

Does the invasion of *Prosopis juliflora* cause the die-back of the native *Manilkara hexandra* in seasonally dry tropical forests of Sri Lanka?

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Abstract: Invasion by *Prosopis juliflora* that would lead to the die-back of *Manilkara hexandra* in tropical semi-deciduous forests at Bundala National Park, Sri Lanka, was examined by conducting both *in vitro* and *in vivo* experiments. Individuals of the two species were enumerated in sixteen 20 × 20 m² experimental plots established in forests over 4 disturbance regimes. *In vitro* experiments to detect the presence of allelopathic chemicals in *P. juliflora* were carried out through a seed germination bio-assay, while the effects of these chemicals on seedling growth performance of *M. hexandra* and the competition between the two species were examined under glass house conditions. Results revealed that the abundance of *P. juliflora* and the number of dead individuals of *M. hexandra* in the forests were positively correlated. Seed germination bio-assay confirmed the presence of allelochemicals in *P. juliflora*. Further, pot experiments revealed that *P. juliflora* could not outperform *M. hexandra* in well moist soil conditions. However, fast growing *P. juliflora* can efficiently draw ground water through its extended root system, which probably creates a water scarcity during drought periods and may lead to the die-back of *M. hexandra*. Water soluble allelochemicals of *P. juliflora* may easily be washed away with rain water and, thus, may not create a severe impact on *M. hexandra* under well moist soil conditions. This reiterates the necessity of controlling this invader in seasonally dry environments.

Key words: Allelopathic chemicals, Bundala National Park, competition, tropical semi-deciduous forests, water stress.

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Introduction

Plant invasions are widely accepted as one of the major threats to global biodiversity across the planet. Massive declines in biodiversity have often been reported in areas where the alien plants are heavily invaded (Cronk & Fuller 1995; Pauchard & Shea 2006; Vitousek *et al.* 1997; Wilcove *et al.* 1998). Although the impacts of exotic plant invasions on plant diversity, community structure and ecosystem processes are well acknowledged (e.g. Cronk & Fuller 1995; Joshi *et al.* 2015), only a few of those have tested whether these effects

truly arise through competition, allelopathy, alteration of ecosystem variables or through other processes (Levine *et al.* 2003).

Based on non-native plant invasions at various spatio-temporal scales, several theories and hypotheses have been put forward by researchers. All these imply that the invasive potential and/or the invasibility of the ecosystem may determine the invasion by a given alien exotic plant in a given locality. Both habitat characteristics and species attributes also determine the rate of spread of alien plant species (Dar & Reshi 2015). However, as Lee (2002) explains, studies on the

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evolutionary genetics of invasive species suggest that the invasion success of many species might depend on their ability to respond to natural selection than on broad physiological tolerance or plasticity. Therefore, genomic approaches would be better alternatives to determine the invasive mechanisms, though this has not shown much progress to date.

The ability of an exotic plant to compete efficiently with native species is an important attribute in plant invasions (Levine *et al.* 2003). Evolution of increased competitive ability through novel pathways (Callaway & Aschehoug 2000), such as the presence of allelopathic chemicals (Elton 1958; Sax & Brown 2000) or through features like greater reproductive potential (Cronk & Fuller 1995) are often cited as facilitating alien exotics to become competitively superior to native plants. As Richardson *et al.* (2000) explain, many introduced plant species rely on mutualisms in their new habitats to overcome barriers against establishment and to become naturalized. For instance, animal mediated pollination and seed dispersal and, symbioses between plant roots and microbiota often facilitate invasions.

On the other hand, the invasibility of the ecosystem appears to be affecting the process of invasion by several ways. Disturbances in 'potentially invading ecosystems' (Cronk & Fuller 1995), which lead to short term fluctuations of resources (Davis *et al.* 2000; Walker *et al.* 2005) are reported as common features that lead to plant invasions. Invaders are better able to exploit new niches created by anthropogenic changes (MacDougall & Turkington 2005; Shea & Chesson 2002). However, more diverse communities have less unused niche spaces, which prevent invasions by alien plants (Elton 1958; Hierro *et al.* 2005; Kennedy *et al.* 2002; Levine 2000; Levine *et al.* 2004; MacArthur & Levins 1967; Stachowicz & Tilman 2005). In addition, by migrating to a novel ecosystem, alien plant species are escaped from their native parasites, pathogens or other natural enemies that occur in an invading host's native range (Blossey & Nötzold 1995; Darwin 1859; Keane & Crawley 2002; Mitchell & Power 2003; Torchin & Mitchell 2004) whereas the native populations are always depressed by the pathogens and other natural enemies.

Thus, the competitive performance of invasive species is often habitat-dependent (Daehler 2003; Joshi *et al.* 2015) and the relative performance of native and invasive species could vary depending on the amount of environmental stress (Alpert *et al.*

2000). There is ample evidence to elaborate that tolerance to drought (Cleverly *et al.* 1997), flood (Newman *et al.* 1996), turbidity (Thomsen & McGlathery 2007), low resources (Funk & Vitousek 2007) and lead contamination (Zhang *et al.* 2008) allowed some invasive species to outperform native species in a stressful environment.

