Relative lack of regeneration of shade-intolerant canopy species in some South African forests

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As a consequence of a general survey of the floristics and size–class distributions of some forest patches in Natal[1] and the Cape Province,[2,3] it became apparent to us that in some coastal/lowland forests certain canopy species are apparently not recruiting *in situ*. Results of a later survey, in the same or similar forests, of leaf nitrogen concentration of forest species, indicated that the species with inadequate recruitment tended to have high leaf nitrogen levels.

In forests, leaf nitrogen concentration has been shown to be positively related to rates of photosynthesis (and therefore growth) and inversely related to leaf longevity. Shade-tolerant species usually retain their leaves for many seasons, each leaf having a relatively low photosynthetic rate.[4,5] Shade-tolerant species therefore tend to have low concentrations of nitrogen. In contrast, shade-intolerant species often have shorter leaf durations and higher levels of leaf nitrogen.[4,5] Leaf nitrogen levels are thus useful for determining relative shade-tolerance. In this article we synthesise some of the data from the two surveys on size–class distributions and leaf nitrogen, for species from from some coastal South African forests.

Methods

We sampled a range of coastal forests from the southern Cape to northern Zululand (see Table 1). Mean canopy height varied from about 10 m (Groenvlei) to 20 m (Amangwe). In all cases we sampled within extensive tracts of forest that were in conservation or semi-conservation

areas. The forests we sampled represent all the major coastal forest types of Cooper[6] except swamp and mangrove forests, which are very restricted and specialized types.

Leaf nitrogen concentration was analysed from fully expanded leaves from well-lit branches of at least three individuals of each species. Leaves were collected in October (i.e. they were recently flushed), dried and then ground up prior to being analysed using the standard Kjeldahl assay technique.

The demography of tree species should ideally be studied from population age-structures. However, it is not possible to obtain ages for most South African tree species from increment bores.[7] We have therefore relied on size–class distributions. Our choice of species was focused on common canopy species which best demonstrate the continuum of seemingly adequate recruitment to inadeqate recruitment. In general this resulted in a comparison between evergreen *Podocarpus* spe-cies (which often recruit abundantly and in shade[8]) and the deciduous species *Celtis africana*.

Forests were surveyed for size–class information in two different ways; in some areas we walked a randomly located straight-line transect and noted the size of all individuals of the selected species in a 10-m belt centred on the transect. At other forests a number of randomly located circular plots, each 400 m² in area were laid out approximately 100 m apart (Table 1). In these plots, all woody individuals more than 10 cm high were enumerated. Because these plots are relatively large (compared to scale of disturbance due to tree-falls) and randomly located we feel they adequately represent each forest area. From the survey data we determined total numbers of stems per size and height class.

Results

Our data indicate that some species, such as *Celtis africana*, are experiencing relative recruitment bottlenecks (Table 2), because there are usually fewer recruits [i.e. individuals <20 cm diameter at breast height, (dbh)] than canopy individuals. The species with low recruitment tend to have higher concentrations of leaf nitrogen (Table 2), suggesting that they are shade-intolerant species. Similarly, the canopy species which are recruiting ade-

quately have low levels of leaf nitrogen (Table 2).

Data showing nitrogen concentrations of other species which may not be recruiting adequately enough to maintain their canopy abundance, but from previous studies of other coastal forests, can be added to Table 2. In the Alexandria forest, species with high leaf nitrogen such as *Vepris lanceolata* (leaf N 30.8 mg g^{-1}) and *Erythrina caffra* (leaf N 59.6 mg g^{-1}) are recruiting poorly compared to *Podocarpus falcatus* (leaf N 15.3 mg g^{-1}).[3]

