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ABSTRACT

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The evolutionary pathways and adaptational responses of the Australian flora to Late Tertiary-Quaternary climate change are yet to be fully elucidated. Congeneric species distributed across a precipitation gradient should possess different responses to water deficit, which may provide an opportunity to investigate the adaptations of plants to such climate changes. In southeastern Australia, four *Pittosporum* species (*P. bicolor*, *P. undulatum*, *P. revolutum* and *P. angustifolium*) occupy habitats with contrasting rainfall regimes. Climate analyses showed important differences in the climates of these species to be the higher temperatures and predominantly summer rainfall of sites supporting tropical and arid species, grading to winter-spring rainfall in the southernmost part of their distributions, compared with the temperate species.

Patterns of seasonal water relations indicated the greater ability of *P. angustifolium*, in comparison to the more mesic *P. undulatum* and *P. revolutum*, to decrease leaf water potential whilst maintaining low stomatal conductance during periods of maximum water deficit. Nevertheless, the latter two species exhibited considerable differences in the seasonal and diurnal water relations. Under common conditions of drought, species responses were broadly consistent with their seasonal field water relations. Maintenance of transpiration, stomatal conductance and high osmotic potential by *P. bicolor* indicated its low resistance to water deficit. *P. undulatum* exhibited high drought resistance, incorporating stomatal closure, osmotic adjustment and increased water use efficiency. *P. revolutum* and *P. angustifolium*, which decreased leaf water potential and displayed intrinsically low rates of transpiration and osmotic adjustment to water deficit, appear to possess very high resistance to water deficit.

The seed and seedling biology of these species revealed considerable intra- and interspecific variation in growth and biomass allocation variables, with seedlings of *P*. *undulatum* exhibiting the highest RGR. Species differed significantly in seed mass, with a broad pattern of decreasing seed mass with increasing latitude. Seedlings of species inhabiting permanently or seasonally dry environments exhibited higher specific leaf area and root:shoot ratio but lower specific root length, with the opposite pattern for those of species from wetter environments.

Species' responses to environmental variables were compared in terms of comparative germination rate and quotient. A lack of germination by *P. bicolor* seed indicated primary dormancy due to after-ripening or alternating temperature requirements. For other species, germination responses to temperature were broadly consistent with temperature variables across their distributions. *P. angustifolium* and *P. undulatum* seed germinated most rapidly but across a narrower range of temperatures than the more slowly-germinating *P. revolutum*. The slower germination and lower quotients of *P. angustifolium* and *P. revolutum* seed from populations subject to low rainfall and/or high seasonality illustrated their high degree of intraspecific variation. While *P. angustifolium* seed germinated readily under suitable field conditions of temperature and soil moisture, there was no seedling survival. However, this species demonstrated a high capacity for vegetative reproduction and a capacity to adjust reproductive allocation in response to climatic or biotic factors.

The close relationship between *P. bicolor* and *P. angustifolium* suggests the recent evolution and spread of the latter species into arid environments. However, differences between these species in selected life-history traits, and similarities in these traits amongst other *Pittosporum* species, contrast with their purported phylogenetic positions. This may be of evolutionary importance, as it suggests a capacity among these species for broad adaptive shifts, possibly in response to climate changes during the Late Tertiary-Quaternary, in life history traits such as seed size and germination biology, biomass allocation and reproductive strategy.

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DECLARATION

To the best of my knowledge, this dissertation does not contain material that has been accepted for the award of any other degree or diploma in any university or other institution and does not contain material previously published or written by another person, except where due reference is made in the text.

I agree that this thesis may be made available for photocopying and for consultation within the university. I note that my consent is required only to cover the three-year period following the approval of my thesis for the award of the degree of Doctor of Philosophy.

Gerry Rayner

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CHAPTER 1. GENERAL INTRODUCTION

Australia's arid and semi-arid zones, which together cover more than 80% of the continent (Fig. 1.1; Burbidge 1960; Truswell and Harris 1982), are characterised by low to very low and unpredictable rainfall and often extreme daytime temperatures. Nevertheless, these areas exhibit a high degree of spatial heterogeneity and floristic diversity (Williams 1982). The origins and evolutionary pathways leading to the development of Australia's semi-arid and arid zone flora are not yet fully understood, due largely to limitations and biases in the plant fossil record and problems with accurate determinations of fossil pollen affinity (Truswell and Harris 1982). There is, on the other hand, appreciation of the importance of climate as a determinant of plant species distribution and greater understanding of the role of climate change as a driving force for non-anthropogenic, long-term changes in vegetation. Thus, knowledge of the differences in life history traits among closely related species distributed across an environmental gradient from mesic to arid might provide information about the ways that the Australian flora responded to the marked climate changes of the late Tertiary.

Climate and other environmental variables, including disturbance, are major determinants of plant distribution and the composition and extent of vegetation communities. Thus, changes in climate may greatly affect plant distribution and vegetation composition, but also rates of plant evolution and the adaptations that arise in response to such changes. The broad scale climatic changes of the Tertiary, together with the dramatic climatic oscillations of the Pleistocene, must have had profound impacts on the nature of the dominant plant groups and their distribution. As Martin (1994) noted, it is taxa rather than vegetation communities that migrate and/or evolve in response to climate change, with changes in vegetation occurring at both a relatively constant rate through species migration and extinction, as well as over quite short time scales. Plant migration is affected by a number of factors, including rates of climate change, inherent characteristics of species including regeneration and reproductive biology and morphological and physiological attributes, and biotic interactions including propagule dispersal and predation. Climatic and tectonic changes that culminated in the development of Australia's arid zone flora began during the Cretaceous, when spreading between the Indo-Australian and Antarctic plates resulted in the formation of a proto-Southern Ocean, approximately 110 Ma (Veevers 1984; Veevers *et al.* 1991; Wilford and Brown 1994; Frakes 1999). During this period, Australia's climate was warmer and wetter than at present (Kemp 1981) with rainforest-type vegetation dominating at both spatial and temporal scales (Truswell 1993). By the mid-Eocene (*c.* 45 Ma), the continued northward drift of Australia had resulted in the initiation of weak westerly currents in the Southern Ocean. However, a full circum-Antarctic current was not to develop until circa 40 Ma (Wilford and Brown 1994) or perhaps even as late as 30 Ma (Quilty 1994), presumably following final separation of South America from Antarctica (Parrish 1987). The climatic effects of this current included increased cooling of Antarctica and adjacent marine areas, and the development of a dominant westerly airstream that prevails to the present day in southern Australia.

The northward movement of Australia also sharpened the latitudinal gradient in sea surface temperatures, resulting in a repositioning and intensification of a belt of subtropical high pressure cells over central-southern Australia (Bowler 1982). The long-term effects of these dry, descending air masses included decreasing rainfall and more defined rainfall seasonality (Bowler 1982), with predominantly winter rainfall (Kemp 1978). From about 10 Ma, the expansion of Antarctic ice exacerbated the existing aridity in Australia, particularly in the interior (Wilford and Brown 1994).

Thus, during the late Tertiary, large areas of Australia experienced substantial changes in climate, including decreased precipitation and the development of seasonal periods of water stress. In south-eastern Australia, there was a gradual but significant decrease in annual rainfall from around 2000 mm in the late Eocene to levels of between 800-500 mm in the late Pliocene-Pleistocene (Martin 1990a). Increasing aridity in south-eastern Australia was accompanied by other climate changes, including decreasing mean temperatures (Sluiter 1992) and increased temperature seasonality (Truswell 1993). In terms of ecological significance, Bowler (1982) considered the hydrologic oscillations over the last 400,000 years to have had the biggest impact on the flora due to their amplitude and rapidity of change. As a consequence of the major climatic changes described above, there was a gradual fracturing of the complex Australian rainforest expanse during the mid-Tertiary, which accelerated about 15 million years ago (Kershaw 1992; Martin 1994). This culminated in the (present day) restriction of rainforest to a series of disjunct refugia along the eastern seaboard (Kershaw et al. 1991; Bowman 2000) and the development and expansion of open woody and herbaceous communities. The transition from rainforest to open communities is considered to have been a gradual process, lasting from the late Miocene to the Late Pliocene or even into the Pleistocene (Kershaw 1988). In southeastern Australia, the vegetational changes included a shift from the tropical Nothofagus brassii type to the N. fusca and N. menziesii types typical of the present day floras in New Zealand, southern South America and Tasmania (Christophel 1995; Kershaw 1988). While sclerophyllous taxa, including occasional grassland types, first appear in the late Eocene, it is during the Miocene that such taxa (including *Eucalyptus*) diversify and become more apparent in the fossil record (Truswell and Harris 1982; Boland et al. 1990; Martin 1990b; Hill et al. 1999). Although the radiation and abundance of sclerophyll-type taxa indicate a drier inland environment, none of the assemblages could be classified as truly xerophytic (Martin 1994).

Following further climatic declines in the Pliocene, extant grasslands and woodlands supporting species belonging to the Poaceae, Chenopodiaceae, and Asteraceae expanded greatly throughout present day semi-arid and arid Australia (Truswell and Harris 1982; Truswell 1990; Sluiter 1992; Kershaw *et al.* 1994; Martin 1994). Nevertheless, truly arid landforms such as linear sand dunes and salt lakes do not appear until the Pleistocene (Wasson 1982), which indicates that inland aridity did not reach its present proportions until *c.* 500,000 years ago (Bowler 1982). Together with the massive expansion of the eucalypts in the later part of the Pleistocene (Hill *et al.* 1999; Sluiter and Kershaw 1982; Sluiter 1992; Dodson and Kershaw 1995), these findings support the hypothesis that the current Australian arid zone flora may not have been fully developed until the mid-to-late Pleistocene (Burbidge 1960; Martin 1982).

Thus, in Australia's desiccated interior during the late Tertiary, habitats were being created for woody taxa pre-adapted to a climatic regime of mid-to-high temperatures, low humidity, shallow, sandy and nutrient poor soils, and, critically, low and unpredictable rainfall. However, as Bowler (1982) pointed out, the exploitation of such

habitats by plants may lag significantly behind the climatic or ecological changes to which such plants respond. Superimposed upon these longer-term climate changes are the effects upon vegetation of periodic El Nino Southern Oscillation events, to which semi-arid Australian taxa may also possess unique adaptations (Nicholls 1991). In considering the above aspects of climate change, a question arises as to the timing, origin and evolution of xeromorphism in the Australian flora. The geographic isolation of the Australian Plate for much of the Tertiary (Frakes *et al.* 1987), exacerbated by the location of developing aridity towards the interior of the Australian continent, would have prevented dispersal by the vast majority of suitably adapted taxa from Africa or the Americas. Furthermore, semi-arid communities supporting suitably-adapted flora do not appear until the mid-Miocene in East Africa (Van Couvering 1980) and the Pliocene in Chile (Arroyo *et al.* 1995). These factors, compounded by large differences in soil fertility between Australia and these continents, support the hypothesis that Australia's arid and semi-arid flora is largely autochthonous in nature (Martin 1982).

There has been considerable debate regarding the origins and purported migration routes of Australia's present-day arid flora (Carolin 1982). The hypotheses proposed to account for this can be classified into two main groups. The first hypothesis is that the flora is derived from species that occupied the area before it became arid, as well as from proximate rainforest species that already poss_____d some degree of tolerance to drought and high incident radiation loads (Truswell and Harris 1982; Werren and Sluiter 1991). This hypothesis is supported by the long-recognised taxonomic affinity between xeric and mesic vegetation (Herbert 1950) as well as links between arid and rainforest elements (Sluiter 1992). The second hypothesis is that elements of the flora have evolved from pre-adapted littoral species that invaded the region as aridity developed. Support for this hypothesis is based upon similarities in floristics and structure between arid and littoral vegetation (Gillison 1987), a proposition that develops and extends an idea first suggested by Tate (1887) and later supported by Smith-White (1959) and Burbidge (1960).

XEROPHYTISM AND ITS EVOLUTION

Australian arid and semi-arid environments support species from a diverse range of families. Xerophylly (by definition) represents the end-product of evolution of characteristics that minimize water loss in arid environments. These characteristics may be inherent aspects of the morphology and physiology of species, or may develop at different stages in the life history of a plant, in response to ontogenetic or environmental cues.

Adaptively important seed and seedling traits of xerophytes include the promotion of germination or maintenance of dormancy in response to environmental conditions or cues. Thus, many arid species produce seed that will germinate only after several wetdry cycles (Lush *et al.* 1984) or sufficient rainfall to leach inhibitory materials from the seed coat (e.g. Beadle 1952). Another characteristic of arid zone species is the production of different seed types, the proportions of which vary, depending upon such factors as soil moisture availability during seed set or the timing of flowering during the year (Anderson 1982).

The seedlings of many arid zone woody taxa exhibit rapid rates of root elongation, which enables such plants to access soil water from increased depth following rainfall events, thereby increasing their likelihood of survival following germination. Arid and semi-arid species often have extensive root systems, comprising a network of surface roots that access soil moisture resulting from rainfall pulses, as well as taproots that can access more stable reserves of water (Noy-Meir 1973).

Morphological characteristics associated with xerophytism mostly relate to minimising water loss and include seasonal reductions in leaf surface (Cunningham and Strain 1969), leaf loss (Orshan 1963), or changes in leaf inclination, which serves to increase light reflectance from the leaf surface, thereby reducing thermal loads and rates of transpiration (Anderson 1982). Leaf inclination is often tied to other leaf characteristics, such as increased waxiness or pubescence, which further reduce cuticular or stomatal water loss. Other leaf characteristics that restrict water loss include the possession of a thick cuticle and few but relatively large stomata, which may be sunken or enclosed beneath projections of the leaf surface and a more than one layer of palisade parenchyma (Jordaan and Kruger 1992).

Many xerophytic taxa display very low leaf water potentials, often a result of osmotic adjustment, which increases their ability to extract water from a drying soil. They may exhibit higher intrinsic water use efficiency during periods of seasonal water stress (Anderson 1982), by stomatal closure or other mechanisms that result in reduced transpiration. This, together with the normally high allocation of resources to root structures (Stafford Smith and Morton 1990), means that many xerophytes are slow-growing (Parsons 1968), which is nevertheless advantageous where they have continued access to soil water (Noy-Meir 1973).

Many arid zone species are able to time flowering, seed set, dispersal and germination with climatic conditions that are most favourable for successful reproduction. However, for many other species, germination is largely a trial-and-error strategy almost every year, although seed maturation may occur over a long period, thereby increasing the slim likelihood of successful germination and seedling survival. Many xerophytes have the capacity for vegetative reproduction, which reduces the requirement for seedling establishment and increases longevity (Bond and Midgley 2001).

Although there is an extremely diverse range of traits that enable species to inhabit arid and semi-arid environments, as Anderson (1982) pointed out, none of these traits could be reasonably regarded as a unique adaptation to aridity. Rather, it is a combination of such traits in a plant that enables it to survive in environments characterised by high and fluctuating diurnal temperatures and provision of little rainfall, the delivery of which is an unpredictable and largely stochastic occurrence.

The response of an organism to its environment is the product of genetically derived aspects of morphology and physiology, interacting with environmental variables, and modified through processes such as competition and predation (Nix 1982). Patterns of plant life histories, and the suites of characteristics that comprise them, including the modes and timing of reproduction, seed biology and germination requirements, growth and biomass allocation, plant longevity, physiological responses to disturbance and environmental stresses, and leaf anatomy and morphology may frequently be adaptive in nature. The integration of these plant life-history traits may provide a better understanding of the patterns of species dominance at large spatio-temporal scales (Zavala *et al.* 2000). In addition, a more thorough understanding of the interactions

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between organisms and environmental variables should provide valuable information about the timing and pathways of adaptation within phyletic groups, and of broader scale patterns of plant response to climate change (Nix 1982). Such study is essential in order to better understand the nature of a plant's 'fit' in its environment and the ways that species may respond to local or more widespread environmental changes. Therefore, a better understanding of the links between functional ecology and adaptation and the subtle differences in these between phylogenetic units may be powerfully predictive, for both adaptive shifts that have occurred in the past, as well as those that may occur in the future.

Pathways of speciation in phyletic groups may be difficult to discern, but are important in terms of questions about plant responses to long-term changes in climate. The physiological and morphological differences among members of a taxonomic group (e.g. within a genus) are likely to be much smaller than those between groups (Smith and Huston 1989). This may be useful where related species share many characteristics of their biology, but are distributed across an environmental gradient. Hence, the study of such characteristics within a taxonomic group, in conjunction with environmental variables, may provide insights into the adaptations of plants to past climate changes (Gibson 1996), such as occurred in Australia during the late Tertiary and Pleistocene (Hope and Kirkpatrick 1988) and is a powerful way of predicting future responses to environmental change (Anderson *et al.* 2000). At the community level, measurement of the ecophysiological variability among taxa provides a better understanding of the history of Australian forests (Hope and Kirkpatrick 1988).

Truswell (1993) suggested that in order to gain an accurate understanding of the ways in which Tertiary desiccation shaped the phytogeography of the Australian flora, research must include not only that of palaeoclimate and the fossil record, but also the comparative ecophysiology of species. Ecophysiological studies of closely related species occupying latitudinal or environmental gradients have been most useful in that respect, as plant water relations of species, due to the interrelated suite of characters, may be less flexible in evolutionary terms to climatic change than changes in photosynthetic responses to temperature or frost resistance (Read *et al.* 1990). Such comparisons have also provided valuable information regarding phylogeny (e.g. Robichaux *et al.* 1986) and the evolution of adaptations to stress (Mooney 1980).

Elucidation of the ecophysiclogical variables of species occupying distinct sites may provide important information about the relationship between climate and distribution (e.g. Scarano *et al.* 2001). Selection for ecophysiological traits resulting in intraspecific variation in drought tolerance may occur over small gradients in soil moisture availability (Farris 1987). Slight shifts in morphology, such as variation in the length or density of epidermal trichomes, or physiological performance including temperature acclimation or osmotic adjustment, have been shown to result in an increased ability to survive water stress (Anderson 1982).

In addition to the ecophysiological characteristics of established plants, relationships between the physical environment and aspects of seed germination, including dormancy, germination rate and seedling growth and survivorship have been recognized as vital in determining the distribution and population dynamics of species (Grubb 1977; Bazzaz 1979; Rhodes *et al.* 1996). For widely-distributed species, once the degree of intraspecific variation in germination and seedling biology is known, interspecific comparisons of germination biology can be made, allowing development and testing of theoretical models for the adaptive nature of germination response to different environments or to changes in climate (e.g. Clauss and Venable 2000).

Australia's arid environments are relatively young, and a study of xeromorphic and sclerophyllous species that have evolved in response to the stresses imposed by changes in climate provides opportunities to both better understand the mechanisms of past responses to climate change, and predict how species might respond to future changes in climate. Most previous studies have examined characteristics of arid zone taxa and inferred adaptive significance. However, as a genotype may express different phenotypes in different environments, an indication of its phenotypic plasticity (Bradshaw 1965; Sultan 2000), it is necessary to gain an understanding of the morphological and physiological variation within species before ascribing potential adaptive value.

Whilst phenotypic plasticity can be expressed either morphologically or physiologically, all changes are physiological in origin, and therefore plasticity is essentially physiological in origin (Bradshaw 1965). Furthermore, plasticity may involve metabolic adjustments that do not alter the development and morphology of an individual plant (Hughes *et al.* 1993). As phenotypic plasticity can be responsive to environmental changes, if the metabolic or morphological adjustments allow an individual to survive environmental stress, then they must be of some adaptive value (Smith 1990). The difficulty in understanding the causes and mechanisms of phenotypic plasticity is due both to the complexities of developmental and physiological pathways and the interactions between such pathways and the environment (Bradshaw 1965). As phenotypic plasticity and genetic differentiation may be considered to be alternative adaptive strategies, it is therefore possible that one species may exhibit the former strategy in response to an environmental factor, while a closely related species displays the latter.

RESEARCH AIMS AND APPROACH

In south-eastern Australia, four *Pittosporum* species (family Pittosporaceae) are distributed across a precipitation gradient, from *Pittosporum bicolor* in cool temperate rainforests and wet sclerophyll forests, through *P. undulatum* and *P. revolutum* in wet sclerophyll forest and seasonally dry rainforest, to *P. angustifolium* in semi-arid and arid open woodlands. The species appear to be closely related and have been grouped within a larger subset of the Australian species (Cayzer *et al.* 2000: Fig. 1.2). If the general paradigm for the evolution of Australia's xeric flora is from rainforest progenitors with mesic traits, because of its distribution *Pittosporum* is an ideal genus upon which to test these ideas. The over. 'I aim of this thesis was to use these four species to explore the nature of evolved plant responses to water deficits.

The main questions to be explored are:

- 1. How do these closely related species differ in their responses to water deficit?
- 2. How do these different plant responses relate to differences in the rainfall regimes of these species?
- 3. How do these different plant responses relate to the phylogenetic relationships among these species? In particular, is there evidence of pathways of development of drought resistance traits?
- 4. What do these patterns indicate about the autochthonous / allochthonous origin of Australia's arid and semi-arid flora?

There are two main methods for elucidating the effects of long-term changes in climate on plants. The first is by studying pollen and macrofossil material dated to a specific time, and correlating this with aspects of their physiology and distribution. In such comparisons, the assumption is that the ecophysiological characteristics being measured will not have changed substantially in the intervening period, with differences among species representing selection that confers increased fitness across the environmental gradient. However, many taxa lack a suitable fossil record. In the second method, comparisons of the morphological, reproductive and ecophysiological attributes of extant species, either of species assemblages from contrasting environments or of closely-related species distributed across an environmental gradient can potentially provide valuable insights into evolved responses to climate, particularly when the phylogeny of the taxa has been established.

The advantage of comparing species assemblages from contrasting environments is a better understanding of the general adaptations, due to convergent or parallel evolution, in such environments. However, such comparisons may be difficult to interpret due to variation in the responses of species to interacting variables. The advantage of comparing closely related species is that physiological or morphological differences that reflect selection for adaptations to their different environments can be mapped onto their phylogeny, thereby allowing the pathway of adaptation to be traced with the evolution of the species. The disadvantage, of course, is phylogenetic constraint, which may lead to pathways being highly specific to those taxa, rather than generalized among broader groups of taxa.

Previous investigations of the interspecific variation in drought tolerance have commonly used single populations of each species. However, as many plant species exhibit considerable intraspecific variation in a wide variety of traits including seed biology and germination rate, drought resistance, growth rate and reproductive output (Venable 1984), investigation of the intraspecific variation in selected characteristics was carried out to better establish the genetic 'distances' between species.

PITTOSPORACEAE

Pittosporaceae is a family of some 200 to 240 species (Willis 1973; Carlquist 1981) belonging to ten genera (Cayzer *et al.* 2000). *Pittosporum*, the type genus for the family, comprises approximately 150 species, distributed throughout the Indo-Australasian region. Two genera, *Hymenosporum* (1 sp.) and *Citriobatus* (6 spp.), have species in southeast Asia (Carlquist 1981), and the other seven are endemic to Australia. Apart from *Rhytidosporum* and *Billardiera*, several of the endemic genera are xerophytic, which Schodde (1971) suggested is a result of late Tertiary desiccation in Australia.

At the family level, there is great diversity in both physiology and morphology. In revisions of the family by Bentham and Hooker (1862) and subsequently by Pritzel (1930), the family was divided into two tribes, the Pittosporae and Billardiereae (syn. Billardieae). This was also the system adopted by Morley and Toelken (1988). Subfamily classification was based on fruit succulence, with the former tribe comprising genera that produce woody or leathery capsules, while those in the latter produce more succulent berries (Cooper 1956). An alternative phylogeny for the family, initially proposed by Crisp *et al.* (1989) and recently tested and extended by Cayzer *et al.* (2000) is that *Citriobatus* (in the Billardieae of Bentham and Hooker (1862) and Pritzel (1930) is congeneric with *Pittosporum*, and should be included in that genus.

The distribution of the Pittosporaceae, together with the high degree of endemism at both genus (Cayzer *et al.* 2000) and family levels and degree of diversity among species, support the contention that the Indo-Australian region is the centre of origin for the family (Cooper 1956; Burbidge 1960). Although Tate (1896 cited by Carolin 1982) suggested that *Pittosporum*, the type genus for the family, was a component of a "cosmopolitan" flora that existed from the Cretaceous to the Paleocene, and Cooper (1956) considered the family to be reasonably ancient, the fossil material found to date is not unequivocal. This may be due in part to the indistinct nature of the pollen, but also to a distinct lack of macrofossil material. *Pittosporum* is considered to have been a component of subtropical forests in southern Japan from the Late Eocene to the mid Miocene (Tanai 1972). Macrofossil material ascribed to *Pittosporum* includes leaves in lower Oligocene and Miocene sediments from New Zealand (Oliver 1928; Cooper

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1956), a single capsule from upper Pliocene sediments in New Zealand (Hayward 1974) and leaves from upper Pliocene sediments in Portugal (Teixeira 1974).

The absence of the Pittosporaceae in South America is unusual, given the degree of diversity within the family in Australia, and the cosmopolitan and distinctly Gondwanan distribution of *Pittosporum* (Balgooy 1966; Crisp *et al.* 1989). Crisp *et al.* (1989) suggested that this absence is due to the evolution of an ancestral form in eastern Gondwana, distant enough from South America to prevent its dispersal to that continent. This is supported to a degree by Schatz's (1996) suggestion that the Madagascan species of *Pittosporum* are Gondwanan relicts from the late Cretaceous-early Tertiary. If Crisp *et al.* (1989) are correct, the Pacific Island *Pittosporum* species would therefore be the product of comparatively more recent dispersal and speciation.

PITTOSPORUM

The generic name *Pittosporum* is derived from the Greek words 'pitta' for pitch or tar, referring to the sticky mucilage that commonly surrounds the seeds of species within this genus, and 'sporos' a seed. *Pittosporum*, which has been described as an 'Old World' genus (Balgooy 1971; Balgooy *et al.* 1996), is the only genus in the Pittosporaceae extending beyond the broad Indo-Australasian region. It has naturally occurring species in Australia, New Zealand, the Pacific islands, Japan and China, India, Madagascar and Africa (Haas 1977; Gowda 1951; Cooper 1956; Schodde 1971). The genus has been most recently reviewed by Cayzer *et al.* (2000) for Australia, with other revisions by Cooper (1956) for Australia and New Zealand, Schodde (1971) for Papuasia, Haas (1977) and Gemmill *et al.* (2002) for the Pacific Islands, Gowda (1951) for the Sino-Indian region, and Friis (1987) for Africa.

The Australian species of *Pittosporum* occupy diverse habitats over a range of altitudes from sea level to approximately 1500 m, although the majority of species are restricted to tropical, subtropical and temperate forests along the Australian eastern seaboard. Habitats include monsoon forest, rocky and sandy seashores, mangrove and swamp margins, dry savannas (e.g. *P. melanospermum*), as well as more extreme environments such as montane forests and subalpine woodlands (e.g. *P. bicolor*). Although some species occur on drier rainforest margins (*P. revolutum*) and others are occasionally

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found in locally drier sites (e.g. *P. undulatum, P. spinescens*) (Cayzer *et al.* 2000), the general phytogeography of *Pittosporum* in Australia – 15 of 20 species occupy rainforests – and elsewhere suggests a long affinity with rainforest vegetation.

Although the Pittosporaceae is characteristically Australian in terms of generic diversity and endemism (Cooper 1956), there are only 20 naturally-occurring Australian species of *Pittosporum* (Cayzer *et al.* 2000), which nonetheless demonstrate a high degree of morphological diversity. In contrast, the much smaller Papuasian region supports 13 species belonging to one relatively large division (Schodde 1971), and the Pacific islands of New Zealand, Hawaii and New Caledonia support, respectively, 20, 23 and 29 species, belonging to 2 large groups (Haas 1977). In the Sino-Indian region, approximately 53 species have been assigned to two groups (Gowda 1951) and in the Madagascar-Africa region 10 species have been classified into a single group (Friis 1987).

The relative paucity of Australian *Pittosporum* species may be due to a number of factors, including the strong association between the Pittosporaceae and rainforest-type vegetation (Hope 1994), with such vegetation presently comprising relictual, small and isolated remnants. This may have prevented the persistence of a large number of *Pittosporum* species during the gradual desiccation of the late Tertiary and Quaternary, and been an impediment to the evolution of new species, as competitive pressures in such shrinking rainforest communities during this period must have been enormous.

The overall lack of Australian *Pittosporum* species is paralleled by the very low number of cool temperate (only 1 - *P. bicolor*) and arid and semi-arid species (only 3 - *P. angustifolium*, *P. ligustrifolium*, *P. phillyreoides*). The low number of arid and semiarid taxa is intriguing given that aridity is considered a stimulant of rates of evolution (Stebbins 1949). One explanation for the relative paucity of xerophytic species of *Pittosporum* is that the migration and radiation of such taxa into arid and semi-arid environments has occurred comparatively recently, a hypothesis that West (1982) proposed to account for the current distribution and diversity of Australian *Dodonaea* species.

A second explanation for the low number of xerophytic *Pittosporum* species is that it represents the product of speciations and extinctions during the climatic amplitudes of

the Pleistocene. Some new species may well have briefly emerged and flourished, only to be lost during subsequent periods of extreme aridity/cooling. Increasing aridity may induce certain responses in plants including reduction in foliage canopy (Lane *et al.* 2000), extinction, or decreases in the number of taxa (Sanderson *et al.* 1990). Thus, although arid communities may not presently support many species, because of a more rapid turnover in the species composition, such habitats may have supported as many or more species than mesic ones over the whole scale of geological time (Stebbins 1949). Schodde (1989) refined this hypothesis for Australia, by describing the central arid zone as a sink, occupied during favourable climatic conditions by speciation from coastal regions, and then abandoned due to extinction during subsequent arid periods.

Aspects of the reproductive biology, biogeography and fire sensitivity of the Australian Pittosporum species support the above suggestion of a rainforest lineage for the genus. Indeed Webb and Tracey (1981) classified Pittosporum as a rainforest genus. Approximately 80% of the Australian species are mesic and inhabit tropical, subtropical or temperate rainforest and sclerophyll forest communities along coastal northern and eastern Australia, with the highest diversity of species in areas that may have acted as rainforest 'refugia' during the climatic extremes of the Late Quaternary (Webb and Tracey 1981) (Fig. 1.3). The conspicuous terminal inflorescences and brightly coloured capsules and seed of Australian Pittosporum species are common traits of rainforest trees (Cameron 1992). P. undulatum and P. bicolor are commonly associated with temperate rainforests from which fire has been absent for long periods. P. undulatum also has thin, resinous bark and has a low capacity to withstand fire (Gleadow and Ashton 1981). Furthermore, P. angustifolium, the most xerophytic Australian Pittosporum species, possesses few of the regeneration-related morphological characteristics commonly associated with semi-arid and arid adapted species, such as rhizomes, corms, bulbs, tubers, epicormic budding or lignotubers. This species may also be fire sensitive, as it occurs largely on sites that are subject to only occasional fire. Together, these observations suggest a relatively recent speciation and subsequent migration of P. angustifolium, P. ligustrifolium and P. phillyreoides (formerly comprising the single species P. phylliraeoides) into semi-arid and arid environments.

i.

THE STUDY SPECIES

<u>P. undulatum</u>

Pittosporum undulatum, Sweet Pittosporum (Syn. Mock Orange, Native Laurel, Waveleaved Pittosporum, Engraver Wood, Victorian Box, Victorian Laurel, Native Daphne) is a slender branched shrub (Cronk and Fuller 1995) or small bushy tree, up to 30 m tall (Cooper 1956; Floyd 1989), with a wide canopy (Plate 1). The shiny, bright-green, alternate leaves have wavy margins and range in length from 7 to 15 cm (Floyd 1989). Terminal clusters of white, fragrant flowers appear in spring, followed by yellow to orange, globular fruits, 8-12 mm in diameter, which reach maturity between February and August (Floyd 1989) (Plate 1). Each fruit contains between 10-25 small, orangebrown seeds, which are consumed and dispersed by a range of native frugivorous birds, including crimson rosellas, silvereyes, pilotbirds, pied currawongs and bulbuls (Cooper 1959; Forde 1986; Floyd 1989). The seed also forms a large part of the diet of the introduced English blackbird (*Turdus merula*) (Gleadow 1982) and is occasionally eaten by brush-tailed possums.

P. undulatum is originally endemic to coastal vegetation communities in south-eastern Australia, from sub-tropical rainforests in south-east Queensland and northern NSW (Cronk and Fuller 1995), warm temperate rainforests and wet sclerophyll forests in NSW and Victoria (Cameron 1992), and dry rainforests in eastern Victoria (Cameron 1992; Sluiter 1992) (Fig. 1.4). It occurs naturally at latitudes of 24.4-39°S, from sea level up to 1200 m in altitude. The moderately broad latitudinal range of *P. undulatum* indicates a capacity to inhabit climates ranging from subtropical to warm-temperate, subject to temperature maxima in the range 22-27°C and minima from 0.5-6°C, with annual precipitation of 600-2000 mm.

In the past 50 years or so, this species has spread far beyond its natural distribution in south-eastern Australia, and now occupies dry sclerophyll forests in central and western Victoria and the Mount Lofty Ranges in South Australia, and wet sclerophyll forests in Tasmania. In Victoria, *P. undulatum* is a declared environmental weed, is classified as a serious threat to at least one vegetation formation (Carr *et al.* 1992) and its spread into areas outside its natural range is listed as a potentially threatening process under the

Victorian Flora and Fauna Guarantee Act (FFG 1995). This species hybridises freely with *P. bicolor*, with hybrids recorded in sclerophyll forests of western Gippsland and the Otway Ranges (Floyd 1989), the Dandenong Ranges and Tasmania (Elliott and Jones 2000). The previously described *P. undulatum* subsp. *emmettii* from Tasmania has been recently reclassified as a *P. undulatum* x *P. bicolor* hybrid (Cayzer *et al.* 2000).

Sweet Pittosporum has been widely cultivated as an ornamental, hedge or shelter plant in Australia, New Zealand, Chile, Colombia, Bolivia, Jamaica, Bermuda, the Azores, the Canary Islands, France, Israel, India, Sri Lanka, China, mainland United States and the Hawaiian Islands (Cooper 1956). Consequently, it has also become a moderate to serious environmental weed in many of these countries, including fynbos vegetation in South Africa (Cronk and Fuller 1995), and a threat to the habitat of native fauna (e.g. see Ramos 1996). The ability of this species to inhabit a wide diversity of vegetation types across a range of edaphic, climatic and hydrological gradients suggests a high degree of physiological tolerance (Cronk and Fuller 1995).

<u>P. bicolor</u>

Pittosporum bicolor, Banyalla (syn. Cheesewood, Tallow-wood, Whitewood, Dragon's Blood Pittosporum) is most often a small, densely bushy shrub or tree up to 18 m in height, with juveniles occasionally growing as epiphytes in the crowns of soft tree ferns (Floyd 1989). The dark green, narrow, alternate leaves, the lighter green abaxial surfaces of which are covered in silvery hairs, may be crowded towards the ends of the branchlets (Jones 1986) (Plate 2). Yellow or purplish flowers, which appear from September to December, are approximately 3-6 mm long and cluster at the ends of leafy branches on long peduncles (Floyd 1989). These are followed by ovoid, orange capsules approximately 15-20 mm long, which dehisce when mature to reveal 15-35 small, angular, bright red seeds enclosed in a sticky mucilage (Plate 2).

Banyalla is distributed from Captains Flat, in the Southern Tablelands of New South Wales to Maatsuyker Island, off the southern coast of Tasmania (Floyd 1989) (Fig. 1.5), at elevations from 0-1450 m. In Victoria, *P. bicolor* occurs throughout the Victorian highlands and Wilson's Promontory and as a disjunct population in the Otway Ranges (Fig. 1.2). The species is largely restricted to areas with mild summers (mean maximum temperatures 17-25°C, mean precipitation 150-500 mm) and cold winters (mean minimum temperatures of -2.5-6°C). Annual precipitation is variable, ranging from 600-2800 mm.

P. bicolor is a common understorey component of cool temperate rainforest, often in association with Eucryphia moorei, Elaeocarpus holopetalus, Nothofagus cunninghamii or Atherosperma moschatum (Floyd 1989). It also occurs in wet and moist sclerophyll forests dominated by Eucalyptus fastigata, E. fraxinoides, E. cypellocarpa and Acacia melanoxylon. In Victorian forests dominated by E. regnans and E. obliqua, P. bicolor is often found in association with Pteridium esculentum, Pomaderris spp., Monotoca scoparia and various tree ferns.

<u>P. angustifolium</u>

Pittosporum angustifolium, Weeping Pittosporum [syn. Inland Pittosporum, Western Pittosporum, Wild Apricot, Butter Bush, Berrigan, Locket Bush, Butterwood, Bell's Orange, Native Willow, Quinine Tree, Poison-berry Tree, Apricot Tree, West Australian Willow, Snotty Gobbles, Macla (Paroo River Aborigines) Derrine (Dubbo Aborigines)] commonly grows as a tall woody shrub or small tree, but on sandy, shaded sites in north-west Victoria, individuals may surpass 10 m in height (Garnet 1965). Its common name derives from its pendulous habit (Plate 3), a characteristic it shares with many other arid and semi-arid species. Its linear-oblong, glabrous leaves are 5-10 cm in length and 2-10 mm wide. Cream coloured, axillary flowers are 9-12 mm in length (Bennett and George 1981). Floral dimorphism in this species (Cooper 1956; Cayzer *et al.* 2000) may indicate a degree of dioecy, although this requires further investigation.

P. angustifolium is the most widespread Australian *Pittosporum* species. It is recorded from all mainland states, being sporadically distributed over much of arid and semi-arid inland Australia (Fig. 1.6), at elevations from 30-1000 m. It inhabits flood plain and mallee communities, grassy eucalypt woodlands, sandy plains and the margins of inland lakes and drainage lines in more arid areas (Bennett and George 1981; Cayzer *et al.* 2000). Associated species in these communities include *Acacia harpophylla*, *A. aneura*, *Casuarina cristata*, *Myoporum platycarpum* and *Santalum spicatum* (Boland 1984). As its distribution suggests, *P. angustifolium* will grow on a wide range of soil types, on sands and sandy loams in Victoria (Costermans 1981) to loams to clays, including calcrete platforms in Western Australia (Mitchell and Wilcox 1988). It occurs as far east as Warwick (southeastern Qld), in dry eucalypt woodlands on the western slopes of the Great Dividing Range.

The wide distribution of this species indicates its tolerance of a broad range of climatic conditions, with mean maximum temperatures from 29-40°C, mean temperature minima of 1-12°C, and annual precipitation of 125-900 mm. *P. angustifolium* has been successfully cultivated as a hedge, windbreak and ornamental shrub in the United States, France, Australia and New Zealand (Cooper 1956).

There appears to be a cline in the phenology of this species across its range. In the most arid part of its distribution, flowers appear in late winter, with seed reaching maturity by late winter of the following year (Friedel *et al.* 1993). In the Wyperfeld National Park region of north-east Victoria, demarking the south-eastern limit of its range, flowers appear in late spring, with mature seed exposed by dehisced capsules during late winter-early spring of the following year. Seed capsules contain between 15-30 comparatively large (4-6 mm diam.), bright-red seeds bound within a resinous mucilage. Seeds may be shed over a several months, with the vast majority consumed and dispersed by avian frugivores (Forde 1986; Milewski 1986; pers. obs.). Sexually-reproducing *P. angustifolium* plants often produce abundant seed, although seedlings are rarely observed in the field. It more commonly regenerates vegetatively by root suckers, which may over time form quite distinct clumps or stands of freestanding ramets, arising at various distances from the parent plant (ortet) and attached to it and to one another by a network of shallow roots ranging in diameter from one to several centimetres (pers. obs.).

Although Cooper (1956) had difficulty delimiting varieties in *P. phylliraeoides*, as mentioned above, in their review of the genus, Cayzer *et al.* (2000) reinstated or confirmed three distinct species - *P. angustifolium*, *P. phillyreoides* and *P. ligustrifolium* - in a subgroup of the Australian Pittosporum. Of the three, P. phillyreoides and *P. ligustrifolium* are restricted to islands and the coastal limestone plain along the west coast of Western Australia, the former from Dampier Archipelago to Kalbarri and the latter from south of Point Perron to Rottnest Island. Interestingly, Cayzer *et al.* (2000) include the cool temperate rainforest species, *P. bicolor* within this subgroup, aligning it most closely with *P. phillyreoides* (Fig. 1.2), as did Cooper (1956).

<u>P. revolutum</u>

Pittosporum revolutum, Rough-fruited Pittosporum (syn. Yellow-flowered Brisbane laurel, Wild Yellow Jasmine, Mock Orange) (Williams 1987; Walsh and Albrecht 1996) occurs as a bushy but sparse shrub to 6 m in height. The trunk and smaller branches of this species are often covered in small, white lenticels. The abaxial surfaces of its dark green, slightly recurved leaves, which are crowded towards the ends of shoots (Plate 4), are covered in a dense, rusty pubescence (Jones 1986). In late spring and early summer, plants produce terminal clusters of yellow, bell-shaped flowers each approximately 1.5 cm in diameter, followed by large, reddish, warty capsules containing between 30-100 red seeds, each between 4-6 mm in diameter (pers. obs).

P. revolutum is the most widely distributed eastern *Pittosporum* species and one of the most variable in the genus (Cayzer *et al.* 2000). It inhabits coastal and near-coastal communities (altitudinal range 0-1100 m) along the eastern seaboard, from Cooktown in northern Queensland to far eastern Victoria (Fig. 1.7), where it is rare (Gullan *et al.* 1990). In the east and north-east of its range, *P. revolutum* is largely restricted to the understorey of tropical and subtropical rainforests, but at latitudes greater than 30°S, it is both an understorey and marginal component of temperate rainforests.

In New South Wales, *P. revolutum* has been recorded in littoral rainforest pockets on coastal sand dunes (Werren and Allworth 1982), in dry sclerophyll forests dominated by *Eucalyptus muelleriana* and *E. cypellocarpa* and from a range of other communities, including vine scrub and dry rainforests dominated by *E. botryoides, Alectryon subcinereus* and *Livistona australis* (NSW Herbarium records). In Victoria, *P. revolutum* occurs as an understorey component of coastal wet sclerophyll forests dominated by *Eucalyptus fastigata* (Loyn *et al.* 1992). The most southerly record for *P. revolutum* occurs on the eastern slope of Mt Nowa Nowa in East Gippsland. Preliminary excavations suggest that this population, comprising a number of small shrubs that flower only sporadically and do not set seed, may be one clonal plant (pers. obs.).

The distribution of this species, from tropical to warm-temperate environments (mean maximum temperature 22-33°C, mean minimum temperature 2-14°C), with 700-2500 mm of precipitation annually, suggests a capacity to grow over a range of climatic conditions. In spite of its broad distribution and rainforest affinity, little is known of the autecology of *P. revolutum*. It is able to regenerate from seed or vegetatively via root suckers following disturbance (pers. ebs), a characteristic that it shares with *P. angustifolium*, as well as the similarly distributed temperate rainforest species *Acmena smithii* (Ashton and Frankenburg 1976). There are clines in capsule and seed size along a latitudinal gradient (pers. obs.), and in north-east Australia a cline from coastal rainforest to higher altitudes, with variation in leaf characteristics between plants from deep shade and those in more exposed sites (Cayzer *et al.* 2000).

Phylogenetically, *P. revolutum* has been placed closest to *P. bracteolatum*, *P. ceylonicum* and *P. moluccanum*, although its position is still unclear, with some analyses clustering it closer to *P. undulatum* (Cayzer *et al.* 2000). The latter grouping is supported by reported hybridisations between *P. revolutum* and *P. undulatum* (Harden 1993). *P. revolutum* also shares with *P. undulatum* an interesting floral dimorphism, with female plants possessing fewer but larger flowers than male plants.

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Figure 1.1 Delineation of arid and semi-arid zones in Australia (adapted from Burbidge 1960; Truswell and Harris 1982).



Figure 1.2 Purported cladistic analysis of a subgroup of *Pittosporum*, containing the four species (in **bold font**), based upon Cayzer *et al.* (2000). The dashed line indicates the incomplete resolution of the position of *P. revolutum*, which in other analyses by Cayzer *et al.* is clustered with *P. undulatum*.

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Figure 1.3 Distribution of the Australian *Pittosporum* species plotted by isoflors. These delineate areas with equal numbers of species, but not necessarily the same species. Shaded areas are the purported north Queensland rainforest 'refugia' of Webb and Tracey (1981).



Plate 1. Foliage and capsules of *P. undulatum*. The scale bar represents 2 cm.



Figure 1.4 Current distribution of *P. undulatum*. Note that occurrences in Tasmania and west of Wilson's Promontory have occurred post-European settlement.

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Plate 2. Foliage of *P. bicolor*. The scale bar represents 2 cm.



Figure 1.5 Distribution of P. bicolor.


Plate 3. Foliage of *P. angustifolium*. The scale bar represents 2 cm.



Figure 1.6 Distribution of P. angustifolium



Plate 4. Habit and foliage of *P. revolutum*. The scale bar represents 5 cm.



Figure 1.7 Distribution of P. revolutum.

CHAPTER 2. CLIMATE ANALYSIS

The distribution of plant species in space and time is the result of a complex series of interactions between their ecophysiological attributes and the environmental conditions to which they are subjected. This fundamental ecological concept has been demonstrated in the present-day phytogeography of many species (Read and Hope 1996), and has also been used to make palaeoclimatic and palaeophytogeographic constructs (Martin 1990a). Climate interacts with vegetation as a series of limiting factors, acting upon individual plants of each constituent species. It consists of a number of variables, the most important of which to plants are those related to temperature and precipitation (Newnham 1968). Other factors which may influence the phytogeography of species and which shape the composition and structure of vegetation communities include light availability (Nix 1982), soil fertility (Swaine 1996) or chemistry (Read 2001), and fire and other disturbances (Lindenmayer *et al.* 2000).

Previous investigations of the role of climate in the phytogeography of woody species have found a consistent interrelationship between particular temperature and precipitation variables, for Australian taxa (Busby 1986; Read and Busby 1990) as well as those occurring elsewhere in the world (Parker 1994; Franklin 1998; Fang and Li 2002). For other species, patterns of mean annual precipitation may be less important, with interactions between temperature (e.g. frost tolerance) and actual water deficit, evapotranspiration balance or the availability of soil moisture during the growing season being stronger determinants of distribution (Cao *et al.* 1995; Huntley *et al.* 1995; Sykes *et al.* 1996).

