Bothalia 25,1: 121–126 (1995)

Vegetation structure and small-scale pattern in Miombo Woodland, Marondera, Zimbabwe

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Keywords: disturbance, miombo woodland, small-scale patterning, soil properties, vegetation structures, woody species, Zimbabwe

ABSTRACT

The aim of this paper is to describe woodland structure and small-scale patterning of woody plants at a miombo site, and to relate these to past disturbance and soil properties. *Brachystegia spiciformis* Benth. and *Julbernardia globiflora* (Benth.) Troupin were the most frequent woody plants at the five hectare site, with size-class distributions which were markedly skewed towards the smaller size classes. The vegetation structure at the site and the increase in basal area over the past thirty years point to considerable disturbance prior to the present protected status. Six woodland subtypes were identified, grouped into two structural types: open and closed woodland. The distribution of woodland subtypes related closely to certain soil properties. It was hypothesized that the distribution of open and closed woodland is stable and a positive feedback mechanism by which this occurs is postulated.

UITTREKSEL

Die doel van hierdie artikel is om die bosveldstruktuur en kleinskaalse patroonvorming van houtagtige plante by 'n miombo-terrein te beskryf, en om hierdie verskynsels met versteuring in die verlede en met grondeienskappe in verband te bring. *Brachystegia spiciformis* Benth. en *Julbernardia globiflora* (Benth.) Troupin was die veelvuldigste houtagtige plante op die vyf-hektaar terrein, met grootte-orde verspreidings wat merkbaar na kleiner grootte-ordes geneig het. Die plantegroeistruktuur van die terrein en die toename in basale area oor die afgelope dertig jaar dui op aansienlike versteuring voor die huidige beskermde status. Ses bosveld-subtipes is geïdentifiseer en in twee strukturele tipes gegroepeer: oop en geslote bosveld. Die verspreiding van bosveld-subtipes het 'n noue verband met sekere grondtipes getoon. Aanspraak word daarop gemaak dat die verspreiding van oop en geslote bosveld stabiel is en 'n positiewe terugvoermeganisme waarvolgens dit plaasvind, word gepostuleer.

INTRODUCTION

Spatial heterogeneity is a universal attribute of natural vegetation (Greig-Smith 1979). Patterning exists and can be studied at various levels of biological organization and at widely different spatial and temporal scales (Allen & Starr 1982). For savanna vegetation, most studies have been concerned with regional and community patterns and their determinants and correlates (Walker 1987). Small-scale patterning (within community spatial heterogeneity) has received scant consideration (but see, for example, Macdonald 1978; Belsky 1983). Particularly the occurrence, determinants and dynamics of small-scale vegetation patterns in savannas remain poorly documented and understood. For instance, although Malaisse (1978), Celander (1983) and Chidumayo (1993) have given details of general miombo structure, no information is available on small-scale pattern. In this study, small-scale patterning of the woody vegetation and correlates between woodland subtypes and various soil properties were investigated for a miombo woodland near Marondera, Zimbabwe.

SITE DESCRIPTION

The five ha study site is one of the intensive research sites of the Tropical Soil Biology and Fertility (TSBF) Programme (Swift 1985). The site is located on the central plateau of Zimbabwe at Grasslands Research Station, 55 km southeast of Harare (18°10'S, 31°30'E). Altitude is 1 640 m. The climate is strongly seasonal, with over 80% of the mean annual rainfall of 885 mm (30 year average) falling between November and March. Mean monthly temperatures range from 11.7° C in June to 19.0° C in November. Night frost is not uncommon from mid-May until early August. Soils are strongly leached alfisols derived from granite. The site is on a gentle, north-facing slope.

The climax vegetation of the plateau, much of which has been cleared, comprises Deciduous Miombo Savanna Woodland (Wild & Barbosa 1967), in which the dominant species are *Brachystegia spiciformis* Benth. and *Julbernardia globiflora* (Benth.) Troupin. White (1983) classifies this vegetation as Zambezian Miombo Woodland (the drier version). Fire and large herbivores have been excluded from the site for about the last thirty years.

METHODS

The occurrence and abundance of woody species was recorded during April 1986 in 36 contiguous 10 × 10 m plots, along three linear transects which were located with randomly selected starting points and a randomly selected direction within 20° of easterly (Figure 1). In each plot the identity, height and basal area at 1.3 m of all 'trees' (individuals with a circumference at breast height of at least 90 mm) were recorded. Heights were estimated visually to the nearest metre. For trees with multiple stems, the basal area of each stem was measured and these

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MS. received: 1992-11-17.

