

## **Chapter 7**

### **Conclusions**

This project used the resource availability hypothesis (Coley *et al*, 1985) as a framework for investigating the relationship between resource availability, leaf traits, insect herbivore damage and insect community structure on a wide variety of plant species of varying growth forms from paired low and higher resource sites within the same region. The study was performed in Sydney, Australia, providing a temperate, southern hemisphere complement to most previous studies on herbivory conducted in the tropics and the northern hemisphere (Coley, 1988; Aide & Londono, 1989; Bryant et al. 1989; Jing & Coley, 1990; Coley & Aide, 1991; Bolser & Hay, 1996).

The paired sites on infertile and more fertile soils were situated in two localities: Ku-ring-gai Chase National Park and Royal National Park. The paired sites were within 5 km of each other, had similar climate and were subject to similar regional insect herbivore fauna. Resources were defined in terms of soil characteristics: - soil moisture, percent organic matter, nitrogen and phosphorus concentrations.

The project had five components. Comparisons between low and higher resource sites were made in terms of:

1. Leaf traits of mature and immature leaves
2. Phenology of leaf maturation
3. Herbivore damage in the field and laboratory
4. Diversity and abundance of herbivorous insect fauna
5. Ability to recover from herbivory

## **Mature and immature leaves**

The first and second components tested the hypothesis that leaves of plants from low resource environments would be better defended, longer-lived, and have slower growth rates compared to leaves of plants from higher resource environments. Mature, immature and expanding leaves were analysed for a number of chemical and physical characteristics in order to answer three major questions:

- ◆ Do the leaves of plants from resource poor environments have higher concentrations of chemical and physical defences than plants from resource-rich environments?
- ◆ Do leaves from low resource environments live longer and have slower expansion rates than leaves from higher resource environments?
- ◆ Do leaves of plant species from resource-poor environments become better defended at a faster rate than plant species from environments that are richer in resources?

It was found that both immature and mature leaves of dry sclerophyll species from low resource environments contained higher concentrations of total phenols and condensed tannins than leaves of mesic species from higher resource environments. Though several mesic species tested positive for alkaloids or cyanogenic glycosides (N-based compounds), low-resource plants appeared to be better defended by carbon-based chemical compounds than higher-resource plants. In addition, dry sclerophyll leaves were more fibrous, contained less nitrogen and water, and had higher carbon:nitrogen ratios than mesic leaves, suggesting dry sclerophyll leaves were less palatable than mesic leaves.

Leaves from low resource habitats did not have longer leaf lifespans than leaves from higher resource environments. Within the mesic plant groups, temperate rainforest plants at the highest nutrient site had leaf lifespans that were significantly longer than dry and wet sclerophyll leaves. In addition, wet sclerophyll leaf lifespans did not differ significantly from dry sclerophyll leaf lifespans.

Expanding dry sclerophyll leaves toughened faster initially than expanding mesic leaves, but reached their 90<sup>th</sup> percentile toughness in approximately the same length of time. It was also found that the majority of mature, fully-expanded dry sclerophyll leaves were not significantly tougher than mesic leaves. The plants with the toughest leaves in this study were monocotyledonous mesic species. As leaf toughness is generally thought to be one of the most important physical defences, it is concluded that low resource plant species are not defended better by physical defences.

Dry sclerophyll leaf expansion rates did not differ greatly from the expansion rates of mesic leaves. Leaves from higher resource plants are therefore vulnerable to herbivory for a similar length of time as leaves from lower resource plants.

Previous leaf trait studies have generally used one or more plant species from a single resource site (eg. Basset, 1990; Gowda, 1996; Cornelissen et al. 1997; Winn, 1999; Wright & Cannon, 2001; Bragg & Westoby, 2002). The species studied have often belonged to a single plant family or growth form (Macauley & Fox, 1980; Edwards, 1982; Reich et al. 1991; Matsuki & MacLean Jr. 1994; Suzuki & Kudo, 1997; Gras et al. 2005), and analyses for a small number of chemical, physical or phenological traits have usually been made on either mature or immature leaves (McKey, 1974; Oghiakhe & Jackai, 1992; Shure & Wilson, 1993; Stock et al. 1993; Cooper & Ginnett, 1998; Edwards et al. 2000; Wright & Cannon, 2001; Arnold & Schultz, 2002; Iddles et al. 2003).

