Does the foliage of *Acacia* spp. determine their distribution? A study to determine how two different leaf forms may alter the distribution of *Acacia* spp. in relation to phosphorus concentration, mean annual precipitation and temperature within Australia and South Africa.

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Abstract

The genus *Acacia* consists of over 1000 species, of which most are native to Australia. An intriguing aspect of this genus is their divergence into two major groups that poses entirely different leaf structures. The first of these groups consist of *Acacias* have fern like bi-pinnate leaves, that are subdivided into small leaflets. The other group posses' what are known as phyllodes which are also called 'simple leaves'. The evolution of phyllodes within the genus *Acacia* seems to have been localized, occurring largely within Australia. Many hypotheses have been put forward in the past to try and explain what advantages phyllodes incur on the species that bear them. Many studies have indicated drought tolerance and resistance as a main evolutionary driver of phyllodes. However due to the very low concentrations of nutrients particularly P within Australia and the generally longer life span exhibited by phyllodes compared to normal compound leaves, we hypothesized that phyllodes were in fact an adaptation to nutrient limitation, and provide a way in which to limit nutrient loss back to the environment.
In order to test our hypothesis we analysed the distributions of 6 *Acacia* spp., three of which were phyllodinous and three of which bore compound leaves, in relation to soil P concentrations, mean annual precipitation and temperature. Due to all 6 of these species being invasive within South Africa we compared their distribution of these species both within Australia and South Africa to determine wither species were following similar trends.
In this study we determined that phyllodinous *Acacia* spp. were occurring on low P soils at significantly higher frequencies to species bearing compound leaves. The reverse relationship however was also recorded for areas of high P with compound leaf bearing species being more dominant. Species followed similar trends between continents, however due to these species being invasive in SA it was assumed that species had not reach their ideal or potential distribution ranges which may mean that trends may become stronger with time. Temperature and rainfall did not show any relationship to foliage type and it was there for concluded that phosphorus concentrations have been the main evolutionary driver of the phyllode.

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Introduction

The genus *Acacia* is very well known and common to both South Africa and Australia. In Australia, Acacias are the largest, most widely spread and ecologically and economically important genus in the Fabaceae family (Warick & Thukten, 2006). The genus consists of over 1000 species, most of which are native to Australia and predominantly in the subgenus *Phyllodineae*. Perhaps one of the most intriguing aspects about the genus *Acacia* is their divergence into two major groups that poses entirely different leaf structures. The first of these groups consist of *Acacia* spp. that poses fern like bi-pinnate leaves, which are subdivided into small leaflets. The other major group posse's phyllodes that are analogous to "simple" leaves.

Phyllodes of *Acacia* species vary considerably in size, shape and vestiture, however, anatomically they are rather less diverse than bi-pinnate leaves (Boughton, 1986). Interestingly, phyllode bearing *Acacia* spp. are restricted to Australia and a few Pacific and Indian Ocean islands (Fig. 1A). The isolation of this group deserves an explanation because *Acacia* spp. which produce normal bi-pinnate leaves are found in Australia, Africa, America and certain parts of Asia (Fig. 1B) (Armstrong, 1998). When phylodinous Acacias first germinate they are no different to any other *Acacia* sp. and produce bi-pinnate leaves, however these leaves are succeeded by phyllodes after a period of weeks to years (Brodribb & Hill,1993). This ontogenetic pattern indicates that phyllodes are a derived character occurring on plants in which bi-pinnate leaves are the ancestral state. The bi-pinnate leaves of *Acacia* spp. have thin cuticles with very little structural thickening and virtually all tissue devoted to photosynthesis (Brodribb & Hill.1993). In contrast, phyllodes are more robust with a very thick cuticle and a high percentage of lignified tissue (Brodribb & Hill, 1993). This increase in structural support means that only about half of a phyllode is photosynthetically active, but that the structure is much longer lived when compared to bi-pinnate leaves. Comparisons of different plant communities around the world have suggested that different leaf types are typical of different environments (Cunningham *et al.,* 1999). For example leaves of rain forest species share characteristics that distinguish them from plants of low-fertility heaths or low-rainfall deserts; these differences suggest that rainfall and soil fertility have been important factors in selecting for different leaf types.

The functional significance of the derived phyllodes has entertained ecophysiologists for some time. Two main hypotheses have been put forward as to why phyllodes have evolved. The first, proposed by Boughton (1986), states that the thick cuticles of phyllodes are an adaptation to drought stress. For this reason *Acacia* phyllodes are generally described as xeromorphic, with phyllodinisation itself being described as a Xeromorphic characteristic (Broughton 1986). The second, proposed by Pedly (1986), suggests that phyllodes evolved due to shady conditions faced by ancestral rainforest *Acacia* spp. and provided a means of increasing their photosynthetic area.

Soils of Australia are in general quantitatively, rather than qualitatively, different from those of other continents (Keely 1992). The high proportion of nutrient-poor soils found in Australia is unique, with soils generally being depleted of both N and P. The most depleted and limiting nutrient of these two is P (Orians & Milewski 2007). On average it is estimated that Australian soils have a total-P concentration of 300 ppm, however some regions have been recorded to have as little as 1 ppm P (Orians & Milewski 2007). For this reason P in particular has been emphasised as a major determinant of the composition and structure of Australian vegetation (Beadle 1954; Specht 1963; Adam *et al.* 1989). A survey of 77 samples from arid-zone soils in Australia revealed a mean P level of 240 ppm, compared to 643 ppm P recorded for 38 soils sampled in arid-zones on other continents (Charley & Cowling 1986; Stafford Smith & Morton 1990).

The significantly low concentrations of P found in Australia have been attributed to the high proportion of soils which are derived from sedimentary rocks low in P (Thomson & Leishman 2004). However, P and other nutrients have also been further depleted by weathering and leaching process which have been occurring for millions of years (Thomson & Leishman 2004) in a climatic stable region resulting in Australia being one of the most highly eroded landscapes in the world.

In areas where soil fertility is low, selection favours plants that have low nutrient requirements (Cunningham *et al.,* 1999). Leaf loss is always associated with the loss of a proportion of the nutrients in the leaf that are not recoverable during senescence. Due to the fact that leaf replacement bears a significantly higher nutrient cost, attributes which increase leaf longevity, such as increased leaf toughness and schlerophylly are important (Cunningham *et al.,* 1999). Retention of nutrients in evergreen foliage and efficient nutrient resorption from foliage before shedding are also effective strategies (Wright & Westoby 2003). A low requirement for nutrients or a low requirement for the limiting nutrient may also be effected by a reduction in plant size and aerial parts (Beadle 1996). All of the above tactics are widespread among phyllodinous *Acacias* and require an investment of energy, rather than nutrients.

In the past it has been postulated that soil phosphate is primarily responsible for the delimitation of mesomorphic and schlerophyllous communities within Australia (Beadle 1966). Although phyllodes have been studied comprehensively with regards to their ability to tolerate or resist droughts, few studies have examined how phyllodes may aid in allowing *Acacia* spp. to inhabit areas of low soil nutrients, in particular low P. We hypothesised that *Acacia* spp. developed phyllodes as schlerophylls in order to thrive on P-deficient soils. We assessed how the distribution of six Australian *Acacia* species was related to soil P availability, rainfall and temperature. Three of the species selected possessed phyllodes (*A. saligna, A. cyclops & A. pycnantha)* while the other three possessed bi-pinnate leaves (*A. dealbata, A. elata & A. baileyana*).Due to the fact that these six species are invasive in South Africa we compared their distributions both in Australia and South Africa to determine wither species showed similar trends on both continents. We predicted that phyllodinous *Acacia* spp. would have a higher frequency of occurrence within low phosphorus zones compared to bi-pinnate leaf bearing *Acacia* spp. and that if phyllodinous *Acacias* are adapted to low P conditions they will be of a small stature.

Materials & Methods

Distribution Maps

A.saligna, A.cyclops, A.pycnantha, A.dealbata, A.elata & *A.baileyana* in Australia and South Africa were chosen for this study as they represent species from both foliage types, three of them being phyllodinous species and three compound leaf bearing species. The reason we chose to look at their distributions within both South Africa and are Australia was to determine wither there were any significant trends in distribution linked to either P level, rainfall or temperature. These six species are also invasive within South Africa. Distribution maps of each *Acacia* species for Australia were obtained using Australia's Virtual Herbarium (Royal Botanic Gardens, Melbourne), while distributions of *Acacia* species for South Africa were obtained from the book "Alien weeds and invasive plants" (Henderson, 2001).

Distribution maps of all species in both countries were then digitally overlaid onto maps representing phosphorus levels, mean annual rainfall and mean annual temperature. Phosphorus maps for both Australia and South Africa were obtained from the Natural Resource Conservation Service (NRCS) (World Soil Resources, Washington D.C.). Mean annual rainfall and temperature maps for Australia were obtained from Australia's Virtual Herbarium (Royal Botanic Gardens, Melbourne). Mean annual rainfall and mean annual temperature maps for South Africa were obtained from the South African Atlas of Agrohydrology and Climatology (Schultze, 2001). After the vegetation distribution and the climatic/edaphic maps had been overlaid, each individual distribution point for all 6 species in South Africa and Australia was scored for soil P, rainfall and mean annual temperature.

Statistical analysis

Kruskal-Wallis Tests with multiple comparisons were performed on all species for all recorded variables (rainfall, temperature and phosphorus level) using Statistica 7. A cluster analysis using complete linkage and Euclidean distance to show similarities between species due to phosphorus levels was also performed using the Community Analysis Package (CAP, Pisces 2002).

Results

Biogeography of Acacia spp. (Figures 2 & 3)

***A. saligna*:** The distribution of *A. saligna* with in Australia tends to be mostly limited to the south-western coast and some inland parts of the continent. With only a few of it's distribution points being scattered along Australia's south-eastern coast. In South Africa we can see that *A. saligna* distribution is again limited, however this time mainly to the southern most parts of the country particularly along the coast.

***A. cyclops*:** The distribution of *A. cyclops* seems to follow a similar trend to that of *A. saligna*, as it is restricted largely to the south-western part of the country. However in the case of *A. cyclops* its distribution is limited mostly to areas in close proximity to the coast. There are however again a few other distribution points which have been recorded further east as with *A. saligna*. In South Africa it can be seen that again *A. cyclops* shows similar trends in distribution to that of *A. saligna* as it occurs in the southern most part of the country along the coast.

