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Woody overstorey and herbaceous understorey biomass in *Acacia harpophylla* (brigalow) woodlands

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Abstract

Extensive areas of Acacia harpophylla *(brigalow) woodlands have been cleared for pasture production in Queensland. The woody regrowth of* A. harpophylla *influences pasture production and composition following initial development of these woodlands.*

Biomass component regressions were developed using tree basal area as the predictor variable and used to estimate component yields of regrowing A. harpophylla *communities. Leaf biomass of* A. harpophylla *reached a maximum of 12 t ha^{-1} with a leaf area index of 2.5 when regrowing plants were 2.5 m high and about 10 years old. Pasture production, pasture basal area and the proportion of sown pasture species were lower at higher tree basal area of* A. harpophylla. *The greatest decrease was seen between 0 and 2 m^2 ha^{-1} tree basal area. Annual grasses and broadleaf herbaceous species represented a greater proportion of pasture biomass at high tree basal area.*

The poor control achieved by herbicide sprays on A. harpophylla *plants that are 2–2.5 m tall would be partly due to poor coverage of the herbicide spray, as leaf area index is at a maximum at this stage. A density of 1000 plants ha^{-1} is a threshold value above which regrowth control would be necessary at some stage to maintain acceptable pasture production and composition.*

The non-linear regression relationship between pasture production and tree basal area was similar to that observed in Eucalyptus *spp. However, in the equation that relates pasture yield (Y) to tree basal area (X),* $Y = A + B * e^{(-kX)}$ *the value of* k *for* A. harpophylla *communities was generally higher than observed in* Eucalyptus *spp. communities with the same potential pasture production in the absence of trees. Within even-aged stands, the use of tree leaf biomass to predict pasture production showed no advantage over the use of tree basal area as the predictor. However, there are advantages in using tree leaf biomass as a predictor when comparing communities with different size- or age-class structures.*

Introduction

The *Acacia harpophylla* (brigalow) forests of Queensland (Isbell 1962) have largely been cleared of original vegetation and developed into farming and grazing country (Johnson 1964; DPI 1976). The soils supporting *A. harpophylla* have a high nutrient status and sown pastures developed on these soils in Central Queensland have a high stock-carrying capacity compared with native pasture areas within *Eucalyptus* spp. communities in the same region (Rudder 1977).

Woody regrowth poses a serious threat to extensive areas of the *A. harpophylla* region with pasture productivity adversely affected in about 50% of localities (Anderson *et al.* 1984). The major regrowth species is *A. harpophylla* itself, which grows from root suckers following the initial scrub pulling/clearing operation (Johnson 1964). Moderate densities (3000–5000 stems ha^{-1}) of even-aged sucker regrowth are common. Effective control measures include blade ploughing (Scanlan & Anderson 1981) and aerial application of the herbicide tebuthiuron, both of which are expensive. Cheaper treatments (repulling and burning) may reduce the size but not the density of *A. harpophylla* regrowth.

Pasture productivity is much higher after initial clearing and sowing of introduced pasture species than in the original forest. Pasture production in cleared pastures declines after several years due to reduced nitrogen availability (Graham *et al.* 1981) and to competition from regrowing woody plants. The rate of woody regrowth and corresponding pasture production decrease determine the economic success of particular control strategies.

Tree basal area is a good predictor of pasture productivity in mature *Eucalyptus* spp. woodlands (Walker *et al.* 1972, 1986; Scanlan & Burrows 1990). However, leaf biomass is directly related to water use by the woody overstorey and should provide a better indication of competition than tree basal area in communities where competition for water is strong. Sapwood basal area and canopy cover can be used to estimate leaf biomass (Kaufmann & Troendle 1981; Baldwin 1989; Maguire & Hann 1989) and water use (Kline *et al.* 1976; Jordan & Kline 1977). Thus, a knowledge of the biomass partitioning of regrowing *A. harpophylla* could be used to interpret pasture productivity data following clearing and sowing of pasture species.

