SPECIES ASSOCIATIONS IN *IPS GRANDICOLLIS* GALLERIES IN *PINUS TAEDA*

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ABSTRACT

This 15-month study examined the species composition and abundance of communities of invertebrates and fungi in *Ips grandicollis* Eichhoff galleries in billets of *Pinus taeda* L. from two localities in north-eastern New South Wales, Australia. Based on monthly sampling of billets which were examined 30 to 60 days after felling, a total of 32 species of insects, six species of Collembola, 30 species of mites, 15 species of nematodes, and 14 species of fungi were recovered. Species constellations were produced for each locality. Species phoretically or parasitically associated with *I. grandicollis* formed a colonising guild, while those species not known to possess such host relationships formed a decay guild. Fungal species had the greatest number of positive associations with species of insects, mites, and nematodes associated with *I. grandicollis*. Total number of mites and of nematodes per unit sampling area was positively correlated to the development stage of *I. grandicollis*. The relationship between billet aspect and percentage moisture content of bark plus cambium influenced gallery nematode counts.

Keywords: bark beetle; community; mites; nematodes; fungi; *Ips grandicollis*; *Pinus taeda*.

INTRODUCTION

A commonly observed feature of bark beetle (Scolytidae:Coleoptera) communities in North America and Europe is the diversity and number of associated organisms present in the subcortical brood galleries (e.g., Dahlsten 1982; Mills 1983). The four dominant groups of organisms present in these subcortical communities are insects, mites, nematodes, and fungi. Barras (1979) has described the scolytid subcortical ecosystem as a "supra-organism" because of the co-evolutionary relationships existing between the bark beetle and its complex of associated organisms.

Insect associates, particularly parasitic Hymenoptera and predaceous Coleoptera, have been extensively surveyed as a prelude to determining their role in regulating bark beetle populations (Kolomietz & Bogdanova 1980; Mills 1983). Dahlsten (1970) catalogued over 70 species of insects associated with the western pine beetle (*Dendroctonus brevicormis* Le Conte) in California, while Moser *et al.* (1971) identified more than 90 species of insects in bolts of *Pinus taeda* infested by the southern pine beetle (*Dendroctonus frontalis* Zimmermann) in Texas. The diversity of mites present in bark beetle galleries has been highlighted in surveys conducted by McGraw & Farrier (1969), Kinn (1971), Moser & Roton (1971), and Moser *et al.* (1974). Species in about 60 families have been recorded as associates of bark beetles (Moeck & Safranyik 1984), using the beetles for transport (phoresy), and feeding either on bark beetle

broods or on some other component of the bark beetle gallery habitat such as nematodes, other mites, fungi, or detritus. The diversity of mites is paralleled by and interrelated with nematode associates of bark beetles. Studies by Rühm (1956) in Europe and Massey (1974) and Poinar (1975) in North America revealed the integral role nematodes play in the scolytid community. Most interest has centred on the numerous endoparasitic nematode species. Fungi have received considerable attention because many species have symbiotic or mutualistic relationships with bark beetles (Graham 1967) and are involved in the processes of overcoming the living trees' defence mechanisms. Thirty-eight genera of fungi have been identified as associates of conifer-killing bark beetles in North America (Whitney 1982).

Ips grandicollis is the most economically important of a small number of bark beetles established in species of *Pinus* in Australia (Neumann 1987). Several studies have been completed on aspects of biology of *I. grandicollis* in Australia (Morgan 1967; Neumann & Morey 1984; Witanachchi 1980, 1986; Witanachchi & Morgan 1981) but little has been published on the associates (Vaartaja 1967; Gibb & Fisher 1986; Simpson & Stone 1988; Stone 1988). As well as determining the species composition and species associations of the mite, insect, nematode, and fungal populations in *I. grandicollis* subcortical communities in infested *Pinus taeda* billets from two different localities in north-eastern New South Wales, this study was designed to examine the effects on species abundance of the following factors: percentage moisture content of the billet barks; aspect (i.e., bottom or top, north- or south-facing surfaces of the billet); stage of bark beetle's phenological development within its brood galleries.

MATERIALS AND METHODS

Two *P. taeda* plantations were selected in November 1986 for the survey. One plantation, in Barcoongere State Forest (S.F.), sited on coastal sandy surface soil deposited over older clay, has an elevation of 20 m and is located 41 km north of Coffs Harbour. The second plantation, in Mount Mitchell S.F., sited on Permian adamellite, has an elevation of 980 m and is located 35 km east of Glen Innes. Clearfelling and thinning operations in both plantations had produced large amounts of logging debris which supported large *I. grandicollis* populations. Records of the daily temperature and rainfall were obtained from two thermohygrographs, both housed in Stevenson's screens, and two raingauges, sited at either the study plot in Barcoongere S.F. or at a nearby forest camp in Mt. Mitchell S.F.

On the first day of each month, a single *P. taeda* tree, planted in 1962, was sampled at each site. The sample trees were of approximately equal height, diameter at breast height over bark (dbhob), and symmetry. After felling, two billets of 70 cm length and approximately 15 cm diameter over bark were cut from each tree. Care was taken to ensure that the billets were free of branches and the bark was not damaged. The billets were then aligned east-west on the ground and their ends and upper surface labelled to indicate this orientation. Each billet was left in the plantation and exposed to *I. grandicollis* attack for either 28 days or 58 days before being sealed in individual PVC cylinders and transported by rail to Sydney. A further 2 days were allowed for rail transportation and so either 30 days or 60 days elapsed between the time the trees were felled and the billets were initially exposed to *I. grandicollis* attack, and the time when the billets were received in the laboratory for examination.

In the laboratory each billet was marked into quadrants (i.e., top, bottom, north side, or south side) according to its previous orientation on the ground. Seven *I. grandicollis* entrance holes were selected randomly in each quadrant and a 4-cm square was marked on the bark around each. If fewer than seven *I. grandicollis* entrance holes were present, all holes were marked for sampling. Marked bark squares from each quadrant were chiselled out, removing a layer of outer sapwood, the cambium-phloem tissues, and bark. The squares were immediately placed into separate, new, small plastic bags. *Ips grandicollis* gallery systems weaken the cambial interface between the inner bark and outer sapwood, hence each bark square consisted of an outer sapwood layer and an inner bark layer with the galleries present on both surfaces where they met. Three bark squares from each quadrant were randomly selected and used for sampling insects, mites, and fungi, another three for sampling nematodes, and the seventh to determine bark moisture content.

Insects and mites were sampled by examining the gallery systems in each bark square under a stereomicroscope and picking off the specimens for storage in 70% ethanol. Care was taken to break up beetle frass to collect any mites not initially visible. Mites were subsequently mounted in Hoyer's medium and examined under a compound microscope. Fungi present in the *I. grandicollis* galleries were qualitatively assessed in each bark square that had been sampled for insects and mites. Fungal species were identified after direct microscopic examination or after subculturing on 1.2% malt extract agar.

Nematodes were sampled using a modified Baermann funnel technique. The inner surface of the sapwood layer was placed on a paper tissue nestled in an 8-cm-diameter 500-mm-mesh sieve. The sieve, slightly elevated on plasticine, was placed in a glass petri dish with enough water to moisten the galleries. After an overnight soaking the extracted nematodes were washed into a circular nematode-counting dish and counted. Subsamples taken from the three inner circles of the counting dish were fixed in a formalin:propionic acid:glycerol:water solution (8:1:2:89) and then taken through two changes of Stanhorst's solution before being mounted in glycerol for microscopic examination (Massey 1974).

