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Woody legumes: a (re)view from the South

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Summary This review is focused on woody legumes from the southern continents. We highlight that the evolution of the Caesalpinioideae and Mimosoideae with old soils, with variable supplies of water and also with fire has produced a suite of advantageous physiological characteristics. These include good potential for nitrogen fixation and mechanisms for acquiring P. The latter includes the ability to form cluster roots and produce extracellular phosphatase enzymes. Further, many of the species in these subfamilies are known to synthesize in significant amounts osmotically compatible solutes, such as pinitol and other cyclitols/polyols, that help them cope with even severe drought conditions. In many cases, these species regenerate prolifically after fire from seed. Such species and their beneficial characters can now be better exploited to help sequester carbon, provide key nutrients such as nitrogen and phosphorus for companion crops and other plants and provide feedstocks for a range of industries, including energy industries.

Keywords: Acacia, drought, nitrogen, old soils, phosphorus, water.

Introduction

Almost all of the progress in understanding the process of biological nitrogen fixation/diazotrophy has been stimulated by the importance of nitrogen in agriculture. Fisher and Newton (2004), as well as Newton (2004), provide significant insights into the history of the subject as part of a multi-volume treatise. They point out that, while beneficial effects of legumes in rotations with cereals were known since Greek and Roman times, it took till 1888 for Hellriegel and Wilfarth (1888) to build on the work of Boussingault and Lawes and Gilbert (and others) and finally provide proof that nitrogen fixation by legumes was due to an association with bacteria. In a recent review of the phylogeny of legumes, Wojciechowski et al. (2004) noted that we now recognize more than 19,400 species worldwide. They also stated that this places legumes ‘second only to Poaceae in agricultural and economic importance’. Such a view is strongly justified by their widespread adoption in agriculture: ‘Grain and forage legumes are grown on some 180 million Ha, or 12% to 15% of the Earth’s arable surface’ (Graham and Vance 2003). By comparison with the obvious impetus provided by the importance of legumes in agriculture and research developments in the 19th century, research on woody legumes languished till well into the latter half of the 20th century. Indeed, it is arguable that research into woody legumes only gained any significant momentum once there were large areas of land and soil that had been degraded by poor agricultural practices and further areas of land that had been cleared but ultimately proved unsuitable for agriculture. It took till well into the 1970s and even the 1980s (e.g., Allen and Allen 1981) for there to be a significant body of research into woody legumes. By then, we knew that diazotrophy was an energetically expensive process, requiring that N-fixing symbioses had available to them significant supplies of phosphorus. Forestry played a role in the development of interest in woody legumes since, obviously, harvesting and fires remove nitrogen, and such losses must be considered in relation to inputs from nitrogen fixation—the balance between inputs and outputs of nitrogen being perhaps one of the keys to assessing the sustainability of management (e.g., Likens et al. 1970, Johnson et al. 1982, Dyck et al. 1994).

The southern continents have played a leading role in the development of knowledge of woody legumes. In Africa and South America, a focus on food production and the advent of agroforestry led to many screening studies of the suitability of tree legumes, and their potential contributions of N, to companion crop plants. These studies are summarized in works by modern ‘fathers’ of agroforestry—P.K. Nair (Nair et al. 1984, Nair 1993) and a decade later by Pedro Sanchez (Sanchez 1995). That work continues (e.g., Aronson et al. 1992, 2002, Arredondo et al. 1998, Cervantes et al. 1998),
while much early work was captured and refined through the creation of the International Centre for Research in Agroforestry, now the World Agroforestry Centre, and has been published under that banner (e.g., Palm 1995, Shepherd et al. 1995).

In Australia, the many and long-standing observations of how well legumes colonize disturbed land and how quickly they re-establish after fire led to the recognition of their importance to the N balance of forests: ‘The contribution of leguminous species is identified as critical to this balance and demands further study’ (Baker and Attiwill 1981). However, it was probably the issue of large areas of land requiring restoration and rehabilitation, which has been particularly acute for large areas of old soils in the tropics and in the South more generally, that led to a southern focus on woody legumes.

