

Interactive effect of water and nutrient on survival and growth of tree seedlings of four dry tropical tree species under grass competition

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Abstract: The increasingly degrading dry tropical forests due to anthropogenic perturbations may further show significant species and individual loss under changing climate condition. It is attributed to the later effect on soil water and nutrient availability, which may variably change the competitive ability, and thus survival of tree species seedlings. Currently, determining the response of tree species seedlings to environmental changes in dry tropical ecosystem is a key challenge. Therefore, understanding of factors, which govern the seedling characteristics, are necessary for maintenance and regeneration of these forests. Here, we aim to examine that how nutrient, water and grass interactively affect the tree seedling survival and growth of four dry tropical species viz., *Ziziphus mauritiana* and *Terminalia arjuna* (non-leguminous), and *Acacia nilotica* and *Acacia catechu* (leguminous). These four species were subjected to eight different combinations of treatments based on water availability, nutrient supplementation and grass competition. Their responses in terms of survival and growth parameters (i.e. height, circumference, aboveground dry weight, number of leaves, leaf area and relative growth rate) were recorded in each combination. It was observed that water and nutrient interactively affected the seedling growth significantly. Under all treatment combinations, leguminous species exhibited higher survival than non-leguminous species, however, a reverse trend was observed for seedlings growth parameters. Presence of grass had significant negative effect on seedling growth in all treatment combinations; however non-leguminous species showed more pronounced effect than leguminous species. We observed a considerable variation in the seedlings growth response of different tree species to the variation in growth conditions in dry tropical environment. The study provides a mechanistic insight about the change in forest community structure with the environmental changes, which would help in devising some management strategies to conserve and restore the dry tropical forest.

Key words: Grasses, leaf nutrients, plant community, survival, tropical dry forest, water.

Introduction

Dry tropical forests are among the most vulnerable ecosystems of the world (Murphy & Lugo 1986). In recent years, increased human perturbations such as mining, agriculture, herbivory and fire has resulted in a considerable

destruction and modification of these forests to open secondary forest or savanna systems (Holechek *et al.* 2004; Jha *et al.* 2005). These forests reflect slow vegetation recovery possibly due to complex interactions among site, propagules and climatic conditions (Khurana & Singh 2001). In India, most of the dry tropical forest occurs in

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nutrient poor soils (Singh *et al.* 1989). Therefore, the composition and successional traits of these forests (i.e. pioneer and non-pioneer), nitrogen fixing ability, tree size, habitat preferences may respond differently to the gradient of resource (such as light, water and nutrient) availability and disturbance (such as herbivory and grass competition) (Chapin *et al.* 2000; Tilman 1987).

Seedlings are the very sensitive and important stage of plant life (Cappers *et al.* 2005; Shevtsova *et al.* 2009). Processes that affect the seedling stage act as strong selective filter in controlling the future plant community structure (Wright *et al.* 2005). In dry tropical ecosystem, seedling germination and establishment occurs within a limited period, having favorable light, nutrients and water conditions (Bhadouria *et al.* 2016, 2017). Soil water availability is a key factor influencing the growth rate and survival of juvenile tree seedlings, thus, plant communities in dry tropical forests (Lugo *et al.* 1978; Yavitt & Wright 2008). For example, soil water limitation can increase the rate of tree mortality, reduces photosynthesis, change the leaf and reproductive phenology and increase the susceptibility of forests to fire. Further, high rainfall variability in this region may affect plant nutrient uptake and storage and, thus, plant growth. The vegetation recovery options can be viewed only after thorough understanding of how seedlings of individual species in a community perform under changed climatic conditions, and by identifying the key regulatory environmental factors for seedling survival and growth (Bhadouria *et al.* 2017).

The studies on dry tropical tree seedling growth have mostly focused on the spatio-temporal pattern of seedling recruitment. The growth response of seedlings, varying in life history traits has been investigated in relation to the availability of light (Rincan & Huante 1993; Tripathi & Raghubanshi 2014), soil nutrients (Mills *et al.* 2013), soil water (Chaturvedi *et al.* 2013; Gómez-Aparicio *et al.* 2008; Rysavy *et al.* 2014) and elevated CO₂ (Khurana & Singh 2004). These studies suggested that combined application of regular watering and nutrient additions increases the seedling growth. In a study, Lawrence (2003) found an increase in the biomass and relative growth rate (RGR) in 80% species among 41 tree species subjected to nutrient treatment. Further, Khurana & Singh (2004) observed an increase in biomass and relative growth rate under different levels of water addition for two slow growing and

three fast growing tropical tree species in India. Moreover, water stress leads to reduction in plant biomass and RGR to a greater extent in fast growing species as compared to the slow growing species (Khurana & Singh 2004).

