observed negative effects on the reproductive potential of *C. versicolor* caused by the activities of *O. glabriculus* and *C. boleti* (Chapter IV) were, however, limited to the short term and to effects on fruit bodies. This snapshot view overlooks long term effects on the fruiting behaviour and fitness of the fungus as well as feedback effects that fungivory on fruit bodies may have on the mycelial activities other than reproduction.

Any interactive system in which the life span of at least one of the parties extends significantly beyond the time available for experimentation has limited predictive power due to potential disparities between short term and long term responses. The system of the Mexican bean beetle, *Epilachna varivesties* **Mulsat** (Coccinellidae) and soybean, *Glycine max* **(L) Merril** (Fabaceae), provides a clear example of disparities between short term and long term responses. It has been observed that in the short term, herbivory by the beetle on soybean induces defence mechanisms in the plants, so that previously damaged plants are less susceptible to further herbivory, presumable due to defence activation by the previous experience. In the long term plants exposed to herbivores appear to develop susceptibility and suffer higher levels of consumption than previously non-consumed plants (Underwood 1998).

The mycelium of wood-rotting fungi such as *C. versicolor* is in effect restricted to a single log or stump or part of these due to interactions with other individuals of the same or different species (see Williams et al. 1981b). In such habitats, the available surface for the production of fruit bodies is limited for the fungal mycelium. Fungivory on fruit bodies could, therefore, have an overall positive effect on the fitness of *C. versicolor* if the activities of the consumers increase the turnover of fruit-bodies over the seasons, compensating for any short term losses. On the other hand, the drain of resources resulting from producing successive rounds of fruit bodies could lead to more rapid exhaustion of the mycelium or its habitat. In the present study no significant long term effects were detected but there was a tendency for genets exposed to the activities of fungivores to produce more new primordia than those genets that were kept fungivore-free. The inability to demonstrate statistically significant long-term effects may have been due simply to the limited period available for experimentation.

If the observed short term effects on the fitness of the host fungus are cumulative in the long term, one would expect that the host fungus will respond in ways that minimise the damage inflicted by fungivory. By analogy with the recurrent interpretation of the presence of secondary metabolites in plants as an evolutionary response to herbivory or pathogen attack, one may expect to observe similar patterns in wood-rotting fungi as a response to fungivory by ciid beetles. However, alternative evolutionary responses may be envisaged: for example given that fungivory by ciid beetles is restricted to fruit bodies, the fungal mycelium may respond by suppressing fruiting. The intermittent and irregular (i.e. unpredictable) appearance of fruit bodies of wood-rotting fungi may, therefore, be an ecological or evolutionary consequence of fungi escaping fungivory. An analogy of this may well be found in the evolution of prime-numbered and synchronised life cycles of cicadas (Heteroptera: Cicadacea). Periodical cicada nymphs feed underground on root xylem fluids for precisely 13 and 17 years before emerging at a given locality synchronously usually in very large numbers (Williams & Simon 1995). One hypothesis for the evolution of prime-numbered life cycles postulates that prime numbers (13 and 17) are favoured for as life cycles because these cycles are least likely to coemerge, hybridise and break down with other synchronised cycles, as well as to be least likely to be match for potential predators' life cycles (Yoshimura 1997; Karban 1997).

