Tree size as a factor influencing leaf emergence and leaf fall in *Acacia nigrescens* and *Combretum apiculatum* in the Kruger National Park

P. NOVELLIE

Novellie, P. 1989. Tree size as a factor influencing leaf emergence and leaf fall in *Acacia nigrescens* and *Combretum apiculatum* in the Kruger National Park. — *Koedoe* 32 (1): 95-99. ISSN 0075-6458.

In *Acacia nigrescens* and *Combretum apiculatum* saplings tended to retain leaves over the dry season, whereas the mature trees generally lost most of their leaves. In *Acacia nigrescens* the production of new leaves over the dry season was more commonly observed in saplings than in mature trees.

Key words: Phenology, Kruger National Park, browse availability.

P. Novellie, Mammal Research Institute, University of Pretoria, Pretoria, 0002 Republic of South Africa. (Present address: *Mountain Zebra National Park, Private Bag X66, Cradock, 5880 Republic of South Africa.)*

Introduction

Differences in growth patterns between old and young trees is a widespread phenomenon, having been recorded in a variety of temperate and tropical species (Borchert 1976, 1980; Rutherford & Panagos 1982; Milton 1987). This paper describes size-related differences in leaf emergence and retention during the dry season in two of the most common woody plants in the Kruger National Park, *Acacia nigrescens* Oliv. and *Combretum apiculatum* Sond.

Study area

The study area was at the Nwamuriwa Hills, situated 4,5 km east of the Tshokwane Ranger Station in the central district of the Kruger National Park. There are two hills which rise abruptly from the surrounding plain: Nwamuriwa, the larger southern one (highest point 410 m above sea level) and Nwamuriwane, to the north of it (highest point 330 m above sea level). There is a sharp break in profile between the steep (roughly 30°) hill slopes and the gently sloping (5 ° — 10 °) to almost level ground surrounding the hill base (termed the pediment). The soils of the slopes tend to be shallower and lower in clay content than those of the pediment (Coetzee 1977).

The dominant woody plant on the pediment and lower slopes is *Acacia nigrescens,* a species which favours clay soils (Van Wyk 1972). On the upper slopes *Combretum apiculatum* is

dominant. This species is virtually confined to well drained sandy or rocky soils (Van Wyk 1972). As might be expected *C. apiculatum* occurs mainly on the hill slopes, few specimens being present on the pediment.

The region is one of hot humid summers and cool dry winters. Eighty-five per cent of the annual precipitation falls between October and March. The mean annual precipitation recorded at the Tshokwane Ranger Station for the period 1935 to 1979 was 561 mm (Gertenbach 1980).

Methods

Observations on the phenology of *Acacia nigrescens* and *Combretum apiculatum* were made during the course of a survey of the species composition of the woody vegetation of the Nwamuriwa Hills (Novellie 1983). Species composition was estimated by means of belt transects, following the procedure of Walker (1976). These transects were 4 m wide, and were aligned at right angles to the hill base. They ran from the hill base to 80 m up the slopes (or as far as the crest of the hill if this was lower than 80 m from the base) and varying distances out from the base across the pediment. A total of 14 such transects, covering an area of 1,21 ha, were surveyed during the study period (October 1975 to August 1977). Each woody plant taller than 0,5 m rooted within the transect was recorded, and note was made of (i) whether new leaves were present and (ii) whether leaves were falling. *Acacia nigrescens* and *Combretum apiculatum* plants were divided into three height classes (i) 0,5 — 1,0 m (ii) 1,1 — 2,0 m and (iii) taller than 2,0 m. For *A. nigrescens* height-related differences in leaf emergence and loss during the dry season were examined in each of two habitats, the hill slopes and the pediment (described above). As noted, *C. apiculatum* was rare on the pediment and so results are given for the slopes only. The data presented here were collected during the dry seasons of 1976 and 1977 (the results for the two years were similar and so they were pooled).

Results

In *A. nigrescens* the smaller trees retained leaves over the dry season to a greater extent than the trees over 2 m tall (Table 1). Similarly, a greater proportion of smaller *A. nigrescens* trees carried new leaves during the dry season than was the case for those over 2 m tall. These new leaves were the result of flushes of new growth which appeared on a proportion of the saplings in the early dry season.

There is some evidence of differences between the two habitats (Table 1), for example the smallest (<1 m) *A. nigrescens* on the slopes lost leaves to a greater extent than those on the pediment. Such differences in phenology possibly reflect differences between habitats in soil moisture availability (see Borchert 1980). However, the relationships between tree height and leaf flush or fall described above were apparent in both habitats.

In *C. apiculatum* the smaller trees also shed their leaves to a lesser extent than the taller ones (Table 2), although the difference between the height classes was less marked than was the case for *A. nigrescens*. In contrast to *A. nigrescens, C. apiculatum* did not produce much new leaf over the dry season, and there were no substantial differences between the height classes in the presence of new leaves (Table 2).

