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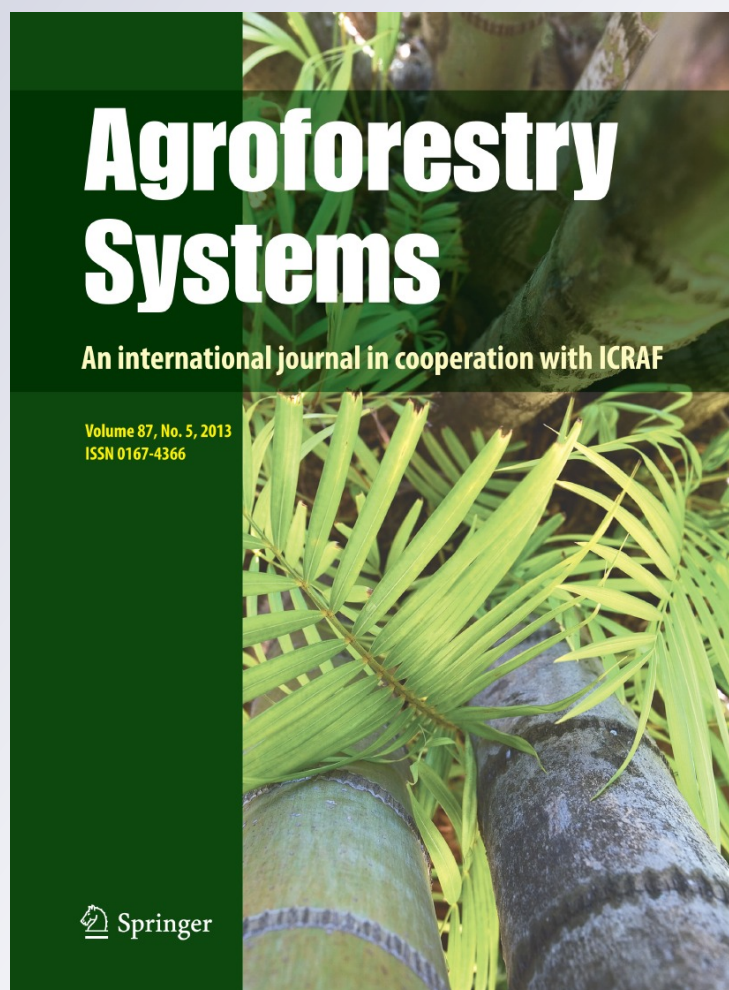Agroforestry Systems

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Seedling growth and water relations of three *Cedrela* species sourced from five provenances: response to simulated rainfall reductions

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Abstract The effects of different simulated rainfall regimes on water relations, growth, and biomass production and allocation of five provenances of *Cedrela fissilis*, *C. saltensis* and *C. balansae* were assessed in a pot-grown seedling experiment in greenhouse under uncontrolled conditions. Four simulated rainfall regimes were applied: 600 mm year^{-1} (severe water deficit), 800 mm year^{-1} (mild water deficit), 1,000 mm year^{-1} (mild wet), and 1,200 mm year^{-1} (well-watered) used as control. Provenances were compared in terms of water relations (midday leaf water potential, Ψ_{md} and relative water content, RWC), growth (root, shoot and leaf length, neck diameter), growth rate (shoot- and neck growth rate, SGR and NGR), biomass production (root, shoot and leaf dry weight), and biomass allocation (root:shoot ratio, RSR). Multivariate analyses revealed that water relations differed significantly under all simulated rainfall treatments by means of several variables throughout time. Effects of species × treatment, and provenance nested within species × treatment interactions significantly were important. SGR and RSR also were important to explain differences in Ψ_{md} and RWC between treatments and provenances. Broadly *C. balansae* and *C. saltensis* provenances seem to display a better performance than *C. fissilis* provenances under severe water deficit only. However, despite differences between provenances, it was not possible to clearly separate them according to their origin, based on water relations and growth performance. Even though the results of this study performed on pot-grown seedlings are based on relatively few observations and require additional confirmation, they allow an opportunity for speculation on the factors that are related to intraspecific variations that are likely to occur during the growth of seedlings from different geographical sites in field condition.

Keywords *Cedrela* · Growth · Rainfall · Water deficit · Water relations

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Introduction

Tree seedling growth and species composition of tropical and subtropical forests greatly depend on the plasticity of species to face environmental variables (Khurana and Singh 2001; Engelbrecht et al. 2007). Although these forests receive substantial rainfall, available data suggest that hydrological fluctuations i.e. the length of dry period and cumulative water deficit are important ecological drivers of species distribution (Slot and Poorter 2007). Drought can be regarded as one of the most damaging environmental disasters, which occurs as a result of extreme climatic changes that are driven by natural variability, but may also be exacerbated by anthropic activity (Sheffield and Wood 2008). Drought effects are highly dependent on the severity of water deficit and plant phenological stage (Engelbrecht et al. 2007). Seedlings are the most critical development stage of trees because they have shallow roots and limited access to soil water, being key in the life story of woody plants (Garkoti et al. 2003). In tropical forests some species are very sensitive to drought and cannot tolerate it, while others have developed strategies to avoid it. However, there is not a single strategy to drought, because adaptive mechanisms of trees include different morphological, anatomical, biochemical, and physiological responses (McDowell et al. 2008). Tropical tree seedlings have developed two major adaptive strategies to drought, each one with its specific functional traits: a) desiccation delay, or avoidance; b) desiccation tolerance (Tyree et al. 2003). Desiccation delay is achieved by increasing the water access and by reducing water loss. This mechanism involves morphological and/or physiological adaptations or a combination of both. In morphological terms, seedlings usually show high biomass investment to develop a deep root system. They also exhibit slow rate of plant growth as a common evolutionary response to habitats where the dry season is long. Slower plant growth rate is often associated with smaller leaf surface area, which may be a way to reduce the risk of high transpiration and soil drought (Garkoti et al. 2003). Moreover, when the plant can no longer maintain a positive carbon balance the shedding of leaves occurs (Borchert et al. 2002). Physiological adaptations include reduction of stomatal conductance and low cuticular

transpiration to reduce the water loss (Motzer et al. 2005). Delaying drought stress can be also achieved by deciduousness. Deciduous species drop their entire canopy and hence do not transpire at significant rates during the dry season. Deciduousness is a strong predictor of seedling survival during drought, but comes at the expense of a shorter growing season and regular biomass loss (Poorter and Markesteijn 2008). Desiccation tolerance is achieved through stomatal regulation (Ryan 2011), osmotic adjustment (Serraj and Sinclair 2002), and by increasing tissue elasticity (Fu et al. 2012). These traits allow that gas exchange and water transport occur at low water potential. Drought-tolerant species also reduce the probability of xylem embolism (Engelbrecht and Kursar 2003). Moreover, osmotic adjustment capacity is a valuable drought-adaptive feature of tree seedlings. Establishment of tree species populations depends on prevailing rainfalls in their naturally occurring habitats, so predominant species are adapted on the basis of a long series of hydroperiods generated by rainfall fluctuations (Miller and Zedler 2003). However, quantity and distribution of rainfalls in many areas of the world do not show regular distribution patterns (Miao et al. 2009). Currently there is a generalized consensus of the strong impact of ongoing anthropic-induced climate change on hydrological fluctuations of the world's forests (IPCC 2001; Allen et al. 2010). Even under a more conservative scenario, it is claimed that the climate change will include significant increases in frequency and severity of drought periods (Burke et al. 2006). Despite the anthropic influence, most of the global climate variability is driven by El Niño-Southern Oscillation (ENSO), which impacts on tropics and subtropics as well as on many regions in mid latitudes. The ENSO event causes plant-available soil water to stay below a critical threshold level during a prolonged period. Furthermore, models of climate change prediction anticipate that tropical regions of South America and Southeast Asian could experience a shift in precipitation patterns leading to more frequent and/or more severe drought periods in the future (Rolim et al. 2005). According to Allen et al. (2010), increases in frequency, duration, and/or severity of drought periods associated with climate changes could seriously affect the physiological functions of trees and fundamentally it would alter the composition, structure, and biogeography of

forests in many regions and possibly it would lead to widespread tree mortality. Seedling is generally considered the key stage for species establishment because its limited root system is most vulnerable to water shortage, thus insight into drought tolerance mechanisms of seedlings from different provenances is needed. It has been observed that in a common water stress environment, seedlings originating from seeds collected from drier areas of a species' range have slower plant growth rates than those collected from wetter areas (Li and Wang 2003). Further, plant responses to water deficit that are out of their natural environments depend on their native habitats (Otieno et al. 2005). Therefore, understanding physiological responses to drought by species originating from habitats with different rainfall patterns may be important to predict consequences of the climatic change on tree seedling performance and species distribution.

