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Phenology and water relations of tree sprouts and seedlings in a tropical deciduous forest of South India

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Abstract The phenology of sprouts (>1 year old, up to 1.5 m in height) and seedlings (<1 year old) of six woody species (four deciduous, one brevi-deciduous, and one evergreen) was examined during the dry season in a tropical deciduous forest of South India. Xylem water potential (Ψ_x), leaf relative water content (RWC; % turgid weight), and xylem specific conductivity (K_S ; $\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$) of sprouts were measured on two occasions during the dry season. In addition, K_S of seedlings (<1 year old) of one deciduous and one evergreen species was determined to allow comparison with sprouts. Ψ_x of deciduous species was significantly higher at the second sampling date and was accompanied by a significant increase in K_S and RWC, while the brevi-deciduous and evergreen species did not show any difference in Ψ_x . Seedlings of *Terminalia crenulata* (deciduous) and *Ixora parviflora* (evergreen) had significantly lower K_S compared to sprouts, while seedlings of all four deciduous species shed their leaves much earlier in the dry season than did conspecific sprouts. More favorable water relations of sprouts compared to seedlings during the peak of the dry season may explain the

lower rates of die-back and mortality of sprouts observed in dry deciduous forests of India.

Keywords Monsoonal forests · Hydraulic conductivity · Phenology · Drought effects

Introduction

Tropical dry forests are the most threatened of lowland tropical forests (Mooney et al. 1995). Anthropogenic activities such as grazing cattle and using fire to clear land have led to a significant loss in tree diversity by killing juvenile individuals and slowing regrowth (Cavelier et al. 1998; Gillespie et al. 2000; Saha and Howe 2003). A large percentage of stems in dry deciduous forests grow as sprouts from the base of stems that have died-back due to fire or grazing (Bond and Midgley 2001). Sprouts are predicted to have an advantage over true seedlings in a highly seasonal environment due to their connection to an established root system. Nevertheless, the water relations of sprouts in seasonally dry forests have received little attention.

The primary objective of this study was to compare the phenology and water status of conspecific sprouts and seedlings during the dry season. Six species with contrasting phenological patterns were examined, although only two species had sufficient numbers of seedlings for collection of the tissues needed for xylem water potential (Ψ_x), stem hydraulic conductivity and leaf relative water content (RWC) measurements. We predicted that seedlings and sprouts would differ in vegetative phenology due to differences in root system morphology. Establishment represents a critical phase in the life cycle of any plant and thus differential responses to seasonal drought will have a disproportionate effect on species diversity. Thus, understanding factors influencing regeneration of seedlings and sprouts contributes to our overall understanding of the resilience of these forests to both anthropogenic disturbance and climate change (Corlette and LaFrankie 1998; William et al. 2003).

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Materials and methods

The study was conducted in Biligiri Rangaswamy Wildlife Sanctuary (11–13°N and 77–78°E) in the state of Karnataka in South India. The primary vegetation type within the sanctuary is dry deciduous forest and the climate is tropical monsoonal, with most of the 1,484 mm of annual precipitation occurring between May and November (Murali et al. 1996). Sampling was confined to two dry deciduous forest patches located 3 km apart. Six species belonging to three phenological categories were sampled: *Diospyros melanoxylon* Roxb. (Ebenaceae), *Emblica officinalis* Gaertn. (Euphorbiaceae), *Pterocarpus marsupium* Roxb. (Fabaceae), and *Terminalia crenulata* Roth. (Combretaceae) are deciduous tree species that as adults are leafless for 2–4 months; *Ixora parviflora* Vahl (Rubiaceae) an evergreen tree in which leaf-shedding is not associated with the dry season; and *Acacia pennata* (L.) Willd. (Fabaceae) a brevi-deciduous liana that is leafless for 1 month.

