3sc+ model YJARE : 1975 Prod.Type:FTP pp.1–12(col.fig.:NIL) ED:Dibyendu PAGN:BhaskaraYS SCAN:

ELSEVIER

Journal of Arid Environments ▮ (▮▮▮▮) ▮▮▮–▮▮▮

Journal of Arid Environments

www.elsevier.com/locate/jaridenv

Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South African savanna

Donald M. Iponga[a], Suzanne J. Milton[a,*], David M. Richardson[b]

[a]*Centre for Invasion Biology, Conservation Ecology Department, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa*
[b]*Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag, Matieland 7602, South Africa*

Received 14 July 2007; received in revised form 28 September 2007; accepted 3 October 2007

Abstract

Invasion of ecosystems by woody alien plant species is a widespread phenomenon. Interspecific competition has often been suggested as a mechanism for replacement of one species by another, but this is rarely tested. We investigated the potential of an invasive alien tree to transform vegetation by quantifying the relative abilities of the alien tree *Schinus molle* and dominant native trees *Acacia tortilis* and *Rhus lancea* to compete for light when growing in association within a South African semi-arid savanna. Due to dispersal of its fruits by birds, seedlings *of S. molle* establish under tree canopies. Using canopy symmetry as an index of ability to compete for light, we found that the alien *S. molle* consistently out-competes the dominant native tree species. The results also show that pod production of *A. tortilis* was higher when it grew alone compared to when it grew with *S. molle* or *R. lancea*. The percentage of dead branches was higher on *A. tortilis* trees growing in association with the *S. molle.* The outcome is that the alien tree will gradually increase in abundance, changing woodland structure and ecosystem processes. Our findings provide evidence for the role of competition in the process of alien plant invasions. We suggest that *S. molle*, previously considered a benign naturalized species in South Africa, should be declared a noxious weed in some parts of that country.

Keywords: Biological invasions; Coefficient of tree symmetry (TS); Shade; Symmetry technique; Woodland structure

1. Introduction

Invasive alien plants (sensu Richardson et al., 2000) have caused substantial changes to the structure and functioning of ecosystems in many parts of the world. By replacing native species and altering vegetation structure, plant invasions potentially drive ~~further~~ changes in community pattern, soil nutrient status, species interactions, ecosystems services and disturbance regimes (Hobbs and Mooney, 1986; Richardson and van Wilgen, 2004; Traveset and Richardson, 2006). The tendency of invasive to become spatially or numerically

---

[*] Corresponding author. Tel.: +27 23 5411556; fax: +27 23 5411828.
E-mail address: sukaroo@telkomsa.net (S.J. Milton).

0140-1963/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2007.10.001

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

dominant in their adopted ranges may contribute to homogenization of biotas (McKinney and Lockwood, 1999).

Spatial patterns in plant communities have been attributed to a range of processes, including interactions between individuals of different plant species, localized dispersal abilities, and disturbance regimes. One interaction with the potential to affect species distribution in communities invaded by alien species is competition for resources at local scales (Pauchard and Shea, 2006). The effects of the invaders on disturbance regimes or other ecosystem processes are generally much more dramatic than any effect attributable to competitive interactions among individuals (e.g. Brooks et al., 2004). Nonetheless, competitive interactions are crucial in some cases and need to be better understood to facilitate effective management strategies.

Schwinning (1996) stated that resources can be divided in proportion to the biomass of competing individuals (relative symmetric competitors), or they can be divided so that large competitors get more than their proportional share (asymmetric competition). In reviewing the mechanisms underlying the impacts of alien plant invasion in terrestrial systems, Levine et al. (2003) found that competition for resources was often hypothesized to be important but that its role was seldom verified through experimentation.

Light and water are among the most limiting resources for plant life, as they are essential for the acquisition of carbon and mineral nutrients (Townsend et al., 2000). Whereas competition for direct sunlight is generally asymmetric, competition for soil resources is generally symmetric (Yokozawa and Hara, 1992). Two interacting plants may compete for resources and this may lead to the exclusion of one by the other. However, the interactions between pairs of species are often mediated by other species, and the indirect effects of such interactions often result in a reduction in the competitive ability of one of the directly interacting species, altering the fitness of both the interacting individuals (Kareiva, 1994; Miller, 1994).

Particular architectural features, such as the growth form of the plant, the size, angles, distributions, and spatial relations of its leaves and branches may give alien plants an advantage in certain habitats (Morris et al., 2002). Consequently, plant architecture and structure may be important for interpreting plant performance and competitive ability when plants are growing close to one another (Morris et al., 2002).

Two species can coexist if they have neutral or positive effects on one another (MacArthur and Levins, 1967). Coexistence often occurs when, for example, each of the interacting species is a superior competitor for different resources in the habitat (Bolker and Pacala, 1999). Nevertheless, one species could out-compete the other if it can grow faster or deplete a limiting resource more rapidly or efficiently (Schwinning, 1996). In this way, differences in competitive ability may explain the dominance in some plant communities.

The genus *Schinus* L. (Anacardiaceae) is native to South America and includes approximately 29 species (Barkley, 1957). Members of the genus have been introduced to many parts of the world outside their natural ranges as ornamentals and for spice production (Morton, 1978). One of the *Schinus* species introduced to South Africa is *Schinus molle* L., a long-lived and drought tolerant hardy evergreen tree native to the arid zone of ~~Peru~~. Introduced in the mid 1800s, the species has been planted in villages and on farms since around 1900 and along national and provincial roads in South Africa over the past 50 years. Unlike many other alien trees introduced to South Africa (Richardson et al., 1997), *S. molle* has, until recently, shown little sign of becoming invasive. It is, nonetheless, included in a recent, objectively derived, list of "major invaders" in South Africa (Nel et al., 2004). Bioclimatic analyses suggest that the species has the potential to expand its range in South Africa (Rouget et al., 2004).