The objectives of this study were: (i) to determine woody biomass partitioning in regrowing *A. harpophylla*; (ii) to identify changes in pasture production and composition in regrowing *A. harpophylla*; and (iii) to compare overstorey–understorey relationships in regrowing and mature woodland communities.

Methods

Component biomass estimation

Component biomass determinations were made at the Brigalow Research Station (24°50′S 149°48′E), 30 km north-west of Theodore in central Queensland, during the first week of November 1982. The original vegetation at the site was *A. harpophylla/Eucalyptus cambageana* (Dawson gum) woodland. Most of the area had been cleared and repulled at different times so that a range of *A. harpophylla* regrowth sizes was available for study. The duplex soil had a sandy-clay loam surface (Db1.13, Northcote 1974), and site slope was 1%.

Twenty-nine *A. harpophylla* stems were selected, ranging in height from 0.45 to 5 m, and in density to 20 000 stems ha^{-1}. The following measurements were made on each stem:

- basal circumference (at 30 cm above ground);
- height;
- canopy size (two measurements at right angles); and
- number and basal circumference of all other woody plants within a 2 m radius of the sampled tree.

The plants were then cut off at ground level and taken to a laboratory for separation into components. The diameter inside bark and diameter of heartwood at the stem base were measured at the laboratory and used to calculate the cross-sectional area of sapwood.

Leaf, branch, stem bark and stem wood components were separated, oven-dried and weighed. Branches were defined as less than 2 cm in diameter; larger branch material was included in the stem component. On trees greater than 3 m tall, the bark was separated from sections of the stem. A mean percentage bark figure was obtained and applied to the whole stem. Leaf area was obtained by photocopying 20 leaves from each plant and determining the area of these using a planimeter. These leaves were also weighed to obtain mean leaf area, mean leaf weight, specific leaf area, total leaf number and total leaf area.

Stem circumference, sapwood basal area, height and canopy area were compared as predictors of biomass components. Bias occurs when using regression analysis with logarithms for determining the arithmetic Y values. Transformation from the logarithmic scale back to arithmetic units gives the median rather than the mean value (Baskerville 1972). The bias correction factor used in this study (the antilogarithm of half the residual mean square of the regression) was taken from Baskerville (1972), with the remaining bias (Beauchamp & Olson 1973) being ignored as was done by Harrington (1979) (see caption and footnote in Table 1).

Community development

Six areas of *A. harpophylla* were selected within the site from which the plants for component analyses were taken. On each area, *A. harpophylla* size was relatively uniform while among areas, *A. harpophylla* ranged from under 2 year old regrowth to almost mature trees. Basal circumference and height of all *A. harpophylla* plants within a sampling strip of 50 m × 2 m were measured. Regression equations were then applied to individual stems to obtain an estimate of component yields in each sampled area.

Overstorey–understorey relationships

Pasture production During April 1983, pasture yields were determined for each of 9 plots (50 m × 50 m) in the same area as above. A 2-stage sampling method (BOTANAL; Tothill *et al.* 1978) was used for pasture yield assessment. Some pasture samples were taken for hand separation into current growth and previous seasons' growth to enable pasture production to be estimated rather than simply herbaceous standing crop. Within each plot, two parallel transects each 30 m × 2 m were defined and the basal circumference of all *A. harpophylla* plants was recorded. These data were then used to estimate leaf and total plant biomass by applying the regressions from the first part of this study.

A similar study was set up to examine pasture production in an area containing *Eremophila mitchellii* (false sandalwood) regrowth. The site chosen had been used for a herbicide screening trial with 12 plots (10 m × 10 m) of varying densities (Scanlan & Fossett 1984). Woody basal area was obtained by measuring the basal circumference of all woody plants in each plot. Pasture production was determined using the same technique as for *A. harpophylla* areas.

Non-linear regression analysis (NONLIN module of SYSTAT program; Wilkinson 1988) was utilized to relate pasture yield to woody biomass parameters.