All measurements were made in the mid-dry season (February and March). This time period was selected because it encompasses the period when adult trees of deciduous species both shed their old leaves and produce new ones. Both the months were rainless but the average midday temperature in March is higher than in February (Saha and Hiremath 2004). At the time of this study no systematic data on the phenology of juvenile plants of these species were available. Juveniles were classified into two categories: tree seedlings <1 year old (based on morphology) and sprouts >1 year old up to or <1.5 m in height. It was impossible to distinguish between seedlings and sprouts of *A. pennata* due to aboveground damage inflicted by herbivores, and thus all individuals of this species were assumed to be sprouts.

Phenology

Observations on leaf phenology were made on 20 individuals of both sprouts and seedlings at 2-week intervals starting from the first week of February until the last week of March. At each sampling interval, each individual was classified as having healthy (green), senescing (yellow/brown), expanding, or no leaves.

Shoot water potential

Measurements of Ψ_x were made on sprouts of all six species during 10–15 February and 17–20 March. Midday Ψ_x was measured with a pressure chamber (PMS Instruments, Corvallis, Oreg.) on five stems per species. Sampled individuals were at least 5 m apart. One leaf-bearing twig per stem was covered with a plastic bag for 1 h prior to excision to ensure equilibration between leaf water potential and Ψ_x of the shoots. Values of Ψ_x were log transformed and compared between February and March using a *t*-test.

Relative water content

RWC of sprouts was measured on leaves collected from four to five stems per species. Stems were cut in the morning at 7 a.m., wrapped in plastic bags to prevent water loss, and transported to the laboratory. Leaves were removed in the laboratory, and their fresh weight determined. Saturated weight was measured after allowing leaves to soak in water for 24 h. Leaves were then oven-dried at 80°C and re-weighed. RWC was calculated following Turner (1981) as:

$$\text{RWC} = (\text{fresh weight} - \text{dry weight}) / (\text{saturated weight} - \text{dry weight}) \times 100.$$

RWC values were arcsine transformed and comparisons were made for each species between the 2 months using a *t*-test.

Xylem hydraulic conductivity

Measurements of xylem hydraulic conductivity were made on sprouts of all six species during 10–15 February and 17–20 March. In addition, xylem hydraulic conductivity of seedlings of *I. parviflora* and *T. crenulata* was measured in March, which allowed comparisons of seedlings and sprouts of these two species. Fifteen stems per species were sampled. We determined xylem specific conductivity (K_s) of stems as $K_s = JL/\Delta PA$, where J is the flow rate (kg s^{-1}), L is the length of the stem segment (m), P is the pressure drop across the segment (MPa), and A is the cross-sectional area of the xylem (m^2). A was obtained by subtracting the cross-sectional area of the pith, measured with callipers, from the total stem cross-sectional area. Stems were cut under water to prevent air from entering the xylem and the cut ends were kept immersed in water during transport to the laboratory. The time between cutting and measuring hydraulic conductivity was approximately 30 min.

Once in the laboratory, the stem segments were re-cut under water and connected to a reservoir of dilute HCl (pH 2) with a pressure head of 50 cm (5 kPa). The HCl solution was perfused through the stem segments and collected from the distal end into Eppendorf tubes, which were weighed periodically on an electronic balance (± 0.001 g). Stem segments ranged between 5 and 10 cm in length, which was, in all cases, longer than the longest vessel length, determined as described in Scholander (1958). Sprout K_s measured between February and March, and seedling and sprout K_s measured for two species in March were compared using *t*-tests.

Results

Leaf phenology

All sprouts had healthy leaves in February, although leaves of *P. marsupium*, *E. officinalis*, and *T. crenulata* had started

to senesce as indicated by a change in their coloration. By the end of March the sprouts of these three species had dropped 50–100% of their leaves accompanied by new leaf production. In contrast, sprouts of brevi-deciduous *A. pennata* and evergreen *I. parviflora*, as well as the deciduous *D. melanoxylon* had healthy leaves in March with no indication of leaf senescence. Seedlings of *P. marsupium*, *E. officinalis* and *D. melanoxylon* had a combination of healthy and senescing leaves in February and were leafless in March, seedlings of *I. parviflora* had healthy leaves both in February and March, while seedlings of *T. crenulata* had healthy leaves in February and a combination of healthy and senescing leaves in March.