Wilson et al. (2007) showed that the extent of invasiveness of woody plants in South Africa is determined by a complex interplay of many factors, including the traits of the species, their residence time, the extent of human-mediated dissemination, and the locality of initial plantings relative to the most favourable sites for the species in the entire region. Consequently, the current limited extent of invasion by *S. molle* may be an artefact of the observation timescale and initial planting sites. In South Africa, *S. molle* invades savanna and grassland and has also naturalised along drainage lines and roadsides in semi-desert Karoo (Henderson, 2001).

This study investigates the ability of *S. molle* to compete for light with the dominant native trees *Acacia tortilis* (Forssk.) Hayne (Fabaceae: Mimosoidea) and *Rhus lancea* L.f. (Anacardiaceae) in a semi-arid savanna in South Africa. Since the study species are trees with long life cycles, it was impractical to study interactions directly in manipulative experiments (Richardson et al., 2004). However, the widespread coexistence of the study species over large areas provides a useful natural experiment for gaining insights in this regard. *S. molle* trees frequently grow in association with indigenous trees where their seeds are dispersed by birds (Milton et

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

al., 2007). If the alien species is able over-top indigenous tree species and to outcompete them for light, then the alien species would become structurally dominant, possibly altering the functioning of the ecosystem. Our aim was to ascertain whether this occurs in *S. molle*-invaded ecosystems.

Using canopy symmetry as an index of ability to compete for light, we tested the hypothesis that the evergreen native *R. lancea* and alien *S. molle* would both out-compete the microphyllous and semi-deciduous *A. tortilis* for light, but that *S. molle* would not be able to displace the evergreen native *R. lancea*. We expected symmetry to be correlated with other indicators of fitness including canopy health and seed production.

2. Material and methods

2.1. Study site

The study was conducted in semi-arid savanna vegetation near the town of Kimberley in the Northern Cape Province of South Africa, (28°48′S, 24°46′E, altitude 1198 m above sea level). Kimberley has warm, relatively moist summers, and cold, dry, winters. The annual rainfall (1961–1990) averages 414 mm and mean daily temperature range between 18 and 33 °C in January, and 3 °C and 19 °C in July (South African Weather Bureau, 2003). The vegetation is classified as Kimberley Thornveld, a component of the Eastern Kalahari bushveld bioregion (Mucina et al., 2006), and is characterized by C_4 grasses and scattered trees. The study took place on approximately 200 ha comprising the Diskobolos Military Base (Aleksanders Fontein) and part of the adjacent farm Rooifontein, 2 km south of Kimberley. Here the landscape is flat, lacking hills or drainage lines, and soils fine textured. Tree cover varies from 5% to 15% at landscape level. The dominant tree species, *Acacia tortilis*, usually has an understorey of fleshy fruited shrubs (*Ehretia rigida*, *Lycium* spp., *Solanum* spp.) and tree saplings including the native species *R. lancea* and *Ziziphus mucronata*, and more recently the invasive alien tree *S. molle*.

2.2. Study species

S. molle is dioecious and female trees produce large crops of small bright pink berries arranged in bunches on pendulous stems. These are eaten and dispersed by birds in California (Nilsen and Muller, 1980) and in South Africa (Milton et al., 2007), and young plants generally establish below perch sites, mainly other trees. Most *S. molle* saplings and trees are thus rooted below the canopies of dominant native trees, as are *R. lancea* trees, the seeds of which are also bird-dispersed. Seeds of mammal- or wind-dispersed *Acacia* species, including *A. tortilis*, generally establish in the open grassland away from tree canopies (Milton and Dean, 1995; Yeaton and Romero-Manzanares, 1986).

Fleshy fruited tree species appear to outlive and succeed their *Acacia* host trees (Milton and Dean, 1995). The outcome of interactions between the invader and the host tree are thus crucial for determining whether the invader can maintain its position and also for determining the impact of the invader. Growth inhibition on the shaded part of a tree canopy would result in the formation of an increasingly lopsided or asymmetrical canopy. We therefore assumed that trees showing large asymmetry in canopy radius from a vertical median, or any sign of distortion, are less competitive for light.

2.3. Methods

2.3.1. Coefficient of tree symmetry

We applied the technique developed by Flores-Flores and Yeaton (2000). This compares the asymmetry or distortion of canopies of trees that are growing in association with one another by means of an index, the coefficient of tree symmetry (TS) that indicates which individual of a pair of contiguous trees is competing more successfully for light. The technique, developed to predict the outcomes of competition between species pairs (*Acacia– Larrea*, *Prosopis– Acacia*, *Opuntia– Yucca*) in the southern Chihuahua Desert, Mexico (Flores-Flores and Yeaton, 2000), confirmed outcomes previously inferred from tree mortality (Yeaton and Romero-Manzanares, 1986).

