Chapter 4
Insect herbivory and resource availability

4.1 Introduction

The resource availability hypothesis predicts that levels of herbivory will vary in environments in which resources are differentially available (Coley et al., 1985). According to the hypothesis, plant species in higher resource habitats have the potential for rapid growth, the ability to replace tissues lost to herbivores, and thus less need to invest in chemical and physical defences (Coley et al., 1985). As resources become limiting, potential growth rates decline, replacement of tissues lost to herbivores becomes more costly, and investments in anti-herbivore defences become more cost effective (Coley et al., 1985; Landsberg & Ohmart, 1989). The resource availability hypothesis subsequently predicts herbivory to be relatively high on fast-growing plants in resource-rich habitats and low on slow-growing, well-defended plants in resource-limited environments (Coley et al. 1985).

Few studies have investigated the relationship between herbivory and resource availability at the plant community level (e.g. Cebrian & Duarte, 1994; Louda et al., 1987). Maiorana (1981) found cultivated garden plants were more vulnerable to herbivores in shade than in direct sunlight. Louda et al. (1987) observed the opposite trend, concluding herbivore damage on perennial forb species in the Rocky Mountains was related more to plant and leaf size than to light levels. Landsberg and Gillieson (1995) noted a rise in herbivory rates with increasing soil nutrients in eucalypt forests in southeastern Australia. Below average rainfall has also been correlated with insect outbreaks (White, 1969; Landsberg & Wylie, 1983; Mattson & Haack, 1987), although a causal relationship is not always clear (Wagner & Frantz, 1990; Willis et al., 1993).

Numerous plant characteristics have been attributed to reducing the feeding, growth and survival of herbivores (Zamora, Hódar & Gómez, 1999; see also chapter 3). Barbs, thorns and spines can repel large organisms (Cooper et al., 1986; Grubb, 1992), while trichomes can prevent some sucking and chewing insects from feeding and moving about on leaves (Hoffman & McEvoy, 1985; Ramalho et al., 1984; Oghiakhe et al., 1992). Leaf toughness and fibre content can inhibit herbivory (Hochuli, 1996; Iddles et al., 2003; Lucas et al., 2000), and influence densities of herbivorous insects (Terra et al., 1987; Ferreira et al., 1992; Peeters, 2002b). Secondary metabolites such as condensed tannins, alkaloids and cyanogenic glycosides can reduce herbivory by affecting plant nutritional quality (Robbins et al., 1987) and disrupting the nervous systems and cardiac functions of herbivores (McKey, 1974; Jones et al., 1978; van Alstyne, 1988; Behmer et al., 2002). Leaf age can also affect rates of herbivory (Coley & Aide, 1991; Jackson et al., 1999; Landsberg, 1988; Landsberg and Cork, 1997, Moles & Westoby, 2000). Young leaves are vulnerable to herbivores because they contain higher concentrations of nitrogen and water, have less fibrous tissue and lower toughness compared to older leaves (Bowers & Stamp, 1993; Coley, 1983; Feeny, 1970; Read et al., 2003). The main defences against herbivores for young leaves are higher concentrations of chemical compounds (Bowers & Stamp, 1993; Krischik and Denno, 1983), and phenological strategies such as synchronous leaf production (Kursar & Coley, 1992; Aide et al., 1989; Aide, 1993). Once a leaf has expanded fully, leaf structure becomes more complex and leaf toughness increases dramatically (Coley, 1983; Ernest, 1989; Lowman & Heatwole, 1992). This has the potential effect of lowering rates of herbivory (Coley & Aide, 1991, Landsberg, 1988, Landsberg & Cork, 1997).

This chapter presents results of field surveys and laboratory experiments designed to monitor herbivore selection and damage on plants growing in nutrient-poor and nutrient richer soils. I test the hypothesis that plants from low resource environments will suffer less herbivore damage than plants adapted to higher resource environments. The specific questions addressed were:

1. Do plants from low nutrient environments suffer less herbivory than plants from higher nutrient habitats?

2. How much plant tissue is lost to herbivores in the field and laboratory?
3. Is herbivore damage correlated with:
    - nutritional value of the foliage (percent nitrogen, fibre content),
    - concentration of chemical defences (total phenols),
    - physical defence (toughness, lamina thickness),
    - and/ or other leaf traits (specific leaf area, water content)?

4.2 Methods

4.2.1 Field monitoring

Herbivore damage was monitored between August 2002 and August 2004 at the sites previously described.

Thirty common plant species, a subset of the 45 species analysed in the mature and immature leaf trait projects (see chapter 3), were used in the field herbivory study. Plant species were chosen to represent a wide range of growth forms (trees, shrubs and vines) and plant families (Fig. 4.1), and comprised eleven temperate rainforest, nine wet sclerophyll, and ten dry sclerophyll species (Fig. 4.1).

For each plant species, four individuals were selected for study. A single growth point on each tree, shrub or vine was tagged with wiremarker tape. Leaves that formed from these growth points were monitored until maturity or senescence using a Canon PowerShot G2 digital camera with a 7-21 mm zoom lens mounted on a frame. The camera frame had a 33 cm arm attached to a 27 cm x 30 cm board. Images were recorded monthly for two years. Leaves were positioned on the board by manipulating the stem. Unnecessary handling of the leaves was avoided (Cahill et al. 2001).

For each leaf image, the surface area and area of damaged/ missing tissues were measured using Image J software, a public domain processing program developed by Wayne Rasband from the National Institute of Mental Health, Marylands, USA. Chewing and sucking damage were measured separately, with sucking damage

defined as the area of brown necrotic tissue surrounding a puncture point, and chewing damage the area missing from a particular leaf. Brown necrotic tissue that was not associated with a puncture was categorised as “necrosis”. Herbivory was expressed as the proportion of chewing or sucking damage on a particular leaf per month.

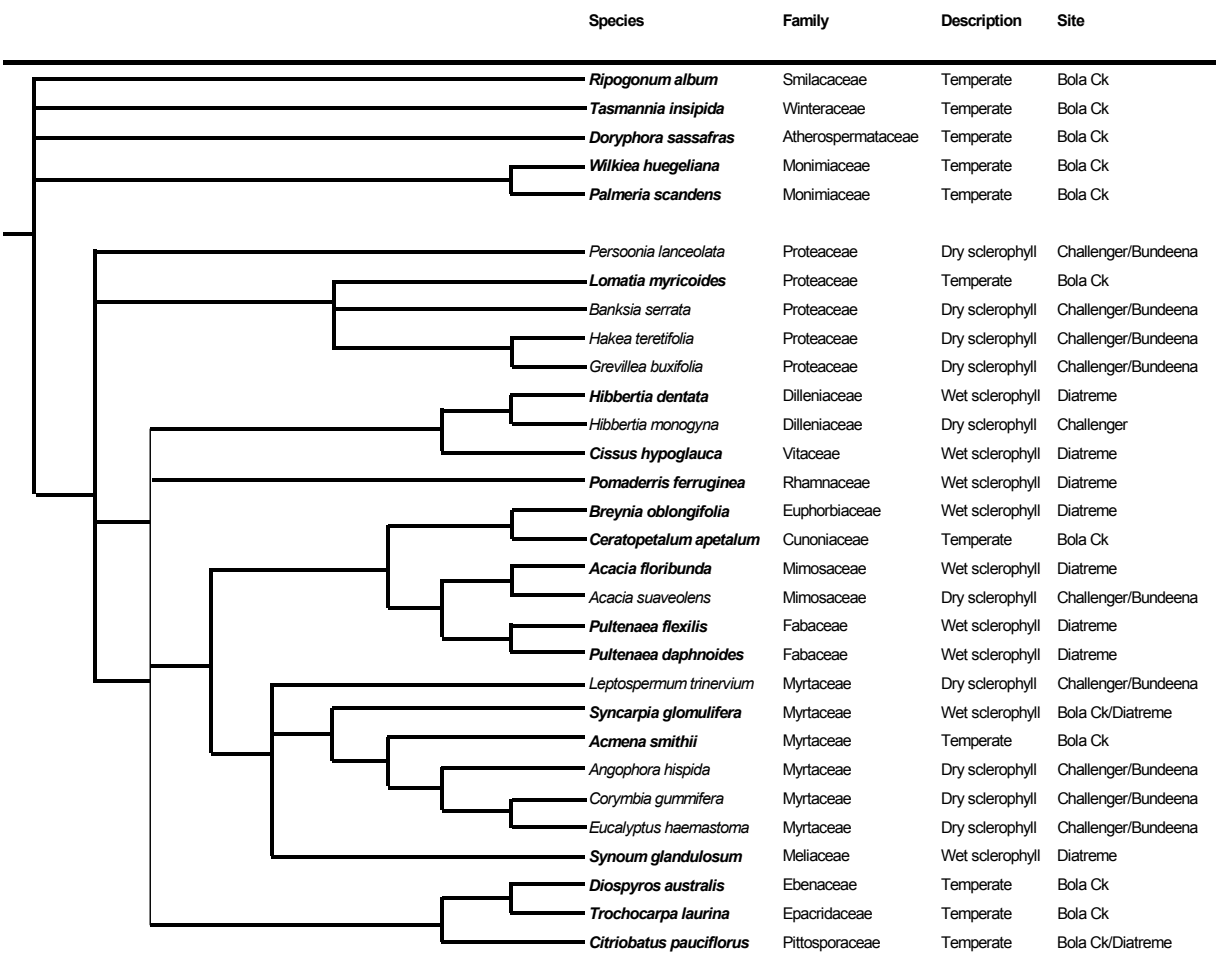


Figure 4.1 Phylogenetic relationships of plant species from high and low resource sites monitored for insect herbivory (August 2002-August 2004). Branch lengths are not proportional to time since evolutionary divergence. Mesic plant species in bold.

The percentage of ambient light available to each leaf being monitored for herbivory was measured with a LI-188B Integrating Quantum Photometer. Readings were recorded using the 10 seconds integration period.

4.2.2 Cafeteria experiments

Cafeteria experiments provide useful information about herbivore preferences for a broad range of plants. Plant tissues are offered simultaneously to herbivores under standardised conditions to determine palatability by observing herbivore food choice, time prior to consumption, and amount of tissue consumed (Grime et al., 1968; Cates and Orians, 1975; Grime et al., 1996; Perez-Harguindeguy et al., 2003).

Three cafeteria laboratory experiments, each consisting of three trials, were conducted in January 2005 at room temperature. The first experiment used the garden snail, *Helix aspersa*. The second experiment used the cricket, *Acheta domestica*. Both the snail and cricket species are generalist herbivores that originated from Europe. The third experiment used an Australian phasmid *Extatosoma tiaratum*. All animals used in the trials were naïve, having no experience of the plant species offered.

Snails were collected from *Agapanthus praecox* in local gardens in the suburb of St Ives, NSW one month prior to commencement of the experiments. They were kept in a covered plastic container in the dark and fed on lettuce and cabbage. To keep them active, they were kept cool and moist. Crickets were supplied by Pisces Enterprises (Australia). They were fed on lettuce for at least a month and kept in a dry, low light environment. Three-month old phasmids were borrowed from a laboratory population at Macquarie University. They were fed on *Agonis flexuosa* (Mrytaceae), a plant endemic to Western Australia (Blombery, 1977). Test herbivores were deprived of food 48 hours before the experiments began.

Twenty plant species were used in the study: four wet sclerophyll, six temperate rainforest, and ten dry sclerophyll plant species (Fig. 4.2). Mature but non-senescing leaves were collected from the field a few hours before the experiments began. Leaves were cut into 1cm x 1cm squares and stored in plastic bags between wet towelling in a refrigerator until all leaves were prepared. Mid-ribs were avoided on all but the smallest leaves (eg. *Hibbertia monogyna*). The needle-shaped leaves of *Hakea teretifolia* were cut into 1cm lengths. Four lengths were pinned to form a 1cm x 1cm grid. The narrow leaves of *Hibbertia monogyna,*

Grevillea buxifolia and *Acacia suaveolens* required only two lengths of leaf to form a grid (Plate 4.1).

There were three trials per experiment. Five squares (or equivalents) were cut for each species per trial. Leaf squares were randomly assigned positions, with 1cm separation, and pinned to the base of a foam 35cm x 22cm x 6cm box. Grid paper pinned to the floor of the cage facilitated positioning of leaf squares (Plate 4.1).

Plate 4.1 Arrangement of leaf squares for the cricket cafeteria experiment

Ten snails, ten crickets and five phasmids were used in each of their respective trials. Snails were kept in the dark and occasionally sprayed with water to promote maximum activity. Crickets were given a transparent polyethylene lid and were covered by a piece of muslin to provide a sheltered environment. As stick insects tend to hang from leaves when they feed, their trial boxes stood upright throughout the experiment. Fly mesh prevented phasmids from escaping.

Trial boxes were photographed every six to twelve hours using a Canon PowerShot G2 digital camera with a 7-21 mm zoom lens mounted on a frame. The

camera was mounted 35.5 cm from the base of the frame, which was 52 cm x 37 cm long. Extra lighting for photography was provided by two 40 watt fluorescent tubes on either side of the camera frame.

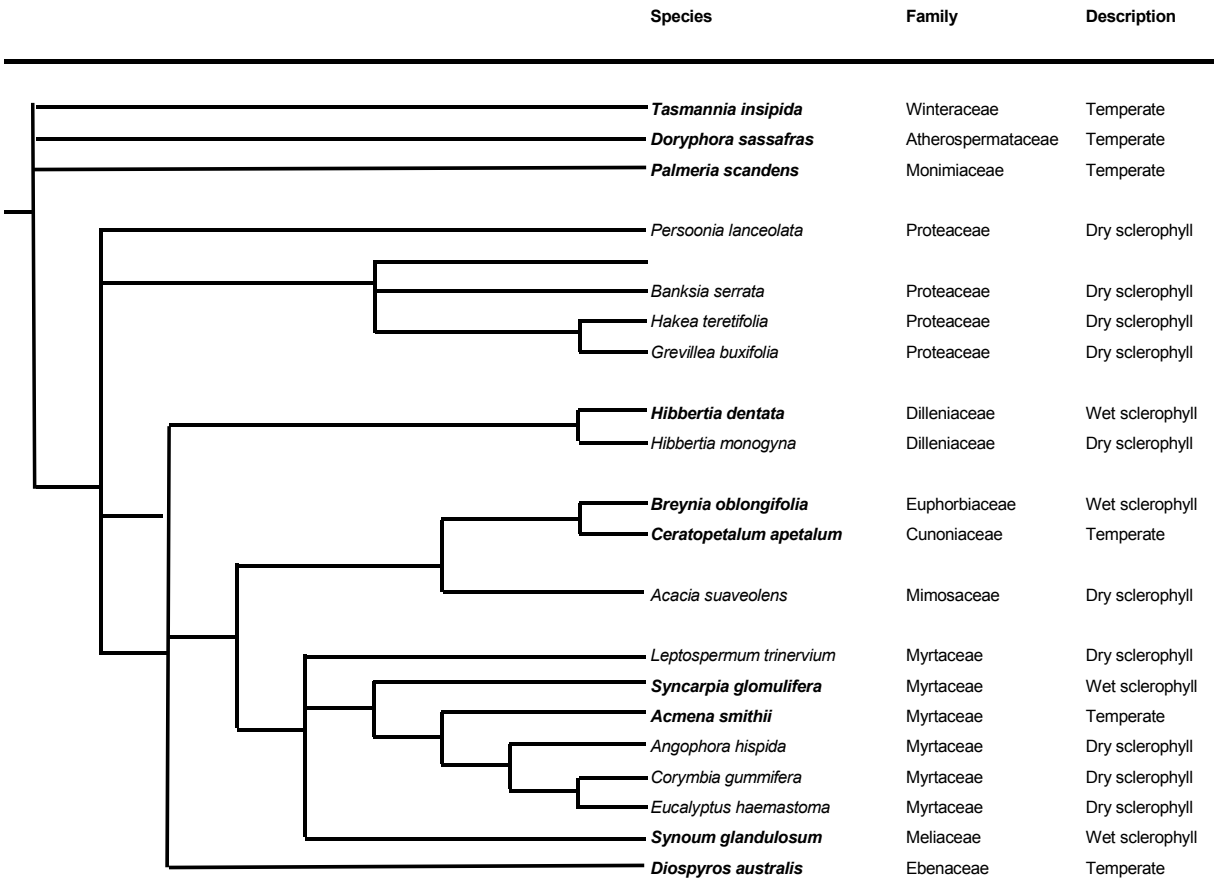


Figure 4.2 Phylogenetic relationships of plant species from high and low resource sites monitored for insect herbivory in each cafeteria experiment. Branch lengths are not proportional to time since evolutionary divergence. Mesic species in bold.

At the end of each trial, the amount of tissue removed and projected leaf areas were measured using the Image J software. Herbivory was expressed as a proportion of total leaf area.

4.3 Statistical analysis

Multiple linear regressions were used to identify and rank variables that predicted consumption of leaves by leaf-chewers and sap-suckers in the field, and

consumption by test organisms in the laboratory. The leaf trait results for the mature leaf trait study were used in the analyses. Preliminary exploration of the data using boxplots and quantile-quantile plots demonstrated the highly skewed nature of the data. Data were subsequently transformed. Due to the small size of the transformed dataset, not all leaf trait variables could be included in the analyses. Variables were selected to represent physical and chemical leaf characteristics.

Wilcoxon rank-sum tests and Welch Two Sample t-tests were used to test for differences between rates of herbivory in low versus higher resource environments, and between expanding versus mature leaves (field data). These tests were also used to test for differences in the palatability of mesic and dry sclerophyll plant species (cafeteria data).

4.4 Field herbivory results

Monitoring of insect herbivory at the four field sites occurred during a period of below average rainfall (Fig. 2.5). The drought caused delays in the production of new leaves by *Banksia serrata, Leptospermum trinervium*, *Hibbertia monogyna*, *Grevillea buxifolia* and *Acacia suaveolens*. It also resulted in a number of trees and shrubs dying. The small shrubs *Hemigenia purpurea* and *Platysace linearifolia* (Plate A2.1), for instance, were removed from the original monitoring programme following the death of the majority of plant replicates. During monitoring, leaf damage was observed to expand proportionally with leaf growth, confirming findings by Lowman (1987).

Plant species from the more fertile sites did not experience significantly more herbivore damage than plants from the nutrient-poor sites (Fig. 4.3). Of the two damage types compared, chewing was the most common type found on leaves in both localities. Mean overall rates of chewing damage for the higher nutrient sites was 0.9 ± 1% per month or 11.2% per year, compared to 0.8 ± 1% or 10% per year for the lower nutrient sites (P = 0.14). Sucking damage on leaves growing in nutrient richer soils was 0.08 ± 0.3% per month compared to 0.04 ± 0.06% per month for dry sclerophyll foliage (P = 0.35). Necrosis damage averaged 0.1 ±

0.3% per month and 0.06 ± 0.07% per month for the higher and low nutrient sites (*P* = 0.12) (Table A5.1).

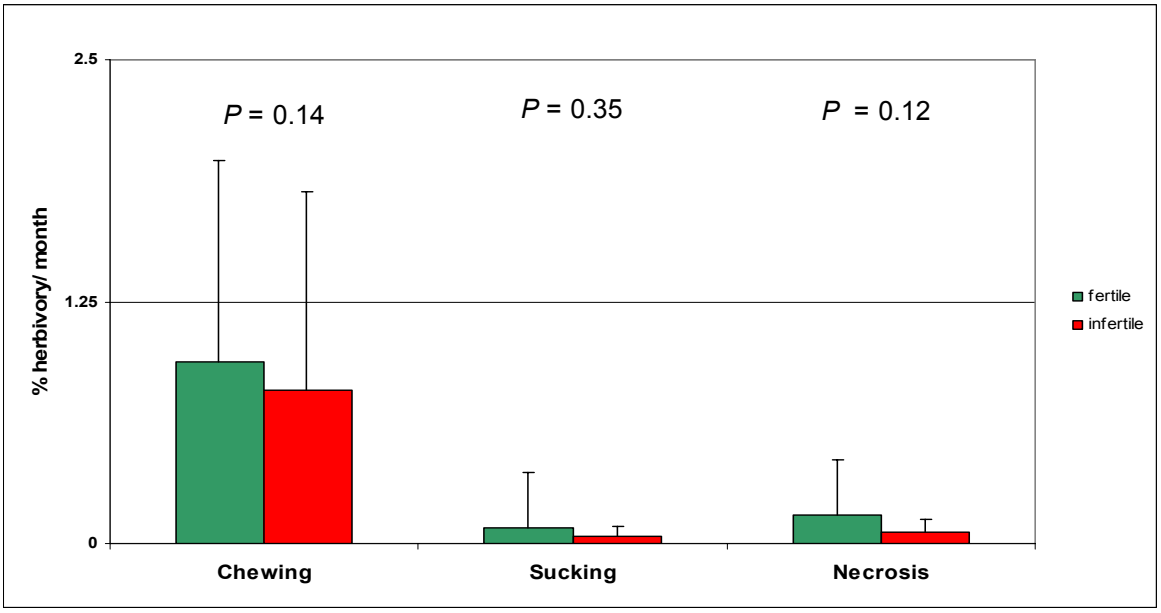


Figure 4.3 Overall rates of herbivory for low and higher resource sites. Results for Welch Two Sample t-tests shown.

The highest rates of herbivory occurred in the Royal National Park, though differences were not significant (Fig. 4.4). Average chewing damage for the higher and low nutrient sites in RNP were 1.2 ± 1% per month (14.6% per year) and 1.0 ± 1% per month (12% annually). In comparison, the average rates of chewing damage for the higher and low nutrient sites in Ku-ring-gai Chase National Park were 0.6 ± 0.7% per month and 0.5 ± 0.6% per month (both 7% annually) respectively. Rates of sucking damage at the two localities ranged from 0.01 ± 0.01% for the higher resource site in RNP to 0.2 ± 0.4% per month at the higher resource site in KCNP. Necrosis damage did not exceed 0.2% per month for any site (Fig. 4.4; Table A5.2).

Rates of herbivory did not vary significantly between plant growth forms (*P* = 0.96, Fig. 4.5). Mesic vines, shrubs and trees had rates of 1.3 ± 1.5% per month, 1.4 ± 1.0% per month and 0.7 ± 0.9% per month respectively. In comparison, dry

sclerophyll shrubs and trees had herbivory rates of 0.05 ± 0.06% per month and 1.0 ± 1.1% per month respectively.

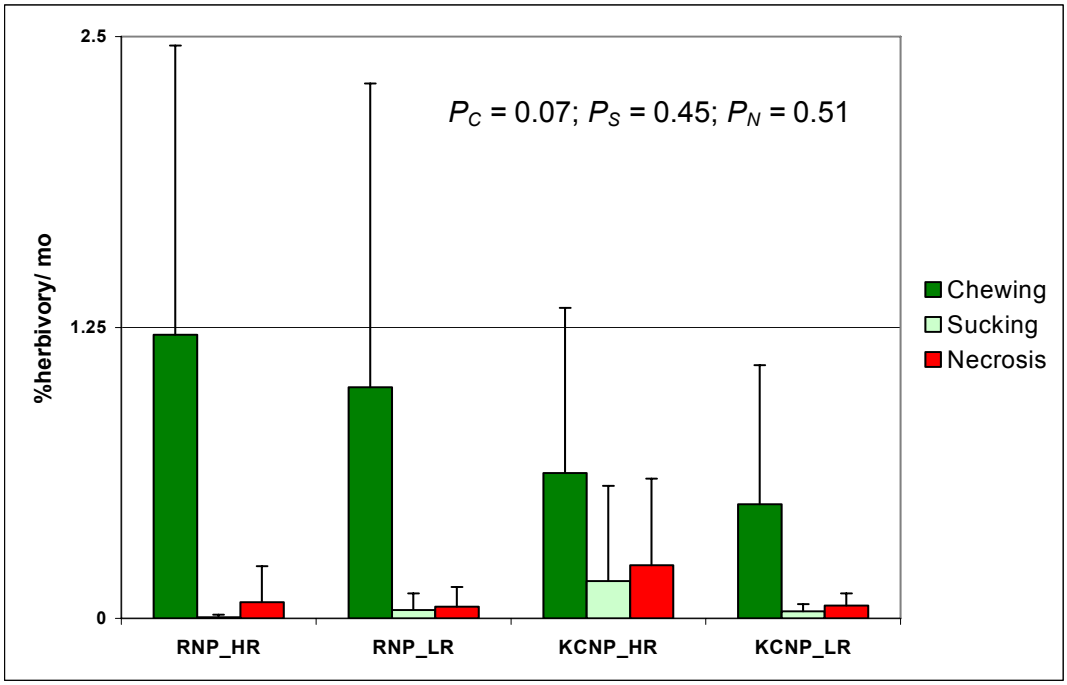


Figure 4.4 Mean rates of herbivory at high (HR) and low (LR) resource sites within Royal National Park (RNP) and Ku-ring-gai Chase National Park (KNP). Welch Two Sample t-tests compare damage type between localities for chewing (P_C), sucking (P_S) and necrosis (P_N).

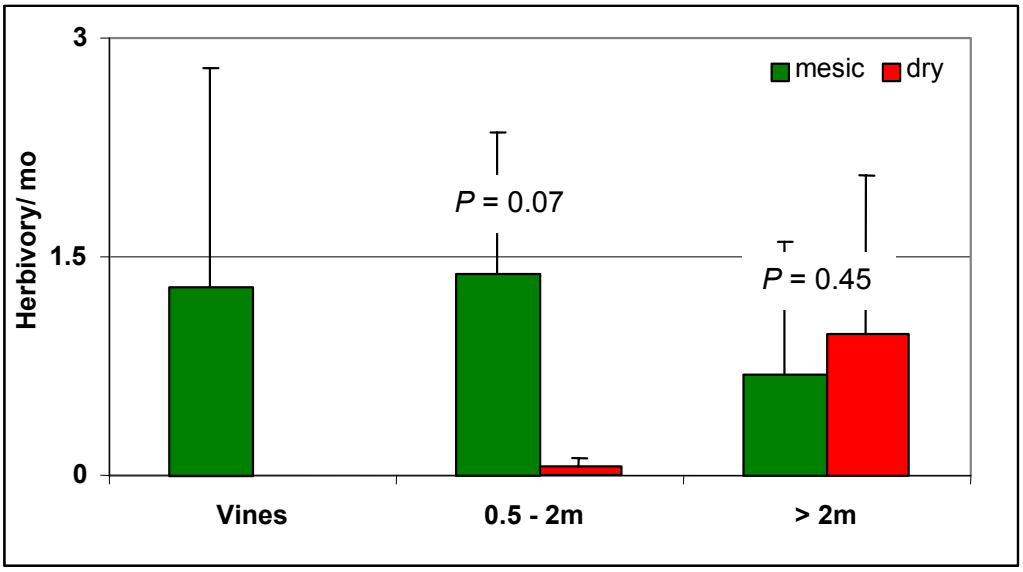
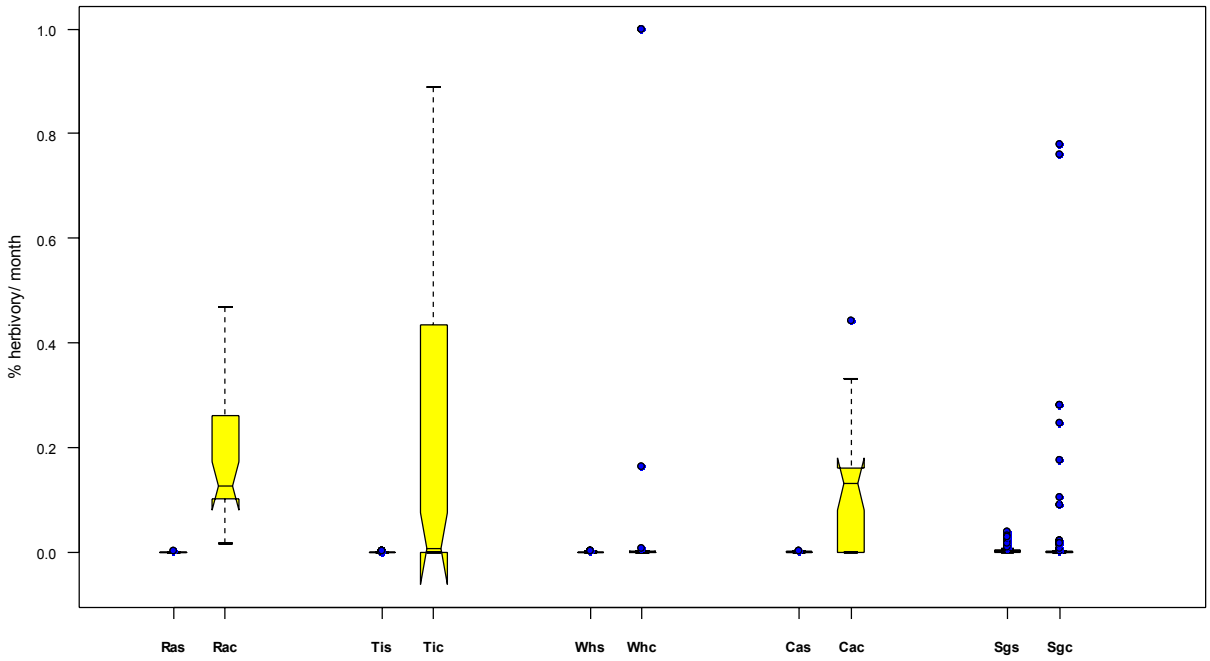


Figure 4.5 Mean rate of chewing damage for mesic and dry sclerophyll (dry) shrubs (0.5-2m) and trees (>2m) and mesic vines. Welch two-sample t-tests compare damage between resource type for shrubs and trees.

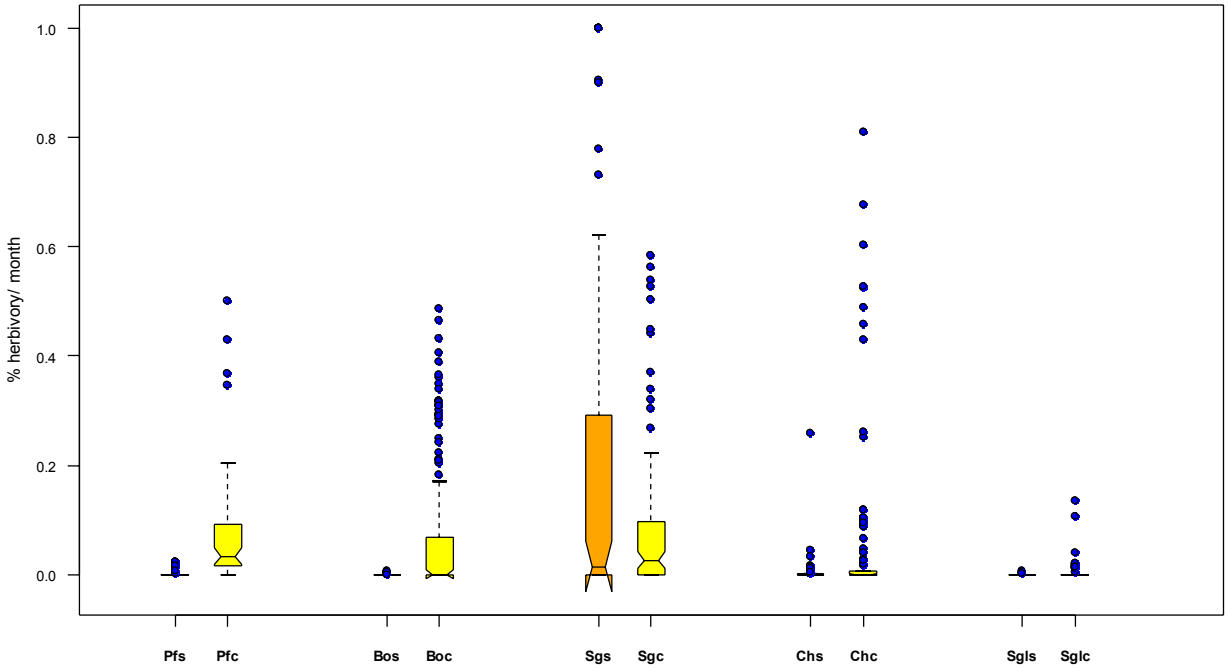
Mesic species at the higher resource sites that sustained the greatest levels of herbivory were *R. album, T. insipida, C. apetalum* (Fig. 4.6), *S. glomulifera* and *P. ferruginea* (Fig. 4.7). Whilst damage by Hemiptera was negligible, median consumption rates by chewers ranged from 1.7% for *R. album* to 2.3% for *C. apetalum* (Fig. 4.6) and *S. glomulifera* (Fig. 4.7).

