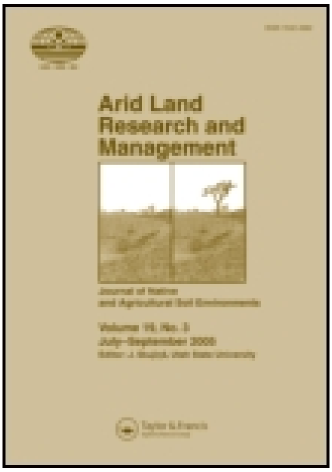

Arid Land Research and Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/uasr20

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Published online: 24 Jun 2013.

To cite this article: Eunice W. Githae , Charles K. K. Gachene , Jesse T. Njoka & Stephen F. Omondi (2013) Nitrogen Fixation by Natural Populations of Acacia Senegal in the Drylands of Kenya Using ^{15}N Natural Abundance, Arid Land Research and Management, 27:4, 327-336, DOI: 10.1080/15324982.2013.784377

To link to this article: http://dx.doi.org/10.1080/15324982.2013.784377

Arid Land Research and Management, 27:327–336, 2013

ISSN: 1532-4982 print/1532-4990 online
DOI: 10.1080/15324982.2013.784377

Nitrogen Fixation by Natural Populations of *Acacia Senegal* in the Drylands of Kenya Using ^{15}N Natural Abundance

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Nitrogen (N) fixation was estimated for three Acacia senegal (L.*)* (A. senegal) *Willd. varieties (*A. senegal *var.* senegal*,* kerensis*, and* leiorhachis*) growing naturally in different sites in the dryland areas of Kenya. The quantities of N_2 fixed were estimated by the ^{15}N natural abundance method, using leaves as the sampling material.* Balanites aegyptiaca (B. aegyptiaca) *was selected as the reference species growing in the same area. Soil samples were also collected under* A. senegal *trees for nodule assessment. Leaf ^{15}N natural abundance values ($\delta^{15}N$) were significantly different between* A. senegal *and* B. aegyptiaca*. These values averaged 6.35, 4.67, and 3.03‰ for* A. senegal *var.* kerensis*,* leiorhachis*, and* senegal*, respectively, and were lower than those of the adjacent reference species. There were also significant differences in the amount of N_2 fixed (%Ndfa) among the varieties.* A. senegal *var.* senegal *showed the highest levels of N_2 fixation with a mean of 36% while* A. senegal *var.* kerensis *and* leiorhachis *had equal estimates of 25%. However, no nodules were observed in the collected soil samples. Leaf N values were significantly different among the varieties with a mean of 2.73, 2.46, and 4.03% for* A. senegal *var.* kerensis*,* leiorhachis*, and* senegal*, respectively. This study shows that the three varieties of* A. senegal *are able to fix N_2 in their natural ecosystems and the differences could probably be due to soil properties and nutrient availability under the different environments. The species can hence be utilized as plantations in agriculture and land rehabilitation programs.*

Keywords arid lands, legumes, natural ecosystem, semiarid lands

Received 4 September 2012; accepted 5 March 2013.
This study was funded by the Rockefeller Foundation through Regional University Forum for Capacity Building in Agriculture (RUFORUM). We also acknowledge the Kenya Forestry Research Institute, Narok University College, and University of Nairobi for technical assistance.
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Introduction

Nutrient depletion in the soil is one of the major forms of soil degradation and declined soil fertility in the drylands of Africa and hence considered as the major threat to food security (Sanchez, 2002). A potential solution is to promote the utilization of indigenous N_2-fixing legume species that are able to improve soil fertility and sustainability (Binkley, 2005). The use of deep-rooted legume trees is often recommended in agroforestry systems, serving, among other things, as a direct and indirect source of nutrients for shallow rooted herbaceous species (Aronson et al., 2002). Legume trees improve soil fertility and structure in the arid and semi-arid environments through N_2 fixation (Sprent and Gehlot, 2010). Among them is *Acacia senegal* (L.) (*A. senegal*) Willd–a multipurpose drought tolerant species that is widely distributed in the drylands of Africa. It is valued for its stem exudate named "gum Arabic" that is essential in dryland farming systems where pastoralism is the major source of livelihood. This gum is used internationally for food, pharmaceuticals and cosmetics industries. The species is also used as a source of fodder during the dry season, provides shade and bee forage and restores soil fertility (Maundu and Tengnäs, 2005; Eisa et al., 2008).

