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REVIEW PAPER

African legumes: a vital but under-utilized resource

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Abstract

Although nodulated legumes have been used by indigenous peoples in Africa for centuries, their full potential has never been realized. With modern technology there is scope for rapid improvement of both plant and microbial germplasm. This review gives examples of some recent developments in the form of case studies; these range from multipurpose human food crops, such as cowpea (*Vigna unguiculata* (L.) Walp.), through to beverages (teas) that are also income-generating such as rooibos (*Aspalathus linearis* (Burm. f.) R. Dahlgren, honeybush (*Cyclopia* Vent. spp.), and the widely used food additive gum arabic (*Acacia senegal* (L.) Willd.). These and other potential crops are well-adapted to the many different soil and climatic conditions of Africa, in particular, drought and low nutrients. All can nodulate and fix nitrogen, with varying degrees of effectiveness and using a range of bacterial symbionts. The further development of these and other species is essential, not only for African use, but also to retain the agricultural diversity that is essential for a changing world that is being increasingly dominated by a few crops such as soybean.

Key words: *Acacia senegal*, cowpea, gum arabic, honeybush, nodulation, rooibos, *Vigna*.

Introduction

Africa has a vast array of indigenous legumes, ranging from large rainforest trees to small annual herbs, listed in Lock (1989). However, in recent years, there has been a tendency in agriculture and forestry to use exotic species such as soybean (*Glycine max* (L.) Merr.) and peanut (*Arachis hypogaea* L.) for crops, and eucalypts (e.g. *Eucalyptus camaldulensis* Dehnh.) and Australian acacias (e.g. *Acacia mangium* Willd.) for wood. As has been pointed out several times over nearly 30 years, most recently in Anon (2006), by the US National Academy of Sciences, this ignores the potential of the native species, which are arguably better adapted to their environment. For this review, some of the nodulated indigenous genera with known uses have been selected to illustrate the problems and potential for their better exploitation. By means of case studies, ways in which modern methods can be used to improve a range of products for both food and income generation are discussed.

Since the publication of the comprehensive checklist of African legumes (Lock, 1989), there have been changes in names, both of species and their assignment to genera. The species names can be checked in the International Legume Database and Information Service (www.ildis.org) and the USDA Germplasm Information Resources Network (www.ars.grin.gov) databases and the genera in *Legumes of the world* (Lewis *et al.*, 2005, and references therein). Whilst there are many large and important native timber trees in African rainforests, many of these are unable to nodulate (Sprent, 2009*a*) and they will not be considered here.

A number of genera either have their major centres of diversity in Africa or are confined to certain regions of Africa, such as the Cape Floristic Region (CFR). The former include the genus *Vigna* Savi and parts of *Acacia* Mill., and the latter numerous endemic genera. These will be considered in turn. As well as the host legumes, the nodule endosymbionts also vary widely in Africa and include newly described members of both α and β branches of the Proteobacteria, now often referred to as α- or β-rhizobia, even though they do not have 'rhizobium' as part of their generic names (Sprent, 2009*a*).