***A. pycnantha*:** The distribution of *A. pycnantha* within Australia does not seem to follow the same trend as that of the other two phyllodinous *Acacia* spp., and occurs largely in the south-eastern parts of the country. There are however a few distribution points dotted along the south-western coast in similar areas to where both *A. saligna* and *A. cyclops* are distributed. In South Africa *A. pycnantha* tends to follow similar distribution patterns to those recorded for the other two phyllode bearing species, with all distribution points occurring in the Southern most part of the country. In SA one will also notice that there are a lot fewer recorded distributions for *A. pycnantha* compared to those of the other two species.

***A. dealbata*:** The distribution of *A. dealbata* within Australia tends to be limited mostly to the south-eastern part of the country, with a few distribution points recorded on the south-western coast. In South Africa *A. dealbata* tends to occur in the central and north-eastern parts of the country, and does not occur along the coast.

***A. baileyana*:** The distribution of *A. baileyana* in Australia is very similar to that of *A. dealbata*, as most of the recorded distribution points occur in the south-eastern part of the country, with a few isolated points being recorded on the south-western coast. In South Africa *A. baileyana* again shows very similar distribution patterns to *A. dealbata* with a large number of its distribution points occurring in the central and north-eastern parts of the country. However there are a few distribution points scattered along the east coast as well as in the southern most parts of the country.

***A. elata*:** The distribution of *A. elata* with in Australia is similar to the two other *Acacias* which posses' compound or bi-pinnate leaves (*A. dealbata* & *A. baileyana*), that is that it occurs on the south-eastern part of the country. Its distribution however is far more restricted than those of the other two species.

In South Africa *A. elata* occurs along the southern coast, however there are very few recorded distribution points for *A. elata* in South Africa.

Distributions in relation to phosphorus Levels

Australian phyllodinous *Acacia* spp. tend to occur on low-phosphorus soils at a much high frequency, compared to on soils which have moderate, high or very high P levels (Fig. 4A). This trend was common across all three species sampled. However phyllode bearing species do not seem to be restricted to low-P soils and also occur across all four soil types. It is also evident from this data that *A. saligna* has a much larger number of recorded distribution points compared to the other two species. From the data recorded for Australian compound leaf bearing species it is evident that *A. elata* and *A. dealbata* occurred most commonly in areas that have very high P levels. *A. baileyana* on the other hand tends to have a more general distribution occurring quite evenly across soils that have moderate, high and very high P levels (Fig 4C). It must also be noted that *A. dealbata* has a much larger number of recorded distribution points compared to the other two compound leaf bearing species.

In South Africa compared to Australia there are far fewer recorded distribution points for both compound leaf bearing species and phyllodinous species (Fig 4). However species still tend to follow similar trends to those species occurring in Australia, with all phyllode-bearing species occur on either low or moderate P soils (Fig 4B). In South Africa, however, phyllodinous species tend to occur more commonly on moderate-P soils compared to low-P soils. There are also no records of any of the phyllodinous species occurring on high or very high-P soils. Compound leaf bearing species *A. baileyana, A. elata* and *A. dealbata* in South Africa show a very different distribution pattern compared to species occurring in Australia (Fig 4D). In this figure (Fig. 4D), all three species show the highest frequency of occurrence on soils which have moderate levels of phosphorus. *A. dealbata,* however does have a large number of distribution points which occur in areas of very high P which is consistent with its distribution in Australia.

In Figure 5 the distribution of phyllode bearing *Acacia* spp. in Australia is mirrored in a way by the bi-pinnate leaf bearing species. This is due to the fact that phyllodinous *Acacia* spp. occur predominantly within low P soils, while *Acacias* with compound leaves tend to occur in soils with high P levels. It is also visible from this figure that phyllodinous *Acacia* spp. have a larger number of distribution points with in Australia. In South Africa it is clear that the distribution of *Acacia* spp. do not follow the same trends as seen in Australia (Fig. 5); however there do seem to be some similarities as a large number of distribution points belonging to phyllodinous spp. tend to occur in low P soils. Most distribution points with in South Africa however for both phyllode and bi-pinnate leaf bearing species occur in soils which have moderate soil P.
Figure 8 is a cluster analysis representing the similarity between *Acacia* spp. distributions in Australia according to phosphorus level. As is evident from this figure phyllodinous species are clearly separated from species bearing compound

leaves. In this dendrogram *A. cyclops* and *A. pycnantha* are the two most similar species, with *A. saligna* being quite similar to both of them. *A. elata* and *A. baileyana* are also indicated to be very similar. *A. dealbata* is shown to be similar to both *A. elata* and *A. baileyana*. All phyllodinous species were also shown to be significantly different from compound bearing species according to a Kruskal-Wallis Tests. Figure 9 shows the similarity between species distributions due phosphorus levels in South Africa. From this figure we can see that *A. cyclops* and *A. saligna* are the most similar species. Once again as in Australia *A. elate* and *A. baileyana* are very similar to each other. A. dealbata is shown to be the most dissimilar from of all the species, while *A. pycnantha* is show to be similar to both *A. elate* and *A. baileyana*.

Distributions in relation to Mean Annual Precipitation

Both *A. saligna* and *A. cyclops* in Australia occur in areas which have similar amounts of rainfall. The largest numbers of individuals in both species tend to occur within areas receiving 500-600mm of rain a year (Fig. 6A). *A. pycnantha* also tends to occur in area of similar rainfall to *A. saligna* and *A. cyclops* however its mean distribution range is shifted slightly towards higher rainfall sites (Fig. 6A), as is evident by the large number of recorded distribution points occurring within areas receiving 600-800mm of rain a year. The distribution of *A. saligna* in Australia has the widest rainfall distribution, occurring in areas that receive as little as 250mm up to areas receiving as much as 1100mm of rain a year. The distribution of the three bi-pinnate or compound bearing *Acacias* in Australia (Fig. 6C) do not share the same means but they all seem to occur within similar rainfall regions. The distribution of *A. dealbata* tends to indicate that it has the ability to handle a large range of rainfalls; however it occurs mostly in areas that receive between 800 – 1000mm of rain (Fig. 6C). *A. elata* on the other hand tends to occur in areas which receive 1000-1600mm of rain, while *A. baileyana* prefers regions that receive 600-800mm of rain (Fig. 6C).

In South Africa *A. saligna* has the widest distribution range in terms of mean annual precipitation occurring in areas with as little as 175 – 850 mm precipitation (Fig. 6B). In South Africa, unlike in Australia, *A. saligna* and *A.*

cyclops do not share the same means in rainfall. Rather the largest numbers of distribution points for *A. saligna* occur within areas receiving 300-400mm, while *A. cyclops* occurs mostly in areas receiving 400-500mm (Fig. 6B). Similar to Australia *A. pycnantha* does not follow the same trends as the other two phyllodinous species, rather it tends to occur in moister sites with most recorded data points occurring in areas which receive 500-600 mm of rain a year (Fig. 6B). The distribution of all three bi-pinnate species within South Africa (Figure 6D) seem to have the same means as all of them occur at the highest frequency in areas that receive 600-700mm. In SA *A. baileyana* seems to occur across the widest scale of rainfall areas occurring in areas receiving as little as 350mm up to areas receiving as much as 1100 mm. *A. elata* occupied the narrowest range in rainfall only occurring in areas receiving 500-1000mm of rain.

From our results it would seem that in Australia the phyllodinous *Acacia* spp. occur within drier sites compared to bi-pinnate leaf bearing species. Large numbers of phyllodinous species were recorded in low rainfall sites, as well as the shift of compound leave bearing species to moister sites. In South Africa *Acacia* spp. tend to show similar trends to those species occurring in Australia, this is evident due to the fact that there is a general shift of phyllodinous species to dryer sites while *Acacia* spp. bearing compound leaves tend to occur in much moister areas.

The cluster analyses for Australian (Fig. 9) and South African (Fig. 10) *Acacias,* show similarities between species in terms of mean annual precipitation, it is evident from these figures that there are no visible trends in relation to foliage type.

Distributions in relation to mean annual temperature

The distribution of phyllodinous *Acacias* spp. do not seem to follow any significant trends with temperature (Fig. 7). All species in Australia have different mean temperature ranges (Fig. 7A). *A. cyclops* and *A. pycnantha* appear, however, to occur in similar temperature ranges, occurring predominantly in areas with temperatures of 20-22°C (Fig. 7A). However the means of these two species are significantly different with the highest frequency of distribution points of *A. cyclops* occurring in areas with a temperature of 22°C while the mean of *A. pycnantha* was 20°C. The distribution of *A. saligna* in terms of temperature indicates a shift towards warmer climates as it has a temperature range of 20-30 °C, with a mean of 24 °C. In Australia the distribution of *A. elata* and *Abaileyana* tends to occur in areas of similar temperature as both species share the same mean value of 22 °C (Fig. 7C). *A. dealbata* on the other hand seems to be favouring lower temperatures as it has a mean of 20 °C, but has a large number of distribution points in areas with temperatures between 16-18 °C (Fig 7C).

Unlike in Australia *A. saligna* and *A. cyclops* in South Africa share the same mean temperature range of 16-18°C. It is also noticeable that the average temperatures for all species are around 2°C lower than those recorded in Australia (Fig. 7B). The distribution of *A. pycnantha* in South Africa seems to indicate that this species' mean temperature range is slightly lower than both *A. saligna* and *A. cyclops*, ranging from 14-16. In South Africa (Fig. 7D) all three compound leaf bearing species tend to share the same mean temperature of between 16-18 °C, again one will notice that the temperature in which these species are occurring in SA are much lower than the temperatures recorded for the same species in Australia.

We can see from these figures that there are not clear cut trends in the distribution of *Acacia* spp. in relation to temperature, however it does appear that phyllodinous spp. are occurring within warmer sites while the other species tend to occur within lower temperatures. In South Africa there does not seem to be any kind of trend either however is seems as though *Acacia* spp. bearing bi-pinnate leaves are occurring within warmer temperatures compared to those of phyllodinous species.
Figures 12 & 13 represent cluster analyses for Australian and South African *Acacias* in terms of similarity due to annual mean temperature. As is evident from these there does not seem to be any kind of trend related to foliage type.

