display a polarised size class profile, with most stems in the small and the very large size classes, with few stems of intermediate size. Under prolonged or intense harvesting the larger sizes classes also diminish for fuelwood purposes, construction purposes or because of a lack of recruitment into the large size-classes to replace natural senescence. The net result is a reduction in the range of size classes represented.

13.3 IMPACTS ON WOODY PRODUCTION AND ASSOCIATED PROCESSES

Although harvesting generally leads to a reduction in attributes of woody community structure, the same does not necessarily apply to woody productivity (McGregor 1994). The key reasons for this appear to be the increase in resources and a decrease in competition associated with a reduction in community density, basal area and biomass (Smith & Goodman 1986). A reduction in these attributes leads to an increase in light and soil moisture per remaining unit of woody biomass. Soil nutrients may also be increased but this is probably related to harvesting intensity. Turnover of nutrient pools may be stimulated because of higher root turnover, and decomposition of root systems associated with dead stumps. However, under severe harvesting the reduced woody biomass may be inadequate to immobilise available nutrients, with more thereby being lost through leaching to deeper layers of the soil profile (Meredith 1987, Mou et al. 1993). Such losses are interactive with changing soil moisture dynamics on disturbed sites, including clearing. However, Chidumayo (1993) concluded that repeated clearing of miombo in Zambia had no discernable impact on soil nutrient status. Shackleton (1993) reported no differences in soil carbon content between a harvested area and adjacent protected area.

The result of the greater access to resources for the remaining biomass is enhanced woody productivity of the remaining trees (Chap. 16). This applies to all components of woody production, including wood, leaves and fruits (Smith & Goodman 1986, Schaecht et al. 1992, Smit 1994), and presumably roots. It is hypothesised that the increase will be related to the intensity of harvesting and reduction in woody biomass. With light harvesting, some competition may still occur because interplant distances are not greatly changed relative to unharvested areas. With heavier harvesting, interplant distances will be increased to such a degree that each remaining plant will have very little impact or interference on its neighbour, now some distance away. In this situation growth enhancement may be up to three fold that of unharvested areas, although more likely to be 30 - 100 % greater (Smit et al. 1996). This growth enhancement per individual tree will remain for a number of years, but will steadily decline as stand biomass increases.
Whether or not woody productivity is enhanced depends upon the intensity of harvesting and the magnitude of enhanced growth of the remaining stems. If harvesting impact is severe and reduces woody biomass to levels below which it cannot utilize all available resources because there are effectively ‘wasted’ spaces between stems, then woody community productivity will also be low. As regeneration occurs community productivity will increase because of (1) small stems grow faster than large stems, and the regenerative phase will be dominated by small coppice stems and saplings rather than large established stems, and (2) density will increase to a level were there are no wasted spaces, and the woody biomass captures an optimal amount of water, nutrients and light, but still with relatively little interference between neighbouring plants. As regrowth continues, it is argued that competition will play an increasing role, so individual tree productivity levels off or declines. This is compensated for to some degree by increased productive woody biomass, but ultimately stand productivity declines (Strang 1974, Chidumayo 1993). It is also dependent upon the frequency of reharvesting. If the community composition is maintained as one dominated by relatively small stems, even at high densities, community productivity in percentage terms will be higher than unharvested areas, but possibly not in absolute terms.

Harvesting also changes the compartmentalisation of woody production. The effect is most marked on fruit production, which may be reduced to zero if all stems of reproductive size are removed. As stated earlier, this usually occurs only under severe harvesting pressure. Harvesting also changes the ratio of wood to leaf production. This is significant if the harvesting occurs in conjunction with browsing. The lowered stature of harvested communities brings a greater proportion of leaf mass into a height accessible by browsers. This may serve to maintain the community in a more a productive state dominated by smaller regrowth stems, and will retard the establishment of a more normal community physiognomy represented by a range of size classes and heights (Trollope 1974). There is evidence that the mere act of browsing stimulates leaf production at increased levels relative to non-browsed trees (Pellew 1983b, Stuart-Hill & Tainton 1988).

The increased productivity may not only be directly due to increased resources per unit remaining biomass. The change to a community dominated by small stems, possibly at higher stem densities than the original community, will result in increased woody production due to the higher growth relative growth rates of smaller stems. Additionally, community phenology changes. Thinned communities dominated by large trees retain leaves longer and show higher flowering and fruiting success than similar sized trees in unthinned stands (D. Wright, pers comm.). Leaf emergence in small trees precedes that of large trees, and small stems retain leaves longer at the end of the growing season (Milton 1987, Novellie 1989). In this

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manner, the growing season is extended, allowing opportunity for greater production, given adequate resources.

Harvesting frequently has marked impacts on recruitment of new stems. Vegetative reproduction through coppicing is stimulated from the cut stem directly or from the remaining root stock (Sect. 14.4). Sexual reproduction and establishment of seedlings is also affected by harvesting (Murati et al. 1996). Firstly, the density of reproductive stems is reduced, potentially leading to lowered reproductive output. This may be compensated for by increased output per remaining stem of reproductive size provided the harvesting impact does not lead to the removal of most reproductive stems. Second, reduced woody biomass usually results in a higher herbaceous biomass (Schacht et al. 1992, Teague & Smit 1992). The higher herbaceous biomass will offer increased competition to establishing woody plant seedlings. Lastly, loss of woody cover may represent a loss of potential nursery sites for canopy species that require protected, subcanopy habitats to establish, such as *Acacia karroo* (Morgan 1991, O'Connor 1995). Clearly, seed recruitment of species not requiring such sites will benefit from the more open canopy and reduced competition from established trees, including several *Acacia* species (Smith & Goodman 1986).

The microprocesses influencing productivity in harvested communities are spatially variable depending upon the interaction of the structure of the woody community prior to harvesting, the severity of harvesting, the species composition of the community and post-harvesting management, notably grazing and browsing. The role of abiotic variables is relatively unknown. Consequently, predictability of the overall effects is poor, other than to state the obvious that woody biomass is decreased and this may or may not improve community productivity depending on the interacting factors. This requires more attention through empirical studies as well as appropriate scaling up from studies on single trees.
14.1 INTRODUCTION

The cutting or lopping of trees is a common phenomenon throughout all African savannas, whether it be caused by humans or large mammals. Felling by humans is usually more severe than the effects of large herbivores, but may range from selective removal of particular individuals (species and/or sizes) within a stand, through to almost clear felling of an entire area. Both occur in support of subsistence (fuelwood collection, patch clearance for small-scale arable plots) and commercial orientated endeavours (e.g. charcoal industries, bush-clearing programmes), and both have significant impact on the actual and potential productivity at the site (Chidumayo 1993).