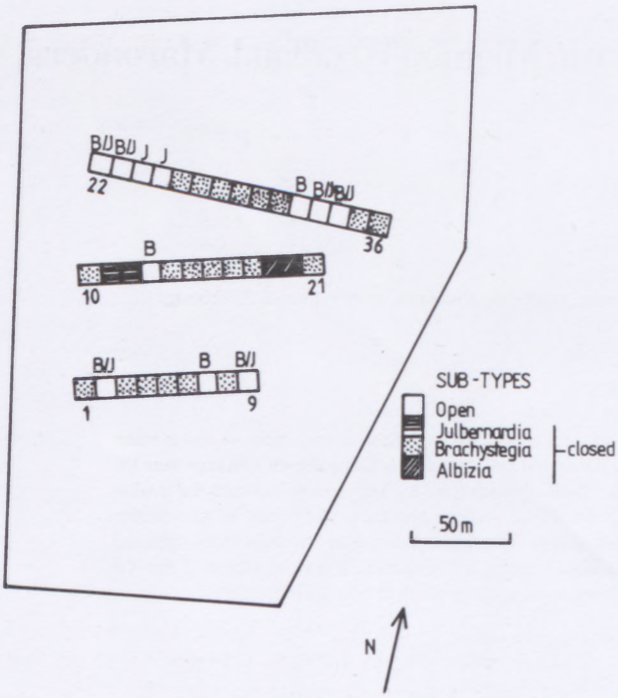

FIGURE 1.—The study site, showing the distribution of the woodland subtypes on the three transects. The transects and study area are drawn to scale. The subtypes of open woodland are indicated by B, *Brachystegia*; J, *Julbernardia*; and B/J, mixed *Brachystegia* and *Julbernardia*.

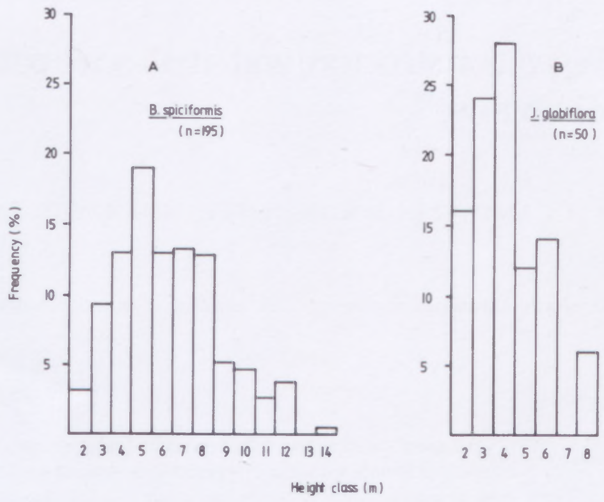

FIGURE 2.—Frequency distributions of tree heights for A, *B. spiciformis* and B, *J. globiflora* in a miombo woodland stand, Marondera.

values were summed to give a total basal area for the individual. Woodland subtypes were identified using a cluster analysis (Campbell 1978) of the plot by species matrix, with basal area, on an ordinal scale, as the importance value.

Soil samples, each comprising four random subsamples bulked together, and infiltration rates were collected for each of the four woodland subtypes from the middle transect (Figure 1). The soil samples were from the top 100 mm. Infiltration rates were recorded as the seconds taken for 250 ml of water to infiltrate after pouring into an infiltration ring of 100 mm diameter. Soil analytical techniques followed Anderson & Ingram (1989).

Aerial photographs dating from 1946, 1967, 1973 and 1981 were used to determine past vegetation patterns and disturbance.

RESULTS

Woody vegetation structure

B. spiciformis, which occurs in 94% of the plots, dominates the stand with eight times greater basal area than either of the species with the next highest basal area (*J. globiflora* and *Albizia antunesiana* Harms) (Table 1). In terms of density, *B. spiciformis* comprised 70% of all trees, and *J. globiflora* 18%. Average height did not exceed 7 m for any species (Table 1). Very few individuals exceeded 10 m in height, with the tallest tree encountered being 14 m.

Size-class distributions for *B. spiciformis* and *J. globiflora*, show that for both species there are many small individuals (Figures 2, 3). *B. spiciformis* individuals are markedly larger than those of *J. globiflora* in terms of both height and basal area. *B. spiciformis* and *J. globiflora* both have many individuals with multiple stems, with 39% and 36% of individuals respectively being multi-stemmed. It is particularly the larger individuals of the two species that have more than one stem (Table 2).

TABLE 1.—Frequency and means of tree density, stem density, basal area and height for the tree species in 36 plots in a miombo woodland, Marondera

Species	Frequency (%)	Tree density (#/ha)	Stem density (#/ha)	Basal area (m^2/ha)	Height (m)
Brachystegia spiciformis	94	547	864	7.73	6.25
Julbernardia globiflora	44	139	211	0.90	4.08
Albizia antunesiana	31	53	67	0.91	6.11
Ekebergia benguelensis Sparrm.	11	11	17	0.04	4.25
Terminalia sericea	6	11	14	0.04	3.75
Acacia sieberiana	3	6	14	0.26	6.50
Others (six spp.*)	17	19	19	0.03	2.67
TOTAL	100	786	1206	9.91	5.71

* Other species were *Ochna pulchra* Hook., *Parinari curatellifolia* Benth., *Strychnos cocculoides* Baker, *Strychnos spinosa* Lam., *Uapaca kirkiana* Müll. Arg. and *Vangueria infausta* Burch.