Discussion

When comparing the distributions of phyllodinous and compound bearing *Acacia* spp. in both Australia and South Africa it is evident that the species are follow similar trends in both countries. In Australia *A. saligna* and *A. Cyclops,* both phyllodinous species, occur within the south-western part of the country. This part of the country is generally considered to have lower concentrations of phosphorus and lower amounts mean annual precipitation compared to the south-eastern parts. It is therefore expected that if phyllodinous *Acacia* spp. are adapted to living in harsher environments and in particular on low-P soils they would tend to be more dominant in the south-western parts of the country, as was recorded in this study. *Acacia* spp. with compound leaves on the other hand would be expected to occur in the south-eastern parts of the country where P-levels and precipitation are higher. The only species which does not follow this trend is *A. pycnantha* which occurs almost entirely in the south-eastern part of the continent.

In South Africa *Acacia* spp. show a similar trend to that in Australia. However, P and rainfall decrease from the north-eastern parts of the country southwards. If phyllodinous *Acacia* spp. are adapted to low P soils, we would expect an increase in abundance of these species in the southern most parts of the country. Compound leaf bearing species on the other hand should show the opposite response and decrease in abundance as one moves southwards. As is evident from our results, *Acacia* spp. follow this predicted trend quite closely, except for *A. elata,* a compound leaf bearing species, which has only been recorded within the southern parts of South Africa. This trend, however, may just be due to the fact that these species are invasive in South Africa and therefore have not had enough time to reach their potential distributions.

The results of this study indicated that, particularly in Australia, phyllodinous *Acacia* spp. occur at higher frequencies in areas which have lower soil P concentrations compared to compound leaf bearing species. The reason that phyllodinous spp. can occur within these low nutrient soils is due to the evolution of phyllodes. This assumption is supported by the 'leaf economic spectrum' (Wright *et al.* 2004), which predicts that leaf traits form a spectrum of variation among plant species. This spectrum runs from species with short-lived leaves that have high leaf area per mass, high nutrient concentrations and high carbon assimilation rates, to species with long-lived leaves, low nutrient concentrations and lower maximum physiological rates (Wright *et al.* 2005). In other words this spectrum can be characterised as running from species that invest in cheap but frequently replaced leaves to those that are more adapted to a nutrient-conserving 'lifestyle' (Reich *et al.* 1997). Due to the presence of a thick, central parenchymatous mesophyll layer and two palisade layers, phyllode lamina depth is typically thicker and/or denser than the those of their leaf counterparts. This increased thickening however leads to a reduction in foliage area per unit foliage mass (SLA) (Bought 1986; Atkin *et al.* 1998). Consequently, lamina depth has been shown to generally increase as water or nutrient levels decrease (Cunningham *et al.* 1999). Across a variety of different nutrient concentrations mean leaf lifespan and SLA have consistently been shown to be negatively correlated (Wright *et al.* 2005). This along with the fact that photosynthetic rates per unit leaf mass of phyllodes are typically lower compared to that of leaves, indicates that phyllodinous and compound leaf bearing *Acacia* spp. are on opposite ends of the 'leaf economic spectrum' with pyllodes being more adapted to a nutrient-conserving lifestyle, while bi-pinnate leaves are adapted more to a quick returns strategy.

A long leaf lifespan in resource-poor environments is generally thought to enhance nutrient conservation, and provide a longer time for the amortization of leaf construction costs in species with low rates of carbon gain (Wright *et al.* 2001). Another way in which phyllodes have adapted to occurring in low nutrients soils is through nutrient resorption. This is the process in which nutrients are withdrawn from the leaves prior to abscission; these nutrients are then redeployed to developing tissue, or stored for later use. On average around 50% of leaf N and P in phyllodes is recycled via resorption (Wright & Westoby 2003); however some pyllodes like those from A. *holosericea* have been recorded to remobilize as much as 85% of their total P before leaf fall (Langkamp & Dalling 1982). Due to the fact that low levels of P are often associated with a reduction in overall plant size (Breadle 1966; Cunningham *et al.* 1999), it may be expected that phyllode bearing *Acacia* spp. are smaller than bi-pinnate bearing species. In species we examined, all the compound leaf producing species were 4 m taller than the phyllodinous species (Table 1). The bi-pinnate leaved A. *dealbata* with the highest frequency of distribution points in areas of high P concentrations was the tallest of the species we examined providing further evidence that phyllodes evolved in *Acacias* as an adaptation to low nutrient soils and not to water stress.

Mean annual precipitation did not explain the distribution of *Acacia* species in relation to their foliage type as well as did soil P concentrations. Species distributions within Australia and South Africa did not follow the same trends, thus indicating that rainfall was probably not the major driver of the evolution phyllodinous foliage. However, in previous studies phyllodes have been shown to confer some advantages in areas which are water limited (Warwick & Thukten 2006; Nativ *et al.* 1999). The reasons why phyllodes are believed to be an adaption to low rainfall areas is due to the fact that their stomata are more sensitive to vapour pressure deficits, they have higher water use efficiencies and greater longevity compared to bi-pinnate leaves (Warwick & Thukten 2006; Nativ *et al.* 1999). Although shortage of water might appear to offer different physiological challenges compared to shortage of nutrients, some authors have argued that shortage of either resource leads to a common "stress", and that stress tolerance leads to a common set of adaptations (Grime 1977). Four reasons have been put forward as to why low-nutrient and low-rainfall adaptations may converge. The first is that low growth rate is generally the primary response to limited availability of either resource (Cunningham *et al.* 1999). Secondly, nutrient limitation can slow the growth of roots, leading to limited asses to water

(Givnish 1987). The third reason is that low rainfall can often lead to low nutrient availability because nutrients are not available unless in solution (Kunchenbunch *et al.* 1986). The fourth and final reason is that low growth rates, through whatever limiting factor, might select for greater structural support and leaf longevity (Coley *et al.* 1985). For these reasons it is important that we state that phyllodes although not shown in this study may indeed help *Acacia* spp. occur within areas of low rainfall.

Temperature was shown not to play a major role in determining the distribution of phyllode and bi-pinnate bearing *Acacia* species. This is interesting as previous studies have tried to link the distribution of *Acacia* spp. to temperature, assuming that phyllodes are adapted to help plants survive in warmer climates. In Australia and South Africa temperature ranges of *Acacia* spp. showed similar distributions with no significant patterns to do with foliage type.

Conclusions

Our results indicated that the distribution of *Acacia* is largely dependent on phosphorus concentration within the soil. During the evolution of the genus *Acacia* phyllodes have evolved to help species occur in low nutrient soils by conserve nutrients. These adaptations are mainly in the form of stronger longer lived foliage which does not need to be replaced as often as normal bi-pinnate leaves. These findings are particularly interesting in the context of South Africa where these species are invasive. Our results suggest that depending on their foliage *Acacia* species, will tend to invade areas that they are adapted to with phyllodinous *Acacia* spp. being more competitive on low P soils, such as in the Cape fynbos biomes while the compound leaf bearing *Acacia* spp. will be more invasive in areas of high P concentrations. Further studies are needed in this field however to determine wither these trends are true for all phyllodinous and compound bearing species.

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References

- Armstrong W. 1998. The Unforgettable Acacias. *Zoonooz* Volume 71 (8): 28-31.
- Beadle, NC (1954). Soil phosphate and the delimitation of plant communities in eastern Australia. *Ecology* **35**: 370–375.
- Beadle N., 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with specicial reference to xeromorphy and sclerophylly. *Ecology* **47**: 992-1008
- Brodribb T. & Hill RS. 1993. A physiological comparison of leaves and phyllodes in *Acacia melanoxylon*. *Australian Journal of Botany* **41**, 293-305pp
- Broughton VH 1986. Phyllode structure, taxonomy and distribution in some Australian acacias. *Australian Journal of Botany* **34:** 663-674
- Charley JL & Cowling RW 1968. Changes in soil nutrient status resulting from overgrazing and their consequences in plant communities of some arid areas. *Proceedings of the Ecological Society of Australia* **3**: 28–38.
- Cunningham, S.A., Summerhayes, B. & Westoby, M., 1999 Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecological Monographs* **69**: 569–588.
- Keeley JE 1992. A Californian's view of fynbos. In The Ecology of Fynbos. Nutrients, Fire and Diversity (ed. R. M. Cowling) 372– 388. Oxford University Press, Cape Town.
- Langkamp P & Dalling M. 1982. Nutrient Cycling in a Stand of *Acacia holosericea* A. Cunn. ex G. Don. 11* Phosphorus and Endomycorrhizal Associations. Aust J. Bot **30,** 107-19

- Orians HG & Milewski AV 2007 . Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biological Reviews* **82:** 393–423
- Reich PB, Walters MB & Ellsworth DS 1997. From tropis to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Science USA* **94:** 13730-13734
- Stafford Smith DM & Morton SR 1990. A framework for the ecology of arid Australia. *Journal of Arid Environments* **18**: 255–278.
- Thomson VP & Leishman MR 2004. Survival of native plants of Hawkesbury Sandstone communities with additional nutrients: effect of plant age and habitat. *Australian Journal of Botany* **52:** 141-147
- Wright I.J., Reich PB, Westoby M., 2001**.** Strategy-shifts in leaf physiology, structure and nutrient content between species of high and low rainfall, and high and low nutrient habitats. *Functional Ecology* **15**: 423–434.
- Wright I.J & Westoby M. 2003. Nutrient concentration, resorption and lifespan: leaf traits of Australia sclerophyll species. *Functional Ecology* **17:** 10-19
- Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Garnier E, Hikosaka K, Lamont BB, Lee W, Oleksyn J, Osada N, Poorter H, Villar R, Warton DI and Westoby M. 2005. Assessing the generality of global leaf trait relationships. *New Phytologist* **166:** 485-496
- Warwick N & Thukten 2006. Water relations of phyllodinous and non-phyllodinous *Acacias*, with particular reference to osmotic adjustment. *Physiologia Plantarum* **127:** 393-403

Figure Legends

Table 1: The six *Acacia* spp. used in this study along with their dominate foliage type, size and average maximum recorded plant heights

Figure 1: Map showing the world wide distribution of Acacia subgenus *Phyllodineae (A)* and the world wide distribution of the genus Acacia (B) (Wattle.)

