J. For. Res. (2021) 32(5):2099–2110
https://doi.org/10.1007/s11676-020-01200-z

ORIGINAL PAPER

Morphophysiological responses of forest seedling species subjected to different water regimes

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Received: 23 February 2020 / Accepted: 3 June 2020 / Published online: 12 August 2020
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Abstract Water availability is a limiting factor for the establishment and development of forest species. To understand the appropriate conditions for the initial post-transplanting phase, it is necessary to understand the specific morphophysiological characteristics of the species, such as the leaf water potential and the efficiency of photosystem II. We aimed to identify the influence of different water regimes on the morphophysiological aspects of young plants of two forest species (*Cedrela fissilis* Vellozo and *Eucalyptus saligna* Sm.). Two greenhouse experiments were conducted for 28 days; one for each species. The design was completely randomized, and the treatments consisted of six different water regimes. Leaf water potential (Ψw) and chlorophyll *a* fluorescence were evaluated every 7 days. At the end of the experiment, morphological attributes (height, collection diameter, root volume, and dry matter) were measured and histological blades were made. The water demand of *E. saligna* was higher than that of *C. fissilis* and required greater replacement within a shorter period. The rehydration from $\Psi w = -2$ Mpa allowed for a fast recovery of the young *C. fissilis* plants ($\Psi w = -1.5$, $Fv/Fm = 0.796$), which indicated good physiological plasticity of this species when submitted to water stress at a level that is not severe. The total dry matter allocation was different among species. Seedlings of *E. saligna* presented the best responses when submitted to a continuous water supply regime, while *C. fissilis* seedlings presented the best response under intermittent irrigation conditions.

Keywords Leaf water potential · Chlorophyll fluorescence · Irrigation · *Cedrela fissilis* Vellozo · *Eucalyptus saligna* Sm

Introduction

Climatic changes affect the morphological, physiological, and anatomical characteristics of plants and influence their productivity (Madani et al. 2018). Species responses to such changes include the development of tolerance and resilience mechanisms, adaption to adverse conditions, or migration to regions with more favorable environmental conditions. In extreme cases, climatic changes can lead to species extinction (Moritz and Agudo 2013).

Studies on climate change have shown that the future water balance will vary under different scenarios due to changes in precipitation, evapotranspiration, and water availability that will shape future flood and drought events (Ponpang-Nga and Techamahasaranont 2016; Jafarnia et al. 2018). For South America, such simulations indicate a significant increase in air temperature and changes in the distribution and amount of precipitation (Chou et al. 2014). Such

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Project funding: This work was supported by the Council for Scientific and Technological Development (CNPq) and the Coordination for the Improvement of Education Personnel (CAPES).

The online version is available at http://www.springerlink.com.

Corresponding editor: Yu Lei.

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conditions will certainly affect forest productivity (Condon et al. 2002; Deeba et al. 2012) on different spatio-temporal scales (Urrutia-Jalabert et al. 2015).

Water availability is a limiting factor for the establishment and development of forest species because it affects survival as well as morphological and physiological characteristics (Whitehead and Beadle 2004; Hodecker et al. 2018). Plants respond to water restriction through various adaptive processes, such as stomatal closure and the reduction of photosynthetic activity, which occur at the expense of maintaining the leaf water potential (Flexas and Medrano 2002; Flexas et al. 2006).

Studies on the effect of induced water stress have been carried out in greenhouses and in the field in order to understand tolerance mechanisms and morphophysiological responses in different species (Otto et al. 2013; Hodecker et al. 2018; Jafarnia et al. 2018). The results of these studies have been used for genotype selection, in different afforestation projects, and for the development of strategies for forest stand implantation in areas with extreme characteristics. Strategies for the selection of species to be planted in areas prone to water deficits depend on understanding the changes caused by low water availability during the initial development period (Hodecker et al. 2018).

In Brazil, forest plantations occupy 7.84 million ha, of which approximately 70% contain *Eucalyptus* species (Gonçalves et al. 2008; IBA 2018) that have been cultivated and studied in the country for more than a century. The *E. saligna* Sm (Myrtaceae) ARA 32864 clone is widely cultivated and used as a source of raw material for obtaining cellulose in Brazil that shows adaptation to different sites but growth restrictions in soils with a severe water deficit in the dry season (Paludzyszyn Filho and dos Santos 2013). Despite this, the critical values of water potential and drought resistance of the clone are unclear.

On the other hand, native tree species with h wood potential are still cultivated in the country but poorly studied, such as *Cedrela fissilis* Vellozo (Meliaceae). *C. fissilis* occurs naturally from southern Brazil (30° S) to Central America (10° N) and is restricted to areas where there are no long periods of low rainfall (Siqueira et al. 2019). Among the factors that explain its wide geographical distribution is its ability to adapt physiologically to different light conditions (Sanches et al. 2017) and a decisiveness that allows adaptation to environments with water deficits (Muellner et al. 2010). With regard to edaphic factors, the species shows a preference for clayey and well-drained soils (Reitz 1984). Additionally, *C. fissilis* has high ecological and economic value (Coradin et al. 2011), which has led to a predatory exploitation for timber that has resulted in the species being currently classified as Vulnerable (Martinelli and Moraes 2013).

Planted forests play a key role in socioeconomic scenarios and generate employment and income while providing environmental services to the country (Longue Júnior and Colodette 2013). In addition, the increasing demand for forest products has contributed to plantation expansions in regions with low quality agricultural soils, low soil fertility, and water restrictions (Silva et al. 2016), which has made it difficult to initially establish plants. We aimed to identify the influence of different water regimes on the morphophysiological aspects of young *C. fissilis* and *E. saligna* plants (clone ARA 32864).