At the lower resource sites, the dry sclerophyll plant species that suffered the most damage were *B. serrata*, *E. haemastoma*, *C. gummifera* and *A. hispida.* Median monthly chewing damage for *B. serrata* in Royal National Park (Fig. 4.8) was 1.0%, compared to the rate of 0.2% at Ku-ring-gai Chase National Park (Fig. 4.9). Median herbivory rates for *E. haemastoma* ranged from 0.04% at KCNP to 1.2% at RNP. Both *C. gummifera* and *A. hispida* suffered around 0.4% removal of leaf tissue by chewers each month. Damage by suckers did not exceed a median of 0.04% monthly for any heathland species.



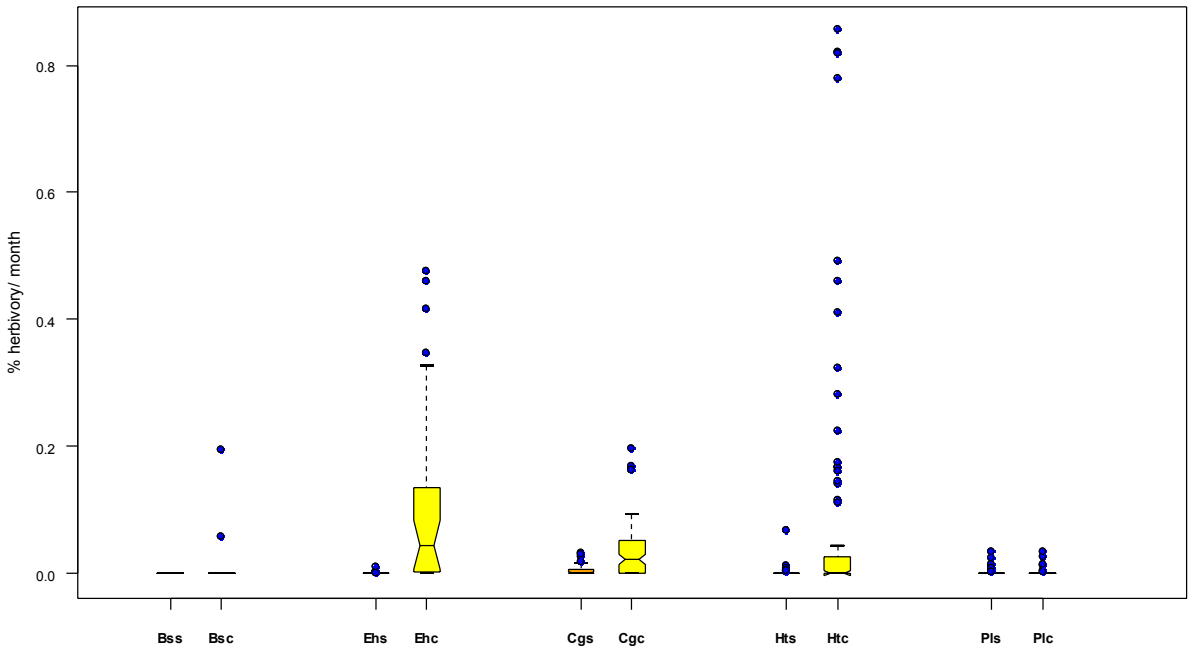
(Ra – *Ripogonum album*; Ti – *Tasmannia insipida*; Wh - *Wilkiea huegelianna*; Ca – *Ceratopetalum apetalum*; Sg – *Syncarpia glomulifera*; s – sucking damage; c – chewing damage)

Figure 4.6 Percent herbivory per month for five temperate rainforest plant species from Bola Creek, Royal National Park. Boxplots indicate data are highly skewed.



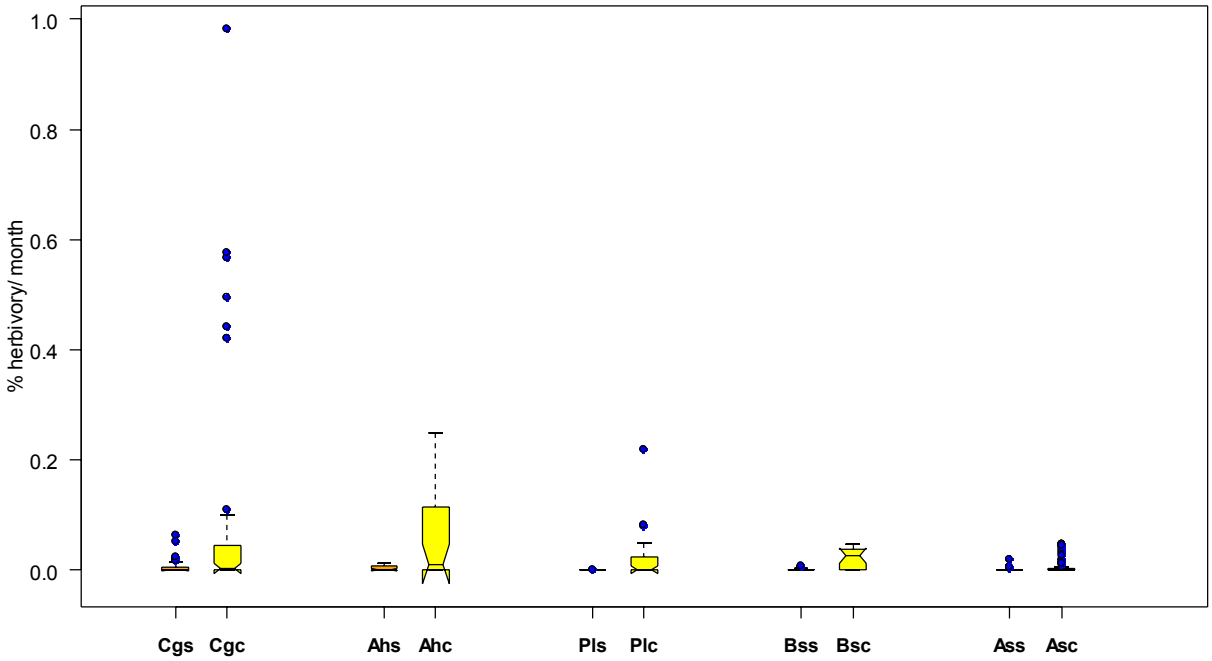
(Pf – *Pomaderris ferruginea*; Bo – *Breynia oblongifolia*; Sg – *Syncarpia glomulifera*; Ch – *Cissus hypoglauca*; Sgl – *Synoum glomulifera*; s – sucking damage; c – chewing damage)

Figure 4.7 Percent herbivory per month for five wet sclerophyll plant species from the Dyke site, Ku-ring-gai Chase National Park. Boxplots indicate data are highly skewed.



(Bs - *Banksia serrata*; Eh - *Eucalyptus haemastoma*; Cg - *Corymbia gummifera*; Ht - *Hakea teretifolia*; Pl - *Persoonia lanceolata*; s - sucking damage; c - chewing damage)

Figure 4.8 Percent herbivory per month for five dry sclerophyll plant species from the Bundeena site, Royal National Park. Boxplots indicate data are highly skewed.



(Cg – *Corymbia gummifera*; Ah – *Angophora hispida*; Pl – *Persoonia lanceolata*; Bs – *Banksia serrata*; As – *Acacia suaveolens*; s – sucking damage; c – chewing damage)

Figure 4.9 Percent herbivory per month for five dry sclerophyll plant species from Challenger track, Ku-ring-gai Chase National Park. Boxplots indicate data are highly skewed.

The most important variables associated with herbivory in the field were leaf area, lamina thickness and fibre content (Tables 4.1, 4.2). Leaves that sustained the highest levels of chewing damage had large leaf areas (Table 4.1), whilst leaves with high sucking damage had thick lamina and low fibre content (Table 4.2). Other variables that influenced chewing insects were low leaf toughness and narrow lamina thickness (Table 4.1). Large leaf areas and low concentrations of total phenols also influenced consumption by Hemiptera. (Table 4.2)

Ambient light had no direct effect on herbivory rates (Tables 4.1, 4.2). This had been a concern during the design stage as many temperate rainforest plants live beneath the forest canopy in dappled light.

Table 4.1 Multiple linear regression results for chewing damage of mesic and dry sclerophyll leaves in Ku-ring-gai Chase and Royal National Parks.

```
Coefficients:
            Estimate  Std Error t value Pr(>|t|)
(Intercept)  -0.70     0.64   -1.09    0.29

Area          0.92      0.43    2.14    0.04 *
Tg           -0.77      0.57   -1.36    0.19
LT           -0.51      0.38   -1.35    0.19
NDF           1.66      1.40    1.19    0.25
SLA          -0.77      0.74   -1.05    0.31
N            -0.54      0.52   -1.02    0.32
TP           -0.86      0.92   -0.94    0.36
Water        -0.94      1.30   -0.72    0.48
L             0.51      0.93    0.55    0.59

Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1
```

Residual standard error: 1.126 on 27 degrees of freedom. Multiple R-Squared: 0.3403, Adjusted R-squared: 0.1203. F-statistic: 1.547 on 9 and 27 DF, p-value: 0.182

Variable codes: Area – leaf area; Tg – leaf toughness; LT – lamina thickness; NDF – fibre content; SLA – specific leaf area; N – nitrogen; TP – total phenol concentration; W – water content; L – light levels.

Table 4.2 Multiple linear regression results for sucking damage of mesic and dry sclerophyll leaves in Ku-ring-gai Chase and Royal National Parks.

```
Coefficients:
            Estimate  Std Error t value Pr(>|t|)
(Intercept) -1.10    0.32 -3.43   0.002 **

LT            0.56     0.19    2.96   0.006 **
NDF          -1.75     0.70   -2.48   0.02   *
Area          0.35     0.22    1.60   0.12
TP           -0.65     0.46   -1.41   0.17
SLA           0.37     0.37    1.01   0.32
Tg            0.23     0.28    0.82   0.42
W            -0.41     0.65   -0.63   0.54
N             0.06     0.26    0.23   0.82
Light        -0.74     0.46   -1.59   0.12

Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1
```

Residual standard error: 0.5642 on 27 degrees of freedom. Multiple R-Squared: 0.4992, Adjusted R-squared: 0.3322. F-statistic: 2.99 on 9 and 27 DF, p-value: 0.0132.

Variable codes: Area – leaf area; Tg – leaf toughness; LT – lamina thickness; NDF – fibre content; SLA – specific leaf area; N – nitrogen; TP – total phenol concentration; W – water content; L – light levels.

In general, young leaves were more vulnerable to insect herbivory than mature leaves (Fig. 4.10). The dry sclerophyll species *A. hispida* and *E. haemastoma* suffered 6.9% chewing herbivory during expansion and 0.9% to 3.4% respectively when leaves were mature (Fig. 4.11). The expanding mesic leaves of *P. ferruginea* had average chewing damage rates per month of 6.6% compared to 1.2% for

mature leaves. *Ripogonum album*, *T. insipida*, *W. huegelianna* and *C. apetalum*, all mesic species, lost between 4.4% and 6.4% of tissue monthly when leaves were young compared to 0.01% to 3.8% when fully expanded (Fig. 4.11).

Not all plant species, however, suffered greater rates of herbivory during leaf formation and expansion (Fig. 4.10). Following maturity, chewing damage rates doubled for *S. glomulifera*, *C. hypoglauca* (both mesic species) (Fig. 4.11) and for *H. teretifolia* (a dry sclerophyll species) (Fig. 4.11). There was also an increase in the rate of consumption by Hemiptera on mature *C. gummifera, C. hypoglauca* and *E. haemastoma* leaves.

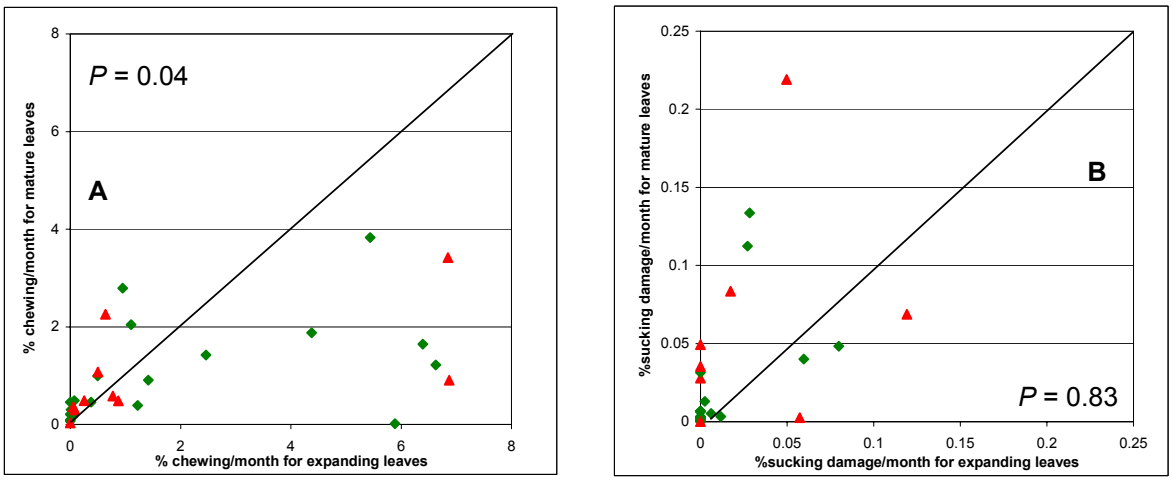
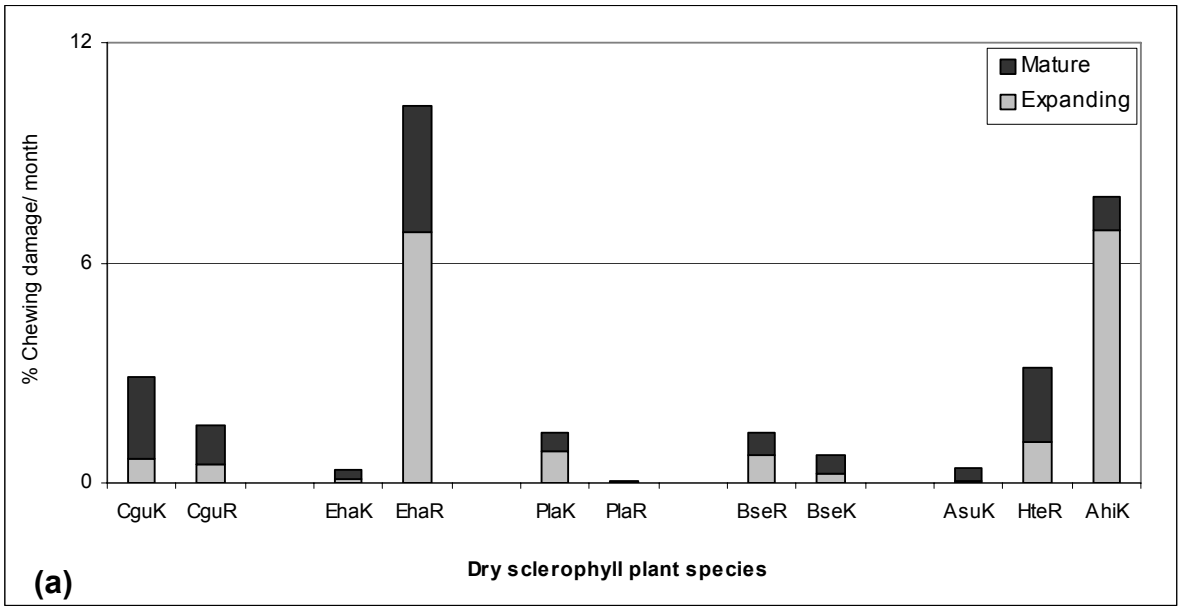
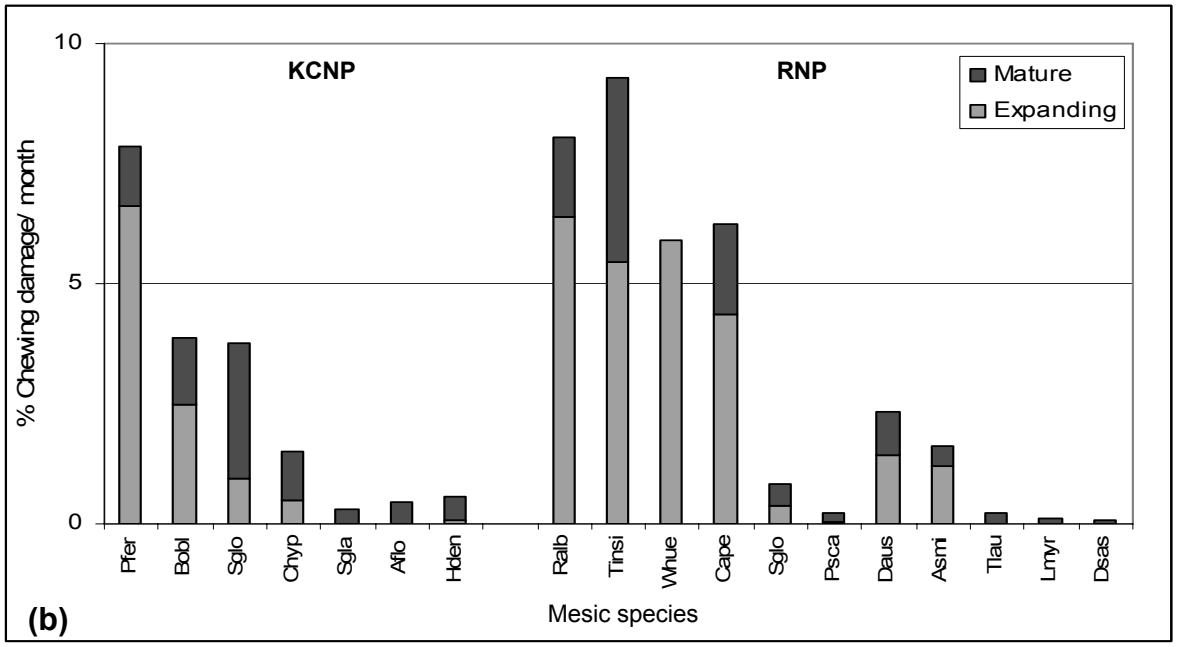


Figure 4.10 Average percent herbivory occuring on expanding and mature leaves per month from high (green) and low (red) resource sites in Royal National Park and Ku-ring-gai Chase National Park. Scatterplots: (A) % chewing damage; (B) % sucking damage. Welch Two Sample t-test results shown.



Cgu – *Corymbia gummifera*; Eha - *Eucalyptus haemastoma*; Pla – *Persoonia lanceolata*; Bse – *Banksia serrata*; Asu – *Acacia suaveolens*; Hte – *Hakea teretifolia*; Ahi – *Angophora hispida*; K – Ku-ring-gai Chase NP; R – Royal NP



Pfer – *Pomaderris ferruginea*; Bobl – *Breynia oblongifolia*; Sglo – *Syncarpia glomulifera*; Chyp – *Cissus hypoglauca*; Sgla – *Synoum glandulosum*; Aflo – *Acacia floribunda*; Hden – *Hibbertia dentata*; Ralb – *Ripogonum album*; Tinsi – *Tasmannia insipida*; Whue – *Wilkiea huegelianna*; Cape - *Ceratopetalum apetalum*; Psca – *Palmeria scandens*; Daus - *Diospyros australis*; Asmit – *Acmena smithii*; Tlau – *Trochocarpa laurina*; Lmyr – *Lomatia myricoides*; Dsass – *Doryphora sassafras*

Figure 4.11 Percent chewing damage per month for expanding and mature dry sclerophyll (A) and mesic (B) leaves in higher and low resource environments.

4.5 Herbivore preference and consumption under laboratory conditions

After being starved for 48 hours, snails, crickets and stick insects took approximately another 35 hours to begin consuming leaf squares. When the test species finally began to feed, temperate rainforest and wet sclerophyll leaves were preferred to leaves from dry sclerophyll plants. Snails selected *Tasmannia insipida*, *Doryphora sassafras*, *Palmeria scandens* and *Breynia oblongifolia* leaves at regular intervals. They tried *Hibbertia dentata*, *Synoum glandulosum* and much later *Syncarpia glomulifera*, *Diospyros australis* and *Acmena smithii*. Snails did not attempt to feed on many of the dry sclerophyll leaves, which suggests this introduced generalist herbivore found heathland plants unpalatable (Fig. 4.12).

Crickets tested more sclerophyll heathland leaves for palatability than the other two herbivores (Fig. 4.12). They preferred the leaves of the wet sclerophyll plants *Breynia oblongifolia, Synoum glandulosum* and *Syncarpia glomulifera*, which they consumed over a period of 52 hours. The rainforest plants *Palmeria scandens* and *Doryphora sassafras* were also tasted.

Stick insects preferred *Synoum glandulosum* and *Doryphora sassafras* leaves. *Hakea teretifolia*, *Banksia serrata*, and *Palmeria scandens* were amongst the leaves that were tried and rejected (Fig. 4.12).

In general, wet sclerophyll and rainforest leaves were consumed at a greater rate than dry sclerophyll leaves. Stick insects and snails consumed wet sclerophyll leaves at rates averaging 0.06% and 0.05% total area per hour respectively. Snails ate rainforest leaves at a rate of 0.03% per hour (Fig. 4.13) compared to stick insects and crickets that had consumption rates of 0.01% and 0.004% total area per hour. The stick insects ate the highest proportion of dry sclerophyll leaves (Fig. 4.13).

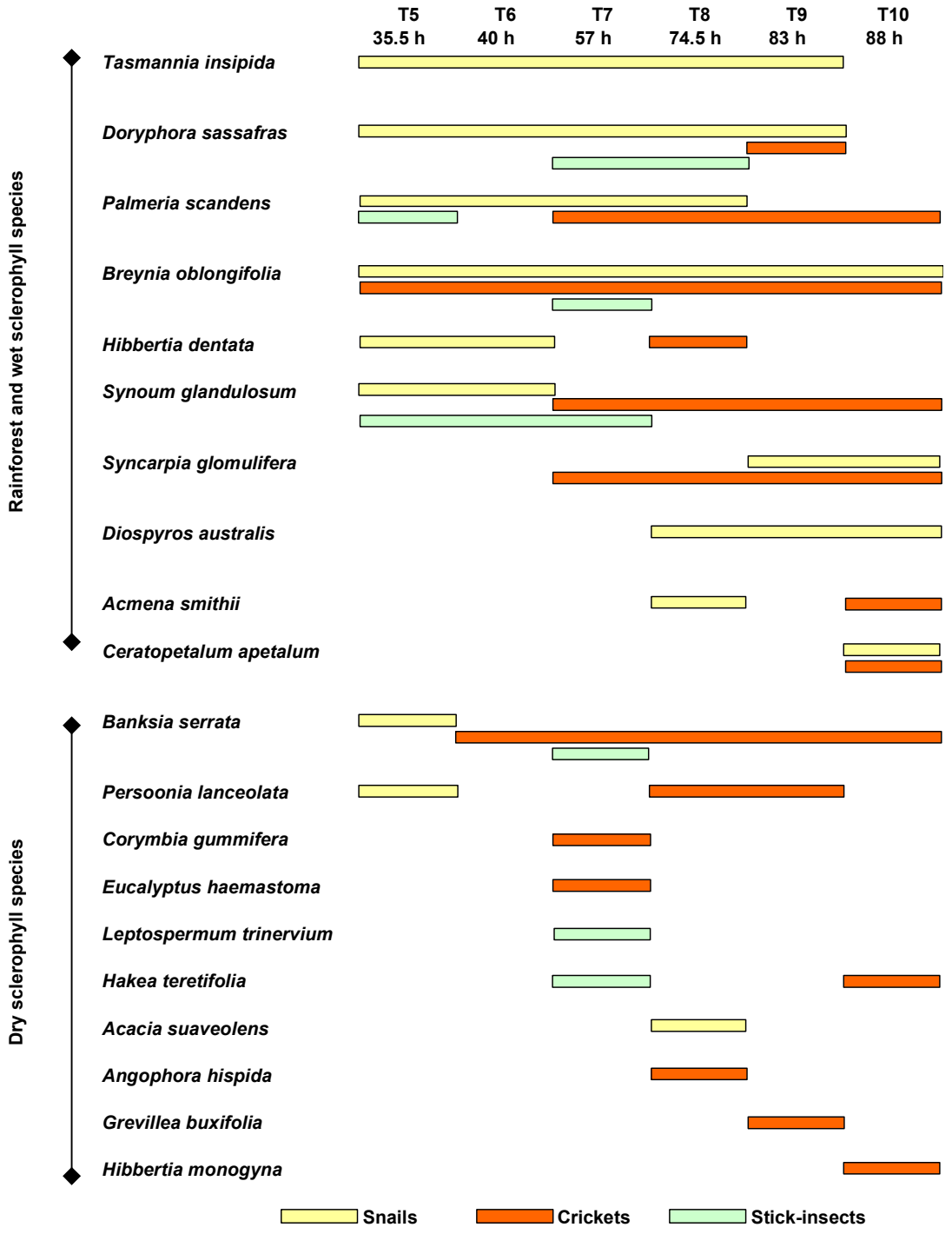


Figure 4.12 Plant selection and preference for three invertebrate herbivores under laboratory conditions. Snails, crickets and phasmids generally preferred Rainforest and wet sclerophyll leaf squares.

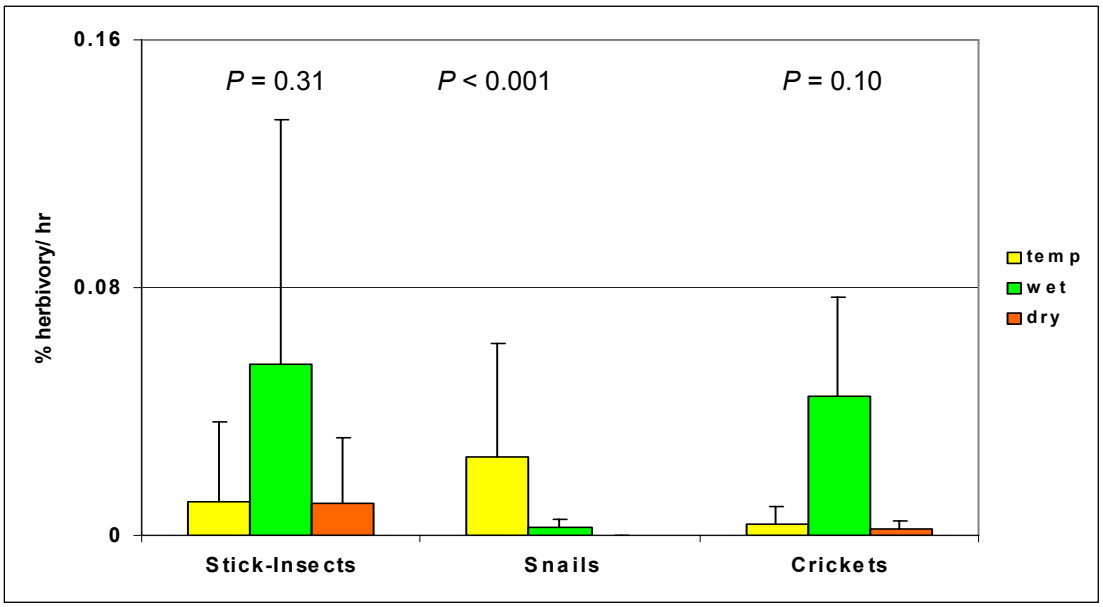


Figure 4.13 Percent consumption of rainforest, wet sclerophyll and dry sclerophyll leaves per hour by three invertebrate herbivores under laboratory conditions. Wilcoxin rank-sum tests compare the rates of consumption of mesic versus dry sclerophyll leaves.

Basic statistics for some plant species consumed by snails, crickets and stick insects are shown in Table 4.3. Data were highly skewed and variable. Only a small number of leaves were eaten by the invertebrates. A total of 18 leaves out of 300 were partially consumed by the stick insects, and both snails and crickets consumed 23 out of 300 leaves.

The most important leaf characteristics associated with consumption of leaves in the cafeteria experiments were lamina thickness, fibre content and water content (Tables 4.4, 4.5, 4.6), with only lamina thickness and fibre content having significant associations with consumption. Consumption by stick insects was predicted mainly by thick lamina and high fibre content and to a lesser extent by higher total phenol concentrations and leaf toughness (Table 4.4). Snails seemed to prefer fibrous leaves, though total phenols and water content may also predict consumption by snails (Table 4.5). No variable significantly predicted consumption by crickets (Table 4.6).

Table 4.3 Proportion of leaf tissue consumed per hour by test organisms in cafeteria experiments

Plant species	Description	Trial	No. leaves eaten during trial (%)	Maximum rate/h	Minimum rate/h	Mean rate/h
Doryphora sassafras	Rainforest	Snail Cricket Stick	40 20 20	0.6 0.1 0.8	0 0 0	0.08 0.01 0.06
Palmeria scandens	Rainforest	Snail Cricket Stick	53 20 6.7	0.3 0.1 0.001	0 0 0	0.03 0.01 0
Breynia oblongifolia	Wet sclerophyll	Snail Cricket Stick	20 27 6.7	0.03 0.6 0.8	0 0 0	0.01 0.07 0.05
Tasmannia insipida	Rainforest	Snail Cricket Stick	47 0 0	0.1 0 0	0 0 0	0.01 0 0
Syncarpia glomulifera	Wet sclerophyll	Snail Cricket Stick	20 40 0	0.1 0.6 0	0 0 0	0.01 0.04 0
Diospyros australis	Rainforest	Snail Cricket Stick	20 0 0	0.04 0 0	0 0 0	0.01 0 0
Synoum glandulosum	Wet sclerophyll	Snail Cricket Stick	6.7 33 40	0.01 0.4 1.0	0 0 0	0 0.04 0.2
Banksia serrata	Dry sclerophyll	Snail Cricket Stick	20 20 27	0.002 0.01 0.37	0 0 0	0 0.01 0.05

Table 4.4 Multiple linear regression results for stick insect consumption during a cafeteria experiment conducted under laboratory conditions.

```
Coefficients:
            Estimate  Std Error t value Pr(>|t|)
(Intercept)  4.89     5.08   0.96   0.36

LT            1.32     0.40    3.31   0.007 **
NDF           5.12     1.62    3.16   0.009 **
TP            1.36     0.91    1.49   0.16
Tg            0.04     0.51    0.08   0.94
N             0.31     3.61    0.09   0.93
W             1.41     1.48    0.96   0.36
CN           -6.17     7.47   -0.83   0.43

Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1.
```

Residual standard error: 1.001 on 11 degrees of freedom. Multiple R-Squared: 0.7699, Adjusted R-squared: 0.6235. F-statistic: 5.258 on 7 and 11 DF, p-value: 0.00761.
Variable codes: LT – lamina thickness; NDF – fibre content; TP – total phenols; Tg – leaf toughness; N – nitrogen; W – water content; CN – carbon:nitrogen ratios.

Table 4.5 Multiple linear regression results for snail consumption during a cafeteria experiment conducted under laboratory conditions.

```
Coefficients:
            Estimate  Std Error t value Pr(>|t|)
(Intercept)  0.57   3.59   0.16   0.88

NDF          2.59    1.15   2.26   0.04 *
TP          -0.79    0.64  -1.22   0.25
W           -1.005   1.04  -0.96   0.36
Tg          -0.20    0.36  -0.57   0.58
CN          -1.00    5.27  -0.19   0.85
LT          -0.04    0.28  -0.13   0.90
N            0.16    2.55   0.06   0.95

Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1
```

Residual standard error: 0.7062 on 11 degrees of freedom. Multiple R-Squared: 0.5952, Adjusted R-squared: 0.3375. F-statistic: 2.31 on 7 and 11 DF, p-value: 0.1035.
Variable codes: LT – lamina thickness; NDF – fibre content; TP – total phenols; Tg – leaf toughness; N – nitrogen; W – water content; CN – carbon:nitrogen ratios.