The change in productive potential of an area after cutting is manifest at the scale of an individual tree. A key attribute of the resilience and productivity of savannas is the ability of damaged trees to regrow from the remaining stump. Survival of the cut stem and growth rate of the resultant coppice shoots is influenced by several factors, including size of the tree, height of cutting, and root/shoot ratio after felling (Tschaplinski & Blake 1989). Some of these can be manipulated by the manager or harvester to maximise or suppress subsequent regrowth rates. Moreover, replacement is faster through coppice growth than through recruitment because (1) coppice shoots grow faster than stems resulting from seedling recruitment (Tschaplinski & Blake 1989, Chidumayo 1993), certainly in the early stages, but this difference may decline as apical dominance is re-established, and (2) mortality is less (although values of seedling mortality are heavily dependent upon the age/size at which the seedlings are monitored). Therefore, it is necessary to have an understanding of the external management and site factors that influence coppice regrowth. Such an understanding is well established regarding species with silvicultural importance, from both an anatomical (e.g. Burrows 1990, Paukkonen et al. 1992a, b) and management (e.g. Bowersox et al. 1990, Johansson 1992a, b) perspective, but not for indigenous savanna species.

An added intervention open to the harvester or manager is pruning of a proportion of the coppice regrowth, which may affect subsequent productivity. Regrowth after cutting is usually rapid, with numerous buds
breaking out from both the rootstock and cut stump. After a time the number of shoots is reduced through inter-shoot competition, and eventually apical dominance is re-established favouring one or a few shoots to the detriment of the rest (Johansson 1992a). The suppressed shoots may wither and die, or remain on the stump, but never attain a meaningful size. It can therefore be hypothesised that pruning of most of the coppice shoots would re-establish apical dominance sooner, and thereby accelerate regrowth since resources would not be allocated to fated secondary shoots. This is a well established principle in silvicultural and horticultural practices, but requires consideration as a means of managing the productivity of natural woodlands. This study sought to examine the effects of pruning on a widespread savanna species.

*Terminalia sericea* Burch. ex DC is widely distributed throughout southern Africa, especially on deep sands. It frequently occurs in dense, relatively mono-specific stands, indicating the upper slope transition zone between sands and clays on granitic derived catenas (Tinley 1982). It is favoured by rural communities for fuelwood, construction, carving and medicinal purposes (Shackleton *et al*. 1994, Shackleton *et al*. 1995).

**14.2 Objectives**

The objectives of this study were to determine the (1) influence of cutting height and stem size on resultant coppice yield of a range of savanna species, and (2) the influence of controlled post-harvest pruning, original stem size, and cutting height on the regrowth rate of a common savanna species, namely *Terminalia sericea*.

**14.3 Methods**

**14.3.1 Coppice regrowth of different species**

In the Bushbuckridge district two villages were selected in communal lands at each of three points across the rainfall gradient; high rainfall (Miloro A and Miloro B), intermediate rainfall (Skagula and Timbavati) and low rainfall (Athol and Welverdend). At each village two plots (20 x 20 m) were judgementally located, one in catenal toplands, and one in catenal bottomlands. In each plot all cut stems were examined,
and the following determined: (1) species, (2) cutting height, (3) basal circumference at 5 cm above the ground (if it had been cut at a height lower than this, then the basal circumference was measured below 5 cm), and (4) the number of coppice shoots, irrespective of size or length.

Since there were no significant effects of rainfall or catenal position on the mean number of shoots per stump, data were pooled by species across the plots. Species for which twenty or more stumps were recorded were subjected to stepwise linear regression with number of coppice shoots as the dependent variable, and the height of cutting, basal circumference, and stump surface area as independent variables. A Mann-Whitney test was used to test the significance of differences between species groups. The relationship between mean stump surface area per coppice shoot and potential height of the tree was examined via linear regression. Potential tree height was obtained from a random selection of one third of all the vegetation plots collected to describe the three intensive monitoring sites (n=60) (Chap. 2). The data were pooled, and sorted according to species and height per stem. The mean of the ten tallest stems per species was taken as the potential tree height. Analysis of residuals of the initial unsignificant regression indicated the presence of potential outliers. Subsequent analysis of the significance of potential outliers indicated that *Pilostigma thonningii* and *Albizia harveyii* were significant (p<0.01 and p<0.05, respectively). These two species were then omitted from the final regression analysis relating coppice density per stump and mean potential height of a species.

14.3.2 Regrowth of *Terminalia sericea*

In December 1991 a 3-way factorial experiment was set up to examine the relationship between original stem size, cutting height and post-harvesting pruning on resultant coppice yield. At each of two sites 108 *T. sericea* trees were randomly selected, 36 each in one of three size classes: large (> 30 cm basal circumference), medium (15 - 20 cm) and small (5 - 11 cm). In each size class, half the trees were felled at 50 cm above ground level, and half were felled at 20 cm. The length of each coppice shoot per stem was recorded monthly, as well as if the coppice shoot was sprouting from the cut stem (stem coppice) or from the base of the cut stem below the soil surface (root coppice). Three months after the original treatment application three pruning treatments were applied; single - only the longest coppice shoot was left; double - the two longest shoots were kept; all - no pruning, all coppice shoots were kept. Thus, there were six replicate stems per treatment (size x height x pruning) per site. Monitoring was on a monthly basis for the
first growing season. If more coppice shoots appeared on the single and double pruning treatments they were removed. Regrowth was measured on three occasions during the second growing season, and twice each in the third and fourth growing seasons. The final measurement was in May/June 1995, three and one half years after the initial felling.

At the end of the monitoring period 30 shoots were randomly collected and weighed. A significant relationship was evident between shoot length (cm) and fresh mass (g) summarised as:

\[
\log (\text{fresh mass}) = 0.0053 \times (\text{length}) + 1.734 \quad (r^2 = 0.97, p < 0.0001; n=30)
\]

Browsing of the regrowth was evident after the second month. Whilst probably effecting subsequent growth rates, this represents a more realistic management situation than if the experimental areas had been fenced. A coppice shoot was recorded as browsed if the apical tip of the shoot had been removed.