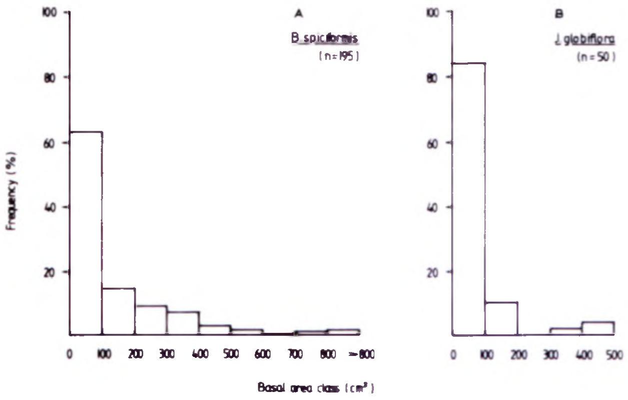

FIGURE 3.—Frequency distributions of basal areas for A, *B. spiciformis* and B, *J. globiflora* in a miombo woodland stand, Marondera.

TABLE 2.—Stem numbers per individual in relation to size for *B. spiciformis* and *J. globiflora* in a miombo woodland stand, Marondera

Size class		*B. spiciformis*		*J. globiflora*	
		n	Mean no. stems	n	Mean no. stems
Height (m)	0–3	25	1.32	20	1.40
	4–6	87	1.36	27	1.48
	7–9	61	1.89	3	2.66
	10–15	22	2.09		
			***		*
Basal area (cm^2)	0–100	123	1.30	42	1.31
	101–200	28	1.68	5	1.80
	201–400	30	2.10	1	4.00
	>400	14	3.00	2	4.00
			***		***

ANOVA: * = $p < 0.05$; *** = $p < 0.001$.

Within-stand pattern of woody vegetation

Numerical classification of the plots based on woody species composition produced six readily interpretable groups or subtypes of woodland (Figure 4). These six groups can in turn be placed into two woodland types according to structural criteria: open woodland and closed woodland (Table 3). The open woodland subtypes are dominated by *Brachystegia*, *Julbernardia* or a mixture of the two species, whereas the closed woodland is dominated by *Albizia*, *Brachystegia* or *Julbernardia*. Compared to closed woodland, open woodland is characterized by being less dense and by having shorter and slimmer trees (Table 3). The open *Julbernardia* subtype is particularly sparse and has the lowest total basal area and density per ha as well as the lowest richness and diversity of woody plants. In terms of the tree floristics, the open and closed woodland types are not distinctive (Figure 4), as the two most frequent tree species, *B. spiciformis* and *J. globiflora*, are dominants in subtypes of both groups (Table 3).

The closed *Brachystegia* subtype is by far the most frequent at the site (Table 3). The distribution of subtypes along the transects is not random, with plots making up a subtype often being contiguous (Figure 1). The distribution amongst plots of the less frequent trees was also by no means random. For instance, for both *Terminalia sericea* DC. and the large trees of *A. antunesiana*, all individuals that were sampled occurred in adjacent plots.