Pasture composition Pasture species composition data were obtained from a study carried out by Anderson *et al.* (1984). A total of 166 sites in central Queensland dominated by *A. harpophylla* was surveyed, with estimates of pasture basal area, species composition, and woody regrowth density and height being made. Height was used to estimate basal circumference using data from the first part of this study, and this enabled total *A. harpophylla* basal area to be estimated for each site. Sites where species other than *A. harpophylla* made up more than 10% of estimated tree basal area were excluded from this study. These data were pooled to give 11 categories of woody plant basal area.

Results

Component biomass yields

Biomass partitioning between components of *A. harpophylla* could be predicted from basal circumference of individual *A. harpophylla* stems (Table 1). Branch and leaf contribution to total yield declined as size increased (Fig. 1), while the proportion of stem increased as the size of *A. harpophylla* increased.

Sapwood basal area was a slightly poorer predictor of component biomass than basal circumference, as judged by coefficients of determination and visual goodness of fit (data

TABLE 1. Predictive equations for component biomass (g) of *A. harpophylla* (Y) using circumference (mm) at 30 cm above ground as the predictor variable (X) in the power curve regression equation $Y = e^{(A + B * \ln X)} * e^{(s^2/2)}$

Biomass component	A	B*	s.e.$_b$	s^2†	R^2
Leaf (g/plant)	−3.284	2.042	0.123	0.109	0.91
Leaf weight (g/leaf)	−1.951	0.187	0.073	0.023	0.27
Leaf area (cm²/leaf)	1.465	0.157	0.069	0.021	0.22
Leaf number (no./plant)	−1.156	1.811	0.169	0.120	0.87
Leaf area (cm²/plant)	0.311	1.967	0.166	0.116	0.89
Branch (g/plant)	−3.818	2.092	0.133	0.128	0.90
Stem bark (g/plant)	−7.235	2.809	0.126	0.115	0.94
Stem wood (g/plant)	−6.436	2.747	0.152	0.167	0.92
Stem total (g/plant)	−6.083	2.774	0.135	0.130	0.94
Total biomass (g/plant)	−3.568	2.384	0.093	0.062	0.96

*All slopes have $P < 0.05$.
†Residual mean square of regression; used to calculate the bias correction factor [exp($s^2/2$)].