Table 4.6 Multiple linear regression results for cricket consumption during a cafeteria experiment conducted under laboratory conditions.

```
Coefficients:
            Estimate  Std Error t value Pr(>|t|)
(Intercept)  0.35    2.47   0.14   0.89

W            1.44    0.72   2.00   0.07 .
LT          -0.30    0.19  -1.52   0.16
N           -1.42    1.76  -0.81   0.44
TP           0.19    0.44   0.43   0.67
NDF          0.10    0.79   0.13   0.90
CN          -0.44    3.64  -0.12   0.91
Tg           0.03    0.25   0.11   0.92

Signif. codes:  0 `***' 0.001 `**' 0.01 `*' 0.05 `.' 0.1 ` ' 1
```

Residual standard error: 0.4871 on 11 degrees of freedom. Multiple R-Squared: 0.4554, Adjusted R-squared: 0.1089. F-statistic: 1.314 on 7 and 11 DF, p-value: 0.3288.
Variable codes: LT – lamina thickness; NDF – fibre content; TP – total phenols; Tg – leaf toughness; N – nitrogen; W – water content; CN – carbon:nitrogen ratios.

4.6 Discussion

Contrary to the expectation of the resource availability hypothesis that plants from higher resource environments should suffer greater levels of herbivory than plants from low resource environments (Coley et al., 1985), no relationship was found between soil nutrients and rates of herbivory in this study.

Damage to leaves in the field by insects was highly variable. Consumption rates varied between resource sites, between localities, between and within sites, between and within plant growth forms and between and within species. Herbivory also varied over time, with consumption rates decreasing as leaves matured for about 52% of the species and increasing for about 44% of the species. Whilst mesic leaves were preferred over dry sclerophyll leaves in the laboratory experiments, it was found that insect herbivory was not significantly greater at the higher resource sites compared to the lower resource sites. Insect herbivory did not differ significantly between soil type, vegetation type, or light availability. Nor was it significantly predicted by chemical and physical characteristics such as total phenols and leaf toughness.

Annual insect herbivory rates for the dry sclerophyll species at the low resource sites were 5.9% and 12% at KCNP and RNP respectively, compared to 7.6% and 14.6% for the mesic species at the higher resource sites. These levels of insect consumption were within the range of values in other Australian studies. Mangrove forest communities lose between 0.3% and 35% leaf area each year (Robertson & Duke, 1987). Rainforest plant species such as *Toona australis* and *Denrocnide excelsa* receive up to 5% and 33% annual defoliation by insects respectively (Lowman, 1985, 1992). Rates of herbivory for Acacias can range from 13% to 23% per year (Andrews and Hughes 2005), and Eucalypt species can suffer between 5% and 70% defoliation annually (Journet 1981; Fox and Morrow 1983, 1986; Ohmart 1984; Lowman and Heatwole 1992; Gras et al. 2005). In the current study, rates of herbivory per year for *Acacia suaveolens* was about 1% and *Eucalyptus haemastoma* from <1% to 28%.

Dry sclerophyll leaves from lower nutrient sites did not suffer less herbivory than mesic leaves from higher nutrient sites. In a previous study (Laxton and Hughes in review), it was found that dry sclerophyll leaves were better defended chemically by phenols and less nutritious than mesic leaves (as they contained more lignin, less nitrogen and water, and had higher C:N ratios). The current study either implies that mesic species are employing different strategies to defend their tissues from herbivores, or that phenols have functions other than defence. Close and McArthur (2002) and Weinig et al. (2004) argued and demonstrated that

phenols act as antioxidants, reducing the photo-destruction of exposed tissues by increasing concentrations as ultraviolet-light levels increase. These findings, combined with the lack of correlation between phenolics and herbivory in several other studies (eg. Coley 1983, Hatcher and Paul 1994, Read et al. 2003), are not supportive of the RAH (Coley et al. 1985). Dry sclerophyll species from low nutrient sites do not appear more capable of defending themselves against herbivores than mesic species from higher nutrient sites.

The leaf characteristics that significantly predicted insect consumption in the field were leaf age, leaf area, lamina thickness and fibre content. Plant species with relatively large leaf areas suffered higher rates of chewing damage than plant species with small leaf areas. Since large leaves expand more slowly than small leaves (Moles & Westoby, 2000) and young leaves are consumed at greater rates than mature leaves, these findings suggest large expanding leaves are vulnerable to chewing herbivores longer than expanding small leaves.

Another explanation that may contribute to the correlation between insect herbivory in the field and leaf area is “apparency” (Feeny, 1976). Large leaves may be discovered by insect herbivores more easily than small leaves, and they may be exposed to a wider range of insects that complete their larval development on individual leaves (Moles & Westoby, 2000). The susceptibility of an individual leaf to discovery by herbivores may be influenced by leaf size, plant growth form, persistence, and the relative abundance of the plant species in the overall community (Feeny, 1976).

Leaves in the field with thick laminas and low fibre content were more vulnerable to sucking insects. This may indicate that the studied leaves only had thin upper cuticles, a characteristic that has been negatively correlated to densities of cicadellids (Peeters, 2002a). Interestingly, nitrogen and water content were not predictors of sucking damage in this study. This was a surprise as previous studies have demonstrated that levels of plant nitrogen can regulate rates of insect herbivory, and sucking insects have been significantly correlated with leaf nitrogen and water (Landsberg & Gillieson, 1995; Majer et al. 1992; Waring & Cobb, 1992; Peeters, 2002a). The unexpected results are likely due to this study being based

on actual herbivore damage, as opposed to previous research that is based on arboreal insect surveys (eg. Peeters, 2002a,b). However, the lack of correlation may also be the result of necrosis or damage caused by sucking insects being monitored over time, as opposed to the actual amount of cytoplasm removed by Hemiptera.

During the cafeteria laboratory experiments, test organisms mainly targeted wet sclerophyll leaves. Snail and stick insect consumption was significantly predicted by high fibre content, whilst cricket consumption appeared not to be influenced by any of the analysed variables. Herbivores are attracted to different plant species that are often characterised by specific leaf traits (Peeters 2002a,b). The decision to feed is based upon information gained from olfaction, chemoreception, mechanoreception and vision (Prokopy & Owens, 1983; Bernays & Chapman, 1994; Chapman, 1998). Diet may be predicted by the form of mouthparts (Ruppert & Barnes, 1991; Chapman, 1998; Harvey & Yen, 1997; Hochuli, 1996), and the structure of the gut can reflect the mechanical properties and the nutrient composition of the food eaten (Gullan and Cranston, 1998).

Any deviations from previous studies may be due to differences between Australian or Southern Hemisphere ecosystems and those in the Northern Hemisphere (Branagan et al. 1979; White, 1994; Edwards et al. 2000). It is also possible that differences may be due to previous studies making comparisons between rates of herbivory at sites separated by considerable distance, such as comparing herbivory in temperate forests with those in the tropics or comparing herbivore consumption on opposite sides of a continent (Coley & Aide, 1991; Majer et al. 1992; Recher et al., 1996a,b). Under these circumstances, the relationship between herbivory and resource availability is confounded by differences in climate, soil structure, vegetation assemblages and regional insect herbivore fauna.

In conclusion, the expectation of the resource availability hypothesis, that herbivory would be greater in resource rich environments, was not supported by these data. While phasmids, crickets and snails preferred wet sclerophyll and temperate rainforest leaves under laboratory conditions, consumption rates in the

field did not differ significantly between resource sites and vegetation types. The variables that predicted consumption were leaf age, leaf area, lamina thickness and fibre content in the field, and lamina thickness and fibre content in the laboratory. Variables expected to influence rates of herbivory, namely leaf toughness, phenol concentration and nitrogen content, were not correlated to herbivory. In this study, therefore, variables traditionally regarded as anti-herbivore defences did not provide effective barriers against consumption. Either mesic species are employing other strategies to defend photosynthetic tissues, or factors such as phenols have functions other than defence.

Chapter 5
Insect communities and resource availability

5.1 Introduction

The distribution and abundance of insects has been attributed to various combinations of abiotic and biotic factors. Increased soil nutrients can elevate nitrogen concentrations in foliage, providing a more nutritious food source for canopy arthropods (Walde, 1995; Recher et al., 1996a). Rainfall fluctuations can alter leaf physiology and promote new leaf production (Janzen & Schoener, 1967; Denlinger, 1980; Lowman, 1982; Landsberg & Wylie, 1983; Itioka & Yamauti, 2004), which may affect insect communities by increasing the growth rates (Wint, 1983) and fecundity of herbivorous insects (Ohmart et al., 1985). Solar radiation can elevate the concentration of soluble nitrogen in sun-leaves and limit leaf production. This in turn may accelerate growth rates and affect survivorship of thrips and psyllids (Journet, 1980; White, 1984; Barone, 1998).

Insect herbivore distribution and abundance has been related to several leaf and host plant characteristics (Basset, 1991). Plant structure can affect the distribution and abundance of arthropod communities by providing “niches” that can be exploited (Lawton, 1978; Strong et al., 1984; Recher et al., 1996a; Recher et al., 1996b). Leaf age and synchronous leaf production influence insect abundance and spatial distribution by affecting nutritional quality and quantity of food (Coley, 1980; Raupp & Denno, 1983; Basset, 1991; Kursar et al., 1991; Aide, 1993). Leaf toughness can deter herbivore consumption and subsequently affect growth rates by wearing the mandibles of insects that attempt to feed (Coley, 1983; Lowman & Box, 1983; Raupp, 1985; Aide & Zimmerman, 1990; Choong et al., 1992; Choong, 1996; Hochuli, 1996; Lucas et al., 2000). Plant trichomes can interfere with insect oviposition, attachment, feeding, and ingestion (Stephens et al., 1961; Gallun et al., 1973; Webster et al., 1973; Ramalho et al., 1984; Hoffman et al., 1985; Makanjuola et al., 1992). They can also provide herbivores with physical defensive

barriers against predators (Levin, 1973; Makanjuola et al., 1992). Condensed tannins, phenols and lignin can act as anti-herbivore substances by forming complexes with plant proteins and carbohydrates (Rhoades, 1979). Along with various protein derived molecules, these substances interfere with the absorption of nutrients by disrupting digestive enzymes, increasing the absorption of toxic substances and damaging insect midguts (Falco et al., 2001; Silva et al., 2001; Pompermayer et al., 2001).

The resource availability hypothesis (Coley et al., 1985) states that variation in herbivore pressure between plant species can be largely understood in terms of the resources available to plants. Plant species growing in resource-limited environments are expected to have long-lived, heavily defended leaves that suffer less intense herbivory. By contrast, plants growing in resource-rich environments are predicted to have faster growing, short-lived leaves that have fewer defences and as a consequence suffer higher levels of herbivore consumption.

This chapter tests a corollary of the resource availability hypothesis, that plants from higher resource environments will have more palatable leaves and therefore be able to attract and support a greater diversity and abundance of insect herbivores than plants from low resource environments. Resources were defined in terms of total nitrogen and total phosphorus levels in the soil (Table 2.2). Invertebrates were collected from a wide variety of plant species from paired sites at two localities in the Sydney region. Both localities are subject to the same climate and regional herbivore fauna. The specific questions addressed were:

1. Does the structure of insect communities differ: (i) between plant species within a site, (ii) between sites of different resource availability, and (iii) between localities?

2. Are specific leaf traits correlated with the diversity or abundance of particular insect orders/ families/ and guilds?

5.2 Methods

Fifteen common plant species per site were sampled (n = 46 species in total). Plant species were selected to represent the plant communities at each site, and a wide range of growth forms (trees, shrubs and vines) and plant families (Fig. 3.1).

Invertebrate collections were made seasonally between April 2002 (autumn) and February 2004 (summer), a total of eight collections. Flowering plants were avoided because the presence/ absence of flowers can significantly affect the abundance of most invertebrate orders (Woinarski & Cullen, 1984). Four replicates per plant species were chosen randomly on each sampling occasion and sampled for organisms using two collection methods: pyrethrum spraying and branch clipping.

Pyrethrum spraying is an effective sampling method because the majority of organisms on the sprayed plant are collected. However the technique has the potential of introducing bias. Unlike several studies that sampled only one or a few plant species (Andrew et al., 2004; Andrew et al. 2005 a,b,c; Recher et al. 1992, 1996), this is a comparative project dealing with plant species of varying size, shape and foliage density. By supplementing pyrethrum spraying with branch clipping and determining the number of organisms per dried unit of biomass, it was possible to calibrate results for variation in size and shape of plants and for differences in the density of foliage.

Prior to pyrethrum spraying, up to four 30 cm x 60 cm collection trays were placed beneath each plant. The plant was then sprayed with a 0.6% pyrethrum/ water solution. The maximum height of canopy sprayed was 2.7 m from ground level. Plant shape, canopy height and width, and proportion of plant sprayed was recorded to calculate the volume of canopy sampled. After 30 minutes, the sprayed plant was shaken vigorously to dislodge remaining organisms, collection trays were retrieved, and the contents washed into 500-mL storage containers with 70% ethanol.

For branch clipping, a portion of foliage was bagged and then cut from either a plant designated for pyrethrum spraying or a nearby plant of the same species. Branch clipping occurred before fogging. Samples were taken from the field and frozen in commercial freezers for at least three days to kill the organisms. Once removed from the freezers and defrosted, branches were shaken vigorously in a closed vessel and organisms washed into 500-mL storage containers with 70% ethanol. Branches were separated into leaves, stems, and fruits and dried at 70^{o}C for over 7 days, then weighed.

All collected organisms were sorted to order. Arthropods were assigned to one of six feeding guilds: predators, leaf chewers, sap suckers, fungivores, scavengers, and "various". The orders Araneae (spiders), Lepidoptera (caterpillars), Orthoptera (grasshoppers), Thysanoptera (thrips), Collembola (springtails), Psocoptera (psocids), Blattodea (cockroaches), and Hymenoptera (ants, wasps and bees) were placed into the feeding guilds shown in Table 5.1. Feeding guilds were based on Harvey and Yen (1997).

Table 5.1 Taxonomic groups and feeding guilds for orders

Name (Taxon)	Common Name	Feeding Guild
Mantodea	Preying Mantids	Predators
Araneae	Spiders	Predators
Lepidoptera	Caterpillars	Leaf chewers
Gastropoda	Snails	Leaf chewers
Phasmatodea	Stick insects	Leaf chewers
Orthoptera	Grasshoppers	Leaf chewers
Thysanoptera	Thrips	Sap suckers
Blattodea	Cockroaches	Scavengers
Pscocoptera	Bark lice	Scavengers
Collembola	Springtails	Scavengers
Isopoda	Slaters	Scavengers
Acarina	Mites	Various
Diptera	Flies	Various
Hymenoptera	Ants, Wasps, Bees	Various

Coleoptera (beetles) and Hemiptera (bugs) were subdivided further as families within these orders have different feeding habits (Table 5.2). Family identification and feeding habits of beetles and bugs were based on Lawrence and Britton

Table 5.2 Taxonomic groups and feeding guilds for Coleoptera and Hemiptera

Name (Taxon)	Common name	Feeding Guild
Coleoptera: Coccinellidae	Ladybirds	Predator
Coleoptera: Staphylinidae	Rove Beetles	Predator
Coleoptera: Pselaphidae		Predator
Coleoptera: Carabidae	Ground Beetles	Predator
Coleoptera: Corylophidae		Predator
Coleoptera: Trogossitidae		Predator
Hemiptera: Nabidae		Predator
Hemiptera: Reduviidae	Assassin Bugs	Predator
Coleoptera: Chrysomelidae	Leaf Beetles	Leaf chewer
Coleoptera: Curculionidae	Weevils	Leaf chewer
Coleoptera: Brentidae	Weevils	Leaf chewer
Coleoptera: Buprestidae	Jewel Beetles	Leaf chewer
Coleoptera: Cerambycidae	Longicorn Beetles	Leaf chewer
Hemiptera: Psyllidae	Leaf Hoppers	Sap sucker
Hemiptera: Cicadellidae	Leaf Hoppers	Sap sucker
Hemiptera: Membracidae	Leaf Hoppers	Sap sucker
Hemiptera: Fulgoridae	Leaf Hoppers	Sap sucker
Hemiptera: Eurymelidae	Leaf Hoppers	Sap sucker
Hemiptera: Flatidae	Leaf Hoppers	Sap sucker
Hemiptera: Ricaniidae	Leaf Hoppers	Sap sucker
Hemiptera: Aphididae	Aphids	Sap sucker
Hemiptera: Pseudococcidae		Sap sucker
Hemiptera: Margarodidae		Sap sucker
Hemiptera: Tingidae		Sap sucker
Hemiptera: Delphacidae		Sap sucker
Hemiptera:Aleyrodidae	Whiteflies	Sap sucker
Hemiptera: Coreidae	Squash bugs	Sap sucker
Hemiptera: Aradidae		Fungivore
Hemiptera: Endomychidae		Fungivore
Hemiptera: Cryptophagidae		Fungivore
Coleoptera:Laemophloeidae		Fungivore
Coleoptera: Lathridiidae		Fungivore
Coleoptera:Mycetophagidae		Fungivore
Coleoptera: Cerylonidae		Fungivore
Coleoptera: Silvanidae		Fungivore
Coleoptera: Zopheridae		Fungivore
Coleoptera: Tenebrionidae	Tenebrionids	Scavenger
Coleoptera: Clambidae	Clambids	Scavenger
Coleoptera: Nitidulidae		Scavenger
Coleoptera: Mordellidae		Scavenger
Coleoptera: Salpingidae		Scavenger
Coleoptera: Ptiliidae		Scavenger
Coleoptera: Scarabaeidae	Scarab Beetles	Scavenger
Coleoptera: Aderidae	Aderids	Scavenger
Coleoptera: Anthicidae	Anthicids	Scavenger
Coleoptera: Melyridae		Scavenger
Coleoptera: Ptilodactylidae		Scavenger
Hemiptera: Miridae	True Bug	Various
Coleoptera: Elateridae	Click Beetles	Various
Hemiptera: Pentatomidae		Various
Hemiptera: Lygaeidae	True Bug	Various

(1991) and Carver *et al* (1991) respectively.

Once the invertebrates were sorted and subdivided, the number of individuals present were converted into density estimates (i.e. for pyrethrum samples: number of organisms per cubic metre sprayed, and for branch samples: number of organisms per gram dried leaf biomass).

5.3 Statistics

Principal component (PC) biplots or multivariate scatterplots produced by the R-statistical program were used to explore the relationship between plant species, soil nutrients and: (i) invertebrate orders, (ii) insect feeding guilds, (iii) coleopteran families and (iv) hemipteran families. Points in the matrix were obtained by transforming the data by logging abundances, and then standardising the data by subtracting the variable (column) mean from the species (cell) mean and dividing the subsequent value by the variable or column mean (Gabriel, 1971; Gabriel and Odoroff, 1990). Though the principal components underlying each biplot are not themselves displayed, the length of one unit in the X-axis direction (1st principal component) is identical to the length of one unit in the Y-axis direction (2nd principal component).

To accompany the PC biplots, PAST was used to perform an analysis of similarity (ANOSIM) comparing dry sclerophyll and mesic species (Hammer et al. 2001). The ANOSIM used an Euclidean distance with 5000 permutations and was performed on the transformed dataset to reduce the colinearity and multidimensionality of the original data (Quinn & Keough 2002).

Canonical correspondence analysis (CCA), based on the work of ter Braak (1987) produced in S-Plus, was used to identify mature leaf characteristics that could potentially predict the presence of: (i) invertebrate orders, (ii) insect feeding guilds, (iii) coleopteran families and (iv) hemipteran families. Prior to analyses, the data were assessed for regularity by using multiple p-variate quantile-quantile plots (Hadi, 1994). As outlying points particularly undermine CCA analysis, the quantile-

quantile plots guided the construction of the CCA data matrix. Outlying points were suppressed, and CCA analysis could proceed with some degree of confidence.

Wilcoxon rank-sum tests and one-way ANOVAs were performed on insect densities to test the significance of: (i) plant growth form and (ii) sampling method. To satisfy the requirements for ANOVA, data were transformed by logging prior to analysis.

5.4 Pyrethrum sampling results

5.4.1 Arthropod community composition and structure

A total of 110 181 animals were collected during the two year study. Of these, 44 organisms belonged to the phylum Annelida and Mollusca, and the rest were of the phylum Arthropoda. The arthropods were represented by the classes Insecta, Arachnida, Collembola, Diplopoda and Malacostraca (Table 5.3). Acarina made up 30% of all animals captured, and Collembola contributed 21%, Diptera 11%, Thysanoptera 9%, Coleoptera and Hymenoptera 7% each, Araneae and Hemiptera both 6%, and Psocoptera 2%. All other remaining groups such as the Lepidoptera and Orthoptera together totalled 1%.

Over 47 800 insects representing twelve orders were collected during the study (Table 5.3). Of these, over 7 500 were beetles and 6 600 were bugs (Table 5.3). Twenty-nine Coleoptera and 22 Hemiptera families were identified in the collection (Table 5.2). Five of the beetle families and 14 of the bug families were phytophagous (Table 5.2).

There were approximately 106 morphospecies of phytophagous beetles. The most dominant phytophagous beetle families were the Curculionidae (about 54 morphospecies) and the Chrysomelidae (approximately 40 morphospecies). Brentidae, Buprestidae and Cerambycidae were represented by three, five and four beetle morphospecies respectively.

Over 60% of the collected Hemiptera were juveniles, making reliable identification to species level impossible. Cicadellidae, Psyllidae, Fulgoridae and Miridae dominated Hemiptera assemblages.

Table 5.3 Taxonomic composition and abundance of arboreal invertebrate fauna collected using pyrethrum spraying at the four sites. (RNP - Royal National Park; KCNP – Ku-ring-gai Chase National Park; LR- Low resource site; HR – Higher resource site)

Taxa			Abundance of organisms			
			Bundeena RNP/ LR	**Challenger KCNP/ LR**	**Dyke KCNP/ HR**	**Bola Ck RNP/ HR**
Phylum Arthropoda						
Class	**Insecta**		**(14 748)**	**(10 910)**	**(12 103)**	**(10 094)**
	Order	Blattodea	77	52	85	11
		Mantodea	3	10	1	1
		Orthoptera	99	79	78	104
		Phasmatodea	2	2	1	2
		Psocoptera	344	332	832	642
		Hemiptera	2701	1758	1480	689
		Thysanoptera	3321	3450	2198	460
		Coleoptera	3064	1252	1441	1752
		Siphonaptera	5	0	11	4
		Diptera	1694	1743	3333	4935
		Lepidoptera	123	64	64	44
		Hymenoptera	2884	1831	2078	1180
		Misc. larvae	431	337	501	270
Class	**Arachnida**		**(13 114)**	**(13 447)**	**(7817)**	**(5070)**
	Order	Araneae	1262	1152	2296	1893
		Acarina	11 852	12 295	5521	3177
Class	**Collembola**					
	Order	Collembola	7524	6767	4224	4270
Class	**Diplopoda**		0	0	1	1
Class	**Malacostraca**					
	Order	Amphipoda	0	0	0	27
	Order	Isopoda	8	4	2	6
Phyllum Annelida						
Class	**Hirudinea**					
	Order	Arhynchobdellida	1	0	6	4
Phyllum Mollusca						
Class	**Gastropoda**		0	0	2	31
	Total		**35 395**	**31 128**	**24 155**	**19 503**

5.4.2 Community structure and resource availability

Principal component analysis revealed there were two distinct groups of arthropods found on plants at the high and low resource sites in Ku-ring-gai Chase National Park and Royal National Park (Fig. 5.1). Group 1 arthropods comprised the Hemiptera (bugs), Acarina (mites), Thysanoptera (thrips), Blattodea (cockroaches), and Phasmatodea (stick insects). Group 2 arthropods consisted of Coleoptera (beetles), Orthoptera (crickets/ grasshoppers), Collembola

(springtails), Psocoptera (psocids) Lepidoptera (caterpillars), and Araneae (spiders).

Dry sclerophyll plant species such as *Pultenaea elliptica*, *Grevillea buxifolia*, *Isopogon anethifolius*, *Leucopogon microphyllus*, and *Hibbertia monogyna* supported large numbers of group 1 arthropods, while wet sclerophyll and temperate rainforest plants like *Syncarpia glomulifera*, *Allocasuarina torulosa*, *Trochocarpa laurina*, and *Acmena smithii* supported lower numbers of group 1 fauna (Fig. 5.1).

Group 2 arthropods were found in relatively high numbers on the wet sclerophyll and temperate rainforest plant species *Citriobatus pauciflorus*, *Pomaderris ferruginea*, *Wilkiea huegelianna,* and *Palmeria scandens* (Fig. 5.1). Dry sclerophyll species with group 2 fauna were *Banksia serrata*, *Corymbia gummifera*, *Eucalyptus haemastoma* and *Pultenaea elliptica* (Fig. 5.1).

The major leaf characteristics that predicted the presence of invertebrate orders on plants were leaf area, total phenol concentration, specific leaf area, and lamina thickness (Fig. 5.2). Coleoptera were found on plants with relatively thick lamina and higher water content. Hemiptera were negatively correlated with leaf toughness and positively correlated with nitrogen concentration. Orthoptera and Thysanoptera were positively correlated with water content, but negatively correlated with leaves high in nitrogen. Psocoptera tended to be found on plants with large leaf areas and specific leaf areas, and on plants with tough, fibrous leaves. Lepidoptera larvae were positively correlated with total nitrogen (Fig. 5.2).

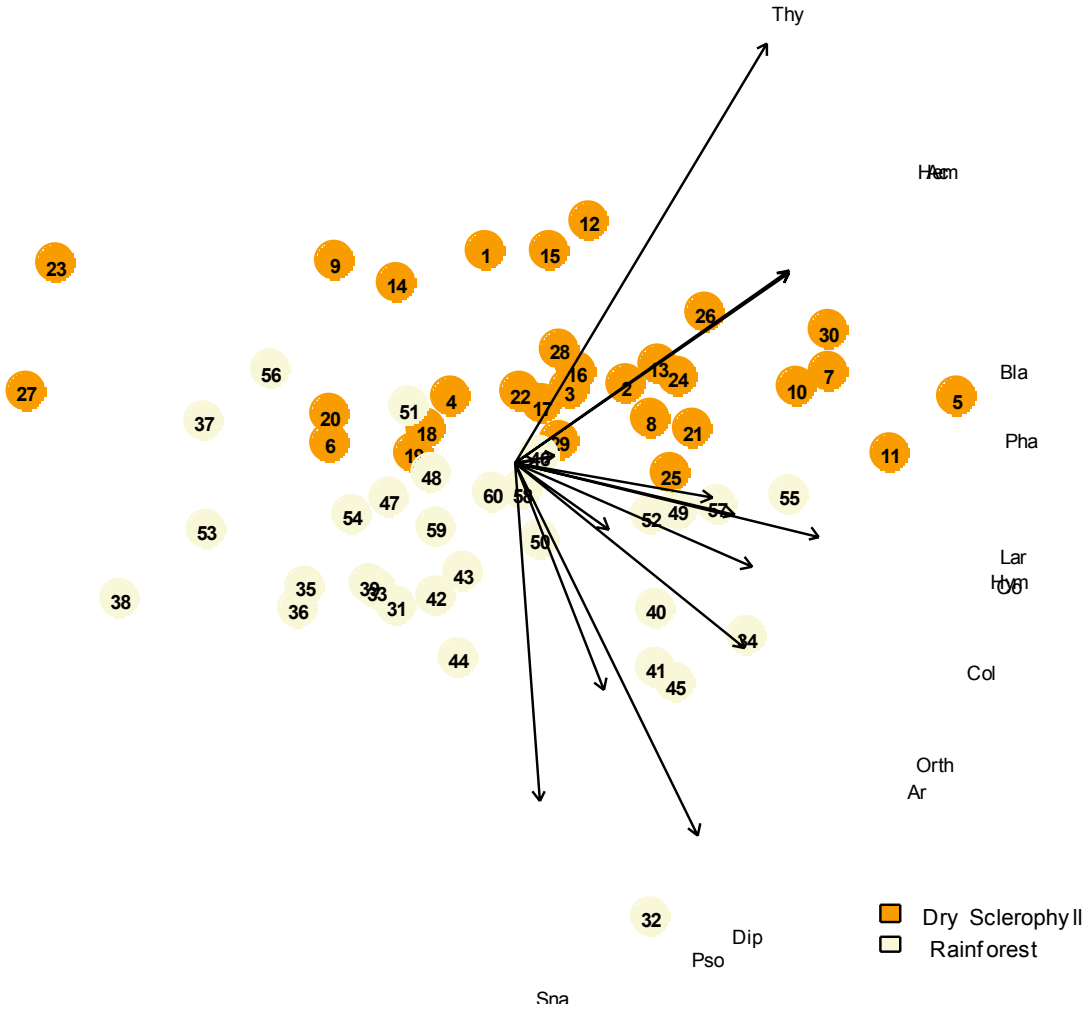


Figure 5.1 Invertebrate orders found on dry sclerophyll, wet sclerophyll and temperate rainforest plant species in Royal and Ku-ring-gai Chase National Parks (2002-2004) (PC biplot goodness-of- fit: 72.4; ANOSIM: R = 0.26, p = 0.0001)

Dry sclerophyll plants Bundeena rd, RNP	**Dry sclerophyll plants Challenger track, KNP**	**Rainforest plants Bola Creek, RNP**	**Wet sclerophyll plants Dyke, KNP**
1 *Acacia suaveolens* 2 *Allocasuarina distyla* 3 *Angophora hispida* 4 *Banksia serrata* 5 *Caustis recurvata* 6 *Corymbia gummifera* 7 *Grevillea sphacelata* 8 *Hakea teretifolia* 9 *Hemigenia purpurea* 10 *Isopogon anethifolius* 11 *Leptospermum trinervium* 12 *Leucopogon microphyllus* 13 *Persoonia lanceolata* 14 *Platysace linearifolia* 15 *Pultenaea elliptica*	16 *Acacia suaveolens* 17 *Angophora hispida* 18 *Banksia serrata* 19 *Corymbia gummifera* 20 *Eucalyptus haemastoma* 21 *Grevillea buxifolia* 22 *Hakea teretifolia* 23 *Hemigenia purpurea* 24 *Hibbertia monogyna* 25 *Leptospermum trinervium* 26 *Leucopogon microphyllus* 27 *Patersonia glabrata* 28 *Persoonia lanceolata* 29 *Platysace linearifolia* 30 *Pultenaea elliptica*	31 *Acmena smithii* 32 *Blechnum cartilagineum* 33 *Ceratopetalum apetalum* 34 *Citriobatus pauciflorus* 35 *Diospyros australis* 36 *Doryphora sassafras* 37 *Gymnostachys anceps* 38 *Livistona australis* 39 *Lomatia myricoides* 40 *Palmeria scandens* 41 *Ripogonum album* 42 *Syncarpia glomulifera* 43 *Tasmannia insipida* 44 *Trochocarpa laurina* 45 *Wilkiea huegelianna*	46 *Acacia floribunda* 47 *Allocasuarina torulosa* 48 *Breynia oblongifolia* 49 *Cissus hypoglauca* 50 *Citriobatus pauciflorus* 51 *Hibbertia dentata* 52 *Lepidosperma laterale* 53 *Livistona australis* 54 *Macrozamia communis* 55 *Pomaderris feruginea* 56 *Pteridium esculentum* 57 *Pultenaea daphnoides* 58 *Pultenaea flexilis* 59 *Syncarpia glomulifera* 60 *Synoum glandulosum*
Invertebrate Orders: Col Coleoptera (beetles) Hem Hemiptera (bugs) Orth Orthoptera (crickets) Pha Stick insects	Ac Acarina (mites) Ar Araneae (spiders) Hym Ants and wasps Sna Snails	Dip Diptera (flies) Co Collembola (springtails) Thy Thysanoptera (thrips)	Pso Psocoptera (psocids) Lar Lepidopteran larvae Bla Blattodea (cockroaches)

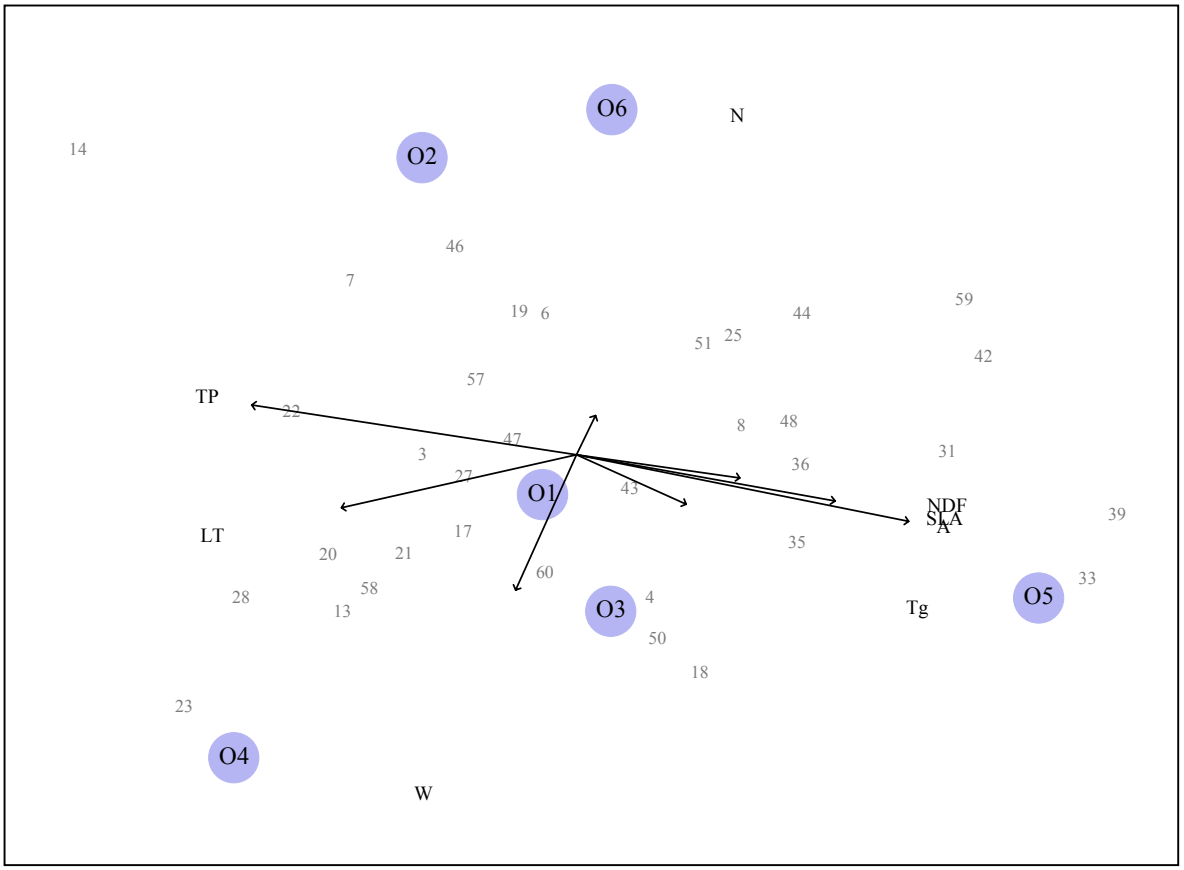


Figure 5.2 Leaf characteristics predicting the presence of six invertebrate orders on plant species in Ku-ring-gai Chase National Park and Royal National Park between the years 2002-2004. (CCA biplot goodness-of- fit: 87.73 %)

TP – Total Phenols; LT – Lamina Thickness; N – % Nitrogen; W – Water content; NDF – Fibre content; Tg – Leaf Toughness; A – Leaf Area; SLA – Specific Leaf Area; O1 – Coleoptera; O2 – Hemiptera; O3 – Orthoptera; O4 – Thysanoptera; O5 – Psocoptera; O6 – Lepidoptera (caterpillars)

Dry sclerophyll plants Bundeena rd, RNP	Dry sclerophyll plants Challenger track, KNP	Rainforest plants Bola Creek, RNP	Wet sclerophyll plants Dyke, KNP
3 *Angophora hispida* 4 *Banksia serrata* 6 *Corymbia gummifera* 7 *Grevillea sphacelata* 8 *Hakea teretifolia* 13 *Persoonia lanceolata* 14 *Platysace linearifolia*	17 *Angophora hispida* 18 *Banksia serrata* 19 *Corymbia gummifera* 20 *Eucalyptus haemastoma* 21 *Grevillea buxifolia* 22 *Hakea teretifolia* 23 *Hemigenia purpurea* 25 *Leptospermum trinervium* 27 *Patersonia glabrata* 28 *Persoonia lanceolata*	31 *Acmena smithii* 33 *Ceratopetalum apetalum* 35 *Diospyros australis* 36 *Doryphora sassafras* 39 *Lomatia myricoides* 42 *Syncarpia glomulifera* 43 *Tasmannia insipida* 44 *Trochocarpa laurina*	46 *Acacia floribunda* 47 *Allocasuarina torulosa* 48 *Breynia oblongifolia* 50 *Citriobatus pauciflorus* 51 *Hibbertia dentata* 53 *Livistona australis* 57 *Pultenaea daphnoides* 59 *Syncarpia glomulifera* 60 *Synoum glandulosum*

5.4.3 Guild composition and structure

The greatest proportion of invertebrates collected were classified in the feeding guild “Various”, which in this study includes the Hymenoptera (predominantly ants and wasps) (Fig. 5.3). Predators were relatively common at the wet sclerophyll

and temperate rainforest sites at the Dyke (KNP) and Bola Creek (RNP). Leaf-chewers and sap-suckers represented less than 16 percent of guild composition at each site. Fungivores were relatively uncommon in the dataset (Fig. 5.3).

