



**The Intensity of Competitive Interactions as a  
Function of Fertility, in Mediterranean-type old  
fields in South Australia**

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"The isolated man can supply but a very small proportion of his wants; all his power lies in association, and in the intelligent combination of universal effort"

Joseph Pierre Proudhon (1863)

"Freely giving more than one expects to receive from his neighbours, is proclaimed as being the real principle of morality-a principle superior to mere equivalence, equity, or justice, and more conducive to happiness. And man is appealed to be guided in his acts, not merely by love, which is always personal, or at the best tribal, but by the perception of his oneness with each human being. In the practice of mutual aid, which we can retrace to the earliest beginnings of evolution, we thus find the positive and undoubted origin of our ethical conceptions; and we can affirm that in the ethical progress of man, mutual support-not mutual struggle-has had the leading part. In its wide extension, even at the present time, we also see the best guarantee of a still loftier evolution of our race"

Petr Kropotkin (1902).

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This thesis contains no material which has been accepted for the award of any other degree or diploma in any University and to the best of my knowledge and belief the thesis contains no material previously published or written by another person, except where due reference is made in the text. I consent to this thesis being made available for photocopying and loan if it is accepted for the award of the degree.

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## **Abstract**

I studied the establishment of tree seedlings in Mediterranean-type oldfields in South Australia, to test for a correlation between habitat fertility and the intensity of competition. I also investigate whether resource competition and invertebrate herbivory were confounded with each other, so that it was possible to evaluate the Unified Concept of Competition (UCC), with both a mechanistic, and a phenomenological definition of competition. The species of tree that I studied are dominant in the over-storey of grassy woodlands in the Adelaide Hills. This community type has been extensively cleared and is heavily infested with exotic grasses and herbs. I tested for a correlation between fertility and the relative intensity of competition. To do this I used a quantitative literature review in combination with field and glasshouse experiments. Although experimental tests of this relationship are abundant, they have produced conflicting results. Studies that use natural fertility gradients generally support the argument that the two are positively correlated, while studies that use artificial nutrient gradients generally refute this argument. Artificial gradients may differ from natural gradients because they include a lower range of fertilities, because artificial gradients are less complex than natural gradients, or simply because different species and/or phenotypes are present at different points along natural gradients, but not necessarily on artificial gradients. I used a wide range of fertility levels creating an artificial resource gradient that was multivariate in nature. I also used a range of different species. In the glasshouse experiment the relative intensity of competition (RIC) increased with fertility in a logarithmic fashion. There was also a positive relationship between fertility and RIC in the field, and in the literature

review. However, the results from the glasshouse experiment suggest that the positive relationship between fertility and RIC in the field, and in the literature review may have been related to the magnitude of the gradients, rather than the complexity of the gradients, or to the range of competitors considered. These results demonstrate that physical resource gradients can produce dynamics similar to those observed on gradients of standing crop, and that a definition of environmental adversity that is based upon the physical environment is possible.

I also performed a comparative study with two species of eucalypt, to determine why *E. camaldulensis*, and *E. microcarpa* have such markedly different populations structures within the Waite Hills Reserve. Previous experiments have shown that competition may be an important process operating in this system, and that it may limit the establishment of eucalypt seedlings. I found that a lack of *E. microcarpa* establishment in the reserve may be attributable to interference from exotic grasses. This suppression is caused by two related mechanisms. I found evidence of resource competition between *Avena barbata* and the relevant eucalypts, and also found evidence that *Avena* may modify abiotic conditions, so that germination of *E. microcarpa* occurs in highly competitive neighbourhoods. In contrast to *E. microcarpa*, *E. camaldulensis* requires high temperatures to germinate, and may therefore germinate when winter annuals (e.g. *Avena barbata*) are senescent. As a consequence it may experience less competition from exotic pasture grasses during the critical seedling establishment phase. The results from this study suggest that direct effects (e.g. resource competition), and indirect effects (e.g. invertebrate herbivory) may be heavily confounded, and that a positive correlation between fertility and the intensity of competition, is most

probable when a phenomenological definition of competition is used. I argue that a phenomenological definition of competition is reasonable because a number of direct and indirect effects are confounded at this, and other field sites, and because it may speed the development of ecological theory.



## Chapter 1

### Introductory Remarks

Competition is a process that has been observed and measured in most ecological systems. The importance of competition as a process, and as a concept, is apparent from the distinguished list of ecologists that have used competition in the development of their theories and hypotheses. Examples, among others, include Darwin (1859) with the theory of natural selection, Hairston *et al.* (1960) with the green earth hypothesis, Hutchinson (1961) with the paradox of the plankton, MacArthur & Wilson (1967) with r/&K selection, the various versions of the habitat templet presented by Grime (1977) Keddy (1989) and Southwood (1977; 1988), and the resource ratio theory developed by Tilman (1982). There have also been large numbers of empirical studies that have focused upon competition (see reviews by Connell, 1983; Goldberg & Barton, 1992; Gurevitch *et al.* 1992; Goldberg *et al.*, 1999; Wilson & Lee, 2000).

Even though competition has a central place in the historical development of ecological thinking, we still do not quite understand what controls the intensity of competition. I have, therefore, chosen to make competition the central theme in my thesis. This is an acknowledgement that the way to see further, is to stand upon the shoulders of giants; the cumulative, synthetic nature of science is obvious, and has obvious advantages. Two examples are sufficient to illustrate this point. Darwin's (1859) theory of natural selection was preceded by the work of geologists, who argued that sedimentary rocks take millions of years to form,

and Tilman's (1982) resource ratio theory was developed in response to questions posed by Hutchinson (1959; 1961). Because of the cumulative, synthetic nature of scientific progress I have chosen to use the habitat templet as one of the central themes in this thesis. This concept has inspired a large number of empirical studies (reviewed by Wilson and Lee, 2000) and is therefore a solid foundation for further experimentation. In this Chapter I outline the historical development of this concept, the criticisms that have been levelled at it, and outline how my work is intended to add to this growing body of work.

### **The Habitat Templet**

The habitat templet has been under construction for many years, and has been described as:

‘the assertion (Macleod 1894, Ramenskii 1938, MacArthur and Wilson 1967, Odum 1969, Grime 1974, Southwood 1977, Whittaker and Goodman 1979, Greenslade, 1983) that some avenues of adaptive specialisation are of universal occurrence and have resulted in the presence throughout the world of plants and animals which conform to basic functional types’ (Grime *et al.*, 1997).

The immense diversity of life on earth has arisen from a small number of progenitors, and has radiated to fill an apparently endless niche-space, which Hutchinson (1957) described as the N-dimensional hyper volume. Thirty three million special cases (the number of species on earth?) may have aesthetic appeal, but is a poor foundation for prediction. Hutchinson (1959) thus paid homage to Santa Rosalia, and posed the question: ‘Why are there so many kinds of animals?’ In a similar vein Hutchinson (1961) also questioned how such a great diversity of plankton could coexist in an unstructured habitat (the water column), the so-called ‘paradox of the plankton’. Tilman (1982, page 136) demonstrated that changing the nutrient composition of a growing medium could alter the outcome of

competition between plankton, and that niche partitioning/divergence could help explain the paradox of the plankton.

Another equally valid response to the questions posed by Hutchinson has been the development of a simplified model of the niche, an attempt to reduce the N-dimensional hyper volume to something theoretically tractable, with a reduced number of dimensions. The best and most widely cited examples are the habitat templet presented by Southwood (1977; 1988), and the C-S-R model presented by Grime (1977). Both authors argue that the niche may be adequately described with two variables. These are environmental adversity (stress), and durational stability (disturbance).

This thesis deals exclusively with a single assumption of this type of model. This assumption/argument is the unified concept of competition (UCC). Under the UCC competitive intensity increases as a function of fertility and/or habitat productivity (which is the same as saying that there is a negative relationship between environmental adversity and competitive intensity) (see Wilson & Lee, 2000). This argument/assumption has been subjected to a large number of empirical tests. However, these empirical tests support and refute this argument in roughly equal measure (reviewed by Wilson & Lee, 2000). The validity of this argument/ assumption has therefore been intensely debated.

### **The Unified Concept of Competition**

On the one hand it is argued that plants in productive habitats can achieve high relative growth rates, and as a consequence they can deplete resources quickly, and are more likely to have overlapping resource depletion zones. Thus natural

selection favours plants with high relative growth rates (RGR) and low levels of reproductive effort. This would allow the rapid development of organs used for resource acquisition, and the subsequent ability to pre-empt both above and below ground resources simultaneously (Grime, 1977). This argument is described as the unified concept of competition (UCC), because the ability to capture above- and below-ground resources is thought to be linked by positive feedback (Donald, 1958 cited in Grime *et al.*, 1997): Access to mineral nutrients results in the ability to construct photosynthetic enzymes, and these produce energy, which promotes the uptake of mineral nutrients. As a consequence fertile environments (which are relatively favourable for plant growth) are thought to sustain relatively high levels of competition.

The alternative argument is that competition occurs at all levels of fertility because plants are differentiated in their ability to compete for above and below ground resources. Plants that are good competitors for below ground resources are thought to be poor competitors for above ground resources - resources allocated to nutrient uptake (roots) cannot be simultaneously allocated to light capture (stems and leaves) (see Newman, 1973 and Tilman, 1988).

There is a wealth of anecdotal evidence consistent with both arguments, examples of plants in which the ability to compete for above and belowground resources is linked by positive feedback, and examples where there appears to be trade-offs (see Wilson & Lee, 2000 and papers therein). There is also a wealth of empirical studies that have measured the intensity of competition as a function of fertility or productivity. These studies have used both natural and artificial productivity gradients, and there are a number of published articles in support of both hypotheses (**for papers that support the UCC see:** Friedman & Orshan, 1974; Gurevitch, 1986; Wilson & Keddy, 1986; Reader & Best, 1989; Reader, 1990;

Shipley *et al.*, 1991; Kadmon, 1995; Berkowitz *et al.*, 1995; Nicotra & Rodenhouse, 1995; Bonser & Reader, 1995; Briones *et al.*, 1998; Sammul *et al.*, 2000; Keddy *et al.*, 2000. **For papers that refute the UCC see:** Welden *et al.*, 1988; Wilson & Shay, 1990; Wilson & Tilman, 1991; DiTommaso & Aarssen, 1991; Campbell & Grime, 1992; Turkington *et al.*, 1993; Wilson, 1993; Wilson & Tilman, 1993; Reader *et al.*, 1994; Wilson & Tilman, 1995; Belcher *et al.*, 1995; Gaudet & Keddy, 1995; Miller, 1996; Peltzer *et al.*, 1998; Nash-Suding & Goldberg, 1999; Cahill, 1999; Fonseca *et al.*, 2000).

### **Criticisms of C-S-R**

In addition to a large volume of empirical research that is inconsistent with the UCC, Grime's (1977) C-S-R model (which assumes UCC) has been criticised on conceptual grounds. Crawley (1986) argues that the utility of the model is limited because it is hard to define stress and disturbance. Stressful conditions for one species may be optimal for another. For example, being submersed in water constitutes a stress for terrestrial vegetation, but many aquatic plants depend upon it for support. Loehle (1988) argues that the representation of plant strategies on a triangular continuum is a distortion of reality. He emphasises that selection for one trait may not result in a unit for unit decrease in other traits. Certain characteristics provide a number of benefits (e.g. sclerophyllous leaves are inexpensive in terms of nutrients and are resistant to attack from herbivores). Another criticism of the model developed by Grime (1977) is the invalidity of the assumption that plants cannot occupy environments with high levels of both stress and disturbance. The annuals, which colonise wholly mobile sand dunes or mobile dune tops in arid environments, persist even though they are subject to high levels of both disturbance and stress (Grubb, 1985).

## Defining Competition

The sometimes-intense debate over the validity of the unified concept of competition may, in part, be attributable to the use of different definitions of competition. Both Grime (1977) and Tilman (1982; 1988) use mechanistic definitions of competition. Grime defines competition as 'the tendency of neighbouring plants to utilise the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space'. Tilman (1987a) also argues that competition is defined by its mechanisms: proof of competition requires that resources are 'explicitly considered'. A good example is the study by Burton & Bazzaz (1995), in which patches of *Solidago altissima* inhibited photosynthesis in woody seedlings, by reducing the amount of  $\text{NO}_3$  in the soil, to a level where rubisco construction was limited. However, implicit in many of the studies that support the UCC is a phenomenological definition of competition (e.g. Wilson & Keddy, 1986). When a phenomenological definition is used, competition is said to occur: 'when an increase in the density of one species leads to a decrease in the density of another, and vice-versa' (Tilman, 1987a).

With such a definition indirect effects such as apparent competition can be confounded with resource competition (Tilman, 1987a). Indirect effects are a common phenomena in ecological systems and need to be considered, thus a phenomenological definition or understanding can be useful in the development of theory, even though mechanistic understanding should be our ultimate goal (see Pickett *et al.*, 1994, page 107).

## Objectives

Even with a wealth of empirical evidence that is inconsistent with the unified concept of competition, and a number of criticisms of the conceptual validity of the C-S-R model and its assumptions (e.g. UCC), the C-S-R model may be ‘the most comprehensive and coherent theory for community ecology’ to date (Wilson & Lee, 2000). The objective of this study was to investigate some of the reasons empirical results relating to the UCC may be inconsistent. This was done using a combination of field (Chapters 5 & 6) and glasshouse experiments (Chapters 5 & 7), and a quantitative review of the literature (Chapter 3).

In the quantitative review of the literature (Chapter 3) the sole focus was upon studies of competition. I assessed how the methods used to study competition affected the results, and also looked for broad ecological patterns. I measured whether surveys and experimental studies yielded comparable estimates of competitive intensity, asked whether the range of neighbour densities affected the intensity of competition, and compared the intensity of competition in controlled environments and in the field. I also assessed whether habitat productivity and the intensity of competition are positively correlated, whether the intensity of intra- and interspecific competition were comparable, whether the intensity of competition varies as a function of taxonomic grouping, and assessed whether there is a correlation between the importance and intensity of competition<sup>1</sup>.

In Chapter 5 I assessed whether aspects of methodology can determine whether or not a positive correlation between fertility and competitive intensity are detected. I tested whether the range of fertilities used in an experiment can be a source of bias in the interpretation of the results. I also tested for a positive correlation between fertility and competitive intensity using a range of different species on an

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<sup>1</sup> The distinction between the ‘importance’ and ‘intensity’ of competition is described in detail in the methods section of Chapter 3 (pages 31 & 32).

artificial fertility gradient that was multivariate in nature. I was therefore able to test whether the complexity of a resource gradient, or the range of species used could influence the relationship between fertility and competitive intensity. I also assessed whether resource competition and invertebrate herbivory were confounded, to determine whether the data support the unified concept of competition when both phenomenological and mechanistic definitions of competition are used. In Chapter 6 I report the results from an experiment that assessed whether competition occurs in an abiotically harsh environment, and measure the level of invertebrate herbivory to determine how these two processes are related in this environment. In chapter 7 I report the results from an experiment in which I assessed the response of two species of eucalypt to resource additions. I was therefore able to test whether species from more favourable environments have a greater potential to respond to resource addition with increased growth (a more plastic growth response). I also compared how the intensity of competition varies as a function of fertility for the relevant species.

In addition to the experimental investigation of the unified concept of competition, this study includes a comparative investigation of the germination ecology of two species of eucalypt (*Eucalyptus camaldulensis* & *E. microcarpa*), that are relatively abundant in the Southern Mount Lofty Ranges (a description of the field site, and some of the dominant species is given in Chapter 2). *Eucalyptus camaldulensis* seeds are 4-5 times as heavy as *E. microcarpa* seeds and I hypothesised that these extra seed reserves may aid *E. camaldulensis* seedlings in competition with exotic pasture grasses. I also assessed the effect of variation in abiotic variables that are modified by pasture grasses (e.g. light, temperature, and water potential) upon the level germination for the two species of eucalypt.

Regrettably logistical problems (rats and/or possums broke into the shade house) prevented the use of *E. microcarpa* seedlings in the field experiment presented in



Chapter 5, and *Allocasuarina verticillata* seedlings had to be used as a substitute. This undoubtedly reduces the continuity of the thesis as a whole, but may be reasonable because both *E. microcarpa* and *A. verticillata* have similar ecological requirements: both species are generally restricted to the relatively poor soils on the hilltops, and form mixed stands at my field site.

## Chapter 2

### **The Experimental System: A Description of the Field Site and Some of the Species Found There**

#### **The Region:**

The vegetation and ecology of the Mount Lofty Ranges are profoundly influenced by the geology and climate of the region. The Mount Lofty Ranges are located in South Australia, and are flanked by lowland areas (plains) on the eastern and western sides of the range. The range was formed by the reactivation of old fault lines during the early tertiary period, and this faulting activity finished roughly 2.5 million years ago. Since then erosion/weathering has been the most significant geological process. During the last 2.5 million years the soil on exposed hilltops has eroded away leaving behind a skeletal soil that can only sustain low levels of primary production. However, in the valleys where there is more protection from the elements, and where rich alluvial soils may accumulate, higher levels of net primary production generally occur.

The level of net primary production is heavily influenced by rainfall which ranges between 1600mm/pa near the summit, to as low as 500mm/pa near the coast at Sellicks Beach. The Mount Lofty Ranges are a relatively small mountain range; mean height is only 300m above sea level, and the highest point (Mount Lofty) is only 720m above sea level. However, even with its small stature, the range has a significant impact upon the local climate. Because of its orientation, the Range traps rainfall from the low-pressure systems that circle the Antarctica, and as a

result the amount of rainfall on the Adelaide Plains (500mm/pa), and on the Mount Lofty Ranges greatly exceeds the level of rainfall in other parts of the state. If the Mount Lofty Ranges were flattened rainfall would probably be in the vicinity of 300mm/pa.

In addition to geology and climate it is essential to be aware of the impact that humans have had upon the ecology of the region. The Aboriginals used fire to flush out game, and to promote the growth of plants, used as fodder by game. The native flora therefore possesses a host of adaptations to fire. Large numbers of species are serotinous and have hard woody capsules that release seeds when exposed to fire (e.g. *Hakea rostrata*, *Banksia marginata*, *Allocasuarina verticillata* and *Eucalyptus microcarpa*). Other species produce large persistent seeds with a hard seed coat, that require fire or physical damage to promote germination (e.g. *Acacia* spp.), and a number of species can resprout after a fire from epicormic buds (e.g. *Eucalyptus* spp.). All aspects of the natural history of the region (including the geology, climate, biota, and anthropology) are discussed at greater length in Twidale *et al.* (1976).

### **The Field Site:**

Peter Waite bequeathed The Waite Hills Reserve to Adelaide University in 1914. The Waite Hills Reserve was pastoral land of exceptional quality. The original community of vegetation was a eucalyptus savannah (pers. comm. Prof. Dudley Pinnock) with 20-30m tall trees. Dominant over storey species included *Eucalyptus camaldulensis*, *E. microcarpa* and *Allocasuarina verticillata*. The under storey was dominated by native perennial bunch grasses such as - *Themeda*

*triandra* (kangaroo grass), *Austrodanthonia* sps. (wallaby grass) and *Austrostipa* sps. (spear grass). The extent of grassy woodlands in the Waite Hills Reserve, and in the rest of Southern Australia has been severely reduced because of pastoral mis-management. As an example, the aerial application of fertiliser in an effort to 'improve' pastures, has placed native grasses at a competitive disadvantage with exotic grasses, which have had a much longer association with the types of anthropogenic disturbance now common to Australian ecosystems (e.g. eutrophication). As a result invasive grasses, such as large quaking grass (*Briza maxima*), silver grass (*Vulpia myuros*), bearded oat (*Avena barbata*), canary grass (*Phalaris aquatica*), Kikuyu (*Pennisetum clandestinum*) and clovers have displaced large areas of native grass. High stocking rates have also had a negative impact upon the native flora (Wallace, 1986).

The climate in this region is Mediterranean with wet cool winters and hot dry summers. The mean annual rainfall is 690mm with 80% of the rain falling during April-October (Autumn to Spring). The average maximum temperature is 12.9°C in winter (June to August) and 26.8°C in the summer (December to February).

The Waite land was used as cattle pasture until 1930, sixteen years after the land was donated to the University of Adelaide. From 1930 to 1991, the land has been used as pasture for domesticated herbivores by researchers at the Waite Agricultural Research Institute. Consequently the Waite Hills Reserve is host to large number of exotic species (primarily pasture grasses and olives). However, because the land has not been used for commercial grazing, remnants of the natural system still persist. Since 1991 the land has been released from grazing by

domesticated animals, and a significant effort has been made to control olives (*Olea europaea*) and other weeds. The response of the native vegetation to this release from herbivory and competition has been mixed. There has been some recruitment of native grasses and herbs, and good recruitment of shrubs such as *Acacia pycnantha*. A large number of *E. camaldulensis* seedlings have established, particularly in the gullies. However, establishment of *E. microcarpa* and *A. verticillata* has been less abundant. The removal of domesticated herbivores has also been beneficial for a number of exotic species, particularly those that are preferentially consumed by herbivores (e.g. bearded oats and olives). As a result competition from exotic species may now be a significant barrier to the re-establishment of the native flora within the reserve.

#### **Species Descriptions:**

*Themeda triandra* Forsk: Kangaroo Grass is a densely tufted perennial, 30-150cm high. The inflorescence is a terminal compound panicle 10-20cm long. It is common to benign habitats throughout Australia; it is absent in the Australian Alps, and it is not found in arid areas away from watercourses. It is widely distributed throughout temperate Australia. It grows mostly in the summer reflecting its tropical affinities; it is a C4 grass and has an optimal temperature range of 25-35°Celsius (Lamp *et. al.*, 1990). Kangaroo grass is a bunch grass, thus in grasslands dominated by this species there are numerous bare patches where trees might establish.

*Eucalyptus microcarpa* (Maiden) Maiden: Greybox is a medium sized tree to 20m in height. It has a fibrous, stringy bark and has alternate leaves. Its white flowers

are borne in clusters of 3-7. Each cluster is borne on a common stalk 5-10mm long and these clusters form a terminal panicle. Buds are 6-7mm long, the cap is conical, and as long or longer than the base (Cunningham *et al.*, 1992).

*Eucalyptus microcarpa* was once common in the foothills of the Mount Lofty Ranges. However, as this land was prime pastoral country and is now urbanised, very few *E. microcarpa* woodlands remain. In the Waite Hills Reserve and the Belair National Park, *E. microcarpa* forms open woodlands with an understorey dominated by exotic pasture species and native perennial grasses such kangaroo grass. The seeds are retained on the parent plant in hard woody capsules that are released *en masse* when the parent plant dies. This may be an adaptation to fire and/or a form of masting behaviour to satiate seed predators (ants).

*Eucalyptus camaldulensis* Dehnh: River-redgum is a medium to large tree, 25-40m high. It has rough, persistent bark at its base. The rest of its bark is smooth and deciduous, forming a mosaic of dull white and light grey. The leaves are alternate and lanceolate. The flowers are cream and are borne in clusters of 5-10. The buds are 6-10mm long, 4-5mm wide; the cap is beaked and is 1.5-2.5 times longer than the base (Cunningham *et al.*, 1992). River red gums are one of the few Eucalypts that release their seeds, usually about one year after flowering (Bonney, 1994). The river red gum has a wide distribution and as the common name suggests, it is common on floodplains and along watercourses. In the Mount Lofty Ranges and foothills it is common along creek lines and in valleys.

*Acacia pycnantha* Benth: Golden Wattle is a large shrub to 5m in height (in the Mount Lofty Ranges it may have a thin stemmed habit and grow in thickets after fires). The bark is rough and dark brown with a high concentration of tannin. The

'leaves' are actually phyllodes (petioles that perform the function of leaves). They are lanceolate-falcate to broadly oblanceolate and are variable in their length and width. The flowers are bright yellow and extremely small, and are grouped in dense globular heads 6mm in diameter. Each globular head has 60-80 flowers (Cunningham *et al.*, 1992). Golden Wattles produce relatively large, persistent seeds with a hard seed coat that requires fire or physical damage for germination. They form a mutualistic relationship with nitrogen fixing bacteria (*Rhizobium* spp.), and with ants. *Acacia pycnantha* secretes nectar through glands called extra-floral nectaries. As a result ants are commonly observed foraging in their foliage, and this may offer some protection from herbivorous insects (Wallace, 1986).

*Allocasuarina verticillata*: Drooping sheoak is a tree 5-7m high with dark-green drooping ribbed branchlets. The plants are dioecious, the male spikes are 4-10cm long, the anthers are yellow and 3mm long. Female plants bear cones that are globular to ovoid, 2.5-5cm long and 2-3cm wide, the valves of the cone are prominent, acute, and pubescent (hairy) inside (Black, 1963). In the Waite Hills Reserve it occurs on shallow, rocky soils. Seeds of this species show no dormancy, and are retained on the parent plant in hard woody cones, that are released *en masse* when the parent plant dies. Again, this may be an adaptation to fire and/or a strategy to satiate seed predators (ants).

*Avena barbata* (Pott ex Link): Bearded Oat is a tufted annual to 1.7m high, with soft-erect, hollow stems. Stems and leaves are hairless; the flower head is one-sided, and the spikelets have 2-3 flowers with outer husks 2-2.5cm long. The florets are clothed with pale hairs with two bristles at the tip and bear a long

slender bent awn, which is twice as long as the floret (Cunningham *et al.*, 1992). The bearded oat is a winter annual and grows in areas with high winter rainfall, and responds well to fertilisation. This species is exotic and may have originated in the Mediterranean (Wallace, 1986) or in Central Asia (Lamp *et al.*, 1990). The pale hairs, which cover the florets, assist them in passing through animals undigested and protect them in the soil. They may therefore accumulate in the seed bank. Control of this weed is therefore problematic.

*Pennisetum clandestinum* Hochst ex Chiov: Kikuyu grass is a perennial that spreads by stolons and rhizomes. It grows as high as 50cm, and the rhizomes are clothed in bracts. The leaf blades have finely serrated margins and are bright green to yellowish green. The leaf sheath is softly hairy, and hairier than the leaf blade. The inflorescence is a small spike with 2-4 spikelets. The spike is enclosed in the uppermost leaf-sheath so that only the anthers and style are visible in the field. Anthers are exerted on long slender filaments. The style is 2-fid and is usually finished by the time the anthers are exerted. Kikuyu originated in the highlands of central East Africa. It has been introduced to the Americas, Australia, South Africa, New Zealand and South East Asia for use as a pasture plant and is often used on playing fields because it is resistant to trampling (Lamp *et al.*, 1990). Kikuyu is a C4 grass and is dormant in the winter (Cunningham *et al.*, 1992). Unlike kangaroo grass Kikuyu spreads by rhizomes and therefore pre-empt all the available space, providing little scope for the establishment of tree seedlings. There are a number of other exotic species that have infested the Waite Hills Reserve, such as clovers; however, the bearded oat and Kikuyu are the dominant weeds in the oldfields that are the focus of this study.