Prosopis juliflora (Sw.) DC., which was reported as an aggressive invasive plant species in the world (Pasiiecznik *et al.* 2001), shows a wide spectrum of adaptations that enable it to successfully establish in new habitats. It has been recorded that this species produces some allelopathic compounds (Nakano *et al.* 2003; Noor *et al.* 1995) which may be the reason for the retardation of radical growth of wheat (Siddiqui *et al.* 2009) and mung bean (Perera *et al.* 2009). The presence of a deep-feeding (Raven *et al.* 2005) and well spreading (Pasiiecznik *et al.* 2001) root system was recorded for *P. juliflora* which enables efficient water absorption by the species, especially during drought periods, and thereby successfully compete with other native natural forest species. Mwangi & Swallow (2005) reported that native species in *P. juliflora* invaded areas in Kenya do suffer from water stress while several researchers have reported that the alien exotic species such as *Carpobrotus edulis* (L.) N.E. Br. (D'Antonio & Mahall 1991) and *Bromus tectorum* L. (Melgoza *et al.* 1990) cause to reduce the availability of water to native plants in some drought prone habitats. Like many other invasive species, *P. juliflora* could also be able to tolerate environmental stress conditions (Kumar & Mathur 2014), which can drive the species to invade into new habitats (Kercher & Zedler 2004; Uveges *et al.* 2002).

The current study focused on the competition between the exotic *P. juliflora* and the native canopy dominant tree *Manilkara hexandra* (Roxb.) Dubard in Bundala National Park (BNP), Sri Lanka. *Manilkara hexandra* forms a single species dominant canopy in Tropical Semi-deciduous (TSD) forests in BNP (Perera 2012) but dying back of individuals of the species is seen in *P. juliflora* invading areas in these forests. Dense thickets of *P. juliflora* were present closer to lagoons and inland water bodies. However, *M. hexandra* trees in such sites were found to be dead already. This highlighted the importance of studying the factors behind the invasion of *P. juliflora* and simultaneous die-back of *M. hexandra* in the same habitat. Therefore, field, glass house and laboratory experiments have been conducted to: (1) reveal whether *P. juliflora* is competitively superior to the native

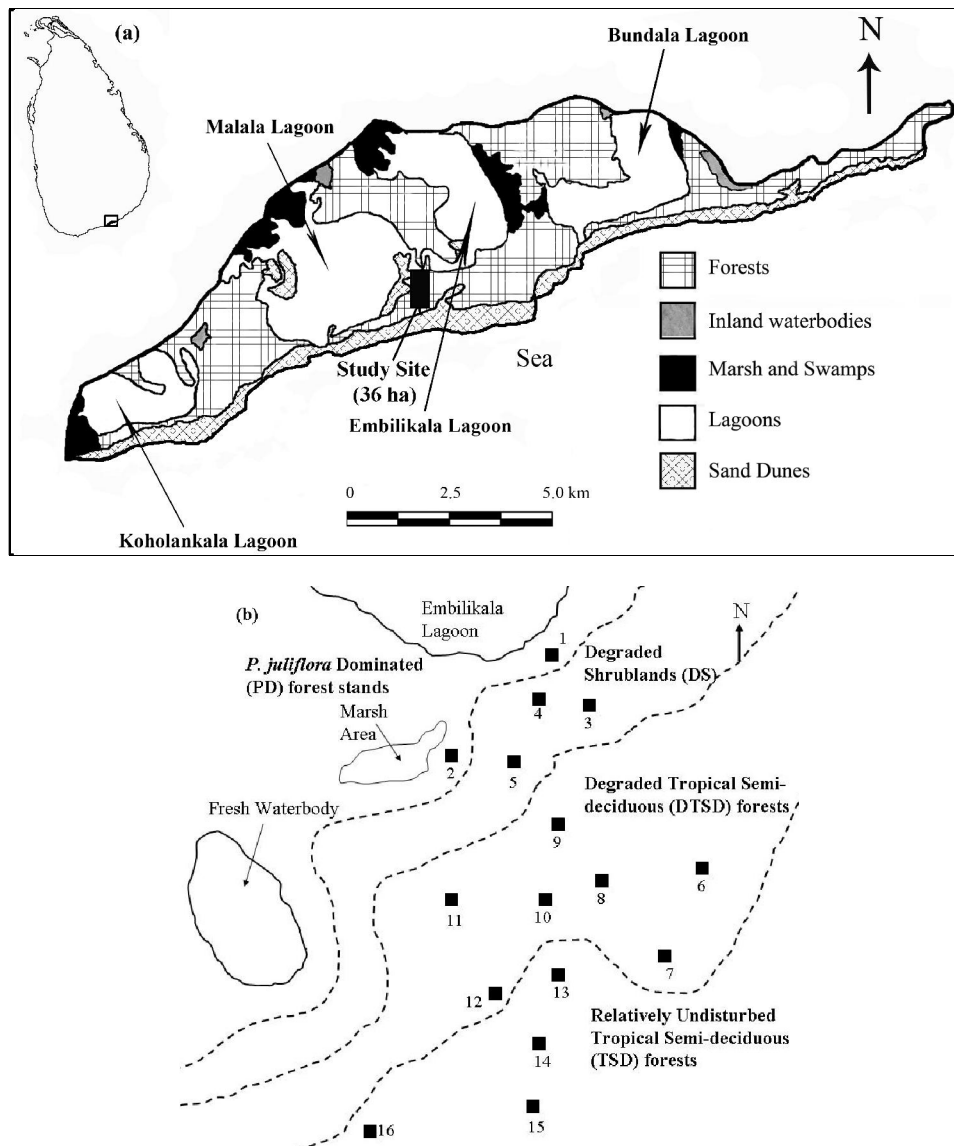


Fig. 1. (a) Map of Bundala National Park showing the study site and (b) Detailed diagram of the study site showing the distribution of experimental plots in different vegetation types.

M. hexandra, (2) investigate specific invasive traits of *P. juliflora*, which make it a successful invader in coastal habitats in the dry tropical areas in Sri Lanka and (3) predict that the die-back of the native dominant canopy tree species, *M. hexandra*, in the invading habitat could be an artefact of the invasion by *P. juliflora*.

Materials and methods

The methodology followed consisted of four major parts; field enumeration of *P. juliflora* and *M. hexandra* to detect the correlation between the abundances of the individuals of *P. juliflora* and

the dying back individuals of *M. hexandra*, seed germination bio-assay to demonstrate the presence of allelo-chemicals in the root extracts of *P. juliflora* and, two pot experiments to detect the competition between the two study species and the impacts of root extracts of *P. juliflora* on the growth performance of seedlings of *M. hexandra*.