Rainfall during the first growing season was considerably less than normal, being the severest drought on record for that region (54 % of the mean). The second season was 32 % above the mean, and the third and fourth seasons less than average (76 % and 78 % of the mean, respectively).

Data from Shackleton (1993) were used to characterise the dimensions of T. sericea poles in fuelwood bundles of rural harvesters in the Timbavati communal lands to allow calculation of harvest intervals.

Data from each site were pooled after statistical analysis for the second and fifth monitoring period failed to detect any significant differences between sites. The actual number of stems per treatment varied because of (1) death of stems (2) loss of three stems (possibly died) and (3) error in the random assignment of pruning treatments. The smallest number of replicate stems for any treatment was eight. Cumulative length data were log transformed and percentage values (percentage browsing and percentage of shoots being root coppice) arcsine transformed. Data for the final sampling period were subject to 3-way analysis of variance.
14.4 RESULTS

14.4.1 Coppice regrowth of different species

All species exhibited a strong coppicing potential following cutting. The number of shoots per stump was most frequently related to cutting height. Two species showed no relationship with cutting height. For *E. crispa* a significant relationship was established with stump surface area. For *A. exuvialis* no significant relationships were established (Table 14.1). It was hypothesised that the strong relationship with cutting height is manifest through the influence of cutting height on the surface area of the stump. However, surface area was not a frequent predictor variable.

Table 14.1. Relationship between number of coppice shoots per cut stump and independent variables

(ht = height of cut stump; surfarea = surface area of cut stump).

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>n</th>
<th>r²</th>
<th>RELATIONSHIP</th>
<th>P VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>All species</td>
<td>348</td>
<td>0.37</td>
<td>S = 0.13(ht) + 6.0</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><em>Acacia exuvialis</em></td>
<td>20</td>
<td>0.16</td>
<td></td>
<td>no</td>
</tr>
<tr>
<td><em>Acacia gerrardii</em></td>
<td>21</td>
<td>0.55</td>
<td>S = 0.11(ht) + 5.8</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><em>Albizia harveyi</em></td>
<td>24</td>
<td>0.63</td>
<td>S = 0.16(ht) + 3.9</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><em>Combretum apiculatum</em></td>
<td>29</td>
<td>0.33</td>
<td>S = 0.09(ht) + 6.6</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td><em>Combretum colinum</em></td>
<td>25</td>
<td>0.70</td>
<td>S = 0.19(ht) + 1.7</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><em>Combretum hereroense</em></td>
<td>22</td>
<td>0.31</td>
<td>S = 0.16(ht) + 6.2</td>
<td>&lt;0.008</td>
</tr>
<tr>
<td><em>Dichrostachys cinerea</em></td>
<td>21</td>
<td>0.42</td>
<td>S = 0.17(ht) + 5.2</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td><em>Euclea crispa</em></td>
<td>21</td>
<td>0.53</td>
<td>S = 0.00064(surfarea) + 6.2</td>
<td>&lt;0.0002</td>
</tr>
<tr>
<td><em>Euclea natalense</em></td>
<td>24</td>
<td>0.73</td>
<td>S = 0.24(ht) - 0.02</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><em>Peltophorum africanum</em></td>
<td>25</td>
<td>0.67</td>
<td>S = 0.23(ht) + 3.3</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><em>Piliostigma thonningii</em></td>
<td>20</td>
<td>0.23</td>
<td>S = 0.11(ht) + 5.0</td>
<td>&lt;0.04</td>
</tr>
<tr>
<td><em>Terminalia sericea</em></td>
<td>22</td>
<td>0.35</td>
<td>S = 0.23(ht) + 8.3</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>
There were clear differences between species with respect to the number of shoots per unit surface area, or the inverse, unit area per shoot (Table 14.2). The species with most coppice shoots per stump area (*Albizia harveyii*) had almost ten times more than the species with the least, *Piliostigma thonningii*. There was no relationship with wood density. However, there was a significant difference ($U_{1,5} = 30, p < 0.05$) in mean unit area per shoot of those species for which cutting height was the most significant predictor variable of coppice stem number ($\bar{x} = 683.6 \pm 117.1; n=7$), and those for which height was not ($\bar{x} = 365.0 \pm 73.9; n=5$), even though it may have been significant.

Table 14.2. Mean unit area per coppice shoot per species (ordered from highest to lowest) (Unlike letters in the Significant Difference column between species indicates a statistically significant difference; like letters indicate no significant difference between those species).

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>UNIT AREA (cm²)</th>
<th>SE</th>
<th>n</th>
<th>SIG. DIFF.</th>
<th>MEAN POT. HEIGHT (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Piliostigma thonningii</em></td>
<td>1258.7</td>
<td>285.3</td>
<td>20</td>
<td>a</td>
<td>4.63</td>
</tr>
<tr>
<td><em>Acacia gerrardii</em></td>
<td>850.9</td>
<td>150.7</td>
<td>21</td>
<td>b</td>
<td>7.90</td>
</tr>
<tr>
<td><em>Combretum collinum</em></td>
<td>761.6</td>
<td>86.5</td>
<td>25</td>
<td>bc</td>
<td>10.40</td>
</tr>
<tr>
<td><em>Peltophorum africanum</em></td>
<td>622.4</td>
<td>53.9</td>
<td>25</td>
<td>bcde</td>
<td>5.69</td>
</tr>
<tr>
<td><em>Dichrostachys cinerea</em></td>
<td>588.4</td>
<td>54.1</td>
<td>21</td>
<td>bcede</td>
<td>3.56</td>
</tr>
<tr>
<td><em>Combretum hereroense</em></td>
<td>491.0</td>
<td>75.6</td>
<td>22</td>
<td>cde</td>
<td>4.19</td>
</tr>
<tr>
<td><em>Combretum apiculatum</em></td>
<td>468.05</td>
<td>74.5</td>
<td>29</td>
<td>de</td>
<td>3.96</td>
</tr>
<tr>
<td><em>Euclea crispa</em></td>
<td>401.1</td>
<td>56.0</td>
<td>21</td>
<td>def</td>
<td>2.96</td>
</tr>
<tr>
<td><em>Terminalia sericea</em></td>
<td>389.0</td>
<td>93.0</td>
<td>22</td>
<td>def</td>
<td>10.72</td>
</tr>
<tr>
<td><em>Euclea natalense</em></td>
<td>332.2</td>
<td>43.0</td>
<td>24</td>
<td>ef</td>
<td>1.98</td>
</tr>
<tr>
<td><em>Acacia exuvialis</em></td>
<td>316.6</td>
<td>42.9</td>
<td>20</td>
<td>ef</td>
<td>3.60</td>
</tr>
<tr>
<td><em>Albizia harveyii</em></td>
<td>130.0</td>
<td>14.3</td>
<td>24</td>
<td>g</td>
<td>8.09</td>
</tr>
</tbody>
</table>

