Performance of seedlings of the invasive alien tree *Schinus molle* L. under indigenous and alien host trees in semi-arid savanna

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Abstract

We assessed the importance of host trees in influencing invasion patterns of the alien tree *Schinus molle* L. (*Anacardiaceae*) in semi-arid savanna in South Africa. Recruitment of *S. molle* is dependent on trees in its invaded habitat, particularly *Acacia tortilis* Hayne. Another leguminous tree, the invasive alien mesquite (*Prosopis* sp.), has become common in the area recently, but *S. molle* rarely recruits under canopies of this species. Understanding of the association between these species is needed to predict invasion dynamics in the region. We conducted experiments to test whether: (i) seedling survival of *S. molle* is better beneath *A. tortilis* than beneath mesquite canopies; (ii) growth rates of *S. molle* seedlings are higher beneath *A. tortilis* than beneath mesquite. Results showed that growth and survival of *S. molle* did not differ significantly beneath the native *A. tortilis* and the alien *Prosopis* species. This suggests that microsites provided by canopies of mesquite are as good for *S. molle* establishment as those provided by the native acacia. Other factors, such as the failure of propagules to arrive beneath mesquite trees, must be sought to explain the lack of recruitment beneath mesquite.

Key words: biological invasions, facilitation, invasion dynamics, invasive species, microsites, transplanting

Résumé

Nous avons évalué l'importance des arbres hôtes dans les facteurs qui influencent les schémas d'envahissement de l'arbre exotique *Scinus molle* L. (*Anacardiaceae*) dans une savane semi aride d'Afrique du Sud. Le recrutement de *S. molle* dépend des arbres de l'habitat qu'il envahit, et particulièrement de l'*Acacia tortilis* Hayne. Un autre arbre de la famille des légumineuses, l'envahissant « mesquite » (*Prosopis* sp.), est devenu commun dernièrement dans la région, mais *S. molle* recrute rarement sous la canopée de cette espèce. Il est nécessaire de bien comprendre l'association entre ces espèces pour prévoir la dynamique des envahissements dans la région. Nous avons réalisé des expériences pour tester si : i) la survie des jeunes plants de *S. molle* est meilleure sous une canopée d'*Acacia tortilis* que de « mesquite »; ii) le taux de croissance des jeunes plants de *S. molle* est supérieur sous les *A. tortilis* que sous les « mesquite ». Les résultats montrent que la croissance et la survie de *S. molle* ne sont pas significativement différentes sous les espèces natives *Acacia tortilis* natifs et sous les espèces exotiques de *Prosopis*. Ceci suggère que les microsites constitués par les canopées de « mesquite » sont aussi bons pour l'établissement de *S. molle* que ceux qu'offrent les acacias natifs. D'autres facteurs, tels que le fait que les propagules ne parviennent pas à arriver jusque sous les « mesquite », pourraient être invoqués pour expliquer le manque de recrutement sous ces arbres.

Introduction

The invasion of woody plants into grasslands or savannas is often initially slow, especially for fleshy-fruited alien plants (Scholes & Archer, 1997; Briggs, Hoch & Johnson, 2002). In the initial phase, isolated trees represent focal points for bird activity, and therefore for recruitment of bird-dispersed indigenous and alien plants (Flores-flores & Yeaton, 2000; Dean *et al.*, 2002; Milton *et al.*, 2007). Once founder trees mature and propagule pressure increases,

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subsequent displacement of grassland vegetation can occur rapidly (Van Auken, 2000; Briggs *et al.*, 2002). Abundant seed input (high propagule pressure) can play a role in accelerating invasions by woody plants, particularly for bird-dispersed species (Berlow, D'Antonio & Reynolds, 2002). More specifically, species with bird-dispersed seeds can potentially infiltrate natural nucleation processes, thereby disrupting crucial processes in savanna ecosystems (Milton *et al.*, 2007).

Schinus molle L. (Anacardiaceae; Peruvian pepper tree), an alien tree from South America, recently started invading natural semi-arid savannas near Kimberley in South Africa's Northern Cape province. In this area, *S. molle* usually occurs in association with, and frequently overtops, the native tree *Acacia tortilis* Hayne (Fabaceae: Mimosoidea) (Milton *et al.*, 2007; Iponga, Milton & Richardson, 2008b), but seldom occurs in association with another widespread and common tree in the area, the invasive alien mesquite (*Prosopis* sp. – a hybrid of several *Prosopis* species; also Fabaceae: Mimosoidea). This pattern could be due to: (i) the failure of seeds of *S. molle* to arrive below mesquite canopies; (ii) the inability of *S. molle* seeds to germinate below mesquite canopies; or (iii) the failure of *S. molle* seedlings to survive beneath mesquite trees. This study addresses potential reasons for third point mentioned above, and compares the performance of *S. molle* seedlings planted under the canopies of the two trees species to determine whether either species is facilitating or limiting recruitment of *S. molle* seedlings.