Cedrela is a tree genus of the New World (common denomination of the American continent) that comprises at least seven species occurring naturally from Mexico and the Southern Caribbean islands to Argentina (Smith 1960), and it is being introduced to cultivation in Uganda, Tanzania, Ghana, Madagascar and South Africa, Australia, and several countries of the Southeast Asian (Patiño Varela 1997; Glencross and Nichols 2008). *Cedrela* is one of the most important woody genus of the world and their species have a long history of intense timber exploitation. *Cedrela odorata*, the most widespread species, and at least some of the other species (i.e. *C. fissilis*, *C. lilloi* and *C. balansae*) have been over-exploited due to their valuable timber, both for domestic use and international trade (Blaser et al. 2011). In several countries, populations of *Cedrela* species are now much reduced in their native ranges and many of them were categorized in the IUCN Red List of Threatened Species as globally Vulnerable, some of them, such as *C. fissilis* and *C. lilloi*, currently being classified as Endangered (http://www.iucnredlist.org). Furthermore, indiscriminate logging of timber trees and inefficient timber processing have led to fragmentation of *Cedrela* populations with the unavoidable consequences it can have (Kageyama et al. 1998). Moreover, selective logging leads to habitat modification and forest disturbance, thus effective size of populations decreases leading to an increasing spatial

isolation among remnant trees. Little is known about interspecific variation of seedling growth traits in relation to water availability among species from different forest types (Poorter and Markesteijn 2008). To our knowledge no study to date has experimentally tested differences among *Cedrela* species, except for *C. odorata*, in their water relations and growth responses to increasing rainfall reductions. The aim of this study was to measure water relations and growth parameters in seedlings of different provenances of *C. fissilis*, *C. balansae* and *C. saltensis* species growing under different simulated rainfall regimes in order to determine which species and/or provenance could be better adapted to tolerate rainfall shortage. We hypothesized that growth of seedlings of different *Cedrela* species and provenances in a given area exhibits distinct responses to rainfall variations depending on their geographical origin.

Materials and methods

Seed collection and nursery locations

Cedrela balansae, *C. fissilis* and *C. saltensis* species were selected as study material because they are valuable timber trees widely distributed in tropical and subtropical forests of South America (UNEP-WCMC 2008). Seeds corresponding to six provenances were from two northwestern and northeastern argentinean subtropical forests (Table 1). The climate of both forests is characterized by two distinct seasons: a) dry season, extending from late April to mid September, b) wet season, encompassing the rest of year. On average, over 80 % of rains fall from October to March, in all seed sampling sites. Seeds of *C. balansae* and *C. saltensis* provenances were from the northwestern forest and were collected in June 2006 whereas seeds of *C. fissilis* provenances were from the northeastern forest and were collected in August 2006. For each provenance, seeds were obtained from mature fruits of adult healthy trees (Monteverde 2006). After harvested, fruits were sun dried to make easy their manual opening and release of seeds, as recommended by Lorenzi (1992). Seeds were removed from fruits and manually were selected in order to constitute a uniform lot in relation to size and external characteristics.

Table 1 Origin and geographic location of *Cedrela* species and provenances

Species	Provenance	Province	Latitude	Longitude	Altitude (m a.s.l.)	Temperature (°C)			Precipitation (mm year-1)		
						Min	Max	Mean	Min	Max	Mean
C. balansae	Río Seco	Salta	22°31′S	63°55′W	700	14	30	22[a]	750	1,300	1,000[a]
C. balansae	Yuto	Jujuy	23°38′S	64°28′W	349	14	36	25[b]	332	1,419	863[c]
C. fissilis	San Antonio	Misiones	26°04′S	53°45′W	600	16	36	26[d]	1332	2,934	2,130[e]
C. fissilis	Guaraní	Misiones	26°54′S	54°15′W	490	14	39	26[f]	1,402	2,900	2,140[f]
C. saltensis	Calilegua	Jujuy	23°41′S	64°51′W	1,168	12	29	21[a]	1,165	2,830	2,000[a]
C. saltensis	Pintascayo	Salta	22°51′S	64°36′W	900	14	29	22[a]	950	2,000	1,500[b]

Compiled data of maximum, minimum and mean averages of annual temperatures and rainfall recorded in sampling sites

[a] Las Yungas: Biosphere Reserve: http://www.rbyungas.org.ar (2012)

[b] Brown et al. (2001)

[c] Bianchi and Yáñez (1992)

[d] Servicio Meteorológico Nacional: http://www.smn.gov.ar (2013)

[e] Pérez (2009)

[f] Pahr et al. (1997)

Site management, experimental design, and data collection

Trials were carried out in the National Institute of Agricultural Technology (INTA–EEA) (Famaillá, Tucumán province, 27°03′S, 65°25′W, 450 m a.s.l.). Before sown, seeds were disinfected in 1 % calcium hypochlorite water solution for 10 min and then thoroughly washed with distilled water. Seeds were sowed in January 2007 in well-drained 13 cm diameter, 45 cm deep pots, filled with a local loamy type soil, with one seed per pot and 15 replications for each provenance and each simulated rainfall treatment in a randomized arrangement. Prior to sowing, pots were watered at field capacity. Pots were assumed to be at field capacity after they were thoroughly watered and kept in a basin partly filled with water overnight. After that, pots were removed from the water basin and left to drain the excess of water for 24 h. After sowing, pots were transferred to a greenhouse under uncontrolled conditions in order to exclude the natural rainfall. Pots were maintained nearly to field capacity until the beginning of simulated rainfall treatments. Pots were rotated regularly in their positions to avoid confounding effects of light and temperature gradients. No fertilizer was added and no pest control was performed. Seeds of Calilegua provenance of *C. saltensis* species showed a very low germination rate and were discarded. Beginning in August 2007,

6-month-old seedlings were supplied with different water volumes to simulate annual rainfalls of 600 mm (severe water deficit), 800 mm (mild water deficit), 1,000 mm (mild wet), and 1,200 mm (well-watered) that served as control. These simulated rainfall regimes could represent different water shortage scenarios that can be occur in tropical and subtropical forests of both Central and South America under the ENSO effects (Allen et al. 2010). For each simulated rainfall treatment, monthly watering volumes were calculated according to the monthly distribution pattern of annual rainfall established for the northwestern subtropical region of Argentina (Bianchi and Yáñez 1992). In addition this rainfall pattern is closely related to one described for the Paranaense rainforest (southeastern Brazilian region) (Cook and Vizy 2008). Between August (cold and dry season ending) and December (warm and wet season) the pots were watered every 6 days with equal fractions of water until complete the corresponding monthly volume of each simulated rainfall treatment. In all simulated rainfall treatments no water drainage was observed. Temperature data were obtained from the INTA–EEA weather station (Table 2).

