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Annual production fraction of aboveground biomass in relation to plant shrubbiness in savanna

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ABSTRACT

A new means of estimating the annual production fraction of aboveground biomass of woody plants along a full shrub-tree continuum in savanna is presented. A measure of shrubbiness was found to be quantitatively definable over a shrub-tree continuum, to closely relate to the annual production fraction and to provide a single criterion for defining shrub and tree forms in South African savanna vegetation. It is proposed that in South African savanna, shrubs be defined as perennial woody plants with an annual production fraction of greater than 10% and trees with that less than or equal to 10%.

INTRODUCTION

Data on aboveground plant biomass in certain South African savannas have recently become more readily obtainable. Particularly total aboveground biomass is already known for some areas while in other more shrubby savannas the relative ease of direct total harvesting has been demonstrated. Methods have become more standardized to establish relationships with good correlation between the aboveground dry biomass of the plant and, for example, plant height, stem size and canopy or plant volume (Rutherford, 1979a). These relationships make it possible to determine, with acceptable accuracy, total plant biomass in many areas.

Data on annual production of woody plants are less readily available. Although data on annual shoot (leaf and twig) production are available for some areas of savanna these are more difficult to acquire by harvest owing to labour intensive, time consuming separation and sorting of the parts of the plant canopy. Further difficulty may arise in recognizing current growth of twigs in the absence of bud scar marks (Rutherford, 1979b). Correlation of whole-plant size parameters with the annual production component is sometimes less satisfactory than with total plant biomass.

The annual shoot production is important as a potentially utilizable fraction of plant biomass and renewable browse resource. It is particularly in shrub-sized plants that browse availability increases through an inverse relationship with plant height *per se* and through an increase in the annual production fraction of the plant. The annual production fraction is referred to as APF and is defined as

$$APF = 100\left(\frac{P}{B}\right)$$

where P is annual shoot production and B total aboveground biomass without dead branches, and for convenience is expressed as a percentage. Although determined for separate plant individuals, APF is also useful when applied to fairly homogeneous plant stands. APF corresponds approximately to the reciprocal of Biomass Accumulation Ratio of Whittaker (1970) in the form of

$$APF = \frac{100}{BAR+1}$$

where BAR is the Biomass Accumulation Ratio.

The objective of the present study was to investigate ways of predicting the Annual Production Fraction of aboveground biomass for woody plants along a full shrub-tree continuum for given savanna vegetation. If possible, prediction was to be considered independent of the plant species studied, to allow for extensive application.

PLANT SHRUBBINESS

It is notoriously difficult to find a commonly acceptable basis for distinguishing between trees and shrubs in many areas of South African savanna. Plant size has often been considered as a measure and applied in different ways (Edwards, 1976; Van der Meulen, 1979). Various measures of stem size have been used effectively for biomass relations, but become impracticable to apply in multi-stemmed shrubs. Plant volume, computed as a cylinder in cubic meters, is more easily applied to both trees and shrubs. One formula is

$$V = \left[\frac{D_1 + D_2}{4}\right]^2 \pi H$$

where V is plant volume, D_1 and D_2 long and short axis canopy diameters and H plant height. The concept of 'shrubbiness' of a plant involves more than plant size and requires consideration of additional factors.

Consider Whittaker's (1970) ranges of Biomass Accumulation Ratios for different terrestrial biome types and the conversions to Annual Production Fraction in Table 1. The terrestrial biome types corresponding to South African woody savannas are shrublands and woodlands. From the data it is clear that the Annual Production Fraction increases with a transition from woodlands to shrublands. It appears that some measure of how shrubby a woody savanna plant is, that is, its 'shrubbiness', is required to associate with this transition. General associations are that shrubbiness, although subject to the genetic constraints of the species concerned, normally increases with past fire treatment and with aridity but is inversely related to plant age. Shrubbiness of a plant

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TABLE 1.—Biomass Accumulation Ratio and Annual Production Fraction according to terrestrial biome type (After Whittaker, 1970)

