Responses of potted *Acacia natalitia* and *Scutia myrtina* saplings to type of nitrogen fertilizer and rate of application

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Two experiments were conducted to study the responses of two savanna trees species *Acacia natalitia* (deciduous legume) and *Scutia myrtina* (evergreen non-legume) to nitrogen (N). Experiment 1 tested the responses of the species to three N-source fertilizers, namely; limestone ammonium nitrate (LAN), a composite fertilizer NPK3:1:5(26) containing slow release nitrate and an “organic” fertilizer (Accelerator). Experiment 2 tested the responses of the species to five LAN rates equivalent to 0, 3.4, 5.7, 23.1 and 34.6 gN m\(^{-2}\). *A. natalitia* formed functional nodules with soil-born rhizobial species, and hence, responded less to applied N compared with the non-legume tree species *S. myrtina*. The source of applied N was inconsequential to the growth of *A. natalitia*, but in *S. myrtina*, LAN produced the most positive growth response. The biomass of *S. myrtina*, responded positively to increasing LAN application over the entire range of rates tested, whereas that of *A. natalitia* showed an optimum at LAN rates equivalent to between 23.1 and 34.6 gN m\(^{-2}\). The stimulation of *S. myrtina* growth by N increased the allocation of dry matter (DM) to the shoots at the expense of the roots in an N rate-dependent manner, whereas *A. natalitia* generally allocated more DM to the roots.

**Key words:** Biomass, browse, growth, herbivore, nitrogen, savanna, tree.

INTRODUCTION

Models proposed to explain the responses of plants to defoliation and the allocation of resources to plant parts consumed or avoided by herbivores emphasise to greater or lesser extents the role of resources in determining the type and magnitude of response (Stamp, 2003). Trees growing along resource gradients, where the trees grow at different rates, are required for testing certain predictions of such models, e.g., trees at the resource-rich end of the gradient will respond to herbivores by increasing growth rate, or trees at either end of the gradient will have low concentrations of C-based secondary metabolites (Stamp, 2003). Usually these experiments are done in greenhouses, under highly controlled conditions where nutrients are supplied in solution at machine-controlled steady rates and seedlings are either mechanically damaged or exposed to insect herbivores (Glynn et al., 2007). Such methods are not practically or financially possible in many situations, or may not be desirable according to the objectives of the experiment, which show that a larger scale experiment done with established saplings in irrigated fields or large pots accessible to mammal herbivores (e.g., goats) would be more appropriate.

Very few useful experiments have been done to test the responses of trees in savannas to variations in resource availability, although the value of such experiments is gaining recognition, especially for savanna modellers. The main resources for plants in savannas are nutrients and water (Scholes, 1997). Given that resources are distributed heterogeneously in savannas, and seedlings are sensitive to browsing, it should be important to understand how the effects of herbivory on seedlings depend on variations in resources (Scogings, 2003; Scogings and Macanda, 2005; Wiegand...
et al., 2006). However, some recent studies that aimed to do this have yielded non-significant effects of fertilizer treatments. Applying the right fertilizer in the right doses to achieve the desired effect is not always straightforward (Scogings and Mopipi, 2008; Fynn and Naiken, 2009). Fertilization with nitrogen (N) has been found to have no effect on growth of woody legumes in some experiments, which may be anticipated because the N₂-fixing ability of legumes makes them less likely to respond to N addition (Högberg, 1986; Fulco et al., 2001; Cash and Fulbright, 2005). In addition, the high volatility of N can make infrequent application to woody plants unsuitable for maintaining elevated N fertility of the soil in experiments conducted over a few months (Rogers and Siemann, 2002; Gowda et al., 2003; Katjiua and Ward, 2006), which may also explain non-significant effects.