For each bark square, the average stage of development of the beetles was assigned a rank according to the following categories:

1 = nuptial chamber only and/or galleries commenced, no eggs;
2 = eggs only and/or eggs plus first instar larvae;
3 = first instar larvae only and/or second instar larvae;
4 = third instar larvae only or third instar larvae plus pupae;
5 = pupae only and/or callow adults
6 = most of the callow adults emerged.

Moisture content of bark squares was estimated gravimetrically by oven drying at 105 °C for 24 hours. Moisture content was expressed as a percentage of dry weight.

Computation of the Shapiro-Wilk statistic (W) on the count data indicated that the data were non-normal. Logarithmic and square root transformations failed to normalise the data so non-parametric analysis techniques were used. Comparisons were made using Chi-squared tests and correlation between variables determined by calculating Spearman rank correlation coefficients (r_s). In the analysis associated with

the bark percentage moisture content, billet aspect and the ranks assigned to the developmental stages of *I. grandicollis*, multiple mean comparisons, analysis of variance, analyses of covariance, and regressions were undertaken on the normalised rank scores using the Blom option of the Rank Procedure in the SAS® version 6 statistical package (Anon. 1985).

Two matrices based on a coefficient of association presented by Krebs (1978) were prepared for the 25 most commonly collected species from Barcoongere and for 21 species from Mt. Mitchell (all species occurring less than five times in the total sample were excluded from the analysis). The two species association matrices have been diagrammatically illustrated as species "constellations" showing the positive association relationships between each species (Fig. 1 and 2). The size of each symbol represents the relative abundance of each species within each of the four groups (insects and collembolans, mites, nematodes, or fungi).

RESULTS

Species Composition, Abundance, and Associations

Total numbers of arthropods collected from the bark squares sampled at both Barcoongere and Mt Mitchell after either 30 or 60 days' exposure to *I. grandicollis* over the survey period of 15 months are presented in Appendices 1 and 2. A total of 67 arthropod species was recovered, consisting of six species of Collembola, 32 species of insects, and 30 species of mites. The relative abundance of the 15 nematode species sub-sampled from the nematode extraction procedure is shown in Appendix 3. The number of bark squares from which each fungal species was identified is given in Appendix 4. The life stages sampled and the probable feeding habit of each species are also listed. Data on feeding habits were obtained either from dissection or from previous reports.

Over-all differences in species abundance between the two sites were highly significant for each group of associates ($p \leqslant 0.001$). Forty-five associate species had significantly different ($p \leqslant 0.05$) counts, with the greatest proportion of significant numerical differences between the two sites being among nematode species. Over-all, more organisms were collected from the Barcoongere site than from Mt Mitchell. The highest total monthly counts for insects, mites, and nematodes were obtained during the summer months at both sites and total monthly counts for mites and nematodes were greater in spring than in autumn.

The mycetophagous mite *Histiostoma varia* Woodring and Moser was numerically the dominant mite species, accounting for more than half the total number of mites collected. The second most abundant mite species was *Macrocheles boudreauxi* Krantz which is a generalist predator, while the mycetophagous mite *Pygmephorus bennetti* Cross and Moser was the third most abundant mite species identified. All three species of mites were observed adhering to *I. grandicollis* adults, with *H. varia* being in the form of hypopi densely clustered within the elytral declivity.

The number of nematodes sub-sampled for species identification was linearly correlated to the total number of nematodes collected ($0.37 \leqslant r_s \leqslant 0.45$, $p \leqslant 0.001$) and therefore represented a constant proportion of the total number of nematodes sampled. The most numerous dominant nematode species, *Parasitorhabditis hastulus* Massey, accounted for more than half of the nematodes sub-sampled. The other two

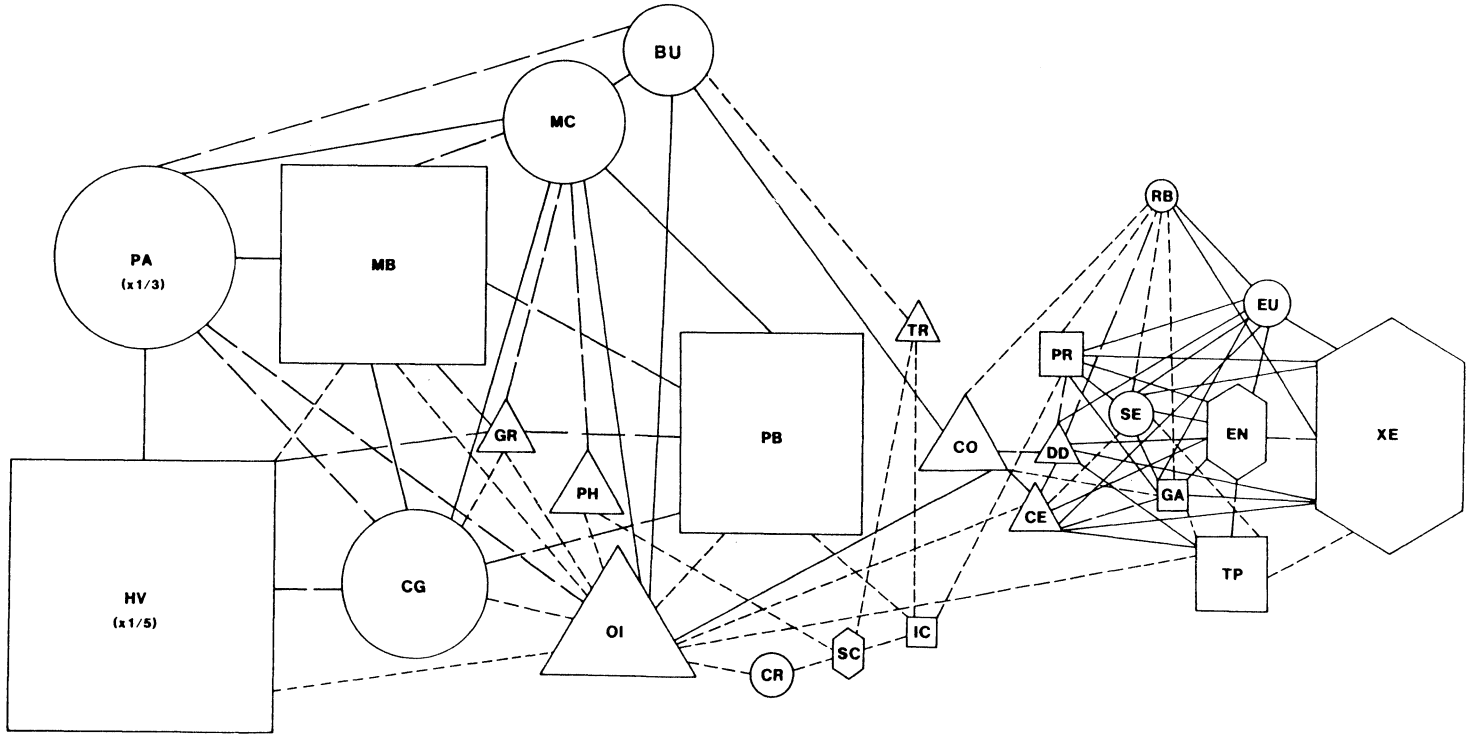

FIG. 1–Species "constellation" based on a coefficient of association (Krebs 1978), showing positive correlations of the 25 most abundant *Ips grandicollis* brood gallery associates sampled from *Pinus taeda* billets exposed to *I. grandicollis* attack in Barcoongere S.F. for either 30 or 60 days, over a period of 15 months. The size of the symbols represents the relative abundance of the species.