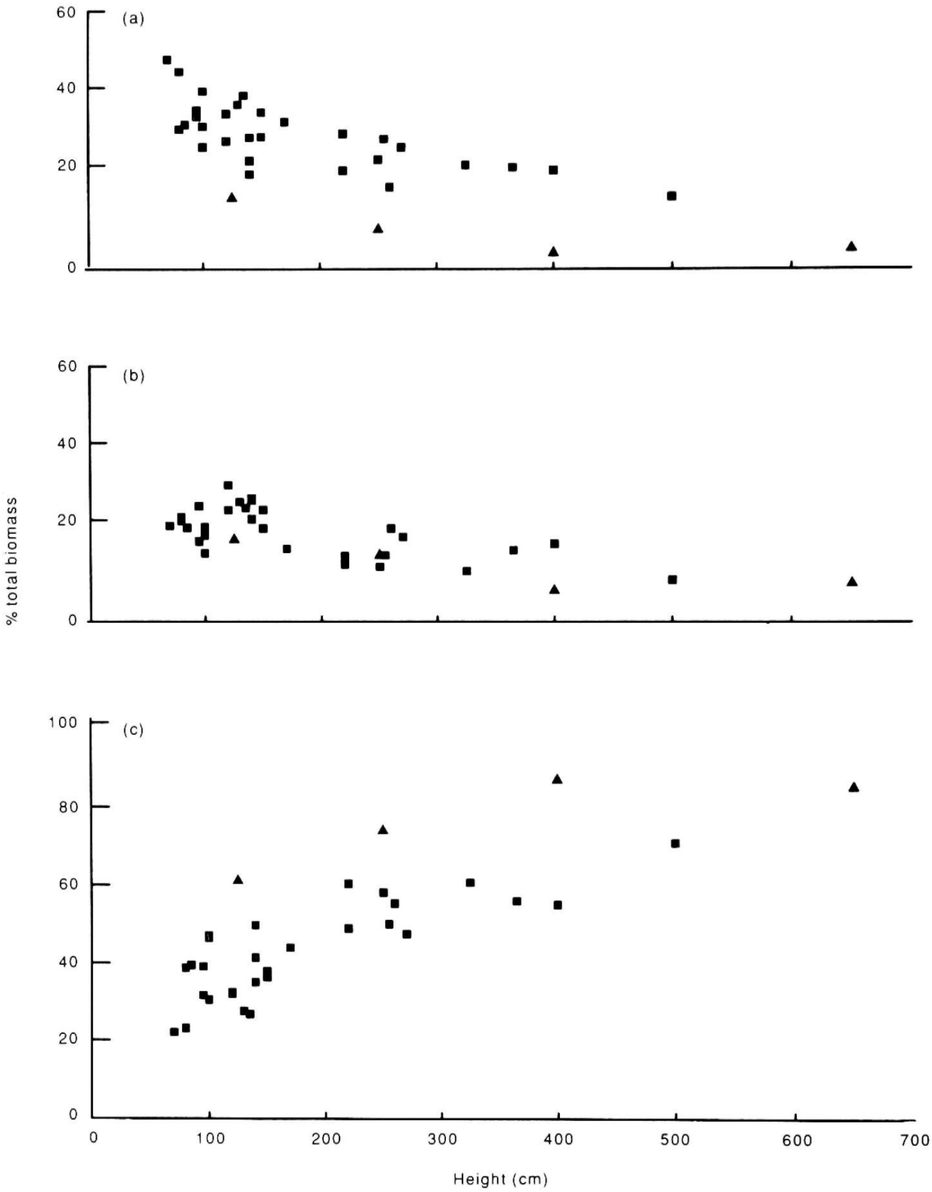

FIG. 1. Component biomass for (a) leaf, (b) branch and (c) stem of *Acacia harpophylla* plants of various sizes sampled in central Queensland. Data from this study (■) and data calculated from Moore *et al.* (1967; ▲) are shown.

not shown). Leaf weight was proportional to sapwood basal area, with 1410 kg leaf m^{-2} of sapwood area (s.e. = 110). Height was a poorer predictor variable for leaf and branch yield but it has the obvious advantage of being much more easily recorded or estimated in the field. Regressions are shown in Table 2.

Multiple linear regression analyses relating component yields to basal circumference and density or basal area of neighbouring *A. harpophylla* plants (within a 2 m radius) accounted for less than 50% of observed variation. Therefore, woody regrowth density was not included in further aspects of this study.

Community development

Tree basal area reached a maximum of 12–16 m^2 ha^{-1} at a wide range of densities (2750–15 000 stems ha^{-1}; Table 3). Stem density decreased as plant size increased. Leaf area

TABLE 2. Predictive equations for component biomass (g) of *A. harpophylla* (Y) using height (cm) as the predictor variable (X) in the power curve regression equation*

Component**	A	B†	s.e.$_b$	s^2‡	R^2
Leaf	−2.840	1.629	0.259	0.493	0.60
Branch	−4.056	1.805	0.233	0.401	0.69
Stem bark	−8.332	2.579	0.232	0.396	0.82
Stem wood	−8.009	2.621	0.200	0.296	0.87
All stem	−7.490	2.611	0.206	0.314	0.86
Total	−4.303	2.150	0.205	0.311	0.86

*Equation given in Table 1.
**Units as in Table 1.
†All slopes have $P<0.05$.
‡Residual mean square of regression; used to calculate the bias correction factor [$\exp(s^2/2)$].

index and leaf biomass reached a maximum for 10 year old regrowth and declined with maturity (Tables 3, 4). Biomass of branch and stem components increased markedly with increased age/size of individual plants within the stand, especially once the plants reached 2.5 m.