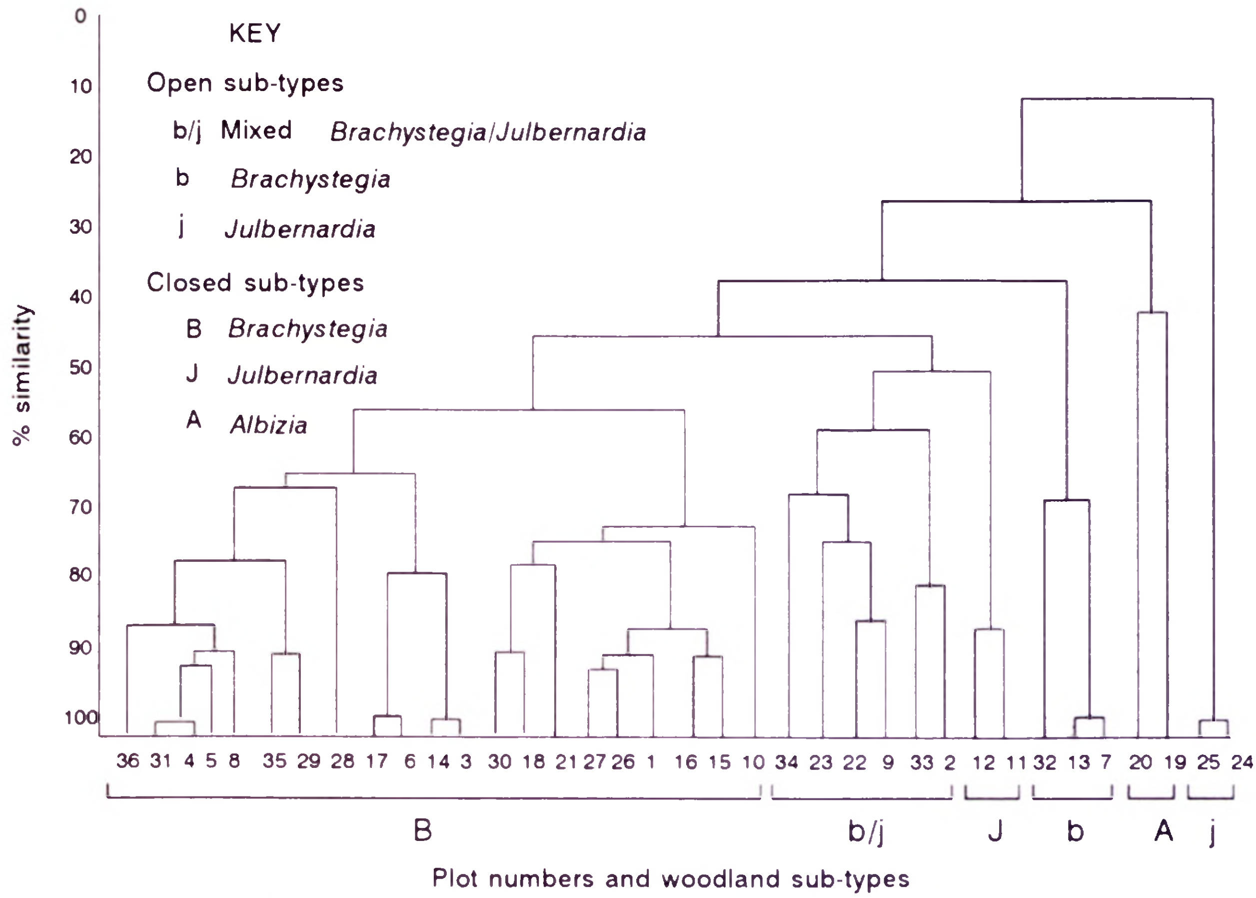

FIGURE 4.—Cluster analysis of 36 plots from a miombo woodland, Marondera, on the basis of woody species composition.

TABLE 3.—Characteristics of plots and trees of six woodland subtypes in a miombo woodland stand, Marondera

Woodland structural type	Open Woodland			Closed Woodland			Significance of ANOVA among all subtypes	Significance of contrast between open and closed woodland
Woodland subtype	*Brachystegia*	*Brachystegia/ Julbernardia*	*Julbernardia*	*Albizia*	*Brachystegia*	*Julbernardia*		
Plot statistics								
Number of plots	3	6	2	2	21	2		
Mean tree density (#/ha)	433	600	200	800	910	1150	NS	**
Mean stem density (#/ha)	567	833	300	1300	1429	1750	*	*
Mean basal area (m^2/ha)	1.5	3.1	0.9	18.2	12.7	13.8	***	**
Dominant species (> 25% of individuals)	*Brachystegia*	*Brachystegia/ Julbernardia*	*Julbernardia*	*Albizia Brachystegia*	*Brachystegia*	*Julbernardia*		
Dominant species (> 25% of basal area)	*Brachystegia*	*Brachystegia*	*Julbernardia*	*Albizia Acacia*	*Brachystegia*	*Julbernardia Brachystegia*		
Species richness (mean no. of species per plot)	1.3	2.7	1.0	2.5	2.2	2.5	NS	NS
Shannon-Weiner diversity index based on tree density	1.06	1.40	1.00	1.42	1.21	1.30	***	*
Tree statistics								
Number of individuals	13	36	4	16	191	23		
Mean basal area (cm^2)	34	52	43	228	140	120	***	*
Mean height (m)	4.1	3.9	3.8	7.9	6.1	5.2	***	***
Mean number of stems	1.31	1.39	1.50	1.63	1.57	1.52	NS	NS

NS = P > 0.05; * = P < 0.05; ** = P < 0.01; *** = P < 0.001.

whereas for both *Acacia sieberiana* DC. and *Vangueria infausta* Burch., all individuals sampled were located on a single plot. In this stand the shape and extent of open woodland patches along the transect, as observed on aerial photographs, have remained unchanged since 1946 when the earliest photographs were taken.

Amongst the closed woodland subtypes, which together occupy about 70% of the stand, there is a high degree of similarity in woodland height, basal area and density (Table 3). Accordingly, much of the small-scale variation within the stand is variation in species composition rather than variation in structure (Campbell *et al.* 1988). This is particularly so since the dominant trees of the three closed subtypes (*A. antunesiana*, *B. spiciformis* and *J. globiflora*) are similar in physiognomy, canopy shape, structure, leaf form and leaflet size.

Soil properties and woody vegetation pattern

The closed *Albizia* woodland subtype is located on termitaria and has soils which differ from those of the other woodland subtypes in having higher contents of clay, silt, organic matter, moisture, calcium and magnesium (Table 4). Amongst the other three woodland subtypes present on the middle transect, the surface soils from the closed *Brachystegia* and *Julbernardia* plots are extremely similar, both in texture and chemical properties (Table 4), and therefore it is unlikely that soil properties are dictating the pattern amongst these woodland subtypes. In contrast, soils from the open woodland, although similar in texture to soils from the closed *Brachystegia* and *Julbernardia* plots, differ considerably from these in being more acidic and having lower infiltration rates, organic matter, moisture and nutrient contents (Table 4). The open woodland patches are strongly capped with a microfloral crust.

DISCUSSION

Based on woody species composition and abundance, the site is typical of miombo woodland as described by Wild & Barbosa (1967) and White (1983), and has a similar stature, basal area and density to another, previously described miombo woodland that had also been protected from fire and cutting for 30 years (Strang 1974). However, when compared to miombo of sites with higher rainfall from Zambia, Zaïre and Tanzania, the trees are considerably smaller and the plot basal area is lower (Celander 1983; Malaisse 1978; Chidumayo 1993). It is difficult, however, to determine whether the differences are due to site potential or disturbance regimes.