Figure 2: Maps showing the distribution of the six *Acacia* spp. in Australia with reference to phosphorus concentrations, mean annual precipitation and temperature.

Figure 3: Maps showing the distribution of the six *Acacia* spp. in South Africa with reference to phosphorus concentrations, mean annual precipitation and temperature.

Figure 4: Frequency distribution of phyllodinous and compound leaf bearing *Acacia* spp. in Australia (A & C) and South Africa (B & D) according to their occurrence on soils of different phosphorus concentrations.

Figure 5: Average frequency distribution of all phyllode and bi-pinnate bearing *Acacia* spp. in Australia and South Africa according to their occurrence on soils of different phosphorus concentrations.

Figure 6: Frequency distribution of phyllodinous and bipinnate leaf bearing *Acacia* spp. in Australia (A & C) and South Africa (B & D) according to their distribution within areas of different mean Annual precipitation

Figure 7: Frequency distribution of phyllodinous and compound leaf bearing *Acacia* spp. in Australia (A & C) and South Africa (B & D) according to their distribution within areas of different mean Annual temperatures.

Figure 8: Cluster analysis showing the similarity between *Acacia* spp. in Australia due to their distribution on 4 different soil phosphorus levels. Complete linkage and Euclidian distance were used to measure similarity. Letters (AB) indicate significant differences at the $p=<0.5\%$ level (post-hoc Tukey test).

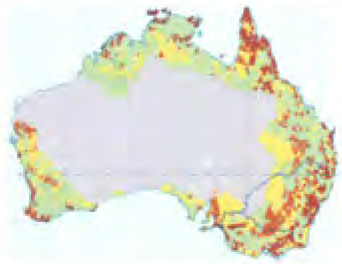
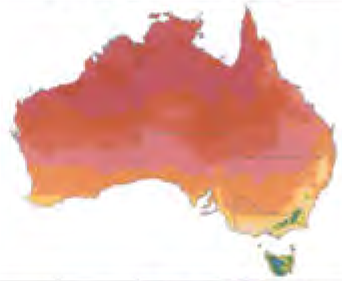
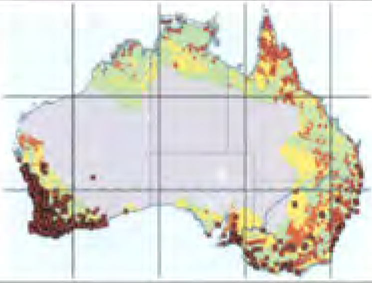
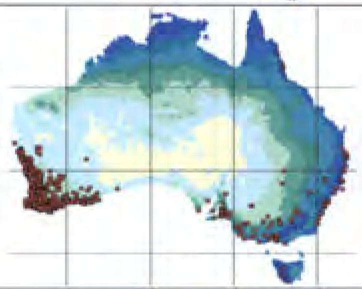
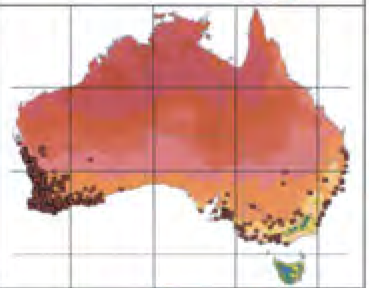
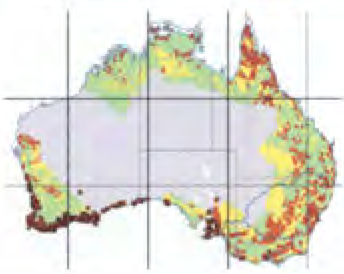
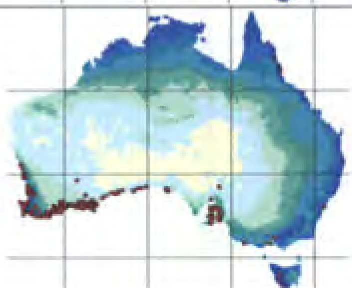
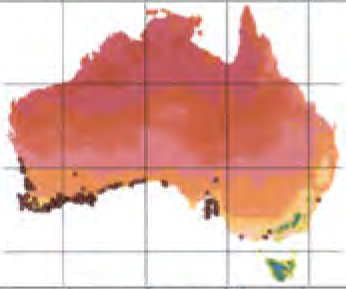
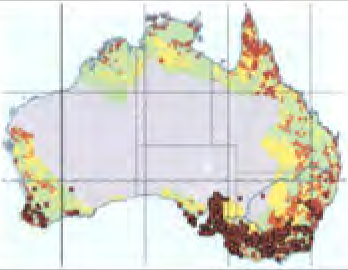
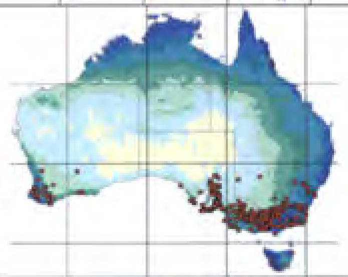
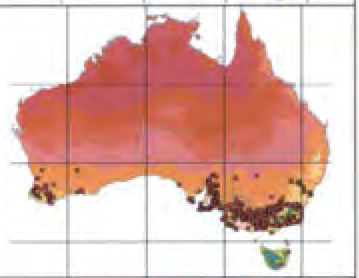
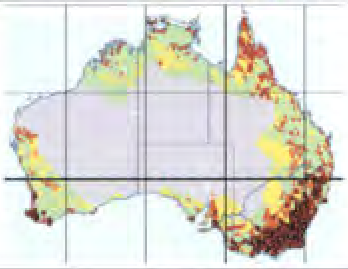
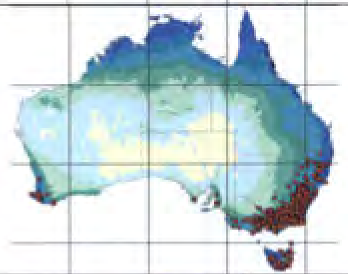
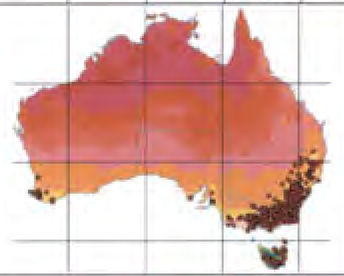
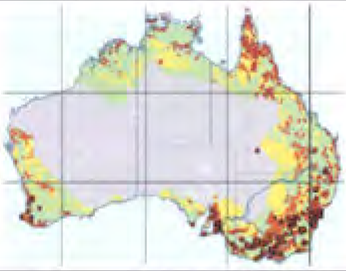
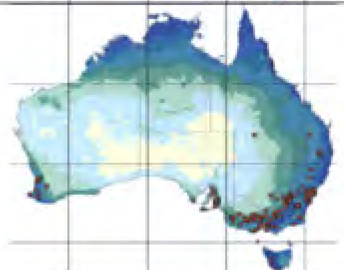
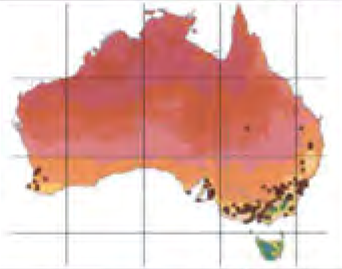
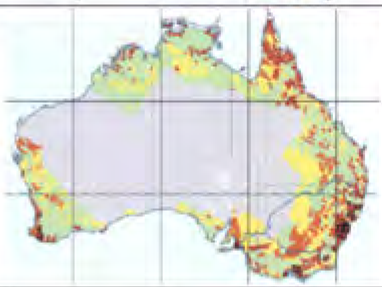
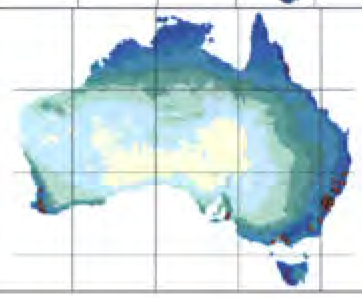
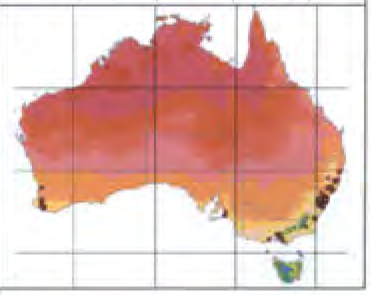
Figure 9: Cluster analysis showing the similarity between *Acacia* spp. in South Africa due to their distribution on 4 different soil phosphorus levels. Complete linkage and Euclidian distance were used to measure similarity. Letters (ABC) indicate significant differences at the p=<0.5% level (post-hoc Tukey test).

