

DEMOGRAPHIC PATTERNS OF STINKWOOD (*Ocotea bullata*) IN THE FORESTS AT WEZA, KWAZULU-NATAL: DIVERGENT MODES OF REGENERATION

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Abstract

Across a gradient of three forests at Weza, KwaZulu Natal (Bangeni, Mpetsheni, Ngele) divergence of Stinkwood (*Ocotea bullata*) demographics, notably regarding regeneration, was noted within the context of a broader forest dynamics monitoring and research programme. The possible underlying reasons for detected population differences were investigated, with the particular objective of increasing our understanding of stinkwood regeneration ecology. Site differences were established and population performance of selected stinkwood cohorts (population structure, growth and survival patterns) compared between the three study forests. Underlying causal mechanisms for the divergent modes of regeneration were explored with reference to disturbance regime impacts, bark harvesting effects, site effects and responses to site constraints. The outcome of the study suggests that divergent modes of regeneration (continuous versus episodic regeneration) are driven by plant metabolic trade-off responses to site constraints. Enhancement of regeneration success through heterosis was furthermore implicated.

1. Introduction

A research project to study aspects of the dynamics of forest patches in the forests at Weza, KwaZulu-Natal (South Africa) was initiated in 1993. The three study forests Bangeni (121ha), Mpetsheni (705 ha) and Ngele (693 ha) belong to the Eastern Mistbelt Forests (Von Maltitz *et al.*, 2003). These forest can be subdivided into two main forest subtypes: *Podocarpus henkelii* / *Ocotea bullata* moist forest and mixed dry forests. The study sites are situated in the former and cover 10,7; 12,4 and 13,2 ha respectively.

The study was focused on the two co-dominating species *Podocarpus henkelii* and *Ocotea bullata*. On the study sites the presence and height of seedlings (S), as well as diameters of saplings (A: > 3m h – 10 cm DBH), poles (10 – 20 cm DBH), subcanopy trees (20 – 30 cm DBH) and canopy trees (> 30 cm DBH) were recorded at each measurement event (1993, 1995, 1999). The occurrence of subadult trees in gaps of small, medium and large-sized gaps was noted. Selected structural and chemical soil parameters representing the three study forests were established. More details regarding methods will be available in Seydack *et al.* (*in prep.*).

Initial investigation of the data revealed strikingly divergent diameter class structures of stinkwood (*Ocotea bullata*) between the three study forests; with a notable absence of regenerating cohorts at Ngele. This study was accordingly directed towards elucidation of the possible causal mechanisms underlying the divergent demographic patterns of stinkwood. Understanding stinkwood demography was considered of great importance for effective conservation and sustainable utilization of this species. Stinkwood can be considered as one of the most important indigenous tree species for utilization since both its timber (high quality furniture) and bark (medicinal purposes) are highly valued (Geldenhuys, 2004).

2. Objectives of study

Divergent population structures of stinkwood over the three study forests are depicted in figure 1. Clearly evident is the absence of seedlings and paucity of saplings and poles at Ngele suggesting the absence of successful sexual reproduction for over 100 years. This is strongly contrasted by the prominence of regenerating cohorts at Bangeni. Figure 1 furthermore suggests accelerated adult tree mortality at Ngele.

In an attempt to explain prevailing demographic patterns, we explored the following potentially explanatory hypotheses.

- I.) Disturbance regime: Is the rate of canopy disturbance and hence light availability insufficient for the regeneration of stinkwood at Ngele?
- II.) Bark harvesting effects: In contrast to the other two forests, bark harvesting impacted on adult stinkwood trees at Ngele. Any possible effect on stinkwood demography was explored.

- III.) Marginality of site conditions: Edapho-climatic features, notably moisture stress (*vide* Schulze, 1997) were contrasted between the three study forests and evaluated in relation to the southern and eastern Cape where the species occurs prominently and is absent respectively. The objective here was to establish whether the conditions at Ngele are marginal for stinkwood as a species.
- IV.) Resource constraints and metabolic responses: At a more complex level, resource conditions (nutrient availability and resource seasonality) were characterized for the three forests and divergent metabolic responses of stinkwood to these investigated.