Materials and methods

Location and experimental installation

The experiments were carried out in a greenhouse in the Forest Nursery of the Federal University of Santa Maria (UFSM; 29° 43′ S and 53° 43′ W) in Brazil. According to the Köppen classification, the local climate is subtropical (Cfa) with four well defined seasons (Alvares et al. 2013). The research was conducted from September to November during spring, which is the most suitable period to plant seedlings in southern Brazil. During the experimental period, the minimum and maximum temperatures varied from 7.2 to 20.2 °C and 17.2 to 32 °C, respectively.

Two experiments were carried out, one with *C. fissilis* and another with *E. saligna*. *Cedrela fissilis* seedlings were ~ 180 days old and were produced in a greenhouse at the Forestry Nursery of the Federal University of Santa Maria. *Eucalyptus saligna* (clone ARA 32864) seedlings were produced in the forest nursery by the CMPC Celulose Riograndense Company (Barra do Ribeiro, Brazil) and were 150 days old. The quantitative morphological and physiological attributes of the seedlings at the time of the experiment installation are presented in Table 1.

Red Argissolo (Embrapa 2013) soil was used for plant cultivation. The soil was collected in the municipality of Santa Maria (29° 43′ 02″ S and 53° 43′ 38″ W) from the 0.0–0.20 m in-ground soil layer. The chemical analysis indicated that the soil had a pH of 4.9 and was composed of P (Mehlich; 20.3 mg dm^{-3}), MO (0.7%), K (40.0 mg dm^{-3}), SB (20.9%), H + Al (10.9 $Cmol_c$ dm^{-3}), Ca (1.7; $Cmol_c$ dm^{-3}), Mg (1.0; $Cmol_c$ dm^{-3}), and CTC pH7 (13.8 $Cmol_c$ dm^{-3}). After collection, the soil was air dried and sieved (2 mm mesh). To raise soil pH to 5.5, dolomitic limestone (PRNT 76%) was applied based on the recommendation for eucalyptus cultivation (SBCS 2016). After 30 days of incubation, the soil was placed in an oven at 60 °C until it reached a constant mass.

For plant cultivation, 2.0 dm^3 of dry soil was added to each pot. After which, 902 mL of water was added to raise the field capacity (c.c) to 100%. Seven days after this procedure, the seedlings were transplanted to the vessels. The c.c

Table 1 Initial characterization of the seedlings used in the experimental installation

Species		*H* (cm)	SD^1 (mm)	LA (cm^2)	TDM (g)	SD^2 (stomata mm^{-2})	PWP (MPa)	MWP (MPa)	*Fv*/*Fm*
Cedrela fissilis	Mean	17.50	7.87	472.31	3.44	107	−0.7	−0.7	0.50
	SD	3.81	1.18	145.67	0.70	21.05	0.02	0.05	0.12
Eucalyptus saligna	Mean	28.75	2.95	145.05	1.79	363	−0.7	−0.7	0.54
	SD	1.85	0.43	6.78	0.36	48.34	0.14	0.06	0.05

H height, *SD^1* stem diameter, *LA* leaf area, *TDM* total dry mass, *SD^2* stomatal density, *PWP* pre-dawn water potential, *MWP* mid-day water potential, *Fv*/*Fm* maximum quantum yield of PSII, *SD* standard deviation

was maintained at 60% by weighing the vessels with a precision analytical balance (0.01 g), and the vessel and transplanted seedling weights were subtracted. Subsequently, the vessels were installed in a greenhouse where different irrigation treatments were carried out for 28 days.

Treatments and experimental design

The experimental design was completely randomized, considering six treatments with 12 replicas of each treatment for a total of 72 plants per experiment. The treatments consisted of six water regimes: (1) HR28, continuous daily irrigation up to 28 days after transplanting (DAT); (2) HR21, daily irrigation up to 21 DAT; (3) HR14, daily irrigation to 14 DAT; (4) HR1_7/14_21, intermittent irrigation from 1 to 7 DAT and from 15 to 21 DAT; (5) HR1/8/15, intermittent irrigation performed only on 1, 8, and 15 DAT; and (6) HR7, daily irrigation from 1 to 7 DAT (Table 2). For each water regime, three vessels were used as references of the soil surface to observe water loss through evaporation.

The daily measurements of the amount of water applied to the vessels were obtained with an analytical balance (accuracy of 0.01 g). Irrigation was performed between 5:00 pm and 6:00 pm, according to the water regime adopted. Before each irrigation, each pot was weighed and the difference between the current and initial weights due to the amount of water replaced. The daily loss results were obtained by measuring water consumption in mL d^{-1}.

Attributes analyzed

Leaf water potential (Ψw) and chlorophyll a fluorescence were evaluated weekly in three plants per treatment for each species. The Ψw evaluations were performed at 05:00 am and 12:00 am with the aid of a pressure chamber (model 600; PMS Instruments, Corvallis, USA; Scholander et al. 1965). A branch (~ 12 cm in length) with at least one pair of completely expanded leaves located in the middle third of the plant was selected. The plant was sectioned and inserted into the chamber, and pressure was applied until the first exudation droplets were evident, at which time the pressure applied was recorded in MPa.

The measurement of the fluorescence emission of chlorophyll *a* took place between 07:00 and 10:00 am, with sun and without the presence of clouds (Berghetti et al. 2019; Turchetto et al. 2016). The analyses were performed using a JUNIOR-PAM portable light fluorometer (Walz, Effeltrich, Germany). A fully expanded pair of leaves from the middle third of each plant was adapted to the dark for 30 min by means of an aluminum foil envelope to determine initial fluorescence (F_0). The leaves were subsequently subjected to a saturating light pulse (10,000 µmol m^{-2} s^{-1}) for 0.6 s to determine the maximum quantum yield of PSII (*Fv*/*Fm*), which was consequently calculated by the ratio of variable fluorescence (*Fv*) to maximum fluorescence (*Fm*).