KEY: ———— $p < 0.1\%$; ——— ——— $1.0\% > p > 0.1\%$; — — — — — $5.0\% > p > 0.1\%$

mites □
nematodes ○
fungi △
insects/Collembola ⬡

BU *Bursaphelenchus* sp.
CE *Ceratocystiopsis* sp. B
CG *Contortylenchus grandicolli*
CO Coelomycete sp. A
CR *Cryptophelenchus* sp.
DD *Dactylaria superba*
EN *Entomobrya* sp.
EU *Eudorylaimus* sp.
GA *Gamasellodes* sp.
GR *Graphilbum* sp.
HV *Histiostoma varia*
IC *Iponemus confusus oriens*
MB *Macrocheles boudreauxi*
MC *Mikoletzkya calligraphi*
OI *Ophiostoma ips*
PA *Parasitorhabditis hastulus*
PB *Pygmephorus bennetti*
PH *Phanerochaete* sp.
PR *Proctolaelaps australis*
RB *Rhabditonema* sp.
SC *Bradysia* sp.
SE *Seinura* sp.
TP *Tyrophagus putrescentiae*
TR *Trichoderma* sp.
XE *Xenylla* sp.

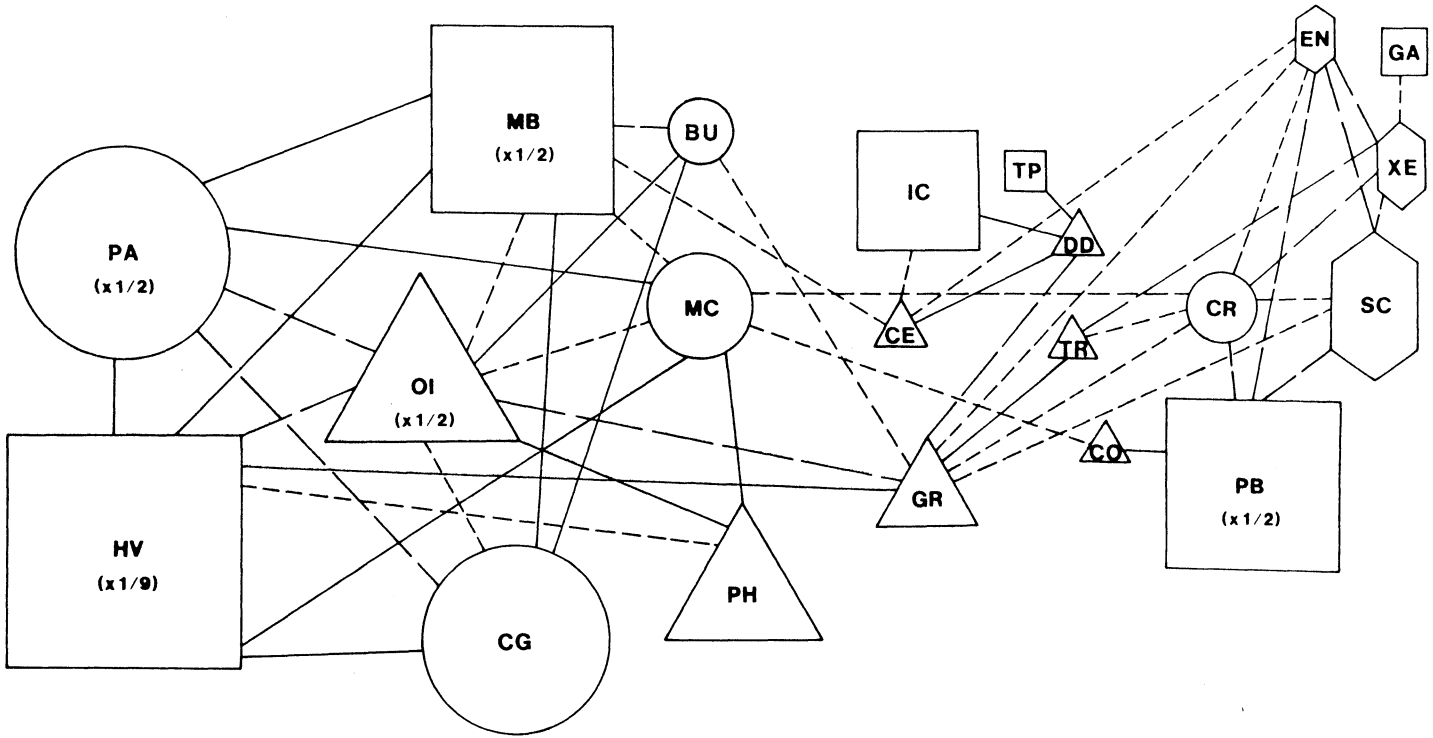

FIG. 2–Species "constellation" based on a coefficient of association (Krebs 1978), showing positive correlations of the most abundant *Ips grandicollis* brood gallery associates sampled from *Pinus taeda* billets exposed to *I. grandicollis* attack in Mt Mitchell S.F. for either 30 or 60 days, over a period of 15 months. The size of the symbols represents the relative abundance of species.

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numerically dominant nematode species, *Mikoletzkya calligraphi* Massey and *Contortylenchus grandicolli* (Massey), are both mycetophagous and parasitic depending on their life stage and *M. calligraphi* was frequently observed in a dauer juvenile stage in small clusters along the dorsal inter-segmental folds of *I. grandicollis* adults. The dauer stage of a fourth nematode species, *Bursaphelenchus* sp., was commonly observed in radial clusters centred on one or more of the abdominal spiracles of adult beetles. The free living stages of this nematode were, however, sampled only infrequently.

Although six species of Collembola and 32 species of Insecta were collected from the bark squares, the majority of species were recovered at very low frequencies (Appendix 1). Only two collembolan species (an *Entomobrya* sp. and *Xenylla* sp.) and a sciarid species (*Bradysia* sp.) were recovered regularly and these were generally from galleries where the *I. grandicollis* brood had developed beyond the early larval stages. Three *I. grandicollis* biological control agents, *Roptrocerus xylophagorum* (Ratz), *Dendrosoter sulcatus* Mues., and *Temnochila virescens* (F.), had been introduced at both sites in autumn 1986; however, during this trial their impact appeared to be minimal, since they occurred within the *I. grandicollis* subcortical galleries at very low densities. The fungal species most frequently recovered from the bark squares was *Ophiostoma ips* (Rumb.) Nannf., a sapwood-staining fungus commonly found associated with *I. grandicollis* in North America. The second and third most commonly sampled fungi were *Phanerochaete* sp. and a coelomycete species (Appendix 4). Yeasts were observed in the brood galleries but were not identified.

The species "constellation" produced from the matrix of coefficients of association for species collected from Barcoongere (Fig. 1) possesses two distinct clusters of species with strong positive associations within each cluster and with four fungal species linking the two clusters. In the left-hand side cluster there are six mycetophagous species but only predators, omnivores, or saprophages occur in the second cluster. The left-hand sections of both constellation diagrams possess the same species with very similar associations; however, the right-hand sides of the two diagrams differ in that more species are present in the Barcoongere diagram and the associations between these species are highly significant ($p \leqslant 0.001$). The right-hand side of the Mt Mitchell diagram (Fig. 2) does not form a distinct cluster and the associations are weaker ($p \leqslant 0.05$). The constellation diagram structures show those species phoretically or parasitically associated with *I. grandicollis* positioned on the left and centre of each diagram while those species not known to possess such host relationships occur on the right-hand side. Numerical dominance of a particular species is not related to the number of strong positive associations (e.g., *H. varia*). Fungal species possess the greatest number of positive associations with other species.