Woodland cover was removed from the Grasslands Research Station after its establishment in 1929 (J. Clatworthy pers. comm.) and it is likely that the study site received this treatment. The high proportion of individuals with multiple stems attests to previous disturbance at the site. The fact that the smaller individuals in particular tend to be single-stemmed suggests that the site has been relatively free from disturbance over the last few decades. The present disturbance-free regime goes back at least to the mid-1950s, and the single aerial photograph from 1946 shows no major difference between the vegetation at that time and at present.

Strang (1965) estimated the combined basal area for *B. spiciformis* and *J. globiflora* at this Marondera site to be 7.2 m^2 per ha in 1963 as compared to 8.6 m^2 per ha as recorded in this study (Table 1). Therefore it appears that the woodland at the site is still maturing, albeit with minimal annual increment in basal area. The size distributions of the two most frequent species are more skewed towards the smaller size classes than are any of the distributions of the six common trees from the Nylsvley savanna in South Africa (Walker *et al.* 1986). This is further evidence that the woodland is still maturing. Some individuals present at the site were probably not felled when stumping took place, as was the case for an adjacent area in which the woodland was thinned out to a parkland containing seven to eleven large trees per ha (Rattray 1948). This would account for the low density (8.3 trees per ha) of very large (basal area greater than 800 cm^2) *B. spiciformis* individuals.

TABLE 4.—Characteristics of soils from four woodland subtypes in a miombo woodland stand, Marondera

	Open *Brachystegia*	Closed *Albizia*	Closed *Brachystegia*	Closed *Julbernardia*	Total no. samples	d.f.	Signif.
Clay content (%)	14.3	24.3	12.4	13.0	8	4.4	*
Silt content (%)	1.6	4.0	2.0	2.6	8	3.4	NS
Sand content (%)	84.1	71.7	85.6	84.4	8	3.4	NS
Moisture content (%)	3.1	8.1	3.8	3.2	8	3.4	***
Organic matter content (%)	1.9	6.5	2.6	2.4	8	3.4	***
Infiltration rate (April) (seconds)	86.8	88.4	31.2	29.8	20	3.16	*
Infiltration rate (July) (seconds)	85.3	25.6	9.1	12.4	40	3.36	***
pH (April)	5.0	5.5	5.8	5.7	8	3.4	NS
pH (July)	4.8	5.5	5.7	5.4	24	3.20	***
Potassium (mg/100g Dw soil)	0.21	0.54	0.53	0.52	8	3.4	NS
Magnesium (mg/100g Dw soil)	0.97	3.59	1.74	1.97	8	3.4	NS
Calcium (mg/100g Dw soil)	0.24	1.39	0.76	0.76	8	3.4	NS
Phosphorus (mg/100g Dw soil)	0.13	0.18	0.67	0.30	8	3.4	*

ANOVA: NS = $p > 0.05$; * = $p < 0.05$; *** = $p < 0.001$.

There is considerable small-scale patterning of woody vegetation at the site. Some of this is simply explained by termite activity (Dangerfield 1990, 1993). The effects of mound-building termites on soils and vegetation are well documented (for example see Wild 1952; Hesse 1955; Glover *et al.* 1964; Lee & Wood 1971; Miedema & Van Vuure 1977). The result is the creation of nutrient-rich microsites which carry a characteristic flora.

It is hypothesized that the current distribution of open woodland is related to past human activities. It is suggested that past human activities have resulted in soil compaction and reduced infiltration. It is further hypothesized that a positive feedback mechanism prevents the re-establishment of closed woodland from open woodland. Open woodland occupies areas where the soil is strongly capped with a microfloral crust and water infiltration is low. Runoff from these areas is likely to be high, resulting in the removal of litter and seeds. This, in turn, will contribute to a low soil organic matter content. Conditions of low soil moisture, organic matter and nutrient levels, combined with low availability of propagules are unlikely to be conducive to the establishment of tree seedlings in these areas. Small-scale patterning of seedling recruitment at this site has been demonstrated by Grundy *et al.* (1994). Lack of seedling establishment will perpetuate the condition of low vegetation cover for these areas, and so the present soil conditions will be reinforced by this positive feedback loop. According to this argument, it can be predicted that the distribution of open and closed woodland should be relatively stable, unless root-coppicing has been substantial. This stability was confirmed through aerial photographic analysis. Campbell *et al.* (1988) suggest that the re-establishment of closed woodland on open woodland sites must await some disturbance that destroys the soil crust, such as the initiation of a termite mound. It is also possible that successful seedling establishment may occur in the open woodland areas under exceptional climatic conditions. Belsky (1986) and Macdonald (1978) have suggested a similar positive feedback mechanism, based on different water infiltration rates, for the stable persistence of two discrete herbaceous vegetation phases in grasslands, on soils which are derived from the same parent material and which do not differ in particle-size distribution.

CONCLUSIONS

Considerable small-scale pattern was found to exist within the woody vegetation at this site, and it is suggested that these patterns are relatively stable through time. Much, but not all, of the spatial heterogeneity in the woody vegetation correlates to various physical and chemical soil properties. Such small-scale vegetation patterning will have significant impact on patterns of within-stand nutrient cycling and hence soil properties, as discussed by Campbell *et al.* (1988).