This review is focused on the woody legumes that originate in the southern continents. The comparatively good knowledge and moderately frequent review of the legumes used in agriculture, especially those that grow in the northern hemisphere or wet tropics, are drawn upon for comparison, as are some of the ecological and physiological characteristics of woody legumes that now grow and prosper in the North or the tropics as invasive plants. We have deliberately taken the view that phylogeny and biogeography provide crucial contexts for the understanding of rates of N fixation, tolerance of drought and ability to acquire phosphorus—physiological features of this fascinating group of plants. We have not dealt in detail with the plant–bacteria association of N-fixing symbioses in woody legumes. That subject is covered by others, in particular by Janet Sprent and co-workers (e.g., Sprent 1995, 2003, 2005, 2007, Sprent and James 2007, Sprent et al. 2009) and most emphatically in her recent book (Sprent 2009). It is also well covered for the genus Acacia, in the recent report by Brookwell et al. (2005). Nor have we attempted to cover the basic physiology and biochemistry of nitrogen fixation per se. That is very well described elsewhere in books (e.g., Postgate 1998), reviews (e.g., Colebatch et al. 2002) and collated proceedings of the frequent conferences on the general topic of nitrogen fixation at regional, national and international levels (e.g., Dakora et al. 2008).

Phylogeny

Similarly to Sprent (2007), we have adopted the terminology of Lewis et al. (2005) that divides the Leguminosae into three subfamilies: Caesalpinioideae, Mimosoideae and Papilionoideae. Two aspects of the phylogeny of woody legumes are noteworthy in the above context. First is that their phylogeny is not the same as that of nitrogen fixation among angiosperms in general. Among the angiosperms, symbiotic nitrogen fixation is not limited to the Leguminosae. Drawing on recent papers by Wojciechowski et al. (2004) and Sprent (2007), we note nitrogen-fixing symbioses have become broadly distributed within the angiosperms, including a range of non-leguminous woody genera such as Casuarina, Alnus and Myrica. Secondly, and more specifically with respect to the Leguminosae, molecular data illustrate what is currently regarded as the evolutionary pattern within the family—the Caesalpinioideae evolved first, followed by the Mimosoideae and then the Papilionoideae. As discussed by Sprent (2007), nodulation is most common in the latter of the three subfamilies and least common in the first. Also, as discussed by Sprent (2007), members of the Leguminosae that are native to or flourish in the warm temperate to arctic regions are mostly in the Papilionoideae, which also includes the great majority of the forage and grain legumes. The ‘more southern’ woody legumes are mostly Mimosoideae and Caesalpinioidae, and these are the subfamilies that form the basis of this review. Immediately, we can note that there is good empirical evidence for the poorer nodulation and N-fixation capacity of the Caesalpinioideae relative to the Mimosoideae, in tropical forests at least (e.g., Ometto et al. 2006).

Biogeography

In an analysis of the distribution of legumes in terrestrial ecosystems, including analysis of their ecological significance, Crews (1999) made a number of points including:

(i) Legumes comprise an important component of canopy trees in lowland mesic and wet tropical forests throughout the world.

(ii) Woody legumes have also been successful in drier tropical environments.

(iii) Legumes in late seral stages and woody legumes in general are notably absent in temperate regions.

Crews went on to cite dry tropical thorn-scrub communities of Mexico, Africa and Australia as examples of his second point, including members of the genus Acacia. While noting that many of the Australian acacias are not ‘thorny’ in the sense applied to African species, we concur with Crews’ overall assessment that ‘potentially nodulating, woody legumes are common and often dominant’ in many tropical ecosystems on most continents. We would, from a southern perspective, note that this is true for Africa and Australia and South America. Beyond this point, however, we must diverge a little from Crews’ view of legumes in temperate regions.

There are large areas of non-tropical Australia and Africa where woody legumes, mainly of the genus Acacia Mill., are far from absent in either late seral stage or in absolute terms—they are either a major component of the overstorey or are the dominant overstorey species (e.g., Johnson and Burrows 1993). Best examples include Mulga (Acacia aneura F. Mueller ex Benth., dominates ∼1.5 × 106 km2 or ∼20% of Australia), Myall (Acacia pendula A. Cunn. & G. Don) and Brigalow (Acacia harpophylla F. Mueller ex Benth.) woodlands of inland Australia. Altogether, acacias cover vast areas southwards from the Tropic of Capricorn to at least as far as 35°S. While it is true that much of this area is arid (e.g., <250 mm annual
of Mediterranean climate regions of the world. The proportion of Mediterranean climate regions to total state or country size is given in parenthesis. Data adopted from Arianoutsou and Thanos 1996.

