Journal of Plant Ecology Advance Access published April 10, 2009

Journal of
Plant Ecology
PAGES 1–7
doi: 10.1093/jpe/rtp006

Comparative response of seedlings of selected native dry tropical and alien invasive species to CO_2 enrichment

Purnima Raizada[1,*], *Anamika Singh*[2] *and A. S. Raghubanshi*[1]

[1] *Ecosystems Analysis Laboratory, Centre of Advanced Study in Botany, Banaras Hindu University, Varanasi 221005, Uttar Pradesh, India*
[2] *Department of Botany, Punjab University, Chandigarh 160014, Punjab, India*
*Correspondence address. Ecosystems Analysis Laboratory, Centre of Advanced Study in Botany, Banaras Hindu University-221005, India. Tel: 05422368399; Fax: 05422368174; E-mail: purnimaraizada@gmail.com

Abstract

Aims
Global climate change and ongoing plant invasion are the two prominent ecological issues threatening biodiversity world wide. Among invasive species, *Lantana camara* and *Hyptis suaveolens* are the two most important invaders in the dry deciduous forest in India. We monitored the growth of these two invasive species and seedlings of four native dry deciduous species (*Acacia catechu*, *Bauhinia variegata*, *Dalbergia latifolia* and *Tectona grandis*) under ambient (375–395 μ mol mol^{-1}) and elevated CO_2 (700–750 μ mol mol^{-1}) to study the differential growth response of invasive and native seedlings.

Methods
Seedlings of all the species were exposed to ambient and elevated CO_2. After 60 days of exposure, seedlings were harvested and all the growth-related parameters like plant height; biomass of root, stem and leaves; total seedling biomass; R/S ratio; allocation parameters; net assimilation rate (NAR) and relative growth rate (RGR) were determined.

Important Findings
Biomass, RGR and NAR of all the species increased under elevated CO_2 but the increase was higher in invasive species and they formed larger seedlings than natives. Therefore under the CO_2-enriched future atmosphere, competitive hierarchies could change and may interfere with the species composition of the invaded area.

Keywords: dry deciduous seedlings • elevated CO_2 • global change • plant invasion

Received: 7 January 2009 Revised: 5 March 2009 Accepted: 8 March 2009

INTRODUCTION

Tropical dry deciduous forests occupy 28.6% of the forested area in India (MoEF 2006). These forests are under great pressure due to increasing industrialization, repeated lopping of trees and shrubs for fuel wood or leaf fodder and heavy grazing (Jha and Singh 1990). All these factors lead to loss of biodiversity (Jha *et al.* 2005), and could promote occurrence of non-native opportunistic species in these forests. These non-native invasive species are now among the most urgent ecological problems and will be an increasingly prominent issue in the foreseeable future (Drake *et al.* 1989). Further, these species are likely to emerge more competitive in the global change scenario (Dukes and Mooney 1999; Mooney and Hobbs 2000).

Among the principal global changes, increased atmospheric loading of CO_2, which leads to global warming, is the most important. Atmospheric CO_2 has been rising continuously from 280 μ mol mol^{-1} at the start of industrial revolution to its current level of 379 μ mol mol^{-1}. This continuously increasing CO_2 due to fossil fuel burning and deforestation is expected to reach 550 μ mol mol^{-1} in the middle of this century and to exceed 700 μ mol mol^{-1} by its end (Alley *et al.* 2007). The elevated CO_2 affects plants either by increasing carbon fixation due to repression of photorespiration and increased substrate supply or by decreased water loss due to partial closure of stomata or by CO_2-driven changes in ecosystem nutrient dynamics and changed soil structure (Singh *et al.* 2006); thus, population dynamics will be affected. This will ultimately

affect ecosystem functions and subsequently evolution (Gutschic 2007; Körner 2003; Ward and Kelly 2004). The rise in CO_2 availability directly impacts photosynthetic processes, evoking a wide range of physiological and morphological responses in plants. These vary among species, depending on differences in photosynthetic pathways, intrinsic growth rates and other properties. Prominent responses include changes in growth rates (Poorter 1993), allocation patterns (Bazzaz 1990), water use efficiency (Nowak *et al.* 2004) and nutrient uptake rates (Jackson and Reynolds 1996). Further, rising atmospheric CO_2 concentration may favourably affect seedling growth in the forest understorey, and might contribute to improved establishment of invasive species (Bond and Midgley 2000; Dukes 2000; Dukes and Mooney 1999; Hattenschwiler and Körner 2003; Polley *et al.* 2003; Salo 2005; Song *et al.* 2009; Weltzin *et al.* 2003; Ziska 2003).