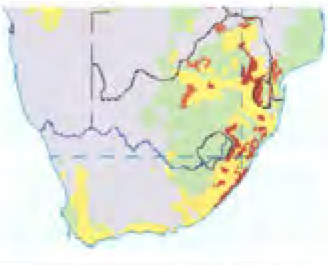
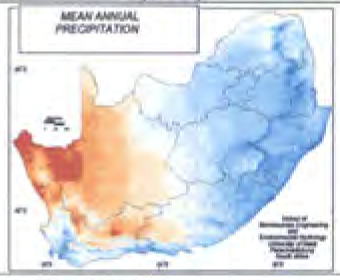
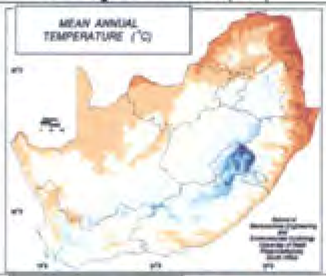
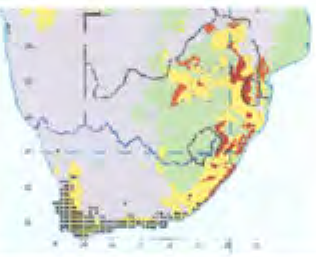
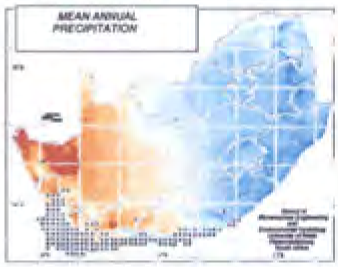
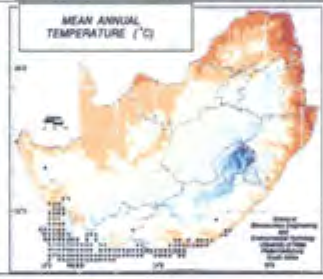
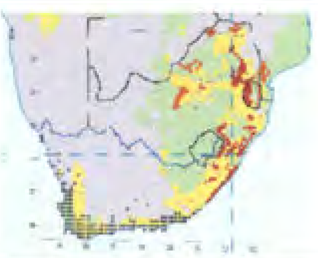
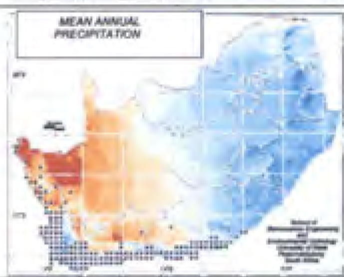
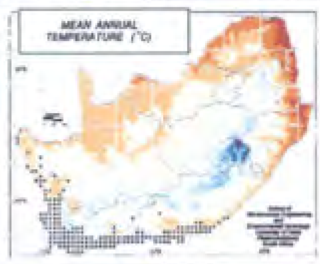
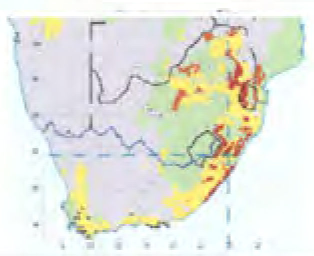
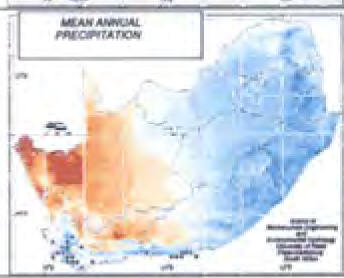
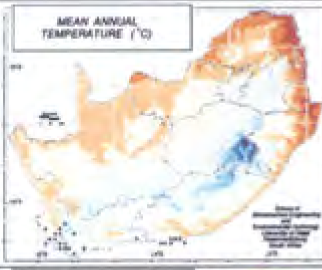
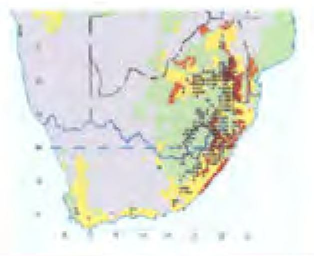
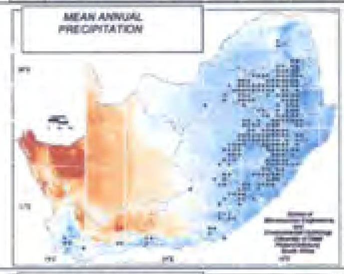
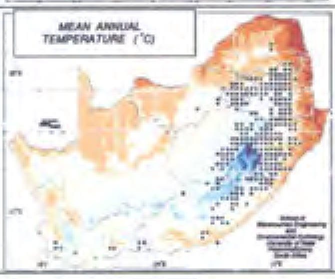
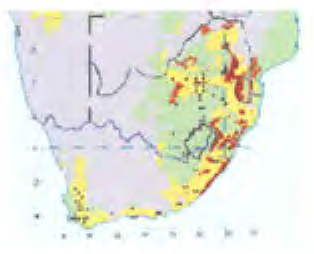
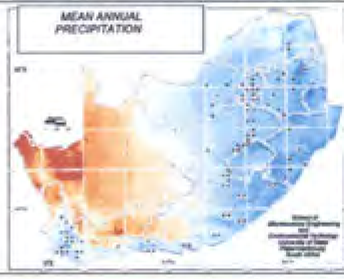
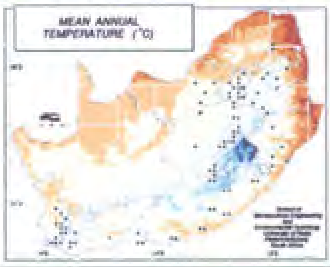
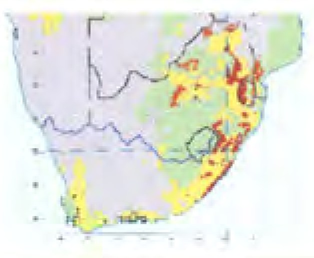
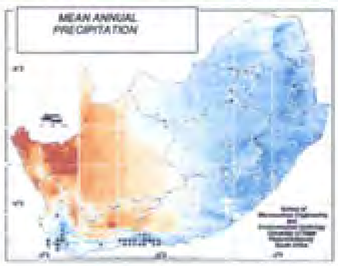
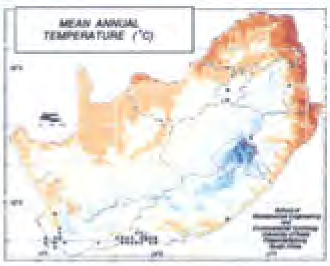
Figure 10: Cluster analysis showing the similarity between *Acacia* spp. in Australia due to their distribution in areas receiving different amounts of rainfall. Complete linkage and Euclidian distance were used to measure similarity.

Figure 11: Cluster analysis showing the similarity between *Acacia* spp. in South Africa due to their distribution in areas receiving different amounts of rainfall. Complete linkage and Euclidian distance were used to measure similarity.

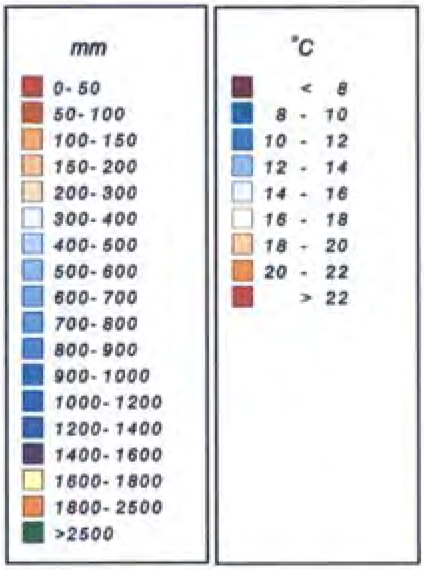
Figure 12: Cluster analysis showing the similarity between *Acacia* spp. in Australia due to their distribution in areas with different mean annual temperature. Complete linkage and Euclidian distance were used to measure similarity.

Figure 13: Cluster analysis showing the similarity between *Acacia* spp. in South Africa due to their distribution in areas with different mean annual temperature. Complete linkage and Euclidian distance were used to measure similarity.

Species	Foliage	Phosphorus Level	Mean Annual Precipitation (mm)	Mean Annual Temperature (^{o}C)
				
A.saligna	**Phyllode**			
A.cyclops	**Phyllode**			
A.pycnantha	**Phyllode**			
A.dealbata	**Bi-pinnate**			
A.baileyana	**Bi-pinnate**			
A.elata	**Bi-pinnate**			

Species	Foliage	Phosphorus Level	Mean Annual Precipitation (mm)	Mean Annual Temperature (°C)
				
saligna	Phyllode			
A.cyclops	Phyllode			
.pycnantha	Phyllode			
A.dealbata	Bi-pinnate			
.baileyana	Bi-pinnate			
A.elata	Bi-pinnate			

Temperature and rainfall key for Australia



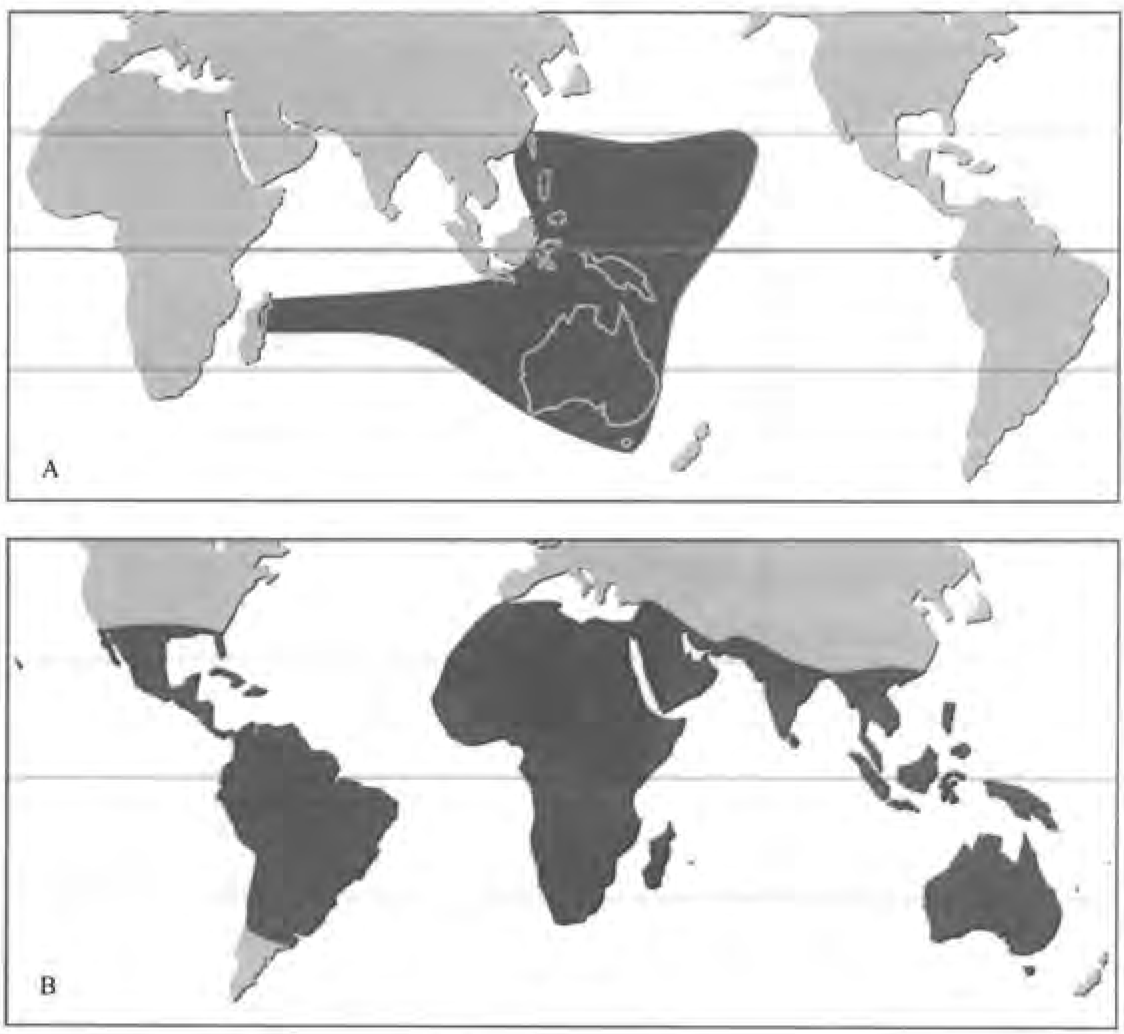
Temperature and rainfall key for South Africa