<table>
<thead>
<tr>
<th>Region</th>
<th>Extent of Mediterranean climate region (km²)</th>
<th>Legumes (% of the total flora)</th>
</tr>
</thead>
<tbody>
<tr>
<td>California</td>
<td>42,397 (10)</td>
<td>3.9–6.9</td>
</tr>
<tr>
<td>Chile</td>
<td>37,848 (5)</td>
<td>3.8</td>
</tr>
<tr>
<td>South Africa</td>
<td>36,631 (3)</td>
<td>7.3–10.9</td>
</tr>
<tr>
<td>Australia</td>
<td>1,675,845 (22)</td>
<td>8.8–13.3</td>
</tr>
</tbody>
</table>

rainfall) to semi-arid (<350 mm), there are still large expanses of Acacia-dominated land, well south of the tropics, that receive up to 900 mm of annual rainfall and may reach almost to the coast. There is almost as much Acacia-dominated land in the band between 350 and 500 mm as there is between 250 and 350 mm. Johnson and Burrows (1993) list at least 18 identifiable Acacia open forests, woodlands and tall shrublands (where one or more Acacia spp. is the canopy dominant).

A similar scenario is true also for southern, non-tropical Africa. The following owes much to the work of Lewis et al. (2005). Acacia spp. dominate large areas of Africa well south of the equator (as well as to the north). For example, Acacia nilotica L. and its numerous subspecies are found throughout much of Africa and over a broad range of edaphic conditions that include an altitudinal range of around 2000 m, a rainfall range of 250–1500 mm. Together with Acacia karoo Hayne (which copes with a narrower range of edaphic conditions), it is the dominant tree in large areas of savanna grassland in much of southern Africa. Likewise, Brachystegia spp. together with Baikiaea ghesquiereana J. Léon. and other members of the leguminous subfamily Caesalpinioideae, dominate some $2.4 \times 10^6$ km² of Miombo woodlands in Angola, Botswana, Burundi, Democratic Republic of Congo, Malawi, Mozambique, Namibia, Tanzania, Zambia and Zimbabwe.

Finally, in non-tropical America, the mesquites or algarobas (Prosopis spp.) dominate large areas. As stated by Isomaki and Ghandi (2004), algarobas are native to ‘the semi-arid savanna, cerrados and caatingas of Brazil, at the edges of the desert on the west coast of South America, on the lower slopes of the Andes, and in many parts of the grasslands of Argentina, in the pampas, and in Patagonia. Algarobas are, in vast areas, the dominant tree species.’ They thrive in arid, semi-arid and even sub-humid conditions. In Brazil, algarobas are a key part of semi-arid vegetation that covers some $5 \times 10^5$ km².

The point we make is that legumes are dominant elements of the woody vegetation in much of Africa, Australia and South America. A simple summary (Table 1) is taken from Arianoutsou and Thanos (1996). To us, there seems little evidence of any absence of legumes in temperate parts of the Southern Hemisphere, and, indeed, they may dominate in large areas of the temperate and subtropical ‘South’. Where legumes do not dominate, they may often, as stated by Crews (1999), become dominant for short periods after fires. This is a well-known phenomenon in much of the southern half of Australia, for example, where Acacia spp. may germinate in large numbers after fire and contribute strongly to the N budget for up to a decade later (see May and Attiwill 2003). We will return to this shortly.

### Ecophysiology—nitrogen fixation, phosphorus and old soils

In a review of woody legumes, it is obvious that we might begin any discussion of their ecophysiology with nitrogen fixation. A strong framework is provided by Houlton et al. (2008), who recently provided a major summary of global patterns of N fixation. From their analysis, it is very clear that N fixation is strongly temperature dependent, displaying a highly normal temperature distribution with a maximum at around 25 °C. This result accords with known biochemical properties of many enzymes. A little more surprising was their analysis that showed that, through enzyme activity, N-fixing plants are also able to increase the availability of P in soil. Houlton et al. (2008) showed that the activity of phosphatase enzymes in soil is up to three times greater when N-fixing plants were present. Using a model to integrate these results into the broader issues of growth and nutrient limitation, Houlton et al. (2008) showed that it seems most likely that P released by phosphatase activity is of direct benefit to the N-fixing plants that produced that activity.