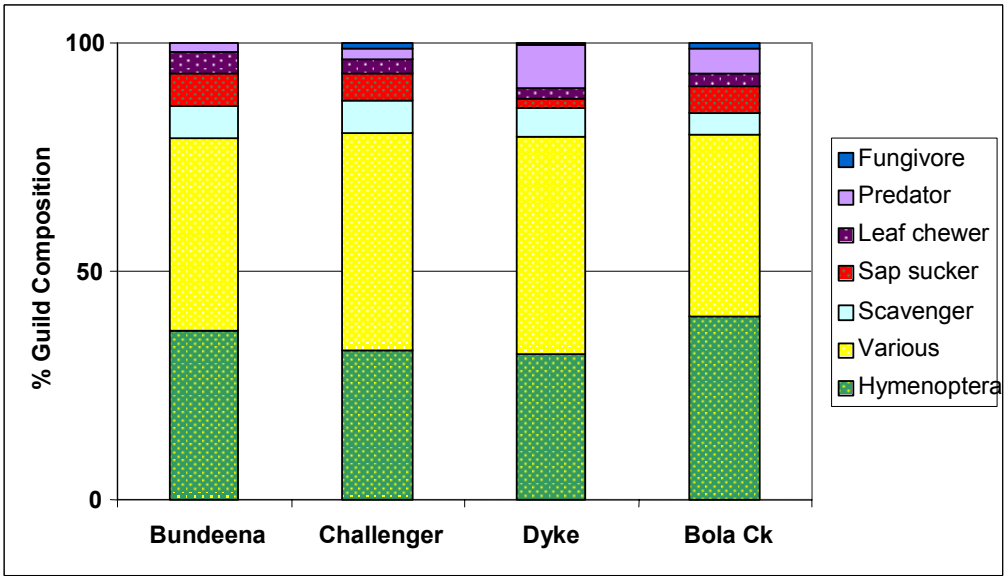


Figure 5.3 Percent composition of invertebrate feeding guilds for sites in Ku-ring-gai Chase and Royal National Parks (2002-2004)

Soil nutrient availability and/or vegetation type may be a predictor of invertebrate feeding guild presence. Dry sclerophyll plant species such as *Caustis recurvata*, *Acacia suaveolens*, *Leptospermum trinervium* and *Grevillea sphacelata* supported relatively high densities of leaf chewers, sap suckers, predators and scavengers. Wet sclerophyll and temperate rainforest plants generally had below average representation of these feeding guilds. (Fig. 5.4).

The major leaf characteristics that predict feeding guild presence were total phenols, lamina thickness, leaf area, specific leaf area, and fibre content. Leaf chewers and sap suckers were highly positively correlated with total phenols and lamina thickness and negatively correlated with leaf area, specific leaf area, fibre content and nitrogen concentration (Fig. 5.5). Fungivores were closely associated with tough leaves, whilst scavengers and the guild “various” were negatively correlated with leaf toughness (Fig. 5.5). Predators were found on leaves with high SLAs, water content and high percent fibre content (Fig. 5.5).

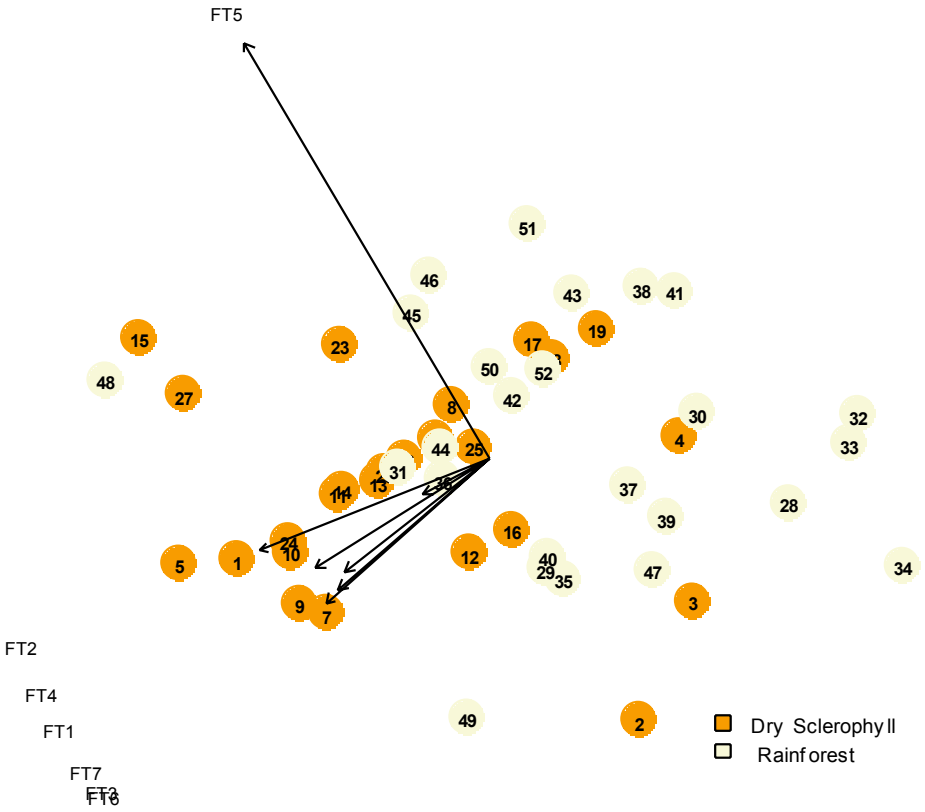


Figure 5.4 Insect Feeding Guilds found on dry sclerophyll and rainforest plant species in Royal and Ku-ring-gai Chase National Parks (2002-2004) (PC biplot goodness of fit: 78.01%; ANOSIM: R = 0.24, p = 0.0001)

Dry sclerophyll plants Bundeena rd, RNP	**Dry sclerophyll plants Challenger track, KNP**	**Rainforest plants Bola Creek, RNP**	**Wet sclerophyll plants Dyke, KNP**
1 *Acacia suaveolens* 2 *Allocasuarina distyla* 3 *Angophora hispida* 4 *Banksia serrata* 5 *Caustis recurvata* 6 *Corymbia gummifera* 7 *Grevillea sphacelata* 8 *Hemigenia purpurea* 9 *Isopogon anethifolius* 10 *Leptospermum trinervium* 11 *Leucopogon microphyllus* 12 *Persoonia lanceolata* 13 *Platysace linearifolia* 14 *Pultenaea elliptica*	15 *Acacia suaveolens* 16 *Angophora hispida* 17 *Banksia serrata* 18 *Corymbia gummifera* 19 *Eucalyptus haemastoma* 20 *Grevillea buxifolia* 21 *Hemigenia purpurea* 22 *Hibbertia monogyna* 23 *Leptospermum trinervium* 24 *Leucopogon microphyllus* 25 *Persoonia lanceolata* 26 *Platysace linearifolia* 27 *Pultenaea elliptica*	28 *Acmena smithii* 29 *Blechnum cartilagineum* 30 *Ceratopetalum apetalum* 31 *Citriobatus pauciflorus* 32 *Diospyros australis* 33 *Doryphora sassafras* 34 *Lomatia myricoides* 35 *Palmeria scandens* 36 *Ripogonum album* 37 *Syncarpia glomulifera* 38 *Tasmannia insipida* 39 *Trochocarpa laurina* 40 *Wilkiea huegelianna* 41 *Gymnostachys anceps*	42 *Acacia floribunda* 43 *Allocasuarina torulosa* 44 *Breynia oblongifolia* 45 *Cissus hypoglauca* 46 *Citriobatus pauciflorus* 47 *Hibbertia dentata* 48 *Pomaderris feruginea* 49 *Pultenaea daphnoides* 50 *Pultenaea flexilis* 51 *Syncarpia glomulifera* 52 *Synoum glandulosum*
Guilds: FT1 Leaf Chewers FT2 Sap Suckers	FT3 Scavengers FT4 Predators	FT5 Fungivores FT6 Various	FT7 Hymenoptera

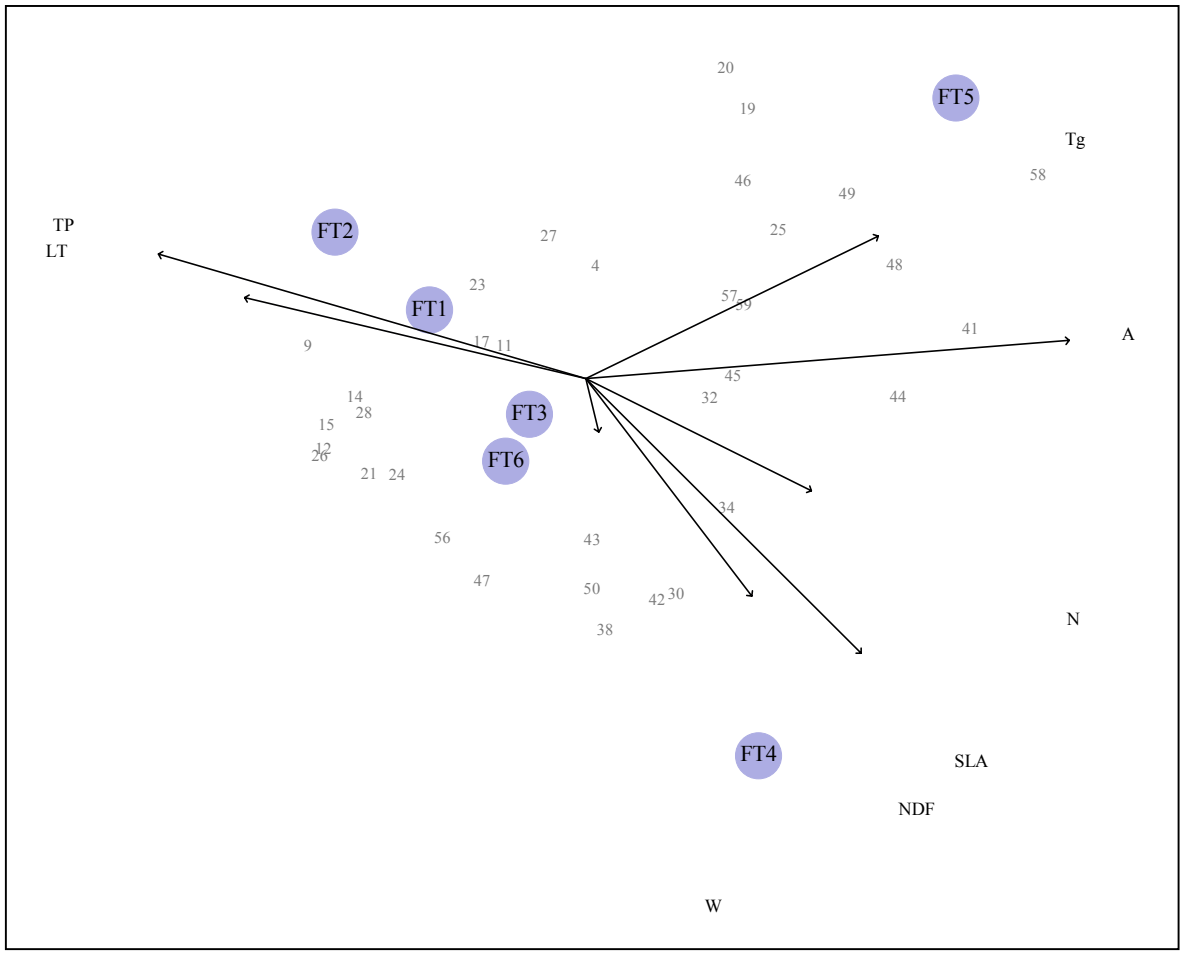


Figure 5.5 Leaf characteristics predicting the presence of invertebrate feeding guilds on plant species in Royal and Ku-ring-gai Chase National Parks (2002-2004). (CCA biplot quality of fit: 86.86%)

TP – Total Phenols; LT – Lamina Thickness; N – % Nitrogen; W – Water content; NDF – Fibre content; Tg – Leaf Toughness; A – Leaf Area; SLA – Specific Leaf Area; FT1 – Leaf Chewers; FT2 – Sap Suckers; FT3 – Scavengers; FT4 – Predators; FT5 – Fungivores; FT6 – Various.

Dry sclerophyll plants Bundeena rd, RNP	**Dry sclerophyll plants Challenger track, KNP**	**Rainforest plants Bola Creek, RNP**	**Wet sclerophyll plants Dyke, KNP**
3 *Angophora hispida* 4 *Banksia serrata* 9 *Hemigenia purpurea* 11 *Leptospermum trinervium* 12 *Leucopogon microphyllus* 13 *Persoonia lanceolata* 14 *Platysace linearifolia* 15 *Pultenaea elliptica*	17 *Angophora hispida* 19 *Corymbia gummifera* 20 *Eucalyptus haemastoma* 21 *Grevillea buxifolia* 23 *Hemigenia purpurea* 24 *Hibbertia monogyna* 25 *Leptospermum trinervium* 26 *Leucopogon microphyllus* 27 *Persoonia lanceolata* 28 *Platysace linearifolia*	30 *Acmena smithii* 32 *Ceratopetalum apetalum* 34 *Diospyros australis* 38 *Lomatia myricoides* 41 *Syncarpia glomulifera* 42 *Tasmannia insipida* 43 *Trochocarpa laurina* 44 *Wilkiea huegelianna*	45 *Acacia floribunda* 46 *Allocasuarina torulosa* 47 *Breynia oblongifolia* 48 *Cissus hypoglauca* 49 *Citriobatus pauciflorus* 50 *Hibbertia dentata* 56 *Pultenaea daphnoides* 57 *Pultenaea flexilis* 58 *Syncarpia glomulifera* 59 *Synoum glandulosum*

5.5 Coleoptera, Hemiptera and Lepidoptera in low and higher resource sites

Coleoptera, Hemiptera and Lepidoptera comprised only a small proportion of the total fauna collected. Despite this, they were the focus of the study because they constituted the most conspicuous herbivores in the collection.

The density of Coleoptera and Lepidoptera larvae did not differ significantly between sites of contrasting resource levels (Wilcoxon rank sum tests: $P = 0.20$ and $P = 0.13$ respectively, Fig. 5.6). Beetle and caterpillar densities at the dry sclerophyll sites averaged 95 beetles and 16 caterpillars m^{-3} of vegetation compared to 57 beetles and 14 lepidopteran larvae m^{-3} at the higher nutrient sites.

Significantly higher numbers of Hemiptera were found on dry sclerophyll plants compared to wet sclerophyll and temperate rainforest plants (Wilcoxon rank sum test: $P < 0.01$). An average of 99 bugs m^{-3} was found on dry sclerophyll plants, compared to 46 bugs m^{-3} on wet sclerophyll and temperate rainforest plants (Fig. 5.6). The greatest number of Hemiptera (110 bugs m^{-3}) and Coleoptera (130 beetles m^{-3}) were collected from the dry sclerophyll site along Bundeena road, RNP (Fig. 5.7), and the lowest densities of Hemiptera (24 bugs m^{-3}) and Coleoptera (56 beetles m^{-3}) were collected from the temperate rainforest at Bola Creek, RNP (Fig. 5.7).

Herbivore densities did not differ significantly between plant growth forms in dry and wet sclerophyll environments (Fig. 5.8 and Fig. 5.9). For example, there was an average of 118 and 107-beetles m^{-3} on the dry (Fig. 5.8) and wet sclerophyll shrubs (Fig. 5.9), compared to 17 and 22 beetles m^{-3} on plants less than 0.5 m in height. Trees (plants greater than 2m in height) had means of 63 and 44 beetles m^{-3} of foliage in dry and wet sclerophyll environments respectively (Figs 5.8 and 5.9).

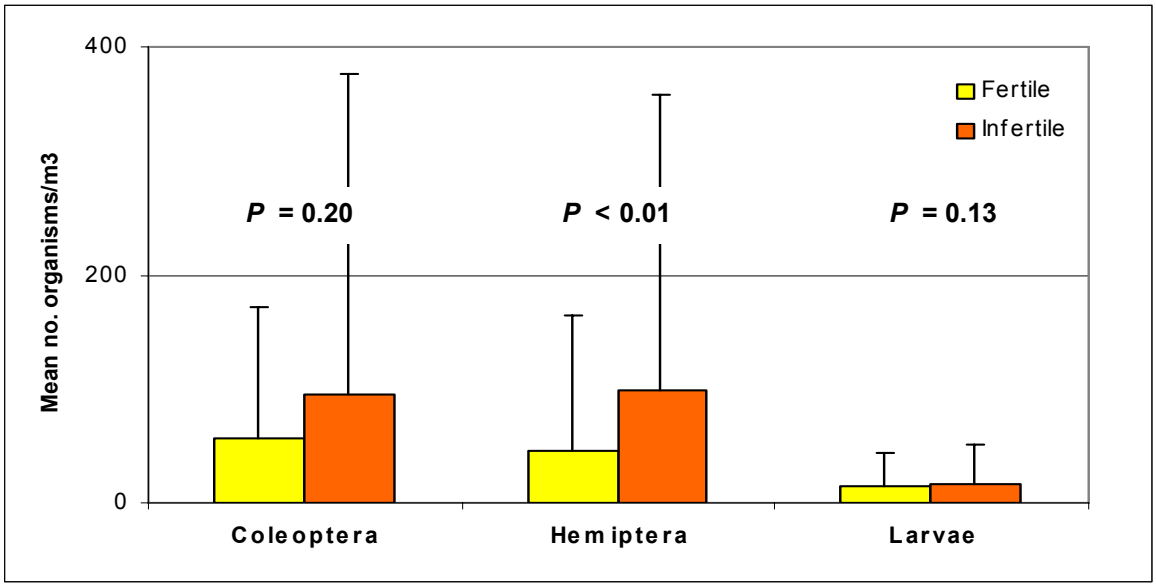


Fig. 5.6 Overall number of Coleoptera (beetles), Hemiptera (bugs) and Lepidoptera larvae (caterpillars) found at low and higher resource sites in Ku-ring-gai Chase and Royal National Parks (2002-2004). Wilcoxon rank sum test results shown.

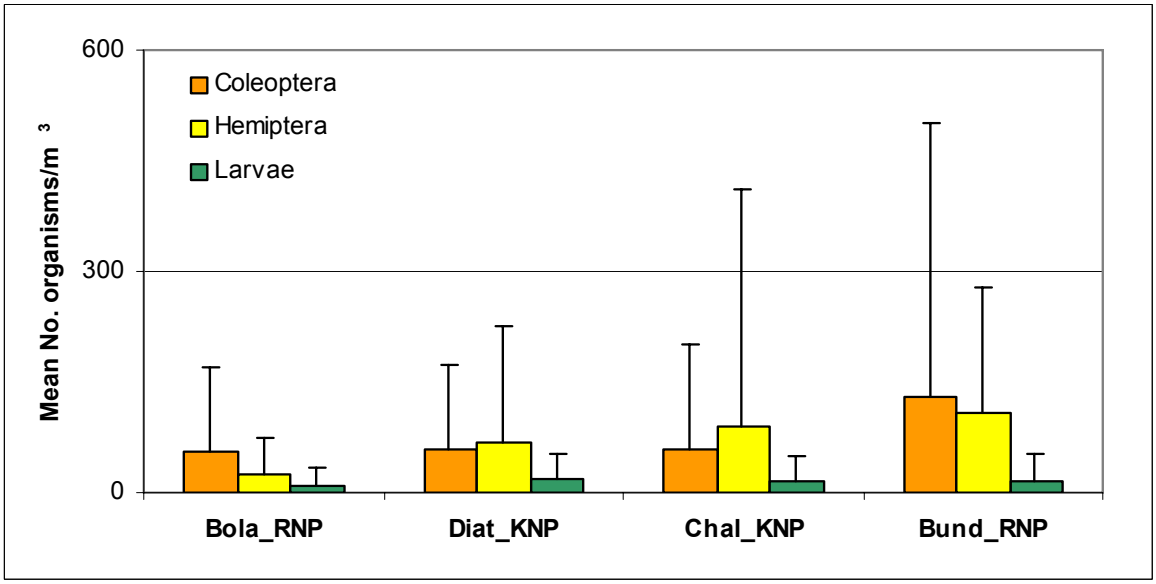


Fig. 5.7 Mean number of Coleoptera (beetles), Hemiptera (bugs) and Lepidoptera larvae (caterpillars) found on plant species at sites in Ku-ring-gai Chase (KNP) and Royal (RNP) National Parks (2002-2004)

There was no significant difference in the number of herbivores on trees, shrubs and vines in the temperate rainforest along Bola Creek (Fig. 5.10). A mean of 166

beetles m^{-3} and 47 bugs m^{-3} were found on vines, and an average of 83 beetles m^{-3} and 38 bugs m^{-3} were collected from shrubs (Fig. 5.10). Plants less than 0.5 m in height had a mean of 65 beetles and 19 bugs m^{-3} of foliage. Few Coleoptera (18 beetles m^{-3}) and Hemiptera (14 bugs m^{-3}) were found on trees (Fig. 5.10). Lepidopteran larvae ranged from 4 caterpillars m^{-3} on tree species to 28 caterpillars m^{-3} on vines (Fig. 5.10).

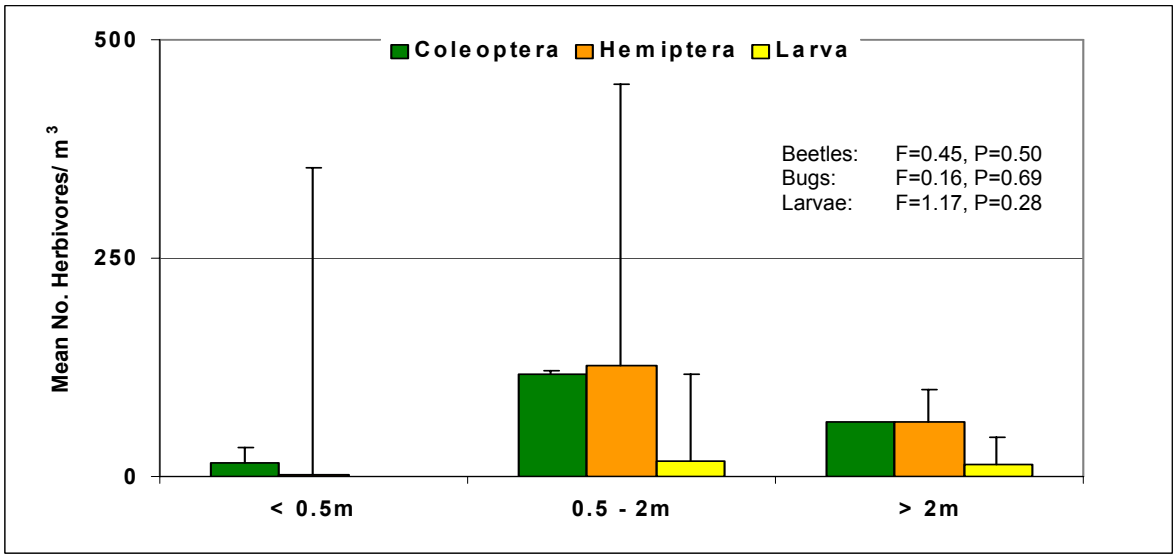


Fig. 5.8 Mean number of Coleoptera (beetles), Hemiptera (bugs) and Lepidoptera larvae found on dry sclerophyll herbs (< 0.5m), shrubs (0.5 – 2m), and trees (> 2m) in Royal and Ku-ring-gai Chase National Parks (2002-2004). ANOVA results shown.

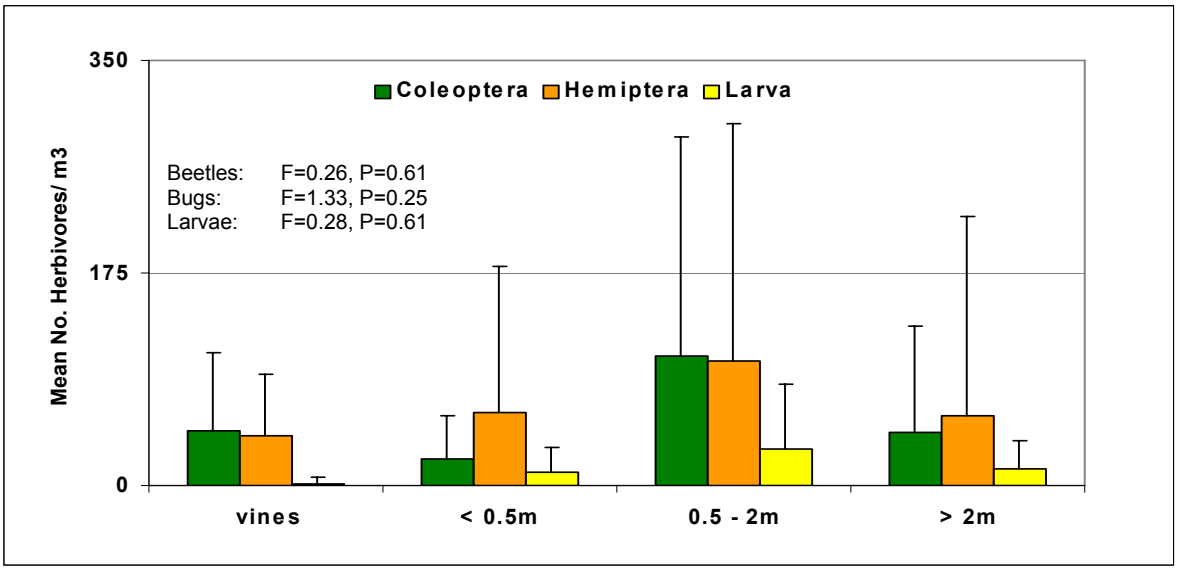


Fig. 5.9 Mean number of Coleoptera (beetles), Hemiptera (bugs) and larvae found on wet sclerophyll vines, herbs (< 0.5m), shrubs (0.5 - 2m) and trees (> 2m) at the dyke, Ku-ring-gai Chase National Park. ANOVA results shown.

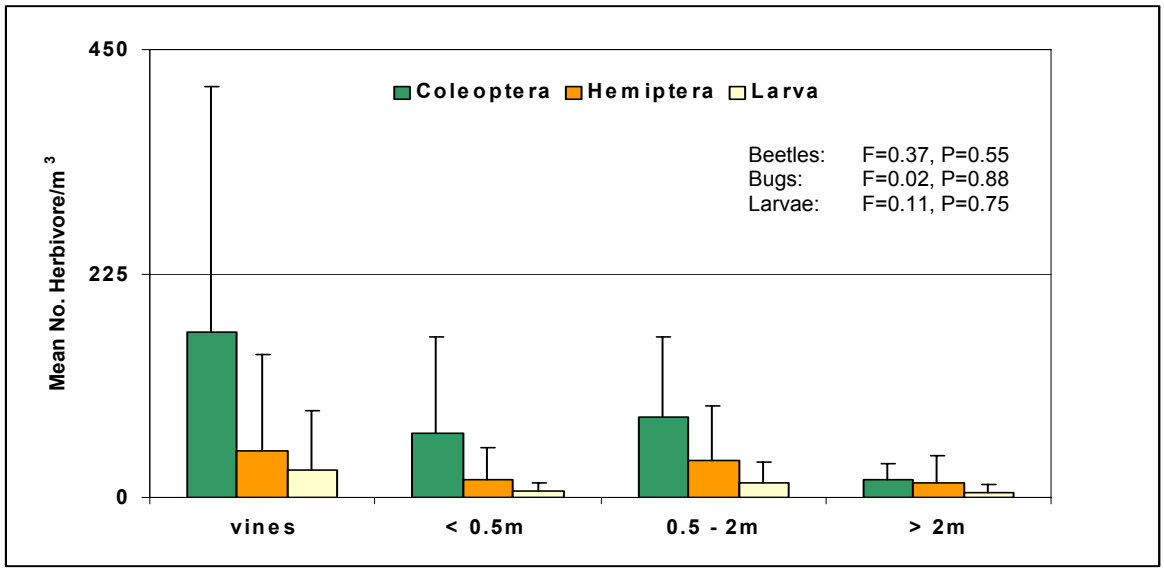


Fig. 5.10 Mean number of Coleoptera (beetles), Hemiptera (bugs) and larvae found on temperate rainforest vines, herbs (< 0.5cm), shrubs (0.5 - 2m) and trees (>2m) at Bola Creek, Royal National Park

5.5.1 Family richness

The greatest average number of coleopteran families were found on plants at the higher nutrient sites, whilst the highest mean number of hemipteran families were found on plants at the nutrient poor sites (Fig. 5.11). The number of beetle families collected from plant species during the two-year study ranged from two families on *Acacia suaveolens* to 23 families on *Leptospermum trinervium (*Table A6.13). *Hemigenia purpurea, Platysace linearifolia* and *Leucopogon microphyllus* were among those plant species supporting small numbers of hemipteran families *(*Table A7.9). The plant species with the highest number of bug families included *Allocasuarina distyla* (17 families), *Leptospermum trinervium* (17 families), and *Angophora hispida* (16 families) (Table A6.13).