Vigna

Vigna is a genus of the important legume tribe Phaseoleae (which also contains soybeans and the so-called common bean, *Phaseolus vulgaris* L.) and has been and still is the subject of much taxonomic shuffling (Schrire, 2005). Early in the present decade it was though to have over 100 species, but some of those from the New World are being split off and the final number is likely to be much lower. In a recent extensive analysis of *Vigna*, Maxted *et al.* (2004) list 99 species overall, with slightly more than half being native to Africa. Some, including important food species such as the grams (*V. radiata* (L.) R. Wilczek, green gram, also known as mung bean, and *V. mungo* Hepper, black gram, both of these species having many other local names) are native to the Indian subcontinent. All species are herbaceous, both annual and perennial, some are climbing, and they often grow in well-drained, low-fertility soils (Schrire, 2005). In legume terms, they are relatively young, having diverged from their relatives about 10 Ma (Lavin *et al.*, 2005), nodulated legumes, in general, evolving about 60 Ma (Sprent, 2007). However, evolution has continued and there is a clear distinction between those subgenera that are native to Africa (though not necessarily exclusively so) and those native to other regions, usually Asia. The largest subgenus, *Vigna*, section *Vigna*, contains 19 species, all but one of which are native to Africa. *Vigna marina* (Burm.) Merr., is given as African in ILDIS, but Maxted *et al.* (2004) record it as being introduced there. Because of its strong affinity with African vignas, it is included in Table 1, which lists some of the African species that may be used as human food. Some of these are described at length in the excellent National Academy of Sciences (USA) publication *Lost crops of Africa*' (Anon, 2006), and Maxted *et al.* (2004) deal in detail with the taxonomy, genetics, and biogeography of *V. unguiculata* and *V. subterranea* (L.) Verdc. Half the species listed in Table 1 are valued for their tubers, an organ seldom appreciated in the developed world as being a legume product, but produced by many perennial herbaceous tropical and subtropical species, not only of *Vigna*. However, there is renewed interest in some of these, such as *V. vexillata* (L.) A. Rich., used as 'bush tucker' by indigenous people in Australia (Grant *et al.*, 2003; illustrated in Sprent, 2009*a*). As well as being perennating organs, tubers enable the plants to store nutrients (including water) over dry periods and thus tuber crops are a useful resource in this increasingly dry, infertile world. In almost all cases, the plants listed in Table 1 have multiple uses (see the case study for cowpea), not only for human food, but also as medicine and for animal feed. *V. marina* is interesting because it grows in saline coastal areas, including mangrove swamps and salinity is, like drought, an increasing global problem. At the moment it is used for seed, tubers, and soil improvement more in the Indian subcontinent than in Africa. Being in the same subgenus as both *V. luteola* (Jacq.) Benth. and *V. subterranea*, it is a candidate for breeding salinity tolerance into these other crops. Attempts to cross it with *V. unguiculata*, which is in a different subgenus, have so far not been successful (Maxted *et al.*, 2004). However, *V. unguiculata* is a large and diverse species, having 11 subspecies, 10 of which are perennial and one annual, and some of which are native to dry coastal areas (Maxted *et al.*, 2004), meaning that it has a great deal of infrageneric diversity to serve as a base for breeding programmes. *V. subterranea*, Bambara groundnut, has two subspecies and is one of several legumes where the seed develops underground. It is thus analogous to the rather distantly related peanut (groundnut), *Arachis hypogaea* L. The latter is native to South America, but widely grown elsewhere, including Africa, where it has been displacing the

Table 1. Some African species of *Vigna* that are used for human food

A '+' after major use indicates other uses. Only the most common 'common name(s)' is given. All have many synonyms, but only those still in use are given.

Species	Synonym	Common name	Major use	Comments
heterophylla	*ambacensis*	None known	Tuber	Native to many countries in drier regions of Africa
luteola	*fischeri*	Various local names	Tuber	Native to wetter areas of much of Africa, also Papua New Guinea and Andaman Islands
marina[a]		Beach pea	Seed +	Pantropical, salt-tolerant
subterranea		Bambara groundnut	Seed	Probably originated in Nigeria and nearby, now widespread in Africa
vexillata	*lobatifolia*	None known	Tuber	Widespread
unguiculata				Seven subspecies
subsp. *sesquipedalis*		Yard-long bean	Seed +	Widely grown
subsp. *unguiculata*		Cow pea, black-eyed pea	Seed +	Widespread

[a] Although this species is listed as native to Africa in ILDIS, Maxted *et al.* (2004) think that it is introduced to Africa.

local, and arguably better, Bambara groundnut. Bambara can tolerate drier and less fertile soils, and, although having a lot less oil and a little less protein than peanut, is a very balanced source of food and can, on its own, support human life (Anon, 2006). A large programme to develop the genetic potential of this species was supported by the European Commission and has resulted in the development of specific molecular tools such as microsatellite markers (Basu *et al.*, 2007). These studies did not take nodulation into account. However, in their native soils, all species of *Vigna* seem to nodulate freely, using mainly slow-growing bradyrhizobia, but, as can be seen in the case study on cowpea, there are differences in effectivity and room for improvement of both plant and rhizobial germplasms for optimizing nitrogen fixation. Preliminary evidence from two sites in Ghana found between 31% and 84% of nitrogen in Bambara groundnut came from fixation, with large variations between cultivars (FD Dakora, unpublished observations).