There was a strong relationship between the mean surface area of stump per shoot (shoot density) and potential height of each species (ignoring outliers; see 14.3), summarised in the form:

---

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\[ y = 234.4 \cdot \ln(\text{potential height}) + 157.7 \]  
\( r^2 = 0.48; \ p < 0.03; \ n = 10 \)

Thus, the taller the potential height of a species, the fewer the coppice shoots per stump surface area.

14.4.2 Effects of original stem size on regrowth of *T. sericea*

The largest stems of *T. sericea* tended to produce a greater number of coppice shoots than either of the two smaller classes (Fig 14.1). The difference was significant by the last sampling period (\( p < 0.0001 \)). However, for most of the first growing season, the largest stems had the least number of shoots. This changed late in the first growing season or during the second growing season, such that in all treatments the larger stems produced a greater number of shoots than stems in the medium and small category. For stems cut at 50 cm the medium-sized stems produced more shoots than those in the small size-class. This was not apparent for stems in the small size-class. The interaction term between size-class and cutting height was significant.

The mean shoot length differed according to original stem size, with the largest stems producing longer coppice shoots (\( p < 0.00001 \)) for all treatments. The medium size class tended to have longer shoots than the smallest size-class but this was not significant (Fig 14.2). In most instances, immediately after cutting the largest size-class had the shortest shoots, with the smallest size-class have the longest. This changed late in the first growing season or during the second growing season.

The effects of size-class were most marked in terms of cumulative coppice length per stump, with a significant difference between all three size-classes (\( p < 0.00001 \)); the largest size-class having the greatest cumulative length and the smallest size-class having the least (Fig 14.3). As with number of shoots and mean shoot length this was not the situation immediately after cutting. Initially, the small or medium size-class had a greater cumulative length then the large size-class, but this changed a few months later. Clearly larger stems took longer to respond to the initial shock, but once had done so, soon grew at a faster rate, possibly a result of their greater root system.

14.4.3 Effects of cutting height on regrowth of *T. sericea*

Stems cut at 50 cm produced more shoots than stems cut at 20 cm in the large and medium size-classes (Fig...
Figure 14.1. Number of coppice shoots per stump under different treatments.
Figure 14.2. Mean coppice shoot length per stump under contrasting treatments (20 cm ———, 50 cm ————)

all shoots - ▼■; 2 shoots - ▽□; 1 shoot - X)

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Figure 14.3. Cumulative coppice shoot length per stump under contrasting treatments (20cm ----; 50 cm ------; all shoots - ▼/■; 2 shoots - ▽/□, 1 shoot - X)
The same generally applied for the small size-class, but at times the opposite applied. Overall, the effect of cutting height on number of shoots was significant by the last sampling date (p<0.05). There was a significant interaction term between cutting height and stem size.

Although the higher cutting height resulted in more shoots the mean shoot length tended to be shorter, although not significantly so. Results were inconsistent between treatments. The same applied with respect to cumulative coppice length (Fig 14.2 and 14.3).

14.4.4 Effects of pruning on regrowth of *T. sericea*

The unpruned treatment consistently had a greater number of coppice shoots than either of the pruning treatments (p<0.00001) throughout the sampling period (Fig 14.1). However, the number of shoots per stump in the unpruned treatment tended to decrease after reaching a maximum during the second growing season. The reduction was least for the largest stumps.

The no prune treatment had the shortest mean shoot length at all sampling dates and treatments. This was significant at the last date (p<0.00001) (Fig 14.2). Generally the longest shoot length occurred under the single pruning treatment, but on occasions the double treatment had a greater mean length per shoot (for example the large size-class cut at 20 cm).

The three pruning treatments resulted in a significantly different cumulative shoot length per stump (p<0.0001), with the no prune treatment having the greatest, the single prune the least, and the double prune being intermediate between these two (Fig 14.3). The only exception to this was for the small size-class cut at 50 cm, where on the last two sampling dates the double prune treatment had the longest cumulative length. The greater cumulative length of the no prune treatments led to a greater mass of coppice for this treatment. Although coppice shoots were frequently thinner for this treatment overall productivity was greatest for the no prune treatment.
14.4.5 Harvester requirements and return time

The issue of primary concern in terms of management of coppice regrowth relates to the return time, i.e. the amount of time required for cut stems to regrow to a size adequate for reharvesting. Of particular concern in the study region is the provision of fuelwood. Table 14.3 summarises the dimensions of *T. sericea* logs in fuelwood bundles cut by local harvesters from the Timbavati communal land, where *T. sericea* is a favoured species.

Table 14.3. Dimensions of *T. sericea* logs in fuelwood bundles cut by local harvesters.

<table>
<thead>
<tr>
<th>SUMMARY STATISTIC</th>
<th>T. sericea ONLY (n = 397 poles)</th>
<th>ALL SPECIES (n = 627 poles)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length (cm)</td>
<td>Circum. (cm)</td>
</tr>
<tr>
<td>Mean</td>
<td>194.3</td>
<td>19.2</td>
</tr>
<tr>
<td>(± SE)</td>
<td>(2.3)</td>
<td>(0.3)</td>
</tr>
<tr>
<td>Maximum</td>
<td>305.0</td>
<td>38.0</td>
</tr>
<tr>
<td>Minimum</td>
<td>24.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Median</td>
<td>214.0</td>
<td>19.0</td>
</tr>
<tr>
<td>Mode</td>
<td>214.0</td>
<td>19.0</td>
</tr>
</tbody>
</table>

By the last sampling date between 6% and 82% of the coppice regrowth stems, depending on treatment, were longer than the mean length measured in fuelwood bundles (Table 14.4). Extrapolation of the growth rates for the contrasting treatments suggests that a return time of approximately 3 - 4 years for large stems, 4 - 5 years for medium stems, and 4 - 9 years for small stems, based on average stem length. Some stems will reach the stipulated length in a shorter period, whilst others will take longer, or will die beforehand. These rates are conservative because of (1) the extreme drought at the study site during the first growing season, and (2) the reduction in elongation due to a high browsing impact, which would also delay the re-establishment of apical dominance.
Table 14.4. The influence of cutting height, stem size, and pruning on the harvest interval.