In response to recent calls for multifactorial experiments to study interactions between browsing and resources, and the recently reported difficulties with fertilizer treatments in experiments (Scogings and Mopipi, 2008; Fynn and Naiken, 2009), together with the lack of standardised protocols for such experiments, we conducted two experiments on each of two woody species that are very different in their functional traits. *Scutia myrtina* is an evergreen, broad-leaf species, while *Acacia natalitia* (formerly part of *A. karroo*) is a deciduous, fine-leaf legume. Both species are spinescent, but *S. myrtina* has short, hooked thorns, while *A. natalitia* has long, straight spines. Both are common in mesic savanna areas on the eastern seaboard of southern Africa and both are utilized, among other uses, as fodder for domestic livestock. It would, therefore, be useful to understand more about their responses to resources. Our aim was, therefore, to address the afore-mentioned difficulties with fertilizer treatments in experiments by exploring the following questions: (1) Do young savanna trees achieve faster growth when fertilized at recommended rates with slow release N fertilizer compared to other types? (2) Do young savanna legumes differ in growth performance in response to different N fertilizers? (3) What dose of N fertilizer yields the fastest growth rate in young savanna trees? (4) Is nodule formation in *Acacia* affected by N availability in the growth medium? (5) Does the availability and source of N affect the biomass allocation pattern of young savannah trees?

**MATERIALS AND METHODS**

The study, consisting of two experiments, was conducted at the University of Zululand (28° 51′ 26″ S; 31° 50′ 34″ E). In both experiments, *S. myrtina* and *A. natalitia* saplings were grown in 6 L pots containing washed sand and housed under polycarbonate roofing that allowed 90% of sunlight to pass through, but no rainfall, and thus facilitating regulated irrigation. Potted plants were used because of logistical reasons, but we acknowledge that potted plants may experience conditions that do not necessarily replicate field conditions, e.g., restricted root growth, or different patterns of water/nutrient movements.

Experiment 1 was aimed at testing the effects of three types of fertilizer as sources of N on growth and biomass allocation of the two species. One N-source fertilizer was limestone ammonium nitrate (LAN), while the other sources were an “organic” fertilizer (OM) and a composite fertilizer NPK 3:1:5(26) containing slow release nitrate. The LAN and fertilizers were both products of Wonder™. The composite fertilizer was recommended by the manufacturer for flowering shrubs and fruit trees. The organic fertilizer (Accelerator) was a product of Gromor, and consisted of pelleted chicken manure. The LAN contained 28% N, while the NPK contained 8.7, 2.9 and 14.4% N, P and K, respectively. The organic fertilizer contained 3, 1.6 and 2% N, P and K, respectively, as well as a range of micro-nutrients. Each fertilizer was applied at a rate equivalent to 5 g N m⁻² based on the assumption that pulses of N mineralisation in savanna systems seldom yield N doses exceeding 5 g N m⁻² (Fynn and Naiken, 2009). An additional treatment involving no fertilizer application was included as a control. The four treatments, each having 15 replicates for each species, were arranged in a randomized complete block design (Underwood, 1997; Robinson et al., 2006). There were five blocks, each containing three replicates of each treatment.

Experiment 2 was aimed at testing five doses of LAN on the growth and biomass allocation of each of the same two species. There were five treatments of LAN viz; 0, 0.07, 0.42, 2.85 and 4.29 gLAN pot⁻¹, being equivalent to 0, 3.4, 5.7, 23.1 and 34.6 g N m⁻², respectively. The LAN treatments were replicated 10 times and arranged in a randomized complete block design. For each treatment, there were five blocks, each with two replicates.