Grasses are the intrinsic component of ground layer vegetation; therefore, a competition for resources may exist between tree seedlings and grasses. Competition between seedlings and grasses may be stronger or weaker in these ecosystems depending on other environmental conditions. For examples, grasses compete poorly for soil nutrients than the trees, while acts as superior competitor for the soil water under arid conditions (Donzelli *et al.* 2013). However, limited studies are available for elucidating the competitive inhibition versus resource limitation for the growth of seedlings (see: Kraaij & Ward 2006). In general, grasses suppress the seedling growth of tree species (Kambatuku *et al.* 2011) due to aboveground and belowground resources competition. In contrast, a few studies reported the neutral (O'Connor 1995) or facilitative behavior of grasses for tree seedling growth (Barbosa *et al.* 2014). Thus, it is still a matter of research to understand the interactive effect of grass-seedling growth behavior under variable resource availability.

In India, dry tropical forests are dominated by a mixture of leguminous and non-leguminous species. These functional groups respond differently under variable environmental conditions. Therefore, a study encompassing different plant functional traits under interactive set of environmental variables may enhance our understanding of tree seedling survival and growth in dry tropical environment. However, limited studies are available so far elucidating the key determinants for individual tree species seedlings growth in these ecosystems. Therefore, determining tree seedling responses to variation in soil nutrient, water and grass competition will improve our understanding of how natural variation in nutrient availability affects the forest community dynamics. Moreover, it would help us to better understand the impacts of the widespread human-induced fertilization and watering of natural ecosystems on seedling establishment in the regeneration of these forest ecosystems. In the present study, two leguminous and two non-leguminous tree species were taken to understand their seedling growth responses to different nutrient and water conditions under grass competition.

Material and Methods

Plant Material

In the present study, four common dry tropical tree species (*viz.* *Ziziphus mauritiana* Lam., *Acacia nilotica* Willd., *Acacia catechu* Willd., *Terminalia arjuna* Bedd.) having different life history traits were selected (*see*: Table 1). These are light demanding species and have great economic values (Troup 1921).

Experimental setup and growth conditions

Study was conducted in the experimental plot of Botanical Garden of the Banaras Hindu University (BHU), Varanasi (25°18'N, 83°03'E, and 129 m above mean sea level) during 2011–2012. The climate of the study area is monsoonal with three seasons, *viz.* winter (November to February), a summer (April to June) and a rainy season (July to September). During the study period, mean monthly temperature ranged from 17 to 39 °C and relative humidity was 42 to 87%. The mean annual rainfall averages 1100 mm, of which 85% falls during the rainy season.

Experimental setup contains three replicate blocks of 9×9 m² which further consisted of two plots of 4×4 m² with 1 m buffer zone. Each plot consisted of four sub-plots of 1×1 m² (total 24 plots) with 0.5 m to 1 m buffer zone. Four seedlings of each species were planted in this 1×1 m² sub-plot. In each plot, different combination of treatments such as water availability [regular watering (W1) or no watering (W0)]; nutrient [no nutrient addition (N0) or added nutrient (N1)], and grass competition [with grass (G1) or without grass (G0)], were applied. Water was treated at plot level (4×4 m²), whereas grass and nutrient were applied at sub-plot level (1×1 m²). There were total 8 treatment combinations in each block. The seedling density in the plots was 16 seedlings m⁻², which was lower than the naturally occurring seedling density in tropical forest (more than 60 seedlings m⁻²) (Kitajima & Tilman 1996).

To examine how the scarcity of water and rainfall variability affects the growth of tree seedlings of different species, we set up two water treatments. For regular water treatment (W1) rain-out shelters were used to exclude natural rainfall and plots were well watered on every 5th days for 18 months of the experiment (July 2011 to December 2012). For no water treatment (W0), water was added only during the seedling

establishment stage *i.e.* in the first two weeks after planting of seedlings for establishment and was left open to receive only natural rainfall. Two nutrients (*i.e.* added nutrient (N1) and no nutrient addition (N0)) and grass (grass presence (G1) and absence of grass (G0)) treatments were selected to observe the growth and resource utilization competition behavior of four tree seedlings.