Field sampling of individuals of M. hexandra and P. juliflora

Field enumeration of individuals of *P. juliflora* and *M. hexandra* was carried out in tropical semi-deciduous forests at the southern part of the Embilikala and Malala lagoons in BNP (Fig. 1a)

situated along the south coast of the Hambantota District in the low country dry zone of Sri Lanka ($6^{\circ} 08' - 6^{\circ} 14' N$, $81^{\circ} 08' - 81^{\circ} 18' E$) (CEA/Euroconsult 1993). The mean annual temperature of the area was $27.8^{\circ} C$ while the mean annual rainfall was 1059 mm (Fig. 2). The highest monthly rainfall is received in November during the North-East monsoon period. Although the mean annual relative humidity in the area varies between 54.6 - 91.9 %, it is higher than the annual average (75.9 %) only during the major rainy season (Gunarathne & Perera 2014).

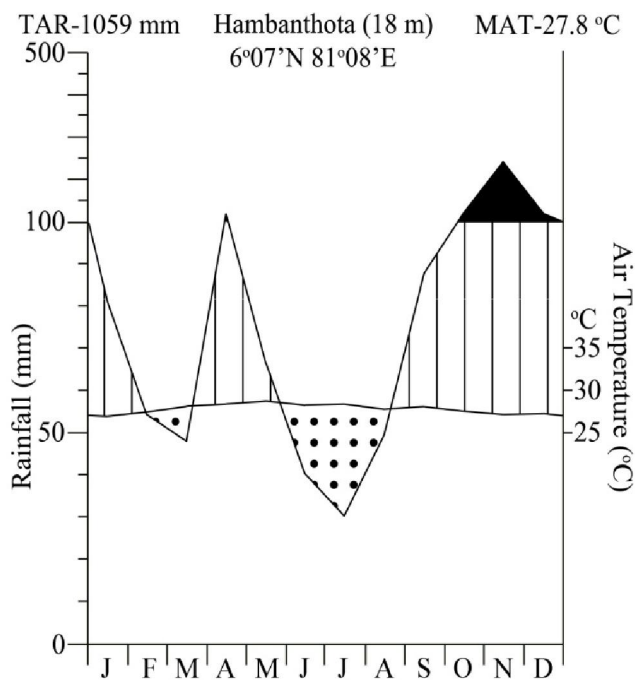


Fig. 2. Climatic diagram for the study area. Rainfall and temperature data were collected from the meteorological station at Hambanthota (5 km away from the study area) from 1995 to 2008.

The BNP extends over an area of 3698.01 ha. An area of 36 ha at the southern part of the Embilikala and Malala lagoons (Fig. 1b) containing four different forest physiognomies were demarcated by considering the features of the vegetation (forest structure and species composition) and the nature of disturbances operating in the area (mainly based on the presence of alien exotic plants and the amount of dead or dying-back individuals of *M. hexandra*). These four vegetation physiognomies include *P. juliflora* Dominated (PD) forest stands, Degraded Shrublands (DS), Degraded Tropical Semi-deciduous (DTSD) forests and Rela-

tively Undisturbed Tropical Semi-deciduous (TSD) forests (Gunarathne 2014) (Table 1).

Table 1. Distribution of experimental plots in various forest stands where different levels of disturbances operated.

Description of the vegetation type	Nature of disturbances	Plot number in Fig. 1b
<i>P. juliflora</i> Dominated (PD) forest stands	Heavily disturbed by tree dieback and by the invasion of alien exotics especially <i>P. juliflora</i> .	1, 2
Degraded Shrublands (DS)	Heavily disturbed by tree dieback and animal activities. Alien exotic plants also common.	3, 4, 5
Degraded Tropical Semi-deciduous (DTSD) forests	Moderately disturbed due to tree dieback, presence of unhealthy canopy trees and animal activities.	6, 7, 8, 9, 10, 11, 12
Relatively Undisturbed Tropical Semi-deciduous (TSD) forests	Less disturbed due to occasional tree dieback and animal activities may be present.	13, 14, 15, 16

Sixteen random points, devised using a random number generator, were marked on a digitized map of the selected study site using ArcGIS 9.3.1® software, and their locations (latitude and longitude of each point) were noted. In the field, the sixteen locations were identified and $20 \times 20 m^2$ experimental plots and established centering each selected point, in a Complete Randomized Design (Fig. 1b). The number of individuals of *P. juliflora* and *M. hexandra* in these experimental plots were counted over a period of two months. Individuals of the two species were examined in the experimental plots established and were recorded as healthy, dying-back or as dead trees. *Manilkara hexandra* is a brevidciduous tree which defoliates seasonally but shows about 10 - 15 % defoliation even out of season of the leaf shedding event (Gunarathne &

Perera 2014). Therefore, if the percentage defoliation of an individual was less than 15 % of the total crown area, it was considered as a healthy tree.

Competition between P. juliflora and M. hexandra

One month old seedlings of *M. hexandra* and *P. juliflora* were grown together in plastic pots according to the experimental protocol described by Donald (1958) enabling four competition conditions to operate (four different treatments as given in Table 2). As depicted in Fig. 3, the pots were partitioned using plastic sheets to prevent the below ground competition where necessary. To avoid the above ground competition, a transparent polythene sheet was used. Thus, in the treatment 1 (control experiment), any above or below ground competition between the individuals of the two species was not present as the two individuals were separated at both above and below ground levels. In the treatment 2, above ground competition was allowed but below ground competition was absent because the two species were planted in two different compartments. In the treatment 3, below ground competition was allowed as both species were planted in the same compartment but the above ground competition was absent. However, in the treatment 4, both above ground and below ground competition was allowed to operate. Thus, forty seedlings of *M. hexandra* were grown with a similar number of *P. juliflora* seedlings so as to have 10 replicates per treatment.