## Chapter 3

### A Quantitative Review of Experiments That Measured Competition

#### Introduction

Competition has probably been studied more than any other process by ecologists. There have been large numbers of empirical studies (see reviews by Connell, 1983; Schoener, 1983; Goldberg and Barton, 1992; Gurevitch *et al.*, 1992; Underwood, 1996), and numerous theoretical treatments of the subject (Hutchinson, 1959; Slobodkin *et al.*, 1967; Grime, 1977; Huston, 1979; Tilman, 1982; Goldberg and Werner, 1983; Southwood, 1988; Keddy, 1989; Grace, 1991 and 1995). Although processes other than competition undoubtedly affect evolution (Janzen, 1966; Bertness and Callway, 1994), few ecologists would argue that competition is not a potent force of natural selection and community structure. Given the large amount of research into this process, it may be our best opportunity to develop generalizations. However, we still debate several issues....

#### *Methodology Questions*

There is a great diversity of methods used to study nature, and studies of competition are no exception. Some researchers use descriptive approaches (e.g. surveys), whilst others use manipulative experiments. Experiments can be conducted in controlled environments or in the field. To make sense of these varied sources of information, comparisons of the effectiveness of the different approaches is required. Literature reviews have been valuable for highlighting deficiencies in approach, and demonstrating that experimental design may bias the outcome of a study. For example, literature reviews have highlighted the propensity for caged animals to compete more intensely than their free roaming

companions (Gurevitch *et al.*, 1992), and have emphasized the need for proper replication (Underwood, 1986; Gurevitch *et al.*, 1992, see also Clements, 1916 and Fisher, 1951).

Our understanding of the role of competition in ecological systems will be improved by identifying factors that may bias an estimate of competitive intensity. To this end I have compared the intensity of competition in controlled environments and in natural habitats. I included studies that were based upon observation (e.g. surveys) and compare the intensity of competition in those studies, with the intensity of competition in studies that used experimental approaches. Connell (1983) advocated the use of biologically realistic densities of competitors and/or to measure the temporal and spatial variability in neighbour population density so that experiments could be placed in an ecological context. The point seems to have been well taken as a large number of researchers (see Appendix 3.1) conducted pilot studies to determine neighbour densities, before conducting their experiments. I compare studies that did, and did not report the results from a pilot study, to determine the natural range of neighbour densities, and ask whether the presence of such a pilot study affected the conclusions reached by the researchers.

With regard to questions of methodology I tested the following null hypotheses: (A) The measured strength of competition is the same in controlled environments and the field, (B) The measured strength of competition is comparable in surveys and experiments, and (C) The measured strength of competition is comparable in experiments with, and without pilot studies to determine neighbour densities.

### ***Ecological Questions***

In addition to helping to define the appropriate experimental approaches to study competition, quantitative literature reviews are an excellent tool for finding general patterns in nature. Because the data collected for a review are drawn from a broad range of habitats and include a broad range of taxa, they enable us to look at the big picture in a way that a single experimental manipulation cannot. For example, modifying resource availability at a single site to test the relationship between productivity and competitive intensity, introduces an artefact by increasing levels of resources above those native to the system (e.g. the resource level that the species at the site usually experience). Reviewing results from several competition experiments conducted at areas with different levels of resources enables comparison of competitive intensities, at different levels of resource availability, with the advantage that the relevant species are adapted to the conditions.

### ***Are Habitat Productivity and the Intensity of Competition Positively Correlated?***

This question has been the subject for a large number of empirical studies, and has been addressed in previous literature reviews. Goldberg and Barton (1992) reviewed articles that specifically address this question. They found that, in studies where a natural resource gradient was used, the data supported the unified concept of competitive ability (UCC), as advocated by Grime (1977), Southwood (1977; 1988) and Keddy (1989, page 146). However, Goldberg & Barton (1992) also found that, where an artificial resource gradient was used, the results supported the rejection of the UCC by Newman (1973), Grubb (1985) and Tilman (1987b). Gurevitch *et al.* (1992) also used a literature review to test for a

correlation between RIC and productivity. They used a system of classification with two levels of productivity. Prairies, meadows and old fields were defined as productive environments, and arctic meadows and deserts were defined as unproductive environments. They found that competition was equally intense in both categories. The results from both of these literature reviews have highlighted some important considerations in this debate. For example, why should the results from natural and artificial resource gradients support alternative arguments? Belcher *et al.* (1995) argue that a logarithmic relationship between fertility and RIC may exist. The lack of correlation between RIC and fertility on artificial gradients may therefore reflect the fact that a limit (the flat portion of the log curve) has been approached or used in studies with artificial gradients. In an effort to account for this complicating factor, I have devised a relative index of productivity, so that there is an objective, numerical basis for determining the level of productivity, in any given system (study).

### ***Is the Relative Intensity of Intra and Inter-specific Competition Comparable?***

Explaining how so many species can coexist when they all require similar resources or why competitive exclusion does not occur, is another ecological question that has a long history of investigation (Hutchinson, 1959). Intense intraspecific competition, relative to interspecific competition (niche partitioning) has been suggested as a mechanism, which may promote coexistence of marine gastropods (Underwood, 1978; Creese and Underwood, 1982). Connell (1983) measured the outcome of studies that used a similar experimental design to that of Creese and Underwood (1982). In this design both the total density (both neighbour and target species), and the ratio of competitors is varied (see

Underwood, 1986 for a discussion of this experimental design). Consistent with Creese and Underwood (1980), Connell (1983) found that in 75% of the studies he considered, the intensity of intraspecific competition outweighed the intensity of interspecific competition.

Goldberg and Barton (1992) also addressed this question, although they restricted their review to plants. They found that intraspecific competition was more intense than interspecific competition in only one of four cases. They suggest that niche partitioning may be of less importance in promoting the coexistence of plants. They argue that environmental variability (Chesson and Werner, 1981; Chesson and Huntly, 1997), and equivalence among competing plants (Goldberg and Werner, 1983) also help to maintain diversity within plant communities. In agreement with Goldberg and Barton (1992), a meta-analysis of the ecological literature by Gurevitch *et al.* (1992), suggests that intra and interspecific competition are of equal intensity for primary producers and carnivores. And in agreement with Connell (1983), Gurevitch *et al.* (1992) report that intraspecific competition was more intense than interspecific competition among herbivores. I also measured the intensity of intra and interspecific competition for studies in which both types of competition were measured simultaneously.

#### ***Are the Importance and the Intensity of Competition correlated?***

Weldon and Slauson (1986) argue that the intensity and the importance of competition are not necessarily related to each other; although they do concede the possibility that the two may be related (Weldon and Slauson, 1986). The first observation they use to support this argument is that historically important competition may be of low intensity at any given moment in time, because

competition has already caused niche divergence (the ghost of competition past). Hence historically important competition could be of low intensity. Secondly, they suggest that the importance of competition can only be judged relative to other processes (e.g. predation, abiotic stress, disturbance etc.), whereas the intensity of competition is not necessarily related to these factors. I test the equivalence of competitive intensity and importance.

***Is the Intensity of Competition for Plants, Insects and Unrelated Taxa Equivalent?***

This was not a question that I had intended to address at the outset of this review. However, the information was easy to extract from the Appendix, and was interesting because it highlighted an important limitation of data generated by quantitative analysis of the literature (see discussion). I therefore compare the intensity of competition for these three taxonomic groups. Sample sizes were too small to compare the relative strength of interspecific competition for other taxonomic groups (e.g. birds, mammals, reptiles and amphibians).

With regard to ecological questions, the specific null hypotheses that I test are:

(A) There is no correlation between RIC and productivity, (B) intra and interspecific competition is of equal intensity, (C) the importance and intensity of competition are equivalent, and (D) the intensity of competition between plants, between insects and between unrelated taxa is equivalent.

## Methods

### *General Considerations*

Because of the great diversity of methods used in ecology, a quantitative review of competition is not a straightforward matter. A possible solution to this impasse is to consider a broad range of journals, and use papers with comparable methodology (see reviews by Connell, 1983; Goldberg and Barton, 1992; Gurevitch *et al.*, 1992). I used a more restricted set of papers, and aimed to develop a method for including studies with a diversity of methods. I assume that this sample accurately reflects the character of the literature because it is a snapshot of the literature, rather than a collection of articles with methodology that I consider appropriate. Researchers working in different systems, with different organisms will inevitably face different practical/methodological and logistical problems, and will tailor their experiments to deal with these. The articles that I used in this review were published in *Oecologia* and *Ecology* between 1990 and 1997 (Appendix 3.1). To determine whether or not the intensity of interspecific competition for plants was positively correlated with habitat productivity, it was necessary to expand the literature search to a broader range of journals (see below).

Because the 'modification of the microenvironment by removal of vegetation is an aspect of interference, hard to separate from resource uptake' (McLellan and Fitter, 1997), I have used a phenomenological definition of competition. That is a: 'decrease in the fitness of a plant (*or animal*)...due to the presence of another plant (*or animal*), without any necessity that the decrease in fitness be due to differential consumption of a limiting resource' (Shipley *et al.*, 1991, *italics are mine*). It has been convincingly argued that resource competition can be

confounded with indirect effects (see Connell, 1990; Reader, 1992; Burger and Louda, 1994 and Leonard, 2000). Tilman (1990) correctly argues the only way to be certain that resource competition is occurring is to measure resources (e.g. the studies by Fonteyn and Mahall, 1981; Naeem, 1990; Tyler and D'Antonio, 1995; Burton and Bazzaz, 1995). However indirect effects (Slobodkin *et al.*, 1967), and interaction modifications (Morin *et al.*, 1988; Wootton, 1994; Facelli, 1994) may be a common property of ecological systems. I thus agree with Leonard (2000) who argues that a synthetic approach is required. While mechanistic understanding should be our objective, it should also be recognised that both direct and indirect effects may operate in the field, and that phenomenological understanding can promote the development of ecological theory (Pickett *et al.*, 1994). Perhaps the word competition should be replaced with 'interference', 'inhibition' or 'associational susceptibility' in this context. However, the proliferation of terminology is not always desirable, and I have retained the term competition. This may be reasonable because (a) Many researchers use a phenomenological definition in their studies of competition (e.g. Wilson & Keddy, 1986), and (b) I have stated explicitly that I am using a phenomenological definition.

For each paper in this review I recorded whether or not the experiment was conducted in the field, the type of experimental design used, and whether pilot studies were conducted to determine naturally occurring levels of neighbours. I recorded the taxa studied, whether intra or interspecific competition was measured and the 'importance' or relative intensity (RIC) of the two types of competition. How importance and intensity were calculated is described below under the



heading: 'Are the Importance and the Intensity of Competition correlated?' It should also be noted that importance and intensity of competition were equivalent (see Results section). I therefore made no distinction between these two measures in any of the analyses, with the exception of the analysis that specifically addressed this question. For studies that measured the response of more than one organism to competition, or measured competition at a number of sites I used the average value so that each paper was of equal weight.

### *Methodology Questions*

**Experimental Conditions:** For the analysis of the intensity of competition in the field and in artificial environments I restricted the analysis to a subset of the data that included only plants. The reason for restricting the data set to this subset was that the intensity of competition varied significantly as a function of taxa; interspecific competition was generally more intense for plants, than it was for insects (Figure 3.5, see below), and plants provided the largest sample size (n=18).

**Methods:** I also investigated whether the intensity of competition varied as a function of the methods used to detect it. The methods I compared were density manipulations, removal experiments and surveys. Removal experiments are strictly speaking a subset of the experiments described as density manipulations. However, density manipulations (as defined in this review) differ from removal experiments because wider ranges of neighbour densities were generally used (e.g. 0x, 1x, 2x, 3x & 4x) than in removal experiments (0x & 1x). Furthermore, with density manipulations neighbour densities were determined by the researcher, as opposed to removal experiments where neighbour densities were dictated by natural

conditions. To address this question I again used a subset of the complete data set. I used insects because they provided the largest sample size ( $n=20$ ). Neither of the data sets was normally distributed and both were highly skewed. I therefore chose non-parametric statistics (the Wilcoxon test) to analyse the data. Non-parametric statistics were used because they are conservative. I used non-parametric pairwise comparisons (the default option in the statistical program 'Jump') for the post-hoc tests.

***Neighbour Densities:*** I also compared the intensity of competition in studies where neighbour densities were determined with a pilot study, and in studies that used arbitrary densities of neighbours. This data was analysed with the Wilcoxon test.

### ***Ecological Questions***

#### ***Are Habitat Productivity & the Intensity of Competition Positively Correlated?***

The unified concept of competitive ability has also been proposed for invertebrates (Southwood, 1977; 1988), but I only considered plants, and only included articles when time series data or relative growth rates (RGR) were presented. When time series data were presented, it was possible to calculate RGR, and therefore to test Grime's (1977) model - a high RGR being one of the factors that defines a competitive species.

Because direct measures of productivity were seldom provided, I had to estimate the productivity of the systems that were studied. I assumed that plants were able to grow faster in more productive (fertile) environments. The relative growth rates

of the relevant plants in the treatments without competition were used as a measure of productivity. Because different researchers measure different variables for their analyses, and conduct their experiments with organisms at varied levels of development, a meaningful comparison requires that data be relative (see Grace, 1995; Miller, 1996; McLellan and Fitter, 1997). To make the data relative I assumed that the value of the dependant variable at the conclusion of the experiment represented 1 unit. The difference between the dependant variable at the start, and at the conclusion of the experiment was expressed as a proportion, and divided by the time (number of days) taken to conduct the experiment. The growth rate was plotted on the x-axis, and RIC was expressed as a function of growth rate. I analysed the data with linear regression.

Restricting the literature search to articles published in *Ecology* and *Oecologia* between 1990 and 1997 yielded only two articles with the data I required (Steinger and Muller-Scharer, 1992; Shabel and Peart, 1994). The limiting factor in the compilation of this dataset was the scarcity of papers with repeated measures over time, or a measure of the dependant variable at the commencement of the experiment. I therefore expanded the literature search to address this particular question. I checked in *Ecology*, *Oikos*, *Oecologia* and the *Journal of Ecology* (1980 to 2000) for articles with the information that I needed. I found a further eight articles in which the dependant variable was measured at the start of the experiment. The papers from this extended literature search were written by: Lorimer *et al.* (1994), Coombes and Grubb (1998), Frost and Rydin (1997), Cottam *et al.* (1986), McConnaughay and Bazzaz (1987), Ehleringer (1984), Whigham (1984) and Gurevitch (1986).

### ***Is the Relative Intensity of Intra and Interspecific Competition Comparable?***

To test whether intraspecific competition was more or less intense than interspecific competition I again used a subset of the data. In this instance I only included studies if they measured both types of competition simultaneously (n=15). For this data set I simply counted the number of studies in which the strength of intraspecific competition was greater than interspecific competition, the number of studies in which the inverse was true, and the number of studies in which the intensity of the two types of competition was equal. For this subset of data I have included all species, but drew a distinction between studies with animals, and studies with plants - brown algae (Reed, 1990) are included in the plant category.

### ***Are the Importance and the Intensity of Competition correlated?***

Very few researchers explicitly state the importance or relative intensity of competition (RIC), so I estimated RIC and importance with one of three methods. When data were analysed with analysis of variance (ANOVA), the value of the sum of squares (SS) for a given factor, such as density, expressed as a percentage of the total sums of squares, is a measure of the 'importance' of that factor (Weldon and Slauson, 1986; Morin *et al.*, 1988; Sammul *et al.*, 2000). When the necessary information was published I used this method for calculating the importance of competition. With studies that used linear regression in the analyses, I used the  $r^2$  value to estimate of the importance of competition (after

Weldon and Slauson, 1986). In instances where no statistical information was given I calculated the relative intensity of competition (RIC). That is:

$$\frac{NC - C}{NC},$$

where NC is the value of the dependent variable (e.g. biomass) in the treatment without competition, and C is the value of the dependent variable in the treatment with competition (see Wilson and Tilman, 1991).

Because the intensity of competition varied as a function of the methods used to detect it, the types of organism used, and the type of competition studied (intra vs. interspecific competition), it was necessary to use a subset of the complete data set. I compared the importance of competition with the intensity of competition, in studies of intraspecific competition, conducted in the field, using invertebrates because this subset of data provided the largest sample size (n=13). The data were analysed using the non-parametric Wilcoxon test.

The methods used to determine RIC and importance are not without limitations. Calculating RIC only makes use of mean values and therefore ignores variation within studies. Meta-analysis may have been an improvement because variability within studies is considered in this type of analysis (see the special issue in *Ecology*, 1999, volume 80(4)). The potential for using quantitative analysis of the literature to discern general patterns in nature is discussed at greater length in the discussion. A further limitation is that when using sums of squares to calculate importance, larger experiments generally produce larger values for (Underwood,

1992). Furthermore, although I made the data on the y-axis relative (the intensity of competition), it could be argued that doing the same for the data on the x-axis (the density of neighbours), would have improved the study. A competition experiment with neighbour densities set at four times their average field density, clearly differs from a removal experiment. However, many of the papers that I reviewed did not report neighbour densities. It was therefore impossible to express the effect of competition as a function of the relative density of neighbours. The method I have used is similar to the vote count used by Connell (1983). The basic difference between Connell's (1983) approach and my own, is that Connell (1983) used binary data to measure the importance of competition (based upon statistical significance), whereas I have weighted each vote by measuring RIC or importance in each study.

### ***Is the Intensity of Interspecific Competition for Plants, Insects and Unrelated Taxa Equivalent?***

I measured the intensity of competition between plants, competition between insects, and competition between unrelated taxa (e.g. water striders and fish). Other taxonomic groups (e.g. mammals) were excluded because of small sample sizes. The data was analysed with a non-parametric Wilcoxon test, and a nonparametric pairwise comparison (the default option in Jump).

## **Results**

### ***Methodology Questions***

Competition (RIC) was less intense in the field than it was in controlled environments (Wilcoxon,  $p < 0.004$ , Figure 3.1). There was no significant

difference in the intensity of competition between insects when it was measured with density manipulations, removal experiments and surveys (Wilcoxon,  $p < 0.12$ , Figure 3.2). Competition was more intense in studies with arbitrary densities of neighbours than it was in studies where pilot studies were performed to determine a biologically realistic range of neighbour densities (Wilcoxon,  $p < 0.005$ , Figure 3.3).

### ***Ecological Questions***

There was a strong positive relationship between RIC and productivity (Figure 3.4,  $r^2 = 0.87$ ,  $P < 0.0002$ ). I found a total of fifteen studies that measured the intensity of intra and interspecific competition simultaneously. In nine, or 60% of those studies, intraspecific competition was more intense than interspecific competition. In three studies they were of equal intensity, and in three cases the intensity of interspecific competition outweighed the intensity of intraspecific competition. In studies with animals intraspecific competition was more intense than interspecific competition in 8 of 10 studies. In studies with plants intraspecific competition was more intense than interspecific competition in 2 of 5 studies, in 2 cases there was evidence of competitive equivalence, and in the fifth study interspecific competition was relatively intense (see Appendix 3.1). There was no significant difference between the importance and the relative intensity of competition in studies of intraspecific competition for invertebrates conducted in the field (Wilcoxon test,  $P < 0.7694$ ). Interspecific competition between plants was more intense than interspecific competition between insects ( $P < 0.015$ , Figure 3.5), and interspecific competition among distantly related taxa was particularly intense ( $P < 0.015$ , Figure 3.5).

## Discussion

### *Methodology Questions*

**Experimental Conditions:** Studying how different factors interact, or studying the relative importance of alternative mechanisms, is efficient in a setting where confounding factors such as indirect effects can be controlled. However, nonlinearities are an inherent property of biological systems (May, 1999), and if the intensity of a process is significantly inflated, there is no guarantee that results generated in such a setting will have relevance to natural conditions. Plants grown in glasshouses can generally achieve higher levels of productivity than plants grown in the field, and this may have resulted in more intense competition (Figure 3.1) in controlled environments. However, the intensity of competition may also have been greater because other processes (e.g. herbivory) may have been largely eliminated, thereby artificially inflating the importance of competition. Because competition is generally more intense when measured in controlled environments, I conclude that experiments conducted under controlled conditions need to be planned carefully and interpreted with caution.

**Methods:** At the outset of this review I was distrustful of the results obtained from surveys because of the possibility of confounding the effects of competition with other processes (Watkinson, 1997; Shipley and Peters, 1990 cited in Shipley, 2000). The results suggest that my suspicions were unfounded. Given that surveys and experiments result in similar estimates of competitive intensity, observational studies may be a reasonable method for gathering basic information about competition in nature. In some cases surveys could be preferable because artefacts introduced by experimental design (e.g. cages) cannot affect a survey (see



Underwood and Denley, 1984; Connell, 1983 and Gurevitch *et al.*, 1992 for discussions on cages). I do not wish to convey the idea that I favour observational studies over experiments; causality cannot be demonstrated without an experimental approach. However surveys may be a valuable and complementary source of information about nature.

*Neighbour Densities:* Since Connell's (1983) review a large number of researchers have conducted pilot studies to determine biologically meaningful neighbour densities for their experiments. My results suggest that such studies often provide a lower estimate of the intensity of competition in nature. However, with the exception of Feminella and Resh (1990) few researchers have gone a step further and placed their experiment in an ecological context (see Connell, 1983). Feminella and Resh (1990) performed a density manipulation of a caddisfly population and found significant density effects. In addition to the density manipulation they present survey data, and demonstrate that densities reach levels where competition occurs only 10% of the time (see also Andrewartha & Birch, 1960). A single study is hardly statistical evidence but it highlights the complementary nature of descriptive and experimental data. It reinforces the idea that surveys have been a neglected source of information. If we wish to obtain more reliable understanding of the role of competition in nature we need to repeat experiments in different times and/or places, perform experiments that manipulate a large number of ecological processes simultaneously (Underwood, 1992), or like Feminella and Resh (1990), place our experiments in their ecological context.

## *Ecological Questions*

### *Are Habitat Productivity & the Intensity of Competition Positively Correlated?*

The unified concept of competition, and Grime's C-S-R model in particular has been widely criticised (reviewed by Wilson & Lee, 2000). There have also been a large number of empirical studies that suggest that there is no correlation between fertility and intensity of competition (see Wilson & Lee, 2000). Regrettably there are more papers relevant to the unified concept of competitive ability, than could be considered or listed in a brief review. However, the core of this controversy can be found in Grime (1977), Wilson and Keddy (1986), Tilman (1987a & b), Wilson and Tilman (1995), Belcher *et al.*, (1995), Peltzer *et al.*, (1998), Wilson and Lee (2000) and Sammul *et al.* (2000). Even though a significant amount of the literature on this subject does not support the unified concept of competition, it should be noted that one of the hallmarks of a good theory is that it stimulates empirical research (MacArthur and Wilson, 1967). My data support the suggestion by Grime (1977), Southwood (1977 and 1988) and Keddy (1989, page 146), that as productivity increases so does the intensity of competition. However, this does not invalidate many of the criticisms of the UCC. I used a phenomenological definition of competition and cannot conclude that the intensity of resource competition (strictly defined) increases with productivity. It is, however, possible to conclude that the multitude of processes that can be defined as inhibition (e.g. resource competition, invertebrate herbivory, predation, parasitism) are generally more intense in more productive environments.

### ***Is the Relative Intensity of Intra and Interspecific Competition Comparable?***

My results relating to the relative intensity of intra and interspecific competition are consistent with previously published results (see Connell, 1983; Goldberg and Barton, 1992). In studies with animals intraspecific competition was generally more intense than interspecific competition. This supports the idea that niche partitioning is an important factor promoting species coexistence within animal communities (Underwood, 1978; Creese and Underwood, 1982; Connell, 1983; but see Chesson & Huntly, 1997). However, it should be noted that this means of coexistence appears to be of more importance for animals than plants.

In studies with plants no such general consensus emerged. There were five studies that measured the relative strengths of intra- and interspecific competition in plants. Only two of these studies found that intraspecific competition to be stronger than interspecific competition. One study found the inverse, and the other two studies found evidence of competitive equivalence (*sensu* Goldberg and Werner, 1983). The effect of a variable environment in promoting coexistence among plants is also well established (Grubb, 1977; Huston, 1979; Chesson & Warner, 1981; Chesson & Huntly, 1997). The reduced importance of intraspecific competition in plants may reflect a more limited potential for niche diversification in plants, or may simply reflect the small sample size (n=5).

### ***Are the Importance and the Intensity of Competition correlated?***

The argument that importance of competition, and its intensity are not necessarily related to each other has been made repeatedly (see Menge, 1978a,b cited by Underwood, 1992), and is irrelevant because 'intensity' and 'importance' were of

a similar magnitude in the studies used in this review (see Appendix 3.1). Whilst it is undoubtedly true that ‘the ghost of competition past’ does in fact exist, it may also (simultaneously) be true that competition is an important force of natural selection and community structure, in both a historical context, and in the present time. Furthermore, when experiments are conducted in the field and processes other than competition (e.g. predation, inclement weather) are of more importance than competition, then this will be apparent when both intensity and importance are calculated. I find it hard to imagine a situation in which competition or density could explain a large amount of variation in an ecological data set, and in which the relative intensity of competition could assume a relatively low value.

***Is the Intensity of Competition for Plants, Insects and Unrelated Taxa Equivalent?***

A closely related result to the data discussed in the section on the relative strengths of intra- and interspecific competition was the finding that interspecific competition between plants, was generally more intense than interspecific between insects (Figure 3.5). This may reflect the limited potential that plants have for niche partitioning relative to animals, and/or the fact that insects are a more diverse trophic group in which natural selection is caused by a larger number of variables.

The relatively intense competition between the distantly related taxa documented in this study (Figure 3.5), highlights a very serious limitation of literature reviews. I am not convinced that all unrelated taxa compete as intensely as the examples cited in this study. It is more likely studies of competition only proceed when the

researcher has the impression that competition is occurring. As a result, the literature on competition is probably a biased sample of nature, and quantitative analysis of the literature has major limitations. Although quantitative analysis of the literature is a poor substitute for large-scale experimentation with orthogonal design (e.g. Reader *et al.*, 1994), it does at least give a broad overview of the character and direction of ecological research. Furthermore, because of its comparative nature it is an excellent tool for determining which methods are most appropriate for studying nature.