Terrestrial Biome Type	Biomass Accumulation Ratio	Annual Production Fraction (APF %)
Desert	2 — 10	9,1 — 33,3
Grassland	1,5 — 3	25,0 — 40,0
Shrubland	3 — 12	7,7 — 25,0
Woodlands	10 — 30	3,2 — 9,1
Mature Forests	20 — 50	2,0 — 4,8

is affected by number of leader shoots and stems of the plant and it is relevant that in many South African savanna types, single stemmed plants are usually a special case of the multi-stemmed norm. These considerations appear to point to a basis for defining shrubbiness quantitatively and to providing for a continuum from distinct forms of shrubs to those of trees. The essence of shrubbiness is taken to be that which increases with number of growing leader shoots but decreases with increase in plant height. Number of basal stems often correlate positively with the number of leader shoots so that a Shrubbiness Index (SI) is given by

$$SI = C - \ln\left(\tfrac{H}{N}\right)$$

where H is plant height in centimeters and N the number of basal stems. The constant C is set to 7 so that the SI value increases with increased shrubbiness and allows for one-stemmed trees up to about 11 m height. These largest trees have, therefore, a Shrubbiness Index defined as zero. The current limits of application are based on the data collected and are discussed below. Wiens & Rotenberry (1981) relate shrubbiness to the amount of plant material in the 0,3 to 0,6 m height interval. This measure appears restricted to a range of smaller shrubs and is probably not suited to a shrub-tree continuum.

METHOD

Twenty generally deciduous plants ranging from distinct tree forms to distinct shrub forms were destructively sampled after completion of their seasonal shoot growth in three of Acocks's (1975) Veld Types. These were Mixed Bushveld, Arid Sweet Bushveld and Kalahari Thornveld in the Transvaal. Shrubs were particularly well represented in the two last mentioned more arid types. A range of plant species was sought and included *Acacia tortilis* (Forssk.) Hayne subsp. *heteracantha* (Burch.) Brenan, *Burkea africana* Hook., *Combretum apiculatum* Sond. subsp. *apiculatum, C. zeyheri* Sond., *Dombeya rotundifolia* (Hochst.) Planch., *Grewia flava* DC., *G. flavescens* Juss., *G. monticola* Sond., *Mundulea sericea* (Willd.) A. Chev., *Ochna pulchra* Hook., *Peltophorum africanum* Sond., *Tarchonanthus camphoratus* L. and *Terminalia sericea* Burch. ex DC. Plant height varied from 0,5 to 11,0 m. Measurements taken were vertical plant height (H), long and short axis canopy diameter (D_1; D_2) and count of number of basal stems (N). All current season's shoot growth was clipped and total plant and shoots weighed excluding dead branches. Subsamples were taken for dry mass (at 85°C) conversion of data. Basal stem counts did not include branches that originated more than 0,1 m above ground level nor that originated above 5% of plant height in smaller plants less than two metres tall. On plants greater than 1,5 m tall, fine basal coppice shoots less than 5 mm in diameter at base were sampled for weighing but were excluded from the stem count.

RESULTS AND DISCUSSION

Plant size in the form of plant volume, as defined above, was found to relate exponentially to the Annual Production Fraction (Fig. 1) but with a correlation coefficient less than 0,90. Greatest variation in the relation occurred in smaller plants with volume of less than about 6 m^3. An essentially no better relationship was obtained by first relating plant volume to total plant biomass (r = 0,99), then to annual shoot production (r = 0,89) and dividing the one regression formula by the other. Plant volume appears to be unsatisfactory for more precise estimation of Annual Production Fraction.

The components of the Shrubbiness Index (SI) are given graphically in Fig. 2 and the limits of application indicated. The data do not necessarily apply to plants less than 0,5 m height, plants with more than 80 countable basal stems, geoxylic suffrutices or tall polycormic trees. The present data and unpublished