From a Southern perspective, this model analysis represents a step forward from other models (e.g., Rastetter et al. 2001, Menge et al. 2009) because it explicitly considers the problems of poor supplies of P in soils. By scientists studying northern plants, this is one of the least well-understood aspects of Australia and Africa in particular but also large parts of South America. Old soils dominate Australia and Africa, and P is often in chronically short supply. The ability of woody legumes to acquire P is thus of paramount importance to their role as N fixers.

Taking as a starting point the summaries presented in 1986 by Hayman and in 1989 by Alexander, a considerable number of both herbaceous and woody legumes were known then to be mycorrhizal. Since then, the list has grown considerably, albeit still with a focus on herbaceous species used in agriculture. Nevertheless, the beneficial effects of mycorrhizas on P availability and uptake by Acacia spp. and many other woody legumes from the South are now well established for both tropical and temperate zones (e.g., Fournoune et al. 2002a, 2002b, 2002c, Duponnois and Plenchette 2003, Giri et al. 2004, Duponnois et al. 2007). A considerable portion of our current knowledge of the beneficial effects of vesicular–arbuscular mycorrhizas on Acacia spp. is due to the work of Drs Lynette Abbott and David Jasper at the University of Western Australia (Jasper et al. 1988, 1989a, 1989b, Jasper 1994). They showed clearly that the availability/viability of vesicular–arbuscular mycorrhizas was a serious con-
Figure 1. Growth of cluster roots and nodules of five woody legumes in a ‘choice’ experiment. All plants were container-grown in sand without added N or P (but with other mineral nutrients supplied via solution), and lateral roots could grow out into each of four different regions. In two regions, the sand was simply white quartz (WS), that had no inherent capacity to hold P and negligible endogenous P, or WS augmented with an insoluble iron phytate (∼80 ppm P). In the other two, a yellow sand (YS) that had ∼2 ppm endogenous available P was either provided alone or augmented with ash generated from native forest species (∼6 ppm P). Data presented are the masses of nodules and cluster roots growing on lateral roots in each of the four regions. Data are recalculated from Adams et al. (2002).

The variety of methods used to make estimates of N fixation is well covered elsewhere as are the sources of error.
inherent to each approach. We regard most of the estimates listed in Table 2 as conservative, while some earlier estimates of N fixation by acacias were questioned as being ‘too large’ and due to errors associated with assay methods (such as the acetylene reduction technique). However, when earlier results are revisited, usually with a variety of 15N-based approaches (e.g., Guinto et al. 2000, May and Attiwill 2003), earlier estimates are revised upwards.

Taken together with the observations of Houlton et al. (2008), the Southern woody legumes, especially species from the subfamily Mimosoideae, play major roles as ‘ecosystem engineers’. Their ability to remobilize P and to fix atmospheric

### Table 2. Annual rates of nitrogen fixed by species from the Mimosoideae subfamily of the Leguminosae from the Northern and Southern Hemispheres. For comparison purposes, we have listed some species from the Papilionoideae at the bottom of the table.