Leaf water relations

For each provenance and simulated rainfall treatment, ten seedlings were sampled to study water relations.

Table 2 Monthly percentage of total rainfall recorded in the northwestern region of Argentina (Bianchi and Yáñez 1992)

Month	Monthly watering (%)	Monthly watering (mm)				Temperature average (°C)	
		1,200	1,000	800	600	Maximum	Minimum
January	20.03	240.36	200.30	160.24	120.18	29.5	20.3
February	16.95	203.40	169.50	135.60	101.70	29.5	20.2
March	15.72	188.64	157.20	125.76	94.32	26.6	18.0
April	7.71	92.52	77.10	61.68	46.26	25.3	14.9
May	3.05	36.60	30.50	24.40	18.30	18.3	8.7
June	1.59	19.08	15.90	12.72	9.54	19.2	5.0
July	0.93	11.16	9.30	7.44	5.58	18.5	2.1
August	1.15	13.80	11.50	9.20	6.90	19.4	3.8
September	2.00	24.00	20.01	16.04	12.00	25.7	10.9
October	5.77	69.24	57.70	46.16	34.62	27.4	15.9
November	10.40	124.80	104.00	83.20	62.40	28.9	16.4
December	14.70	176.40	147.00	117.60	88.20	30.4	18.4

Monthly water volume applied to each pot for each simulated rainfall. Corresponding monthly water volume was divided into equal fractions, which were applied individually every 6 days. Monthly maximum and minimum temperature averages recorded at the experimental site

Midday leaf water potential (Ψ_{md}) and leaf relative water content (RWC) were measured each 2 months between August and December. Measurements of Ψ_{md} were taken between 12:00 and 14:00 h when water stress will be maximized, using a PI-6 Schölander-type pressure chamber (Bio-Control, Argentina). All measurements were made on the second pair of fully expanded leaves, counted from the top bud and immediately after excision. Measurements were performed on two leaflets of each leaf end. We did not measure predawn leaf water potential (Ψ_{pr}) because at midday, greater differences in leaf water potential exist between water-stressed and well-watered plants (Girona et al. 2006). After complete Ψ_{md} measurements, RWC was determined using fresh weight (FW) at excision, turgid weight (TW) after 12 h rehydration in distilled water at 4 °C in dark, and dry weight (DW) after oven drying 48 h at 70 °C.

$$RWC(\%) = [(FW - DW)/(TW - DW)] \times 100$$

TW and DW were also used to calculate TW:DW ratio of *Cedrela* provenances.

Growth parameters and biomass production

Shoot height (SH) and neck diameter (ND) were also measured every 2 months. Shoot height corresponds to distance between soil surface and top bud, and was

performed by using a tape measure (1 mm accuracy). Neck diameter was measured at soil surface level (root collar) using a digital calliper (ECO5 Tresna, China). Shoot height and neck diameter measurements were used to make respective estimators of growth rate. Both shoot growth rate (SGR) and neck growth rate (NGR) were calculated by dividing measured values recorded after the initial 2-months treatment by values obtained in August (month = 0) and thereafter by values corresponding to immediately previous 2-months period. At the end of the experiment seedlings were harvested and washed thoroughly. Length of root and fully expanded leaf (first basal leaf) and leaf number were measured in ten seedlings for each provenance and each simulated rainfall treatment. After that, seedlings were divided into shoot, root and leaves which were dried in an oven at 70 °C for 48 h to obtain corresponding dry weights (DWs). In order to depict carbon allocation to root and shoot biomass, we also calculated the root:shoot DW ratio (RSR).

Statistical analyses

Since water potential and water content are very important physiological parameters related to seedling survival under drought conditions, a multivariate analysis of variance (MANOVA, type III decomposition) was applied to analyze the effects of four

simulated rainfall treatments on water relation parameters i.e. Ψ_{md} and leaf RWC in seedlings of three *Cedrela* species and also to test if there were significant variations among species and provenances nested within species throughout time. Analyses of several interactions were also included. Due to SGR, NGR and RSR parameters may affect water relations, were considered as covariates and then a multivariate analysis of covariance (MANCOVA) was also performed to assess effects and interactions of simulated rainfall treatments on the performance of species and provenances throughout time. Following the MANOVA and MANCOVA analyses, obtained data were subjected to univariate repeated-measures analysis of variance (RM-ANOVA) and covariance (RM-ANCOVA). These statistical approaches were applied to mitigate potential effects of pseudoreplications that may inflate type I error (Tabachnick and Fidell 2001). Data for statistical analyses were averages of measurements recorded repeatedly during the experiment for each seedling and provenance at the corresponding simulated rainfall treatment. Post hoc mean comparisons were made by Duncan's test and the level of confidence was established at 95 %. All statistical analyses were performed using the STATISTICA (Version 7.0, 2004, StatSoft, Tulsa, OK) data analysis software system by mean of the General Linear Modeling with Gaussian error.

Results

Leaf water relation parameters (both Ψ_{md} and RWC)

MANOVA analysis applied on midday leaf water potential (Ψ_{md}) and leaf RWC revealed that simulated rainfall treatment (*Pillai's* = 0.86, $F_{6,36} = 4.54$, $P = 0.0016$), species (*Pillai's* = 1.50, $F_{4,36} = 26.73$, $P < 0.0001$), provenance nested within species (*Pillai's* = 0.52, $F_{4,36} = 3.14, P = 0.0258$), and time (*Pillai's* = 1.47, $F_{4,36} = 24.84, P < 0.0001$) significantly influenced water relations. Seedling performance respect to water relations was also significantly different throughout time depending on species (time × species interaction, *Pillai's* = 0.85, $F_{8,36} = 3.35, P = 0.0057$). Other interactions among analyzed parameters were not significant ($0.5 < Pillai's > 0.75; 0.07 < P > 0.6$).

Midday leaf water potential (Ψ_{md})

The evolution of Ψ_{md} in seedlings of *Cedrela* species growing under four simulated rainfall regimes are shown in Fig. 1. A clear difference between northwestern and northeastern forests was observed. Highest values of Ψ_{md} were found in northwestern species whereas lowest (more negative) ones were observed in northeastern species. This difference was notably marked at the end of the experiment under both 800 and 600 mm year^{-1} of simulated rainfall treatments (Fig. 1c, d). In almost all provenances, Ψ_{md} pattern can be divided into two phases. In the first phase from the beginning of simulated rainfall treatments (August to October), water deficit seems affect the water potential more slowly. Whilst during the second phase from October to December it became increasingly more severe especially under highest water deficits when comparing with well-watered control. At provenance level highest decreases of Ψ_{md} was found in provenances from wettest sites (Guaraní and San Antonio of *C. fissilis* species), indicating that they experienced more severe stress. By contrast, in Yuto provenance (*C. balansae*) from the less rainy site, a less reduction of Ψ_{md} was observed. The Pintascayo provenance (*C. saltensis*) from a middle rainy site showed a slightly less reduced Ψ_{md} than the Yuto provenance under severe water deficit condition. The Ψ_{md} pattern of Río Seco provenance from a mild rainy site did not show two different phases and practically stayed without changes during the experiment (Fig. 1a, b). The post-MANOVA univariate RM-ANOVA analysis revealed that simulated rainfall treatment significantly affected the Ψ_{md} ($F_{3,18} = 26.12, P < 0.0001$) with clear differences among species ($F_{3,18} = 59.74, P < 0.0001$). Treatment × species interaction was scarcely significant on Ψ_{md} ($F_{6,18} = 2.54, P = 0.0585$). Further, Ψ_{md} also varied significantly between 2-months measurement periods ($F_{2,18} = 28.41, P < 0.0001$), and this variation was significantly different between species (time × species interaction; $F_{4,18} = 4.7, P = 0.0089$), and provenances (time × provenance nested within species interaction; $F_{4,18} = 3.62, P = 0.0247$). However, provenance nested within species × time × treatment, and time × treatment × species interactions were not significant ($0.21 < F > 1.99, 0.12 < P > 0.81$).

