South African Journal of Botany 104 (2016) 91–97

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Light availability drives tree seedling success in a subtropical coastal dune forest in South Africa

Z. Tsvuura [a,*], M.J. Lawes [a,b]

[a] Forest Biodiversity Research Unit, School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa
[b] Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, NT 0909, Australia

ARTICLE INFO

Article history:
Received 22 June 2015
Received in revised form 16 November 2015
Accepted 18 November 2015
Available online 29 January 2016

Edited by R M Cowling

Keywords:
Ecological filter
Isoglossa woodii
Phenotypic clustering
Shade tolerance
Specific leaf area

ABSTRACT

In subtropical coastal dune forests of South Africa, the microenvironment of tree seedlings is largely influenced by a pervasive understorey woody herb, *Isoglossa woodii*. We examined whether the additional shading by *I. woodii* explains the competitive response of tree seedlings from these forests. Seedlings of four common mid- to late-successional tree species (*Diospyros natalensis*, *Euclea racemosa*, *Sideroxylon inerme* and *Apodytes dimidiata*) were grown at three densities of *I. woodii* in a common garden experiment under greenhouse conditions. The seedlings were grown at 1.6% and 13.5% of full sunlight and supplied with 1% and 10% nitrogen in half-strength Hoagland's nutrient solution. Total biomass and biomass allocation parameters were used to measure the competitive response of the seedlings. Seedlings attained maximum biomass at high light and high nutrient levels and showed species- and light-specific responses to biomass of *I. woodii* neighbours. Seedlings' allocation to roots increased with increasing light levels but decreased at higher nutrient levels. The leaf mass fraction (LMF) response to light and nutrient levels was opposite to that shown by root allocation. Specific leaf area (SLA) and leaf area ratio (LAR) decreased with increasing light conditions but were not responsive to manipulation of nutrients. The presence of *I. woodii* neighbours reduced LMF whilst the responses of SLA to neighbours depended on the light level and species. Leaf trait responses to manipulation of light conditions, *I. woodii* neighbour density and soil nutrient concentration are complex but overall demonstrate an overwhelming role of light in influencing seedling establishment in coastal dune forests. The competitive response of these seedlings to low irradiance reiterates the notion of phenotypic clustering at the seedling stage amongst shade tolerant tree species, which promotes seedling persistence and gradual transition into the tree layer. Our results highlight the role of additional understorey shading by the herb stratum in influencing tree recruitment dynamics and ultimately tree community structure in many of Africa's tropical lowland forests.

1. Introduction

The physical environment for tree recruitment in closed canopy forests may be modified by ubiquitous understorey plants (George and Bazzaz, 1999). In tropical and temperate forest communities, understorey plants have a profound effect on tree recruitment (Nilsen et al., 2001; George and Bazzaz, 2003; Griffiths et al., 2007; Tsvuura et al., 2010). Their influence is often negative, and may include transfer of herbivorous insects and pathogens from overstorey plants to seedlings, and size asymmetric competition for resources between tree seedlings and the understorey (Denslow et al., 1991; Horsley, 1993; Abe et al., 2001; Nilsen et al., 2001). However, understorey plants may also have positive effects on tree regeneration, for example, through promoting hydraulic lift (Dawson, 1996; Brooks et al., 2002). These influences may determine the density, species composition and size structure of tree seedlings.

Tree seedling recruitment in subtropical coastal dune forests of South Africa is influenced by the pervasive understorey herb, *Isoglossa woodii* C.B. Clarke (Acanthaceae). The species reproduces and regenerates synchronously within dense (4–10 stems m^{-2}) and relatively tall (± 2 m) monospecific stands in the understorey that can extend for thousands of hectares (Griffiths et al., 2010; Tsvuura et al., 2011). During its vegetative stages, the herb filters and reduces the light reaching the forest floor to <1% of photosynthetically active radiation (PAR). In general, low levels of PAR reach the seedling stratum in forest ecosystems (Chazdon et al., 1996; George and Bazzaz, 2003). The low levels of PAR in these dune forests may be limiting for tree seedling establishment (Griffiths et al., 2007; Tsvuura et al., 2007, 2010, 2012). Moreover, herbaceous understorey vegetation can compete with or modify nutrients and moisture for woody seedlings whose roots are initially in the superficial layers of the soil alongside those of the herb layer. Hence,

Abbreviations: SLA, Specific leaf area; LAR, Leaf area ratio; LMF, Leaf mass fraction; RMF, Root mass fraction; SMF, Stem mass fraction.