The Bioclimatic Prediction System, BIOCLIM (subsequently expanded as ANUCLIM) has been used by researchers for a number of purposes. These have included analysis of existing distributions of plant and animal species and groups of species (Coates and Kirkpatrick 1999), the prediction of likely distribution and for the testing of hypotheses regarding the climatic controls of organism distribution (Busby 1987). Another application for BIOCLIM, as pointed out by Fox (1999), is the prediction of climatic variables for previous periods, by plotting the distribution of a taxon from fossil evidence, and then integrating this with current day distributional and climatic information for that taxon. A further application may be predicting the short to medium

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term (distributional) response of individual taxa to changes in climate associated with the Enhanced Greenhouse Effect, brought about by increasing global CO₂ levels.

The primary aim of this chapter was to investigate the relationship between climate and distribution for each *Pittosporum* species. A secondary aim of these analyses was to formulate hypotheses about the causes of species distribution limits that could be subsequently tested by experimental means. The specific aims of this chapter were therefore to:

- 1. characterise the climate over the range of each species;
- determine the major ways in which the climate profiles of these species differ, based on their present distributions. It was assumed that this would suggest the climatic determinants of the distributions of these species.

METHODS

BIOCLIM (Holder *et al.* 1999) was used to generate climate profiles and 35 sitespecific climatic variables for each species. These variables are derived from mean weekly climate estimates of maximum and minimum temperature, precipitation, solar radiation and evaporation (Holder *et al.* 1999). The variables are of biological significance as they describe the range, extremes and seasonality of climatic conditions experienced by the species at each recorded location (Lloyd and Kershaw 1997). Of these 35 climate variables, twenty-one of the major temperature, precipitation, radiation and moisture balance variables were selected for comparison and further analysis (Table 2.1).

As many of the derived climate variables are likely to be highly intercorrelated, principal components analysis (PCA) was used to determine which variables explain the majority of the variation in the data set for each species. Site records for each species (latitude, longitude and altitude) were identified from data supplied by State and Territory Herbaria, from flora survey records of the Victorian Department of Natural Resources and Environment, and by personal examination of New South Wales Herbarium records. For between-species comparisons, 140 sites were randomly subsampled from all site records for each species. This was done to prevent potential bias resulting from unequal sample sizes and to simplify interpretation of the factor plots. PCA was again used to determine which climatic variables are most important in distinguishing between species. Data were analysed using SYSTAT® Version 9.0 (SPSS Inc. 1999).

RESULTS

Comparison of climate variables among species

The BIOCLIM analyses showed that even though there were broad biogeographical differences among the four *Pittosporum* species, their climate profiles overlap to some degree (Table 2.2). Nevertheless, the results showed broad patterns both within and between species. One-way ANOVAs carried out on each of the estimated variables indicated significant differences among the four species (Table 2.2). *P. bicolor* had the lowest values for almost all temperature variables and amongst the highest values for precipitation variables, including those for mean annual precipitation, precipitation of the driest quarter and winter precipitation. *P. angustifolium* had the highest values for most temperature variables, and the lowest mean annual precipitation (MAP), values of which were constrained within a reasonably narrow range, with 75% of recorded sites receiving on average less than 400 mm precipitation annually (Table 2.2).

There were significant differences among the species in their values of mean annual temperature (MAT), with *P. angustifolium* and *P. revolutum* exhibiting the highest values, and *P. undulatum* and *P. bicolor* the lowest values for this variable (Table 2.2). *P. revolutum* had the greatest range of MAT, reflecting its broad latitudinal (but predominantly coastal) distribution. *P. undulatum*, on the other hand, showed the lowest range of MAT, which is surprising given its considerable latitudinal range, and comparatively recent range expansion westward through south-eastern Australia. There was a slight increase in temperature seasonality with increasing latitudinal origin of these species, with the highest seasonality derived for *P. angustifolium* (Table 2.2), which is the most 'inland' of the four species (Fig. 1.6). Although *P. undulatum* and *P. angustifolium* do not overlap in distribution (Figs. 1.4 & 1.6), they possess similar values for mean minimum temperature of the coldest week, with a large overlap in their 5-95% ranges for this variable.

For the variables mean temperature of the wettest quarter (TWeQ), mean temperature of the driest quarter (TDQ), precipitation of the warmest quarter (PWaQ) and precipitation of the coldest quarter (PCQ), the species fell into two groups. For *P. undulatum* and *P. bicolor*, mean temperature of the wettest quarter is less than that of the driest quarter, and coldest quarter (winter) rainfall exceeds that of the warmest quarter (summer)

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(Table 2.2). These results indicate that *P. bicolor*, and to a lesser extent *P. undulatum*, are subject to largely winter rainfall. These patterns are reversed for *P. angustifolium* and *P. revolutum*, with wettest quarter temperature means exceeding those of the driest quarter, and warmest quarter precipitation means exceeding those of the coldest quarter, indicating a predominantly summer rainfall regime for these species (Table 2.2). However, for *P. angustifolium*, the differences are less pronounced and the ranges of all variable values are extremely high, reflecting its wide distribution across the summer-winter rainfall divide, which suggest that precipitation seasonality is probably not the primary determinant of its distribution (Table 2.2). The most important climatic determinants for *P. angustifolium* appear to be those related to high temperature (MAT, TWaQ, MTWP) and low annual precipitation (Fig. 2.1d).

There was a trend in precipitation seasonality among the species, with the mid-latitude *P. undulatum* demonstrating the lowest value, *P. bicolor* a slightly higher value, with *P. angustifolium* and *P. revolutum* exhibiting the highest values for this variable (Table 2.2). In relation to this, the climate of *P. angustifolium* exhibited the highest ratio of highest to lowest weekly precipitation among the species (12), followed by those of *P. revolutum* (3), *P. bicolor* (2.6) and *P. undulatum* (2.1) (Table 2.2). In regard to overall water balance, the annual mean moisture index for *P. angustifolium* was significantly lower than values of the other three species (Table 2.2).

Principal components analysis of climatic variables indicated that selected temperature and precipitation variables explain much of the climate variation across the distribution of the four *Pittosporum* species (Table 2.3). Component 1 is positively correlated with temperature variables (maximum temperature of the warmest week, annual mean temperature and mean temperature of the warmest quarter) and negatively with precipitation variables (precipitation of the driest quarter and precipitation of the coldest quarter - Table 2.3). Component 2 is most strongly (and positively) associated with precipitation characteristics, namely precipitation of the warmest quarter, precipitation of the wettest week and precipitation of the driest quarter (Table 2.3). Component 3 is negatively correlated to mean temperature of the driest quarter and minimum temperature of the coldest week and positively with temperature seasonality and annual temperature range (Table 2.3).

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Although there is considerable variation within species and overlap between them, the first two axes largely separate *P. angustifolium* and *P. bicolor*, with *P. revolutum* and *P. undulatum* intermediate (Fig. 2.1a), which corresponds closely with their nonoverlapping distributions, and the relationship on the primary axis between increasing temperature and decreasing precipitation, where *P. bicolor < P. undulatum* & *P. revolutum & P. revolutum < P. angustifolium*. There is considerable overlap of *P. undulatum* with both *P. bicolor* and *P. revolutum* on the first and second axes, and among all species on the second axis (Fig. 2.1a). There is a large degree of overlap among the four species on the third axis (Fig. 2.1b), which corresponds to the broad overlap among them in MTCP, TDQ and TSeas, the principal component of this axis (Table 2.2).

Variation in climate variables within species

P. undulatum

Component loadings of the 21 temperature and precipitation variables for each species and the variance explained by the three principal components are shown in Table 2.4. For *P. undulatum*, precipitation variables contribute most to Component 1, in particular the seasonality of moisture index, mean annual precipitation, precipitation of the wettest week and precipitation of the wettest quarter. The vast majority of *P. undulatum* sites fall within a comparatively narrow range of annual and summer precipitation means (Table 2.2), with considerable variation amongst remaining sites (Fig. 2.2a). The low rainfall / low temperature outlier for this species is located in Tasmania, and is probably an historically recent cultivated specimen or garden escape, as the species does not occur there naturally. Temperature variables contributed most strongly to Component 2, particularly mean annual temperature and mean temperature during summer (Table 2.4). As with precipitation variables, the majority of sites were constrained within a very narrow range of mean annual temperature. (Table 2.2). Component 3 correlates negatively with annual temperature range and temperature seasonality (Table 2.4).

P. bicolor

Component 1 of the PCA for *P. bicolor* correlates negatively with many of the precipitation variables, particularly MAP and PDQ (summer rainfall), but positively with the seasonality of moisture index (Table 2.4). The large variation in rainfall, particularly that falling during summer, across the distribution of *P. bicolor* is consistent with these results (Fig. 2.2b). Component 2 is correlated with winter temperature variables, and Component 3 with summer temperature peaks (Table 2.4).

P. revolutum

For *P. revolutum*, the bulk of the variation is accounted for by mean annual temperature, summer and winter temperature means, precipitation seasonality and radiation variables, all of which are correlated with Component 1 of the PCA (Table 2.4). Its restriction to largely coastal environments along the eastern seaboard, subject to largely summer rainfall reflects this outcome. Component 2 is negatively correlated with the annual temperature range but positively with all precipitation variables, in particular PCQ (winter rainfall - Table 2.4). Component 3 correlates negatively with the seasonality of moisture index and temperature of the driest quarter, which is winter at low latitude sites and summer at higher latitude sites (Table 2.4). A configuration plot demonstrates a three-way interaction between temperature variables, winter rainfall and annual temperature range (Fig. 2.2c).

P. angustifolium

For *P. angustifolium*, Component 1 represents temperature variables, in particular mean annual temperature and summer temperature (Table 2.4). Component 2 is correlated with precipitation variables MAP and PWeQ and Component 3 correlates with winter temperature (Table 2.4). The broad range of factor scores for these temperature and rainfall components is consistent with the very broad distribution of this species (Fig. 2.2d).

DISCUSSION

Comparison of climate profiles of these species indicated the predominant climatic regime under which each operates and the variables that are most important in delimiting them. Nevertheless, a degree of caution is necessary in interpreting the results of these studies. First, climate may exert both direct and indirect influences on the distribution of species, e.g. via its effect on fire regimes or interactions with edaphic factors. Second, the realised niche of a species is also influenced by biotic interactions (competition, herbivory, symbioses), which may vary across its geographic range (Hutchinson 1957). The implications of the results of these climate analyses will be discussed with these constraints in mind.

Comparison of climate variables among species

The importance of selected temperature variables, notably summer and mean annual temperature, together with summer precipitation, in delimiting the distributions of these species is consistent with the results of Hill *et al.* (1988), who found the major climatic determinants of distribution for temperate rainforest species in southeastern Australia to be primarily those associated with temperature, followed by particular rainfall variables. Similarly, Read (1990) found the most important climatic determinants separating temperate and tropical *Nothofagus* species in Australia and New Guinea to be increasing mean annual temperature and greater diurnal and seasonal variation in temperature and precipitation with increasing latitude.

The trends in precipitation seasonality and ratios of highest to lowest weekly precipitation among climates of these species indicate the sharp distinction between wet and dry seasons for both *P. revolutum* and *P. angustifolium*. However, *P. angustifolium* is also subject to a high degree of rainfall unpredictability across much of its range and high temperature seasonality, which increases as a function of increasing latitude and distance from the coast (Nix 1982). The higher summer rainfall for sites supporting these species is likely to be offset however, by increased evaporative losses during this period, particularly for *P. angustifolium*, effectively reducing soil moisture availability. On the other hand, the lack of rainfall and higher temperatures in summer for *P. unc' alatum* and *P. bicolor* may place them under considerable water stress during that period. The parity in MTCP between *P. undulatum* and *P. angustifolium* may be due to

a combination of their similar latitudinal ranges and to the very low overnight temperatures that operate over much of the inland range of *P. angustifolium*.

Variation in climate variables within species

P. undulatum

The distribution of *P. undulatum* across a considerable latitudinal gradient along the southeastern Australian seaboard initially suggests a broad tolerance of temperature. Nevertheless, its narrow range of MAT and the negative correlation between Component 3 and ATR suggests that it may be less tolerant of extremes in temperature. Furthermore, the very narrow ranges of values for MTWP and TWaQ suggest that warmth may determine its northern limit. The considerable clustering of site factor scores for precipitation variables also suggests a narrow precipitation requirement (Gleadow *et al.* 1983).

P. bicolor

Although *P. bicclor* might be expected to be strongly aligned with a winter rainfall climate, it occupies many sites that have relatively high summer precipitation, a characteristic of other cool temperate rainforest species including *Nothofagus cunninghamii* (Read and Brown 1996). A requirement by *P. bicolor* for relatively high summer precipitation may reflect a degree of susceptibility to drought, which is supported by its comparatively narrow precipitation spectrum and low coefficient of variation of weekly precipitation value. However, this pattern may also result from the reduced likelihood in such habitats of fire (Busby 1986; Read and Busby 1990; Read and Brown 1996), to which this species may be particularly vulnerable. The derived climatic variables for *P. bicolor* are very similar to those of other cool temperate rainforest taxa, including *Nothofagus cunninghamii* and *Atherosperma moschatum* in south-eastern NSW is intriguing, but may be due to warmer temperatures (particularly at lower altitudes) or the change from a largely winter to summer rainfall regime that approximates the northern limit of its distribution.

P. revolutum

The climate variables that characterize the distribution of *P. revolutum*, including high annual precipitation and high minimum winter temperatures, together with the interaction between temperature, winter rainfall and annual temperature range, suggest that low growing season temperature may be a factor in limiting its southerly distribution. Restriction of *P. revolutum* to coastal sites with high rainfall and mild winter temperature minima suggests that it may have low frost resistance, which is characteristic of other tropical taxa (Read and Hope 1989). This supports the suggestion that the most important climatic determinant for species requiring tropical or subtropical conditions is minimum temperature of the coldest month (Fox 1999). It may be this factor that prevents the establishment of such species, particularly when the minimum temperature of the coldest period coincides with seed maturation and germination, as it does with the most southerly populations of *P. revolutum*. This is consistent with the suggestion by Grace (1987), that a species' distribution pattern is probably determined by failure at one part of its life cycle, caused by either climatic extremes or unusual combinations of climatic variables.

P. angustifolium

While *P. angustifolium* has a broad distribution, its northern limit occurs at latitude *c*. 18°S, which also demarks the limit of monsoonal rains and the point at which arid conditions commence (Bowman 1996). This coincidence suggests that precipitation seasonality may be a determinant of its northern distributional limit. However, its northern limit also approximates the southerly limits of monsoonal savannas that are subject to frequent fire and to which this species may be particularly sensitive. Together with the PCA results, this implicates a combination of temperature and precipitation variables, which together reduce the incidence of fire, as the principal determinants of the northern extent of this species. The very low mean moisture index (M.I.) for *P. angustifolium* reflects the nature of its distribution and suggests that it may possess a strong degree of drought tolerance. This is reinforced by an apparent correlation between its distribution and the isolines demarking values of M.I. that are less than 0.25 for 26 or more weeks of the year, although in the east its distribution extends closer to the coast, thus overlapping the 0-13 and 13-26 isolines.

Component 3 of the PCA for this species - minimum temperature of the coldest period, which is characteristically the coldest week of winter - may be an important determinant of the southern distributional limit of *P. angustifolium*. Other studies have shown winter temperature to be a potentially important determinant of the distribution of arid and semi-arid species in Australia (Hnatiuk *et al.* 1983) and elsewhere (Retuerto and Carballeira 1990; Franklin 1998).

In summary, climate analyses have demonstrated the importance of temperature and precipitation variables as determinants of the distribution for these species. In regard to precipitation, the high to very high coefficients of variance of weekly precipitation values of *P. revolutum* and *P. angustifolium* suggest they may possess some degree of physiological tolerance of water deficit. Given the apparent importance of water availability in the distribution of these species, they are likely to exhibit differences in diurnal and seasonal water relations, aspects that will be investigated in Chapter 3. Furthermore, as there are broad differences in precipitation seasonality and mean annual temperature between the arid continental (*P. angustifolium*) and tropical coastal (*P. revolutum*) species on the one hand, and the temperate species (*P. undulatum, P. bicolor*) on the other, the mode and degree of seedling drought resistance among these species may be a crucial factor in their distributions. The water relations behaviour of seedlings of these species in response to drought resistance will be explored in Chapter 4.

Seedling growth and biomass allocation may reflect selection for traits of adaptive value, which will be shaped by the phylogeny and genetic diversity within species. As such, the relationships among the growth and biomass attributes of these species and interplay with climatic variables will be explored in Chapter 5. Successful germination and seedling establishment depends upon the provision of suitable environmental conditions, particularly those related to temperature and soil moisture availability. In this respect, the broad distributional overlaps between *P. undulatum* and *P. revolutum* at latitudes above circa 25°S, and between *P. undulatum* and *P. bicolor* above *c.* 36°S suggests that they may share similar aspects of seed biology and germination, attributes that will be investigated in Chapter 6. Reproductive strategies that increase the likelihood of a species' persistence in arid and semi-arid environments may be important life-history components and indicate pathways of evolution during past

periods of climate change. These characteristics will be explored for *P. angustifolium*, the only xerophytic species in the genus, in Chapter 7.

At the regional level, this study has shown the importance of temperature and precipitation (together with associated variables such as relative humidity) as determinants in the distribution of these *Pittosporum* species. However, other factors of importance in delimiting the distribution of these species may include parent rock material (and derived soil type), which has been shown to have an influence on the distribution of several *Eucalyptus* species (Austin *et al.* 1990). Other potentially important factors include the competitive ability of each species at its distributional limits, together with shade tolerance characteristics and susceptibility to and regeneration from fire. At the local level, such as along a stream bank or in a gully, other factors such as light availability, soil pH and aspect are probably important determinants of site suitability for these species.

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Abbreviation	Description
MAT	mean annual temperature
MTWP	maximum temperature of the warmest week
MTCP	minimum temperature of the coldest week
ATR	annual temperature range
TWeQ	mean temperature of the wettest quarter
TDQ	mean temperature of the driest quarter
TWaQ	mean temperature of the warmest quarter
TCQ	mean temperature of the coldest quarter
TSeas	seasonality of mean temperature (coefficient of variation)
МАР	mean annual precipitation
PWP	precipitation of the wettest week
PDP	precipitation of the driest week
PSeas	seasonality of mean precipitation (coefficient of variation)
PWeQ	precipitation of the wettest quarter
PDQ	precipitation of the driest quarter
PWaQ	precipitation of the warmest quarter
PCQ	precipitation of the coldest quarter
AR	annual mean radiation
RS	radiation seasonality
AXMI	annual mean moisture index
MISeas	seasonality of moisture index (coefficient of variation)

 Table 2.1
 Climate variables used in the BIOCLIM analysis.

N Cable	P. angustifolium	P. revolutum	P. undulatum	P. bicolor		
variable	(<i>n</i> =350)	<u>(n=140)</u>	=140) (<i>n</i> =1206)		<u>(n=489)</u>	
MAT	18.3 ± 0.14 (14.8 - 22.7)	17.1 ± 0.25 (13.4 - 22.3)	13.3 ± 0.02 (11.5 - 14.4)	10.0 ± 0.08 (7.2 - 12.7)	2173.8	< 0.001
MTWP	33.3 ± 0.15 (29.8 - 37.8)	$26.6 \pm 0.24 \\ (22.3 - 30.5)$	$\begin{array}{c} 24.7 \pm 0.03 \\ (22.6 - 26.6) \end{array}$	21.9 ± 0.91 (18.8 - 25.2)	3257.6	< 0.001
МТСР	$\begin{array}{r} 3.9 \ \pm 0.09^{a} \\ (1.8 - 7.2) \end{array}$	6.4 ± 0.27 (1.8 - 12.8)	3.8 ± 0.04^{a} (0.5 - 6.2)	1.0 ± 0.11 (-2.3 - 5.0)	423.5	< 0.001
ATR	29.4 ± 0.15 (25.0 - 33.5)	20.2 ± 0.25 (16.4 - 26)	20.9 ± 0.05^{a} (17.1 - 24.2)	20.9 ± 0.13^{a} (15.6 - 25.1)	1308.2	< 0.001
TWeQ	$19.6 \pm 0.41^{\circ}$ (10.5 - 29.3)	$\frac{19.8 \pm 0.39^{a}}{(11.8 - 25.6)}$	12.0 ± 0.06 (8.9 - 16.2)	6.9 ± 0.13 (2.4 - 12.3)	994.1	< 0.001
TDQ	17.7 ±0.20 (11.2 - 22.4)	15.0 ± 0.28^{a} (9.6 - 19.3)	17.1 ± 0.06 (10.2 - 19.3)	$13.4 \pm 0.11^{\circ}$ (8.9 - 17.5)	169.1	< 0.001
TWaQ	24.8 ± 0.15 (20.8 - 29.5)	21.4 ± 0.23 (17.5 - 25.7)	18.1 ± 0.02 (16.6 - 19)	15.0 ± 0.08 (12.7 - 17.5)	3043.1	< 0.001
TCQ	11.3 ± 0.11 (8.5 - 15.6)	12.4 ± 0.26 (8.8 - 18.3)	$8.7 \pm 0.03 \\ (6.4 - 10.3)$	5.2 ± 0.09 (2.2 - 8.8)	1273.5	< 0.001
TSeas	1.8 ± 0.01 (1.4 - 2.2)	1.2 ± 0.02 (1.0 - 1.6)	1.3 ± 0.01 (1.1 - 1.5)	1.4 ± 0.01 (1.0 - 1.7)	1320.8	< 0.001
МАР	352 ± 8.12 (183 - 690)	1275 ± 37.12 (771 - 2181)	936 ± 3.88 (710 - 1198)	1340 ± 15.88 (843 - 1934)	1391.5	< 0.001
PWP	12.0 ± 0.38 (5 - 28)	48.0 ± 2.51 (21 - 116)	23.0 ± 0.14 (5 - 32)	36.0 ± 0.51 (22 - 57)	724.6	< 0.001
PDP	0.0 ± 0.05 (0 - 1)	16.0 ± 0.66 (0 - 18)	11.0 ± 0.12 (1 - 17)	14.0 ± 0.21 (11 - 24)	792.8	< 0.001
PWeQ	135 ± 4.09 (53 - 302)	529 ± 26.1 (257 - 1202)	274 ± 1.47 (178 - 365)	416 ± 5.56 (249 - 626)	793.4	< 0.001
PDQ	50 ± 1.70 (6 - 111)	171 ± 4.68 (74 - 245)	185 ± 0.78 (136 - 244)	241 ± 2.57 (161 - 351)	1665.2	< 0.001
PWaQ	$ \begin{array}{r} 110 \pm 4.09 \\ (32 - 288) \end{array} $	473 ± 21.51 (212 - 988)	198 ± 1.48 (107 - 291)	246 ± 2.56 (168 - 354)	667.1	< 0.001
PCQ	$ \begin{array}{r} 81 \pm 2.35 \\ (20 - 149) \end{array} $	211 ± 5.78 (110 - 325)	245 ± 1.11 (163 - 328)	402 ± 5.82 (219 - 627)	1480.4	< 0.001

Table 2.2Climate profiles of the species derived from BIOCLIM (means \pm sem, 5-95%percentiles in brackets).All temperatures are in °C.All precipitation values are in mm.Shared alphabet letters denote non-significant differences between species for that variable.

Variable	P. angustifolium (n=350)	P. revolutum (n=140)	P. undulatum (n=1817)	P. bicolor (n=489)	F	Р
PSeas	38.0 ± 1.13^{a} (11 - 77)	41.0 ± 2.27^{a} (13 - 97)	$ \begin{array}{r} 16.0 \pm 0.12 \\ (11 - 23) \end{array} $	21.0 ± 0.31 (11 - 32)	601.5	< 0.001
AR	10.5 ± 0.10 (17.3 - 22.7)	16.9 ± 0.11 (15.2 - 19.3)	15.0 ± 0.01 (14.3 - 15.7)	14.0 ± 0.05 (11.4 - 15.4)	2959.9	< 0.001
RS	31.0 ± 0.42 (20 - 42)	29.0 ± 0.75 (18 - 42)	44.0 ± 0.09 (41 - 47)	46.0 ± 0.17 (41 - 53)	1118.8	< 0.001
AXMI	0.22 ± 0.01 (0.06 - 0.44)	0.78 ± 0.01^{a} (0.52 - 0.95)	0.77 ± 0.00^{a} (0.67 - 0.88)	0.89 ± 0.00 (0.79 - 0.98)	6115.7	< 0.001
MISeas	57 ± 0.11 (25 - 95)	26±0.99 (8-52)	33 ± 0.16 (22 - 42)	18 ± 0.39 (3 - 32)	178.4	< 0.001

Table 2.2 continued Climate profiles of the species derived from BIOCLIM.

Variable	Component 1	Component 2	Component 3		
MAT	0.888	0.365	-0.213		
MTWP	0.947	0.113	0.150		
MTCP	0.394	0.320	-0.837		
ATR	0.694	-0.085	0.666		
TWeQ	0.784	0.437	0.072		
TDQ	0.235	-0.262	-0.551		
TWaQ	0.946	0.267	0.019		
TCQ	0.737	0.409	-0.493		
TSeas	0.635	-0.102	0.702		
MAP	-0.833	0.520	0.058		
PWP	-0.508	0.803	0.025		
PDP	-0.873	-0.013	0.203		
PSeas	0.522	0.682	0.068		
PWeQ	-0.572	0.784	0.007		
PDQ	-0.939	0.102	0.119		
PWaQ	-0.336	0.887	0.056		
PCQ	-0.885	0.154	0.064		
AR	0.925	0.208	0.251		
RS	-0.701	-0.573	-0.301		
AXMI	-0.940	0.124	-0.110		
MISeas	0.754	-0.337	-0.311		
Variance explained	56%	19%	12%		
Total variance	Accounts for 87% of the total variance				

Table 2.3Summary of component loadings for PCA carried out on twenty-one site-specific climate variables for 4 species of *Pittosporum*. The highest componentloadings are in bold font.

		P. undulatum	<u></u>		P. bicolor	
Valiable	Component i	Component 2	Component 3	Component 1	Component 2	Component 3
MAT	-0.173	0.901	0.284	0.519	0.764	0.242
MTWP	-0.099	0.587	-0.523	0.704	0.111	0.662
МТСР	-0.494	0.401	0.723	0.062	0.974	-0.071
ATR	0.340	0.032	-0.900	0.421	-0.726	0.503
TWeQ	0.135	0.842	-0.267	0.589	0.347	-0.142
TDQ	-0.285	-0.307	0.273	0.262	0.538	0.499
TW₂Q	-0.112	0.926	-0.008	0.691	0.483	0.491
TCQ	0.303	0.753	0.525	0.05	0.902	0.023
TSeas	0.363	0.001	-0.858	0.307	-0.772	0.490
MAP	0.940	0.009	0.340	-0.929	0.156	0.307
PWP	0.864	0.333	0.296	-0.880	0.234	0.324
. PDP	0.613	-0.431	-0.096	-0.757	-0.262	0.288
PSeas	0.289	0.721	0.213	-0.284	0.556	0.274
PWeQ	0.850	0.363	0.329	-0.881	0.267	0.322
PDQ	0.793	-0.431	0.055	-0.857	-0.187	0.181
PWaQ	0.808	0.551	0.096	-0.825	-0.225	0.156
PCQ	0.657	-0.505	0.442	-0.867	0.310	0.330
AR	0.117	0.831	-0.335	0.790	-0.484	0.240
RS	-0.527	-0.727	0.216	-0.536	0.730	-0.197
AXMI	0.831	-0.349	0.213	-0.897	-0.130	0.001
MISeas	-0.963	-0.006	0.013	0.910	0.196	0.090
Variance explained	34%	32%	17%	47%	27%	11%
Total variance	Account for 83% of the total variance			Account for 85% of the total variance		

Table 2.4 Component loadings for 21 climatic variables for the first three component axesfrom PCA for each species. The highest component loadings are in bold font.

Variable	P. revolutum			P. angustifolium			
Valiable	Component 1	Component 2	Component 3	Component 1	Component 2	Component 3	
MAT	0.961	0.029	-0.049	0.963	0.0156	0.185	
MTWP	0.888	-0.368	0.179	0.925	-0.228	0.047	
МТСР	0.796	0.436	-0.356	0.353	0.261	0.853	
ATR	0.008	-0.806	0.544	0.734	-0.384	-0.450	
TWeQ	0.888	-0.254	0.280	0.896	0.232	-0.262	
TDQ	0.371	0.480	-0.640	-0.472	-0.300	0.705	
TWaQ	0.939	-0.143	0.075	0.975	-0.023	0.042	
TCQ	0.926	0.196	-0.201	0.818	0.315	0.438	
TSeas	-0.207	-0.728	0.615	0.587	-0.424	-0.503	
MAP	0.566	0.691	0.392	-0.200	0.953	-0.172	
PWP	0.819	0.448	0.168	0.203	0.947	0.178	
PDP	-0.697	0.616	-0.030	-0.090	0.163	-0.238	
PSeas	0.954	-0.005	-0.028	0.743	0.355	0.443	
PWeQ	0.796	0.475	0.195	0.145	0.973	0.101	
PDQ	-0.691	0.648	0.242	-0.660	0.486	-0.503	
PWaQ	0.828	0.419	0.294	0.303	0.898	-0.214	
PCQ	-0530	0.720	0.361	-0.753	0.361	0.126	
AR	0.917	-0.323	-0.023	0.952	-0.134	-0.004	
RS	-0.941	0.069	-0.225	-0.894	-0.360	0.129	
AXMI	-0.003	0.717	0.537	-0.745	0.604	-0.064	
MISeas	0.209	-0.227	-0.874	-0.336	-0.298	0.791	
Variance explained	54%	24%	14%	46%	26%	16%	
Total variance	Account for 92% of the total variance			Account f	Account for 88% of the total variance		

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 Table 2.4 continued
 Component loadings for 21 climatic variables for the first three

 component axes from PCA for each species.



Figure 2.1 Configuration plots of PCA of species' climate profiles. *P. bicolor* (\Box), *P. undulatum* (\triangle) *P. angustifolium* (\blacktriangle) and *P. revolutum* (\blacksquare).





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CHAPTER 3. SEASONAL PLANT WATER RELATIONS

Drought is a common climatic phenomenon of the Australian landscape. However, differences in the severity and duration of seasonal water stress across environmental gradients are likely to elicit differences in the evolved responses of species distributed across such gradients. Shantz (1927) recognized several relationships between plants and drought, including plants that are drought-escaping, drought-evading, drought-enduring and drought-resisting. However, the term 'drought resistance' is relatively generic and is currently used to describe a range of mechanisms by which plants survive extended periods without precipitation (Jones *et al.* 1981). Other difficulties with Shantz's model were that some plant species possess various combinations of escape, avoidance, and endurance, whilst other species with quite different strategies were classified as belonging to the same category (Gibson 1996).

Although early models of drought resistance have been considerably refined and expanded, there has been on-going debate about the most appropriate terminology for drought resistance (Levitt 1972, 1980; Turner (1979, 1986a). Levitt (1972, 1980) categorized xerophytes on their possession of one of five strategies for dealing with drought, with perennial plants generally classified as either drought avoiders or tolerators (Fig. 3.1). Turner (1979), on the other hand, eschewed the term avoidance, reiterating the point made by May and Milthorpe (1962) that plants that maintain high internal water status do not avoid drought, which is an environmental condition. Turner thus classified drought resistant plants as either able to 'escape' or 'tolerate' drought, with drought tolerant plants subdivided into those that maintain high water potential by either reducing water loss or maintaining water uptake (Levitt's 'drought avoiders') and those that allow water potential to fall, thereby maintaining cell turgor (Fig. 3.1).

For the purposes of this study, I will adopt with some clarification the system of Levitt, if only because it differentiates more clearly between species that either maintain or reduce leaf water potential in response to water stress (Fig. 3.1). The term 'drought' is therefore defined as a condition resulting from diminished soil water supply due to low rainfall and/or high atmospheric demand. Thus, drought avoiding species are those that are able, under conditions of water stress, to resist the formation of leaf or shoot water deficits by minimizing decreases in water potential. For plants possessing such

mechanisms, 'avoidance' refers to the avoidance of tissue dehydration rather than the specific avoidance of drought (Jones *et al.* 1981). The mechanisms used to maintain high leaf or shoot water potential can be categorized into two major groups. The first comprises strategies that maintain water uptake by increased root density and/or depth, or hydraulic conductance (Turner 1979). The second comprises mechanisms that variously minimize water loss, by means of reductions in stomatal conductance, radiation absorption and/or evaporative surface (Turner 1979; Jones *et al.* 1981; Khalil and Grace 1992) (Fig. 3.1).

Drought tolerant species are able to maintain leaf tissue function whilst experiencing very low values of leaf water potential (Cowan 1981; Jones *et al.* 1981; Bannister 1986). Taxa with the greatest capacity to tolerate drought include xerophytic and sclerophytic species, most of which demonstrate some degree of physiological adaptation to water stress. In such plants, the very low leaf or shoot water potentials resulting from long periods without rainfall are countered by strategies that either maintain cell turgor or directly tolerate desiccation (Jones *et al.* 1981) (Fig. 3.1). Turgor facilitates stomatal opening, cell elongation and expansion (Turner 1986b) and the maintenance of metabolic processes, thereby promoting growth and survival (Turner and Jones 1980; Morgan 1984). Turgor potential at a specific leaf water potential depends upon both the osmotic potential and elasticity of leaf tissue. Thus, one mechanism of turgor maintenance at very low tissue water potentials is that of osmotic adjustment, which involves an increase in the concentration of solutes in the symplast, enabling water to be extracted from drying soil (Turner and Jones 1980; Khalil and Grace 1992).

The second mechanism of turgor maintenance is to increase the bulk elastic modulus, which is a measure of the degree of cell wall stiffness (Grace 1997). Although water stress may occasionally result in reduced cell elasticity (Jones and Turner 1978; Jones *et al.* 1981), the decrease in cell size that often accompanies water stress may serve to increase both cell elasticity and the dry weight:turgid weight ratio of leaf tissue (Turner and Jones 1980).

Ecophysiological variables frequently used to determine the drought stress strategies of species are patterns of diurnal and seasonal leaf water potential (Ψ_L) and stomatal

conductance (g_s) , and the relationship between them. Leaf water potential is the driving force for the movement of water through the plant (Jarvis 1976), and the diurnal range of this variable is regarded as a useful index of the water status of plants (Doley 1981).

A feature of many plants occupying seasonally dry environments is their strong control of gas exchange (Abril and Hanano 1998). Stomatal movement allows a rapid, but reversible, adjustment to environmental changes (Cowan 1982) and g_s is therefore an important variable affecting the exchange of CO₂ and water vapour between the plant and the atmosphere (Hanan and Prince 1997). As such, g_s may also provide an indication of the degree of water stress that a plant is experiencing. A number of studies have revealed a strong correlation between g_s and habitat (Korner *et al.* 1979; Korner 1994; Schulze *et al.* 1994), and variability in diurnal and seasonal movements of g_s can be accounted for by certain environmental variables (Jarvis 1980). Environmental variables that exert a strong influence over g_s include above-ground factors such as irradiance, air temperature, CO₂ concentration, air saturation deficit, as well as belowground variables such as soil water availability (root zone water deficit) (Abril and Hanano 1998; Whitehead 1998). As well as the speed of response to environmental variables, other characteristics that greatly influence the leaf water status include stomatal size, morphology and density.

The different ways that plants cope with drought are numerous, with an enormous range and variability of anatomical and physiological characteristics reported to date. Stomatal behaviour has been rated as the strongest determinant of drought resistance (van Buijtenen *et. al* 1976) or control of transpirational water loss (Jarvis 1981), with root structure and leaf morphology variously reflecting local conditions of soil and climate (Kozlowski *et al.* 1991). Further, the relationship between g_3 and Ψ_L is considered to be a key functional response in understanding how stomata react to water stress and how they exercise their regulatory role (Ludlow 1980).

The life history strategies and functional morphology of plants are often closely linked with seasonality of precipitation (Gibson 1996). Mooney (1980) used seasonality and gradients as foci in a discussion of the evolution of mechanisms in plants that enable them to cope with both short and long term stress. Although field ecophysiological field studies may be difficult to interpret due to the possible influence of two or more

factors, they are very useful in providing both direction and material for the later design of laboratory-based studies (Mooney 1980). It must be acknowledged, of course, that the occurrence of a particular character in a plant exhibiting water stress tolerance does not necessarily demonstrate that it is of adaptive value (Kramer 1983).

The interactions among characteristics that contribute to drought resistance may be complex, and might require a particular temporal sequence of evolution. For example, some species cope with short periods of drought by closing stomata and avoiding water loss. Others growing in the same environment may invest more in root systems and osmotic adjustment that allow transpiration to be maintained during the dry period. However, the latter 'strategy' may require development of the root system before or simultaneously with an 'insensitivity' of stomata to tissue water deficits, otherwise desiccation will occur. Hence, a water saving strategy may be a simpler genetic solution to water deficits than a water spending strategy. While the various physiological and morphological adaptations to water deficit are well documented, relatively little research has focussed on the possible evolutionary pathways of resistance to water deficit. The major aim of this study was to compare the seasonal field water relations of the xerophytic *P. angustifolium* with *P. undulatum* and *P. revolutum*, which occur in habitats that are less exposed to severe water stress.

The specific aims of this study were therefore to:

- 1. determine the pattern of variation in seasonal field water relations of these species from contrasting rainfall regimes;
- 2. determine whether the seasonal water relations patterns of these species are correlated with any environmental factors.

At the time that this field study was carried out, laboratory germination trials had shown little response from seeds of *P. bicolor*, and consideration was given to omitting it from the overall study. Consequently, field observations of the seasonal water relations of *P. bicolor* were not made, even though seed of this species subsequently germinated and it was thereafter included in all investigations of drought resistance, growth rate and allocation and germination biology.

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METHODS

The study sites

The two sites selected for comparisons of seasonal water relations among these species were: (i) for *P. revolutum* and *P. undulatum*, in Croajingolong National Park, north-east of Mallacoota Inlet in East Gippsland; (ii) for *P. angustifolium*, in Wyperfeld National Park, situated within the Mallee region of north-west Victoria.

The Mallacoota site (37.49°S, 149.78°E, 20 m asl) is situated in a shallow gully in coastal moist sclerophyll forest dominated by *Eucalyptus sieberi* and *E. obliqua*, with occasional *E. cypellocarpa* and *E. muellerana*. The understorey comprises a variety of shrub and small tree species, including *Elaeocarpus reticularis*, *Tristaniopsis laurina*, *Goodenia ovata* and various *Acacia* species. *P. revolutum* individuals selected for study were all tall shrubs (height range 2-2.5 m), and those of *P. undulatum* were tall shrubs or small trees (height range 2.5-3 m). Plants of both species selected for study were all growing within 15 m of each other, and although there may have been small differences in microclimate between plants, this arrangement allowed for rapid movement among plants to carry out leaf measurements. This site, which represents the scuthern distributional limit for *P. revolutum*, is subject to the climate of coastal south-easterm New South Wales, which, together with consistent physiography, impacts significantly upon the floristics of the area. The climate is characterized by mild temperatures, with relatively regular precipitation throughout the year (Fig. 3.2a).

The Wyperfeld National Park site (35.63° S, 142.02° E, 80 m asl) is situated on the margin of the western edge of the Outlet Creek floodplain, close to the Park's southern entrance. This semi-arid region is subject to a strongly Mediterranean-type climate, with cool winters and hot, dry summers, and large amplitudes of diurnal temperature. Mean annual rainfall is in the range 350-380 mm, most of which falls during spring (Fig. 3.2b), although its annual evaporation of c. 1300 mm greatly exceeds annual rainfall (LCC 1987). Frosts are common between May and September (LCC 1987; Foreman and Walsh 1993). Soils are alkaline, finely textured grey sandy-loams, essentially duplex in structure (Foreman and Walsh 1993). The study site, which is typical habitat for *P*. *angustifolium* in this part of its range, is located on an ecotone between *E. largiflorens* open woodland and a copi rise dominated by *Callitris gracilis*, with a ground layer of open woodland and a copi rise dominated by *Callitris gracilis*, with a ground layer of various native and exotic grasses. As with the Mallacoota site, all plants selected for study were small trees of similar size (height range 2.5-3 m) and apparent health, growing no further than 15 m apart.

Pre-dawn and diurnal leaf water potential

The pressure-chamber technique (Scholander *et al.* 1965) has been the most widely used method for measurement of water potential in plants growing under field conditions (Koide *et al.* 1989), and was the method used in this study. Water potential, Ψ , is the variable most commonly used to measure the energy status of water in plants (Koide *et al.* 1989). It is defined as:

$$t' = \frac{\mu_w - \mu_w^*}{V_w}$$

where μ_w is the chemical potential of water at constant temperature and atmospheric pressure, μ_w^* is the chemical potential of pure water at the same temperature and pressure and V_w is the partial molal volume of water. As the solute concentration of xylem water is low in leaves and equilibration of water potential between mesophyll cells and the xylem is rapid, the mean water potential of leaf mesophyll can be regarded as the equivalent of the xylem pressure potential in most species (Jarvis 1976).

Using a portable Scholander-type pressure chamber (Scholander *et al.* 1965) and compressed nitrogen gas, measurements of pre-dawn (Ψ_{PD}) and diurnal (Ψ_L) leaf water potential were carried out on three fully expanded leaves from each of three separate plants of each species, at three-hourly intervals from just before dawn to dusk. Minimum diurnal leaf water potential (Ψ_{min}) for each species and season was derived from diurnal observations. Values of Ψ_{PD} and Ψ_{min} were used to determine whether there was a significant decrease in diurnal leaf water potential.

As leaves at different heights in a canopy may have considerably different values of diurnal leaf water potential (Jarvis 1976), leaves were sampled from a standard height of 1.5 m. Due to potential differences in Ψ_L between shade and sun foliage (Kaufmann 1975), leaves were selected from the outer canopy. Measurements were carried out on a sunny day in the final month of each seasonal period, and repeated at three-monthly intervals from November 1995 to August 1996. Leaves were excised from each plant and

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inserted into the pressure chamber, leaving a small section (~5 mm) of the petiole exposed. Because water potential values have been found to decrease significantly in rapidly transpiring leaves (Turner and Long 1980), the time between excision from the tree and placement in the pressure chamber was minimized. Pressure in the chamber was increased slowly by the addition of N₂, until xylem sap appeared at the cut surface of the petiole. At that exact moment, the end-point pressure value was recorded using a fixed hand-lens magnifier. The end-point balance pressure is, under most conditions, considered to equal the symplastic value of Ψ (Koide *et al.* 1989).

Diurnal stomatal conductance

Diurnal measurements of g_s were carried out on the abaxial surface of three fully expanded and illuminated leaves from each of three separate plants of each species, at two-hourly intervals from dawn to dusk. These measurements were taken seasonally, as described above for leaf water potential. Leaf conductance was measured using a steady state porometer (Model AP3, Delta-T Devices, Cambridge, UK), with calibration for the prevailing ambient temperature. Measurements were carried out on the undersurface of the leaves, and are expressed in molar terms (Cowan 1977). The maximum stomatal conductance (g_{smax}) for each species and season were derived from diurnal observations. Values of g_{smax} and noon g_s were used to determine whether there was a significant decrease in diurnal stomatal conductance.

Diurnal measurements of g_s and Ψ_L were only undertaken on days with clear skies. Irradiance was measured during summer, to investigate possible differences in photon flux density between leaves on the trees sampled at each site, and the possible impacts that differences in irradiance might have on g_s and Ψ_L . As stomata may open and close in response to environmental factors other than leaf water status and irradiance (Noggle and Fritz 1983), the porometer was used to monitor air temperature and relative humidity adjacent to the leaf, at a standard height of approximately 1.2 m above the ground.

Statistical Analyses

Assumptions regarding the distribution of data were checked using boxplots. Data did not require transformation. Diurnal measurements were undertaken on the same plant, and therefore two-way repeated measures ANOVA was used to investigate the diurnal variation in each species and how this varied seasonally. One-way ANOVA was used to test differences between Ψ_{PD} and Ψ_{min} , and noon g_s and g_{smax} for each season. For each species, seasonal relationships between Ψ_{PD} and g_{smax} , Ψ_{PD} and precipitation variables, and g_s and environmental variables were analysed by Pearson correlation and linear regression. No corrections were made for multiple comparisons, following the reasoning of Stewart-Oaten (1995). For all hypothesis tests, the critical value used was $\alpha = 0.05$.

RESULTS

Site climates

Rainfall at the Mallacocta site over the 12-month period of this study was approximately 6% above the long-term average. However, seasonal rainfall totals for spring, summer and autumn were considerably different from their long-term means (Fig. 3.3a). Spring 1995 and summer 1996 rainfall totals at the Mallacoota site were both well above average, but the autumn and winter totals were both below average, particularly that of autumn, which experienced almost 40% less rainfall than average.

Over the course of the study period, rainfall at the Wyperfeld site was approximately 21% greater than the long-term average, with above average rainfall during summer, autumn and winter (Fig. 3.3b). Winter rainfall was almost 70% higher than the long-term mean. Rainfall during the spring quarter was approximately 30% lower than the long-term average.

A comparison of the rainfall records indicates that while autumn and winter rainfall during the study period was below average at the Mallacoota site, rainfall was above average for both of these periods at the Wyperfeld site (Fig. 3.3). Although the Wyperfeld site normally receives c. 62% less annual rainfall than the Mallacoota site, due to higher than normal winter rainfall at the Wyperfeld site, for the duration of the study period it received only 56% less rainfall than the Mallacoota site. Field days on which the measurements were taken, had, in general, similar daily temperature maxima (range: 15-32°C) across both sites. Temperature minima on study days followed the pattern for monthly minimum temperatures for each site.

<u>Pre-dawn (Ψ_{PD}), diurnal (Ψ_{I}), and minimum leaf water potential (Ψ_{min})</u>

P. undulatum maintained reasonably uniform Ψ_L across all seasons, with values all higher than -0.6 MPa during autumn, winter and spring (Fig. 3.4a). For these seasons, the overall diurnal pattern of Ψ_L for this species was for a slight decrease after dawn to a minimum value in the early afternoon, after which it increased to approximate pre-dawn values (Fig. 3.4a). There was a significant diurnal decrease in Ψ , but no effect of season on Ψ_L , and no interaction between these variables (Fig. 3.5a). The lack of any seasonal effect on Ψ_L is reflected by the negligible seasonal variation in both Ψ_{PD} and Ψ_{min} with values for these variables being greater than -0.4 MPa and -1.1 MPa respectively (Fig. 3.5a). The decrease from Ψ_{PD} to Ψ_{min} for *P. undulatum* was not significant for any season except autumn (Fig. 3.5a). On a seasonal basis, Ψ_{PD} was not correlated with the actual precipitation of that period, but was very strongly correlated with the long-term average seasonal rainfall (r = 1.00, P = 0.006). As this correlation was based upon four points, it must be considered with a degree of caution.