Case study 1: *V. unguiculata*, subsp. *unguiculata* cowpea

Cowpeas are widely grown in Africa as multipurpose crops. Leaves are eaten raw and cooked, the grain is eaten green or dried, and the haulms are used as forage. It is often grown as an intercrop with sorghum, millet or maize (Fig. 1A). In the 1970s and 1980s there was a great deal of research into the crop, but this was mainly aimed at West African farming systems. It covered what was then mainstream plant physiology, such as responses to photoperiod and temperature, problems of pests and diseases, as well as breeding systems. It was a major part of the research programme of the Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria. Four chapters in the volume edited by Summerfield and Bunting (1980) cover these and related aspects. At that stage, nodulation and nitrogen fixation were not considered to be a major problem. However, this is certainly not true in parts of Africa, where it is becoming apparent that both N and P can limit cowpea production. There are now several research programmes, including the South African Legume project, funded by the McKnight Foundation and covering South Africa, Ghana, and Tanzania, looking at nodulation and nitrogen fixation. It is becoming clear that the bacteria nodulating cowpea are more diverse than earlier thought, when the term 'cowpea miscellany' was used to cover the slow-growing bradyrhizobia nodulating cowpeas and other tropical legumes. Although most isolates are still from the bradyrhizobial group, which are slow-growing, fast-growing strains are also now being identified. For example, in China, where, in

Fig. 1. (A) Cowpea intercrop with sorghum at University of Cape Town experimental farm; (B) gum arabic 'nodules' formed on a branch of an *Acacia senegal* tree 2 weeks after tapping at Dahra, Senegal; (C) rooibos tea processing and packaging factory in Cape Province, South Africa. Note the large brown areas near the 'C' where the fermented tea is put out to dry in the sun.

addition to the more promiscuous bradyrhizobia, some highly specific fast-growing strains were found (Zhang *et al.*, 2007). Within bradyrhizobia there are many different lines nodulating cowpeas, some of which seem particularly suited to southern African (Botswana and South Africa) soils and will probably eventually become new defined species of *Bradyrhizobium* (Steenkamp *et al.*, 2008). Pule-Meulenberg and Dakora (2009, and unpublished data) isolated rhizobia from 100 plants of each of 9 genotypes of cowpea growing in South Africa, Botswana, and Ghana and found great variability both with host genotype and location, with South Africa again having the most diversity and groups of strains distinct from those in other areas. Some host cultivars housed a wider range of bradyrhizobia than others. Clearly with all this variability in bradyrhizobia nodulating cowpea, there is likely also to be great variation in the amount of nitrogen fixed. This is a very difficult parameter to measure in the field. Table 2 gives published values for Africa and clearly shows the wide range of values obtained. The methods listed are fully described in Unkovich *et al.* (2008). Another parameter that is important is the proportion of N in the plant that is derived from fixation (Ndfa), bearing in mind that legumes are very good scavengers of soil N and do not necessarily enrich soil N. Ndfa will depend not only on the efficiency of the nodules, but also on soil fertility and other factors. In a survey of 63 farmers' fields in 12 villages in the Upper West region of Ghana, Naab *et al.* (2009) using the ^{15}N natural abundance method, found that 58.5–91.5% of the N in plant shoots came from fixation. In a study of 25 cowpea genotypes grown in savanna locations in Guinea, Sudan, Ghana, and South Africa, seven consistently derived over 50% of their N from fixation (FD Dakora *et al.*, unpublished data). Commercially these are the types of germplasm that seed producers should be able to market in sufficient quantities to make a profit.

To understand the wider benefits of nitrogen-fixing legumes to soil fertility, it is necessary to know total plant N and relate this to N removed with the crop. Many legumes, especially those adapted to dry areas have very good root systems, to access not only nutrients, but water. Harvesting root systems on any scale is a formidable task, even for annual legumes such as cowpea and there are no such data available yet.