Of those studies that have compared leaf characteristics of plants from environments with differing resource conditions, chemical but not physical traits have often been more closely associated with resource availability. Myers (1987) found nutrient availability had no effect on the production of spines in the prickly pear cactus *Opuntia stricta*, and Campbell (1986) found spinescence did not increase with reduction of nutrients in fynbos vegetation (Campbell, 1986). Grubb (1992) observed that a decrease in rainfall in alpine zones was correlated to an increase in spininess. However, he also noted an association between high-rainfall and spininess in many western European plants (Grubb, 1992). Coley (1983) found shade-tolerant leaves were tougher and contained higher concentrations of

fibre and phenolics than gap-colonizing species. Folgarait and Davidson (1995) demonstrated that phenolic levels could rise when nutrient concentrations declined, and Yates and Peckol (1993) found polyphenolic concentrations in the seaweed *Fucus vesiculosus* were higher at low-nitrogen sites compared with algae from high-nitrogen sites.

The current study differed from previous work by consisting of: (1) a mature leaf trait study, (2) an immature leaf trait study, (3) a phenology of leaf maturation study, and (4) a leaf-lifespan study. Plants from low and higher resource sites were selected to represent a wide range of plant families and growth forms (trees, shrubs, herbs and vines), and young, old and expanding leaves were analysed for a relatively large number of chemical and physical leaf traits. Leaves were also monitored from bud to senescence to determine maximum leaf-lifespans.

To be regarded as “better defended”, a plant must possess chemical and/or physical characteristics that actually prevent or inhibit herbivore consumption. Attempts to determine the efficacy of a particular leaf trait to defend a plant against herbivory would ideally require the researcher to suppress the confounding influences of other leaf traits. It would also be necessary to consider factors such as herbivore feeding method and digestion, and the phenological changes that occur in plants over time and under different levels of resource availability. At present such manipulations are simply not tractable.

Regardless of the difficulties of assessing the effectiveness of a particular leaf trait, several secondary metabolites and physical leaf characteristics have been cited as important anti-herbivore defences (McKey, 1974; Feeny, 1976; Levin, 1976; Jones et al., 1978; Levin et al., 1978; Rosenthal et al., 1979; Coley, 1986). Secondary metabolites such as condensed tannins, alkaloids and cyanogenic glycosides are generally thought to reduce the nutritional quality of plants by binding to digestive enzymes and dietary proteins (Robbins et al., 1987). They disrupt the nervous systems and cardiac functions of herbivores (van Alstyne, 1988), and make plants toxic or bitter tasting (Moles & Westoby, 2000). Physical leaf traits such as toughness, force of fracture and fibre content are thought to inhibit herbivory by wearing out contact parts such as mandibles and teeth. They can also prevent

animals from shearing leaves (Coley, 1983a; Raupp, 1985; Coley & Aide, 1991; Hochuli, 1996; Lucas et al., 2000; Sanson et al., 2001; Iddles et al., 2003; Read et al., 2003).

In summary, this investigation of leaf traits provided only partial support for the first major expectation of the resource availability hypothesis, that leaves of plants from low resource environments would be better defended, longer-lived, and have slower growth rates compared to leaves of plants from higher resource environments. Plants from low resource sites were better defended in terms of carbon-based compounds, but not in terms of nitrogen-based compounds or physical defences such as leaf toughness. Low resource plants did not have longer leaf lifespans than leaves from higher resource habitats, and leaves from low resource sites did not have slower expansion rates than leaves from higher resource sites. If phenols are important anti-herbivore defences, rates of herbivory in higher nutrient sites should be significantly higher than herbivory rates in the lower nutrient sites.

