THE MONOCARPIC HERB, *ISOGLOSSA WOODII*, INFLUENCES SUBTROPICAL FOREST TREE DYNAMICS AND DIVERSITY

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Abstract

Herbaceous plants belonging to the family Acanthaceae are widely distributed in coastal belt forests throughout eastern and southern Africa. They usually grow in dense, monospecific stands that dominate the forest understorey. In addition, many species are monocarpic and have highly synchronized reproduction events followed by mass diebacks. We hypothesize that recruitment opportunities for coastal dune forest trees are limited by the presence of *Isoglossa woodii*, a monocarpic Acanthaceae that flowers every 5-10 years. This species is likely to compete with tree seedlings and prevent the entry of new recruits into the population. Furthermore, *I. woodii* may act as an ecological filter that differentially affects the growth and survival of tree seedling species. *Isoglossa woodii* effects on tree seedling growth were assessed over six years in plots where the *I. woodii* understorey was undisturbed or removed by cutting. Fenced exclosures were also used to assess the effect of vertebrate herbivory on seedlings. *I. woodii* stem density declined as a consequence of self-thinning over the study period while the height of the herb increased. Height of *I. woodii* was lower in unfenced plots, indicating that vertebrate herbivory controls its growth. We found fewer tree seedlings in plots with an intact *I. woodii* understorey and fewer seedling in unfenced areas. The presence of *I. woodii* also affected tree species diversity and composition, lending support to the argument that this herb might selectively filter tree seedlings and therefore influence coastal dune forest regeneration and structure.

1. Introduction

Understorey plant species can have a profound impact on regeneration dynamics in forests (Veblen, 1982; Denslow *et al*., 1991; Nilsen *et al*., 2001; González *et al*. 2002). In South Africa, the understorey of subtropical coastal dune forest is dominated by the native herb *Isoglossa woodii* (Acanthaceae), which forms dense stands that often exceed 2 m in height. An interesting feature of *I. woodii* is that the species is monocarpic and reproduces synchronously every 5-10 years before dying back (Van Steenis, 1978). This results in significant temporal variability in the physical structure of the forest understorey.

Given the dominance of *I. woodii* in the understorey, this species has the potential to influence other plants growing on the forest floor. It has been proposed that tree recruitment might be limited to the dieback period when seedlings are released from competition with *I. woodii* (Midgley, 2000). It is also possible that *I. woodii* acts as an ecological filter that only allows tree species with certain life-history traits (e.g., shade tolerant seedlings) to grow underneath it (George and Bazzaz, 2003). In this manner, the presence of *I. woodii* in the coastal dune forest understorey may limit tree species diversity in the long term.

We hypothesize that *I. woodii* is a selective filter that differentially influences the growth and survival of tree species at the seedling stage, thereby significantly influencing tree species diversity and forest dynamics. In this study we test the predictions that: (1) *I. woodii* reduces the growth and survival of tree seedlings; (2) *I. woodii* lowers seedling density overall; and (3) *I. woodii* causes the seedling pool to have different species composition and size structure compared with areas that are not covered in *I. woodii*.

2. Methods

In order to test the effects of *I. woodii* on coastal dune forests, twenty experimental plots were established at Cape Vidal, in the Greater St. Lucia Wetland Park, KwaZulu-Natal. Each plot measures 10 m × 10 m and is divided into four 5 m × 5 m sub-plots. Two manipulations were applied to these experimental plots: (1) fenced exclosures to evaluate the effect that herbivores (e.g., kudu, bushbuck, red duiker) may have on both seedling and *I. woodii* recruitment and growth and (2) removal of the herbaceous cover of *I. woodii*. A different treatment is applied to each sub-plot following a two-way factorial design (Table 1). All plots were sited under the canopy and in areas where *I. woodii* previously grew. In each sub-plot, five 1m × 1m quadrats have been used to sample seedling establishment. In each plot, all tree seedlings have been identified to species and their height recorded annually since the last *I. woodii* dieback in 2000. The height and stem density of *I. woodii* have also been recorded annually since the last dieback in 2000.