A. senegal is known to be highly variable in growth form. Current classification includes four varieties, namely: *A. senegal* var. *senegal* Schweinf, var. *kerensis* Schweinf, var. *rostrata* Brenan, and var. *leiorhachis* Brenan (Brenan, 1983; Beentje, 1994; Fagg and Allison, 2004; Maundu and Tengnäs, 2005). The differences among them are based on natural distribution and morphological characteristics (Table 1). *A. senegal* var. *senegal* is the most widespread in Africa and the source of more than 80% of commercial gum arabic marketed in the world. In Kenya, three of the varieties are found, namely: *A. senegal* var. *senegal, kerensis,* and *leiorhachis*, sometimes closely distributed, with var. *kerensis* being the most widespread and the main source of commercial gum arabic (Chikamai, 1994). *A. senegal* is one of the N_2-fixing species highly suitable in agroforestry systems (Ballal et al., 2005; Elmqvist et al., 2005; Gaafar et al., 2006) that ensures optimum and sustainable utilization of the natural resources (Eisa et al., 2008). The rare adaptive responses to moisture stress and drought allow this species to produce high biomass in extremely dry environments (Gaafar et al., 2006). The ability of the species to fix N_2 makes it grow better on N-depleted soils thereby restoring fertility of such soils (Hussein, 1983; Deans et al., 1999; Raddad et al., 2005; Fadl and El sheik, 2009) and this would be important in farming systems where the application of fertilizers is limited. Because of their environmental, social, and economic benefits, agroforestry systems based on *A. senegal* are considered one of the most successful forms of sustainable management in tropical drylands (Eisa et al., 2008). In Kenya, despite the potential of this species, there is a lack of knowledge on its potential for N_2 fixation under natural conditions and is therefore underutilized. One potential limitation is the fact that no nodules have been found in mature *A. senegal* trees (Bernhard-Reversat and Poupon, 1980; Anderson, 1984; Jakubaschk, 2002). Considering this lack of information, N_2 fixation by *A. senegal* varieties in the dryland areas of Kenya was estimated for sustainable utilization.

Materials and Methods

Study Sites

Three study sites were selected based on the varieties distribution range since each variety is found growing separately. Kibwezi was selected for the assessment of

Table 1. Distinguishing characteristics of *A. senegal* varieties and their distribution

Variety	Altitude (m)	Distinguishing characteristics	Distribution
A. senegal var. *senegal*	120–1680	A tree up to 15 m high with rounded and spreading crown. Bark on trunk is not papery and peeling but greyish to yellowish-brown, sometimes flaking. Pods rounded to acute, rarely acuminate at apex.	Senegal, Gambia, Mali, Ghana, Niger, Nigeria, Sudan, Ethiopia, Somalia, Central African Republic, Cameroun, Zaire, Rwanda, Uganda, Kenya, Tanzania, Pakistan and India.
A. senegal var. *leiorhachis*	460–910	A tree up to 12 m high, with long straggling branches forming an open irregular crown. Bark on trunk is usually yellow, papery, and peeling. Pods are rounded to acute at apex and larger than in other varieties (up to 19 cm long).	Ethiopia, Somalia, Kenya, Tanzania, Mozambique, Zambia, Zimbabwe, Botswana and South Africa.
A. senegal var. *kerensis*	460–1130	A shrub 1–5 m high branching from base with trunk short or almost absent. Young branchlets are usually pubescent. Pods are rounded to acute at apex, rarely acuminate.	Ethiopia, Somalia, Uganda, Kenya and Tanzania.
A. senegal var. *rostrata*	Near sea level–600	A tree 2–8 m high with a flattened and spreading or slightly rounded crown; sometimes a shrub. Young branchlets are more or less pubescent. Pods markedly rostrate or acuminate at apex.	Mozambique, Zimbabwe, Botswana, South and West Africa. A few specimens from Kenya have pods similar to this variety hence more evidence is required.

A. senegal var. *kerensis*, Magadi for the var. *leiorhachis*, and Kajiado for the var. *senegal* (Figure 1). These sites are located in areas with different environmental and physical conditions (Table 2). The major types of vegetation of these sites are dominated by *Acacia seyal* Del., *Balanites aegyptiaca* (L.) Del., *Combretum*, and