P. revolutum demonstrated a consistent and distinctive pattern of Ψ_L across all seasons (Fig. 3.4b). Maximum values of Ψ_L , recorded at or just after dawn, decreased rapidly to minima in the range -1.5 - -1.8 MPa at 1500 h, after which Ψ_L increased to approximate pre-dawn or early morning values (Fig. 3.4b). There was a significant diurnal decrease in Ψ , but no effect of season on Ψ_L , and no interaction between these variables (Fig. 3.5b). Seasonal Ψ_{PD} ranged from -0.2 to -0.7 MPa, and Ψ_{min} ranged from -1.6 to -2.1 MPa (Fig. 3.5b). The decrease from Ψ_{PD} to Ψ_{min} was significant for each season (Fig. 3.5b).

Patterns of Ψ_L for *P. angustifolium* varied according to the season (Fig. 3.4c). The general pattern of Ψ_L was for maximum values at dawn, followed by a moderate (spring and winter) or rapid (summer) decrease to a minimum Ψ_L during the early afternoon, after which Ψ_L increased to approximately pre-dawn values (Fig. 3.4c). Diurnal values of Ψ_L were lower in spring than in winter and autumn, and for all but the midday and early afternoon values recorded during summer (Fig. 3.4c). The minimum diurnal Ψ_L was reached earlier in the day during summer than for any other season (Fig. 3.4c).

There was a significant diurnal decrease in Ψ , and a significant effect of season on the Ψ_L of *P. angustifolium* but no interaction between these variables (Fig. 3.5c). Thus, the difference between Ψ_{PD} and Ψ_{min} was significant for each season, with significant differences among seasonal values of each of these variables (Fig. 3.5c). Seasonal values of Ψ_{PD} for *P. angustifolium* ranged from -1.4 to -2.1 MPa, and those of Ψ_{min} ranged from -2.2 to -3.5 MPa (Fig. 3.5c). Maximum values of Ψ_{PD} for *P. angustifolium* were always well below zero (Fig. 3.5c), even during winter, when measurements were taken after the occurrence of an above-average amount of rainfall (Fig. 3.3). Neither Ψ_{PD} nor Ψ_{min} was correlated with seasonal or long-term average rainfall.

Comparison of leaf water potential among species

Diurnal values of Ψ_L for *P. revolutum* were considerably more negative than the cooccurring *P. undulatum* (Fig. 3.4), and *P. revolutum* exhibited greater variation in seasonal Ψ_{PD} compared with *P. undulatum* (Fig. 3.5). There was no significant difference in seasonal Ψ_{PD} between *P. undulatum* and *P. revolutum*, except during autumn (F = 10.1, P = 0.029). In contrast, *P. revolutum* had significantly lower values of Ψ_{min} than *P. undulatum* for every season (summer, F = 8.8, P = 0.042; autumn, F =26.6, P = 0.007; winter, F = 11.5, P = 0.028; spring, F = 38.1, P = 0.003). Of the three species, *P. angustifolium* demonstrated the lowest seasonal Ψ_{PD} and Ψ_{min} , and largest amplitude of Ψ_{PD} (Figs. 3.4, 3.5). Although comparisons of diurnal leaf water potential in summer show considerable differences in behaviour among the three species (Fig. 3.4), values of Ψ_{min} for all species occurred during summer, which at both sites is the hottest and driest of seasons. There were significant differences in Ψ_{PD} among species (F = 347.5, P < 0.001) and seasons for each species (F = 12.5, P < 0.001), with a significant interaction between these variables (F = 3.9, P = 0.002).

Diurnal stomatal conductance

The three species demonstrated similar patterns of diurnal g_s , which were essentially sinusoidal in shape and which fell into two broad categories; (i) autumn/winter patterns and (ii) spring/summer patterns (Fig. 3.6). During autumn and winter, g_s peaked during the early morning, after which it decreased to a minimum between midday and 1500 hrs. Conductance then increased in the late afternoon, before decreasing at a steady rate to stomatal closure at dusk (Fig. 3.6). During spring and summer the pattern of g_s was similar to that described above, except that values were considerably lower than for the other two seasons, with a shift forward in the diurnal depression of g_s for *P. undulatum* (Fig. 3.6a) and *P. angustifolium* (Fig. 3.6c). For *P. angustifolium*, diurnal g_s was highest during autumn, and then winter, with all spring and summer values being less than 0.06 mol m⁻² s⁻¹ (Fig. 3.6c).

P. undulatum displayed a significant decrease in diurnal g_s , there a significant effect of season on g_s and a significant interaction between these variables (Fig. 3.7a). There were significant differences among seasonal values of g_{smax} , but not among those of noon g_s (Fig. 3.7a). There was a significant difference between g_{smax} and noon g_s of *P. undulatum* during summer and winter (Fig. 3.7a). Patterns of diurnal g_s were not correlated with any of relative humidity, ambient temperature or light.

For *P. revolutum*, there was a significant decrease in diurnal g_s and a significant effect of season on g_s , but no interaction between these variables (Fig. 3.7b). There were significant differences among seasonal values of both g_{smax} and noon g_s (Fig. 3.7b). The difference between g_{smax} and noon g_s was significant during spring and winter (Fig. 3.7b). Patterns of diurnal g_s were not correlated with any of relative humidity, ambient temperature or light.

P. angustifolium exhibited two-peaked diurnal courses in g_s during spring and onepeaked courses during summer, autumn and winter (Fig. 3.6c). There was a significant decrease in diurnal g_s and a significant effect of season on g_s , but no interaction between these variables (Fig. 3.7c). There were significant differences among seasonal values of both g_{smax} and noon g_s (Fig. 3.7c). The difference between g_{smax} and midday g_s was significant during spring, summer and autumn (Fig. 3.7c). Summer g_s was positively correlated with relative humidity (r = 0.91, P = 0.012), but not with either ambient temperature or light. Winter g_s was negatively correlated with ambient temperature (r = -0.95, P = 0.039) but not with relative humidity or light.

Comparison of stomatal conductance among species

The patterns of diurnal stomatal conductance in winter for the co-occurring *P*. *revolutum* and *P*. *undulatum* were similar, in spite of larger-scale differences in their respective patterns of Ψ_L (Figs. 3.6, 3.8d, 3.8h). Broad patterns of seasonal stomatal conductance were much the same for all three species, with higher g_{smax} during winter and autumn than in spring and summer (Fig. 3.7). The difference in g_{smax} between *P*. *undulatum* and *P*. *revolutum* was not significant for any season except spring, during which g_{smax} of *P*. *undulatum* was significantly higher than that of *P*. *revolutum* ($F \approx$ 7.92, P = 0.048). Seasonally, highest values of g_{smax} were recorded during winter for both *P*. *undulatum* and *P*. *revolutum* (Figs. 3.7a, b), and autumn for *P*. *angustifolium* (Fig. 3.7c). *P*. *angustifolium* had higher midday g_s than both *P*. *undulatum* and *P*. *revolutum* during autumn and winter, and higher g_{smax} during autumn (Fig. 3.7).

Interaction between Ψ_L and g_s

The maintenance by *P. undulatum* of relatively high diurnal Ψ_L , across all seasons, was coupled with fluctuating stomatal conduct \Rightarrow (Fig. 3.8a-d). On a seasonal basis, g_{smax} was not correlated with either Ψ_{PD} or Ψ_{min} . For *P. revolutum*, a minimum Ψ_L by midday or early afternoon was preceded by a lowering of g_s for all seasons (Figs. 3.8eh) except autumn, when g_s actually increased to reach a maximum at circa the same time that the minimum value of Ψ_L was recorded (Fig. 3.8g). For *P. angustifolium*, declines in Ψ_L appeared to precipitate declines in g_s (Fig. 3.8i-1). This occurred both during seasons when g_s was relatively high (autumn, winter), as well as during spring, when it was low. During summer, a decline in Ψ_L was initially accompanied by an increase in g_s , albeit from a low base, until circa 1000 hrs, after which g_s declined to almost zero for the rest of the day (Fig. 3.8j). The diurnal reduction in g_s in response to decreasing Ψ_L was followed by increases in Ψ_L during the afternoon (Figs. 3.8i-1). On a seasonal basis, g_{smax} was not correlated with either Ψ_{PD} or Ψ_{min} .

DISCUSSION

These field measurements of diurnal leaf water potential and stomatal conductance suggest that the three species have quite different strategies for dealing with seasonal changes in soil moisture availability. The overall diurnal patterns of Ψ_L for *P*. *revolutum* and *P. angustifolium* conform to the typical pattern observed in a diverse range of plant species, which is essentially sinusoidal in nature (Klepper 1968; Ritchie and Hinkley 1975; Jarvis 1976). For species exhibiting this behaviour, Ψ_L falls steadily from a high value in the early morning to a minimum during the early afternoon, after which it rises slowly, reaching a maximum again just before dawn. The patterns of Ψ_L for these two species also support the suggestion that midday depression of leaf or shoot Ψ is widespread on sunny days for field plants, regardless of soil water availability (Hsiao *et al.* 1976). Nevertheless, there are considerable differences between *P. angustifolium* and *P. revolutum* in the seasonal values of Ψ_{PD} and the timing and rate of diurnal decline in Ψ_L (Fig. 3.9).

Mean values of g_{smax} and diurnal g_s for the three species fall within broader amplitudes of g_s for woody plants in these environments (Schulze et al. 1994), with seasonal maxima during autumn and winter towards the upper limit of the range (0.06-0.20 mol m⁻² s⁻¹) of evergreen woody plants (Korner et al. 1979). Similarly, the patterns of diurnal stomatal conductance among these species broadly conform to those observed. for field-growing individuals of other woody taxa (Grace 1997). High stomatal conductance at dawn or during the early part of the morning is not surprising given that stomata open in the light due to endogenous circadian rhythms or as a direct response to solar radiation (Fitter and Hay 1987). Stomatal closure during the hottest and driest part of the day (c. 1400-1600 hrs), followed by a slight recovery in late afternoon, has been reported for many species (Kozlowski et al. 1991), and is very common among taxa subject to summer drought or to periods without rainfall (Lange et al. 1982; Resemann and Raschke 1984; Tenhunen et al. 1984; Tenhunen et al. 1985b; Grace 1997). The slight recovery of g_s in the late afternoon may be due to a number of interrelated factors, including the persistence of suitable light levels, a decline in temperature, rise in humidity, and increase in leaf water potential. However, as the degree of water stress may vary considerably in different parts of a tree (Kozlowski et al. 1991), caution must be exercised in drawing conclusions about overall tree water

relations based upon leaves from only one part of the canopy. For example, determination of stomatal conductance was based on mid-canopy leaves, which usually have lower rates of g_s than leaves at the top of the canopy, where conductance is highest (Grace 1997).

Seasonal values of Ψ_{PD} for *P. angustifolium* at Wyperfeld N.P. (range -1.4 to -2.2 MPa) are similar to those recorded for the mesic wet-dry tropical species *E. tetrodonta* (-0.2 to -2.4 MPa: Prior *et al.* 1997) and semi-arid *Eucalyptus leucoxylon* (-0.8 to -2.9 MPa: White *et al.* 2000) and, but slightly higher than those of other semi-arid eucalypts, such as *E. behriana* and *E. microcarpa* (-0.9 to -4.7 MPa: Attiwill and Clayton-Greene 1984; Myers and Neales 1984). The minimum value of Ψ_{PD} for *P. angustifolium* (-3.5 MPa) is considerably less negative than those recorded for *Callitris columellaris* (-6.6 MPa: Attiwill and Clayton-Greene 1984), *Acacia harpophylla* (-7 MPa: Tunstall and Connor 1981) and *A. aneura* (-12 MPa: Slatyer 1962).

The consistently low maximum values of Ψ_{PD} observed for *P. angustifolium* has been reported for other semi-arid taxa (Bennert and Mooney 1979; Milburn 1979; Myers and Neales 1984). Low Ψ_{PD} during winter and spring, when soil water potential should approximate zero, suggests incomplete overnight equilibration of Ψ between the leaves of *P. angustifolium* and the soil. This observation has been made elsewhere (Meinzer *et al.* 1988; Ourcival and Berger 1995; Sellin 1999), even for plants subject to well-watered conditions (Donovan *et al.* 2001). Alternatively, these values of Ψ_{PD} , particularly those of winter and spring, may represent acclimation or adaptation to the increased incidence of frost during such periods (LCC 1987). Severe frosts have previously caused the death of a broad range of woody plant taxa in the Wyperfeld area (O'Brien *et al.* 1986). Low water potentials, resulting from changes in the turgor and/or osmotic pressure of leaf cells, has been proposed as a mechanism for increased frost tolerance in plants subjected to subfreezing temperatures (Kacperska and Kulesza 1987; Valentini *et al.* 1990). Furthermore, frost tolerance has also been linked to drought tolerance in the similarly widespread Mediterranean-climate species *Banksia marginata* (Blake and Hill 1996).

The quite low spring values of Ψ_L for *P. angustifolium* suggest that it may have been compromising water loss with a requirement for growth. However, this is not supported by diurnal g_s , which was comparatively low for this period. Rather, it may have been
unseasonal drought stress, brought about by lower soil moisture availability, that was responsible for the low diurnal Ψ_L and g_s observed during spring. On average, this site receives approximately 27% of its annual rainfall during the spring period, although this was only 16% for spring 1995. On the other hand, high diurnal Ψ_L and g_s during autumn, and to a lesser extent winter, together with the observed effects of season on these variables, is indicative of comparatively high potential photosynthetic capacity (Kramer 1983), suggesting that plants may behave opportunistically in response to soil moisture availability. A similar response has been recorded for other desert shrubs and perennials subject to irregular water availability (Ehleringer and Mooney 1983; Blake-Jacobson 1987).

Summer is the period during which plants inhabiting Mediterranean-type climates are most often subjected to water stress of varying degree (Tenhunen *et al.* 1985a). Very low rainfall, together with higher ambient temperatures and greater solar radiation loads during summer must place considerable pressure on rates of stomatal conductance and transpiration by *P. angustifolium*. During summer, the slight opening of stomata, resulting in low values of conductance, is restricted to a short period in the morning, when temperature and vapour pressure deficit make smaller transpirational demands. Similar behaviour has been recorded for other woody species subjected to very high water stress (Schulze and Hall 1982; Attiwill and Clayton-Greene 1984; Eamus 1999). Under such conditions, the stomata often remain closed until soil water becomes more freely available (Kozlowski *et al.* 1991).

Decreasing diurnal Ψ_L during summer, and to a lesser extent during spring, for *P*. angustifolium, reaching a minimum between 1200-1400 hrs, appears to be the trigger for stomatal closure. As the lowest Ψ in a plant is generally that of the leaf (Comstock and Mencuccini 1998), and due to the physical association between Ψ_L and leaf stomata, Cowan (1965, 1972) suggested the existence of a negative feedback loop between g_s and Ψ_L . An extension to this model is one that encompasses the hypothesis of specific water potential set-points, where stomatal closure is initiated by discrete lower thresholds of Ψ_L (Hsiao 1973; Comstock and Mencuccini 1998; Maier-Maercker 1998). The closure of stomata in response to some threshold level of leaf water content or potential serves to protect the leaf tissue against excessive tissue water loss (Bradford and Hsiao 1982). Threshold levels have been observed to differ among species and to depend upon growing conditions, including the water stress history of the plant (Brown 1974; Hsiao et al. 1976; Kozlowski et al. 1991).

Stomatal behaviour may also be regulated by factors other than leaf water status (Noggle and Fritz 1983). One hypothesis is that stomatal closure is caused by increased concentrations of abscisic acid (ABA), produced by the roots in response to decreasing soil water potential (Zhang *et al.* 1987; Zhang and Davies 1989; Sauter *et al.* 2001). The results of many recent studies support this hypothesis (Gowing *et al.* 1993; Tenhunen *et al.* 1994; Jackson *et al.* 1995; Bunce 1996), although stomatal sensitivity to ABA may vary across a light gradient (Niinemets *et al.* 1999). Possible interactions between soil water potential and increased ABA production in the reduction of g_s cannot be ruled out for *P. angustifolium*, and is worthy of further investigation.

Other environmental factors that may be associated with leaf water status, transpiration rate and stomatal closure include vapour pressure deficit (Nilsen *et al.* 1981; Pallardy and Kozłowski 1981; Sena Gomes *et al.* 1987), ambient temperature and seasonal differences in irradiance (Meinzer 1982). However, the relative importance of each of these will depend upon local climatic conditions and the morphology and physiology of individual species. For example, in a study of the water relations of the semi-arid species *Acacia harpophylla*, Tunstall and Connor (1975) found little difference in the diurnal amplitude of leaf water potential between days of high (summer) and low (spring and winter) total radiant fluxes. Nevertheless, the positive correlation in summer between g_s and relative humidity and negative correlation in winter between g_s and ambient temperature suggest that further study of the role of such variables in the seasonal water relations of *P. angustifolium* is warranted.

Characteristics of drought tolerant species include low minimum values of Ψ_{PD} together with high summer amplitudes of Ψ_L (DeLucia and Schlesinger 1991), as well as a delay in the reduction of g_s following a decrease in Ψ_L (Strain 1975; Bennert and Mooney 1979). These relationships between Ψ_L and g_s are strongly characteristic of the water relations of *P. angustifolium*, and to a lesser extent, those of *P. revolutum*. For these two species, reductions in stomatal conductance and transpirational water loss appear to only occur when leaf water potentials fall below some critical threshold value, or in response to increased ABA production mitigated by low soil water potential. One method of maintaining positive turgor is through osmotic adjustment, which is a common characteristic of drought tolerant species (Turner 1979). Osmotic adjustment can be effective in maintaining turgor pressure during periods of mild water stress, but cannot maintain turgor pressure during severe drought (Nilsen and Orcutt 1996). During osmotic adjustment, a decline in Ψ_L should enable maintenance of g_s and accompanying rates of photosynthesis (Tyree and Jarvis 1982), which is consistent with the relationship between Ψ_L and g_s during autumn and winter for *P. angustifolium* and in autumn for *P. revolutum*. At Mallacoota, growth by *P. revolutum* during autumn should be sustained by adequate conditions of temperature and rainfall.

An alternative explanation for the diurnal patterns of Ψ_{PD} and Ψ_L observed for *P*. angustifolium and *P. revolutum* may be associated with root system depth and extent, which play important roles in the responses of plants to water deficit (Etherington 1975). Thus, the low spring and summer leaf water potentials exhibited by these species may theoretically result from a shallow root system, coupled with primary roots of insufficient length and/or seasonally low soil water potentials at depths accessed by such taproots. Very similar patterns of stomatal closure in response to highly negative leaf water potentials have been recorded for a number of shallow rooted evergreen species inhabiting Mediterranean-type climates (Poole and Miller 1975). However, this is not likely to be the case for *P. angustifolium*, which possesses dual root systems with long taproots (Chapter 7).

Although there are broad similarities between *P. angustifolium* and *P. revolutum* in their patterns of diurnal Ψ_L and g_s , there are subtle differences between them in their rates of decline in diurnal Ψ_L and g_s . *P. revolutum*, whilst subject to quite different abiotic, edaphic and climatic conditions, maintains low rates of stomatal conductance and presumably transpiration for much of the day during summer. Similar behaviour has been recorded for other woody species during periods of seasonal water stress (Pearcy *et al.* 1974). These patterns of stomatal conductance conform to models of stomatal movement (Cowan 1977, 1982; Cowan and Farquhar 1977), which propose that stomata function in such a way as to minimize water losses relative to the quantity of CO₂ taken up. The advantage of a drought tolerance strategy is that by maintaining stomatal conductance, plants are capable of continued photosynthesis and slow growth during short periods of water stress, which may be of adaptive importance in nutrient or water limiting environments.

In contrast with *P. angustifolium* and *P. revolutum*, *P. undulatum* maintained uniformly high diurnal Ψ_L across seasons, although there do not appear to be differences among the species in their diurnal patterns of g_5 . Uniformly high Ψ_L , together with rapid and early stomatal closure during spring and summer, the periods during which water stress is likely to be highest, suggests that *P. undulatum* may utilize a strategy of drought avoidance (Fig. 3.1). As soil water availability declines, drought-avoiding taxa maintain comparatively high leaf water potentials by a rapid reduction in stomatal conductance, thereby reducing transpirational losses (Monson and Smith 1982; Nilsen *et al.* 1984; Kramer 1988). The conservation of water by stomatal closure will depend upon the ability of plants to reach stored water, and the length and intensity of the drought period (Larcher 1961).

An alternative explanation for the maintenance by *P. undulatum* of high diurnal and seasonal Ψ_L in this study could be constant access to adequate soil water, via welldeveloped and/or deep root systems (Bazzaz 1979, 1996) i.e. drought avoidance by continued access to water (Fig. 3.1). Although root system plasticity is a characteristic of *P. undulatum*, and may be a factor in its success in a range of soil types (Gleadow and Ashton 1981), a well-developed root system is unlikely to account for the maintenance of high Ψ_L in this taxon. This is because the maintenance of Ψ_L by access to adequate soil moisture would *not* normally be accompanied by rapid decreases in diurnal and seasonal stomatal conductance, as displayed by *P. undulatum*. These patterns support the suggestion that *P. undulatum* adopts a strategy of water saving by reducing stomatal conductance under diurnal or seasonal conditions of water stress (Fig. 3.9).

The observed maintenance of diurnal and seasonal leaf water potential for *P. undulatum* contrast with the results of Smith (1990), who recorded considerable depression of xylem pressure potential for an individual tree of this species growing in the south-western Cape region of South Africa, where it has become naturalized. Low xylem potentials (c. -2.6 MPa) in summer for *P. undulatum* were proposed by Smith to result from increased root resistance to water uptake. The differences in the water relations behaviour of *P. undulatum* between this study and that of Smith's may be due to a

number of factors, not least of which is that only one plant was used in the fynbos observations. Other possible contributing factors include likely differences in environmental conditions between the sites, in particular the likelihood of a much drier summer in the South African location, as well as factors related to plant genetics, age and height.

Similar patterns of diurnal and seasonal g_s for the co-occurring *P. undulatum* and *P. revolutum* suggest that they share a common period of growth. However, their dissimilar patterns of diurnal and seasonal Ψ_L indicate fundamental differences in their water use strategies, which may result from a number of factors including differences in osmotic responses to soil moisture availability, patterns of biomass allocation, the structure of root and canopy systems and aspects of leaf structure and anatomy (Abrams *et al.* 1994). For example, in a growth trial of 1 month-old seedlings of these species, values for mean specific root length and primary reot length of *P. undulatum* seedlings were significantly higher than those of *P. revolutum* seedlings (Chapter 6). Shallow-rootedness greatly impedes the ability of plants to maintain high leaf water potentials in the absence of sufficient soil moisture. Similar patterns of rapid reductions in Ψ_L in response to soil moisture depletion has been observed for other shallow-rooted shrubs inhabiting a Mediterranean-type environment (Gucci *et al.* 1997).

Alternatively, the differences in Ψ_L between *P. undulatum* and *P. revolutum* may have resulted from factors such as differences in microsite between plants or the size of the plants used in this study. For example, all *P. revolutum* plants used in this study were shrubs *c.* 2-2.5 m in height, whereas *P. undulatum* plants were 2.5-3 m in height with more developed canopies. Larger *P. revolutum* plants may have more developed root systems capable of accessing soils with higher moisture content, therefore maintaining a more consistent supply of water to their leaves, and preventing the observed larger-scale perturbations in Ψ_L . Furthermore, these patterns of Ψ_{PD} , Ψ_L and Ψ_{min} for *P. revolutum* at Mallacoota, which represents the southern-most distributional limit for this species, are not necessarily typical of plants growing at lower latitudes.

Although the seasonal changes in Ψ_{PD} , Ψ_{L} and Ψ_{min} for the three species appear to broadly reflect their respective phytogeographic rainfall and temperature regimes, this study has demonstrated important differences in the patterns of diurnal and seasonal tissue water relations among these species. Co-occurring, similarly-sized individuals of *P. undulatum* and *P. revolutum* appear to have considerably different means of managing water economy (Fig. 3.9). *P. revolutum* had significantly lower seasonal values of Ψ_{min} than *P. undulatum* and demonstrated considerable diurnal depression in Ψ_L , in contrast with *P. undulatum*, which maintains Ψ_L at relatively constant level. However, field studies such as this are unable to separate the role of genetic differences in these patterns of water use from the effects of different environmental conditions, even for co-occurring species. One way of elucidating the role of differences in genetic variation in determining drought resistance among closely related species is to grow them under common environmental conditions. The observations and outcomes of a droughting experiment conducted on the four species of *Pittosporum* grown under such conditions will be examined in the following chapter.

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Figure 3.1 Plant drought resistance mechanisms (modified from Levitt 1972, 1980; Turner 1979, 1987; Nilsen and Orcutt 1996).





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Figure 3.3 Seasonal long-term (open columns) and 1995-96 (shaded columns) rainfall for the (a) Mallacoota and (b) Wyperfeld N.P. study sites. Long-term precipitation means were derived from BIOCLIM. Seasonal rainfall data for 1995-96 were provided by local staff of the Victorian Department of Conservation and Environment.



Figure 3.4 Seasonal diurnal leaf water potential of (a) *P. undulatum* and (b) *P. revolutum* at Mallacoota, and (c) *P. angustifolium* at Wyperfeld N.P. (means \pm sem, n=3).

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Figure 3.6 Seasonal diurnal stomatal conductance of (a) *P. undulatum* and (b) *P. revolutum* at Mallacoota, and (c) *P. angustifolium* at Wyperfeld N.P. (means \pm sem, n=3).

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Figure 3.7 Seasonal variation in midday (\blacktriangle) and maximum (\blacksquare) stomatal conductance of (a) *P. undulatum*, (b) *P. revolutum* and (c) *P. angustifolium*. (means ± sem, *n*=3). Asterisks above points indicate significant differences between midday g_s and $g_{smax}(P < 0.05)$.



Figure 3.8 Patterns of seasonal diurnal leaf water potential (--m-) and stomatal conductance (-- - -). (means $\pm sem$, n=3).



Figure 3.9 Major seasonal water relations characteristics of three of the four species in relation to their purported cladistic positions as per Cayzer *et al.* (2000). The dashed line indicates that the position of *P. revolutum* is yet to be fully resolved.

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CHAPTER 4. COMPARATIVE DROUGHT RESISTANCE

In the previous chapter, field measurements were made of the diurnal and seasonal leaf water potential and stomatal conductance for three species of *Pittosporum* occurring at two sites. Although such studies are useful as indicators of the ways in which plants respond to seasonal water stress, interpretation of patterns is difficult due to differences in environmental variables between sites. The growth of plants under common conditions enables the elucidation of differences in genotype that may cause variation in drought resistance among them. It also enables the measurement of other ecologically-important water relations variables, including transpiration rate and those derived from pressure-volume analyses.

Plant water deficits develop when water is lost from the leaf during the uptake of carbon dioxide from the atmosphere. Patterns of water deficit can vary with weather and soil conditions, with plant water stress developing on very hot days or during drought. While species differ in their response to water stress, the short- to medium-term physiological effects of water stress include reductions in cell growth and cell wall synthesis and the loss of cell turgor and the closure of stomata, leading to the inhibition of photosynthesis and disturbance to nitrogen and carbohydrate metabolism (Hsiao *et al.* 1976; Kramer 1980; Bradford and Hsiao 1982). Long-term water stress may cause a reduction in xylem conductance leading to xylem cavitation and runaway embolism, a decrease in protein synthesis, the hydrolysis of starch to sugars and the accumulation of proline and other intermediates (Tyree and Sperry 1988; Kozlowski *et al.* 1991).

The ability of plants to function effectively under conditions of increasing water stress depends on their capacity to adjust form and function to offset the potentially damaging impacts of negative water potentials (Khalil and Grace 1992). Drought resistance thus results from the integration of a variety of adaptive characteristics and physiological mechanisms (Turner 1979; Jones 1980; Ranney *et al.* 1991). Arid and semi-arid taxa, for example, often exhibit a range of anatomical and physiological adaptations to water stress (see Turner and Kramer 1980; Cowan 1981; Jones *et al.* 1981; Turner and Begg 1981; Atwell *et al.* 1999). As the impacts of water stress are likely to be most critical at the seedling stage, mechanisms of drought resistance have important ramifications for species' patterns of survivorship and distribution.

Plants that are highly drought resistant can be differentiated from less resistant taxa based on a number of water relations variables, in particular those derived from the relationship between water potential and water content (Monson and Smith 1982; Bannister 1986). Such variables include osmotic potential at full and zero turgor and the bulk modulus of elasticity. The relationships between these variables may differ markedly between species, and can influence the ecological range of species (Grace 1997). A common characteristic of highly drought resistant taxa is their capacity to maintain positive turgor (with small changes in water content) in spite of large declines in Ψ_L (Weatherley and Slatyer 1957; Jarvis and Jarvis 1963; Ranney *et al.* 1991; Grace 1997). Turgor pressure is often positively correlated with photosynthesis and plant growth under water stress (Johnson 1978; Osonubi and Davies 1978).

Stomatal response to water stress may also play an important role in determining the ability of a species to resist drought (Kaufmann 1981). As discussed in Chapter 3, variation in diurnal and seasonal patterns of stomatal conductance (g_s) may result from variation in particular environmental variables, including light intensity, temperature, CO_2 , soil water availability and air saturation deficit at the leaf surface (D_s) (Jarvis 1980; Mansfield and Davies 1981). As stomatal conductance has been shown to be very sensitive to changes in D_s (Schulze and Hall 1982), some researchers have concluded that D_s is the most important variable for explaining variation in g_s (Bunce 1985; Aphalo and Jarvis 1991). Other evidence suggests that it is the rate of water loss from the leaf (the transpiration rate, E) that determines stomatal response, as a decline in g_s appears to be the principal cause for a decline in E as water stress develops (Hsiao 1973; Kozlowski *et al.* 1991; Mott and Parkhurst 1991; Monteith 1995).

Another indicator of a plant's drought resistance is its water use efficiency (WUE), which is the ratio of net photosynthesis to transpiration (Sinclair *et al.* 1984). The use of carbon isotope ratios (^{13}C ; ^{12}C) to estimate long-term WUE has become a routine procedure in controlled (Ehleringer 1989; Farquhar *et al.* 1989) and natural ecosystems (Ehleringer and Cooper 1988; Lajtha and Marshall 1994). Carbon isotope ratios in C₃ plants provide an estimate of intercellular CO₂ levels (Farquhar *et al.* 1982), which are negatively correlated with WUE (Farquhar and Richards 1984; Lajtha and Marshall 1994). Decreases in the discrimination of ^{13}C in response to increasing water stress or along altitudinal or precipitation gradients have been recorded for a number of species (Mansfield 1976; Davies *et al.* 1978; Korner *et al.* 1988, 1991; Stewart *et al.* 1995; Arndt *et al.* 2000), although such patterns are not necessarily uniform amongst wider species groups or along environmental gradients (Miller *et al.* 2001).

As drought limits plant growth and reduces the likelihood of survival, selective pressure for adaptation to water stress is often high (Pallardy 1981). Interspecific differences in responses to water stress are therefore important in determining their comparative drought resistance (Kaufmann 1981) and may also provide insights into the co-evolved responses of species and degree of divergence between them. The ability to distinguish between genotypic and phenotypic variation within species, and identification of the degree of phenotypic plasticity within them, are crucial in determining stress adaptations of plant species (Abrams 1994).

The major aims of this experiment were to investigate differences in drought response among the four *Pittosporum* species from contrasting rainfall regimes and evaluate the potential adaptive significance of this for their drought resistance. In contrast with the previous chapter, use of seedlings allowed growth of the four species in a common environment, thus allowing genetically-derived differences to be identified. Given the generality of the term *drought resistance*, the potential importance of determining the specific physiological or morphological characteristics that confer such resistance cannot be understated. The specific aims of this study were to investigate and compare the effects of drought on these four *Pittosporum* species in terms of their:

- 1. rates of transpiration (E) and stomatal conductance (g_s) ;
- tissue water relations, including turgid weight:dry weight ratio, leaf water potential, osmotic potential at full hydration and turgor loss, degree of bulk elastic modulus and relative water content;
- 3. overall drought resistance and possible links between this and aspects of their ecology and distribution.

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METHODS

Seed collection and germination

Between March and July 1995, fully mature seed capsules of *P. undulatum, P. revolutum, P. angustifolium* and *P. bicolor* were collected from at least three trees within a naturally occurring Victorian population of each species (Table 4.1). Seeds were removed from dehisced capsules, wiped clean of mucilage and stored at room temperature for later use. In October, seed was sown in flat trays containing equal parts sand and fine potting mix. Due to predetermined differences between the species in the time taken to commence germination, seed sowing was staggered to facilitate simultaneous germination, enabling comparison of water stress response by similarly-aged plants of each species. Approximately one month after germination, seedlings were planted out into plastic potting bags (20 cm by 10 cm) containing seedling-raising mixture. Seedlings were randomly arranged in a glasshouse, rotated regularly to minimise the effects of environmental variation and top-watered once per week with a dilute solution of Aquasol[®]. Six-month-old seedlings were used in all subsequent experiments.

Transpiration rates with limiting and non-limiting soil moisture

During April 1996, 10 similarly-sized seedlings of each species were selected, watered to near field capacity and then each pot was sealed to prevent direct loss of water from the soil. Seedlings were then divided into two groups. Control seedlings were provided with as much water as required to maintain their initial weight, while water was withheld from droughted seedlings for a period of 79 days. This timeframe enabled the development of slowly increasing water stress, thus simulating field conditions, which is important in comparing the drought responses of species (Kramer 1980).

Transpiration rates of control and droughted seedlings, expressed as mg day⁻¹ cm⁻² leaf area, were measured by weighing the pots every 1-2 days at 7 a.m. The leaf area of each seedling was estimated from leaf dry weight measurements, based on leaf samples from non-experimental seedlings for which leaf area-dry weight relationships were derived by regression. The transpiration rates of droughted seedlings were also calculated as a percentage of *E* of control seedlings for each species.

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Stomatal conductance

Measurements of noon abaxial leaf conductance to water vapour diffusion (g_s) were carried out alternately on five randomly selected droughted and control seedlings of each species, using a steady state porometer (Model AP3, Delta-T Devices, Cambridge, UK). Measurements of g_s were carried out prior to the start of the trial and on days 11, 43, 58 and 79.

Pre-dawn leaf water potential

Pre-dawn leaf water potential (Ψ_{PD} - using a Scholander-type pressure chamber and the procedure described in Chapter 3) was measured on five seedlings at the commencement of the trial, and then on five randomly selected control and droughted seedlings on days 14, 28, 50, 65 and 79. Maximum values of leaf water potential occur just before dawn, due to the equilibrium that arises between soil and plant water potentials in the absence of water flux (Tardieu and Simonneau 1998). As plants growing in soils with decreasing water availability generally have decreasing values of Ψ_{PD} , it is therefore a reliable indicator of the soil water potential operating in the plant root zone. The pressure at which xylem sap appeared at the cut petiole surface was taken as a measure of the pre-dawn bulk leaf water potential. For measurements of Ψ_{PD} , droughted and control seedlings were sampled alternately.

Other tissue water variables

Of the seedlings harvested for measurement of Ψ_{PD} , 27 were also used to compare temporal patterns of tissue water relations among droughted seedlings of the species. Pressure-volume analysis was carried out on three seedlings of each species at the commencement of the trial, and on three control and droughted seedlings on days 14, 28, 50 and 65. On sampling days, after measurement of Ψ_{PD} , each seedling shoot was placed into a beaker with its cut end in distilled water, covered in a black plastic bag and allowed to resaturate for 6-8 hours. The weight of each shoot taken immediately after rehydration was used as its saturated weight. The method used to determine tissue water variables was similar to that of Wilson *et al.* (1979), which is essentially a technique combining measurements of sap expression and air drying over time. This involved the weighing of the resaturated shoot followed immediately by measurement of its balance pressure, which was recorded as the water potential at full saturation. To avoid tissue damage, the chamber pressure was slowly increased in steps of approximately 0.2 MPa sec⁻¹. After determination of the balancing pressure, the pressure was slowly reduced and the shoot removed from the chamber and allowed to transpire freely on a laboratory bench (Hinckley *et al.* 1980; Ritchie and Roden 1985) until the next measurement was taken, usually within *c.* 1 hour. Pressure volume curves and associated water relations variables - osmotic potential at full turgor (π_s) and turgor loss point (π_p), relative water potential at zero turgor (RWC₀) and bulk modulus elasticity (ε_s) - were derived using the program 'Template' (Radford and Lamont 1992). The bulk modulus of elasticity is defined as the change in turgor pressure per change in relative symplastic water content (Jones and Turner 1980).

The tissue relative water content (R') is defined as:

$$R' = \frac{W_s + W_a}{W_s^{\circ} + W_a^{\circ}}$$

where W_s is the total weight of symplastic water in the tissue, W_a is the weight of apoplastic water, W_s^o is the weight of symplastic water at full hydration, and W_a^o is the weight of apoplastic water at full hydration (Koide *et al.* 1989). Essentially, for each measurement of Ψ_L , the corresponding R' value can be calculated as:

$$R' = \frac{fresh \ weight - dry \ weight}{saturated \ weight - dry \ weight}$$

After the final readings of balancing pressure and weight, shoots were dried in a twostage heat-drying process, with 1.5 hours at 100°C followed by 48 hours at 70°C, after which the components were reweighed. This drying procedure approximates the respiratory losses that occur during freeze-drying, while avoiding reduction in total nonstructural carbohydrates that occurs during prolonged drying at 70°C (Chiariello *et al.* 1989).

Carbon isotope discrimination was measured on leaf tissue from control and droughted plants harvested on day 79 of the trial. A small quantity (1 to 2 mg) of sample was combusted with CuO in quartz tubes at 1000°C to liberate CO₂. This was cryogenically purified and analysed on a Finnigan MAT 252 dual-inlet mass spectrometer in the School of Geosciences at Monash University. The volume of CO₂ produced was measured to ensure complete combustion has occurred. Analysis of blanks indicated negligible production of CO₂ by the CuO and quartz tubes. Standardization was made against CO₂ of known isotopic composition and the in-house Monash Graphite standard. Duplicates of samples and standards indicated that precision was within 0.2 parts per million. δ^{13} C values were calculated by comparing the 13 C/ 12 C ratio of the sample (R_s) relative to the Pee Dee belemnite standard (R_{PBD}):

$$\delta^{13}C$$
 (‰) = [(R_s/R_{PDB}) -1] x 1000

For interspecific comparisons of WUE, the relationship between WUE and δ^{13} C rests on the assumption that plants will be physiologically active at the same time of the year, with leaves subjected to similar leaf-to-air vapour pressure deficit (DeLucia and Schlesinger 1991). All seedlings utilised in the trial were similarly aged and grown under uniform glasshouse conditions, which largely satisfies these assumptions.

Statistical Analyses

Assumptions were checked using boxplots. Data did not require transformation. Differences between treatments and among species were investigated using ANOVA. Among species, *post hoc* Tukey's tests were used for multiple comparisons. Associations among physiological and environmental variables were tested using Pearson correlation. No corrections were made for multiple comparisons, following the reasoning of Stewart-Oaten (1995). R^2 values of individual variables derived using 'Template' were in all cases greater than 0.97. For all hypothesis tests, the critical value used was $\alpha = 0.05$. All statistical analyses were carried out using SYSTAT® Version 9.0 (SPSS Inc. 1999).

RESULTS

Transpiration rates

Before the commencement of droughting, there was an almost three-fold variation in mean E among the four species (Table 4.2). The species fell into two groups, with the transpiration rates of P. undulatum and P. bicclor significantly higher than those of P. revolutum and P. angustifolium (Table 4.2). Droughted seedlings of seedlings of P. undulatum and P. bicclor had higher average rates of transpiration than control seedlings for the first ten days of droughting (Fig. 4.1). Over the course of the trial, the transpiration rates of control seedlings of all four species initially increased, after which they slightly decreased (Fig. 4.1), although significant differences in E between the two species groups were maintained (Fig. 4.2a). The mean daily transpiration rate was strongly correlated with maximum temperature of the glasshouse for control seedlings of P. undulatum (r = 0.65, P < 0.001) and P. revolutum (r = 0.65, P < 0.001) but not for P. angustifolium or P. bicolor.

Following the commencement of the droughting treatment, the transpiration rate of all four species decreased (Fig. 4.1). Additionally, the daily transpiration rate of each species was strongly correlated with maximum glasshouse temperature (*P. undulatum*: r = 0.92, P < 0.001; P. revolutum: r = 0.88, P < 0.001; P. angustifolium: r = 0.91,<math>P < 0.001; P. bicolor: r = 0.90, P < 0.001). Of the species, *P. undulatum* reacted earliest to decreasing soil water availability, with a decline in *E* commencing after approximately 10 days without water (Fig. 4.1). *P. revolutum* and *P. bicolor* maintained normal rates of transpiration for approximately 22 and 30 days respectively (Fig. 4.1).

Between days 13-28 after the withholding of water, the rate of decline in E was 4.5 mg day⁻¹ cm⁻² for P. undulatum, 3.4 mg day⁻¹ cm⁻² for P. bicolor, 2.9 mg day⁻¹ cm⁻² for P. angustifolium and 2.4 mg day⁻¹ cm⁻² for P. revolutum. The difference in E between control and droughted seedlings became significant at 28 days for P. undulatum (F = 8.24, P = 0.024), 29 days for P. revolutum (F = 6.66, P = 0.042) and P. angustifolium (F = 9.12, P = 0.017), and 35 days for P. bicolor (F = 12.5, P = 0.008) (Fig. 4.1). At the cessation of the trial, the transpiration rate of droughted compared to control seedlings was 35% for P. bicolor, 21% for P. revolutum, 11% for P. undulatum

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and 4% for P. angustifolium (Fig. 4.3). By day 65 of the trial there was a significant difference among species in the mean transpiration rates of droughted seedlings (F = 12.3, P < 0.001; Table 4.3).

Stomatal conductance

Prior to the withholding of water, there were no significant differences in g_s among the four species (Table 4.2). For control seedlings of these species, the trend was an apparent increase in mean g_s for the first 11 (*P. revolutum*, *P. angustifolium*) or 43 days (*P. undulatum*, *P. bicolor*), followed by a gradual decrease in mean g_s over the remainder of the experiment (Fig. 4.4). The pattern of g_s in droughted seedlings was very similar to the general pattern of g_s in control seedlings for all species except *P. undulatum*, droughted seedlings of which showed an apparent immediate decrease in g_s (Fig. 4.4), such that by day 43 following the withholding of water, the g_s of such seedlings was significantly lower than that at the commencement of the trial (F = 191.6, P < 0.001).

Significant differences in g_s between control and droughted seedlings were established by day 43 for both *P. undulatum* (F = 199.6, P < 0.001) and *P. revolutum* (F = 7.9, P = 0.027) and day 58 for *P. bicolor* (F = 64.6, P < 0.001). There was no significant difference in mean g_s between control and droughted seedlings of *P. angustifolium* for the duration of the trial although at cessation of the trial, the average g_s of droughted *P. angustifolium* seedlings was 25% lower than that of control seedlings (Fig. 4.5). Among the other species, the reduction in g_s was 58% for *P. revolutum* (F = 11.5, P = 0.009), 65% for *P. bicolor* (F = 38.3, P < 0.001) and 94% for *P. undulatum* (F = 108.9, P <0.001; Fig. 4.5). By day 65 there was a significant difference in g_s of droughted seedlings among the species (F = 6.9, P = 0.004; Table 4.3).

Among control seedlings, *P. undulatum* had the highest rate of transpiration for a given value of stomatal conductance, followed by *P. bicolor* and *P. angustifolium*, with *P. revolutum* demonstrating the lowest amount of water loss for a given g_s (Fig. 4.6). Control seedlings of all four species showed only slight decreases in *E* for comparatively large decreases in g_s (Fig. 4.6). However, for all species except *P. bicolor*, the rate of change in *E* for a relative change in g_s appears to be higher in droughted compared to control seedlings (Fig. 4.6).

The relationship between g_s and E in droughted seedlings of each species appears to conform to one of three patterns. The first, which is characteristic of P. undulatum, is one in which decreasing g, is strongly correlated with a decline in E (from an initially high comparatively value) (r = 0.99, P = 0.001), with both variables approaching zero by cessation of the trial (Figs. 4.6a; 4.7a). The second is similar to the first in that g, and E are strongly correlated, but in this case there is the maintenance of moderate g_s as E approaches zero. This correlation between g_s and E is characteristic of P. revolutum (r = 0.92, P = 0.027) and P. angustifolium (r = 0.94, P = 0.017) (Figs. 4.6b, c; 4.7b, c). The third pattern, which is characteristic of P. bicolor seedlings, is one where there is no correlation between g_s and E (Fig. 4.6d). In this species, plants maintained high g_s for a long period following the commencement of droughting, in spite of decreasing Eand increasing water stress (increasingly negative Ψ_{PD}), until there is a sudden and dramatic decline in g_s (Fig. 4.7d). This relationship is characterized by the maintenance of low rates of E, even as g_s approaches zero. While there was no correlation between g_s and E for droughted seedlings of P. bicolor, there was a correlation for control seedlings (r = 0.93, P = 0.025).

Leaf water potential

Prior to the withholding of water, Ψ_{PD} of *P. revolutum* seedlings was significantly lower than that of the other three species (Table 4.2). There was very little temporal variation in the Ψ_{PD} of control seedlings of *P. revolutum* and *P. bicolor*, and the Ψ_{PD} of control seedlings of *P. undulatum* and *P. angustifolium* remained above -1 MPa for the duration of the trial (Fig. 4.8). Mean Ψ_{PD} of droughted seedlings of *P. revolutum*, *P. bicolor* and *P. angustifolium* gradually declined over the course of trial, although for *P. angustifolium* mean Ψ_{PD} was not significant lower than that of control seedlings (Fig. 4.8). Droughted seedlings of *P. undulatum* displayed very little change in Ψ_{PD} until day 65, when the difference in this variable between control and droughted seedlings first became significant (F = 8.7, P = 0.019) (Fig. 4.8a). For other species, there was no significant difference in Ψ_{PD} between control and droughted seedlings until day 28 for *P. bicolor* (F = 16.8, P = 0.003) and day 50 for *P. revolutum* (F = 8.2, P = 0.021; Figs. 4.8b, 4.8d). There was no significant difference in Ψ_{PD} between control and droughted seedlings of *P.* angustifolium for the duration of the trial. By day 65 of the trial there were significant differences among the species in the Ψ_{PD} of droughted seedlings (Table 4.3).

The relationship between stomatal conductance and leaf water potential among the four species appears to conform to three patterns (Fig. 4.9). The first is one in which there is no correlation between g_s and Ψ_{PD} (and thus Ψ_L). In this response to decreasing soil water availability, which is characteristic of *P. undulatum*, as g_s declines values of Ψ_{PD} are maintained within the range -0.5 to -1 MPa for much of the trial (Fig. 4.9a). The second response, which characterizes seedlings of *P. revolutum* and *P. angustifolium*, is one in which there is a positive relationship between g_s and Ψ_{PD} (and thus Ψ_L) (Figs. 4.9b,c). The third response, displayed by droughted seedlings of *P. bicolor*, is an apparent negative correlation between g_s and Ψ_{PD} for the first 45 days of the trial, after which it becomes positive (Fig. 4.9d).