Table 1. Two-way factorial design for experimental plots

		Isoglossa woodii	
		Present	**Absent**
Herbivores	**Unfenced**	No manipulation (CU)	*I. woodii* cut back (CC)
	Fenced	*I. woodii* left intact; Herbivores excluded (EU)	*I. woodii* cut back; Herbivores excluded (EC)

All analyses of woody seedling abundance and species richness were conducted using repeated measures ANOVA and based on a split-plot experimental design. Analyses were conducted in SPSS 13.

3. Results

There is an obvious effect of herbivory on *I. woodii* height; *I. woodii* grows taller in plots that are fenced to exclude herbivores (Figure 1). In all plots, the height of *I. woodii* has increased since the first year of monitoring, but the height seems to have reached a plateau at an average maximum height of around 2 m (Figure 1). *I. woodii* density has decreased yearly since monitoring began, indicating that the species is self-thinning and that density decreases as height increases (Figure 2).

Seedling species density has increased in all plots since monitoring began, but the degree of response varied among treatments (Figure 3). Fenced areas with *I. woodii* removed (the EC treatment) have the highest number of seedling species ($F_{1,72}$ = 21.6, P<0.0001), followed by unfenced areas with *I. woodii* removed (the CC treatment) ($F_{1,72}$ = 10.3, P<0.002). Seedling species density was lowest in treatments where *I. woodii* was present, indicating that *I. woodii* cover significantly restricts the number of species that can survive underneath it ($F_{1,54}$ = 96.7, P<0.0001).

Seedling density also increased in all plots since monitoring began (Figure 4). There are more seedlings in fenced areas with *I. woodii* removed (the EC treatment) than in any other treatment and the fewest number of seedlings overall in the unfenced areas with *I. woodii* present (the CU treatment).

To explore the possibility that *I. woodii* acts as an ecological filter of the seedling community, we used a multi-response permutation procedure (MRPP). This analysis tested for differences in the seedling community composition. We found that treatments had significantly different species composition, particularly when comparing the fenced, *I. woodii* removed treatment with others (Table 2). This indicates that a different seedling community develops under ideal conditions when there is no herbivory and *I. woodii* cover. The implication of this finding is that there is the potential for a more diverse seedling community to develop in the forest but factors such as herbivory and *I. woodii* limit regeneration.

Table 2. T-statistic values (with significance values based on a Bonferroni-adjusted P) from an MRPP analysis showing differences in seedling community composition between treatments

	CU	**EC**	**EU**
CC	-2.5 (n.s.)	-3.2 (n.s.)	-3.4 (n.s.)
CU		-9.3 (< 0.001)	-0.4 (n.s.)
EC			-6.0 (< 0.001)

We also carried out an indicator species analysis on the 55 seedling species in our experimental plots and found that 12 species were significantly more likely to occur in fenced plots where *I. woodii* was removed. It is difficult to separate the effects of *I. woodii* and herbivory but we did find that where only *I. woodii* was removed only two species were more likely to occur. Given this finding, it is clear that where herbivory rates are low, *I. woodii* has the potential to significantly affect the seedling community composition.

4. Discussion

The findings of this study help us to better understand the regeneration dynamics of coastal dune forests. We found strong evidence that *I. woodii* inhibits the recruitment of trees, which supports results from other studies on dominant understorey species (Veblen, 1982; Monk *et al.*, 1985; Clinton & Boring, 1994; Baker & Van Lear, 1998; Nilsen *et al.*, 2001; González *et al*., 2002; George & Bazzaz, 2003). Seedling density was reduced in areas with *I. woodii* cover, as was seedling species richness, suggesting a species-specific effect of the herb on tree regeneration at the seedling stage. Indeed, some species were unable to grow in conditions created by *I. woodii*, yielding differences in seedling community composition between areas with and without *I. woodii* cover. The clear separation we found in seedling communities between plots with and without *I. woodii* cover is commensurate with the ecological filter model proposed by George and Bazzaz (2003) in their study on the effect of ferns in northern hardwood forests.