Overstorey–understorey Relationships

Pasture yield Pasture yield ranged from 190 kg ha^{-1} to 2430 kg ha^{-1}, with corresponding values (for *A. harpophylla*) of 9.7 m^2 ha^{-1} and 0.7 m^2 ha^{-1} for basal area, 5800–400 kg ha^{-1} for leaf biomass and 18 800–1000 kg ha^{-1} for total biomass. The details of regressions relating pasture yield to *A. harpophylla* parameters are shown in Table 5. The use of leaf or total yield of *A. harpophylla* did not improve the predictions of pasture yields that were obtained using *A.*

TABLE 5. Details of regressions relating pasture yield, Y (kg ha^{-1}) to X (woody plant parameters: basal area (m^2 ha^{-1}), leaf and total biomass (kg ha^{-1}) for *A. harpophylla*; basal area (m^2 ha^{-1}) for *Eremophila mitchellii*) using the equation $Y=A+B*e^{(-kX)}$

Attribute	A	B*	k**	R^2
A. harpophylla				
Basal area	−40	2988	0.223	0.95
	(448)†	(437)	(0.086)	
Leaf yield	296	1920	0.00084	0.81
	(330)	(466)	(0.00061)	
Total yield	274	1783	0.00027	0.80
	(314)	(410)	(0.00019)	
E. mitchellii				
Basal area	205	2850	0.170	0.96
	(357)	(368)	(0.059)	

*All slopes have $P<0.05$.
**Only values for Basal area have $P<0.05$.
†Value in parentheses are standard errors of estimate.

TABLE 3. Density, basal area and leaf area index of *A. harpophylla* at various stages of development

Age (years)	Height (cm)	Circumference (mm)	Density (no. ha^{-1})	Basal area (m^2 ha^{-1})	Leaf area index
1.5	45	29	19 000	1.36	0.21
2.5	70	41	15 000	2.04	0.33
4	120	86	12 000	6.90	1.48
10	250	99	15 000	15.90	2.48
15	275	104	12 350	12.69	2.00
Unknown	600	300	6 600	15.14	1.80
Mature*			2 750	12.5	

*Estimated using density data and the mean size of diameter classes from Moore *et al.* (1967).

TABLE 4. Component yields (kg ha^{-1}) of dry matter for developing *A. harpophylla* regrowth using density data from Table 3

Age (years)	Height (cm)	Leaf	Branch	Stem bark	Stem wood	Total dry matter
1.5	45	701	388	102	159	1350
2.5	70	1140	679	252	400	2470
4	120	2190	1440	811	1310	5750
10	250	12 300	9170	9120	15 300	45 800
15	275	10 600	8030	8030	14 400	41 600
Unknown	600	8550	9520	13 300	44 200	75 500
Mature*		7700	11 000		100 100**	119 000

*Data from Moore *et al.* (1967).
**Total stem material (bark and wood).

harpophylla basal area. At the *Eremophila mitchellii* site, the pattern of pasture dry matter production in relation to woody plant basal area was the same as that of the *A. harpophylla* site (Table 5) as indicated by the similar magnitudes of regression coefficients.

Pasture composition Pasture basal area was lower at high basal areas of *A. harpophylla* (Fig. 2a), with the largest decrease in the range of 0–2 $m^2\,ha^{-1}$. This also represented the basal area range in which native perennial grasses replaced the sown pasture species (Fig. 2b). At higher basal areas, the contribution by native perennial grasses was slightly less than the maximum and these were replaced by broadleaf species and annual grasses.