### Chapter 3: A Quantitative Review of Experiments that measured Competition

#### APPENDIX 3.1: Papers used in the literature review

<i>Oecologia</i>									
Study #	Authors	Substrate	Method of calculation	Survey?	Treatments, observations, experimental design	Taxa	Type	RIC	RIC-average
1	Poiani et. al. (1990)	field	ANOVA	NA	survey -7 years and different sites	birds	inter	0.57	0.57
2	Dickman (1991)	field	RIC	NA	removal experiment	mammals	inter	0.25	0.305
							inter	0.36	
4	Bronmark et. al. (1991)	field	R	no	density manipulation (Underwood design) and response curve experiment.	amphibians/ molluscs	intra	0.93	0.93
							inter	0.49	0.49
5	Bradshaw & Holzapfel (1992)	field	RIC	yes	density manipulation of two species (mono-cultures and both monocultures together)	insects	inter	0	0
		field		yes	density manipulation of two species (mono-cultures and both monocultures together)	insects	inter	0	
		field		yes	density manipulation of two species (mono-cultures and both monocultures together)	insects	inter	0	
6	Morris (1992)	field	ANOVA	NA	removal experiment (competitors, predators and water for the host plant present or absent).	insects	inter	0.03	0.015
		field		NA	removal experiment (competitors removed or increased in abundance, predators and water for the host plant present or absent).	insects	inter	0	
7	Wise & Wagner (1992)	field	ANOVA	Yes	density manipulation(0x, .25x, 1x, and 4x natural densities).	spiders	intra	0.1	0.1
8	Steinger & Muller-Scharer (1992)	artificial	RIC	no	competition, root herbivory and nitrogen shortage present or absent.	plants	inter	0.67	0.67
9	Gotelli & Spivey (1992)	field	R	NA	survey (regression of density and distance to resource).	barnacles	intra	0.56	0.56
10	Krebs et. al. (1992)	artificial	RIC	no	density manipulation (3 resource types, Underwood design).	insects	intra	0.8	0.735
							inter	0.78	0.54
							intra	0.67	
							inter	0.3	
11	Englund et. al. (1992)	field	RIC	NA	removal experiment	fish/insects	inter	0.75	0.75
12	Young et. al. (1993)	artificial	RIC	no	density manipulation(hybrid of replacement series and response curve experiment.	leeches	inter	0	0
								0	
13	Griffiths (1993)	field	RIC	NA	survey(measured spatial distribution)	insects	intra	0.35	0.35
14	Mesleard et. al. (1993)	artificial	RIC	no	density manipulation(hybrid of replacement series and response curve experiment with two levels of salinity).	plants	intra	0.96	0.935
							inter	0.81	0.84
							intra	0.91	
							inter	0.87	

15	Nilsson (1994)	artificial	ANOVA	NA	removal experiment, root competition present or absent. Allelopathy also present/absent.	plants	inter	0.58	0.54
		field		NA	removal experiment, root competition present or absent. Allelopathy also present/absent.	plants	inter	0.5	
16	Shabel & Peart (1994)	field	RIC	NA	removal experiment (with herbivores present/absent) at sites with different levels of disturbance.	plants	inter	0.59	0.59
17	Burger & Louda (1994)	field	RIC	NA	removal experiment	plants	inter	0.5	0.5
18	Resetarits (1995)	artificial	ANOVA	no	density manipulation (Underwood design)	fish	intra	0.11	0.11
							inter	0.18	0.205
							inter	0.23	
19	Hougen-Eitzman & Karben (1995)	field	RIC	no	density manipulation (competitors added or not at different times in the season, also presence/absence of a predator).	insects	inter	0.37	0.37
20	Robertson (1995)	field	RIC	NA	removal experiment	fish	inter	0.15	0.15
21	Skelly (1995)	field	RIC	yes	density manipulation (response curve experiment).	amphibians	intra	0.42	0.42
							inter	0	0
22	Forrester (1995)	field	R	NA	removal experiment and observational data, also monitored resources.	fish	intra	0.5	0.5
23	Human & Gorden (1996)	field	RIC	no	observation and density manipulation (present/absence).	insects	inter	0.51	0.47
							inter	0.53	
							inter	0.37	
24	Holmer & Stenlid (1996)	artificial	RIC	no	density manipulation with six species present or absent.	fungi	inter	1	0.642
							inter	1	
							inter	0.68	
							inter	0.4	
							inter	0.13	
25	Fox et. al. (1996)	artificial	R	no	density manipulation	insects	inter	0.37	0.285
		artificial		no	density manipulation	insects	inter	0.2	
26	Debouzie et. al. (1996)	field	RIC	NA	removal experiment	insects	intra	0.02	0.08
							intra	0.14	
29	Retuerto et. al. (1996)	artificial	RIC	no	density manipulation (three density treatments), two wind speed treatments and two levels of CO2.	plant	intra	0.86	0.86
30	Harris (1996)	field	ANOVA	NA	observation	lichens	inter	0.14	0.14

<i>Ecology</i>									
study #	authors	substrate	Method of calculation	survey?	treatments, observations, experimental design	taxa	type	RIC	RIC-average
1	Reed (1990)	field	ANOVA	no	density manipulation (Underwood design)	algae	intra	0.45	0.415
							inter	0.13	0.125
							intra	0.38	
							inter	0.12	
2	Mitchell et. al. (1990)	field	RIC	no	density manipulation (Underwood design)	mammals	intra	0.07	0.25
							inter	0.07	0.05
							intra	0.43	
							inter	0.03	
3	Moran & Whitham (1990)	field	RIC	NA	removal (exclusion) experiment and survey	insects	inter	0.22	0.235
							inter	0.25	
4	Rice (1990)	artificial	ANOVA	no	density manipulation (three density treatments).	plants	intra	0.72	0.72
5	Settle & Wilson (1990)	field	RIC	no	density manipulation (Underwood design).	insects	intra	0.52	0.43
							inter	0.67	0.715
							intra	0.34	
							inter	0.76	
6	Anholt (1990)	field	ANOVA	yes	density manipulation (two resource levels, two levels of habitat complexity and three densities of competitors).	insects	intra	0.04	0.32
		field		yes	density manipulation (four levels of resource and 5 levels of competitor).	insects	intra	0.28	
7	Wilson & Shay (1990)	field	RIC	NA	removal experiment crossed with nutrient and disturbance (fire) treatments.	plants	inter	0.42	0.495
								0.57	
8	Smith (1990)	field	RIC	yes	density manipulation with ambient and low levels.	amphibians	intra	0.53	0.53
9	Schmitt & Holbrook (1990)	field	RIC	NA	removal experiment	fish	inter	0.17	0.115
							inter	0.06	
11	Porter & Savignano (1990)	field	RIC	NA	observation (spatial survey)	insects	inter	0.7	0.715
							inter	0.73	
12	Feminella & Resh (1990)	field	R	yes	density manipulation (with 3 levels), also measured effect of disturbance upon density with a survey.	insects	intra	0.76	0.43
								0.1	
13	Swank & Oechel (1991)	field	RIC	NA	removal experiment with herbivores, water and nutrients also present or absent.	plants	inter	0.33	0.33
14	Bertness (1991a)	field	RIC	NA	removal experiment	plants	inter	0.17	0.31125
							inter	0.04	
							inter	0.3	
		field		NA	removal experiment with transplants	plants	inter	0.4	
							inter	0.08	
							inter	0.55	
15	Bertness (1991b)	field	RIC	NA	removal experiment with transplants	plants	inter	0	0.475
							inter	0.95	



16	Hemphill (1991)	field	RIC	NA	removal experiment, plus disturbance and control treatments.	insects	inter	0.34	0.17
17	Auerbach (1991)	field	RIC	NA	observation, surveyed causes of mortality ie. parasitism, predation and competition.	insects	intra	0.12	0.12
18	Buskirk & Smith (1991)	field	RIC	yes	density manipulation with 4 density levels.	amphibians	intra	0.33	0.33
19	Pennings & Callaway (1992)	field	RIC	NA	removal experiment	plants	intra	0.7	0.57
							inter	0.6	0.715
							intra	0.44	
							inter	0.83	
20	Grosholz (1992)	field	ANOVA	yes	density manipulation, Underwood Design with presence/absence of a virus.	isopods	intra	0.25	0.25
21	Evans (1992)	field	ANOVA	NA	density manipulation (removed individuals used to augment plots with competition).	insects	intra	0	0
22	Faeth (1992)	field	ANOVA	NA	removal of a resource and observation, surveyed causes of mortality.	insects	intra	0.18	0.18
							inter	0.02	0.02
23	Denno & Roderick (1992)	artificial	RIC	yes	density manipulation (Underwood design)	insects	intra	0.66	0.33
							inter	0.09	0.01
							intra	0	
							inter	0	
24	Griffith & Poulson (1993)	field	RIC	NA	observation (correlation of density and interference).	insects	intra	0.28	0.28
25	Pantastico-Caldas & Venable (1993)	artificial	RIC	NA	removal experiment with 3 levels of removal at three different sites.	plants	intra	0.22	0.185
							inter	0.22	0.185
							intra	0.15	
							inter	0.15	
26	Christensen & Whitham (1993)	field	RIC	NA	removal experiment, survey and regression of harvest rate with density (in time and space).	insects/birds & mammals.	inter	0.59	0.62
								0.61	
								0.66	
27	Buskirk (1993)	field	ANOVA	yes	observation (regression of density and fitness).	insects	intra	0.36	0.36
28	Heske et. al. (1994)	field	RIC	NA	removal experiment	mammals	inter	0.44	0.44
29	Callaway (1994)	field	RIC	NA	removal experiment	plants	inter	0.55	0.183
								0	
								0	
30	Tonn et. al. (1994)	field	RIC	yes	density manipulation (individuals removed from low density ponds added to high density ponds).	fish	intra	0.22	0.22
31	Bergman & Greenberg (1994)	field	R	no	density manipulation (response curve experiment, effect of increasing density of the neighbour species upon its own fitness also measured).	fish	intra	0.81	0.81
							inter	0.62	0.31
							inter	0	
32	Hughes (1994)	field	RIC	NA	removal experiment	mammals	inter	0.13	0.13
33	Bertness & Ming (1994)	field	RIC	no	density manipulation with two densities of competitors.	plants	intra	0	0
							inter	0	0

### The Relative Intensity of Competition Between Plants in the Glasshouse and in the Field

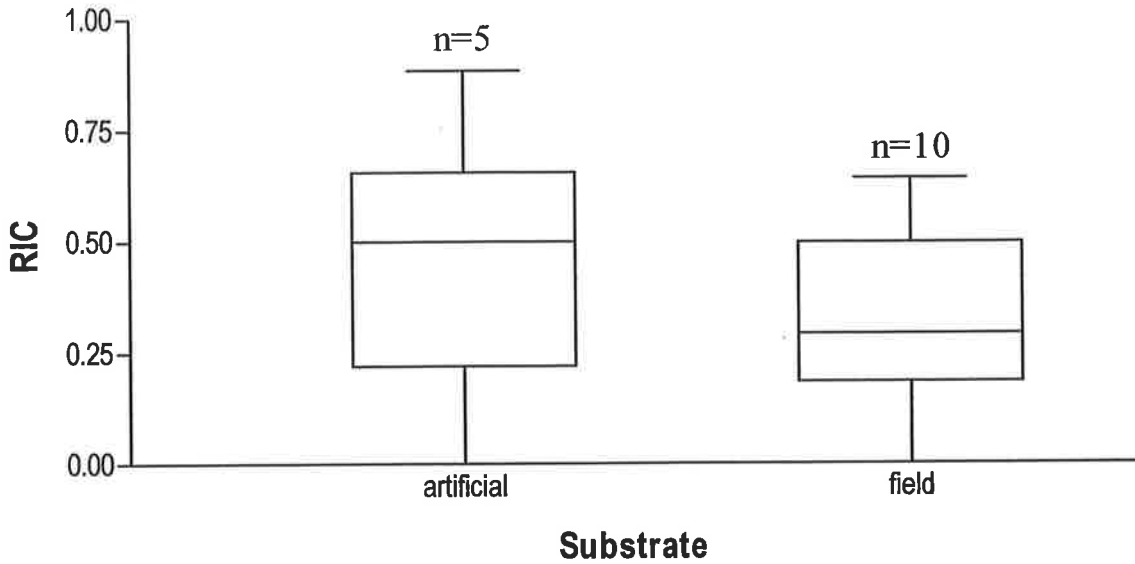


Figure 3.1. Box & Whiskers Plot. The intensity of competition is significantly different for the two categories (Wilcoxon test,  $P < 0.004$ ). The middle line of each box represents the median value, the lines above and below the median represent the 75th and 25th percentile respectively and the upper and lower 'error bars' are zero and 100th percentile.

### The Intensity of Competition Between Insects as a Function of Experimental Method

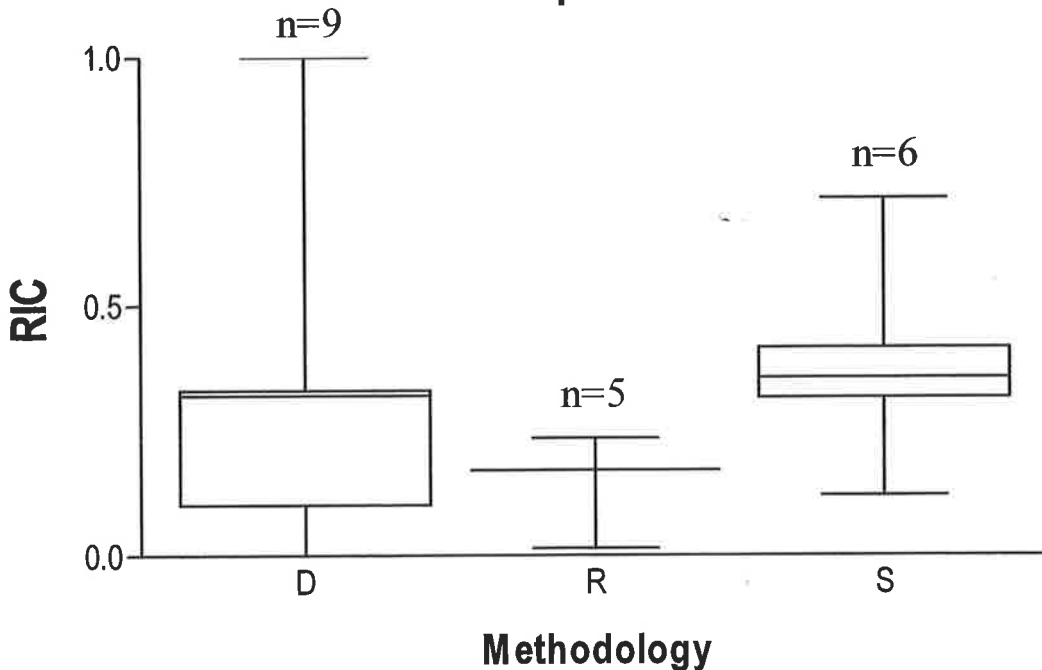


Figure 3.2. Box & Whiskers Plot. D=density manipulation; R=removal experiment; and S=survey. No significant differences between methods (Wilcoxon test,  $P < 0.12$ ). See figure 3.1 for more detail.

### The Relative Intensity of Competition in Studies With and Without Pilot Studies

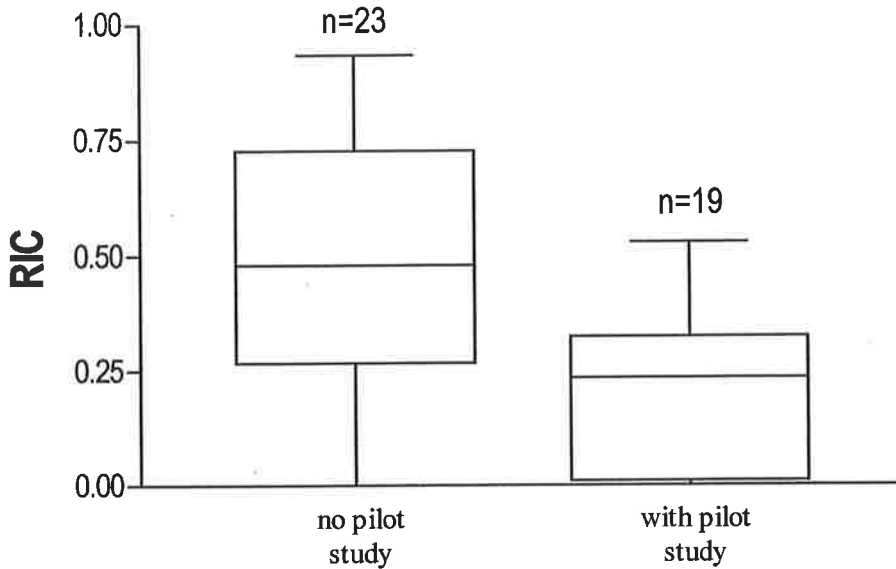


Figure 3.3. Significant differences were detected with the non-parametric Wilcoxon test ( $p < 0.005$ ). See figure 3.1 for more detail.

### The relative intensity of competition as a function of productivity

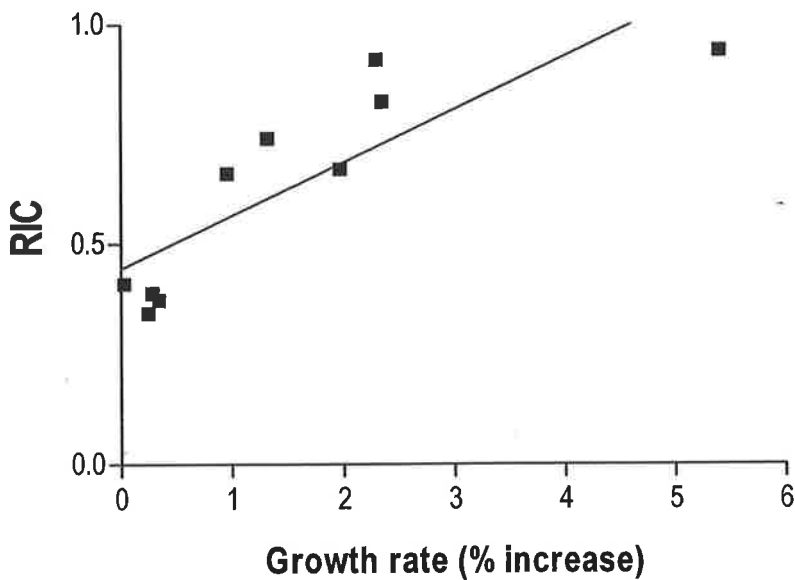


Figure 3.4. The relationship between relative growth rate and the intensity of competition. When  $n=10$ :  $y=0.12x+0.45$ ,  $r^2=0.71$ ,  $P<0.0022$ . Note that the removal of the extreme high value does not dramatically change this relationship. When  $n=9$ :  $y=0.21x+0.35$ ,  $r^2=0.87$ ,  $P<0.0002$ .

### Intensity of Competition Between Plants, Insects and Between Unrelated Taxa.

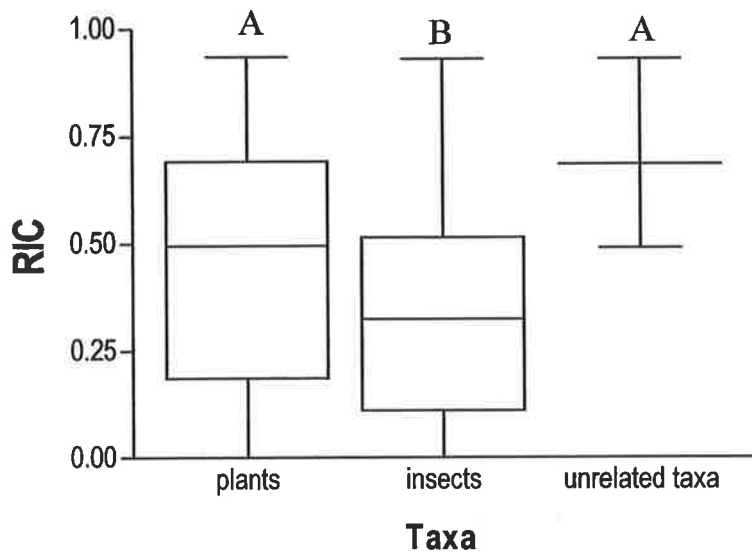


Figure 3.5. Box & Whiskers Plot. Note that for competition between plants:  $n=18$ ; insects:  $n=24$ ; unrelated taxa:  $n=4$ . There is no discrimination between intra & interspecific competition. The intensity of competition is significantly different among categories (Wilcoxon test,  $P<0.015$ ). Columns with the same letter are not significantly different (non-parametric pairwise comparison). See figure 3.1 for more detail.

## Chapter 4

### Emergence, growth and survival of *Eucalyptus camaldulensis* and *E. microcarpa* in response to competition from *A. barbata*

#### Introduction

Establishment is the most critical phase in the life cycle of plants because seeds and seedlings are extremely vulnerable to a range of environmental conditions. The probability of death for a tree seedling declines continuously from birth (Watkinson, 1997). The disparity between the vigour of seedlings and mature trees has prompted some authors to consider these two stages in the life cycle separately (Grubb, 1977; Grime 1979). One of the most significant influences upon tree seedling establishment is competing vegetation. This interaction can be both direct and indirect, can be positive or negative, and can have opposite effects upon emergence and subsequent growth/survival. For example, DeStevens (1991a & b) found that competing herbs reduced the growth and survival of tree seedlings, but promoted their emergence.

Examples of direct inhibition of tree seedlings by competing herbs and grasses are numerous. Hughes and Vitousek (1993) found that grass cover can reduce light levels to 1-10% of background levels (also see D'Antonio *et al.*, 1998). Burton and Bazzaz (1995) found that patches of *Solidago altissima* inhibited photosynthesis in woody seedlings, by reducing the amounts of nitrate in the soil to a level where Rubisco synthesis was limited. Herbaceous vegetation can also inhibit tree seedling growth by reducing air and soil temperatures (see Ball *et al.*, 1997 and Cater & Chapin III, 2000 respectively). Reductions in soil temperature

can inhibit growth by decreasing the availability of nitrogen (Cater & Chapin III, 2000). Annuals can also inhibit the growth of tree seedlings by reducing soil water potential (Gordon *et al.*, 1989; Gordon & Rice, 2000).

In addition to depriving tree seedlings of the resources they require, herbs may modify the microenvironment so that it is more suitable for invertebrate herbivores. Southwood *et al.* (1988) found that thick grass vegetation provides habitat for small mammals and mollusks, and thereby increases the mortality of woody seedlings (see also Gill and Marks, 1991 cited in Berkowitz *et al.*, 1995; Reader, 1992; Burger and Louda, 1994). The litter produced by herbs can also increase tree seedling mortality, because it provides habitat for invertebrate herbivores (Facelli, 1994), and/or pathogenic fungi (Facelli *et al.*, 1999). Resource competition and invertebrate herbivory are often confounded (Facelli, 1994; Bonser & Reader, 1995), and such indirect effects are clearly an important aspect of interference in the field. However, teasing apart the relative contributions of direct and indirect effects can be difficult (McLellan & Fitter, 1997; Bonser and Reader, 1995). Interference under field conditions and the relative importance of direct and indirect effects is therefore considered separately, and at greater length in Chapter 5.

In addition to competing for resources and providing habitat for natural enemies, herbaceous vegetation can affect tree seedling establishment by preventing germination. Herbs can affect tree seedling emergence primarily through modification of abiotic conditions. Cater & Chapin III (2000) argue that the removal of herbs may increase soil temperature, thereby increasing the availability

of nitrogen, and promoting its uptake: nitrate levels are an important influence on the level of germination (Vleeshouwers *et al.*, 1995). Furthermore, grass cover can significantly reduce minimum air temperatures (Ball *et al.*, 1997), and thereby have a significant influence upon the level of germination in tree seedlings (Yates *et al.*, 1996; Bell, 1999).

Light availability and composition are also important cues for germination of some tree seeds (Facelli & Ladd, 1996; Bell, 1999), and herbs can reduce the quantity of light by as much as 90% (Hughes & Vitousek, 1993), and change its composition so that it contains a higher proportion of far-red light (Van Hinsberg, 1998). Reduction in soil water potential caused by grasses (Gordon *et al.*, 1989; Gordon & Rice, 2000) may also cause reduced emergence because reductions in water potential can severely reduce the level of germination in some trees (Facelli & Ladd, 1996).

I investigated the effect of competition from herbaceous vegetation, and the effect of a range of abiotic variables upon the establishment of two species of eucalyptus. At my field site (the Waite Hills Reserve) *Eucalyptus camaldulensis* seedlings are more common than *E. microcarpa* seedlings. *Eucalyptus camaldulensis* seedlings form thick mono-specific stands in some parts of the reserve, whereas *E. microcarpa* seedlings are present but occur in much lower abundances and are more isolated. The Reserve is heavily infested with exotic pasture grasses (e.g. *Avena barbata*). I thus hypothesised that the differential recruitment into the two eucalypt populations within the reserve, was related to their ability to compete with exotic grasses when in the seedling stage. *Eucalyptus camaldulensis* seeds

weigh 4-5 times as much as *E. microcarpa* seeds, and these extra seed reserves may make them better competitors early in the establishment phase. I used glasshouse experiments that compared the growth, survival and emergence of *Eucalyptus camaldulensis*, and *E. microcarpa* in response to competition from *Avena barbata*.

In the glasshouse experiments on competition, *Avena barbata* had similar net effects upon the growth and survival of the two species of eucalypt. However patterns of seedling emergence for the two species of eucalypt, in response to increased densities of *A. barbata* showed marked differences (see results). I therefore exposed Eucalypt seeds to a range of abiotic conditions that are modified by herbaceous vegetation. My goal was to understand the mechanistic basis of the differential emergence of the two species of Eucalypt in response to competition from *Avena barbata*.

## **Methods**

### ***Competition Experiments***

I assessed the effect of *Avena* density upon the emergence, growth and survival of *E. microcarpa* and *E. camaldulensis* using two glasshouse experiments that were performed in consecutive years. The experiment with *E. microcarpa* commenced on 23 February 1998 and was concluded on 25 May 1998. The experiment with *E. camaldulensis* began on 22 March 1999 and ran until 1 July 1999. I terminated the experiments when *Avena barbata* (Bearded Oat) flowered.



For both competition experiments I used a single factor, the density of *Avena barbata*. In the experiment with *E. microcarpa*, *A. barbata* was sown at 0, 0.5, 1, 1.5 and 2 times its average field density. In the experiment with *E. camaldulensis*, *A. barbata* was sown at 0, 1, and 2 times its average field density. A reduced number of levels were used in the second experiment, because the large numbers of levels in the first experiment proved to be superfluous. To determine a biologically realistic range of densities for *A. barbata* I collected soil from underneath a circle with a diameter of 9cm, to a depth of 3cm, at five different sites in the Waite Hills Reserve during summer 1997/1998. *Avena barbata* does not grow during the hot, dry summer months, but persists in the seed bank, and this seed bank was used as a source of competitors.

Each of the five sites from which the *A. barbata* seed bank was collected was at least 500m distant from the next closest site, and each site was host to dense mono-specific stand of *A. barbata* (present as dead individuals). The mean weight of soil in those five samples (Mean $\pm$ SE: 450 $\pm$ 23g) was used as a baseline, which was considered the baseline density of *A. barbata*. Because the seed-bank is concentrated in the top 3cms of the soil (Facelli & Ladd, 1996), and the diameter of the pots that I used is 9cms, 450 grams of soil should result in a density of *A. barbata* in each pot typical of the situation in the field. Using portions of soil that weigh 900 grams doubles the seed input, and should result in a density of *A. barbata* which is roughly double the average in the field. Although some spatial variability in the *A. barbata* seed bank should be expected, this variability is likely to inflate the error term in ANOVA, and therefore make any analysis more conservative.