Xylem water potential

Midday Ψ_x of the sprouts of the four deciduous species were significantly greater in March than in February. In contrast, evergreen *I. parviflora* and brevi-deciduous *A. pennata* did not exhibit significant differences in midday Ψ_x between February and March (Table 1).

Relative water content

Leaf RWC of sprouts increased from February to March in *D. melanoxylon*, *E. officinalis*, *P. marsupium* and *T. crenulata* (Table 1), with a significant increase only for *P. marsupium* ($P < 0.01$, $df=9$). No significant difference was found between the 2 months for the evergreen *I. parviflora* and brevi-deciduous *A. pennata*.

Xylem hydraulic conductivity

Between February and March, K_S increased significantly in sprouts of the four deciduous species: *E. officinalis* ($n=15$, $P < 0.05$), *T. crenulata* ($n=15$, $P < 0.01$), *D. melanoxylon* ($n=15$, $P < 0.01$), and *P. marsupium* ($n=15$, $P < 0.01$). In contrast, there was no significant change in K_S for either the evergreen *I. parviflora* or brevi-deciduous *A. pennata* (Table 1).

Xylem hydraulic conductivity of *T. crenulata* seedlings was significantly lower than in sprouts ($n=5$ each, $P < 0.01$).

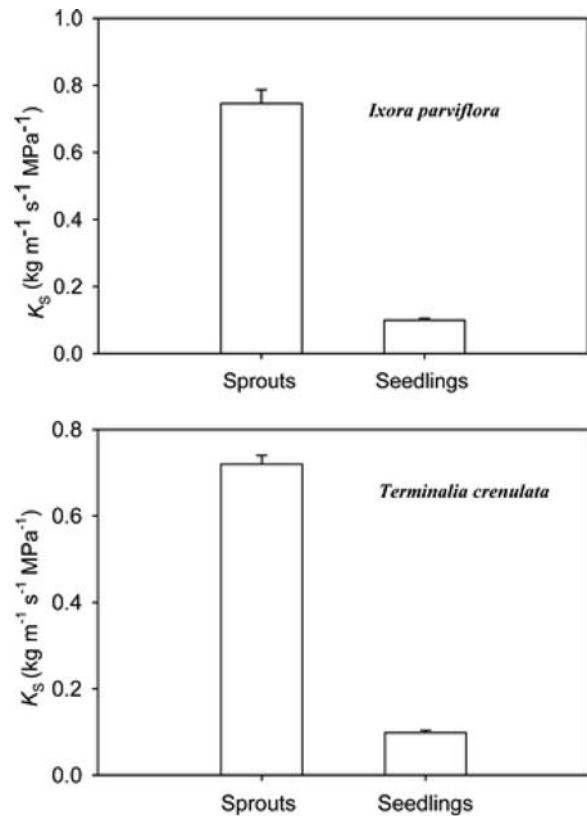


Fig. 1 Xylem specific conductivity (K_S) of sprouts and seedlings of evergreen *Ixora parviflora* (upper panel) and deciduous *Terminalia crenulata* (lower panel) in March at the peak of the dry season. For both species, K_S was significantly lower in seedlings compared with sprouts. Data are means \pm SEs

The same trend existed for *I. parviflora* seedlings compared to sprouts ($n=5$ each, $P < 0.01$, Fig. 1).