Table 1

Differences between tree sizes in the occurrence of leaf fall and new leaves in Acacia nigrescens *during the dry season. Percentages of trees in each phenological class are compared between two habitats, the hill slopes and the pediment. N = number of trees observed*

I LEAF FALL

	TREE HEIGHT CLASS (m)					
	PEDIMENT			HILL SLOPES		
	0,5–1,0	1,1–2,0	>2,0	0,5–1,0	1,1–2,0	>2,0
No leaves falling	82%	40%	19%	45%	60%	18%
Some leaves falling	18%	60%	81%	55%	40%	82%
N	72	57	16	42	20	11

II NEW LEAF

	TREE HEIGHT CLASS (m)					
	PEDIMENT			HILL SLOPES		
	0,5–1,0	1,1–2,0	>2,0	0,5–1,0	1,1–2,0	>2,0
Some new leaves	28%	28%	13%	33%	40%	9%
No new leaves	72%	72%	87%	67%	60%	91%
N	72	57	16	42	20	11

Table 2

Differences between tree sizes in the occurrence of leaf fall and new leaves in Combretum apiculatum *during the dry season. Percentages of trees in each phenological class are shown for the hill slopes. N = number of trees observed.*

I LEAF FALL

	TREE HEIGHT CLASS (m)		
	0,5–1,0	1,1–2,0	>2,0
No leaves falling	65%	47%	50%
Some leaves falling	35%	53%	50%
N	23	15	12

II NEW LEAF

	TREE HEIGHT CLASS (m)		
	0,5–1,0	1,1–2,0	>2,0
No leaves falling	9%	20%	8%
Some leaves falling	91%	80%	92%
N	23	15	12

Discussion

The differences in growth patterns between old and young trees found in this study are similar to those described in many other species (Borchert 1976). Commonly shoot growth ceases earlier in the growing season in adult trees than in saplings. Recurrent growth flushes, sometimes extending almost throughout the year, have been recorded in the saplings of several genera, whereas in mature trees growth tends to be limited to one or two annual flushes. Among southern African savanna species Milton (1987) found that *Acacia burkei* Benth. saplings retained leaves longer than adult trees in the dry season. Exceptions to the general rule have, however, been reported: Rutherford & Panagos (1982) found that smaller *Ochna pulchra* Hook. plants initiated leaf drop earlier than larger ones, and that leaf loss did not correlate with tree height in *Burkea africana* Hook.

Borchert (1976) considered that many of the observed differences between adult and juvenile trees are the direct consequence of the increase in complexity and size (e.g. the increasing distance between the roots and growth points, and the increasing proportion of supportive tissues) that occurs with aging. The ubiquitous nature of the association between tree size and leaf growth discussed above lends support to this view, but a variety of environmental factors may also act to produce age-related differences in growth patterns. Borchert (1980) found that water stress in a tropical tree *Erythrina poeppigiana* O.F. Cook was affected by tree size, and in consequence large trees at dry sites passed through leaf change earlier in the dry season than smaller trees.

Milton (1987) suggested that leaf retention by saplings might represent a response to damage by browsing animals. Defoliation tends to stimulate late summer growth, and leaves produced during the late growing season are retained over the following dry season. Rutherford & Panagos (1982) ascribed the early leaf loss of small *Ochna pulchra* plants to a possibly less effective water uptake in younger root systems and the greater exposure of leaves of smaller plants to lower temperatures nearer the ground. Mooney, Parsons & Kummerow (1974) suggested that the demands of reproduction might account for size-related differences in growth patterns: growth may cease earlier in mature than in immature plants because the mature plants divert resources from vegetative growth to reproductive parts.

The differences in leaf retention between old and young trees implies that the age distribution of woody plants in a community may be an important determinant of resource availability for browsing herbivores. It appears that leaf abundance would, in general, vary less between the wet and dry seasons in habitats which have a high proportion of immature trees than in habitats where most plants are mature.

Acknowledgements

Funds and equipment for the study were provided by the Mammal Research Institute, University of Pretoria and by the National Parks Board. Earlier drafts of the paper benefited from the comments of Sue Milton and an anonymous referee.

References

BORCHERT, R. 1976. The concept of juvenility in woody plants. *Acta Horticulturae* 56: 21-36.

BORCHERT, R. 1980. Phenology and ecophysiology of tropical trees: *Erythrina poeppigiana* O.F. Cook. *Ecology* 61: 1065-1074.

COETZEE, B. 1977. Phytosociological survey, Central District, Kruger National Park. Internal Report: National Parks Board. Unpubl.

GERTENBACH, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe* 23: 35-43.

MILTON, S.J. 1987. Phenology of seven *Acacia* species in South Africa. *S. Afr. J. Wildl. Res.* 17: 1-6.

MOONEY, H.A., D.J. PARSONS and J. KUMMEROW. 1974. Plant development in Mediterranean climates. Pp. 255-267. *In*: H. LEITH (ed.). *Phenology and Seasonality Modelling*. New York: Springer-Verlag.

NOVELLIE, P.A. 1983. *Feeding ecology of the kudu* Tragelaphus strepsiceros *(Pallas) in the Kruger National Park*. D.Sc. thesis. Univ. Pretoria.

RUTHERFORD, M.C. and PANAGOS, M.D. 1982. Seasonal woody plant shoot growth in *Burkea africana — Ochna pulchra* savanna. *S. Afr. J. Bot.* 1: 104-116.

VAN WYK, P. 1972. *Trees of the Kruger National Park*. Volumes I and II. Cape Town: Purnell.

WALKER, B.H. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *S. Afr. J. Wildl. Res.* 6: 1-32.