Other tissue water variables

Values of π_s and π_p for control seedlings of these species did not vary significantly over the course of the study (Figs. 4.10, 4.11), except for π_s for *P. bicolor*, for there was a significant decrease between commencement and termination of the trial (F = 19.6, P = 0.047). In contrast to the general lack of decreases in π_s and π_p of control seedlings of these species, droughted seedlings commonly exhibited decreases in these variables (Figs. 4.10, 4.11). At harvest, the π_s of droughted seedlings was lower than that of control seedlings for each species, but this difference was only significant after 29 days for *P. angustifolium* (F = 10.2, P = 0.033), and by 65 days for *P. revolutum* (F = 206.0, P = 0.004) and *P. undulatum* (F = 29.0, P = 0.013) (Fig. 4.10). There was no significant difference in π_s between control and droughted *P. bicolor* seedlings during the trial. *P. angustifolium* was the only species to show a significant effect of droughting on π_p . The difference in π_p between droughted and control seedlings became significant after 29 days without water (F = 34.0, P = 0.004) (Fig. 4.11c).

For each species, there was no significant difference in turgid weight:dry weight ratios between control and droughted seedlings at any stage during the trial (Fig. 4.12). At commencement of the trial, *P. bicolor* seedlings had a significantly higher mean turgid weight:dry weight ratio (TW:DW) than those of the other species (F = 89.5, P < 0.001).

By day 65, the TW:DW ratio in droughted seedlings of *P. bicolor* was significantly lower than that at the commencement of the trial (F = 176.8, P = 0.005).

Temporal patterns of ε_s were difficult to discern, although values recorded for both control and droughted seedlings of all species fall within the range previously recorded for other woody taxa (Turner 1986a). Droughted *P. bicolor* seedlings demonstrated the highest change in ε_s , with an increase from c. 6 MPa to 10 MPa by cessation of the trial (Fig. 4.13d). Over the course of the trial, droughted seedlings of *P. undulatum* also demonstrated an increase in ε_s (Fig. 4.13a). Trends in relative water content values are equivocal (Fig. 4.14). There were no significant differences among species in ε_s , π_s , π_p or the TW:DW ratio of droughted seedlings 65 days after withholding water (Table 4.3).

The mean δ^{13} C of control seedlings of *P. bicolor* harvested at completion of the trial was significantly lower (more negative, i.e. greater discrimination against ¹³C) than that of the other three species (Table 4.4). This implies that under non-limiting soil moisture conditions, the intrinsic WUE of *P. bicolor* is lower than that of the other three species. Mean values of δ^{13} C for droughted seedlings of all four species were higher than those of control seedlings, although this difference was only significant for *P. bicolor* and *P. undulatum* (Table 4.4). This suggests that by completion of the trial, the WUE of droughted *P. bicolor* and *P. undulatum* seedlings was significantly higher than that of control seedlings. There was a significant difference between *P. bicolor* and *P. undulatum* in the mean δ^{13} C of droughted seedlings (*F* = 7.9, *P* = 0.022) (Table 4.4).

Among control seedlings, there was a strong positive correlation between δ^{13} C and leaf water potential (r = 0.99, P = 0.011). For droughted seedlings, δ^{13} C values were positively correlated with leaf water potential (r = 1.00, P = 0.002), but δ^{13} C was not correlated with either E or g_s. In regard to climate variables of the collection sites, for control seedlings δ^{13} C was positively correlated with mean annual temperature (r = 0.99, P = 0.007) and summer temperature (r = 0.96, P = 0.043), but negatively with most precipitation variables. Among droughted seedlings there was a strong negative correlation between E and the mean temperature of the warmest quarter (r = -1.00, P = 0.005) but a weak positive correlation between E and winter rainfall (r = 0.95, P = 0.049). These correlations must be considered with some caution as they are the product of only four paired data points.

DISCUSSION

Seedlings of these four *Pittosporum* species exhibited differences in both their day-today water relations and in their drought response strategies (Fig. 4.15). Furthermore, seedling responses to drought were very similar to the seasonal water relations of more mature, field growing plants, as discussed in the previous Chapter. Droughted seedlings of the species differed most in their rates of decline in transpiration rate and stomatal conductance and in their relationships of g_s with E and g_s with Ψ_{PD} . In congeneric taxa belonging to the same functional group, the physiological mechanisms of drought resistance might reasonably be expected to vary in the rapidity and/or degree of response, rather than being based on substantially different strategies. Consequently, the broad scale differences in water relations and responses to drought among these closely-related species may be important indicators of the physiological adaptations that may evolve in dry environments.

P. bicolor appears to possess low-moderate drought resistance. This conclusion is based upon its maintenance of high stomatal conductance in response to decreasing soil water availability, resulting in continued high rates of transpiration, a comparatively large decrease in tissue water content per unit reduction in leaf water potential and an apparent inability to adjust osmotically to decreasing leaf water potential. The maintenance of high stomatal conductance under conditions of decreasing soil water availability and leaf water potential is consistent with the previously discussed hypothesis of critical or threshold Ψ_L , a common response among species subject to seasonal drought (Sobrado and Turner 1983).

P. bicolor seedlings also demonstrated high rates of transpiration under non-stressful conditions and an early reduction in leaf water potential and maintenance of relatively high osmotic potentials per unit fall in leaf water potential following the imposition of water stress. These characteristics are all consistent with a water-spending drought response strategy (Levitt 1972; Monson and Smith 1982; Kalapos 1994), although under most circumstances this would result in the maintenance of Ψ_L , rather than the decline in this variable observed in *P. bicolor*. Alternatively, a water spending response to drought is exhibited by species that are able to consistently access soil water, via well-developed root systems with large absorptive surfaces and possibly high root:shoot

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ratios (Fig. 3.1). The relationships between these variables in the four species are discussed in the next chapter.

The ecological consequence of a water spending strategy is that under mild water-stress conditions, changes in diurnal transpiration rate and leaf water potential do not result in significant stomatal closure, which occurs only when reductions in soil water potential cause considerable decreases in leaf water potential (Jarvis 1980). When this occurs, water-spending taxa become water savers (Levitt 1980). The initial maintenance of g_s and E by droughted P. bicolor seedlings is similar to that of Nothofagus cunninghamii, and may be an important physiological mechanism for species normally subject to only mild water deficit during summer but to cold winters that largely prevent photosynthesis (Read and Farquhar 1991). Thus, in environments where water deficits are relatively rare, a water spending strategy under conditions suitable for growth, possibly resulting in mild water stress, may be of adaptive importance. As *P. bicolor* inhabits communities that are only rarely subject to long periods without rainfall, the response to drought of its seedlings is consistent with the broad application of this hypothesis.

The significantly higher WUE of droughted compared to watered seedlings of *P*. *bicolor*, inferred from δ^{13} C values, suggests that this species has some capacity for drought acclimation. As δ^{13} C analyses were conducted at the cessation of the trial, it is not possible to determine whether the inferred increase in WUE was initiated early during soil drying or as a consequence of the reduction in *g*_s observed approximately 6 weeks after the withholding of water. The decrease in turgid weight:dry weight ratio and increase in ε_s of droughted *P*. *bicolor* seedlings might reflect some minor degree of structural acclimation, possibly resulting in an increase in cell wall thickness, or a decrease in cell size, which as mentioned above often accompanies water stress (Turner and Jones 1980).

P. undulatum appears to possess moderate-high drought resistance. Its seedlings maintain relatively high Ψ_L in spite of decreasing soil water availability, which probably results from simultaneous reductions in g_s and *E*. This behaviour is also consistent with seasonal patterns of Ψ_{PD} and g_s of this species growing in the field (Chapter 3). Rapid stomatal closure, which is the most common of all plant responses

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to water stress (Jones *et al.* 1981), is considered to be characteristic of drought avoiding taxa (Oechel *et al.* 1972; Levitt 1980; Pallardy 1981). Rapid stomatal closure may account for its increase in water use efficiency, inferred from higher δ^{13} C. High stomatal sensitivity to water deficit, coupled with increased WUE, is also consistent with a drought avoidance strategy (DeLucia and Schlesinger 1991; Dawson and Ehleringer 1993). Moreover, a rapid reduction in *E* in response to declining soil moisture availability is characteristic of high drought resistance (Nunes 1967). Taxa demonstrating an ability to maintain relatively high leaf water potential during drought are known as isohydric species (Bates and Hall 1981; Meinzer and Grand 1990; Khalil and Grace 1992; Loewenstein and Pallardy 1998). The control of water status in such species reinforces the important role of stomata in the prevention of damaging water deficits (Jones and Sutherland 1991), which as discussed above have the capacity to cause xylem cavitation and possibly runaway embolism (Tyree and Sperry 1988). Species that demonstrate a strategy of drought avoidance are common in environments subject to a moderate degree and/or duration of water strates (Levitt 1980).

Other mechanisms of drought avoidance during periods that would otherwise cause water stress include the possession of deep root systems and/or effective methods of water uptake (Turner 1986b). The limited root biomass and architecture of six-monthold tubed seedlings is unlikely to account for the maintenance of Ψ_L . Hence, rapid stomatal closure appears to be the primary mechanism of drought avoidance for *P. undulatum* seedlings exposed to water stress in this experiment. The apparent response of stomata to soil water depletion, prior to any significant change in the leaf water status, suggests that for *P. undulatum*, g_s may be more closely correlated with soil water availability than with Ψ_L . This supports the hypothesis that stomatal closure is effected by signals generated within the root system and transported to leaves via the transpirational stream (Blackman and Davies 1985; Zhang and Davies 1990; Gowing *et al.* 1990; Trejo and Davies 1991; Khalil and Grace 1992).

The drought avoidance strategy of *P. undulatum* seedlings in maintaining leaf water potential continues to a possible threshold level of soil water potential, after which leaf water potential declines rapidly. The concomitant decreases in Ψ_L and π_s , suggests that *P. undulatum* seedlings had begun to adjust osmotically in order to maintain cell turgor, a response that is more characteristic of drought tolerant species (Turner and Jones 1980), although a strategy of drought avoidance coupled with a capacity for osmotic adjustment has been observed in other drought resistant species (Arndt *et al.* 2000).

Gleadow and Rowan (1982) proposed a strategy of drought tolerance for *P. undulatum*, based on such factors as its speed of recovery after water stress and its possession of thin leaf cuticles, shallow roots and glabrous leaves that do not abscise when stressed. A drought tolerance strategy is also supported by the ability of *P. undulatum* seedlings to maximise a decrease in leaf water potential per unit decrease in water content, which is common among stress tolerant, sclerophytic taxa (Cowan 1981; Kramer 1983). The drought resistance behaviour displayed by *P. undulatum* is similar to that of *Acmena smithii* (Melick 1990), with which it shares strong distributional and vegetation links (Floyd 1989).

These observations suggest that *P. undulatum* is capable of both drought avoidance and tolerance strategies, each of which is expressed at different degrees of water stress. The sequential expression of physiologically adaptive mechanisms has been observed in other drought resistant taxa (Riga and Vartanian 1999). It may be this suite of physiological mechanisms that enables *P. undulatum* to successfully inhabit a wide range of habitat types, from temperate rainforest and sclerophyll forests that under normal conditions are subjected to only moderate water stress, through to communities subject to low annual rainfall or strongly seasonal conditions.

The most drought resistant of these species appear to be *P. revolutum* and *P. angustifolium*, which display day-to-day rates of transpiration and stomatal conductance that are significantly lower than the other two species. A decrease in leaf water potential in response to water stress, whilst maintaining low rates of transpiration, together with osmotic adjustment in response to decreasing soil water availability, support a strategy of drought tolerance for these species (Fig. 4.15).

The minimization of transpiration by plants conforms to three broad strategies: (i) reduction in plant leaf area, expressed by variables such as leaf area ratio; (ii) reduction in radiation absorption per unit leaf surface area; (iii) increased resistance to water vapour in the transport pathway (Bradford and Hsiao 1982). The leaf characteristics of

P. angustifolium that conform with strategies (i) and (ii) include comparatively low leaf surface area and vertical orientation, which are important in limiting transpirational water loss in other arid and semi-arid taxa (Forseth and Ehrlinger 1983; Smith and Ullberg 1989; King 1997). However, a low *E* may also result from restriction of transpiration to a short period during the day, which is characteristic of more mature field-growing individuals of this species (Chapter 3). This suggestion is further supported by the observed lack of reduction in noon stomatal conductance of droughted seedlings. It may be that where glasshouse temperature reached a maximum, stomata opened for a short period of time to reduce thermal stress. Consequently, it may be physiological attributes, rather than leaf morphology, that contributed most to the very low transpiration rate of droughted *P. angustifolium* seedlings.

The significantly lower E of control seedlings of P. revolutum, compared with that of other species, may relate to strategies (ii) and (iii) of Bradford and Hsiao (1982). Young leaves of this species possess high densities of trichomes on their abaxial surfaces (pers. obs.; Wilkinson 1992), which may serve to increase the reflection coefficient of solar radiation, resulting in lower leaf temperature and a reduction in potential transpirational water loss (Cowan 1981). However, the absence of trichomes on adaxial leaf surfaces of P. revolutum suggests that its low transpiration rate probably results from increased leaf diffusion resistance to water loss, which may also be associated with comparatively high instantaneous water use efficiency (Ripley et al. 1999). The low mean transpiration rate of P. revolutum seedlings is consistent with the water use strategies of more mature, field growing plants, which demonstrate low stomatal conductance during periods of minimum soil water availability (Chapter 3).

For droughted seedlings of *P. revolutum* and *P. angustifolium*, the strong correlation between declining values of g_s and Ψ_{PD} is consistent with models of the relationship between these variables for plants subjected to long-term stress (Jones and Rawson 1979; Hall 1982). This correlation, together with only minor reductions in stomatal conductance accompanying almost total reductions in transpiration rate, suggests that these species may be maintaining physiological functions by means of osmotic regulation. This is supported by the capacity of these species, compared with *P. bicolor* and *P. undulatum*, to maintain higher stomatal conductance at lower leaf water potentials. For example, at a Ψ_{PD} of -2 MPa, values of g_s for *P. angustifolium* and *P. revolutum* were 0.08 and 0.06 mol m⁻² s⁻¹ respectively, higher than those for *P. undulatum* and *P. bicolor* (0.01 and 0.04 m ol m⁻² s⁻¹ respectively). The strong positive correlations between g_s and *E*, and g_s and Ψ_{PD} observed for *P. angustifolium* and *P. revolutum* have been reported for a range of other drought tolerant taxa (Turner *et al.* 1978; Jones and Rawson 1979; Jones 1998). The early and rapid decrease in π_s of droughted *P. angustifolium* seedlings suggests that they possess adaptations that enable them to respond more rapidly than seedlings of the other three species to decreasing soil water availability. The nature and timing of physiological responses such as osmotic adjustment and turgor maintenance are regarded as critical for seedling survival under drought stress (Meier 1992).

Many xeromorphic taxa are known to accumulate high concentrations of solutes irrespective of water stress, and are thus able to maintain turgor and normal cellular function during periods when leaf water potential declines (Jones *et al.* 1981). Such behaviour would be reflected in comparatively low values of π_s under stress-free conditions. Both *P. angustifolium* and *P. revolutum* exhibited winter depression of Ψ_L in the field (Chapter 3), and control seedlings of these species exhibited low values of π_s , although these were not significantly lower than values for *P. undulatum* and *P. bicolor*. Together, these results suggest that solute accumulation by *P. angustifolium* and *P. revolutum* probably occurs only in response to some degree of water stress.

Although comparatively high values of δ^{13} C (and by inference, of WUE) in droughted seedlings of *P. revolutum* and *P. angustifolium* suggest a drought avoidance strategy, the lack of significant differences in WUE between control and droughted seedlings of these species suggests that they may be using other mechanisms to maintain physiological functioning. The combined effects of photosynthetic rate and stomatal behaviour upon WUE may be important in this respect. The lack of clear relationship between drought tolerance and carbon isotope composition has been reported elsewhere (Zhang *et al.* 1997; Miller *et al.* 2001), which suggests that if, under uniform conditions, δ^{13} C is correlated with WUE, then drought tolerance and WUE may not be related. Alternatively, because retained water could be used by competing vegetation, a high WUE may *not* be selected for in arid and semi-arid environments (Passioura 1982; Zhang *et al.* 1997). The lack of a broad trend in δ^{13} C values among these species may be due to the use of populations of these species from the most temperate parts of their ranges, as in other studies, an increase in δ^{13} C (decrease in discrimination) occurs only at the drier end of an environmental gradient (Lajtha and Getz 1993; Korol *et al.* 1999).

Among droughted seedlings of these species, the inferred correlation between WUE (from δ^{13} C) and Ψ_{PD} probably reflects the rapidity of stomatal closure, with a decrease in δ^{13} C discrimination in leaf tissue under conditions of increasing water stress. The lack of correlation between WUE and other tissue water variables suggests that the maintenance of comparatively high leaf water potentials may be a stronger indicator of WUE than has been previously recognised.

The overall reductions in transpiration rate during the trial of *control* seedlings of all species may have resulted from seasonal decreases in temperature and light availability over the course of the trial. Trees and shrubs exhibit both daily and seasonal transpiration cycles, with E in moist soils largely controlled by atmospheric conditions (Kozlowski *et al.* 1991). The strong positive correlation between E and glasshouse temperature for control seedlings of P. *undulatum* and P. *revolutum* is consistent with this general observation. As a consequence, interspecific comparisons of transpiration rate, stomatal conductance and tissue water relations of control and droughted seedlings must also consider the effects of increasingly cooler temperatures on growth and physiological behaviour.

For *P. undulatum* and *P. bicolor*, the reduction in *E* of control seedlings may also be related to decreasing values of π_s and π_p , which may reflect seasonal osmotic adjustment in response to temperature and irradiance cues. In the case of *P. bicolor*, which occurs in areas subject to cold winters, a seasonal reduction in π_s and π_p may reflect winter hardening, which is common among other cold winter taxa (Ritchie and Shula 1984; White *et al.* 1996). However, this is unlikely to account for the patterns of π_s and π_p observed in *P. undulatum*, which inhabits sites that are not subject to extremely cold winters.

The development of water stress in droughted seedlings of the four species over the course of the study was reflected in general (but not uniform) decreases in both E and g_s . Such behaviour is consistent with the response of seedlings of other species subjected to seasonally or experimentally induced drought (Pallardy 1981; Blake-Jacobson 1987; Kozlowski *et al.* 1991), and is very common in species subject to summer drought. This is reinforced by the correlation, among these species, between E and mean summer temperature, which demonstrates the ability of species subjected to high summer temperatures to minimise transpirational water loss.

For *P. undulatum* and *P. revolutum*, the correlation coefficients between *E* and glasshouse temperature are higher in droughted seedlings than control seedlings. Similarly, these variables become correlated for *P. angustifolium* and *P. bicolor* only after the withholding of water. This suggests that the retention of water under drought conditions becomes increasingly important in all four species, including the seedlings of species with transpiration rates that under non-stressful conditions are less closely aligned with ambient temperature. This is also reflected in the higher implied water use efficiency of droughted compared to control seedlings of the four species. Such behaviour should not be unexpected given that the conservation of water is at least as important as its capture under conditions of water stress (Lambers and Poorter 1992). It also suggests that even when subjected to moderate-to-high water stress on days of higher than normal ambient temperature, these seedlings increase stomatal conductance and transpiration in order to prevent the development of temperatures that may be injurious to leaf tissues.

The observed interspecific differences in drought resistance are underpinned to some extent by differences in the relationship between π_s and π_p in response to drought, which is often adaptive in nature (Monson and Smith 1982). High osmotic potentials, which are characteristic of *P. bicolor*, are often associated with low drought resistance, while the maintenance of low osmotic potentials under water stress, a feature of *P. revolutum*, is more strongly associated with drought tolerance (Bennert and Mooney 1979). Nevertheless, the absence of significant differences in osmotic or elastic variables among droughted seedlings of these species may indicate more about what these species have in common than what separates them. The lack of any pattern in the adjustment of these variables for much of the trial is consistent with previous reports in which the

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adaptive significance of such adjustments is questioned (Munns 1988; Blake and Tschaplinski 1992; White *et al.* 1996). Thus, stomatal behaviour and rates of transpiration may not be closely correlated with the maintenance of turgor, which suggests that among these species, tissue water relations may not acclimate significantly in response to water stress.

One limitation of this experimental design is that except for sharply-defined seasonal environments, periods of drying are often cyclic in nature, with plants experiencing slowly increasing levels of water stress as the periods between rainfall events gradually increase. Furthermore, the stomatal response of seedlings may change as a result of one of more drying cycles, and may be affected by plant age (Jordan *et al.* 1975). Thus it is possible that the water relations behaviour resulting from the imposition of drought on seedlings, for the timeframe used in this trial, may be atypical of more mature plants of these species growing under normal field conditions. Nevertheless, the imposition of water stress on plants growing in a uniform environment has been shown to elicit responses that mimic the behaviour of field plants (Camarcho *et al.* 1974).

The observed differences in drought response among these *Pittosporum* species demonstrate their modes of drought resistance and the mechanisms used for physiological adjustment to water stress (Fig. 4.15). The resultant water stress response strategies of these species reflect to some degree their current distributions and reinforce the hypothesis that the evolution of xeromorphy may have involved not just substantial changes in morphology, but also the evolution of physiological mechanisms of drought tolerance. If the proposed hierarchy of drought resistance among these spr cies is correct, it is somewhat paradoxical that the closely related, similarly-distributed *P. revolutum* and *P. undulatum* possess different strategies of drought resistance, in contrast with the similar modes of *P. revolutum* and *P. angustifolium*, which inhabit distinctly different biogeographic zones. Such a similarity may be of considerable importance, as it suggests the co-evolution of drought tolerance mechanisms in semi-arid and arid environments as well as those characterised by strong rainfall seasonality.
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Species	Latitude	Longitude	Altitude	Altitude TWO		PWO	PDO
Population	(°S)	(°E)	(m a.s.l.)				.~~
P. undulatum Mallacoota	37.49	149.78	20	13.0	18.1	283	217
<i>P. revolutum</i> Mallacoota	37.49	149.78	20	13.0	13.1	283	217
P. angustifolium Wyperfeld N.P.	35.69	142.05	60	11.7	21.1	103	62
P. bicolor Mt Worth	37.76	145.70	680	7.0	15.1	446	245

Table 4.1Selected climatic variables of seedling populations. TWQ – Temperaturewettest quarter; TDQ – Temperature driest quarter; PWQ – Precipitation wettestquarter; PDQ – Precipitation driest quarter [temperatures in °C; precipitation in mm].

Species	E	<i>gs</i>	Ψ _{РD}
	(mg day ⁻¹ cm ⁻²)	(mmol m ⁻² s ⁻¹)	(MPa)
P. undulatum	90.7 ^a	97.7 ^a	-0.70ª
	(8.31)	(1.71)	(0.08)
P. revolutum	37.5 ^b	80.7 ^a	-1.02
	(4.48)	(13.14)	(0.04)
P. angustifolium	34.7 ^b	80.8ª	-0.62 ^a
	(3.17)	(12.29)	(0.05)
P. bicolor	77.7*	84.6ª	-0.78 ^a
	(6.87)	(14.69)	(0.07)
F	14.8	0.5	8.00
Р	< 0.001	0.700	0.002

Table 4.2 Transpiration rate (E), noon stomatal conductance (g_s) and pre-dawn leaf water potential (Ψ_{PD}) of seedlings prior to droughting (means \pm sem, n=5). Shared alphabet letters denote non-significant differences between means of species for that variable.

Table 4.3 Transpiration rate (*E*), noon stomatal conductance (g_s), pre-dawn leaf water potential (Ψ_{PD}), osmotic potential at full turgor (π_s) and turgor loss point (π_p), relative water potential at zero turgor (RWC₀), bulk modulus elasticity (ε_s) and turgid weight:dry weight ratio (TW:DW) of six-month-old seedlings 65 days after commencement of droughting (mean ± sem, n=5). Shared alphabet letters denote non-significant differences between means of species for that variable.

Species	E (mg day ⁻¹ cm ⁻²)	E s (mmol m ⁻² s ⁻¹)	Ψ _{PD} (MPa)	π _s (MPa)	π _p (MPa)	RWC ₀ (%)	ε _s (MPa)	TW:DW
P. undulatum	6.7ª	4.9	-1.0ª	-2.4ª	-3.2ª	82.1 ^a	15.8ª	2.8ª
	(1.4)	(1.4)	(0.1)	(0.3)	(0.5)	(1.2)	(5.7)	(0.13)
P. revolutum	6.9ª	41.1 ^{ab}	-2.3 ^{ab}	-2.3ª	-3.4ª	72.6ª	12.4 ^a	3.1°
	(1.8)	(16.0)	(0.7)	(0.0)	(0.3)	(7.1)	(3.5)	(0.10)
P. angustifolium	1.7	80.0ª	-1.6 ^{ab}	-2.3ª	-3.2ª	74.9ª	15.0ª	3.1ª
	(0.2)	(15.7)	(0.3)	(0.1)	(0.3)	(5.2)	(1.3)	(0.06)
P. bicolor	21.4	30.1 ^b	-2.7 ^b	-2.1ª	-3.1*	65.9*	9.9ª	3.1ª
	(4.6)	(8.0)	(0.4)	(0.1)	(0.2)	(6.0)	(4.5)	(0.08)
F	12.3	6.9	3.6	1.0	0.6	2.7	0.2	1.4
P	< 0.001	0.004	0.038	0.445	0.628	0.140	• 0.862	0.326

Table 4.4 δ^{13} C of control and droughted seedlings measured on day 65 of the trial.Values are means for five seedlings with standard errors in brackets. Shared alphabetletters denote non-significant differences between means across species for eachtreatment.

Species		Control	Droughted	F	Р
P. undulatum		-29.5 (0.22) *	-27.7 (0.46) ^b	12.4	0.008
P. revolutum		-29.4 (0.32) ^a	-29.0 (0.41) ^{ab}	0.7	0.431
P. angustifolium		-29.4 (0.32) ^a	-28.2 (0.54) ^{ab}	4.0	0.082
P. bicolor		-30.7 (0.26)	-29.2 (0.32) ^a	12.2	0.008
Species	F	5.4			
	p	0.004			
Treatment	F	22.1			
	P	< 0.001			
Species * Treatment F		1.2			
	р	0.312			



Figure 4.1 Transpiration rate of control (solid symbols) and droughted (open symbols) seedlings (mean, n=5). Arrows indicate the time after which there is a significant difference in transpiration rate between control and droughted seedlings. Daily maximum glasshouse temperatures are also shown.



Figure 4.2 Mean (a) transpiration rate, (b) noon stomatal conductance and (c) pre-dawn leaf water potential of control seedlings of the four species (mean + sem, n=5). Shared alphabet letters denote non-significant differences between means.



Figure 4.3 Mean transpiration rates of droughted seedlings expressed as a percentage of rates for control seedlings. $\Box - P$. bicolor; $\blacksquare - P$. revolutum; $\triangle - P$. undulatum; $\blacktriangle - P$. angustifolium; .



Figure 4.4 Temporal changes in noon stomatal conductance of control (solid symbols) and droughted (open symbols) seedlings. Asterisks above points indicate significant differences between control and droughted seedlings (mean \pm sem, n=5).

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Figure 4.6 Transpiration rate plotted against stomatal conductance of control (solid symbols) and droughted (open symbols) seedlings of (a) *P. undulatum*, (b) *P. revolutum*, (c) *P. angustifolium* and (d) *P. bicolor* (n = 5). Regression lines are shown. Dotted lines indicate non-significant relationships between *E* and *g*.



Figure 4.7 Temporal changes in transpiration rate (\blacksquare) and stomatal conductance (\blacktriangle) of droughted seedlings over the course of the trial (means ± sem, n=5).



Figure 4.8 Pre-dawn leaf water potential of control (solid symbols) and droughted (open symbols) seedlings. Asterisks above points indicate significant differences between control and droughted seedlings (mean \pm sem, n=5).



Figure 4.9 Patterns of stomatal conductance (\blacktriangle) and pre-dawn leaf water potential (\diamond) of droughted seedlings (mean \pm sem, n=5).



Figure 4.10 Osmotic potential at full turgor of control (solid symbols) and droughted (open symbols) seedlings (mean \pm sem, n=3). Asterisks above points indicate significant differences between control and droughted seedlings.





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Figure 4.12 Turgid weight: dry weight ratio of control (solid symbols) and droughted (open symbols) seedlings (mean \pm sem, n=3).



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Figure 4.13 Bulk modulus of elasticity of control (solid symbols) and droughted (open symbols) seedlings (means \pm sem, n=3).

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Figure 4.14 Relative water content at zero turgor of of control (solid symbols) and droughted (open symbols) seedlings (means \pm sem, n=3).



Figure 4.15 Major drought response variables of the four species in relation to their purported cladistic positions as per Cayzer *et al.* (2000). The dashed line indicates that the position of *P. revolutum* is yet to be fully resolved.

CHAPTER 5. SEED BIOLOGY AND GERMINATION

Seed germination and seedling establishment are critical stages in the life history of all plants, yet represent phases of maximum vulnerability to environmental changes and minimal capability for homeostatic response or physiological adjustment (Angevine and Chabot 1979). Seeds must therefore respond to the correct set of environmental cues in order to maximize the likelihood of successful establishment and survival (Bell *et al.* 1993). This is particularly important for arid and semi-arid species as well as those of seasonal environments where there is a distinct period that is unfavourable for seedling establishment (Nishitani and Masuzawa 1996). Angevine and Chabot (1979) recognized two basic strategies of germination behaviour: (i) avoidance of conditions that are difficult for seedling growth and (ii) tolerance of such conditions.

The relationship between regeneration characteristics such as the timing of seed germination and the distribution and dynamics of species has been extensively researched (e.g. Grubb 1977; Harper 1977; Bazzaz 1979; Fenner 1935). Furthermore, seed and seedling biology may be critical in determining rates of change of species' distributions in response to changes in climate. For example, Leishman *et al.* (1992) suggested that species distributed across broad gradients in environmental conditions may be able to more rapidly or successfully respond to changes in climate due to inherently broader amplitudes in germination behaviour, growth rates and ecophysiology in relation to temperature and soil water content compared to narrowly-distributed species.

A limitation of most comparative ecophysiological studies of plant species is their dependence upon the responses of a single population of each species (Kirkpatrick and Gibson 1999). This is despite the fact that plant species may display considerable intraspecific geographical variation in germination response or in responses to environmental factors, with patterns of differentiation of populations tending to follow patterns of environment very closely (Bradshaw 1984). Thus, investigations of the germination biology of species should encompass the response of populations spread over geographic or environmental gradients. Quinn and Colosi (1977) suggested that to consider germination ecology at the species level is to ignore the population as the ecological unit. While there is a large body of literature supporting the concept that germination strategies are adaptive at the species level (Angevine and Chabot 1979), studies investigating intraspecific variation in germination biology are less common (Thompson 1981; Meyer *et al.* 1989). This is despite general acceptance that variation exists in the germination responses of different populations of a species (Harper 1965; Thompson 1973). Given this, a more comprehensive understanding of within-species variation in germination response to climatic variables such as temperature may greatly assist in modelling both past and future responses of plant species to climate change.

Dormancy is a phenomenon in which seeds, when exposed to environmental conditions (water and temperature) considered favourable for germination and subsequent seedling growth, fail to germinate. While there has been much research on dormancy (e.g. Heydecker 1973; Fenner 1985; Murdoch and Ellis 1992; Bewley and Black 1994; Egley 1995; Baskin and Baskin 1998), a clear consensus for defining it is yet to be reached. The terminology of this study conforms to the definition by Baskin and Baskin (1998), who categorize the two principal forms of dormancy as *innate* (or primary) and *induced* (or secondary). Thus, control of germination exists at two levels: dormancy, the first of these, is related to the physiological state of the seed (*internal control*); the second involves the influence of environmental factors on both dormancy and germination (*external control*) (Bewley and Black 1994). The ecological advantages of seed dormancy include avoidance of conditions unfavourable for seedling growth and distribution of germination events over time, factors that combine to increase the likelihood of survival to reproductive maturity of some plants (Bewley and Black 1994).

A seed may represent a complex of adaptive traits, including those related to maintenance of genetic diversity, dispersal, and as a module capable of surviving extremely difficult environmental conditions for long periods of dormancy (Anderson 1982). As field germination behavior may not be under rigid genetic control, but represent an integration of genetic and environmental factors (Meyer *et al.* 1989), interpretations of intraspecific variation in germination behaviour should avoid the presumption that such variation is necessarily adaptive. Rather, it is the differences among plant populations that confer an increased ability to survive and reproduce in their own environment that provide direct evidence of adaptation (Bradshaw 1984).

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Soil moisture availability is a primary requirement for germination through its effect on the rate of imbibition (Bell 1999) and is thus a major factor limiting the regeneration of species occupying arid, semi-arid and strongly seasonal environments (Noy-Meir 1973). Variation in germination response over rainfall gradients may be discernible at the level of populations (Meyer *et al.* 1997; Anella and Whitlow 1998) or species (Thompson 1973). Germination attributes that increase the likelihood of seedling establishment in arid, semi-arid or strongly seasonal environments may have adaptive significance and indicate pathways of adaptation during periods of climate change. Adaptations of woody perennial species to arid environments often include a requirement for a long period of exposure to moisture.

Despite the obvious requirement for water in seed germination, temperature may be the most critical factor influencing germination (Thompson 1973; Heydecker and Coolbear 1977; Beardsell and Richards 1987), due to both its direct impact on germination and also its dominant role in controlling seed dormancy (Bouwmeester and Karssen 1992, 1993). Therefore, even though soil moisture levels may be amenable to germination during a particular phase of the year (season), temperatures suitable for germination may not (Bell *et al.* 1995). For example, the seeds of a range of Australian arid and semi-arid species germinate optimally at temperatures that approximate the winter rainfall period (Bellairs and Bell 1990; Bell and Bellairs 1992; Bell *et al.* 1995; Bell and Williams 1997). Elsewhere, many arid and semi-arid taxa exhibit a slow or poor germination response at high temperature (Meyer *et al.* 1997).

The broad aim of this study was to examine the germination response to cold stratification, light and temperature within and among these *Pittosporum* species and evaluate the potential adaptive significance of these responses in relation to their contrasting rainfall regimes.

The specific aims of the germination trials were therefore to:

- establish whether seeds of these species exhibit dormancy or other delayedgermination characteristics;
- investigate intra- and interspecific variation in germination response to light, stratification and temperature;
- explore possible relationships between the germination traits of these species and particular environmental variables.

While the germination response of seeds of these species to moisture is also of interest, seed availability prevented further investigation.

METHODS

Seed dormancy and responses to stratification and light

An initial trial was carried out to investigate dormancy in freshly collected seeds of each species, and to determine germination responses to various conditions of light and cold stratification. The suitability of constant or alternating temperatures for germination experiments has been the subject of considerable debate, and it might be expected that seed would be more responsive to some pattern of alternating or fluctuating temperature than to overall mean daily temperature. The results of research to date are mixed, with the seeds of many species germinating more rapidly or to higher percentages at constant rather than alternating temperatures (Gulliver and Heydecker 1973; Thompson and Grime 1983; Conner and Conner 1988). However, for many other species, the opposite trend is apparent (Steinbauer and Grigsby 1957; Harty and McDonald 1972; Thompson and Grime 1983; Curtis 1996). Compounding this is a lack of data regarding diurnal fluctuations in soil temperature at sites supporting these *Pittosporum* species, creating difficulties in selecting an appropriate regime of alternating temperatures for all species. Nevertheless, a mean, constant temperature is thought to approximate the effects of a fluctuating temperature regime on germination in the field (Ross 1976). Given this, as well as limitations in the availability of suitable equipment, preliminary experiments were designed to examine dormancy status and response to light under conditions of constant temperature, with subsequent trials to investigate more fully the germination response of these species to temperature.

Capsules of *P. undulatum* and *P. revolutum* were collected from Harrison's Creek, situated on the eastern side of Mallacoota Inlet, of *P. bicolor* from the Dandenong Ranges, and *P. angustifolium* from Wyperfeld National Park (Table 5.1). The capsules were mature at the time of collection, and were obtained from a minimum of five trees of each species. After the capsules dehisced, seeds were extracted and the resinous mucilage removed with a non-abrasive cloth. After being combined and incubated at 20°C for 14 days, half the seeds were kept at room temperature with the remainder stratified at 5°C for 21 days. Seeds were treated in this way to determine: (i) the dormancy status, and (ii) if dormancy exists, whether stratification has any effect on the germination response. Stratification at 5°C has been found to be the most effective means of initiating germination in dormant seeds (Bewley and Black 1982a). Seeds were then surface sterilised in "Fongarid" and placed in 4 cm petri dishes on double layers of filter paper over wicks of folded filter paper, which maintained a moist surface for the seeds. Seeds were incubated at a constant 20°C in a single germination cabinet, subject to one of the following three treatments:

- (i) under constant white light, consisting of five Growlux[®] fluorescent tubes emitting total photon flux density of 50-70 μmol m⁻² s⁻¹ at a distance of 30 cm;
- (ii) in permanent darkness (by covering petri dishes in aluminium foil);
- (iii) under a 12 hr alternating white light/dark regime.

For each treatment there were three replicate dishes of 10 seeds, arranged in random blocks. Petri dishes were checked daily, and distilled water was added when necessary. Germination was considered to have occurred when the radicle had extended approximately 2 mm beyond the seed testa. The seeds were monitored for up to 90 days

or until germination had ceased, which was effectively 10-12 days without further germination.

The viability of ungerminated seeds was tested using a 5% aqueous solution of tetrazolium chloride (Moore 1973). Each seed was inspected and those infected with fungi were recorded as non-viable and discarded. Derived variables were the minimum time to the onset of germination (T_{min}) , maximum time to completion of germination (T_{max}) and final germination percentage. The time to the onset of germination is a useful indicator of germination rate, which under field conditions may be a critical factor in seedling establishment and survivorship (Kaufmann and Eckard 1977).

Germination of P. bicolor

P. bicolor failed to germinate under any of the above treatments (see **Results** section). This may have been due to a requirement of seed for a period of after-ripening, during which changes occur that subsequently facilitate germination (Mayer and Poljakoff-Mayber 1989). Other possible reasons for lack of germination may include seed non-viability or factors associated with innate dormancy, such as endosperm or seed coat characteristics that restrict germination, or the requirement for some pre-germination treatment.

Treatments known to promote seed germination of woody Australian taxa include stratification (Pryor 1954; Boden 1957; Grose 1957; Battaglia 1993), heat (Cavanagh 1980; Auld and O'Connell 1991), plant-derived smoke (Dixon *et al.* 1995), and hormones such as gibberellic acid (Bachelard 1967; Bell *et al.* 1995). Physical treatments such as seed scarification (Richmond and Chinnock 1994) or digestion by avian fragivores (Noble 1975; Glyphis *et al.* 1981; Letnic *et al.* 2000) have also been observed to increase seed germination in some species.

On the basis of the initial lack of germination for this species and the above observations, trials were conducted to examine the germination response of *P. bicolor* seed to the following pre-treatments: (i) cold stratification; (ii) heat; (iii) scarification; (iv) simulated bird digestion; (v) exposure to smoke-derived compounds.

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Mature seeds of *P. bicolor* used in these trials were collected from a minimum of five trees in naturally-occurring populations from Brown Mountain (south-east NSW), Warburton, the Dandenong Ranges and Otway Ranges (Victoria) and Francistown in south-east Tasmania (Table 5.1). Following the appropriate treatment (see below), seeds were placed on moistened filter paper in petri dishes as described previously, incubated at 15°C under constant light and monitored twice weekly for 300 days. Filter papers were changed regularly to maintain hygiene. Five replicates of 10 seeds were used for each treatment and control.

(i) cold stratification

Seeds of *P. bicolor* were stratified in continuous darkness at 5°C for 28 days, after which they were placed on moistened filter paper and incubated as described above. Control seeds were maintained at room temperature for 28 days and then imbibed at 15°C and incubated as described above.

(ii) heating

Seeds were immersed in distilled water at 100°C for 5, 10, or 20 minutes, after which they were placed on moistened filter and incubated as described above. Control seeds were immersed in distilled water at room temperature for the above time periods, after which they were incubated as per treated seeds.

(iii) scarification

Seeds were lightly rubbed for 10 seconds with fine emery paper, after which they were incubated as above. Controls were maintained as above.

(iv) bird digestion

Dunlop and Galloway (1984) used Pancreatin[®], an enzyme-based compound derived from porcine pancreas, to simulate bird digestion of *P. angustifolium* seed, and found that it effected small increases in both the rate of seed germination and final germination percentage. Solutions containing various concentrations of Pancreatin (Sigma Chemical Co Lot 13H0347) were used to simulate bird digestion of *P. bicolor* seed. Both the concentration of digestive enzyme and duration of 'ingestion' were tested, with seeds immersed in 10% or 50% solutions of Pancreatin (in KH₂PO₄ buffer)

at 35°C for 30, 60, 120 or 240 min. Control seeds were immersed in 90% or 50% KH₂PO₄ buffer at 35°C for the same time periods. Treated and control seeds were then incubated as described above.

(v) smoke-derived compound

The role of smoke in the enhancement of seed germination was first reported for South African fynbos species (De Lange and Boucher 1990; Brown 1993; Brown *et al.* 1993, 1994). It has subsequently been reported for many Australian taxa (Dixon *et al.* 1995; Read *et al.* 2000; Roche *et al.* 1997, 1998). As *P. bicolor* occupies wet sclerophyll vegetation that is subject to occasional fire, smoke may play a role in the breaking of dormancy in this species. Kirstenbosch[®] "instant smoke plus" seed primers, developed by the National Botanical Institute of South Africa, are paper discs impregnated with chemicals derived from plant-derived smoke. Two Kirstenbosch seed primer papers were immersed in 100 ml of distilled water for 2 hours, and then *P. bicolor* seeds were soaked in distilled water for 24 hrs and then incubated as above. Control seeds were soaked in distilled water for 24 hrs and then incubated as described above.

Gibberellic acid (GA₃)

Seeds of *P. bicolor* again failed to germinate under any of the above treatments. As temperature plays an important role in germination, and to test for a possible afterripening requirement in this species, further trials were conducted to test the effects lower temperature and different concentrations of gibberellic acid (GA₃) on the germination of its seed. Gibberellic acid appears to mediate the phytochrome responses of seeds to red and far red light (Thomas 1992), and is associated with the breaking of various types of dormancy in a wide range of species (Lang 1965; Halmer *et al.* 1975; Jones and Stoddard 1977; Karssen *et al.* 1989; Bell *et al.* 1995).

Phase I trial: Three replicates of 100 seeds from two populations (Dandenong Ranges and Brown Mountain) of *P. bicolor* were incubated in petri dishes on filter paper saturated with 10, 50, or 100 μ M solutions of GA₃, maintained at constant temperatures of 10°C, 15°C or 20°C. Small quantities of the GA₃ solutions were added to petri dishes daily to maintain moist conditions. Controls were kept moist with distilled water maintained at each of the above temperatures.

Phase II trial: There was limited germination of seed treated with 50 and 100 μ M GA and incubated at 15°C (see Results). Consequently, a further trial was conducted to investigate the germination response of seeds treated with 1000 μ M GA and incubated at 3 temperatures (10, 15 and 20°C). Five seed populations were utilised (Table 5.1), with final germination percentages recorded and T₅₀ values estimated as described above.

At the conclusion of the above trials, the remaining ungerminated control seeds were sown into trays containing seed-propagating mix, and placed in a glasshouse on a thermal germination bed maintained at 20°C. Seeds were watered daily, and subjected to normal diurnal light conditions.

Effects of temperature on germination of P. undulatum, P. revolutum and P. angustifolium.

After establishing that seeds of *P. undulatum*, *P. revolutum* and *P. angustifolium* are able to germinate freely under conditions of constant light and temperature (see Results section), experiments were carried out to examine the effects of temperature on the germination of seed collected from different populations.

Undehisced, fully-mature capsules of the three species were provided or collected from naturally-occurring populations during March-April 1995 (Table 5.1). Seed capsules were collected from a minimum of six plants except for *P. revolutum* from Atherton (two trees), and *P. angustifolium* from Palm Valley (two trees). Capsules and seeds were individually weighed and then combined by population and stored at room temperature for a minimum of 3 weeks. Dry storage is considered to reduce the degree of innate dormancy (as defined by Harper 1977) evident in the vast proportion of newly shed seed (Probert 1992).

Seeds were treated as above, with five petri dishes containing 10 seeds from each population of each species arranged randomly in four identical growth cabinets

maintained at 10°C, 15°C, 20°C and 25°C (\pm 1°C) and two controlled temperature rooms, maintained at 5°C and 30°C. The incubation temperatures encompass the range of seasonal mean temperatures across the range of habitats from which the seed populations were collected (Table 5.2). Seeds were incubated under conditions of constant light, with petri dish positions re-randomised every week.

As cumulative germination curves were predominantly sigmoidal, a three-variable Gompertz-type non-linear regression model: $y = a^{exp}(-exp(b-cx))$ (Ratkowsky 1990) was fitted to estimate T₅₀ (the time to reach 50% of the final germination) values for all species and populations. Gompertz-type models have been shown to be superior to other growth curve models in germination studies (Tipton 1984), with the one used being asymmetric about its inflection point, a characteristic that is prevalent in biological systems (Ratkowsky 1990). The T₅₀ value, which is used as an indication of germination rate, has an advantage over other indices, such as mean time to germination (Kotowski 1926) or germination energy index (Grose 1963), of being relatively insensitive to long-tailed or slightly skewed distributions (Nichols and Heydecker 1968; Battaglia 1993). The maximum rate of germination was derived from the regression model of T₅₀ for each population of each species. The other derived variable was final germination percentage, which provides a useful index of seed viability and germination potential for a species (Ross 1976). Germination rate and final germination percentage were used to determine the optimum incubation temperature for each species.

Statistical Analyses

For the initial germination trial on the effects of light treatments and stratification, values of minimum time to the onset of germination and maximum time to the completion of germination were calculated and log_e-transformed prior to ANOVA. Final germination percentages were arcsin-square root transformed prior to ANOVA. A three-way ANOVA was used to examine the variation between species in minimum time to commence germination, the time to complete germination and final germination percentages as a function of light and stratification. Within species, the effects of stratification and light treatments were analysed by two-way ANOVA. Where a

treatment had no significant effect but the interaction term was significant, one-way ANOVA was used to clarify the treatment effect. Significant differences between means were determined *post hoc* using Tukey's tests.

