Perspectives in Plant Ecology, Evolution and Systematics 16 (2014) 11–20

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

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

Research article

Herbivory effects on saplings are influenced by nutrients and grass competition in a humid South African savanna

Snehalatha Vadigi, David Ward*

School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, Pietermaritzburg 3209, South Africa

ARTICLE INFO

Article history:
Received 26 June 2013
Received in revised form 28 October 2013
Accepted 29 October 2013
Available online 4 November 2013

Keywords:
Acacia
Browsing
Grazing
Mesic savanna
Tree sapling biomass
Woody plant encroachment

ABSTRACT

Woody plant encroachment is a common consequence of disturbance in savannas. Grazers and browsers interfere with sapling establishment dynamics by direct consumption of plant tissue, changing soil nutrient status (through fertilization and trampling) and grass competition. Studies evaluating the effects of herbivory on sapling establishment have mostly been extrapolated from single species. In a controlled field experiment, we studied the effects of clipping (simulating grazing and browsing), nutrients, grass competition, and their interactive effects on sapling survival and growth of four dominant humid and four dominant mesic savanna species. We conducted this experiment in a humid South African savanna. We found no effects on sapling survival by the treatments provided. However, clipped saplings of all species increased their investment in relative growth rate of stem length (RGR_L). Clipping had a greater negative impact on relative growth rate of more humid than mesic species in terms of stem diameter (RGR_D), total dry biomass and proportion of leaf biomass. Nutrients had a positive effect on the RGR_L and sapling biomass of three mesic species. Positive effects of nutrients on RGR_L of one humid and two mesic species were observed in their clipped saplings only. Grass competition had a strong negative impact on all growth parameters measured. Clipped saplings of one humid and two mesic species had lower RGR_L with grass competition whereas intact saplings showed no significant response. After clipping, humid savanna species were more vulnerable to grass competition than mesic species, with reduced ability to use nutrients. In conclusion, herbivory increases sapling vulnerability to grass competition, with humid species being more susceptible than mesic species, indicating that woody-plant control strategies are more likely to be effective in humid savannas.

Introduction

Tree sapling establishment in savannas is rare in the presence of fire, herbivory and grass competition (Ward, 2005; Lehmann et al., 2009), yet woody plant encroachment has become a global phenomenon. Reconciling this apparent paradox has been a central theme of savanna research (Ward, 2005; Wiegand et al., 2006; Bond, 2008), and several possible causes have been proposed for the spread of woody plants in savannas. These include the removal of grasses (and therefore fuel loads for fires) by intense grazing (Scholes and Archer, 1997; Briggs et al., 2005), and global climate change effects such as increased photosynthetic efficiency under higher carbon dioxide levels of C_3 trees relative to the C_4 grasses that predominate in tropical and subtropical savannas (Bond and Midgley, 2000; Ward, 2010). Here we investigate how herbivory affects the sapling survival and growth of eight dominant African species from mesic and humid savannas through defoliation, nutrient addition and grass competition.

Large mammalian herbivores play a role in altering the dynamics of nutrients and grasses on trees. Apart from incurring obvious negative effects, herbivores can have a direct positive effect on savanna tree growth. For example, browsers may stimulate shoot re-growth in fertile soils (Du Toit et al., 1990) and grazers help sapling establishment by removing grass competition (Roques et al., 2001). Large herbivores also indirectly affect savanna vegetation structure by enriching local soil nutrient levels, through dung and urine deposits (Van Der Waal et al., 2011). Increase in nutrients promotes tree growth, but heavy nutrient utilization by grasses might enhance competitive stress on woody saplings (Van Der Waal et al., 2009). Grass competition is one of the major factors restricting tree recruitment, particularly when the rainfall is high (Goheen et al., 2010; Grellier et al., 2012). However, grasses may also exert potential positive effects on tree establishment by protecting the saplings from mammalian browsers (Seymour, 2008). Hence, by removing grasses, grazers may facilitate browsing of woody saplings and create more negative effects than the benefit achieved by removing

* Corresponding author. Tel.: +27 33 2606018; fax: +27 33 2605105.
E-mail addresses: ward@ukzn.ac.za, davidmercerward@gmail.com (D. Ward).

1433-8319/$ – see front matter
http://dx.doi.org/10.1016/j.ppees.2013.10.002

grass competition. Therefore, the interplay between grazers and browsers, through their mediation into soil nutrients and grass competition, significantly determine success of trees in savannas.

Many studies evaluating herbivory effects on the role of sapling establishment in woody plant encroachment have been based on single species (Kraaij and Ward, 2006; Riginos and Young, 2007; Scogings and Mopipi, 2008; Goheen et al., 2010). Understanding sapling establishment dynamics of multiple species with respect to herbivory can help predict changes in vegetation at an ecosystem level. Success of saplings is mainly affected by their ability to resist herbivory. This is often achieved by growth allocation to stems (Clarke et al., 2013), resulting in fast growth rates in height (Palo et al., 1993) and diameter (Gignoux et al., 1997).