<table>
<thead>
<tr>
<th>SIZE CLASS</th>
<th>CUTTING HEIGHT</th>
<th>PRUNING</th>
<th>Mean shoot length (cm) at June 1995</th>
<th>% of stems &gt; mean fuelwood pole length (194 cm) by June 1995</th>
<th>Predicted time (months) required to reach mean fuelwood pole length</th>
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<tr>
<td></td>
<td>50 cm</td>
<td></td>
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<tr>
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<td>227.2</td>
<td>67</td>
<td></td>
<td>33</td>
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<tr>
<td></td>
<td>Double</td>
<td>199.8</td>
<td>65</td>
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<td>38</td>
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<tr>
<td></td>
<td>All</td>
<td>141.7</td>
<td>25</td>
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<td>20 cm</td>
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<tr>
<td>Medium</td>
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<td>120.9</td>
<td>14</td>
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<td></td>
<td>All</td>
<td>72.5</td>
<td>6</td>
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<tr>
<td></td>
<td>Single</td>
<td>187.7</td>
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<tr>
<td></td>
<td>Double</td>
<td>155.1</td>
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<td>48</td>
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<tr>
<td></td>
<td>All</td>
<td>82.4</td>
<td>6</td>
<td></td>
<td>89</td>
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</table>

14.4.6 Root coppice of *T. sericea*

The proportion of coppice shoots being root coppice increased across the sampling period (Fig 14.4). This seems to be the result of two factors. Firstly, root coppice took longer to initiate, possibly because it is a
secondary reaction, it is inherently slower, or it simply takes more time for it to be observed because it has to grow some distance through soil before breaking the surface and becoming visible. Secondly, the steadily decreasing numbers of shoots per stump during the third and fourth growing seasons is a result of higher shoot mortality of stem coppice shoots rather than root coppice shoots.

Figure 14.4. The proportion of root coppice shoots throughout the study.

14.4.7 Browsing of regrowth of T. sericea

During the first growing season after cutting browsing frequency was greater than 50 % (Fig 14.5). This is probably a result of (1) the low height of the regrowth making it readily accessible to even small browsers, (2) the new regrowth being relatively nutritious, and (3) the severe drought during this period resulting in a relative poor fodder supply. At the start of the second growing season approximately 20 % of the coppice had been browsed. Browsing frequency declined throughout the second growing season and remained at less than 5 % for the remainder of the study.
Figure 14.5. Browsing frequency throughout the study.

14.5 DISCUSSION

The results indicate that through a combination of easily applied management considerations and actions the resultant number and regrowth rate of coppice can be manipulated. The first consideration is which tree to cut based on its size. It seems that either (1) increasing stem size results in increasing number of coppice shoots, or (2) has no effect. Where an effect is evident it is probably a result of the greater surface area per stump, and greater root/shoot ratio. After the first or second growing season larger stems of T. sericea also had a greater mean shoot length and cumulative length per stump. During the first few months this was not the case, suggesting that larger stems take longer to respond to the initial shock, but once recovered have the capacity to regrow at a rate faster than that of smaller stems, possibly a result of their greater root system (Tschaplinski & Blake 1989). However, a positive relationship was evident for only eight of the twelve species examined. Bowersox, et al. (1990) found no relationship between these two parameters, but Whitesell et al. (1985) (in Bowersox et al. 1990) also recorded a positive relationship. Some authors have found a negative relationship. For example, McDonald & Powell (1983) found a decreasing survivorship of stumps and number of shoots per stump with increasing stump size for Acer
saccharum. Khan & Tripathi (1986) found decreasing coppicing ability with increasing stem size for four sub-tropical forest species, as did Chidumayo (1993). This has been ascribed to the increased bark thickness of larger stems hindering emergence of the bud (Khan & Tripathi 1986). This did not apply in this study, where only D. cinerea had a negative relationship between shoot number and stem size.

Clearly the consideration of what size tree to fell is the result of several factors, including what the timber will be used for, ease of transportation, and what is available. Potential regrowth dynamics is another to add in.

Having selected the size of tree the manager or harvester has options regarding the height at which to cut the tree. Increased cutting height appears to have a positive effect on the number of coppice shoots. This is supported by data from other species and vegetation types (e.g. Harrington 1984, Khan & Tripathi 1986, Bowersox et al. 1990, Huang 1990). This may be related to stump surface area (Canadell et al. 1991), but many studies did not investigate the influence of area, but just height. Survival of the cut tree is also positively related to cutting height (Bowersox et al. 1990, Johansson 1992a). The T. sericea study indicated that the greater number of shoots with increasing cutting height need not lead to a reduction in mean shoot length, or total cumulative shoot length per stump. The positive effects of increased cutting height must be balanced against the loss of useful timber that is left behind as stump. However, changing cutting height is an easy management action to implement, with marked effects on the resultant coppice number and regrowth rate, and hence harvest turnover time.

The survey component of this study did not take account of changing numbers of coppice shoots per stump with time since cutting, or of cutting season. In the first few months after cutting, shoot number increases up to a maximum; thereafter it declines as inter-shoot competition and apical dominance increases as shown by this study and others (Khan & Tripathi 1986, Lubbe 1990, Chidumayo 1993). Studies from other species and biomes have indicated an effect of season of cutting (Johansson 1992b, Chidumayo et al. 1996). Stumps in this study were of different ages and had been cut in different seasons. Therefore, some of the species comparisons in this study may be inaccurate. However, the wide range of sites, localities and tree sizes, should ensure that variance due to time since cutting would have minimal influence on the overall findings of this study. This was also the primary reason for using number of coppice shoots as an index of regrowth rather than mass of coppice growth.
Post-harvest pruning is a more intensive management action than selecting tree size and choice of cutting height. Moreover, it requires repeated application until apical dominance is established, which in this study, was towards the end of the second growing season. However, pruning has a significant impact on resultant coppice growth, including the number of shoots per stump, mean shoot length, and cumulative shoot length. The effects of pruning are interactive with those of initial stem size. After four growing seasons mean shoot length for the single prune treatment was 54% greater than the no prune treatment, whilst the double prune was 40% greater.