Table 2. Estimates of N_2 fixation by cowpea in experimental plots in Africa

Country	N-fixed (kg ha^{-1})	Technique used[a]	Reference
Ghana	200	N difference	Dakora *et al.*, 1987
Kenya	24–29	N difference	Ssali and Keya, 1984
Burkina Faso	50–115	^{15}N fertilization	Bado *et al.*, 2006
Nigeria	122	^{15}N fertilization	Eaglesham *et al.*, 1981
Zimbabwe	68–138	^{15}N fertilization	Rusinamhodzi *et al.*, 2006
Zimbabwe	4–29	^{15}N fertilization	Ncube *et al.*, 2007
Ghana	32–67	^{15}N natural abundance	Adjei-Nsiah *et al.*, 2008
Ghana	29–179	^{15}N natural abundance	Belane and Dakora, 2009
South Africa	25–70	^{15}N natural abundance	Ayisi *et al.*, 2000
South Africa	46–87	^{15}N natural abundance	Makoi *et al.*, 2009
Tanzania	70	^{15}N natural abundance	Vesterager *et al.*, 2008

[a] For details of techniques, see Unkovich *et al.* (2008).

In addition to the traditional use of cowpeas as a multipurpose crop, analysis of the iron content of its leaves suggest that it could be developed as a source of minerals in areas where there are dietary deficiencies. Leaf and grain mineral content was measured in the same plants of the 25 genotypes used in the assessment of Ndfa (above). Although values varied with genotype and location, on balance, cowpea leaves were particularly rich in iron, much greater than in spinach, often used as a dietary source of iron (399 μg g^{-1} compared with 241 μg g^{-1}, AK Belane and FD Dakora, unpublished data). The average for legume forage is 222 μg g^{-1} (Spears, 1994, cited by Tola *et al.*, 2009). For comparison, Tola *et al.* (2009) found values of 300 μg g^{-1} for *Sulla coronaria* (also known as *Hedysarum coronarium*) and considered this to be very high and only possible because of specially modified 'shovel' roots. Since mineral deficiency is a widespread problem in many parts of Africa, this is another reason for encouraging the growth of cowpeas.

Acacia

Even more than *Vigna*, *Acacia* is undergoing major taxonomic changes. It has been known for many years that it is a rather heterogeneous genus and was divided into three subgenera, *Phyllodineae*, *Acacia*, and *Aculeiferum* (Ross, 1979). With the use of molecular methods, these subgenera were found not to be monophyletic and to be in two different tribes of subfamily Mimosoideae. Five distinct genera are now being recognized, but their names have been causing international controversy (discussed in Sprent, 2009*a*, where the currently known nodulated species are divided according to the subgenera). For the present purposes, the name *Acacia* will be retained for the species of interest, noting that the Australian species introduced to Africa are from a different genus and tribe. Subgenera *Acacia* and *Aculeiferum* can usually be distinguished by the presence of prickles and thorns, respectively. They all have pinnate, drought deciduous leaves, rather than the phyllodes of most Australian acacias. These native shrubs and trees are major components of the flora of drier areas of Africa, as well as parts of South America and the southern USA, with a few in Asia. African acacias have been the subject of many studies, and the former Oxford Forestry Institute has published a number of monographs on particular species. These cover practical issues such as diversity of germplasm and methods of propagation, but also the multiple uses to which the species is put. Table 3 gives the uses for *A. erioloba* E. Mey. (subgenus *Acacia*) and *A. senegal* (subgenus *Aculeiferum*). The latter is a very complex species, economically important for the production of gum arabic and is the subject of case study 2. All African acacias are important in the culture of local communities. Although most of them can and do nodulate, there are

Table 3. Some uses of *Acacia erioloba* and *A. senegal*, taken from Barnes *et al*. (1997) and Fagg and Allison (2004), respectively