**Plant management and processing**

Saplings of *S. myrtina* and *A. natalitia* were raised in pine bark medium in plastic sleeves for one year in the case of Experiment 1 and for two years in the case of Experiment 2. At transplanting to the experimental pots, saplings of similar size were shaken free of the pine bark medium and individually placed in the pots, which were half filled with sand. More sand was then added to fill the pots, firmly pressed down and thoroughly watered with deionised water. In both experiments, the fertilizer treatments were imposed at two weeks after transplanting. In those treatments that required fertilizer application, the fertilizer was top dressed as per treatment. The pots were kept moist throughout the growth of the plants with deionized water, and the watering was done in such a way that no water seeped through the bottom of the pots, this being done to avoid leaching of the fertilizers. The plants were harvested after four and six months of growth in Experiment 1 and 2, respectively. At harvest, nodule density on roots of *A. natalitia* in Experiment 1 was visually assessed on a score of 0 to 5. A score of 5 indicated a high nodule density and 0 indicated absence of nodules on the roots. The harvested plants were separated into tops, twigs and roots. These plant parts were oven-dried at 60°C until constant weight, and their dry matter (DM) determined. A subsample of leaf material from Experiment 1 was analysed for N concentration at the Plant Analysis Lab, Cedara.

**Data analysis**

In both Experiment 1 and 2, an ANOVA procedure was performed on all data collected using Genstat discovery version 3.0 (VSN International, 2008). Means of the treatments were separated by least significant difference at 5% level (LSD0.05). In addition,
Table 1. Effects of N application and N-fertilizer type on dry matter of *A. natalitia* and *S. myrtina* plant parts (n=15).

<table>
<thead>
<tr>
<th>Nitrogen fertilizer type</th>
<th>Root dry weight (g)</th>
<th>Leaf dry weight (g)</th>
<th>Twigs and thorn dry weight (g)</th>
<th>Above ground part dry weight (g)</th>
<th>Whole plant dry weight (g)</th>
<th>Shoot/root ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. natalitia</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>None</td>
<td>18.87</td>
<td>5.71</td>
<td>12.88</td>
<td>19.19</td>
<td>37.5</td>
<td>1.07</td>
</tr>
<tr>
<td>LAN</td>
<td>20.97</td>
<td>4.89</td>
<td>13.06</td>
<td>18.44</td>
<td>38.9</td>
<td>0.97</td>
</tr>
<tr>
<td>NPK</td>
<td>20.96</td>
<td>5.45</td>
<td>11.95</td>
<td>17.95</td>
<td>38.4</td>
<td>1.02</td>
</tr>
<tr>
<td>OM</td>
<td>20.95</td>
<td>5.18</td>
<td>12.47</td>
<td>18.41</td>
<td>38.3</td>
<td>0.99</td>
</tr>
<tr>
<td>Mean</td>
<td>20.44</td>
<td>5.26</td>
<td>12.59</td>
<td>18.41</td>
<td>38.3</td>
<td>0.99</td>
</tr>
<tr>
<td>LSD&lt;sub&gt;0.05&lt;/sub&gt;</td>
<td>NS</td>
<td>NS</td>
<td>2.42</td>
<td>NS</td>
<td>NS</td>
<td></td>
</tr>
</tbody>
</table>

| **S. myrtina**           |                     |                     |                               |                                 |                           |                  |
| None                     | 5.75                | 3.21                | 3.79                          | 7.3                             | 12.74                     | 1.44             |
| LAN                      | 10.8                | 12.42               | 10.87                         | 23.91                           | 34.09                     | 2.37             |
| NPK                      | 9.01                | 6.23                | 5.71                          | 12.55                           | 20.95                     | 1.49             |
| OM                       | 7.12                | 4.17                | 4.79                          | 9.37                            | 16.07                     | 1.37             |
| Mean                     | 8.17                | 6.51                | 6.29                          | 13.28                           | 20.96                     | 1.66             |
| LSD<sub>0.05</sub>       | 2.01                | 2.21                | 1.9                           | 4.02                            | 5.1                       | 0.55             |

Table 2. Effects of N application and N-fertilizer type on DM distribution to the roots and shoots of *S. myrtina* and *A. natalitia* (n=15).