I tested this method of density manipulation with a pilot study. I grew *A. barbata* at the baseline density, and at twice the baseline density. I had 12 replicates of each density level, and harvested four replicates from each level, every week, for three weeks. The experiment was performed in a glasshouse in January 1998 (Figure 4.1). This method for manipulating the density of *A. barbata* was effective for a short period of time (Figure 4.1). From day 8, to day 20 of the experiment there was more *A. barbata* biomass in pots that were sown with twice the average field density of *A. barbata* seeds. However, as the experiment progressed it is likely that pot size became the main limiting factor, and the biomass of *A. barbata* sown at its average field density, and at twice that density equilibrated (figure 4.1). However, for the critical window in time in which the bulk of the eucalypt seeds germinated, there were significant differences between the amounts of *A. barbata* biomass in the two different levels (see Facelli & Ladd, 1996).

After the baseline density of *A. barbata* was established, further soil samples were collected from the Waite Hills Reserve and used in the competition experiments. To obtain densities of *A. barbata* above and below the baseline I used samples of soil that weighed 0, 225, 450, 675 and 900 grams. These samples produced levels with *A. barbata* at zero, half, one, one and a half and two times its baseline density. For the experiment with *E. camaldulensis* I only used soil portions that weighed 0, 450 and 900 grams. These samples produced levels with *A. barbata* at zero, one and two times its baseline density. The heavier soil samples (e.g. the 900g samples) contained more seeds, but they also contained more of the heavy

clay soil from the field site. To avoid this potentially confounding factor all soil samples were crushed with a roller and sieved. A 2mm sieve was sufficient to retain the seeds, and permit standardisation of the samples by removing most of the clay soil.

Eucalypt seed was sown into 9cm diameter pots filled with commercial potting mix. For the *E. microcarpa* experiment, ten replicates were used for each density, which gave a total of 50 pots. For the experiment with *E. camaldulensis* there were 15 replicates for each density - a total of 45 pots. I randomised the position of each pot within the glasshouse and used overhead misters to water the pots for 3 minutes every day. The temperature in the glasshouse was controlled with an electronic thermostat so that the temperature did not exceed 27<sup>0</sup>C. *Eucalyptus microcarpa* and *E. camaldulensis* seeds were obtained from a commercial supplier and were sprinkled on the soil surface after the seedbank from the Waite Hills Reserve had been added to each pot. I used 0.2 grams of *E. microcarpa* seed and 0.4 grams of *E. camaldulensis* seed per pot. Emergent seedlings were counted every second day. The first five seedlings to emerge in each pot were marked and all seedlings that emerged subsequently were removed. The five marked seedlings in each pot were used to measure biomass and mortality.

### ***Statistical analysis***

The germination, mortality and biomass data for *E. microcarpa* were analysed with one-way ANOVA, using *A. barbata* density as the relevant factor. Where ANOVA showed significant differences I used the Tukey-Kramer HSD test for post-hoc comparison. I performed the same set of analyses for *E. camaldulensis*.

To compensate for the fact that different absolute numbers of *E. camaldulensis*, and *E. microcarpa* seeds were used in the two experiments, I made the germination data relative. For each species the level of emergence in each pot, was expressed as a proportion of the level of emergence in the pot with the highest level of emergence. Each species of eucalypt was considered independently.

### ***Impact of Abiotic Factors on Germination***

I used constant environment cabinets with a 12-hour light/dark cycle to study how the interaction of temperature and light affected the level of germination in *E. camaldulensis* and *E. microcarpa*. A factorial design with 3 different temperature regimes, and three different levels of light was used. The temperature regimes were 6/12°C, 12/22°C and 20/32°C (dark/light periods, respectively). These temperature regimes were chosen because they are typical of conditions in the field in winter through to late spring. For the light treatments seeds were exposed to: light, light that had been filtered through leaf litter, or darkness. Leaf litter may act as a filter, which increases the proportion of far-red light relative to red light (Vazquez-Yanes *et al.*, 1992). Leaf litter is therefore analogous to oldfield vegetation in the way that it changes the quality and composition of light (see Van Hinsberg, 1997).

For each combination of species, light and temperature there were ten replicates. Petri dishes with filter paper, filtered water and seeds were placed in trays, and the trays were wrapped in plastic to maintain a humid microenvironment. To manipulate the light environment one tray (with ten petri dishes per tray) was exposed to light (trays were placed one metre from a 400 watt – high pressure

sodium globe), one was covered with leaf litter (one metre from the light source) and another was covered with a piece of wood. In the petri dishes with *E. camaldulensis* 0.3 grams of seed were used, and in the petri dishes with *E. microcarpa* 0.2 grams of seeds. The experiment ran for 20 days. I analysed the germination data for each species separately and used two-way ANOVA, with temperature and light as factors. I used Tukey-Kramer HSD test when ANOVA showed significant differences.

To investigate the effect of water potential upon the germination of the two eucalypts I used a simplified version of the germination trial just described. This germination trial also ran for 20 days. Seed were exposed to aqueous solutions of poly-ethylene glycol-6000 to create three different levels of water potential (0-reverse-osmosis water, -0.55Mpa, and -1.05Mpa), following the method described in Kaufmann (1969).

There were five replicates of each treatment. In the petri dishes with *E. camaldulensis* 0.15 grams of seed were used, and in the petri dishes with *E. microcarpa* 0.1 grams. Petri dishes with *E. camaldulensis* seed were kept in a growth cabinet set at 12/22°C (dark and light respectively). Petri dishes with *E. microcarpa* seed were kept in a growth cabinet set at 12/22°C, but were left in constant darkness. Slightly different abiotic conditions were used for each species because the results from the previous germination trial suggest that the respective conditions were optimal for each species (see Results). Otherwise the experimental design was identical to the experiment just described. Data were calculated as a proportion of the number of emergent seedlings in the petri dish

with the largest number of emergent seedlings; each species of eucalypt was considered independently. The data were analysed with one-way ANOVA, and the Tukey-Kramer HSD test when ANOVA showed significant differences.

## **Results**

### ***Competition Experiments***

The emergence of *E. microcarpa* seedlings was greatest at intermediate levels of *A. barbata* density, and declined when *A. barbata* was sown at higher and lower densities (ANOVA,  $P < 0.0003$ , Figure 4.2). There was linear, and positive correlation between the densities at which *A. barbata* was sown, and the level of mortality for *E. microcarpa* seedlings (ANOVA,  $P < 0.0003$ , Figure 4.3). The biomass of the seedlings that did survive (mean value per pot) decreased as a function of the density at which *A. barbata* was sown (ANOVA,  $P < 0.0027$ , Figure 4.4). In contrast, increasing the density of *Avena barbata* had a negative effect upon the emergence of *E. camaldulensis* seedlings (ANOVA,  $P < 0.0144$ , Figure 4.5). Relatively low numbers of *E. camaldulensis* seedlings emerged in the pots sown with high densities of *A. barbata*. Increased densities of *A. barbata* also increased the level of seedling mortality for *E. camaldulensis* (ANOVA,  $P < 0.0004$ , Figure 4.6), and reduced the mean weight of the seedlings that did survive (ANOVA,  $P < 0.0001$ , Figure 4.7).

### ***Impact of Abiotic Factors on Germination***

The germination for *E. microcarpa* was affected by light, temperature, and the interaction of the two factors (ANOVA,  $P < 0.0001$ , Figure 4.8). The combination of high temperatures and exposure to light inhibited germination of *E. microcarpa*

(Figure 4.8). The level of germination for *E. camaldulensis* was also affected by light, temperature, and the interaction of the two factors (ANOVA,  $P < 0.0001$ , Figure 4.9). However, it was a combination of low temperature and darkness that most profoundly inhibited the germination of this species (Figure 4.9). The highest level of germination for *E. microcarpa* occurred at  $-0.5\text{Mpa}$  (ANOVA,  $P < 0.0035$ , Figure 4.10). Water potentials above and below this level inhibited germination (Table 4.1, Figure 4.10). Water potential did not significantly affect the level of germination for *E. camaldulensis* (ANOVA,  $P < 0.275$ , Figure 4.11).

## Discussion

Increased densities of *A. barbata* caused similar reductions in the survival and biomass of the two species of eucalypt. I thus reject my initial hypothesis. The extra seed reserves available to *E. camaldulensis* did not enable this species to compete more effectively with *A. barbata*. However, on the question of seed size and resistance to competition in general, these results are inconclusive because I used such a small range of seed sizes (see Fenner, 1986 cited in Westoby *et al.*, 1992). However for the limited case of the two species of eucalypt used in this study, I conclude that seed size does not account for the relatively poor recruitment of *E. microcarpa* in the Waite Hills Reserve.

The differing emergence response of the two species of eucalypt to manipulations of *A. barbata* sowing density may have been related to the physiology of the relevant seeds. The data from the germination trials suggest that the two species of eucalypt use different abiotic factors as cues for germination. The level of germination for *Eucalyptus camaldulensis* was lowest when seeds were deprived

of light and subjected to low temperatures. In comparison, the level of germination for *E. microcarpa* was most profoundly influenced by variations in water potential, and showed little response to variations of temperature and light. The emergence response of *E. microcarpa* in relation to the sowing density of *Avena barbata*, and to variations in water potential, bear a remarkable similarity and may have been related. I hypothesize that the water potential of *E. microcarpa* seeds is somewhere between  $-1$  &  $-0.5$  Mpa so that water moves into seeds when the surrounding environment is around  $-0.5$  Mpa. More negative water potentials (e.g.  $-1$  Mpa) may draw water out of *E. microcarpa* seeds and inhibit germination, whereas more positive water potentials (e.g.  $0$  Mpa) may be anoxic. The hump shaped emergence response of *E. microcarpa* in response to *A. barbata* sowing density may thus be related to the effect of *A. barbata* upon soil water potential. Physical measurements of abiotic conditions (e.g. water potentials), in pots sown with different densities of *A. barbata* would strengthen this hypothesis. However, the hump shaped emergence response curve for *E. microcarpa* was not apparent until the competition experiment had concluded, and the growing season had ended. Measurement of physical conditions (e.g. water potential,  $O_2$  availability) in relation to *A. barbata* density will, therefore, have to be assessed in the future.

The data presented by Witje & Gallagher (1996) are consistent with this hypothesis. They tested the effects of oxygen availability and salinity upon the germination of *Phragmites australis* and found that both variables produced a similar hump shaped emergence response. The emergence response that I have detected could thus be related to solute concentrations (e.g. nitrogen), water



potential, or to oxygen availability (Noe & Zedler, 2000). Again, further experiments will be required to differentiate between these alternatives.

The differential emergence responses of the two species of eucalypt, to the experimental treatments used in this study, may be understood by considering the natural history of the two species. *Eucalyptus microcarpa* is a serotinous species that releases seeds *en masse* from its hard woody capsules following disturbance (e.g. fire). The small seeds produced by this species are therefore released into an environment where resources are abundant, and competition is of relatively low intensity. *Eucalyptus camaldulensis* produces relatively large seeds, and releases them annually, irrespective of disturbance history. As a consequence, it often releases seeds into an environment that is subject to high levels of competition. In Western Australian plants from genera such as *Hakea*, *Eucalyptus*, and *Banksia*, there is a linear relationship between seed mass and nutrient content (Milberg *et al.*, 1998). Relatively large seeds in the Western Australian flora may represent an adaptation to harsh environmental conditions such as drought, competition, shade and burial under litter (see Richards & Lamont, 1996; Milberg & Lamont, 1997; Milberg *et al.*, 1998). The differential emergence response of *E. microcarpa* and *E. camaldulensis* in relation to the experimental treatments imposed in this study could be interpreted in a similar fashion.

The emergence responses of the two species of eucalypt (*E. microcarpa* and *E. camaldulensis*) may also be related to their phenology. Bell (1999) notes that *Eucalyptus oleosa*, an arid zone eucalypt, has an optimal rate of germination at 10-20°C. Germination therefore coincides with the winter rains. In comparison,

seeds of *E. rudis* are found in more mesic coastal environments along creek margins, where water may be available further into the dry summer months, and these seeds germinate optimally at 20-30°C (temperatures typical of the springtime). At my field site *E. camaldulensis* occurs along creek lines whereas *E. microcarpa* is more common on the shallower and drier soils on ridge tops. Because the environment occupied by *E. microcarpa* is drier than the environment occupied by *E. camaldulensis*, the optimal temperature for germination of that species may be lower. My results are thus consistent with Bell's (1999) observation. However, the significant interactions between light and temperature in this study highlight the diverse mechanisms by which plants can acquire information about their environment (see Aphalo & Ballare, 1995), and the need to consider a number of variables (e.g. water potential-Figures 4.10 & 4.11; see also Smith *et al.*, 1999 and Bell *et al.*, 1999).

It should also be noted that seeds can detect the absence of competitors by alternating temperatures or the level of nitrate (Vleeshouwers *et al.*, 1995). Indeed the failure to consider nitrogen is a major limitation of this study. The effect of water potential and/or *Avena* density upon *E. microcarpa* emergence may have been indirect. The availability of nitrogen is heavily influenced by the availability of water. When water is scarce it will slow the diffusion of nitrogen, and when water is freely available it will dilute the concentration of nitrogen (Karssen & Hilhorst, 1992). Nitrogen is worth considering because it is the most important chemical cue of germination (Fenner, 1985), and is most freely available when conditions for plant growth are best (Fenner, 1985). It is also a cofactor in phytochrome action (Bell *et al.*, 1999). Testing whether nitrogen availability is

implicated in the patterns that I have observed may provide greater insight and will require further experimentation, using a combination of different water potentials, and oxygen and nitrogen availabilities.

A further limitation of this study was the small number of growth cabinets that were used. For each of the nine different combinations of 'light and 'temperature' (which were repeated for each species of eucalypt), the 10 replicate petri dishes for each combination of factors were grouped in only one tray. These replicates lacked independence, being pseudo replicated (Morrison & Morris, 2000). The same criticism could also be levelled at the germination trials that measured germination as a function of water potential. The only possible manner in which this problem could have been overcome would have been using a larger number of growth cabinets, or using the same growth cabinets a larger number of times. To avoid the problem of pseudo replication it would have been necessary to run 30 growth cabinets for 20 days (for the light vs temperature trial alone). The prohibitive cost of such an exercise excluded it as a possibility. Even with their limitations, I'm confident that the results from these trials provide reliable data, and that the results reflect mostly treatment effects, rather than cabinet or tray effects.

Even with their limitations, my results suggest that *A. barbata* may be directly responsible for the comparatively poor recruitment of *E. microcarpa* in the reserve. Both species of eucalypt had increased levels of mortality and reduced levels of growth when subjected to competition with *Avena*. However only *E. microcarpa* showed enhanced levels of seedling emergence in highly

competitive neighbourhoods. I therefore conclude that the current management of the reserve, which focuses upon weed control, is appropriate. However, the factors controlling the establishment of tree seedlings (or lack thereof) may be affected by a number of variables. Indirect effects may operate in the field and compound or offset the effect that *A. barbata* had in the glasshouse. The importance of indirect effects is discussed in Chapter 5.

Perhaps the most significant finding in this study was the positive density dependence between the emergence of *E. microcarpa* and *A. barbata*. Although there are examples in the literature where high densities of seedlings result in enforced seed dormancy (see Murray, 1998), there are few studies that report that high densities of competitors can promote germination (but see Linhart, 1976; Miller *et al.*, 1994; Dyer *et al.*, 2000). Dyer *et al.* (2000) measured accelerated seedling emergence for *Nasella pulchra* (a perennial bunch grass) in neighbourhoods with high densities of *Avena triuncialis*, but not neighbourhoods with high densities of *Bromus hordeaceus*. Because of the species specificity, they argue that a chemical cue may be involved. Whilst my results cannot falsify this argument, they do at least suggest that modification of abiotic factors (e.g. water potential, O<sub>2</sub> availability) by *Avena* is also a potential explanation.

## Chapter 4

Table 4.1. Summary statistics for ANOVA's from the competition experiments, and from the germination trials

<i>Source of Variation</i>	<i>df</i>	<i>SS</i>	<i>F</i>	<i>Pr &gt; f</i>
<b><i>Competition Experiments</i></b>				
<b><i>E. microcarpa</i></b>				
<b>GERMINATION</b>				
Competition	4	48.68	6.49	0.0003*
error	45	84.3		
<b>MORTALITY</b>				
Competition	4	48.68	6.49	0.0003*
error	45	84.3		
<b>BIOMASS</b>				
Competition	4	0.0022	4.7	0.0027*
error	45	0.0052		
<b><i>E. camaldulensis</i></b>				
<b>GERMINATION</b>				
Competition	2	19.19	6.64	0.0144*
error	42	60.7		
<b>MORTALITY</b>				
Competition	2	43.3	9.33	0.0004*
error	42	97.46		
<b>BIOMASS</b>				
Competition	2	2.29	27.84	0.0000*
error	42	1.72		
<b><i>Germination Trials</i></b>				
<b><i>E. microcarpa</i></b>				
<b>LIGHT AND TEMPERATURE</b>				
temperature	2	0.254	15.22	0.0001*
light	2	0.463	27.77	0.0001*
temp*light	4	0.437	13.09	0.0001*
error	81	0.675		
<b><i>E. camaldulensis</i></b>				
<b>LIGHT AND TEMPERATURE</b>				
temperature	2	3.94	324.35	0.0001*
light	2	0.295	24.31	0.0001*
temp*light	4	0.438	18.02	0.0001*
error	81	0.493		
<b><i>E. microcarpa</i></b>				
water potential	2	0.339	9.4	0.0035*
	12	0.21		
<b><i>E. camaldulensis</i></b>				
water potential	2	0.017	1.43	0.275
	12	0.07		

\* Indicates factors significant at the .05 level.

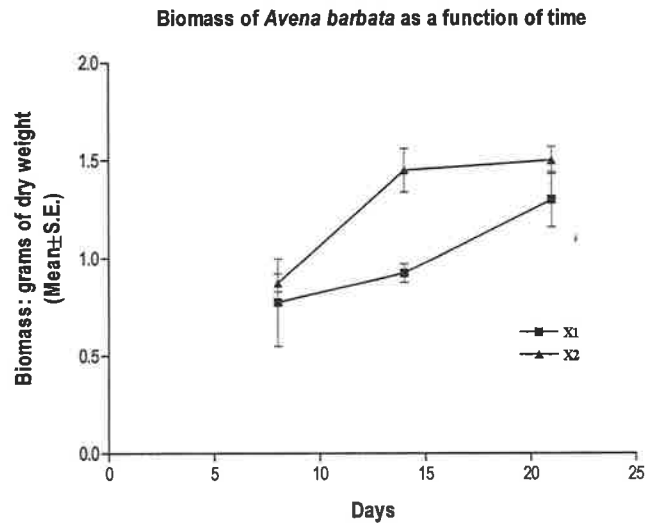


Figure 4.1. X1= *Avena* sown at its average field density, X2 = *Avena* sown at twice its natural field density.

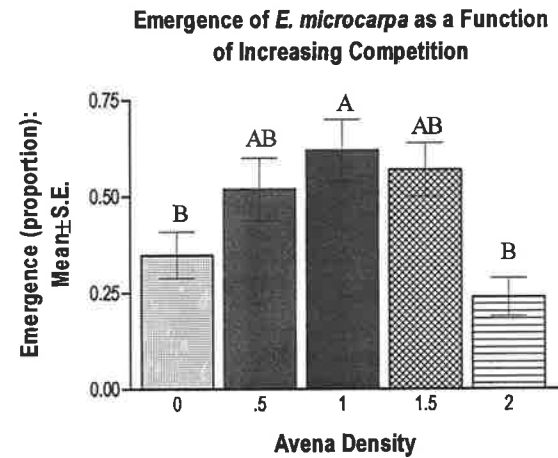


Figure 4.2. 1 represents the baseline level of competition (see text), other levels are densities of *Avena* above and below this baseline. At each level N=10. Levels with the same letter are not significantly different (Anova,  $P < 0.0137$  and Tukey Kramer HSD test).

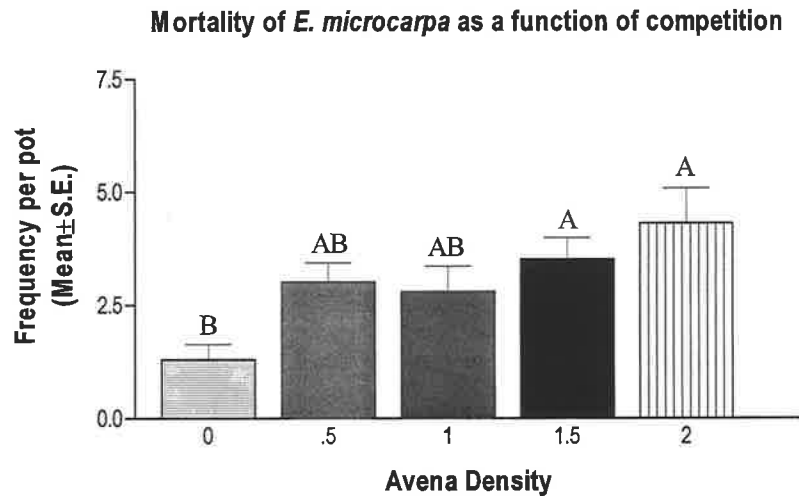


Figure 4.3. Levels with the same letter are not significantly different (Anova,  $P < 0.0003$  and Tukey Kramer HSD test). See figure 4.2 for more detail.

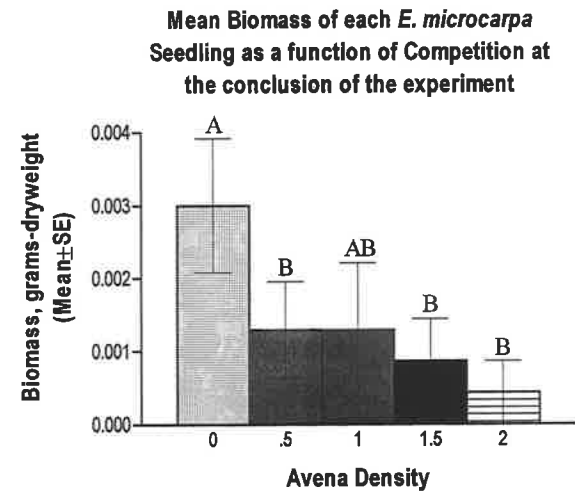


Figure 4.4. See figure 4.2 for more detail. For each level N=10. Levels with the same letter are not significantly different (ANOVA,  $P < 0.0027$  and Tukey-Kramer HSD test).

The number of emergent seedlings for *E. camaldulensis* at three different levels of Competition

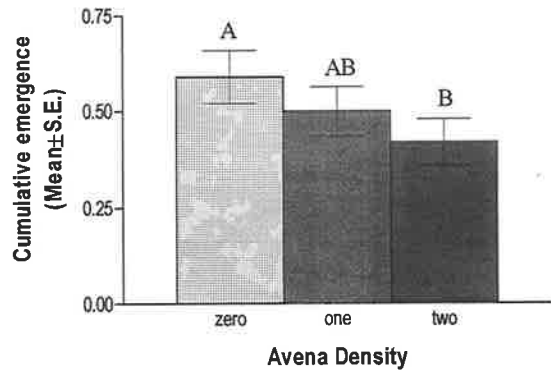


Figure 4.5. See figure 4.2 for more detail. For each level of *Avena* n=15. Levels with the same letter are not significantly different (ANOVA,  $P < 0.0144$  and Tukey-Kramer HSD test).

Mortality of *E. camaldulensis* as a function of increasing Competition

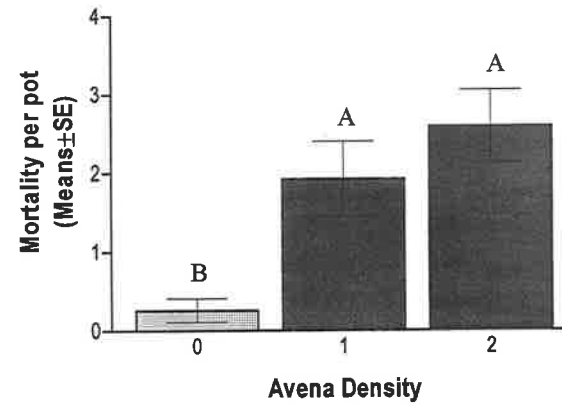


Figure 4.6. See figure 4.2 for more detail. For each level N=15. Levels with the same letter are not significantly different (ANOVA,  $P < 0.0004$  and Tukey-Kramer HSD).

Biomass of *E. camaldulensis* Seedlings as a function of Competition

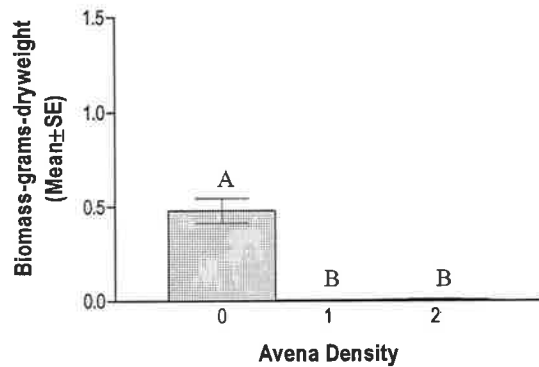


Figure 4.7. See figure 4.2 for more detail. For each level N=15. Data have been transformed:  $\text{Log}_{10}$  for statistical tests, whilst raw data are presented on the histogram. Levels with the same letter are not significantly different (ANOVA,  $P < 0.0001$  and Tukey-Kramer HSD test).

The interactive effects of light and temperature upon germination of *E. microcarpa*

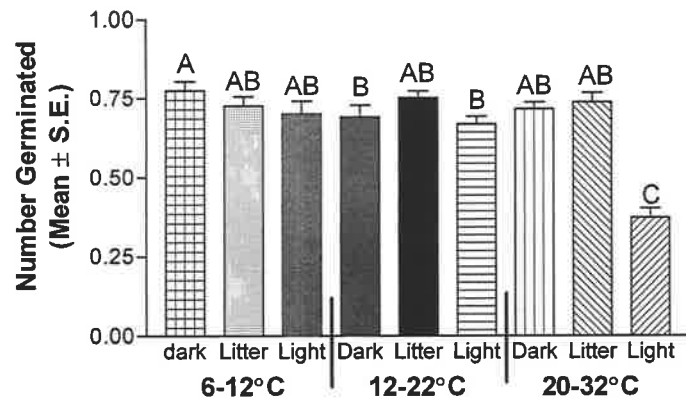


Figure 4.8. Columns with the same letter are not significantly different (ANOVA  $P < 0.0001$  and Tukey-Kramer HSD test).