Part of plant	*A. erioloba*	*A. senegal*
Wood	Firewood, charcoal, construction	For poles, cartwheels, too small for major construction
Bark	Building huts	Tannin, rope production
Gum	Eaten by bushmen, very nutritious	See case study 2
Foliage and pods	Fodder for animals, both green and dry; may contain cyanogenic glycosides	Highly nutritious fodder
Flowers	Eaten by stock	Important for honey
Pods and seeds	Pulped and used for humans and stock	Pods, seeds, and germinating seeds used for human food
Various	Bark, gum and roots have medicinal uses	All parts except wood are used for medicinal purposes
Other uses	Valuable shade tree, soil improvement	Soil improvement

a few species of a section of subgenus *Aculeiferum* that have lost this ability (Sprent, 2001). The nodulating bacteria are from a variety of mostly fast-growing rhizobia, from genera *Rhizobium* and *Sinorhizobium* (Nick, 1998; Odee *et al.*, 2002). Nodulation with slow-growing bradyrhizobia is less common than for the Australian acacias, which also, in many cases, have the ability to form dual mycorrhizas, unlike African acacias (Sprent, 1994). Rates of nitrogen fixation vary greatly and it has been argued that, since growth of many of these acacias in their natural environment may be limited by water, N acquisition may be a lesser priority (Sprent, 2009*a*, and references therein). This suggestion is supported by the fact that some important food legumes, such as Ye-eb (*Cordeauxia edulis* Hemsl.), that has very nutritious nuts and has supported nomads in Somalia through serious droughts, and marama bean (*Tylosema esculentum* (Burch.) A. Schreib., which has both edible beans and very large, nutritious underground tubers, prized by Bushmen of the Kalahari, are non-nodulating members of subfamily Caesalpinioideae.

Case study 2: gum arabic

Gums are important products with wide uses in the food industry and for medicine, paper production etc. A number of important gums are produced by legumes. These include guar gum, from the endosperm of *Cyamopsis tetragonoloba* (L.) Taub., which is a galactomannan with no protein component (http://wwwl.lsbu.ac.uk/water/hygua.html, accessed 17 August 2009) and gum arabic whose major component is a low molecular weight ($\sim0.25\times10^6$) polysaccharide with a minor component of a higher molecular weight ($\sim2.5\times10^6$) hydroxyproline-rich glycoprotein (http://www.lbsu.ac.uk/water/hyarabic.html, accessed 17 August 2009). It is produced, in response to wounding, by the stems of several acacias, including *A. seyal* Delile and *A. senegal* (Fig. 1B). Its composition and yield are very variable, both with host genotype and growing conditions (climate, soil, agronomic practice). Because it has been extensively tested for its properties and licensed by agencies such as the EU and FAO, *A. senegal* is the most important species for production of material for the export trade. In 2006, the EU imported 40 000 and the USA 20 000 tonnes [United Nations Statistics Division (UNSD), 2009)], with Sudan accounting for about 60% of world production (Muller and Okoro, 2004). An international programme, largely funded by the EU, is currently looking at how sustainable production of gum arabic can be improved. Figure 2 outlines the approach that is being used.

A. senegal is part of a complex of about 20 species, and *A. senegal* alone has four varieties, *senegal*, *kerensis*, *leiorhachis*, and *rostrata*, which vary in form from trees with a single stem to large bushy shrubs (Ross, 1979). They also vary in their distribution, *rostrata* being restricted to Southern Africa. Only variety *senegal* will be considered in detail as this produces the bulk of current gum production. It is diploid ($2n$=26) exclusively outcrossing, and mainly pollinated by bees. Production of honey is one of the many important other uses of dryland acacias in Africa. A number of provenances of this variety were sampled from across its natural range, from the west of Senegal through to India, where it is grown for commercial gum and other uses. When grown in a Sudano Sahelian climatic region of Africa at Bambey, Senegal, annual rainfall 400 mm, there was wide variation both within and between provenances in the amount of gum produced (Table 4). One of the factors that may contribute to this wide variation is the level of nodulation and nitrogen fixation. Faye *et al.* (2006) reported improved gum arabic yield production of mature (10-year-old) *A. senegal* trees inoculated with a mixture of selected rhizobial strains at Rotto, Senegal. There have been a number of studies on the nodulation of *A. senegal* and there is a range of rhizobia that have been shown to form nodules on it (as opposed to being isolated from its nodules, which is not necessarily the same). These are four species of *Sinorhizobium* (which is now often called *Ensifer*), *S. arboris*, *S. kostiense*, *S. saheli*, and *S. terangae* (McInroy *et al.*, 1999; Nick *et al.*, 1999; Odee *et al.*, 2002), plus *Rhizobium leguminosarum* and *Mesorhizobium plurifarum* (Wolde-Meskel *et al.*, 2005). All of these belong to the α-Proteobacteria. There are now many reports of β-Proteobacteria nodulating legumes from tropical and subtropical regions (Sprent, 2009*a*) and there is evidence that some species of African acacia (but not yet including *A. senegal*) can be nodulated by *Burkholderia phymatum* (EK James, JI Sprent, DW Odee, unpublished observations), so the range of bacteria nodulating *A. senegal* may well increase. In addition, the numbers of rhizobia capable of nodulating *A. senegal*, found in areas where the species is grown, vary widely. For example, in the EU supported