Discussion

The results of this study concur with the findings that trees in tropical deciduous forest are not completely dormant even during the peak of the dry season (Borchert 1994; Brodribb et al. 2002). Water status improved with the severity of the dry season among sprouts of the deciduous species. Similar reports of improved water status following

Table 1 Xylem specific conductivity (K_S ; $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) and xylem water potential (Ψ_x , MPa) of shoots and relative water content (RWC) among sprouts in February and March. Values are means \pm SEs

Species	Phenology	February Ψ_x	March	February RWC	March	February K_S	March
<i>Acacia pennata</i>	Brevi-deciduous liana	-2.63 ± 0.01	-2.77 ± 0.15	0.93 ± 0.04	0.95 ± 0.01	1.66 ± 0.001	1.62 ± 0.006
<i>Diospyros melanoxylon</i>	Deciduous tree	$-1.67 \pm 0.12^{**}$	-0.71 ± 0.21	0.53 ± 0.08	0.60 ± 0.05	$0.04 \pm 0.009^{**}$	0.08 ± 0.004
<i>Emblia officinalis</i>	Deciduous tree	$-1.12 \pm 0.06^{**}$	-0.54 ± 0.12	0.58 ± 0.13	0.73 ± 0.08	$0.06 \pm 0.003^*$	0.08 ± 0.001
<i>parviflora</i>	Evergreen tree	-1.09 ± 0.20	-1.15 ± 0.15	0.84 ± 0.08	0.80 ± 0.12	0.77 ± 0.002	0.74 ± 0.140
<i>Pterocarpus marsupium</i>	Deciduous tree	$-1.94 \pm 0.18^{**}$	-0.38 ± 0.05	$0.19 \pm 0.07^{**}$	0.83 ± 0.06	$0.10 \pm 0.004^{**}$	1.33 ± 0.040
<i>Terminalia crenulata</i>	Deciduous tree	$-1.89 \pm 0.17^{**}$	-1.03 ± 0.18	0.58 ± 0.60	0.79 ± 0.17	$0.07 \pm 0.002^{**}$	0.80 ± 0.005

* $P < 0.05$, ** $P < 0.01$

leaf shedding have been reported for deciduous trees in Costa Rica (Borchert 1994; Brodribb et al. 2002), and deciduous species in monsoonal savannas of Australia that rehydrated and initiated leaf expansion before the arrival of the rainy season (Williams et al. 1997).

The midday Ψ_x observed in the juvenile stems was not as low as among species occurring in Mediterranean ecosystems (<-7 MPa among sclerophyllous shrubs; Hart and Radosevich 1987), or among adult trees in tropical deciduous forests of Mexico (<-4 MPa in the late dry season; Fanjul and Barradas 1987), and Costa Rica (<-4 MPa, Borchert 1994), but was within the range reported for deciduous species that rehydrate after leaf-fall is complete (Borchert 1994). Water potential values increased for all the deciduous species as the dry season intensified. In contrast, there was no change in leaf water potential in the breviceducious and evergreen species during the same period.

The liana *A. pennata* had the greatest K_S among all the species in the study. Ewers (1985) and Gartner et al. (1990) found that the specific conductivity among morphologically diverse species was greatest for climbers and attributed this to greater xylem conduit diameter among the liana species they studied. Xylem conduit diameter was greatest for *A. pennata* compared with all the species sampled in the present study, but precise measurements of maximum vessel diameter were not undertaken. Hydraulic conductivity rose by as much as eightfold for all species as the dry season progressed. Thus the increase in K_S paralleled the increase in water potential and initiation of leaf flushing in all four deciduous species. Whether this increase in K_S is due to the production of new xylem or the re-filling of cavitated vessels is not known.

Seedling K_S measured in March was significantly lower than K_S of conspecific sprouts in both the evergreen species, *I. parviflora*, and the deciduous species, *T. crenulata*. This could be due to differences in age and morphology of seedlings and sprouts. Height growth of sprouts remains arrested for several years, during which time they continue to accumulate root biomass, which allows them to extract water from deeper soil layers. In contrast, the seedlings belonging to the same height class are much more limited in their water extraction ability because their root systems are less well developed. Seedlings had lost 75% of their leaves in March and, unlike the sprouts, had not initiated leaf flushing.