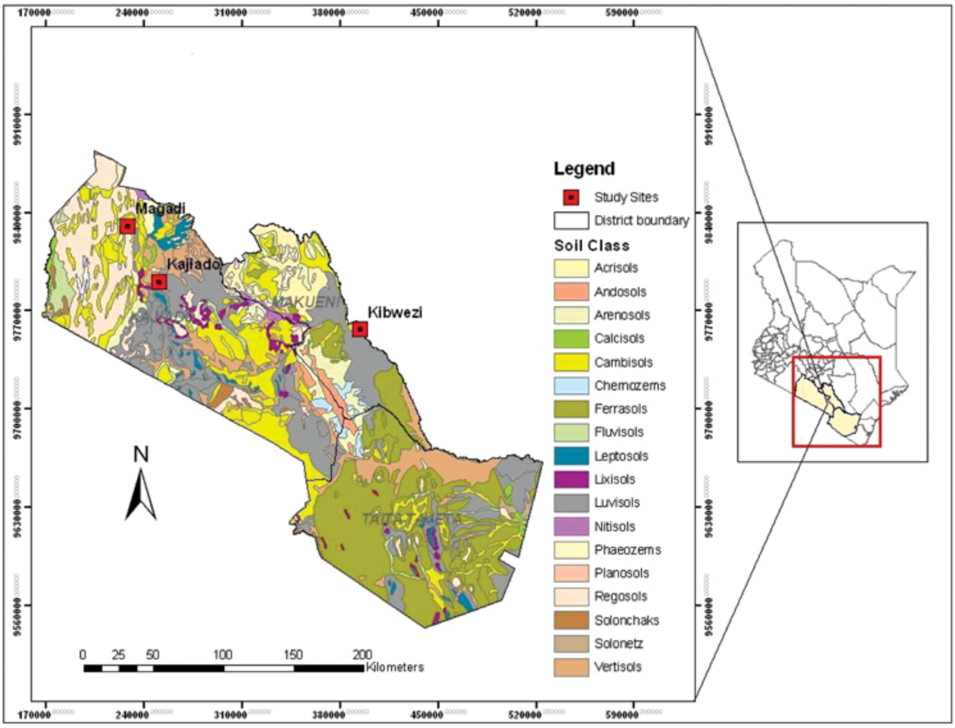

Figure 1. Location of the study sites in the Kenyan drylands. (Figure available in color online.)

Commiphora spp. (Maundu and Tengnäs, 2005). The major source of livelihood in these areas is pastoralism due to unreliable rainfall for agriculture.

Sampling of Leaves

Ten trees were randomly selected for sampling in each population during the early flowering period. Mature green leaves were collected evenly from the upper to lower branches to form a single sample for analysis. *Balanites aegyptiaca* (Balanitaceae) was selected as the reference species growing in the same environments due to

Table 2. Environmental and physical characteristics of three sites where three varieties of *A. senegal* are distributed in Kenya

Population	Altitude (m)	Mean-annual rainfall (mm)	Condition	Mean-annual temperature (°C)	Soil type	Soil texture	Variety of *A. senegal* found
Kajiado	1730	300–900	Semi-arid	21–32	Chromic Luvisols	Sandy clay loam	*senegal*
Kibwezi	731	300–1200	Semi-arid	23–32	Luvisols/ Ferralsols	Loamy sand	*kerensis*
Magadi	1460	300–600	Arid	28–33	Vertisols	Sandy loam	*leiorhachis*

similarities in duration and pattern of growth (Maundu and Tengnäs, 2005). This species has been used as a reference species in several studies (for example by Schulze et al., 1991; Sylla et al., 2002; Raddad et al., 2005) that indicate similarities in N sources with the N_2-fixing species.

Nodulation Assessment in the Field

Soil samples were collected under *A. senegal* trees at an area of 25 by 25 centimetres at a depth of 0–25 cm and cored at 0, 1, and 2 metres distant from the trunk in order to cover the maximum horizontal distribution of fine roots under the canopy. The soils were then spread on a thin film and carefully checked for nodules.

^{15}N Natural Abundance Method

The ^{15}N natural abundance method has become increasingly popular as a method for estimating N_2 fixation by leguminous shrubs and trees in their natural ecosystems (Boddey et al., 2000). It is a non destructive sampling technique that provides an integrated measure of N_2 fixed under field conditions (Spriggs et al., 2003). The potential of the legume to fix N_2 is indicated by the differences between the natural isotopic composition of the legume and that of the non-N_2-fixing reference species (Shearer and Kohl, 1986). An assumption of the method is that the natural abundance of ^{15}N in relation to the atmosphere (δ^{15}N) of the reference plants is identical to the δ^{15}N of soil N utilized by the legume. To increase the likelihood of this assumption, reference species should exploit the same soil N pool as the legume, have a similar duration of growth and pattern of N uptake as the legume and receive no significant transfer of fixed N_2 from the legume if they are growing in close association (Boddey et al., 2000). This method is widely used in studies on woody legumes and has been suggested in many studies to be the most reliable method for quantifying N_2 fixation in natural ecosystems (Shearer and Kohl, 1986; Boddey et al., 2000; Sylla et al., 2002; Brockwell et al., 2005; Raddad et al., 2005). However, difficulties arise from determining the reference species with similar growth patterns and N sources as that of the N_2-fixing species (Boddey et al., 2000).