<table>
<thead>
<tr>
<th>Species</th>
<th>Study country</th>
<th>Stand age (years)</th>
<th>Rate of N fixation (kg ha(^{-1}) year(^{-1}))</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mimosoideae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Acacia alata</em></td>
<td>Zimbabwe</td>
<td>2</td>
<td>61</td>
<td>Hansen et al. 1987</td>
</tr>
<tr>
<td><em>Acacia angustifolia</em></td>
<td></td>
<td>6</td>
<td>9.5</td>
<td>Aronson et al. 2002</td>
</tr>
<tr>
<td><em>Acacia caven</em></td>
<td>Australia</td>
<td>2</td>
<td>12-32</td>
<td>Adams and Attiwill 1984</td>
</tr>
<tr>
<td><em>Acacia dealbata</em></td>
<td>Australia</td>
<td>5</td>
<td>50</td>
<td>May and Attiwill 2003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>50+</td>
<td>2.1</td>
<td>Pfautsch et al. 2009</td>
</tr>
<tr>
<td><em>Acacia extensa</em></td>
<td>Australia</td>
<td>1–6</td>
<td>0.1</td>
<td>Hansen et al. 1987</td>
</tr>
<tr>
<td><em>Acacia holoserica</em></td>
<td>Senegal</td>
<td>–</td>
<td>36-108</td>
<td>Peoples and Herridge 1990</td>
</tr>
<tr>
<td><em>Acacia holostrera</em></td>
<td>Senegal</td>
<td>–</td>
<td>&lt;12</td>
<td>Peoples and Herridge 1990</td>
</tr>
<tr>
<td><em>Acacia magnifolia</em></td>
<td>Brazil</td>
<td>2.5</td>
<td>66</td>
<td>Boulillet et al. 2008</td>
</tr>
<tr>
<td><em>Acacia mearnsii</em></td>
<td>Australia</td>
<td>7</td>
<td>0.75</td>
<td>Lawrie 1981</td>
</tr>
<tr>
<td><em>Acacia melanoxylon</em></td>
<td>Australia</td>
<td>7</td>
<td>0.005</td>
<td>Lawrie 1981</td>
</tr>
<tr>
<td></td>
<td></td>
<td>50+</td>
<td>31.6</td>
<td>Pfautsch et al. 2009</td>
</tr>
<tr>
<td><em>Acacia paradoxa</em></td>
<td>Australia</td>
<td>7</td>
<td>0.042</td>
<td>Lawrie 1981</td>
</tr>
<tr>
<td><em>Acacia pentatula</em></td>
<td>Australia</td>
<td>3</td>
<td>12</td>
<td>Langkamp et al. 1979</td>
</tr>
<tr>
<td><em>Acacia pulchella</em></td>
<td>Australia</td>
<td>1–13</td>
<td>2.2</td>
<td>Monk et al. 1981</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.3–1</td>
<td>6</td>
<td>Hingston et al. 1982</td>
</tr>
<tr>
<td><em>Acacia senegal</em></td>
<td>Sudan</td>
<td>4</td>
<td>7–12</td>
<td>Raddad et al. 2005</td>
</tr>
<tr>
<td><em>Acacia verniciflua</em></td>
<td>Australia</td>
<td>–</td>
<td>38</td>
<td>Turvey and Smethurst 1983</td>
</tr>
<tr>
<td><em>Albizia lebbeck</em></td>
<td>Nigeria</td>
<td>1</td>
<td>60–120</td>
<td>Kadiata et al. 1996</td>
</tr>
<tr>
<td></td>
<td></td>
<td>–</td>
<td>94</td>
<td>Danso et al. 1992</td>
</tr>
<tr>
<td><em>Albizia falcata</em></td>
<td>Hawaii</td>
<td>–</td>