Sub-plots were supplemented with NPK based inorganic fertilizer in the ratio of 3:1:2 to N1 treatment plots three times (at interval of 6 months) during the experimental period. The fertilizer addition to the experimental plots was done at the rate of 4 g N m⁻² per application, which represents a high dose of nutrient application in dry tropical forests (Kraaij & Ward 2006). For observing the effect of grass competition, a local grass species *Eragrostis tenella* was seeded one month before the transplantation of tree seedlings in experimental plots. Regular manual weeding was done to control naturally germinated grass in G0 and G1 plots.

Seeds of *Z. mauritiana*, *A. nilotica*, *A. catechu* and *T. arjuna* species were collected from the nearby dry tropical areas. Healthy seeds were surface sterilized for 30 seconds by immersion in 0.1% HgCl₂ and washed thoroughly with distilled water. Seedlings were raised in Botanical Garden of Banaras Hindu University (BHU). Seeds were sown in nursery bags filled with experimental field soil, one month before the experiment. Four seedlings of each species were randomly transplanted in each sub-plot at the initiation of the experiment.

Soil samples were collected randomly from 10 locations from the experimental field for various physico-chemical properties at the time of commencement of the experiment. Soil was thoroughly mixed and sieved to pass through a 2 mm sized sieve. Standard methods were used to estimate the soil organic C (Walkley & Black 1934), total Kjeldahl N (Jackson 1973), total P (Olsen & Sommers 1982), soil pH (Anderson & Ingram 1993) and soil texture (Sheldrick & Wang 1993). Soil organic C, total N, total P and soil pH were 5.91±0.85 mg g⁻¹, 0.59±0.08%, 0.17±0.05% and 7.2±0.81, respectively. Soil texture was silty loam with a sand, silt and clay contents of 23.4±2.33%, 73.2±0.56% and 3.5±0.12%, respectively.

Measurements of seedling growth parameters

Initial measurements for stem length, root length, girth, number of leaves, leaf area, dry

Table 1. Vegetation characteristics of the Four studied tree species (based on Troup 1921).

Species	<i>Ziziphus mauritiana</i>	<i>Acacia nilotica</i>	<i>Acacia catechu</i>	<i>Terminalia arjuna</i>
Family	Rhamnaceae	Mimosaceae	Mimosaceae	Combretaceae
Growth	Fast	Slow	Moderate	Fast
Successional status	Pioneer	Pioneer	Pioneer	Non-pioneer
Tree size	Moderate	Small	Moderate	Large
Habitat preferences	Disturbed	Disturbed	Disturbed	Undisturbed
Functional group	Non-legume	Legume	Legume	Non-legume
Soil	Sandy/alluvium	Alluvium/black	Cotton sandy	Alluvial loam

weight of leaf and whole plant for calculating the relative growth of tree seedlings were recorded for 10 seedlings of each species. Further, stem length (from soil surface to tip), girth (1 cm above the ground) and number of leaves were recorded for individual species for 18 months at an interval of 1 month. Number of surviving seedlings per species per treatment combination was recorded at the end of the experiment. Six seedlings of individual species from each treatment were harvested randomly after 18 months and were separated into leaf and stem for further analysis. Leaf surface area was measured by a leaf area meter (SYSTRONICS leaf area meter-211, India). Separated plant parts were oven dried to constant mass at 70 °C for 48 hours. Foliar-N content was determined by macro-Kjeldahl method (Jackson 1973) and P by perchloric acid extraction method (Olsen & Sommers 1982). Relative growth rate in height (RGR_H), stem diameter (RGR_D), dry weight (RGR_w) were calculated by following Hunt (1978) to observe the response of individual species under variable resource and disturbance conditions. Cumulative values of 18 months for different growth parameters of the study are presented further.

Statistical Analysis

ANOVA was performed to observe the effect of different treatments on the tree seedling survival, growth and foliar nutrient contents of different tree species. Tukey's Post-Hoc test was performed to observe the significant differences for the studied parameters between the treatment combinations. All statistical analysis was performed using the SPSS package (ver. 16, SPSS Inc., Chicago, USA, SPSS 1997).