<table>
<thead>
<tr>
<th>Nitrogen fertilizer type</th>
<th>A. natalitia</th>
<th>S. myrtina</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Percentage DM root</td>
<td>Percentage DM stem</td>
</tr>
<tr>
<td>None</td>
<td>50.1</td>
<td>51.7</td>
</tr>
<tr>
<td>LAN</td>
<td>53.1</td>
<td>48.2</td>
</tr>
<tr>
<td>NPK</td>
<td>52.2</td>
<td>49.3</td>
</tr>
<tr>
<td>OM</td>
<td>54.3</td>
<td>47.2</td>
</tr>
<tr>
<td>Mean</td>
<td>52.43</td>
<td>49.1</td>
</tr>
<tr>
<td>LSD&lt;sub&gt;0.05&lt;/sub&gt;</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

mathematical functions expressing correlations and regression relationships between N dose and the biomass of the plants and plant parts were obtained in Experiment 2 using the curve fitting programme of TableCurve™ 2D v3 for Win32 (Jandel Scientific, 1994). The same programme was also used to determine relationships between N dosage and root: shoot ratio and those between whole plant biomass and shoot or root biomass.

RESULTS

Experiment 1

Biomass response

The application of N and type of N-fertilizer was inconsequential to the growth of *A. natalitia* since none of the measured growth parameters differed significantly between the N-fertilizer treatments (Table 1). *S. myrtina* was more responsive to N application compared with *A. natalitia*, and the magnitude of the response was influenced by the type of N-fertilizer applied. The growth of *S. myrtina* was more enhanced when N was applied as LAN compared with the compound NPK fertilizer or OM. The LAN fertilizer stimulated shoot growth more than that of the roots resulting in a higher shoot-root ratio compared with the other fertilizer treatments.

Dry matter distribution

There were differences in the pattern of DM allocation of *A. natalitia* and *S. myrtina* to the roots and shoots. Generally, the proportions of DM distributed to the roots and the above ground parts of *A. natalitia* were equal with no significant effect of the type of N-fertilizer (Table 2). By contrast, dry matter apportioning to the roots and shoots of *S. myrtina* was significantly affected by the source of N, and the DM apportioning appeared to favour the shoot
Table 3. Effect of N application and N-fertilizer type on rhizobial nodule density on roots of A. natalitia and tissue N concentration in A. natalitia and S. myrtina.

<table>
<thead>
<tr>
<th>Nitrogen fertilizer type</th>
<th>Nodule density on A. natalitia roots (Visual score scale 0-5)¹</th>
<th>Tissue N concentration in A. natalitia leaves (%)²</th>
<th>Tissue N concentration in S. myrtina leaves (%)²</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>3.7</td>
<td>3.56</td>
<td>1.51</td>
</tr>
<tr>
<td>LAN</td>
<td>1.3</td>
<td>3.64</td>
<td>2.74</td>
</tr>
<tr>
<td>NPK</td>
<td>2.2</td>
<td>3.53</td>
<td>1.42</td>
</tr>
<tr>
<td>OM</td>
<td>2.8</td>
<td>3.63</td>
<td>1.49</td>
</tr>
<tr>
<td>Mean</td>
<td>2.5</td>
<td>3.59</td>
<td>1.79</td>
</tr>
<tr>
<td>LSD₀.₀₅</td>
<td>1.06</td>
<td>0.38 (NS)</td>
<td>0.26</td>
</tr>
</tbody>
</table>

¹ Nodule density is the mean of a visual score for 15 plants per treatment on a scale of 0 to 5, where 0 indicates absence of nodules and 5 indicates highest nodule density. ² Tissue N concentrations are means of 9 plants.

Figure 1. Pictogram showing large elongated nodules (on left side of the pen) and smaller rounded nodules (on the right hand side of the pen) on roots of A. natalitia.