Influence of Bark Percentage Moisture Content and Billet Aspect

Total annual rainfall was similar for the two sites (Barcoongere 1563 mm; Mt Mitchell 1597 mm). Although seasonality was similar between the two sites, Mt Mitchell had a monthly mean temperature approximately 5° to 6°C lower than Barcoongere. Percentage moisture contents of bark squares sampled from billets exposed to 30 days of *I. grandicollis* attack from both Barcoongere and Mt Mitchell

were positively correlated with the respective monthly total precipitation ($0.67 \leq r_s \leq 0.95$, $p \leq 0.01$).

When mean percentage moisture contents of bark squares were compared with quadrants, it was found that the billet surface resting on the ground (bottom quadrant) had a significantly higher ($p \leq 0.05$) mean percentage moisture content than the other three quadrants for Barcoongere at both 30-day and 60-day exposure periods and for Mt Mitchell after 60 days' exposure to *I. grandicollis* attack (Table 1). Bark samples from each billet quadrant from Mt Mitchell had a bark moisture content approximately 20% higher than the corresponding samples from billets from Barcoongere (Table 1). The percentage moisture content after 60 days' exposure to *I. grandicollis* was higher than that from billets exposed to *I. grandicollis* for only 30 days (Table 1) for both sites.

TABLE 1–Percentage moisture content of 4-cm bark squares sampled from the four aspects on *Pinus taeda* billets exposed to *Ips grandicollis* attack for 30 or 60 days over a period of 15 months in Barcoongere or Mt Mitchell State Forests

Barcoongere S.F.				Mt Mitchell S.F.			
30 days		60 days		30 days		60 days	
Billet aspect*	Mean moisture content of bark (%)	Billet aspect	Mean moisture content of bark (%)	Billet aspect	Mean moisture content of bark (%)	Billet aspect	Mean moisture content of bark (%)
B	68.5 a†	B	72.3 a	B	89.9 a	B	90.8 a
S	64.1 ab	S	65.9 ab	S	83.8 a	S	81.7 b
T	61.2 b	N	64.6 b	T	82.8 a	N	80.4 b
N	60.4 b	T	64.5 b	N	81.9 a	T	78.9 b
d.f.	270		294		225		289

* B = bottom, S = south-facing, T = top, N = north-facing, d.f. = degrees of freedom

† The means designated by the same letter in each column are not significantly different ($p > 0.05$) using Tukey's Studentised Range (HSD) Test

For the Barcoongere billets, significantly more mites were collected from the top quadrant than from the bottom quadrant (Table 2). Comparison of nematode counts per 4-cm bark square from each of the four billet quadrants produced a statistically more highly significant difference ($p \leq 0.0001$) than was obtained for the mite counts ($p \leq 0.05$) and it occurred to a greater extent (Table 2). The order of quadrants in terms of nematode counts was similar to that of mite counts (Table 2).

Analysis of variance on normalised ranks obtained from nematode counts per 4-cm bark square between date of collection and billet aspect revealed a highly significant ($p \leq 0.0001$) interaction. Examination of the total nematode counts from each billet for every month revealed the reason for this interaction. In the cooler months, bark squares from the top quadrant produced the highest numbers of nematodes; however, in the hotter months, the highest number of nematodes were extracted from either the north-facing or occasionally the south-facing billet quadrants. Bark squares from the billet's bottom surface or occasionally the south-facing quadrant had the fewest nematodes.

TABLE 2–Mite and nematode counts per 4-cm bark square from the four aspects on billets exposed to *Ips grandicollis* attack for 30 or 60 days in Barcoongere or Mt Mitchell State Forests, utilising the Tukey's Studentised Range Test on normalised ranks

Barcoongere S.F.				Mt Mitchell S.F.			
30 days		60 days		30 days		60 days	
Mites							
Top	a*	Top	a	Top	a	Top	a
North	ab	North	ab	North	a	North	a
South	ab	South	ab	South	a	South	a
Bottom	b	Bottom	b	Bottom	a	Bottom	a
d.f. 230		246		193		253	
Nematodes							
Top	a	Top	a	Top	a	North	a
North	a	North	b	North	b	Top	a
South	b	South	c	South	c	South	b
Bottom	c	Bottom	d	Bottom	d	Bottom	c
d.f. 288		292		199		252	

* Billet aspects followed by the same letter are not significantly different ($p > 0.05$)

To determine if there were interactions between nematode counts and other measured factors, several covariance analyses were carried out using normalised rankings of the nematode counts (details of analysis of covariance results not presented). There were significant interactions between billet quadrant and the three variables — monthly mean temperature, monthly total precipitation, and bark square percentage moisture content ($p \leq 0.0001$) for the three interactions). Examination of the nematode counts at each level of each factor revealed a similar trend in that the relative magnitude of nematode counts per billet aspect varied through the season as was observed for the collection dates. No significant interactions were detected for the mite counts when examining these relationships with the factors collection date, temperature, precipitation, or bark percentage moisture content against billet aspect ($p \leq 0.1$ for the four interactions).

Influence of *I. grandicollis* on Associate Species

Ips grandicollis is solely responsible for the physical construction of the brood gallery system from which all the associate species have been recovered. These species were totally absent from the cambium-inner bark interface in billets that had not been attacked by *I. grandicollis* after 30 or 60 days' exposure on the ground at Barcoongere or Mt Mitchell. The only exceptions were some ubiquitous, airborne, fungal species which can enter this subcortical region via the billet ends. After 60 days, however, hyphae penetration rarely exceeded 10 to 15 cm from the ends.

In Appendices 1 to 4 the numbers of each associate species are compared for both 30 days' and 60 days' exposure. Thirty species out of a total of 78 species collected from Barcoongere and 20 species out of a total of 55 for Mt Mitchell had significantly different counts ($p \leq 0.05$) between the 30-day exposure period and the 60-day exposure period. At both localities, the numbers of insect, collembolan, and mite species and total counts of insects and collembolans increased when the exposure

period was extended from 30 to 60 days (Appendices 1 and 2). Nematode total counts, however, noticeably decreased with the longer period of exposure (Appendix 3).