Results

Seedling Survival

Seedling survival (i.e. seedlings that survived till the end of experiment) varied significantly ($P < 0.001$) across the species, water availability, nutrient addition and grass competition. However, it showed no variations under their interactions (Table S1). Across the species, seedling survival was higher under regular watering with added nutrient in absence of grasses (Table 2). Across the treatment combinations, the seedling survival of leguminous species was relatively higher than non-leguminous species. It ranged from 50 to 100% (Table 2) and showed highest value in *A. nilotica* followed by *A. catechu*, *T. arjuna* and *Z. mauritiana* across treatment combinations. Water stress showed a significant negative effect on seedling survival. It was observed highest under regular water treatment than natural water regime (Table 2). Grass competition exerted a significant impact over seedling survival, which was relatively more pronounced under the natural water regime. Nutrient supplementation improved the seedling survival. However, grass competition under water stress condition reduced the favorable effect of nutrient supplementation on seedling survival (Table 2).

Seedling growth parameters

The growth parameters varied significantly across the species (Table S2). Seedling height, girth (circumference), total dry weight, leaf area and number of leaves were significantly affected by water availability, nutrient addition and grass competition (Table S2). Different treatment and their

Table 2. Survival (%) of tree seedlings of four tree species under eight treatment combinations.

Species	W1G0N0	W1G0N1	W1G1N0	W1G1N1	W0G0N0	W0G0N1	W0G1N0	W0G1N1
<i>Z. mauritiana</i>	67	92	58	67	50	67	50	50
<i>T. arjuna</i>	67	92	50	67	50	58	50	58
<i>A. nilotica</i>	92	100	83	92	58	83	58	58
<i>A. catechu</i>	75	100	67	75	50	75	58	50

W1 – regular watering; W0 – no watering; N1 – added nutrient; N0 – no supplementary nutrient; G1 – presence of grass; G0 – absence of grass.

Table 3. Effect of different treatment combinations on seedling growth parameters.

Species	W1G0N0	W1G0N1	W1G1N0	W1G1N1	W0G0N0	W0G0N1	W0G1N0	W0G1N1
Height (cm)								
<i>Z. mauritiana</i>	194.3 ^c	219.3 ^a	183.2 ^c	197.0 ^b	103.2 ^e	128.3 ^d	98.7 ^e	126.7 ^d
<i>T. arjuna</i>	179.2 ^b	200.2 ^a	162.3 ^c	181.2 ^b	92.2 ^{ef}	112.0 ^d	85.7 ^f	100.2 ^e
<i>A. nilotica</i>	166.3 ^a	176.0 ^a	154.2 ^b	173.5 ^a	85.3 ^e	115.2 ^c	89.0 ^e	99.2 ^d
<i>A. catechu</i>	165.2 ^{bc}	190.2 ^a	159.0 ^c	170.8 ^b	89.2 ^f	118.3 ^d	83.3 ^f	101.3 ^e
Circumference (cm)								
<i>Z. mauritiana</i>	6.30 ^c	7.53 ^a	5.93 ^{cd}	7.00 ^b	4.32 ^f	5.47 ^{de}	3.93 ^f	5.17 ^e
<i>T. arjuna</i>	7.50 ^c	9.85 ^a	6.50 ^d	8.05 ^b	4.58 ^g	6.07 ^e	4.08 ^h	5.33 ^f
<i>A. nilotica</i>	4.53 ^{cd}	6.03 ^a	3.95 ^{def}	5.38 ^{ab}	3.78 ^e	5.02 ^{bc}	3.72 ^f	4.45 ^{cde}
<i>A. catechu</i>	5.10 ^c	6.52 ^a	4.67 ^c	5.93 ^b	3.77 ^d	4.72 ^c	3.60 ^d	4.05 ^d
Dry weight (g)								
<i>Z. mauritiana</i>	46.93 ^c	63.59 ^a	39.77 ^d	49.37 ^b	26.43 ^g	31.70 ^e	28.83 ^f	27.60 ^{fg}
<i>T. arjuna</i>	29.53 ^c	38.73 ^a	28.73 ^c	34.90 ^b	22.57 ^d	28.53 ^c	19.70 ^e	23.53 ^d
<i>A. nilotica</i>	21.00 ^c	34.54 ^a	21.57 ^{bc}	23.53 ^b	14.77 ^d	20.70 ^c	15.15 ^d	16.01 ^d
<i>A. catechu</i>	22.67 ^{bc}	31.71 ^a	19.13 ^{cd}	25.14 ^b	13.40 ^e	19.90 ^e	13.53 ^e	13.70 ^e
Leaf number								
<i>Z. mauritiana</i>	286 ^b	357 ^a	270 ^b	278 ^b	192 ^c	206 ^c	191 ^c	196 ^c
<i>T. arjuna</i>	115 ^b	155 ^a	114 ^b	119 ^b	70 ^{cd}	84 ^c	68 ^d	77 ^{cd}
<i>A. nilotica</i>	130 ^b	162 ^a	128 ^b	133 ^b	85 ^{cd}	95 ^c	81 ^e	86 ^{cd}
<i>A. catechu</i>	121 ^b	141 ^a	128 ^c	115 ^{ab}	64 ^d	86 ^c	68 ^e	69 ^{cd}
Leaf area (cm ²)								
<i>Z. mauritiana</i>	13.88 ^{ab}	15.06 ^a	13.26 ^{ab}	14.16 ^{ab}	12.80 ^b	13.40 ^{ab}	12.47 ^b	12.93 ^b
<i>T. arjuna</i>	28.79 ^a	30.38 ^a	28.19 ^a	29.09 ^a	27.97 ^a	28.51 ^a	27.94 ^a	28.49 ^a
<i>A. nilotica</i>	2.98 ^{bc}	3.70 ^a	2.92 ^{bcd}	3.14 ^b	2.50 ^{de}	2.80 ^{bcde}	2.40 ^e	2.65 ^{cde}
<i>A. catechu</i>	3.76 ^{bc}	4.41 ^a	3.51 ^{bcd}	3.93 ^b	3.37 ^{cd}	3.63 ^{bcd}	3.26 ^d	3.49 ^{bcd}