For seed populations of *P. bicolor* subjected to various combinations of GA_3 and temperature, final germination values were recorded and arcsine-square root transformed. T₅₀ values were calculated as described above and log transformed. Within populations, these variables were analysed using a two-way ANOVA.

For the germination trial on the effects of temperature on populations of *P. undulatum*, *P. revolutum* and *P. angustifolium*, final germination percentages were recorded and T_{50} values estimated as described above. These variables were arcsin-square root and log_e transformed respectively, in order to improve the normality of the data, to reduce the influence of outliers and to overcome problems associated with proportions or percentages. The optimum incubation temperature for each species was derived from a regression of the plot of T_{50} against temperature, using population values as replicates.

A partly nested (or split plot) ANOVA design was used to analyse the variation in T_{50} and final germination percentages as a function of temperature effects across populations within species. Pairwise comparisons were carried out using Tukey's tests to determine which variable means were significantly different from one another. Relationships between T_{50} values and selected climatic variables derived from BIOCLIM were analyzed by Pearson correlation. No corrections were made for multiple comparisons, following the reasoning of Stewart-Oaten (1995). For all hypothesis tests, the critical value used was $\alpha = 0.05$. All statistical analyses were carried out using SYSTAT[®] Version 9.0 (SPSS Inc. 1999).

RESULTS

Seed dormancy and responses to stratification and light

There was no germination of *P. bicolor* under any of the initial treatments (see 'Germination of *P.* bicolor' below). While *P. bicolor* seed readily imbibed water, the embryos of ungerminated seeds appeared quite under-developed after 8 months incubation at 20°C.

Seeds of *P. undulatum*, *P. revolutum* and *P. angustifolium* differed significantly in their minimum time to the onset of germination, the time to final germination and in their final germination percentages (Table 5.3). Stratification prevented germination or had a significant effect on the final germination percentage, but did not have an overall effect (all species combined) upon the time to the onset or completion of germination (Table 5.3; Fig. 5.1). Stratification also appeared to reduce the viability of ungerminated seeds (Table 5.4). T_{min} and final germination percentage were significantly affected by light, and there were significant interactions between light and stratification for T_{min} and final germination was not significantly affected by light or stratification (Table 5.3).

Seeds of the three species germinated optimally when not stratified and under conditions of continuous light (Table 5.5). Using only the results for seeds subjected to this treatment combination, there were significant differences in final germination percentage between *P. angustifolium* and both *P. undulatum* and *P. revolutum* but not between the latter two species (Table 5.5). *P. revolutum* seeds took significantly longer to commence germination than that of *P. undulatum* and *P. angustifolium* (Table 5.5). Seeds of *P. revolutum* also took significant longer to reach the final germination percentage (i.e. it germinated more slowly) than those of both *P. undulatum* and *P. angustifolium* (Table 5.5).

The lack of a significant effect of light on the time to complete germination, but significant species x light and species x stratification x light interactions demonstrated that species differed in their germination response to light and the combination of light

and stratification (Table 5.3). Consequently, two-way ANOVA was carried out on the effects of light and stratification for each species, as discussed below (Table 5.6). For *P. undulatum*, stratification had a significant effect on both T_{min} and T_{max} (Table 5.6). Stratified seeds subjected to either continuous light or dark took significantly less time to complete germination (i.e. smaller values of T_{max} - faster germination rate) than equivalent non-stratified seeds (Table 5.6). There was no effect of light treatment on T_{min} or T_{max} , but there was a significant interaction between stratification and light treatment for T_{max} (Table 5.6). Consequently, one-way ANOVA was carried out on the effects of light treatment on the time to complete germination for each of stratified and non-stratified seeds. These showed that under light/dark conditions, the T_{max} of stratified seeds was significantly higher (i.e. a slower germination rate) than under constant light or dark conditions (F = 10.7, P = 0.010). There was, however, no effect of light treatment on T_{max} of non-stratified seeds. Stratification and light treatment each had a significant effect on the final germination percentage of *P. undulatum* seeds, with no significant interaction between these variables (Fig. 5.1a).

For *P. revolutum*, stratified seeds failed to germinate under any of the light treatments (Fig. 5.1b). Light treatment had a significant effect on T_{min} , i.e. seeds incubated in permanent darkness took significantly longer to commence germination than those under continuous light or alternating light/dark (Table 5.6). However, there was no effect of light treatment on T_{max} (Table 5.6). Stratification and light treatment both had a significant effect on final germination percentage, with a significant interaction between these factors, indicating that the magnitude of response to stratification varied among light treatments (Fig. 5.1b).

Both stratification and light treatment had a significant effect on T_{min} for seeds of *P*. angustifolium, i.e. under light and dark conditions, non-stratified seeds took significantly less time to commence germination (i.e. lower T_{min}) than did stratified seeds under any light treatment and non-stratified seed subject to alternating light/dark (Table 5.6). While there was no effect of stratification on T_{max} , light treatment significantly affected T_{max} (Table 5.6). Stratification and light treatment both had a significant effect on final germination percentage of *P*. angustifolium seeds and there was a significant interaction

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between these factors, indicating that the magnitude of response to stratification varied among light treatments (Fig. 5.1c).

Germination of P. bicolor

Seeds of *P. bicolor* failed to germinate in the preliminary trial and following cold stratification, heating, scarification, simulated bird digestion and treatments with smoke-derived compounds. For the Phase I GA trial, germination was very slow and after 326 days, the only seeds to germinate were those incubated at 15°C and treated with 50 and 100 μ M GA₃ (7% and 15% germination respectively).

In the Phase II trial, seeds from all populations except Francistown failed to reach 50% germination (Fig. 5.2). Consequently, statistical analyses were used to examine the effects of GA₃ and temperature on the final germination percentage (not T_{50}) of each seed population. Both incubation temperature and the addition of gibberellic acid had a significant effect on the final germination percentage of all seed populations, with a significant interaction between these treatments for all populations except those from Brown Mountain and the Otway Ranges (Table 5.7). The significant interaction term was caused by a varying magnitude of effect of GA₃ across the temperature treatments.

The optimum incubation temperature for this species appeared to be 10°C, although GA₃treated seeds from Francistown had a slightly higher final germination percentage and a significantly higher germination rate (F = 35.6, P = 0.029) at 15°C than at 10°C (Fig. 5.2). At 20°C, the only seeds to germinate were GA₃-treated seeds from the Otway Ranges and Francistown populations, albeit at very low percentages (Fig. 5.2). Warburton seeds not treated with GA₃ did not germinate at any temperature and those from the Dandenong Ranges, Brown Mountain and Otway Ranges failed to germinate at 15°C and 20°C (Fig. 5.2).

Ungerminated control seeds remaining from the initial trials began to germinate c. 6 months after being placed on seed-raising mixture in the glasshouse. However, some seeds took up to 12 months to germinate after being planted out, approximately 18 months after initial commencement of this trial.

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Effects of temperature on germination of P. undulatum, P. revolutum and P. angustifolium.

All three species exhibited sigmoidal cumulative germination responses, which is typical of vigorously-germinating, non-dormant seeds (Bewley and Black 1994). Gompertz-type regression models fitted these cumulative germination responses tightly, with small coefficient errors and high adjusted R^2 values (range 0.94-0.99).

P. undulatum

Seeds from all three populations demonstrated similar patterns of germination response, both in terms of germination rate (Fig. 5.3a) and final germination percentages (Fig. 5.4). Final germination percentages were high for seeds incubated at 10°C, 15°C and 20°C, and Mallacoota seeds also germinated to a high final percentage at 25°C (Table 5.8, Fig. 5.4a). Myali Lakes seeds germinated slowest at all temperatures (Figs. 5.3a, 5.4) and had the poorest germination response at 25°C and 30°C (Table 5.8). For all populations, incubation temperature affected T_{50} values, with seeds incubated at 10°C and 25°C taking considerably longer to reach 50% germination than those at 15°C and 20°C (Fig. 5.3a).

Seeds of *P. undulatum* from all populations failed to germinate at 5°C for the first 90 days. After transfer to 20°C, these seeds began to germinate within 16-18 days, in all cases reaching high final germination percentages after an additional 40 days (Fig. 5.4). Seeds from all three populations incubated at 30°C also failed to germinate for the first 90 days. After transfer to 20°C, these seeds began to germinate within 16-18 days, reaching moderate (Myall Lakes, Bunya Mountains) to high (Mallacoota) final germination percentages after 40 days (Fig. 5.4). The cardinal incubation temperatures for this species are a minimum between 5-10°C, an optimum between 15-20°C and a maximum between 20-25°C. For all populations, the temperature eliciting the highest final percentage germination (15°C) was lower than that which produced the highest rate of germination (20°C) (Fig. 5.4).

Of the three *P. undulatum* populations, the seed cohort from Mallacoota had the highest germination rate, with the lowest T_{50} values at all temperatures (Fig. 5.3a). There were

significant effects of temperature and seed population on T_{50} and a significant interaction between these factors (Table 5.9a).

P. revolutum

Seeds from all populations germinated readily across the range of temperatures from 15-30°C (Fig. 5.3b). There was variable germination at 10°C, with Carmila seeds failing to germinate at this temperature, and those from Atherton showing a poor germination response. Seeds from all populations failed to germinate at 5°C until transfer to 20°C, after which there was a moderate (Mallacoota) to weak (all other populations) germination response (Fig. 5.5). The cardinal temperatures for this species are a minimum between 5-10°C, an optimum between 15-20°C (Mallacoota, Carmila) or 20-25°C (Atherton, Myall Lakes Brisbane F.P.) and a maximum slightly above 30°C.

For T₅₀ values, temperature optima for all *P. revolutum* populations lie within the range 20-25°C, with the lowest latitude population demonstrating the highest optimum incubation temperature. Seeds from the Brisbane Forest Park population took the longest time, at almost all temperatures, to reach 50% germination (Fig. 5.3b). Two-way ANOVA showed that both temperature and seed source significantly affected T₅₀, with a significant interaction between these variables (Table 5.9b). Among these seed populations there was a strong positive correlation between optimum incubation temperature and mean summer rainfall (r = 0.94, P = 0.017) and a strong negative correlation between maximum germination rate and annual temperature range (r = -0.98, P = 0.003).

P. angustifolium

Seed populations from Wyperfeld, Peak Hill and Bell displayed very similar germination responses to temperature. They had similar T₅₀ values and final germination percentages, germinated over a similar range of temperatures and when incubated at 5°C and 30°C, began to germinate after transfer to 15°C (Table 5.8; Figs. 5.3c, 5.6). In contrast, seed from Palm Valley germinated more slowly and over a smaller range of incubation temperatures, and seed incubated at 5°C failed to germinate after relocation to 15°C (Table 5.8). The highest germination rate was obtained at 20°C for seed from Bell, Peak Hill and Wyperfeld and 15°C for seed from Palm Valley

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(Figure 5.3c). Palm Valley seed incubated at 10°C reached higher final germination percentages than similarly treated seed from all other populations (Fig. 5.6; Table 5.8). Conversely, incubation temperatures of 25°C and 30°C prevented germination of Palm Valley seed. When transferred to 15°C, these seeds commenced germinating within 30 days, culminating in moderate (25°C) to poor (30°C) germination responses. The cardinal temperatures for *P. angustifolium* appear to be a minimum between 5-10°C, an optimum between 15-20°C and a maximum in the range 25-30°C.

All *P. angustifolium* seed populations achieved highest mean final germination percentages at 15°C, although there was no significant difference in values for all populations (except Peak Hill) across the range 15-20°C. Temperature and seed source significantly affected T_{50} values, with a significant interaction between these variables (Table 5.9c). Among populations, the optimum incubation temperature was positively correlated with winter precipitation (r = 0.96, P = 0.040). Seed weight was positively correlated with precipitation of the wettest quarter (r = 1.00, P = 0.012). Caution must be expressed with this result, as the correlation is based on the results of only four populations.

Comparison of germination biology among species

Based on germination rate, the optimum focubation temperatures for seeds of P. undulatum and P. angustifolium were found to be 18.4°C and 17.9°C, respectively (Fig. 5.7), with maximum final germination percentages for both at an incubation temperature of 15°C (Table 5.8). Incorporating germination data for P. bicolor, there were significant differences among the four species in their optimum incubation temperature (Fig. 5.7). Of the four species, P. revolutum germinated across the broadest amplitude of temperatures (10-30°C), although after transfer to 20°C, seeds of this species previously incubated at 5°C germinated more slowly than similarly-treated seeds of P. undulatum and P. angustifolium.

For all species, there were significant effects of population and temperature on both the rate of germination and final germination percentage, and a significant interaction between population type and temperature for these variables across all species (Table

5.9). There were significant differences among species in the final germination percentages of seed incubated at temperatures of 5°C and 10°C, but not at temperatures of 15°C and higher (Table 5.10). There was a significant difference among species in their germination rate (Table 5.11): *P. angustifolium* was the most rapidly germinating species at incubation temperatures in the range 10-20°C (Fig. 5.3) and pooling populations, *P. angustifolium* germinated significantly faster at its optimum incubation temperature than all species except *P. undulatum* (Fig. 5.8). Final germination percentages varied significantly among species and among populations within species (Table 5.12). When incubated at the temperature inducing the most rapid germination rate for each species, the final germination percentage of *P. bicolor* seeds was significantly lower than that of the other species (Fig. 5.9).

Pooling populations within species, there was a negative correlation between maximum germination rate and mean winter precipitation (r = -0.96, P = 0.041), i.e. species native to sites with wetter winters germinated more slowly than those from sites with drier winters.
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DISCUSSION

Seed dormancy and responses to stratification and light

P. undulatum seed germinates relatively rapidly and to high percentages, lacks dormancy attributes and germinates optimally under conditions of continuous light. The reduction in germinability of stratified seed may have resulted from damage induced by the low temperature or by induction of secondary or conditional dormancy (Baskin and Baskin 1998). As soil seedbank temperatures of 5°C are likely to be rare for naturally-occurring *P. undulatum*, the reduced germination response of seed stratified at this temperature is not surprising, although whether this was due to the imposition of secondary dormancy or low-temperature induced injury requires further investigation. The imposition of secondary dormancy may provide *P. undulatum* with a mechanism to avoid seedling damage from frosts, which occur sporadically during the autumn-winter seed fall in parts of the distribution of this species.

The more rapid commencement of germination of stratified *P. undulatum* seed implies an increase in germination rate, which has been reported for seeds of a range of species subjected to such treatment (Battaglia 1993; Al-Helal 1996; Edwards and El-Kassaby 1996; Walck *et al.* 1997). This supports the suggestion that for some species, the process of germination may actually commence during stratification (Battaglia 1993). Lack of germination by stratified seeds of *P. revolutum* suggests that they may have been damaged by exposure to low temperature, although it is possible that such seed may have undergone secondary dormancy. Seed injury resulting from exposure to low temperature is common among annual species (Baskin and Baskin 1986, 1989), but appears to be rare for woody taxa.

The days to first and final germination for non-stratified seeds of *P. angustifolium* under continuous light approximated those recorded by Kullmann (1981) for seeds of this species from Western Australia. The germination response of *P. angustifolium* seed to the light and stratification treatments was similar to that of *P. undulatum*, except that it appeared to more deleteriously affected by stratification than *P. undulatum*.

The lower final germination percentages and increased time to commence germination for dark-treated seeds indicates that germination of these species is stimulated by light, which is common among Australian taxa (Willis and Groves 1991; Plummer and Bell 1995), including rainforest and sclerophyll forest species (Beardsell and Richards 1987; Bell 1999). It is less common, however, among woody species occupying more open vegetation (Grose and Zimmer 1957), although higher germination in the light has been reported for a number of large-seeded species associated with high light environments (Bell 1994; Bell *et al.* 1995). The differences between the treatments may have been even more pronounced had not dark-only seed been exposed to the light whilst germinants were counted, which is sufficient-enough time to induce seed germination in other taxa that have a light requirement (Zohary *et al.* 1975; Mott and Groves 1981).

Germination of P. bicolor

The dormancy observed in seeds of *P. bicolor* is a common characteristic of many species, occupying a diversity of environments (Bewley and Black 1982a; Mayer and Poljakoff-Mayber 1989; Burrows, 1996; Bell 1999). Causes of dormancy can be summarized as: (i) true dormancy, imposed by some biochemical means, which may include the presence of inhibitory compounds in the seed contents or testa; (ii) embryo immaturity; (iii) environmental constraint, resulting from unsuitable external conditions; (iv) or physical constraint, imposed by thick, water-impervious seed coats (Burrows 1996).

Based on the observed lack of embryo development in long imbibed but ungerminated seeds and the subsequent germination of seed c. 18 months post initial imbibition, embryo immaturity (ii above) is strongly implicated as the cause of dormancy in *P. bicolor*. Baskin and Baskin (1998) classified this condition as 'morphological dormancy'. Seed displaying such dormancy often requires a considerable period of time, during which the embryo completes its development, before the commencement of germination. This form of dormancy has been proposed for two New Zealand species of *Pittosporum* demonstrating germination delays (Burrows 1996). Furthermore, morphophysiological dormancy, which also involves an after-ripening requirement, has been previously recorded for a number of species belonging to the Pittosporaceae

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(Baskin and Baskin 1998). The effectiveness of gibberellic acid in breaking the dormancy of *P. bicolor* seeds has also been recorded for *Pittosporum obcordatum* (Moore *et al.* 1994) and other species with seeds that have an after-ripening requirement (Hidayati *et al.* 2000). In such species, field germination often occurs during the second spring or autumn period following maturity (Hidayati *et al.* 2001).

The pattern of delayed germination observed in seeds of *P. bicolor* is similar to that of the cool-temperate rainforest species *Tasmannia lanceolata* (Howard 1974) and *Phyllocladus aspleniifolius* (Read 1989). The germination delay in *P. bicolor* suggests the maintenance of an active soil seed bank, which together with active seed dispersal by birds, may facilitate rapid re-establishment following fire or other disturbance.

It is also possible that seasonal or diurnal changes in temperature and/or light periodicity in the glasshouse may have played a role in facilitating germination in *P. bicolor*. The germination of a number of hard-seeded species occupying Mediterranean-type climates is promoted by a regime of diurnal temperature fluctuations, similar to those experienced on an exposed soil surface during the summer months and which act to increase seed permeability (Quinlivan 1961).

As mentioned above, cold stratification of seeds has been observed to break dormancy in many species. For many species, the effects of chilling can be replaced by the addition of a gibberellin (usually gibberellic acid GA₃, GA₄ or GA₇), an observation that has led researchers to conclude that cold stratification induces the biosynthesis of this hormone in such species (Bewley and Black 1994). As cold stratification appears to influence neither the state of dormancy nor initiation of germination in seeds of *P*. *bicolor*, then either the process is not inducing GA synthesis in such seeds, or it is induced, but not to concentrations sufficiently high to break dormancy. However, the significant effect of GA₃ on germination of *P*. *bicolor* seed indicates its dormancybreaking role, most likely by the speeding-up of embryonic growth (Jones and Stoddard 1977).

Of the other factors tested on *P. bicolor* seed, a requirement for smoke-derived compounds was considered to be unlikely for germination, and the results support this.

Furthermore, the presence of *P. bicolor* in cool temperate rainforests, a vegetation community that develops only in the absence of frequent fire, suggests that it may be fire sensitive rather than fire responsive.

The seeds of many plant species are consumed and dispersed by a range of bird and mammal species (Howe 1986). The passage of seeds through the guts of birds may facilitate the breaking of dormancy, resulting in higher germination percentages compared to undigested seeds, a phenomenon reported for many plant species (Swank 1944; Krefting and Roe 1949; Traveset 1998) including woody Australian taxa (Glyphis 1981; Gill 1985). This does not mean that the breaking of dormancy is dependant upon consumption by frugivores, as the loss of physical dormancy may still occur in unconsumed seed as a result of environmental factors (Baskin and Baskin 1998). The above results suggest that the breaking of dormancy in *P. bicolor* seeds is unlikely to depend upon digestion by birds.

Finally, among bird-dispersed plant species, a general negative relationship has been recorded between seed size and dormancy, which may also be related to comparative degrees of establishment success and/or herbivory (Rees 1996). *P. bicolor* seeds are small in comparison to those of closely-related non-dormant species (see Chapter 6), suggesting that dormancy may be related to seed size in this species.

The optimum incubation temperature of 10°C for seeds from all populations of *P. bicolor* is dissimilar to that of southern Australian cool temperate rainforest species (range 17-25°C, Read 1989), but is not unexpected for a species restricted to sites with mean annual temperatures in the range 4.8-13.9°C. Moreover, for the Francistown, Dandenong Ranges, Otways and Warburton sites, 10°C approximates the mean temperatures of May and September, months that also provide consistent and predictable rainfall at these sites. For Brown Mountain, 10°C approximates mean temperatures of March-April, during which there is normally abundant, regular rainfall (BIOCLIM analyses). This temperature also approximates the optimum incubation temperature of cool temperate species occurring elsewhere in the world (Bewley and Black 1982b). The lack of germination at incubation temperatures higher than 15°C may be of adaptive importance, as a low temperature requirement would prevent

summer germination at most sites within its range. It might also play an important role in determining the northern limits to the distribution of *P. bicolor*.

Effects of temperature on germination of P. undulatum, P. revolutum and P. angustifolium.

These germination studies indicate that even for non-dormant seeds of these *Pittosporum* species and their populations, germination is possible only within well-defined temperature limits - the maximum and minimum temperatures - beyond which germination is prevented.

P. undulatum

The observed intraspecific differences in final germination percentage and germination rate of *P. undulatum* indicate the likelihood of ecotypes within this taxon. The poor germination response at high temperature and comparatively slow germination rate of seeds from Myall Lakes are surprising, particularly as this site has the highest annual precipitation, much of which falls during summer. As this population occurs on very sandy soils, is possible that soil moisture sufficient to sustain seedling establishment and survival may not be available until the cooler winter months. This study has shown that *P. undulatum* seeds are able to survive a long period of high temperature-induced dormancy and germinate to high final percentages when released from such dormancy. As seeds of this species normally begin to develop during summer, their germination response may be determined to some extent by summer temperature, which is a critical factor in the conditioning processes leading to germination in other species (Thompson and Cox 1978).

The observed optimum incubation temperature of 20°C for *P. undulatum* seeds largely concurs with the results of Gleadow (1982) and Gillespie *et al.* (1996). The maintenance of viability by *P. undulatum* seeds incubated for 90 days at both 5 and 30°C, and their rapid germination after transfer to 15°C, demonstrates an ability to withstand exposure to temperature extremes, even though exposure for such duration would not normally be expected across its distribution. It also shows that while low

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temperature prevents seed germination, it does not induce secondary dormancy in seeds of this species.

The expansion of *P. undulatum* throughout south-eastern Australia in the last 50 years has been attributed to a number of factors including its extensive cultivation as an ornamental (Gleadow 1982), its high fecundity (Cameron 1992) and dispersal by native and introduced vectors, and changes to natural fire regimes of sclerophyll forests (Gleadow and Ashton 1981). The ability of *P undulatum* seeds to germinate rapidly across a relatively wide range of temperatures has undoubtedly contributed to this process.

P. revolutum

The broad variation in germination response to temperature $\operatorname{amon}\circ$ populations of *P*. *revolutum* reinforces the suggestion that germination responses are highly plastic, undergoing selection by environmental factors to generate adaptive changes that distinguish different populations (Thompson 1973). The degree of variation among populations may be correlated with the geographic range of the species, with narrowly confined species demonstrating less variation than those such as *P. revolutum* with broader distributions. *P. revolutum* is able to germinate over a broad range of temperatures, although most of the seeds incubated at 5°C appeared to be impaired sufficiently to prevent germination when later transferred to 20°C.

The higher optimum incubation temperature of northern compared with southern populations of this species probably reflects trends in mean annual temperature, but may also be related to the strong precipitation seasonality to which mid- and lower latitude populations of this species are subjected. At lower latitudes (summer-dominated rainfall), seeds of *P. revolutum* typically reach maturity during July-August, which is seasonally cool (mean temperature 18°C) and dry (30-49 mm of rainfall, with few rain days) (Bureau of Meteorology 1989). The inhibition of germination at such temperatures avoids the likely danger to germinants of lower soil water availability at that time of the year.

The significantly higher T_{50} value of Brisbane Forest Park seeds, compared to those of the other populations, indicates that even for seeds at the optimum incubation temperature, germination is spread over a long period. At this site, *P. revolutum* seeds mature between April-July, during which conditions of temperature and rainfall are unfavourable for successful germination and seedling establishment. Spreading the germination period over a longer period of may time increase the likelihood of encountering conditions suitable for both germination and subsequent seedling survivorship. The lower germination rate of seeds from this population may also explain the very low RGR of its seedlings in comparison to those of more-rapidly germinating populations of this species (Chapter 6). At the southern end of its distribution, plants of *P. revolutum* produce seeds that mature during March-May, and thus an ability of such seeds to readily germinate at temperatures approximating those of the autumn period (13-16°C) would be distinctly adaptive, given that frost is rare.

The negative correlation between germination rate and annual temperature range among these populations of *P. revolutum* is interesting. It may be that increasing amplitude of annual temperature equates with increased environmental unpredictability, which selects for lower rates of seed germination in ecotypes subjected to strongly seasonal conditions. Selection for delayed seed germination in other species has been suggested as a response to climatic unpredictability (Andersson 1996). In relation to this, annual temperature range may reflect the length and intensity of drought, which has been shown to reduce the rate of seed germination among Sahelian rangeland species (Elberse and Breman 1990).

P. angustifolium

The relatively low optimum incubation temperature (16.4°C) obtained for *P. angustifolium* seeds from Palm Valley, compared with the other populations studied here, concurs with the results of germination trials on seeds of this species from Rottnest Island (Dunlop and Galloway 1984). This optimum temperature is very close to the long term June average (16.8°C) for Palm Valley (BIOCLIM-derived), which coincides with the early winter rainfall period in inland Australia (Bell 1999) and just precedes the peak period of fruit ripening previously reported for plants of this species in this region (Friedel *et al.* 1993). In contrast, Jurado and Westoby (1992b) determined

28°C to be the optimum incubation temperature for seeds of *P. angustifolium* collected from the Alice Springs area, which suggests a summer germination regime for this species. In Jurado and Westoby's germination trial, seeds incubated at 20°C and 12°C produced germination responses of only 28% and 4% respectively.

The difference between this study and that of Jurado and Westoby (1992b) may be due to a number of factors including the criteria used to determine the temperature optimum, genetic differences between the populations, differences in seed handling or storage and differences in experimental design. Based on the results of each trial, the last factor is the most plausible explanation for the observed differences in germination response. Jurado and Westoby maintained seeds in permanent darkness except for a small period of exposure to light when germinants were counted. As seeds may be light-requiring at one temperature but not at another (Pons 1992), it is possible that high temperature obviates the requirement for light, which is necessary for germination at lower temperatures. However, the two factors of high temperature *and* light availability might actually serve to inhibit germination in *P. angustifolium*, which would explain the total lack of germination of seeds incubated at 30°C in this trial.

Seeds of *P. angustifolium* from the arid Palm Valley population may require sufficient rainfall to provide adequate soil moisture for germination, together with a temperature regime sufficiently low enough to prevent rapid loss of soil water and/or high evapotranspirational stress. For species (or populations of species) demonstrating such behaviour, although water availability is the main limiting factor and primary controller of germination, temperature may be a secondary controller that acts when a soil moisture threshold has been reached (Kigel 1995). Conditions of temperature and soil moisture suitable for germination are therefore only likely to occur after a sustained period of rainfall during the cooler winter-spring period. Such a germination strategy increases the likelihood of successful seedling establishment in arid and unpredictable environments such as central Australia. A similar germination response has been recorded for a range of other arid and semi-arid species (Silcock 1973; Bellairs and Bell 1990; Bell *et al.* 1993; Bell 1994; Richmond and Chinnock 1994; Bell and Williams 1997). It is also characteristic of Mediterranean species (Perez-Garcia *et al.* 1995; Thanos and Doussi 1995) and those of arid environments elsewhere in the world (Went

and Westergaard 1949; Ackerman 1979; Al-Helal 1996). The slow germination rate of Palm Valley seeds, in comparison to other populations, indicates a requirement for a longer period of hydration at temperatures in the range 10-20°C before germination will proceed. This would greatly reduce the potential for summer field germination in arid central Australia, as temperatures are usually high and soils do not normally remain moist for long periods. Slower germination rates have been recorded for low rainfall ecotypes of other widely distributed species (Ali 1968; Ladiges 1974).

The lower overall mean germination fraction and slow germination rate of P. angustifolium seeds from Palm Valley fits the bet-hedging strategy for arid and semiarid species (Letnic et al. 2000). This strategy involves non-committal of the end e seed cohort to germination, which occurs over a longer than normal period of time, thereby reducing the probability that all seedlings will die before reproducing (Bulmer 1984; Leon 1985). Such a strategy makes ecological sense, given that for central Australia, initial effective rain, which is the amount required to initiate plant growth, is likely to occur on average only once every two years during summer and only three times every two years during winter (Stewart and Perry 1962). This supports the suggestion that a combination of uncharacteristically high winter rainfall and mild temperatures may facilitate the recruitment of perennial, arid and semi-arid woody species such as P. angustifolium. For example, during 1973, when precipitation was recorded for every month in the Alice Springs area, resulting in annual rainfall of 448 mm, 50% higher than the long-term average, seedlings of a large number of species were recorded in the field (Maconochie 1982). Furthermore, in arid and semi-arid Eucalyptus-dominated scrubs and shrublands, seedling regeneration of Acacia sowdenii has been reported only three times in the past century, with above average rainfall occurring on each occasion (Lange and Purdie 1976).

In contrast to the germination behaviour of Palm Valley seeds, those from Wyperfeld, which is characterized by mild, rainy winters and hot, dry summers, demonstrated rapid rates of germination across a broad range of incubation temperatures. Seed, of P. *angustifolium* at Wyperfeld mature between May-October, which coincides with the autumn and winter rainfall in north-western Victoria. Rapid germination at suitable temperatures is therefore possible following the first substantial autumn-winter rains in

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this region. Nevertheless, the hot, dry summers at Wyperfeld mean that seeds maturing in late spring are unlikely to germinate and successfully establish seedlings, an element of the phenology of this species that will be explored in Chapter 8.

Comparison of germination biology among species

The consistent trend of optimum temperature for germination rate being higher than that for total germination among these *Pittosporum* species has been reported for other Australian plant taxa, including some from central Australia (Ross 1976). It is possible that lower temperatures facilitate slower but more thorough germination in these species, while higher temperatures favour a more rapid germination response, with slightly less overall final germination.

These species display broad differences in their germination response to temperature, (Fig. 5.10). The most conservative species, in terms of germination rate and the amplitude of temperatures across which it will germinate, appears to be *P. bicolor*. It is also the most mesic and narrowly-distributed of the four taxa. In contrast, *P. angustifolium* and *P. revolutum*, which exhibited the highest germination rates across a broad range of temperatures and high degrees of intraspecific variation in germination biology (Fig. 5.10), are the most widely-distributed and have populations in environments subject to on-going or strongly seasonal water deficit. Similar behaviour has been reported for other widely distributed taxa (Thompson 1973; Meyer and Kitchen 1994), which suggests that it may be a common strategy of such taxa. However, populations of *P. angustifolium* and *P. revolutum* from extremely arid or seasonal habitats demonstrated the narrowest germination response to temperature and the lowest germination quotient at all temperatures. For such populations, selection for adaptive syndromes appears to realign the germination response toward that of more narrowly distributed taxa such as *P. bicolor* (Fig. 5.10).

The generally rapid germination of P. angustifolium conforms with the suggestion that the seeds of xerophytic taxa will respond more rapidly to water availability than those of more mesic taxa (Jurado and Westoby 1992b). Nevertheless, the slower germination rate and lower overall germination quotient of seeds from the most arid population of P. angustifolium demonstrates the high degree of intraspecific variation within this species and suggests selection for traits that will increase the likelihood of germinant survival and growth to reproductive maturity. A similar pattern of lower germination fractions has been observed in the most xeric populations of other species (Clauss and Venable 2000).

The higher optimum incubation temperature for *P. revolutum* than the other species reflects the climate across its distribution, in particular the less extreme coastal temperatures and largely summer-dominated rainfall operating along much of Australia's east coast. The positive correlation between the distribution of *P. revolutum* and summer rainfall, and negative correlation with low winter minimum temperature have been previously discussed (Chapter 2). This, together with the lack of germination and subsequent loss of viability or imposition of secondary dormancy in seeds incubated at 5°C, suggests that winter temperature minima may be an important factor in defining the southern distributional limit of *P. revolutum*. Minimum winter temperature has been suggested as a critical determinant in the distribution of various plant species (Woodward 1997).

The negative correlation between germination rate and winter precipitation among these species largely divides them by seed mass, with large-seeded species occupying arid or low winter rainfall sites (*P. angustifolium* and *P. revolutum*) germinating more rapidly than those (*P. bicolor* and *P. undulatum*) occupying sites with high winter rainfall. This pattern may relate to patterns of winter temperatures in areas with high winter rainfall not being conducive to rapid rates of germination. Alternatively, assuredness of winter rainfall may preclude a requirement for rapid germination, resulting in a slower response of species in higher rainfall sites to the availability of soil moisture.

It is possible that the observed differences in germination response among populations of these species might have been due to a 'preconditioning' effect of the climate during seed maturation. Baskin and Baskin (1973) suggested that before genecological significance can be assigned to differences in the responses of seeds from different populations of a species, plants from each population should be grown for several generations in a uniform environment. While seeds for these trials were collected over

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a short period of time, thereby reducing the possible magnitude of this effect, there would have been differences in climate of each population during seed development. Given that temperatures operating at the site of each population during seed maturation were typical of the long-term trends at these sites, it presents difficulties in distinguishing between the genetic and environmental components of the germination response of these species and their populations. In regard to this, as Mallacoota represents the southerly limit to the distribution of *P. revolutum*, climate might be expected to be less favourable for seed development, resulting in decreased germination performance. However, the Mallacoota population had the fastest germination rate at incubation temperatures in the range 15-25°C. Broad differences in the germination response of co-occurring populations of *P. undulatum* and *P. revolutum* diminishes the importance of preconditioning but reinforces the importance of genotype as the main determinant of germination behaviour among these species. This suggests that genetic differences play an important role in determining the phytogeographic zones that these species are able to inhabit.

The dissimilar germination characteristics of the Mallacoota populations of *P*. undulatum and *P*. revolutum contrast with the quite similar germination response to temperature of *P*. undulatum and *P*. angustifolium, which have non-overlapping distributions. Furthermore, the proximal optimum incubation temperatures of *P*. angustifolium and *P*. bicolor indicate that comparatively low optimum incubation temperature may be advantageous in contrastingly arid and higher-latitude mesic environments. Together, these results suggest that environmental factors additional to the effects of temperature on seed germination are important determinants of distribution for these species of *Pittosporum*.

Intra- and interspecific variation in the germination response of these species to temperature is consistent with selection for traits that will maximize the chances of germination during periods when there is a high probability of subsequent establishment. Germination attributes that are likely to have significant adaptive value in arid environments include a requirement for a suitable combination of light, moisture and temperature, a rapid rate of germination and inhibition of germination at temperatures above 25°C (Fig. 5.10). For populations of species such as *P. revolutum*

that inhabit seasonally dry environments, adaptive traits include germination at temperatures approximating those of the summer rainfall period, a comparatively slower rate of germination and an ability to maintain seed viability for a considerable period under conditions not suitable for germination.

Further research into patterns of germination within and between closely related species should include an investigation of the relationship between germination rate and osmotic potential, particularly as the germination of all seeds is ultimately determined by the availability of water. This research could explore Summerson's (1986) concept of 'hydrothermal time', which is derived by combining the environmental factors of water potential and temperature and linking these with time. Such research might provide links between germination biology and the water relations of seeds, seedling and adult plants of these species.

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Species	Population	Latitude (°S)	Longitude (°E)	Altitude (m a.s.l.)
	Bunya Mountains	26.83	151.58	1000
P. undulatum	Myall Lakes	32.56	152.30	60
	Mallacoota	37.49	149.78	20
	Atherton	17.25	145.42	1100
	Carmila	21.87	149.17	200
P. revolutum	Brisbane Forest Park	27.40	152.78	350
	Myall Lakes	32.56	152.30	60
	Mallacoota	37.49	149.78	20
	Palm Valley	24.05	132.56	650
	Bell	26.50	151.50	475
P. angustifolium	Peak Hill	32.72	148.19	350
	Wyperfeld N.P.	35.69	142.05	60
	Brown Mountain	36.60	149.40	1200
P. bicolor	Warburton	37.76	145.70	680
	Dandenong Ranges	37.92	145.44	240
	Otway Ranges	38.75	143.55	255
	Francistown	43.55	146.90	40

 Table 5.1
 Locations of seedlots used in germination experiments.

Table 5.2 Selected temperature and precipitation data for *Pittosporum* species collection sites (TWaQ – Mean Temperature of the Warmest Quarter; TCQ – Mean Temperature of the Coldest Quarter; TWeQ – Mean Temperature of the Wettest Quarter; TDQ – Mean Temperature of the Driest Quarter; MAP – Mean Annual Precipitation). (Temperatures are in °C; Precipitation is in mm).

Species	Site	TWaQ	TCQ	TWeQ	TDQ	МАР
	Bunya Mountains	20.0	8.5	20.0	9.7	924
P. undulatum	Myall Lakes	21.2	11.7	14.5	16.2	1295
	Mallacoota	18.1	10.5	13.0	18.1	959
	Atherton	21.5	14.2	21.0	16.2	1598
P. revolutum	Carmila	25.7	16.4	25.6	17.8	1100
	Brisbane Forest Park	22.3	12.7	22.1	13.7	1266
	Myall Lakes	21.2	11.7	14.5	16.2	1295
	Mallacoota	18.1	10.5	13.0	18.1	959
	Palm Valley	28.2	12.2	27.5	13.7	261
P. angustifolium	Bell	23.1	11.4	23.1	12.2	744
	Peak Hill	23.5	9.0	23.5	10.1	581
	Wyperfeld N.P.	21.6	9.4	11.7	21.1	392
	Brown Mountain	13.8	2.9	11.7	3.8	1157
P. bicolor	Warburton	15.2	5.3	7.0	15.1	1061
	Dandenong Ranges	17.5	8.0	9.8	17.5	1134
	Otway Ranges	15.6	8.1	8.1	15.6	1269
	Francistown	14.0	7.5	7.5	14.0	740

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Table 5.3 Effects of species, cold stratification and light treatments on the minimumtime to germination, the maximum time to germination and final germinationpercentage for seed of P. undulatum, P. revolutum and P. angustifolium. Data areresults of a three-way ANOVA. T_{min} : minimum time to the onset of germination; T_{max} : maximum time to the completion of germination.

	T _{min} (days)		T _{max} (days)		Final germination percentage	
Species / Effect	F	Р	F	Р	F	P
Species	93.9	< 0.001	67.8	< 0.001	50.1	< 0.001
Stratification	2.9	0.094	2.7	0.114	153.7	< 0.001
Light	31.3	< 0.001	0.2	0.802	9.5	< 0.001
Species x Stratification	19.6	< 0.001	0.1	0.780	21.2	< 0.001
Stratification x Light	21.4	< 0.001	0.3	0.730	8.3	< 0.001
Species x Light	31.3	< 0.001	10.9	< 0.001	7.2	< 0.001
Species x Stratification x Light	12. 1	< 0.001	3.2	0.039	0.6	0.668

Table 5.4 Percentage viability, determined by tetrazolium staining, of ungerminated seeds of *Pittosporum undulatum*, *P. revolutum*, *P. undulatum* and *P. bicolor* following stratification or non-stratification and incubation under different light regimes for approximately 90 days at 20°C. The number of seeds examined (*n*) is given in parentheses.

	Lig	ght	Dai	ſk	Light/Dark	
Species	Stratified	Non- stratified	Stratified	Non- stratified	Stratified	Non- stratified
P. undulatum	33.3 (12)	50.0 (6)	57.9 (19)	73.3 (15)	41.2 (17)	46.7 (15)
P. revolutum	16.6 (30)	62.5 (8)	23.3 (30)	43.8 (16)	23.3 (30)	61.1 (18)
P. angustifolium	36.7 (30)	58.8 (17)	33.3 (27)	40.0 (10)	27.3 (22)	58.8 (17)
P. bicolor	36.7 (30)	76.7 (30)	40.0 (30)	56.7 (30)	33.3 (30)	50.0 (30)

Table 5.5 The minimum time to germination, the maximum time to germination and final germination percentage for non-stratified seed of *P. undulatum*, *P. revolutum* and *P. angustifolium* subjected to constant light. Data are means with sem in brackets, n=3. Shared alphabet letters denote non-significant differences (P < 0.05) between species. T_{min} : minimum days to the onset of germination; T_{max} : maximum time to the completion of germination.

Species	T _{min} (days)	T _{max} (days)	Final germination percentage
P. undulatum	26.0 (0.0) ^a	57.3 (6.4) *	80.0 (5.7) ^a
P. revolutum	47.0 (0.0)	132.7 (4.3)	73.3 (8.8) ^a
P. angustifolium	25.0 (1.0) ^a	62.3 (6.3) ^a	43.3 (3.3)
F	463.0	53.8	9.4
Р	< 0.001	< 0.001	0.011

Table 5.6 Effects of cold stratification and light treatments on germination of the four species. Data are means with scm in brackets, n=3. T_{min}: minimum time to the onset of germination; T_{max}: maximum time to the completion of germination. Shared alphabet letters denote non-significant differences (P < 0.05) between treatment means. N/A denotes zero seed germination.

		L	ight	I	Dark	Ligi	nt/Dark		
Species	Variable	Stratified	Non-stratified	Stratified	Non-stratified	Stratified	Non-stratified	Effects	
								Stratification: $F = 9.6$,	P = 0.009
	T _{min} (days)	24.6 ^{ab} (1.3)	26.0 ^{ab} (0.0)	24.0 ^ª (2.0)	29.0 ^{ab} (1.0)	27.0 ^{ab} (0.6)	31.0 ^b (2.0)	Light: $F = 3.8$,	P =0.053
D. undulatum								Strat x Light: $F = 1.0$,	<i>P</i> =0.407
P. unaulalum								Stratification: $F = 14.9$,	<i>P</i> = 0.002
	T _{max} (days)	36.7 ^{bc} (2.2)	57.3° (6.4)	35.3 ^b (0.9)	54.7° (4.6)	48.3 ^{sc} (3.0)	43.7 ^{ab} (2.7)	Light: $F = 0.1$,	<i>P</i> = 0.868
								Strat x Light: F=7.3,	P = 0.008
							47 0 ⁸ (1 7)	Stratification:	N/A
	T _{min} (days)		47.0 ^a (0.0)		73.3 (1.2)		47.0 (1.7)	Light: F=156.0,	P < 0.001
P. revolutum		N/A		N/A		N/A		Strat x Light:	N/A
								Stratification:	N/A
	T _{max} (days)		132.7ª (4.3)		142.7° (4.7)		129.0*(3.2)	Light: $F = 3.0,$	<i>P</i> = 0.126
					<u></u>			Strat x Light:	<u>N/A</u>
								Stratification: $F = 4.8$,	P = 0.048
	T _{min} (days)		25.0ª (1.0)	39.0 ^b (3.1)	24.0 ^a (1.0)	39.0 ^b (3.1)	41.0 ⁶ (4.6)	Light: $F = 5.0, I$	<i>P</i> = 0.027
P. angustifolium		N/A						Strat x Light: $F = 1.6$,	P = 0.251
								Stratification: $F = 4.0$,	P = 0.080
	T _{max} (days)		62.3°(6.3)	39.0 (3.1)	60.3 ^a (13.4)	81.0 ⁶ (3.2)	88.0 ^b (1.0)	Light: F = 24,3,	P = 0.091
			·····					Strat x Light: $F = 1.0$,	<i>P</i> = 0.340
P. bicolor	<u></u>	N/A	N/A	N/A	N/A	N/A	N/A		

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Population / Effect	df	F	Р
a. Warburton			
Temperature	2	61.0	< 0.001
GA3	1	196.0	< 0.001
Temperature x GA ₃	2	61.0	< 0.001
b. Dandenong Ranges			
Temperature	2	34.3	< 0.001
GA ₃	1	42.0	< 0.001
Temperature x GA ₃	2	12.3	0.004
c. Brown Mountain			
Temperature	1	90.8	< 0.001
GA3	1	137.2	< 0.001
Temperature x GA ₃	1	0.6	0.457
d. Otway Ranges			
Temperature	1	7.5	0.052
GA₃	1	20.3	0.011
Temperature x GA ₃	1	3.9	0.121
e. Francistown			
Temperature	2	32.4	0.001
GA ₃	1	40.1	0.001
Temperature x GA ₃	2	5.8	0.040

Table 5.7 Effects of temperature and GA_3 on the final germination percentage of seedof five populations of P. bicolor.

Species	Incubation temperature (°C)					
Population	5	10	15	20	25	30
P. undulatum						
Mallacoota	98 (2.0) [*]	100 (0)	100 (0)	100 (0)	92 (2.4)	68 (11.1)
Myall Lakes	88 (3.7) [*]	94 (4.0)	100 (0)	98 (2.0)	24 (5.1)	46 (9.8) [•]
Bunya Mts	84 (6.0)*	86 (2.5)	100 (0)	98 (2.0)	38 (6.6)	54 (9.3) [*]
P. revolutum						
Mallacoota	44 (7.5) [•]	52 (9.7)	94 (2.5)	96 (4.0)	90 (3.2)	64 (6.8)
Myall Lakes	24 (8.7) [•]	20 (3.2)	94 (2.5)	96 (2.4)	98 (2.0)	72 (5.8)
Brisoane Forest Park	14 (7.5) [•]	14 (4.0)	46 (2.4)	64 (5.1)	70 [°] (4.5)	48 (2.0)
Carmila	28 (3.7)*	0	62 (5.8)	88 (2.0)	50 (8.9)	30 (17.0)
Atherton	18 (3.7)*	2.0 (2.0)	94 (2.5)	94 (4.0)	9 4 (2.4)	82 (4.9)
P. angustifolium				· •· · •· •· •· •		
Palm Valley	0**	78 (14.0)	87 (2.2)	87 (4.1)	54 (2.4)**	32 (5.8)**
Wyperfeld N.P.	58 (8.0) ^{**}	70 (4.5)	100 (0.0)	98 (2.0)	94 (4.0)	90 (3.2) ^{**}
Bell	88 (3.7) ^{**}	72 (6.6)	100 (0.0)	98 (2.0)	96 (2.4)	86 (4.0)**
Peak Hill	34 (5.1)**	50 (4.5)	100 (0.0)	94 (2.4)	40 (9.5)	96 (2.4) ^{**}

Table 5.8 Final germination percentage of seed of three *Pittosporum* species from different provenances, incubated over a range of temperatures (means \pm sem, n=5). (* - seed transferred to 20°C after 90 days; ** - seed transferred to 15°C after 90 days).