Nitrogen Fixation Estimates

Leaf samples were oven dried at 50°C for 3 days and then milled to fine powder. The powdered samples were analyzed at the Stable Isotope Facility at the University of California, Davis using a PDZ Europa spectrometer with a combustion system (PDZ Europe LTD, UK). The contribution of N_2 fixed from the atmosphere (Ndfa), takes into account the difference between the N isotopic composition of N_2-fixing species and that of the reference plants using the following equation (Shearer and Kohl, 1986):

$$\%\text{Ndfa} = \left(\delta^{15}N_0 - \delta^{15}N_t/\delta^{15}N_0 - \delta^{15}N_a\right) \times 100$$

where $\delta^{15}N_0$ is the Non-N_2-fixing reference plant; $\delta^{15}N_t$ is the N_2-fixing plant; and $\delta^{15}N_a$ is the N_2-fixing plant grown in a nitrogen free media.

Boddey et al. (2000) reported that $\delta^{15}N_a$ value ranges from −2.0 to 1.0‰ for most tree legume species. These two values were used in this study to estimate the range of %Ndfa for *A. senegal* from the lowest under assumption 1 (using $\delta^{15}N_a$ value of −2.0‰) to the highest under assumption 2 (using $\delta^{15}N_a$ value of 1.0‰).

Statistical Analysis

In order to compare the levels of N_2 fixation and leaf N among the three varieties of *A. senegal*, one-way analyses of variance were carried out. Significant differences between means were determined using t-test at $p < 0.05$. Data was analyzed using the statistical software SPSS ver. 10 for Windows.

Results

Significant differences were observed between the leaf δ^{15}N values of *A. senegal* and *B. aegyptiaca*. The leaf δ^{15}N values of each variety were lower than those of the corresponding reference species (Table 3). On average, *A. senegal* had leaf δ^{15}N values of 4.68‰ while *B. aegyptiaca* had a mean of 6.51‰. The mean contribution of N_2 fixed from the atmosphere for the three varieties of *A. senegal* ranged from 21 to 35% (Table 3). These values were significantly different ($p = 0.002$) among the varieties. *A. senegal* var. *senegal* showed the highest %Ndfa with a mean of 36%.

Leaf N concentrations varied significantly among the three varieties. These averaged 2.73%, 4.03% and 2.46% for *A. senegal* var. *kerensis, senegal*, and *leiorhachis*, respectively, with a mean of 3.07%. The reference species *B. aegyptiaca* had an average leaf N of 3.76%, which was higher than that of *A. senegal*. This difference was also valid for each population of the reference species, where the leaf N concentrations were 3.64% in *A. senegal* var. *kerensis* population, 4.05% in the var. *senegal* population, and 3.58% in the var. *leiorhachis* population.

During the nodule assessment in the field, no nodules were found in the soil samples collected under the canopies of the three *A. senegal* varieties.

Table 3. Leaf nitrogen isotopic composition (δ^{15}N) of three varieties of the legume *A. senegal* and of the non-legume *B. aegyptiaca*; and amount of N_2 fixed from the atmosphere (%Ndfa) using the natural abundance method

			%Ndfa		
Site	Plant species	δ^{15}N (‰)	Assumption 1 (Lowest)	Average	Assumption 2 (Highest)
Kibwezi	*kerensis*	6.35 ± 0.58	20.63 ± 5.81	25 ± 2.04	28.86 ± 5.72
	B. aegyptiaca	8.52 ± 0.23	–	–	–
Kajiado	*senegal*	3.03 ± 0.60	25.92 ± 11	36 ± 3.01	46.44 ± 13.1
	B. aegyptiaca	4.79 ± 0.30	–	–	–
Magadi	*leiorhachis*	4.67 ± 0.18	18.86 ± 7.66	25 ± 1.15	29.69 ± 7.54
	B. aegyptiaca	6.22 ± 0.34	–	–	–
Mean	*A. senegal*	$4.68 \pm 1.66^{*}$	21.80 ± 9.33	$30 \pm 1.06^{**}$	35.00 ± 9.27
	B. aegyptiaca	$6.51 \pm 1.88^{*}$	–	–	–

$^{*}p = 0.003$; $^{**}p = 0.002$.