W1 – regular watering; W0 – no watering; N1 – added nutrient; N0 – no supplementary nutrient; G1 – presence of grass; G0 – absence of grass.

Different superscript indicates significant differences at $P < 0.05$ between different treatment combinations; values are given for 18 month old tree seedlings of four dry tropical species.

interactions such as species \times water availability, species \times grass, species \times nutrient, water \times grass, water \times nutrient, and grass \times nutrient also showed significant effect on the growth parameters for different plant species (Table S2).

Seedling growth parameters (e.g. height, girth, total dry weight, leaf area, number of leaves) were affected by different growth conditions (Table 3). Nutrient addition had a positive effect on all the growth parameters. Seedling height, girth, total dry

Table 4. Effect of different treatment combinations on relative growth rate of tree seedlings.

Species	W1G0N0	W1G0N1	W1G1N0	W1G1N1	W0G0N0	W0G0N1	W0G1N0	W0G1N1
RGR _H (cm cm ⁻¹ month ⁻¹)								
<i>Z. mauritiana</i>	0.166 ^{ab}	0.173 ^a	0.163 ^{ab}	0.167 ^{ab}	0.131 ^c	0.143 ^{bc}	0.128 ^c	0.142 ^{bc}
<i>T. arjuna</i>	0.158 ^a	0.164 ^a	0.152 ^{ab}	0.158 ^a	0.121 ^c	0.132 ^{bc}	0.117 ^c	0.125 ^c
<i>A. nilotica</i>	0.136 ^a	0.140 ^a	0.132 ^a	0.139 ^a	0.099 ^c	0.116 ^b	0.092 ^c	0.108 ^{bc}
<i>A. catechu</i>	0.149 ^a	0.156 ^a	0.147 ^a	0.151 ^a	0.114 ^c	0.130 ^b	0.111 ^c	0.121 ^b
RGR _D (cm cm ⁻¹ month ⁻¹)								
<i>Z. mauritiana</i>	0.067 ^{bc}	0.077 ^a	0.064 ^{bc}	0.072 ^{ab}	0.046 ^{de}	0.059 ^{cd}	0.041 ^e	0.056 ^{cd}
<i>T. arjuna</i>	0.086 ^{bc}	0.101 ^a	0.078 ^{cd}	0.090 ^b	0.059 ^{fg}	0.074 ^{de}	0.052 ^g	0.067 ^{ef}
<i>A. nilotica</i>	0.074 ^{bc}	0.090 ^a	0.066 ^{cd}	0.083 ^{ab}	0.064 ^{cd}	0.080 ^{ab}	0.063 ^d	0.073 ^{cd}
<i>A. catechu</i>	0.084 ^{bc}	0.098 ^a	0.079 ^{cd}	0.092 ^{ab}	0.067 ^{de}	0.079 ^{bcd}	0.065 ^e	0.071 ^{cde}
RGR _W (g g ⁻¹ month ⁻¹)								
<i>Z. mauritiana</i>	0.257 ^b	0.274 ^a	0.247 ^c	0.259 ^{bc}	0.225 ^d	0.235 ^d	0.230 ^d	0.227 ^d
<i>T. arjuna</i>	0.256 ^{bc}	0.271 ^a	0.255 ^c	0.265 ^{ab}	0.241 ^d	0.254 ^c	0.234 ^d	0.243 ^d
<i>A. nilotica</i>	0.263 ^b	0.291 ^a	0.265 ^b	0.269 ^b	0.244 ^c	0.262 ^b	0.245 ^c	0.248 ^c
<i>A. catechu</i>	0.265 ^b	0.284 ^a	0.256 ^b	0.271 ^{ab}	0.238 ^c	0.258 ^b	0.239 ^c	0.239 ^c