Suppression of sexual reproduction by wood rotting fungi may have significant effects on the rate of wood decomposition. In fungi such as *C. versicolor* that are physically restricted within the boundaries of localised supplies of resources [i.e. unit-restricted according to Cook and Rayner (1984)] there may be trade-offs between mycelial activity, decomposition, and sexual reproduction once all the available space has been occupied by the fungal mycelium. Every unit of energy from the resource expended in mycelial turnover, i.e. vegetative growth, cannot be made later available for sexual reproduction since there is not storage organs in these fungi. Therefore, the suppression of sexual reproduction in unit-restricted fungi may be accompanied by a decrease in mycelial turnover, a process that would maximise energy conservation for future sexual reproduction, but consequently, will decrease the rate of wood decomposition. On the other hand, in non-unit restricted fungi (such as *Armillaria mellea* **(Vahl. ex Fr) Kummer.** or *Phallus impudicus* **Pers.**) capable of mycelium extension beyond immediate resource supplies, suppression of sexual reproduction in a particular resource unit may be accompanied by accelerated mycelium metabolic activity, and consequent decomposition, since resources can be translocated through the mycelium network (cords or rhizomorphs) (see Boddy & Watkinson 1995; Donnelly & Boddy 1997; Wells & Boddy 1995a; Wells & Boddy 1995b; Wells et al. 1998) from areas with incidence of fungivory into fungivore-free areas which may maximise sexual reproduction.

The effects that fungivores may have on the dynamics of wood decomposition are not only of academic interest but are relevant to the conservation, management and restoration of woodland ecosystems. If fungivory on fruit bodies has the potential to affect dynamics of wood decomposition by shifting the allocation of energy from reproduction into mycelial activity and accelerated decomposition (as may be expected in non-unit restricted fungi) or by decreasing mycelium metabolic activities and consequently slowing down decomposition (as may be expected to occur in unit-restricted fungi), human activities such as the picking of fruit bodies may not be as innocuous as is generally thought. Since fruit bodies of wood-rotting fungi are homes for most ciid beetles undirected removal of fruit bodies may have consequences on the diversity and functionality of woodland ecosystems. The same conclusion would apply to the too-prompt removal of dead trees, thus depriving the fungi that occupy them of the opportunity to decay the wood *in situ* and to produce fruit bodies.

To conclude, the acknowledgement of the dynamic nature of wood-rotting fungus-ciid beetle interactions has potentially wide-ranging implications. These range from purely academic aspects such as the use of fungus-fungivore systems for the testing and expansion of ecological and evolutionary theories to more applied issues such as conservation, management and restoration of both specific and functional diversities in woodland ecosystems.

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APPENDIX

1. Mycelium isolations

Fruit bodies of 67 potentially distinct genets were collected for a two-years period. Mycelium was isolated from the inside (flesh) young fruit bodies on 2% malt-agar medium poured in 90 mm petri plates in aseptic conditions. The initial isolations were sub-cultured after three days when mycelium started to develop in order to reduce the risk of contamination. Then, I sub-cultured the isolates every 4 weeks by transferring small section of agar+mycelium from the 4-weeks old plates into plates containing fresh medium. All initial isolates and sub-cultures were incubated at 23° C ±2° C in darkness.

2. Pairing

I used paired-cultures in order to establish whether each mycelium isolate was a genetically distinct individual (see Cook & Rayner 1984; Willimas et al 1981b). The same procedure used to sub-culture was followed to establish paired cultures with the difference that two small sections of agar+mycelium were transferred into the plate containing fresh medium; each section corresponded to a different isolate and they were place toward the centre of the plate with 1 cm gap between them. The plates were then incubated under the same conditions above mentioned. After 3 weeks I checked the plates for the presence of demarcation lines between the isolates. Pigmentation of the demarcation lines varies from light yellowish to highly melinised depending, at least in part, on the strength of the incompatibility between isolates with more pigmented lines between least genetically similar isolates, therefore, least compatibles. When isolates were genetically identical, i.e when they are clones of each other, no demarcation lines were present since the two initial mycelia merge into a single mycelium.

3. Genets in the field

Based on the information from paired cultures and external morphology (i.e. colour and pattern of concentric rings) of fruit bodies I identified the limits for each fruiting genet in the study site. Additional mycelium isolations, sub-culturing and paring were necessary when the morphology of newly formed fruit bodies did not correspond to the morphology of previouly identified genets on the same log section.

From the initial 67 isolates 53 genetically distinct genets were discriminated and delimited in the field. These genets were followed in field studies described in Chapter III.