Discussion

We are not suggesting that these patterns apply to all forests. For example, regeneration appears to be adequate for canopy dominants in the southern Cape forests[2] and the Umtiza forest.[8] Our point is that in some coastal forests, recruitment of some canopy species is less than at replacement levels and that such species tend to be intolerant of shade. We have no mortality data to determine whether regeneration levels are insufficient for replacement. However, it is well known that podocarps grow slowly but may become large and old. Therefore turnover rates are probably lower for canopy individuals of these shade-tolerant species than for shade-intolerant ones, due to these differences in growth rates and longevity. In some cases the advantage of greater longevity is traded off against the disadvantage of slow growth rates. Each recruit of the shade-intolerant species may have a higher probability of achieving the canopy because their faster growth rates confer greater competitive ability for capturing gaps. However, this strictly applies only when the whole cycle of recruitment occurs in a gap. However, this strictly applies only when the whole cycle of recruitment occurs in a gap. It does not apply when recruitment is from advanced regeneration (such as arises with a bank of saplings waiting for release from the shade, by a gap in the canopy).[2] Our point is that in the absence of better demographic data, size–class distributions are a rough indication of demographic processes and such information as we have suggests recruitment failure of some shade-intolerant trees.

Table 1. Details of the forest type (Acocks[12] veld type in parentheses), position, altitude and sampling strategy for each study site.

Site	Forest type	Position	Altitude	Sample
Dukuduku	Lowland (1)	32°15'S 28°22'E	<100 m	54 × 400 m²
Zinawe	Sand (1)	32°20'S 27°48'E	<200 m	1-km transect
Amangwe	Lowland (1)	32°10'S 28°10'E	<100 m	3-km transect
Mapelane	Dune (1)	32°21'S 28°21'E	<100 m	90 × 400 m²
Gants	Sand (1)	32°00'S 28°00'E	<100 m	8 × 400 m²
Groenvlei	Cape-dune (4)	34°02'S 23°02'E	<100 m	2-km transect

Table 2. Size–class distribution of selected species in several South African forests (C = *Celtis*, P = *Podocarpus*, V = *Vepris*, A = *Albizia*, D = *Diospyros*, S = *Strychnos*, W = *Wrightia*, Pt = *Pteleopsis*, N = *Newtonia* and C= *Cleistanthus*).

Site	Species	Mean leaf nitrogen	<5m (ht)	<10 cm	>10 cm	>20 cm	>30 cm	>40 cm	>50 cm	% <20 cm
Amangwe	C. africana	36.7	1	–	1	6	9	9	21	4.3
	P. falcatus	20.0*	4	4	9	3	1	–	3	70.8
	A. adianthifolia	38.0	–	–	–	2	9	10	28	0.0
Mapelane	C. africana	32.5	7	3	2	17	10	10	26	16.0
	D. natalensis	15.7	611	34	42	33	10	7	1	93.0
Gants	W. natalensis	47.0	2	2	3	6	4	4	2	30.4
	Pt. myrtifolia	22.5	19	2	0	1	–	2	2	75.0
Groenvlei	C. africana	26.9†	1	–	5	14	16	23	–	10.2
	P. falcatus	15.3†	38	1	2	3	2	5	8	69.5
Zinawe	N. hildebrandtii	27.7	–	1	3	12	12	28	29	8.8
	C. schlecterii	21.2	1	9	88	49	6	–	3	65.3
Dukuduku	C. africana	36.7	8	11	25	14	9	–	–	28.4
	S. madagascar	17.0	57	20	17	12	7	9	5	60.6

*Estimate based on maximum value obtained for *P. falcatus* in four other forests.

†Nitrogen values obtained at Alexandria, which is a similar forest also on deep coastal sands.

What factors, either natural or man-made, may have caused this apparent decline in shade-intolerant species? We briefly discuss some narratives which may explain this situation. Periodic large-scale events such as fire, cyclones or drought may open up the canopy and thus facilitate the periodic regeneration of shade-intolerant species. There is no information on the occurrence, or importance, of such events in the dynamics of coastal forests, although we suspect that they are relatively unimportant because recruitment bottlenecks appear to be occurring on a large geographic, and hence climatic, scale. Excessive tree harvesting in the past or higher rates of tree mortality due to disturbance by megaherbivores, such as elephants, may have favoured excessive recruitment of the shade-intolerant species in two ways; large canopy openings would have been made, thus favouring recruitment of shade-intolerant species, and shade-tolerant ones (such as podocarps), as the preferred timber species, may have been disproportionately reduced in abundance.