Leaf relative water content (RWC)

Excepting *C. balansae* (Río Seco provenance) in all simulated rainfall treatments the RWC practically showed the same temporal pattern in all provenances (Fig. 2). Similarly to Ψ_{md} the RWC also showed a biphasic pattern. It decreased from August to October and subsequently increased between October and December. No clear difference of RWC values between northwestern and northeastern provenances was observed. Further, for all simulated rainfall treatments the Río Seco provenance showed the less variability of RWC pattern (Fig. 2a–d). The increase of RWC observed between October and December in all treatments probably was due to enhanced simulated rainfall volumes that lead to soil moisture increment. When a post-MANOVA univariate RM-ANOVA analysis was accounted for RWC, no significant effects of simulated rainfall treatments have been detected ($F_{3,18} = 0.38$, $P = 0.7665$). However, significant variations were observed among species ($F_{2,18} = 26.92$, $P < 0.0001$), provenance nested within species ($F_{2,18} = 9.22$, $P = 0.0018$), and time ($F_{2,18} = 22.02$, $P < 0.0001$); being the temporal pattern independent of the other factors (non-

significant interactions; $0.49 < F > 2.36$, $0.09 < P > 0.81$).

Turgid weight to dry weight ratio (TW:DW)

TW:DW ratio showed a similar temporal pattern in almost all species and provenances, either in well-watered control or under severe water deficit. From August to October under all simulated rainfall treatments, TW:DW ratio slower increased in *Cedrela* provenances, except in *C. fissilis* (San Antonio provenance) whose TW:DW remains practically unchanged throughout the experiment. From October to the end of the experiment TW:DW slightly decreased (data not shown).

Shoot height and neck diameter

Shoot height (SH) showed a similar pattern in all provenances under all simulated rainfall treatments (Fig. 3). From August to October SH remained practically unchanged, but from this point it increased in all species and provenances, being more pronounced in *C. saltensis* (Pintascayo provenance) and less in *C. balansae* (Yuto provenance) (Fig. 3d). Neck

Fig. 1 Midday leaf water potential (Ψ_{md}) in *Cedrela* seedlings growing under four simulated rainfall regimes: **a** 1,200 mm year^{-1}, **b** 1,000 mm year^{-1}, **c** 800 mm year^{-1} and **d** 600 mm year^{-1}. Values are means of 10 different measurements. Vertical bars represent ± standard error ($P < 0.05$)
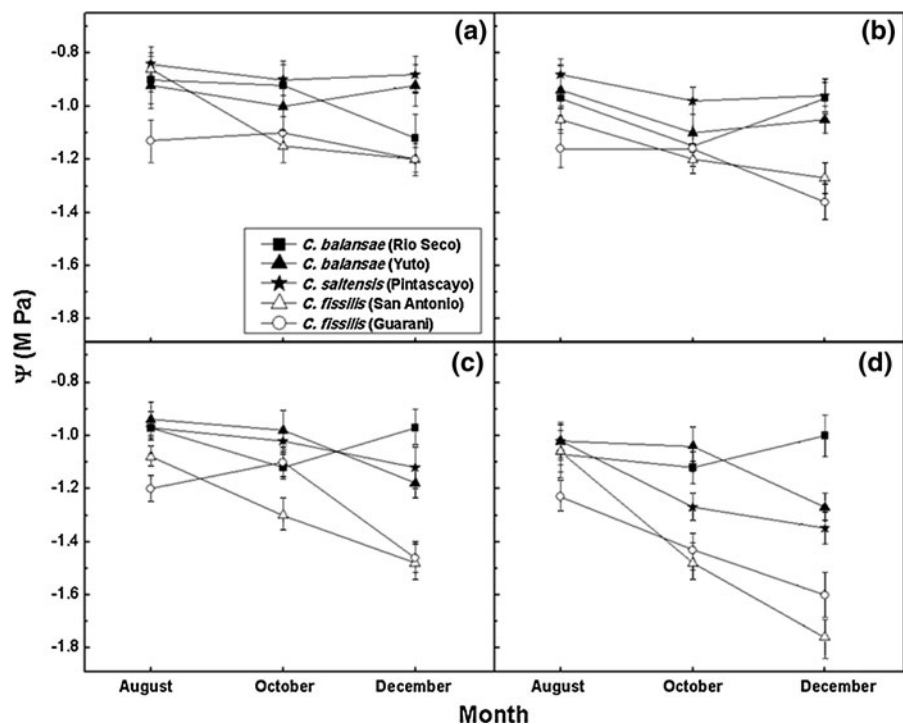
Fig. 2 Leaf RWC in *Cedrela* seedlings growing under four simulated annual rainfall regimes: **a** 1,200 mm year^{-1}, **b** 1,000 mm year^{-1}, **c** 800 mm year^{-1} and **d** 600 mm year^{-1}. Values are means of 10 different measurements. Vertical bars represent ± standard error ($P < 0.05$)
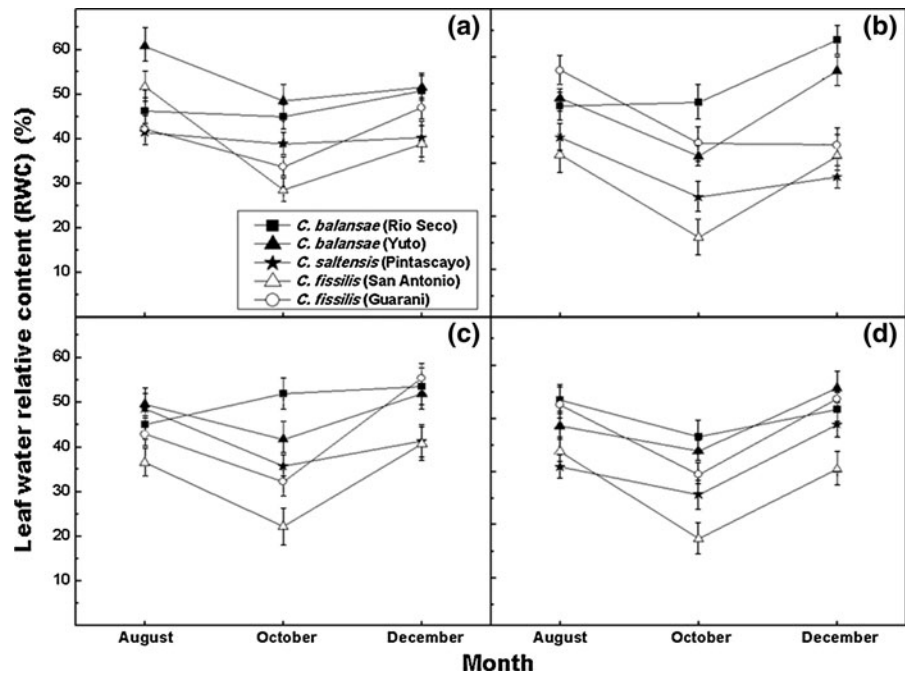
diameter (ND) increased in all species and provenances during the experimental period under all simulated rainfall treatments (Fig. 4). From August to October the ND showed a more pronounced increase than observed from October to the end of the experiment. Interestingly, *C. saltensis* (Pintascayo provenance) showed highest intraprovenance increases of SH and ND occurring under severe water deficit (Figs. 3d, 4d). Statistical analyses were not carried out, however, the effects of simulated rainfall treatments on both PH and ND per species were distinct and similar in all provenances.