W1 – regular watering; W0 – no watering; N1 – added nutrient; N0 – no supplementary nutrient; G1 – presence of grass; G0 – absence of grass.

Different superscript indicates significant differences at $P < 0.05$ between different treatment combinations; values are given for 18 month old tree seedlings of four dry tropical species.

weight, leaf area and number of leaves were higher under treatment plots having regular watering, nutrient addition and absence of grass (W1N1G0) across the studied species (Table 3). Stem height of 18 month old individual seedlings ranged from 85.3 to 219.3 cm. Maximum height was attained by *Z. mauritiana* under W1N1G0 and minimum by *A. catechu* under W0G0N0. Girth ranged from 3.7 to 9.9 cm. Maximum girth was observed for *Z. mauritiana* and minimum for *A. nilotica* under W0G1N0 treatment. Total dry weight ranged from 13.5 to 63.0 g. Maximum dry weight was observed for *Z. mauritiana*. All the growth traits were extremely suppressed under natural water treatments (W0 treatments). There was no effect of presence or absence of grass on height across the species under natural water treatment without nutrient addition. Similar results were found under regular watering without nutrient addition, except *A. catechu*. Under natural water regime, grass competition and nutrient supplementation did not affect seedling growth (especially girth) (Table 3). Grass competition had no effect on height across the species under natural water treatment without nutrient addition. Overall, nutrient addition showed a positive effect on all the growth parameters.

Relative growth rate for height (RGR_H), stem diameter (RGR_D), dry weight (RGR_W) showed significant variations across the species, water

availability, nutrient addition and grass competition (Table S2). RGR_H ranged from 0.10 to 0.17 cm cm⁻¹ month⁻¹ (Table 4). Maximum RGR_H was observed for *Z. mauritiana* under regular watering with nutrient addition in absence of grass competition (W1G0N1); whereas minimum RGR_H was shown by *A. nilotica* under natural water without nutrient addition in presence of grass competition. RGR_D ranged from 0.06 to 0.11 cm cm⁻¹ month⁻¹ (Table 4). *Terminalia arjuna* exhibited maximum RGR_D under regular watering with added nutrient in absence of grasses; whereas minimum RGR_D was exhibited by *T. arjuna* under natural water and no nutrient addition, in presence of grasses. RGR_W ranged from 0.23 to 0.30 mg mg⁻¹ month⁻¹ (Table 4). Maximum RGR_W was observed for *Z. mauritiana* under regular watering and added nutrient in absence of grass competition (W1G0N1); whereas, minimum RGR_W was observed for *A. catechu* under natural watering with no added nutrient condition in presence of grasses (W0G1N0). RGR_H was found higher for non-leguminous seedling, whereas RGR_D and RGR_W were found higher for leguminous seedlings.