Both total mite counts and total nematode counts per 4-cm bark square were positively correlated to the developmental stage of *I. grandicollis* (mites, $0.205 \leq r_s \leq 0.50$, $p \leq 0.05$; nematodes, $0.26 \leq r_s \leq 0.41$, $p \leq 0.01$). There was a strong relationship between mite numbers per 4-cm bark square and developmental stage of *I. grandicollis* in billets from Barcoongere after 30 days' exposure (Fig. 3a). After 60 days' exposure

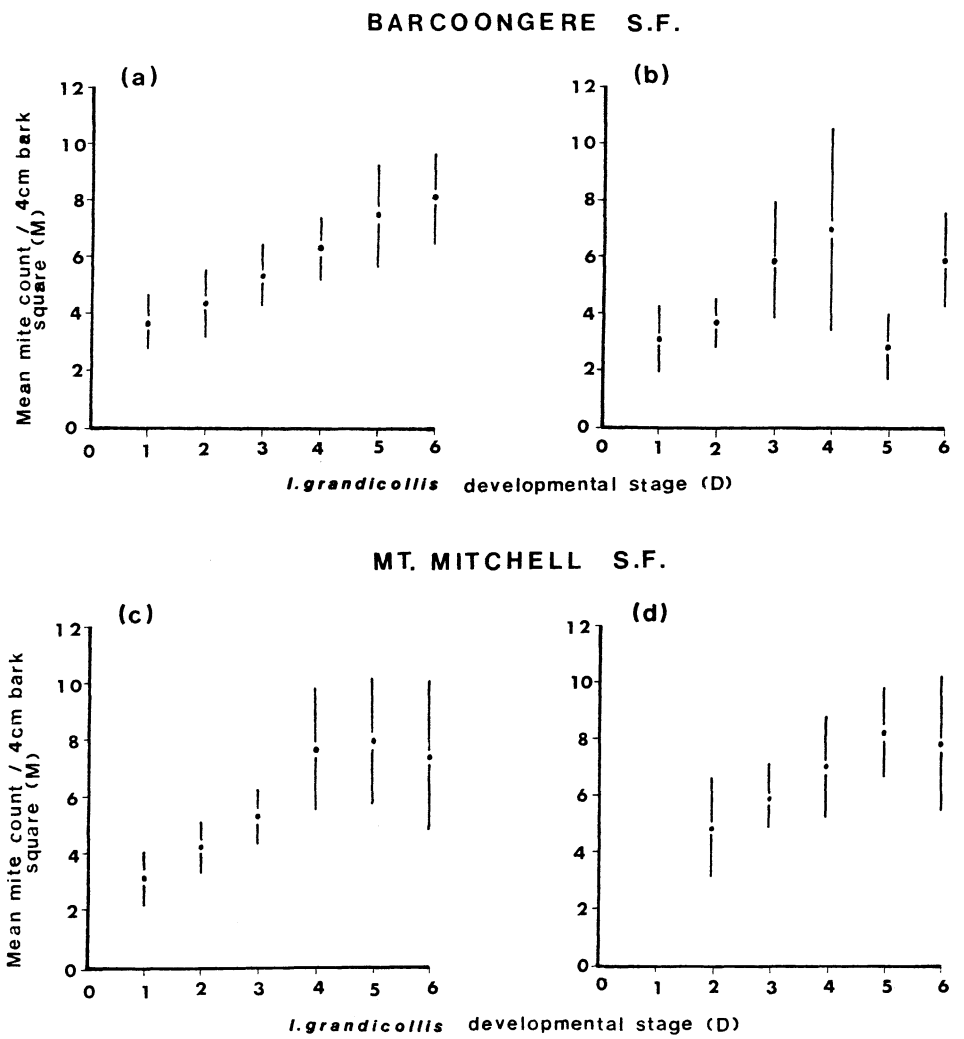

FIG. 3–Mean mite counts per 4-cm bark square against *Ips grandicollis* development stage ranking (1–6): (a) for Barcoongere after 30 days' exposure, $M = 4.7\ LnD - 1.5$, $r^2 = 0.98$, $p = 0.0001$; (b) after 60 days' exposure, $M = 0.56\ D + 2.2$, $r^2 = 0.24$, $p = 0.26$; (c) for Mt Mitchell after 30 days' exposure, $LnM = 0.98\ LnD + 0.4$, $r^2 = 0.95$, $p = 0.0008$; (d) after 60 days' exposure, $M = 4.6\ LnD - 1.5$, $r^2 = 0.97$, $p = 0.0001$. The vertical bars around each point represent the 95% confidence limits.

there was a linear increase in mite numbers up to developmental rank No. 4 (presence of *I. grandicollis* third instar larvae and/or pupae) when mite numbers significantly decreased, only to increase again when most of the *I. grandicollis* callow adults had emerged (Fig. 3b). Comparable results were obtained from Mt Mitchell and are best described by logarithmic equations (Fig. 3c and 3d). A similar pattern was observed when nematode numbers were plotted against *I. grandicollis* developmental stage (Fig. 4a–d) including the distinct decrease and subsequent increase after *I. grandicollis* developmental stage No. 5 (Fig. 4b).

At Barcoongere there was a gradual increase of species of fungi until *I. grandicollis* stage No. 5, after which callow adults had emerged (rank No. 6) and there was a dramatic increase in the frequencies of the fungal species. Though the increase in frequency of occurrence of fungi from bark squares from Mt Mitchell was not linear, the dramatic increase at callow emergence still occurred. Insect and Collembola abundance behaved very similarly to the fungi when plotted against *I. grandicollis* developmental stage, with a large increase in the occurrence of both larval and adult forms after *I. grandicollis* callow emergence.

Finally, in an attempt to determine the relative importance of *I. grandicollis* developmental stage and bark square percentage moisture content in influencing mite and nematode numbers, stepwise regression was done utilising the normalised rank procedure. Although the models for both mite and nematode counts were significant ($p \leq 0.05$) the resultant coefficients of determination (r^2) were relatively small (approximately 0.2 to 0.4). The *I. grandicollis* developmental stage accounted for at least 65% of the total value of the coefficient of determination (r^2) for all four sampling regimes for the mite counts (i.e., for Barcoongere and Mt Mitchell and for 30- and 60-day exposure periods) and for nematodes for the 30-day exposure period at both sampling sites. However, bark percentage moisture content contributed more to the total model coefficient of determination (r^2) than the *I. grandicollis* developmental stage factor for nematode counts from Barcoongere and Mt Mitchell after 60 days' exposure to *I. grandicollis* attack.

DISCUSSION

There appears to be no single published report that has attempted to investigate all the arthropod fauna, as well as the abundant nematode and fungal associates of a bark beetle subcortical community. Although the most extensive listing of species associates of *I. grandicollis* in Australia is presented in Appendices 1 to 4, the species diversity is much less than that presented in listings of bark beetle associates from either North America or Europe (e.g., Moser & Roton 1971; Massey 1974). The probable reason for this is that *I. grandicollis* is not indigenous to Australia and neither is the host *P. taeda.*

The relative complexities of the communities collected from Barcoongere and Mt Mitchell are illustrated in the species constellations produced from the pair-wise association matrices (Fig. 1 and 2). At each locality there appear to be two guilds of organisms, a colonising guild and a decay guild, with several linking fungal species. The colonising guild, occurring on the left-hand side of each diagram, consists of organisms known to be phoretically associated with *I. grandicollis.* All of these species, with the possible exception of the *Bursaphelenchus* sp., have been recorded previously in North America and are presumed to have been introduced into Australia with the bark beetle.