Morphological attributes were evaluated at the end of the experiments (28 days after transplanting) considering three plants per treatment for each species. Height (H) was measured from the apical bud of the plant to the surface of the soil with a millimeter ruler, and the collection diameter (SD) was measured using a digital caliper (accuracy of 0.01 mm). The root volume (RV) was quantified by immersing the roots in a graduated cylinder containing a known volume of water, and the root volume was obtained by measuring the water displacement.

In order to quantify leaf dry matter (LDM), stem dry matter (SDM), and root dry matter (RDM), the seedlings were sectioned into the aerial (stem and leaves) and root portions. The roots were washed in flowing water with a mesh sieve (2 mm). Subsequently, the plant material of each section was oven dried with air circulation at 65 °C until a constant weight was achieved. Total dry matter (TDM) was obtained by summing LDM, SDM, and RDM. The root/shoot ratio was determined by dividing root dry matter by the sum of the leaf and stem dry matter (Benincasa 1998).

For plants maintained under continuous irrigation (WR28), the total dry mass increment (TDMI) was obtained by subtracting the initial TDM from the final TDM. For this treatment, the water use efficiency (WUE), or coefficient of transpiration, was obtained from the relationship of water consumed (transpiration) and TDMI (da Silva et al. 2004).

Table 2 Description of the water regimes tested on *Eucalyptus saligna* (clone ARA 32864) and *Cedrela fissilis* for 28 days after initial transplanting

Water regimes	Experimental period (days)																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
HR28	×[a]	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
HR21	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×							
HR14	×	×	×	×	×	×	×	×	×	×	×	×	×	×														
HR1-7/14-21	×	×	×	×	×	×	×								×	×	×	×	×	×	×							
HR1/8/15	×							×							×													
HR7	×	×	×	×	×	×	×																					

[a] Days in which seedling irrigation was carried out in each treatment. HR28, continuous daily irrigation up to 28 days after transplanting (DAT); HR21, daily irrigation up to 21 DAT; HR14, daily irrigation to 14 DAT; HR1_7/14_21, intermittent irrigation from 1 to 7 DAT and from 15 to 21 DAT; HR1/8/15, intermittent irrigation performed only on 1, 8, and 15 DAT; and HR7, daily irrigation from 1 to 7 DAT

For the qualitative anatomical analysis, samples were taken from the seedling stem base of all treatments and preserved in 70% ethanol. Due to the fragility of the material, an inclusion technique with Polyethylene glycol 2000 was used (Mady 2007). Microtomy was performed at the Madeira Anatomy Laboratory of the Federal University of Santa Maria following the standard technique recommended by Burger and Richter (1991). The prepared blocks were cross sectioned in a Leica model, and the anatomical sections were dyed with blau (safranin 30% and astra blue 70%). Afterwards, they were washed with distilled water, dehydrated in an alcoholic ascending series (30%, 50%, 70%, 90%, and twice in absolute alcohol), and diaphanized in xylol. The permanent slides were assembled with Entellan, and photomicrographs of the anatomical structure were taken under a Bioval® microscope with a coupled digital camera.

Statistical analysis

Normality and homogeneity of variance were evaluated by the Shapiro–Wilk and Bartlett tests, respectively. An analysis of variance (ANOVA) was performed according to below model:

$$Y_{ij} = m + t_i + \delta_{ij} \tag{1}$$

where Y_{ij} is the observed value, m is a constant, t_i is the effect of the treatment, and δ_{ij} is the effect of the random error present in each experimental unit. When a significant effect was detected ($p < 0.05$), a post hoc analysis was performed using Tukey's test in the R Software package (R Core Team 2018).

Results

Due to the availability of adequate water (c.c 60%), *E. saligna* seedlings presented higher water consumption compared to that of *C. fissilis* and consequently required a higher water reuse rate (approximately 20%). The water consumption peaks during the experiment coincided with high temperatures and low relative humidity (Fig. 1).

The mean leaf water potential (Ψw) for *E. saligna* and *C. fissilis* seedlings at the beginning of the experiments was − 0.7 Mpa, and this value varied from − 0.5 to − 1.0 for the HR28 treatment over the 28 experimental days (Fig. 2). With regard to HR21 and HR14, *C. fissilis* plants maintained potential at − 1.0 MPa, while *E. saligna* showed Ψw values below the critical level of − 2.0 Mpa when irrigation ceased at 22 and 15 DAT, respectively (Fig. 2b, c).

Seven DAT, *E. saligna* showed reduced Ψw, which continued to decline and reached critical values below − 2.0 MPa at 14 DAT, after which we observed seedling