Table 2. Nature of competition operating between seedlings of *P. juliflora* and *M. hexandra* in each treatment.

Treatment no.	Nature of competition
1 (control)	No above or below ground competition between two species
2	Above ground competition may be present but no below ground competition
3	Below ground competition may be present but above ground competition is absent, suppression by allelopathic compounds may be present
4	Both above ground and below ground competition and suppression by allelopathic compounds may be present

The potting mixture for the experiment included well drained garden soil:sand:compost at a ratio of 4:1:1 and the pots were arranged according to the Complete Randomized Design (CRD). During the experimental period, all pots were maintained at optimal moisture levels and, thus, a similar volume of water (10 ml) was provided to each four compartments to keep the soil at near field capacity levels. Height, root collar diameter and number of leaves of each seedling of *M. hexandra* were recorded monthly. After 17 months, at the end of the experiment, seedlings were carefully uprooted and rinsed with tap water. Subsequently, roots were separated from shoots and collected in separate, labeled paper bags. These samples were oven dried at 55 °C until a constant weight was reached. Finally, the weight measurements were taken using a precision balance (Denver Instrument, XP-300®).

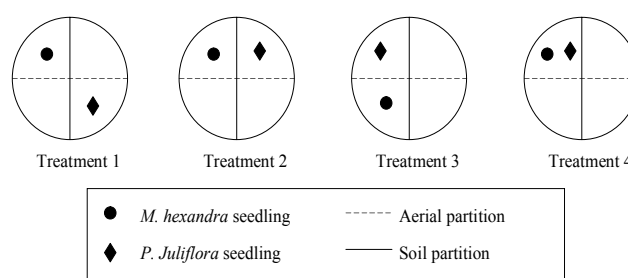


Fig. 3. Layout of seedlings grown in different treatments to depict how the above and below ground competition between *P. juliflora* and *M. hexandra* seedlings was manipulated.

Seed germination

Seeds of Mung bean [*Vigna radiata* (L.) Wilczek] and mustard [*Brassica juncea* (L.) Czern.] were used in the bio-assay as these two species germinate robustly with a high percentage germination. First, an aqueous root extract of *P. juliflora* was prepared by grinding 10 g of the root tissues with 100 mL of distilled water, shaking for six hours in an orbital shaker (at 60 rpm) and filtering through a 'Whatmann-42' filter paper using a suction pump. Seeds of Mung bean (*V. radiata*) were soaked in a concentration series of root extract of *P. juliflora* (0 %, 0.1 %, 2 %, 5 % and 10 %) for 48 h in six replicates. Each treatment consisted of 300 healthy seeds. Soaked seeds were placed in labeled sterilized plastic Petridishes (14.4 cm in diameter) on tissue papers wetted with the relevant concentration of the root extract (25 ml). These Petridishes were placed in sterilized

growth chambers in Completely Randomized Design. Growth chambers were maintained at a temperature between 25 - 30 °C, a humidity of 70 % and 12 hour dark and 12 hour light conditions. These were observed over a period of 10 days and the number of seeds germinated was recorded. As no new seeds in the control experiment germinated after five days of the commencement of the experiment, the total number of seeds germinated in all treatments by the fifth day was counted for analyses. The same procedure was followed for mustard (*B. juncea*) seeds and the number of seeds germinated was recorded after five days.

Effects of root extracts from P. juliflora on the growth performance of M. hexandra seedlings

Fifty seedlings of *M. hexandra* at two different age groups, i.e. 10 months old seedlings (32 seedlings) and 17 month old seedlings (18 seedlings) were used for this study. Seedlings were grown in pots containing a well-drained, fertile soil mixture (garden soil:sand:compost; 4:1:1). These were provided with adequate amount of water at near field capacity levels and allowed to be established over a period of 2 months. Then, seedlings of each age category were separated into two groups. One set of seedlings was treated daily with 25 ml of 1 % freshly prepared root extract of *P. juliflora*. After three months from the starting date of the experiment, the concentration of the extract applied was increased up to 5 %. The other set of seedlings was treated as the control experiment and 25 mL of distilled water was applied to these instead of the root extract. The height, root collar diameter and the number of leaves in each seedling were recorded once a month. After 9 months, at the end of the experiment, the seedlings were uprooted and the root biomass and shoot biomass of each individual was measured.

Data analyses

Relative densities of *M. hexandra* and *P. juliflora* were calculated with respect to the four vegetation types identified, and these were statistically compared by performing Kruskal-Wallis test while the correlation between the number of individuals of *P. juliflora* and the number of dead individuals of *M. hexandra* per plot was detected by performing a Pearson product moment correlation test using the MINITAB statistical package (Version: 16.1.0.0). For the seed germination bioassay, the percentage germination of mung bean and mustard seeds was calculated and these values

were statistically tested using two-way ANOVA using MINITAB statistical package (Version: 16.1.0.0). Statistical tests were performed using MINITAB statistical package (Version: 16.1.0.0) to find out the growth performance of seedlings among different treatments. Except for the seedling biomass data, the difference between initial and final readings of each parameter measured was considered in the statistical analyses. Where applicable, root/shoot ratio of *M. hexandra* and *P. juliflora* was calculated and the variation of this parameter between the two species was statistically compared by performing two-sample t-test using MINITAB statistical package (Version: 16.1.0.0). The Competitive Balance Index (C_b) was calculated using the following equation described by Wilson (1988).

$$C_b = \log_e \frac{W_{ab}/W_{ba}}{W_{aa}/W_{bb}}$$

where,

W = dry weight per original planted plant

a = *M. hexandra* seedling

b = *P. juliflora* seedling

W_{aa} = dry weight of *M. hexandra* seedlings in monoculture

W_{bb} = dry weight of *P. juliflora* seedlings in monoculture

W_{ab} = dry weight of *M. hexandra* growing in association with *P. juliflora*

W_{ba} = dry weight of *P. juliflora* growing in association with *M. hexandra*

Results

Many mature individuals of *M. hexandra*, which grew closer to lagoons and inland water bodies appeared to be dead or dying-back. However, those situated far away from water bodies appeared to be healthy. In contrast, almost all individuals of *P. juliflora* present in the study area did not show any disease symptoms. Therefore, firstly, the spatial patterns of the two study species were described and secondly, whether the death of *M. hexandra* could be due to the competition or allelopathic effects of *P. juliflora* was proven through several *in vitro* experiments as given below.