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

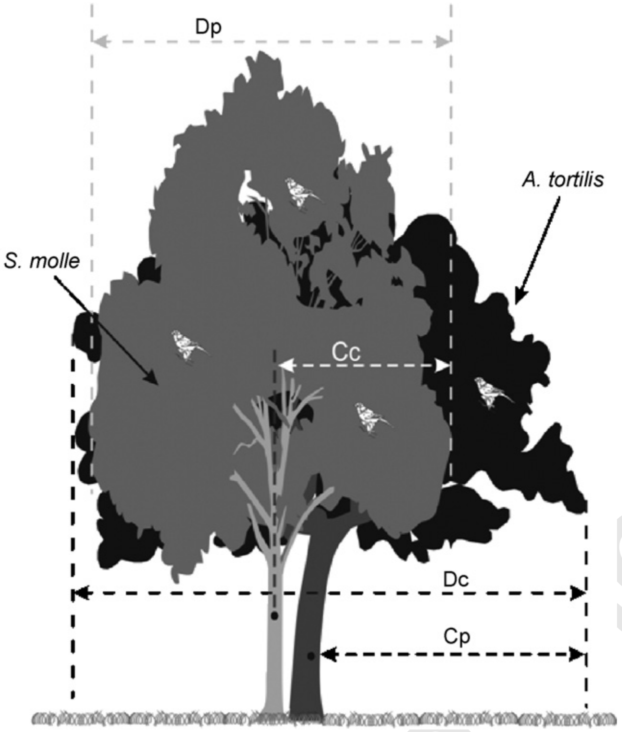

Fig. 1. Schematic representation of light competition assessment between *Schinus molle* (alien) and *Acacia tortilis* (native) in semi-arid savanna in South Africa. The coefficient of tree symmetry (TS), an index developed by Flores-Flores and Yeaton (2000), is calculated by dividing the longest diameter of the complete canopy of a given tree (Dp for *S. molle*, Dc for *A. tortilis*), by the distance from its trunk to the canopy edge that is not in contact with its neighbour (Cc for *S. molle*, Cp for *A. tortilis*). The coefficient of tree symmetry (TS) is calculated as Dc/Cp, and the lower this value, the weaker the ability of the tree to compete for light.

The sampling method requires that canopies of two individual trees of different species be in contact. In the plain determined by the two tree trunks, the longest diameter of the complete canopy of each tree (Dc) is measured. This is complemented with the measurement of the distance from the centre of each single or multi-stemmed plant (Cp) to the edge where there is no contact. The assumption is that there will be a tendency for more growth in this direction (Fig. 1). TS, the coefficient of TS is calculated as

$$\mathrm{TS} = \mathrm{Dc}/\mathrm{Cp}.$$

The more even the canopy of the tree, the closer TS will be to 2 (i.e. for a perfectly symmetrical tree, TS = 1.0/0.5 = 2). The smaller the TS ratio, the weaker is the ability of a species to out-compete its neighbour for light. If one tree is being affected strongly by its neighbour it will have a TS = 1 (i.e. Dc = Cp). In this case, the whole canopy is escaping the effect of competition and the canopy is completely asymmetrical. Over time, such a tree will probably be replaced by the neighbour that is competing more strongly for light. In this way, an index of the likelihood that a species with a tall dense canopy will replace one with a lower more open canopy can be calculated and some inference can be made about whether this will happen in the medium or long term. The weaker competitor for light will possibly die or fall over due to the asymmetrical growth of the canopy (Fig. 2).

2.4. Sampling

2.4.1. Coefficient of tree symmetry

To understand whether *S. molle* will out-compete indigenous savanna trees (*A. tortilis* and *R. lancea*), whether *A. tortilis* trees have symmetrical canopies when growing alone and whether *R. lancea* may also out-compete *A. tortilis* in semi-arid savannas, 171 pairs of tree species were sampled around Kimberley. Canopies