### **Herbivore damage in the field and laboratory**

Few studies have monitored individual leaves for herbivore consumption over extended periods of time (Lowman, 1985, 1992a; Lowman & Heatwole, 1997; Andrew & Hughes, 2005a). Most studies have used one or a few plant species from one site or several similar sites (in terms of resources) (Journet, 1981; Fox & Morrow, 1983, Robertson & Duke, 1987; Andrew & Hughes, 2005a). Even fewer studies have compared rates of herbivore consumption under laboratory conditions to herbivore consumption rates in the field (Perez-Harguindeguy et al. 2003), and have correlated herbivory with chemical and physical leaf traits (Coley, 1983; Andrew & Hughes, 2005a).

Component 3 tested the hypothesis that plants from low resource environments would suffer less insect herbivore damage than plants from more fertile areas (Coley et al. 1985). Herbivore damage was monitored monthly for two years in the field, and experiments testing the palatability of leaves were conducted on three invertebrate herbivores in the laboratory. The specific questions addressed were:

- ◆ Do plants from low resource environments suffer less herbivory than plants from more fertile habitats? (ii) How much plant tissue is lost to herbivores in the field and laboratory?
- ◆ Is herbivore damage correlated with (i) nutritional value (percent nitrogen, fibre content) of the foliage, (ii) concentration of chemical defences (total phenols), (iii) degree of physical defence (toughness, force of fracture, lamina thickness), (iv) other leaf traits (specific leaf area, percent water)?
- ◆ How is the herbivore damage distributed amongst insect feeding guilds (chewing, sucking etc), and is this distribution different at sites with differing resources?

In the field study it was found that chewing damage was the most common type of herbivory on leaves, and that young leaves were more vulnerable to insect herbivory than mature leaves. Plant species from low resource sites did not suffer significantly more herbivore damage (chewing and sucking) than plants from higher resource sites. Chewing damage on leaves in dry sclerophyll heathland average 0.79% per month or 9.5 % per year, compared to 0.95% per month or 11.2% per year for mesic leaves from the higher resource sites. Sucking damage on leaves averaged 0.08% per month for mesic leaves and 0.03% per month for dry sclerophyll foliage. The most important variables predicting herbivory in the field were leaf area, lamina thickness and fibre content. Leaves that sustained the highest levels of chewing damage tended to have large leaf areas, whilst leaves that suffered the highest levels of sucking damage tended to have thicker laminas and low fibre content.

Leaf traits cited by previous studies as having an influence on herbivore food choice include leaf toughness, fibre content, phenol concentration and nitrogen content (McKey, 1974; Feeny, 1976; Levin, 1976; Jones et al., 1978; Levin et al., 1978; Rosenthal et al., 1979; Coley, 1986). That the majority of these variables did not correlate with insect herbivory in this study may indicate or confirm that:

- ◆ insect herbivores, which have long and close associations with various plant species, can overcome the chemical and physical defences of the subset of plants on which they feed (Chapman, 1998; Gullan & Cranston, 1998);

- ◆ variables such as phenolic compounds have functions other than defence. Phenols act as antioxidants to reduce the photodestruction of exposed tissues (Close & McArthur, 2002). High concentrations of total phenols may indicate a leaf's ability to withstand harsh sunlight, whilst low concentrations may indicate the reduced photodamage risk for plants beneath a partially closed canopy;
- ◆ monitoring of herbivore damage does not reveal the full extent of tissues lost to herbivores (eg the amount of cytoplasm removed by Hemiptera can not be estimated by measuring the area of sucking damage); and/or
- ◆ previous studies may not reflect true correlations between herbivory and leaf traits because they were based on arboreal insect surveys as opposed to actual damage by herbivores (Stork, 1987; Cornell & Kahn, 1989; Shuter & Westoby, 1992).