Alternatively, the present lack of recruitment may be related to recent increased levels of herbivory. Species with high levels of nitrogen may be prone to herbivory because they are poorly defended.[9,10] Possibly the historical elimination or reduction of numbers of large carnivores, or even megaherbivores, may have led to a relative increase in small ungulates and thus a reduction in their preferred food species. Terbough[11] previously suggested a similar hypothesis aimed at seed-predation (about which we know very little in South African forests), rather than seedling herbivory. He suggested that loss of large carnivores in parts of Amazonia has led to an increase in mammals which eat large seeds. This in turn has led to a decline in plant species with large seeds.

Celtis africana and *Vepris lanceolata*, two typical shade-intolerants, have small berries. *Newtonia hildebrandtii*, easily the most important Sand Forest dominant and a species for which it is very hard to find small stems, is wind-dispersed. It is therefore unlikely that the poor recruitment of these species is due to the disruption of specialized dispersal mechanisms. If anything, a species like *Podocarpus falcatus*, which has larger berries that are dispersed by relatively large birds and/or bats (C. Geldenbuys pers. commun.), should be more prone to dispersal failure.

Finally, in many coastal forests we observed that tree-fall gaps were a tangled mass of spinescent species, lianas and dense stands of the herb *Isoglossa woodii*. These species appear to have taken over the 'recruitment space' of shade-intolerant canopy species. It is possible that large herbivores, like elephants, may have previously opened gaps and thus had a role in preventing rapid gap closure by these weedy non-canopy species. This, in turn, may have improved the probability of recruitment of shade-intolerant species.

We suggest there is a possibility of a change in relative dominants in some coastal South African forests. South Africa is not well endowed with forests.[6] Further work is therefore needed on the regeneration dynamics of our coastal forests to determine whether this succession is an important management issue or not. It may no longer be appropriate to assume that forests do not need active management if it is possible that important biotic interactions and disturbance regimes, which determine relative canopy dominance, are no longer functioning.

1. Everard D.A., Midgley J.J. and van Wyk G.A functional classification of Natal forests using size–class distributions and ordinations. (Submitted to *Aust. J. Bot.*)

2. Midgley J.J., Seydack A., Reynell D. and McKelly D. (1990). Fine-grain pattern of Southern Cape plateau forests. *J. Veg. Sci.* 1, 539–546.

3. Midgley J.J. (1992). Aspects of the dynamics of the high forest at Langebos (Alexandria Forest Type). *Jl S. Afr. For. Ass.* 161, 19–22.

4. Reich P.B., Uhl C., Walters M.B. and Ellsworth D.S. (1991). Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* 86, 16–24.

5. Reich P.B., Walters M.B. and Ellsworth D.S. (1992). Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecol. Monogr.* 62 (3), 365–392.

6. Cooper K.H. (1985). *The conservation status of indigenous forests in Transvaal, Natal and O.F.S., South Africa*. Wildlife Society of South Africa. Durban.

7. Lilly M.A. (1977). An assessment of the dendrochronological potential of indigenous tree species in South Africa. Occasional Paper No. 18. University of the Witwatersrand, Johannesburg.

8. Midgley J.J. and Gobetz P. (1993). The dynamics of the forest in Umtiza Nature Reserve. *Bothalia* 23 (1), 111–116.

9. Coley P.D., Bryant J.P. and Chapin F.S. (1985). Resource availability and plant antiherbivore defense. *Science* 230, 895–899.

10. Gulmon S.L. and Mooney H.A. (1986). Costs of defense and their effects on productivity. In *On the Economy of Plant Form and Function*, ed. T.J. Givnish, pp. 681–698. Cambridge Univ. Press, Cambridge.

11. Terbough J. (1988). The big things that run the world – a sequel to E.O. Wilson. *Conserv. Biol.* 2 (4), 402–403.

12. Acocks J.P.H. (1975). *Veld Types of South Africa*, 2nd edn. *Mem. bot. Surv. S. Afr.* 40, 1–127.

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