The interactive effects of light and temperature upon germination of *E. camaldulensis*

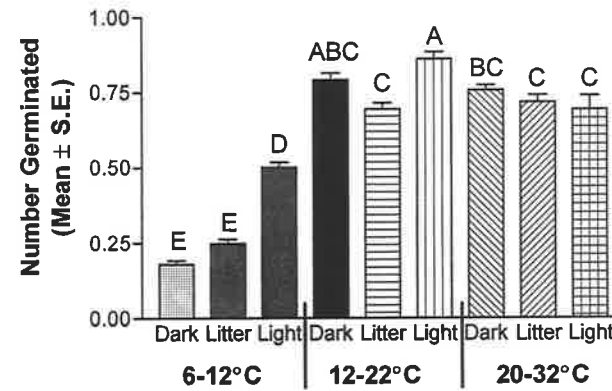


Figure 4.9. Columns with the same letter are not significantly different (ANOVA  $P < 0.0001$  and Tukey-Kramer HSD test).



**Germination of *E. microcarpa*  
as a function of water potential**

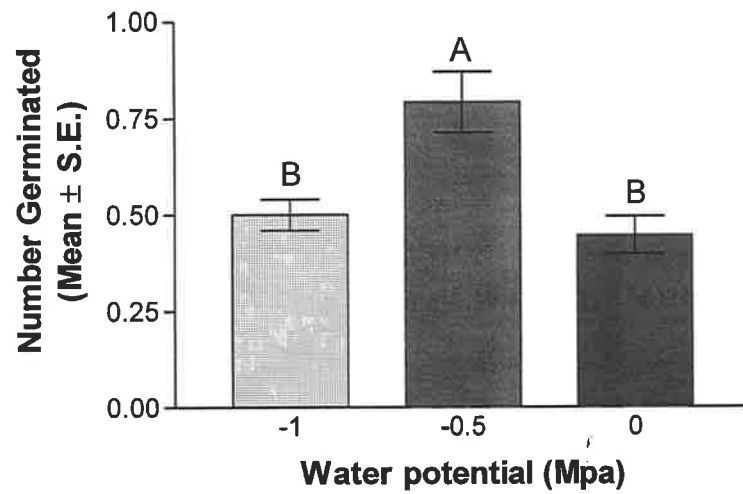


Figure 4.10. Levels with the same letter are not significantly different (ANOVA  $P < 0.0035$ , and Tukey-Kramer HSD test).

**Germination of  
*E. camaldulensis* as a function  
of water potential**

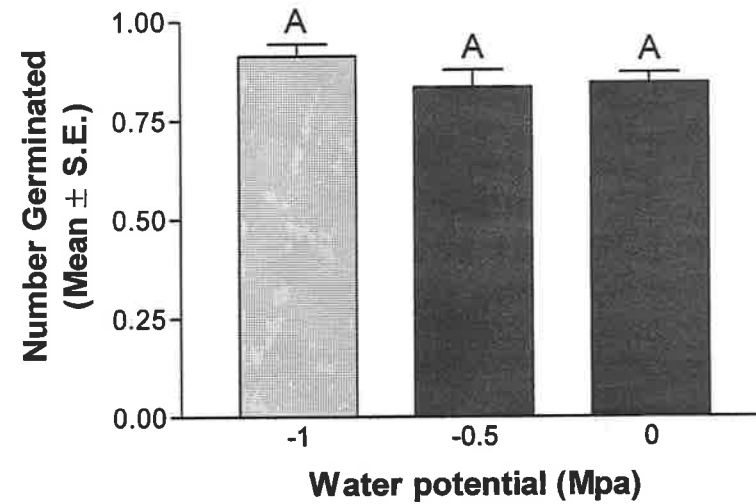


Figure 4.11. Levels with the same letter are not significantly different (ANOVA  $P < 0.275$ , and Tukey-Kramer HSD test).

## Chapter 5

### **The response of *Allocasuarina verticillata* and *Eucalyptus camaldulensis* to the interaction of fertility and competition**

#### **Introduction**

In the early 1960's Hutchinson (1961) first described 'the paradox of the plankton'. He argued that determining how such a great diversity of plankton could coexist in an apparently unstructured habitat (the water column) would be a productive avenue for ecological research. Tilman's (1982) experiments and his theory of resource ratios show how insightful this view was. Tilman (1982, page 136) demonstrated that changing the nutrient composition of a growing medium could alter the outcome of competition between plankton. He, therefore, considered heterogeneity in resource availability in time and/or space, and subsequent niche partitioning as a plausible explanation for 'the paradox of the plankton'. He also developed the resource-based theory of competition from this work.

Tilman (1988) further developed this model in an attempt to explain coexistence among higher plants. In this model he argued that competition for soil resources decreases, and competition for light increases along gradients of fertility. Tilman argues that a trade-off exists because biomass and energy used to acquire soil resources cannot be used to acquire light. Thus there is competition at all levels of fertility, but the resources that are the object of competition change (Tilman, 1987b; Wilson & Tilman, 1991; see also Newman, 1973 and Grubb, 1985).

Grime (1977) also invoked the niche as the explanation for coexistence among higher plants. However, Grime's (1977) work was not directly related to questions posed by Hutchinson (1959; 1961). It was an attempt to synthesise the r-K continuum proposed by MacArthur & Wilson (1967), and the functional classifications of vegetation, which were first proposed by botanical geographers (see Macleod, 1894 & Ramenskii, 1938, cited in Grime *et al.*, 1997). Grime (1977) aimed to develop a general model in which two factors drive speciation. He argued that each species of plant is best adapted to a unique combination of disturbance and productivity. Productivity was defined as the ability of the environment to sustain growth (the inverse being stress), and disturbance as the total or partial destruction of biomass. Grime argues that competitive intensity increases with fertility because the ability to capture above- and below-ground resources is linked by positive feedback; the production of sugars through photosynthesis provides energy, which can be used to acquire mineral nutrients, which may increase a plant's photosynthetic capacity. Because it is argued that the ability to capture above- and below-ground resources is correlated by positive feedback, this argument is referred to as the unified concept of competition (UCC) (after Donald, 1958 cited in Grime *et al.*, 1997). Southwood (1977; 1988) and Keddy (1989) have advanced similar arguments (see also Belcher, Keddy & Twolan-Strutt, 1995). A variation or extension of this argument is well represented in more recent ecological literature. Callaway & Walker (1997) and Brooker & Callaghan (1998) both argue that the intensity of competition declines, and that the importance of positive interactions (facilitation) increases, as abiotic conditions become less favourable for plant growth.

The sometimes-acrimonious debate between the proponents of these arguments may be partly attributable to the use of different operational definitions of competition. Tilman (1990) argues that competition cannot be demonstrated unless it can be shown that one competitor has used resources that are required by another. It is a strictly mechanistic definition of competition (see Tilman, 1987a). However, implicit in many of the studies that support the UCC is a phenomenological definition of competition, that is: a 'decrease in the fitness of a plant...due to the presence of another plant, without any necessity that the decrease in fitness be due to differential consumption of a limiting resource' (Shipley *et al.*, 1991).

Invertebrate herbivory and other processes are often confounded with resource competition because of the way in which plants can modify their environment (see Southwood *et al.*, 1988; Connell 1990; Reader, 1992; Burger and Louda, 1994; Facelli, 1994; Bonser & Reader, 1995 and Leonard, 2000). For example, the perennial forb – *Machaeranthera canescens* cannot survive in the vicinity of the shrub – *Gutierrezia sarothae*. This is attributable to relatively high levels of herbivory by *Hesperotettix viridis* (grasshoppers) in the vicinity of the shrub, as opposed to resource competition (Connell, 1990).

A large number of the studies that have found support for the UCC have used a phenomenological definition of competition (see Goldberg & Barton, 1992 and Wilson & Lee, 2000 and references therein). Thus if we employ a strict mechanistic definition of competition, then evidence in support of the UCC is meagre. However, both indirect effects (Slobodkin *et al.*, 1967), and interaction

modifications (Morin *et al.*, 1988; Wootton, 1994), are reasonably common and need to be considered in any comprehensive model of the plant niche. I thus agree with Leonard (2000), who argues that a synthetic approach is required, and with Pickett *et al.*, (1994) who argue that phenomenological understanding can be useful in the development of theory, even though mechanistic understanding should be our ultimate goal.

There have been a large number of studies that have investigated the influence of fertility upon the intensity of competition, and there is support for both hypotheses (reviewed by Wilson & Lee, 2000). The literature on facilitation is similarly ambiguous (Teilborger & Kadmon, 2000; Ibáñez & Schupp, 2001). One dichotomy that is apparent, in the large body of work on competition, is that experiments conducted with artificial nutrient gradients generally refute the UCC. However, experiments that use natural gradients generally support this argument (Goldberg & Barton, 1992; Belcher *et al.*, 1995; Goldberg & Novoplansky, 1997). Although exceptions to this general pattern exist (Nash-Suding & Goldberg, 1999; Reader, 1990), the vast majority of studies do conform to this pattern.

One possible difference between natural and artificial nutrient gradients is their magnitude – natural gradients often include a wider range of productivity than artificial gradients (Belcher *et al.*, 1995; Bonser & Reader, 1995; Foster, 1999). Another fundamental difference between natural fertility gradients and artificial ones is their complexity. Rainfall gradients are a good example. Rainfall may have a direct positive effect upon plant growth, it is generally neutral in terms of pH (acid rain being an obvious exception), and this may increase the availability

of nutrients. Increased levels of transpiration may also promote the uptake of nutrients, so that in areas with high rainfall, more nutrients can be absorbed at a minimal energetic cost (although this has an upper limit, above which nutrient acquisition may be retarded (Schuur & Matson, 2001)). Furthermore, if water is not limiting, then stomata can remain open longer and a plant can absorb more carbon dioxide. The activity of soil microbes also increases with water availability, and the actual species or genotypic composition of the plant community may change along a natural gradient, but does not necessarily change along artificial resource gradients. Processes such as invertebrate herbivory may also be confounded with resource competition on natural productivity gradients (Cebrián & Duarte, 1994; Bonser & Reader, 1995; Strong *et al.*, 2000; Scheidel & Bruelheide, 2001; Grone & Ayal, 2001). Because of the obvious differences that exist between artificial nutrient gradients, and natural productivity gradients; I conducted a set of experiments to determine whether the contradictory results generated in previous studies are attributable to the methods used, and in particular to the type of gradient(s) used.

The first question I addressed is whether or not the magnitude of a productivity gradient could bias the outcome of an experiment. If a logarithmic relationship exists between fertility and the relative intensity of competition (RIC), then experimental tests of this hypothesis could reasonably find support for either hypothesis, depending on which portion of the resource gradient was used for the test. Previous research, which suggests that such a logarithmic relationship exists, comes from field studies (see Belcher *et al.*, 1995; Bonser & Reader, 1995; Foster, 1999) where productivity and disturbance can be confounded (Wilson & Tilman,

1993; Peltzer *et al.*, 1998). I tested for a logarithmic relationship between fertility and RIC, in a glasshouse where disturbance and fertility could not be confounded. Another equally plausible possibility is that artificial fertility gradients generally refute the UCC because they lack the complexity that natural productivity gradients possess. I created an artificial fertility gradient in the field that was multivariate in nature, using water and fertiliser (with a full range of both macro- and micronutrients) in combination (terminology after Wilson & Keddy, 1986). I also measured the relative intensity of competition for a range of different species at the different levels of fertility. In addition I deployed pitfall traps and measured leaf damage to determine whether resource competition and invertebrate herbivory were associated. This allowed an assessment of the UCC using a phenomenological definition of competition

The specific null hypotheses that are tested in this set of experiments are:

- (1) The magnitude of a fertility gradient or the range of fertilities used does not determine whether a positive relationship between RIC and fertility is detected (essentially I tested for a logarithmic relationship between fertility and RIC on an artificial resource gradient).
- (2) The relative intensity of competition does not vary as a function of fertility on an artificial resource gradient that is multivariate in nature.
- (3) Resource competition and invertebrate herbivory are not associated.

## Methods

### *Study Site*

This study was carried out in an oldfield dominated by exotic annuals such as *Avena barbata* (bearded oat), within the Waite Hills Reserve. A full description of the field site is given in Chapter 2.

### *Glasshouse Experiment*

I used a glasshouse experiment to measure the response of *E. camaldulensis* to competition from exotic annuals (mainly *Avena barbata*), fertilisation and the interaction of those factors. I began this experiment on 23 February 1999, and it concluded on 24 July 1999. I collected *E. camaldulensis* seeds from the Waite Hills Reserve in the spring of 1998 and sprinkled half a gram of the seed/chaff mixture in 60 - 2 litre pots, after the pots were filled with potting mix. I watered these pots with overhead misters for 3 minutes every day. I used a factorial design to measure the effect of *Avena* density, fertilisation and the interaction of those factors on the emergence, survival and biomass of *E. camaldulensis*. I fertilised 20 pots with Native Osmocote™ (Scotts Pty. Ltd.) at the recommended rate (one kilogram/25 metres<sup>2</sup>: 3g/pot), fertilized 20 pots at half that rate, and I left 20 pots unfertilised. At each level of fertility *E. camaldulensis* seedlings were grown with or without *A. barbata*. For each combination of fertility and *Avena* density there were 10 replicates.

To obtain a density of *A. barbata* representative of the conditions in the field, I used the seedbank at the Waite Hills Reserve. The climate in Southern Australia is Mediterranean, and exotic annuals survive the hot-dry conditions in summer by



producing a persistent seed-bank. Most of the seeds produced by annual plants can be found in the top three centimetres of the soil. I collected soil from the top 3cm of an oldfield at Waite Hills Reserve. I then determined the diameter of the 2L pots (9cms), and the weight of soil required to fill these pots to 3cms (450g). I then extracted the seeds from 450g portions of dirt using bread rollers and sieves, and placed those seeds in pots that were assigned competition.

The pots were placed in a random order on a glasshouse bench. I counted all the *E. camaldulensis* seedlings that emerged in each pot. However, the first five to emerge were marked with wooden skewers and all seedlings in excess of five were removed to avoid intraspecific competition. The five seedlings that were marked in each pot were used to measure mortality and biomass. At the conclusion of the experiment I harvested the *A. barbata* biomass in the relevant pots and oven dried it for three days at 80°C. The eucalypt seedlings that survived received the same treatment.

I used a one-way ANOVA to determine whether the application of fertiliser affected the above ground biomass of *A. barbata* and used a Tukey-Kramer HSD test for post-hoc comparison. I used a two-way ANOVA to analyse the effect of fertility, weed density and their interaction upon emergence, biomass and survival of *E. camaldulensis*. I used a Tukey-Kramer HSD test for post hoc comparisons. In addition I calculated the relative intensity of competition (RIC) of *E. camaldulensis* and *A. barbata* at three levels of fertility, using biomass and survival data. RIC was calculated as:

$$\frac{NC - C}{NC},$$

where NC is the performance of the target species (e.g. biomass) in the pots with no competition, and C is the performance of the target species in the pots with competition (see Sammul *et al.*, 2000). I also calculate RIC with two different subsets of biomass data derived from the fertility gradient. The first compared RIC at the lower end of the fertility gradient: in the pots with no fertiliser (0g/pot) and in the pots with half the recommended application (1.5g/pot). The second subset of data was taken from the top end of the fertility gradient. The intensity of competition was compared in the pots with half the recommended application (1.5g/pot), and in the pots with the full application (3g/pot). Each replicate value for eucalypt survival or biomass in the treatments with *A. barbata* was randomly paired with a value for eucalypt survival or biomass when there was no competition. I analysed these ratios with ANOVA and Tukey-Kramer HSD test.

### ***Field Experiment***

I investigated the effect of microhabitat (the identity of competitor), fertility and the interaction of those factors upon the establishment of *Allocasuarina verticillata* and *Eucalyptus camaldulensis*. I grew *A. verticillata* and *E. camaldulensis* in four microhabitats, at two levels of fertility. The four microhabitats that I used were: quadrats with exotic grasses (W), *Acacia pycnantha* (AP), *Themeda triandra* (KG), and no vegetation (NW). I refer to these microhabitats as 'biological neighbourhood' for the remainder of this paper. The creation of these biological neighbourhoods was initiated 2 years before the target organisms were introduced into the experiment. To create biological

neighbourhoods with *A. pycnantha* I purchased seedlings from a commercial supplier, and planted these seedlings in the field in May 1998. *Themeda triandra* was grown in commercial seedling tubes, in a shade house, from seed that was germinated in a constant environment cabinet in June 1998. The *T. triandra* 'seedlings' were transplanted into the field (the Waite Hills Reserve) at the end of winter 1999 (10/8/99). Whilst the experiment ran I used glyphosate once in spring, and once in autumn to control exotic grasses in the 1m buffer strips that surrounded each quadrat. I also pre-treated the *A. pycnantha* and *T. triandra* quadrats with glyphosate, to allow these species to establish without competition from exotic grasses. Quadrats with *A. pycnantha*, *T. triandra* and no vegetation were weeded by hand, three times a year whilst the experiment ran, whereas the quadrats with exotic grasses were left un-weeded (control). During the summer of 1999/2000 I watered the quadrats with *A. pycnantha*, and *T. triandra*, once a month to ensure good establishment. Each type of biological neighbourhood was created within a 1m<sup>2</sup> quadrat.

I used a randomised, complete block experimental design. There were ten plots, and each plot contained one replicate of all four biological neighbourhoods. Five of these plots were left untreated, and the other five received additional resources; fertile plots were watered with 10L/m<sup>2</sup>, once a month during the dry summer months (October-March), and were fertilised twice a year with Native Osmocote, at the recommended rate for horticulture (40g/m<sup>2</sup>). Each plot was oriented on a north-south axis, and the order of the biological neighbourhoods was randomised within each plot. I planted 3 *A. verticillata* and 2 *E. camaldulensis* seedlings in each quadrat on 23/5/00.

I measured the performance of the tree seedlings twice during the course of the experiment. The first census was on 13/9/00 (spring), and the second census was on 23/3/01 (autumn). At the first census I recorded survival of *A. verticillata*. *Allocasuarina verticillata* seedlings have photosynthetic organs analogous to pine needles, and the seedlings that I planted in the field were still very small by 13/9/00. I had intended to measure the number and length of photosynthetic organs, but it would have resulted in an unreasonable level of disturbance to the experimental plot. By the time of the first census it was apparent that invertebrate herbivores would have a major influence upon the results generated in this study, hence the lack of desire to disturb their activities. For *E. camaldulensis* seedlings I counted survival, the number of leaves, and the number of leaves that had been damaged by herbivores.

In addition to measuring the performance of the tree seedlings, I set up pitfall traps. Each pitfall trap consisted of a 300ml plastic cup buried to the rim, in the centre of each quadrat. The traps were filled with a 30% ethanol solution and were deployed from 10/9/00 to 13/9/00. At the second census I measured the biomass and survival of *E. camaldulensis* and *A. verticillata* seedlings. The above ground biomass of the surviving tree seedlings was harvested and oven dried at 80°C for 48 hours, and then weighed, on the 25<sup>th</sup> of March 2001.

### *Variables Measured and Statistical analyses:*

#### *Spring Census - 2000:*

No analysis of *E. camaldulensis* survival was performed because all seedlings survived until the first census. I used a two-way ANOVA to determine whether fertility, biological neighbourhood, or the interaction of the two factors affected the number of leaves on *E. camaldulensis* seedlings. I also used the same type of analysis to determine whether the number of leaves that had been damaged by herbivores, was affected by the experimental treatments. Because biological neighbourhood significantly affected the number of leaves on *E. camaldulensis* seedlings (see below), the percentage of damaged leaves (on each seedling) was used in the analysis of leaf damage. This measure of leaf damage is extremely conservative because leaves that have been completely removed by herbivores, do not contribute to the total. For *A. verticillata* seedlings only the presence or absence of seedlings was recorded. *Allocasuarina verticillata* survival data were analysed with a two-way ANOVA, using fertility and biological neighbourhood as factors.

I calculated the relative intensity of competition for *E. camaldulensis* and *A. verticillata* in three different biological neighbourhoods (AP, KG & NW), at two levels of fertility. For *E. camaldulensis* I used leaf number data to calculate RIC, and for *A. verticillata* I used survival data. I analysed the data with a two-way ANOVA, using fertility and biological neighbourhood as the relevant factors.

The data derived from the pitfall traps was analysed with a two-way ANOVA with fertility and biological neighbourhood as factors. I analysed the effect of fertility

and biological neighbourhood upon the frequency of each type of invertebrate individually – statistical comparisons were not made between the different types of invertebrate. If the ANOVA was significant for any of the above analyses, then Tukey-Kramer HSD test was used for the post-hoc comparison. Data were not always normally distributed, and some of the frequency distributions of the data were skewed. However, I did not use transformations because ANOVA is reasonably robust to departure from these assumptions (Underwood, 1997).

### ***Summer Census - 2001:***

For the final census I compared survival and biomass of *E. camaldulensis* and *A. verticillata* seedlings, using two-way ANOVA, with fertility and biological neighbourhood as factors. Statistical comparisons were not made between *E. camaldulensis* and *A. verticillata*. Where ANOVA showed significant differences I used Tukey-Kramer HSD test for post-hoc comparison. I used both biomass and survival data to calculate the RIC for *E. camaldulensis*, and *A. verticillata*, in the three different biological neighbourhoods (AP, KG & NW), at two levels of fertility. Where ANOVA showed significant differences I used Tukey-Kramer HSD test for post-hoc comparison.

## **Results**

### ***Glasshouse Experiment***

The application of fertiliser increased the biomass of *A. barbata* (ANOVA;  $P < 0.0001$ , Figure 5.1a). Increasing the density of *Avena barbata* resulted in lower levels of emergence for *E. camaldulensis* (ANOVA;  $P < 0.003$ , Figure 5.1b, Table 5.1). Fertility, and the interaction of *A. barbata* density and fertility had no effect

upon eucalypt emergence (ANOVA;  $P < 0.25$  &  $P < 0.27$  respectively, Table 5.1). Increased densities of *A. barbata* reduced the survival of *E. camaldulensis* seedlings (ANOVA;  $P < 0.0002$ , Figure 5.1c). Fertility and the interaction of fertility and *A. barbata* density did not affect *E. camaldulensis* survival (ANOVA;  $P < 0.2174$ ,  $P < 0.3326$  respectively, Table 5.1). The interaction of fertility and *A. barbata* density significantly affected the growth (final biomass) of *E. camaldulensis* seedlings (ANOVA;  $P < 0.0001$ ). At low fertility the density of *A. barbata* did not significantly affect biomass of *E. camaldulensis*. However, in the pots with fertiliser, *A. barbata* caused a significant reduction in the growth of *E. camaldulensis* seedlings (Table 5.1, Figure 5.1d). When biomass data were used to calculate RIC, increased fertility resulted in more intense competition (ANOVA;  $P < 0.0014$ , Figure 5.1e). When a subset of data taken from the lower end of the fertility gradient was used for analysis, increased fertility resulted in more intense competition (ANOVA;  $P < 0.0087$ , Figure 5.1f). However, with the subset of data taken from the top-end of the fertility gradient, increased fertility did not result in more intense competition (ANOVA;  $P < 0.1347$ ). When survival data were used to calculate RIC, increased fertility does not result in more intense competition (ANOVA;  $P < 0.1347$ ).

### ***Field Experiment***

#### ***Spring Census - 2000:***

*Allocasuarina verticillata* survival was lower in quadrats with exotic grasses than in quadrats without vegetation or quadrats with *A. pycnantha*. However, survival in quadrats with *T. triandra* was not significantly different from survival in quadrats with exotic grasses, no vegetation or *A. pycnantha* (ANOVA,  $P < 0.0001$ ,

Table 5.2, Figure 5.2a). Fertility and the interaction of fertility and biological neighbourhood did not affect *A. verticillata* survival (ANOVA,  $P < 0.1991$ , &  $P < 0.7473$  respectively). Fertility and the interaction of fertility and biological neighbourhood did not affect the number of leaves on *E. camaldulensis* seedlings (ANOVA,  $P < 0.7143$ , &  $P < 0.2534$  respectively). However, *Eucalyptus camaldulensis* seedlings growing in quadrats with exotic grasses and *T. triandra* had fewer leaves than seedlings growing in quadrats with *A. pycnantha* and no vegetation (ANOVA,  $P < 0.0053$ , Figure 5.2b). The proportion of leaves on *E. camaldulensis* seedlings with evidence of insect damage was significantly affected by biological neighbourhood (ANOVA,  $P < 0.0001$ ), the interaction of fertility and biological neighbourhood (ANOVA,  $P < 0.0011$ ), but not by fertility alone (ANOVA,  $P < 0.273$ ) (see Table 5.2, Figure 5.2c). Insect damage was highest in quadrats with exotic pasture grasses and *T. triandra* (ANOVA,  $P < 0.0001$ , Figure 5.2c). The RIC for *A. verticillata* and *E. camaldulensis* was affected by biological neighbourhood (ANOVA,  $P < 0.0032$  &  $P < 0.0217$  respectively), but not fertility or the interaction of fertility and biological neighbourhood (ANOVA,  $P < 0.479$  &  $P < 0.726$  respectively, Figures 5.2d & 2e respectively) - For both *E. camaldulensis* and *A. verticillata* there was evidence of a facilitative relationship with *A. pycnantha*.

The abundance of invertebrates was never significantly affected by fertility, or the interaction of fertility and biological neighbourhood (Table 5.3). However, biological neighbourhood significantly affected the abundance of some invertebrates. For example, there were more spiders in quadrats with *A. pycnantha* than in quadrats with exotic pasture grasses or *T. triandra* (ANOVA,



$P < 0.0015$ , Figure 5.2f). Ants were more abundant in quadrats with *A. pycnantha* than in quadrats with no vegetation, exotic pasture grasses (weeds) and *T. triandra* (ANOVA,  $P < 0.000$ , Figure 5.2f). There were more slugs in quadrats with exotic grasses, than in any other type of quadrat, more Portuguese millipedes (*Ommatoiulus moreleti*) in quadrats with *A. pycnantha* than there were in quadrats with *T. triandra*, and there were more collembolans in quadrats with no vegetation and *A. pycnantha*, than there was in quadrats with exotic grasses and *T. triandra* (see Table 5.3, Figure 5.2f).

#### **Summer Census - 2001:**

Biological neighbourhood, fertility, and the interaction of fertility and biological neighbourhood all affected the biomass of *E. camaldulensis* seedlings (Table 5.4). *Eucalyptus camaldulensis* seedlings growing in fertile plots, without competition attained higher levels of biomass than seedlings growing in quadrats with any other combination of fertility and biological neighbourhood (ANOVA,  $P < 0.0002$ , Figure 5.3a). Survival of *E. camaldulensis* seedlings was not affected by fertility or the interaction of fertility and biological neighbourhood (ANOVA,  $P < 0.1501$  &  $P < 0.5124$  respectively). However, biological neighbourhood did affect *E. camaldulensis* survival (ANOVA,  $P < 0.0001$ ). Survival was lowest in quadrats with exotic grasses, intermediate in quadrats with *T. triandra*, and highest in quadrats with *A. pycnantha*, and no vegetation (Table 5.4, Figure 5.3b).