If the native and invasive species respond differentially to CO_2 enrichment, competitive hierarchies may change, and structure and function of the forest may be affected. In the present paper, we investigated how the seedlings of widespread invaders *Lantana camara* L. and *Hyptis suaveolens* Poit. respond to elevated CO_2 in comparison to those of native woody species.

MATERIALS AND METHODS

Study area

The present study was conducted in the experimental plots of the Botanical Garden of the Department of Botany, Banaras Hindu University, Varanasi. The Botanical Garden is located at 25°18′ N latitude and 80°01′ E longitude at 126 m above the mean sea level. The soil of the study area has been characterized as Banaras Type III by Agarwal and Mehrotra (1953).

Species selection

Native dry deciduous tree species, *Acacia catechu* Willd., *Bauhinia variegata* Roxb., *Dalbergia latifolia* Roxb. and *Tectona grandis* Roxb. and invasive species *L. camara* L. and *H. suaveolens* Poit. were selected for the study. These two invasive species pose a considerable threat to the integrity of Vindhyan forests and are well known for their ability to colonize productive lands by displacing the natural flora and are also included among the top 10 invasive species of India (Raghubanshi *et al.* 2005).

Seed germination and seedling acclimatization

Mature fruits of all species were collected from full-grown flowering branches of approximately 50 plants from the local populations near the study site. Seeds were first surface sterilized by immersion in 0.1% $HgCl_2$ for 30 s, washed thoroughly with water and then kept in Petri plates for germination. Another set of Petri plates was kept in CO_2 enrichment chamber to study the effect of elevated CO_2 on seed germination. Both the germination experiments were performed in triplicate. One-week-old seedlings of each species, visually uniform in size, were transplanted into earthen pots (≈1 700 cm^3) on one seedling per pot basis. The soil in the pots was sandy loam inceptisol (33% sand and 16% clay) having 33% water holding capacity (WHC). Organic C, total N and total P in the soil were 2.4, 0.18 and 0.03%, respectively (Singh *et al.* 2007). The transplanted seedlings were equally well watered during the first 3 weeks and subsequently subjected to two CO_2 levels, ambient (375–395 μ mol mol^{-1}) and elevated (700–750 μ mol mol^{-1}). In the present study, no significant effect of elevated CO_2 on seed germination was observed.

CO_2 enrichment experiment

For exposing seedlings to elevated CO_2, a method described by Devakumar *et al.* (1996) and Khurana and Singh (2004) was followed. This is a low-cost method using decomposing organic matter as a source of CO_2 and provides nearly natural conditions to the growing seedlings. In this method, elevated CO_2 was generated by the decomposition of organic manure in rectangular trenches, which were roofed by polythene-covered frames. Seedlings were exposed to elevated CO_2 between 3:30 p.m. and 11:00 a.m. Thus, each day seedlings were exposed to elevated CO_2 for 19.5 h, which included 7-day light hours.

For ambient CO_2 level, another set of trenches was left uncovered without organic matter. Other types of low-cost methods are also recommended by Idso (1997). During the study period, CO_2 concentration was measured with LC 'pro' portable photosynthesis system (ADC, 1985; Scinoken International, UK) that was calibrated against known CO_2 standards. Excess buildup of CO_2 gas was released by small outlets in the polythene frames to the desired level of CO_2. The experiment was conducted in triplicate. Total 12 (2 treatments × 3 replicates × 2 samplings) pots per species were used in the experiment. Treatment comprised ambient (375–395 μ mol mol^{-1}) and elevated CO_2 (700–750 μ mol mol^{-1}). The moisture level in the pots was measured at every alternate day and kept constant at 50% WHC using Theta probe (Delta T Device Ltd., England) during the study period to avoid any effect of variation in soil moisture on seedling growth.

Plant sampling and data analysis

From the total 12 plants, a set of 3 plants per species was harvested prior to exposure to elevated CO_2 for recording initial growth data for each species. After 60 days of exposure to elevated CO_2, three seedlings of each species per treatment were randomly harvested; roots were thoroughly washed with water. The harvested plants were transported to the laboratory. Plants were then separated into leaves, stem and root. Height, root length and number of leaves were recorded for each plant. All plant parts were oven-dried at 80°C to constant weight and their biomass was recorded. Total biomass (per plant) is reported on a dry weight basis. Different biomass partition parameters like root shoot ratio, root mass fraction, stem mass fraction, leaf mass fraction and leaf area ratio were determined.