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

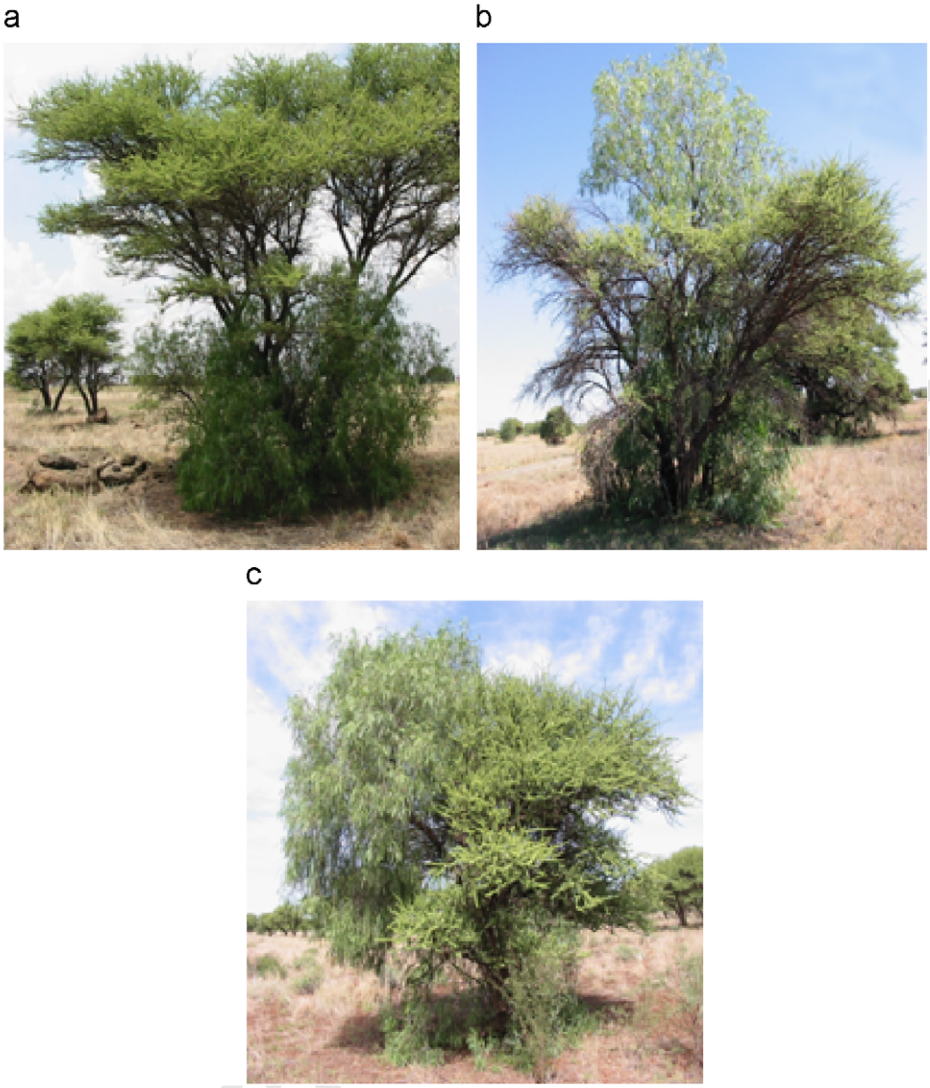

Fig. 2. The succession scenario between *Schinus molle* (alien) and *Acacia tortilis* (native) in semi-arid savanna in South Africa. ~~Arrows indicates *S. molle* development under the canopy of *A. tortilis*.~~ Following seed deposition by birds, *S. molle* will germinate under the canopy of *A. tortilis* (a), *S. molle* will grow in almost perfect symmetry and overtop the host tree (b), then due to the shading effect by *S. molle*, *A. tortilis* will develop canopy distortion as it grows toward light and away from its neighbour (c). ~~The asymmetrical canopy of *A. tortilis* might cause the tree to fall, for example, due to a strong wind.~~

of the individuals in each of the tree pairs selected for study were in physical contact. A total of 123 pairs of *S. molle* and *A. tortilis* were sampled, and 48 pairs of *S. molle* and *R. lancea* were sampled. Fifty-one pairs of *A. tortilis* and *R. lancea* close to one another were sampled, as were 100 *A. tortilis* trees growing alone. TS was calculated for each tree.

2.4.2. *Plant health and fitness*

To assess whether competition for light with *R. lancea* or *S. molle* increases mortality rates for *A. tortilis*, we recorded the status (% of dying *A. tortilis* with and without *R. lancea* and *S. molle*) of 100 *A. tortilis* growing alone, 51 pairs of *A. tortilis* growing with *R. lancea*, and 68 pairs of *A. tortilis* and *S. molle*. The health and fitness quantification was only done for *A. tortilis* due to its dominance in the woodland. Other reasons were that *A. tortilis* plays the role of a nucleus founding species (Milton et al., 2007; Pausas et al., 2006) facilitating

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

the recruitment of other bird dispersed plants in these savannas (Dean et al., 1999), and because this species is more likely to be affected by fleshy fruited alien plant species than any other tree in these savannas.

The percentage of canopy dieback (0%; $<25\%$; 26–50%; 51–75% and $>75\%$) was used as an indication of tree health. As an additional indication of health, we also examined the abundance of pods on *A. tortilis* by recording, in categories, the percentage of the canopy covered by pods (0%; $<25\%$; 26–50%; 51–75% and $>75\%$). Basal diameter of *A. tortilis* alone, and growing with *R. lancea* and *S. molle* was measured to determine: (a) at what stage fleshy-fruited trees began to be associated with *A. tortilis*, and (b) whether with competition from *R. lancea* or *S. molle* caused *A. tortilis* to die at a smaller size than when this species grew alone.

2.4.3. Statistical analysis

One-way analysis of variance (ANOVA) was used after checking the normality and homogeneity of the data; this was followed by bootstrapping analysis to test the non-normal data. Then, differences in TS between pairs of tree species were tested separately and differences in means were illustrated graphically using a significance level of $p<0.05$. A Scheffé post hoc test was also done to determine significant effects between TS of trees in pairs (STATISTICA 6.1, StatSoft, Inc., 2003).

To understand the impact of the alien *S. molle* on indigenous trees, the analysis compared the coefficient of TS of *A. tortilis* and *S. molle* in the pair and the TS *R. lancea* and *S. molle* in the pair. There could be also exclusion between two indigenous species growing together. The difference between *A. tortilis* and *R. lancea* TS values were therefore also tested when the two species were growing together. The analysis also tested the difference between TS of *A. tortilis* growing alone with the TS of *A. tortilis* growing with *S. molle* and *A. tortilis* growing with *R. lancea*. Then another comparison was also made between TS of *A. tortilis* growing alone with those of *A. tortilis* with *S. molle*, *A. tortilis* with *R. lancea*, and *R. lancea* with *S. molle*.

To reject the null hypothesis that all the category classes (percentage of dead branches and presence of pods) used to assess *A. tortilis* performance, have the same uniform distribution when this species is growing alone or with *S. molle* or *R. lancea*, we used a χ^2 goodness of fit test to test this hypothesis for each of the five percentage category classes (Gotelli and Ellison, 2004, p. 376). We used linear regression, between *A. tortilis* basal area and the proportion of the population *A. tortilis* growing with *R. lancea* or with *S. molle*, to determine whether the association with fleshy-fruited trees increased as *A. tortilis* aged. We assumed that stem basal area increased with tree age.

3. Results

3.1. Coefficient of tree symmetry

The results showed that the mean coefficient of TS of *S. molle* was significantly higher than both *A. tortilis* ($F_{1,244} = 17.999$; $p<0.0001$; Fig. 3a) and *R. lancea* ($F_{1,94} = 7.284$; $p<0.005$; Fig. 3b), indicating that *S. molle* is causing asymmetrical canopy growth in both those species. However, the distortion was greater for *R. lancea* than for *A. tortilis* ($F_{1,100} = 5.155$; $p<0.05$; Fig. 3c) when these two species grew together.

Acacia tortilis growing alone in the woodland had a significantly higher TS than when this species grew with *S. molle* ($F_{1,221} = 74.854$; $p<0.0001$; Fig. 3d). However, no difference was found between *A. tortilis* growing alone and when it grew with *R. lancea* ($F_{1,149}$; $p = 0.533$; Fig. 3e). The results also show that the TS of indigenous trees (*A. tortilis* and *R. lancea*) when growing in association with non-indigenous *S. molle* were significantly lower than the TS of *A. tortilis* growing alone and *A. tortilis* growing with *R. lancea*. On the other hand, *A. tortilis* experiences significantly greater impact when growing with *S. molle* than when growing with *R. lancea* (Scheffe post hoc test, $p<0.0001$, Fig. 3f).