* Corresponding author at: Life Sciences Division, Multidisciplinary Research Centre, University of Namibia, Private Bag 13301, 340 Mandume Ndemufayo Avenue, Pionerspark, Windhoek, Namibia.

E-mail addresses: tsvuuraz@yahoo.co.uk (Z. Tsvuura), michael.lawes@cdu.edu.au (M.J. Lawes).

http://dx.doi.org/10.1016/j.sajb.2015.11.009
0254-6299/

understorey vegetation may suppress seedling establishment in closed canopy forests (Denslow et al., 1991).

A suppressive understorey comprising species that are different to the overstorey is common in African and some Asian forests (Richards, 1963; Chapman et al., 1999; Carine and Scotland, 2000; Fashing and Gathua, 2004; Meyer and Lavergne, 2004). In particular, *I. woodii* and other Acanthaceous herbs are abundant in the understorey of African forests (Struhsaker, 1997; Fashing and Gathua, 2004; Paul et al., 2004; Griffiths et al., 2007). Understanding the effects of a dominant herbaceous understorey on tree seedling establishment and on the composition of the tree species community and its dynamics is essential for understanding ecological succession in African forests (Struhsaker, 1997; Paul et al., 2004; Lawes and Chapman, 2006; Griffiths et al., 2007; Tsvuura et al., 2010, 2011).

The *I. woodii* understorey may be a selective ecological filter that shapes the abundance, structure, species composition, and species interactions of trees that constitute the overcanopy layer (Chapman et al., 1999; Griffiths et al., 2007; Tsvuura et al., 2010, 2012). In particular, *I. woodii* may create a light regime on the forest floor that favours species whose seedlings are tolerant of deep shade. An extension of this view predicts phenotypic clustering, whereby the dominance of *I. woodii* and its relatively long maturation time has selected against light demanding tree species, which have therefore been progressively lost from the community (Tsvuura et al., 2010). Here, we investigate whether morphological traits of selected representative tree species from coastal dune forests are consistent with predictions of ecological filtering and phenotypic clustering of shade tolerance in the tree community (Griffiths et al., 2007; Tsvuura et al., 2010).

This paper experimentally examines patterns of phenotypic plasticity in morphological traits of representative dune forest tree species under different light and nutrient conditions that reflect the range found in these forests. We emphasise the potential species-sorting role of the suppressive herb *I. woodii* particularly at the seedling stage. A previous paper (Tsvuura et al., 2012) compared relative growth rate and biomass-based performance of tree seedlings grown with *I woodii*, using the competition index of Armas et al. (2004). We complement that earlier study by presenting analyses of interaction terms (viz. competition × resource) for each biomass allocation parameter and morphological traits of seedlings of the same tree species, and relate these parameters to survival and persistence in the understorey. This approach allows us to expand on the findings of our earlier (Tsvuura et al., 2012) paper. We examine the following questions: (1) to what extent is the competitive response of coastal dune forest tree seedlings explained by their biomass allocation patterns and morphological traits; and (2) what is the influence of *I. woodii* neighbours on tree seedling responses to light and nutrient manipulation?

We hypothesise that *I. woodii* competes with tree seedlings by preempting nutrient and light resources, which results in species-sorting patterns that reflect adaptation (shade tolerance) and plasticity of response to resource availability. We predict that: (1) at low light levels, tree seedlings allocate more biomass to capturing light (Aerts, 1999; Poorter, 1999; Poorter and Nagel, 2000), represented by high leaf mass fraction and high SLA; (2) at high light levels and low nutrients, leaf mass fraction and SLA will decrease as biomass is allocated belowground; (3) leaf mass fraction will decrease with density of neighbouring *I. woodii* plants i.e. increasing competition for belowground resources; and (4) SLA will increase with neighbour density in response to lower light levels.