We conducted a field experiment to evaluate the effects of simulated grazing and browsing (by clipping both grass and tree saplings), nutrient availability and grass competition on sapling survival and growth of eight dominant indigenous savanna tree species in a humid South African savanna. In order to test whether savanna tree species from different climate types have a similar or different growth patterns, we selected four humid savanna species (>1000 mm mean annual precipitation (MAP)) i.e. *Acacia karroo* (Hayne) (a subtropical coastal variety from Richards Bay (Ward, 2011)), *Acacia sieberiana* (Burtt Davy), *Schotia brachypetala* (Sond.) and *Strychnos spinosa* (Lam.) and four species from mesic savannas (approx. 750 mm MAP), i.e. *Acacia nigrescens* (Oliv.), *Acacia tortilis* (Hayne), *Combretum apiculatum* (Sond.) and *Colophospermum mopane* (J. Kirk ex J. Léonard). Tree species were selected based on dominance in their respective climate types. The most widespread grass species in South Africa, *Eragrostis curvula* (Schrad.) Nees was used to study the effects of grass competition in relation to herbivory on the tree sapling growth. We performed our study under irrigated conditions to control for variation in rainfall which may directly interfere with our study by affecting sapling survival and growth. Water, amounting to the long-term mean annual rainfall (1250 mm) of the study area, was supplied to plants at regular time intervals over the 6 month study period. Based on the individual factor and interactive effects on sapling survival and growth, we predicted that:

1. Tree saplings will resprout and grow fast after clipping. Very young savanna tree seedlings have the ability to resprout and invest root reserves rapidly in growth after herbivory (Bergström, 1992). Herbivore impact on plants is greatest on nutrient-rich soils as they prefer feeding on plants with high nutrient content (Levick and Rogers, 2008). Mesic tree species evolved in eutrophic soils with high browsing pressure (Du Toit, 1995). Therefore, mesic species should be well adapted to herbivory and grow better with clipping treatment than humid species.
2. Nutrient addition will increase the survival and growth of tree saplings (Wakeling et al., 2010). Plants invest in root biomass more than stem biomass when soil nutrients are limited (Poorter et al., 2012). Humid species grow under high rainfall conditions and on nutrient-poor soils, whereas mesic species occur in areas with low rainfall and nutrient-rich soils (Du Toit, 1995). Therefore mesic species, adapted to their native soil conditions, will perform better than humid species in the presence of nutrients.
3. Grass competition should have a strong negative effect on tree sapling survival and growth (Kambatuku et al., 2011; Ward and Esler, 2011; Grellier et al., 2012). Savanna seedlings increase their investment in root mass at the expense of shoots in the presence of grass competition (Kambatuku et al., 2011). Grasses may provide moist microclimatic conditions (Grellier et al., 2012) conducive for sapling establishment in mesic savannas (less evapotranspiration), but may be inhibitory to sapling establishment (due to low light availability) in humid savannas. Thus, species that evolved under humid conditions will be more negatively affected by grass competition than mesic species.
4. Survival and growth will be highest in clipped saplings treated with nutrient supplementation and no grass competition whereas intact saplings will exhibit lowest survival and growth with no nutrient supplementation and in the presence of grass competition.

Materials and methods

Study site

The experimental study was conducted on Mondi nursery grounds, KwaMbonambi which is situated in the north-eastern coastal region of KwaZulu-Natal, South Africa (28°35′59.20″ S, 32°10′47.22″ E). The long-term mean annual rainfall (1984–2010) of the study area is 1250 mm. Rainfall occurs predominantly in the summer months, with peaks in November and February. The terrain at KwaMbonambi is generally flat and is comprised of Quaternary alluvial sediments of clayey sands of aeolian deposition (Mucina and Rutherford, 2006). The high permeability of the soils allows rapid leaching of the nutrients due to the heavy rainfall in these areas. The vegetation is classified as Maputaland wooded grassland (Mucina and Rutherford, 2006).

Experimental design and treatments

The experimental site was fenced to exclude large mammalian herbivores (>5 kg) from the area. The site was cleared of all vegetation prior to the application of the treatments and was not previously fertilized. Topsoil samples (up to 15 cm depth) were randomly collected from the experimental site and were sent to the University of KwaZulu-Natal laboratory, Pietermaritzburg, South Africa for soil N and P analysis. Nitrogen was analyzed in a LECO Truspec Nitrogen Analyser (LECO corporation, Michigan) using the Dumas combustion method and phosphorous was analyzed using a Technicon Autoanalyser II (Technicon Industrial Systems, Tarrytown, N.Y.). The topsoil in the study area contained a mean (±SE) of 0.1051 (±0.013) % total N and 0.0236 (±0.0021) % total P on a dry matter basis (n = 12 samples).

We adopted a split-plot design with irrigation provided at a whole-plot level. Ten 7 m × 7 m whole-plots were randomly scattered within the fenced area in an open, non-wooded and topographically flat 70 m × 50 m area. Clipping treatment with two levels, clipped and non-clipped, was performed at a whole-plot level. The two sub-plot treatment factors of nutrient fertilization (N) and grass (G), each had two levels, *viz.* presence and absence, within a given whole-plot treatment. Four sub-plots of 2 m × 2 m area with 0.5 m distance between them were situated at the centre, leaving a peripheral width of 1.25 m, of the whole-plot. “Osmocote exact” was the fertilizer applied to all sub-plots provided with nutrient treatment. It was a water soluble, granular, controlled-release fertilizer. The nutrient composition was 15% of N, 9% of P_2O_3, 11% of K_2O, 2.5% of MgO and other trace elements. This fertilizer was chosen for the steady and continuous release pattern over a 12 month period, although this experiment was terminated after 6 months. Nitrogen is an important limiting factor for plant growth in tropical savannas (Tilman, 1987) and was used to determine the level at which we applied the fertilizer. The fertilizer was applied once-off in October 2009 at the rate of 4 g N m^{-2} month^{-1}, to conform to levels applied in similar experiments in a global savanna experiment, Global Experiments on Savanna Tree seedlings (GEST) (see e.g. Tomlinson et al., 2013). This amount was approx.