By selectively filtering the tree seedling community *I. woodii* might have an important long-term influence on the structure of the forest. Other Acanthaceous herbs, such as *Acanthus pubescens* in Kibale forest in Uganda, are also known to limit forest regeneration (Chapman *et al*., 1999; Chapman & Chapman, 2004; Paul *et al*., 2004). However, it is possible that during periods of *I. woodii* dieback, canopy tree species establish in the understorey and grow out into the canopy. Thus, while *I. woodii* cover clearly inhibits seedling establishment and diversity in the short-term, dieback of *I. woodii* may maintain tree species diversity over the long term in these forests.

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Addendum

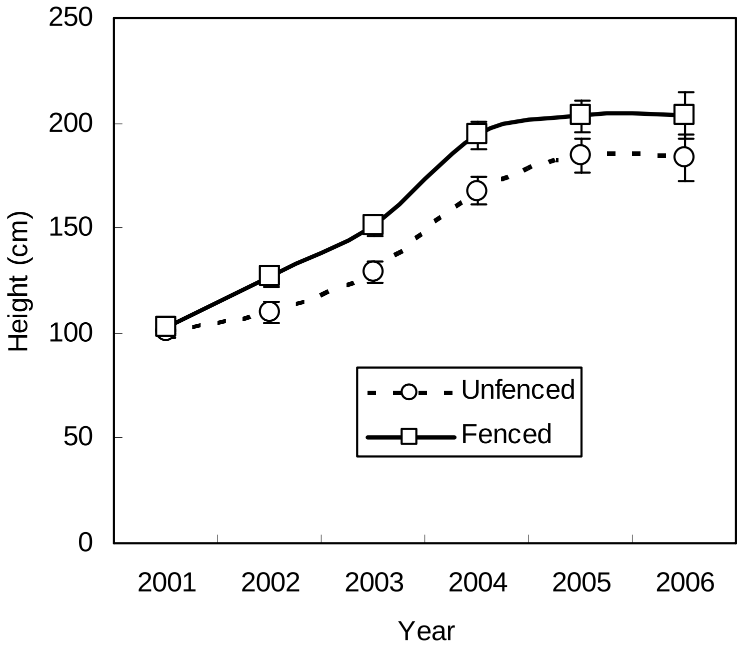

Figure 1. Comparison of the heights of *Isoglossa woodii* between fenced (herbivores excluded) and unfenced treatment levels.

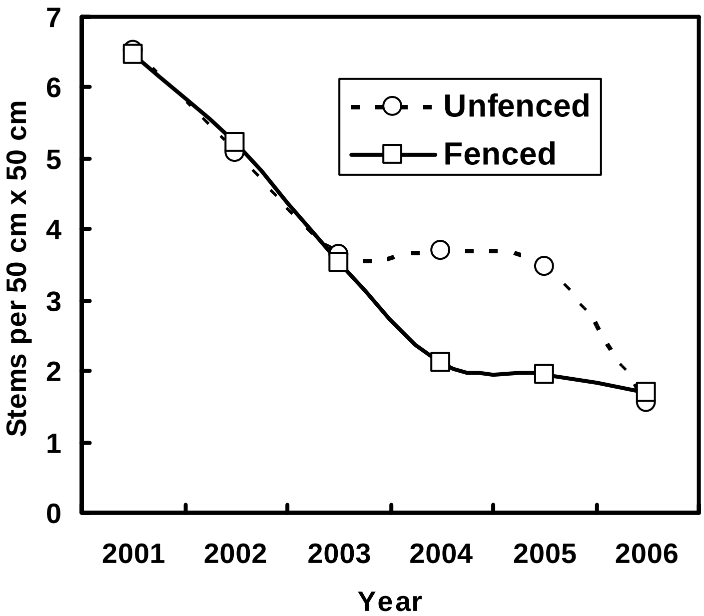

Figure 2. Density of *Isoglossa woodii* over time.