Impact of growth rate parameters (SGR and NGR) on water relations

To assess the effects of SGR on Ψ_{md} and RWC a multivariate MANCOVA analysis was performed. Broadly water relations were significantly affected by SGR (*Pillai's* = 0.55, $F_{2,16} = 9.65$, $P = 0.0018$). Impact of SGR on water relations showed significant variations among simulated rainfall treatment (*Pillai's* = 0.96, $F_{6,34} = 5.22$, $P = 0.0007$), species (*Pillai's* = 1.62, $F_{4,34} = 36.23$, $P < 0.0001$), provenance nested within species (*Pillai's* = 0.66, $F_{4,34} = 4.22$, $P = 0.0070$), and time (*Pillai's* = 0.82, $F_{4,34} = 5.85$, $P = 0.0011$). The inclusion of SGR as a covariate in the multivariate model showed that water relations varied significantly between species and provenance throughout time (time × species interaction; *Pillai's* = 1.12, $F_{8,34} = 5.42$, $P = 0.0002$, and time × provenance nested within species interaction; *Pillai's* = 0.87, $F_{8,34} = 3.29$, $P = 0.0069$). This indicates that a significant proportion of time-dependant variation related to water relations among provenances, is be associated to variation of SGR among seedlings. Other interactions between factors were not significant ($1.24 < F > 1.69$; $0.11 < P > 0.28$). Post-MANCOVA univariate RM-ANOVA analysis showed that SGR significantly and negatively affected the Ψ_{md} (estimate: $\beta = -0.61 \pm 0.14$, $t = -4.247$, $P = 0.0005$). Significant effects were also observed for treatment × species, and time × treatment interactions. It is noted that in RM-ANOVA analysis accounted for Ψ_{md} these effects practically were not significant (Table 3). By contrast, SGR did not account for RWC variation (estimated: $\beta = 0.18 \pm 0.29$, $t = 0.613$, $P = 0.548$). Respect to NGR, the MANCOVA analysis showed that NGR have not effects on water relations (*Pillai's* = 0.18, $F_{2,16} = 1.74$, $P = 0.2064$).

Root and leaf length, leaf number

Both root and leaf lengths were reduced in all provenances, except the root length of Yuto provenance, under severe water deficit when compared with

Fig. 3 Shoot height of *Cedrela* seedlings growing under four simulated annual rainfall regimes: **a** 1,200 mm year^{-1}, **b** 1,000 mm year^{-1}, **c** 800 mm year^{-1} and **d** 600 mm year^{-1}. Vertical bars represent ± standard error ($P < 0.05$)
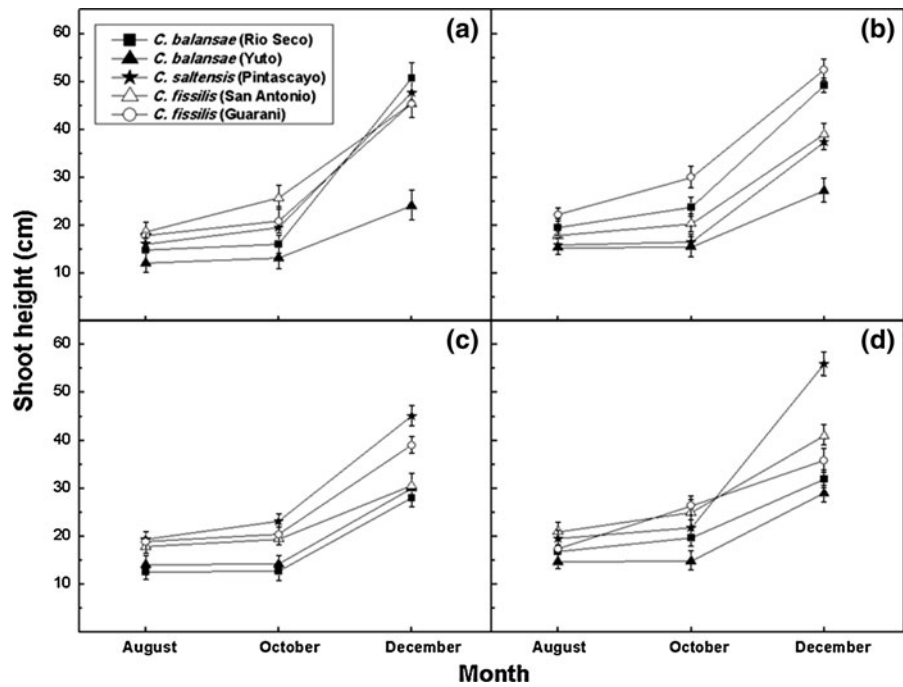
Fig. 4 Neck diameter (ND) of *Cedrela* seedlings growing under four simulated annual rainfallregimes: **a** 1,200 mm year^{-1}, **b** 1,000 mm year^{-1}, **c** 800 mm year^{-1} and **d** 600 mm year^{-1}. Values are means of 10 different measurements. Vertical bars represent ± standard error ($P < 0.05$)
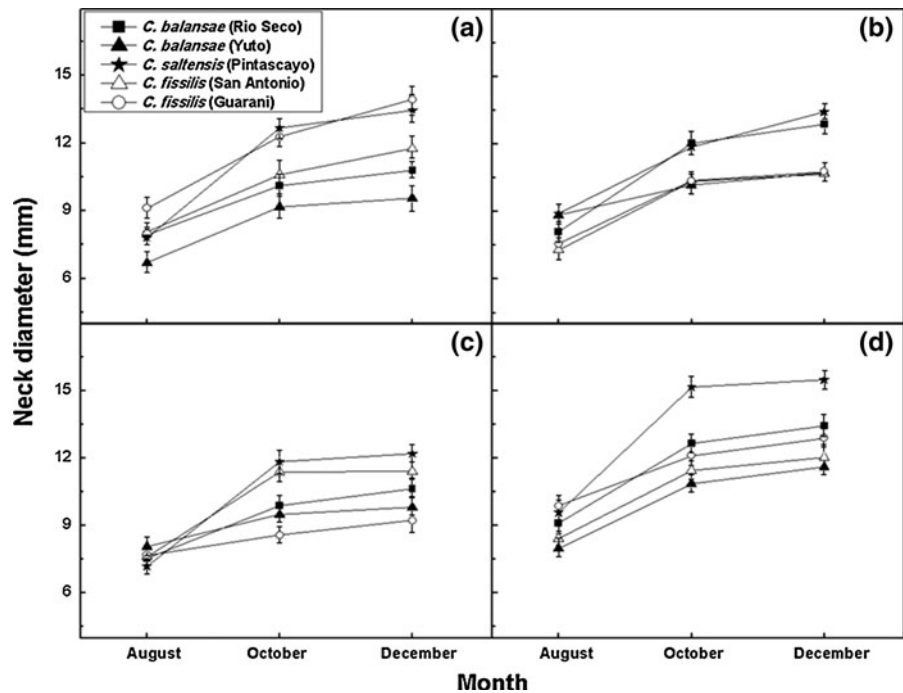
well-watered control plants (Fig. 5). Highest reductions of root length were 92.5 % in *C. fissilis* (San Antonio provenance) and 74.7 % in *C. saltensis* (Pintascayo provenance) (Fig. 5a), while in left length they were 30.5 % in *C. fissilis* (Guaraní provenance)

and 27.5 % in *C. saltensis* (Pintascayo provenance) (Fig. 5b). Further, the percentage of root length into total axis length (root + shoot) did not show significant changes, except in *C. fissilis* (San Antonio provenance) and *C. saltensis* (Pintascayo provenance)

Table 3 Summary of univariate repeated-measures ANOVA (RM-ANOVA) on effects of four simulated rainfall treatments on midday leaf water potential (Ψ_{md}) throughout time in *Cedrela* seedlings

Source of variation	df	MS	F	P
Treatment	**3**	**0.18**	**56.67**	**0.00000**
Species	**2**	**0.40**	**125.01**	**0.00000**
Provenance nested within species	2	0.00	1.51	0.24821
Treatment × species	**6**	**0.01**	**4.12**	**0.00978**
Time	**2**	**0.05**	**15.25**	**0.00016**
Time × treatment	**4**	**0.02**	**5.40**	**0.00276**
Time × species	**12**	**0.04**	**13.67**	**0.00004**
Time × treatment × species	4	0.01	1.68	0.15833
Time × provenance nested within species	**6**	**0.03**	**9.61**	**0.00030**
Shoot growth rate (SGR)	**1**	**0.06**	**18.04**	**0.00054**
Error	17	0.00		

Significant effects are highlighted in bold

Treatment, species, provenance nested within species, and treatment × species interaction represent between-effects; time and interactions with time represent the within-effects; SGR is the covariate. See Materials and Methods for details. *MS* mean squares, *df* degrees of freedom, *F* F-statistic, *P* significance level $P < 0.05$

(data not shown). On the other hand the leaf number was not affected by all simulated rainfall treatments and no plant death occurred (data not shown).