Whilst cafeteria experiments are poor substitutes for field monitoring (eg. test organisms are generally not endemic, the influence of predators can not be quantified, plant architecture and spatial relationships are factored out), they nevertheless provide useful information about herbivore preferences for a broad range of plants. By observing food choice, time prior to consumption and amount of tissue consumed, researchers can potentially determine the palatability of leaves offered simultaneously to herbivores under standardised conditions (Grime et al. 1968; Cates & Orians, 1975; Grime et al. 1996; Perez-Harguindeguy et al. 2003).

Prior to the beginning of the cafeteria experiments, test organisms were starved for 48 hours. Despite this, snails, crickets and stick insects took approximately another 35 hours to begin consuming leaf squares. When the test species finally began to feed, mesic species were preferred to dry sclerophyll species, though only 18 to 23 leaf squares out of 300 were partially consumed by the invertebrates, and consumption rates never exceeded a mean of 0.06% per hour. The most important leaf characteristics influencing consumption of leaves in the cafeteria experiment were lamina thickness, fibre content and water content. 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. Snails

had preferences for fibrous leaves, though low total phenol concentrations and water content may also influence snail consumption. Cricket consumption was not influenced by any of the variables.

In summary, my findings did not strongly support the second major expectation of the resource availability hypothesis that plants from low resource environments would suffer less insect herbivore damage than plants from more fertile areas. There was no significant difference between the amount and rate of consumption of leaves from low and higher resource sites in the field, and whilst test organisms tended to prefer mesic leaves, consumption rates were low for all plant species used in the cafeteria experiments.

An issue that has not been addressed in this study is the potential importance of vertebrate herbivores. Vertebrates can have major impacts on plant communities. Ungulates can reduce the abundance, distribution and stature of willows and other vascular plants (Singer et al. 1994; Grellmann, 2002), and increase plant species richness in semi-arid grasslands (Rambo & Faeth, 1999). Rabbits and sheep have transformed alpine vegetation in Tasmania (Bridle & Kirkpatrick, 2001), and introduced possums and rodents continue to have a profound effect on forests in New Zealand (Miller & Miller, 1995; Wilson et al. 2003; Bach & Kelly, 2004).

The Ku-ring-gai Chase National Park and Royal National Park shelter many native herbivorous and omnivorous vertebrates such as the common ringtail possum (*Pseudocheirus peregrinus*), brushtail possum (*Trichosurus vulpecula*), greater glider (*Petauroides volans*), and the swamp wallaby (*Wallabia bicolor*). Exotic species such as the rabbit (*Oryctolagus cuniculus*) can be found in Ku-ring-gai Chase National Park, and rusa deer (*Cervus timorensis*) were introduced to Royal National Park in the latter half of the nineteenth century (Strahan, 1983). The effects of exotic native vertebrates on native vegetation have been well-documented (eg. Hamilton, 1981; Rambo et al. 1999; Stewart, 2001; Keith et al. 2005). However, in the current study, vertebrate herbivory was not a confounding factor. The low consumption rates and patterns of damage on leaves indicated herbivory on the studied plants was caused by invertebrates only.

## **Diversity and abundance of herbivorous insect fauna**

The fourth component of this research tested the hypothesis that plants in low resource environments would support fewer insect herbivores than plants from more fertile areas. The diversity and abundance of insect herbivores in the field were measured using two collection methods: pyrethrum spraying and branch clipping. The orders Coleoptera, Hemiptera and Lepidoptera were the focus of this study. The questions addressed were:

- ◆ Does the structure of insect herbivore communities differ: (i) between plant species within a site (ii) between sites of different resource availability at a location (iii) between locations?
- ◆ Are specific leaf traits correlated with particular insect orders/ families/ guilds?

It was found that dry sclerophyll plant species from low resource environments supported higher densities of leaf-chewers and sap-suckers than plants from more fertile habitats. The major leaf characteristics predicting the presence of leaf-chewers and sap-suckers were small leaf areas, high concentrations of total phenols, thick lamina, low fibre content and low nitrogen concentrations.