Nodule production and tissue N

At transplanting, the roots of A. natalitia did not posses rhizobial nodules. However, functional nodules were observed on roots of A. natalitia at harvest, the source of inoculum being the sand soil. The nodules were significantly more abundant in plants raised without N than in plants that were supplied with N (Table 3). The nodule number was significantly higher in the OM treatment among the fertilizer treatments that contained N. There were two distinct types of nodules based on morphology, indicating that there was more than one species of rhizobium that infected the plants. One type of nodule was small, roundish and determinate, whilst the second type was larger, elongated and indeterminate (Figure 1). The former type was numerous, whereas the later was not as profuse. The two nodule types were not found on the same plant, which strongly suggested that they were mutually exclusive of each other on the host system. This was more pronounced in S. myrtina plants supplied with LAN fertilizer (Table 2), and which also produced the most plant growth response (Table 1).
plants. Both types had leg-hemoglobin, which indicated that they were functional, and therefore suggested that *A. natalitia* could be promiscuous with respect to rhizobial species that can form effective symbiotic associations with it.

Because of rhizobial N fixation in the nodules, there were no significant differences in the concentration of tissue N between the N-source fertilizer treatments in *A. natalitia* (Table 3). In the case of *S. myrtina*, a non-legume, the leaf N concentration in plants that received NPK fertilizer or OM was similar to that of plants that did not receive N fertilizer, but was approx. 1.8-fold higher in plants that received LAN fertilizer (Table 3).

**Experiment 2**

**Biomass response**

Nitrogen application rate had significant (P < 0.01) effects on the growth of both *A. natalitia* and *S. myrtina* (Figure 2), with root biomass (Figure 2A and B) and shoot biomass (Figure 2C and D) as well as plant biomass (Figure 2E and F) being highly correlated ($r^2 = 0.878$-966) with the N application rate. Also, the leaf biomass and twig plus thorn biomass were closely correlated with N application rate (Figure 3). However, the two species differed in the magnitude as well as in the nature of the responses of some of these parameters to increasing N application rate (Figures 2 and 3).

In *S. myrtina*, the plant biomass responded positively to increasing N application rate over the entire range of the N rates tested (Figure 2F), whereas that of *A. natalitia* plants appeared to show an optimum between 23.1 and 34.6 g N m$^{-2}$ N application rates (Figure 2E). In addition to this difference in the responses of the two species to increasing N application rate, the effects of N application rate on plant biomass of *A. natalitia* were smaller than for *S. myrtina*.

The shoot biomass increased with increasing N application in both *A. natalitia* (Figure 2C and D). In *S. myrtina* (Figure 2D), but the response of root biomass of the species (Figures 2A and B) differed from that obtained for shoot biomass (Figure 2C and D). In the case of *A. natalitia*, the root biomass increased to an optimum at 23.1 g N m$^{-2}$ and declined at higher N application rate (Figure 2A). In *S. myrtina*, the root biomass rapidly increased to reach a plateau at 5 g N m$^{-2}$ (Figure 2B).

There was a tendency for the leaf biomass of *A. natalitia* to decrease with increasing N application rate at 0 and 23 g N m$^{-2}$ (Figure 3A). This was accompanied by increases in twig and thorn biomass (Figure 3C). With further increase in N application rate, the twig and thorn biomass of *A. natalitia* showed a declining trend, whilst that of the leaves increased sharply at 34.6 g N m$^{-2}$. By contrast, a decline was absent in leaf biomass of *S. myrtina*, which increased as the N application rate was increased from 0 to 34.6 g N m$^{-2}$ (Figure 2B) in the same way as the response of shoot biomass to increasing N application rate (Figure 3D). The response of *S. myrtina* twig and thorn biomass to increasing N application rate (Figure 3D) was also different from that obtained for the twigs and thorns of *A. natalitia* (Figure 3C) by showing no biomass increment when N application was increased from 5.7 and 23.10 g N m$^{-2}$, but registered a significant increase when the N application was raised from 23.10 to 34.6 g N m$^{-2}$.