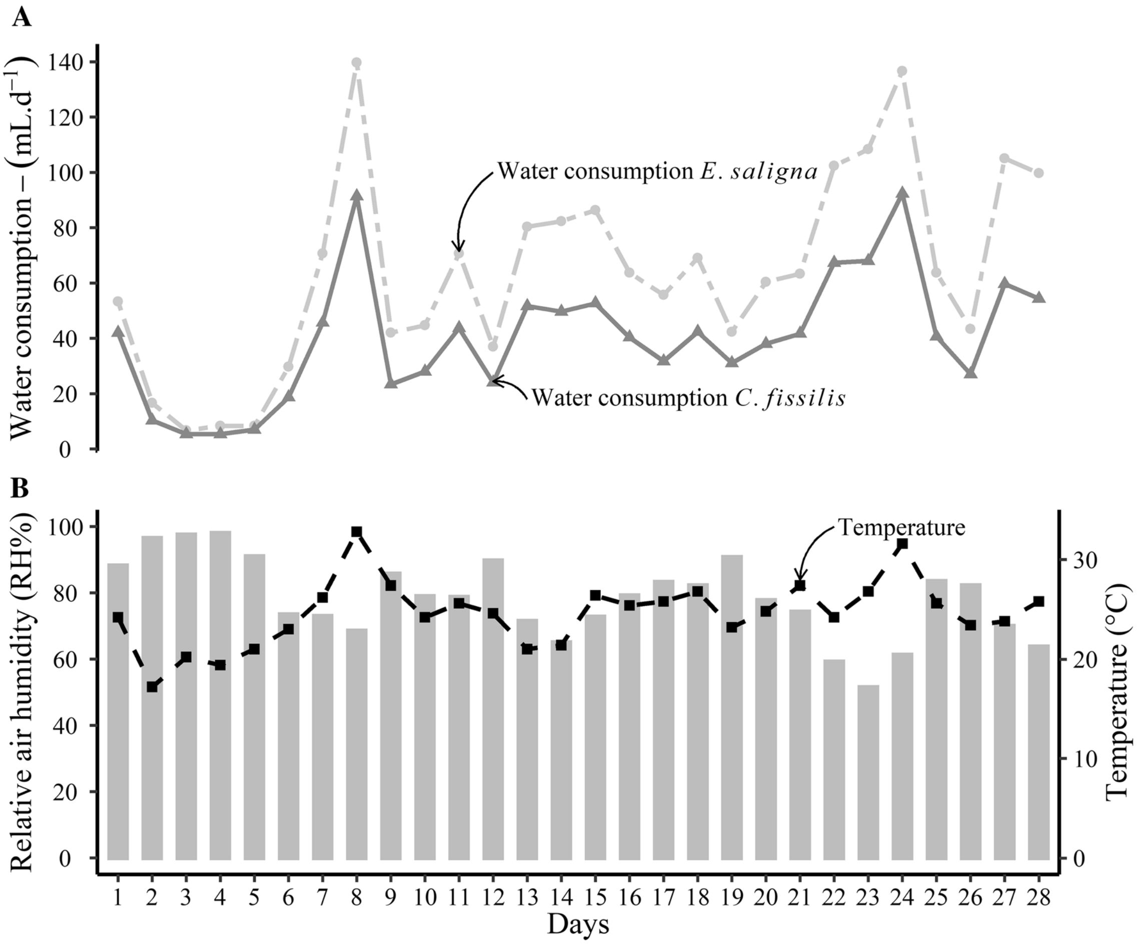

Fig. 1 **a** Daily water consumption of *Cedrela fissilis* and *Eucalyptus saligna* (mL d^{-1}) seedlings with adequate water availability, **b** percent relative humidity (RH%), and maximum daily temperatures (°C) recorded during the study in Santa Maria, RS, Brazil

mortality (Fig. 2d, f). On the other hand, *C. fissilis* individuals were more resilient, even reaching values close to – 2.0 Mpa at 14 DAT and were able to re-establish *Ψw* under HR1-7/14-21 rehydration conditions (Fig. 2d).

When we adopted an intermittent water regime (HR1/8/15), we verified that the plants managed to retain Ψw values of approximately – 1.0 (*C. fissilis*) and – 1.5 (*E. saligna*) until 14 DAT; however, after seedling irrigation at 15 DAT, seedlings were no longer able to recover and presented Ψw values below the critical level at 22 DAT (Fig. 2e).

Under water restriction conditions, the reduction in water availability significantly compromised the water status of *E. saligna* seedlings, which reached the point of permanent wilt due to the loss of 7.7% of soil moisture. However, with regard to c.c., *Cedrela fissilis* seedlings presented higher resistance to moisture loss compared to that of the *E. saligna* seedlings. After the first stress level, seedlings with a water potential of – 2.0 Mpa were restored (Fig. 2d) at 14 DAT, even with a moisture loss of 7.2%.

The water regimes adopted had no significant effect on the quantum efficiency of PSII (*Fv*/*Fm*). In general, *Fv*/*Fm* values close to 0.70 were observed while the plants of both species were adequately hydrated (Table 3). However, due to extreme water stress, *E. saligna* seedlings presented dehydrated leaves and stems, while *C. fissilis* presented leaf abscission, which made it impossible to quantify this physiological variable (Table 3).

After 28 treatment days with increasing water stress, we observed a reduction in *Fv*/*Fm* for *C. fissilis* (0.529) plants under the HR1-7/14-21 treatment, which was characterized by intermittent irrigation, and under the HR21 treatment, which included the suspension of irrigation at 21 DAT (0.586; Table 3). For *E. saligna* plants, only individuals cultivated under the HR28 treatment survived until the end of the experiment and showed *Fv*/*Fm* values equal to 0.714.

At the end of the experiment, we observed the highest values of the morphological variables analyzed in *E. saligna* seedlings in the continuous irrigation treatment (HR28; Table 4). In this treatment, the increase in height