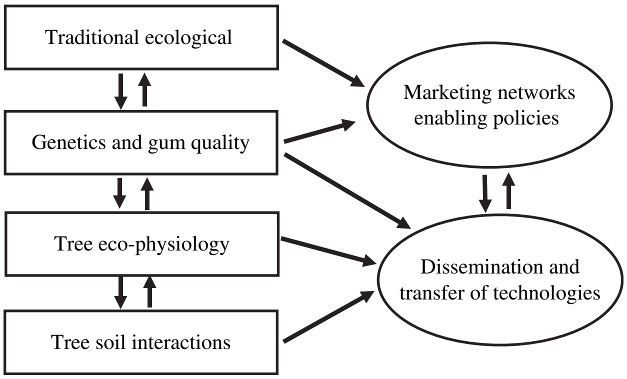

Fig. 2. A schematic presentation of the programme for development of *Acacia senegal* in Africa (Courtesy 'EU ACACIAGUM PROJECT'). Gum arabic yield and quality are important traits and their improvement requires an integrated approach to ensure sustainability in its provision of socioeconomic well-being and ecosystem services in the arid and semi-arid lands of Africa.

Table 4. Variation in gum arabic producing trees and yield of 8-year-old *Acacia senegal* provenance trial at Bambey, Senegal (I Diallo *et al., unpublished data)*

Provenance (country)	No. of tapped trees	No. of gum producing trees	Range of gum produced (g tree^{-1})
Aite (Mali)	6	3	38–186
Kirane (Mali)	6	2	38–52
Somo (Mali)	8	5	40–392
Bissiga (Burkina Faso)	5	1	6
Burkina Di (Burkina Faso)	3	2	180–384
Daiba (Senegal)	8	3	26–334
Diamenar (Senegal)	10	10	22–420
Kidira (Senegal)	9	7	18–808
Ngane (Senegal)	7	2	62–66
Djigueni (Mauritania)	6	3	26–82
Kankossa (Mauritania)	7	3	398–650
Jodhpur (India)	3	1	16
Karofane (Niger)	7	6	10–92
Sodera (Ethiopia)	6	2	24–448
Kordofan (Sudan)	8	6	64–800

study, values from 0 to 5.9×10^3 cells g^{-1} soil were found (DW Odee *et al.*, unpublished data) and these numbers varied with the particular variety of *A. senegal* used to trap the rhizobia. Thus it is not surprising that estimates of nitrogen fixation vary greatly, both under greenhouse conditions and field trials. In an experiment with eight provenances of *A. senegal* grown on various soil types in a common garden experiment in the Blue Nile region of the Sudan, Raddad and Luukkanen (2006) found that the proportion of N in the plant obtained from fixation varied from 24–61%. If gum arabic is to be produced under sustainable conditions, these values must be improved. This is one of many characters, in addition to gum quality and amount produced, that are being assessed against DNA-based molecular markers (RAPD, SSR, and cpSSR) found in the host plant and correlated with environmental parameters. Assoumane *et al.* (2009) have isolated and characterized a set of microsatellite markers from a range of provenances and these are now being used to assess variation in populations of trees in Kenya and elsewhere and these data are being linked to traits such as gum production.