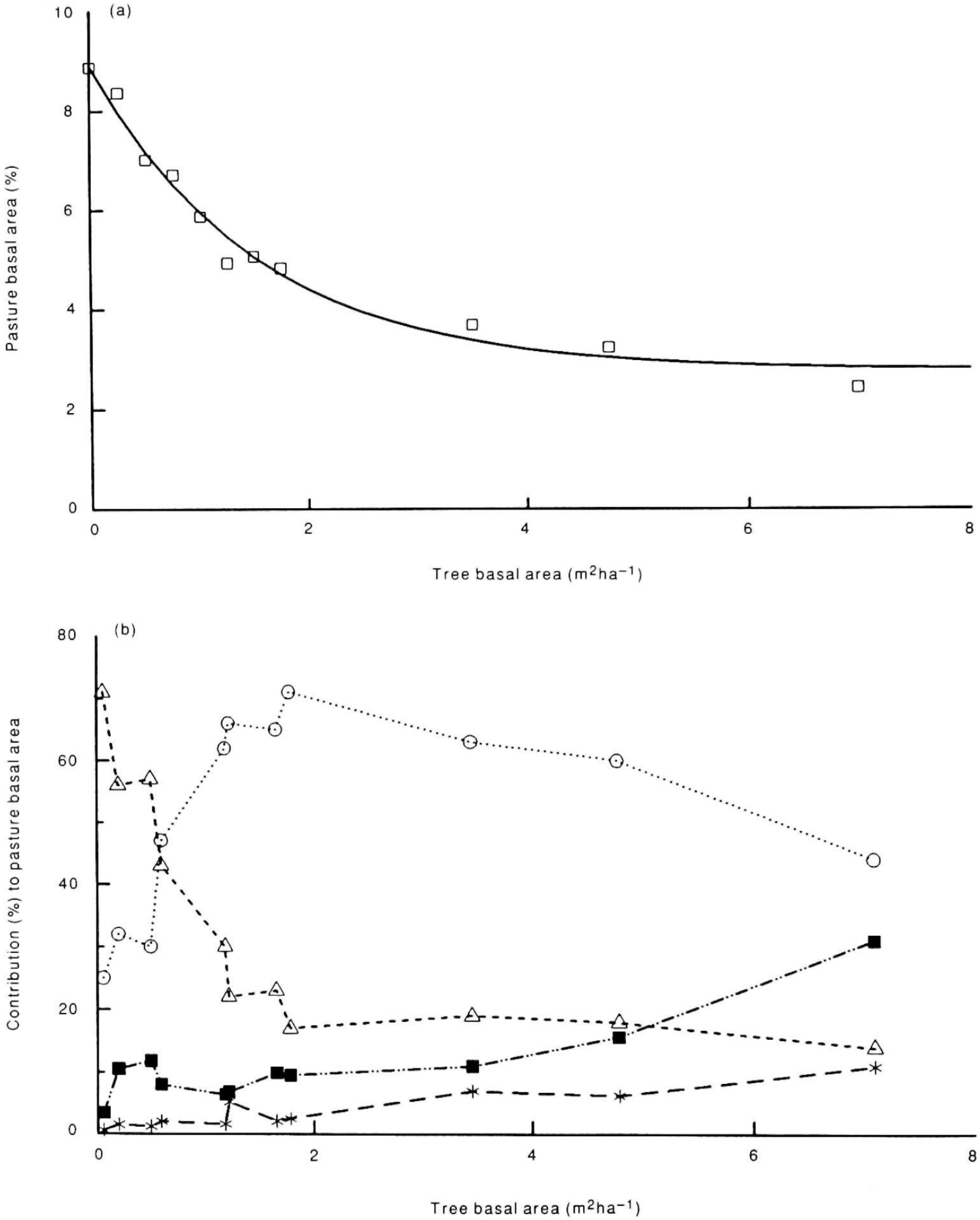

FIG. 2. Pasture (a) basal area and (b) composition for native perennial grass (○), native annual grass (■), sown grass (△) and broadleaf species (∗) as influenced by tree basal area of *Acacia harpophylla* regrowth in central Queensland (data recalculated from Anderson *et al.* 1984).

Discussion

As individual plants of *A. harpophylla* become larger (taller and greater basal circumference of stems), the proportion of wood increased and the proportion of leaf declined. Pasture production decreased as basal area of *A. harpophylla* increased, and the proportion of sown pasture species decreased rapidly.