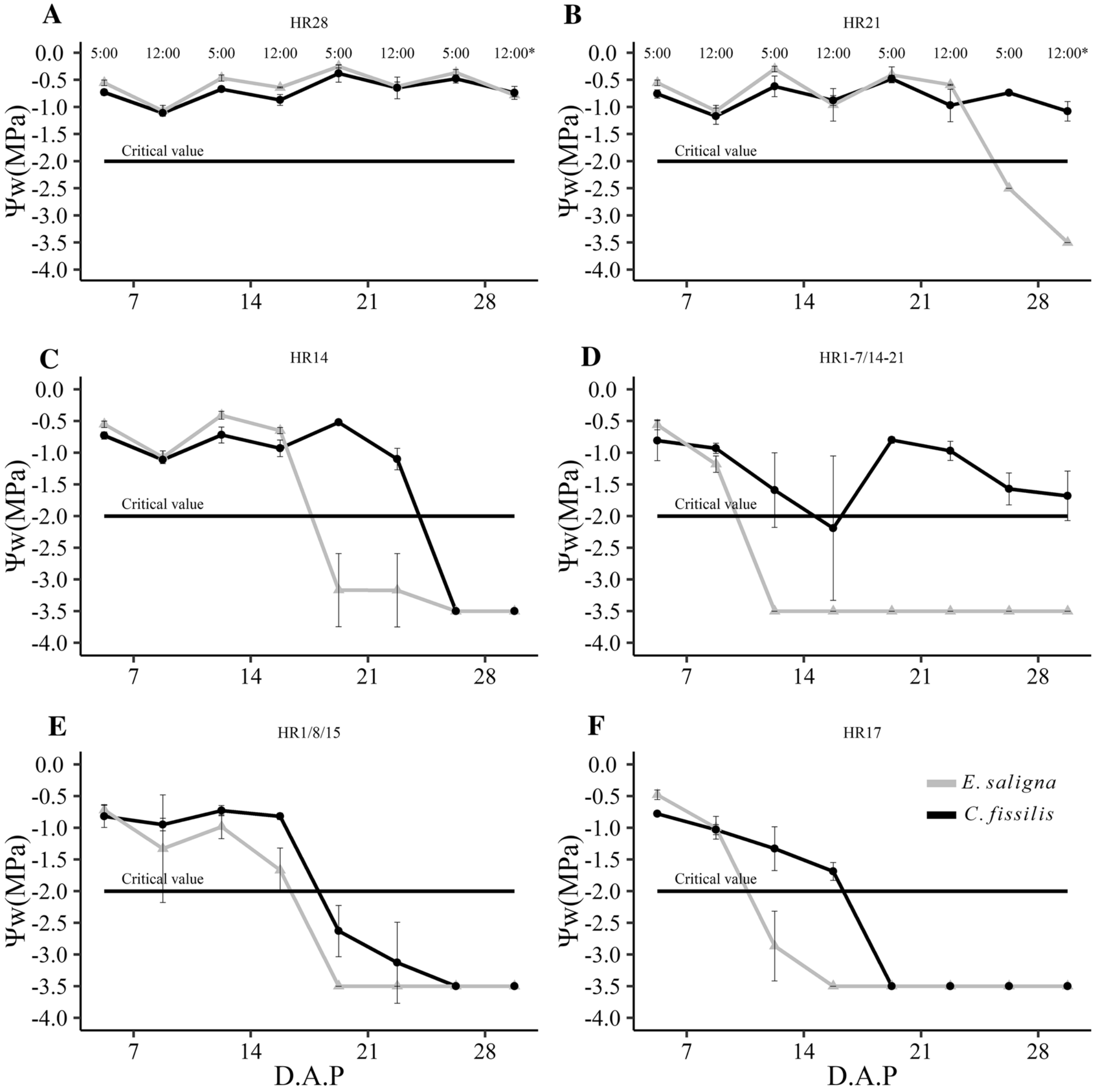

Fig. 2 Leaf water potential (*Ψw*) at pre-dawn (05:00 am) and mid-day (12:00 pm) of *Cedrela fissilis* and *Eucalyptus saligna* (clone ARA 32864) seedlings during the experiment. *Note*: Days after transplanting (DAT) critical value adopted according to Taiz et al. (2017). HR28, continuous daily irrigation up to 28 DAT; HR21, daily irrigation up to 21 DAT; HR14, daily irrigation to 14 DAT; HR1_7/14_21, intermittent irrigation from 1 to 7 DAT and from 15 to 21 DAT; HR1/8/15, intermittent irrigation performed only on 1, 8, and 15 DAT; and HR7, daily irrigation from 1 to 7 DAT. *indicates the times for measuring leaf water potential

(IH), collection diameter (ISD), root volume (IVR), and total dry matter (IMST) for *E. saligna* was 22.9, 39.3, 418.5, and 107.1%, respectively. For *C. fissilis*, the corresponding values were 15.05, 0.89, 83.3, and 4.54%. In the HR28 treatment, *C. fissilis* and *E. saligna* seedlings presented water use efficiency values of 431.8 and 484.96 g^{-1}, respectively.

Water stress significantly affected total dry matter yield and stem dry matter in both species as well as the leaf dry matter of *E. saligna* ($p < 0.05$). There was no significant difference in the dry matter yield of the roots for either species.

The highest total dry matter and stem yields were found in the HR1-7/14-21 and HR28 treatments of *C. fissilis* and in the HR28 and HR21 treatments of *E. saligna* (Fig. 3). In addition, there was a decrease in total dry matter accumulation of 26.76% for *C. fissilis* and of 41.30% for *E. saligna* when HR1/8/15 was used compared to that of the continuous irrigation treatment (HR28).

The highest values of leaf dry matter production (LDM) for *E. saligna* were observed in the HR28 and HR21 treatments (Fig. 3). *Eucalyptus saligna* plants submitted to continuous irrigation (HR28) presented 2.4-fold higher values than those of *C. fissilis* seedlings under the same treatment conditions.

Table 3 Mean values of the maximum quantum yield of PSII (*Fv*/*Fm*) of *Cedrela fissilis* and *Eucalyptus saligna* (clone ARA 32864) plants submitted to different water regimes in Santa Maria, RS, Brazil

Species	Treatment days	HR28	HR21	HR14	HR1-7/14-21	HR1/8/15	HR7	ANOVA
Cedrela fissilis	7 days	0.670^{ns}	0.743	0.584	0.644	0.668	0.735	$p=0.08$
	14 days	0.557	0.723	0.738	0.684	0.601	0.667	$p=0.17$
	21 days	0.765	0.79	0.787	0.796	–	–	$p=0.90$
	28 days	0.601	0.586	–	0.529	–	–	$p=0.74$
Eucalyptus saligna	7 days	0.797	0.745	0.702	0.792	0.633	0.767	$p=0.06$
	14 days	0.625	0.719	0.637	–	0.638	–	$p=0.82$
	21 days	0.832	0.708	–	–	–	–	$p=0.10$
	28 days	0.714	–	–	–	–	–	

^{ns}not significant at 5% probability; (–) indicates seedling mortality. HR28, continuous daily irrigation up to 28 days after transplanting (DAT); HR21, daily irrigation up to 21 DAT; HR14, daily irrigation to 14 DAT; HR1_7/14_21, intermittent irrigation from 1 to 7 DAT and from 15 to 21 DAT; HR1/8/15, intermittent irrigation performed only on 1, 8, and 15 DAT; and HR7, daily irrigation from 1 to 7 DAT