3.2. Plant health and reproductive performance

The presence of pods appeared to be a good indicator of health and performance of *A. tortilis* in semi-arid savannas. Solitary *A. tortilis* trees produced more pods than those growing with *S. molle* ($\chi^2 = 117.13$, $df = 4$,

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

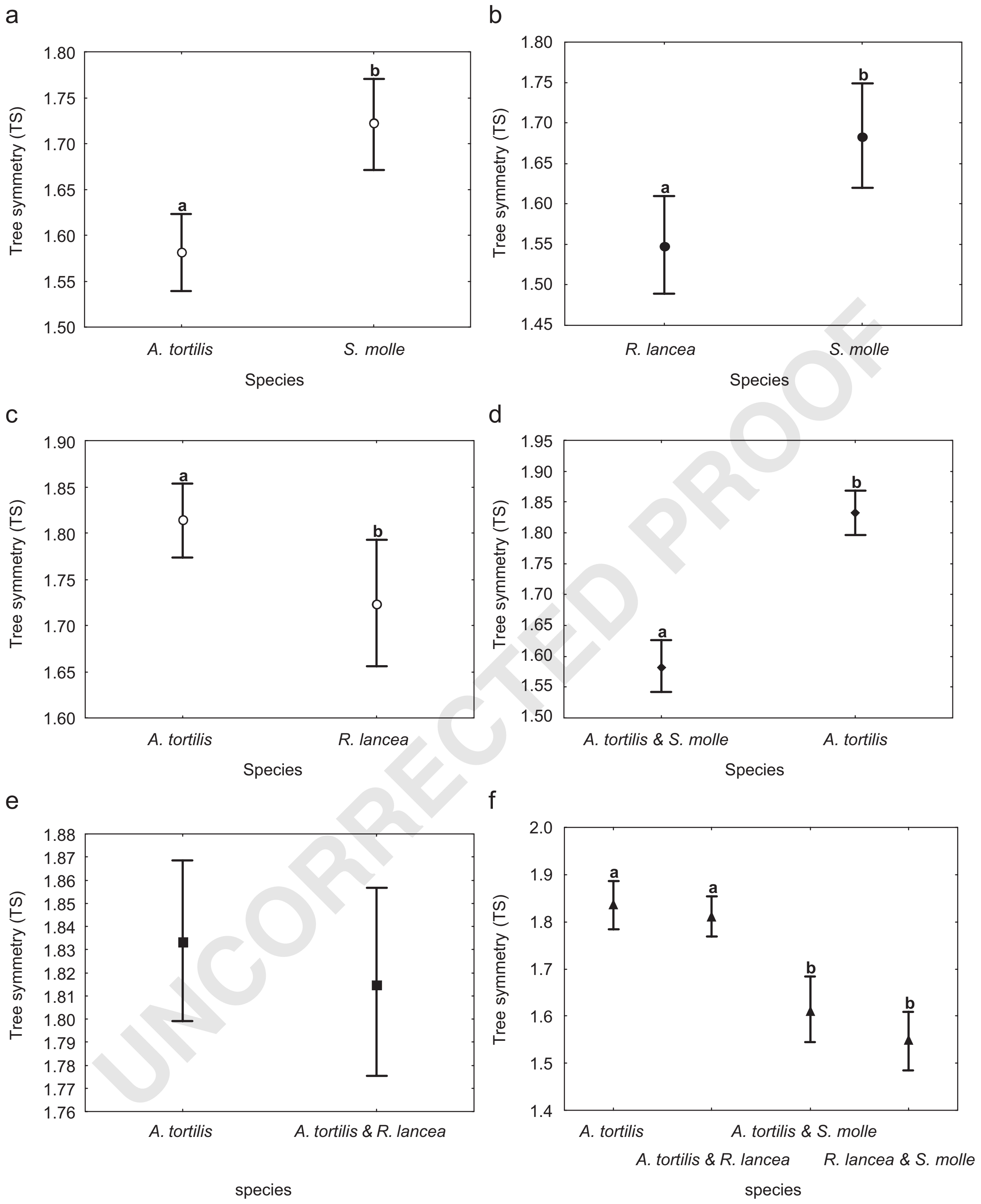

Fig. 3. Mean coefficient of tree symmetry (TS) of *Acacia tortilis* (native) vs. *Schinus molle* (alien) (a); *S. molle* vs. *Rhus lancea* (native) (b); *A. tortilis* vs. *R. lancea* (c); *A. tortilis* growing alone vs. *A. tortilis* growing with *S. molle* (d); *A. tortilis* growing alone vs. *A. tortilis* growing in association with *R. lancea* (e); and *A. tortilis* growing alone vs. *A. tortilis* growing with *R. lancea*, vs. *A. tortilis* growing with *S. molle*, vs. *R. lancea* growing with *S. molle* (f). Vertical bars indicate standard deviations from the mean and different letters above the bars indicate significant differences.

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

Table 1
Number of *Acacia tortilis* in each pod abundance category (0–>75% cover of canopy by pods) for *A. tortilis* growing alone, or growing with *Schinus molle* and with *Rhus lancea*

Canopy cover of pods (%)	*A. tortilis* alone	*A. tortilis* with *S. molle*	*A. tortilis* with *R. lancea*
0%	4	6	2
<25	7	**18**	8
26–50	**25**	**22**	7
51–75	**31**	**17**	**20**
>75	**33**	5	**14**
Totals (*N*)	100	68	51

Bold type highlights numbers larger than 10.