The application of pruning or not depends upon local management circumstances and objectives. The return time is shortest for the single prune treatment. The double prune treatment provides two poles in only a slightly longer period, and the no prune treatment provides several poles in a period of approximately 1½ times that of the single prune. Consequently, in areas of low wood supply and high demand, pruning may be a viable option because it reduces the interval between harvests. At the opposite extreme of low demand and good supply, pruning would probably not be worth the added effort since there is sufficient wood supply between harvest intervals. A longer return time, with ultimately perhaps a few more shoots is a better strategy in this situation.

Tietema (1992) estimated that regrowth of *Acacia tortilis* would take between 7 and 14 years to reach preharvesting biomass at a semi-arid site in Botswana (MAR = ± 500 mm). The duration of the experiment was characterised by an extreme drought. Linear extrapolation of the data of Schacht et al., (1992) indicates that tree biomass of all species in a semi-arid tropical woodland (MAR = 788 mm) in Brazil would attain preharvesting levels after 8 - 9 years. Using a more curvilinear relationship indicates recovery in approximately 12 years. This is comparable to the estimated 14 years required for attainment of preharvesting basal area of *Colophospermum mopane* stands at an arid site (MAR = ± 500 mm) in South Africa (Scholes 1990b). Most of these estimates of regrowth rates are greater than extrapolated for *T. sericea*. It must be remembered that the *T. sericea* estimates are for the period required to attain a size adequate for reharvesting as fuelwood, and not recovery of the stand basal area or biomass to preclearing levels, but indicates that the *T. sericea* extrapolations are of the right order of magnitude.

This study focused on the impact of pruning, assuming that humans would be the cause of the pruning. However, it is possible that natural pruning could occur through a variety of agents, namely fire, frost, or browsing (Chidès 1984). The impacts of these agents frequently impair the growth of some of the coppice...
shoots on a stump, thereby allowing the undamaged or unpruned shoots to grow out, and eventually suppress the remaining shoots through apical dominance. Browsing of *Ocotea bullata* coppice shoots retarded elongation by 66% relative to protected shoots during the first two years after felling (Lubbe 1990). Browsing by wild or domestic animals in most management situations in African savannas should be taken into account.

The relationship between mean potential height and the number of coppice shoots per stump provides a differentiating variable regarding plant growth form. In shorter, shrubby species new growth goes into multiple shoots, whereas for taller, tree species, new growth is concentrated into fewer shoots. The lower density of shoots will result in faster growth rates. Thus, tall species allocate resources in a manner permitting them to regain a height advantage after felling. Shorter species allocate resources into more shoots that would grow at a slower rate. This appears to suggest another growth allocation pattern in addition to the two already recognised, namely (1) height growth species, and (2) crown growth species (Hara, et al. 1991). The relationship with maximum potential tree height tends to reinforce the positive relationship found with stem diameter and coppice shoot number, since height and diameter are well correlated for most tree species.
15.1 INTRODUCTION

Harvesting of woody stems is a common feature of commercially and communally managed savannas. In the former, bush-clearing or thinning is widely practised throughout savanna regions to retard a perceived trend towards increasing density of woody plants (Skarpe 1990). It is usually driven by a commercial, aesthetic or ecological need (Scholes 1987). In communal systems, harvesting is predominantly for domestic household requirements such as fuelwood, building or fencing materials, although some removal for commercial gain may occur, either by fuelwood vendors, or specialised use of key species, such as those used by woodcarvers. The key difference between tree removal in commercial and communal systems is that in the former, post-cutting actions generally include some treatment to prevent regrowth of the cut stem.

The removal of a single stem has several potential impacts. It affects the growth of the cut stem (Chap. 14). It also impacts, on a localised scale, water, light, nutrient pools and fluxes in the vicinity of the removed stem. Nutrient enhancement due to the former presence of the cut tree (Belsky et al. 1989, Belsky 1994) will cease until another stem occupies that space, either a new recruit or regrowth of the original stem to a meaningful size. In the short-term, however, a nutrient flush may be experienced resulting from die back or death of the root system (Gage 1995), frequently resulting in higher herbaceous production for a limited period (Grossman et al. 1980, Teague & Smit 1992, Scholes & Archer 1997). Finally, neighbouring stems could benefit depending upon their proximity to the cut stem. It is widely hypothesized that benefits would accrue to any stems close to the cut stem because of (1) a reduction in any competitive interactions, (2) potential access to an increased pool of resources, including water, soil nutrients and light, that was previously used by the cut stem, and (3) a nutrient flush from decay of all or some of the roots of the cut stem (Teague & Smit 1992). It is assumed that these benefits would be translated into increased productivity of the neighbouring stems.

Despite the widespread assumption of benefits to neighbouring stems, there is little empirical data to
confirm or reject it, since most studies have focused on responses of the herbaceous layer (Scholes & Walker 1993, Smit 1994). The few studies in the literature dealing with the woody layer report variable or simply anecdotal results, or are at a plot scale (e.g. Schachet et al. 1988, Scholes 1990b), rather than at the scale of the individual neighbouring tree. Most studies of competition between trees have been through nearest neighbour analysis rather than thinning experiments (Scholes & Archer 1997). This study sought to measure the response of neighbouring trees directly.

15.2 OBJECTIVES

To test the hypothesis that growth beneficitation to neighbouring trees is inversely related to the distance away from the cut tree and the size of the cut tree, i.e. the closer a neighbouring tree is to a the cut tree, the greater will be the growth enhancement of the neighbouring tree for a specific size of cut tree. The greater the size of the cut tree, the greater will be the benefit to the neighbour at a specific distance.