<td>100–200</td>
<td>Binkley and Giardina 1997</td>
</tr>
<tr>
<td><em>Calliandra calothyrsus</em></td>
<td>Australia</td>
<td>2</td>
<td>67–93</td>
<td>Stahl et al. 2002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>76</td>
<td>Purwarianti et al. 1996</td>
</tr>
<tr>
<td><em>Calliandra calothyrsus</em></td>
<td>Kenya</td>
<td>0.6</td>
<td>24</td>
<td>Gathumbi et al. 2002</td>
</tr>
<tr>
<td><em>Inga edulis</em></td>
<td>Costa Rica</td>
<td>1–2</td>
<td>100</td>
<td>Leblanc et al. 2007</td>
</tr>
<tr>
<td><em>Leucaena spp.</em></td>
<td>Nigeria</td>
<td>–</td>
<td>304</td>
<td>Danso et al. 1992</td>
</tr>
<tr>
<td><em>Leucaena leucocephala</em></td>
<td>Malaysia</td>
<td>–</td>
<td>934</td>
<td>Peoples and Herridge 1990</td>
</tr>
<tr>
<td></td>
<td>Nigeria</td>
<td>1–4</td>
<td>238</td>
<td>Sanginga et al. 1996</td>
</tr>
<tr>
<td></td>
<td>Puerto Rico</td>
<td>1.5–3.5</td>
<td>71–74</td>
<td>Parrotta et al. 1996, 1994</td>
</tr>
<tr>
<td></td>
<td>Tanzania</td>
<td>4</td>
<td>110</td>
<td>Högberg and Kvarnström 1982</td>
</tr>
<tr>
<td><em>Prosopis glandulosa</em></td>
<td>USA</td>
<td>1</td>
<td>40</td>
<td>Shearer and Kohl 1986</td>
</tr>
<tr>
<td></td>
<td></td>
<td>–</td>
<td>25–30</td>
<td>Rundel et al. 1982</td>
</tr>
<tr>
<td>*Prosopis spp./<em>Acacia caven</em></td>
<td>Chile</td>
<td>–</td>
<td>80–590</td>
<td>Urzúa 2000</td>
</tr>
<tr>
<td><strong>Papilionoideae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Erytina lanceolata</em></td>
<td>Costa Rica</td>
<td>6</td>
<td>82.5</td>
<td>Salas et al. 2001</td>
</tr>
<tr>
<td><em>Erytina poepigiana</em></td>
<td>Costa Rica</td>
<td>1–2</td>
<td>60–160</td>
<td>Leblanc et al. 2007</td>
</tr>
<tr>
<td><em>Erytriana fusca</em></td>
<td>Costa Rica</td>
<td>1–2</td>
<td>80</td>
<td>Leblanc et al. 2007</td>
</tr>
<tr>
<td><em>Gliricidia sepium</em></td>
<td>French Antilles</td>
<td>8</td>
<td>147</td>
<td>Dulormne et al. 2003</td>
</tr>
<tr>
<td></td>
<td>Nigeria</td>
<td>–</td>
<td>108</td>
<td>Danso et al. 1992</td>
</tr>
<tr>
<td></td>
<td>Indonesia</td>
<td>1.3</td>
<td>700</td>
<td>Catchpoole and Blair 1990</td>
</tr>
<tr>
<td></td>
<td>Sumatra</td>
<td>1</td>
<td>35–38</td>
<td>Hairiah et al. 2000</td>
</tr>
<tr>
<td></td>
<td>Philippines</td>
<td>1.5</td>
<td>126</td>
<td>Ladha et al. 1993</td>
</tr>
</tbody>
</table>
N at considerable rates is of benefit to many other plants and animals. It is arguable that, in systems where fire is common or even prevalent, members of the Mimosoideae and perhaps the Caesalpinioideae are truly keystone species.