Table 2
Number of *Acacia tortilis* in each branch mortality category (0–>75% volume of canopy comprising dead branches) on *Acacia tortilis* growing alone, with *Schinus molle* and with *Rhus lancea* for different percentage classes

Branch mortality category (%)	*A. tortilis* alone	*A. tortilis* with *S. molle*	*A. tortilis* with *R. lancea*
0%	5	1	0
<25	**56**	**17**	**26**
26–50	**36**	**27**	**21**
51–75	2	**18**	4
>75	1	5	0
Totals (*N*)	100	68	51

Bold type highlights numbers larger than 10.

$p<0.001$) or with *R. lancea* (χ^2 16.679, $df=4$, $p<0.01$), but *S. molle* clearly depressed pod production more severely than did *R. lancea* (Table 1).

Association with *S. molle* appears to cause branch mortality of *A. tortilis*. Since a greater proportion of *A. tortilis* trees growing with *S. molle* were found in high classes of percentages of dead branches (51–75% and >75%) than those growing alone ($\chi^2=70.636$, $df=4$, $p<0.0001$). Proximity to the native *R. lancea* did not significantly increase branch mortality of *A. tortilis* (Table 2).

The proportion of *A. tortilis* growing alone decreased significantly with stem basal area class, whereas the proportion of *A. tortilis* growing in association with fleshy fruited trees tended to increase with stem basal area (Fig. 4). The increase in *A. tortilis* association with *S. molle* with size was significant ($r^2=0.737$; $p<0.05$), whereas association with *R. lancea* was non-significant.

4. Discussion

Competition for light is often seen as one of the most important mechanisms whereby invasive alien plants cause changes in invaded communities (Hobbs and Mooney, 1986; Hutchinson and Vankat, 1997; Richardson et al., 2000). This study was designed to examine the impact of non native *S. molle* distribution on two indigenous tree species (*A. tortilis and R. lancea*) in semi-arid savanna of South Africa, and also to test whether *S. molle* will be better competitor for light when growing with *A. tortilis and R. lance*a. If *S. molle* is able to out-compete the native host, this could have a marked influence on vegetation structure in the long-term. Vegetation structure and tree architecture influence bird perching, foraging and nesting behaviour, which in turn influence ecosystem functioning (Dean et al., 2002; Milton et al., 2007; Seymour, 2006).

This change in canopy symmetry of those indigenous species caused by competition with an alien species is probably due to their intolerance of shading by *S. molle.* As a result, canopies of both species, when growing in association with *S. molle*, will develop asymmetrically as shoots extend sideways to capture light. The results

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

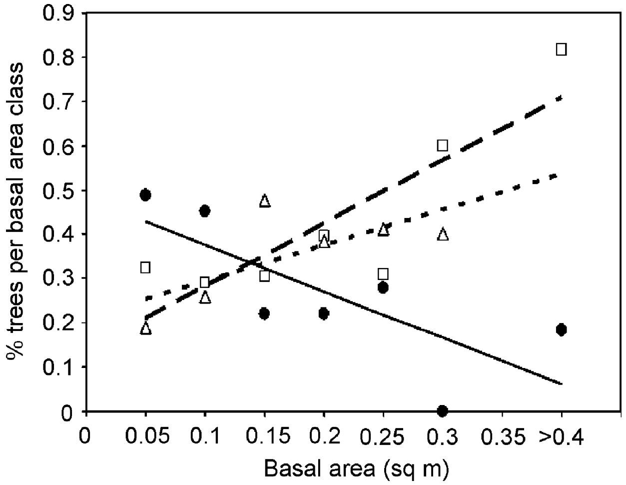

Fig. 4. Fitted curves for the proportions of *Acacia tortilis* trees in various basal area classes growing alone (filled circle, $n = 100$, $r^2 = 0.580$, $p < 0.05$), *or* growing in association with *Schinus molle* (open square, $n = 68$, $r^2 = 0.737$, $p < 0.05$) and or *Rhus lancea* (open triangle, $n = 51$, $r^2 = 0.497$, n.s.).

also indicate that *S. molle* is a stronger competitor for light since its canopy remains symmetrical as it overtops native neighbours.

Studies have suggested that large plants can pre-empt light from smaller neighbours by overtopping and shading them (Diggle, 1976; Hara, 1984) and as competition for light increases, there are greater advantages to be gained by investing in vertical crown expansion than through horizontal crown expansion to minimize shading by neighbours (Baruch et al., 2000; Poorter and Werger, 1999). The arrangement of branches and leaves of plants can be closely linked with environment conditions, particularly with regard to light (Poorter and Werger, 1999).

Our results show that *S. molle* can out-compete the dominant native trees in semi-arid savanna. We also show that the pod production of *A. tortilis* was higher when it grew alone than when it grew with *S. molle* or *R. lancea*. The percentage of dead branches was also high on *A. tortilis* trees growing with the alien *S. molle.* The performance of *A. tortilis* growing with *S. molle* could be limited due to the low light interception, which could ~~lead to~~ increase the percentage of dead branches and decrease the pods production. The process of replacement of native by alien trees is at an early stage at our study site, as shown by the size-class distribution of the population. It seems certain that invasive *S. molle* trees are poised to cause a marked change in the composition of these plant communities.

A limitation of this study was that we tested only the individual performance of canopy structure of pairs of plants. Other competitive interactions, such as for water and nutrient uptake, may also influence the response of the species to light, and may interact with those for light to mediate the outcome of the results. However, for well-established mature trees such factors are probably less important since competition for water and nutrients are most important at the seedling stage (Bakker and Wilson, 2001; Iponga et al., 2005; Walters and Reich, 2000). Canopies of pairs of trees where *S. molle* was not emerging or overtopping the neighbouring indigenous species were not measured.