Legumes of the Cape Floristic Region (CFR)

The CFR is one of the world's biodiversity hotspots (Myers *et al.*, 2000). It has a long and varied history in terms of climate and geomorphology (Cowling *et al.*, 2009), with the result that there are numerous relatively small areas with unique combinations of characters, such as soil pH and nutrient content. This, in turn, has resulted in a high level of endemism and the evolution of families with genera and species found only in this region. These endemics include numerous nodulated legumes. Unlike other parts of Africa, there is only one record of a non-nodulated legume in the CFR (Sprent, 2009*a*), suggesting that nodulation is an important attribute. It is now becoming clear that the diversity of host legumes is accompanied by diversity of their nodulating bacteria. The great potential of these symbiotic systems is now being realized and developed. For example, a multi-disciplinary collaboration between South African and Australian scientists is leading to the identification of several forage legumes that could be developed for the increasing area of agricultural land exposed to drought. Unlike the dry areas in which African acacias are dominant and where soil pH is usually slightly alkaline or neutral, many of the soils in the CFR are acid and of low nutrient content. In their natural state, most of the CFR legumes are short-lived perennials, that are either destroyed by periodic fires, a natural part of the ecosystem (Manning, 2007) or have woody rootstocks (xylopodia) from which they can regenerate after either fire or prolonged drought (Sprent, 2009*a*, *b*). Howieson *et al.* (2008) outline the processes needed to take wild material and turn it into acceptable agronomic varieties. Crucial is the matching of host and bacterial genotypes, which, in the case of some of the CFR legumes, involves newly discovered bacterial genera and species. For example, *Lotononis angolensis* Baker is nodulated by a pink pigmented bacterium that will be assigned to a new genus of α-rhizobia (Yates *et al.*, 2007), and Garau *et al.* (2009) found *Rhynchosia ferulifolia* Harv. to be nodulated by a new species of the β-rhizobial genus *Burkholderia*.

In addition to looking for new forage species, development and marketing of traditional beverage crops is proceeding rapidly. The pros and cons of the legume teas, rooibos (*Aspalathus linearis*) and honeybush (*Cyclopia* sp.) are considered in case study 3.

Case study 3: legume teas, rooibos and honeybush

Taxonomically, the large (~280 species) and exclusively South African genus *Aspalathus* is in tribe Crotalarieae, which also includes *Lotononis* (see above) and is also largely African (Van Wyk, 2005*a*). *Cyclopia* has 24 species and is a member of the small Cape Region endemic tribe Podalyrieae (Van Wyk, 2005*b*). Unlike traditional teas made from species of *Camellia* L., rooibos (red bush) and honeybush teas are caffeine-free and low in tannins. Both are low shrubs, with xerophytic characters, such as reduced leaf size, and shoots rather than leaves are harvested. Most of the harvested material is fermented (as in black tea from *Camellia*). This used to be, and still is for local use, carried out in heaps. In these, the temperature varies greatly as does the microbial flora. Fermentation in large-scale production is now carried out in ovens where conditions are closely controlled (Joubert *et al.*, 2008). Following fermentation, the 'tea' is dried in the sun (Fig. 1C) before further processing and packing. During the process of fermentation, many of the allegedly healthy ingredients (see below for individual teas) become greatly reduced in amount. For example, aspalathin in rooibos drops from 13.5 to 1.1 mg 100 ml^{-1} and mangiferin in honeybush from 3.7 to 0.3 mg 100 ml^{-1} (Joubert *et al.*, 2009). As is the case with traditional teas, unfermented or green rooibos and honeybush teas are now being produced in increasing amounts. They are an important part of the South African economy and are likely to become more so as the market for 'healthy' products grows.