Discussion

Nitrogen-fixing legumes are always associated with root nodules but in the present study, no root nodules were found in the collected soil samples under *A. senegal*. These findings are similar to previous observations of this species (Raddad et al., 2005), as well as others like *A. nilotica* var. *tomentosa* (Benth.) A.F. Hill (Faye et al., 2007), *Albizia adianthifolia* (Schum.) W.F. Wight (Dossa et al., 2008), *Pterocarpus amazonum* (Benth.) Amshoff (Kreibich et al., 2006) and *P. lucens* Lepr. ex Guill. & Perrott (Sylla et al., 2002). Mohamed (2005) excavated different sizes of *A. senegal* root systems during two rainy seasons and found no nodules even during the most active growth period. Similarly, Bernhard-Reversat and Poupon (1980) reported that no N_2-fixing nodules existed under mature *A. senegal* trees, assuming that symbiotic fixation occurs during the first years of tree life, but rarely in adult trees. However, root nodules have been observed in *A. senegal* seedlings (Raddad et al., 2005). This indicates that rhizobia might be present in the soil but are not able to infect the plant under natural environments. It is however assumed that, in some cases, the nodules may not be observed even if they are present due to their rapid decomposition, micro-size, or they may be located at lower depths below 5 m (Johnson and Mayeux, 1990).

The percentage of plant N derived from the atmosphere for *A. senegal* in this study averaged 30% with the highest values of 36% reported for *A. senegal* var. *senegal*. This variety prefers soils with high clay content compared with the other two varieties (Githae et al., 2011). In general, the levels of N_2 fixation in *A. senegal* seedlings have been reported to be higher at 43% using the same method (Ndoye et al., 1995; Raddad et al., 2005). Sylla et al. (2002) also reported a mean of 35% of N_2 fixed in *Pterocarpus lucens*. in a semi-arid ecosystem while Kreibich et al. (2006) reported an average of 44% of N_2 fixed by nineteen trees in a secondary forest. A study conducted by Reis et al., (2010) reported levels of N_2 fixation at 21% in seven mimosa species in a semi-arid region while Shearer et al. (1983) reported 52% Ndfa in *Prosopis* spp growing under conditions of very low mineral nutrients. These results suggest that N_2 fixation under natural conditions is highly variable and can be influenced by several factors including micro-symbionts efficiency (Ndiaye and Ganry, 1997), plant age and condition (Raddad et al., 2005), soil properties and nutrient availability (Pons et al., 2007; Isaac et al., 2011).

In this study, leaves were used as the sampling material for both *A. senegal* and the reference species. It is recommended that, if possible, entire plants should be sampled to assess biological N_2 fixation with the natural abundance technique due to differences in N isotopic composition in different plant parts (Boddey et al., 2000). However, *Pterocarpus lucens*, a similar dryland tree to *A. senegal*, showed no significant differences in N isotopic composition among different plant parts (Sylla et al., 1998).

A. senegal had significantly lower leaf δ^{15}N values than the non-legume *B. aegyptiaca*. In general, this difference reveals that the N_2-fixing species is able to effectively fix a significant amount of N_2 (Kreibich et al., 2006) and in this case, it implies that *A. senegal* has a potential to fix N_2 with little dependence on soil N (Githae et al., 2011). In this study, there was variation in the leaf δ^{15}N values among the three *A. senegal* varieties. These values are reported to vary depending on the local environmental factors, rooting depth and leaf longevity (Schulze et al., 1991; Raddad et al., 2005). In contrast, Kreibich et al. (2006) studied 22 leguminous species in periodically flooded forest of the central Amazon over two hydrological cycles and reported that the leaf $\delta^{15}N$ values did not vary over the two seasons. This lack of variation was possibly due to the significant high seasonal N losses through leaching.

The significant differences of leaf N observed among the three *A. senegal* varieties could probably be due to differences in N mineralization in the different soil types. This can be grounded by the fact that sampling was done at the end of the rainy season after a prolonged dry period when the rate of mineralization is high. Differential soil compaction in our study sites may also explain the observed differences in leaf N among *A. senegal* varieties. This is because plants with roots restricted by compaction may show low amount of N than others even when adequate N is present in the soil (Eckert and Martin, 1994).

This study indicates that *A. senegal* varieties are able to fix N_2 in their natural ecosystems and their plantations can be utilized in agriculture and land rehabilitation programs. The differences observed in N_2-fixing potential and N accumulation in leaves could probably be due to differences in soil properties and nutrient availability under the different environments. Further research should address the seasonal patterns of variations in N_2 fixation across the three different agro-ecological regions and also relate with gum arabic production for the purposes of *A. senegal* domestication.

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