15.3 METHODS

At each reserve a monospecific stand was selected for thinning in mid-November 1993. The species were *Combretum apiculatum* (arid site), *Terminalia sericea* (semi-arid) and *Parinari curatellifolia* (mesic). Within the stand twenty relatively uniformly sized trees were selected (hereafter termed the 'point tree') in a stratified random manner. For each point tree the initial resource space available to it was calculated as

\[
\text{Resource space} = \sum_{n=1}^{k} \left( \frac{a_n}{a_n + a_i} \right) \times d_i
\]

where 
- \( a_n \) = basal area of point tree;
- \( a_i \) = basal area of nearest tree in quarter 1;
- \( d_i \) = distance of nearest tree in quarter 1 from the marked tree.
Thereafter, the resource space was increased by felling a varying number of trees adjacent to the point tree. The magnitude of increment in resource space ranged from approximately 10% to 150% for a given point tree. Coppice regrowth was largely limited by browsers, but what little was evident was removed by hand from the felled stumps once every three months.

The stem circumference and height was recorded for the point tree, the initial nearest neighbours, and the new nearest neighbours. Productivity was indexed as the change in basal area of the point tree which was remeasured at the end of each of the two growing seasons following thinning, as well as shoot length measured at the end of the first season only.

15.4 RESULTS

There was no influence of a relative (%) increase in resource space on basal area increment. Rather, basal area increment was related to the absolute resource space available to the point tree after thinning for both the first \( r^2 - 0.085; n=60; p<0.05 \) and second growing seasons \( r^2 =0.066; n=60; p<0.05 \) (Fig 15.1).

\[
\text{Relative basal area increment (\%)} = 0.45(\text{resource space}) + 4.28 \text{ (1st season)}
\]

\[
\text{Relative basal area increment (\%)} = (0.43)\text{resource space} - 0.05 \text{ (2nd season)}
\]

The slope of the relationship was consistent for the two seasons. There was no relationship between shoot length and resource space.

15.5 DISCUSSION

The amount of space available to an individual tree is a primary determinant of its growth rate, since it defines the pool of resources available to it. This study has demonstrated a significant, but weak linear relationship in this regard. It is hypothesised that some asymptote will be reached as the available space

Harvesting, Chap. 15: Plant level impacts of harvesting: effects on neighboring tree
Figure 15.1. Relative basal area increment relative to newly created resource space (■ - first year; ▼ - second year).

is too large for the tree to utilise fully. Quantification of this point would be useful in that it would indicate allow calculation of the optimum resource space required, and therefore the number of trees per unit area to maximise productivity per unit area for a stand of trees of that size. The absence of a clear asymptote suggests that this upper limit was not reached in this study. It is well documented that lateral spread of roots in dystrophic broadleaved savannas can be several times greater than the above-ground canopy spread (Rutherford 1983, Belsky 1994).

There is little comparative data from similar thinning studies. Smit (1994) recorded several attributes of Colophospermum mopane growth on plots thinned to differing intensities. A positive relationship was evident between thinning intensity and growth of the remaining trees indexed through shoot length, duration of leaf retention, proportion of trees flowering and setting seed, and seed size. Smith & Goodman (1986) thinned all trees within five metres of fifteen tagged Acacia nilotica trees (± 1.5 m tall) and compared growth attributes relative to control trees around which no thinning was done. The mean resource space around the control trees was not quantified. At the end of one growing season after thinning, trees
around which thinning occurred had a higher basal area increment, longer shoots, and a greater number of new shoots relative to trees around which no thinning occurred. There was no difference in height increments between the thinned and control situation. At a gross scale, division of the area-based woody production estimates of Schacht et al. (1988) by the number of stems per hectare in two thinning treatments in Brazilian tropical woodland, indicates that mean production per stem was over 20% greater in the less thinned treatment.

The absence of a relationship between the percentage increase in resource space and the basal area recorded is contrary to previous work. This indicates that either the species studied were characterised by different growth dynamics relative to those of previous studies or there were methodological problems associated with this study. Accepting the results indicates that there was very little overlap of rooting zones for any of the species studied, and/or each has only a limited ability to exploit a newly created opening. Perhaps monitoring should have continued for a longer period after thinning. Interpretation is confounded by the fact that the growth rate was not expressed as a change in rate relative to some previously known growth rate for each individual stem (of x size and y resource space), as was the resource space. Thus, the resource space of two stems may be equal after the thinning process, resulting in each having similar growth rates. However, prior to thinning, they may have had different resource spaces, and hence different growth rates. The initial resource space was quantified, but not the initial growth rate. Hence, the percentage increase in resource space could be calculated, but the percentage increase in growth rate, relative to an unknown initial rate, could not.

A direct relationship between available resource space and growth rate implies competitive interactions between the point tree and its neighbours. The further away the neighbours are, relative to their size, the greater the absolute growth rate. This is contrary to the nearest neighbour analysis study (Chap. 6), but in concurrence with previous literature (see Chap. 6).
COMMUNITY LEVEL IMPACTS OF FIRE ON WOODY PRODUCTIVITY:
IMPACT ON WOODY COMMUNITY STRUCTURE

16.1 INTRODUCTION

Fire has long been recognised as an essential determinant of the structure of savannas (Trollope 1982, Skarpe 1992, Scholes & Walker 1993). It may have a profound impact on the structure and productivity of the herbaceous layer (Trollope 1982, Mentus & Tainton 1984), with herbaceous material being an important component of the fuel required to maintain a fire. Through this mechanism, the impact of fire on the woody stratum is also dependent upon the nature of the herbaceous layer. The greater the herbaceous layer fuel-load, the greater the resulting fire intensity, and the greater the impact on woody plants.

Most work pertaining to fire in southern African savannas has concentrated on the herbaceous species composition and productivity (Scott 1984) and the proportion of woody stems killed. Integration and scaling up of woody mortality rates to community level has not been attempted, other than the results of complete fire protection (Trapnell 1959, Angus & Spence 1971). Whether or not fire induced changes at the plant level, i.e. stem death and stimulation of coppice growth, is maintained at the community level, or do they simply balance out, is under reported, and has not been considered in relation to fire frequency. If the sum total of fire effects at the plant level is manifest as a change in woody community structure, it can be readily hypothesised that fire will also, therefore, alter woody community productivity as argued by several authors (Smit & Teague 1992, Skarpe 1992, Scholes & Walker 1993).