ACKNOWLEDGEMENTS

Funding for this research was obtained from the Swedish Agency for Research Cooperation with Developing Countries (SAREC), the Research Board of the University of Zimbabwe and the Meikles Scholarship Trust. Fumi Mizutani, Paul de Jager and Tim Lynam assisted with data collection and also commented on an earlier draft of this manuscript.

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Book Reviews

A KEY TO AUSTRALIAN GRASSES, 2nd edn, by B.K Simon. 1993. *Queensland Department of Primary Industries*, GPO Box 46, Brisbane, Qld 4001. ISBN 0 7242 5381 5. Pp. vii + 206. Price: soft cover, Australian $35.00.

This second edition, like its predecessor, can be recommended for its simplicity and user-friendly layout. It incorporates numerous new features such as the larger font which makes for much easier reading.

The introduction is divided into a number of subheadings. It gives a short overview on the construction and history of the layout. There is a note on the different characters used to classify grasses from the days of Palisot de Beauvois (1812) to the modern day works of Watson *et al.* (1985) and Clayton & Renvoize (1986). The author then gives his own classification of the Australian grasses. Under notes on grass identification, reasons are given as to why artificial botanical keys are more practical for identification than natural keys. There are a few useful hints on the dissection of a spikelet, followed by a short but clear explanation on computer-generated keys using the DELTA (**DE**scription **L**anguage for **TA**xonomy) system. The differences between the generic concepts of Watson and co-workers and those of the author are discussed.

A very useful glossary explains scientific terminology used in the book. Under the heading 'Illustrations' there are stylized drawings showing the structure of a grass spikelet and the diagnostic characters of Australian grass tribes and subtribes. The use of shading for highlighting the different parts of the spikelet is very effective.

There are two keys to the genera. Key 1 was generated by the author himself around the same framework as that in edition 1. Key 2, extracted from the world database of Watson & Dallwitz (1992), was supplied by Watson. In key 1 the couplets are brief and therefore tend to be easy to use. However, the novice may find certain characters difficult to use without additional information. An example is the very difficult character 'Annual or perennial'. The inclusion of key 2 may alleviate the difficulty to some extent since other and/or more features are often employed. But in computer-generated keys the characters used are often difficult to see or are not present on herbarium specimens. An example is the question 'shoots aromatic' or not.

The genera are arranged in alphabetical order. Related genera are consequently not grouped together but the index need not be referred to continually. This arrangement also tends to be more stable since advances in knowledge often result in changes to the classification. At the beginning of each genus a few abbreviated references are mentioned. These are then given in full at the end of the book before the index.

The keys to species are similarly short, with the current name in bold followed by the distribution in Australia in brackets. Although the use of abbreviations rather than symbols is an improvement, the map of Australia should have been retained. Below each name the most recent synonym and/or misapplied name is given in italics. Naturalised entities are marked by an asterisk (*) throughout the book. This is very useful, especially to scientists in applied fields.

A few minor technical points worthy of attention in future editions: include the abbreviation 'auct.' in the glossary; distinguish between dashes and hyphens; on p. 61 add under 'Key to species' the meaning of × in front of the genus or plant name and repeat explanation for *; p. 143 under *Pentaschistis*, cite Linder & Ellis (1990); p. 147 line 5 from below: lemmas 2.0–2.5 mm; p. 149 line 3 from below: nerves; p. 150 couplet 49: 'internerves' of what?; p. 180 line 3 : Plantarum; p.178–183 references: at least minimal use of end-of-line hyphenation should be considered; p. 199 column 1 line 2 from below: Parodi. The following terms should be added to the glossary: spicate, nodular, internerves.

This second edition, with the expanded and informative introduction, the glossary, the additional computer-generated key to genera and the updated taxonomic information, is a clear advance on the first edition and is highly recommended.

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FLORA OF AUSTRALIA Volume 49: Oceanic Islands 1, edited by A.E. Orchard & A.J.G. Wilson. 1994. *Australian Government Publishing Service*, GPO Box 84, Canberra ACT 2601. Price: Cat. No. 93 1664 3 Paperback $54.95; Cat. No. 93 1665 5 Hard cover $64.95.

Like Volume 50, which preceded Volume 49, this work deals with all the vascular plants present on two major islands off the east coast of Australia. The islands in question are Norfolk and Lord Howe Islands, which together comprise 51.16 km^2, a minute portion of the earth's surface. There are 361 naturalised plants in addition to the 345 indigenous species, of which 149 (44.9%) are endemic. Unfortunately, it is not clear whether endemic refers to only these two islands or whether it includes other major, adjacent islands such as New Caledonia and New Zealand. If the former, $^3\!/_{10}{}^7$ of the world's surface supports $^6\!/_{10}{}^4$ of the world's flora that does not occur elsewhere. The degree of endemism at the specific level is thus extremely high and, with the exceptionally high score of seven endemic genera, this publication is of particular interest.