The density of Coleoptera and Lepidoptera larvae did not differ significantly between sites of contrasting resource levels. However, the beetle family Curculionidae was found in higher numbers at the low resource sites compared to the higher resource sites. It was also found that the major leaf characteristics predicting the presence of Curculionidae was small leaf area, thick lamina, relatively high concentrations of total phenols, and water content.

Significantly higher numbers of Hemiptera were found on dry sclerophyll plant species compared to mesic species. Hemipteran families distinguishing dry sclerophyll faunal assemblages were the Cicadellidae, Membracidae and Psyllidae. Membracids were common on plants high in fibre, whilst psyllids were negatively correlated with fibre content. Cicadellids were not associated with any of the leaf trait variables.

Herbivore densities did not differ significantly between plant growth forms in dry and wet sclerophyll environments. In addition, 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. The ratio of carnivores:herbivores did not vary significantly between the resource sites.

Previous studies have demonstrated that the distribution and abundance of insects can be determined by various combinations of abiotic and biotic factors such as soil nutrients, rainfall fluctuations, host plant characteristics and predator abundance (eg. Lawton, 1978; Lowman, 1982; Basset, 1991; Walde, 1995; Recher et al. 1996a). Peeters (2001), working in a low-resource site in Victoria, found insect feeding guild densities and assemblages varied significantly amongst plant species (Peeters, 2001). Sucking insects were strongly associated with high nitrogen and water concentrations, and chewing insects were correlated with low levels of fibre and lignin (Peeters, 2002b). Sessile phloem feeders and rostrum chewers were negatively correlated with specific leaf weight, lamina and cuticle thickness, vascular tissue depth and stomate length, and were positively correlated with stomate density (Peeters, 2002a). External chewers were negatively correlated with percent lignified vein area, and positively correlated with leaf area (Peeters, 2002a).

For variables such as leaf area, lamina thickness and fibre content, these data often varied from my findings in terms of direction (Peeters, 2001, 2002a, b). However, the essential messages were the same. Insect herbivore densities and assemblages vary significantly among plant species, and herbivore assemblages are closely associated with various physical (structural) and chemical leaf traits (constituents).

In summary, the hypothesis that plants from higher resource habitats would support a greater abundance of insect herbivores than plants from low resource environments was not supported by this study. Instead, it was found that low resource plant species 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 family richness and abundance was highest at the nutrient poor sites, and there was no significant difference between the mean densities of beetles and caterpillars found on plants growing in low and higher resource habitats. Dry sclerophyll plants supported relatively large numbers of phytogamous bugs such as Cicadellids, Membracids and Psyllids, and the beetle family Curculionidae were more common at the low resource sites compared to the more fertile sites.

### **Ability to recover from herbivory**

The fifth component tested the hypothesis that plant species from low resource environments have less ability to recover from herbivore damage than species from higher resource environments. This component consisted of a glasshouse experiment designed to monitor recovery rates of dry sclerophyll and mesic plant species following artificial herbivory. The questions investigated were:

- ◆ 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?
- ◆ Do plant species from infertile environments recover faster from defoliation when they have access to greater concentrations of soil nutrients?

It was found that 50 percent removal of foliage from dry sclerophyll and mesic plant species had positive, negative, or no effects on compensatory growth. 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 also decreased the root:shoot ratio for five dry sclerophyll and three mesic species; increased the root:shoot ratio for two mesic species; and had no effect on the root:shoot ratio for three species.

Overall median rates of leaf and biomass production did not vary greatly between mesic and dry sclerophyll plants. In addition, higher nutrient soils did not significantly increase compensatory growth for the majority of dry sclerophyll species. Out of seven species, six produced fewer leaves than controls in higher nutrient soils, while one species produced more leaves than controls. Higher nutrient soils had the effect of raising the root:shoot ratios for four species, and had no discernible effect on three species. It was also found that the higher nutrient soils 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.