Three factors confound the ability to determine and interpret the impact of fire on woody community structure, and hence productivity. The first is that it can be expected that the impact of fire will be highly variable because of the variability in season, intensity and frequency of burning (Trollope 1982, 1984, Gitzenstein et al. 1995). For example, does a single intense fire impact community structure in the same manner as several less intense fires? Knowing that stem mortality is greatest in short stems, it is hypothesised that the answer to this question will be negative. A single intense fire may induce significant mortality of stems. These will be replaced by coppice regrowth and seedling recruitment. If there is not another fire for several years, sufficient time for the new stems (coppice or new recruits) to grow tall enough to be relatively immune to another fire, then community structure will be little
altered except for the few years immediately after the fire. If there is another fire within a relatively short period, then the coppice regrowth and new recruits will still be short enough to be affected by the subsequent fire. Thus, frequent burning will tend to limit the probability of new stems growing through to larger size classes. The effects of fire intensity are evident more at the scale of an individual stem, whereas fire frequency is a function of community level process. The variation in season of burn may change these effects through its influence on fire intensity. Consequently, this study examined the effects of fire frequency on woody community structure.

The second problem with the determination of the effects of fire is that fire impact cannot always be isolated from the effects of post-fire management (van Wyk 1971, Trollope 1982, 1984). For example, burnt areas are attractive to a variety of herbivores (Moe, et al. 1990). Thus, there may be a period of intense grazing and browsing on new regrowth following a fire, the effects of which are inversely related to the size of the burnt area. What are the impacts of this relative to the impacts of the fire, and what impacts are a result of both events in succession? Herbivore impact can be diluted if large enough areas are burnt relative to the density of herbivores. If not, any contrasts of fire frequency cannot be isolated from the simultaneous effects of herbivores, which if at high densities will probably serve to reduce woody biomass (Strang 1974). The effects of herbivory also interact with fire frequency and intensity because grazing reduces the rate of fuel-load accumulation, thus reducing fire intensity and possibly frequency, but at the same time maintains the new coppice growth at a height that is susceptible to a repeat fire (Trollope 1982, Sweet & Mphinyane 1986).

The last problem is the measurement of woody productivity directly in burnt areas. Pre-marking of stems requires fire resistant markers. Even when that is achieved, the charring of bark on woody stems may lead to an erroneous interpretation that productivity per tree (through change in basal area) decreases after fire because stem circumference has decreased. Hence an indirect approach is required. This study approached it through the question of impact on community structure, given the correlation between some index of woody biomass and community productivity (Chap. 3).

16.2 OBJECTIVES

The objective of this section was to assess the effect of increasing fire frequency on woody community structure.
16.3 METHODS

Controlled burning block, contrasting fire season and frequency, have been maintained in Kruger National Park since 1953, in each of the major vegetation types. Of interest to this study were four of the treatments of different fire frequency, namely, annually, biennially, triennially, and a fire exclusion treatment. In 1983 two additional treatments were added, a four year and a six year rotation. Prior to 1983 the four year rotation treatment plot had been burnt biennially, and the six year rotation had been burnt triennially.

Treatment plots are arranged in a row, and treatments randomly assigned to plots within the series. Four replicate series, several kilometres apart, were established per vegetation type. In this study three replicates (Satara, Meraya and Nwanetsi) of the Satara region were assessed. Thus, a total of eighteen plots were measured during this study (6 treatments x 3 replicate blocks).

The area is classified as *Sclerocarya birrea* - *Acacia nigrescens* savanna by Gertenbach (1983). Woody communities are dominated by *Acacia nigrescens*, *Sclerocarya birrea* and *Pterocarpus rotundifolius*. The shrub layer dominants are *Dichrostachys cinerea*, *Securinega virosa* and *Grewia* species. The area is underlain by basalts, giving rise to eutrophic clay soils, with a clay content of 25 - 50 % (Gertenbach 1983). Mean annual rainfall at Satara is 548 mm.

Within each plot woody vegetation was stratified into two layers; less than 4.5 m high, and greater than 4.5 m high. This was necessary because of the low total biomass, and the low density of large trees in all the treatments except the fire exclusion plot. Thus, large individuals would have been undersampled by means of random transects, and if one was included it had a disproportionate impact on the resulting mean biomass and associated confidence limits. The double sampling approach described below overcame these problems.

Woody individuals less than 4.5 m were sampled in each plot by means of five randomly located transects (50 x 5 m). Within each transect all woody stems were identified and the basal circumference (at 35 cm above ground level) and height recorded. A visual estimate of the total biomass that was dead was also noted. If a stem greater than 4.5 m was located within the transect, it was ignored, except for the fire exclusion plots.

Thereafter for all treatments other than the fire exclusion, all stems greater than 4.5 m within the entire
plot were counted, and assessed as dead or alive. At every third stem the basal circumference was measured, and height determined from trigonometric conversion after measurement of the angle to the top of the tree from a known distance away (Shackleton 1993). The density of stems greater than 4.5 m was sufficient in the fire exclusion plots to sample them by means of the random transects. However, even for the fire exclusion treatment analyses were performed separately for the two height layers.

Regenerative stems were taken as any stems of 2 cm or less in circumference. This definition includes seedlings as well as new stems resulting from vegetative reproduction.

At two randomly located 5 m segments of the 50 m transects all woody litter was collected and weighed. This was abandoned after no woody litter was recorded for the first five plots assessed.

Five A-horizon soil samples were collected systematically from the annual, triennial and fire exclusion plots. They were analysed in the laboratory for pH (1 M KCl), CEC, Ca, Mg, K, Na (atomic absorption spectrosopy), P (Ambic 1), total N (Kjeldahl) and organic carbon (Walkley-Black).

All data were tested for normality and appropriate transformations made where necessary. Basic analysis was via ANOVA with subsequent analysis of residuals. For significant ANOVAs treatment means were compared further using the Least Significant Difference (LSD).

Overgrazing of the fire plots is considered an important confounding variable in the Kruger National Park experimental plots (van Wyk 1971).

16.4 RESULTS

16.4.1 Biomass

The biomass of stems less than 4.5 m tall was significantly greater in the fire exclusion than the fire treatments (F=13.3; d.f. = 5; p < 0.0001) (Table 16.1). Biomass in the annual, biennial and triennial burn plots was approximately 10% of that in the fire exclusion. Similarly, the biomass in the taller stratum was also greatest in the fire exclusion treatment (F= 2.99; d.f.=5; p=0.05). In the taller stratum, there was an increasing biomass with increasing fire frequency except for the 6 year burn.