2. Methods

2.1. Study site and species

The study plants were sourced from coastal dune forest at Cape Vidal (28°16′S, 32°29′E) in the iSimangaliso Wetland Park in KwaZulu-Natal (KZN) Province, South Africa. Cape Vidal has a subtropical climate with mean annual precipitation of approximately 1200 mm and mean annual temperature of 21 °C (Schulze, 1997). The soils are deep sands of low fertility (Boyes et al., 2010). The forest is part of the Indian Ocean Coastal Belt forest, which has a subtropical component in eastern South Africa and southern Mozambique, and a tropical component that extends into southern Somalia (Tinley, 1985; Mucina and Rutherford, 2006).

I. woodii (Acanthaceae) is a broad-leaved, semi-woody herb that dominates the understories of coastal dune forests of eastern southern Africa. The species is a clonal synchronous monocarp (Griffiths et al., 2010) that produces flowers and fruits at 4–10 year intervals and regenerates from seed within a year of reproduction (Van Steenis, 1978; Tsvuura, 2010). Four tree species from Cape Vidal were selected for growing trials with *I. woodii*, to investigate the effects of the herb on forest regeneration, using contrasting light and nutrient treatments in a common garden experiment under greenhouse conditions. The four tree species are relatively abundant with >20 ind. ha^{-1} (Nzunda et al., 2007). *Diospyros natalensis* (Harv.) Brenan and *Sideroxylon inerme* L. are late-succession species, the former mainly a reseeder and the latter mainly a resprouter, with contrasting seedling densities in the forest (Appendix 1; Nzunda et al., 2007). *Euclea racemosa* Murray is a mid- to late-succession mature phase subcanopy resprouter whilst *Apodytes dimidiata* E. Mey ex Arn. is a non-resprouting mid-successional species (Appendix 1; Tsvuura et al., 2012). All four tree species are evergreen. As these species belong to different genera, they will be referred to using their genus names.

2.2. Experimental design

To determine the density effects of *I. woodii* on tree seedling leaf traits and growth, seedlings of *Diospyros*, *Euclea*, *Sideroxylon* and *Apodytes* were grown with seedlings of *I. woodii* in 4 L pots (185 × 244 × 206 mm: bottom diameter × top diameter × height) in a greenhouse (mean daytime temperature of 24 °C from May to August, and 27 °C from October to April) at the University of KwaZulu-Natal, Pietermaritzburg. The pots had perforated bases and contained sterilised sand collected from the field site. Sand was sterilised to prevent the germination of any seeds collected with the soil, which would confound our experiment.

We used a factorial design with nutrients, light and *I. woodii* density as main factors. Half-strength Hoagland's nutrient solution (Hewitt, 1966) containing either 1% or 10% nitrogen was used as the nutrient source and 100 ml (increased to 200 ml after 10 months) were applied every third day. The lower level of N was based on soil samples from the field. We used half-strength nutrient solution because of the low native fertility of the soil (Boyes et al., 2010). The plants were provided with additional water at weekly intervals. The light treatment was imposed by manipulating sunlight transmission in the greenhouse to achieve specified levels of photosynthetically-active radiation (PAR). The "shade" treatment (1.6% PAR, 15.4 ± 4.0 μmol m^{-2} s^{-1} at 1200 h on a sunny day) was located inside a shade structure made from commercially available 80% shade cloth, whilst the "sun" treatment (13.5% PAR, 160.3 ± 13.0 μmol m^{-2} s^{-1}) was positioned outside, but adjacent to, the shade structure in the greenhouse. These light levels are consistent with the conditions beneath the understorey (ca. 1%) and above it (8%), respectively (Griffiths et al., 2007). The lower light level (15.4 μmol m^{-2} s^{-1}) is one order of magnitude greater than the light compensation point of many species from these forests (Tsvuura et al., 2010), and may drive positive photosynthesis as expected of tree seedlings growing beneath *I. woodii* thickets and gaps (Griffiths et al., 2007). Both *I. woodii* habitats occur beneath the tree canopy. For each tree species, a single seedling was grown with zero, one or three *I. woodii* seedlings as neighbours in the same pot in an additive design (Goldberg and Scheiner, 2001). The densities of *I. woodii* used were inferred from those observed in the field at early (1–2 years old) and late (4–7 years) vegetative stages, which range from ca. 30 stems to 10 stems per m^2, respectively (Tsvuura et al., 2010). Our replicated factorial design required 192