Biomass production and root:shoot DW ratio (RSR)

Data of biomass production (root, shoot and leaf DW) and root:shoot DW ratio (RSR) are shown in Table 4. Compared with well-watered condition, root DW decreased under 600 mm year^{-1} of simulated rainfall treatment, being found highest reductions in *C. balansae* (Río Seco provenance) (69.9 %) and *C. fissilis* (Guaraní provenance) (55.7 %), respectively. Of interest, in Guaraní and Pintascayo provenances highest values of root DW were found under 1,200 mm year^{-1} whereas in the rest of provenances were observed under 1,000 mm year^{-1} of simulated rainfall. Shoot DW showed a similar pattern to root DW with decreases of 20.2 and 49.5 % in Río Seco and Guaraní provenances under severe water deficit condition. In an opposite trend, shoot DWs of Yuto, San Antonio and Pintascayo provenances were increased by 20.4, 45.1 and 85.1 %, respectively. Leaf DW also decreased under 600 mm year^{-1} of simulated rainfall, with highest reductions (65.1 and 38.9 %) occurring in Guaraní and Río Seco provenances. Similar to root DW highest values of leaf DW

of these provenances were observed at the mild wet condition (1,000 mm year^{-1}). The RSR did not show a uniform trend under all simulated rainfall treatments. In *C. balansae* (Río Seco provenance) increased from well-watered condition to severe drought condition, while in *C. fiisilis* (Guaraní provenance) increased from well-watered to mild wet condition only. In the rest of species and provenances, RSR generally decreased with decreasing simulated rainfall supply.

Impact of RSR on water relations

MANCOVA analysis showed that RSR significantly affected water relations (*Pillai's* = 0.36, $F_{2,16} = 4.55$, $P = 0.0272$). By using this multivariate model the impact of RSR on water relations showed significant variations between simulated rainfall treatment (*Pillai's* = 0.94, $F_{6,34} = 5.06$, $P = 0.0008$), species (*Pillai's* = 1.29, $F_{4,34} = 15.59$, $P < 0.0001$), provenance nested within species (*Pillai's* = 0.66, $F_{4,34} = 4.18$, $P = 0.0074$), and time (*Pillai's* = 1.55, $F_{4,34} = 29.22$, $P < 0.0001$). Temporal response significantly varied among species (time × species interaction; *Pillai's* = 0.96, $F_{8,34} = 3.93$, $P = 0.0022$). Similarly to SGR, the inclusion of RSR as covariate in the multivariate model showed that water relations also varied significantly among provenance throughout
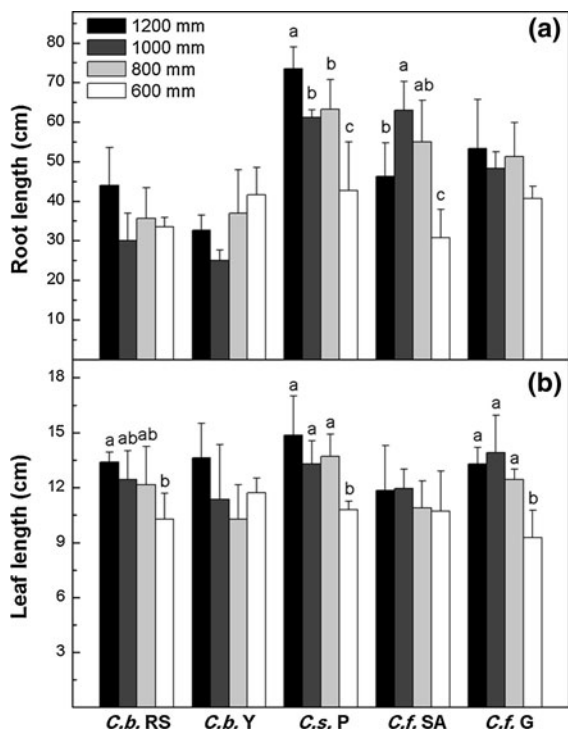
Fig. 5 Root length **a** and leaf length **b** of *Cedrela* seedlings growing under four simulated rainfall regimes. Values are means of 10 different measurements. For each provenance, means followed by different letters are significantly different from each other ($P < 0.05$). ***C.b.* RS**: *C. balansae* Río Seco provenance; ***C.b.* Y**: *C. balansae* Yuto provenance; ***C.s.* P**: *C. saltensis* Pintascayo provenance; ***C.f.* SA**: *C. fissilis* San Antonio provenance; ***C.f.* G**: *C. fissilis* Guaraní provenance

time (time × provenance nested within species interaction; *Pillai's* = 0.71, $F_{8,34}$ = 2.33, P = 0.0411). This indicates that temporal differences between provenances respect to water relations also depend upon variation of RSR among seedlings. However, there was only marginally significant effect of treatment × species interaction (*Pillai's* = 0.84, $F_{8,34}$ = 2.03, P = 0.0519). Other interactions between factors were not significant ($1.02 < F > 2.03$; $0.42 < P > 0.45$). Following the MANCOVA analysis, the univariate RM-ANOVA test showed that RSR significantly and positively affected leaf RWC (estimate: $\beta = 0.86 \pm 0.30$, $t = 2.868$, $P = 0.0107$). Further, there was significant effect of treatment × time × species interaction (Table 5). Of interest, these effects are not significant if covariate is not included in the model. On the other hand, RSR did not account for Ψ_{md} variation (estimated: $\beta = 0.10 \pm 0.11$, $t = 0.9127$, $P = 0.374$).

Discussion

This study sheds light on the relationship between rain deficit and growth in five provenances of three *Cedrela* species. By withholding water in the greenhouse to simulate different rainfall patterns, were induced substantial changes in leaf midday water potential (Ψ_{md}) and leaf RWC. These changes varied significantly in the degree of change over time in relation to both species/provenances and water deficit intensity. Both Ψ_{md} and RWC showed a biphasic temporal pattern assuming as first phase the growth period between August and October and as second one the October to December growth period. Biphasic pattern of RWC was more pronounced than Ψ_{md} pattern and also showed a higher similarity among provenances. Moreover, RWC and Ψ_{md} biphasic patterns have the same break month, but two phases did not show similar trends. During the first phase both RWC and Ψ_{md}, in general, decreased in practically all provenances under all simulated rainfall treatments. However, during the second phase whereas RWC showed a sustained increase, the decreasing tendency of Ψ_{md} continued until the end of the experiment (Figs. 1,2). This contradictory trend of water relation parameters, may suggest that the combination of dry season with little amount of simulated rainfall (first phase) followed by increasing temperature and rainfall amount during early wet season (second phase) has a severe impact on water status of *Cedrela* seedlings. To explain responsiveness of *Cedrela* RWC to early increases of rainfall amount must be noted that a gradual increase of soil water content occurs as the rainy season progresses. After a time-lapse of 1–3 months following starting of rainy season, the water content of soil may surpass a threshold level and seedlings can maintain a positive water balance throughout the rest of wet season, even in short dry periods (Brienen and Zuidema 2005). Moreover the responsiveness to rainfall that exhibit many seedlings of tropical species is quite similar, with highest sensitivity during the early rainy season and with no significant effect in the late rainy season (Dunisch et al. 2003; Fichtler et al. 2004). In agreement with these assumptions our data showed between October and December (second phase), concomitantly with the rise of temperature and amount of simulated rainfall, a pronounced increase of RWC in *Cedrela* provenances takes place (Table 2, Fig. 2). Similar insights were applied to explain the impact of severe