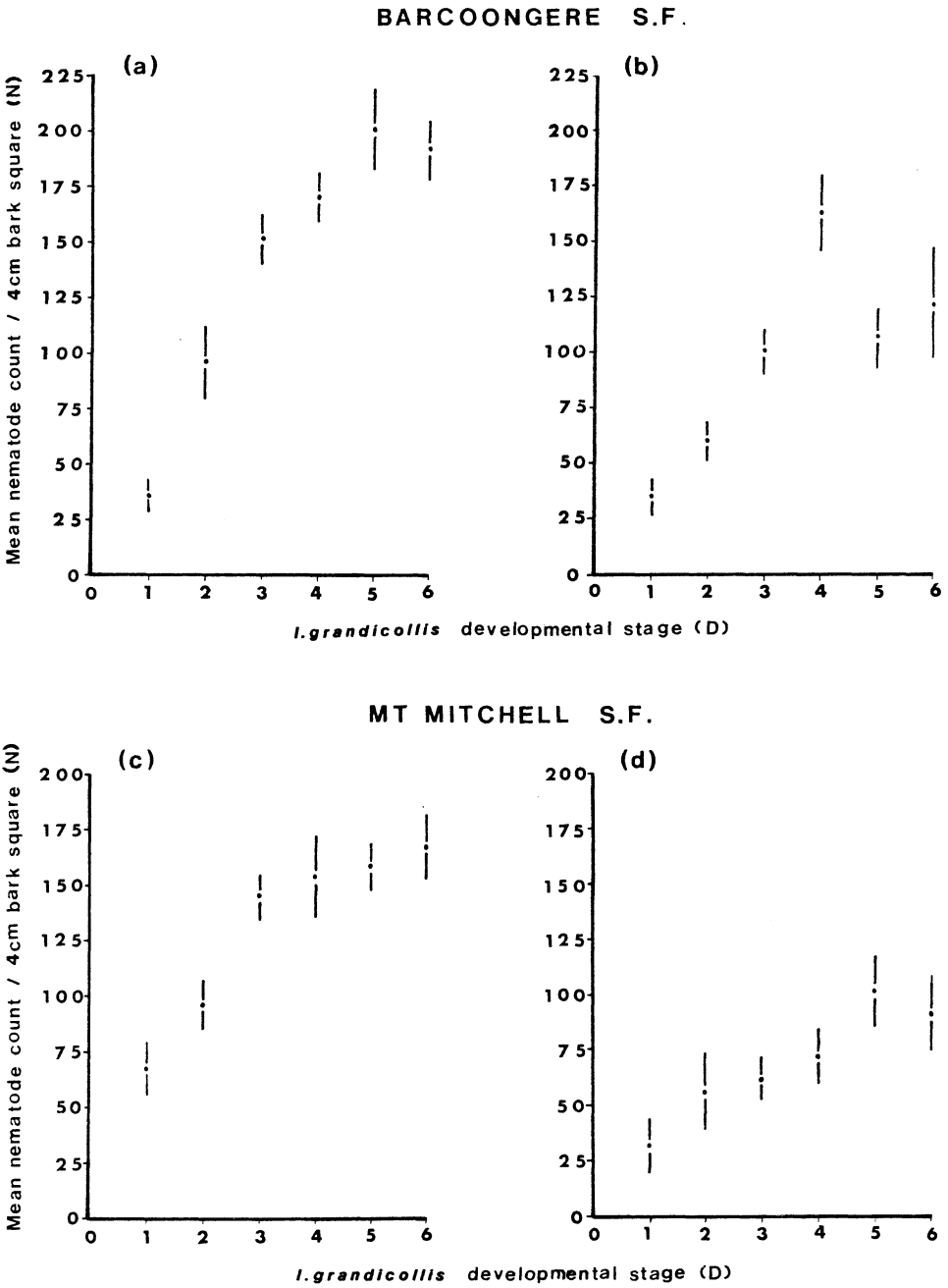

FIG. 4–Mean nematode counts per 4-cm bark square against *Ips grandicollis* developmental stage ranking (1–6): (a) for Barcoongere after 30 days' exposure, N = 130.7 LnD – 62.6, $r^2 = 0.95$, p = 0.0002; (b) after 60 days' exposure, N = 13.7D + 30.1, $r^2 = 0.32$, p = 0.18; (c) for Mt Mitchell after 30 days' exposure, N = 108.7 LnD – 39.6, $r^2 = 0.96$, p = 0.0004; (d) after 60 days' exposure, N = 58.3 LnD – 15.8, $r^2 = 0.88$, p = 0.0017. The vertical bars around each point represent the 95% confidence limits.

The second cluster or decay guild comprises organisms that become numerically dominant on completion of the larval stages of the bark beetle. Many of these organisms could not be identified to species level with the available taxonomic keys, and the majority of species are presumed to be native to Australia. The colonising guild converts the fresh intact tissues of the inner bark and cambium into frass material and, hence, greatly alters the chemical and physical nature of the substrate. Organisms of the decay guild exploit the frass. Thus the requirements of the two guilds of organisms are different.

A major difference between the billets collected from Barcoongere and Mt Mitchell was the frequency of recording the sixth ranking of *I. grandicollis* developmental stage (i.e., majority of callow adults emerged). This occurred much more frequently in billets from Barcoongere than from Mt Mitchell and can be attributed to the higher monthly mean temperatures recorded from Barcoongere. This also explains why a greater number of species were recovered from the Barcoongere billets. Colonising guilds at the two sites have very similar species compositions. However, under the cooler conditions occurring at Mt Mitchell, the 60-day exposure period was not long enough for the complete transition into the decay guild. It is anticipated a decay guild would have been more clearly defined in the species constellation diagram for Mt Mitchell if billets were exposed to *I. grandicollis* attack for 70 to 80 days.

The numerically dominant mite and nematode species within the colonising guilds from both sites were mycetophagous. These species were observed feeding directly on the fungal species known to be transmitted by the adult bark beetle (e.g., *O. ips*). Although several mite species belonging to genera known to be predaceous were collected (e.g., *Proctolaelaps* spp. and *Asca* spp.). only one predatory mite species was prominent in the colonising guild and this was *Macrocheles boudreauxi*. The adult females of this aggressive generalist predator were often observed in numbers of one to five clinging to emerging callow *I. grandicollis* adults. The other predatory mites did not become abundant until after the callow adults had begun to emerge. Similarly, insect and collembolan species in either larval or adult stage, did not become obvious until after the *I. grandicollis* larvae had pupated. These species may be attracted to the decaying frass material generated by the *I. grandicollis* larvae.

The frequency of the fungal xylobionts also greatly increased on completion of the bark beetle larval stages. This would be due to both the time exposure factor and the altered micro-environmental conditions. There is some evidence to suggest that the significant increase in fungi occurring after *I. grandicollis* pupation could contribute to the observed decline in abundance of the mobile mesofauna species that belong to the colonising guild. Although the number of species increases as organisms belonging to the decay guild move into the subcortical community, the over-all numerical abundance of organisms actually decreases with the decline of the numerically dominant species belonging to the colonising guild. This correlation can also be observed on a monthly basis with an increase of fungi occurring in the autumn months compared to the spring months, especially for Barcoongere billets after 30 days' exposure, while there were lower numbers of mites and nematodes present in the *I. grandicollis* brood galleries during the autumn months than in the spring months.

Percentage moisture content of the bark and cambium region was shown to influence the subcortical community through the observed relationship between billet

aspect and bark percentage moisture content and mite or nematode counts (Tables 1 and 2). The observed increase in bark percentage moisture content with increased length of exposure to the bark beetle has also been reported by Wallace (1953). In his study of insect fauna of pine stumps, Wallace related increased moisture content to increased decay.

Although annual rainfall was similar at the two sampling sites, the lower ambient temperatures at Mt Mitchell State Forest ensured that mean bark moisture contents were approximately 20% higher than those recorded from Barcoongere billets. The lower temperatures may also explain the lack of any significant difference in bark moisture content between the four billet quadrants for Mt Mitchell after 30 days' exposure. For the other three sampling regimes, bark squares from the bottom billet quadrant which is in constant contact with the ground, were significantly moister than squares from the other billet aspects. The moister bottom billet aspect could have been the site of entry for soil- and litter-borne fungi and their associated arthropods into the subcortical community. Those soil-borne fungi may be less favoured by the mycetophagous mites and nematodes of the colonising guild than those fungal species directly associated with *I. grandicollis*, e.g., *O. ips*. The significant decrease in mite and nematode counts in the bottom quadrant compared to the top quadrant from billets from Barcoongere, however, is most likely to be due to the observed preference of *I. grandicollis* for the warmer (top and north-facing) quadrants, especially during the spring and autumn months. It was not until the warmer months when the *I. grandicollis* populations attained higher attack densities that adults attempted to enter the subcortical region near the bottom surface of billets.