Density and healthiness of M. hexandra and P. juliflora

The relative density of *P. juliflora* was significantly higher in heavily disturbed vegetation (PD forest stands and DS) than in

moderately disturbed (DTSD) forests (Kruskal-Wallis test, $P = 0.007$) but no individuals of *P. juliflora* were found in relatively less disturbed TSD forest plots (Fig. 4). DTSD forests also consisted of a significantly higher number of dead individuals of *M. hexandra* (Kruskal-Wallis test, $P = 0.007$). Thus, a strong positive correlation was observed between the number of individuals of *P. juliflora* and the number of dead individuals of *M. hexandra* over the study area ($r^2 = 0.846$, $P < 0.001$, $n = 16$). All individuals of *M. hexandra* in relatively less disturbed TSD forest plots were healthy but a majority of the individuals of the species in DTSD forest plots showed signs of tree die-back.

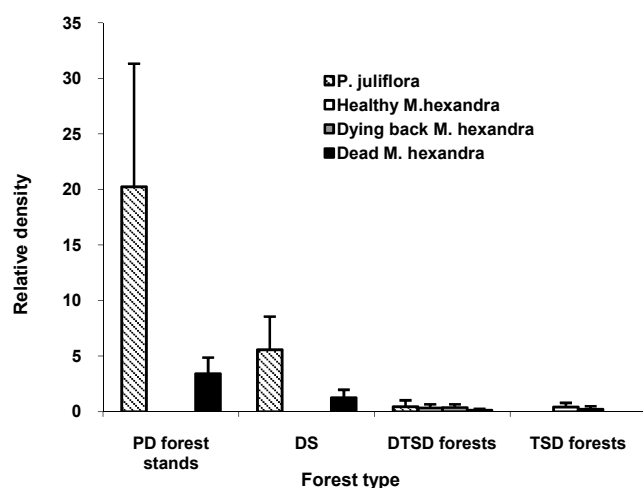


Fig. 4. Relative density of individuals of *M. hexandra* and *P. juliflora* in forests at different disturbance regimes with 95 % confidence limits.

Growth performance of M. hexandra under competition exerted by P. juliflora

No significant differences were found between initial and final measurement of each parameter among four treatments (one-way ANOVA - for root collar diameter: $F_{(3, 35)} = 0.28$, $P = 0.84$; for height: $F_{(3, 35)} = 0.36$, $P = 0.78$; for number of leaves: $F_{(3, 38)} = 1.90$, $P = 0.15$; and for number of branches: $F_{(3, 35)} = 1.49$, $P = 0.23$) (Fig. 5). Shoot, root and total biomass of seedlings of *M. hexandra* (Fig. 6) were slightly higher in the control experiment than in the other treatments but these variations were also not statistically significant (one-way ANOVA - for shoot biomass: $F_{(3, 35)} = 1.08$, $P = 0.37$; for root biomass: $F_{(3, 35)} = 0.24$, $P = 0.87$; and for total biomass: $F_{(3, 35)} = 0.78$, $P = 0.509$).

The growth rate of *P. juliflora* in the control

experiment was greater than that of *M. hexandra*. The increment of the root collar diameter (Fig. 7a) and the total biomass (Fig. 7b) of *P. juliflora* were significantly higher than that of *M. hexandra* when the two species were grown separately (t-test - for the increment of root collar diameter: $t = 6.90$, $df = 17$, $P < 0.001$; and for total biomass: $t = 10.08$, $df = 8$, $P < 0.001$). However, the root:shoot ratio of *M. hexandra* was significantly higher than that of *P. juliflora* (t-test: $t = 2.53$, $df = 12$, $P = 0.027$) (Fig. 7c). The calculated values for the competitive balance (C_b) for the shoot and root competitions between *M. hexandra* and *P. juliflora* were as low as 0.15 and 0.16, respectively (Fig. 7d).

Seed germination

Percentage germination of mung bean and mustard seeds were significantly different between the treatments and species with a significant interaction (Two way ANOVA - for the concentration of the root extract: $F_{(4, 92)} = 30.77$, $P < 0.01$; for the species, $F_{(1, 92)} = 14.66$, $P < 0.01$; for interaction: $F_{(4, 92)} = 7.68$, $P < 0.01$). Percentage germination of seeds of mung bean decreased with the increased concentration of the root extract of *P. juliflora* (Table 3). However, the percentage germination of mustard seeds was reduced only at higher concentrations of the root extract.

Impact of allelopathic compounds of P. juliflora on growth performance of M. hexandra seedlings

The average height increment, increment of number of leaves and number of branches, root biomass, shoot biomass and total biomass of *M. hexandra* did not vary significantly among the seedlings of two different ages, i.e., initially 10 month and 17 month old seedlings for both control and treatment groups (t-test, $P > 0.05$). Therefore, these growth performance parameters were further analysed to find out the differences between the seedlings in control (without root extract of *P. juliflora*) and treatment (with the root extract of *P. juliflora*) groups irrespective of the seedling age and the results are given in Table 4. However, there were no statistically significant differences among the seedlings in treatment and control groups for any of the studied seedling growth performance parameters (t-test; $P > 0.05$) when they do not experience any environmental stress conditions such as water stress.