Nutrient addition showed a significant positive effect on RGR_H, RGR_D and RGR_W. Regular watering with nutrient addition favors RGR_H, RGR_D and RGR_W across the species (Table 4). Further, grasses showed a significant competition

with seedling for water and nutrient as revealed by decreased RGR_H , RGR_D and RGR_W in presence of grass (Table 4).

Discussion

Effect of water, nutrient and grass competition on seedling survival

Seedling survival was found sensitive to the resource and disturbance combinations and different species showed different survival rates. It was higher under regular watering with added nutrient and without grass competition. This finding indicates that water availability induces the nutrient dissolution at higher rate under nutrient supplemented treatments, and thus improves the seedling survival at early stages of plant life. The negative effect of grass competition on the seedling survival in the present study suggests that belowground competition for resources plays a very important role in the seedling establishment (see also Kambatuku *et al.* 2011). It is possibly due to reduction in the period of suitable growing conditions for the tree seedlings survival. Further, the higher seedling survival under nutrient addition with regular watering condition suggests that the availability of water and nutrient are the key determining factors for tree seedling survival under dry tropical environment.

In the present study, survival of leguminous species was observed higher than non-leguminous species in presence of grass. It suggests that competition by grass for nutrients would enable the leguminous species to survive better than non-leguminous species due to increased nodulation in the former under such conditions. It is reported that N_2 fixation ability of leguminous species might be an important attribute, which allows them to survive under competition with grasses when tree seedlings compete with grasses for nutrient (Cramer *et al.* 2007). The higher survival of *A. nilotica* and *A. Catechu* than *Z. mauritiana* and *T. arjuna* in the present study suggests that survival of non-leguminous species was affected more by grass competition under regular watering than leguminous species. Indeed, both the leguminous species are pioneer and can survive in stressed environmental conditions (Winkler *et al.* 2014). Overall, the present study reveals that nutrient supplementation improves the seedling survival and growth; however, this effect is reduced under grass competition and water stress.

Effect of water, nutrient and grass competition on seedling growth

Marked differences were observed in height, girth, total dry weight, leaf area and number of leaves of 18 months old tree seedlings of dry tropical tree species. It was also found that all the species grew better under regular watering with nutrient supplementation. Soil water availability is considered as a main driving factor for the regeneration, survival and growth of tree seedlings in tropical dry forest (Bauweraerts *et al.* 2014). Considerable reduction under water stress condition in the present study might be due to hydraulic-failure and carbon starvation, with their relative importance depending on the intensity and duration of draught stress (McDowell *et al.* 2008). The hydraulic-failure theory predicts that reduced soil water supply, together with high evaporative demand, cause xylem cavitations and desiccation of plant tissue resulting in the mortality of tree seedlings (Niu *et al.* 2008). Significant reduction in height, girth, total dry weight and number of leaves in response to water stress, as observed in the present study demonstrates the ability of species to tolerate in broad range of water levels by plastic response (Hibbs *et al.* 1995). Present study showed a significant reduction in growth parameters in natural water treatment. It is consistent with some studies conducted in dry tropical environment, suggesting that water stress limits the seedling growth and survival (Gómez-Aparicio *et al.* 2008; Kraaij & Ward 2006).

All the studied species in the present study performed better under regular watering condition with nutrient addition. It is consistent with the results obtained by Khurana and Singh (2001) under similar nutrient and water conditions in dry tropical ecosystems. Our findings were also found in agreement with a fertilization experiment conducted by Singh & Singh (2001), in which fertilization showed comparatively greater impact on the non-leguminous species than leguminous species. Increased seedling height, girth and total dry weight with nutrient addition under regular watering condition further provides an evidence of co-limitation for water and nutrient conditions (Donovan *et al.* 2014). In general, the effects of nutrient addition on seedling growth may result indirectly from the changes in soil processes such as N mineralization rate. Our finding is also consistent with many fertilization studies conducted in a variety of tropical dry forests (Kaspari *et al.* 2008;

Santiago *et al.* 2012). All the studied species showed an enhanced growth with nutrient addition, suggesting that water availability may increase the nutrient availability resulting into better growth and development. The differential responses among growth forms of different species suggest that N enrichment has the potential to change the plant community structure and biodiversity in terrestrial dry ecosystems (Zavaleta *et al.* 2003).