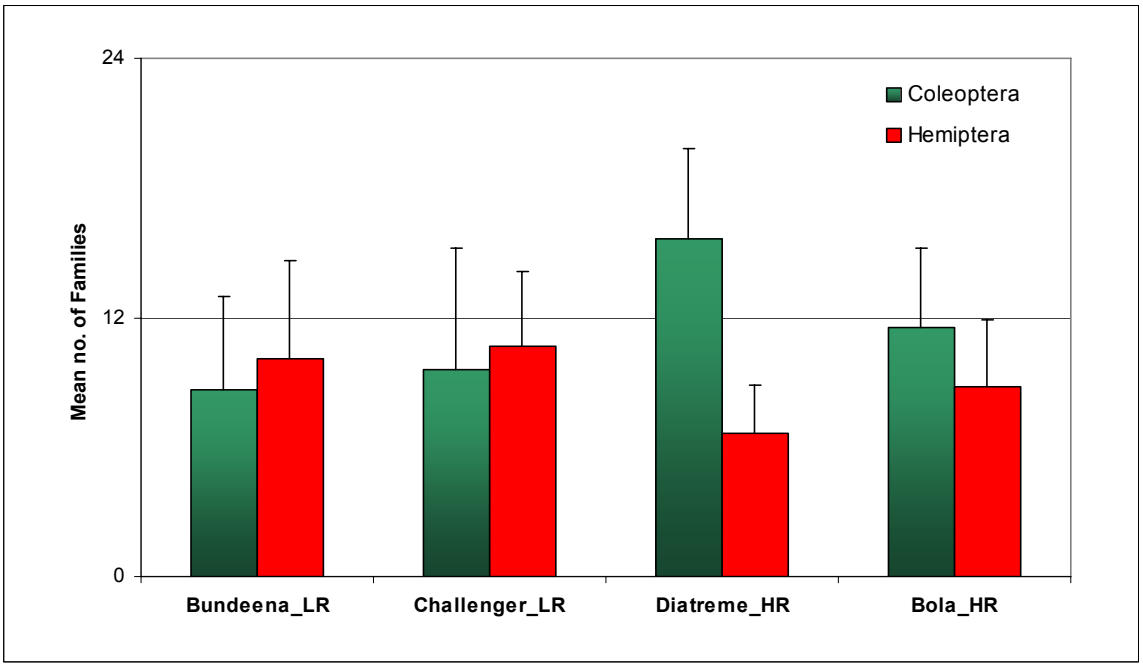


Fig. 5.11 Average number of coleopteran and hemipteran families found on plant species in high (HR) and low (LR) resource sites in Royal National Park and Ku-ring-gai Chase National Park (2002-2004).

5.5.2 Coleopteran assemblages

Principal Component Analysis showed coleopteran families in the Ku-ring-gai Chase National Park and Royal National Park formed two distinct groups (Fig. 5.12). The first group was associated with both high and low resource plant species and comprised the predators Staphylinidae (rove beetles), Pselaphidae, Corylophidae, Coccinellidae (ladybirds) and Trogossitidae; the leaf chewers Chrysomelidae (leaf beetles); and the scavengers Ptiliidae (Fig. 5.12). The second group of beetles included the phytophagous Curculionidae (weevils) and the fungivores Lathridiidae. These families, along with the Elateridae and Aderidae ("various" and scavengers respectively), were found commonly on dry sclerophyll plant species and rarely on rainforest and wet sclerophyll plants (Fig. 5.12).

High numbers of group 1 beetles were found on the mesic plant species *Palmeria scandens*, *Ceratopetalum apetalum*, *Trochocarpa laurina* and *Acmena smithii*, and

on the dry sclerophyll shrubs *Hemigenia purpurea* and *Leucopogon microphyllus* (Fig. 5.12). *Banksia serrata*, *Angophora hispida*, *Blechnum cartilagineum* and *Ripogonum album* were among those plants characterised by below average abundances of group 1 beetles (Fig. 5.12).

Group 2 beetle families were abundant on dry sclerophyll plant species such as *Acacia suaveolens*, *Isopogon anethifolius*, *Leptospermum trinervium*, and *Grevillea buxifolia.* Examples of wet sclerophyll and temperate rainforest plant species with below average densities of weevils and Lathridiidae were *Cissus hypoglauca*, *Pultenaea flexilis*, *Hibbertia dentata* and *Ripogonum album* (Fig. 5.12).

The major leaf characteristics that predicted the presence of beetle families on dry sclerophyll and mesic plant species were lamina thickness, water content and leaf area. Fibre content, leaf toughness and specific leaf area also influenced beetle families, but to a lesser degree (Fig. 5.13). The herbivorous beetle family Curculionidae was found on plant species characterised by thick lamina, and relatively high concentrations of total phenols and water content. They appear to be predominantly associated with small leaves, low in nitrogen with small specific leaf areas (Fig. 5.13). The second most dominant herbivorous beetle familiy, the Chrysomelidae, were positively correlated with fibre and negatively correlated with large specific leaf areas and nitrogen concentration (Fig. 5.13). The Lathriidae, which are fungivores, were negatively associated with fibrous tissue (Fig. 5.13).

5.5.3 Hemiptera assemblages

The hemipteran families distinguishing dry sclerophyll faunal assemblages from wet sclerophyll and temperate rainforest assemblages were the Cicadellidae, Membracidae, Psyllidae, and Miridae (Fig. 5.14). Dry sclerophyll plant species supporting high densities of these insects included *Leptospermum trinervium*, *Acacia suaveolens*, and *Grevillea buxifolia* (Fig. 5.14). Rainforest and wet sclerophyll plants such as *Trochocarpa laurina*, *Acacia floribunda* and *Allocasuarina torulosa* supported only low densities of Cicadellidae, Membracidae, Psyllidae, and Miridae (Fig. 5.14).

The major leaf characteristics that appear to influence Hemiptera were total phenol concentrations, leaf area, lamina thickness and fibre content (Fig. 5.15). Small lamina thickness predicted the presence of Fulgorids and Aphids on plants. Membracids were highly positively correlated with leaf fibre content, and psyllids were negatively correlated to percent fibre. Pentatomidae were found mainly on plants with large leaf areas and high total phenol concentrations. They were also found on plants with small specific leaf areas, low water content, and low concentrations of nitrogen (Fig. 5.15).

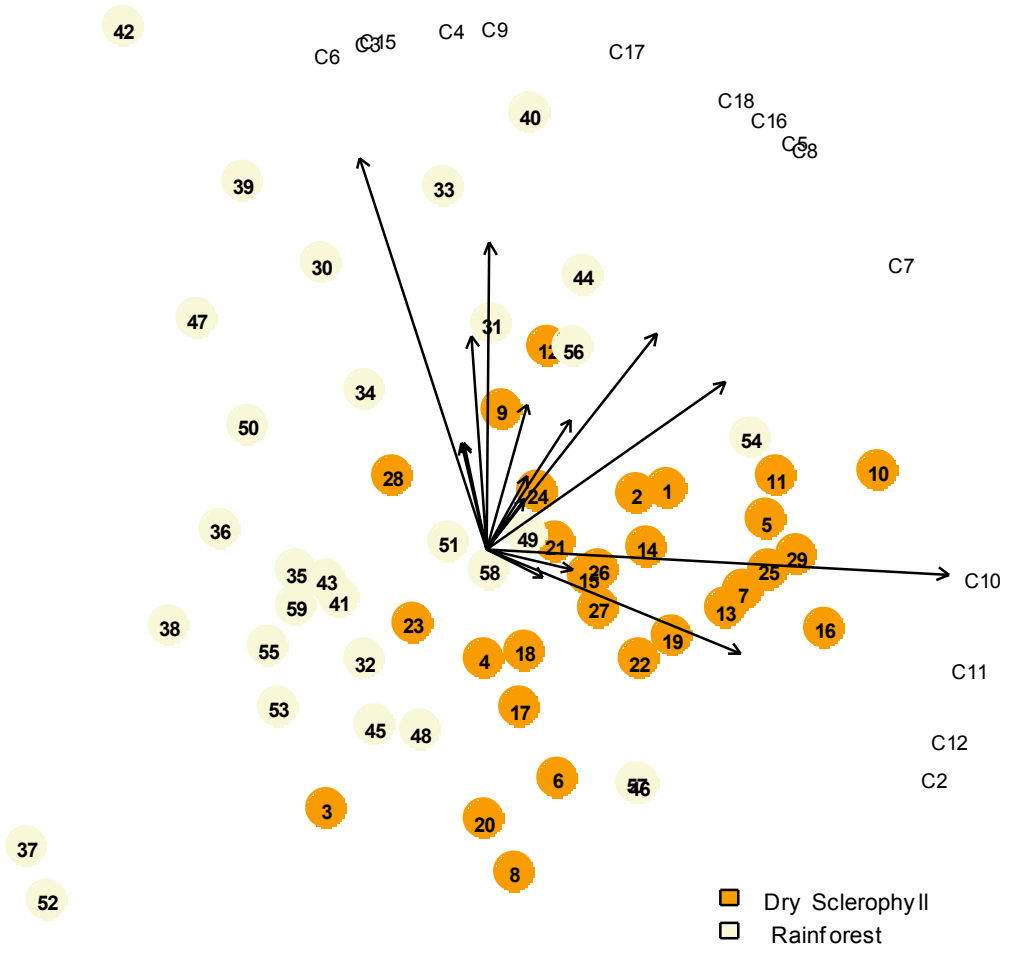


Figure 5.12 Major coleopteran families found on dry sclerophyll and rainforest plant species in Royal and Ku-ring-gai Chase National Parks (2002-2004) (PC biplot goodness of fit: 38%; ANOSIM: R = 0.25, p = 0.0001)

Dry sclerophyll plants Bundeena rd, RNP	Dry sclerophyll plants Challenger track, KNP	Rainforest plants Bola Creek, RNP	Wet sclerophyll plants Dyke, KNP
1 *Acacia suaveolens*	16 *Acacia suaveolens*	31 *Acmena smithii*	46 *Acacia floribunda*
2 *Allocasuarina distyla*	17 *Angophora hispida*	32 *Blechnum cartilagineum*	47 *Allocasuarina torulosa*
3 *Angophora hispida*	18 *Banksia serrata*	33 *Ceratopetalum apetalum*	48 *Breynia oblongifolia*
4 *Banksia serrata*	19 *Corymbia gummifera*	34 *Citriobatus pauciflorus*	49 *Cissus hypoglauca*
5 *Caustis recurvata*	20 *Eucalyptus haemastoma*	35 *Diospyros australis*	50 *Citriobatus pauciflorus*
6 *Corymbia gummifera*	21 *Grevillea buxifolia*	36 *Doryphora sassafras*	51 *Hibbertia dentata*
7 *Grevillea sphacelata*	22 *Hakea teretifolia*	37 *Gymnostachys anceps*	52 *Lepidosperma laterale*
8 *Hakea teretifolia*	23 *Hemigenia purpurea*	38 *Livistona australis*	53 *Livistona australis*
9 *Hemigenia purpurea*	24 *Hibbertia monogyna*	39 *Lomatia myricoides*	54 *Macrozamia communis*
10 *Isopogon anethifolius*	25 *Leptospermum trinervium*	40 *Palmeria scandens*	55 *Pomaderris feruginea*
11 *Leptospermum trinervium*	26 *Leucopogon microphyllus*	41 *Ripogonum album*	56 *Pteridium esculentum*
12 *Leucopogon microphyllus*	27 *Patersonia glabrata*	42 *Syncarpia glomulifera*	57 *Pultenaea daphnoides*
13 *Persoonia lanceolata*	28 *Persoonia lanceolata*	43 *Tasmannia insipida*	58 *Pultenaea flexilis*
14 *Platysace linearifolia*	29 *Platysace linearifolia*	44 *Trochocarpa laurina*	59 *Syncarpia glomulifera*
15 *Pultenaea elliptica*	30 *Pultenaea elliptica*	45 *Wilkiea huegelianna*	60 *Synoum glandulosum*
Beetle Key:			
C2 Aderidae	C6 Staphylinidae	C10 Curculionidae	C16 Nitidulidae
C3 Clambidae	C7 Chrysomelidae	C11 Elateridae	C17 Trogossitidae
C4 Pselaphidae	C8 Coccinellidae	C12 Lathridiidae	C18 Scarabaeidae
C5 Ptiliidae	C9 Corylophidae	C15 Nemonychidae	

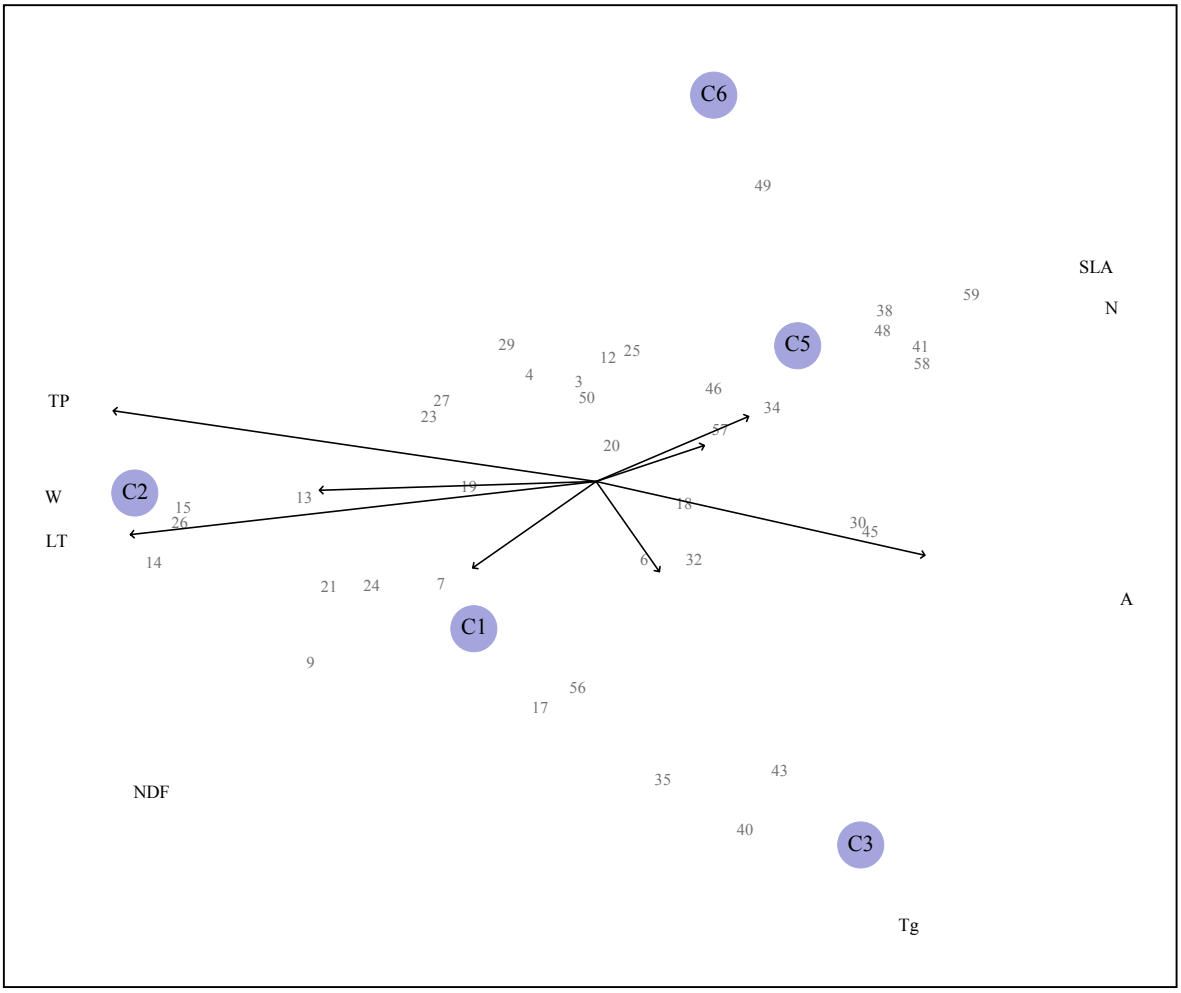


Figure 5.13 Leaf characteristics predicting the presence of six beetle families on plant species in Ku-ring-gai Chase National Park and Royal National Park between the years 2002-2004 (CCA biplot quality-of-fit: 96.82)

TP – Total Phenols; LT – Lamina Thickness; N – % Nitrogen; W – Water content; NDF – Fibre content; Tg – Leaf Toughness; A – Leaf Area; SLA – Specific Leaf Area; C1 – Chrysomelidae; C2 – Curculionidae; C3 – Ptiliidae; C5 – Coccinelidae; C6 – Lathriidae

Dry sclerophyll plants Bundeena rd, RNP	**Dry sclerophyll plants Challenger track, KNP**	**Rainforest plants Bola Creek, RNP**	**Wet sclerophyll plants Dyke, KNP**
3 *Angophora hispida* 4 *Banksia serrata* 6 *Corymbia gummifera* 7 *Grevillea sphacelata* 9 *Hemigenia purpurea* 12 *Leucopogon microphyllus* 13 *Persoonia lanceolata* 14 *Platysace linearifolia* 15 *Pultenaea elliptica*	17 *Angophora hispida* 18 *Banksia serrata* 19 *Corymbia gummifera* 20 *Eucalyptus haemastoma* 21 *Grevillea buxifolia* 23 *Hemigenia purpurea* 24 *Hibbertia monogyna* 25 *Leptospermum trinervium* 26 *Leucopogon microphyllus* 27 *Persoonia lanceolata* 29 *Pultenaea elliptica*	30 *Acmena smithii* 32 *Ceratopetalum apetalum* 34 *Diospyros australis* 35 *Doryphora sassafras* 38 *Lomatia myricoides* 40 *Ripogonum album* 41 *Syncarpia glomulifera* 43 *Trochocarpa laurina*	45 *Acacia floribunda* 46 *Allocasuarina torulosa* 48 *Cissus hypoglauca* 49 *Citriobatus pauciflorus* 50 *Hibbertia dentata* 56 *Pultenaea daphnoides* 57 *Pultenaea flexilis* 58 *Syncarpia glomulifera* 59 *Synoum glandulosum*

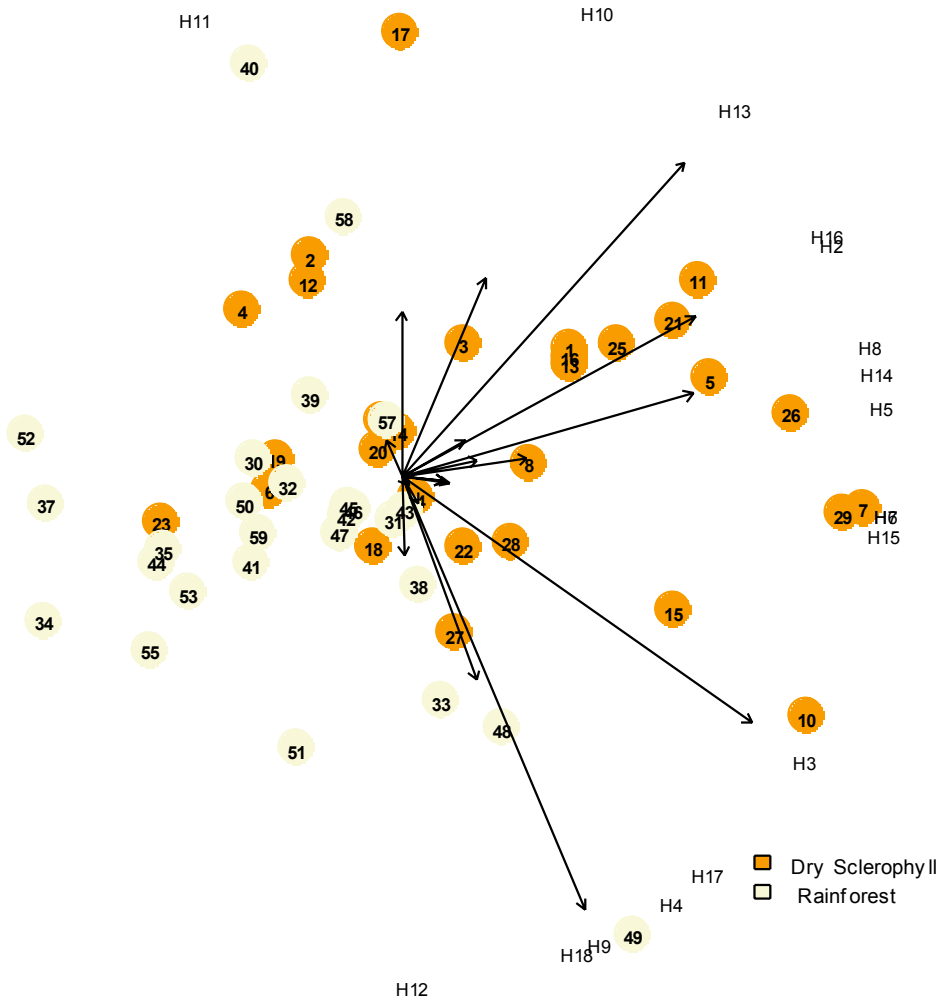


Figure 5.14 Major hemipteran families found on dry sclerophyll and rainforest plant species in Royal and Ku-ring-gai Chase National Parks (2002-2004) (PC biplot goodness of fit: 37%; ANOSIM: R = 0.24, p = 0.0001)

Dry sclerophyll plants Bundeena rd, RNP	Dry sclerophyll plants Challenger track, KNP	Rainforest plants Bola Creek, RNP	Wet sclerophyll plants Dyke, KNP
1 *Acacia suaveolens*	16 *Acacia suaveolens*	30 *Acmena smithii*	45 *Acacia floribunda*
2 *Allocasuarina distyla*	17 *Angophora hispida*	31 *Blechnum cartilagineum*	46 *Allocasuarina torulosa*
3 *Angophora hispida*	18 *Banksia serrata*	32 *Ceratopetalum apetalum*	47 *Breynia oblongifolia*
4 *Banksia serrata*	19 *Corymbia gummifera*	33 *Citriobatus pauciflorus*	48 *Cissus hypoglauca*
5 *Caustis recurvata*	20 *Eucalyptus haemastoma*	34 *Diospyros australis*	49 *Citriobatus pauciflorus*
6 *Corymbia gummifera*	21 *Grevillea buxifolia*	35 *Doryphora sassafras*	50 *Hibbertia dentata*
7 *Grevillea sphacelata*	22 *Hakea teretifolia*	36 *Livistona australis*	51 *Lepidosperma laterale*
8 *Hakea teretifolia*	23 *Hemigenia purpurea*	37 *Lomatia myricoides*	52 *Livistona australis*
9 *Hemigenia purpurea*	24 *Hibbertia monogyna*	38 *Palmeria scandens*	53 *Macrozamia communis*
10 *Isopogon anethifolius*	25 *Leptospermum trinervium*	39 *Ripogonum album*	54 *Pomaderris feruginea*
11 *Leptospermum trinervium*	26 *Leucopogon microphyllus*	40 *Syncarpia glomulifera*	55 *Pteridium esculentum*
12 *Leucopogon microphyllus*	27 *Persoonia lanceolata*	41 *Tasmannia insipida*	56 *Pultenaea daphnoides*
13 *Persoonia lanceolata*	28 *Platysace linearifolia*	42 *Trochocarpa laurina*	57 *Pultenaea flexilis*
14 *Platysace linearifolia*	29 *Pultenaea elliptica*	43 *Wilkiea huegelianna*	58 *Syncarpia glomulifera*
15 *Pultenaea elliptica*		44 *Gymnostachys anceps*	59 *Synoum glandulosum*
H1 Aleyrodidae	H6 Lygaeidae		
H2 Cicadellidae	H7 Pseudococcidae	H11 Pentatomidae	H15 Flatidae
H3 Fulgoridae	H8 Psyllidae	H12 Piesmatidae	H16 Reduviidae
H4 Eurymelidae	H9 Aphididae	H13 Miridae	H17 Ricaniidae
H5 Membracidae	H10 Coreidae	H14 Acanthosomatidae	H18 Tingidae

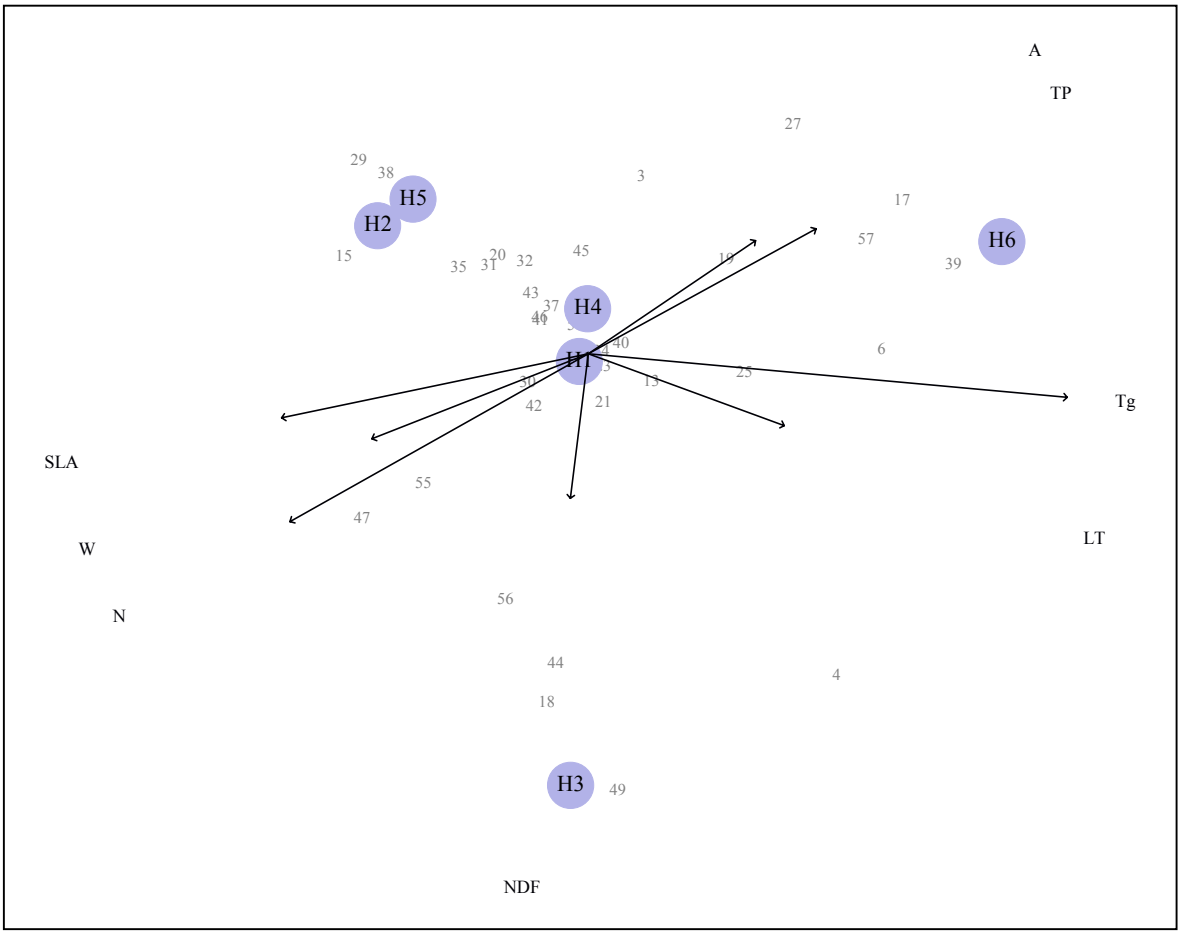


Figure 5.15 Leaf characteristics predicting the presence of six hemipteran families on plant species in Ku-ring-gai Chase and Royal National Parks (2002-2004). (CCA biplot quality of fit: 76.68%)

TP – Total Phenols; LT – Lamina Thickness; N – % Nitrogen; W – Water content; NDF – Fibre content; Tg – Leaf Toughness; A – Leaf Area; SLA – Specific Leaf Area; H1 – Cicadellidae; H2 –Fulgoridae; H3 – Membracidae; H4 – Psyllidae; H5 –Aphididae; H6 – Pentatomidae.

Dry sclerophyll plants Bundeena rd, RNP	**Dry sclerophyll plants Challenger track, KNP**	**Rainforest plants Bola Creek, RNP**	**Wet sclerophyll plants Dyke, KNP**
3 *Angophora hispida* 4 *Banksia serrata* 6 *Corymbia gummifera* 13 *Persoonia lanceolata* 15 *Pultenaea elliptica*	17 *Angophora hispida* 18 *Banksia serrata* 19 *Corymbia gummifera* 20 *Eucalyptus haemastoma* 21 *Grevillea buxifolia* 23 *Hemigenia purpurea* 25 *Leptospermum trinervium* 27 *Persoonia lanceolata* 28 *Platysace linearifolia* 29 *Pultenaea elliptica*	30 *Acmena smithii* 31 *Blechnum cartilagineum* 32 *Ceratopetalum apetalum* 34 *Diospyros australis* 35 *Doryphora sassafras* 37 *Lomatia myricoides* 38 *Palmeria scandens* 39 *Ripogonum album* 40 *Syncarpia glomulifera* 41 *Tasmannia insipida* 42 *Trochocarpa laurina* 43 *Wilkiea huegelianna*	44 *Acacia floribunda* 45 *Allocasuarina torulosa* 46 *Breynia oblongifolia* 47 *Cissus hypoglauca* 49 *Hibbertia dentata* 55 *Pultenaea daphnoides* 56 *Pultenaea flexilis* 57 *Syncarpia glomulifera* 58 *Synoum glandulosum*

5.5.4 Relationship between herbivores and herbivory

It has often been implied that the density of insect herbivores equates to higher levels of insect herbivory (eg Lieberman and Lieberman, 1984; Basset, 1991; Basset, 1992; Jones and Lawton, 1991). In this study it was found that there was no relationship between the number of herbivores found on a particular plant species and the actual mean percent herbivory that occurred each month (Chapter 4; Fig. 5.16). Plant species that sustained relatively high levels of herbivory did not support large numbers of herbivores. Therefore, greater numbers of herbivores on plants does not necessarily imply a high level of herbivory.