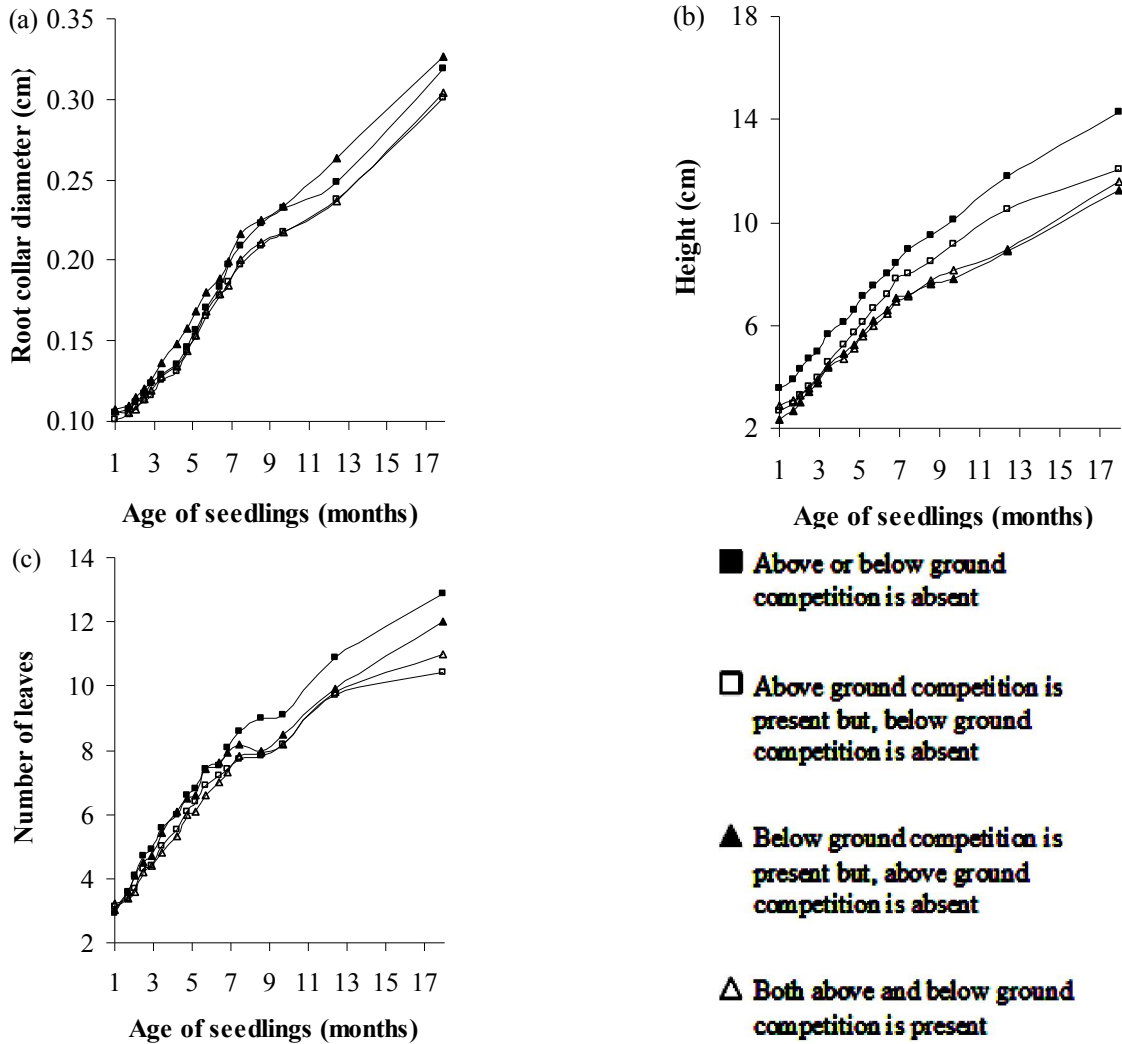


Fig. 5. Growth performance of *M. hexandra* seedlings over a period of 17 months given as average values of: (a) root collar diameter, (b) height and (c) number of leaves.

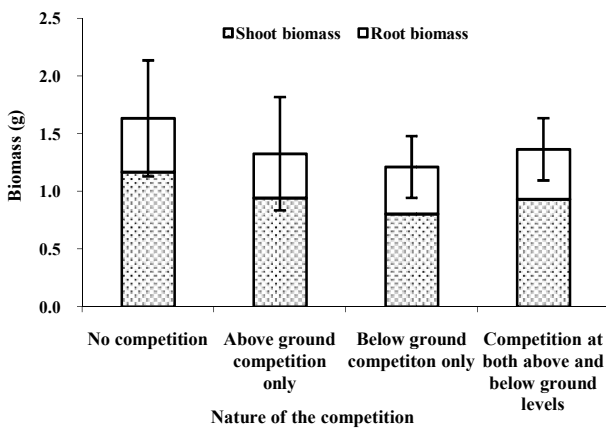


Fig. 6. Shoot and root biomass of *M. hexandra* seedlings in four competition regimes (95 % confidence limit is given for the total biomass).