Community development

Biomass allocation varied as plant size increased. For young stems all components (leaf, branch and stem) contributed about equally to total yield while regrowth 3 m tall was composed of *c.* 60% stem material. The data presented by Moore *et al.* (1967; for *A. harpophylla* at Meandarra in southern Queensland; 27°19′S 149°55′E) support the data presented here, although the leaf yield is slightly lower and stem yield slightly higher for the latter study (Fig. 1).

Leaf yield of *A. harpophylla* reached a maximum of 12 t ha^{-1} when the mean plant height was about 2.5 m. The decline in leaf biomass in stands with a mean height above 2.5 m occurred because the decrease in plant number was greater than the increase in leaf yield per plant. It is interesting to note that at this stage *A. harpophylla* regrowth is extremely hard to kill with aerially applied 2,4,5-T ester (Johnson 1964). This poor control has been attributed to inadequate coverage and some inherent resistance to the herbicide at this stage of growth. These data suggest that coverage would be a problem: the leaf area index for *A. harpophylla* regrowth, 2.5 m high, was 2.5, which is 10 times the figure for regrowth 45 cm tall (the growth stage recommended for treatment with 2,4,5-T).

The total yield of *A. harpophylla* increased for many years, although leaf yield peaked within 10 years of disturbance. Stem wood was the most important contributor to this increase in yield and in the virgin state may contain 80% of total nutrients present (Moore *et al.* 1967). This large nutrient pool is mobilized during the pulling and burning operations and, once dissipated, cannot be totally replenished. The rapid development of high leaf yields results in retention of these nutrients within the nutrient cycle, thereby reducing losses from the system.

Overstorey–understorey relationships in A. harpophylla *communities*

Pasture basal area and productivity were low at high basal areas of *A. harpophylla* (Table 5; Fig. 2). The decline in pasture dry matter production was greater than the decline in pasture basal area and, therefore, the productivity per unit basal area also declined as woody basal area increased. Pasture response to removal of woody plant cover may be due to an increase in production per unit of grass basal area and an increase in grass basal cover. The percentage of sown pasture species declined rapidly (from 70% to 17%) over a relatively small range of woody plant basal area (0–2 m^2 ha^{-1}; Fig. 2). This may occur over a period of 2–4 years if *A. harpophylla* regrowth is very dense (as in the study site). However, in most commercial situations, regrowth densities are usually lower and a woody plant basal area of 2 m^2 ha^{-1} would not be reached for a much longer period. The important feature of these results is that the decline in sown species cannot be attributed solely to declining fertility with time from clearing (c.f. Graham *et al.* 1981).

A woody plant basal area of 1 m^2 ha^{-1} reduces grass basal area to about 70% of the maximum, and sown pasture species and native perennial grasses are present in similar quantities. This is suggested as a tree basal area at which some tree treatment should be undertaken to prevent further declines in pasture productivity. One thousand plants per hectare, each 2.5 m high, would have a basal area of 1 m^2 ha^{-1}, and this could be used as an indicator of the need for treatment.

Overstorey–understorey relationships in regrowth vs *mature communities*

The use of leaf or total yield of *A. harpophylla* did not appear to give any advantage over the use of woody plant basal area for the estimation of pasture production in even-aged *A. harpophylla* regrowth communities. Previous work has shown that pasture production (Y) in mature *Eucalyptus* spp. communities can be predicted from tree basal area (X) (Scanlan & Burrows 1990) from the equation:

$$Y = A + B * e^{(-kX)}$$

The same form of equation was used in these trials (Table 5). The value of k in this equation

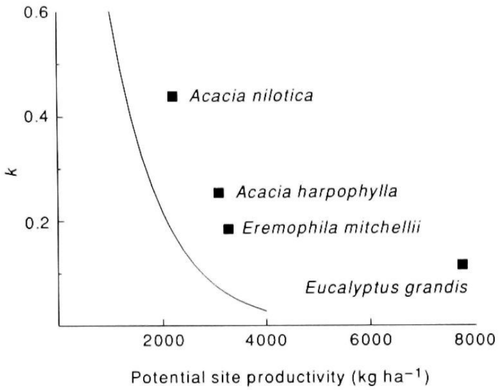

FIG. 3. Comparison of k values in the equation $Y = A + B * e^{(-kX)}$, which relates pasture production (Y) to tree basal area (X) for mature and regrowing woody plant communities in Queensland. (Line represents data from Scanlan & Burrows 1990; data for *Acacia nilotica* from J. O. Carter, pers. comm.); data for *A. harpophylla* and *Eremophila mitchellii* from this study; data for *Eucalyptus grandis* saplings from Cameron *et al.* 1989.