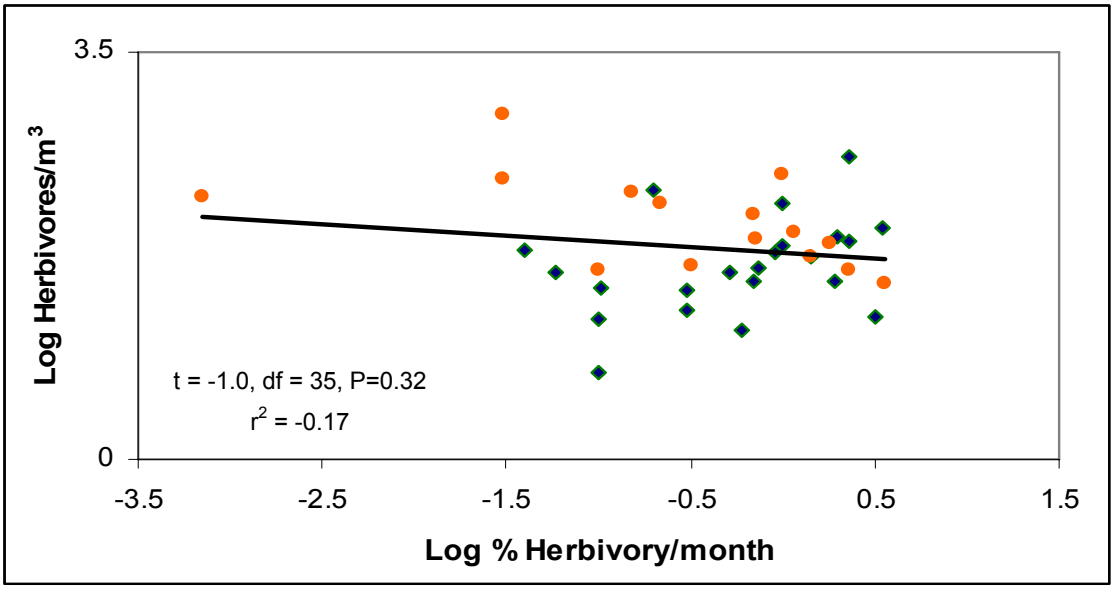


Figure 5.16 Mean percent herbivory per month against mean number of herbivores per m^3. P-value from Welch Two Sample t-test and the correlation coefficient shown. Orange spots represent dry sclerophyll plant species. Green diamonds represent mesic plant species.

5.6 Branch clipping results

While the density of Coleoptera and Hemiptera was significantly higher in the branch collections compared to the pyrethrum samples (ANOVA: F = 7.83, P = 0.019), there were no significant differences in the proportions of Coleoptera and

Hemiptera between sampling methods (ANOVA: F = 1.615e-31, P = 1.0). The density of Coleoptera (ANOVA: F = 3.39, P = 0.32) and hemiptera (ANOVA: F = 0.75, P = 0.55) did not differ significantly between vegetation types in the branch collection. Coleoptera (ANOVA: F = 3.50, P = 0.31) and Hemiptera (ANOVA: F = 120.35, P = 0.06) in the pyrethrum collection also did not differ significantly between vegetation types (Fig. 5.18).

The ratios of carnivores to herbivores did not vary significantly between the resource sites (Fig. 5.17). However, the temperate rainforest site at Bola Creek, RNP supported the highest number of predators, and the lowest ratios occurred at the Bundeena site, RNP. The carnivore to herbivore ratios from the pyrethrum collections did not differ significantly from the branch collection ratios (ANOVA: F = 2.96, P = 0.09).

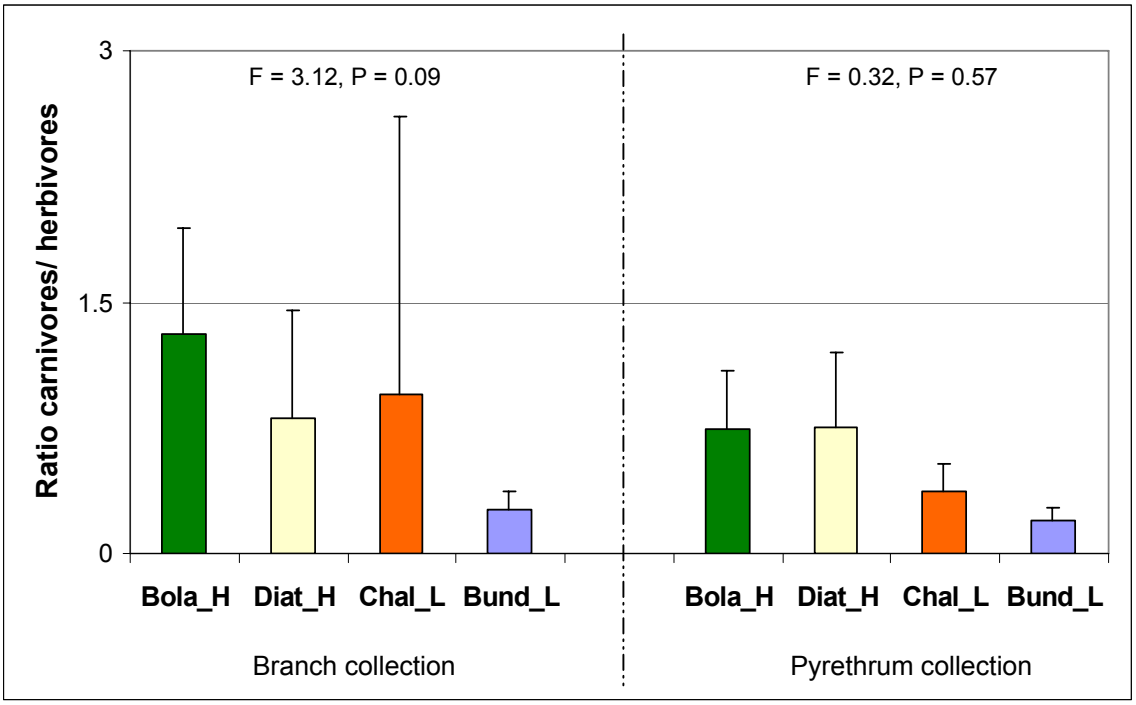
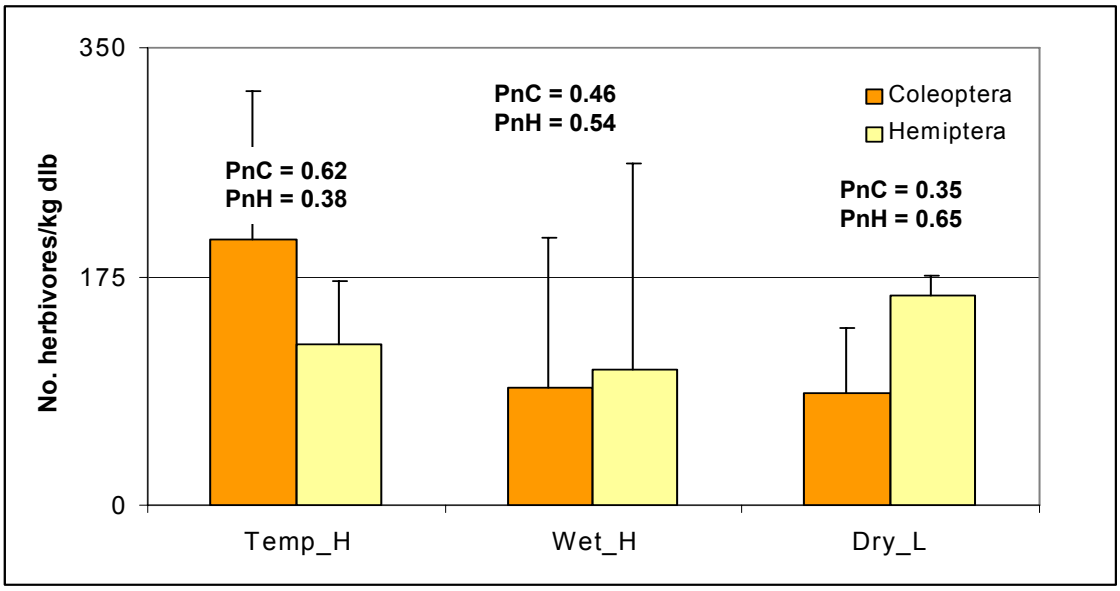
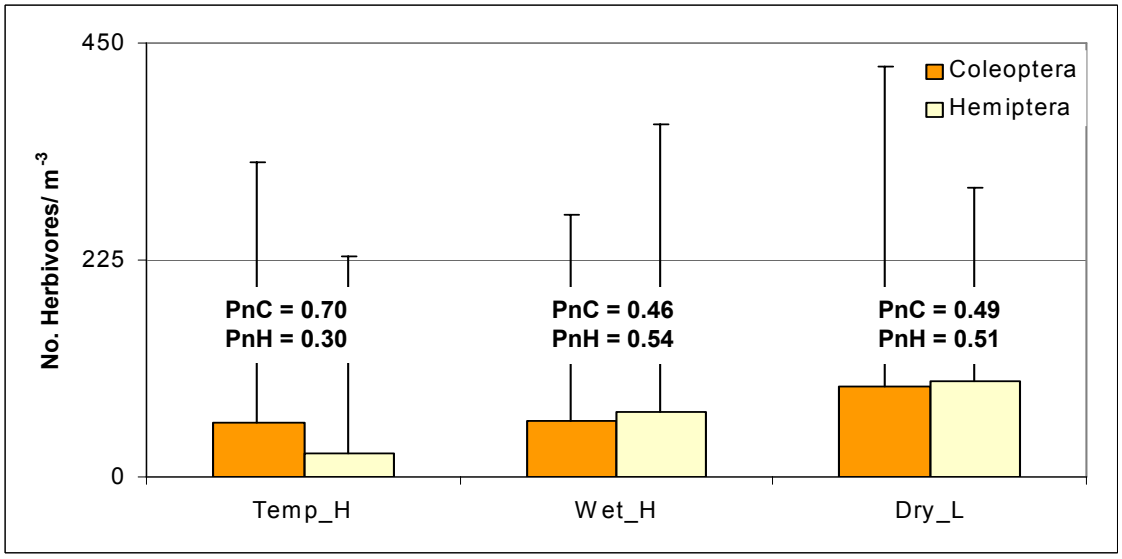


Figure 5.17 Ratio of carnivores to herbivores associated with plant species at each site. Compares branch and pyrethrum sampling results. H – high resource site, L – low resource site. ANOVA results shown.



(A) Average number of Coleoptera and Hemiptera per kg dried leaf biomass (dlb). Proportions of Coleoptera (PnC) and Hemiptera (PnH) shown for each vegetation type.



(B) Average number of Coleoptera and Hemiptera per cubic metre. Proportions of Coleoptera (PnC) and Hemiptera (PnH) shown for each vegetation type.

Fig. 5.18 Average number of Coleoptera and Hemiptera found on temperate rainforest, wet sclerophyll and dry sclerophyll plants using (A) branch clipping method and (B) pyrethrum collection method. H - high resource site, L - low resource site.

The branch clipping method gave the same overall conclusions as the pyrethrum collection method (Figs 5.17-5.20). Any deviations between the pyrethrum and branch clipping results (Fig. 5.19) may be due to differences in plant structural characteristics.

Plant species with the smallest leaf areas had the highest densities of insect herbivores per kilogram of dried leaf biomass (Fig. 5.20A). As leaf area declined, leaf density increased and herbivore abundance rose. This pattern was observed on plant communities at low and higher resource sites (Fig. 5.20A), and was reflected in the pyrethrum results (Fig. 5.20B).

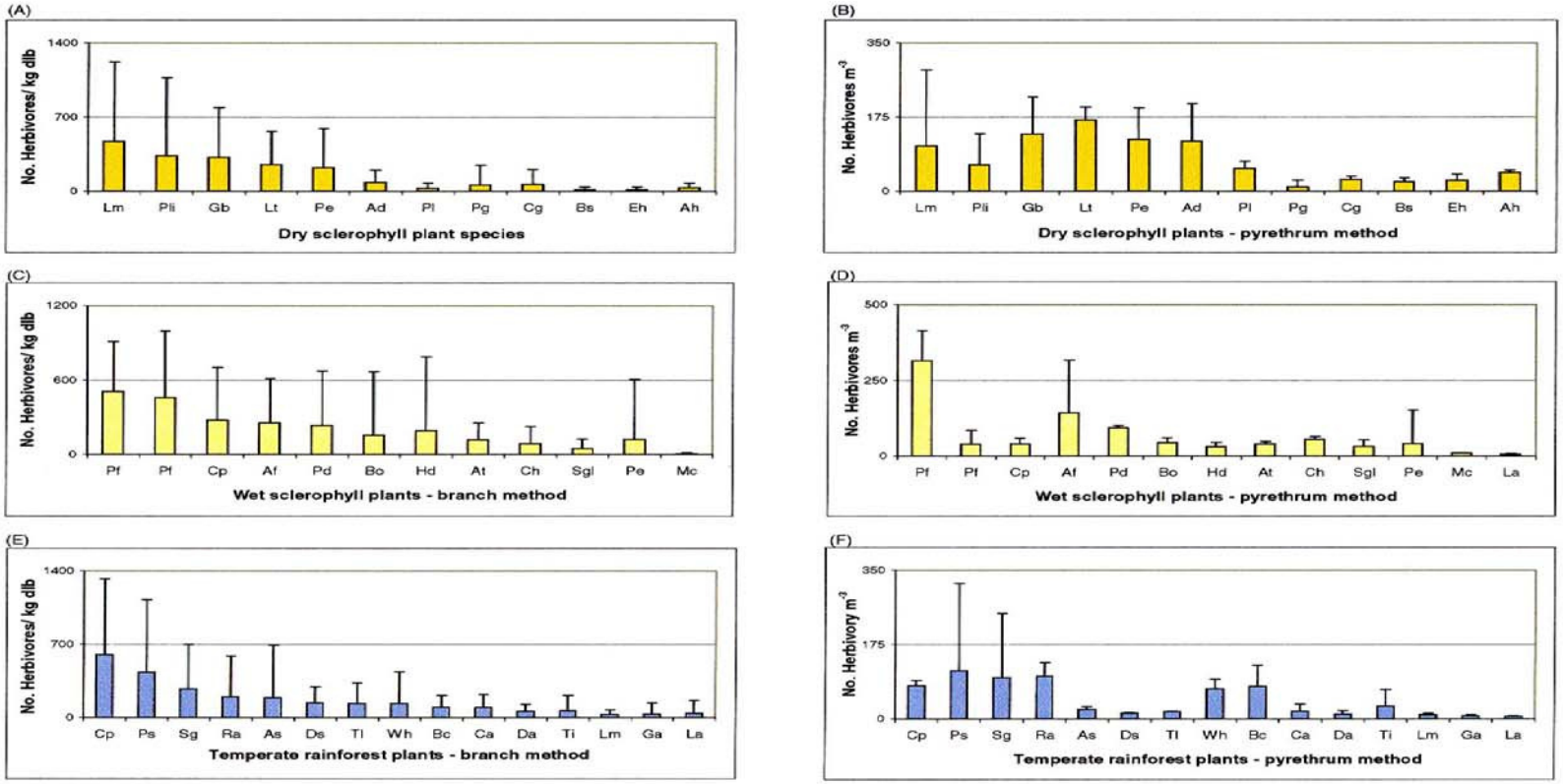


Figure 5.19 **Mean number of insect herbivores on dry and wet sclerophyll and temperate rainforest foliage. Comparison of pyrethrum spraying and branch clipping methods (2002-2004).**

Average number of herbivores and standard deviations on (A-B) Dry sclerophyll, (C-D) Wet sclerophyll, and (E-F) Temperate rainforest plant species.

Key
(A and D) Dry sclerophyll plant species: Lm - *Leucopogon microphyllus;* Pli - *Platysace linearifolia*; Gb - *Grevillea buxifolia*; Lt - *Leptospermum trinervium*; Pe - *Pultenaea elliptica*; At - *Allocasuarina torulosa*; Pl - *Persoonia lanceolata*; Pg - *Patersonia glabrata*; Cg - *Corymbia gummifera*; Bs - *Banksia serrata*; Eh - *Eucalyptus haemastoma*; Ah - *Angophora hispida*
(B and E) Wet sclerophyll plant species: Pf - *Pomaderris ferruginea*; Pf - *Pultenaea flexilis*; Cp - *Citriobatus pauciflorus*; Af - *Acacia suaveolens*; Pd - *Pultenaea daphnoides*; Bo - *Breynia oblongifolia*; Hd - *Hibbertia dentata*; At - *Allocasuarina torulosa*; Ch - *Cissus hypoglauca*; Sgl - *Synoum glandulosum*; Pe - *Pteridium esculentum*; Mc - *Macrozamia communis*; La - *Livistona australis*
(C and F) Temperate rainforest plant species: Cp - *Citriobatus pauciflorus*; Ps - *Palmeria scandens*; Sg - *Syncarpia glomulifera*; Ra - *Ripogonum album*; As - *Acmena smithii*; Ds - *Doryphora sassafras*;
Tl - *Trochocarpa laurina*; Wh - *Wilkiea huegelianna*; Bc - *Blechnum cartilagineum*; Ca - *Ceratopetalum apetalum*; Da - *Diospyros australis*; Ti - *Tasmannia insipida*; Lm - *Lomatia myricoides*; Ga - *Gymnostachys anceps*; La - *Livistona australis*
dlb - dried leaf biomass

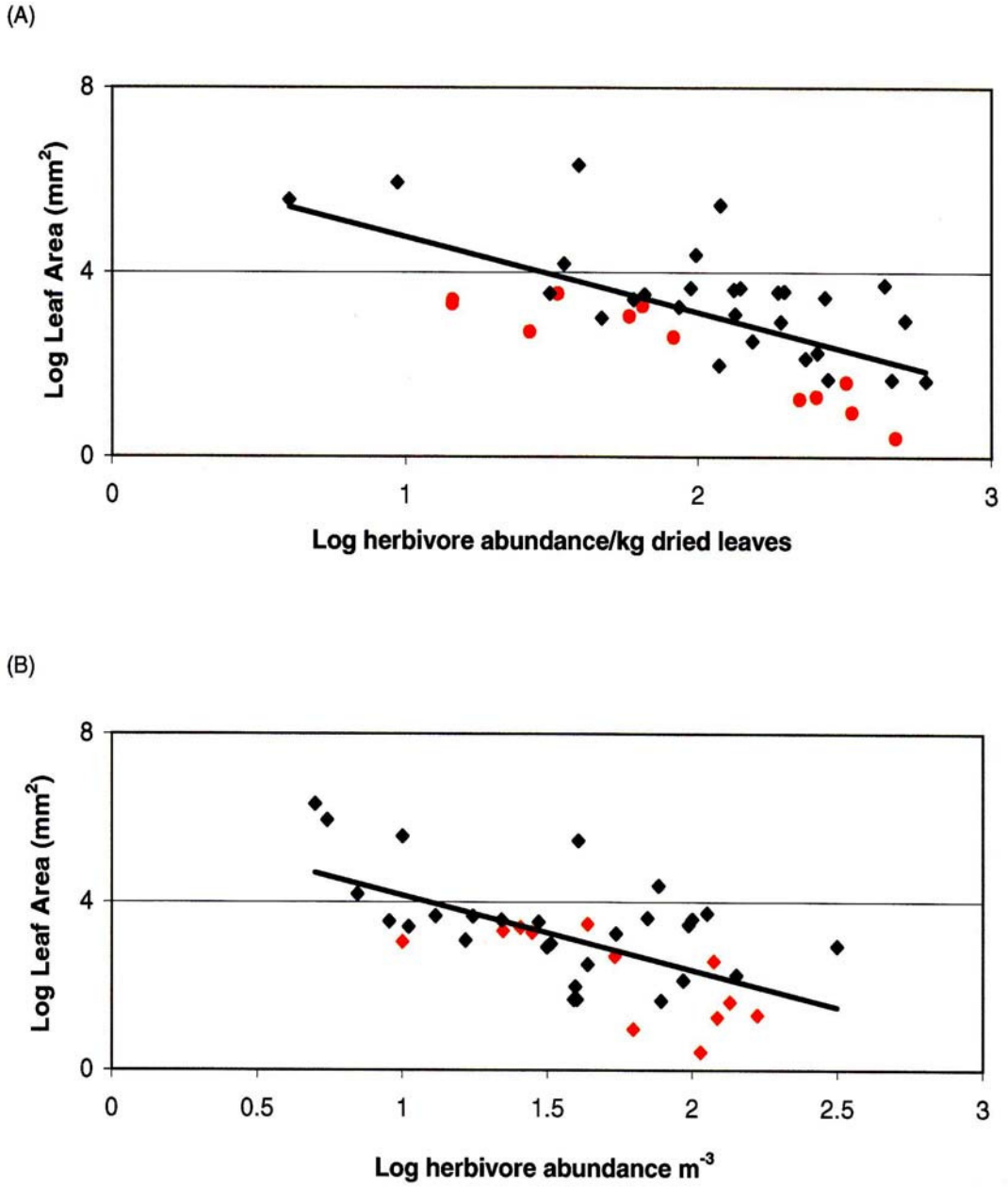


Figure 5.20 Mean leaf area against (A) mean number of herbivores per kilogram dried leaf biomass, and (B) mean number of herbivores per m-3 for dry sclerophyll (orange) and mesic (blue) plant species.

5.7 Discussion

In this study, plants from low resource environments supported the greatest densities of phytophagous insects. Leaf-chewers and sap-suckers were more

abundant on dry sclerophyll plants growing in nutrient poor soils than wet sclerophyll and temperate rainforest plants in more fertile soils. Hemipteran abundance was highest at the nutrient poor sites, although there was no significant difference between the mean densities of beetles and Lepidoptera larvae found on plants growing in the two habitats. Dry sclerophyll plants supported relatively large numbers of phytopagous bugs such as Cicadellids, Membracids and Psyllids, and the beetle family Curculionidae was common at the low resource sites compared to the more fertile sites. The high resource sites supported the greatest diversity of Coleoptera families compared to the low resource sites, and the greatest diversity of Hemiptera families was found at the low resource sites.

Whilst the current study does not show insect herbivore abundance to correlate with higher nutrient soils, some previous studies have found positive relationships between insect abundance and resource availability (eg. Janzen & Schoener 1967, Janzen 1973, Louda et al. 1987; Landsberg et al. 1995; Progar et al. 2002). An increase in water availability can alter leaf physiology and promote leaf production, which can influence invertebrate communities by affecting the growth and fecundity of insects (Janzen & Schoener 1967; Denlinger 1980, Itioka & Yamauti 2004). Higher light levels can increase the concentration of soluble nitrogen in leaves, and potentially accelerate the growth rates and improve the survivorship of insects (Journet, 1980; White, 1984; Barone, 1998). A study has also shown that increased soil nutrients can elevate nitrogen concentrations in foliage, providing a potentially more nutritious food source for canopy arthropods (Walde, 1995).

Differences between this and previous studies may be due to differences between Australian or southern hemisphere ecosystems and those in the northern hemisphere, or because previous studies have mainly focused on a single plant species, genus, or growth form (Ohmart et al. 1983; Stork, 1987; Cornell & Kahn, 1989; Basset, 1991; Abbott et al. 1992; Basset & Arthington, 1992; Shuter & Westoby, 1992; Recher et al. 1996; Basset & Novotny, 1999; Peeters, 2001). It is also possible that differences are due to the fact that past studies compared insect herbivore communities at sites separated by considerable distance (Coley & Aide,

1991; Majer et al. 1992; Recher et al., 1996a,b). For researchers to gain any insight into the relationship between insect communities and resource availability, they would have to firstly consider the confounding effects of climate, soil structure, vegetation assemblages and regional insect herbivore fauna.

Another potential explanation for differences in results may be sampling method, which did not include invertebrate faunal surveys of the upper wet sclerophyll and temperate rainforest canopies. Studies have shown that understorey leaves can suffer higher rates of insect damage than canopy leaves (Coley and Barone, 1996; Schulze et al., 2001). However, several studies have demonstrated that rainforest canopies consist of many microhabitats that have the potential to support a greater diversity and abundance of insect herbivores than the understorey (e.g. Erwin and Scott, 1980; Erwin, 1982; Lowman, 1983; Lowman, 1985; Stork and Brendell, 1990; Lowman, 1992; Nadkarni, 1994). There is a possibility that insect herbivore abundance has been under-estimated at the higher resource sites in this study.

As in previous studies (Peeters, 2001, 2002), this work found the presence of insect orders, insect feeding guilds, and bug and beetle families were predicted by an array of chemical and physical leaf characteristics. A major expectation of the resource availability hypothesis is that plants with physical and chemical defences and less palatable leaves would attract fewer herbivores and subsequently suffer less intense herbivory (Coley et al., 1985). This expectation was supported at the ordinal level, but not at the feeding guild level, or the beetle and bug family level. At the ordinal level, Coleoptera were highly correlated with lamina thickness and water content; Hemiptera were negatively correlated with leaf toughness and positively correlated with nitrogen content; and lepidopteran caterpillars were found on plants with high concentrations of foliar nitrogen. Leaf-chewers and sap-suckers, on the other hand, tended to be associated with plants that had leaves high in phenol concentrations and low in nitrogen. Phytophagous beetles such as Curculionids were found on plants with thick lamina, high concentrations of total phenols, and low percent nitrogen, and Cicadellidae and Psyllidae were unaffected by leaf toughness and fibre content.

A factor that influenced the abundance of insect herbivores on wet and dry sclerophyll and temperate rainforest plant species was plant architecture. Shrubs between the heights of 0.5 m – 2 m supported the greatest densities of Coleoptera and Hemiptera, followed by trees and small shrubs. Plants with the smallest, most densely clustered leaves, supported the greatest densities of phytophagous insects, while plants with the largest, least densely clustered, leaves had the lowest densities of herbivores. Plant architectural characteristics such as growth form, plant size, and leaf size and shape can influence insect abundance and diversity by providing phytophagous insects with a greater variety of feeding, resting and hiding places (Lawton & Schroder, 1977; Lawton, 1978; Lawton, 1983). Increased above-ground complexity may also provide insects with more potential oviposition sites (Lawton, 1983).

There is anecdotal evidence that fire influenced insect communities in Royal National Park. In late December 2001, 60% of Royal National Park was burnt, including one side of Bundeena road. In 2002, insect surveys were conducted solely on the unburnt section. By 2003, due to a concern that field activities were detrimentally affecting the site, insect surveys began to be conducted on both sides of the road. Plants in the burnt section had younger, “fresher” looking leaves that supported higher densities of insects than any other site. Past studies have found fire can cause physiological changes in plants by increasing nutrient concentrations in the soil (Prieto-Fernandez et al., 1993). This can increase the concentration of nitrogen, potassium, phosphorus and carbohydrates in leaves; affect plant growth rates; and increase photosynthetic rates and efficiency (Rieske, 2002; Rieske et al., 2002; Brys et al., 2005). These physiological changes have the potential to influence insect abundance (Vieira, 1996).

In conclusion, the hypothesis that plants from resource-limited environments would be better defended and subsequently support a smaller density of herbivores compared to plants from higher resource habitats was not supported by these data. Dry sclerophyll plants supported higher densities of leaf-chewers and sap-suckers compared to the mesic species. Coleoptera abundance was not significantly different between the resource sites, and weevils (Curculionidae) were

more abundant on the dry sclerophyll plants compared to the mesic plant species. In addition, the hemipteran families Cicadellidae, Membracidae, Psyllidae and Miridae were found on dry sclerophyll plants in greater densities.

The major physical and chemical leaf characteristics attributed to predicting the presence of insect herbivores on plants were lamina thickness, leaf area, nitrogen and water content, leaf toughness and fibre content.

Chapter 6
Influence of resource availability on recovery from herbivory

6.1 Introduction

Herbivory can have many detrimental effects on plants, such as decreasing fruit and seed production (Rockwood, 1973; Foster, 1984; Hendrix, 1984; Louda, 1984; Edwards, 1985; Whitham and Mopper, 1985; Crawley, 1987), altering plant community structure and distribution (Harper, 1969; Kulmon, 1971; Parker et al., 1981; Louda, 1983; Fraser & Grime, 1999), and reducing fitness and competitive ability (Marquis, 1984; Dirzo & Harper, 1982). However, some plants can be positively effected by herbivory (Chew, 1974; Dyer, 1975; Mattson and Addy, 1975) with biomass, fruit and seed production increasing and photosynthetic capacity improving (eg McNaughton 1983, Caldwell et al. 1981, Inouye 1982, Heichel & Turner 1983, Cargill et al. 1984, Mutikainen et al. 1993, Paige & Whitham 1987, Trumble et al. 1993, Gadd et al. 2001).

The response of plants to herbivory varies according to prevalent biotic and abiotic conditions (Maschinski and Whitham, 1989; McNaughton, 1986). Factors known to influence compensatory growth include the intensity of grazing; nutrient, water and light availability; defoliation history; and type and age of tissue consumed (Clark & Clark, 1985; Mendoza et al., 1987). The timing of herbivory is also a major factor affecting regrowth. Seedlings are extremely vulnerable because they have fewer defences than older plants, and do not possess the root systems and photosynthetic machinery needed to replace removed tissues efficiently (Whitham et al., 1991). The combination of timing and intensity of herbivory determines the degree to which a plant can compensate for herbivore consumption (Turnipseed, 1972; Smith and Bass, 1972). Variation in nutrient and water availability and the type of tissue eaten can produce a gradient of plant compensatory responses (Cox & McEvoy, 1983; Crawley, 1983; McNaughton et al., 1983; Maschinski &

Whitham, 1989). Low light levels can also stress plants and affect growth (Whitham et. al., 1991).

A major expectation of the resource availability hypothesis (Coley et al., 1985) is that plants from resource-limited environments have slower growth rates than those from higher resource habitats. Growth rates are predicted to increase along a gradient as soil nutrients, water, and/ or light become available. A major corollary of this hypothesis is that plants from low resource environments will recover more slowly from herbivory than plants from higher resource habitats.

The current study presents the results of a glasshouse experiment designed to answer two questions:

(1) Do plant species from vegetation communities growing in more fertile environments recover faster from artificial herbivory than plant species from communities in less fertile environments?
(2) Do plant species from infertile environments recover faster from defoliation when they have access to greater concentrations of soil nutrients?

6.2 Methods

Plant species were chosen as a set of phylogenetically independent contrasts (Felsentein, 1985; Burt, 1989; Armstrong and Westoby, 1993), based on within-family taxonomies from the *Flora of Australia* (1982, 1984, 1988) (Fig. 6.1). Phylogenetically independent contrasts (PICs) use phylogenetic relationships to establish independent cases of evolutionary divergence (Armstrong & Westoby, 1993). Each PIC serves as a statistical replicate for testing the relationship between nutrients in the soil and recovery from herbivory.

The glasshouse experiment was conducted at Macquarie University, Sydney Australia between April - December 2002, and August 2003 - April 2004. For logistic reasons, different species were grown at different times, though synchronized planting occurred for species within each PIC.

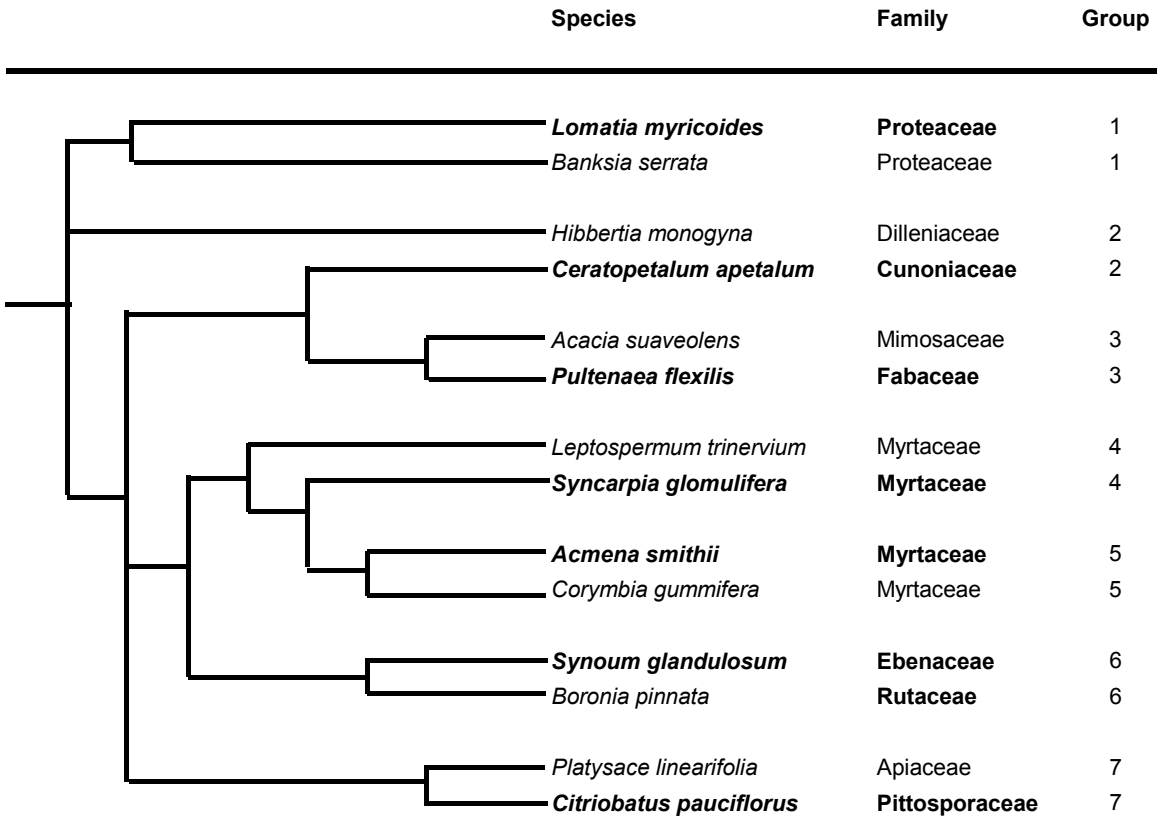


Figure 6.1 Phylogenetic relationships of plant species used in glasshouse experiments 1 and 2. Branch lengths are not claimed to be proportional to time since evolutionary divergence. Mesic species in bold.