Table 4 Dry mass accumulation in root shoot and leaf of *Cedrela* seedlings at the end of the experiment under four simulated annual rainfall regimes

Rainfall (mm)	C. balansae (RS)	C. balansae (Y)	C. saltensis (P)	C. fissilis (SA)	C. fissilis (G)
Root (g DW)					
1,200	$4.86 \pm 0.97_{aA}$	$3.12 \pm 0.32_{aA}$	$7.19 \pm 0.53_{aB}$	$3.98 \pm 0.58_{aA}$	$5.62 \pm 0.92_{aAB}$
1,000	$5.17 \pm 0.76_{aA}$	$4.16 \pm 0.36_{bB}$	$4.11 \pm 0.13_{bB}$	$5.39 \pm 0.74_{bA}$	$5.36 \pm 0.39_{aA}$
800	$5.17 \pm 0.94_{aA}$	$2.93 \pm 0.62_{acB}$	$4.73 \pm 0.55_{bA}$	$3.85 \pm 0.57_{aB}$	$3.93 \pm 0.25_{bBC}$
600	$2.86 \pm 0.78_{bA}$	$3.52 \pm 0.52_{abA}$	$5.99 \pm 0.56_{cB}$	$2.97 \pm 0.51_{aA}$	$3.61 \pm 0.33_{bA}$
Shoot (g DW)					
1,200	$6.19 \pm 0.32_{aA}$	$3.18 \pm 0.63_{aB}$	$3.22 \pm 0.40_{aB}$	$3.48 \pm 0.56_{aB}$	$6.43 \pm 0.32_{aA}$
1,000	$5.29 \pm 0.94_{aA}$	$5.06 \pm 0.73_{bA}$	$3.42 \pm 0.13_{aB}$	$5.90 \pm 0.62_{bA}$	$5.80 \pm 0.49_{aA}$
800	$4.88 \pm 0.42_{abA}$	$3.46 \pm 0.72_{aB}$	$3.32 \pm 0.14_{aB}$	$3.32 \pm 0.36_{aB}$	$3.37 \pm 0.22_{bB}$
600	$3.07 \pm 0.42_{cA}$	$3.83 \pm 0.70_{abA}$	$5.96 \pm 0.14_{bB}$	$5.05 \pm 0.47_{bAB}$	$4.30 \pm 032_{cAC}$
Root:Shoot ratio (RSR)					
1,200	$0.78 \pm 0.07_{a}$	$0.98 \pm 0.08_{a}$	$2.23 \pm 0.14_{a}$	$1.14 \pm 0.10_{a}$	$0.87 \pm 0.11_{a}$
1,000	$0.98 \pm 0.11_{b}$	$0.82 \pm 0.09_{a}$	$1.20 \pm 0.11_{b}$	$0.91 \pm 0.11_{b}$	$0.92 \pm 0.13_{a}$
800	$1.06 \pm 0.09_{b}$	$0.85 \pm 0.06_{a}$	$1.42 \pm 0.10_{b}$	$1.16 \pm 0.09_{a}$	$1.17 \pm 0.08_{b}$
600	$0.93 \pm 0.09_{b}$	$0.92 \pm 0.09_{a}$	$1.00 \pm 0.10_{bc}$	$0.59 \pm 0.06_{c}$	$0.84 \pm 0.08_{a}$
Leaf (g DW)					
1,200	$3.80 \pm 0.55_{aA}$	$1.70 \pm 1.29_{aB}$	$3.45 \pm 0.39_{aA}$	$3.20 \pm 0.65_{aA}$	$6.64 \pm 0.21_{aC}$
1,000	$5.24 \pm 0.94b_{A}$	$3.78 \pm 1.23_{bB}$	$2.70 \pm 0.74_{aB}$	$5.55 \pm 0.48_{bA}$	$5.90 \pm 0.20_{aA}$
800	$3.56 \pm 0.47_{aA}$	$2.49 \pm 0.99_{aA}$	$3.57 \pm 1.44_{aA}$	$3.79 \pm 0.29_{aA}$	$4.56 \pm 0.54_{bB}$
600	$2.32 \pm 0.67_{cA}$	$2.61 \pm 0.70_{aA}$	$3.07 \pm 0.38_{aA}$	$4.03 \pm 0.65_{aB}$	$2.32 \pm 0.57_{cA}$

RS Río Seco, *Y* Yuto, *P* Pintascayo, *SA* San Antonio, *G* Guaraní

For root, shoot, leaf DW and RSR, means followed by the same lowercase letter within each column, and for root, shoot and leaf DW, means followed by the same uppercase letter within each row, are not significantly different at $P < 0.05$ using Duncan's test (n = 10)

Table 5 Summary of univariate repeated-measures ANOVA (RM-ANOVA) on effects of four simulated rainfall treatments on leaf RWC throughout time in *Cedrela* seedlings

Source of variation	df	MS	F	P
Treatment	**3**	**58.35**	**3.27**	**0.04698**
Species	**2**	**675.39**	**37.82**	**0.00000**
Provenance nested within species	**2**	**286.46**	**16.04**	**0.00012**
Treatment × species	6	37.05	2.07	0.11067
Time	**2**	**550.99**	**30.85**	**0.00000**
Time × treatment	6	12.14	0.68	0.66826
Time × species	**4**	**59.01**	**3.30**	**0.03551**
Time × treatment × species	12	22.73	1.27	0.31633
Time × provenance nested within species	4	28.33	1.59	0.22327
Root:shoot ratio (RSR)	**1**	**146.93**	**8.23**	**0.01065**
Error	17	17.86		

Significant effects are highlighted in bold

Treatment, species, provenance nested within species, and treatment × species interaction represent between-effects; time and interactions with time represent the within-effects; RSR is the covariate. See Materials and Methods for details. *MS* mean squares, *df* degrees of freedom, *F* F-statistic, *P* significance level $P < 0.05$

chronic rainfall reduction on the leaf physiology of *Quercus suber* trees growing in a Mediterranean mesothermic humid site with hot and dry summer and cool and wet winter (Grant et al. 2010). Since trees adapted to drought conditions tend to maintain a higher water content and a relatively low water potential (Li and Wang 2003), *C. balansae* and *C. saltensis* provenances seem to display a better performance than *C. fissilis* provenances under severe water deficit condition. Because only one provenance of *C. saltensis* was assayed, further studies are needed to get a more reliable data on this assumption. On the other hand, lower values of Ψ_{md} found at the end of the experiment in *C. fissilis* (Guaraní and San Antonio provenances) under increasing water deficit (Fig. 2b,d) could agree with the assumption of Stoneman et al. (1994). Stoneman's assumption considers that decrease of water potential but not RWC under drought is a feature of species tending to inhabit moist sites. Seeds of *C. fissilis* provenances were from sites with a mean annual rainfall higher than 2,000 mm. Interestingly, Ψ_{md} of the Río Seco provenance did not show a biphasic pattern and practically stayed without changes during the experiment. This fact could indicate that at least in this provenance other strategies such as stomatal closure also contribute to cope with water deficit to stabilize the seedling water potential. Although the trigger of stomatal closure is not fully understood, leaf water potential is one of the major factors in stomatal regulation because stomatal aperture directly responds to guard cell turgor (Franks et al. 1995). However, the interspecific relationship between Ψ_{md} and midday stomatal conductance (g_s) has not been well established, and the mechanism by which stomata respond to and control Ψ_{md} is unclear (Brodribb and Holbrook 2003). Notably, the ability of a plant to maintain high Ψ_{md} during active transpiration is related to plant hydraulic system i.e. those species with high water transport would be able to replace transpirational water loss more quickly and therefore maintain higher Ψ_{md} (Zhang and Cao 2009). Consequently, a positive relationship between water transport and maximum photosynthetic rate has been found in different plant taxonomic groups and different ecosystems (Brodribb et al. 2003). Midday g_s also seem to be related to plant hydraulic conductance (Lo Gullo et al. 2003). Decreased g_s at midday slows down further water loss, consequently, it has an adaptive significance in protecting the plant vascular system from