**Root: shoot ratio**

Generally, the root: shoot ratio of *A. natalitia* varied less than that of *S. myrtina* in response to increasing N application rate (Figure 4). Furthermore, the response of the root: shoot ratio differed in the two plant species. In *A. natalitia*, the root: shoot ratio was highest at 23.10 g N m$^{-2}$, and tended to decline at N application rates that were lower or higher (Figure 4). By contrast, in *S. myrtina*, the ratio: shoot ratio was highest in plants that were not supplied with N fertilizer. As the N application was increased from 0 to 34.6 g m$^{-2}$, there was a large decline in the root: shoot ratio of *S. myrtina* with the first increment in N application rate of 3.4 g N m$^{-2}$ followed by smaller decreases with larger increments in N application rate. Thus, the root: shoot ratio of *S. myrtina* declined curvilinearly with increasing N application rate. Whilst the root: shoot ratio of *S. myrtina* in plants that were not supplied with N fertilizer was significantly higher than that of *A. natalitia* at any of the N application rates, it was significantly smaller in all N application rate treatments (Figure 4). The mean root: shoot ratio of *S. myrtina* (0.65) was significantly lower than that (0.83) for *A. natalitia*.

**Relationships root and shoot biomass with total plant biomass**

Significant correlations were obtained between plant biomass and shoot or root biomass (Figure 5). The root biomass of *A. natalitia* (Figures 5A and B) increased in a linear manner with increasing plant biomass, but the root biomass of *S. myrtina* (Figure 5B) increased in a sigmoid manner with increasing plant biomass, which indicated a greater control and regulation of root growth.

**Biomass allocation**

Dry matter partitioning to various plant parts was greatly influenced by the N application rate (Figure 6). Generally, *S. myrtina* showed larger changes than *A. natalitia* in the
Figure 2. The response of shoot (A, B), root (C, D) and plant (E, F) biomass to increasing N application rate (data points are means of 15 plants). Note the smaller responses of root and plant biomass in *A. natalitia* compared with *S. myrtina* to increasing N application rate.
allocation of DM to most plant parts in response to increments in N application rate (Figure 6). Also, there were notable differences in the way the two species partitioned DM among the various plant components in response to increasing N application. In A. natalitia, the allocation of DM to the leaves decreased with increasing N application rate to reach a minimum at 23.1 g m\(^{-2}\) N, and then increased at 34.6 g m\(^{-2}\) N to almost the same amount as that allocated with no N application (Figure 6A). In S. myrtina, the DM allocated to the leaves increased with increasing N application rate (Figure 6B). The DM allocation to the twigs plus thorns of both A. natalitia and S. myrtina registered a large increase with the first increment in the rate of N application, but in A. natalitia, there was a very slow decline in DM allocation to the leaves (Figure 6C) whilst that in S. myrtina (Figure 6D) continued to increase, albeit slowly, with progressively larger increments in N application rate. Changes in

**Figure 3.** Effects of N application rate on biomass of leaves (A, B) and twig plus thorns (C, D) of two plant species (data points are means of 15 plants). Note that the effects of N application rate were much smaller in A. natalitia than in S. myrtina.
the amount of DM portioned to the whole shoot system (above-ground parts) with increasing N the leaves in both species (Figures 6E; F). The changes in the DM apportioned to the shoot system of A. natalitia (Figure 6E) were however much smaller than those recorded for S. myrtina (Figure 6F).

The percentage of plant DM partitioned to the roots in S. myrtina with no N application was ca. 49% (Figure 6H), and decreased with increasing N application to approx. 29% at the highest N application rate. By contrast, in A. natalitia, the changes in the DM allocated to the roots were small and showed an optimal at 23.1 g N m$^{-2}$ (Figure 6G).

On average S. myrtina allocated more DN to the leaves than did A. natalitia, but allocated smaller amount to the twigs plus thorns and to the root system compared with A. natalitia (Figure 7). However, although the DM allocated to the twigs plus thorns in S. myrtina was smaller than that in A. natalitia, the DM allocated to the whole shoot system was larger in S. myrtina because of the much larger DM allocated to the leaves (Figure 7).