The fact that the water status of juvenile sprouts improved during the dry season has implications for understanding the response of tropical dry forests to disturbance. Experimental studies of Mediterranean ecosystems suggest that water potentials of resprouting vegetation are less negative than in adjacent unburned vegetation (Hart and Radosevich 1987; Shelden and Sinclair 2000). Anthropogenic fires, which occur frequently in the dry season in the seasonal tropical forests of India lead to stem die-back of sprouts, but rarely kill the entire plant. In contrast, seedlings are often killed, with their numbers significantly reduced following fire (Saha and Howe 2003). It is possible that sprouts, which are less vulnerable to seasonal drought, can withstand fire better than seedlings because the interactive effect of fire

and drought has a more negative impact on seedlings than sprouts.

This study represents the first demonstration of rehydration among juvenile trees in the dry season in a dry deciduous forest of India. However, to achieve a better understanding of plant water relations and diversity of responses among woody species in the dry forests, the water relations of a wider variety of species should be assessed during the different seasons of the year. It is also important to determine if seedlings suffer a loss of xylem hydraulic conductance due to cavitation, and to what degree this can be repaired as the dry season progresses.

References

- Bond WJ, Midgley J (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol Evol* 16:45–51
- Borchert R (1994) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75:1437–1449
- Brodribb TJ, Holbrook NM, Gutierrez MV (2002) Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant Cell Environ* 25:1435–1444
- Cavelier J, Aide TM, Santos C, Eusse AM, Dupuy JM (1998) The savannization of moist forests in the Sierra Nevada de Santa Marta, Colombia. *J Biogeogr* 25:901–912
- Corlett RT, LaFrankie JV (1998) Potential impacts of climate change on tropical Asian forests through an influence on phenology. *Climatic Change* 39:439–453
- Ewers FW (1985) Xylem structure and water conduction in conifer trees, dicot trees and lianas. *IAWA Bull* 6:309–317
- Fanjul L, Barradas V (1987) Diurnal and seasonal variation in the water relations of some deciduous and evergreen trees of a deciduous dry forest of the western coast of Mexico. *J Appl Ecol* 24:289–303
- Gartner BL, Bullock SH, Mooney HA, Brown VB, Whitbeck JL (1990) Water transport properties of vine and tree stems in a tropical deciduous forest. *Am J Bot* 77:742–749
- Gillespie TW, Grijalva A, Farris CN (2000) Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecol* 147:37–47
- Hart JJ, Radosevich SR (1987) Water relations of two Californian chaparral shrubs. *Am J Bot* 74:371–384
- Mooney HA, Bullock SH, Medina E (1995) Introduction. In: Bullock SH, Mooney HA, Medina E (eds) *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, pp 1–8
- Murali KS, UmaShankar RU, Shaanker K, Ganeshiah, Bawa KS (1996) Extraction of non-timber forest products in the forests of the Biligiri Rangan Hills, India. 2. Impact of NTFP extraction on regeneration, population structure, and species composition. *Econ Bot* 50:251–269
- Saha S, Howe HF (2003) Species composition and fire in a dry deciduous forest. *Ecology* 84:3118–3123
- Saha S, Hiremath A (2004) Anthropogenic fires in India—a tale of two forests. *Arid Land Newslett* 54
- Scholander PF (1958) The rise of sap in lianas. In: Thimann KV (ed) *The physiology of forest trees*. Ronald Press, New York, pp 3–17
- Shelden M, Sinclair R (2000) Water relations of feral olive trees (*Olea europaea*) resprouting after severe pruning. *Aust J Bot* 48:639–644
- Williams RJ, Myers BA, Muller WJ, Duff GA, Eamus D (1997) Leaf phenology of woody species in a north Australian tropical savanna. *Ecology* 78:2542–2558
- Williams SE, Bolitho EE, Fox S (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proc R Soc Lond Ser B* 270:1887–1892
- Turner NC (1981) Techniques and experimental approaches for the measurement of plant water status. *Plant Soil* 58:339–336