Nematodes require a continuous water film in which to move. This reliance on moisture is reflected in the observed differences in nematode counts between several of the billet aspects from each sampling regime. The sensitivity of nematodes to moisture content partially explains the observed interactions between billet aspect and the external factors, ambient temperature and precipitation, as well as bark percentage moisture content. Nematode counts were highest during the hottest months, on the north- and south-facing billet quadrants. However, during the cooler months more nematodes were recovered from the top billet quadrant. Mite populations appeared to be less dependent on bark percentage moisture content. No significant differences in mite counts were detected between the quadrants in the Mt Mitchell billets while, for billets from Barcoongere there was a significant difference only between the top and bottom quadrants.

The changes that occur in mite and nematode abundance at the time of callow adult emergence are illustrated in Fig. 3 and 4. There is a well-defined inflection point in the curves for billets from Barcoongere after 60 days' exposure. However, it appears to be just commencing in those billets from Mt Mitchell. This is in accordance with the results illustrated in the species constellation diagrams. It is suggested that the point of inflection on the plots in Fig. 3b and 4b represents the transitional phase between the colonising guild associated with *I. grandicollis* and the initial decay guild. As was mentioned earlier, if the exposure period was extended to approximately 80 days, this transitional phase would probably be detected in billets from Mt Mitchell.

The regressions of mite and nematode counts *v. I. grandicollis* developmental stage or bark percentage moisture content summarise the relative impact these two factors

have on both mite and nematode abundance. During the period from initial gallery construction to pupation the bark beetle dominates the subcortical community which is represented by the colonising guild. However, after pupation, the influence of *I. grandicollis* rapidly declines, while influence of bark percentage moisture content increases, especially on nematode abundance. Also of importance is the significant increase in the frequency of several fungal species which could influence this transitional phase between the two guilds.

The introduced bark beetle *I. grandicollis* is the predominant insect colonising subcortical tissues of logging slash and dead trees of *Pinus* spp. in Australia. The presence of subcortical communities created by only one scolytid species provided a rare opportunity to study a discrete subcortical community which was not complicated by other similarly behaving beetle species. Thus it has been possible in this study to present specific information on the species composition and structure of the associated community occurring in the brood galleries of *I. grandicollis* from two sites in north-eastern New South Wales.

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APPENDIX 1

HEXAPOD BROOD GALLERY ASSOCIATES OF *IPS GRANDICOLLIS* INFESTING *PINUS TAEDA* BILLETS

Total number of bark squares from which each species was collected and total number of individuals collected per 4-cm bark square sampled over a period of 15 months from either Barcoongere or Mt Mitchell State Forests after 30 or 60 days' exposure to *I. grandicollis* attack, life stages sampled from the subcortical galleries, and proposed feeding habit for each species

Class, order, family, and species	No. of bark squares from which each species was counted	Total number of individuals counted				Life stage	Feeding habit
		Barcoongere		Mt Mitchell			
		30 days N = 130*	60 days N = 146	30 days N = 102	60 days N = 113		
Class Collembola							
Order Collembola							
Hypogastruridae							
Xenylla sp.	47	5	140	9	19	A, N†	Saprophagous or mycetophagous
Neanuridae							
Setanodosa sp.	1				1	A	Saprophagous or mycetophagous
Entomobryidae							
Entomobrya sp.	29	2	62		12	A, N	Saprophagous or mycetophagous
Sinella sp.	1		1			A	Saprophagous or mycetophagous
Isotomidae							
Cryptopygous sp.	2	1	1			A, N	Saprophagous or mycetophagous
Folsomia sp.	1		1			A	Saprophagous or mycetophagous
Class Insecta							
Order Thysanura							
Lepismatidae							
Heterolepisma sp.	1	1				A	Saprophagous or mycetophagous
Order Blattodea							
Blaberidae							
sp. B	1	1				A	Saprophagous?
Order Isoptera							
Rhinotermitidae							
Coptotermes sp.	1		3			W	Cellulose
Order Psocoptera							
sp. C	3	1	1	1		N	Saprophagous or mycetophagous
Order Coleoptera							
Anobiidae							
Ernobius mollis (Linnaeus)	2			1	1	A	Phloem/cambium
Colydiidae							
Bitoma serricollis Pasc.	13	2	28			A, L	Predaceous or mycetophagous
sp. D	5			5	3	A, L	Predaceous or mycetophagous
Curculionidae							
Aesiotes notabilis Pascoe	3				3	A	Phloem/cambium
Xyleborus perforans (Wollaston)	2		1		1	A	Sapwood

APPENDIX 1 cont.

Laemophilidae							
Laemophiloeus amabilis (Olliff)	7		10			A, L	Saprophagous or mycetophagous
Nitidulidae							
Brachypeplus koebelei Blkb.	6		19			A, L	Omnivorous or mycetophagous
Silvanidae							
Hyliota militaris Erichson	1				4	L	Mycetophagous
Silvanus lateritius (Brown)	7	6	3			A, L	Mycetophagous?
Silvanus sp.	1		1			A	Mycetaphagous?
Staphylinidae							
Atheta sp. A	3		3			A	Predaceous?
Atheta sp. B	2			1	1	A	Predaceous?
Conosoma sp.	2				3	A	Predaceous?
Eleusis sp.	2	1	1			A	Predaceous?
Gyrophaema sp.	1		1			A	Predaceous?
Neoxantholinus sp.	1		1			A	Predaceous?
Trogossitidae							
Temnochila virescens (F.)	1	1				A	Predaceous
Order Diptera							
sp. E	6	6	3			L	Saprophagous
sp. F	4			2	2	L	Saprophagous
Cecidomyiidae							
sp. G	6	1	5		4	L	Saprophagous?
Drosophilidae							
sp. H	9		5	1	15	L	Mycetophagous
Sciaridae							
Bradysia sp.	23	23	12	23	29	L	Saprophagous
Plastosciara sp.	3		17			L	Saprophagous
Order Hymenoptera							
Chalcididae							
sp. J	3			1	2	A	Parasitic
Formicidae							
Pheidole sp.	3		1		5	A	Scavenger?
Rhytidoponera sp.	2		6			A	Scavenger?
Torymidae							
Roptrocerus xylophagorum (Ratz)	12	7	3	5	4	P, L	Parasitic
Braconidae							
Dendrosoter sulcatus Mues.	2	2				P, L	Parasitic
Class Chilipoda							
sp. M	1				1	A	Predaceous
Class Symphyla							
sp. N	3		4			A	Detritus

* Total number of bark squares sampled

† A = adults, ♂ or ♀ ; N = nymph; W = worker; L = larvae; P = pupae

APPENDIX 2

MITE BROOD GALLERY ASSOCIATES OF *IPS GRANDICOLLIS* INFESTING *PINUS TAEDA* BILLETS

Total number of bark squares from which each species was collected and total number of individuals collected per 4-cm bark square sampled over a period of 15 months from either Barcoongere or Mt Mitchell State Forests after 30 or 60 days' exposure to *I. grandicollis* attack, life stages sampled from the subcortical galleries, and proposed feeding habit for each species