**DISCUSSION**

**Growth responses to fertilizer type and rate of N application**

Data obtained in Experiment 1, which tested the effect of N fertilizer type on the growth of A. natalitia and S. myrtina, showed that the growth of A. natalitia was insensitive to type of N fertilizer compared to S. myrtina (Table 1). The lack of growth stimulation in A. natalitia by N application in Experiment 1 could be attributed to N fixation by nodular rhizobium which may have supplied enough nitrogen for plant growth in treatments. Plants that were not supplied with N fertilizer had a higher proliferation of nodule formation compared with those that were supplied with N fertilizer.

In the case of S. myrtina, the LAN fertilizer registered the highest growth stimulation compared with NPK or OM (Table 1). The more favourable effects of LAN fertilizer on the growth of S. myrtina are difficult to explain, since this fertilizer contained only Ca and N compared with NPK which in addition to N contained P and K, or OM which contained more additional nutrients essential for plant growth. Noteworthy, however, was that S. myrtina plants supplied with LAN showed higher N concentration in the leaves compared with plants supplied with NPK or OM (Table 3), suggesting that N was more readily available from LAN compared to the other sources.

Notwithstanding the lack of growth response to N applications involving fertilizer types in Experiment 1, A. natalitia did respond to increasing N application supplied as LAN in Experiment 2, albeit the growth responses were lower than those registered for S. myrtina (Figures 2 and 3). High nitrogen application (> 23.1 g N ha$^{-1}$) appeared to negatively influence root growth of A. natalitia (Figure 2A).
Figure 5. Relationship between root biomass (A, B), shoot biomass (C, D) plant biomass in *A. natalitia* (A, C) and *S. myrtina* (B, D).

**Biomass partitioning**

Generally, *A. natalitia* allocated more DM to the roots than did *S. myrtina*, especially in treatments in which N was applied (Table 2, Figures 6 and 7). The difference between the two species in the amount of DM invested in the roots widened with increasing N application (Table 2, Figure 6G and H). *S. myrtina* invested considerably more DM to the leaves than did *A. natalitia* (Figures 6A, B and 7) leading to substantially greater overall DM allocation to the shoot system of *S. myrtina*, especially at higher N application rates. The stimulation of *S. myrtina* growth by N in Experiment 1 and 2 increased the allocation of DM to the shoots (Figure 6F) at the expense of the roots (Figure 6H) in an N rate-dependent manner. *S. myrtina* showed higher plasticity compared with *A. natalitia* in the allocation of DM to the shoot and root systems in response to change in N level in the growth medium (Figure 6).

The difference between *A. natalitia* and *S. myrtina* in
Figure 6. Relationships between N rate and the proportions of plant dry matter invested in the above-ground and below ground parts of *A. natalitia* and *S. myrtina* (data points are means of 10 plants).
the pattern of DM allocation to the roots and shoots suggests that the two species have different survival strategies. Generally, plants under mesic conditions put less DM to the roots compared with the shoot system (Celano et al., 1999; Creelman et al., 1990; Li et al., 2006) because of the need to maintain a large photosynthetic apparatus (Li et al., 2006) as well as providing a larger framework for reproduction (Klinkhammer et al., 1992; Sugiyama and Bazzaz, 1998). This, however, occurs in situations where nutrients, especially N and phosphorus (P), are abundant and readily available to plants. In nutrient-poor soils the need to forage for nutrients, e.g. N and P, over a wider area and larger soil volume may necessitate investment of higher amounts of DM to the root system than to the shoot system (Muller et al., 2000; Hermans et al., 2006). In the case of *A. natalitia*, the larger proportion of DM distributed to the roots than to the shoots suggests that this species might be adapted to nutrient-poorer soils compared with *S. myrtina*, which tended to invest more DM in the shoot system than in the root system.