Table 4 Increase in height (IH), stem diameter (ISD), root volume (IRV), total dry mass (ITDM), and water use efficiency (WUE) of *Cedrela fissilis* and *Eucalyptus saligna* (clone ARA 32864) seedlings with continuous irrigation (HR28) after planting

Species	IH (cm)	ISD (mm)	IRV (mL)	ITDM (g)	WUE (g g^{-1})
Cedrela fissilis	2.63 ± 3.62	0.07 ± 1.08	5.0 ± 2.91	0.16 ± 0.54	431.8
Eucalyptus saligna	6.58 ± 3.8	1.16 ± 0.7	9.42 ± 5.12	1.49 ± 0.83	484.96

The value after ± is standard deviation. HR28, continuous daily irrigation up to 28 days after transplanting (DAT); HR21, daily irrigation up to 21 DAT; HR14, daily irrigation to 14 DAT; HR1_7/14_21, intermittent irrigation from 1 to 7 DAT and from 15 to 21 DAT; HR1/8/15, intermittent irrigation performed only on 1, 8, and 15 DAT; and HR7, daily irrigation from 1 to 7 DAT

The root/shoot ratio differed significantly among treatments for *E. saligna*, and the highest values were observed in the HR1/8/15 treatment, while the lowest values were observed in the HR28 treatment. No significant difference was observed among treatments for *C. fissilis* (Table 5).

When analyzing the plant stem anatomy, we found that the parenchyma cells that composed the marrow (Me) of *E. saligna* in the HR28 treatment and *C. fissilis* in the HR28, HR21, and HR1-7/14-21 treatments presented no damage after the 28 experimental days (Fig. 4a–c). On the other hand, the *E. saligna* seedlings submitted to the HR1-7/14-21 treatment presented a complete loss of cell turgor and consequently the rupture of these cells, which resulted in the formation of a hole along the medulla (Fig. 4d).

Discussion

Our study demonstrates that water restriction significantly affected the survival as well as the physiological, morphological, and anatomical attributes of the *Cedrela fissilis* and *Eucalyptus saligna* seedlings. In general, we observed that *C. fissilis* presented a higher tolerance to water stress, although this species presented a smaller increase in height, diameter, root volume, dry matter, and water use efficiency under continuous irrigation conditions (Table 4).

We observed that the survival and growth of *E. saligna* was associated with adequate water availability, given that the water leaf potential was significantly reduced (− 2.0 MPa) in all treatments without the maintenance of the field capacity (60%) for a short period (≅ 7 days). Plant water stress is considered low from − 0.5 to − 1.0 Mpa, moderate from − 1.0 to − 1.5 Mpa, and high at values < − 1.5 Mpa (Ritchie et al. 2010). Thus, we verified that the water stress in *E. saligna* (− 2.0 MPa) occurred soon after the suspension of irrigation and was more rapidly observed than that of *C. fissilis*. Taiz et al. (2017) point out that stomatal conductance and photosynthesis tend to reduce beginning at − 1.0 MPa and cease at − 2.0 MPa.

In this sense, the differences observed in leaf water potential among the studied species were the result of a greater control of the transpiration rate of *C. fissilis* and lower environmental water loss (Fig. 1). Plants with low soil water supply, which is the main mechanism responsible for the efficient control of transpiration rates (Cordeiro et al. 2009), possibly ensured the survival of *C. fissilis* on days without irrigation. Noulèkoun et al. (2017) evaluated the effects of water availability on five tree species and also found that slow-growing species showed better performance in the field and higher survival rates compared to that of fast-growing species.

In general, the plants submitted to intermittent irrigation once a week (HR1/8/15) were more tolerant when compared to plants in treatments that included a water supply suspension after continuous irrigation (Fig. 2e). This may be associated with the acclimation of the plants to conditions of