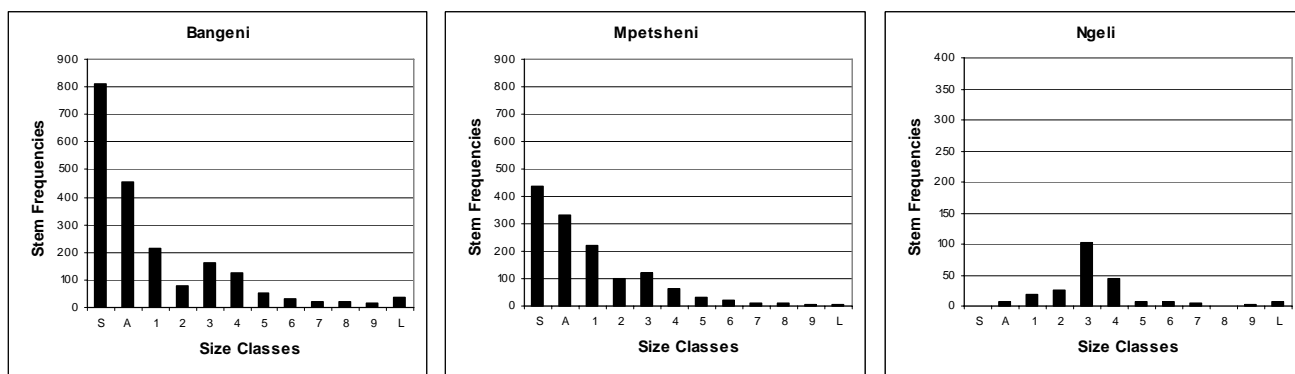


Figure 1. Population structures of stinkwood over the three study forests.

The investigation culminated in the question of whether the divergent patterns of regeneration were the result of direct impacts or merely representing divergent modes regeneration (continuous *in situ* regeneration versus episodic regeneration dynamics).

3. Results and discussion

3.1 Direct impacts potentially impacting on regeneration

3.1.1 Disturbance effects

Stinkwood is considered shade tolerant as a species (Van Daalen, 1993; Geldenhuys, 2004). Furthermore a higher incidence of gaps was recorded at Ngele (Table 1).

Table 1. Percentage Stinkwood stem frequencies in canopy gaps (n)

	Bangeni	Mpetsheni	Ngele	G
<i>Ocotea bullata</i>				
Saplings	3,2 (468)	17,0 (330)	-	45,75 ***
Seedlings	1,7 (534)	5,5 (421)	-	10,46 ***
<i>Podocarpus henkelii</i>				
Saplings	6,4 (78)	21,1 (156)	33,3 (427)	32,84 ***
Seedlings	3,5 (567)	24,1 (617)	24,6 (491)	140,20 ***

The forest with poor regeneration (Ngele: Figure 1) was found to have the highest incidence of gaps, whereas at Bangeni, the forest with a low occurrence of canopy gaps, regenerating cohorts were particularly well-represented. We accordingly conclude that insufficiency of disturbance (canopy gaps) cannot be implicated as factor resulting in the absence of regeneration at Ngele.

3.1.2 Bark harvesting effects

Bark harvesting impacts were recorded for about one-third of adult stinkwood trees in the study area at Ngele (Table 2). Of the affected trees 19% died during 1993 – 1999, whereas less than 2% of non-affected

Table 2. Incidence and effects of bark harvesting on Stinkwood canopy trees at Ngele (1993 – 1999)

	Alive	Died		%
No debarking impact	135	2	137	65,5
Various degrees of debarking impact	58	14	72	34,5
(G = 21.16, P<0,005)			209	100

trees were lost to mortality during the same period. These results suggest debarking-related accelerated adult mortality at Ngele (Figure 1). This is consistent with the findings of Geldenhuys (2004). However, since two-thirds of adult trees had been unaffected by bark harvesting, no link can be made to the absence of seedlings in the study area at Ngele.