		T ₅₀	value	Final germination percentage		
Species / Effect	df	F	Р	F	Р	
a. P. undulatum	<u> </u>	<u></u>			<u> </u>	
Population	2	77.2	< 0.001	44.7	< 0.001	
Temperature	3	163.7	< 0.001	38.0	< 0.001	
Population x Temperature	6	2.6	0.029	31.4	< 0.001	
b. P. revolutum						
Population	4	34.2	< 0.001	36.6	< 0.001	
Temperature	4	227.7	< 0.001	26.4	< 0.001	
Population x Temperature	14	7.7	< 0.001	4.8	< 0.001	
c. P. angustifolium						
Population	3	22.7	< 0.001	14.1	< 0.001	
Temperature	3	96.1	< 0.001	47.1	< 0.001	
Population x Temperature	9	6.3	< 0.001	9.3	< 0.001	

Table 5.9 Effects of population and temperature on the time to 50% germination (T_{50}) and final germination percentage for seed of three *Pittosporum* species.

 Table 5.10
 Final germination percentage of seed of three *Pittosporum* species incubated over a range of temperatures. Data are means of populations within species with sem in brackets. Shared alphabet letters denote non-significant differences between species' means for each temperature.

Species	Incubation temperature (°C)								
Species	5	10	15	20	25	30			
P. undulatum	90.0 (4.2) ^a	93.3 (4.1) ^a	100.0 (0) *	98.7 (0.7)ª	51.3 (20.8)"	56.0 (6.4)ª			
P. rcvolutum	25.6 (6.8) ^b	17.6 (9.1)	78.0 (12.4)*	87.6 (8.3) ^e	80.4 (6.4)*	59.2 (5.5) ⁴			
P. angustifolium	45.0 (22.4) ^{ab}	67.5 (2.1) ^a	96.8 (3.8) ⁴	94.3 (3.2) ^a	71.0 (11.8) ^a	76.0 (16.2) ^a			
F	7.3	23.5	2.5	1.3	1.1	0.9			
Р	0.013	< 0.001	0.138	0.308	0.379	0.451			

Source of variation df F Р Species 2 126.1 < 0.001 Population within species 13.2 9 < 0.001 Temperature 4 193.0 < 0.001 Species x Temperature 107.2 < 0.001 6

Table 5.11 Effects of species, population within species and temperature on the timetaken for seed of three *Pittosporum* species to reach 50% germination. Data are resultsof a partly-nested ANOVA.

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Table 5.12 Effects of species, population within species and temperature on the finalgermination percentage for seed of three *Pittosporum* species. Data are results of apartly-nested ANOVA.

Source of variation	df	F	Р
Species	2	17.1	< 0.001
Population within species	9	10.4	< 0.001
Temperature	4	31.4	< 0.001
Species x Temperature	7	29.5	< 0.001



Figure 5.1 Final germination percentages of (a) *P. undulatum*, (b) *P. revolutum* and (c) *P. angustifolium* seed subject to light and stratification treatments and incubated at 20°C. Data are means with sem, n=3. *F*- and *P*-values from ANOVA were calculated using transformed data, and where these were significant (P < 0.05), shared alphabet letters above columns denote no significant difference between means. Note: There was zero germination of *P. bicolor* for all treatments.

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Figure 5.2 Final germination percentage of control and GA₃-treated seed from five populations of *P. bicolor*, incubated at 10, 15 and 20°C (mean + sem, n=3). Within populations, shared alphabet letters denote non-significant differences between means.



Figure 5.3 Time to 50% germination for seed populations of (a) *P. undulatum*, (b) *P. revolutum* and (c) *P. angustifolium* incubated over a range of temperatures (mean \pm sem, n=5.



Figure 5.4 Cumulative germination percentages of seed from three populations of *P. undulatum*, incubated at 5-30°C. Data points are means of five replicates. Note: After 90 days without germination, seed incubated at 5°C and 30°C was



Figure 5.5 Cumulative germination percentages of seed from five populations of *P. revolutum*, incubated over the temperature range 5-30°C. Data points are means of five replicates. Note: After 90 days without germination, seed at 5°C was transferred to 20° C.



Figure 5.6 Cumulative germination percentages of seed from four populations of *P. angustifolium*, incubated over the temperature range 5-30°C. Data points are means of five replicates. After 90 days without germination, seed from Palm Valley at 5° C, 25° C and 30° C, and that from Wyperfeld, Peak Hill and Bell at 5° C and 30° C was transferred to 15° C.



Figure 5.7 Optimum incubation temperature for seed of four *Pittasporum* species, based on germination rate. Data are means of populations with sem. Shared alphabet letters above columns denote no significant difference between species.



Figure 5.8 Time to 50% germination at the optimum incubation temperature for seed of four *Pittosporum* species. Data are means of populations with sem. Shared alphabet letters above columns denote no significant difference between species.



Figure 5.9 Final germination percentage for seed of each species based on its optimum incubation temperature. Data are means of populations with sem. Shared alphabet letters above columns denote no significant difference between species.



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Figure 5.10 Major germination characteristics of the four species in relation to their purported cladistic positions as per Cayzer et al. (2000). The dashed line indicates that the position of *P. revolutum* is yet to be fully resolved.

CHAPTER 6. GROWTH AND BIOMASS ALLOCATION

Seed and seedling characteristics are important determinants of the types of vegetation communities that a species can inhabit and the microsites where seedlings can establish (Grubb 1977). One of the most influential of these is growth rate, with interspecific variation in seedling growth rate considered to be one of the primary spectra of plant adaptation (Saverimuttu and Westoby 1996). Growth may refer to several interrelated characteristics, including changes in size, form and/or number of plant parts (Chiariello *et al.* 1989). Furthermore, growth rate can be measured in absolute or relative terms, although the former provides little information about a plant's efficiency of dry matter production and is often proportional to plant size (Causton and Venus 1981). Thus, the most commonly accepted and measured form of growth is relative growth rate (RGR), which is the increase in plant material per unit of material per unit time (Hunt 1982).

As RGR is independent of the scale of an organism, it is an important central component of physiological strategies (Evans 1972; Hunt 1990; Nilsen and Orcutt 1996) and may thus be related to adaptive features such as drought resistance (Atwell *et al.* 1999). Growth analyses may also provide insights into population dynamics (Bonan 1988) and are a means of modeling species' responses to climate change (Newbery *et al.* 1999). Such studies can thus provide an environmental basis for aspects of plant demography, as growth rate determines plant biomass, which influences plant competitiveness, survivorship and reproductive maturation and output (Chiariello *et al.* 1989).

Plant growth rates reflect a range of contributing variables and constraints, primarily genetics, climate and soil nutrient availability, with the direct on and magnitude of intraand interspecific differences in RGR resulting from the interaction among these variables (Hunt 1982). The ecological advantages of interspecific variation in RGR have been extensively studied (Grime and Hunt 1975; Mooney *et al.* 1978; Poorter and Remkes 1990; Lambers and Poorter 1992; Villar *et al.* 1998), with conclusions mostly based on the characteristics of single populations of species. Studies of intraspecific variation in RGR are less common (cf. Ashton 1958; Ladiges and Ashton 1974; Kolb and Steiner 1990; Messina *et al.* 2002), in spite of the evolutionary implications of such variation for species (Chiariello *et al.* 1989; Kozlowski *et al.* 1991) and the importance of establishing whether intraspecific variation in RGR is less than that between species *before* scaling up to higher levels of ecosystem and climate (Cornelissen *et al.* 1998). Given this, it is perhaps not surprising that studies combining both intraspecific and interspecific comparisons of growth rate and patterns of biomass allocation appear to be extremely rare (cf. Hunt and Lloyd 1987, van Andel and Biere 1989, Cornelissen *et al.* 1996).

Growth analyses have traditionally compared the effects of environmental variables such as soil nutrient and water availability, temperature, light intensity and/or carbon dioxide on the RGR of a species or their populations (Causton and Venus 1981). Slow growth typifies plants from habitats subject to limiting levels of environmental factors (Parsons 1968; Hunt 1982; Grime *et al.* 1988; Chapin *et al.* 1993), including soil nutrients (Bradshaw *et al.* 1964), water or light (Grime and Jeffrey 1965). Low growth rates may also be associated with higher levels of resistance against herbivores (Coley 1986; Sagers and Coley 1995) or disease (Hoffland *et al.* 1998).

These general patterns suggest that low RGR in limiting or otherwise unfavorable habitats is advantageous to particular species (Rorison 1968; Higgs and James 1969), with high RGR placing others at a selective disadvantage (Grime and Jeffrey 1965; Loach 1967). In considering this pattern, an important question is whether low growth rate forms the basis of adaptation or is rather a by-product of selection for other plant characteristics that are in some way advantageous in such environments. The latter hypothesis is supported by the results of a number of nutrient-limiting growth trials, in which the RGR of all species was reduced, but fast-growing species maintained faster rates of growth than inherently slow-growing species (Poorter 1989; Lambers and Poorter 1992).

In contrast to the growth rates of species inhabiting limiting environments, species inhabiting favorable or non-limiting environments generally have inherently high RGR (Ladiges and Ashton 1974; Grime and Hunt 1975; Poorter and Remkes 1990; Villar *et al.* 1998). The ecological advantages of high RGR are those associated with competition for resources or the basis of a plant life form (e.g. stress avoidance by rapid completion of the annual life cycle) (Lambers and Poorter 1992). In light of the relationships between RGR and various environmental variables, establishment of the

potential RGR of species and comparisons between them must be made under nonlimiting conditions, so as to separate the effects of genetics from environment (Grime and Hunt 1975).

Whilst RGR provides a convenient integration of the combined performances of the various components of a plant (Hunt 1978), a plant allocates proportionally more biomass to structural materials as it grows, resulting in a decline in RGR, which becomes a progressively poorer measure of productive efficiency (Hunt 1982). A better measure of productive efficiency is the net gain in mass per unit of leaf area, the Unit Leaf Rate (Briggs *et al.* 1920), now more commonly known as Net Assimilation Rate (NAR; Gregory 1926). NAR is an estimate of the carbon-assimilatory capacity of a plant and is a product of resource availability (particularly light) and leaf display (Chiariello *et al.* 1989).

Although RGR and NAR define the growth characteristics of a plant, they do not explain its leafiness. A quantitative measure of plant leafiness is Leaf Area Ratio (LAR), the ratio of total leaf area to whole plant dry mass, broadly representing the ratio of photosynthetic to respiratory material within the plant (Hunt 1982). Although LAR is considered to be a morphological component, it may be affected by chemical composition, leaf anatomy and biomass allocation (Lambers and Poorter 1992). The growth rate of a plant is therefore the product of the efficiency of its leaves as producers of now material (NAR – the physiological component), and its leafiness (LAR – the morphological component) (Hunt 1982). LAR may be further subdivided into Leaf Mass Ratio (LMR – also known as the leaf weight fraction, LWF), the ratio of leaf to total plant mass, and Specific Leaf Area (SLA), the leaf area per unit leaf mass.

Another potentially important contributor to RGR is seed mass, which influences species distribution and thus has important evolutionary consequences (Silvertown 1989). Considerable research has been carried out on the relationship between seed mass and plant distribution (e.g. Foster and Janson 1985; Foster 1986; Leishman and Westoby 1994; Westoby *et al.* 1996), and clear correlations have been made between them (Schimpf 1977; Sorenson and Miles 1978; Silvertown 1989; Stromberg and Patten 1990). Although many crop species maintain a high degree of constancy of seed mass over many generations (Harper *et al.* 1970), many non-crop species exhibit considerable

phenotypic plasticity and low heritability in this variable (Michaels et al. 1988; Ellison 2001).

The interrelationships between growth and biomass variables may be influenced by the degree of phenotypic plasticity within species. For example, species exhibiting high potential growth rates, characteristic of high resource environments, show higher morphological plasticity in comparison to species characteristic of low resource environments (Grime *et al.* 1986; Hutchings and de Kroon 1994). For woody plants inhabiting low resource habitats, plasticity is expressed primarily through rapid, reversible physiological changes (Grime *et al.* 1986).

As growth reflects the net movement of resources into and out of a plant, patterns of biomass allocation within and among species provide insights into their adaptive mechanisms and physiological balance (Cody 1966; Abrahamson and Caswell 1982). The primary determinants of biomass allocation are biotic and abiotic environmental factors, genetics and physical constraints to plant architecture (Niklas 1994). As such, there are substantial differences among woody plant species in their patterns of biomass allocation, resulting in morphologies that directly relate to their ability to compete for soil resources and light (Tilman 1988). Thus, a morphology that allows a plant to be a superior competitor at one rate of nutrient supply may be inferior to other morphologies in habitats with higher or lower soil nutrient or moisture status. Given the above-discussed relationship between competitive ability and growth rate, variation in patterns of biomass allocation within or among species distributed along an environmental gradient should affect not only their competitiveness, but also their relative rates of growth.

Patterns of biomass allocation to roots and root system architecture are ecologically important as they determine rates of water and nutrient uptake by plants (Fitter 1997) and are interrelated with the RGR of a species and its geographic distribution (Villar *et al.* 1998). Root system architecture can be measured as the ratio of total root length to root dry weight biomass, the specific root length (SRL).
Rates of stem elongation and height at maturity are important for long term survival and reproductive success, as they determine the amount of light capture (Grime 1979b; Givnish 1982), with slight differences in height greatly affecting light-capturing capacity (Harper 1977) and seed dispersal. However, height is energetically expensive due to the increased costs of transporting nutrients, water and photosynthate, as well as the requirement for a high biomass allocation in order to cope with compressive stresses and instability associated with increased height (Tilman 1988). Ultimately, there are trade-offs between growth rate and plant longevity, with plants with rapid shoot elongation tending to be overtopped and eventually outcompeted by more slowly growing, shade tolerant species (Crawley 1997). Rainforest taxa typically exhibit high ratios of stem length to stem biomass (specific stem length – SSL), which serve to increase height and the likelihood of greater light capture (Poorter 1999).

These considerations of plant growth variables and biomass allocation generate a number of interesting questions, including what drives intra- and interspecific variation in RGR and biomass allocation and what are the potential ecological advantages to a species in its patterns of RGR and biomass allocation? The broad aim of this study was to investigate intra- and interspecific variation in growth variables and the importance of such variation in regard to drought resistance. This chapter presents the results of an investigation of the intra- and interspecific variation in seed mass, RGR and related growth variables of the four study species of *Pittosporum*, and the relationships between these variables and climatic variables for each species.

The specific objectives of this study were to:

- investigate intra- and interspecific variation in seed biology, growth variables and patterns of biomass allocation among these species;
- determine whether links between the life history traits of these species and certain bioclimatic variables may confer increased drought resistance.

METHODS

The seed of naturally occurring populations of *P. bicolor*, *P. revolutum*, *P. undulatum* and *P. angustifolium* were collected as previously described (Chapter 4). Populations were selected from a range of sites differing in aspects of climate and/or soil nutrient status, across the distribution of each species (Table 6.1).

Mean seed mass was determined from one hundred oven-dried (70°C for 48 h) seeds from each population of each species. This was used as Weight 1 (W1) in all subsequent growth analyses. As species vary widely in their germination biology, in order to obtain similarly aged seedlings, seed dormancy and germination characteristics were first established (as described in Chapter 5) and germination was then staggered so as to obtain evenly-aged seedling cohorts. Seed was sown onto seed-raising mixture on a propagating bed. Ten days after germination, 10 seedlings of each provenance of each species (except for *P. bicolor*, for which there were 5 seedlings of each population) were planted out into individual polythene propagation pots (10 cm square, 25 cm deep) containing Debco[®] potting mixture. This container size was used to minimize the likelihood of restricting root elongation. Seedlings were randomly arranged in a glasshouse, rotated every three days to minimize any effects of environmental variation and top-watered once per week with a nutrient solution of Aquasol[®].

Plants were harvested 20 days after planting by cutting stems at ground level. This time period was decided upon for three reasons: (i) it allowed sufficient time for seedlings to acclimate to the container and glasshouse environment before measurements were taken; (ii) as rates of plant growth tend to be exponential, this life history stage is considered optimal for intra- and interspecific comparisons of RGR (Grime and Hunt 1975; Cornelissen *et al.* 1996; Hunt and Cornelissen 1997a) and avoids problems in establishing mean RGR of older seedlings due to ontogenetic drift (Walters *et al.* 1993); (iii) for woody perennials, the most meaningful measure of SRL for a seedling's root system is obtained in the early stages of growth, before the development of significant secondary thickening (Wright and Westoby 1999). Seedlings were harvested over a period of 10 hours. For the duration of the growth trial, mean glasshouse temperature was 23.4°C, with a mean minimum of 17.8°C and a mean maximum of 29.1°C.

top leaf (crown height). Seedling leaves were removed and allowed to saturate by wrapping them in wet tissue paper, after which they were sealed in a polythene bag and stored at 5°C for 12 hours. Before being weighed, the surfaces of saturated leaves were patted dry with tissue paper. The total leaf area for each seedling was then measured using image analysis (BioscanTM Image Analysis, Monash University).

Seedling root systems were separated from the soil matrix by immersion in a basin of tap water, after which the roots were rinsed with distilled water to remove remaining soil particles. Root systems were straightened (but not stretched), and the numbers of primary and secondary roots were counted and their lengths measured with a ruler. Following completion of wet weight, leaf area and length measurements, all leaves, stems and roots were placed into paper bags and dried in the two-stage heat-drying process described previously (Chiariello *et al.* 1989), after which the components were reweighed. Plant growth attributes (Table 6.2) for seedling populations of each species were then derived from the primary data. The calculation of NAR, which is a measure of the efficiency with which the photosynthetic machinery produces biomass, is considered to be valid only when leaf area and plant dry mass are linearly related (Hunt 1978). Linear regressions of these variables satisfied this condition for populations of all species except *P. angustifolium* (Table 6.3).

Statistical Analyses

Several plant growth variables, including seed mass and plant dry mass variables were log_e -transformed, in order to overcome problems associated with non-normality of dry mass distributions and to reduce the influence of outliers. Nested ANOVAs were used to determine variation in seedling growth variables among species, and among populations within species. Pairwise comparisons were carried out using Tukey's tests to determine significant differences among variable means of species and populations. Among species, relationships among seedling growth and climate variables were analyzed by Pearson correlation and linear regression. No corrections were made for multiple comparisons, following the reasoning of Stewart-Oaten (1995). For all hypothesis tests, the critical value used was $\alpha = 0.05$. Principal components analysis (PCA) was carried to summarize the major axes of variation in growth and seed mass variables. All statistical analyses were carried out using SYSTAT® Version 9.0 (SPSS Inc. 1999).

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RESULTS

Variation in growth and biomass allocation within species

Within *P. angustifolium*, seedlings from the Bell population had significantly higher values of seed mass, final mass, RGR, NAR, root mass ratio and root:shoot ratio, but significantly lower SLA, LAR, specific root length, specific stem length and stem mass ratio than those from Wyperfeld (Table 6.4). Although the populations did not differ significantly in primary root length, secondary roots of Bell seedlings were significantly longer than those of Wyperfeld seedlings (Fig. 6.1a). Ratios of secondary to primary root length were 2.8 and 1.4 for seedlings from Bell and Wyperfeld respectively.

There were also significant differences in most growth variables among the populations of *P. revolutum* (Table 6.4). Populations of this species were characterized by comparatively low values of RGR, with the Brisbane F.P. population exhibiting negative growth during first 30 days following germination (Table 6.4). There was a greater than five-fold difference in final mass among the three populations (Table 6.4). Of the growth variables, RGR was the highest contributor to the variation in the final mass of seedlings. Among populations of *P. revolutum*, there was a trend for slightly higher biomass allocation to roots than leaves, except for seedlings from Brisbane F.P., which had a significantly higher mean allocation to leaves and a concomitant reduction in allocation to root biomass than the other two populations (Table 6.4). The primary and secondary roots of Brisbane F.P. seedlings were significantly shorter than those of the other two populations (Fig. 6.1b). Ratios of secondary to primary root length were 9.2 (Atherton), 4.0 (Brisbane F.P.) and 8.6 (Mallacoota).

Among seedling populations of *P. undulatum*, there were significant differences in almost all seed and seedling growth variables (Table 6.4). Bunya Mountains seedlings had the lowest final mass, significantly lower RGR and SLA, but higher SSL and heavier seed than that of the other two populations (Table 6.4). Mallacoota and Myall Lakes seedling populations differed significantly in primary root length (Fig. 6.1c). Myall Lakes seedlings had significantly longer secondary roots than the other two populations (Fig. 6.1c). Ratios of secondary to primary root length were 1.9 (Bunya Mountains), 4.9 (Myall Lakes) and 1.7 (Mallacoota). There were few significant differences in growth and seed mass variables among populations of *P. bicolor*, possibly a result of the smaller sample size and broad variation in variables among seedlings of each population. The variables LAR, SLA and specific stem length differed significantly among populations of this species, with the highest specific stem length recorded for Brown Mountain seedlings (Table 6.4). Brown Mountain seedlings also exhibited the lowest RGR, NAR, root mass ratio and final seedling mass of the three populations (Table 6.4). Dandenong Ranges seed was significantly lighter than that of the other two populations (Table 6.4). Populations did not vary significantly in primary or secondary root length (Fig. 6.1d). Ratios of secondary to primary root length were 4.1 (Dandenong Ranges), 2.3 (Brown Mountain) and 3.2 (Mount Worth).

Comparison of growth characteristics among species

The considerable intraspecific variation in most variables meant that patterns of the relationships between RGR and other growth and biomass variables were difficult to discern (Fig. 6.2). The negative RGR for Brisbane F.P. seedlings of *P. revolutum* was the only one recorded for any populations of these species. Species varied considerably in seed and seedling growth variables, with significant differences among them for all variables except LAR (Figs. 6.3, 6.4). There was a 6-fold difference in RGR among the species, from 8.1 mg gm⁻¹ day⁻¹ (*P. revolutum*) to 51.9 mg gm⁻¹ day⁻¹ (*P. undulatum*) (Fig. 6.3). There was no significant difference in RGR between *P. angustifolium* and *P. bicolor* (Fig. 6.3).

The variables most strongly correlated with RGR were NAR and LAR, although neither correlation was significant (Table 6.5). The population of each species with the highest NAR had the lowest SLA and SRL but highest root biomass allocation (RMR) and root:shoot ratio, and for three out of four species, the highest RGR (Table 6.4). There were significant differences among species in final seedling mass, with *P. angustifolium* seedlings having a significantly higher mean final mass than both *P. undulatum* and *P. bicolor* seedlings (Fig. 6.4). Of the leaf variables, the leaf mass ratios of rainforest or open forest seedlings (*P. revolutum*, *P. undulatum*, *P. bicolor*) were considerably higher than those of *P. angustifolium* (Fig. 6.3). Conversely, *P. angustifolium* seedlings had

significantly higher values of RMR and root:shoot ratio than the other three species (Fig. 6.4). There were negative correlations between NAR and stem mass ratio and between LMR and root:shoot ratio (Table 6.5).

Of the root variables, there was a twofold difference in SRL among these species, from 29.5 (*P. angustifolium*) to 59.6 (*P. bicolor*) mm mg⁻¹ (Fig. 6.4). SRL was negatively correlated with final seedling mass (Table 6.5). Primary root growth varied from approximately 8 mm day⁻¹ for populations of *P. angustifolium* and *P. undulatum*, down to 1.5 mm day ⁻¹ for the Brisbane F.P. population of *P. revolutum*. There was a significant difference in mean length of primary root among species, with *P. angustifolium* and *P. undulatum* higher than *P. revolutum* and *P. bicolor* (Fig. 6.5). *P. undulatum* had significantly longer secondary root length than *P. bicolor* (Fig. 6.5). For co-occurring populations of *P. undulatum* and *P. revolutum*, *P. undulatum* seedlings had significantly higher RGR (F = 34.6, P < 0.001), primary root length (F = 82.1, P = 0.004) and specific root length (F = 6.1, P = 0.024), than those of *P. revolutum*.

In relation to climate variables of the seed source, seed mass was positively correlated with precipitation seasonality but negatively with radiation seasonality (Table 6.6). Final seedling mass was positively correlated with most temperature variables, in particular mean annual temperature and summer temperature, but negatively with precipitation variables, in particular with winter rainfall (Table 6.6). Net assimilation rate was negatively correlated with the maximum precipitation of the wettest period, and mean precipitation of both the wettest and warmest quarters (Table 6.6). Of the leaf variables, SLA was negatively correlated with mean annual precipitation, maximum precipitation of the wettest week and mean precipitation of the wettest quarter (Table 6.6). LMR was negatively correlated with temperature seasonality and stem mass ratio positively correlated with summer rainfall (Table 6.6).

Of the root variables, root:shoot ratio was positively correlated with temperature seasonality and annual temperature range, but negatively with annual mean moisture index. Root mass ratio was positively correlated with temperature seasonality. Specific root length was positively correlated with the maximum precipitation of the coldest week and precipitation of the coldest quarter, but negatively with mean annual temperature, the maximum temperature of the warmest week, summer temperature and

mean annual radiation (Table 6.6). The broad patterns of biomass allocation indicate negative correlations of LMR with temperature variables and positive correlations with precipitation variables (Table 6.6). The converse is apparent in regard to biomass allocation to roots, with positive correlations of root mass ratio and root:shoot ratio with a number of temperature variables but negative correlations with specific precipitation variables (Table 6.6).

The first three component axes of a PCA carried out on the growth and seed variables explained 83% of the variation among them (Table 6.7). Component 1 was positively correlated with the variables NAR, root mass ratio and final seedling mass, and negatively with leaf mass ratio and specific root length (Table 6.7). Component 2 was correlated with seed mass - increasing factor scores indicate decreasing values of this variable. Seedling SLA was the main component of the third axis (Table 6.7); increasing values of the third axis indicated increasing values of this variable. Although there is little segregation of species along Component 1, *P. revolutum* is segregated from the other three species along Component 2 (Fig. 6.6a). *P. bicolor* is largely segregated from the other three species along Component 3 (Fig. 6.6b).

A PCA of the climate variables of the four species (Chapter 2) showed Component 1 to be positively correlated with summer temperature, mean annual temperature and annual radiation and negatively with winter precipitation and the annual mean moisture index. There is a positive correlation between species seed mass and Climate Component 1 (r = 0.95, P = 0.047, using species means of populations: Fig. 6.7).

DISCUSSION

Variation in growth and biomass allocation within species

P. angustifolium

The lower RGR and NAR of *P. angustifolium* seedlings from Wyperfeld, compared with those of Bell seedlings, conforms to observed patterns of lower potential growth rates for species or ecotypes of species inhabiting nutrient limiting or otherwise unfavorable environments (Townsend and Roberts 1973; Ladiges and Ashton 1974; Pallardy 1981). The siliceous sands of the Big Desert, of which Wyperfeld N.P. forms part, are characteristically low in soil nutrients (Blackburn and Wright 1989) and are likely to be considerably less fertile than the black vertosols of the Darling Downs region, which supports the Bell population of this species. Furthermore, the mean annual precipitation of the Bell provenance is more than twice that of the Wyperfeld site. Selection for slower-growing ecotypes in more limiting environments may be strongly adaptive, and is common in widely distributed species (Wang et al. 1994; Johansson and Tuomela 1996). Alternatively, slow growth rate may result from selection for physiological traits related to drought resistance that have effects on net assimilation or patterns of biomass allocation.

The significantly lower values of SRL and higher ratio of secondary to primary root length of Bell seedlings, compared with those from Wyperfeld, suggests development of substantially thicker roots in Bell seedlings. This may reflect the greater availability of soil nutrients and moisture to Bell seedlings and/or a requirement by Wyperfeld seedlings to maximize the acquisition, per unit mass of root, of less available soil nutrients and water. These differences are consistent with patterns of biomass allocation of other taxa from nutrient-poor habitats, which had narrower roots and higher values of SRL than those from nutrient-rich habitats (Berendse and Elberse 1989; Fitter 1997), but may also may relate to the greater annual rainfall of the Bell site. Rapid root development during the seedling stage, resulting in higher SRL and potentially greater soil moisture uptake, would be of adaptive value in dry environments. Long root systems are characteristic of seedlings and adult plants inhabiting semi-arid, sand plain environments, where the water table lies at great depth below the soil surface (Weaver 1926; Salisbury 1952; Parker 1968; Crawley 1997).

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The significant difference in seed mass between these *P. angustifolium* populations is consistent with the suggestion that in unpredictable or highly heterogeneous environments, a high degree of phenotypic plasticity in seed mass may be of adaptive importance (Fenner 1987).

P. revolutum

Populations of *P. revolutum* exhibited considerable variation in seed mass and seedling growth and biomass variables. The comparatively low values of RGR may result from selection for traits that increase water conservation and decrease herbivory. For example, seedling leaves and branchlets of this species are characterized by dense rusty pubescence, which may restrict energy load, leaf temperature and transpiration, but which may also decrease photosynthetic capacity (Ehleringer 1980), resulting in comparatively lower rates of growth. Low RGR in seedlings of this species may also result from selection for traits that will increase tolerance to the shaded environments that this species typically inhabits. Low RGR is typical of shade-adapted species (Lambers and Poorter 1992) and commonly results from a low NAR i.e. a physiological mechanism, rather than a low LAR i.e. a morphological mechanism (Poorter 1989; Ryser and Wahl 2001).

The negative RGR for Brisbane F.P. seedlings is intriguing given the rarity of such behaviour among woody taxa (Swanborough and Westoby 1996), although a loss of plant dry mass, particularly during the first 20 days or so following germination, is not uncommon among herbaceous angiosperms (Hunt 1978). The loss in dry mass in these seedlings was most likely due to the expenditure of seedling resources in cell division and morphological development, prior to the ability of newly differentiated leaves to contribute to carbon assimilation. The significantly higher values of LAR, LMR and SSL, and significantly lower values of RMR, root:shoot ratio and root lengths of Brisbane F.P. seedlings, compared with other populations, suggests that seedlings of this population maximize biomass allocation to leaf tissue, possibly in response to a shaded environment, at the expense of biomass allocation to roots.

The high ratios of secondary to primary root length and low-moderate values of SRL common among populations of *P. revolutum* suggest the development of dense, fibrous but comparatively shallow root systems.

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P. undulatum

The association between RGR and final seedling mass for *P. undulatum* populations conforms with that in other woody species (Lambers and Poorter 1992), and together with the relationship between RGR and seed mass, suggest that for this species, RGR is more important than seed mass in determining seedling mass. Variation in SLA among the populations of *P. undulatum* may reflect selection for leaf morphologies that most suit the environment of the seed collection sites. This is supported to some extent by the similar values of SLA, LAR and LMR for co-occurring populations of *P. undulatum* and *P. revolutum*, in spite of considerable differences between them in other growth and life history traits.

P. bicolor

Differences in growth variables between the Victorian populations of *P. bicolor* on the one hand, and the Brown Mountain population on the other, may result from broad climatic and/or edaphic differences between them. The lower growth, assimilation and biomass variables of Brown Mountain seedlings, compared to those of the other two populations, may be related to the large differences in climate or light availability between Brown Mountain and the Victorian sites. As discussed previously, low growth rate is associated with shaded environments, and this trait may have been selected for in seedlings from Brown Mountain, the seed of which was sourced from a cool temperate rainforest with very low light availability.

Comparison of growth characteristics among species

The range in RGR among these *Pittosporum* species is considerably greater than that reported for less-closely related species (e.g. 3.3 in Poorter and Remkes 1990; 2.5 in Marañón and Grubb 1993). Broad intraspecific variation in RGR creates difficulties in detecting patterns of RGR among these species based on characteristics of their distributions and/or life form. Nevertheless, RGR values for all species are at the lower end of a scale of values derived for other Australian woody taxa from a range of habitats (Wright and Westoby 1999), suggesting that low rates of growth may be characteristic of *Pittosporum*. Low RGR may reflect selection for traits that suit the growth conditions of populations used in this study, all of which are limiting in at least one of

the factors of light, nutrients or water (Table 6.1). The lack of a significant difference in RGR between *P. angustifolium* and *P. bicolor*, the phylogenetically closest of the four species, may reflect phylogenetic constraint. Alternatively, if *P. angustifolium* evolved from a precursor of *P. bicolor*, then low growth rate may have been a pre-adaptation to its expansion into a sub-optimal environment, e.g. semi-arid and arid habitats. This is countered by the broad differences between these species in seed mass and patterns of specific root length and other biomass allocation variables (Fig. 6.8). However, similarities between these species in all of the leaf variables suggest a close relationship between RGR and leaf characteristics such as SLA, LAR and LMR, although this is not consistent among all species.

The higher RGR and NAR of Mallacoota seedlings of *P. undulatum*, compared to those of the co-occurring *P. revolutum*, suggests inherently lower rates of growth and assimilation in the latter species. This is supported by relatively low RGR values for other populations of *P. revolutum*, as well as by germination studies, in which seed of *P. undulatum* had significantly faster germination rates than that of *P. revolutum* at three out of four temperatures (Chapter 5). Furthermore, under non-limiting conditions, *P. undulatum* seedlings have significantly higher rates of transpiration than those of *P. revolutum* (Chapter 4), suggesting a greater intrinsic rate of photosynthesis in the former species, which would account for the observed differences in RGR. While stomatal behaviour may play only a small role in determining rates of photosynthesis within species (Jones 1998), it is a major determinant of interspecific differences in assimilation rate (Jones 1985).

The lack of a relationship between RGR and LMR among *Pittosporum* populations or species does not concord with Tilman's (1988) prediction that for species or genotypes with similar physiological variables, these variables will be positively correlated. However, negative correlations between RGR and LMR among closely-related species have been recorded elsewhere (Ryser and Wahl 2001). Given that much of the mass of thicker leaves may be structural rather than photosynthetic in nature, a better measure of photosynthetic capacity may be LAR rather than LMR. The negative correlation between LMR and root:shoot ratio is characteristic of other woody taxa and reinforces the tenet of trade-offs in biomass allocation between shoots and roots among species. However, this pattern between LMR and root:shoot ratio, together with the relationship

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of root:shoot ratio with both SLA and final seedling mass does not support the proposition that plants that allocate more biomass to roots will necessarily produce less overall biomass than those that invest proportionally more in shoot biomass (Poorter and Lambers 1991).

The importance of NAR as a determinant of RGR in these species, together with the lack of a strong relationship between RGR and SLA, does not conform to the usual pattern for woody taxa, for both northern hemisphere (Lambers and Poorter 1992; Cornelissen *et al.* 1996, 1998) and Australian taxa (Wright and Westoby 1999). Nevertheless, strong correlations between RGR and NAR have been previously reported (Poorter 1989; Brown 1997). Although NAR is considered to represent the 'physiological' component of RGR, it is a complex variable that is determined by rates of photosynthesis and respiration, and influenced by biomass allocation (Lambers *et al.* 1989). Thus, analyses of photosynthesis and respiration might provide a better understanding of variation in growth rate within and among these species.

The considerable variation in RGR and the positive relationships between RGR and both NAR and biomass allocation to roots are similar to patterns observed elsewhere, although for closely-related species, RGR is usually more strongly correlated with LAR than NAR (Poorter and Lambers 1991; Tilman 1991). Together, the relationships between these variables suggest that it may be physiological variation among these species, rather than biomass allocation, that is responsible for variation in potential RGR (Hunt and Cornelissen 1997b). In regard to phytogeography and soil moisture availability, there is little information on relationship between RGR and RMR, although Wright and Westoby (1999) suggested that the lack of a relationship between RMR and either site favourability or RGR might be the rule rather than the exception.

Differences in plant biomass may result from a number of plant variables including seed mass, germination speed or variation in RGR (van Andel and Biere 1989; Swanborough and Westoby 1996; Van Rijn *et al.* 2000). Although not significant, the positive trend of increasing seed mass with seedling mass is consistent with the results of other studies (Grime and Jeffery 1965; Fenner 1983; Stanton 1984; Wulff 1986; Winn 1988), and may have important ecological implications. For example, a higher seedling mass may result in an increased ability to compete for nutrients, water and light, thereby

facilitating a higher probability of successful seedling establishment and longer-term survival (Silvertown 1982), as has been reported for a number of species (Fröborg and Eriksson 1997; Eriksson 1999). These results support the hypothesis that largeseededness is competitively advantageous (Harper *et al.* 1970; Fenner 1980) in open, arid and semi-arid communities (Leishman and Westoby 1994; Caddick and Linder 2002), as well more shaded tropical and temperate vegetation types (Foster and Janson 1985; Foster 1986).

For species such as *P. angustifolium* that have higher root mass ratio than stem mass ratio, much of the root biomass appears to be allocated to development of a taproot, at the expense of more shallow lateral or secondary roots. This pattern of biomass allocation has been reported for other semi-arid and arid zone taxa (Anderson 1982; Enright and Lamont 1992). The negative correlation between NAR and stem mass ratio is consistent with that observed for individual species and reinforces the importance of the fine balance between biomass allocation and assimilatory capacity.

The negative correlation between SLA and annual rainfall is paradoxical, as species from low rainfall environments generally have smaller leaves and lower SLA (Cunningham *et al.* 1999) than those from higher rainfall sites. Smaller leaves are, in general, subject to lower temperature loading and transpirational losses (Begg 1980). Moreover, high values of LAR and SLA are considered to be advantageous in low-light environments such as tropical rainforests, where light capture is of primary importance (Poorter 1999), or in optimal environments where high SLA and RGR are selected to maximize competitiveness (Monteith 1972, 1977).

One explanation for the observed relationship between SLA and mean annual rainfall might be that higher SLA in more xeric taxa is linked during the seedling stage to selection for growth and biomass attributes that will enable rapid accumulation of plant biomass, thereby allowing the development of deeper roots that will enhance the likelihood of longer-term survival and establishment. During periods that facilitate germination and seedling establishment in xerophytes, soil moisture is likely to be nonlimiting. The maximization of carbon acquisition by means of increased SLA may facilitate the development of longer roots, which would increase the likelihood of seedling survival during the first summer following germination. However, the sclerophytic nature of adult leaves of this species indicates that at some stage, perhaps prior to the first period of water stress, seedlings must begin to exhibit decreases in SLA.

The positive correlation between specific root length and precipitation variables (in particular winter precipitation) among these species is consistent with the results for studies of other woody Australian taxa, with lower values of specific root length among species in environments subject to limited soil water and/or nutrient availability (Wright and Westoby 1999; Nicotra et al. 2002). Whilst this is perhaps unexpected, it may be due to the tendency of species in higher rainfall environments to produce a greater number of growing tips than those in low rainfall environments (Nicotra et al. 2002), although similar increases in SRL could also be achieved by fewer, very long roots. As root fineness and density, the variables that comprise SRL, can have potential nullifying effects in response to different environmental conditions (Ryser 1998), it may be difficult to elucidate the ecological significance of the interspecific variation in SRL. Lower overall values of SRL for P. angustifolium could therefore be a product of lower tissue density relative to the other species, rather than the fineness of their root systems. The converse of this, i.e. high root tissue density, may account for the root system variables of *P. bicolor* seedlings, which demonstrated the lowest values of secondary root development, but among the highest SRL values.

As an indicator of root architecture, Wright and Westoby (1999) suggested that SRL might be considered to be analogous to SLA for leaves, as it similarly reflects the potential for resource acquisition per unit mass, and is affected by both tissue density and root diameter. Among these species, whilst SLA is positively correlated with temperature variables and negatively with precipitation variables, specific root length is conversely correlated. These patterns suggest that under non-limiting growth conditions, the seedlings of species inhabiting the dry end of a precipitation gradient exhibit higher SLA and lower specific root length, with those at the wetter end displaying low SLA and high specific root length.

The negative correlation between root:shoot ratio and moisture index suggests that along a gradient of increasing precipitation, there may be a shift in strategy from belowto above-ground maximization of resource acquisition (Fig. 6.8). These results are

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consistent with the pattern for other woody species distributed across moisture gradients (Zimmer and Grose 1958; Monk 1966; Whittaker 1975; Breymeyer 1980; Kummerow 1980; Bloom *et al.* 1985), although exceptions may occur due to life history traits or site-specific environmental factors (e.g. light availability). There may be considerable adaptive value in the allocation by arid zone taxa of proportionately more biomass to non-structural, absorptive tissues such as roots.

The flip side of the relationship between root:shoot ratio and moisture availability is the negative, although not statistically significant, relationship between RGR and stem mass ratio, which suggests a tendency for slow-growing species to allocate a higher proportion of biomass to structural rather than non-structural tissue (Wright and Westoby 1999). This may be related to the relationship between stem mass ratio and summer rainfall, as sites with high soil moisture availability during the growing season are strongly associated with high productivity and competition for light, and the value of increased biomass allocation to the shoot may be considerable (Villar *et al.* 1998).

The consistent patterns in biomass allocation among these species, with leaf biomass negatively correlated with temperature variables and positively with precipitation variables, and root biomass and root:shoot ratio positively correlated with temperature and negatively with precipitation variables, accord with expectations of optimal foraging theory for essential resources (Bloom *et al.* 1985; Tilman 1988). The broad tenet of this theory is that in any growth-limiting environment, there will be increased biomass allocation to that part of the plant which draws most upon the growth-limiting component of the environment (Hunt and Lloyd 1987). Thus, in shaded communities, typical of high rainfall areas, plants become more leafy while in arid or nutrient-limited environments, plants allocate more biomass to roots.

The positive correlations between seed mass and both precipitation seasonality and the temperature variables of Component 1 of the climate PCA, together with the negative correlation between seed mass and radiation seasonality, accord with the general pattern observed among other taxa, which is for seed mass to decrease with increasing latitude (Lord *et a*! 1997; Baker 1972; Rockwood 1985). Several causal mechanisms have been proposed to account for this pattern, including the relationships between seed mass and both shade tolerance and vertebrate dispersal syndromes and the higher metabolic costs,

in tropical systems, associated with seed germination and seedling establishment (Lord et al. 1997).

It should be acknowledged that whilst these plant growth characteristics may be representative of seedlings 30 days post-germination, growing in a glasshouse under non-limiting conditions of moisture and nutrient availability, their actual growth under normal field conditions is likely to be substantially different. Such a consideration may be significant if glasshouse temperature and light regimes better approximated the field conditions of one provenance, at the expense of other populations. For example, the temperature regime may have had a negative affect on the growth rate of cool provenance populations of these species, although this is unlikely given that species from similar environments often exhibit higher growth rates in the glasshouse than in the field (Cunningham and Read 2003). This may be of particular importance given the differential effects of growth temperature on the relationships between RGR and both SLA and NAR (Loveys *et al.* 2002).

Furthermore, although the seedling stage is critical in the successful establishment and longer-term survival of a plant, it represents only a short phase in its potential life span, and therefore caution must be exercised in modeling growth rate characteristics of mature plants based upon their seedling variables. It is highly likely that both intra- and interspecifically, the nutrient and moisture requirements of plants will change as they mature, particularly under the influence of varying field conditions of light, soil nutrient and moisture availability and from processes such as competition and herbivory. Given these qualifications, although mean RGR values for woody species decline as plants mature, growth rate rankings still broadly reflect their longer-term growth and life history characteristics (Cornelissen *et al.* 1998). Thus, trends in allocation may be better viewed as adaptively plastic responses to resource gradients, rather than as fixed species attributes that determine growth rates (Gleeson and Tilman 1994). This must be borne in mind whenever comparisons of growth rate and biomass allocation are made, whether at intraspecific and/or interspecific levels, or of plant groups across environmental gradients.

Finally, differences in leaf, stem and root anatomy and the potentially important role of mycorrhizae were not investigated in this study. The optimal provision of nutrients and

water during this growth trial may have made redundant the requirement for mycorrhizal fungi. However, for species with fine roots, expressed as high values of specific root length, mycorrhizae may be of particular importance, as thin fungal hyphae increase the volume of exploited soil with only a small increase in biomass (Ryser 1998). In the absence of knowledge of such interactions, care must be taken in deriving the potential ecological significance of trends in growth variables, both within and among species.

In summary, the results of this study indicate that growth variables such as RGR may vary widely among populations of a single species, perhaps even more widely than single populations of congeneric species selected from the same habitat or from sites along environmental or latitudinal gradients. Furthermore, species with large natural distributions appear to possess greater genetic diversity than those with more limited ranges (Wright 1976; Mantovan 2002). Such findings reinforce the importance of accounting for within-species variation in consideration of the adaptive significance of growth rat.) variables (Burdon and Harper 1980). Under uniform growth conditions, the expression of such variation may reflect local selection for morphological and/or physiological traits that will optimize the survivorship and establishment of seedlings subject to local conditions of climatic and soil nutrient status.

Traits that may be adaptive within and among these species of *Pittosporum* include low rates of RGR in environments characterized by low availability of light, nutrients or water, an inverse relationship between biomass allocation to roots and soil moisture availability and the various relationships between seed mass and growth variables. An important finding of this study was that within and among these species of *Pittosporum*, correlations between growth rate and other variables are not consistent with patterns observed previously. i.e. for these species, RGK is more strongly correlated with physiological (NAR) rather than morphological (LAR, SLA) means of assimilation. This may have considerable resonance given that physiological behaviour is inherently linked with the water relations behaviour of these species, which as discussed previously may be less flexible to climatic change than those related to morphology or photosynthesis (Read *et al.* 1990).

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Species	Vecetation to a	Light	Soil Nutrient	Annual
Provenance		availability	status	rainfall
P. angustifolium				
Bell	Open Woodland	High	Moderate	Moderate
Wyperfeld N.P.	Woodland	High	Low	Low
P. undulatum				
Bunya Mountains	Subtropical Rainforest	Moderate	Moderate	Moderate
Myall Lakes	Coastal Woodland	High	Low	Moderate
Mallacoota	Wet Sclerophyll Forest	Moderate	Moderate	Moderate
P. revolutum				
Atherton	Tropical Rainforest	Low	High	High
Brisbane Forest Park	Sub-tropical Rainforest	Low	Moderate	Moderate
Mallacoota	Wet Sclerophyll Forest	Moderate	Moderate	Moderate
P. bicolor			······	
Dandenong Ranges	Moist Sclerophyll Forest	Moderate	Moderate	Moderate
Brown Mountain	Cool Temperate Rainforest	Low	High	High
Mount Worth	Wet Scierophyll Forest	Moderate	Moderate	Moderate

Table 6.1Broad categories of vegetation type, light availability, soil nutrient statusand annual rainfall for seed collection sites of the four *Pittosporum* species.

Note: The above sites are as per Table 5.1, except for Mt Worth (Lat: 38.3°S, Long: 146.1°E). Determinations of light availability are based upon values of percentage projected foliage cover for these vegetation communities (Specht 1970). Annual rainfall is based on long-term averages derived by BIOCLIM (Holder *et al.* 1999). Assessments of soil nutrient status are based upon Ashton (1981) and Northcote and Wright (1982).