Presumably, the differences in the pattern of DM partitioning of *A. natalitia* and *S. myrtina* noted before and also in Experiment 1 relate to different adaptation strategies in the two species. Generally, the partitioning pattern of DM between the above- and below-ground biomass is under strong genetic control (Barnes et al., 1998), and relates to the survival of a plant species in its adapted environment (Bloom et al., 1985; Geber et al., 1990; Enquist et al., 2002). Plants adapted to resource-rich environments are generally highly plastic in their allocation of DM in response to environmental stress or changes in resource availability (Bloom et al., 1985). Often, the plants decrease the amount of roots, whilst they increase that of the foliage as water and nutrient availability increase (Barnes et al., 1998). This was precisely the case in the response of *S. myrtina* to increasing N availability, and similar responses in the allocation of DM to the shoots and roots along gradients of increasing N availability have been documented with other herbaceous species (Barnes et al., 1998). The highly plastic pattern of compensatory allocation observed for *S. myrtina* in response to variation in the supply of N enables the plant to balance and maximize the use of N in a heterogeneous N environment.

The high allocation of DM to the roots coupled with a lack of plasticity in DM apportioning in *A. natalitia* suggest that this plant species is adapted to less fertile conditions than is the case with *S. myrtina*. Plants from resource-poor environments are often less plastic in their allocation
pattern (Tilman, 1988) and have genetically fixed high root: shoot ratios which change very little in response to variations in the environment (Bloom et al., 1985). In part, the high root: shoot ratio arises as an adaptive mechanism in which the root system is used for storage in addition to increasing the capacity for foraging for mineral nutrients and water. When the environment temporarily becomes unfavourable, the plant can fully exploit that environment through storage rather than changing its allocation to some pattern that would be inappropriate for the normal environment (Bloom et al., 1985). In the case of A. natalitia and S. myrtina, the former is deciduous, shedding its leaves in the dry winter months to conserve moisture. The latter is an evergreen, and therefore has slow leaf turnover. In spring, A. natalitia forms new leaves whilst S. myrtina has no need to do so. The production of new leaves in spring by A. natalitia is supported by remobilization of stored food reserves. Thus, the need for forming new leaves every spring may then be one of the driving forces behind its higher DM partitioning to the roots compared with S. myrtina. Furthermore, it is more economic for A. natalitia to invest in the more permanent roots than in the leaves which are periodically lost. In the case of S. myrtina, because the leaves are more permanent, it makes economic sense to invest in the leaves under conditions of favourable resource availability.

Because of the greater DM allocation to the roots and twigs, which may act as storage organs of carbohydrates that are largely inaccessible to herbivory, A. natalitia, is therefore well buffered against herbivory and unfavourable growth periods such as drought and fire than S. myrtina.

**Conclusion**

*Acacia natalitia* and *S. myrtina* saplings differed in their response to N fertilization. Because of its ability to form functional symbiosis with soil-born rhizobial species, *A. natalitia* was less responsive to nitrogen application compared to the non-legume *S. myrtina*. Nitrogen appeared to be more available to the plants when they were supplied with LAN compared with NPK or OM, this being indicated in the higher N concentration in the leaves of plants and its greater stimulatory effect on the growth of *S. myrtina* in Experiment 1. The biomass of *S. myrtina*, responded positively to increasing LAN application rate over the entire range of the rates tested in Experiment 2, whereas that of *A. natalitia* plants appeared to show an optimum between 23.1 and 34.6 g m$^{-2}$ N application rates. Nitrogen application had significant effects on DM distribution in the two species depending on application rate, and the species differed in DM distribution. Generally, *A. natalitia* allocated more DM to the roots than did *S. myrtina*, this being more pronounced as the N was increased. For tree browsing experiments that require an N availability gradient, it is recommended that LAN be used as the N source at rates similar to the ones we used (e.g., 0, 3, 6, 24 and 36 g N m$^{-2}$) to achieve a variety of growth rates. It must, however, be cautioned that the response to N application by leguminous trees that promiscuously form symbiosis with soil-born rhizobia may be limited, unless the soil is first sterilized.

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**REFERENCES**


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