3.1.3 Marginality of site conditions

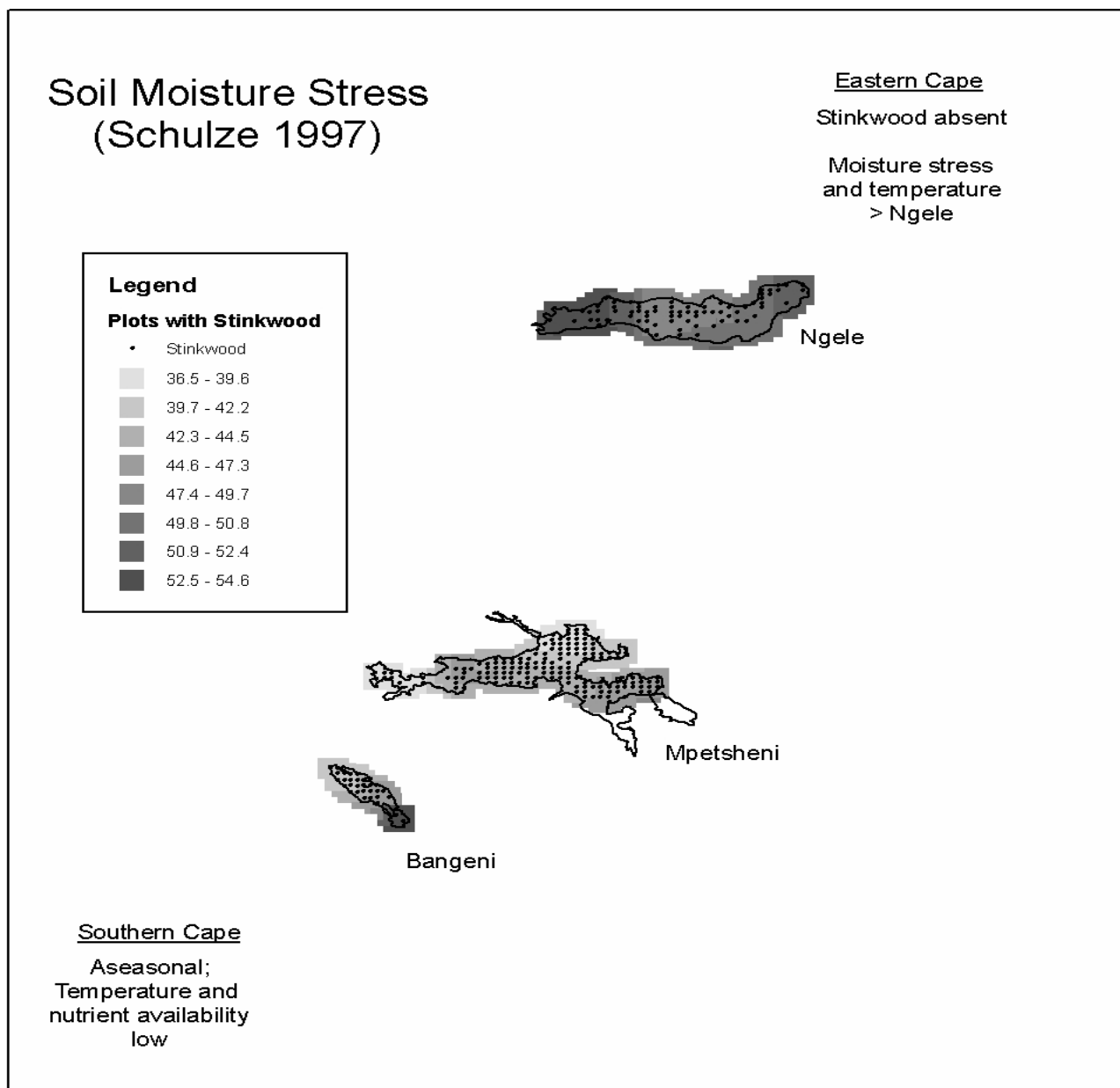


Figure 2. Moisture stress gradient (summer) over the study forests Bangeni, Mpetsheni and Ngele (KwaZulu-Natal); contrasted with conditions in southern Cape (stinkwood present) and eastern Cape forests (stinkwood absent).

A pronounced summer moisture stress gradient (Schulze, 1997) is evident across the study forests (Figure 2). Accordingly, moisture availability for plants is notably lower at Ngele. These results suggest that conditions of moisture availability are marginal for stinkwood at Ngele. The known preference of stinkwood for cool, moist sites is also reflected in the absence of the species in the drier forest types of the Weza forests.