The positive and negative effects of herbivory on plants are well documented (eg McNaughton, 1979; Parker et al., 1981; Louda, 1983; Foster, 1984; Hendrix, 1984; Louda, 1984; Marquis, 1984; Edwards, 1985; Whitham & Mopper, 1985; Crawley, 1987; Paige & Whitham, 1987a,b; Fraser & Grime, 1999; Gadd et al., 2001), as are the factors that effect a plant's ability to recover from herbivory (eg. Turnipseed, 1972; Smith & Bass, 1972; Cox & McEvoy, 1983; Crawley, 1983; McNaughton et al., 1983; Maschinski & Whitham, 1989). Many Australian plant species are well adapted to low-nutrient soils (Smith, 1992; White, 1992). Studies have shown that additional nutrients can adversely affect species and even cause a decline in plant diversity (Specht, 1963; Heddle & Specht, 1975; Thomson and 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.

In summary, the expectation that plant species from low resource environments have less ability to recover from herbivore damage than species from higher resource habitats was not supported by the findings of the glasshouse experiment. Mesic plant species growing in higher nutrient soils did not recover faster from artificial herbivory than dry sclerophyll plants in low nutrient soils. In addition, dry sclerophyll plants growing in higher nutrient soils did not recover faster from artificial defoliation than dry sclerophyll species in low nutrient soils.

## Conclusions

The prediction of the resource availability hypothesis that plants from low resource environments would be better defended was only partially supported by this study. Dry sclerophyll leaves were defended better by carbon-based chemical compounds, but not by physical leaf traits.

Leaf traits associated with particular levels of soil nutrients were total phenol concentrations, percent nitrogen, specific leaf area, lamina thickness and water content. Dry sclerophyll leaves from low resource sites contained higher concentrations of phenols, higher carbon:nitrogen ratios, thicker lamina and higher concentrations of lignin. Wet sclerophyll and temperate rainforest leaves from higher resource sites were characterised by higher concentrations of nitrogen, water and hemicellulose and higher specific leaf areas. Leaf traits that showed inconsistent responses to soil nutrients and did not differentiate low and higher resource leaves were leaf toughness, force of fracture, cellulose and area.

Contrary to the expectation of the resource availability hypothesis that levels of herbivory would be highest in environments rich in resources, there was no significant difference in the levels of herbivore consumption at the low and higher resource sites. In addition, leaf toughness, force of fracture and total phenol concentrations (variables regarded by many as having defensive functions) were not associated either positively or negatively with herbivore consumption. Young leaves with large leaf areas were particularly susceptible to chewing damage, and leaves with thick laminae and low fibre content were vulnerable to sucking damage.

The corollary of the resource availability hypothesis, that higher resource sites would have greater densities of herbivores than low resource sites, was not supported by this study. The density of Coleoptera and Lepidoptera larvae did not differ significantly between resource sites, and the beetle family Curculionidae were found in greater numbers on dry sclerophyll plants. The greatest densities of Hemiptera, particularly the Cicadellidae, Membracidae and Psyllidae, were collected from low resource plants, and the greatest diversity of Hemiptera were

found at the low resource sites. The highest average number of Coleoptera families were found on plants at the higher nutrient sites.

Toughness and force of fracture did not influence invertebrate abundance. The major leaf characteristics predicting the presence of Curculionidae beetles were small leaf area, thick lamina, relatively high concentrations of total phenols, and water content. Membracid bugs were common on plants high in fibre, and psyllids were negatively correlated with fibre content. Cicadellids were not associated with any of the leaf trait variables.

Australian plants from higher resource environments did not have faster recovery rates than low resource plant species. In addition, soil nutrients did not increase the rate of recovery of dry sclerophyll plant species from artificial defoliation.

### **Future directions**

A number of observations were made during the study that are worthy of further investigation:

- (1) The first arose from the mature leaf trait component. Four plant species (3 mesic, 1 dry sclerophyll) periodically tested positive for cyanogenic glycosides. This raised the following questions:
  - I. Which Australian plant species produce cyanogenic glycosides?
  - II. When and why are cyanogenic glycosides produced in Australian plants?
  - III. What mechanisms instigate cyanogenic glycoside production?
  - IV. How effective are cyanogenic glycosides in plant defence?