Ecophysiology—coping with drought

The genus *Acacia* has inspired some of the most seminal and fundamental work on the water relations of all plants. Beginning more than 50 years ago, Ralph Slatyer and colleagues worked first to develop techniques that would yield reliable data and then applied those to species of *Acacia*, most notably *A. aneura* (e.g., Slatyer 1960, 1961, 1962, 1965). The history of this development is covered in some detail by Doley (2004). Much of this work was captured in the iconic text *Plant–Soil Water Relationships* published in 1967 (Slatyer 1967). One of the most striking aspects of the early work is that the Scholander pressure chamber was not introduced till 1964 (Scolander et al. 1964). Thus, Slatyer et al. had to use far more difficult techniques to be able to provide estimates of key aspects of water potential (including osmotic potential)—estimates that are still used as points of reference for researchers that have followed (see summary by Winkworth 1973, also O’Grady et al. 2009).

The water relations of honey mesquite (Prosopis glandulosa Torr.) have been studied in some detail, particularly in the Sonoran Desert (Nilsen et al. 1983). *P. glandulosa* is largely phreatophytic, acquiring water from sources as deep as 4–6 m below the surface. Nonetheless, it still generates xylem pressure potentials of close to –5 MPa at midday in midsummer (Nilsen et al. 1983), when vapour pressure deficits approach 8 kPa. A key to its ability to maintain turgor is undoubtedly its ability to generate solute (osmotic) potentials of between 2 and 4 MPa. This is one of the notable features of Southern woody legumes—their ability to develop significant osmotic potentials as part of their tolerance of drought. Otieno et al. (2005) showed that, for two African acacias—*Acacia tortilis* (Forssk.) Hayne and *Acacia xanthophloea* Benth.—osmotic potential at the turgor loss point accounted for almost 96% of variation in water potential at the same turgor loss point. They went on to speculate that the accumulation of solutes was probably responsible. Johnson et al. (1996) recorded that Colophospermum mopane (J. Kirk ex Benth.) J. Léon., a member of the Caesalpinioideae that is widespread in low-altitude, high-temperature regions of southern Africa, could develop significant concentrations of pinitol (>100 mol m⁻³) in foliage and especially roots in response to drought (or salinity). Significantly, they noted that increased concentrations in roots were not due to loss of water. Liu et al. (2008) found that pinitol content constituted 50% of phyllode total sugars in *Acacia auriculiformis* A. Cunn. ex Benth. in northern Australia compared with 17% for fructose, 20% for glucose and <10% for sucrose. These results accord closely with ‘general knowledge’ for acacias and other mimosoid legumes—they can accumulate significant quantities of pinitol and related compounds. Seigler (2003) provides a good overview of the more general phytochemistry of *Acacia* spp.

Southern woody legumes can clearly become ‘conditioned’ to drought. Conditioning includes a wide range of features in addition to osmotic adjustment, as described recently for *Prosopis* in Argentina by Villagra et al. (2010). As a further example, xylem conductivity of *Acacia* seedlings (Clemens and Jones 1978) can be altered by conditioning to drought and was correlated with stomatal behaviour. Leaf shedding is another mechanism noted as being important to how *Acacia* and other woody legumes such as *Semna, Anadenanthera* and *Machaerium* spp. can adapt to and cope with drought (e.g., Filho and Filho 2000, Gebrekirstos et al. 2006). Noting again the large area (~20%) of Australia dominated by *A. aneura*, O’Grady et al. (2009) presented data that argued for convergence of species-based physiological traits (including *Eucalyptus*) within the arid and semi-arid zones, such that general rules (e.g., for hydrological analysis) could be applied. Even so, data for *A. aneura* usually marked one of the two extremes of the recorded range (e.g., Huber values, wood density, specific leaf area).

Ecophysiology and the future—woody legumes as exotics, invaders and agents of rehabilitation and food and fuel production

Looking to the future requires consideration of changing atmospheric [CO₂] and its likely effects on plants. As far as we are aware, there is still little work done on the response of Southern woody legumes to atmospheric [CO₂], and that published by Schortemeyer et al. (1999, 2002) stands alone for *Acacia* spp. Schortemeyer et al. found that both growth and rates of N fixation by glasshouse-grown seedlings of a range of *Acacia* spp. were generally increased in the presence of increased atmospheric [CO₂], albeit that plants were grown with ample supplies of P.