Figures

Table 1:

Species	Foliage type	Folige size(mm)	Tree height (Max) (m)
A.baileyana	Leaflets	5-8 x 0.7-1.6	10
A.dealbata	Leaflets	1.5-5 x 0.4-0.8	30
A.elata	Leaflets	20-60 x 5-13	20
A.cyclops	Phyllodes	40-95 x 6-15	6
A.pycantha	Phyllodes	90-150 x 10-35	8
A.saligna	Phyllodes	70-250 x 4-20	6

Figure 1:



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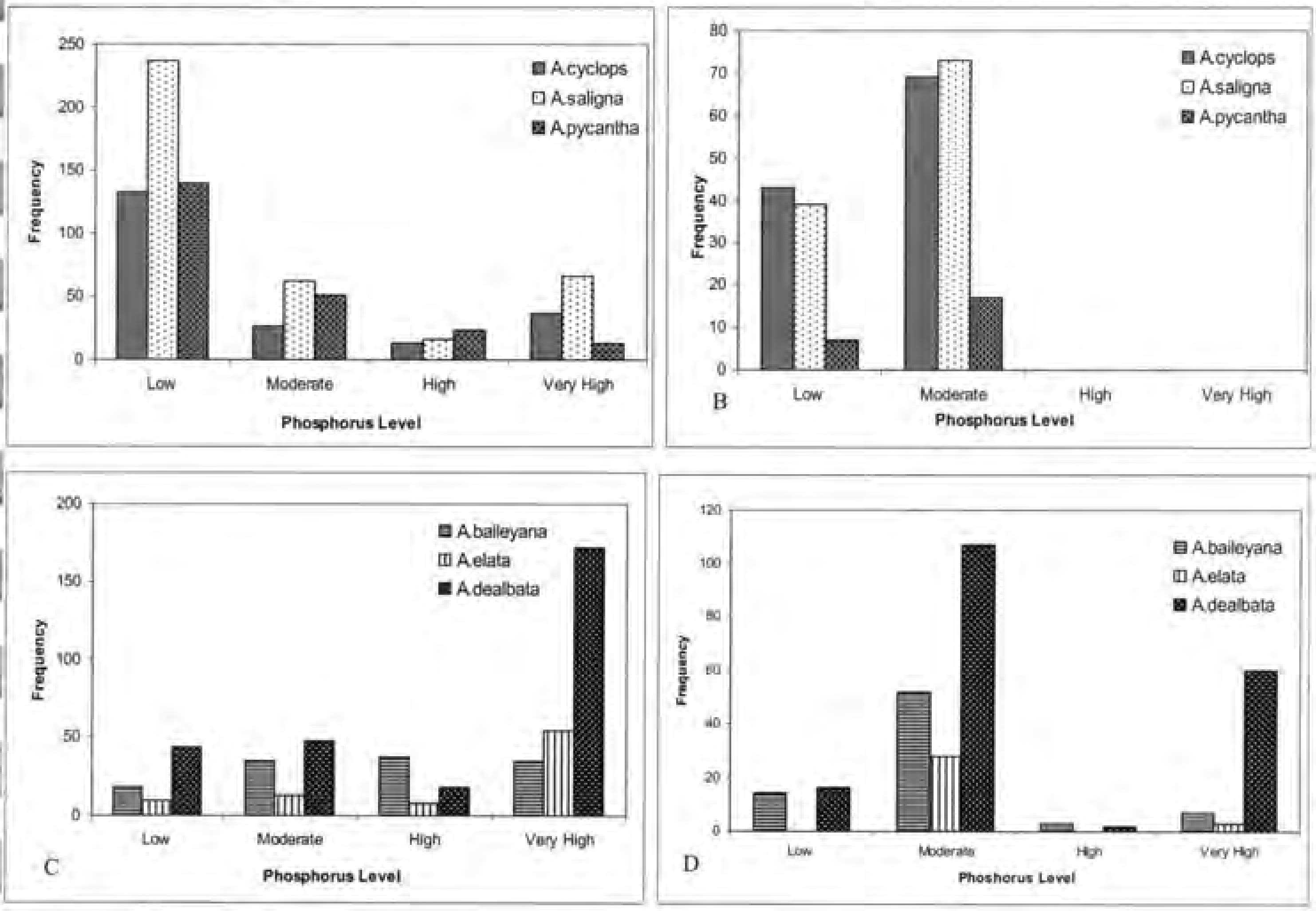

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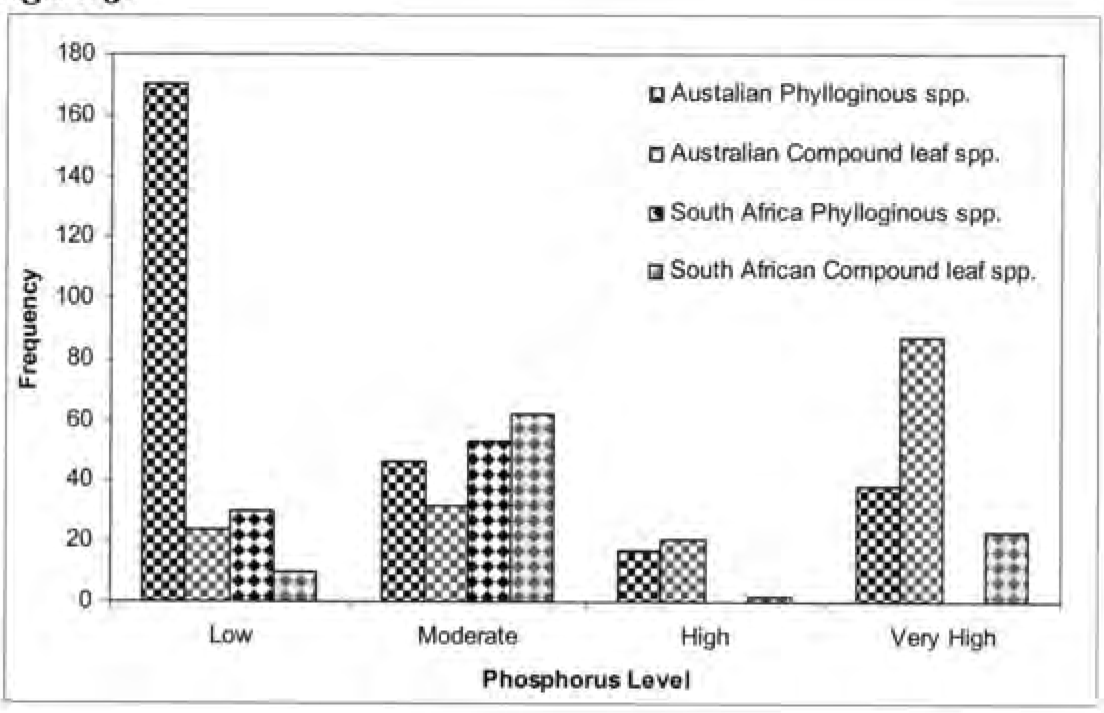