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Abbreviation	Definition	Unit
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	Seed mass	mg
	Final dry weight	mg
RGR.	Relative growth rate: instantaneous rate of dry mass	mg mg ⁻¹ day ⁻¹
	increase per unit dry mass already present.	
	Calculated as: $RGR = (\ln W_2 - \ln W_1)/t$	
	where W_2 is the final seedling weight, W_1 is the initial	
	weight, and t is the period between harvests.	
LAR	Leaf area ratio: leaf area per unit plant dry mass	$mm^2 mg^{-1}$
	Calculated as: LAR = SLA x LMR	
		2 1
SLA	Specific leaf area: total area of leaves per unit dry mass of	mm* mg*
	leaves	
NAR	Net assimilation rate: instantaneous rate of dry mass	mg mm ⁻² day ⁻¹
	increase per unit leaf area per day.	
	Calculated as: $NAR = dW/(dt \times A)$	
	where dW is the change in weight, dt is the duration	
	between harvests, and A is the change in leaf area.	
LMR. SMR. RMR	Leaf, stem or root mass ratio; ratio of leaf, stem or root	-
2	dry mass to plant dry mass	
RSR	Root:shoot ratio. Ratio of root dry mass to shoot dry mass	-
		.1
SRL	Specific root length: root length per unit root dry mass	mm mg ⁻ '
SSL	Specific stem length: stem length per unit stem dry mass	mm mg ⁻¹

 Table 6.2
 Seed and seedling growth and biomass allocation variables used in the study.

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Species			<u>ה</u>
	Population	r	<i>P</i>
P. angustife	olium		
	Bell	0.37	0.291
	Wyperfeld	0.54	0.072
P. revolutu	m		
	Atherton	0.86	0.013
	Brisbane F.P.	0.75	0.012
	Mallacoota	0.78	0.013
P. undulati	(m	· · · · · · · · · · · · · · · · · · ·	
	Bunya Mountains	0.69	0.032
	Myali lakes	0.75	0.013
	Mallacoota	0.69	0.027
P. bicolor	· · · <u>· · · · · · · · · · · · · · · · </u>		
	Dandenong Ranges	0.96	0.044
	Brown Mountain	1.00	0.003
	Mount Worth	0.86	0.042

Table 6.3 Pearson correlation coefficients between leaf area and plant dryweight for seedling populations of four *Pittosporum* species.

Table 6.4 Seed mass and seedling growth variables of populations of four *Pittosporum* species grown under non-limiting conditions. Data are means with sem in brackets. For some variables, F and P values were calculated using log_c-transformed data. Within species, superscript alphabet letters denote non-significant differences between parameter means.

Species	Population	Seed mass (mg)	Final mass (mg)	RGR (mg g ⁻¹ day ⁻¹)	LAR (mm ² mg ⁻¹)	SLA (mm ² mg ⁻¹)	NAR (g m ⁻² day ⁻¹)	LMR	RMR	SMR	Root:shoot ratio	Specific root length (mm mg ⁻¹)	Specific stem length (mm mg ⁻¹)
	Bell	27.96 (0.42)	84.38 (5.28)	35.2 (2.02)	4.77 (0.46)	17.37 (1.19)	29.2 (2.48)	0.27ª (0.015)	0.57 (0.018)	0.16 (0.009)	1.34 (0.01)	19.12 (0.84)	3.24 (0.19)
P. angustifolium	Wyperfeld N.P.	16.57 (0.24)	32.58 (2.15)	22.6 (2.70)	8.58 (0.69)	28.74 (1.67)	10.7 (1.50)	0.30° (0.022)	0.46 (0.026)	0.23 (0.022)	0.92 (0.12)	38.07 (3.85)	5.45 (0.36)
	F	544.9	93.7	19.9	19.1	28.2	105.6	1.2	9.8	759.0	7.0	19.4	26.0
	P	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.284	0.005	0.012	0.016	< 0.001	< 0.001
	Atherton	32,79 (0.96)	74.94 (5.82)	24.9 ^s (2.41)	4.31 (0.19)	13.46 (1.17)	25.1* (2.60)	0.33 ^b (0.016)	0.42 ^a (0.018)	0.25 ^{ab} (0.023)	0.75° (0.06)	22.21 (1.96)	2.28 (0.12)
P. revolutum	Brisbane F.P.	23.94 ^a (0.76)	13.96 (1.17)	-19.2 (3.02)	9.34 (0.60)	18.16ª (1.04)	-14.2 (2.53)	0.51 (0.014)	0.26 (0.023)	0.23* (0.017)	0.36 (0.05)	64.60 (5.47)	7.12 (0.65)
	Mallacoota	23.46ª (0.96)	48.64 (5.38)	21.3* (3.76)	6.44 (0.52)	19.62ª (1.03)	16.1* (3.66)	0.32 ^b (0.018)	0.39 ^a (0.019)	0.28 ^b (0.012)	0.67* (0.06)	32.66 (2.86)	3.55 (0.28)
	F	34.3	38. 9	60.7	18.4	9.2	43.3	40.4	15.1	2.4	13.2	24.3	29 .1
	P	< 0.001	< 0.001	< 0.001	< 0.001	0.001	< 0.001	< 0.001	< 0.001	0.112	< 0.001	< 0.001	< 0.001
	Bunya Mountains	7.85 (0.18)	28.08 ^a (1.23)	43.1 (1.56)	7.29 ^a (0.28)	17.95 (0.72)	17.6 ^b (0.84)	0.41° (0.008)	0.41 ^b (0.008)	0.19° (0.011)	0.69 ^b (0.03)	50.92ª (3.02)	4.86 (0.14)
P. undulatum	Myali Lakes	6.59 ^b (0.34)	43.62 ^b (2.19)	61.6 (1.80)	8.64 ^b (0.35)	21.45° (0.88)	19.7 ⁶ (1.00)	0.40° (0.013)	0.37 (0.011)	0.22° (0.016)	0.60 (0.03)	51.43 ^a (1.73)	3.59 (0.08)
	Mallacoota	7.44 ^b (0.20)	35.89 ^{4b} (3.54)	51.0 (3.11)	7.69 ^{ab} (0.44)	21.38° (1.26)	19.9 ^b (2.21)	0.36 (0.008)	0.43 ^b (0.015)	0.21° (0.010)	0.78 ^b (0.06)	42.09 (2.00)	4.40 (0.26)
	F	6.6	8.0	20.5	3.0	4.2	0.7	5.8	5.8	2.0	4.7	4.3	13.7
	Р	0.002	0.002	< 0.001	[.] 0.067	0.025	0.498	0.008	0.008	0.158	0.018	0.025	< 0.001
P. bicolor	Dandenong Ranges	4.26 (0.14)	12.53 ^{od} (4.67)	31.2 ^{bc} (12.6)	6.96° (0.39)	20.63 (0.71)	12.3 ^{cd} (4.89)	0.34 ^d (0.036)	0.45° (0.055)	0.22 ^d (0.065)	0.84 ^c (0.19)	63.06 ^b (5.95)	6.13 (0.50)
	Mount Worth	6.70° (0.18)	18.80 ^d (1.58)	32.9° (2.87)	5.00 (0.15)	14.45 (0.77)	19.4 ^d (1.68)	0.35 ^d (0.022)	0.45° (0.026)	0.20 ^d (0.018)	0.84° (0.09)	54.93 ^b (6.32)	4.72 (0.44)
	Brown Mountain	6.29° (0.16)	10.60° (3.17)	14.5 ⁶ (9.00)	6.74° (0.18)	17.66 (0.83)	9.4° (4.09)	0.38 ^d (0.012)	0.38° (0.046)	0.24 ^d (0.049)	0.64° (0.12)	62.74 ^b (6.39)	7.69 (0.99)
	F	65.5	2.5	2.2	7.5	14.3	4.2	0.9	1.1	0.3	0.9	0.6	5.2
	Р	< 0.001	0.140	0.168	0.012	0.002	0.051	0.428	0.388	0.767	0.453	0.593	0.032

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 Table 6.5
 Pearson correlation matrix of growth and biomass variables of the species. Correlations with a coefficient >0.96 were significant and are in bold font.

Variable	Seed mass Fina	al mass	RGR	SLA	LAR	ŅAR	LMR	SMR	RMR	Root:shoot ratic r	Specific oot length	Specific stem length
Seed mass	-											
Final mass	0.80	-										
RGR	-0.70 -6	0.15	-									
SLA	0.11 (0.64	0.50									
LAR	-0.24 (0.20	0.73	0.29	-							
NAR	-0.36 (0.24	0.82	0.89	0.44							
LMR	-0.26 -0	0.46	0.02	-0.74	0.42	-0.54	-					
SMR	0.46 -(0.08	-0.78	-0.82	-0.26	-0.97	0.60					
RMR	0.01 (0.36	0.29	0.85	-0.20	0.77	-0.95	-0.82	-			
ratio	0.14 (0.45	0.17	0.85	-0.25	0.70	-0.98	-0.74	0.99			
length	-0.81 -().99	0.19	-0.66	-0.09	-0.25	0.56	0.11	-0.44	-0.54	•	
length	-0.50 -0).85	-0.23	-0.57	-0.68	-0.34	0.05	0.12	-0.08	-0.13	0.77	

Climate variable	Seed mass	Final mass	RGR	LAR	SLA	NAR	LMR	SMR	RMR	Root:shoot ratio	Specific root length	Specific stem length
Mean annual temperature	0.91	0.98	-0.35	0.06	0.48	0.04	-0.41	0.11	0.25	0.36	-0.98	-0.77
Temperature seasonality	0.29	0.57	0.08	-0.25	0.85	0.64	-0.98	-0.66	0.96	0.99	-0.66	-0.23
Maximum temp. warmest week	0.70	0.93	-0.11	-0.02	0.79	0.41	-0.75	-0.31	0.66	0.74	-0.96	-0.65
Minimum temp. coldest week	0.82	0.72	-0.41	0.28	-0.03	-0.37	0.24	0.56	-0.39	-0.29	-0.65	-0.74
Annual temperature range	0.36	0.67	0.09	-0.17	0.88	0.64	-0.95	-0.63	0.93	0.97	-0.74	-0.35
Mean temp. wettest quarter	0.95	0.94	-0.44	0.03	0.35	-0.10	-0.30	0.25	0.12	0.23	-0.93	-0.74
Mean temp. driest quarter	0.14	0.70	0.59	0.58	0.94	0.84	-0.48	-0.70	0.62	0.61	-0.68	-0.79
Mean temp. warmest quarter	0.84	0.98	-0.26	0.01	0.63	0.20	-0.58	-0.07	0.44	0.54	-1.00	-0.73
Mean temp. coldest quarter	0.92	0.91	-0.40	0.16	0.27	-0.15	-0.13	0.33	-0.03	0.08	-0.88	-0.79
Mean annual precipitation	-0.29	-0.75	-0.35	-0.21	-0.98	-0.79	0.78	0.71	-0.84	-0.86	0.78	0.61
Max. precipitation wettest week	0.16	-0.40	-0.67	-0.32	-0.96	-0.97	0.70	0.94	-0.87	-0.83	0.43	0.40
Max. precipitation coldest week	-0.79	-0.97	0.18	-0.02	-0.70	-0.30	0.64	0.18	-0.53	-0.62	0.99	0.72
Precipitation seasonality	0.97	0.71	-0.79	-0.45	0.09	-0.38	-0.39	0.44	0.11	0.24	-0.75	-0.31
Mean precipitation wettest quarter	0.10	-0.46	-0.63	-0.30	-0.98	-0.96	0.72	0.92	-0.88	-0.84	0.49	0.43
Mean precipitation driest quarter	-0.63	-0.92	0.02	-0.04	-0.84	-0.49	0.76	0.39	-0.70	-0.76	0.95	0.67
Mean precipitation warm. quarter	0.41	-0.11	-0.72	-0.19	-0.83	-0.96	0.67	1.00	-0.87	-0.80	0.15	0.10
Mean precipitation cold. quarter	-0.72	-0.99	0.04	-0.22	-0.74	-0.37	0.54	0.22	-0.47	-0.55	0.99	0.84
Mean annual radiation	0.79	0.93	-0.25	-0.12	0.69	0.27	-0.72	-0.18	0.59	0.68	-0.97	-0.61
Radiation seasonality	-1.00	-0.85	0.65	0.21	-0.20	0.28	0.32	-0.39	-0.08	-0.21	0.86	0.54
Annual mean moisture index	0.95	0.91	-0.53	-0.20	0.40	-0.07	-0.51	0.17	0.30	-0.96	-0.94	-0.58
Moisture index seasonality	0.43	0.84	0.22	0.17	0.94	0.68	-0.77	-0.59	0.78	0.82	-0.87	-0.67

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Table 6.6Pearson correlation matrix of the growth, biomass allocation and climate variables of the species. Correlations with acoefficient > 0.96 were significant and are in bold font.

Growth variable	Component 1	Component 2	Component 3
RGR	0.544	0.582	0.040
SLA	-0.181	0.396	0.891
LAR	-0.748	0.208	0.527
NAR	0.911	0.229	-0.096
LMR	-0.851	-0.153	-0.231
RMR	0.868	0.383	0.029
SMR	-0.310	-0.573	0.387
SRL.	-0.866	0.377	-0.277
SSL	-0.813	0.252	-0.089
Root:Shoot Ratio	0.836	0.310	0.043
Seed Mass	0.383	-0.854	0.142
Final Seedling Mass	0.848	-0.399	0.137
Variance explained	52%	19%	12%
Total variance explaine	ed	83%	

Table 6.7 Component loadings of growth and seed weight variables for the firstthree component axes from PCA. The highest component loadings are in bold font.



Figure 6.1 Length cf primary (open columns) and combined secondary roots (shaded columns) in 1-month-old seedlings of (a) *P. angustifolium*, (b) *P. revolutum*, (c) *P. undulatum* and (d) *P. bicolor* (mean with sem). *F* and *P*-values from ANOVA were calculated using transformed data as per Table 5.4. Where these were significant (P < 0.05), shared alphabet letters above bars denote no significant difference between populations.



Figure 6.2 Relationship between RGR and other growth variables for populations of the four species. RGR vs. (a) SLA; (b) LAR; (c) NAR; (d) LMR; (e) specific root length; (f) In seed mass; (g) root mass ratio; (h) stem mass ratio; (i) specific stem length; (j) In final seedling mass; (k) root:shoot ratio. $\blacksquare - P$. angustifolium; $\square - P$. revolutum; $\blacktriangle - P$. undulatum; $\bigtriangleup - P$. bicolor.





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Figure 6.5 Length of (a) primary and (b) combined secondary seedling roots. Data are means of populations with sem. F- and P-values from ANOVA were calculated using transformed data as per Table 5.4. Where these were significant (P < 0.05), shared alphabet letters above bars denote no significant difference between species. ang - P. angustifolium; rev - P. revolutum; und - P. undulatum; bic - P. bicolor.

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Figure 6.7 Populations of four *Pittosporum* species in relation to Component 1 of a climatic variables PCA and seed mass. $\blacksquare -P.$ angustifolium; $\Box -P.$ bicolor; **▲**-*P*. revolutum; \triangle -*P*. undulatum.



Figure 6.8 Summary of the major growth and biomass allocation variables of the four species in relation to their purported cladistic positions as per Cayzer *et al.* (2000). The dashed line indicates that the position of *P. revolutum* is yet to be fully resolved.

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CHAPTER 7. FIELD REGENERATION OF P. ANGUSTIFOLIUM

Flowering plants can reproduce sexually by means of seeds, or asexually by means of vegetative organs. The advantages of sexual reproduction are those associated with the number of propagules, ease of dispersal, the ability to survive adverse conditions, and the adaptive value of genetic flexibility (Fenner 1985). The benefits of vegetative reproduction include the ability of clones to develop immediately and in some cases to grow rapidly, as well as increased longevity and perennation of the parent plant (Bond and Midgley 2001). Plant taxa from all evolutionary levels demonstrate a capacity for vegetative reproduction (Callaghan *et al.* 1992), forms of which include stolons and runners, lignotubers, epicormic shoots, rhizomes, tubers, bulbs, corms, column roots, crown roots, root suckers and adventitious buds and roots (Abrahamson 1980; Jenik 1994).

Variation and specialization of these basic reproductive strategies are numerous. They are linked inexorably with Harper's (1977) hypothesis that the growth forms of perennial plants represent a continuum with two extremes: (i) at one end by plants dominated in their evolution by selective pressures to attain height (and therefore to shade neighbours), leading to the woody habit. For this growth form, the physical integrity of the genet (as a discrete genetic individual) is usually maintained (which describes most trees); (ii) at the other end by plants able to expand laterally to garner limited water and nutrient reserves, leading equally strongly towards the lateral branching, nodal rooting or root suckering habit of clonal plants.

Reproductive success is fundamental to the establishment and persistence of all plant taxa, but is associated with considerable risk in arid and semi-arid environments, where rainfall events are spatially and temporally variable and which are characterized by prolonged drought. For perennial plants inhabiting such environments, the likelihood of recruitment and long-term survivorship by sexual reproduction appears to be very low (Crisp 1978; Wilson and Witkowski 1998). It is not surprising therefore, that regeneration from seed is a rarely observed event for the vast majority of Australian perennial arid zone species (Maconochie 1982; Harrington *et al.* 1984).

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Plants growing on sandy soils in arid and semi-arid habitats are subject to almost constant ablation and deflation of the soil surface (Maun and Lapierre 1984). The seeds of such species may therefore be quickly buried following dispersal or shedding from the parent tree. Burial may hasten, delay or prevent seed germination, increase temporal variation in the germination response of a seed cohort, or increase seed predation by soil fauna (Maun 1998). While the tolerance of species to different degrees of burial has been extensively studied in other environments (Maun and Lapierre 1984; Seliskar 1990, 1994; Sykes and Wilson 1990; Maun 1998), there are few comparable studies in arid and semi-arid systems (Brown 1997). In particular, there is a dearth of studies into the effects of seed burial depth on rates of water uptake, time to germination and seedling survivorship following germination. A better understanding of the population dynamics of arid and semi-arid taxa requires a more thorough understanding of their field dormancy and germination characteristics, the longevity of seeds in the soil, and the comparative germination success of seeds at different soil depths.

Given the low likelihood of successful sexual reproduction in harsh environments, the high frequency of vegetative reproduction among arid and semi-arid taxa is not surprising. Comparative analyses of trait-environment relationships have shown that clonal plants are more abundant in aquatic, alpine and arctic habitats, or in other environments that are resource-limiting (van Groenendael *et al.* 1996). However, many of these taxa utilize both sexual and vegetative means of reproduction, which suggests that subject to suitable environmental conditions, the benefit per investment may be the same for both processes (Abrahamson 1980). Life history strategies that increase the likelihood of survival in harsh or unpredictable habitats, particularly those with sustained periods of climate unfavourable for successful sexual reproduction, may therefore be of considerable adaptive significance.

Root suckering has been recorded in a diverse range of woody plant species belonging to a number of unrelated genera (Lacey and Johnston 1990), including many Australian taxa (Maconochie 1982). Suckering is common among species inhabiting deserts (Kaasas 1966), Mediterranean-type ecosystems (Abrahamson 1980) and semi-desert grasslands subject to frequent fire (Fatubarin 1987), enabling species to regain aboveground biomass more rapidly than those that regenerate solely from seed (Humphrey

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1974). Jenik (1994) suggested that the ramets of root suckering taxa behave as opportunistic organs, the functions of which can be classified into six broad groups: (a) provision of a means of vegetative reproduction; (b) colonization of unoccupied ground; (c) improved ability to compete within a plant community; (d) increasing a genet's chances of survival in marginal habitats; (e) replacement for old or damaged organs; and (f) repetition of the entire architectural model of the genet. Collectively, these functions contribute to two important life history strategies for a clonal population, which are increasing its fitness and the sequestering of space (Fagerstrom 1992).

The vast majority of Australian arid zone, root suckering species are shrub or subshrub taxa, with *P. angustifolium* being one of only four arid zone tree species capable of reproducing by this method (Maconochie 1982). Of the suckering species surveyed by Maconochie, 87% inhabited sand plain and sand dune communities, suggesting that there may be features of these systems that favour the evolution of suckering. These include: (i), the high soil porosity of such habitats, facilitating ease of root expansion and ramet growth; (ii), the availability of soil water in the lower profile, accessible to the taproots common amongst suckering taxa (Specht and Rayson 1957); and (iii), the relatively high incidence in such communities of fire, which suckering species are commonly able to survive. The capacity to survive fire enables suckering plants to rapidly access resources made available by it (Canham and Marks 1985). Root suckering may be stimulated by increases in temperature (Kormanik and Brown 1967), exposure of lateral surface roots following fire (Chesterfield and Parsons 1985) or from combinations of factors such as increased temperature and light (Schier *et al.* 1985).

The success of a species in a stressful habitat is determined by its reproduction and propagation (Bradford and Hsiao 1982). Species able to reproduce sexually and vegetatively may respond, via tradeoffs in the allocation of resources to each reproductive mode, to changing or difficult environmental conditions, thereby increasing their chances of growth, survival and reproduction (Silvertown *et al.* 1993). The ability of *P. angustifolium* to reproduce both sexually and vegetatively, together with the potentially adaptive nature of suckering for arid species, provides an opportunity to investigate the frequency of suckering among its genets and to gain an understanding of the reproductive success obtained from seed production. A better

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understanding of the biology of clonal plants, many of which are extensive and longlived, is considered to be crucial for accurately predicting the impacts of environmental change on the distribution of species and vegetation communities (Callaghan *et al.* 1992). In relation to this, Li *et al.* (1999) suggested that the various traits related to increasing sexual reproduction in time and space have evolved in concert with clonal reproduction in clonal woody species.

The broad aim of this chapter was to investigate the extent and comparative success of sexual and vegetative reproduction in *P. angustifolium*, and patterns in its allocation to each of these forms of reproduction in the field. Given time restraints involved in this work and that the field regeneration biology of at least one of the species (*P. undulatum*) has already been largely established (Gleadow and Ashton 1981; Gleadow and Rowan 1982, 1983), the decision was made to investigate these aspects in the most arid-adapted of the four species. This chapter is therefore an investigation of aspects of the population biology of *P. angustifolium*, including its germination biology, seedling growth and survivorship, and the nature, pattern, and extent of clonal growth, including the allocation to sexual and vegetative reproduction. The specific aims of this study were to:

1. investigate field germination behaviour and seedling survivorship;

 survey the incidence and extent of vegetative growth, and the nature of allocation to sexual and vegetative reproduction among mature genets.
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METHODS

Field germination

Undehisced, fully-mature capsules of *P. angustifolium* were collected during September 1994 from approximately 10 trees in Wyperfeld National Park. In this part of its range, *P. angustifolium* flowers from mid-winter to early summer (Costermans 1983; pers. obs.). Under normal climatic conditions, individuals may set abundant seed, which is consumed and dispersed by a range of avian frugivores. Although seeds may persist in their capsule for a period of time following dehiscence, *P. angustifolium* seedlings rarely occur in the open or in the vicinity of adult trees of this species, with the majority of genets occurring directly beneath overstorey trees such as *Eucalyptus camaldulensis* and *E. leucoxylon* (pers. obs.). The climate, soils and vegetation of the study area have been described previously (Chapter 2). Dehisced capsules, with their full complement of seeds, were weighed, after which the seeds were removed, cleaned of mucilage, weighed and stored at room temperature for 3 weeks.

In November 1994, thirty-five replicates of 10 seeds were buried at depths of 1, 2 and 5 cm in sandy-loam soil on a gentle east-facing slope in the south-east sector of Wyperfeld N.P. The burial trial was initiated in November, as this often approximates the time of capsule dehiscence on parent trees (pers. obs.), although mature capsules of this species may be present from late spring onwards. Holes were augured to a depth of 10 cm, and a 15 cm (diam) x 20 cm (high) nylon mesh basket (mesh 4 mm²) was placed into each and filled to the required depth with some of the removed soil. Seeds were carefully placed onto the soil in each basket and then buried to surface level with the remaining augered soil. Seed burial sites were independent and located 2 m apart, with random positioning of depth/harvest replicates. Control seeds were stored at room temperature.

Following the burial of seeds, the study site was inspected at three-monthly intervals for the emergence of germinants above the soil surface. At each time interval, five replicates of buried seeds at each depth were harvested. The mesh baskets containing soil, together with germinants and ungerminated seeds, were carefully removed from the surrounding soil and placed into plastic bags, which were sealed to prevent water

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loss. For each sample, the number of germinated seeds was recorded, and the hypocotyl and radicle lengths for each germinant were measured. Ungerminated seeds were removed from the soil column, weighed to determine their degree of field imbibition, placed in petri dishes on moistened filter paper and imbibed at a constant temperature of 20°C in a growth cabinet. Controls, comprising fifty randomly selected seeds, were weighed, divided into five replicate lots of 10 seeds, and incubated as described above. Control and ungerminated seeds were monitored on a daily basis for the first three weeks, and then two to three times per week for a further 6 weeks. Cumulative germination curves of treatments and controls were sigmoidally-shaped, so a three-parameter Gompertz-type regression model (equation in Chapter 5) (Ratkowsky 1990) was fitted to estimate T_{50} values (time to 50% germination). The final germination percentages for depth treatments and controls were also recorded.

In order to establish the soil water status at each harvest, soil samples were weighed, dried at 100°C for 48 hours, and then reweighed. From these data, mean percentage soil water content was calculated for each harvest. As soil samples disintegrated during retrieval of germinants and ungerminated seeds, it was not possible to establish percentage water content for different depths of the soil column.

Vegetative reproduction

An investigation of aspects of root suckering in *P. angustifolium* was carried out in Wyperfeld National Park during September 1994. Areas in the Park were traversed along north-south transects roughly 100 m in length, and when a *P. angustifolium* genet was located, its immediate area was surveyed for ramets. Nineteen stands of *P. angustifolium* were surveyed, based upon the presence of a mature plant, either as a solitary (nonsuckering) individual, or as a genet in association with a number of ramets. At each site, all ramets within a radius of 25 m from the genet were identified and the position of each mapped relative to the genet (see below). The height of the genet and ramets, and girth 50 cm above ground level was recorded, together with the distance and direction of the genet from the nearest overstorey tree. The genet and ramets in each stand were inspected for herbivory, the overall degree of which was estimated as zero, low (1-25% leaf area damaged), medium (26-50%), high (51-75%) or very high (76-100%).

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As *P. angustifolium* ramets do not appear to form individual root systems, at least early in their development (pers. obs.), the 'parent' plant (genet) in each stand was identified initially upon position, height and girth measurements, with subsequent verification by soil excavation. Soil excavation was also carried out to verify the attachment of ramets to the genet, to investigate evidence of ramet root system development, to determine the depth of lateral roots and to establish possible patterns of ramet development in terms of distance / height relationships, direction from the genet, or association with open space or timber debris. During soil excavations, care was exercised to minimize disturbance to the genet and ramets in each stand.

At each stand of *P. angustifolium*, inspections were made for seedlings, both beneath the genet and also in the general vicinity of the stand. Each genet was also inspected for flowers, flower buds and capsules, and where these were present, counts were made of each. The aspect, slope, soil type and vegetation at each site were also recorded to investigate their possible effects on the incidence and extent of suckering.

Statistical Analyses

Assumptions regarding the distribution of data were checked using boxplots. Final germination percentages of field-buried seeds were arcsin transformed to improve normality. Two factor ANOVA was carried out to determine the effects of duration and depth of burial on germination. Single factor ANOVA was carried out to determine the effects of seed burial depth upon seed weight, germination rate and seedling hypocotyl and radicle lengths. Pairwise comparisons were carried out using Tukey's tests to determine which parameter means were significantly different from one another. Relationships between selected variables were analyzed by Pearson correlation. No corrections were made for multiple comparisons, following the reasoning of Stewart-Oaten (1995). For all hypothesis tests, the critical value used was $\alpha = 0.05$. All statistical analyses were carried out using SYSTAT® Version 9.0 (SPSS Inc. 1999).

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RESULTS

Field germination

There was very little germination of *P. angustifolium* seeds after three months burial in the field, with only one recorded germinant, from a soil burial depth of 5 cm (Fig. 7.1). There was a significant effect of time, but not of burial depth, on the number of germinants (Fig. 7.1). Ungerminated seeds were intact and in an apparently healthy condition. After six months burial, most seeds at all depths had germinated, with seeds buried deeper in the soil (2 cm and 5 cm) germinating to slightly higher percentages than that buried at 1 cm (Fig. 7.1). However, the hypocotyls of germinants that had reached the soil surface appeared to have been cropped, possibly as a result of herbivory by native or introduced vertebrates. After nine months, no surviving seedlings were observed at the site, and soil samples harvested at that time contained neither ungerminated seeds nor germinants.

The mean weight of ungerminated seeds retrieved after 3 months burial was proportional to the burial depth, with seeds buried at all three depths significantly heavier than control seeds (Fig. 7.2a). Seeds buried at 5 cm was significantly heavier than that buried at 1 cm and 2 cm. The difference in weight between seeds buried at 1 cm and 2 cm was not significant (Fig. 7.2a). After six months, seeds buried at 5 cm were significantly lighter than control seed, as well as that buried at 2 cm (Fig. 7.2b). They were also significantly lighter than seeds retrieved from 5 cm after 3 months burial (F = 44.1, P = 0.006). After 6 months, seeds buried at 1 cm were not significantly heavier than control seeds (Fig. 7.2b). Furthermore, there was no significant change in the mean weight of seeds between 3 and 6 months burial at either 1 cm or 5 cm depth.

Ungerminated seeds collected after three months burial at all depths germinated significantly faster than control seeds (Fig. 7.3). Of the buried seed, that at 1 cm took significantly longer to reach 50% germination than that at 2 cm and 5 cm (Fig. 7.3). However, there was no significant difference in germination rate between seeds buried at 2 cm and 5 cm (Fig. 7.3). Germination rate was strongly correlated with seed burial depth (r = 0.99, P = 0.009). Final germination percentages were comparatively high, without significant differences in this variable among control or buried seeds (Fig. 7.4).

Soil water content was lowest at the start of the trial, had increased slightly by the 3month seed harvest in February, and peaked in May, 6 months after commencement of the study (Fig. 7.5). Between May and August there was a considerable decrease in the water content of the soil, to the extent that the moisture content of soil sampled in August was lower than that sampled in February (Fig. 7.5). Although soil water percentages were strongly correlated with the seasonal rainfall at this site (r = 0.98, P =0.022), seasonal rainfall total during the trial were atypical of the long-term seasonal averages for the site (Fig. 7.5).

Seed burial depth had a significant effect upon hypocotyl length, but not radicle length (Fig. 7.6). Furthermore, hypocotyl length was correlated with the depth of seed burial (r = 1.00, P = 0.036). This correlation must be viewed with caution, as it is derived from only three paired observations. There was a significant difference between hypocotyl and radicle length of seedlings emerging from seeds buried at both 1 cm and 2 cm (1 cm: F = 11.8, P = 0.009; 2 cm: F = 5.8, P = 0.041), but not for those emerging from 5 cm (Fig. 7.6).

Vegetative reproduction

Of the nineteen *P. angustifolium* genets surveyed, fifteen occurred in clonal stands with various numbers of ramets and no evidence of flowering or fruiting, three possessed ramets and were flowering or fruiting and five were solitary flowering or fruiting individuals (Table 7.1). The vast majority of genets were located beneath an overstorey eucalypt, and for individuals or stands where there was no overstorey tree, there was relictual evidence of one. No seedlings of *P. angustifolium* were recorded during the survey, either beneath genets or in the vicinity of the clonal stand. There was no clear pattern in the number, arrangement and distribution of ramets in relation to aspect, slope, soil type or the vegetation at each site, although they occurred less frequently in the direction of or beyond nearby large overstorey eucalypts (Fig. 7.7), often resulting in quite asymmetrical ramet distribution. Furthermore, ramets were often located close to fallen and decomposing overstorey trees or large branches.

In stands of *P. angustifolium* reproducing by only vegetative means, there was a positive correlation between genet height and the number of ramets per genet (Fig. 7.8), and a weak correlation between genet height and the mean distance of ramets from the

genet (r = 0.61, P = 0.046). However, correlations did not exist between mean ramet height and the number of ramets (Fig. 7.9) and between ramet height and its distance from the genet. Although there was no correlation between genet height and ramet height, of the height class frequencies, for genets < 2 m in height, ramets were all < 1.4 m tall. There was no apparent pattern of size cohorts among *P. angustifolium* stands, with ramets falling into a range of size class distributions (Fig. 7.10). Further, there was no apparent pattern of reproduction or ramet number with respect to aspect, slope, vegetation type or soil type at each site (Table 7.1).

The root systems of excavated P. angustifolium stands consisted of a primary taproot, usually in close proximity to the genet, and an extensive, horizontal network of highly branched lateral roots approximately 10-30 cm from the soil surface, from which secondary taproots arose at irregular intervals (Fig. 7.11). As taproots were not fully excavated, whether they branch lower in the soil is unknown. Excavated ramets of P. angustifolium did not appear to possess individual root systems, but were connected to each other and the genet by a wide network of laterals.

Of eight genets that were in flower or had capsules remaining from the previous fruiting season, only three had produced ramets (Table 7.1). The number of ramets for genets reproducing by only vegetative means was significantly higher than that of genets that were reproducing sexually (Fig. 7.12). However, the considerable variation in the mean number of ramets for sexually reproductive stands was predominantly due to only one site (Site 16), which had 62 ramets (Table 7.1). The incidence and extent of herbivory of ramets was quite variable, although there appeared to be a strong correlation between the number of ramets in a stand and degree of herbivory (Fig. 7.13).

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DISCUSSION

Field germination

Under suitable conditions of light and temperature, P. angustifolium seeds will usually begin to germinate within 14-20 days after commencement of imbibition (Chapter 5). Thus, lack of germination in the first three months of burial, followed by high germination percentages, at all depths between three and six months, may have been due to a number of factors. Based on previous trials, dormancy or an after-ripening requirement for seeds of this species can be largely discounted. It is more likely that an unsuitable environmental factor, such as insufficient soil moisture and/or unsuitable soi! temperature, was responsible for the lack of germination. Soil water content, which was low at the commencement of the trial and increased only slightly after three months, is very closely linked with germination in arid and semi-arid environments (Bewley and Black 1994; Kigel 1995). Furthermore, the likelihood of seedling survival is maximized when germination is restricted to periods when soil water potential is sufficiently high to ensure an adequate supply of water to satisfy seedling transpiration requirements (Evans and Etherington 1990). However, as P. angustifolium seeds have an optimum germination temperature in the range 15-20°C, with inhibition of germination but maintenance of viability at temperatures between 25-30°C (Chapter 5), high soil temperature over the summer period may have been responsible for the observed delay in germination. The subsequent germination response between three and six months following burial supports the suggestion that lack of soil moisture and/or high soil temperatures prevented germination during the first three months in the field.

The strong correlation between soil water content and rainfall for the month in which soil samples were taken demonstrates the seasonal nature of soil water availability at the study site. Seeds deposited on or near the soil surface would be exposed to soil water conditions in an almost continuous state of flux, with little upper-surface retention of moisture resulting from precipitation. Due to seepage, buried seeds should benefit from longer term access to soil moisture following such precipitation. This suggestion is supported by the weight of seeds after three months burial, as well as by higher field germination percentages of the most deeply buried seeds after both 3 and 6 months. The cause of the reduction in mean weight of the most-deeply buried seeds is uncertain. This is further compounded by the high soil water content at 6 months, presumably a reflection of the reasonable amount of precipitation that fell during that period. A possible explanation for the reduced seed weight is that prevailing precipitation between February and May fell as a series of light showers, sufficient to rehydrate the first 1-3 cm of the soil profile, without significantly affecting moisture levels deeper in the soil. Further study of the temporal patterns of soil moisture availability at different depths in the soil profile may shed light on this.

The correlation between germination rate and burial depth, together with the significantly higher germination rate and weight of seeds buried at 5 cm compared with control seeds and that buried at 1 cm, indicates the ability of deeply buried seeds to advance more rapidly toward germination, via greater moisture availability for imbibition, than that closer to the soil surface. Similar behaviour has been reported for species inhabiting arid and semi-arid environments elsewhere in the world (Fatubarin 1987; Bowers 1996). In coarse-grained desert soils, the balance between moisture relations, soil temperature and mechanical impedance means that positions deeper in the soil profile are more hospitable for germination (Koller and Hadas 1982). For species such as P. angustifolium that commonly occupy active sand dune and sand plain environments which may cause newly shed seeds to be buried by wind-blown sand, an ability to germinate from lower in the soil profile may be of considerable adaptive value. In contrast, the seeds of many other arid and semi-arid species germinate best on or just below the surface (Yates et al. 1995), where they are exposed to cycles of soil wetting and drying. For some of these species, progress made toward germination in wet periods is conserved during dry periods, a process described by Lush et al. (1984) as 'stop-go' germination. Whether seeds of P. angustifolium employ such a strategy is unknown, although Gibson and Bachelard (1986) suggested that this form of germination may be particularly advantageous for seeds on exposed seed-beds subject to intermittent drying.

The high percentage of seeds that had germinated by six months at all depths, together with a total lack of ungerminated seeds in samples collected after nine months, indicates that the bulk of seeds germinated between three and six months after burial. This supports the results of laboratory trials, in which seeds of *P. angustifolium* germinated quite rapidly under suitable conditions of moisture and temperature (Chapter 5).

Together, these observations suggest that *P. angustifolium* maintains a 'transient' soil seed bank, in which none of the seeds produced in a given year remain viable in the habitat for more than one year (Thompson and Grime 1979). As seeds of this species are non-dormant at maturity, they is likely to be in a transient seed bank for perhaps only 4-8 months and thus may not survive to a second season of seed set and germination. However, the long period of flowering and seed production of this species effectively extends seed dispersal and thus the potential for germination over many months. Together with the capacity for long distance dispersal - the 'spatial disperser' syndrome for avoidance of biotic stress during germination (Angevine and Chabot 1979) - this should increase the possibility of seedling survivorship, due to the increased likelihood of some seedlings encountering favourable environmental conditions.

There are several features that distinguish the seeds of transient soil seed banks, including comparatively large size and an ability to germinate over a wide range of temperatures and in both light and continuous darkness (Thompson and Grime 1979). These features, all of which pertain to seeds of *P. angustifolium*, are thought to facilitate rapid germination soon after dispersal. Transient soil seed banks are characteristic of other woody perennials occupying arid and semi-arid environments (Cowling *et al.* 1987; Yates *et al.* 1995; Adams 1999), including mallee communities (Barbour and Lange 1967). The incidence of very low quantities of soil-stored seed among resprouting species has been noted for a number of semi-arid taxa (Hodgkinson *et al.* 1980), which may be related to the comparative efficiencies of sexual and vegetative reproduction (Hodgkinson and Griffin 1982).

While the results of this study suggest soil seed bank transience for *P. angustifolium*, its observed field germination behaviour may be an artefact of the experimental design used in this study. This is because in general, the number of buried viable seeds of individual species, as well as the total for all species, declines more rapidly in disturbed than undisturbed soil (Roberts and Dawkins 1967; Roberts and Feast 1973), although these studies largely pertain to the longevity of annual seed in arable systems. It is possible that removal and replacement of the soil provided conditions, such as increased light availability, that facilitated germination by *P. angustifolium* seeds earlier or more rapidly than would otherwise have naturally occurred.

The differences in hypocotyl length of germinants from different soil depths may be related to the timing of germination, with seeds buried deeper in the soil having access to greater quantities of soil moisture, imbibing more rapidly, and consequently germinating earlier than seeds buried at more shallow depths. Although the lack of a significant difference in radicle length of seedlings at the three depths might appear to contradict this, it is possible that greater soil water availability at 5 cm precluded a requirement for rapid radicle elongation. The survival of species growing on arid zone sandy soils is dependent upon the maintenance of root elongation ahead of a descending soil drying front (Buckley 1982). The success of seedlings in such environments may be directly related to seed size, with larger seeds able to both generate rapid root growth and also facilitate shoot emergence from greater depths (Buckley 1982; Jurado and Westoby 1992a). Although there are few comparable field studies, the ability of *P. angustifolium* seeds to germinate and reach the soil surface from a depth of 5 cm may be a rare phenomenon among Australian arid and semi-arid woody taxa.

It is difficult to establish the precise timing of germination of seeds at the different burial depths without greater temporal resolution. However, as the first recorded germinant was from seeds buried at 5 cm, and the mean hypocotyl length for seedlings collected at six months was highest from seeds also buried at this depth, it is not unreasonable to suggest that seeds buried deepest in the soil germinated earlier than seed buried at 1 cm and 2 cm. The significant difference between hypocotyl and radicle length of germinants from depths of both 1 cm and 2 cm is not unexpected, given the requirement for such species to establish a primary taproot able to access deep soil water. However, for seedlings germinating from 5 cm, elongation of the hypocotyl at the expense of the radicle may be somewhat unusual. One explanation may be that in order to facilitate leaf development and thus be better equipped to generate resources required for radicle elongation, seedlings emerging from deeper in the soil may preferentially allocate biomass to the hypocotyl. In any case, an inability to reach the soil surface before the depletion of seed endosperm nullifies the benefits of access to greater soil water. If this is correct for seeds of P. angustifolium, it indicates an ability to utilize its seed reserves to maximize the chances of survivorship by trading off allocation to different developmental paths in the maturing seedling.

An increase in the biomass of above-ground components and a reduction in root:shoot ratios has been reported for buried seedlings compared to unburied or partially buried seedlings of a range of dune species (Seliskar 1990; Brown 1997), although other studies have been more equivocal (e.g. Sykes and Wilson 1990). Nevertheless, such behaviour at the incipient seedling stage suggests that a growth strategy of maximizing photosynthetic rates at the expense of root elongation may not be restricted to more mature life history stages of plants. This individual-based aspect of optimal partitioning theory is a refinement of the 'principal of allocation' proposed by Cody (1966), in which organisms with finite resources, in this particular case seed endosperm reserves, must allocate them between competing demands.

The lack of survivorship of *P. angustifolium* seedlings in the field may have been due to a number of factors. Evidence of physical shearing of seedling hypocotyls at six months suggests that herbivory by native (e.g. kangaroos) and/or exotic (e.g. rabbits) mammals, or possibly invertebrate species (e.g. Richmond 1995) caused the death of seedlings in this trial. Herbivory may be the principal cause of lack of short- to medium-term seedling survival of this species in the field, even when climatic conditions favour seed germination and establishment. Grazing by introduced and/or native mammals is regarded as the primary cause for lack of recruitment in a diverse range of Australian arid and semi-arid woody taxa (Tiver and Andrew 1997; Lange and Graham 1983), including *Callitris columellaris* (Johnston 1968), *Acacia burkittii* (Crisp and Lange 1976), *A. oswaldii* (Auld 1995), *A. aneura* (Crisp 1978), *A. melvillei* (Batty and Parsons 1992), *Eremophila leucophila* (Hacker 1984) and *Alectryon oleifolius* (Chesterfield and Parsons 1985; Wisniewski and Parsons 1986).

However, in field studies such as this one, determination of the exact cause of seedling death is notoriously difficult (Fenner 1985). The bulk of buried seeds germinated between February and May and precipitation records suggest that soil moisture in the months following germination was unlikely to have been limiting. However, as adverse conditions lasting only a few hours can be sufficient to cause seedling death (Thompson 1973), any short term drop in soil moisture during April or May, when seedlings were perhaps only 1-2 months old, may have been fatal. Furthermore, even in the absence of herbivores, seedlings may not have survived low soil moisture during the first summer

following germination, as has been noted for other arid and semi-arid taxa (Wellington and Noble 1985; Harrington 1991).

Vegetative reproduction

The high frequency of suckering among *P. angustifolium* genets suggests that it may be a normal component, at least in the area surveyed, of its life history. Although the spontaneous production of new stems is a common characteristic of root-suckering shrubs, it is much less frequent in tree taxa, with suckering mostly occurring only after damage or disturbance (Dei Tredici 2001). Thus, it is possible that climatic, edaphic or biotic factors may be triggers for the onset of root suckering in this species. Alternatively, the high frequency of root suckering may be related to the proximity of the survey area to the latitudinal limit of its distribution. The incidence of sprouting has been observed to increase considerably on sites near the limits of a species altitudinal or latitudinal range (Marr 1977; Koop 1987; Mitton and Grant 1996).

The correlation between genet height and the mean distance of ramets from it may reflect gradual root development and expansion over time. Due to the increased light availability and reduced competition for nutrients and water, newer (younger) ramets might be expected to arise at the periphery of clonal stands (Barnes 1966). However, assuming that ramet height is proportional to its age, ramet position appears to be based upon factors or processes other than simple lateral spread and competition for light, nutrients or water. Hutchings (1997) summarized the factors, some of which are potentially conflicting, that may determine the distance of new ramets from a genet. These include the minimization of competition between ramets and avoidance of competition with other plants, investment and metabolic costs of rhizomes (Eriksson and Jerling 1990), a ramet's ease in acquiring resources from the genet (Caraco and Kelly 1991) and the patchiness of the habitat and size of favourable and unfavourable sites (Hutchings and Bradbury 1986).

Given the nature of the environment and structure of the vegetation in these stands of P. angustifolium, light is not likely to be limiting anywhere within the stand, and in any case, as Salisbury (1942) noted, less light is required for vegetative growth than for flower and seed production. One explanation for the patchy distribution of ramets is that it is the end result of numerous ramet 'births' and 'deaths', with survivors subsequently attached to several unconnected root laterals, as has been reported for American aspens (Barnes 1966). An alternative explanation is that ramets are arising as a consequence of lateral roots simply taking the path of least soil resistance.

A third explanation for patchy distribution of *P. angustifolium* ramets may relate to habitat and resource heterogeneity. Many plants exhibit plasticity of root growth in response to nutrient heterogeneity (Crick and Grime 1987; Campbell and Grime 1994) and clonal growth should therefore be particularly advantageous in environments with patchily distributed soil moisture and nutrients (Harper 1985; de Kroon and Hutchings 1995; van Groenendael *et al.* 1996). Indeed, the preferential production of ramets in high-fertility sites, or in response to microgradients in nutrient or water availability, has been reported for a number of clonal species (Barnes 1966; Abrahamson *et al.* 1991; Hutchings and de Kroon 1994; Stuefer *et al.* 1996) - the 'foraging tactics' of clonal taxa as described by Sutherland and Stillman (1988). This strategy, Abrahamson *et al.* (1991) suggested, makes better use of heterogeneous nutrient resources and serves to increase the overall fitness of the genet. However, this explanation, if correct for *P. angustifolium*, would require ramets to possess their own root systems, which as discussed above has not been observed.