(a) Rooibos: Aspalathus linearis

The species from which rooibos teas is obtained has been called *A. linearis* ssp *linearis*, but now this and another subspecies have been incorporated into *A. linearis* (Dahlgren, 1988, cited in van Heerden *et al.*, 2003). Van Heerden *et al.* (2003) describe the species as 'exceptionally polymorphic' and one for which no satisfactory infraspecific classification has been produced. One of the sources of variation is its fire resistance strategy, with some forms being 'reseeders', i.e. the plants are killed by fire and regeneration is from seed, whereas others are 'resprouters' that have woody rootstocks that can produce new growth after fire. In attempting to classify the different parts of the species, van Heerden *et al.* (2003) list three resprouting and four reseeding types. Only the 'red type' among the reseeders is used for the commercial production of rooibos tea. This is both low in tannins and also high in the flavanoid aspalathin (dihydroxychalcone), which has strong anti-oxidant properties. It is grown from seed, the seedlings transplanted and harvested yearly after 12–15 months, for about five years. Details of its production can be found in Joubert *et al.* (2008) and in many sites on the web, most of the latter also having extravagant claims as to its health-giving properties. It can grow on extremely poor acid soils and, as well as producing nitrogen-fixing nodules, also has cluster roots and mycorrhizas that help in nutrient uptake. Surprisingly little is known about the rhizobia nodulating *A. linearis*, although it is known to be able to fix well over 100 kg N ha^{-1} annually (Muofhe and Dakora, 1999). Total production has risen greatly in the last few years, with an estimated 14 000 tonnes (about 1% of which was unfermented) being harvested in 2007 (Joubert *et al.*, 2008). More than half of the export trade is to Germany with the Netherlands, the UK, Japan, and the USA being smaller players. In addition to teas, rooibos is used to make various cosmetics and pharmacalogical products (Joubert *et al.*, 2009). However, such a large expansion of cropping of *A. linearis* is not without its price and there are now concerns that nutrient mining of some very fragile soils is occurring. In some areas, which have been heavily cropped, fields have been abandoned (JI Sprent, personal observations) and it is not clear when or how these will be restored.

(b) Honeybush tea: Cyclopia *sp.*

There are several species of *Cyclopia* that can yield honeybush tea, but they vary in quality and quantity of product. Like *Aspalathus linearis, Cyclopia* species can be divided into reseeders (e.g. *C. falcata* (Harv.) Kries, syn. *C. subternata* Vogel) and resprouters (e.g. *C. genistoides* Vent.). These two species, together with *C. intermedia* E. Mey. and *C. sessiliflora* Eckl. & Zeyh. are the main ones used commercially. Production is small (<300 tonnes), but growing, and again the major importer is Germany. The characteristic compound of *Cyclopia* is xanthone *C*-glucoside, otherwise known as mangiferin (because it is also found in mangoes) and other phenolics with anti-oxidant activities. Joubert *et al.* (2009) give some interesting comparisons between the flavanols and flavanones in rooibos and honeybush, compared with other fruits, such as mangoes and citrus. Like rooibos, honeybush is used for cosmetic and pharmacological purposes as well as for tea.

Cyclopia root nodules and their endophytic bacteria are much better studied than those of *A. linearis* and include both α- and β-rhizobia (Spriggs, 2004; Elliott *et al.*, 2007). Interestingly the β-rhizobium *Burkholderia tuberum* which nodulated several species of *Cyclopia* did not nodulate *A. linearis* or several other species of this genus, but does appear to nodulate *A. carnosa* (EK James, JI Sprent, FD Dakora, unpublished observations). Taken together with the data cited in the section on the CFR, it is clear that the Cape area is unique for its rhizobia as well as for its host legumes. In the wild, *Cyclopia* species were found to fix up to 90% of the N in the plants (Spriggs and Dakora, 2008), whereas commercial cultivars, even when inoculated with a recommended strain fixed less and responded positively to inoculation with elite strains, both in field and nursery conditions (Spriggs and Dakora, 2009).

Concluding remarks

It is generally accepted that the alleviation of poverty in Africa needs its peoples to be properly fed and also able to generate products that can yield income. With modern technology for improving plant and rhizobial germplasms, better exploitation of native legumes for both of these purposes is achievable, as illustrated by the examples given here.

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