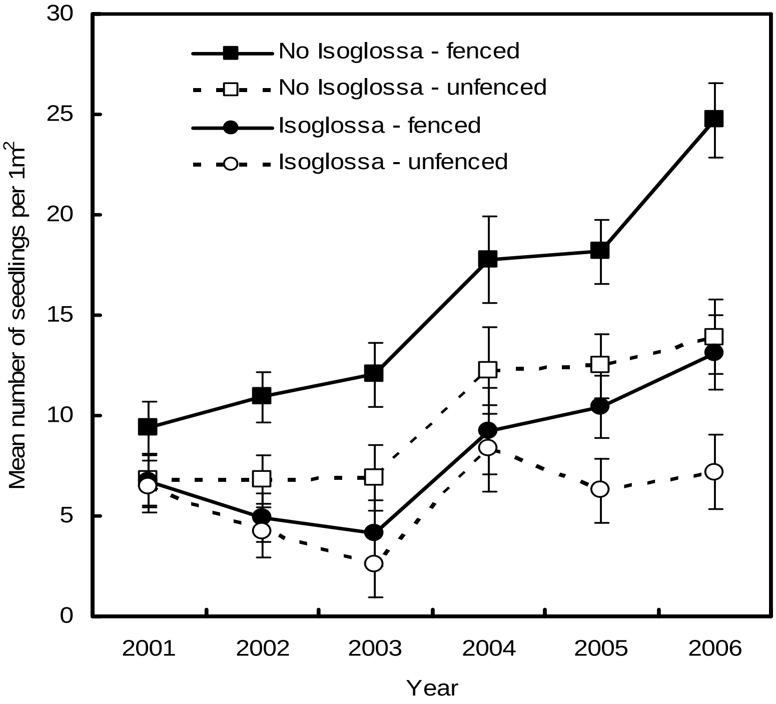

Figure 3. **Comparison of the number of woody seedlings among experimental treatments. Note that woody seedlings are at their most abundant when *I. woodii* and herbivores are excluded, but that seedling numbers are similar between treatments where either *I. woodii* or herbivores are only excluded. The effect of herbivory or the herb appear to be similar on woody seedling establishment.**

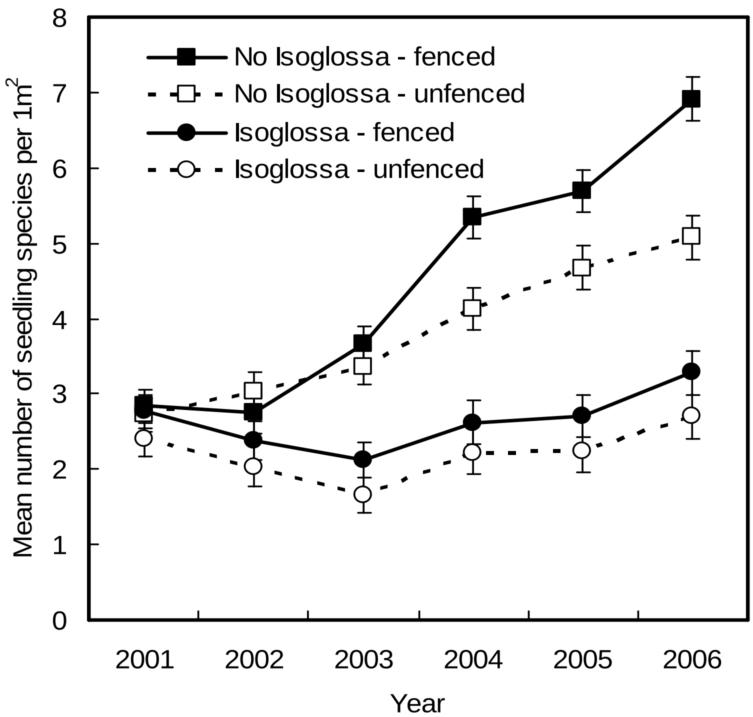

Figure 4. **Comparison of the number of woody species at the seedling stage among experimental treatments. In contrast to seedling abundance trends, the number of species appears to be most affected by the presence of the herb and less so by herbivory.**