In addition to these traits, growth parameters like specific leaf area, relative growth rate and net assimilation rate were assessed in order to elicit response of these species in the CO_2-rich atmosphere. Formulae to analyse different allocation parameters and growth traits are given below.

Root shoot ratio (R/S): Root dry weight/Shoot dry weight

Root mass fraction (RMF): Root dry weight/Plant dry weight

Stem mass fraction (SMF) : Stem dry weight/Plant dry weight

Leaf mass fraction (LMF) : Leaf dry weight/Plant dry weight

Leaf area ratio (LAR) : Leaf area/Plant dry weight

Specific leaf area (SLA) : Leaf area/Total dried leaf biomass

$$\text{Relative growth rate (RGR)} : (\ln W_2 - \ln W_1)/(T_2 - T_1)$$

$$\text{Net assimilation rate (NAR)} : [(W_2 - W_1)/(T_2 - T_1)] \times [(\ln L_2 - \ln L_1)/(L_2 - L_1)]$$

W_1 and W_2 represent total plant dry weight at time T_1 and T_2 and L_1 and L_2 correspond to the total leaf weight at time T_1 and T_2.

Statistical analysis

Effect of different factors, *viz.* species, CO_2 levels and the two-way interactions on seedling growth, were statistically examined through multivariate analysis of variance (ANOVA). Unbalanced ANOVA was conducted to test for significance of differences due to species type (four native and two invasive species), CO_2 and their interaction. Relationship between weight ratios ($biomass_{ele}$/$biomass_{amb}$) at 60 days of exposure to elevated CO_2 and SLA was examined through regression analysis. SPSS package was used for all statistical analyses (SPSS 1997).

RESULTS

In this study, growth performance of seedlings significantly differed across species. CO_2 level significantly affected plant height ($F_{1,24}$ = 46.352, P = <0.001), total biomass ($F_{1,24}$ = 26.022, P = <0.001), SLA ($F_{1,24}$ = 7.165, P = <0.05), RGR ($F_{1,24}$ = 32.695, P = <0.001) and NAR ($F_{1,24}$ = 11.116, P = <0.005). The species × CO_2 level interaction was significant only for plant height ($F_{5,24}$ = 4.326, P = <0.05), total biomass ($F_{5,24}$ = 3.574, P = <0.05) and RGR ($F_{5,24}$ = 5.383, P = <0.005). Except for plant height, total biomass and LMF, all growth parameters differed between native and invasive species (Table 1). Species type × CO_2 level interaction was significant only for total biomass, RGR and NAR.

Elevated CO_2 significantly promoted the growth of seedlings of all six species. At the end of experiment, percent increase in height in the seedlings of invasive species was more than that in the native tree seedlings (Fig. 1). Maximum percent enhancement was observed in *H. suaveolens* followed by *L. camara*. Among the native species, *B. variegata* responded least to elevated CO_2 (Fig. 1) while *D. latifolia* showed maximum increase in height.

Plants accumulated more biomass under elevated CO_2 as exhibited by their weight ratios ($biomass_{ele}$/$biomass_{amb}$) (Fig. 2). Total plant biomass after 60 days varied significantly among species ($F_{5,24}$ = 8.436, P = <0.001) and between CO_2 level ($F_{1,24}$ = 26.022, P = <0.001). Species × CO_2 interaction was also significant ($F_{5,24}$ = 3.574, P = <0.05). Invasive species realized higher plant height and weight ratios than the native dry deciduous seedlings. *Tectona grandis* showed the least increment in biomass and *A. catechu* the maximum weight gain under CO_2-enriched atmosphere. Among invasive species, *H. suaveolens* showed more weight gain than *L. camara*.

Biomass allocation parameters differed significantly among species (RMF: $F_{5,24}$ = 22.161, P = <0.001; SMF: $F_{5,24}$ =47.508, P = <0.001; LMF: $F_{5,24}$ = 14.564, P = <0.001; R/S: $F_{5,24}$ = 18.519, P = <0.001) and between invasive and native plants (Table 1). However, elevated CO_2 did not influence these allocation parameters. All the species allocated maximum biomass to leaves except *H. suaveolens*, which allocated its 54% mass to stem (Table 2). Similar mass allocation pattern was observed for all the species under elevated CO_2 but LMF decreased under elevated CO_2. Contrary to other species, *H. suaveolens* exhibited an opposite pattern and showed 5% increase in LMF under elevated CO_2.