Material and methods

The experiment was conducted between March 2006 and April 2007 on 50- to 80-year-old diamond mining tailings on the De Beers Mine near the town of Kimberley (28.76091178 degrees S; 24.79271270 degrees E) in the Northern Cape province, South Africa. The climate is semi-arid with the mean annual rainfall of 431 ± 127 mm. The mean monthly temperature range is from 35°C to 18°C in January and from 20°C to 3°C in July (South Africa Weather http://www.weathersa.co.za/Climat/Climstats/Kimberleystats.jsp). Over the past 50 years the alien tree *S. molle* has been grown as a shade tree, and planted at many picnic sites along national and provincial roads in South Africa (see Milton *et al.*, 2007 for more details). Both *A. tortilis* and *Prosopis* sp. are deep-rooted, microphyllous leguminous trees belonging to the Mimosoideae that occur in semi-arid savanna. Umbrella Thorn Acacia (*A. tortilis*) is a medium to large microphyllous tree native primarily to savannahs of Africa. *Prosopis* is a genus of about 45 species of leguminous spiny trees and shrubs native to subtropical and tropical regions of the Americas. Several *Prosopis* species introduced to regions outside their native ranges for agroforestry purposes have become invasive (Richardson, Binggeli & Schroth, 2004). In southern Africa the most invasive forms are hybrids of *Prosopis glandulosa* Torr., *Prosopis juliflora* (Sw.) DC and *Prosopis velutina* Wooton (Zimmerman, 1991).

To test the effect of host tree type on seedling performance, ten trees each of *A. tortilis* and *Prosopis* sp. (hereafter acacia and mesquite) with approximately the same canopy size, separated from each other by a distance of approximately 20 m were randomly selected on an old mine tailings of De Beers Mine in Kimberley. Seedlings of *S. molle* were grown in a greenhouse at Stellenbosch University. When seedlings reached a height 80–100 mm they were transplanted into the field, three seedlings beneath the canopy of each host tree at different directions (S, N and E) relative to the tree trunk. A total of 60 seedlings were transplanted in the site, 30 under canopies of each of the two tree species. The performance of each seedling was recorded monthly for fifteen months in terms of height, canopy area, stem basal diameter (measured with vernier callipers), and number of branches produced per seedling.

Canopy area was calculated using the following formula for an ellipse (Bronstein & Semendjajew, 1991): Cover = (Pi/4) .*canopy*1 .*canopy*2 (1), where *canopy*1 and *canopy*2 are two perpendicular diameters of the plant as seen from above. One-way analysis of variance (ANOVA; Statistica 6.1, StatSoft, Inc, 2003) was used to test separately the effect of host tree (acacia versus mesquite) after testing for normality and homogeneity of the data, followed by bootstrapping on the measured seedlings parameters (plant height, canopy area, change in stems basal area and number of branches) at the end of the experiment. Seedling survival at each recording stage was examined in terms of the proportion of seedlings that survived relative to the total number of planted seedlings planted per host tree. Because we used count data, a generalized nonlinear model, with a log-link function to a Poisson distribution was used to test for differences in number of seedlings that survived compare to dead seedlings between host tree type (acacia and mesquite) (Statistica 6.1, StatSoft Inc. 2003).

Results

Schinus molle seedling performance was not significantly different when planted below canopies of acacia and mesquite trees (Table 1). The cumulative proportion of *S. molle* seedling survival was the same beneath canopies of the two species: 40% (Table 2).