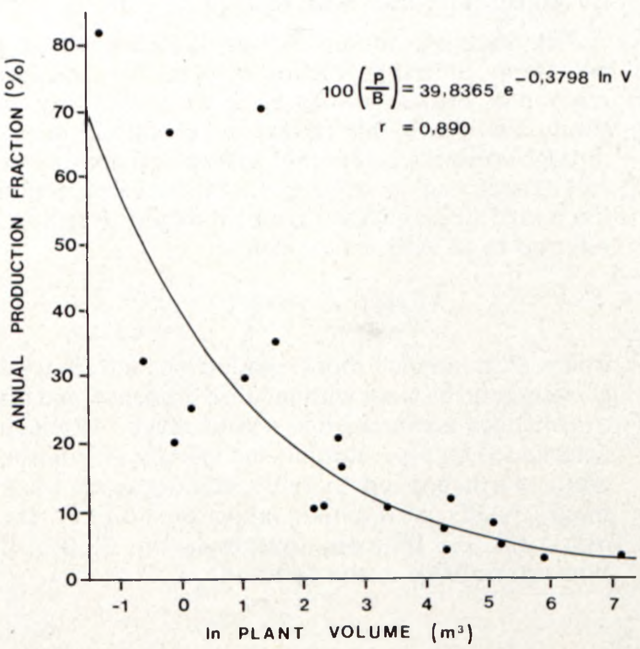

FIG. 1.- -Relationship between plant volume and annual production fraction where 100 ($\frac{P}{B}$) is annual production fraction and V is plant volume and r is correlation coefficient.

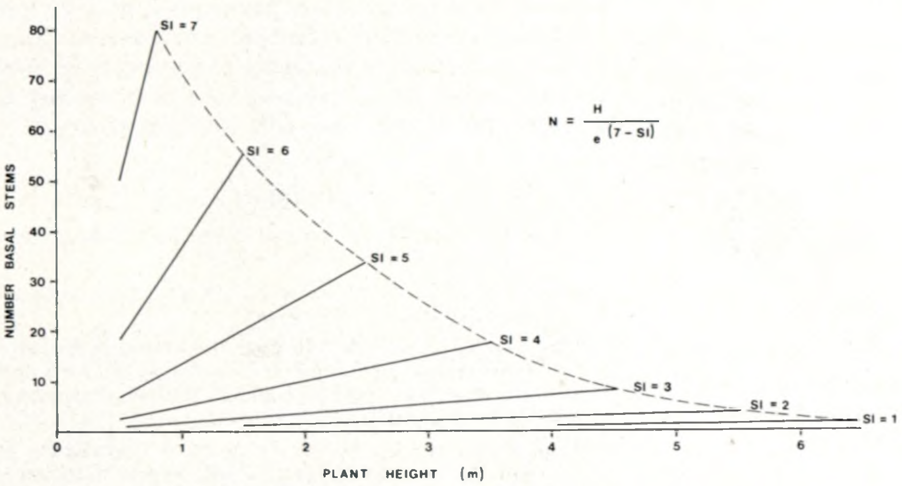

FIG. 2.—Relationships between plant height (H) and number of basal stems (N) for shrubbiness indices (SI) from 1 to 7, number of stems from 1 to 80 and plant height from 0,5 to 6,5 m. Valid application is limited to the area to the left of the broken line.

observations and tests have shown that occurrence of plants that correspond to positions in the upper right section of the graph is rare. Any plants that do occur in this area usually cause an overestimation of the Annual Production Fraction when applied as described below. All plants included have at least one stem and plants more than 7 m high usually have only one stem.

Shrubbiness Index related closely to Annual Production Fraction with a correlation coefficient of 0,964 (Fig. 3). This is a considerably improved exponential relation compared to that using plant size particularly in. the range of smaller plants. A hypothetical example of use of information from both Figs 2 & 3 illustrates the method. For a given area of fairly uniform vegetation, a mean plant height of 2,8 m and 5 basal stems per plant gives a Shrubbiness Index of 3 which in turn results in an expected Annual Production Fraction of 16%. With a known total biomass of say 10,0 tons/ha this results in an annual shoot production estimate of 1,6 tons/ha/year. It is important to note that for very low Shrubbiness Index values, small differences between estimated and actual Annual Production Fraction (data points show APF as low as 3% when 5% is predicted in Fig. 3) when applied to a tall tree can make a relatively large difference to the estimate of absolute annual shoot production.