Table 1: summary of unbalanced ANOVA for the effect of species type (native vs. invasive), CO_2 levels and their interaction on growth-related parameters

Growth-related parameters	Species type ($F_{1,32}$)	CO_2 levels ($F_{1,32}$)	Species type × CO_2 levels ($F_{1,32}$)
Height	0.285^{NS}	18.595***	4.100^{NS}
Total biomass	0.046^{NS}	17.911***	7.698*
RMF	4.275*	0.393^{NS}	0.000^{NS}
SMF	8.526*	0.088^{NS}	0.016^{NS}
LMF	2.749^{NS}	0.193^{NS}	0.277^{NS}
R/S	5.898*	0.009^{NS}	0.270^{NS}
SLA	5.705*	0.001^{NS}	0.000^{NS}
RGR	33.940***	23.774***	9.467**
NAR	47.557***	16.090***	7.416*

*** $P \leq 0.001$,
** $P < 0.005$,
* $P < 0.05$, NS = non-significant.

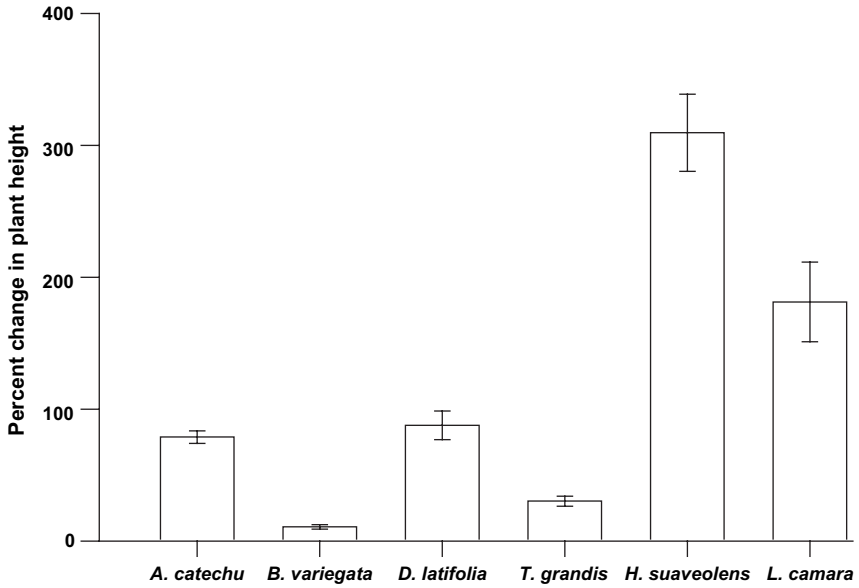

Figure 1: percent increase in seedling height after exposing to elevated CO_2.

After leaves, maximum mass was allocated to roots in *A. catechu* and *L. camara* under both ambient and elevated CO_2. Increased mass allocation to stem was observed for *L. camara* under elevated CO_2. *Acacia catechu* and *D. latifolia* exhibited a decrease in RMF while other species showed increased RMF under elevated CO_2. Among dry deciduous seedlings, maximum R/S ratio was observed for *A. catechu* and lowest for *B. variegata*. Among invasive species, R/S ratio increased in the case of *H. suaveolens* while in *L. camara* it decreased when exposed to elevated CO_2.

All species showed decreased SLA in response to elevated CO_2 except *T. grandis* (Table 3) and RGR of seedlings exposed to elevated CO_2 was higher than those exposed to ambient CO_2 in all species, 28% in *A. catechu*, 18% in *B. variegate*, 17% in *D. latifolia* and 16% in *T. grandis*. Compared to the above, *H. suaveolens* and *L. camara* seedlings showed 112 and 26% higher RGR under elevated CO_2 than those grown under ambient CO_2. NAR was maximum for *L. camara* under both ambient and elevated CO_2. Exposure to elevated CO_2 resulted in greater increase in NAR in invasive species than the native dry deciduous seedlings.