It is suggested that a phenological study be undertaken to discover and monitor the periods when cyanogenic glycosides are produced and present in plants. Monitoring should occur throughout leaf expansion, and prior to and during flower, fruit and seed production. Such a study would shed light on the function and importance of nitrogen-based chemical compounds in Australian

plants. It would also determine whether mesic species were defended more regularly by nitrogen-based chemical compounds than dry sclerophyll species.

- (2) The second observation arose from the phenology study, which monitored leaves from bud to full-expansion. Of the four dry sclerophyll species used in the phenology study, three belonged to the Myrtaceae and one to the Proteaceae. The Myrtaceae were characterised by relatively constant concentrations of nitrogen and carbon:nitrogen ratios, whilst the Proteaceae species showed a slight decrease and increase in concentrations respectively. Further investigation of additional plant species and families would be beneficial to understanding and confirming the existence of a pattern, and may provide further evidence that plants from low resource environments have strategies to reduce the palatability of leaves.
- (3) Another observation from the phenology study that warrants further investigation is that dry sclerophyll leaves seem to reach their 50 percent leaf toughness faster than mesic species. Whilst this is most likely a strategy employed by dry sclerophyll plants to reduce water loss and sun damage to maturing leaves, it would make an interesting project. It is suggested that a larger subset of dry sclerophyll and mesic species be selected and monitored throughout the expansion phase for leaf toughness and force of fracture. Lamina thickness, leaf area, specific leaf area, water content and cuticle thickness should also be recorded.
- (4) In this study, total phenol concentrations were not associated with herbivore consumption, and did not negatively influence herbivore abundance. It has been suggested that the primary role of phenols is to act as a photoinhibitor to protect leaves from harsh sunlight (Close & McArthur, 2002).

It is proposed that an experiment be setup to investigate the primary role of total phenols. The experiment would use mesic and dry sclerophyll species capable of being acclimated to high and low light levels. Species would be grown in their natural soils in a field or glasshouse, and each individual would

be subjected to one of three light-levels: high light levels, partial shade, full shade. At set intervals, leaves would be collected and tested immediately for total phenol and condensed tannin concentrations. This would provide data on any changes of concentrations within and between treatments, and determine if any patterns exist within and between vegetation types.

As part of this research, cafeteria and / or field experiments could be set up to determine whether plants become more or less palatable at different light levels.

- (5) In the field herbivory study, young leaves were particularly susceptible to herbivore consumption. It is suggested that an additional survey be carried out on a monthly or two monthly basis using the branch collection method described by Peeters (2002a). This would determine if herbivore abundance in low and higher resource sites was correlated with leaf age (as well as other traits), and would enable the researcher to compare their results to another region in Australia.
- (6) The effects of seasonally driven plant growth patterns on insect herbivory and communities should be investigated. This could involve phenological leaf trait studies, the regular sampling of arboreal insects each season over a number of years, and long term monitoring of insect herbivory in the field using photography. While this direction of research is peripheral to the core of the resource availability hypothesis, it would provide valuable data.
- (7) Further research could involve transplant experiments. Dry sclerophyll plant species could be transplanted to higher resource environments to determine if additional nutrients in the field lead to increased insect consumption. Reciprocal transplants of mesic species to low resource habitats would be unfeasible, as it would likely result in major plant deaths. Nevertheless, transplant experiments are a useful tool and could assist in testing aspects of the resource availability hypothesis.

- (8) The identification of insects and other arthropods to species may make it possible to determine whether increased soil nutrients ultimately lead to a greater diversity of herbivorous insects and an even greater increase of predators on host plants. The implications of such research would influence evolutionary thought that espouses resources are the basis of the spectacular radiations of animals (eg. Price, 2002).
- (9) The resource availability hypothesis needs to be tested at a greater scale, such as across biomes. Research needs to be replicated on several continents and in both Hemispheres. Only then, will the resource availability hypothesis be finally tested and assessed.