A degree of shade tolerance is generally necessary for tree species to establish (Walters and Reich, 2000). Fleshy fruited seedlings recruit below the canopies of trees because they are dispersed to such sites by birds. As birds disperse the seeds of fleshy fruited species *Rhus* and *Schinus* their seedlings are commonly associated with trees used as perches (Dean et al., 1999, 2002; Milton et al., 2007; Seymour, 2006; Smith et al., 1994). For this reason it would be expected that *R. lancea* would have similar levels of shade tolerance to *S. molle*. Nevertheless, it is clear that *S. molle* is able to out-compete both indigenous trees for light. The results also suggested that *R. lancea* may have less impact on the dominant *A. tortilis* than *S. molle* in the semi-arid savannas.

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

It is probable that the *Acacia* tree in each tree pair sampled would have established before the fleshy-fruited neighbour arrived. This assumption is made because large *A. tortilis* were more frequently associated with fleshy fruited trees and because seeds of fleshy-fruited tree species are usually dropped below perch sites. For this reason *S. molle* seedlings would have established and grown in the shade of *A. tortilis* before emerging from the host tree canopy. We cannot make the assumption for *R. lancea*–*S. molle* pairs, that the alien partner always established beneath the indigenous member of the pair. However, we have observed that *S. molle* can reach reproductive maturity beneath or within the canopies of tall indigenous savanna trees (Milton et al., 2007). *S. molle* is mesophyllous and evergreen (Howard and Minnich, 1989), in contrast to *A. tortilis* that is microphyllous and semi-deciduous losing >80% of leaves in dry winters (Milton, 1987) and *R. lancea* that is mesophyllous and evergreen, but sheds all its old leaves in late spring when new leaves are forming (Palmer and Pitman, 1972). Moreover, the leaves of *S. molle* do not appear to suffer insect or fungal damage (S.J. Milton, personal observation), whereas leaves of *R. lancea* are damaged by fungi (Crous et al., 2003), that may reduce their ability to compete for light. Greater photosynthetic potential may possibly explain the competitive ability of *S. molle*.

Most light competition experiments have been between tree or shrubs seedlings and grasses, or involved the manipulation of light in the laboratory (Siemann and Rogers, 2003). Field experiments on light competition are difficult to perform. However, the response of the alien plant species reported by this study may correspond with that reported in many other studies that found high above-ground productivity of alien plants compared with indigenous species (e.g. Lawrence and Ratzlaff, 1989).

5. Conclusions

We have shown that the performance of two dominant native tree species in semi-arid savannas of South Africa is influenced by alien trees (*S. molle*) that grow in association with them as a result of directed dispersal of its seeds by birds. The ability of *S. molle* to compete strongly for light, and the fact that such competition may lead to changes in vegetation composition, may contribute to the growth of *S. molle* populations and to the transformation of large areas from grassy open savanna with scattered *Acacia*, to less grassy woodland dominated by *S. molle*. This could have cascading effects including the disruption of pollinator and disperser mutualisms, changes in bird communities and reduction of grazing value for cattle and game. Consequently, *S. molle* may pose a threat to the conservation of this vegetation type. A comprehensive strategy for the management of this invasive species is urgently needed.

Acknowledgements

We acknowledge financial support from the DST-NRF Centre of Excellence for Invasion Biology, and thank W.R.J. Dean, J.L. Flores-Flores, and R.I. Yeaton for discussion in Mexico that inspired this study, and two reviewers whose suggestions improved the manuscript.

References

Bakker, J., Wilson, S., 2001. Competition ability of introduced and native grasses. Plant Ecology 157, 117–125.

Barkley, F.A., 1957. A study of *Schinus* L. Lilloa 28, 5–110.

Baruch, Z., Pattison, R.R., Goldstein, G., 2000. Responses to light and water availability of four invasive Melastomataceae in Hawaiian Islands. International Journal of Plant Sciences 161, 107–118.

Bolker, B.M., Pacala, S.W., 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. American Naturalist 153, 575–602.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., Di Tomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. BioScience 54, 677–688.

Crous, P.W., Groenewald, J.Z., Carroll, G., 2003. *Muribasidiospora indica* causing a prominent leaf spot disease on *Rhus lancea* in South Africa. Australasian Plant Pathology 32, 313–316.

Diggle, P.P., 1976. A spatial stochastic model of inter-plant competition. Journal of Applied Probability 13, 662–671.

Dean, W.R.J., Milton, S.J., Jeltsch, F., 1999. Large trees, fertile islands and birds in arid savanna. Journal of Arid Environments 40, 61–78.

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

Dean, W.R.J., Anderson, M.D., Milton, S.J., Anderson, T.A., 2002. Avian assemblages in *Acacia* and *Prosopis* drainage line woodland in the Kalahari, South Africa. Journal of Arid Environments 51, 1–20.

Flores-Flores, J.L., Yeaton, R.I., 2000. La importancia de la competencia en la organización de las comunidades vegetales en el altiplono Mexicano. Interciencia 25, 365–371.

Gotelli, N.J., Ellison, A.M., 2004. A Primer of Ecological Statistics. Sinauer Associates, Sunderland, MA, USA.

Hara, T., 1984. A stochastic model and the moment dynamics of the growth and size distribution in plant populations. Journal of Theoretical Biology 109, 173–190.

Henderson, L., 2001. Alien weeds and invasive plants: a complete guide to declared weeds and invaders in South Africa. Plant Protection Research Institute Handbook 12. PPRI, Pretoria.

Hobbs, R.J., Mooney, H.A., 1986. Community changes following shrub invasion of grassland. Oecologia 70, 508–513.

Howard, L.F., Minnich, R.A., 1989. The introduction and naturalization of *Schinus molle* (Pepper Tree) in Riverside, California. Landscape and Urban Planning 18, 77–95.

Hutchinson, T.F., Vankat, J.L., 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. Conservation Biology 11, 1117–1124.

Iponga, D.M., Krug, C.B., Milton, S.J., 2005. Competition and herbivory influence growth and survival of shrubs on old fields: implication for restoration of renosterveld shrubland. Journal of Vegetation Science 16, 685–692.