Regression analysis between weight ratios and SLA indicated significant positive relationship in two of the four dry deciduous seedlings, *A. catechu* (weight ratio = 0.001 SLA−2.655, r^2 = 0.955) and *D. latifolia* (weight ratio = 0.049 SLA−25.60,

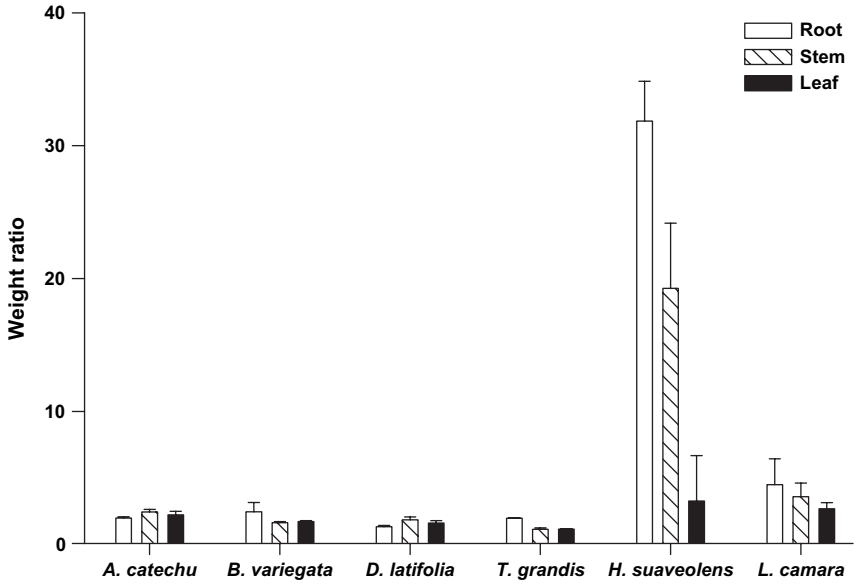

Figure 2: seedling weight ratio (biomass elevated/biomass ambient).

Table 2: biomass allocation parameters of dry deciduous tree species and invasive species in response to elevated CO_2

	Species					
	Dry deciduous tree species				Invader	
Parameter	*Acacia catechu*	*Bauhinia variegata*	*Dalbergia latifolia*	*Tectona grandis*	*Hyptis suaveolens*	*Lantana camara*
R/S ratio						
[CO_2]A	0.47±0.03	0.20±0.03	0.29±0.01	0.28±0.03	0.10±0.04	1.37±0.37
[CO_2]E	0.41±0.01	0.27±0.05	0.23±0.01	0.15±0.01	0.19±0.08	0.97±0.25
RMF						
[CO_2]A	0.32±0.01	0.16±0.01	0.23±0.01	0.13±0.01	0.06±0.02	0.24±0.03
[CO_2]E	0.29±0.01	0.21±0.03	0.19±0.01	0.21±0.02	0.09±0.03	0.24±0.05
SMF						
[CO_2]A	0.23±0.03	0.35±0.04	0.23±0.02	0.21±0.03	0.54±0.02	0.18±0.02
[CO_2]E	0.25±0.02	0.32±0.01	0.27±0.01	0.20±0.02	0.50±0.04	0.25±0.03
LMF						
[CO_2]A	0.45±0.02	0.48±0.22	0.54±0.02	0.66±0.04	0.39±0.02	0.58±0.01
[CO_2]E	0.45±0.01	0.47±0.05	0.55±0.02	0.60±0.04	0.41±0.03	0.51±0.04
LAR (cm^2g^{-1})						
[CO_2]A	838±41.8	109±4.6	261±9.4	102±6.8	63±1.9	113±1.8
[CO_2]E	838±23.6	106±10.1	262±9.8	85±8.5	63±4.6	97±7.8

[CO_2]A = ambient carbon dioxide (375–395 μ mol mol^{-1}), [CO_2]E = elevated carbon dioxide (700–750 μ mol mol^{-1}).

r^2 = 0.962). Whereas in *B. variegata* (weight ratio = 0.362 SLA−78.36, r^2 = 0.386) and in *T. grandis* (weight ratio = 0.029 SLA−3.416, r^2 = 0.791), the trend was positive but non-significant. Both the invasive species showed no significant relationship between weight ratios and SLA ((*H. suaveolens* (weight ratio = −0.004 SLA+3.780, r^2 = 0.220) and *L. camara* (weight ratio = −0.000 SLA+8.879, r^2 = 0.394)).