Seven common sclerophyll and seven mesic plant species were used in the experiment. Sclerophyll plant species were paired with closely related rainforest or wet sclerophyll (mesic) plants to form seven pairs (PICs) (Fig. 6.1). The plant species were a subset of the 45 species analysed for chemical and physical constituents in chapter 3 (Fig. 3.1).

The majority of seedlings were purchased as tubestock from commercial suppliers, the exceptions being *Hibbertia monogyna* and *Synoum glandulosum*, which were grown at Macquarie University from cuttings and seeds respectively. Cuttings and seeds were collected from Ku-ring-gai Chase National Park.

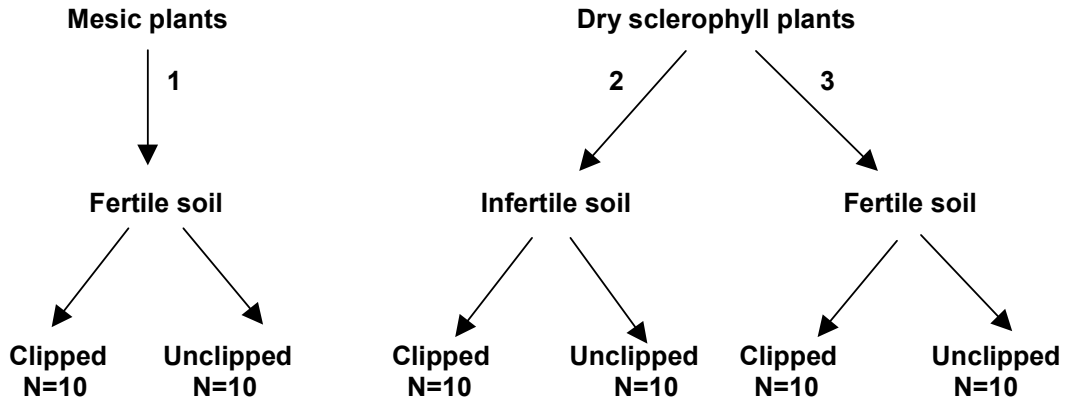


Figure 6.2 Design of glasshouse experiment conducted at Macquarie University during the period 2002-2004. Question 1 compares treatments 1 and 2. Question 2 compares treatments 2 and 3.

Dry sclerophyll plant species were grown in two soil types: (1) infertile sandy soil collected from Ku-ring-gai Chase National Park, and (2) higher nutrient soil from Royal National Park. Mesic plant species were grown in higher nutrient soil only (Fig. 6.2). Soils were collected from a maximum depth of 30 cm and mixed with grade 3 vermiculite (3:1 soil to vermiculite). Air dried soil samples were analysed by State Chemistry Laboratory in Victoria for total nitrogen and total phosphorus concentrations (Table 6.1).

The first question being addressed in this chapter was a comparison between soil treatments 1 and 2. The second question compared soil treatments 2 and 3 (Fig. 6.2).

Table 6.1 Total Nitrogen (%w/w) and total phosphorus (mg/kg) concentrations for infertile and fertile soil used in experiment.

Soil Type	Collection Site	Total N (%w/w)	Total P (mg/kg)
Infertile	Warrimoo track, Ku-ring-gai Chase NP 151° 09'02"E, 33°39'05"S	<0.05	61
Fertile	Lady Carrington Drive Track, opposite Bola creek, Royal National Park 151°01'57.2"E, 34°08'42.8"S	0.42	450

Ten replicate seedlings per plant species were randomly allocated to a clipping treatment to represent removal of tissue by herbivores (ie clipped or unclipped) (Fig. 6.2), and were transplanted from their 50 mm x 100 mm tubes to 170 mm x 170 mm pots. Within each species, seedlings were of similar size.

Plants were grown in natural light for five weeks prior to commencement of the clipping treatment. Plants were randomly distributed throughout the glasshouse and were re-positioned every two weeks. Glasshouse temperatures ranged from 17^{o}C-24^{o}C and plants were watered for 10 minutes every 12 hours.

Plants designated for defoliation had 50% of their foliage clipped. This involved the symmetrical removal of every second leaf. Clipping occurred once only. Leaves from each replicate were placed in paper envelopes and dried at 70^{o}C for 96 hours. Leaves were then weighed to obtain dry biomass of removed tissue.

To monitor regrowth, growing tips of up to 14 branches per plant (depending on the species' architecture) were marked either by cotton thread or permanent marker-pen on every plant at the beginning of the experiment. The number of leaves produced on each branch per individual plant was counted fortnightly for eight months.

Following the final leaf count, plants were harvested and biomass divided into new growth, old growth, and roots. New growth was defined as all plant tissue above the initial marker while old growth was defined as tissue below the marker. For each replicate plant, new and old growth tissues were subdivided into leaves and stems. Separated tissues were placed into separate paper bags to be oven dried (70^{o}C for 96 hours) and later weighed for dried biomass. Soil and vermiculite was washed with care from roots, which were also placed in paper bags, oven dried, and weighed.

6.3 Statistics

Wilcoxon rank-sum tests were used to compare (1) rate of leaf production and (2) rate of biomass production for clipped and unclipped dry sclerophyll and mesic plant species growing in their native soils (Question 1).

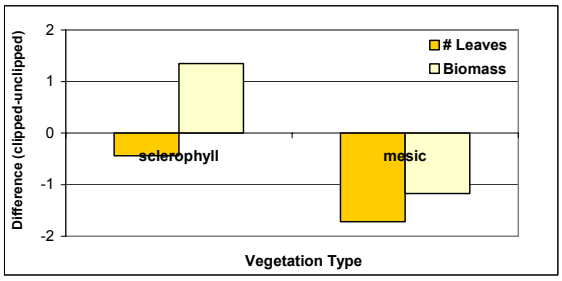
Two-way ANOVAs were used to determine the differences between clipped and unclipped dry sclerophyll plant species growing in low and higher nutrient soils (Question 2).

6.4 Results

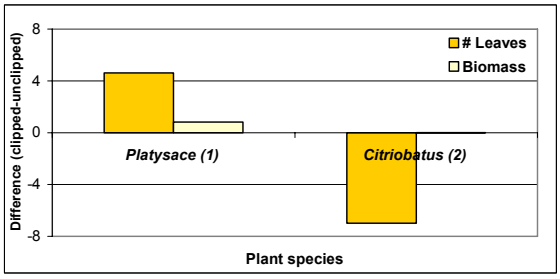
6.4.1 Effects of 50% defoliation on growth and growth rate

Mesic species did not recover faster from defoliation than dry sclerophyll species. The removal of 50% of foliage from seedlings growing in their natural soils affected the regrowth of some dry sclerophyll and mesic plant species positively (clipped plants produced more leaves than controls), some negatively (clipped plants produced fewer leaves than controls) and some not at all. Dry sclerophyll plant species positively affected by the single clipping event were *Platysace linearifolia* (Fig. 6.3B), *Banksia serrata* (Fig. 6.3C), *Leptospermum trinervium* (Fig. 6.3F), *Corymbia gummifera* (Fig. 6.3G) and *Boronia pinnata* (Fig. 6.3H). Clipped mesic species that produced more leaves but less biomass than controls were *Syncarpia glomulifera* (Fig. 6.3F), *Acmena smithii* (Fig. 6.3G) and *Lomatia myricoides* (Fig. 6.3C). The only mesic species to produce more leaves and new biomass (leaves and stem) in clipped plants was *Synoum glandulosum* (Fig. 6.3H).

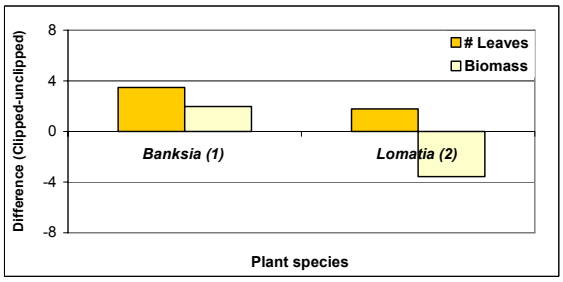
Plant species negatively affected by 50% defoliation were the dry sclerophyll shrub *Hibbertia monogyna* (Fig. 6.3D), and the mesic shrubs *Citriobatus pauciflorus* (Fig. 6.3B) and *Pultenaea flexilis* (Fig. 6.3E). Leaf removal had no discernible effect on the leaf production and total new biomass production of *Ceratopetalum apetalum* (Fig. 6.3D).



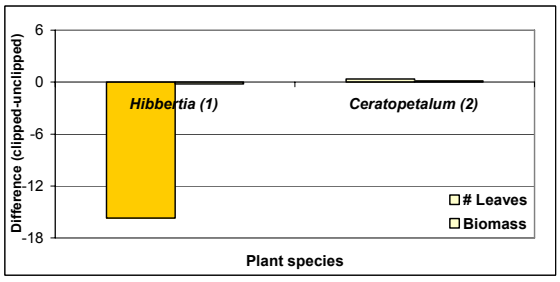
A. Difference in leaf tissue for sclerophyll and mesic plant species



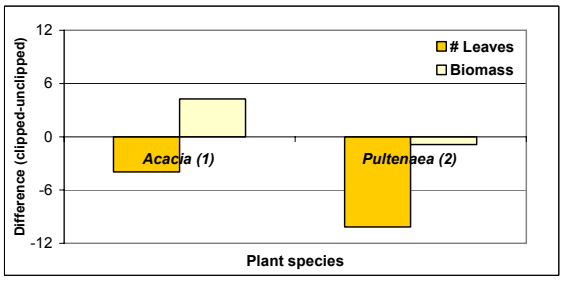
B. Difference in leaf tissue for *Platysace linearifolia* and *Citriobatus pauciflorus*



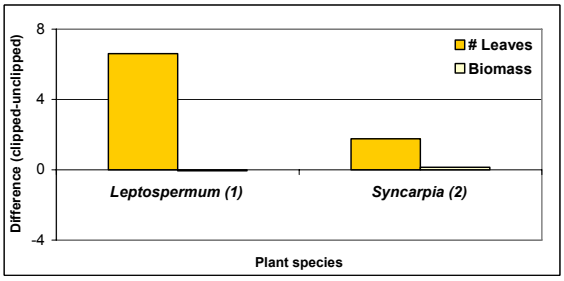
C. Difference in leaf tissue for *Banksia serrata* and *Lomatia myricoides*



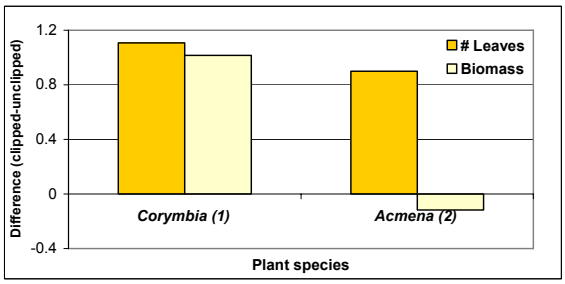
D. Difference in leaf tissue for *Hibbertia monogyna* and *Ceratopetalum apetalum*



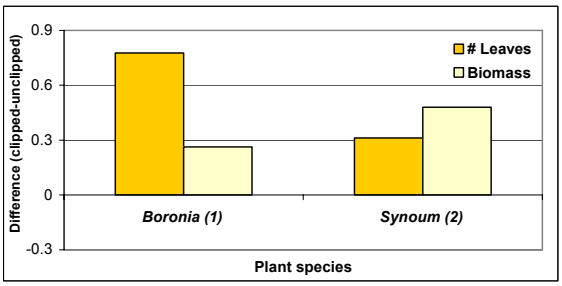
E. Difference in leaf tissue for *Acacia suaveolens* and *Pultenaea flexilis*



F. Difference in leaf tissue for *Acacia suaveolens* and *Pultenaea flexilis*



G. Difference in leaf tissue for *Corymbia gummifera* and *Acmena smithii*



H. Difference in leaf tissue for *Boronia pinnata* and *Synoum glandulosum*

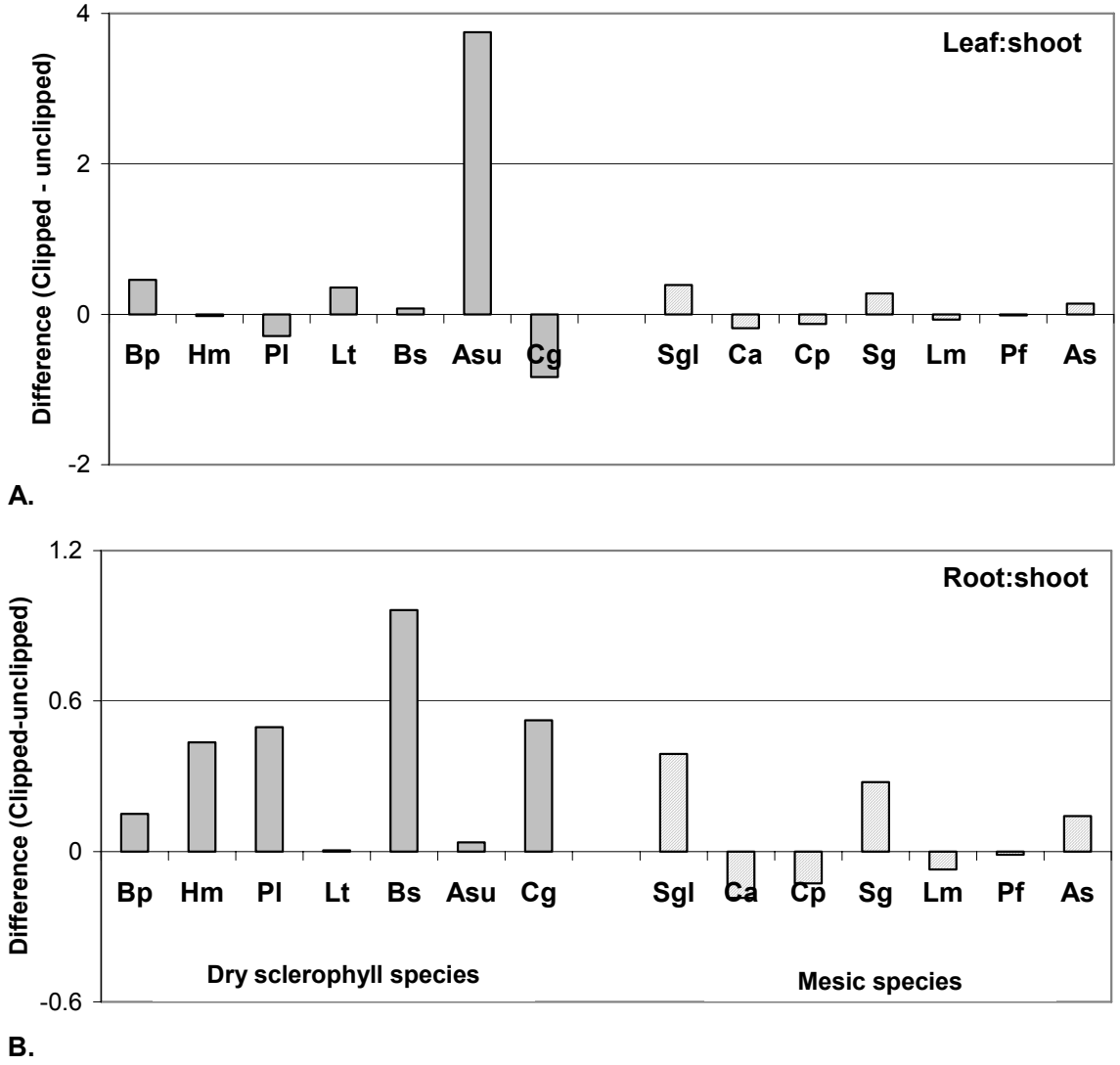
Figure 6.3 Effects of a single defoliation event on the compensatory growth of dry sclerophyll (1) and mesic (2) plant species. Plants grouped into Phylogenetically Independent Contrasts (PICs).

Artificial defoliation increased the leaf:shoot ratio of three dry sclerophyll (*A. suaveolens*, *B. pinnata*, *L. trinervium*) and three mesic species (*A. smithii*, *S. glandulosum*, *S. glomulifera*); decreased the leaf:shoot ratio of two dry sclerophyll

(*C. gummifera*, *P. linearifolia*) and two mesic species (*C. apetalum*, *C. pauciflorus*); and had no effect on two dry sclerophyll (*H. monogyna*, *B. serrata*) and two mesic species (*L. myricoides*, *P. flexilis*) (Fig. 6.4 A). The root:shoot ratio was increased for six dry sclerophyll (*A. suaveolens*, *B. serrata*, *B. pinnata*, *C. gummifera*, *H. monogyna*, *P. linearifolia*) and three mesic species (*A. smithii*, *S. glandulosum*, *S. glomulifera*) and decreased for three mesic species (*C. apetalum*, *C. pauciflorus*, *L. myricoides*). The root:shoot ratios for one mesic (*P. flexilis*) and one dry sclerophyll species (*L. trinervium*) were unaffected by the single defoliation event (Fig. 6.4 B).

The majority of mesic plants did not consistently produce leaves faster than dry sclerophyll species (Fig. 6.5H). Mesic species that produced leaves at a faster rate than their paired dry sclerophyll PIC were *L. myricoides* (Fig. 6.5B), *P. flexilis* (Fig. 6.5D), and *A. smithii* (Fig. 6.5F). Dry sclerophyll plants that produced leaves at a faster rate than their mesic PIC were *P. linearifolia* (Fig. 6.5A), *H. monogyna* (Fig. 6.5C), *B. pinnata* (Fig. 6.5G) and *L. trinervium* (Fig. 6.5E).

Similarly, mesic plant species did not consistently produce new biomass at a faster rate than dry sclerophyll plant species (Fig. 6.6H). The plant species with the highest median rates of biomass production were *L. myricoides* (mesic) (Fig. 6.6B), *B. serrata* (dry sclerophyll) (Fig. 6.6B), *A. smithii* (mesic) (Fig. 6.6F), and *C. gummifera* (dry sclerophyll) (Fig. 6.6F). *Ceratopetalum apetalum* (mesic) (Fig. 6.6C) also had a relatively high median rate of biomass production. The small-leaved *B. pinnata* (Fig. 6.6G) and *H. monogyna* (both dry sclerophyll species) (Fig. 6.6C) had the lowest median rates of biomass production.



Bp – *Boronia pinnata*; Hm – *Hibbertia monogyna*; Pl – *Platysace linearifolia*; Lt – *Leptospermum trinervium*; Bs – *Banksia serrata*; Asu – *Acacia suaveolens*; Cg – *Corymbia gummifera*; Ac – *Acmena smithii*; Ca – *Ceratopetalum apetalum*; Sg – *Syncarpia glomulifera*; Pf –*Pultenaea flexilis*; Lm – *Lomatia myricoides*; Cp – *Citriobatus pauciflorus*; Sgl – *Synoum glandulosum.*

Figure 6.4 Difference between clipped and unclipped plants for root:shoot ratios (A) and leaf:shoot ratios (B) for dry sclerophyll and mesic species following 50% defoliation. Plants organised into phylogenetically independent contrasts.

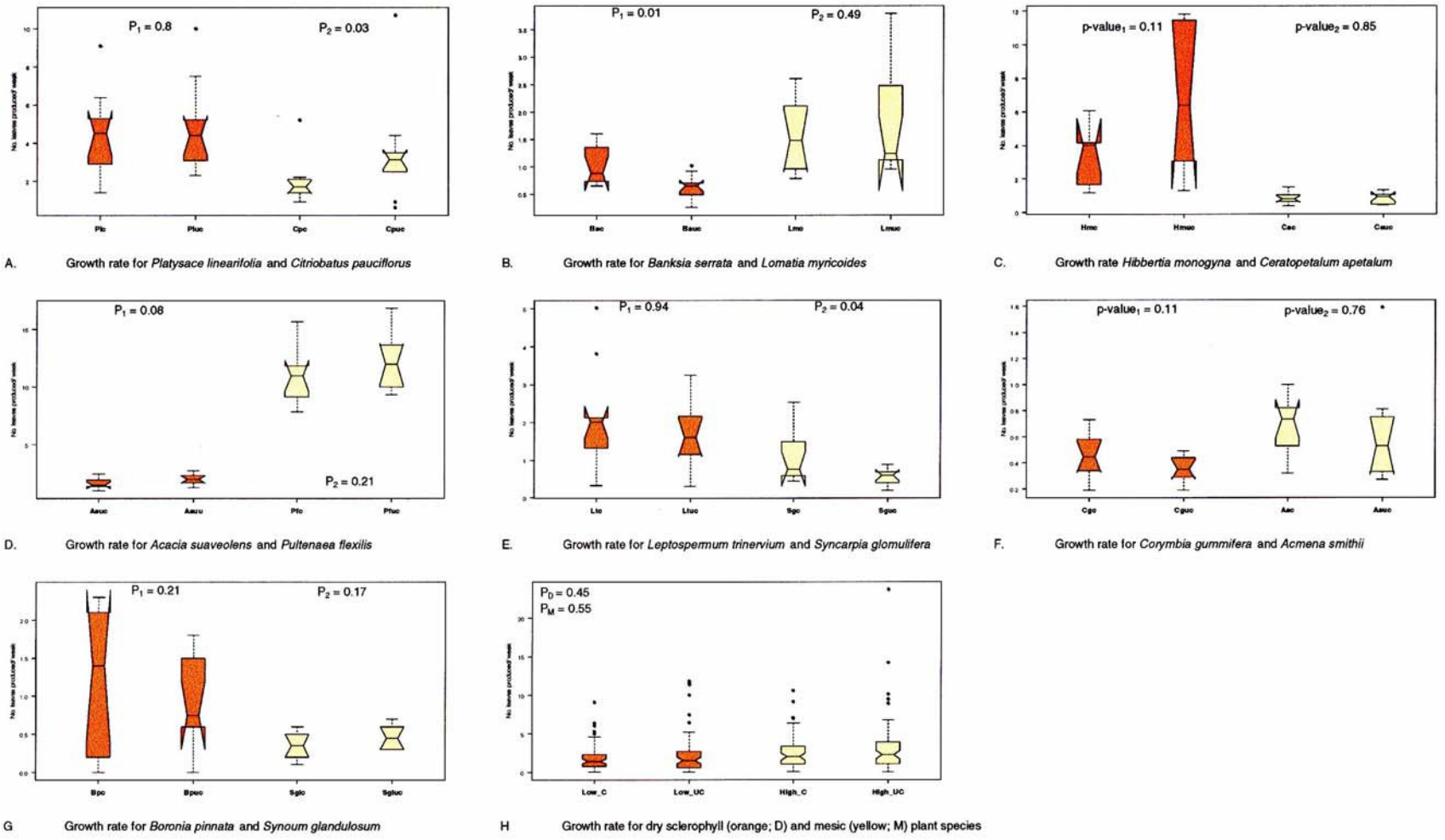
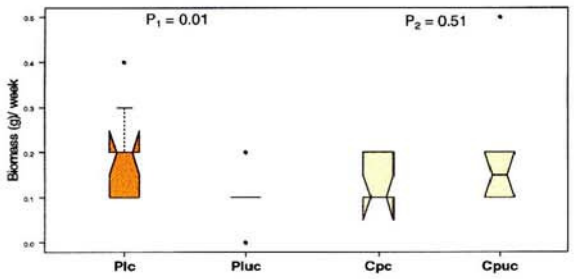
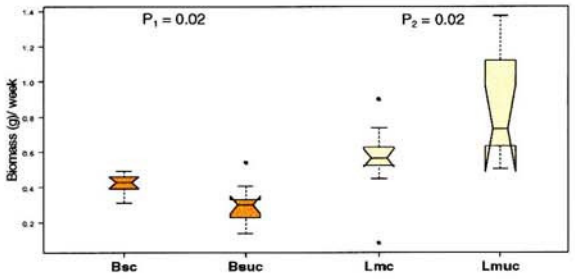


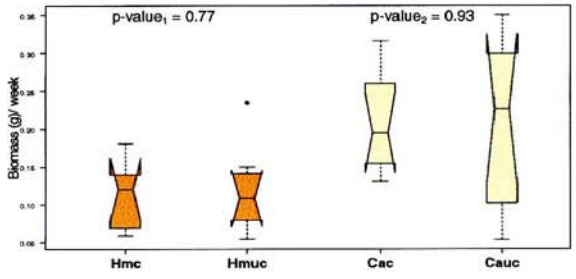
Fig. 6.5 **Minimum, maximum and median number of leaves produced per branch each week for clipped (.c) and unclipped (uc) dry sclerophyll (orange) and mesic (yellow) plant species organised into PIC groups.** * Wilcoxon rank sum tests: P_1 - significance value of clipped vs unclipped dry sclerophyll plants; P_2 - significance value of clipped vs unclipped mesic plants.



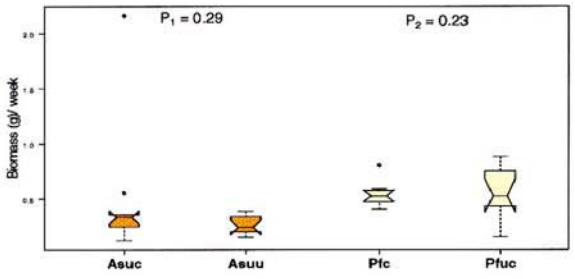
A. Biomass/ wk for *Platysace linearifolia* and *Citriobatus pauciflorus*



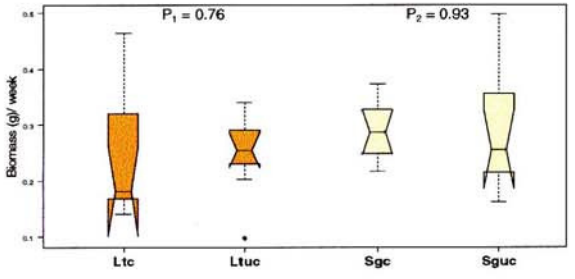
B. Biomass/ wk for *Banksia serrata* and *Lomatia myricoides*



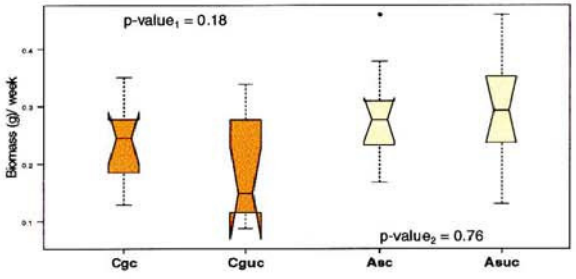
C. Biomass/ wk for *Hibbertia monogyna* and *Ceratopetalum apetalum*



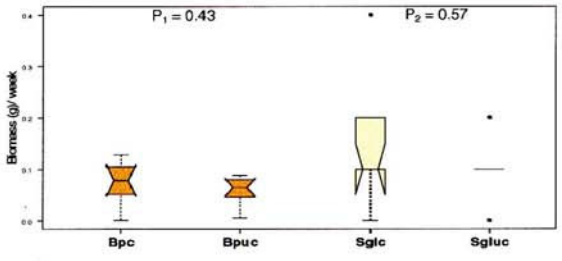
D. Biomass/ wk for *Acacia suaveolens* and *Pultenaea flexilis*



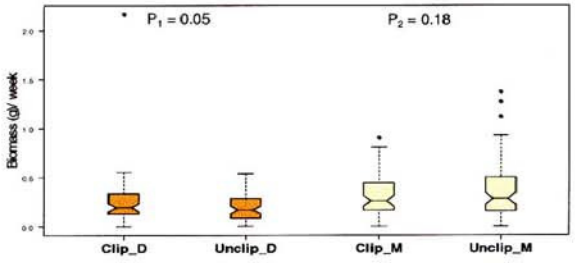
E. Biomass/ wk for *Leptospermum trinervium* and *Syncarpia glomulifera*



F. Biomass/ wk for *Corymbia gummifera* and *Acmena smithii*



G. Biomass/ wk for *Boronia pinnata* and *Synoum glandulosum*



H. Biomass/ wk for dry sclerophyll and mesic plant species

Fig. 6.6 Minimum, maximum and median dried biomass (new leaf and stem) produced/ week for clipped (.c) and unclipped (uc) dry sclerophyll (orange) and mesic (yellow) plant species organised into PIC groups

* Wilcoxon rank sum tests: P-value$_1$ - significance value of clipped vs unclipped dry sclerophyll plants; P-value$_2$ - significance value of clipped vs unclipped mesic plants; L:S - mean leaf:stem.

6.4.2 Responses to defoliation within phylogenetically independent contrasts

In this study phylogenetically independent contrasts were used to detect the effects of defoliation on plants from low and higher resource sites without the potentially confounding effects of phylogenetic relationships. It was found that the response to defoliation was fairly consistent. In terms of number of leaves, four dry sclerophyll species growing in their native soils recovered better than their mesic PIC partner; one mesic species recovered better than their dry sclerophyll PIC partner; and two PIC pairs showed similar responses to clipping (Fig. 6.7 A). In terms of biomass, five dry sclerophyll species growing in their native soils recovered better than their mesic PIC partner, and two PIC pairs had similar responses to clipping (Fig. 6.7 B).

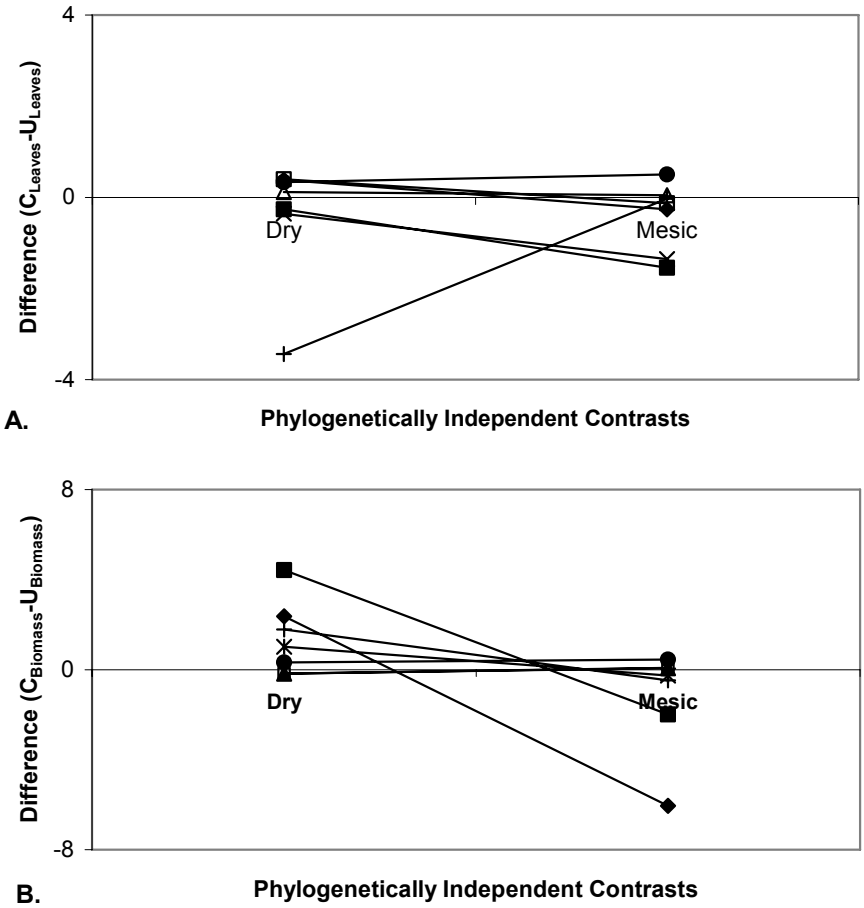


Figure 6.7 Continuity between phylogenetically independent contrasts and the difference between clipped and unclipped dry sclerophyll (Dry) and mesic (Mesic) species, in terms of number of leaves produced per week and biomass produced. Lines connect PIC pairs.