The publication comprises a dedication to Ru Hoogland, a brief introduction to the rationale, scope and presentation of the volume, a brief discussion of the vegetation of the two islands, a bibliography, a key to the families, accounts of all the families, an appendix dealing with some nomenclatural matters, a glossary, a list of abbreviations and contractions, publication dates of previous volumes in the series and an extensive index.

The volume is dedicated to Ruurd Dirk Hoogland in recognition of his contribution to the development of the Australian National Herbarium and the contribution that he made indirectly to the volume by his extensive collections and very extensive notes and indices that he made available to the author. Ru Hoogland died suddenly in December 1994, after an operation in Paris.

The introduction to the rationale, scope and presentation of the volume includes the history of the development of the volumes on Oceanic Islands, the reason for combining the family accounts for the two islands and the arrangement of the volume. A list of the small islands that are included as part of the two larger islands, a note on the authorship of the volume and notes on the composition and presentation of the following sections are included, as are the policy on common names, the source of information on flowering time and the basis for the selection of species for illustration. This is followed by acknowledgements by the Australian Biological Resources Study and Peter Green, the major author, The discussion of the vegetation of the islands includes a general introduction to both islands, and for each island a general introduction, a description of the vegetation and a list of species, indicating which are endemic, indigenous and naturalised. At the end of this section there is a note on conservation on the two islands. The beginning of this section very briefly places the flora of the two islands in context of the southeastern Pacific Ocean flora, but states that an analysis of the floristic affinities of the two islands was beyond the immediate scope of the work.

The key to families is consolidated for both islands (unlike in Volume 50 which has a key for each island). We have tried running a few characteristic families through the numbered, indented key and found that it worked well and was easy to follow. The terminology is simple for botanists but amateurs may find some words rather technical. The list of exceptions to a step (e.g. the first part of step 3 on p. 27) is very helpful, as are the page references for other parts of the couplets (unfortunately step 33 is given as p. 34 instead of p. 33). We would prefer to see lines of dots leading to the family names in the key, but even more helpful would be page numbers on which the families occur, rather than the family numbers. This would reduce the amount of paging that needs to be done or the necessity to look up the page number in the index or table of contents.

The accounts of families, genera and species are neatly laid out and are clear, concise and informative. They cover 706 species in 136 families, the biggest of which are Poaceae (51 genera), Asteraceae (40 genera) and Fabaceae (23 genera). The families are ordered following the system of Cronquist, but we could not discover whether any particular order was used for the genera (they are not alphabetical). They presumably follow some more meaningful phylogenetic arrangement. The inclusion of taxa that have only been recorded in literature and for which there are no voucher specimens (e.g. Ebenaceae, p. 148), is extremely helpful and indicates that the author is aware of the situation. The treatments of families include descriptions, keys to genera, descriptions of genera, discussions, keys to species and accounts of the species. Accounts of species include citation of types, etymology, references to illustrations in other works, descriptions, common names, local distribution, ecological notes, global distribution, vouchers (with herbaria cited) and a discussion.

The nomenclatural appendix includes the description of a new species and subspecies and the lectotypification of a name. The glossary is quite extensive, with approximately 900 terms defined. The lists of abbreviations and contractions cover literature, herbaria, states, territories and nearby countries, general abbreviations and symbols. The single index is comprehensive, including scientific names in current use, synonyms and common names. We prefer single comprehensive indices, to separate indices for scientific names and common names.

There is a helpful comment on the back of the title page indicating how individual contributions should be cited, but it is only in a brief note in the introduction that the issue of authorship is clarified. We believe that a disservice is done to the major author, as few readers dipping into the volume for information on particular groups will actually discover who the author is. We think the situation should have been made clearer on the title page, in the table of contents or on page xi, where the contributors are listed.

There are 104 figures in the volume, including 63 colour plates (figures 1–30 and 50–81), 3 maps (figures 32–34) and 38 plates of line drawings of 4–5 plants each (figures 35–40 and 82–104). The colour plates provide spectacular views of the islands (figures 1–6 & 74) and good illustrations of many of the plants, some of them showing elements of the habitat. Captions include the name of the plant, the name of the island on which the plant was photographed and the name of the photographer. Unfortunately, the family names are omitted, as are magnifications. We feel that the former reduces the educational value of the photographs, because in order to find the family of a featured plant, one has to page to the index, then to the section in the book and then back to the photograph to look for family characteristics. Although generally accurate and clear, we felt that the quality of the line drawings is not of the same very high quality of those in Volume 50, with figure 83. A being a particular case in point.

In our review of Volume 50 (*Bothalia* 24: 262) we hoped that Volume 49 would include an introduction to the floras of all the islands and indicate the relationship to the rest of the Australian flora. Although some information is provided in the introduction to the floras of Norfolk and Lord Howe Islands, there is no information on the relationship of these floras to those of other islands, nor to the Australian flora as a whole. Considering the geographical distance and climatic differences between the islands, it seems that this expectation of ours was unrealistic.

Overall, this volume, like Volume 50, is an excellent piece of scientific work. The volume is presented in a user-friendly and appealing manner and is an example to be followed.

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DIVERSITY AND EVOLUTIONARY BIOLOGY OF TROPICAL FLOWERS by P.K. ENDRESS. 1994. *Cambridge University Press*, The Pitt Building, Trumpington St, Cambridge CB2 1RP. Pp. 511. ISBN 0 521 42088 1. Price: £55.00.