xylem dysfunction. Rather, the significance of diurnal stomatal regulation is probably to maintain stem water potential in the range that will avoid stem xylem embolism during the day (Meinzer et al. 2009). Thus, stomatal conductance seems to be more related to stem water potential than that leaf water potential (Zhang et al. 2013).

The continuous decline of Ψ_{md} irrespective of simulated rainfall treatments observed in all provenances, except the Río Seco provenance, seems to be contradictory with RWC temporal pattern and leads to assume that different to rainfall amount and temperature rise, other mechanisms such as stomata aperture regulation and osmolyte accumulation (Brodribb et al. 2003; Choat et al. 2006) can also be operating in regulating RWC in *Cedrela* provenances. However, we did not carry out a gas exchange analysis to measure CO_2 assimilation rate, stomatal conductance and transpiration rate; also osmotic parameters were not measured. Further, large leaves of plants growing in dry sites can lead to excessive transpiration water loss (Forbes and Watson 1992). Since *Cedrala* species have large paripinnate leaves with many leaflets, grouped towards the end of the branches (15–50 cm long, with pairs of scythe-shaped leaflets, lanceolate to oblong, 7–15 cm × 3–5 cm, with the base obliquely truncated and asymmetric) (Grau et al. 2006), a great transpiration rate is expected. Previous results have demonstrated that in *C. fissilis* leaflets increasing temperature-dependant transpiration occurs (Inoue 1980). At present, we have no explanation for contradictory responses of Ψ_{md} and RWC. Multivariate analysis of combined data of Ψ_{md} and RWC showed that simulated rainfall treatments, species and provenances nested within species, and time significantly influenced water relations. When multivariate analyses were accounted separately for both Ψ_{md} and RWC, was found that Ψ_{md} exhibited higher variability among all analyzed traits than that RWC. Trait interactions were also more variables for Ψ_{md} than for RWC. Water potential and RWC are considered reliable indicators of plants' tolerance to water deficit (Kozlowski and Pallardy 2002). Thus, our results might indicate that RWC is a more conservative parameter of water status than that Ψ_{md} in growing seedlings of *Cedrela* provenances watered with different amounts of simulated rainfall.

Water deficit led to changes in the ratio between leaf weight at full turgor and leaf dry weight

(TW:DW). Lower TW:DW ratios have been related to decreased cell volume and changes in cell wall rigidity (Clifford et al. 1998). Leaf cells become smaller with thick walled causing low TW:DW ratios (Cutler et al. 1977). Drought resistant species might be expected to be adapted to large losses of water without loss of turgor (Liu and Stutzel 2002). In the present study there were no significant variations of TW:DW ratio among provenances even under severe water deficit, indicating that another drought adaptation features could be involved in the tolerance of *Cedrela* seedlings to rainfall reductions. Under field conditions growing seedlings can be especially prone to drought because they have not developed an extensive root system (Poorter and Hayashida-Oliver 2000). Reducing growth is the main strategy employed by seedlings to maintain their water status. Water stress slows the seedling growth sooner than root growth does, and the root:shoot ratio (RSR) becomes a reliable indicator of biomass allocation and drought tolerance (Paulilo et al. 1998). Further, both RSR and RWC are closely associated with survival of seedlings and establishment success (Guarnaschelli et al. 2012). Decreasing amounts of simulated rainfall do not induced proportional biomass allocation to root and shoot in *Cedrela* provenances, and also RSR did not show any definite trend. Under severe water deficit the RSR only increased in *C. balansae* (Río Seco provenance), and *C. fiisilis* (Guaraní provenance) when comparing with well-watered control condition. In the rest of provenances RSR decreased. Similar decreases of RSR in drought-stressed plants have been communicated (Elfeel and Al-Namo 2011; Feng et al. 2012). In seasonal dry sites higher RSR is beneficial due to it contributes to get more water supply (Guarnaschelli et al. 2012). An increased carbon allocation to growing root reduces leaf area and decreases both photosynthesis and plant growth (McDowell et al. 2008). Reductions of shoot height, neck diameter, leaf size, and biomass production have been recognized as common responses of reduced plant growth (Kozlowski and Pallardy 2002). No great changes in shoot height and neck diameter were observed among provenances under all simulated rainfall treatments. Under severe water deficit condition highest shoot height and neck diameter were found in *C. saltensis* (Pintascayo provenance). Leaf length and biomass production were differentially affected by simulated rainfalls. But a definite trend among provenances was

not observed. Covariate analyses using growth- and biomass allocation parameters revealed that shoot growth rate SGR and root DW to shoot DW ratio (RSR) significantly affected water relations at species and provenance levels in all simulated rainfall treatments. Effects of SGR also varied significantly throughout time (time × species interaction and time x provenance nested within species interaction). When Ψ_{md} and RWC were individually analyzed the effects of SGR were only significant on Ψ_{md} whereas RWC was not significantly affected. By contrast, there were no significant effects of NGR on water relations. This fact signify that a significant proportion of time-dependant variation related to water relations among provenances, is be associated to variation of seedling shoot growth. Biomass allocation (RSR) also significantly affected water relations throughout time at species and provenance levels under all simulated rainfall treatments (time × species interaction and time x provenance nested within species interaction). However, there was only marginal significant effect of treatment × species interaction. At individual level RSR significantly affected RWC but not Ψ_{md}. This indicates that temporal differences between provenances respect to water relations also depend upon variation of RSR among seedlings.

Differences drought responses among tree ecotypes growing in tropical and subtropical rain forests have been communicated for many species (Engelbrecht et al. 2007). They are attributed to genetic differences in physiological and morphological adaptative responses (Engelbrecht and Kursar 2003), but many of observed variations cannot be explained by genetic traits and/or environmental factors only (phenotypic plasticity) (Aspelmeier and Leuschner 2004). Therefore, variability among individuals of a given population may be the result of distinct sources of fertilizing pollen and/or microenvironmental differences during the formation and maturity of seeds (Wu 1998). Agreeing with this assumption, in this study great variability regarding water relations and growth parameters was observed among seedlings from seeds of the same provenance. Interestingly, studies performed with pot-grown seedlings are probably the most commons in drought-stressed plant research. However, to simulate severe drought conditions, pots often are supplied with small amounts of water, so that only upper soil layers are wetted. In these conditions, sometimes, total supplied water does

not get to root, and then soil–water–root relationships may vary (Ray and Sinclair 1998). Therefore, responses of pot-grown seedlings to water deficit have several limitations when extrapolating to field condition. Notwithstanding, even though the results of this study performed on pot-grown seedlings are based on relatively few observations and require additional confirmation, they allow an opportunity for speculation on the factors that are related to intraspecific variations that are likely to occur during the growth of seedlings from different geographical sites in field condition.

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