Kareiva, P., 1994. Higher order interactions as a foil to reductionist ecology. Ecology 75, 1527–1528.

Lawrence, T., Ratzlaff, C.D., 1989. Performance of some native and introduced grasses in a semiarid region of western Canada. Canadian Journal of Plant Sciences 69, 251–254.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., Lavorel, S., 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society, London B 270, 775–781.

MacArthur, R., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101, 377–385.

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14, 450–453.

Miller, T.E., 1994. Direct and indirect species interactions in an early old field plant community. American Naturalist 143, 1007–1025.

Milton, S.J., 1987. Phenology of seven Acacia species in South Africa. South African Journal of Wildlife Research 17, 1–6.

Milton, S.J., Dean, W.R.J., 1995. How useful is the keystone species concept, and can it be applied to *Acacia erioloba* in the Kalahari desert? Zeitschrift für Ökologie und Naturschutz 4, 147–156.

Milton, S.J., Wilson, J.R.U., Richardson, D.M., Seymour, C.L., Dean, W.R.J., Iponga, D.M., Procheş, Ş., 2007. Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. Journal of Ecology 95, 648–661.

Morris, L.L., Walck, J.L., Hidayati, S.N., 2002. Growth and reproduction of the invasive *Ligustrum sinense* and native *Forestiera Ligustrina* (Oleaceae): implications for the invasion and persistence of a non native shrub. International Journal of Plant Sciences 16 (6), 1001–1010.

Morton, J.F., 1978. Brazilian pepper—its impact on people, animals and the environment. Economy Botany 32, 353–359.

Mucina, L., Rutherford, M.C., Powrie, L.W. (Eds.), 2006. Vegetation map of South Africa, Lesotho and Swaziland, 1/1000 000 scale sheet map. South Africa National Biodiversity Institute, Pretoria.

Nel, J.L., Richardson, D.M., Rouget, M., Mgidi, T., Mdzeke, N., Le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L., Neser, S., 2004. A proposed classification of invasive alien plant species in South Africa: towards prioritising species and areas for management action. South African Journal of Science 100, 53–64.

Nilsen, E.T., Muller, W.H., 1980. A comparison of the relative naturalizing ability of two *Schinus* species in southern California. I. Seed germination. Bulletin of the Torrey Botanical Club 107, 51–56.

Palmer, E., Pitman, N., 1972. Trees of Southern Africa, vol. 2. A.A. Balkema, Cape Town.

Pauchard, A., Shea, K., 2006. Integrating the study of non-native plant invasions across spatial scales. Biological Invasions 8, 399–413.

Pausas, J.P., Bonet, A., Fernando, T., Maestre, E.T., Climent, A., 2006. The role of the perch effect on nucleation process in Mediterranean semi-arid oldfields. Acta Oecologica 29, 346–352.

Poorter, L., Werger, M.J.A., 1999. Light environment, sapling architecture, and leaf display in six rain forest tree species. American Journal of Botany 86, 1464–1473.

Richardson, D.M., van Wilgen, B.W., 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? South African Journal of Science 100, 45–52.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., Henderson, L., 1997. Alien plant invasions. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp. 535–570.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6, 93–107.

Richardson, D.M., Rouget, M., Rejmánek, M., 2004. Using natural experiments in the study of alien tree invasions: opportunities and limitations. In: Gordon, M.S., Bartol, S.M. (Eds.), Experimental Approaches to Conservation Biology. University of California Press, Berkeley, pp. 180–201.

Rouget, M., Richardson, D.M., Nel, J.L., Le Maitre, D.C., Egoh, B., Mgidi, T., 2004. Mapping the potential spread of major plant invaders in South Africa using climatic suitability. Diversity and Distributions 10, 475–484.

Schwinning, S., 1996. Decomposition analysis of competitive symmetry and size structure dynamics. Annals of Botany 77, 47–58.

Seymour, C., 2006. The influence of size and density of the Camelthorn (Acacia erioloba Mayer) on its keystone role in the Xeric Kalahari. Ph.D. Thesis, University of Cape Town, Cape Town.

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001

Siemann, E., Rogers, W.E., 2003. Changes in light and nitrogen availability under tree may indirectly facilitate tree invasions of grasslands. Journal of Ecology 91, 923–931.

South African Weather service 〈http://www.weathersa.co.za/Climat/Climstats/KimberleyStats.jsp〉.

Smith, T.J., Robblee, M.B., Wanless, H.R., Doyle, T.W., 1994. Mangroves, hurricanes, and lightning strikes: assessment of Hurricane Andrew suggests an interaction across two differing scales of disturbance. BioScience 44, 256–262.

StatSoft, Inc., 2003. STATISTICA (data analysis software system), version 6. 〈http://www.statsoft.com〉.

Townsend, C.R., Jarper, J.L., Begon, M., 2000. Essentials of Ecology. Blackwell Science, MA, USA.

Traveset, A., Richardson, D.M., 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology and Evolution 21, 208–216.

Walters, M.B., Reich, P.B., 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. Ecology 81, 1887–1901.

Wilson, J.R.U., Richardson, D.M., Rouget, M., Procheş, Ş., Amis, M.A., Henderson, L., Thuiller, W., 2007. Residence time and potential range: crucial considerations in modelling plant invasions. Diversity and Distributions 13, 11–22.

Yeaton, R.I., Romero-Manzanares, A., 1986. Organization of vegetation mosaics in the *Acacia schaffneri–Opuntia streptacantha* association, southern Chihuahuan Desert, México. Journal of Ecology 74, 211–217.

Yokozawa, M., Hara, T., 1992. A canopy photosynthesis model for the dynamics of size structure and self-thinning in plant populations. Annals of Botany 70, 314–320.

Please cite this article as: Iponga, D.M., et al., Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South.... Journal of Arid Environments (2007), doi:10.1016/j.jaridenv.2007.10.001