Discussion

Changing forest structure due to plant invasions is a common phenomenon in many invaded habitats (Holway *et al.* 2002). As the forest canopy of tropical semi-deciduous forests at BNP comprises *M. hexandra* alone (Perera 2012) its die-back appears to be changing the ecosystem immensely. The high correlation between the number of dead individuals of *M. hexandra* and the density of *P. juliflora* could be interpreted as an evidence for the adverse impacts of the invasion of *P. juliflora* in this habitat though strategic investigations on the biotic interactions between the two species should be necessary to understand whether the die-back of *M. hexandra* is truly an artefact of the invasion of *P. juliflora*. Testing of

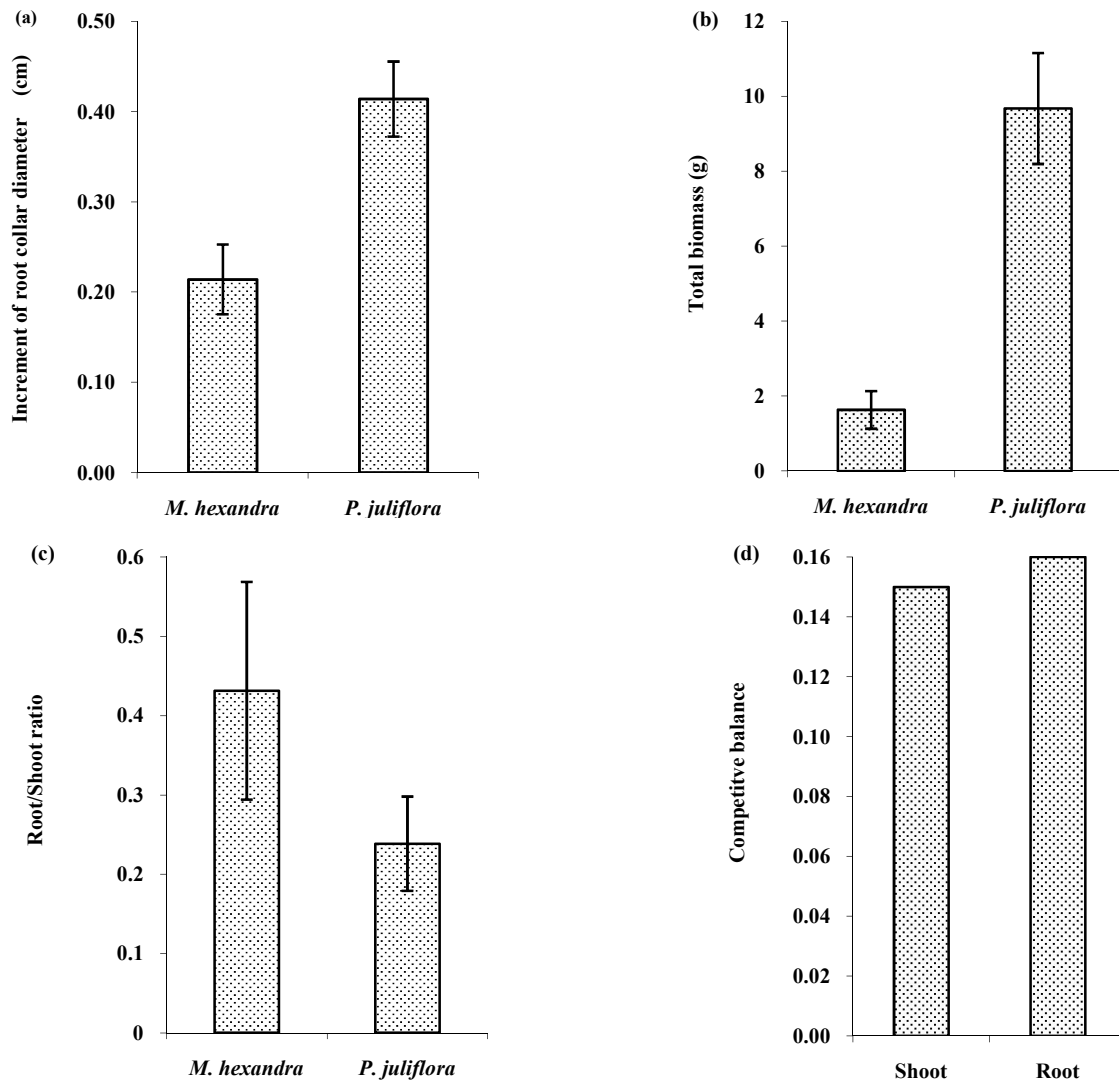


Fig. 7. Growth performance of *M. hexandra* and *P. juliflora* in the absence of competition (control experiment): (a) increment of the root collar diameter, (b) total biomass, (c) root: shoot ratio and (d) competitive balance.

Table 3. Percentage germination of mung bean and mustard seeds at different concentrations of the root extract of *P. juliflora*.

Concentration of the root extract of <i>P. juliflora</i> (%)	Percentage (%) seed germination (with SEM)	
	Mung bean	Mustard
0 (Control)	98.7 ± 0.7	67.8 ± 3.0
0.1	90.6 ± 1.7	70.0 ± 2.5
2	88.7 ± 3.0	65.1 ± 2.7
5	74.8 ± 3.3	57.7 ± 3.0
10	22.8 ± 4.5	44.3 ± 6.2

SEM = standard error of the mean.

the impacts of *P. juliflora* on *M. hexandra* or the competition between the two species is difficult to monitor directly because the water stress conditions similar to field conditions are difficult to create under shade house environments. Therefore, an indirect approach was used to detect the impacts of *P. juliflora* on *M. hexandra*, and the competition between the two species by creating a water-stress free condition assuming that the deviations of the nature of interactions from the field condition if detected could arise due to the lack of seasonal drought stresses.

Results of the pot experiment reveal that *P. juliflora* is not competitively superior than *M. hexandra* in well moist soil conditions. The growth

Table 4. Growth performance of *M. hexandra* seedlings in the presence and absence (control experiment) of the root extract of *P. juliflora*.