The effect of fertility on the biomass of *A. verticillata* seedlings was marginally non-significant (ANOVA,  $P < 0.0806$ ). Biological neighbourhood, and the interaction of fertility and biological neighbourhood both influenced the growth of

*A. verticillata* seedlings (Table 5.4). *Allocasuarina verticillata* seedlings growing in fertile plots without competition achieved higher levels of biomass than seedlings in any other treatment combination (ANOVA,  $P < 0.0270$ , Figure 5.3c). Survival of *A. verticillata* seedlings was not affected by fertility or the interaction of fertility and biological neighbourhood (ANOVA,  $P < 0.3499$  &  $P < 0.7775$  respectively), but biological neighbourhood did affect survival (ANOVA,  $P < 0.0001$ ). No *A. verticillata* seedlings survived in quadrats with exotic grasses or *T. triandra*, whereas significant numbers survived in the quadrats with *A. pycnantha*, and no vegetation (Table 5.4, Figure 5.3d).

When biomass data were used to calculate RIC, fertility, biological neighbourhood, and the interaction of the two factors significantly affected *E. camaldulensis* seedlings (see Table 5.5). This result is attributable to the fact that competition was less intense in quadrats with *A. pycnantha* in the low fertility plots, than in quadrats with any other combination of factors (ANOVA,  $P < 0.01$ , Figure 5.4a). When survival data were used to calculate RIC for *E. camaldulensis*, only biological neighbourhood had a significant effect (ANOVA,  $P < 0.0001$ , see Table 5.5) - the intensity of competition was lowest in quadrats with *A. pycnantha*, intermediate in quadrats with *T. triandra*, and most intense in quadrats with exotic grasses (Figure 5.4b).

Fertility did not affect the RIC for *A. verticillata* seedlings, and this was true when biomass (ANOVA,  $P < 0.1103$ ) and survival data (ANOVA,  $P < 0.1684$ ) were used to calculate competitive intensity. However, biological neighbourhood influenced RIC (ANOVA,  $P < 0.0031$ ); the intensity of competition in the quadrats with

*A. pycnantha* was relatively low, and this was true when biomass (ANOVA,  $P < 0.0031$ , Figure 5.4c), and survival data (ANOVA,  $P < 0.0001$ , Figure 5.4d) were used to calculate RIC. The combined effect (interaction) of fertility and biological neighbourhood was marginally non-significant when biomass data were used to calculate the ratio (ANOVA,  $P < 0.0841$ , figure 5.4c), and not significant when survival data were used (ANOVA,  $P < 0.9835$ ). Because the risk of disregarding an existing interaction is more serious than the risk of accepting a non-significant interaction (Fowler 1990), I prefer to consider the implications of an interdependent effect (see Shrader-Frechette & McCoy 1992 for a discussion of contextualism in the appraisal of Type I and Type II errors). Thus when biomass data were used to calculate RIC, the intensity of competition for *A. verticillata* was lower in unfertilised quadrats with *A. pycnantha*, than in quadrats with any other combination of fertility and biological neighbourhood (ANOVA,  $P < 0.0841$ , Figure 5.4c).

## **Discussion**

Competition, fertility, and invertebrate herbivory all strongly affected the establishment of *A. verticillata* and *E. camaldulensis*. Competition (phenomenologically defined) was the most important process operating in this system. It strongly reduced emergence, survival, and growth of the tree seedlings. In comparison, fertility did not affect emergence, or survivorship, but did result in increased growth of tree seedlings in the absence of competition. Because the effects of fertility and biological neighbourhood were not independent, there was a positive correlation between fertility and the relative intensity of competition

(RIC). However, this relationship was only apparent with biomass data. The comparative value of survival and biomass data are discussed below.

The identity of the competitor had major implications in this study, and this finding would not be apparent from data generated in a controlled environment like a glasshouse, even if a range of competitors were used. Competing plants not only consume resources, they can also modify their environment (Jones *et al.*, 1994). Different microenvironments may harbour different assemblages of invertebrates, and this may affect seedling establishment (see Southwood *et al.*, 1988; Reichert & Bishop, 1990; Facelli, 1994; Bonser & Reader, 1995). Tree seedlings growing in quadrats with exotic grasses and kangaroo grass, were more heavily grazed than tree seedlings in quadrats with *Acacia pycnantha* and no vegetation. They were, therefore, less likely to survive, and attained lower levels of biomass. In addition, the abundance of predators (ants and spiders) and invertebrate herbivores (e.g. slugs) was closely correlated with these patterns.

It could be argued that the difference between the performance of tree seedlings growing in the different biological neighbourhoods, could have been attributable to the different levels of plant biomass that were present in those biological neighbourhoods. However differences in plant architecture (terminology after Lawton, 1983) is a more plausible explanation. The size and biomass attained by *A. pycnantha* greatly exceeded the level of biomass attained by either kangaroo grass or the exotic pasture grasses (personal observation). Furthermore, the extra-floral nectaries of *A. pycnantha*, the data from the pitfall traps, and the leaf damage data all support the argument that the plants used to create the biological

neighbourhoods, indirectly affected tree seedling establishment by modifying the microenvironment. By the end of the experiment it was obvious that tree seedlings growing in the quadrats with *T. triandra* had been subjected to herbivory. However, the pitfall traps proved an ineffective method of catching these invertebrates. The use of suction traps (Southwood, 1978) may provide a better sample of the invertebrate community in patches of *T. triandra*.

The relatively high abundance of invertebrate herbivores in the quadrats with exotic grasses, and in the quadrats with *T. triandra* may be attributable to two factors. These microhabitats could have harboured a relatively high abundance of invertebrate herbivores, because these microhabitats are insulated from desiccating physical conditions. These microhabitats may also have been favourable because of the reduced abundance of predators (e.g. ants and spiders) and/or a reduction in the foraging efficiency of predators (see Groner & Ayal, 2001). It should also be noted that there was a relatively low abundance of collembola in the plots with exotic grasses and *T. triandra*. Collembola may be an important component in the diet of ants (Wilson, 1959), and their relatively high abundance in the quadrats with *A. pycnantha* and no vegetation, may have sustained the relatively large number of predators found there.

The results of this study show that the variable used to assess competitive effects has a major bearing on the conclusions derived. One could draw alternative conclusions, depending upon the choice of variable (Figures 5.1c & 1d). When biomass data is used to calculate RIC the results support the unified concept of competition (Donald, 1958 cited in Grime *et al.*, 1997). However, when survival

data are used to calculate RIC the results favour Newman (1973) and Tilman's (1987b) rejection of the concept. The studies by Reader (1990), Berkowitz *et al.* (1995) and Sammul *et al.* (2000) also suggest that the choice of dependant variable has significant implications. The use of a mathematical function that includes more than one demographic parameter may help resolve this problem (e.g. McPeck & Peckarsky, 1998).

Regrettably the model developed by McPeck & Peckarsky (1998) is of little use because: 'the demographic model used for any particular organism must be tailored to its life history' (McPeck & Peckarsky, 1998), and the life histories of hemimetabolous insects and tree seedlings are quite different. However, the need for a demographic model with more than one parameter may not be as important for plants. Because of their modular construction biomass is often an excellent indicator of plant fitness (e.g. Molofsky *et al.*, 2000). This was the case in this study. Some of the *E. camaldulensis* seedlings in the quadrats with *T. triandra* survived, but did so in very poor condition. For example there were seedlings with only one or two leaves left, and invertebrates had eaten 75% of each remaining leaf. The poor state of health for such seedlings is apparent with biomass data (Figure 5.3a), but not with survival data (Figure 5.3b).

Furthermore, comparable numbers of tree seedlings survived in quadrats with *A. pycnantha* and no vegetation, irrespective of fertility (Table 5.4, Figure 5.3). However, in quadrats with no vegetation and high fertility, *E. camaldulensis* seedlings grew exceedingly well - they were, on average, four times as large as the seedlings growing in the unfertilised quadrats with no vegetation, and roughly 12

times as large as seedlings growing in quadrats with *A. pycnantha* (Figure 5.3a). When survival data are used for analysis, the poor state of health of eucalypt seedlings growing in quadrats with exotic grasses is not apparent. I, therefore, conclude that biomass data, at least in this instance, are more meaningful, and that increased fertility resulted in more intense competition. The positive correlation between fertility and RIC exists because *E. camaldulensis* and *A. verticillata* were better able to increase growth when released from competition in the fertile quadrats (Figures 5.3a & c). Thus my results mirror the results in Reader (1990): Competition in the unfertilised plots may have been constrained by low nutrient supply.

In Grime's (1977) generalised model of the plant niche, competition decreases as environmental adversity increases (terminology after Whittaker, 1975 cited in Southwood, 1977). I hypothesize that this model will be most accurate when a phenomenological definition of competition is used. As fertility increases so does net primary production (NPP) (Whittaker, 1975). The presence of more vegetation provides more habitat for invertebrate herbivores, and may, therefore, result in higher levels of inhibition through herbivory (see Cebrián & Duarte, 1994; Bonser & Reader, 1995; Strong *et al.*, 2000; Scheidel & Bruelheide, 2001; Grone & Ayal, 2001). The positive correlation that is consistently detected between RIC and fertility when a phenomenological definition is used may be less related to resource competition than it is to the action and behaviour of invertebrates. The lack of independence between processes such as herbivory and competition highlights the value of a phenomenological approach, and is a good

example of how our understanding of natural systems may increase when we use a phenomenological definition (see Pickett *et al.*, 1994, pages 104-107).

Both resource competition and invertebrate herbivory may have been operating in this system. The reductions in tree seedling biomass caused by association with *A. pycnantha*, was probably caused by resource competition (as there was no evidence of invertebrate herbivory). Whereas the reductions in tree seedling biomass caused by association with exotic pasture grasses, and *T. triandra*, appeared to be attributable to invertebrate herbivores. Obviously the evidence for resource competition is anecdotal, direct measures of resources such as the concentrations of nutrients in the relevant plants-tissues, would provide more reliable proof that resource competition was in fact occurring (see Tilman, 1987a). Even with their limitations, the results from this study should be placed in the context of the large volume of ecological literature that demonstrates that resource competition, and invertebrate herbivory are often heavily confounded (Southwood *et al.*, 1988; Burger & Louda, 1994; Reader, 1992; Berkowitz *et al.*, 1995; Bonser & Reader, 1995 and Figure 2c). The consistency with which this observation has been made suggests that calls for contingent ecological theory (e.g. Holt *et al.*, 1994) are premature (proponents of contingent ecological theory argue that ecological theory should be developed on a case by case basis because of the complexity of ecological systems. Generalization: the substitution of one theory for many facts (MacArthur & Wilson, 1967) is still a laudable objective.

Previous field studies have shown that there is a logarithmic relationship between standing crop and RIC (Belcher *et al.*, 1995; Bonser & Reader, 1995; Foster,



1999). The existence of a logarithmic relationship between fertility and RIC, suggests that some previous studies may have failed to detect a correlation between fertility and RIC, because narrow ranges of fertility were used, or because only fertility levels characteristic of the upper portions of the relevant gradient were used. However, the results from these field experiments could be criticised because disturbance and fertility can be confounded on gradients of standing crop (Wilson & Tilman, 1991 and 1993; Peltzer *et al.*, 1998). I used an artificial fertility gradient, in a glasshouse, where fertility and disturbance could not be confounded. My results (Figures 5.1d, 5.1e and 5.1f) suggest that the range of fertilities used can bias the results from an experiment, and that RIC does increase with resource availability in a logarithmic fashion.

In contrast to the bulk of studies that have used artificial resource gradients (see Goldberg & Barton, 1992), the results from the field experiment are consistent with the unified concept of competition. However, it was impossible to determine whether the results supported the UCC, because the gradient created was multivariate in nature (and therefore more similar to a natural gradient), or was simply a result of the fact that a sufficiently wide range of fertilities were used. This distinction is perhaps unimportant. The results demonstrate that the relationship between physical resource gradients and RIC, and standing crop and RIC may be similar. A definition of environmental adversity that is based upon physical characteristics of habitat (e.g. rainfall) may therefore be possible. A definition of environmental adversity that is based upon the physical environment would be superior to standing crop because it would avoid suspicions of

circularity (Wilson & Lee, 2000), and because disturbance and standing crop are not confounded on resource gradients.

### ***Facilitation and Environmental Gradients***

My data do not support the argument that positive interactions become of greater importance as the abiotic environment becomes harsher (Brooker & Callaghan, 1998; Callaway & Walker, 1997). In the spring census I found that *A. pycnantha* facilitated the establishment of *A. verticillata* and *E. camaldulensis*, and that fertility did not affect this relationship. Furthermore my experimental system is a Mediterranean one, and the abiotic conditions deteriorated as the experiment progressed. I detected facilitation during the spring census (Figures 5.2d and 5.2e) when the physical conditions for plant growth were excellent, but there was no evidence of facilitation by the end of the hot, dry summer (Figures 5.4a, b, c & d).

Bertness & Callaway (1994, Figure 1) also make predictions about the importance of facilitation on gradients of environmental adversity. However, in their model the axes are defined by concepts. As a result an independent test of this model is difficult. A definition of environmental adversity that is based upon the physical environment may enable independent tests of this hypothesis (see Elton, 1966 *cited in* Southwood, 1977; Wilson & Lee, 2000 & Chapter 8).

### ***Unanswered Questions***

Most experimental tests of the unified concept of competition have used a narrow range of habitats, for example oldfields (this study; Bonser & Reader, 1995; Wilson & Tilman, 1993), herb meadows (Belcher *et al.*, 1995; Sammul *et al.*,

2000), grasslands (Foster, 1999) or deserts (Kadmon, 1995; Briones *et al.*, 1998). Even the study by Reader *et al.* (1994) which used twelve different sites located all over the world used a narrow range of standing crop, only one species, and seeds from a single source. It is worth noting that at the site with the highest range of standing crop in the study by Reader *et al.*, (1994), RIC and standing crop were positively correlated (Belcher *et al.*, 1995). Scale clearly has important implications and requires further empirical investigation.

I hypothesize that the range of species used may also have important consequences for interpretation of experimental tests of the UCC. Plants adapted to extreme temperatures have limited potential to acclimate to more benign temperatures (Björkman, 1981). Physiological adaptations to factors such as drought, frost and salinity increase a plant's ability to survive those conditions, but reduce its potential growth rate (Jones & Jones, 1989). Thus plants adapted to poor physical conditions may not have the potential to respond to a release from competition with increased growth, as the tree seedlings in this study did (Figures 5.3a & c). Furthermore, the intensity of the indirect effect whereby vegetation provides habitat for invertebrate herbivores, may decrease with NPP because of the reduction in suitable habitat. I thus predict that studies that use a broader range of habitats, and species that are adapted to those conditions will provide unequivocal support for the unified concept of competition.

I also hypothesize that the potential for *A. pycnantha* to facilitate establishment of tree seedlings will decrease with decreasing rainfall. In this study ants seem to have protected tree seedlings by reducing the abundance of invertebrate

herbivores. As the environment becomes more arid energetic constraints may limit the production of sugar from foliar nectaries (Janzen, 1966). Consistent with this hypothesis, Mackay (1991) found that ants did not protect eucalypt seedlings from invertebrate herbivory in a semi arid habitat - many of the invertebrate herbivores that he observed were hard bodied (presumably an adaptation to prevent desiccation) and may thus have been more resistant to ants. In this study the abundance of ants was inversely correlated with the abundance of soft-bodied invertebrates such as slugs (Figure 5.2f). It seems reasonable to suggest that as the environment becomes more arid, the proportion of invertebrates with hard-desiccation proof bodies will increase, and the potential for acacia spp. to gain protection from ants will decrease. If this hypothesis is correct then trees (e.g. eucalypts) associated with acacia spp. will also benefit less from the presence of ants.

### ***Summary***

The results presented here suggest that a logarithmic function is a good model of how the relative intensity of competition is related to fertility. In contrast to the bulk of experimental tests of the unified concept of competition, that have used artificial resource gradients (see Goldberg & Barton, 1992) these results support the UCC. This may be attributable to the fact that a relatively large resource gradient was used. It is concluded that a physical description of habitat (after Southwood, 1977) may be possible. However, the axes that define adversity in the models presented by Grime (1977), Southwood (1977) and Keddy (1989), will prove most relevant when a phenomenological definition of competition is used.

This is a result of the fact that invertebrate herbivory and resource competition are often confounded.

## Chapter 5

Table 5.1- Summary statistics for ANOVA's performed on plant attribute data from the glasshouse experiment. BN = Biological Neighbourhood.

Source of Variation	df	SS	F	Pr > f
<b>Avena (Weed) Biomass</b>				
Fertility	2	744.65	61.34	0.0001*
error	24	145.66		
<b>Eucalyptus camaldulensis: Emergence</b>				
Fertility	2	485.91	1.44	0.25
Avena Density	1	2308.84	6.84	0.003*
Fertility*Density	2	902.35	1.34	0.27
error	39	607.2		
<b>E. camaldulensis: Survival</b>				
Fertility	2	6.82	1.58	0.2174
Avena Density	1	40	18.61	0.0001*
Fertility*Density	2	4.86	1.13	0.3326
error	39	83.8		
<b>E. camaldulensis: Biomass</b>				
<i>(with three levels of fertility)</i>				
Fertility	2	42.7	33.88	0.0001*
Avena Density	1	86.27	136.63	0.0001*
Fertility*Density	2	42.77	33.87	0.0001*
error	39	24.62		
<b>E. camaldulensis: Biomass</b>				
<i>(with a low and intermediate level of fertility)</i>				
Fertility	1	25.04	133.05	0.0001*
Avena Density	1	26.39	140.27	0.0001*
Fertility*Density	1	24.83	131.94	0.0001*
error	26	4.89		
<b>E. camaldulensis: Biomass</b>				
<i>(with an intermediate and high level of fertility)</i>				
Fertility	1	1.31	1.38	0.2491
Avena Density	1	127.65	134.9	0.0001*
Fertility*Density	1	1.38	1.46	0.237
error	26	24.59		
<b>RIC of Avena and E. camaldulensis Seedlings:</b>				
<i>RIC Calculated with Biomass data:</i>				
Fertility	2	1.56	11.87	0.0014*
error	12	0.79		
<i>RIC Calculated with Survival data:</i>				
Fertility	2	0.641	2.3	0.1347
error	12	1.61		
<i>RIC Calculated with Biomass data</i>				
<i>(Biomass measured at a low and intermediate level of fertility):</i>				
Fertility	1	1.17	11.88	0.0087*
error	8	0.79		
<i>RIC Calculated with Biomass data</i>				
<i>(Biomass measured at an intermediate and high level of fertility):</i>				
Fertility	1	0	0.404	0.542
error	8	0.00001		

\* Indicates factors significant at the .05 level.

**Table 5.2- Summary statistics for ANOVA's performed on plant attribute data  
Data from the field experiment, spring census (september 2000)  
BN = Biological Neighbourhood.**

<i>Source of Variation</i>	<i>df</i>	<i>SS</i>	<i>F</i>	<i>Pr &gt; f</i>
<i>Allocauarina verticillata survival</i>				
fertility	1	0.136	1.71	0.1991
BN	3	2.38	10.04	0.0001*
fertility*BN	3	0.097	0.0409	0.7473
error	72	2.53		
<i>E. camaldulensis leaf number</i>				
fertility	1	8.45	0.135	0.7143
BN	3	863.35	4.59	0.0053*
fertility*BN	3	260.55	1.38	0.2534
error	72	4505.6		
<i>percentage of E. camaldulensis leaves with damage</i>				
fertility	1	0.0462	1.22	0.273
BN	3	1.96	17.2	0.0000*
fertility*BN	3	0.678	5.96	0.0011*
error	72	2.72		
<i>RIC for E. camaldulensis seedlings (leaf # data):</i>				
fertility	1	0.828	2.69	0.1065
BN	2	2.53	4.11	0.0217*
fertility*BN	2	0.197	0.3208	0.7269
error	24	16.6		
<i>RIC for A. verticillata seedlings (survival data):</i>				
fertility	1	0	0	1
BN	2	2.8	7.37	0.0032*
fertility*BN	2	0.288	0.759	0.479
error	24	4.56		

\* Indicates factors significant at the .05 level.

**Table 5.3- Summary statistics for ANOVA's performed on the abundance of invertebrates: spring census (september 2000)**  
**BN = Biological Neighbourhood.**

<i>Source of Variation</i>	<i>df</i>	<i>SS</i>	<i>F</i>	<i>Pr &gt; f</i>
<b>Spiders</b>				
fertility	1	1.65	0.85	0.3628
BN	3	38	6.55	0.0015*
fertility*BN	3	0.65	0.11	0.9524
error	31	59.9		
<b>Ants</b>				
fertility	1	56.69	0.966	0.333
BN	3	2271	13.37	0.0000*
fertility*BN	3	173	1.02	0.3956
error	31	1755		
<b>Slugs</b>				
fertility	1	0.218	0.098	0.755
BN	3	95.22	14.38	0.000*
fertility*BN	3	9.45	1.42	0.2532
error	31	68.4		
<b>Millipedes</b>				
fertility	1	19.69	1.54	0.2231
BN	3	141.09	3.69	0.0221*
fertility*BN	3	79.26	2.07	0.124
error	31	395		
<b>Collembola</b>				
fertility	1	19	0.735	0.3976
BN	3	13387	172.74	0.000*
fertility*BN	3	33.44	0.4315	0.7319
error	31	800.8		
<b>Dermaptera</b>				
fertility	1	4.89	0.056	0.813
BN	3	9.22	0.958	0.424
fertility*BN	3	3.65	1.8	0.16
error	31	52.8		
<b>Caterpillars</b>				
fertility	1	0	0	1
BN	3	1.35	2.05	0.126
fertility*BN	3	0.2	0.303	0.822
error	31	6.8		
<b>Slaters</b>				
fertility	1	1.104	0.084	0.7737
BN	3	53.69	1.36	0.272
fertility*BN	3	29.05	0.737	0.537
error	31	407.1		
<b>Worms</b>				
fertility	1	8.29	1.69	0.202
BN	3	38.41	2.62	0.068
fertility*BN	3	5.29	0.361	0.781
error	31	151.4		
<b>Beetles</b>				
fertility	1	0.218	1.4	0.244
BN	3	0.474	1.02	0.3967
fertility*BN	3	0.84	1.8	0.1662
error	31	4.8		
<b>Flying Ants</b>				
fertility	1	1.02	1.08	0.306
BN	3	4.06	1.43	0.252
fertility*BN	3	1.82	0.6427	0.593
error	31	29.4		

\* Indicates factors significant at the .05 level.



**Table 5.4- Summary statistics for ANOVA's performed on Plant attribute data. Data from the field experiment, summer census (march 2001). BN = Biological Neighbourhood.**

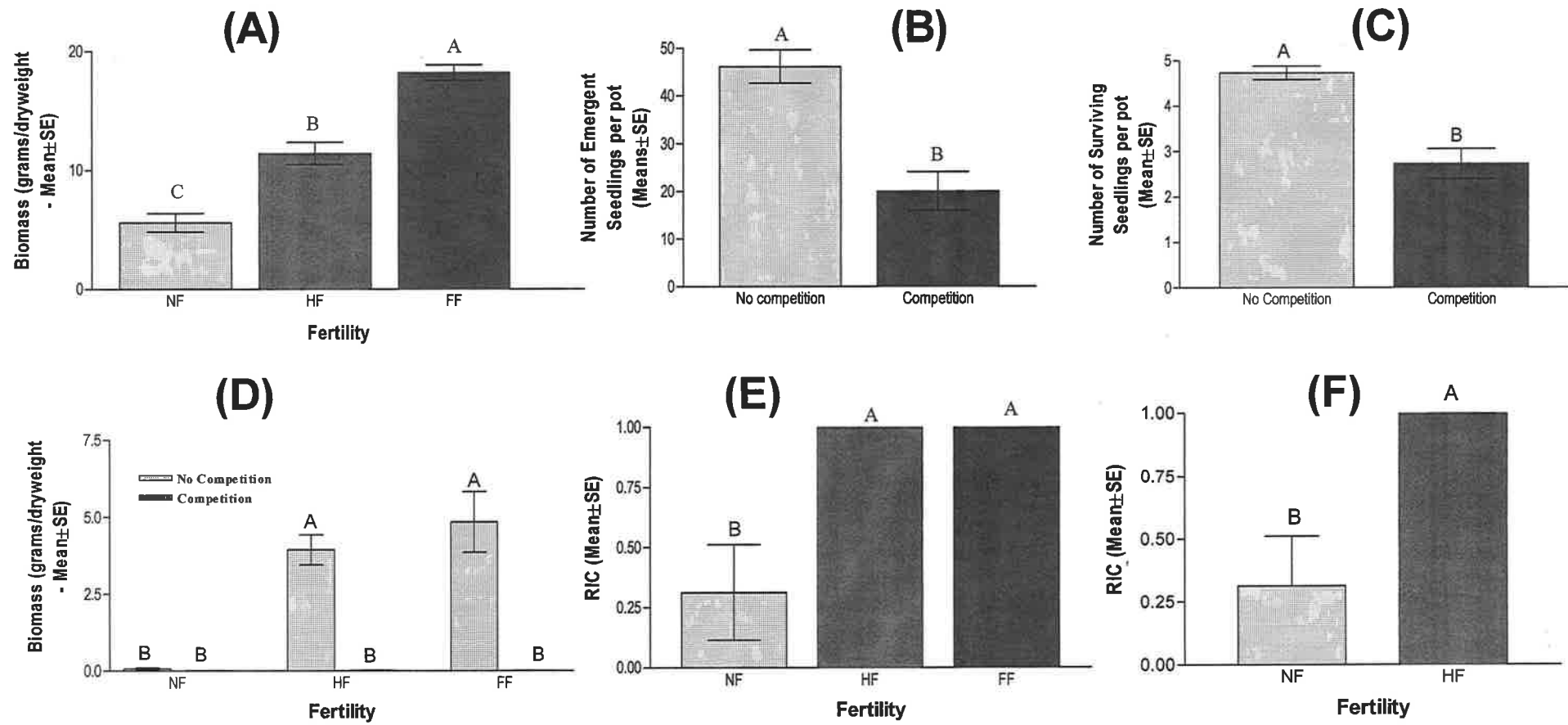
<i>Source of Variation</i>	<i>df</i>	<i>SS</i>	<i>F</i>	<i>Pr &gt; f</i>
<b><i>E. camaldulensis</i></b>				
<i>Biomass</i>				
fertility	1	4605.4	8.34	0.0069*
BN	3	36559.3	22.09	0.0000*
fertility*BN	3	14592	8.81	0.0002*
error	32	17649.6		
<i>survival</i>				
fertility	1	0.625	2.17	0.1501
BN	3	23.475	27.2	0.0000*
fertility*BN	3	0.675	0.78	0.5124
error	32	9.2		
<b><i>Allcasuarina verticillata</i></b>				
<i>Biomass</i>				
fertility	1	5.93	3.25	0.0806
BN	3	99.23	18.14	0.0000*
fertility*BN	3	19.04	3.48	0.0270*
error	32	58.32		
<i>survival</i>				
fertility	1	0.225	0.9	0.3499
BN	3	55.27	73.7	0.0000*
fertility*BN	3	0.275	0.366	0.7775
error	32	8		

\* Indicates factors significant at the .05 level.