The moisture stress index for Kologha forests (eastern Cape), where stinkwood is absent, is 58. This is only slightly higher than the maximum values for Ngele; further substantiating the potential marginality of moisture availability conditions at Ngele. However, the actual presence of seedlings/saplings is not necessarily sensitive to such moisture stress conditions as is indicated by the presence of regeneration in pine plantations adjacent to natural forests in the area (recorded by Geldenhuys, 2004). Moisture stress is expected to be higher in pine plantations than natural forests and moisture deficits are unlikely to explain the complete absence of regeneration within natural forests such as Ngele.

3.2 Resource constraints and metabolic trade-off responses

Since direct impacts possibly underlying the divergent regeneration modes could not be identified, interpretation of demographic patterns according to the G-S metabolic trade-off model was undertaken. According to this model G capacity denoted metabolic competence for maximized growth or peak productive performance, whereas S capacity referred to pronounced survival/persistence, i.e. stress resistance capacity. G and S capacities were postulated to be subject to a trade-off relationship: high G capacity involved lowered S capacity and *vice versa*. Accordingly, the G > S metabolic mode involved maximum capacity for the utilization of resource surplus conditions (high photosynthetic capacity, but at high respiratory costs), but low stress resistance. The S > G metabolic mode involved only intermediate to low photosynthetic capacity, but conferred greater stress resistance (high S capacity: respiratory efficiency). The model finally implies that the G > S metabolic mode is favoured under conditions of pronounced fluctuations in resource surplus levels, whereas the S > G metabolic mode is likely to be superior under constancy of resource deficit levels.

Nutrient availability levels and temporal fluctuations / predictability of resource levels for growth (mainly water and temperature) are thus of relevance in determining which metabolic mode is most appropriate under relevant prevailing conditions. Soil phosphorus values below stinkwood trees at Bangeni (3.96 ppm) were significantly higher than at Ngele (1.89 ppm; $n = 24$; $P < 0,05$). Soil P levels were significantly ($P < 0,05$) positively correlated with soil moisture status ($r = + 0,50$) and depth of the A horizon ($r = +0,44$). A negative correlation was found with pH (water); $r = -0,30$. Soil nitrogen levels were significantly lower at Ngele (2,57% $n = 49$, $P < 0,00001$) compared with those at Bangeni (4,22%) and Mpetsheni (3,95%). These data suggest slower rates of decomposition / mineralization at Bangeni and imply relatively higher nutrient availabilities at Ngele (Louw and Scholes, 2002).

A moisture deficit severity index (summer) was defined as the product of the Penman-Monteith evapotranspiration index (index of plant water requirements: Schulze, 1997) and the moisture stress index of Schulze (1997). The resulting values were 6388 versus 5324 and 5240 for Ngele as compared with Bangeni and Mpetsheni respectively. These results were interpreted to indicate accentuated seasonality at Ngele. Furthermore, lower precipitation is generally associated with greater variability thereof (Davidowitz, 2002), lowering predictability of moisture availability. Accentuated seasonality is also indicated by the higher incidence of *Celtis africana*, a prominent deciduous species, at Ngele (10,7 spha > 30 cm DBH; 2,6 spha at Bangeni; 3,9 spha at Mpetsheni). It is concluded that time span constrained / unpredictable phases of resource surpluses for growth (water, temperature, nutrients) are accentuated at Ngele.

Based on the above findings, resource conditions / constraints relating to the three study forests are characterized as follows:

- Temporally variable / unpredictable phases of resource surpluses: Ngele > Mpetsheni / Bangeni.
- Unconstrained nutrient availability: Ngele > Mpetsheni > Bangeni.

According to the G – S metabolic trade-off model, the conditions at Ngele favour the G > S metabolic mode; i.e. maximized metabolic performance under time-span restricted resource surplus conditions. The associated capacity for high photosynthetic peak performance involves costs of relatively high respiration levels. Following from the G to S capacity trade-off relationship, the G > S metabolic mode is associated with a reduced S capacity; i.e. low stress tolerance, particularly of juveniles under resource deficit conditions (i.e. low light availability). Such constraints are postulated to typically manifest in ephemeral regeneration, i.e. low juvenile / adult ratios and / or discontinuous presence of regeneration; as is evident at Ngele.