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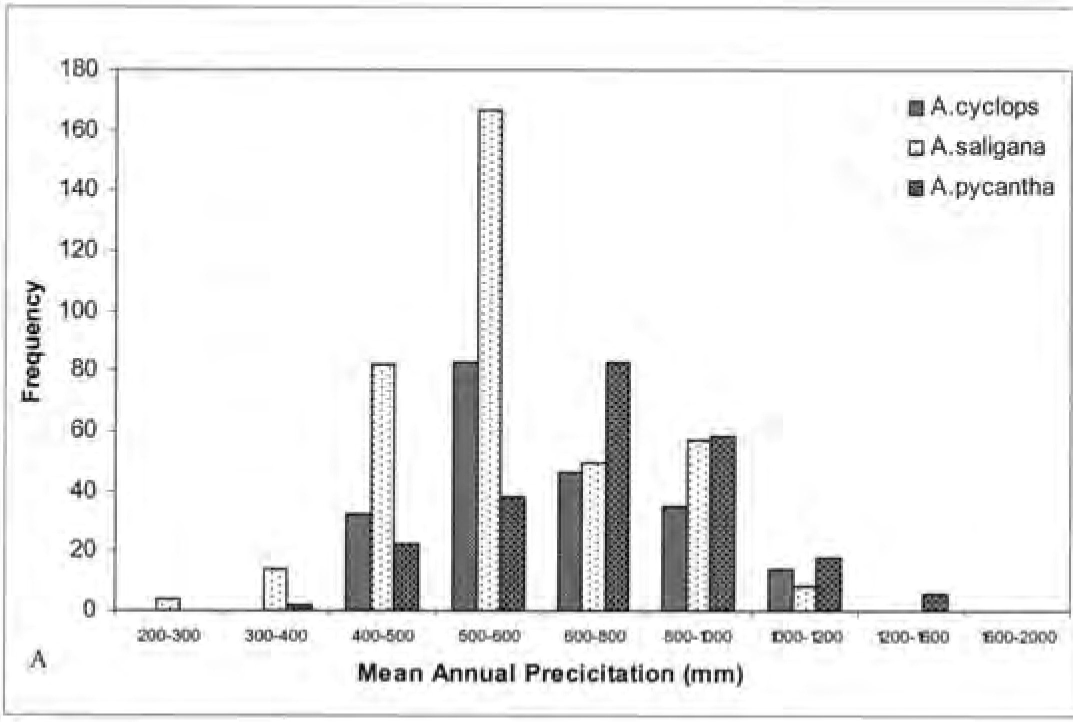
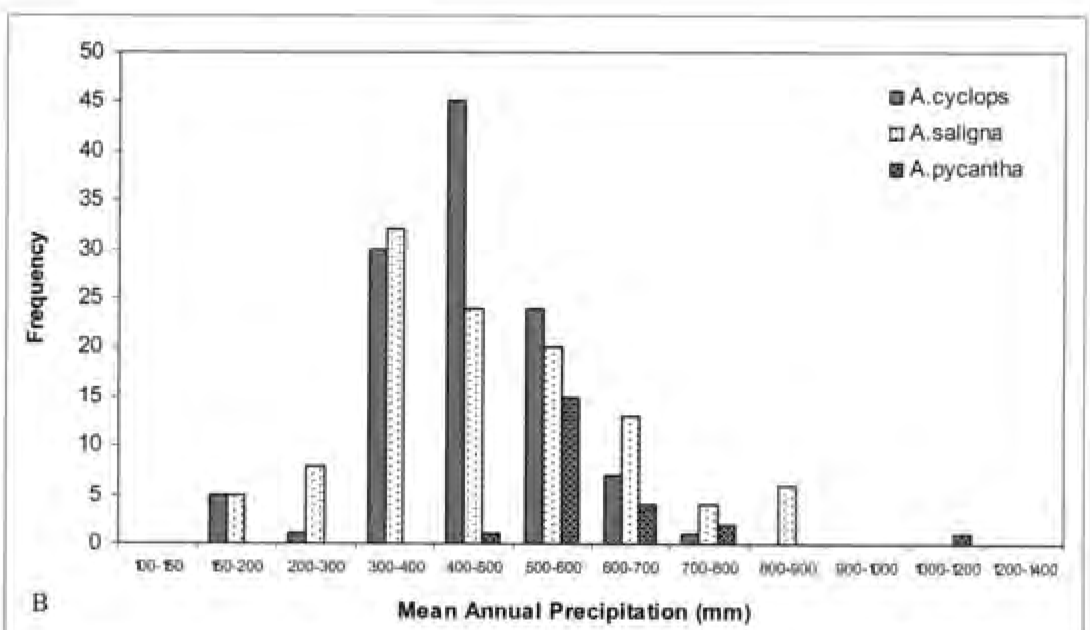
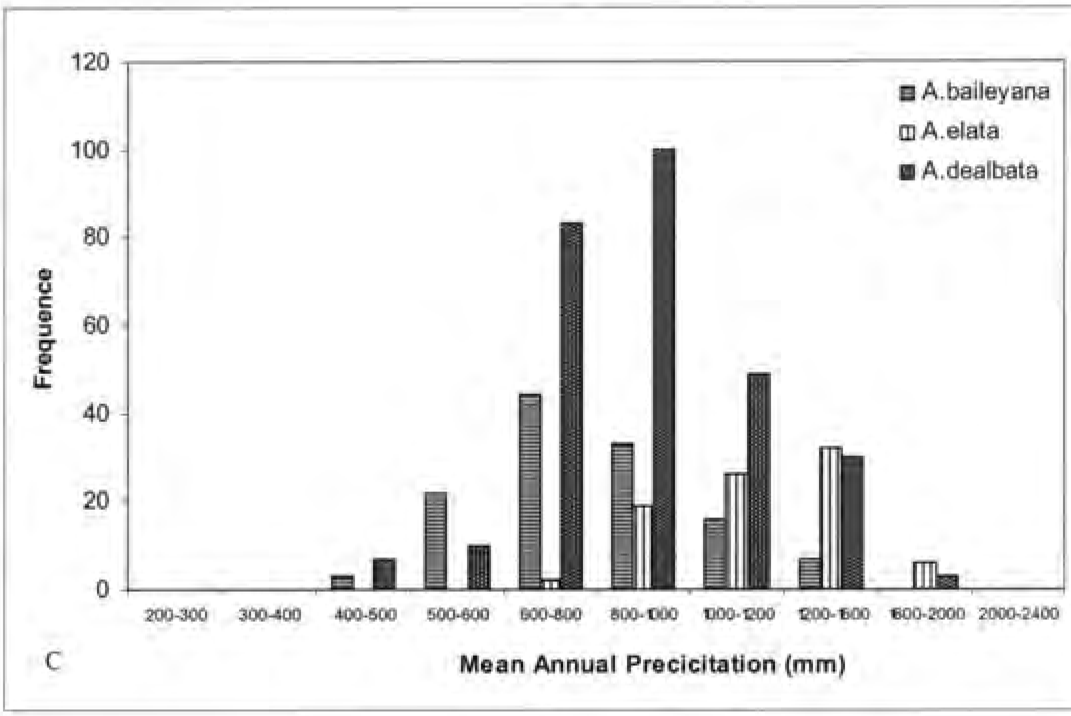
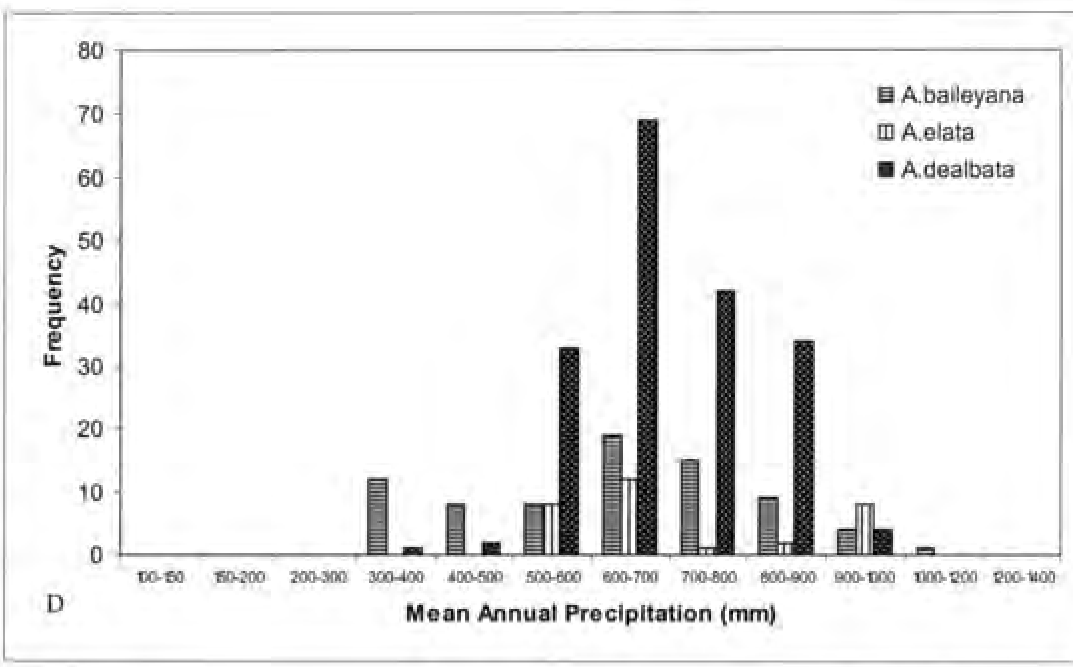

180
160
140
120
100
80
60
40
20
0
Frequency
A.cyclops
A.saligana
A.pycantha
200-300
300-400
400-500
500-600
600-800
800-1000
1000-1200
1200-1600
1600-2000
Mean Annual Precicitation (mm)
A


50
45
40
35
30
25
20
15
10
5
0
Frequency
A.cyclops
A.saligna
A.pycantha
Mean Annual Precipitation (mm)
B



A.baileyana
A.elata
A.dealbata
Frequence
Mean Annual Precicitation (mm)
C



A.baileyana
A.elata
A.dealbata
Frequency
Mean Annual Precipitation (mm)
D

Figure 7:

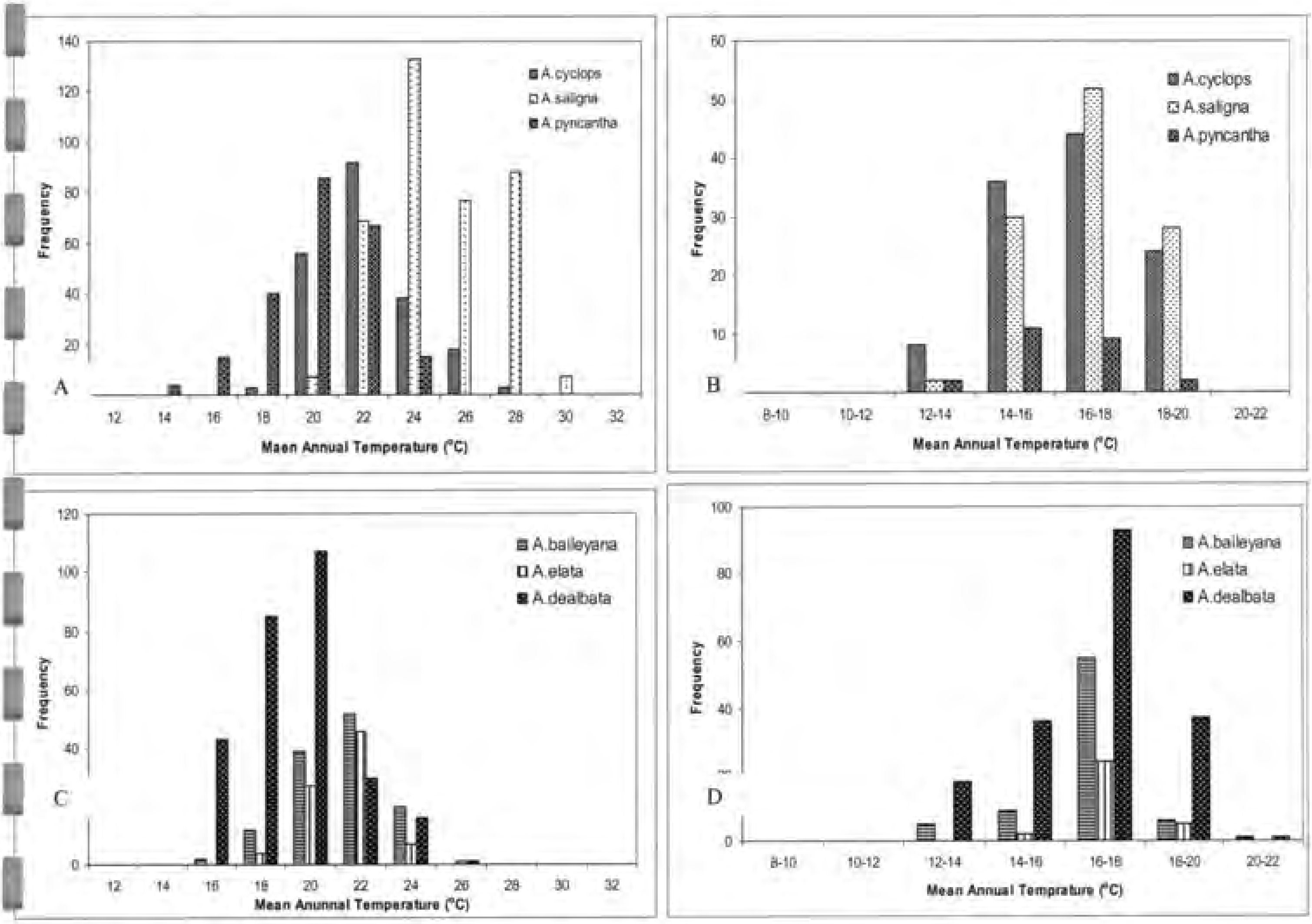
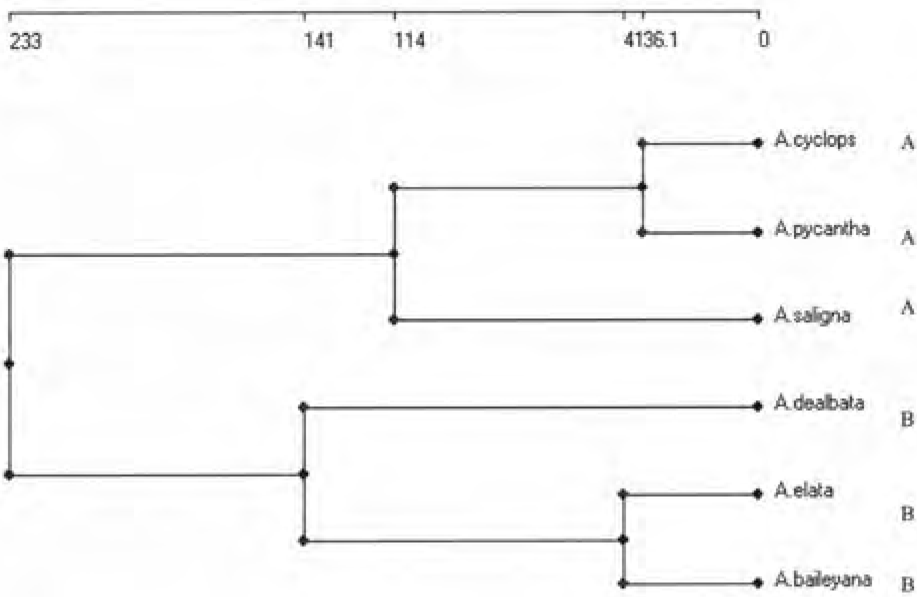

A
A.cyclops
A.saligna
A.pyncantha
Frequency
Maen Annual Temperature (°C)
B
A.cyclops
A.saligna
A.pyncantha
Frequency
Mean Annual Temperature (°C)
C
A.baileyana
A.elata
A.dealbata
Frequency
Mean Anunnal Temperature (°C)
D
A.baileyana
A.elata
A.dealbata
Frequency
Mean Annual Temprature (°C)

Figure 8:



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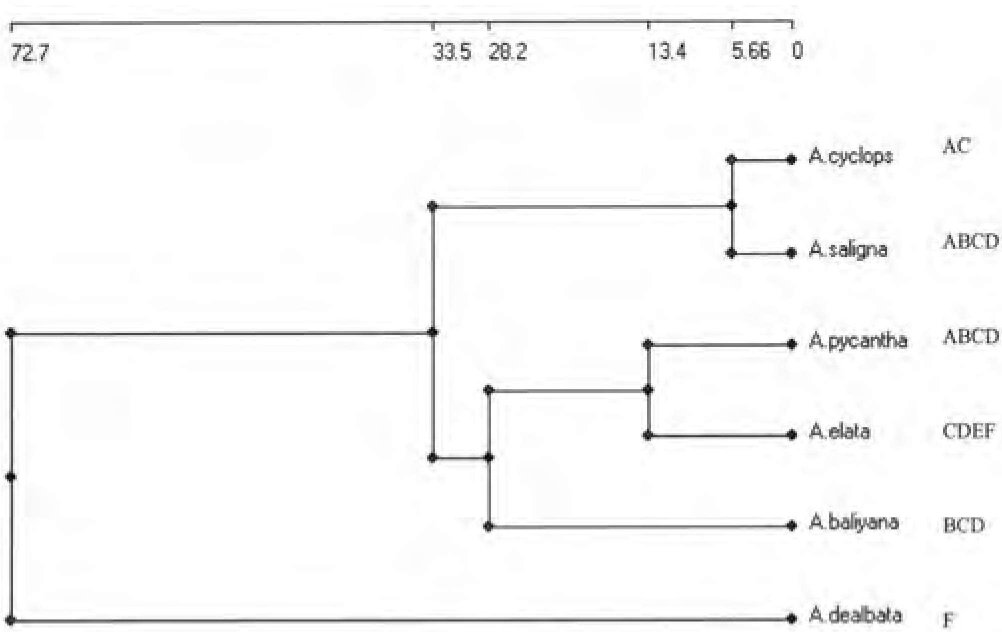

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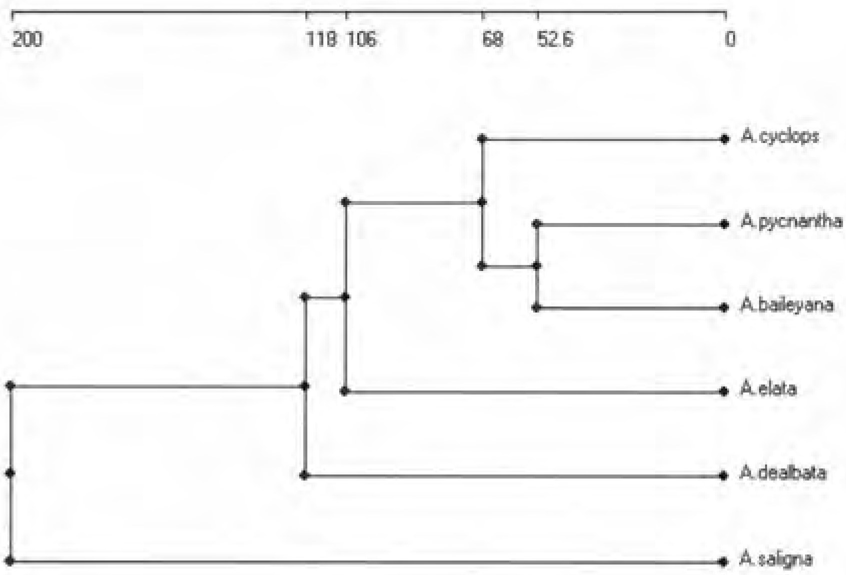

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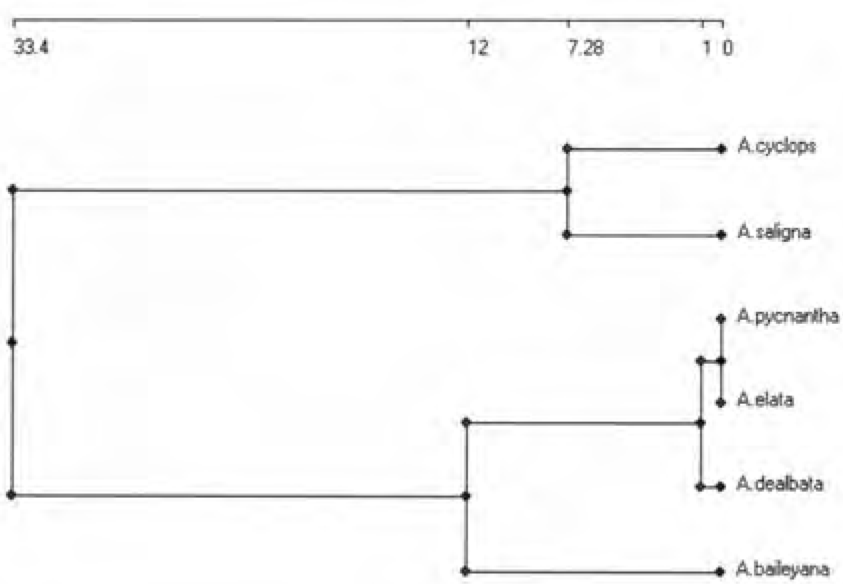

Figure 12

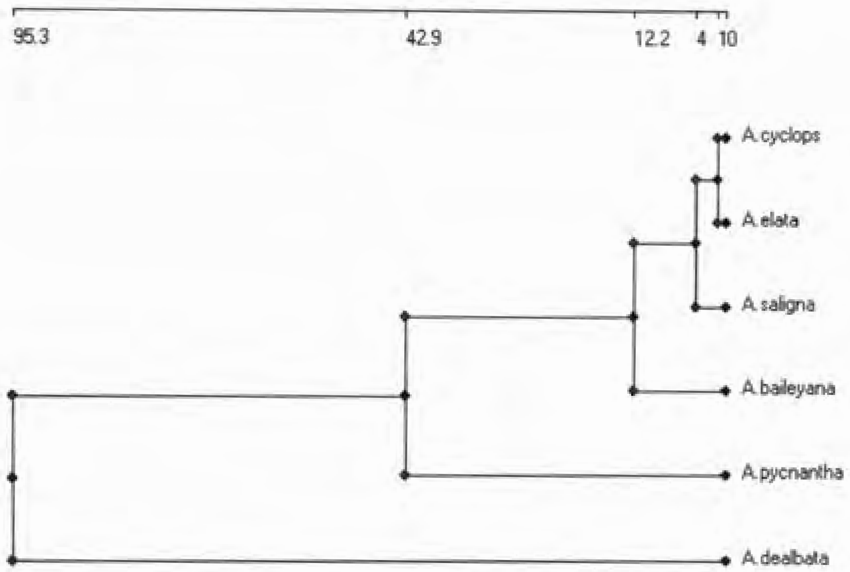

Figure 13