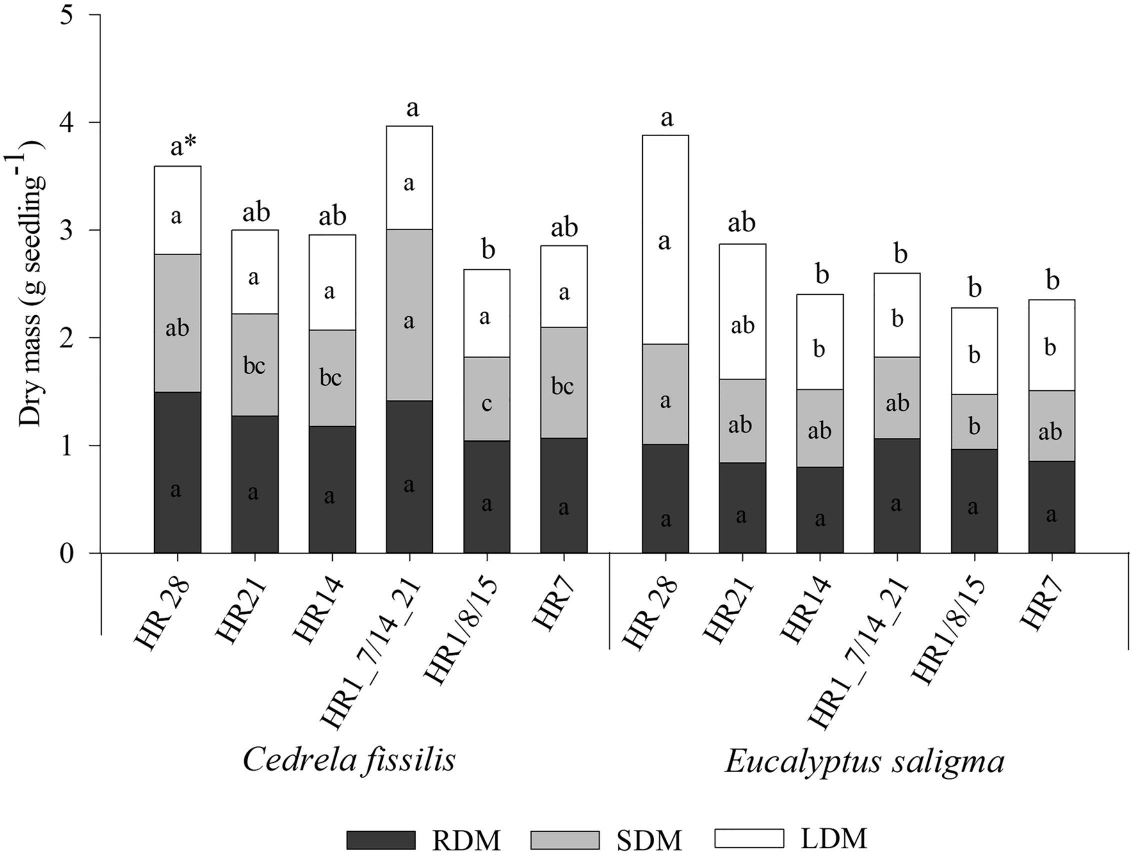

Fig. 3 Mean values of total dry matter, root dry matter (RDM), stem dry matter (SDM), and leaf dry matter (LDM) of *Cedrela fissilis* and *Eucalyptus saligna* (clone ARA 32864) seedlings as a function of the different water regimes at 28 days after planting (DAT) in Santa Maria, RS, Brazil. HR28, continuous daily irrigation up to 28 DAT; HR21, daily irrigation up to 21 DAT; HR14, daily irrigation to 14 DAT; HR1_7/14_21, intermittent irrigation from 1 to 7 DAT and from 15 to 21 DAT; HR1/8/15, intermittent irrigation performed only on 1, 8, and 15 DAT; and HR7, daily irrigation from 1 to 7 DAT

Table 5 Mean values of the root/shoot ratio of *Cedrela fissilis* and *Eucalyptus saligna* (clone ARA 32864) seedlings as a function of the different water regimes at 28 days after planting (DAT) in Santa Maria, RS, Brazil

Species	HR28	HR21	HR14	HR1-7/14-21	HR1/8/15	HR7
Cedrela fissilis	0.717^{ns}	0.735^{ns}	0.662^{ns}	0.556^{ns}	0.781^{ns}	0.648^{ns}
Eucalyptus saligna	0.352 b	0.413 ab	0.497 ab	0.696 ab	0.802 a	0.577 ab

^{ns}not significant; HR28, continuous daily irrigation up to 28 DAT; HR21, daily irrigation up to 21 DAT; HR14, daily irrigation to 14 DAT; HR1_7/14_21, intermittent irrigation from 1 to 7 DAT and from 15 to 21 DAT; HR1/8/15, intermittent irrigation performed only on 1, 8, and 15 DAT; and HR7, daily irrigation from 1 to 7 DAT

Means followed by the same lower case letters on the lines do not differ significantly by the Tukey Test at 5% error probability

reduced water availability as a strategy to maintain cellular turgor for a certain period. A reduction in the irrigation frequency is a recommended technique for seedling preparation in the field (rustification); however, stress should be maintained at a moderate level and should not reach the point of permanent wilting or severe water stress (Ritchie et al. 2010). This situation requires intense planning during the transplantation period to allow for the maintenance of moist soils. However, variable and unpredictable environmental conditions can reduce transplanting success when using more demanding genetic material, such as *E. saligna* (clone ARA 32864).

A higher tolerance of *C. fissilis* to low water availability compared to that of *E. saligna* was further supported when the water use efficiency was analyzed (Table 4). Water use efficiency (WUE) is defined as the amount of carbon assimilated as biomass per unit of water used by the crop (Hatfield and Dold 2019). By comparing the WUE among the species

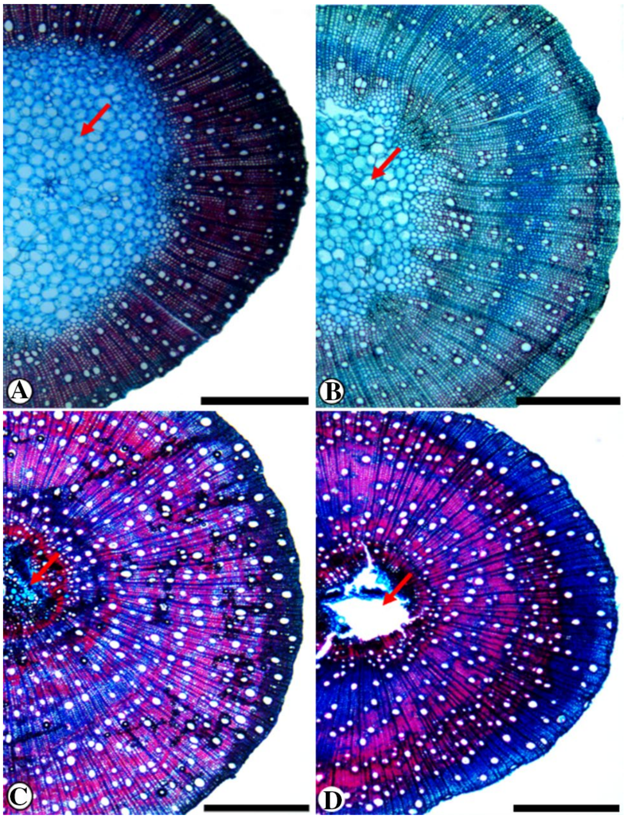

Fig. 4 Cross sections of the stem of the seedlings of *Cedrela fissilis* and *Eucalyptus saligna* (clone ARA 32864). **a** *C. fissilis* (HR28). **b** *C. fissilis* (HR1-7/14-21). **c** *E. saligna* (HR28). **d** *E. saligna* (HR1-7/14-21). Scale bars: 500 µm. Arrows indicate the stem pith

studied, we found that *C. fissilis* presented a higher efficiency (i.e., the lowest transpiration coefficient, 431.8 g^{-1}, gram of water per gram of dry matter produced), while *E. saligna* required a higher amount of water for biomass production (484.96 g^{-1}). Estimates of water use efficiency in C3 plants vary from 333 to 500 g of water per gram of dry matter produced and depend on the environment and the species analyzed (Kramer and Boyer 1995). da Silva et al. (2004) evaluated the water use efficiency of *Eucalyptus grandis* and *Corymbia citriodora* species under conditions of good water availability (field capacity) and found values of 283.8 and 302.2 g^{-1}, respectively.