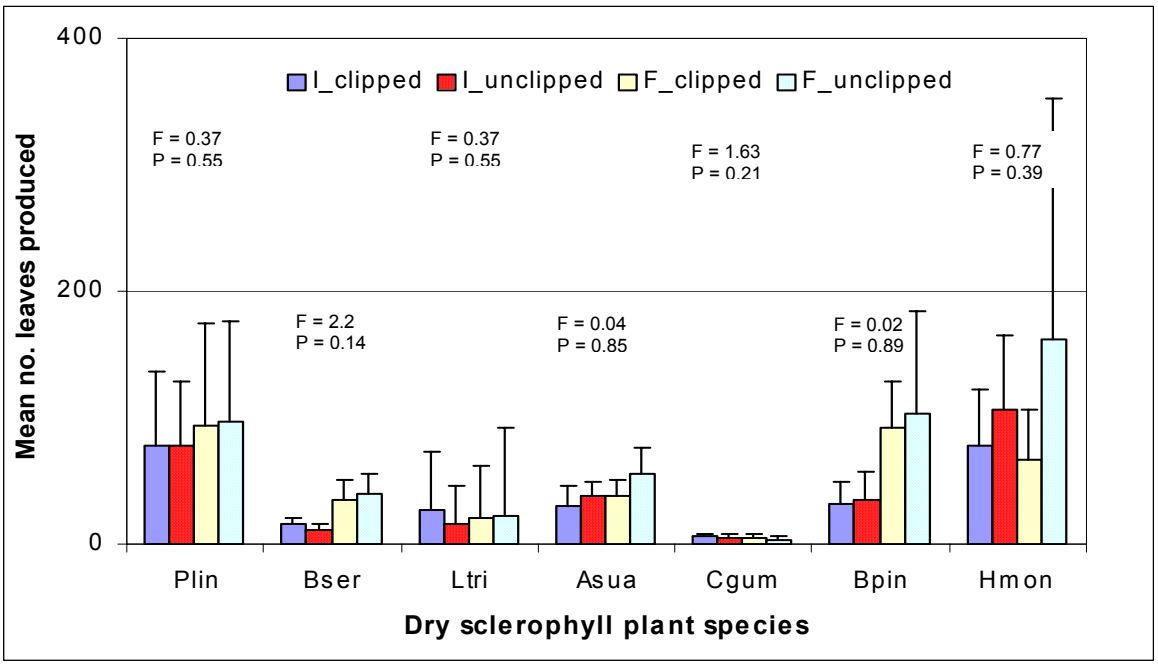
6.4.3 Soil nutrients and recovery from defoliation in dry sclerophyll species

For the majority of dry sclerophyll plant species, provision of higher nutrient soils did not significantly increase compensatory growth after artificial defoliation (Fig. 6.8). Clipped individuals of species such as *Platysace linearifolia* (Fig. 6.9A) and *Banksia serrata* (Fig. 6.9B), growing in higher nutrient soils, actually produced fewer leaves and less dried biomass than clipped individuals growing in low nutrient soils (Fig. 6.9H). Clipped *Leptospermum trinervium* (Fig. 6.9C) and *Boronia pinnata* (Fig. 6.8F) also produced fewer leaves when grown in higher nutrient soils, though no decrease in biomass was observed in these plants. The only departure from this trend was *Corymbia gummifera*, which produced more leaves following defoliation when grown in more fertile soil (Fig. 6.9E).

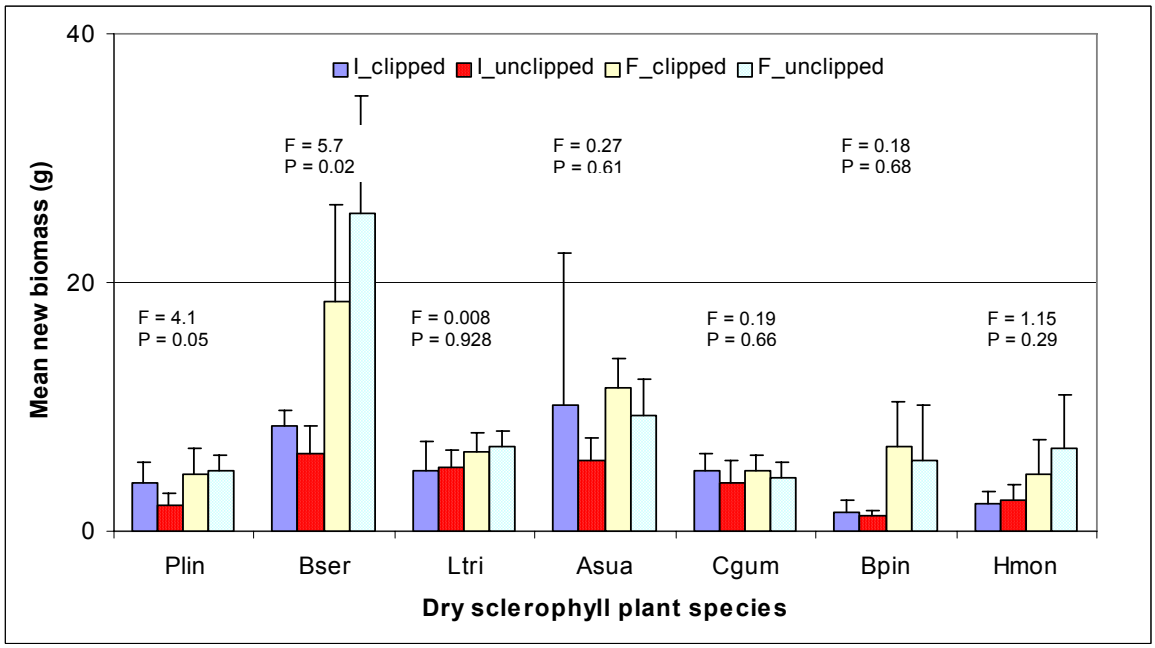
The provision of additional nutrients had the effect of increasing the leaf:shoot ratio for four species (*B. serrata*, *C. gummifera*, *L. trinervium* and *P. linearifolia*), decreasing the leaf:shoot ratio for two species (*A. suaveolens* and *B. pinnata*), and having no effect on the leaf:shoot ratio for one species (*Hibbertia monogyna*) (Fig. 6.10 A). Higher nutrient soils also had varying effects on the root:shoot ratios of dry sclerophyll species. Clipped individuals of five species growing in higher nutrient soils showed a decline in root:shoot ratios (*B. pinnata*, *H. monogyna*, *P. linearifolia*, *B. serrata* and *C. gummifera*), whilst one species showed an increase (*A. suaveolens*) and another no change (*L. trinervium*) (Fig. 6.10 B).

In general, provision of higher nutrient soils had no significant effect on the rate of leaf production (Fig. 6.11H). Rates for *A. suaveolens*, *H. monogyna*, *C. gummifera*, *L. trinervium* and *P. linearifolia* did not differ significantly between soil treatments (Fig. 6.11). For instance, the number of leaves per branch produced each week by *L. trinervium* ranged from a median of 1.41 leaves per branch per week for clipped plants in infertile sandy soil to 1.87 leaves per branch per week for unclipped plants growing in more fertile soil (Wilcoxon test: $p = 0.5$). Only *B. serrata* (Fig. 6.11B) and unclipped *B. pinnata* (Fig. 6.11G) produced leaves at a greater rate when they were grown in more fertile soils.

However, five dry sclerophyll plant species growing in higher nutrient soils had significantly faster rates of biomass (new leaf and stem) production than dry sclerophyll plants in infertile sandy soil (Fig. 6.12). Dry sclerophyll plant species with significantly higher rates of biomass production were *A. suaveolens* (Fig. 6.12A), *B. serrata* (Fig. 6.12B), *H. monogyna* (Fig. 6.12D), *L. trinervium* (Fig. 6.12E) and *B. pinnata* (Fig. 6.12G). Only *C. gummifera* (Fig. 6.12C) and clipped *P. linearifolia* (Fig. 6.12F) had similar rates of growth between soil types.



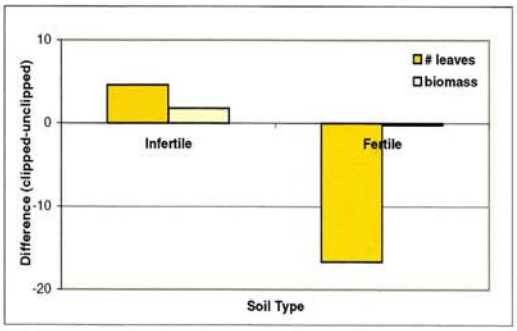
(A)



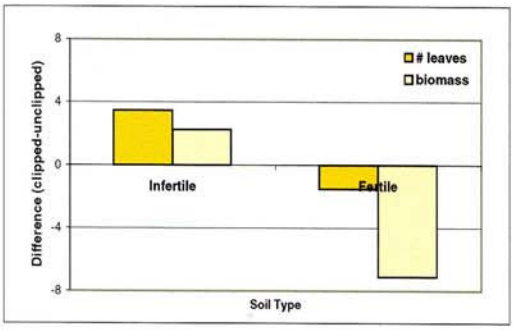
(B)

Plin – *Platysace linearifolia*; Bser – *Banksia serrata*; Ltri – *Leptospermum trinervium*; Asua – *Acacia suaveolens*; Cgum – *Corymbia gummifera*; Bpin – *Boronia pinnata*; Hmon – *Hibbertia monogyna*; I – infertile sandy soil; F – more fertile soil.

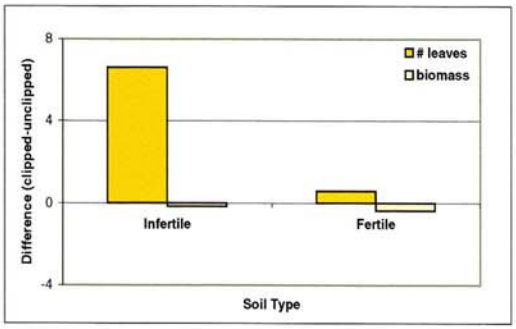
Fig. 6.8 Mean number of leaves (A) and new (leaf and stem) biomass (B) produced by dry sclerophyll plant species growing in low and high nutrient soils after 8 months of growth (experiment 2). F and P values from two-way ANOVAs shown.



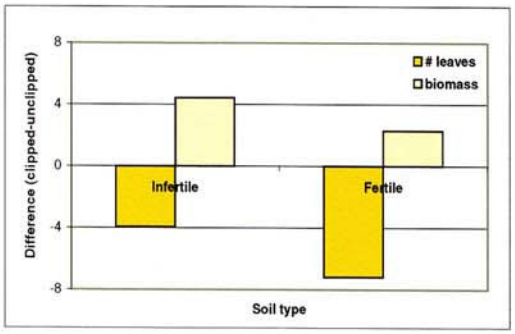
A. Difference in leaf tissue for *Platysace linearifolia*



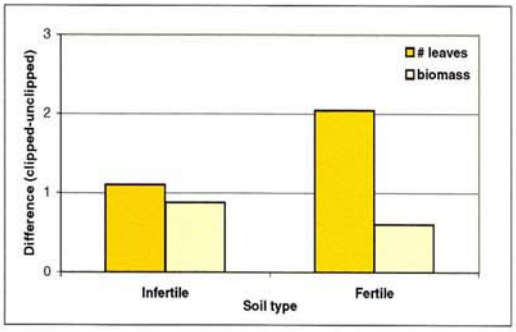
B. Difference in leaf tissue for *Banksia serrata*



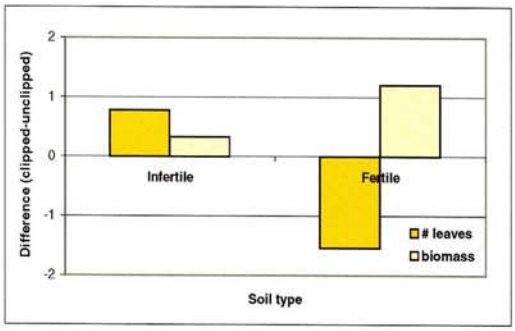
C. Difference in leaf tissue for *Leptospermum trinervium*



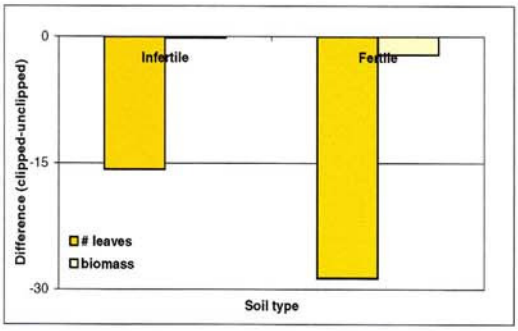
D. Difference in leaf tissue for *Acacia suaveolens*



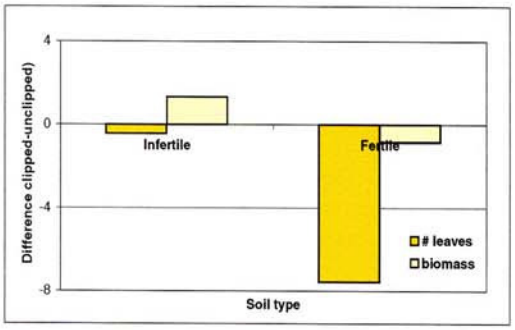
E. Difference in leaf tissue for *Corymbia gummifera*



F. Difference in leaf tissue for *Boronia pinnata*

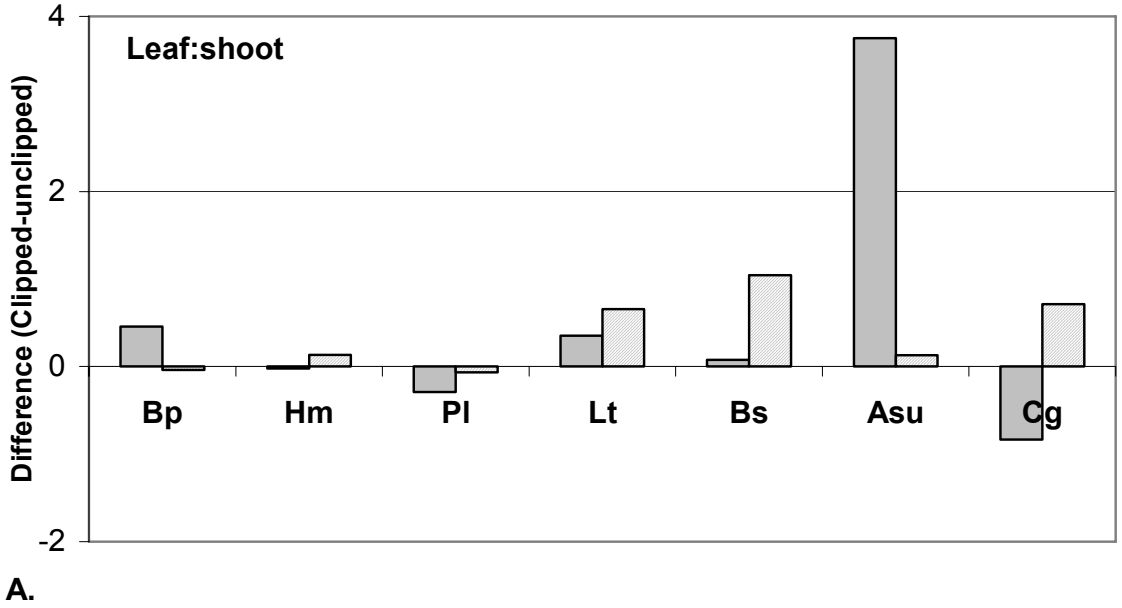


G. Difference in leaf tissue for *Hibbertia monogyna*

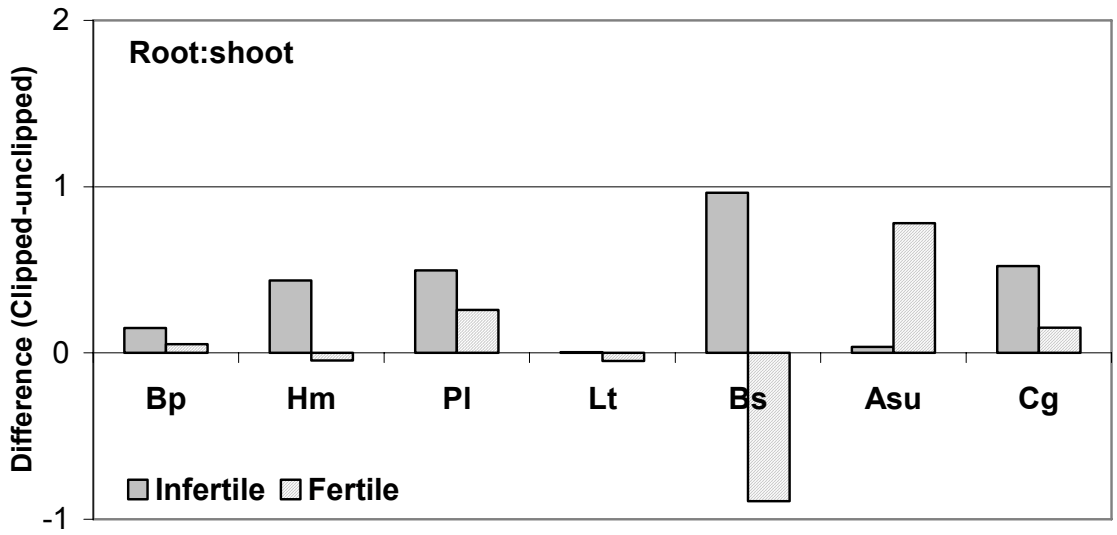


H. Difference in leaf tissue for dry sclerophyll plants in low and high nutrient soils

Figure 6.9 Effect of added nutrients to the compensatory growth of dry sclerophyll plant species in terms of number of leaves produced and new (leaf and stem) biomass.



A.



B.

Bp – *Boronia pinnata*; Hm – *Hibbertia monogyna*; Pl – *Platysace linearifolia*; Lt – *Leptospermum trinervium*; Bs – *Banksia serrata*; Asu – *Acacia suaveolens*; Cg – *Corymbia gummifera*

Figure 6.10 Effects of added nutrients on the compensatory growth of dry sclerophyll species in terms of leaf:shoot (A) and root:shoot ratios (B) following a single defoliation event.

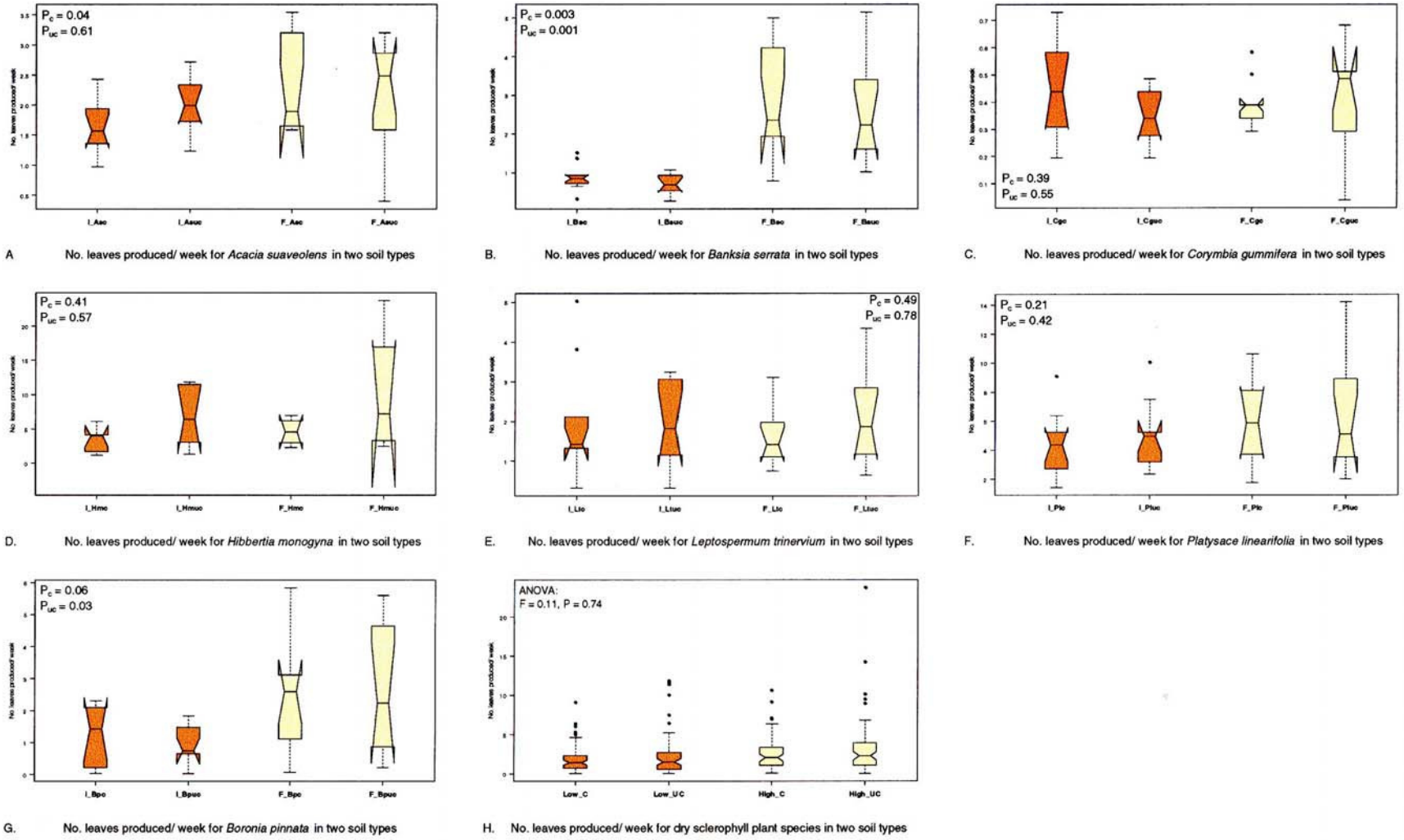
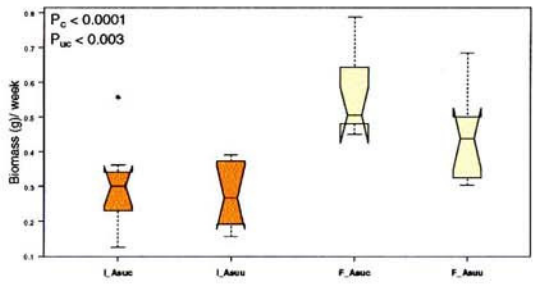
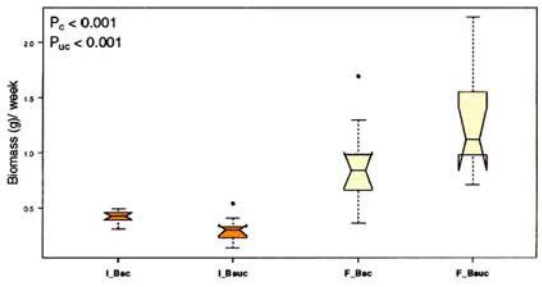


Fig. 6.11 **Minimum, maximum and median number of leaves per branch produced each week for clipped (C) and unclipped (UC) dry sclerophyll plant species growing in low (orange) and higher (yellow) nutrient soils**

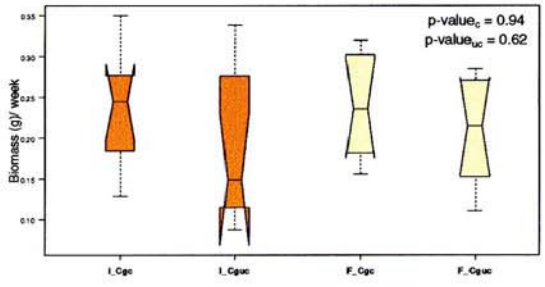
* Wilcoxon rank sum tests: P-value$_C$ is the significance value of clipped plants in dry sclerophyll vs mesic soils; P-value$_{UC}$ is the significance value of unclipped plants in dry sclerophyll vs mesic soils.



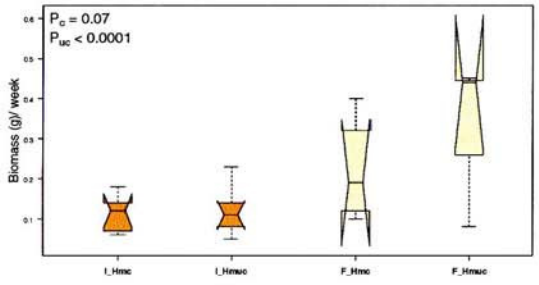
A. Biomass in grams/ week for *Acacia suaveolens* in two soil types



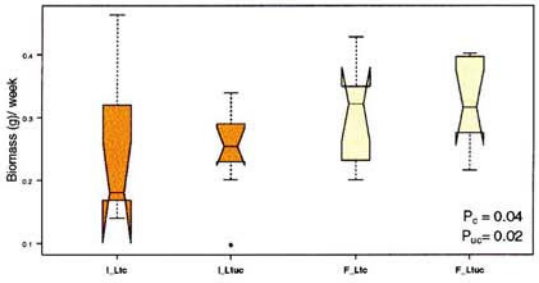
B. Biomass in grams/ week for *Banksia serrata* in two soil types



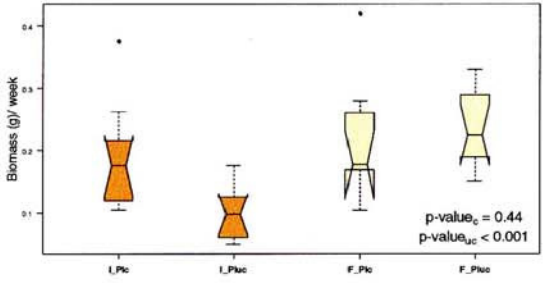
C. Biomass in grams/ week for *Corymbia gummifera* in two soil types



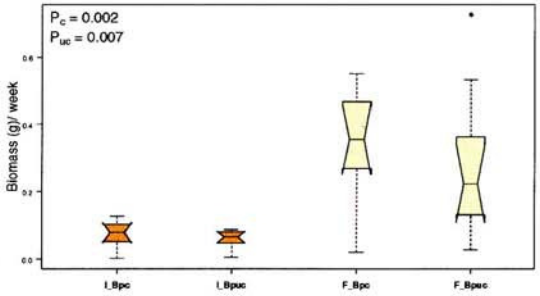
D. Biomass in grams/ week for *Hibbertia monogyna* in two soil types



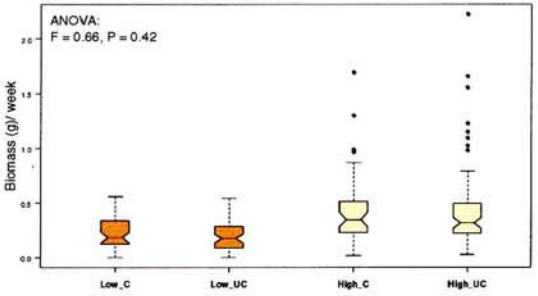
E. Biomass in grams/ week for *Leptospermum trinervium* in two soil types



F. Biomass in grams/ week for *Platysace linearifolia* in two soil types



G. Biomass in grams/ week for *Boronia pinnata* in two soil types



H. Biomass in grams/ week for dry sclerophyll plant species in two soil types

Fig. 6.12 Minimum, maximum and median dried biomass (new leaves and stems) produced/ week for clipped (C) and unclipped (UC) dry sclerophyll plant species in low (orange) and higher (yellow) nutrient soils

* Wilcoxon rank sum tests: P-value$_C$ - significance value of clipped plants in dry sclerophyll vs mesic soils; P-value$_{UC}$ - significance value of unclipped plants in dry sclerophyll vs mesic soils; L:S - mean leaf:stem.

6.5 Discussion

Previous studies have demonstrated that herbivory can negatively effect the fitness, competitiveness and reproductive capacity of plants (Harper 1969, Kulmon 1971, Rockwood 1973, Foster 1984, Hendrix 1984, Louda 1984, Marquis 1984, Dirzo & Harper 1982, Fraser & Grime 1999). However, it has also been shown that defoliation can have positive effects on plants by increasing fruit, seed and biomass production (McNaughton 1979, Caldwell et al. 1981, Inouye 1982, Cargill et al. 1984) and improving photosynthetic capacity (Trumble et al., 1993).

In this study, it was found that removal of 50% foliage from dry sclerophyll and mesic plant species had positive, negative, or no effects on subsequent growth, depending on the species. Out of fourteen species, five dry sclerophyll and four mesic species were positively affected; two dry sclerophyll and two mesic species were negatively affected; and one mesic species was unaffected by defoliation. The clipping treatment increased the root:shoot ratios for five dry sclerophyll and three mesic species; decreased the root:shoot ratios for three mesic species; and had no effect on the root:shoot ratios for three species. In addition, clipping had no effect on the leaf:stem ratios for two dry sclerophyll and two mesic species; increased the leaf:stem ratios for three dry sclerophyll and three mesic species; and decreased the leaf:stem ratios for two dry sclerophyll and two mesic species.

An expectation of the resource availability hypothesis is that plants from higher resource environments would have faster growth rates than plants from low resource environments (Coley et al. 1985). Contrary to this expectation, overall median rates of leaf and biomass production did not vary greatly between mesic and dry sclerophyll plants. Those species that did produce leaves at higher rates tended to be dry sclerophyll plants with smaller leaves than their mesic PIC partner. Small leaves expand faster than large leaves (Moles & Westoby, 2000), which may explain why small-leaved plants had faster leaf production rates, but similar rates of biomass production compared to large-leaved species.

Plant responses to herbivory vary according to prevalent biotic and abiotic conditions (Maschinski & Whitham 1989, McNaughton, 1986). Studies have

demonstrated that the availability of nutrients, water and light can influence a plant's ability to recover from herbivory (Bryant et al. 1983, Cox & McEnvoy 1983, Ruess et al. 1983, McNaughton & Chapin 1985, Clark & Clark 1985, Schmid et al. 1990, Hamilton III et al. 1998). The degree of recovery is also determined by the edaphic tolerances of the species under investigation (Clarkson, 1966; Rorison, 1968) and the abilities of the plants to absorb and transport nutrients efficiently (Christie & Moorby, 1975).

In the present study, it was found that higher nutrient soils did not significantly increase the ability of dry sclerophyll species to recover from defoliation. Out of seven dry sclerophyll species, six produced fewer leaves than controls in higher nutrient soils, while one species produced more leaves than controls. Higher nutrient soils decreased the root:shoot ratios for five species, increased the root:shoot ratio for one species and had no discernible effect on one species. Only three out of seven species growing in higher nutrient soil showed an increase in the leaf:shoot ratio. The higher nutrient soils also did not increase the rate of leaf production for the majority of dry sclerophyll plants. However, the higher nutrient soil did increase the rate of biomass production for four dry sclerophyll species by increasing the production of stem.

Australia is the flattest, driest, least fertile and most bushfire-prone continent on Earth (Smith, 1992). The ancient soils that characterise the Australian landscape are nutrient-deficient after millennia of leaching without renewal from volcanic activity (White, 1992). Australian plants are so well adapted to low-nutrient soils that additional nutrients can adversely affect species and even cause a decline in plant diversity (Specht, 1963; Heddle & Specht, 1975; Thomson & Leishman, 2005). This may explain the lack of response of dry sclerophyll plants to higher nutrient soil following defoliation, and the reason why several of the expectations of the resource availability hypothesis (based predominantly on northern hemisphere observations) are not supported by this study.

Strategies employed by Australian plants to increase the uptake of phosphorus, nitrogen and other nutrients include root symbioses with mycorrhizal fungi and N-fixing bacteria (Hopkins 1995), and the production of cluster or proteoid roots

(Lamont 1993, Skene 1998, Adams et al. 2002, Miller 2005). Mycorrhizal fungi and N-fixing bacteria are associated with many Australian plant families, including the Mimosaceae and Fabaceae. Cluster roots, which are confined to the uppermost 100 mm of the soil profile, occur in almost all the Proteaceae and some Mimosaceae and Fabaceae (Skene 1998, Wrigley & Fagg 2000).

In conclusion, the hypothesis that plants from resource-limited environments have slower growth rates and hence recover more slowly from herbivory was not supported. The majority of mesic species did not produce leaves or new biomass faster than dry sclerophyll plant species. Higher nutrient soils also did not significantly increase the compensatory growth or rate of leaf production for the majority of dry sclerophyll plants. Those species that did show an increase in the rate of biomass production, had lower leaf:stem ratios, indicating a rise in stem production as a result of increased concentrations of soil nutrients.