DISCUSSION

In the present study, growth response to elevated CO_2 varied among species, some showing greater increases in shoot length and biomass accumulation than others. However, biomass accumulation under elevated CO_2 was greater in invasive species than in the woody natives. As native and invasive species differ in their life form therefore their performance is expected to differ in response to elevated CO_2. Since invasive species invade areas harbouring diverse species composition therefore such types of comparative studies are required. Other studies have also shown an increase in overall biomass of invasive species, e.g. *Pueraria lobata* (Sasek and Strain 1988), *Lonicera japonica* (Sasek and Strain 1991), *Bromus tectorum*, *Pueraria lobata*, *Lonicera japonica* (Dukes and Mooney 1999), *Bromus madritensis* (Smith *et al.* 2000), *Prunus laurocerasus* (Hattenschwiler and Körner 2003) and *Mikania micrantha* and *Wedelia trilobata* (Song *et al.* 2009) compared to native tree seedlings. SLA

Table 3: growth traits of dry deciduous tree species and invasive species in response to elevated CO_2

	Species					
	Dry deciduous tree species				Invader	
Parameter	*Acacia catechu*	*Bauhinia variegata*	*Dalbergia latifolia*	*Tectona grandis*	*Hyptis suaveolens*	*Lantana camara*
SLA (cm^2g^{-1})						
[CO_2]A	1862±1.66	226±0.01	482±0.1	173±0.0	162±2.5	194±0.2
[CO_2]E	1851±0.8	227±0.0	481±0.2	174±1.5	155±0.1	192±0.3
RGR (mg $mg^{-1}d^{-1}$)						
[CO_2]A	0.04±0.003	0.06±0.001	0.05±0.0008	0.04±0.001	0.04±0.006	0.08±0.010
[CO_2]E	0.06±0.002	0.07±0.001	0.06±0.0008	0.05±0.001	0.09±0.003	0.101±0.013
NAR (mg $mg^{-1}d^{-1}$)						
[CO_2]A	0.11±0.004	0.11±0.005	0.10±0.004	0.08±0.005	0.12±0.009	0.18±0.05
[CO_2]E	0.14±0.007	0.13±0.011	0.11±0.002	0.09±0.004	0.24±0.013	0.23±0.044

[CO_2]A = ambient carbon dioxide (375–395 μ mol mol^{-1}), [CO_2]E = elevated carbon dioxide (700–750 μ mol mol^{-1}).

generally decreased in response to elevated CO_2 in the present study and this decrease was in conformity with other reports (Delucia *et al.* 1985; Raschi *et al.* 1997; Tolley and Strain 1984). The decrease in SLA may be attributed to increased levels of non-structural carbohydrates/starch in leaves, and/or changes in leaf anatomy (cell wall components and intercellular spaces) and/or accumulation of carbohydrates (Farrar and Williams 1991). NAR as well as RGR increased under elevated CO_2 in all species but the magnitude was higher in the case of invasive species. Dry deciduous seedlings showed a significant positive correlation between NAR and RGR (r^2 = 0.426, P = <0.05) under both ambient and elevated CO_2 environment, whereas invasive species showed such a relationship only under elevated CO_2 (r^2 = 0.9352, P = <0.05). Positive correlation between NAR and RGR exhibit mass-based metabolic differences among species. It may be expected that these invasive species will be more efficient in capturing the light and CO_2 under the climate change scenario. Since RGR is instantaneous rate of dry mass gain per unit total dry mass, higher RGR will lend relative advantage to the invasive species. This advantage to invasive species may help them to maintain dominance under different environmental stresses (Mooney and Hobbs 2000). In conclusion, our study indicated that under the elevated CO_2 in future, growth of invasive species, *H. suaveolens* and *L. camara*, would be more than the woody natives. Greater height and biomass may lower the light reaching to the forest floor and may also interfere with the seedling recruitment in dry deciduous forests. Further formation of taller seedlings in the invasives may also confer advantage to these species as theses species can shade out the native seedlings. The invasive species can invade the shaded areas as their distribution is relatively restricted by the light availability in the dry deciduous forest. Furthermore, invasive species are supposed to be more tolerant to environmental stresses as suggested by Alpert *et al.* (2000) and phenotypically more plastic to a wider range of environmental conditions (Feng *et al.* 2007; Geng *et al.* 2006). These species are expected to perform better than native tree seedlings and this may lead to a shift in community composition as atmospheric CO_2 build up in future. Management of these species may become more difficult in near future because of their rampant growth and better adaptability to the changing climate.

FUNDING

Council of Science and Technology, UP, India

ACKNOWLEDGEMENTS

Critical comments and suggestion from Prof. J.S. Singh are thankfully acknowledged.

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