In general, grass competition is a fundamental hindrance to tree seedling establishment, survival and growth. Our result indicates that grass competition exerts a strong negative effect on tree seedling growth, even in favorable environmental conditions (i.e. regular watering with nutrient addition). It is in agreement with some previous studies (Kambatuku *et al.* 2011; Vandenberghe 2008) who reported that belowground competition for the resources may play a crucial role in the seedling establishment and development. However, the observed higher growth of seedlings across the species under nutrient supplementation with natural watering treatment, even in grass competition, reveals that nutrient supplementation can be a wise strategy to regenerate the tree seedlings in dry tropical conditions. Donzelli *et al.* (2013) suggested that grasses poorly compete for soil nutrients as compared to trees, while are superior competitor for soil water under dry conditions. The better growth of tree seedlings under nutrient supplementation with regular watering even under grass competition supports the above consensus.

Non-leguminous (i.e. *Z. mauritiana* and *T. arjuna*) species were more responsive to nutrient addition than leguminous (*A. catechu* and *A. nilotica*) in terms of height, girth and total dry weight and number of leaves. This might be possibly due to the loss of advantage of legumes over non-legumes under increased N availability (Suding *et al.* 2004). In the present study, a wide variation in response of dry tropical tree seedlings to nutrient addition was observed. Pioneer species responded higher to nutrient supplementation (except *A. nilotica*) than non-pioneer species. Further, these pioneer species also responded better under grass competition as compared to non-pioneer species. The relatively low growth response of *A. nilotica*, even under added nutrient conditions was possibly due to its slow growing nature (Chapin III 1980). Slow growing species usually exhibit a low absorption rate per plant and a very small increase in the absorption rate in response to increasing external concentration

Chapin III 1980; Christie & Moorby 1975). Root absorption capacity (i.e. per g root rather than total absorption per plant) is usually higher in rapidly growing species from fertile habitats than in plants from infertile habitats under all growth conditions (Davy & Taylor 1975; Grondon 1972; Harrison & Helliwell 1979). Further, the negative effect of grass competition on slow growing pioneer species *A. nilotica* was found less under all the treatment combinations, which suggests the wider competition amplitude of this species under dry environments.

In general, leguminous species were able to significantly enhance their RGR due to nutrient supplementation under low water availability, when grass competition was absent. Under same conditions, non-leguminous species were able to enhance RGR_D, only. When experiencing water stress (i.e. natural water condition), seedlings significantly reduce the leaf number and area, which reflects the inherent mechanism of dry tropical species to avoid transpiration loss. Overall, nutrient supplementation along with grass removal and regular watering could be an effective management strategy to enhance tree seedling growth under dry tropical ecosystems. In our study, growth of non-leguminous species was affected higher in regular watering than leguminous species under grass competition. It is also in agreement with the study conducted by Barbosa *et al.* (2014).

Conclusions

Our study suggested that the response of tree seedlings in terms of survival and growth can be enhanced by increased water availability and removal of grasses. The study is in line with the consensus that grasses compete strongly with tree seedlings for above- and below-ground resources. Our study reflected that grass competition severely limits the tree seedling survival and growth under various environmental conditions, which is true even under favorable environmental conditions (i.e. regular watering and nutrient addition). However, nutrient addition can supplement the seedling growth under water stress even in presence of grasses. The responses of tree species belonging to different functional types (viz. legumes, non-legumes, pioneer, non-pioneer) differed significantly under various resource combinations. Seedlings of all the studied species performed better under nutrient addition with regular watering. Interestingly, the leguminous species were identi-

fied as more survival tolerance against grass competition and resource limited conditions. However, a reverse trend was observed for seedling growth parameters. Therefore, a non-field combinatorial experimentation involving key regulatory factors (water, nutrient and grass) with existing functional types is required to understand seedling survival and growth in dry tropical ecosystems in a species or functional group specific manner. It can be a wise strategy to conserve the dry tropical forest and enhance the woody cover in dry tropical environment. Moreover, seedling growth and plant cover can be managed in dry tropics by nutrient supplementation, which is expected to experience water stress condition due to present climatic variability.

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Supporting Information

Additional Supporting information may be found in the online version of this article.

Table S1. Effect of water availability, nutrient addition and grass competition on the survival of tree seedlings.

Table S2. Summary of Analysis of Variance (ANOVA) for the individual and interactive effect of treatments on the seedling growth traits.