The lack of a relationship between ramet height and the number of ramets per genet and absence of any apparent trend in height class frequencies among stands together support the hypothesis that *P. angustifolium* ramets arise in response to patchily distributed resources. In this model, the distribution (and availability) of resources varies both in space and time, and sites with few available 'patches' will support comparatively few ramets. Ramet generation thus may not necessarily depend upon genet age, but rather resource availability. The lack of relationship between ramet height and the number per clonal stand also suggests that between-ramet competition plays only a minor role in stand dynamics, and that the resource acquisition is ramet- rather than genet determined, although without individual root systems, there must be a degree of competition between ramets for soil moisture and nutrients. In stands of *P. angustifolium*, ramets are often spaced wide-apart, and thus may not approach densities at which regulation by self thinning would occur, unlike the more dense packing of some herbaceous clonal taxa, which appear to regulate ramet numbers through correlated ramet production and

extinguishment (Lovett Doust 1981). It is possible that as only a small sample of genets from one population of *P. angustifolium* was surveyed, these results may not represent patterns within the broader population or species.

The close proximity of P. angustifolium genets to overstorey trees is not surprising, as seeds of this species are consumed and dispersed by a range of avian frugivores, which defecate the seeds while perching on the lower lateral branches of such trees. A very similar association between overstorey eucalypts and Pittosporum seedlings has also been noted for P. undulatum (Gleadow 1981), and is common among other arid taxa (Tester et al. 1987). In arid and semi-arid environments, these canopy trees may act as 'nurse trees' (McAuliffe 1984; Suzan et al. 1996; Tewksbury and Lloyd 2001), enhancing the conditions for seed germination and successful seedling establishment by the combined effects of lowering soil temperature and surface evaporative losses (Fulbright et al. 1995; Breshears et al. 1998). Increased soil water availability, resulting from the effects of rainfall channeling, may also contribute to higher seedling survivorship under tree canopies (Slatyer 1961; Pressland 1976). Furthermore, the accumulation of litter beneath the canopy reduces water run-off and allows more time for infiltration (Passioura 1982). It may also result in a localised increase in soil nutrients, as has been reported for arid and semi-arid ecosystems in North America (Tiedemann and Klemmedson 1973; Charley and West 1975) and Australia (Hacker 1984).

The total lack of seedling survivorship in the open habitat used in the field germination trial supports the hypothesis that sites beneath canopy trees may be more favourable for the establishment of *P. angustifolium* seedlings. While germination syndromes in this species are probably more closely linked to season a rainfall and temperature conditions, successful germination and establishment may be augmented by reasonable proximity to canopy trees. In such situations, competition between seedlings and canopy trees for soil water and nutrients may not be great, due to their broad differences in root architecture. The survival of seedlings in close proximity to non-conspecific older trees, purportedly due to differences in rooting depth, has been recorded for other semi-arid taxa (Martens *et al.* 1997).

The root systems of arid and semi-arid zone perennial plants fall into three general categories. These are 'specialized taproot', 'specialized lateral', and 'generalized', based upon the presence of major taproots, a lateral root system without a major taproot, and combined taproot and lateral root system, respectively (Cannon 1949; Kummerow 1980). The root system structure of *P. angustifolium*, which is consistent with other arid and semi-arid taxa (Davis 1970), including Australian species (Specht and Rayson 1957; Maconochie 1982), conforms to the 'generalized' category. These are commonly known as dual root systems (Canadell and Zedler 1995), so-named because they comprise two fundamentally different root morphologies. In such systems, taproots serve to access water stored deep in the soil profile, while lateral roots can access micro-sites suitable for both the sequestering of nutrients (as discussed above) and water and as points of ramet emergence – the 'resource-rich micro-sites' described by Stuefer (1996).

In arid and semi-arid environments, rainfall events generate pulses of moisture that recharge the surface soil layer (Noy-Meir 1973; Schwinning and Ehleringer 2001). Thus it is not surprising that plant life-forms in such environments show specialization in accessing water from different soil horizons at different times of the year (Cody 1986; Smith and Nobel 1986; Flanagan *et al.* 1992). For *P. angustifolium*, a network of surface lateral roots can access water in upper soil horizons during rainfall pulses, with taproot access to deeper soil water between pulses, regardless of the moisture status of the surface horizon. During rainfall pulses, plants with a network of shallow lateral roots also have a greater capacity for carbon gain than plants without shallow roots (Schwinning and Ehleringer 2001), which may be of adaptive and competitive value.

Another advantage of lateral roots may be their role in protection from and regeneration after fires, which in the study area recur at intervals of approximately 20 years (Cheal *et al.* 1979). Resprouting is an important trait for the survival of semi-arid taxa damaged by fire (Hodgkinson and Griffin 1982). In contrast, many tap-rooted species that do not possess a network of subsurface lateral roots are unable to survive fire (Specht and Rayson 1957). Although little is known of the fire sensitivity of *P. angustifolium*, as previously discussed, the majority of Australian *Pittosporum* species are rainforest inhabitants and some species, such as *P. undulatum*, are quite fire sensitive as seedlings or juveniles (Melick and Ashton 1991; Rose and Fairweather 1997). This suggests that

the ability to produce root suckers, which probably increases the likelihood of genet survival during fire, may be highly adaptive in such environments.

The apparent lack of individual root system development by P. angustifolium ramets has been recorded for other woody suckering taxa, including Acacia signata (Dodd et al. 1984). Nevertheless, this trait is unusual, as in most suckering taxa, ramets develop their own root systems and become independent from the genet (Jenik 1994), although for some taxa this may take many years (Grime 2001). The lack of ramet root development may be due to a number of factors, including sucker immaturity, the robustness of the genet, the role of lateral roots in nutrient uptake, or simply that ramet root development has not yet been observed. Where there is a total lack of root development by ramets, they must rely indefinitely upon the genet's root system, with communal death of the entire stand under circumstances of old age or disease. In stands of P. angustifolium surveyed to date, the death of the genet does not appear to result in the death of the entire stand. Therefore, it is likely that deep or secondary taproots remain connected to ramets and continue to supply their moisture and nutrient requirements. Alternatively, the lateral root connections between ramets and the genet may fragment over time, leading to the formation of true clones (Lacey and Johnston 1990), although this would require the development of ramet root systems.

Nevertheless, by remaining interconnected, ramets may be able develop some degree of specialization in nutrient uptake, carbohydrate storage, vegetative spread or sexual reproduction, which have been observed in other suckering taxa (Stuefer 1998; Charpentier and Stuefer 1999). Stuefer (1998) considered this to be comparable to the division of labour in colonies of social animals or in economic systems, the ecological significance of which is increased efficiency of entire clones in exploiting their environments. Furthermore, in nutrient-poor environments, which are characteristic of much of inland Australia, plant fitness may be enhanced by maximizing the lateral exploitation of soil resources, rather than vertical growth and light capture (Noble *et al.* 1979), Harper's (1977) Type (ii) strategy as described above. This strategy, together with the buffering effects of resource-sharing amongst ramets (Bazzaz 1984; Pitelka and Ashmun 1985), may give *P. angustifolium* an important competitive advantage in patchy environments (Alpert 1999).

Clonal growth may be of significant value in arid and semi-arid environments as it eliminates the requirement for seedling establishment, fosters the phenotypic stability of a genotype that is well adapted to this habitat (Lamont 1988), and may substantially increase longevity (Muller 1951; Noble 1986; Bond and Midgley 2001). Individual plants of some species are estimated to be 10,000 years old (Vasek 1980). Even allowing for considerable overestimation, this demonstrates the ability of root suckering individuals to persist for many years.

Other potential advantages of root suckering, particularly in arid and semi-arid environments, may be the ability of ramets to more rapidly produce photosynthetic tissue, and to access greater volumes of subsurface water, than newly-emerging seedlings (Maconochie 1982; De Steven 1989). In such environments, root suckering may also buffer a plant against the periodic impacts of severe frost. For example, although severe frosts during the winter of 1982 in Wyperfeld N.P. caused the widespread death of adult plants of *Leptospermum coriaceum*, it had little impact on the health of their root suckers (O'Brien *et al.* 1986).

While the incidence of root suckering by *P. angustifolium* genets is widespread, at least in the south-eastern part of its range, there is some risk in assuming that it is the result of selection for adaptive functionality with respect to the current environment. This is because it may be phylogenetically based, a remnant of past evolutionary history (Gould and Lewontin 1979) or the by-product of selection for a different trait (van Groenendael *et al.* 1996). The suggested phylogenetic basis for root suckering is supported by the similar ability of *P. revolutum* and *P. undulatum* individuals to sucker, although this requires further investigation (Fig. 7.14).

Reproductive allocation

The low incidence of resource allocation to flowering and seed production observed in stands of *P. angustifolium* with extensive ramet development is common among clonal taxa, particularly those inhabiting severe environments such as those at high altitude or latitudes (Mooney and Billings 1961; Billings and Mooney 1968). This pattern may explain the absence of *P. angustifolium* seedlings beneath or in the vicinity of adult trees, which has been recorded for other clonal taxa (Eriksson 1989), including several

arid and semi-arid taxa (Friedman and Orshan 1975; Hacker 1984). Although the low density of *P. angustifolium* genets across its range may reflect both sporadic reproduction and only occasional seedling survivorship, it is unlikely to result from a widespread pattern of low allocation to sexual reproduction, as some genets produce abundant quantities of viable seeds that will germinate readily under suitable conditions (Chapter 5).

In a number of root-suckering taxa that regularly set large quantities of seed, but for which seedlings are rare or absent due to unfavourable environmental conditions, the degree to which energy is allocated to sexual versus vegetative reproduction may vary, depending on environmental conditions (Lacey and Johnston 1990). For such species, vegetative reproduction occurs during periods of environmental stress, with sexual reproduction restricted to rare short periods of climatic amelioration. Trades-offs in the allocation of resources between sexual and clonal reproduction have been reported for a range of taxa, and may be related to the optimization of plant fitness (Abrahamson and Gadgil 1973). For some species, the allocation to sexual reproduction has been at the expense of growth or clonal reproduction (Law 1979; Snow and Whigham 1989; Primack et al. 1994). In other species, a high allocation to clonal or vegetative reproduction may result in a low allocation to sexual reproduction (Schaffer and Gadgil 1975; Douglas 1981; Bazzaz et al. 1987), which is one explanation for the low rates of seedling recruitment in some clonal species (Wein and Pickett 1989; Eriksson 1992). For *P. angustifolium*, energy partitioning appears to occur at the level of the genet, with a 'decision' to invest either in sexual or vegetative reproduction, but rarely in both.

An alternative explanation for the observed allocation of resources to either sexual or vegetative reproduction is that proposed by Lacey and Johnston (1990), who suggested that the switch from sexual to vegetative reproduction for individuals is mitigated by genotype-environment interactions, commonly resulting from disturbance or damage. Given the sporadic but occasionally severe degree of herbivory of *P. angustifolium* genets and correlation between the degree of damage from browsing and ramet number, the role of herbivore-induced disturbance as a determinant of reproductive allocation in this species may be considerable. The apparent relationship between ramet production and degree of herbivory in *P. angustifolium* accords with the model of Bellingham and

Sparrow (2000), who proposed that the reproductive allocation to sprouting is highest in environments subject to very low or very high disturbance regimes.

A third alternative for these allocation patterns is that *P. angustifolium* is selfincompatible, which together with a low density of genets across its range, could result in poor fertilization and thus low fruit production (Rathcke 1983; Kunin 1993). A positive correlation between fruit production and genet population density has been reported for a number of clonal species (Tammisola 1982; Laverty and Plowright 1988; Eriksson and Bremer 1993), with conflicting results for others (McCall and Primak 1987; Aspinwall and Christian 1992). However, as flower and capsule-bearing genets of *P. angustifolium* may occur in reasonably close proximity to non-flowering or erratically-flowering individuals (pers. obs.), the role of distributional patterns and genet frequency in its lack of allocation to sexual reproduction is somewhat discounted.

If genet height for *P. angustifolium* is a reasonable approximation of its age, then the biomass invested in vegetative growth (based upon ramets per genet) appears to be roughly proportional to genet age. This suggests that individuals may have to reach a certain age before allocating resources to sexual and/or vegetative reproduction, which is common among woody taxa (Worley and Harder 1996), although there are variations and exceptions (Ohlsen 1988). Furthermore, as growth, functional maintenance and reproductive allocation must be drawn from the same finite pool of resources, an increase in any one of these requires trade-offs with competing functions (Cody 1966; Harper 1967). Seedling establishment and the subsequent development of root and shoot systems capable of sustaining the individual plant may demand little or no biomass allocation to reproduction.

Another possible explanation for the relationship between genet age and ramet number is that reproductive investment in ramets is cumulative. i.e. the number of clonal propagules and biomass allocation to them can increase with increasing ramet size (Antlfinger *et al.* 1985), with ramet number being the equivalent of ramet size for *P. angustifolium*. Nevertheless, any increase in the number of ramets must, in the absence of root system development by ramets, increase among-ramet competition for soil resources.

Regardless of the patterns of investment and the actual mechanisms for induction and persistence of clonality in species such as *P. angustifolium*, the capacity to reallocate resources from sexual to vegetative reproduction, if possessed by this species, would be strongly adaptive (Howe and Westley 1997). This may be of particular significance for the long-term persistence of arid and semi-arid taxa like *P. angustifolium*, which are characterized by low population densities that are subject to stresses from herbivory, limited nutrient availability and long periods of water deficit. Nevertheless, there are costs associated with root suckering, the most substantial of which is likely to be resource allocation to ramets, which may result in lower RGR of the genet. Low RGR, which is a feature of this species and of the Wyperfeld N.P. population in particular (Chapter 6), may be a general characteristic of sprouting taxa (Bond and Midgley 2001).

Interestingly, the most southerly, naturally-occurring populations of this species in central Victoria all display extensive clonal growth, with total lack of seed set (pers. obs.), presumably due to the limitations of low mean spring temperature, but not necessarily exclusive of the factors mentioned above. This phenomenon, which is also a feature of the most southerly population of P. revolutum (pers. obs.), reinforces the suggestion that it is low temperature during the period of flowering or fruit set that prevents successful sexual reproduction in southerly populations of these taxa (Fig. 7.14). Thus, although climatic and soil conditions may be adequate for seed germination and suitable for seedling establishment, a local lack of propagules, exacerbated by substantial distances to other such material, may provide effective mechanisms for demarcating the distributional limits of such species. This phenomenon has been recorded for northern Britain populations of Tilia cordata, which have persisted by sprouting since the onset, approximately 5000 years ago, of cooler climatic conditions that have prevented sexual reproduction (Pigott 1993). Alternative explanations for the lack of seed set in the southern-most population of P. angustifolium include possible impacts on seed set due to drought during the year prior to these observations, self-incompatibility and lack of other locally-flowering individuals, or from lack of suitable pollinators.

In summary, this study has shown that although *P. angustifolium* seeds will germinate readily in the field under appropriate conditions of soil moisture, and from different soil depths, seedling survivorship is negligible, reinforcing the observation that successful regeneration from seed is extremely rare. Rapid generation of early root growth

suggests the likelihood of successful seedling establishment under conditions of adequate soil moisture. Nevertheless, while adequate soil moisture is a critical requirement for seedling establishment, other evidence suggests that it is probably not the sole factor of seedling mortality in this species.

Although modes of sexual and vegetative reproduction differ in their adaptive value, the capacity of P. angustifolium for both may be an adaptively powerful life history trait providing an important advantage in resource-limiting, arid and semi-arid environments. Occasional sexual regeneration provides for maintenance of genetic variation and longdistance dispersal, with the rate of genet recruitment important in the distribution and abundance of this species. An ability to reproduce vegetatively may enable its genets to harvest patchily distributed resources and facilitate long-term persistence, thereby increasing the eventual likelihood of successful sexual reproduction. The ability to switch between reproductive methods or to adjust the reproductive allocation to each in response to environmental conditions relating to climate, soil nutrient status, fire, competition or herbivore pressure may be crucial in its establishment and persistence in arid and semi-arid environments. Furthermore, if extended life spans function as a 'genetic memory' of past selection, paralleling the role played by soil seed banks (Fagerstrom 1992), a capacity for extreme longevity by clonal reproduction may be a critical attribute during periods of increasing aridity, such as occurred in Australia during the Late Tertiary.

Site	Genet height	Genet girth	Flowers / genet	Fruits / genet	# Ramets	Ramet height	Degree of herbivory	Community type	Soil type
Genets reproducing by vegetative means only									
1	4.0	26	0	0	13	0.77 ± 0.23	Moderate	BB-RRG	S
2	2.7	23	0	0	1	0.66	Low	BB	S
3	5.6	70	0	0	89	0.50 ± 0.02	Very High	CP-B	SL
5	3.6	7	0	0	4	0.62 ± 0.01	Low	BB	S
9	5.5	6	0	0	54	0.41 ± 0.06	Low	BB-RRG	S
12	2.9	10	0	0	74	0.55 ± 0.28	Moderate	BB	SL
13	7.5	8	0	0	63	0.79 ± 0.06	High	CP-B	S
14	1.5	7	0	0	. 14	0.58 ± 0.08	Low	RRG	SL
15	5.0	47	0	0	50	0.91 ± 0.06	Moderate	BB	SL
17	0.7	6	0	0	8	0.39 ± 0.03	Low	BB	S
18	2.5	12	0	0	22	0.86 ± 0.16	Low	Mailee	LC
Genets reproducing by both vegetative and sexual means									
4	9.5	90	0	~ 100	5	0.55 ± 0.14	Low	BB-RRG	S
8	1.9	10	50	0	1	0.37	Low	BB	S
16	2.8	35	0	400	62	0.97 ± 0.05	High	СР	S
Genets reproducing by sexual means only									
6	5.4	30	0	~ 250	0	-	None	BB	S
7	2.5	12	~ 600	0	0	-	None	BB	S
10	2.6	13	~ 2000	0	0	-	None	BB-RRG	S
11	3.0	34	~ 18000	0	0	-	None	СР-В	S
19	2.0	13	~ 5000	0	0	-	None	BB-RRG	S

Table 7.1 Genet details for surveyed stands of *P. angustifolium* at Wyperfeld National Park(Genet and ramet heights are in m. Genet girth is in cm. Ramet height is mean \pm sem.Flowers and fruits per genet and degree of herbivory are estimates).

Community Type: BB = Black Box; BB-RRG = Black Box - River Red Gum; CP-B = Cypress Pine-Buloke Woodland. Soil Type: S = Sand; SL = Sandy Loam; LC = Loamy Clay).



Harvest / Seed burial depth

Figure 7.1 Percentage germination of *P. angustifolium* seed after three and six months burial in the field at different soil depths. Data are means with sem, n=5. *F* and *P* values were calculated using arcsin-transformed data. Shared alphabet letters above bars denote no significant difference between means. Note: there was zero germination of seed buried at 1 cm and 2 cm after 3 months.



Figure 7.2 Weight of *P. angustifolium* seed buried at different depths in the soil and retrieved after (a) three months and (b) six months Data are means with sem, n=5. Shared alphabet letters above bars denote no significant difference between means.

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Figure 7.3 Time to 50% germination in the laboratory of *P. angustifolium* seed following collection after 3 months burial at different soil depths in the field. Data are means with sem, n=5. Shared alphabet letters above bars denote no significant difference between means.







Figure 7.5 Soil water content (\triangle) and seasonal (\Box) and long term average precipitation (\blacksquare ; 1901-1970) for each sampling period at Wyperfeld N.P. For soil water content and long term precipitation, data are means with sem, n=5 and n=70 respectively. Long term precipitation data from the Bureau of Meterology (1989).



Figure 7.6 Length of the hypocotyl (open columns) and radicle (shaded columns) of *P. angustifolium* seedlings harvested 6 months post seed burial. Data are means with sem, n=5. Shared alphabet letters above bars denote no significant difference between means.

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Figure 7.8 Relationship between the number of ramets per genet and genet height for stands of *P. angustifolium* reproducing by vegetative means only (n=11).



Figure 7.9 Relationship between the number of ramets per genet and mean ramet height for stands of *P. angustifolium* reproducing by vegetative means only (n=11).



Figure 7.10 Genet height and distribution of ramet height classes in stands of *P. angustifolium* reproducing by vegetative means only.







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Figure 7.12 Number of ramets produced by sexually- and vegetativelyreproductive stands of *P. angustifolium*. Data are means with sem.



Figure 7.13 Percentage of total *P. angustifolium* genets displaying sexual (open columns) and/or vegetative (shaded columns) reproduction grouped according to the degree of herbivory. Numbers above columns denote the mean number of ramets for genets in each herbivore impact type.



Figure 7.14 Major regeneration characteristics of the four species in relation to their purported cladistic positions as per Cayzer *et al.* (2000). The dashed line indicates that the position of *P. revolutum* is yet to be fully resolved (Sources of information: Gleadow 1982; Narayan 1993; Friedel *et al.* 1993; Elliot and Jones 2000).

CHAPTER 8. SYNTHESIS AND GENERAL DISCUSSION

This study aimed to investigate life history characteristics of four closely related species from contrasting rainfall environments in order to better understand the evolution of strategies, among the Australian flora, that facilitate survival during periods of moisture stress. Observations of these species, together with the results of experiments, have shown considerable differences in their patterns of germination, growth, seasonal water relations and drought resistance, and provided insights into the population biology of *P. angustifolium*, the most xerophytic species in the genus. This study has also revealed very high intraspecific variation in some of these life history traits, particularly in species such as *P. revolutum* and *P. angustifolium*, which have very broad distributions.

Individual traits of species are most likely not, in isolation, sufficient to facilitate the long-term persistence of a species or population in a community. Rather, it is a suite of characteristics possessed by a species that determines its fitness in specific environments, and variation in these traits among populations is of great importance in its ability to respond successfully to changing biotic and abiotic conditions. For example, although germination response to temperature is conditional upon the availability of water, it may also be determined by dormancy factors that are not related to climate (e.g. after-ripening requirement in *P. bicolor*). Furthermore, the climatic determinants of distribution may equally include the degree of seasonality as well as soil moisture availability and temperature extremes.

In Chapter 2, climate analyses were undertaken to identify the variables that explain the bulk of the variation in the distribution of these species and the differences among them. In a PCA of climate variables, the first axis separates *P. angustifolium* from *P. bicolor*, with *P. revolutum* and *P. undulatum* intermediate. This corresponds closely to their distributions with *P. angustifolium* inhabiting hot, dry environments and *P. bicolor* cooler, wetter environments. The pattern among these species is consistent with the results for a range of other forest taxa (Hill *et al.* 1988; Read 1990). In the northern parts of their ranges, the climates of *P. revolutum* and *P. angustifolium* are marked by a marked degree of precipitation seasonality, indicating the sharp distinction between wet and dry seasons. *P. angustifolium* is also subject to high temperature seasonality and a marked degree of rainfall unpredictability across its range. Evaporative losses largely

offset summer rainfall in environments supporting *P. revolutum* and *P. angustifolium*, effectively reducing soil moisture availability. To a lesser extent, low rainfall and high temperatures during summer for sites supporting *P. undulatum* and *P. bicolor* would place them under some degree of water stress during that period.

Study of the seasonal field water relations of three of these species (Chapter 3) revealed substantial interspecific differences. *P. angustifolium* exhibited the lowest values of Ψ_L and Ψ_{PD} and reductions in g_s during periods of maximum water deficit. It displayed consistently low maximum values of Ψ_{PD} , even during winter, when above-average rainfall should have facilitated values of Ψ_{PD} closer to zero. This pattern of Ψ_{PD} suggests incomplete overnight equilibration of Ψ between leaves and the soil, which if due to increased osmotic potential, may increase its tolerance to frost as well as drought. While the co-occurring *P. undulatum* and *P. revolutum* shared similar patterns of diurnal and seasonal g_s , they exhibited quite dissimilar patterns of diurnal and seasonal Ψ_L . In contrast to *P. undulatum*, which maintained uniformly high diurnal Ψ_L across seasons, the pattern of diurnal Ψ_L for *P. revolutum* was broadly sinusoidal in nature, decreasing from a high value in the early morning to a minimum during the early afternoon, after which it increased, reaching a maximum just before dawn.

Differences among these species in their responses to water deficit were investigated in seedlings grown in a common environment (Chapter 4). The drought response of *P. bicolor* seedlings was consistent with an avoidance-type strategy, initially by means of the maintenance of stomatal conductance, with stomatal closure and an increased water-use efficiency occurring under conditions of extreme water deficit. *P. undulatum* seedlings were highly drought resistant, exhibiting both drought avoidance and tolerance mechanisms. For relatively fast growing species such as *P. undulatum*, drought avoidance by stomatal closure and maintenance of high leaf water potential may cost less metabolically than decreasing leaf water potential by osmotic adjustment.

P. angustifolium and *P. revolutum* exhibited drought tolerance responses to water deficit, largely by means of decreases in leaf water potential via osmotic adjustment and maintenance of low rates of transpiration. These species did not exhibit decreased ¹³C discrimination, suggesting that these mechanisms of drought resistance may preclude a

requirement for increased water use efficiency. Furthermore, increased water-use efficiency may result in a slower rate of water uptake, which would not be advantageous to such species if conserved soil water was able to be exploited by competing species.

These species displayed broad differences in their germination responses to light, stratification and temperature (Chapter 5). Overall, the germination responses of these species to temperature were broadly consistent with climatic variables across their distributions. Of the species, *P. angustifolium* seed germinated more rapidly than that of *P. bicolor* and *P. revolutum*, which accords with hypotheses regarding the germination response of arid zone taxa to moisture availability. *P. bicolor* was the most conservative species in terms of germination rate and the amplitude of temperatures across which it would germinate. The slower germination and lower overall germination quotients of seed from populations of *P. angustifolium* and *P. revolutum* occupying the most marginal habitats demonstrated the high degree of intraspecific variation within them and suggests there has been selection for traits that will increase the likelihood of germinant survival and growth to reproductive maturity. For such populations, selection for adaptive syndromes appears to realign the germination response toward that of more narrowly distributed taxa such as *P. bicolor*.

The considerable intra- and interspecific variation in growth rate and biomass allocation variables among these species (Chapter 6) was surprising, given their phylogenetic relationship and created difficulties in elucidating broad patterns among them. Overall, the four species exhibited lower growth rates than those of other woody Australian taxa, which suggests that a low RGR may be general characteristic of *Pittosporum*. The significant differences in seed mass among these species, a broad pattern of decreasing seed mass with increasing latitude, and correlations between seed mass and particular climate variables may be of evolutionary significance, particularly given the close phylogenetic proximity of these species to one another.

Under non-limiting growth conditions, young seedlings of these species inhabiting the dry end of a precipitation gradient exhibit higher specific leaf area and lower specific root length, with those at the wetter end displaying the opposite pattern. The high SLA of *P. angustifolium* seedlings suggests selection in the juvenile stage for enhanced carbon acquisition by means of increasing leaf area per unit biomass, without

necessarily diverting biomass from roots. Optimisation of carbon gain and growth rates may be important in facilitating maximum root growth, which would increase the likelihood of seedlings surviving their tirst summer. However, as adult leaves of this species are sclerophyllous, there must be an ontogenetically-triggered decrease in SLA, perhaps prior to the first period of water deficit faced by seedlings.

The negative correlation between root:shoot ratio and the moisture index of these species supports the broader trend among species of a shift from above- to below-ground maximisation of resource acquisition along a gradient of increasing water deficit. The considerable variation in RGR and the relationships between growth variables and patterns of biomass allocation among these species suggest that it may be physiological flexibility, rather than biomass allocation, that is responsible for variation in RGR (Hunt and Cornelissen 1997b).

Field germination trials of *P. angustifolium*, the most xerophytic of the Australian species, revealed that although seed germinated readily in the field, there was no seedling survival over the period of the study, most likely resulting from biotic and/or climatic factors (Chapter 7). Seedling survival may depend upon rare events such as wet summers, together with factors (e.g. previous drought, fire) that reduce population densities of mammalian herbivores. However, the capacity of *P. angustifolium* for both sexual and vegetative reproduction may be an adaptively powerful life history trait in low rainfall environments. Its capacity to switch between reproductive methods or to adjust the reproductive allocation to each in response to environmental or biot.c conditions may be crucial in its establic imment and persistence in arid and semi-arid environments.

It is likely that differences in leaf anatomy, morphology and orientation among these species are important contributors to the observed differences in drought resistance. The small surface area, vertical orientation and high degree of waxiness of *P*. *angustifolium* leaves are likely to be very important in limiting transpirational water losses. A high degree of waxiness directly reduces cuticular transpiration and increases light reflectance, which may be important in minimising water loss due to a lower requirement for energy dissipation (Ehleringer 1981). Similarly, the dense pubescence of *P. revolutum* leaves may contribute to its inherently low rates of transpiration.
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Each species exhibited a range of life-history traits that integrate with climate and other environmental variables to generate its realized niche. For *P. bicolor*, there was a strong correlation between rainfall consistency and distribution, which suggests a susceptibility to drought and/or fire. Its water spending behaviour, with high rates of transpiration under non-limiting conditions and apparent inability for osmotic adjustment, support a hypothesis of drought intolerance. Nevertheless, its capacity for increased water-use efficiency, inferred by higher ¹³C:¹²C ratios in the leaves of droughted compared to control seedlings, suggests that it has some capacity to adjust to water deficit. The northern limit of the range of *P. bicolor* coincides with the broad change from winter to summer rainfall. However, its comparatively low optimum germination incubation temperature of *c*. 10°C suggests that an inability to germinate at temperatures above 15°C may be an important determinant of the northern distributional limit of this species in southeastern Australia.

The seed of *P. undulatum* germinated rapidly and its seedlings exhibited the most rapid response to water stress and highest values of RGR. Species with high RGR tend to be highly responsive to environmental stressors and are most often associated with mechanisms of physiological avoidance rather than tolerance (Nilsen and Orcutt 1996). Stress endurance among plant species is highly variable in nature and there appear to be particular complexes of stress resistance, with, for example links between shade tolerance and drought resistance (Hope and Kirkpatrick 1988), although for most species there are trade-offs between these traits (Barton 1993). The rapid response to drought of *P. undulatum* seedlings, together with the maintenance, by seedlings and field-growing mature individuals, of high leaf water potential under moderate to high water stress conditions, broadly support this pattern. Its strong drought resistance is consistent with the diurnal and seasonal water relations of more mature plants growing in the field. It is able to significantly increase its water-use efficiency under drought conditions, thereby facilitating the maintenance of high leaf water potential under conditions of reduced stomatal conductance.

Overall, these characteristics of *P. undulatum*, together with other life history traits, including rapid seed dispersal, fast seedling growth rates, early seed production and variable root system (Gleadow and Ashton 1983), strongly suggest that it utilizes strategies of avoidance to withstand sustained periods of water stress. Species that

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demonstrate a strategy of drought avoidance are common in environments subject to a moderate degree and/or duration of water stress. The high RGR and shade tolerance, and small seed mass of *P. undulatum* contrasts with the usual relationship between these variables, which is one in which shade tolerance usually correlates positively with seed mass and negatively with RGR (Saverimuttu and Westoby 1995). However, *P. undulatum* produces copious amounts of seed that will germinate equally well under light or dark conditions (Chapter 5). While high RGR increases the mortality risk per seedling, the very high number of seeds means that mortality risk is spread more widely, increasing the likelihood of establishment success for at least a small number of seedlings.

Climatic analysis of the site records of *P. undulatum* suggested that maximum and minimum temperatures are important determinants of its distribution. Furthermore, its comparatively narrow germination amplitude, high shade tolerance (Gleadow *et al.* 1983) and sensitivity to fire (Melick and Ashton 1991) suggest that a lack of climatic extremes and absence of large-scale disturbance may be critical requirements in its establishment in areas with lower rainfall and a high natural frequency of fire. Its presence in warm temperate rainforests from which fire has been largely excluded, occupation of scree slopes naturally protected from fire and invasion of wet and dry sclerophyll forests from which fire has been anthropogenically excluded further support this hypothesis. Although this species is able to resprout epicormically following lowmoderate intensity fires, it does not demonstrate a strong capacity for vegetative reproduction, which is characteristic of *P. angustifolium* and has also been observed in *P. revolutum*.

The behaviour of field-growing and droughted seedlings of *P. revolutum* indicated that they maintain physiological function by means of osmotic regulation, a characteristic of drought tolerant taxa. Furthermore, seedlings of this species displayed inherently low rates of stomatal conductance and transpiration, probably resulting partly from norphological factors such as the dense pubescence of their leaves, which act to lower leaf temperature and transpiration but which also limit photosynthetic capacity. Thus, the observed low rates of growth in this species may be a product of morphological adaptations to restrict water loss. Dense leaf pubescence may also represent a greater investment in leaf protection against insect herbivory (Coley 1983; Woodman and Fernandes 1991), which would allow for greater longevity, but the cost for which is slower growth. Alternatively, the low RGR may result from selection for high shade tolerance, which in studies of other rainforest taxa and broader species assemblages correlates with slow growth, high survival, large seed size and relatively low fecundity (Metcalf and Grubb 1995; Hodkinson *et al.* 1998).

P. revolutum and *P. undulatum* share many similar characteristics, some of which are morphological, such as leaf and flower traits, and others which relate to distribution and habitat. However, *P. revolutum* has significantly heavier seeds and its seedlings exhibit inherently lower rates of germination, lower RGR and lower rates of transpiration under non-limiting conditions of water availability than those of *P. undulatum* (Figs. 8.1, 8.2). These differences may reflect selection for trade-offs in life history traits, generating strategies that facilitate establishment and regeneration in similar habitats. Thus, the cooccurrence of *P. undulatum* and *P. revolutum* across a broad latitudinal range may result largely from these differences, as has been shown for other species belonging to different groups or subgenera within a genus (Mohler 1990). Similarly, species belonging to the same subgroup or subgenus, such as *P. angustifolium* and *P. bicolor*, often occur in different habitats, a pattern that is often determined by water availability or deficit (Whittaker 1969).

The distribution of *P. angustifolium* may be restricted in the north by interactions between temperature, precipitation and fire, and to the south by temperatures that prevent flowering and/or seed set. The slightly higher seasonal values of Ψ_{PD} for *P. angustifolium* in comparison with other xerophytic species occupying semi-arid or arid environments may reflect an inability to reduce leaf water potential to the same degree without incurring cell membrane and organelle injury, which may explain its absence from the most xeric parts of its broader distribution. Nevertheless, an ability to survive frosts by lowering leaf water potential, perhaps by osmotic adjustment, may be of adaptive importance in arid and semi-arid habitats where severe frost is relatively common at certain times of the year.

The large differences in seed mass among these four species, in particular that between the closely-related *P. angustifolium* and *P. bicolor*, supports the hypothesis of a strong

relationship between seed mass and habitat (Silvertown 1989). The greater mass of seeds of *P. angustifolium* and *P. revolutum*, the two drought tolerant species, may be linked to the ability of their seedlings to inhabit environments subject to unpredictable (irregular, but of long duration) or seasonal water stress. Links between Late Tertiary drying and the evolution of large-seededness and drought resistance have been suggested for other Australian taxa (Caddick and Linder 2002). Although there may be links between seed mass and other functionally related characters, it is often difficult to correct for constraints in phylogeny. This is less of a problem in this comparison, as the large-seeded *P. angustifolium* and *P. revolutum* are phylogenetically less close to each other than they are to the small-seeded *P. bicolor* and *P. undulatum* respectively (Cayzer *et al.* 2000) (Fig. 8.1). This suggests the possibility of coevolution of such traits as large-seededness, low RGR and high drought resistance among species subjected to ongoing or strongly seasonal water stress conditions.

Another explanation for the patterns of seed mass among these species is that the large mass of *P. revolutum* and *P. angustifolium* seed is a retained, general characteristic of Australian *Pittosporum* species, and that the small-seededness of *P. bicolor* and *P. undulatum* has evolved in response to the cooler mean annual temperatures and minimum temperatures that operate at higher latitudes in southeastern Australia (Fig. 8.1). A negative correlation between seed mass and latitude has been recorded across life-forms and at inter- and intra-familial scales among Australian taxa (Lord *et al.* 1997) as well as in those of other regions (Baker 1972; Rockwood 1985). Lord *et al.* examined the various mechanisms for this pattern, and concluded that it might be result from the higher metabolic costs associated with seed germination and seedling establishment in tropical systems. The flipside of this hypothesis, if correct, is that selection for smaller seed mass in *P. bicolor* and *P. undulatum* may have resulted from the lower metabolic cost of germination and establishment in more temperate environments.

P. revolutum and *P. angustifolium* also demonstrate a high degree of intraspecific variation in germination biology, growth rate and biomass allocation. This is perhaps not surprising, as these species are the most widely distributed in the genus, and intraspecific variation in such traits is not uncommon among widely- or disjunctly-distributed species. Furthermore, over much of their range, *P. angustifolium* and *P.*

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revolutum occupy environments subject to water stress, as on-going and seasonal components respectively. Species inhabiting high stress environments often exhibit low RGR and low responsiveness to environmental stresses, and characteristically possess adaptive mechanisms of stress tolerance rather than avoidance (Nilsen and Orcutt 1996). These results suggest ecotypic selection for a suite of traits including seed mass, rates of germination and early seedling growth and biomass. Strong correlations between these traits and precipitation and temperature parameters of the populations have also been observed among other species (Ager *et al.* 1993).

As inhabitants of environments subject to on-going or seasonal water deficit, the advantage of a strategy of drought tolerance to *P. angustifolium* and *P. revolutum* cannot be underestimated. The suggested drought tolerance strategy of *P. angustifolium* and *P. revolutum* is supported by their slower rates of growth and assimilation compared to *P. undulatum* and *P. bicolor*. Evolutionary trade-offs for greater drought resistance include reductions in growth rate and hence in competitive ability (Grime 1979a; Barnes 1985), which may explain the absence of *P. angustifolium* in more mesic plant communities, although there appears to have been selection for higher RGR ecotypes in the higher rainfall parts of its range.

Both *P. undulatum* and *P. bicolor* are drought-avoiding taxa, by means of water-saving and short-term water-spending, respectively. Their responses to water deficit and the nature of their distributions indicate the comparatively greater ability of *P. undulatum* to inhabit environments subject to greater water deficit. This pattern is typical of the broader relationship between water-saving and water-spending taxa (Levitt 1980), although both types may co-occur (Oppenheimer 1953), which is true of *P. undulatum* and *P. bicolor*.

The suggested evolution of *P. angustifolium* from rainforest progenitors is supported by the fact that almost all other species in the genus are rainforest taxa and that its closest, non-arid congener is the cool temperate species *P. bicolor*. An obvious question is whether *P. angustifolium* evolved from relictual rainforest species that were able to survive increasingly harsh conditions of the Late Tertiary, or rather that it represents the product of a more recent radiation and invasion of the arid region. If the onset of severe aridity has been a relatively recent phenomenon, and one to which *P. angustifolium*

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responded, then a greater number of *Pittosporum* species would be expected in temperate and tropical areas than in arid and semi-arid areas. As has been indicated, this is the case for *Puttosporum* in Australia.

Other factors that support the idea of the recent speciation of P. angustifolium are aspects of the present-day distribution and morphology of the closely related P. *ligustrifolium* and P. *phillyreoides*, the only other arid or semi-arid Australian species in the genus. These two species are the most westerly-distributed of the Australian taxa, being restricted to limestone plains and offshore islands along the west coast of Australia (Cayzer et al. 2000). The three species also exhibit similar morphologica! characteristics, including persistent involucres, terminal, axillary inflorescences and cotyledon number (Cayzer et al. 2000). Together, these factors suggest a recent radiation of P. *ligustrifolium* and P. *phillyreoides* from P. *angustifolium*.

Cayzer et al. (2000) group P. bicolor with P. phillyreoides (Fig. 1.2), which as mentioned above is restricted to the west coast of Western Australia. The extensive distribution of P. angustifolium and its strong affinity with P. phillyreoides and P. ligustrifolium suggest that it may be most closely aligned with P. bicolor, with selection for adaptations to local soil and climatic conditions in the Western Australian west coast taxa generating the observed groupings in the cladistic analysis. The characteristics of other tropical rainforest species in the genus (e.g. P. revolutum - strong affinity with rainforest, poor germination response at low temperature and slow rate of growth) suggest a rainforest progenitor for these species.

In the absence of palynological or macrofossil material, it is difficult to discern the nature and timing of evolution and extinction in *Pittosporum* during the climate changes of the Late Tertiary and the subsequent rapid climatic oscillations of the Pleistocene. Nevertheless, the current high frequency of taxa inhabiting tropical rainforests indicates the preference of the majority of species for climates that encompass high mean annual rainfall and temperature, and low variability in other temperature parameters.

Thus, the current low number of Australian *Pittosporum* species, in contrast with the higher species numbers in Africa, Indo-China, New Guinea and the Pacific Islands, probably reflects the greater contiguous availability, in those regions, of tropical and

subtropical rainforest habitat to which species of this genus are preadapted. This further suggests that there may have been considerable extinction of *Pittosporum* species in south-eastern Australia during the Late Tertiary and Quaternary, perhaps resulting from one or a combination of the lower minimum temperatures, change from a year-round rainfall to winter-dominated rainfall and increased seasonality of temperature and rainfall associated with the climate changes of that period. As Read and Hill (1989) noted, in terms of water deficit and low mean and minimum temperatures, the direction of selection pressures of the Late Tertiary would have been reinforced during the glaciations of the Quaternary.

Of the current Australian Pittosporum species, while P. angustifolium is the most xeromorphic, it is most closely aligned with P. bicolor, which has low drought resistance. This relationship may however, not be as paradoxical as it first appears. First, purported responses of other taxa to Late Tertiary – Quaternary climate change are thought to have included physiological changes leading to cold adaptation in many species, including the Nothofagus species of southeastern Australia (Read et al. 1990). The likely ability of *P. angustifolium* to tolerate frost, via osmotic adjustment, has already been discussed. Based on its distribution and the demonstrated frost tolerance of co-occurring taxa (Sakai et al. 1981), frost tolerance is probably also characteristic of P. bicolor, although the exact mechanism of frost tolerance in this species is not yet known. Second, selection for characteristics that confer frost tolerance (e.g. osmotic adjustment) may also confer some degree of drought tolerance, which may have been of adaptive value with the expansion of drier environments during the Late Tertiary and Quaternary. Third, similarities in leaf size and shape between P. bicolor and P. angustifolium suggest that selection for smaller leaf size during Late Tertiary cooling and drying, which has been recorded for Nothofagus (Hill 1983), may have provided a degree of preadaptation to drought for the progenitor of P. angustifolium.

The putative ancestral characteristics of these four species (Figs. 8.1, 8.2) are primarily based upon an assumed rainforest lineage for *Pittosporum*. Such characteristics include large seed mass (two of the four species, but characteristic of most other Australian *Pittosporum*), high optimum incubation temperature, low growth rate (three of four species), a capacity for vegetative reproduction (three of four species), shade tolerance (three of four species occupy rainforest-type vegetation) and extreme fire sensitivity (all species) (Figs. 8.1, 8.2). In addition, the most parsimonious analysis also includes osmotic adjustment as an ancestral characteristic (three of four species) (Figs. 8.1, 8.2).

The most distinctive difference between the two cladograms is leaf size, which separates *P. revolutum* and *P. undulatum* from *P. bicolor* and *P. angustifolium*. This may be of evolutionary significance given the importance of leaf size and/or thickness as a determinant of the balance between photosynthetic gain and transpiratory costs (Givnish 1987). In his model of the adaptive significance of leaf size, Givnish (1987) proposed that smaller leaves are optimal where resources other than light are limiting, based on the efficiency of carbon gain relative to the costs of supplying water to the leaves, via the influence of leaf size on leaf temperature and thereby on photosynthesis and water loss. Thus, the larger leaf size of *P. revolutum* and *P. undulatum* is predicted to optimise carbon gain in the relatively mild coastal environments that they inhabit. In contrast, the small leaves of *P. bicolor* and *P. angustifolium* are consistent with the cooler environment of the former species (leading to decreasing carbon gain) and the drier environment of the latter (leading to increasing costs of water supply to the leaves).

CONCLUDING REMARKS

This study has illustrated differences among these species, in spite of their phylogenetic proximity, in aspects of their germination, growth and biomass allocation, water relations and drought resistance, as well as the considerable intraspecific variation in these variables for species distributed across broad ranges of latitude and/or longitude. Plant adaptations may be regarded as multi-faceted compromises that enable an individual plant to deal effectively, if not necessarily in an optimal manner, with particular environmental or metabolic constraints (Anderson 1982). It may be a suite of adaptations in *P. angustifolium*, including physiological mechanisms such as low rates of transpiration and osmotic adjustment, together with high root:shoot ratios and ecological strategies related to the timing of flowering and germination and the capacity for vegetative regeneration that enabled its expansion into the developing arid and semi-arid environments during the Late Tertiary and Quaternary in Australia (Figs. 8.1, 8.2). Leaf morphological adaptations for conserving water probably also played an important role in this process, and remain an area for further research.

Based on the adaptive shifts in seed biology, physiology and biomass allocation projected for these *Pittosporum* species, a general evolutionary pathway leading to the evolution of xeromorphy in *P. angustifolium* may have involved an initial reduction in leaf size and a requirement for lower optimum incubation temperatures, followed by further adjustments to leaf anatomy and morphology (e.g. increased waxiness) together with ontogenetic characteristics that maximise leaf area and root development in the seedlings stage (Figs. 8.1, 8.2).

There are difficulties in mapping seed and physiological characteristics of these *Pittosporum* species onto their projected phylogenetic tree. This is due to a number of factors including the fact that their phylogeny has not been resolved to a very high degree (e.g. by molecular markers), which is compounded by the unresolved position of P. revolutum, resulting in different maps of physiological traits (Figs. 8.1, 8.2). Furthermore, the number of characteristics determined by these analyses may not have been sufficient to clearly delineate these species. Finally, there may be genetic tradeoffs between ecophysiological characteristics, for example between stomatal conductance and photosynthetic rate (Dudley 1996), which make it difficult to elucidate differences among species when one of these variables is not measured. Nevertheless, the comparative study of ecophysiological and other life-history characteristics and the mapping of these onto projected phylogenies have provided greater insight into the possible sequence and direction of evolutionary transitions among these Pittosporum species. Further study of the comparative drought resistance and regeneration biology of other genera that include both rainforest and xerophytic species (e.g. Flindersia, Marsdenia, Alectryon) may provide additional information regarding the evolution of adaptations to water deficits during the dramatic climate changes of the Late Tertiary -Quaternary in south-eastern Australia.



Figure 8.1 Ecophysiological and life-history characteristics mapped onto the cladogram of Cayzer *et al.* (2000) (based on morphological analyses), with *P. revolutum* grouped with *P. angustifolium* and *P. bicolor*. Characteristics were mapped on the most parsimonious basis, with putative ancestral characteristics based on a proposed rainforest lineage for the genus.



Figure 8.2 Ecophysiological and life-history characteristics mapped onto the cladogram of Cayzer *et al.* (2000) (based on morphological analyses), with the alternative grouping of *P. revolutum* with *P. undulatum*. Characteristics were mapped on the most parsimonious basis, with putative ancestral characteristics based on a proposed rainforest lineage for the genus.

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