Class, order, family, and species	No. of bark squares from which each species was counted	Total number of individuals counted				Life stage	Feeding habit
		Barcoongere		Mt Mitchell			
		30 days N = 130*	60 days N = 146	30 days N = 102	60 days N = 113		
Subclass Acarina							
Suborder Mesostigmata							
Ascidae							
Asca sp. A	5	1	13			A, N†	Predaceous
Asca sp. B	3	3				A, N	Predaceous
Asca sp. C	11		8		3	A, N	Predaceous
Gamasellodes sp.	51	7	38	21	28	A	Predaceous
Lasioseius sp. A	2	1	1			A	Predaceous
Lasioseius sp. B	3			5		A, N	Predaceous
Lasioseius sp. C	2			2		A	Predaceous
Protogamasellus mica (Athias-Henriot)	11	6	15			A, N	Mycetophagous?
Proctolaelaps australis Stone	44		17	18	25	A, N	Predaceous
Proctolaelaps sp.	27	32	43			A, N	Predaceous
Digamasellidae							
Dendrolaelaps sp.	6			5	8	A, N	Predaceous
Epriariidae							
sp. D	1				1	N	Predaceous
Macrochelidae							
Macrocheles boudreauxi Krantz	244	311	103	190	194	A, N, E	Predaceous
Diplogyniidae							
sp. E	1				1	A	Predaceous
Suborder Prostigmata							
Bdellidae							
sp. F	1				1	N	Predaceous
Paratydeidae							
sp. G	2				2	A	Predaceous

APPENDIX 2 cont.

Class, order, family, and species	No. of bark squares from which each species was counted	Total number of individuals counted				Life stage	Feeding habit
		Barcoongere		Mt Mitchell			
		30 days N = 130*	60 days N = 146	30 days N = 102	60 days N = 113		
Pygmephoridae							
Pygmephorus bennetti Cross & Moser	109	324	181	127	234	A	Mycetophagous
Pediculaster sp. Vitzthum *sensu* Mahunka (1979)							
Nonphoretic form	8	4	8			A	Mycetophagous
Phoretomorph	1		2			♀ only	Mycetophagous
Tarsonemidae							
Iponemus confusus oriens Lindquist	43	15	12	38	89	A, L	Parasitic (on *Ips grandicollis* eggs)
Tarsonemus subcorticalis Lindquist	10	5	30			A, L	Mycetophagous
Suborder Astigmata							
Acaridae							
Acarus sp.	13	1	36		3	A, N	Saprophagous or mycetophagous
Tyrophagus putrescentiae (Schrank)	36	22	114		9	A, N	Omnivore
Anoetidae							
Histiostoma varia Woodring & Moser	426	1207	1326	864	1297	A, N, H	Mycetophagous
Suborder Cryptostigmata							
Hypochthoniidae							
sp. H	1		1			A	Saprophagous or mycetophagous
Nanhermanniidae							
sp. I	1		1			A	Saprophagous or mycetophagous
Liacaridae							
sp. J	1		1			A	Saprophagous or mycetophagous
Carabodidae							
sp. K	1	1				A	Saprophagous or mycetophagous
Oppiidae							
sp. L	2	1	5			A	Saprophagous or mycetophagous
Galumnidae							
sp. M	1		1			A	Saprophagous or mycetophagous
Oribatulidae							
sp. N	5		2	1	2	A	Saprophagous or mycetophagous

* Total number of bark squares sampled

† A = adults, ♂ or ♀ ; N = nymph; E = egg; H = hypopi

APPENDIX 3

NEMATODE BROOD GALLERY ASSOCIATES OF *IPS GRANDICOLLIS* INFESTING *PINUS TAEDA* BILLETS

Total number of bark squares from which each species was collected and total number of individuals identified per 4-cm bark square sampled over a period of 15 months from either Barcoongere or Mt Mitchell State Forests after 30 or 60 days' exposure to *I. grandicollis* attack, life stages sampled from the subcortical galleries, and proposed feeding habit for each species

Phyllum, order, family, and species	Total occurrences of species	Total number of individuals counted				Life stage	Feeding habit
		Barcoongere		Mt Mitchell			
		30 days N = 125*	60 days N = 142	30 days N = 103	60 days N = 113		
Phyllum Nematoda							
Order Tylenchida							
Neotylenchidae							
sp. A	9	1	33	2		A, L†	Saprophagous or mycetophagous
Allantonematidae							
Contortylenchus grandicolli (Massey)	211	374	84	439	246	A, L	Mycetophagous? and parasitic
Aphelenchoididae							
Bursaphelenchus sp.	113	71	62	65	10	A, L, D	Mycetophagous and phoretic
Aphelenchoides sp. A	9	3	9			A, L	Mycetophagous
Aphelenchoides sp. B	6			11		A, L	Mycetophagous
Seinura sp.	28	13	75			A, L	Predaceous
Cryptophelenchus sp.	24	20	50		70	A, L	Mycetophagous
Order Rhabditida							
Diplogasteridae							
sp. C	1	6				A, L	Predaceous or saprophagous
Mikoletzkya calligraphi Massey	119	237	135	150	204	A, L, D	Omnivorous and phoretic
Rhabditidae							
Rhabditonema sp.	18	19	35			A, L	Saprophagous or mycetophagous
sp. E	2	1	2			A	Saprophagous or mycetophagous
Parasitorhabditis hastulus Massey	436	902	740	876	688	A, L	Mycetophagous and parasitic
Order Monhysterida							
Monhysteridae							
sp. F	15	2	24			A, L	Saprophagous or mycetophagous
Order Dorylaimida							
Dorylaimidae							
Eudorylaimus sp.	31	7	87			A, L	Omnivorous
Mononochidae							
Monochus sp.	8		28		1	A, l	Predaceous

* Total number of bark squares sampled

† A = adults, ♂ or ♀ ; L = larvae; D = dauerlarvae

APPENDIX 4

FUNGAL BROOD GALLERY ASSOCIATES OF *IPS GRANDICOLLIS* INFESTING *PINUS TAEDA* BILLETS

Total number of bark squares (4 cm) from which each species was collected and total number of individuals collected over a period of 15 months from either Barcoongere or Mt Mitchell State Forests after 30 or 60 days' exposure to *I. grandicollis* attack.

Class, order, and species	Total number of bark squares from which each species was collected			
	Barcoongere		Mt Mitchell	
	30 days N = 103*	60 days N = 146	30 days N = 102	60 days N = 113
Mycophyta				
Class Hymenomycetes				
Order Aphyllophorales				
Phanerochaete sp.	23	54	20	58
Class Ascomycetes				
Order Ophiostomatales				
Ceratocystiopsis minuta (Siem.) Upadhyay & Kendrick	5	6		5
Ceratocystiopsis sp. B	4	45	4	2
Ophiostoma ips (Rumb.) Nannf.	102	115	100	93
Class Coelomycetes				
Coelomycete sp. A	46	66	5	8
Sphaeropsis sapinea (For.) Dyko & Sutton	10	6	7	
Class Hyphomycetes				
Beauveria bassiana (Bals.) Vuill.	1	1	1	
Cephalosporium sp.	2	3	4	1
Dactylaria superba Corda	6	19	9	10
Graphilbum sp.	27	6	49	
Paecilomyces penicillatus (Hohnel) Samson	1		1	
Penicillium sp.	2	4		
Phialoptora sp.	1		1	
Trichoderma spp.	17	8	11	10

* Total number of bark squares sampled