3.3 Heterosis-enhanced episodic recruitment?

The extant population of adult stinkwood trees represents evidence that successful recruitment can and has taken place at Ngele under particular circumstances. The enhanced metabolic efficiency associated with heterosis constitutes a potential mechanism which may neutralize G versus S metabolic trade-off constraints. Heterosis arises through the combination of genetically divergent / inbred strains; i.e. restoration of heterozygosity levels through gene exchange between populations (Konarev, 1976).

Heterosis commonly manifests in enhanced metabolic efficiency (increased photosynthesis / respiration ratio) over parental forms, but is displayed mainly by F1 progeny (Konarev, 1976). Progeny of subsequent generations often experience inverse heterosis.

Heterosis effects, resulting in relaxed G versus S trade-off constraints, are postulated to have been involved in the facilitation of recruitment / invasion of the extant adult stinkwood population at Ngele. Substantially higher growth rates at Ngele, in spite of site marginality, may possibly be the result of heterosis ($F = 3,23$, $df = 2$, $n = 436$, $P = 0,0406$; Figure 3).

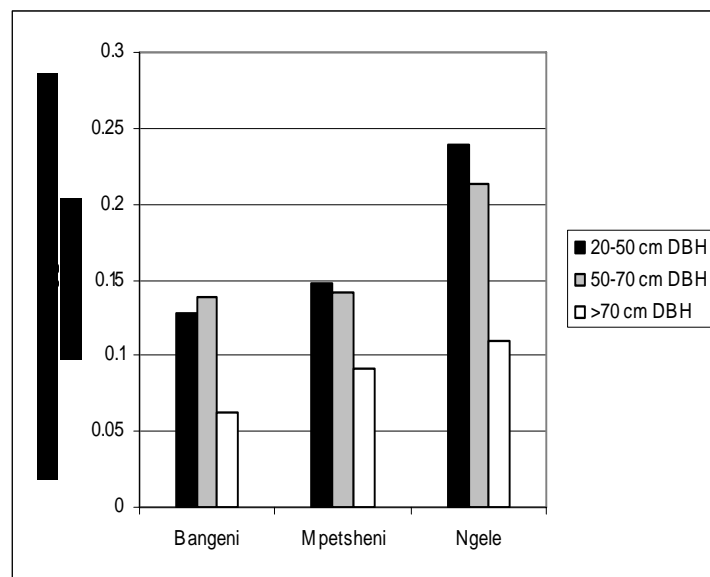


Figure 3. Stinkwood canopy tree increment (cm/annum) on study sites in Bangeni, Mpetsheni and Ngele forests (KwaZulu-Natal); differentiated according to three diameter classes.

Furthermore, the prolonged absence of sexual progeny could be the result of the poor performance of progeny arising from mating between heterotic adults (inverse heterosis). Accordingly, the availability of heterotic progeny for successful reproduction at Ngele is expected to be an episodic / rare event.

The proposed explanatory model for the divergent modes of regeneration across the study forests can now be summarized as follows:

- I.) Prevalence of the $G > S$ metabolic mode at Ngele:
 - Temporally variable/unpredictable and time-span constrained resource surplus conditions: Ngele > Mpetsheni/Bangeni
 - Unconstrained nutrient availabilities: Ngele/Mpetsheni > Bangeni
- II.) G mode regeneration is subject to low S capacity (stress resistance of juveniles), particularly under resource constraints (shade)
- III.) Heterosis is disproportionately advantageous for enhanced metabolic competence ($P/R \uparrow$); conferring both G and S capacity (G versus S trade-off relaxation)
- IV.) Regeneration at Ngele occurs via heterosis-enhanced episodic recruitment or invasion pulses. In contrast, continuous in situ regeneration occurs at Bangeni and Mpetsheni (Figure 1).

4. Conclusions

Direct causative factors possibly resulting in stinkwood regeneration failure at Ngele were not found. Rather, the interpretation of results according to the explanatory model presented suggests that divergent modes of regeneration are involved. According to this model, continuous on-site stinkwood regeneration occurs at Bangeni and Mpetsheni, whereas episodic heterosis-enhanced regeneration events appear to ensure persistence of the species when subject to the constraints of the $G > S$ metabolic mode at Ngele. Verification of the applicability of both the $G - S$ metabolic trade-off model and heterosis through further research is required and ongoing.

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