This is one of the Cambridge Tropical Biology Series and maintains the high standards which have become associated with the Cambridge University Press. Peter Endress, although based in Zürich, has a long and productive association with the tropics and maintains that he actually started this book during the monsoon in Java. Endress is a developmental morphologist who has published extensively on floral structure and development in primitive groups of flowering plants. His approach to the topic in hand is decidedly that of an evolutionary morphologist. This provides a refreshing zest to a topic which is not well documented experimentally and thus liable to an uncritical and even anecdotal exposition. Indeed he starts off by citing the instance of that most familiar of tropical ornamental trees, the Flamboyant, *Delonix regia*. For all its obvious attractions little is known about its reproductive biology in the wild (although I think the fact that it is rare in its natural home in Madagascar might well have something to do with this). But the point is well made nevertheless. The biology of flowers can provide insights into trophic and evolutionary relationships within the community. This facilitates an understanding of community dynamics which could not be gleaned from even the most comprehensive checklist. Anyway, a botanical inventory of the tropics is still far from complete, yet even as new species are being described, others are disappearing and all that is known to Science about them are their names. After all, the most informative aspect of a species is not what it looks like but how it functions. Endress is aware of this, and while nothing in his book is startlingly new, it is a compelling synthesis which provides a firm grounding, both philosophically and intellectually, from which to proceed.

The comparative study of flowers began in the temperate regions. While unusual and highly specialised pollination systems do occur in temperate Europe and America, they are more common in the tropics, probably mostly for the same reasons that there are more species in the tropics. The study of floral biology in all regions of the tropics, but especially the Neotropics, has expanded rapidly over the last three decades and it is Endress' intent in this book to summarise and expose these exciting advances to the general biologist. Not being a reproductive biologist, he is not biased towards any particular thinking on the topic and the sections in his book dealing with these aspects are more in the nature of summaries of published thinking, leaving the reader free to investigate further. His particular intelligence is most evident in the sections on morphology.

The book starts with a brief, whorl by whorl account of the components of the flower, not as a structural stocktake, but as an introduction to the basic tenets of floral organisation and ontogeny. The integrated nature of the parts and their shifting functions are emphasised and various aberrant types mentioned. A strong evolutionary bias permeates this section and all variations are examined from the perspective of their possible evolutionary status. The scanning electron micrographs of uncommon types of anther dehiscence are delightful.

The central part of the book concentrates on floral function. It opens with a summary of various classes of pollinating agents and some floral adaptations. This sets the scene for a basic introduction to current comprehension of the various structural specialisations and behavioural strategies developed by plants for attracting and rewarding pollinators or even avoiding them entirely. These include floral rewards, pollinator attractants, reproductive strategies and breeding systems. Although none of the topics is thoroughly discussed the salient points are there and the accounts serve as good starting points for anyone studying any aspects of floral biology. The importance of floral guilds in tropical communities, for instance, has been greatly overlooked and mention of them here may stimulate field workers to identify and document them more fully. They provide the key to understanding the origin of many particular floral forms which cannot be readily explained when the genus is examined in isolation. By summarising contemporary concepts in the field Endress provides both a wider paradigm for interpreting pollination biology and a convenient source of seminal references. Here in one place is enough to give any biologist a good idea of the kind of advances which have been made and where to start researching further, without getting caught up in detailed examination of specific instances. I challenge any general biologist to read these chapters without being thrilled at the exquisite strategies developed by plants and experiencing again the thrill of real life.

The second half of the book is largely taken up by examples of the structural and biological idiosyncrasies evident in selected tropical taxa. These range from some of the smaller Magnoliid families with rather insignificant flowers through the bizarre Rafflesiaceae, which contain the largest flowers in the kingdom; those masters of symmetry the Passifloraceae, which contrast greatly with the largely asymmetrical Scrophulariales although both exploit a range of similar pollinators; and that ubiquitous tropical group the Fabales, to the Zingiberales and inevitably the Orchidales, along with a number of others. Throughout this section Endress manages to keep the evolutionary thread intact and the examples gain in impact when placed in their functional and phylogenetic context. Something which struck me was the paucity of references to African examples. Studies in pollination biology are in their infancy here, and while some interesting work has been done in the last three years it is too recent for inclusion in this book. With Endress' book now available, we no longer have an excuse.

Endress ends with a miscellany of hints for a better understanding of flowers. It is particularly necessary to be aware of the historical context in which the existing form has developed. Structural constraints are an important legacy of ancestry and influence subsequent elaboration and diversification. No organism can develop structures nor strategies without constraint. In fact the strength of selection is most telling when it can be seen to have resulted in a transference of function. The use of leaves or bracts as attractive structures is an example easily called to mind, but the plants dealt with here provide an array of instances which are far more astounding.

We are only beginning to understand the diversity of living organisms in a way which sheds meaning on the dynamics of existence and exploitation. Endress' book is an admirable introduction to this. His strong evolutionary bias removes it from the ranks of a descriptive guide and makes for a fascinating philosophical introduction to floral form and function. I can never again regard flowers as more or less sculptural agglomerations—read this book, and neither will you.

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