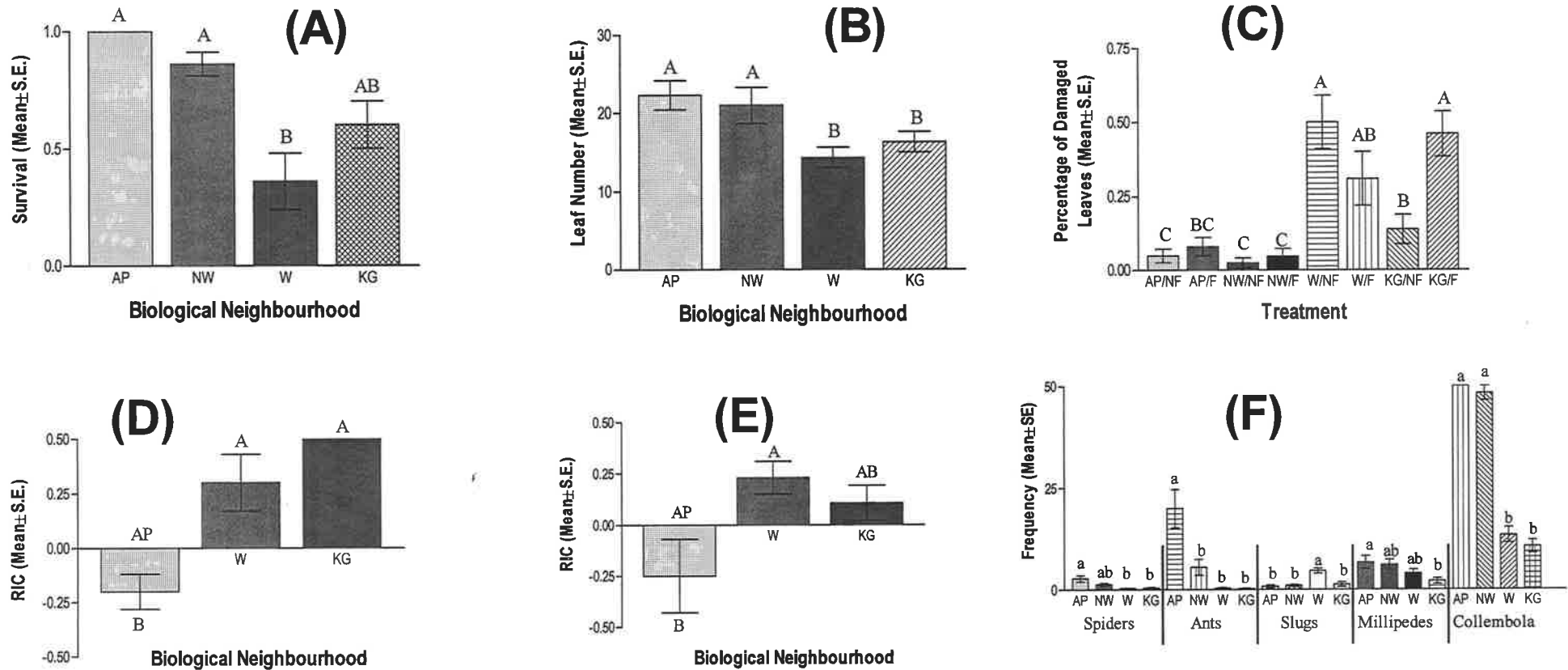
**Table 5.5- Summary statistics for ANOVA's of RIC calculated with biomass & survival data: field experiment, summer census (march 2001). BN = Biological Neighbourhood.**

<i>Source of Variation</i>	<i>df</i>	<i>SS</i>	<i>F</i>	<i>Pr &gt; f</i>
<b><i>Eucalyptus camaldulensis:</i></b>				
<i>RIC calculated with Biomass data:</i>				
fertility	1	0.149	12.48	0.0017*
BN	2	0.328	13.7	0.0001*
fertility*BN	2	0.1339	5.6	0.01*
error	24	0.286		
<i>RIC calculated with Survival data:</i>				
fertility	1	0.208	2.17	0.15
BN	2	4.11	21.4	0.0000*
fertility*BN	2	0.116	0.608	0.5522
error	24	2.3		
<b><i>Allocasuarina verticillata:</i></b>				
<i>RIC calculated with Biomass data:</i>				
fertility	1	0.1025	2.74	0.1103
BN	2	0.5548	7.44	0.0031*
fertility*BN	2	0.205	2.74	0.0841
error	24	0.8948		
<i>RIC calculated with Survival data:</i>				
fertility	1	0.112	2.01	0.1684
BN	2	4.09	36.8	0.0000*
fertility*BN	2	0.0018	0.0167	0.9835
error	24	1.3		

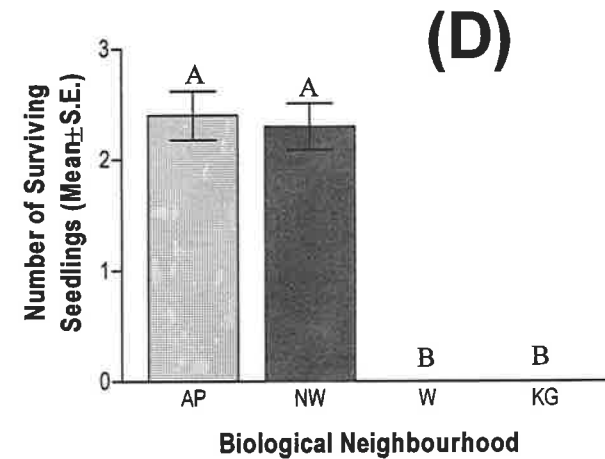
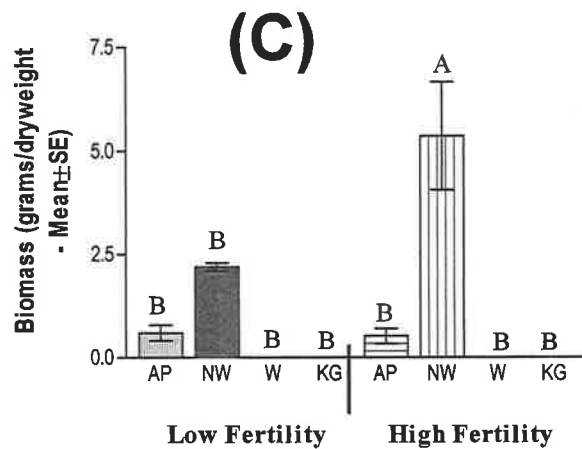
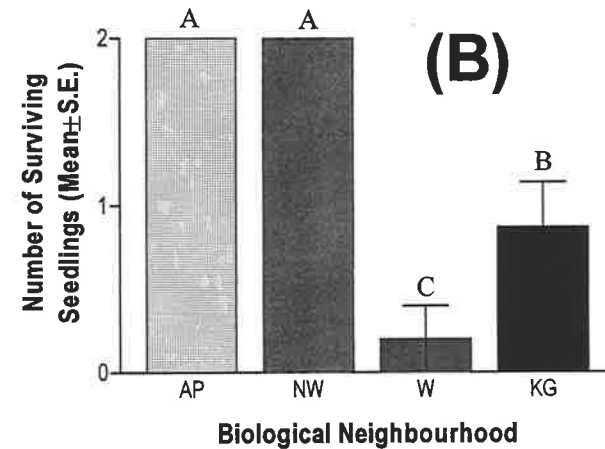
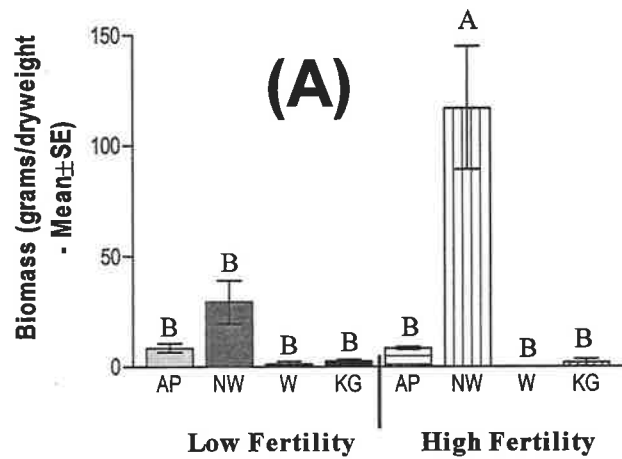
\* Indicates factors significant at the .05 level.



**Chapter 5. Figure 5.1:** (A) The effect of fertiliser application upon *Avena barbata* biomass. FF = fertiliser application at the recommended rate for horticulture (3g /pot). HF = fertiliser application at half that rate, and NF = no application of fertiliser. (B) Number of Emergent *E. camaldulensis* seedlings per pot, in response to increasing densities of *A. barbata*. NC = No Competition and C = Competition. For each level N=30. (C) The number of surviving *E. camaldulensis* seedlings per pot as a function of *A. barbata* density. (D) Biomass (grams of dry weight) of *E. camaldulensis* seedlings, at three levels of soil fertility and two levels of *A. barbata* density. (E) RIC of *A. barbata* and *E. camaldulensis*: RIC calculated with biomass data. (F) RIC of *A. barbata* and *E. camaldulensis* seedlings calculated at a low and intermediate level of soil of fertility (calculated with biomass data). All data (figures A, B, C, D, E & F) were analysed with ANOVA and Tukey-Kramer HSD test (see Table 5.1). Levels with the same letter are not significantly different.

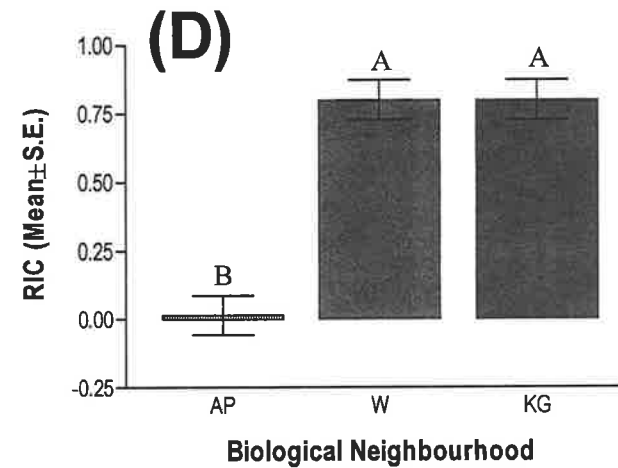
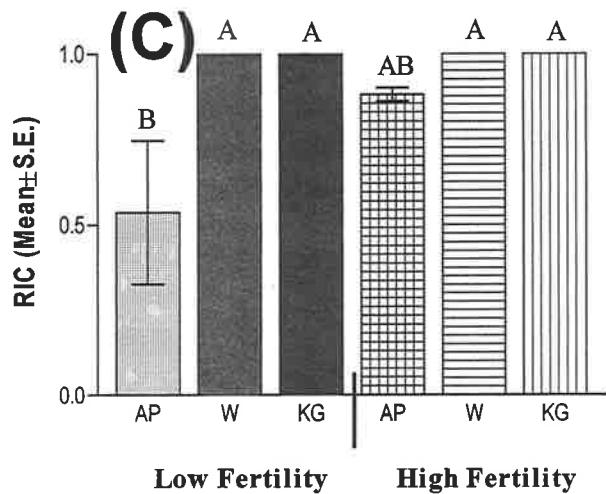
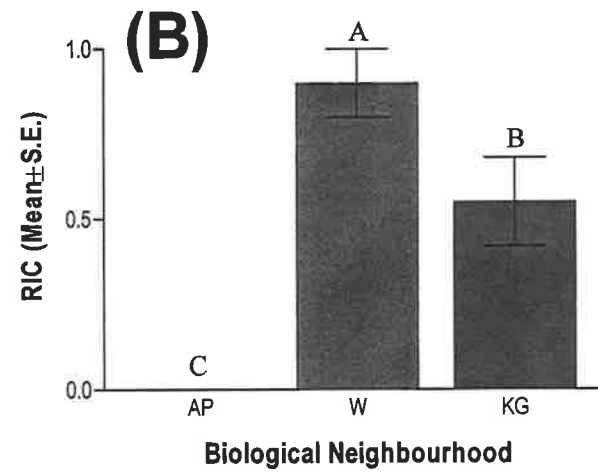
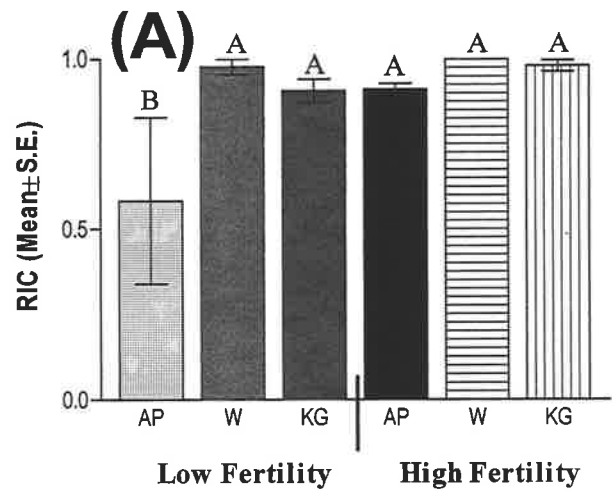


Chapter 5, Figure 5.2: Results from the census 3 months after the tree seedlings had been planted (springtime 2000). All data are analysed with ANOVA (see tables 2 & 3). Columns with the same letter are not significantly different (Tukey-Kramer HSD test). (A). Proportion of *Allocasuarina verticillata* seedlings alive after 3 months. AP = *Acacia pycnantha*, NW = No Weeds, W = Weeds and KG = *Themeda triandra* (Kangaroo Grass). (B). Mean number of leaves on *Eucalyptus camaldulensis* (Redgum) seedlings. (C). Proportion of *E. camaldulensis* Leaves with evidence of Insect Herbivory. NF = No additional fertilizer/water and F = addition of fertilizer and water. See part A for more detail. (D). RIC for *A. verticillata* in three different biological neighbourhoods. (E). RIC for *E. camaldulensis* in three different biological neighbourhoods. (F). The abundance of invertebrates in relation to microhabitat (biological neighbourhood), September 2000.



**Chapter 5, Figure 5.3:** Results from the census at the end of summer - March 2001. All data are analysed with ANOVA and Tukey-Kramer HSD test (see Table 5.4). Columns with the same letter are not significantly different. See Figure 5.2 for descriptions of the abbreviations. (A) Biomass of *E. camaldulensis*. (B) Survival of *E. camaldulensis*. (C) Biomass of *A. verticillata*. (D) Survival of *A. verticillata*.

A.



**Chapter 5, Figure 5.4:** Results from the census at the end of summer - March 2001. All data are analysed with ANOVA and Tukey-Kramer HSD test (see Table 5.5). Columns with the same letter are not significantly different. See Figure 5.2 for more detail. (A) RIC for *E. camaldulensis* when biomass data are used in the calculations. (B) RIC for *E. camaldulensis* when survival data are used in the calculations. (C) RIC for *A. verticillata* when biomass data are used in the calculations. (D) RIC for *A. verticillata* when survival data are used in the calculations.

## Chapter 6

### The effect of diffuse competition upon *Eucalyptus microcarpa* in a harsh abiotic environment

#### Introduction

There are two basic arguments that have been advanced regarding the intensity of competition in unproductive environments. Grime (1977) argues that competition should be of low intensity in harsh environments because the factors that limit the production of dry matter (e.g. abiotic stress) prevent plants from interacting.

Plants in more favourable habitats are able to achieve higher relative growth rates, and are therefore more likely to have overlapping resource depletion zones. In contrast Tilman (1982) argues that a superior competitor is a plant that can reduce the availability of a limiting resource to a level where its competitors are unable to obtain sufficient quantities of the relevant resource. Thus competition occurs at all levels of productivity, even though the resources that are the object of competition may change from light in productive environments, to soil resources in less productive environments. The two theories clearly diverge on the question of whether or not competition occurs when abiotic conditions are harsh.

Empirical studies have produced evidence that supports both arguments. Fowler (1986) reviewed the literature on competition in arid environments and concluded that competition does occur. Kadmon (1995) found evidence of competition between winter annuals (mainly *Stipa capensis*) when mean annual precipitation is as low as 100mm. Field experiments have also shown that the mechanistic basis of the resource ratio hypothesis is sound - plants that can reduce resource levels

below the minimum requirements of their competitors tend to dominate. For example, Burton and Bazzaz (1995) found that patches of *Solidago altissima* may inhibit photosynthesis in woody seedlings by reducing the amounts of nitrate in the soil to a level where rubisco construction is limited. However, there are also examples where harsh abiotic conditions seem to prevent the occurrence of competition. Donovan & Richards (2000) found that competition between *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* was of low intensity in a habitat where soil pH was generally >9.5 and mean annual precipitation averages 140mm. Similarly Harris & Facelli (in press) measured diffuse competition in a habitat dominated by *Carrichtera annua* (wards weed). This habitat has a mean annual rainfall of 230mm, and their data suggest that competition is of low intensity in this abiotically harsh environment.

I performed a competition experiment in a relatively unfavourable habitat. The mean annual rainfall of the field site is 690mm, but I performed the experiment on a ridge top where the soil was extremely shallow and rocky and as a consequence the mature vegetation is stunted. I chose this field site because I have measured relatively intense competition in the deeper soils in the gullies (Chapter 5), and hypothesised that the harsh abiotic conditions on the ridge tops might prevent competition from occurring.

## Methods

I collected seeds from *E. microcarpa* trees in the Waite Hills Reserve in September 1996, and grew *E. microcarpa* seedlings from seed in commercial seedling tubes during the summer of 1996/1997. In late autumn (May 1997) I planted these seedlings in the field, in plots with competing olive seedlings and pasture grasses (e.g. *Avena barbata*), or in plots without olive seedlings and pasture grasses. I had six plots with competition and six without. Into each plot 10 *E. microcarpa* seedlings were planted. Creating the two levels of competition was achieved by removing (hand pulling) olives and pasture grasses from the plots that were assigned no competition. In January 1999 (summer) I took a census of the experimental *E. microcarpa* population. I measured mortality per plot, the height, number of leaves, number of damaged leaves, trunk diameter and number of galls/seedling on all surviving seedlings. These data were analysed with one-way ANOVA. For the analysis of leaf damage I made the data proportional to give some indication of the level of herbivory occurring at the site.

## Results

Competition did not affect mortality, height of surviving seedlings, the number of leaves, trunk diameter, the level of damage inflicted by herbivores or the number of galls that were present on *Eucalyptus microcarpa* seedlings (Table 6.1).



## Discussion

This data supports the argument that competitive intensity is low when abiotic conditions are harsh. However, the results from this study need to be placed in the much larger context of the literature relevant to this question, which is often inconsistent. The fact that competition may be of high (e.g. Kadmon, 1995) or low intensity (this study) when abiotic conditions are harsh highlights the fact that the habitat templet (*sensu* Southwood, 1977; 1988) is a work in progress. There is a clear need to accommodate for the temporal dynamics of ecological systems. Goldberg & Novoplansky (1997) have drawn attention to this with their discussion on the pulsed dynamics of resource availability in arid systems. The importance of a temporal framework, and the pulsed dynamics of resource availability may best be understood by comparing this study (which was conducted in a relatively benign habitat), with the study by Kadmon (1995), which was conducted in an extremely harsh environment where annual rainfall may be as low as 100mm. Even so, Kadmon (1995) detected a positive correlation between productivity and competitive intensity. However, the annuals that Kadmon (1995) studied survive inter-pulse periods by producing seed. In a sense they are confined to the pulse period when resources are relatively abundant, whereas the perennials that I studied must survive the inter-pulse period. Over the relatively short growth season at the Jericho site (Kadmon, 1995), resource availability may have exceeded resource availability at my field site, per unit of time. Given that new studies that are relevant to this debate continue to accumulate, and continue to be inconsistent (e.g. Keddy *et al.*, 2000; Harris & Facelli, in press; Donovan & Richards, 2000; Peltzer *et al.*, 1998; Wilson & Lee, 2000; Sammul *et al.*, 2000; Grime *et al.*, 1997; Foster, 1999; Briones *et al.*, 1998) some basis for comparison

between papers seems warranted. I thus reiterate the need for a physical measurement of habitat (see Southwood (1977) who quotes Charles Elton (1966): 'definitions of habitats, or rather lack of it, is one of the chief blind spots in zoology').

It is important to note that the operational definition of competition that I have used in this experiment is a phenomenological one (a net effect). I measured relatively intense competition in the more productive gullies at my field site, but this competition was heavily confounded with invertebrate herbivory: pasture grasses may have inhibited the movement of predatory insects such as ants, and therefore sustained higher levels of herbivores such as slugs (Chapter 5). Indirect effects may also operate on the less productive ridge tops (this experiment). The low abundance of grasses may result in low levels of invertebrate herbivores. Furthermore, the large numbers of rocks on the ridge-tops may provide extra habitat for predators (e.g. snakes, lizards, scorpions, ants) and thereby reduce the level of herbivory. Regrettably, I did not measure the abundance of invertebrates or reptiles. However, the extremely low levels of herbivore damage on the ridge-top (less than 1% of leaves were damaged), and the extremely high levels in the gully (Chapter 5, Figure 5.2c) are consistent with these hypotheses. At the least, the results from this experiment suggest a line of future research into the character and intensity of indirect effects.

## Chapter 6

Table 6.1 - Summary Statistics for ANOVA's of  
*E. microcarpa* attributes

<i>Source of Variation</i>	<i>df</i>	<i>SS</i>	<i>F</i>	<i>Pr &gt; f</i>
<b><i>Mortality</i></b>				
competition	1	6.75	1.6	0.2345
error	10	42.16		
<b><i>Height</i></b>				
competition	1	26.13	1.437	0.2582
error	10	181.85		
<b><i>Leaf Number</i></b>				
competition	1	27.39	0.433	0.5254
error	10	632.64		
<b><i>Trunk Diameter</i></b>				
competition	1	0.2667	0.1576	0.6997
error	10	16.93		
<b><i>Proportion of damaged leaves</i></b>				
competition	1	0.0002	1.0137	0.3378
error	10	0.002		
<b><i>Number of Insect Galls</i></b>				
competition	1	0.0011	0.0372	0.8508
error	10	0.3024		

\* Indicates factors significant at the .05 level.

## Chapter 7

### A comparison of the growth plasticity of two Eucalypts and their response to competition

#### Introduction

The literature on the relationship between habitat productivity and competitive intensity is extremely inconsistent, and a large amount of this inconsistency may be related to scale (see Chapter 5). I hypothesize that similar considerations will also apply to the range of species used. The unified concept of competition (UCC) is an evolutionary concept and the use of a narrow range of species may be inappropriate. Species from relatively benign habitats have the ability to acclimate to a fairly wide range of physical conditions (Björkman, 1981). However, species that occupy more extreme habitats have a more limited potential for acclimation (Jones and Jones, 1989). Thus plants from favourable habitats may have the ability to respond to a release from competition with increased growth, whereas species adapted to infertile habitats will not possess the same ability, to the same degree. Thus studies that use a narrow range of species, from a narrow range of habitats may be predisposed to find no effect of fertility upon RIC. A large amount of work has been done on the UCC, but typically a narrow range of species has been used. Reader *et al.* (1994) measured RIC at twelve different locations in North America, Europe and Australia. However, they use only one species, from a single seed source, and use a narrow range of standing crop (compare Table 1 in Foster, 1999, with Table 1 in Reader *et al.*, 1994).

I conducted an experiment to determine whether the intensity of competition experienced by two species of eucalyptus increased with fertility. Natural populations of the two species of *Eucalyptus* occur in environments with different abiotic conditions. *Eucalyptus camaldulensis* (river redgum) is common along creek lines at my study site, and *E. microcarpa* (greybox) is more common on ridge tops where the soil is shallower, and the abiotic conditions are generally less favourable. I test the following null hypotheses: (1) The two species have a similar ability to acclimate to improved physical conditions – fertilisation, and (2) the effect of the interaction between fertility and competition is similar for the two species of eucalypt.

## Methods

I performed two glasshouse experiments to test these hypotheses. The first experiment was designed to test whether *E. camaldulensis* and *E. microcarpa* have a similar potential to acclimate to improved physical conditions. I grew the relevant species at two levels of fertility: either without fertiliser, or with fertiliser (Native Osmocote) applied at the recommended rate for horticulture (one kilogram/25 metres<sup>2</sup>: 3g/pot). I used 2 litre pots, filled with commercial potting mix and watered the pots with overhead misters for 10 minutes every second day. I grew 10 *E. camaldulensis* or 10 *E. microcarpa* seedlings in each pot. I had twenty replicates of each combination of species and fertility. I harvested 5 pots from each combination every month for 4 months, and calculated the mean weight of 10 seedlings. The experiment began on 16/4/2001, and finished on 16/8/2001. The tree seedlings that were harvested were oven dried for three days at 80°C. I analysed the data with two-way ANOVA and used fertility and species as factors.

I used the Tukey-Kramer HSD test for post-hoc comparison. Statistical comparisons were not made between harvest dates.

In the second experiment *E. camaldulensis* and *E. microcarpa* were exposed to a factorial combination of fertiliser application and competition from *A. barbata*. I used the same two levels of fertility that were used in the first experiment, and had two levels of competition. Tree seedlings were either grown with or without *Avena barbata*. To obtain a density of *A. barbata* representative of the conditions in the field, I used the seedbank at the Waite Hills Reserve. The experimental system that I used has a Mediterranean type rainfall regime, and there are a large number of exotic annuals that survive the extreme summer as dormant seeds. Most of these seeds can be found in the top three centimetres of the soil. I collected soil from the top 3cm of an oldfield at Waite Hills Reserve, midway between the ridge-tops and the creek-lines. I then determined the diameter of the 2L pots (9cms), and the weight of soil required to fill these pots to 3cms (450g). I then extracted the seeds from 450g portions of soil using a bread roller and sieve, and placed those seeds in pots that were assigned competition.