Therein lies a key issue—will availability of P serve to limit responses of Southern legumes to rising atmospheric [CO₂]? This is an open question. Binkley (2005) noted that rates of cycling of P always seem to be greater under N-fixing species, while Binkley et al. (2003) showed that the metabolic responses (including rates of N fixation) to added P by the woody legume *Faucaltaria moluccana* (Miq.) Barneby & J. W. Grimes (= *Albizia falcatoria*) were far greater than the growth responses. Binkley’s evidence (and that of others) comes mostly from areas where legumes have been planted or introduced, so it is not that legumes have ‘selected’ those areas of soil that have greater availability of P. It seems that legumes in general, including woody legumes from the South, have inherent capability to increase availability of forms of P unavailable to other plants and to enhance N fixation as a result (as noted above and by Houlton et al. 2008).
This capacity also speaks to the potential of woody legumes to succeed and even become invasive, where other plants may fail due to poor supplies of water and P. Clearly, deliberate introductions of species from genera such as *Acacia*, *Prosopis*, *Mimosa*, *Sesbania* and *Parkinsonia* needs careful thought (e.g., Hughes and Styles 1989, Paynter et al. 2003, Jamnadas et al. 2005). Faye et al. (2009) noted recently that relationships among root nodule bacteria, ectomycorrhizal fungi and cohabiting native (*Faidherbia albida* (Del.) A. Chev.) and introduced (*Acacia holosericea* G. Don) woody legumes are far from simple and that negative effects of one association may be offset by others. In many places, Southern woody legumes have become ‘naturalized’ parts of the flora, and they too can become serious pest plants (e.g., Emms et al. 2005). However, this also provides a note of caution—interpretations that climate alone is the cause of increased abundance of woody legumes may well miss the obvious points that such increases could owe as much to the ability of legumes to thrive where other species struggle as it does to any change in climate. In particular, the at least partial dependence of the abundance of woody legumes on fire regimes can easily be confused or confounded with the effects of changing climate. An example is the honey mesquite. Most of the more than 40 species of mesquite are native to South America (Burkhart and Simpson 1977). However, it is a highly successful woody legume in much of the arid and semi-arid areas of both South and North America as well as northern Africa and parts of Asia. At present in the USA, *Prosopis* spp. or mesquite ‘is the dominant woody plant on more than 38 million ha of what has been considered semi-arid southwestern grasslands’ (Van Auken 2000). Most ecologists regard its spread into grasslands as due to the combination of grazing and fire regimes (e.g., Wright et al. 1976, Archer 1989, Archer et al. 1995), especially the active suppression of fire or heavy grazing that removes the fuel and makes fire less likely (Van Auken 2000). As mentioned previously, availability and viability of fungal and bacterial symbionts will continue to be important determinants of the success of efforts to (re)introduce woody legumes as part of rehabilitation or restoration programmes (e.g., Murray et al. 2001, Bell et al. 2003, Thrall et al. 2005, 2007). The many advantages over other plants enjoyed by woody legumes from the South and their association with and responses to fire make assigning causality to their spread a hazardous occupation.

All of the above also suggest that effort to better understand the physiology of the Southern woody legumes will be rewarded—they will play a major role in land rehabilitation and carbon sequestration strategies. Using their ability to fix nitrogen and acquire phosphorus, they can contribute strongly to soil carbon. Their capacity to accumulate cyclitols to very significant concentrations as part of coping with drought is largely unexplored. We believe this last trait offers great potential. For example, SoyOyl® is a trademark product of Dow Chemical that is based on the cyclitols produced by soy beans. SoyOyl® has countless applications and is now widely used in plastics and other industries. A combination of useful physiological traits make Southern woody legumes literally ‘biofactories’.

**Conclusions**

This review has focused on the woody legumes of the South, especially genera such as *Acacia* and *Prosopis*, that have proved to be remarkable for their adaptability to old soils, drought and fire, as much in the North as in the South. While many of the genera in the subfamilies Mimosoideae and Caesalpinioideae are not always nodulated and do not always show evidence of N fixation, under the right conditions, many of their species will nodulate and fix atmospheric N, often at rates approaching those measured for legumes from the Papilionoideae that are more frequently used in agricultural systems. Insofar as we have looked, species of the Mimosoideae and Caesalpinioideae subfamilies show clear adaptations that aid their acquisition of P from soils that frequently lack plant-available P.

Given the increasingly clear economic importance of nitrogen fixation, the ecological significance of woody legumes in the South (and the North) and the still poor general level of knowledge of these remarkable plants, there is an urgent need for further research. Perhaps, the first priority should be the processes that facilitate their acquisition of N and P under often harsh edaphic conditions. A second priority might be investigations as to why the Caesalpinioideae are generally so poor at producing nodules and into their rates of N fixation. In evolutionary terms, it seems odd that they seemingly cannot fix N, yet can be so common or even dominant in areas/regions where N could become a limiting element (most likely due to fire).

Finally, given changing climates (especially potential reductions in rainfall in large parts of southern Africa and Australia and South America) and atmospheric [CO₂] the mechanisms by which the Mimosoideae and Caesalpinioideae adapt to drought and fire deserve far more attention. As a side benefit, we might elucidate further the processes responsible for their accumulating large quantities of cyclitols (e.g., pinitol) and their adaptation to use as feedstocks for biofuels and even their use as ‘biofactories’. We concur with and extend the understated plea of Sprent et al. (2009) for greater investment in research in African legumes. We agree that there is an urgent need to develop African legumes for Africa and Australian legumes for Australia and South American...

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**References**