declines as potential site productivity increases (Fig. 3). Estimates of k from this trial, and from data of Cameron *et al.* (1989) and J. O. Carter (pers. comm.) for developing woody communities exceed those predicted for mature *Eucalyptus* communities where production in the absence of trees is similar (Fig. 3). The consequence of this difference is that, for a given level of potential pasture productivity and tree basal area, the actual production observed will be less in a regrowing woody community than in a mature woodland. The reasons for this difference are important in understanding overstorey–understorey balance.

In woodlands and open forests in Queensland, competition for water is probably the most important reason for reduced pasture productivity. The amount of leaf on woody plants is a good indicator of the amount of water used (Kline *et al.* 1976; Jordan & Kline 1977). The proportion of leaf per plant decreased as plant size increased (Fig. 1) and the amount of leaf supported by each unit of tree basal area changes as plant size changes. Data presented by Harrington (1979) and Pressland (1975) enabled these calculations to be made for *Eucalyptus populnea* and *Acacia aneura* respectively. For both species, more leaf is supported per unit of tree basal area for small trees (regrowth) than for mature trees. Therefore, a regrowing woody community will be more competitive for water (has more leaf) than a mature community of the same tree basal area. This is seen as a higher k value for regrowing communities than for mature communities, as shown in Fig. 3.

Generally, there is a positive correlation between the area of sapwood and the amount of leaf on an individual woody plant (e.g. Snell & Brown 1978; Kaufmann & Troendle 1981; Marchand 1984). Harrington (1979) related leaf weight to tree basal area for *E. populnea* and also presented data to indicate that for larger saplings and trees, the bark thickness averaged 1.03 cm and the thickness of the sapwood was 1.65 cm. These data were used to calculate the sapwood area for *E. populnea* plants of differing size. The regressions provided by Harrington (1979) were then used to estimate leaf biomass for the same size range of plants. The leaf biomass was then divided by sapwood area for each plant size and these data are presented in Fig. 4. As suggested from Kaufmann and Troendle (1981), the amount of leaf per unit sapwood area is relatively constant over a wide range of tree sizes. This was the case also for *A. harpophylla* but only a limited range of stem diameters (1–5 cm) was sampled.

Use of woody leaf biomass would be of benefit if communities of vastly different tree sizes were to be compared. In these situations, sapwood area could be used as an estimate of leaf material. Further analyses of pasture production and woody leaf biomass are necessary if a generalized model of overstorey–understorey competition is to be developed. Particular emphasis needs to be placed on: (i)

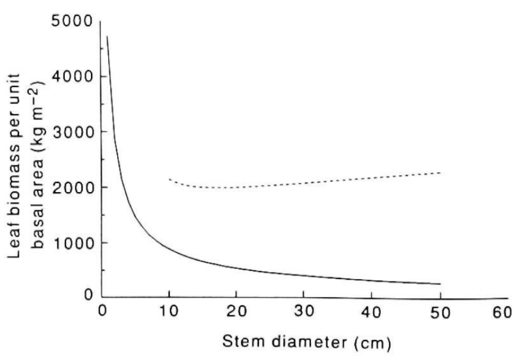

FIG. 4. Leaf biomass per unit of sapwood basal area (– – –) and per unit of tree basal area (—) for *Eucalyptus populnea* trees of varying size (data calculated from Harrington 1979).

tree effects on grass basal area; (ii) relationship between grass basal area and pasture yield; and (iii) competition between trees and herbaceous plants for water and nutrients.

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