Seeds of *Eucalyptus camaldulensis* and *E. microcarpa* were purchased from a commercial supplier (Blackwood Seeds), and a fixed volume of seeds was added to each pot. I had ten replicates for each combination of species, fertiliser and competition (80 pots). I placed wooden skewers by the first 10 seedlings to germinate in each pot. I removed all the seedlings that germinated in excess of ten so that my measurement of seedling survival was standardised. The pots were watered with overhead misters for 10 minutes every second day. The experiment

began on 16/4/2001, and finished on 16/8/2001. The tree seedlings that survived were harvested and oven dried for three days at 80°C. The above ground biomass of *Avena barbata* was also harvested and oven dried at 80°C for three days.

Survival and biomass data for the tree seedlings were analysed with 2-way ANOVA and Tukey-Kramer HSD test. I used fertility and competition as factors and did not make statistical comparisons between the two species of eucalypt. The survival data for *E. camaldulensis* was also analysed with a non-parametric multivariate ANOVA (Freidman test) because of unequal variances. I also calculated the relative intensity of competition (RIC) of *A. barbata* and the tree seedlings. RIC is:

$$\frac{NC - C}{NC}$$

where NC is the dependant variable in the pots with no competition (e.g. biomass), and C is the dependent variable in the pots with competition (see Sammul *et al.*, 2000). I calculated RIC with survival and biomass data, and analysed the data with two-way ANOVA (using species and fertility as factors). Tukey-Kramer HSD test was used for post-hoc comparison.

## Results

Both *E. camaldulensis* and *E. microcarpa* responded to fertiliser application with increased growth. However, there was a significant interaction between species and fertility because *E. camaldulensis* seedlings in pots with fertiliser weighed twice as much as *E. microcarpa* seedlings in pots with fertiliser (ANOVA,

$P < 0.0006$ , Figure 7.1). Competition from *Avena barbata* caused a reduction in the number of *E. microcarpa* seedlings that survived (ANOVA,  $P < 0.038$ , Figure 7.2). The biomass of *E. microcarpa* seedlings was significantly affected by fertility, competition and the interaction of the two factors (Table 7.2). Release from competition resulted in increased biomass of *E. microcarpa* seedlings, but only in the pots with fertiliser (ANOVA,  $P < 0.0001$ , Figure 7.3). Competition caused a reduction in the number of *E. camaldulensis* seedlings that survived (ANOVA,  $P < 0.0014$ ). And this reduction was apparent with both the parametric, and non-parametric ANOVAs (see table 7.2). The effects of fertility and the interaction of fertility and competition were marginally non-significant (ANOVA,  $P < 0.076$  &  $P < 0.076$ , Figure 7.4). The effects of competition and fertility upon the biomass of *E. camaldulensis* seedlings were not independent (Table 7.2): Release from competition only resulted in increased growth of *E. camaldulensis* seedlings in the pots with fertiliser (ANOVA,  $P < 0.0001$ , Figure 7.5).

When biomass data was used to calculate RIC, the effect of species was marginally non-significant (ANOVA,  $P < 0.0694$ ), and the combined effects of species and fertility were additive (ANOVA,  $P < 0.1113$ ); however, the application of fertiliser resulted in more intense competition, and this relationship was similar for both species of eucalypt (ANOVA,  $P < 0.0001$ , Figure 7.6). Fertility, competition and their interaction did not affect RIC when survival data were used to calculate the ratio (see Table 7.2), although the effect of fertility was only marginally non-significant (ANOVA,  $P < 0.0783$ ). The biomass of *A. barbata* was not affected by 'competition' with eucalypt seedlings (ANOVA,  $P < 0.609$ ), or by the interaction of competition and fertility (ANOVA,  $P < 0.129$ ), but there was



more *A. barbata* biomass in pots with fertiliser than there was in pots without fertiliser (ANOVA,  $P < 0.0001$ , Figure 7.7).

## Discussion

The growth of *E. camaldulensis* seedlings in the pots with fertiliser was double the growth of fertilised *E. microcarpa* seedlings. However, the growth of *E. camaldulensis* and *E. microcarpa* seedlings was equally low in pots without fertiliser. These results support the argument that species from fertile microenvironments (e.g. *E. camaldulensis*) may be better able to respond to a release from competition with increased growth, than species from relatively poor microenvironments (e.g. *E. microcarpa*). However, because of the small number of species used ( $N=2$ ) these results lack generality. Furthermore, the results from this set of experiments did not support the second hypothesis. Although *Eucalyptus camaldulensis* was better able to acclimate to improved physical conditions, this did not result in more intense competition for that species. For both species of eucalypt competition was constrained by low nutrient supply (see Chapter 5): In the pots without fertiliser eucalypt seedlings were unable to respond to release from competition, with increased growth, and as a consequence the effects of competition and fertility were not independent. It should also be noted that my failure to falsify the second null hypothesis presented in this Chapter, may be attributable to the fact that I used such a limited range of species.

In retrospect, the glasshouse may have been the wrong place to perform an ecological experiment of this nature. Conditions in the glasshouse are exceptionally good for plant growth. Thus rather than having conditions that are

unfertile (pots without fertiliser) and fertile (pots with fertiliser), it is probable that conditions in the glasshouse were good (pots without fertiliser) and exceptionally good (pots with fertiliser). The failure to measure resources is again a major limitation of in study, and a mistake that I am unlikely to make again. However, the logarithmic relationship between fertility and RIC demonstrated in chapter 5, illustrates the limitations of studies in which the range of fertilities that are used, only represent the upper portions of the relevant fertility gradient.

Interpretation of the results from this experiment are also problematic because in the field *E. microcarpa* is more abundant where soils are shallow (e.g. on hill tops), and the grasses are fairly sparse and are roughly ankle height. Whereas *E. camaldulensis* is more common along creek lines where the conditions for plant growth are much better, and the grasses are densely packed and are more commonly waist height. It is difficult to ascertain the intensity of the biotic variables that each species of eucalypt experiences under field conditions with a glasshouse experiment. Collecting the *Avena* seed bank from ridge tops and creek lines for *E. microcarpa* and *E. camaldulensis* respectively may have improved the experiment (especially if the lower stature of the grasses upon the ridge tops has some genetic component). However, there would still be a need to compensate for the fact that abiotic conditions are harsher on hilltops. However, trying to incorporate these aspects into the experimental design would confound level of competition with species. I therefore conclude that field experimentation is required. This is especially important when indirect effects are considered (see Chapters 5 & 6). As previously stated, neighbouring vegetation may consume resources, but modification of the microenvironment also needs to be considered.

There is generally a greater abundance of invertebrate herbivores when more vegetation is present (Southwood *et al.*, 1988; Facelli, 1994; Bonser & Reader, 1995). Thus indirect modes of inhibition may be more important at productive sites, because of the extra habitat available to invertebrate herbivores (see Chapter 5). Further field experiments, along with a census of the invertebrate community present in the microhabitats occupied by the two species of eucalypt, may be more appropriate to address this question.

## Chapter 7

**Table 7.1 - The Ability of *Eucalyptus microcarpa* & *E. camaldulensis* to acclimate to improved physical conditions (Biomass data).**

<i>Source of Variation</i>	<i>df</i>	<i>SS</i>	<i>F</i>	<i>Pr &gt; f</i>
<b><i>Harvest 1</i></b>				
Species	1	0.21	18.46	0.0006*
fertility	1	0.04	37.27	0.0001*
Species*fertility	1	0.017	15.06	0.0013*
error	16	0.018		
<b><i>Harvest 2</i></b>				
Species	1	0.48	39.64	0.0001*
fertility	1	2.42	199.7	0.0001*
Species*fertility	1	0.54	44.6	0.0001*
error	16	0.093		
<b><i>Harvest 3</i></b>				
Species	1	4.33	23.17	0.0002*
fertility	1	14.71	78.65	0.0001*
Species*fertility	1	4.87	26.02	0.0001*
error	16	2.99		
<b><i>Harvest 4</i></b>				
Species	1	8.32	19.31	0.0005*
fertility	1	57.2	132.6	0.0001*
Species*fertility	1	7.78	18.04	0.0006*
error	16	6.89		

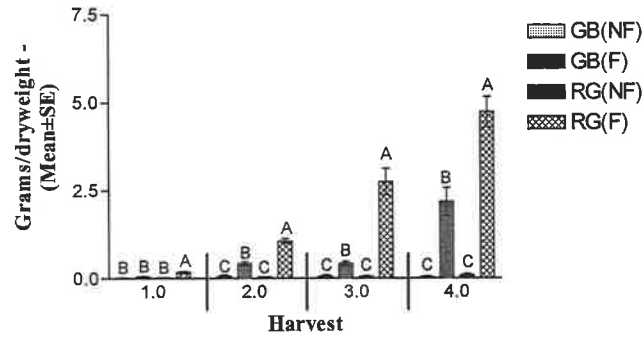
\* Indicates factors significant at the .05 level.

Table 7.2 - Summary of ANOVAs from the competition experiment

<i>Source of Variation</i>	<i>df</i>	<i>SS</i>	<i>F</i>	<i>Pr &gt; f</i>
<b><i>E. microcarpa</i></b>				
<b><i>Survival</i></b>				
fertility	1	0.2	0.03	0.863
competition	1	30.6	4.61	0.038*
fertility*competition	1	4.22	0.636	0.43
error	36	238.9		
<b><i>Biomass</i></b>				
fertility	1	5.61	110.6	0.0001*
competition	1	3.62	71.4	0.0001*
fertility*competition	1	2.85	56.2	0.0001*
error	36	1.82		
<b><i>E. camaldulensis</i></b>				
<b><i>Survival</i></b>				
fertility	1	18.22	3.33	0.076
competition	1	65.02	11.91	0.0014*
fertility*competition	1	18.22	3.33	0.076
error	36	196.5		
<b><i>Survival - non parametric multivariate AVONA (Freidman test)</i></b>				
fertility	1	18.22	3.33	0.0721
competition	1	65.02	11.913	0.0003*
fertility*competition	1	18.22	3.33	0.075
error	36	196.5		
<b><i>Biomass</i></b>				
fertility	1	22.78	1289	0.0001*
competition	1	16.68	944	0.0001*
fertility*competition	1	11.47	649	0.0001*
error	36	0.635		
<b><i>RIC calculated with Biomass data</i></b>				
species	1	0.0417	4.8	0.0694
fertility	1	0.341	39.2	0.0001*
species*fertility	1	0.0346	3.99	0.1113
error	36	0.304		
<b><i>RIC calculated with Survival data</i></b>				
species	1	0.0397	0.3229	0.5735
fertility	1	0.3458	3.2887	0.0783
species*fertility	1	0.0425	0.3458	0.5603
error	36	4.304		
<b><i>Biomass of Avena barbata</i></b>				
species	1	4.53	0.52	0.609
fertility	1	256.18	29.58	0.0001*
species*fertility	1	28.57	3.29	0.129
error	36	311.77		

\* Indicates factors significant at the .05 level.

**Growth of *E. camaldulensis* and *E. microcarpa* in response to fertilizer**



Chapter 7, Figure 7.1. GB = *E. microcarpa* (greybox), RG = *E. camaldulensis* (redgum), NF = no fertilizer and F = fertilizer. Columns with the same letter are not significantly different (ANOVA and Tukey-Kramer HSD test - table 7.1). Statistical comparison were not made between harvest dates.

**Survival of *E. microcarpa* as a function of competition**

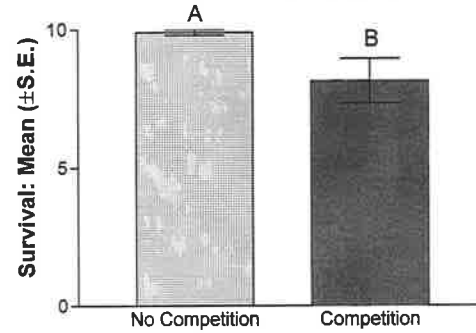


Figure 7.2. Columns with the same letter are not significantly different (ANOVA and Tukey-Kramer HSD test - table 7.2).

**The interactive effects of competition and fertility upon the biomass of *E. microcarpa* seedlings**

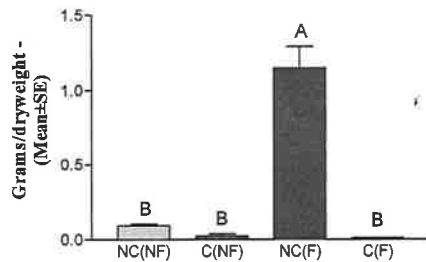


Figure 7.3. NC = No Competition, C = Competition, NF = no fertilizer and F = fertilizer. Columns with the same letter are not significantly different (ANOVA and Tukey-Kramer HSD test - table 7.2).

**Survival of *E. camaldulensis* as a function of fertility and competition**

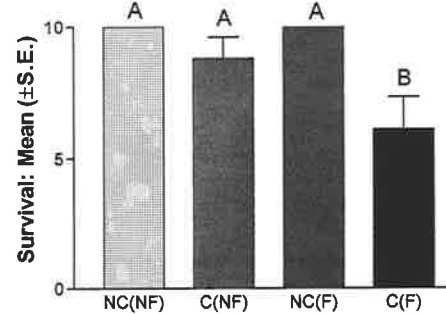


Figure 7.4. See figure 7.3 for more detail. Columns with the same letter are not significantly different (ANOVA and Tukey-Kramer HSD test - table 7.2).

The interactive effects of competition and fertility upon the biomass of *E. camaldulensis* seedlings

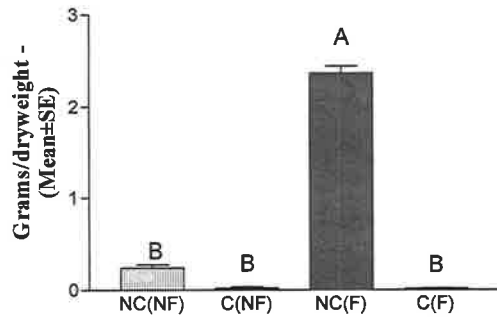


Figure 7.5. See figure 7.3 for more detail. Columns with the same letter are not significantly different (ANOVA and Tukey-Kramer HSD test - table 7.2).

The Relative Intensity of competition for *E. microcarpa* and *E. camaldulensis* as a function of fertility

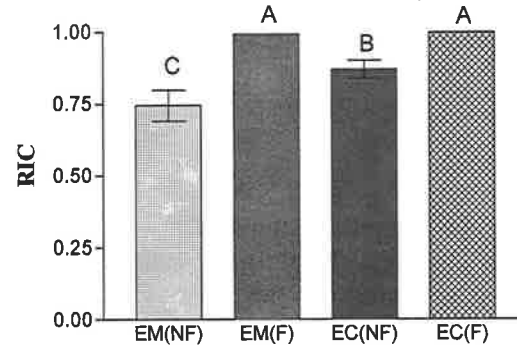


Figure 7.6. EM = *E. microcarpa*, EC = *E. camaldulensis*. See figure 7.3 for more detail. Columns with the same letter are not significantly different (ANOVA and Tukey-Kramer HSD test - table 7.3). Biomass data are used to calculate RIC.

Biomass of *Avena barbata* as a function of fertility

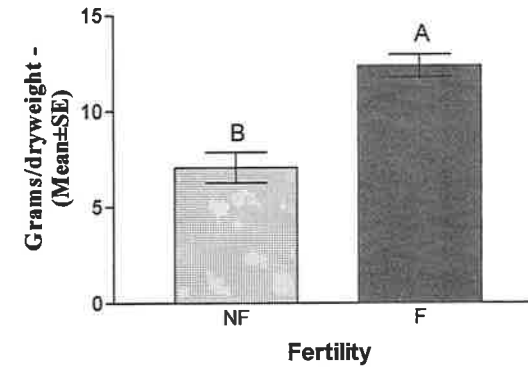


Figure 7.7. See figure 7.3 for more detail. Columns with the same letter are not significantly different (ANOVA and Tukey-Kramer HSD test - table 7.3).

## Chapter 8

### Conclusions and Suggestions for Further Study

The results from the literature review (Chapter 3) suggest that experimental design can have a big influence upon the results generated in an ecological study. Aside from considerations of replication and other factors necessary to meet the requirements of statistical tests, more consideration of logistical factors may be important (e.g. the range of neighbour densities – see Chapters 3 & 4).

Similarly the results from the glasshouse experiment described in Chapter 5 indicate that the range of fertilities used, may determine whether or not a positive correlation between fertility and RIC is detected: The existence of a logarithmic relationship between fertility and RIC suggests that previous studies may have failed to detect a correlation between fertility and RIC, because a narrow range of fertilities were used, and/or because the fertility levels used only represented the upper portions of the relevant gradient.

The results from this study also suggest that the UCC is most appropriate when a phenomenological definition of competition is used. The inhibitory effect of neighbouring vegetation upon the tree seedlings used in this study was in all probability, as much a result of invertebrate herbivory, as it was a result of resource competition. However, in both cases (for resource competition and for invertebrate herbivory), the lack of independence between neighbouring vegetation and fertility was attributable to the same underlying mechanism. In both instances 'competition' was constrained by low nutrient supply (see Reader,



1990). In plots (Chapter 5 & 6) and pots (Chapters 5 & 7) without additional resources, the tree seedlings growing without 'competitors' did not benefit from a release from 'competition', because additional growth was not possible in the absence of additional resources.

In common with a number of previous studies, my results suggest that resource competition and invertebrate herbivory can be heavily confounded (see Chapter 5 and references therein). Highly competitive biological neighbourhoods were also host to a relatively high abundance of invertebrate herbivores, and to a relatively low abundance of predators (see Chapter 5). I therefore conclude that the strict mechanistic definition of competition used by Grime (1977), in his seminal model, may be inappropriate in a generalised model of the plant niche. The model proposed by Grime (1977), and its underlying assumptions (e.g. UCC) should not be preserved in their original format. There is a large volume of empirical work relevant to the UCC, and the results from these studies should be used to modify the general framework (see Southwood, 1977). In the early tests of Grime's (1977) model, by Grime and his co-workers (Campbell & Grime, 1992; Turkington *et al.* 1993), absolute measures of competitive intensity were used. These have been abandoned in favour of relative indices (Grace, 1995 and McLellan & Fitter, 1997 discuss the virtues of relative indices). The use of mechanistic definition of competition should also be abandoned. As previously stated, many of the studies that support the UCC do so only in a phenomenological sense; positive correlations between RIC and productivity may be the result of a number of direct and indirect effects (e.g. resource competition and invertebrate herbivory (see Chapter 5). The substitution of a phenomeno-logical definition of

competition in the place of a mechanistic one is reasonable because both modes of thinking can be useful in the development of theory, and because theories are not static and should be subjected to 'continual revision'.

'Patience is a virtue in the application of theory. Premature rejection of a theory may deprive a field of a tool for integration and unification. Giving up on the development of a pre-theoretic notion can be a mistake. Because scientists are trained to be critical and because they are generally deeply influenced by the hoary philosophy of logical positivism and its falsificationist descendants, the risk of ill-advised acceptance of a young theory seems less of a danger than throwing the theoretical "baby" out with the empirical "gray water from the bath". Rather, we should become better at assessing the status and needs of theory, and discerning when a developing theory can engage in the rigorous discourse with reality.' (Pickett *et al.*, 1994).

This discussion seems particularly relevant to the UCC. Although there are a number of studies inconsistent with the UCC, these studies have generally used a narrow range of productivity and/or fertility. Furthermore the UCC enjoys wide support when a phenomenological definition of competition is used. Thus although there is a patent need for a more comprehensive, mechanistic understanding of the plant niche, the generalised model of the niche first envisioned by Hutchinson (1959; 1961), is at least beginning to emerge.

Although there is a wealth of empirical data relevant to the UCC, there is little consensus (see Wilson & Lee, 2000). In agreement with my predecessors, I therefore, argue that there is a need for a definition of environmental adversity that is based upon the physical environment (after Elton, 1966 *cited in* Southwood, 1977). This would avoid suspicions of circularity (Wilson & Lee, 2000), and such a definition could not be criticized on the grounds that disturbance and productivity are confounded, as they are on gradients of standing crop (Peltzer *et al.*, 1998). Such a definition would also enable comparison between studies. I

therefore propose a model, which expresses or describes 'environmental adversity' as a mathematical function. This model should be viewed as a hypothesis that requires empirical investigation, rather than as a conclusion.

Rainfall may prove to be an excellent parameter for a generalized model of the niche, and for 'environmental adversity' in particular. Experiments that use H<sub>2</sub>O gradients usually support the unified concept of competition (this study; Friedman & Orshan, 1974; Kadmon, 1995; Briones *et al.*, 1998; but see Reader & Best, 1989). Leith (1975) and Whittaker (1975) present a reasonably large dataset relating net primary production (NPP) to mean annual rainfall. They report a strong positive correlation between the two ( $r^2 = 70\%$ ). These data were collected as contributions to the International Biological Program and are predominantly from Europe (Lieth, 1975, Figure 12-2). Updating this data set to include more recent studies, and studies from a broader range of geographical locations may significantly improve the model. However, an  $r^2$  value of 70% is reasonable, and net primary production can be expressed as function of rainfall with an equation of the form:

$$\text{NPP} = M(1 + e^{\alpha\chi})$$

Where  $M$  and  $\alpha$ , are constants,  $e$  is the natural log base and  $\chi$  is rainfall (from Leith, 1975). There is a wealth of evidence to suggest that as NPP and/or standing crop increases, so does the intensity of invertebrate herbivory (see Chapter 5). As a result the intensity of invertebrate herbivory and rainfall may also be positively

correlated, which would further strengthen the case for a UCC, when competition is defined phenomenologically.

Other continuous variables that influence NPP can be incorporated into the model with ease. For example, if you assume that temperature affects NPP in the same way that it affects enzyme kinetics (e.g. with a maximum level of activity in the mid twenties and lower levels of activity above and below this temperature), then NPP can be expressed as a function of rainfall and temperature with an equation of the form:

$$NPP = \frac{M(1 + e^{\alpha\chi})}{(1 + e)^{\beta + \theta(T-25)^2}}$$

Where M,  $\alpha$ ,  $\beta$  and  $\theta$  are constants, e is the natural log base,  $\chi$  is mean annual rainfall, T is mean annual temperature. Figure 8.1 shows the output from an equation of this form at a range of temperatures (-10 to 60°Celsius) and rainfalls (100mm to 3600mm). Maximum temperatures are based upon data in Björkman (1981). The inclusion of temperature is only used as an example to demonstrate the ease with which continuous variables can be incorporated into the model.

Whether mean annual temperature affects NPP in the same way that it affects enzyme kinetics has not been demonstrated empirically to the best of my knowledge, however, it is at least a reasonable inference. The rate of photosynthesis is heavily dependant upon temperature because of the photosynthetic enzymes, and because temperature affects the ease with which CO<sub>2</sub> can diffuse through leaf tissues (Björkman, 1981).

Future research should measure the intensity of competition and herbivory at locations with different levels of rainfall and temperature, and test whether the intensity of either process tracks that of NPP as modelled in Figure 8.1. Soils are patently the Achilles Heel of the model that I present. Producing data inconsistent with this model would be as easy as selecting a field site with high rainfall and poor soil. Soils will complicate any attempt to produce a generalised model of the niche, because they are the N dimensional hyper-volume *par excellence* (see Tilman, 1982; Aerts & Chapin III, 2000). They vary, for example, in their availability of nutrients, their nutrient composition, their pH, and their structure. Soils are clearly an important component of the plant niche, and any comprehensive model would need to include them. However, because of their complexity they are a poor place to begin the construction of a generalised model of the niche. 'As always with classifications of nature, it is easy to find exceptions; the real challenge, the constructive work, is not find the exception, but to use this to improve, modify or even change the general framework' (Southwood, 1977). Soils should thus be used modify the general framework as opposed to being the foundation for a generalised model of the niche.

With regards to the habitat templet in general, studies of disturbance are rare (see Wilson & Lee, 2000), and empirical contributions are urgently required here. A generalised model of the niche that does not consider disturbance would be incomplete. However, with the wealth of inconsistent data generated on the question of competitive intensity and fertility, this empirical vacuum is perhaps

not surprising. Quantifying disturbance and placing it in the context of the habitat templet will be problematic, and represents a massive challenge to ecologists.

### **Summary**

In conclusion I have demonstrated that the intensity of competition may be positively correlated with fertility on an artificial resource gradient. My results also suggest that previous studies, which have used artificial resource gradients may have failed to detect a positive correlation between the two because small ranges of fertilities were used. My results also suggest that a physical description of environmental adversity may be possible, and that resource competition and invertebrate herbivory are so heavily confounded that the use of a phenomenological definition of competition may be reasonable.

## Chapter 8. Figure 8.1.

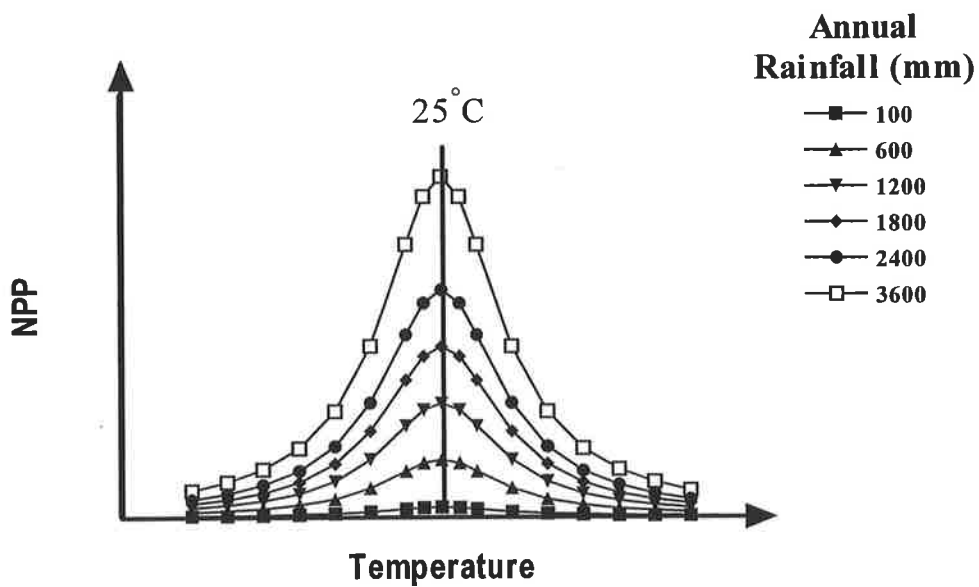


Figure 8.1. A model of Net Primary Production (NPP) as a function of rainfall and temperature. NPP is modelled with the following formula:

$$NPP = \frac{-M(1+e^{\alpha\chi})}{(1+e)^{\beta} + \phi(T-25)^2}$$

$M = 0.9$ ,  $\alpha = 0.00064$ ,  $\beta = 0.013$ ,  $\phi = 0.02$ ,  $e = 2.74..$ ,  $\chi =$  rainfall (mm),  
 $T =$  mean annual temperature, and  $\wedge =$  raised to the power of.

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