Growth performance parameters	Number of seedlings per treatment	Average values and SEM	
		Control experiment	With addition of root extract of <i>P. juliflora</i>
Number of leaves	50	38 ± 3	36 ± 4
Number of branches	50	8 ± 4	7 ± 1
Root collar diameter (cm)	50	0.57 ± 0.03	0.54 ± 0.02
Height (cm)	50	25.7 ± 1.2	25.4 ± 1.6
Shoot biomass (g)	49*	5.80 ± 0.47	5.20 ± 0.53
Root biomass (g)	49*	3.04 ± 0.23	2.80 ± 0.24
Total biomass (g)	49*	8.84 ± 0.65	8.00 ± 0.74

*One seedling was damaged due to pest attack just before harvesting to detect biomass.

performance of *M. hexandra* and *P. juliflora* seedlings that grew together was more or less the same as in the corresponding control experiments (i.e. with no competition) under optimal moisture conditions. Low values of C_b obtained for the above and below ground competition between the two species further confirm a poor competition between the two species in well moist soil conditions. Moreover, higher root : shoot ratio observed for *M. hexandra* seedlings grown in stress free conditions indicates that *M. hexandra* is able to perform well in stress free conditions. Thus, our study agrees with Daehler (2003) that the performance of native species was equal to that of invader, at least, for some growing conditions.

In general, the growth rate of *P. juliflora* is much faster than that of *M. hexandra*, and this was also clearly observed during shade house experiments. Therefore, a significant above ground competition between the seedlings of the two species for space and light might have not existed when these two species were grown together in pots. When the two species naturally grow together in forests, they occupy different synusia as the maximum heights of mature individuals of the two species are different in natural conditions. *Manilkara hexandra* trees grow up to 15-20 m in height and dominate the forest canopy while *P. juliflora* trees grow up to about 10 m and, therefore, the above ground competition may not cause a significant impact on *M. hexandra* despite the fact that *P. juliflora* may heavily compete with the other native species in the same synusia for above ground resources. In contrast, a below ground competition between the two species may exist, especially for water.

Prosopis juliflora is known to fix atmospheric nitrogen through rhizobia in its root nodules (Miettinen 1989; Mwangi & Swallow 2005, 2008; Olivares *et al.* 1988; Zhang *et al.* 1991). Nitrogen is one of the major nutrients that determine the growth of plants (Turner & Lambert 2005), and high nitrogen fertility may cause to reduce the impact of other stresses experienced by *M. hexandra* if soil water is adequately present in shade house experiments.

The root extract of *P. juliflora* possesses allelopathic chemicals as proved by mung bean and mustard seed germination assays. Siddiqui *et al.* (2009) also found that the germination of wheat seeds was suppressed by the root extract of *P. juliflora*. Nakano *et al.* (2003) have identified that L-tryptophan, Syringin and (-)-lariciresinol are the allelopathic compounds present in *P. juliflora*. In natural conditions, these allelopathic compounds of *P. juliflora* may not accumulate in the soil as these are washed away with the rain water (Nakano *et al.* 2003). Similarly, these allelopathic chemicals may be washed away from pots, which are well watered and, hence, may not create a significant adverse impact on the growth performance of *M. hexandra* seedlings grown in pots. However, the allelopathic chemicals of *P. juliflora* may act as good weapons in suppressing the germination of seeds of native plants in dry regions of Sri Lanka (Jayasinghe & Perera 2011; Perera *et al.* 2009), and they may, thus, be able to invade alien habitats in seasonal climatic conditions with fluctuating soil moisture levels.

In BNP, drought periods occur in two seasons per year; the major dry spell from June to September or October and the minor dry spell from

February to March. During these drought periods, the monthly evapotranspiration exceeds the monthly rainfall (Piyankarage *et al.* 2004). Hence, a water scarcity may occur during drought periods and, then, the two species may compete for water. Fast growth rate of *P. juliflora* (estimated by the rate of increment of root collar diameter and the total biomass) indicates that the species requires more water. Mwangi & Swallow (2005) have also pointed out that the lands invaded by *P. juliflora* suffer from water stress as they draw water from the ground water table. The species has several adaptations for the purpose. Highly dispersed root system of *P. juliflora* (Pasiczek *et al.* 2001), which may extend up to about 50 m in the soil (Raven *et al.* 2005) and its fast growth are, thus, good invasive traits, which facilitate the species to invade drought prone lands successfully. Moreover, *P. juliflora* thrives well in BNP where the soils indicate high salinity levels (Perera *et al.* 2002), and this would also be a reason for the high invasibility of *P. juliflora* in this coastal dry habitat.

Manilkara hexandra trees in *P. juliflora* invading areas are gradually dying-back, and the die-back symptoms intensify in subsequent drought periods. Such incidences have been reported from other areas in the world as well. For instance, Khan *et al.* (1994) have reported tree die-back in a tropical dry forest in Gir Lion Sanctuary and National Park, Gujarat, India, where the drought conditions were associated with increased mortality levels of 13 plant species in the park. Such weakened trees are liable to be further attacked by secondary pathogens, such as canker forming fungi, which have been reported on live trees of *M. hexandra* in the study area (Perera 2007). Severe defoliation in dying-back individuals and their ultimate death may change the level of penetration of light to the forest floor and, thus, may pave a way for more individuals of invasive species to establish and spread further in the area.

Conclusions

Although *P. juliflora* possesses specific invasive traits, such as extended root system and allelopathic chemicals, the species is not competitively superior to the native *M. hexandra* in well moist soil conditions. Fast growing *P. juliflora* can efficiently draw ground water through its extended root system, which probably creates a water scarcity during drought periods and may lead to the die-back of *M. hexandra*. Water soluble

allelopathic compounds of *P. juliflora* may be easily washed away with rain water and, thus, may not create a severe impact on *M. hexandra* under well moist soil conditions. This study, therefore, highlights the necessity of controlling the alien exotic *P. juliflora* in vulnerable habitats in seasonally dry environments.

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