The asymptotic trend of the limits of application of the Shrubbiness Index with increasing height in Fig. 2 (uppermost height range not shown) indicates that a Shrubbiness Index value of about 2 may be a convenient delimiter of shrubs and trees in the abovementioned veld types. This points to a definition of shrubs and trees based on a single measure namely the Annual Production Fraction (APF) of the plant and conveniently be set at 10% (corresponding to SI of 1,9). It is therefore proposed that shrubs be defined as those perennial woody plants with an APF greater than 10% and trees as those with an APF of less than or equal to 10%. From this definition and Fig. 2 it follows that in terms of plant height, shrubs can extend to about five and a half metres tall, whereas the lower height limit of trees lies between one and a half and two metres. Outside these two height limits, woody plants are either exclusively shrubs or trees. The Annual Production Fraction of 10% for distinguishing between shrub and tree forms is somewhat higher than the APF of 7,7 to 9,1% indicated by Whittaker (1970) to separate shrublands from woodlands. The Annual Production Fraction of the present study is aimed at the plant individual and not at averages for heterogeneous vegetation. It is for this reason also that the range of APF in this study is far greater than that for Whittaker's (1970) biome types (Table 1). The following correspondences may assist in providing a word picture of Shrubbiness Index values for individual plants: SI of 0 to 1, mainly larger savanna trees; SI of 1 to 2, mainly smaller savanna trees; SI of 2 to 5, majority of common shrubs; SI of greater than 5, mainly smaller shrubs with very many stems.

The use of the SI-APF relationship for the projection of shrub growth forwards of backwards in time is complex and depends on the degree of constancy of basal stem number, the rate of change in

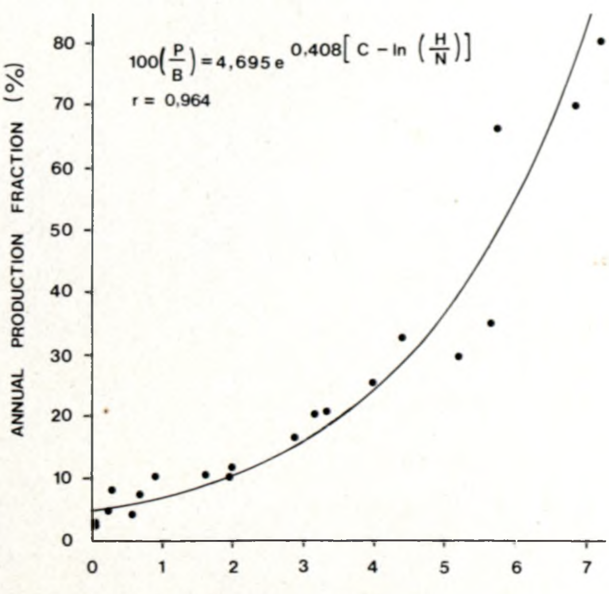

FIG. 3.—Relationship between shrubbiness index and annual production fraction where P is annual production, B is biomass, $100\,(\frac{P}{B})$ is annual production fraction, C is 7, H is plant height, N is number of basal stems and r is correlation coefficient.

plant height and the large and variable deciduous leaf component of shoot production.

The sample size in the present study remains small. Although it encompasses plants of different ages and species with different management treatments from different areas and savanna Veld Types, the Shrubbiness Index-Annual Production Fraction relation should be tested and applied over further variation in savanna to determine its full extent and applicability in South African savanna as a whole.

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UITTREKSEL

'n Nuwe metode vir die beraming van die jaarlikse produksie gedeelte van bogrondse biomassa van houtagtige plante vir 'n volledige struik-boom kontinuum in savanna word gegee. Daar is gevind dat 'n struikagtigheidsmaat kwantitatief definieerbaar is oor 'n volledige struik-boom kontinuum, nou verband hou met die jaarlikse produksie gedeelte en dien as 'n enkele maatstaf om struik- en boomvorms in die Suid-Afrikaanse savanna plantegroei te definieer. Daar word voorgestel dat in Suid-Afrikaanse savanna, struike as meerjarige houtagtige plante met 'n jaarlikse produksie gedeelte van meer as 10% en bome met dié van minder of gelyk aan 10% gedefinieer word.

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