Discussion

In semi-arid savannas of South Africa, microsites provided by large acacia trees increase the growth and survival of alien *S. molle* seedlings (Iponga *et al.*, 2008b). Similar patterns have been reported from grasslands in other parts of the world. For example, shading has been shown to increase the growth of seedlings of both the alien tree *Sapium sebiferum* (L) Roxb. and the native tree *Celtis laevigata* Spreng. in Texas (Siemann & Rogers, 2003). Our study was designed to examine the performance of *S. molle* seedlings planted beneath *A. tortilis* and *Prosopis* sp., similar trees in the sub-family Mimosoideae, one native and one alien. Given that Milton *et al.* (2007) showed that fleshy fruited aliens were confined to sub-canopy sites and that there were more beneath native acacias than beneath alien mesquite trees in the savanna. Our expectation was that *S. molle* seedling performance and survival would be much reduced beneath mesquite canopies relative to that beneath acacia canopies. Possible causes of differences in the sub-canopy environmental between acacia and mesquite might include shade density, root competition or allelopathic influences. This would explain why association between mature *S. molle* and mesquite trees was much less common than that between acacia and *S. molle*. However, results of the transplanting experiment revealed no such differences in seedling performance and survival beneath the two host trees.

Since microsites provided by the two dominant tree species in the region afford similar opportunities for seedling survival and growth, we need to seek other explanations for the failure of mesquite trees to act like acacia in facilitating *S. molle* invasion. The most obvious explanations are: a lack of propagules arriving below mesquite canopies; or high predation of seeds below mesquite canopies. Dean *et al.* (2002) suggested that the canopy architecture of invasive mesquite in the Northern Cape discourages utilization of these trees by local birds. Importantly, most branches of mesquite trees are angled too steeply to provide good perches for birds. Bird species richness and diversity in woodlands dominated by native *Acacia* differed substantially from woodlands invaded by alien mesquites, with a general trend of fewer species and fewer individuals in mesquite-invaded woodland (Dean *et al.*, 2002). Research is required to determine the implications for seed dispersal of *S. molle*, and thus its invasion dynamics, in mesquite-invaded ecosystems. Such work is currently underway.

The seed predation hypothesis was not tested in this study. However, the seeds of the indigenous *Acacia* spp. are heavily parasitized by indigenous bruchid beetles (Coleoptera) and seeds of *Prosopis* spp. are now parasitized by two endophagous Coleoptera introduced for biological control (Zimmermann, 1991). On the other hand, damage to *S. molle* seeds is caused mainly by a southern African wasp species limited to Anacardiaceae (Iponga *et al.*, 2008a). A study of the dispersal of *S. molle* seed in semi-arid savannas in South Africa showed that birds can move seeds distances of up to 320 m from female trees, but that most seeds were deposited within 50 m of putative source trees (Iponga, Milton & Richardson, 2009). It is unlikely that the wasp would parasitize seeds dispersed by birds beneath mesquite more frequently than

Table 1 Mean heights (±SE), mean canopy areas (± SE), mean number of branches (± SE) and mean stem basal diameter (± SE) of surviving seedlings of *Schinus molle* after fourteen months beneath *Acacia tortilis* and *Prosopis* sp.

Variables/treatments	Prosopis sp.	*Acacia tortilis*	*P* values
Height (cm)	39.84 ± 3.46	45.79 ± 3.60	0.24
Canopy areas (cm^2)	215.71 ± 47.54	299.44 ± 49.49	0.23
Number of branches	2.07 ± 0.65	2.91 ± 0.68	0.38
Stem basal diameter (mm^2)	0.32 ± 0.02	0.35 ± 0.02	0.29

P values were obtained through one-way ANOVA.

Table 2 Log-link function to a Poisson distribution of the mean (± SE) number of seedlings of *Schinus molle* that survived for fourteen months for different host tree types (*Acacia tortilis* and *Prosopis* sp.)

Treatments	Dead	% dead	Alive	% alive	Total n
Prosopis sp.	17	56.66	13	43.33	30
Acacia tortilis	18	60.00	12	40.00	30

$\chi^2 = 0.000$; P = NA.

seeds dispersed to acacia sub-canopy sites, particularly as native species of Anacardiaceae are more abundant beneath acacia than mesquite in this woodland (Milton *et al.*, 2007).

We have rejected the seedling performance hypothesis for explaining lack of *S. molle* association with mesquite. Of the alternative explanations, poor dispersal of seeds to mesquite canopies by birds is probably the most convincing. Although Milton *et al.* (2007) showed that *S. molle* can germinate below mesquite tree in this savanna, the seed germination and seed predation hypotheses have not yet been tested.

In conclusion, we believe that invasion of southern African arid savanna by mesquite will have a negative to neutral effect on the rate of invasion of this ecosystem by *S. molle*. However, where mesquite trees are invading grasslands where few other perches are available to birds, the alien host might provide microsite conditions that would advance of the invasion of *S. molle* or other fleshy fruited alien tree species.

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