Higher *Fv*/*Fm* values express the efficiency of the capture of excitation energy by open PSII reaction centers (Baker 1991). In our study, the values found for this attribute in *C. fissilis* and *E. saligna* seedlings did not reach the range proposed by Araújo and Deminicis (2009) for woody plants under optimum environmental conditions (0.75–0.85) even with adequate water availability (HR28). Similar results were found in other studies carried out in southern Brazil with seedlings of some native tree species, showing that values between 0.55 and 0.70 can be considered to be indicators of initial growth (Turchetto et al. 2016; Berghetti et al. 2019).

When we analyzed *Fv*/*Fm* values over the experimental period, a variation in the values of this attribute was observed. However, water restriction was not sufficiently limiting to cause a significant reduction of *Fv*/*Fm* values for plants with leaf water potentials above − 2.0 MPa (Table 3). Nonetheless, we observed that there was a tendency towards the reduction of the *Fv*/*Fm* values with the increase of water stress at 28 DAT for *C. fissilis* in the HR21 and HR1-7/14-21 treatments.

Changes in *Fv*/*Fm* of plants submitted to water stress conditions have been reported by several authors, indicating that the reduction in water availability potentiates photoinhibitory processes (Lage-Pinto et al. 2012; de Campelo et al. 2015). However, Tatagiba et al. (2015) evaluated photosynthesis in young Eucalyptus plants under different soil and climatic conditions and also showed that the maximum quantum yield estimated by the *Fv*/*Fm* ratio did not show a significant difference between dry and rainy seasons. Similar results were observed by Leiva et al. (2018) for *Quercus ilex* plants under water stress and optimal conditions that presented *Fv*/*Fm* values of 0.77 and 0.79, respectively. It is important to point out that it was impossible to evaluate fluorescence in plants that presented Ψw below the critical level (− 2.0 MPa). We were not able to accurately identify the period in which there was a marked decline of the *Fv*/*Fm* ratio since a lack of leaf turgidity made the evaluation of this variable impossible.

The lowest values for the IH, ISD, IVR, and IMST attributes observed in *C. fissilis* plants compared to those of *E. saligna* when analyzed under continuous irrigation conditions (Table 4) were associated with the ecological and silvicultural characteristics of the species. *Cedrela fissilis* is a slow-to-intermediate native species (Araujo et al. 2018), whereas the *E. saligna* clone (ARA 32864) has been improved for cellulose production and presents rapid growth and high productivity (Paludzyszyn Filho and dos Santos 2013).

The influence of the water deficit on dry matter production in plants was confirmed when we analyzed the values obtained for *E. saligna*. The highest values were obtained in the treatments with the highest water content (HR28 and HR21). When evaluating *Eucalyptus urograndis* plants submitted to a water deficit, Pereira et al. (2007) also found a reduction in the performance of morphological characteristics, especially with regard to dry matter.

Cedrela fissilis and *E. saligna* presented different results with regard to the root/shoot ratio (Table 5). For *E. saligna*, the seedlings submitted to the treatment with the highest water deficit (HR1/8/15) had higher mean values, that is, these plants allocated higher biomass to the roots. In young plants such behavior can be explained by the production of abscisic acid (ABA) in response to a water deficit, which induces root growth and stimulates the emergence of lateral roots while suppressing leaf growth (Taiz et al. 2017). This strategy not only prioritizes water absorption but also reduces loss due to leaf transpiration since mass allocation to the leaves is reduced (Figueirôa et al. 2004), as was observed in this study in *E. saligna* plants of the HR1/8/15 treatment.

On the other hand, *C. fissilis* seedlings that presented the highest dry matter production were those submitted to the intermittent irrigation regime (HR1-7/14-21) and did not differ from those of the continuous irrigation treatment (HR28). According to Grossnickle (2012), plant responses to water deficits depend on the phenological and genetic factors of the species as well as on the magnitude and intensity of the stress. In addition, Pimentel (2004) points out that a moderate water deficit can favor the growth and production of biomass. Other studies also demonstrate that the induction of periodic stress can increase resistance to water shortages in the post-transplanting phase, resulting in better performance in the field (Liu et al. 2012; Grossnickle and MacDonald 2018).

Cedrela fissilis did not show a significant difference between the applied treatments regarding the root/shoot ratio. One of the reasons for this behavior may be related to the low growth rates presented by the species, which reflect a balance between the translocation and accumulation of photoassimilates between the root system and aerial portion of the plant. Our results agree with the findings of do Nascimento et al. (2011) who evaluated the behavior of *Hymenaea courbaril* L. seedlings submitted to water stress. According to the author, similarities with regard to biomass allocation among tropical tree species, regardless of water availability, occur due to the low photosynthetic and transpiration rates presented.

The lower tolerance of *E. saligna* to water stress when compared to that of *C. fissilis* is even more evident when we observe the anatomical sections of the stems of both species (Fig. 4). The disruption of the marrow parenchyma cells observed in the *E. saligna* seedlings submitted to treatments with more severe water deficits (HR1-7/14-21, HR1/8/15 and HR7) may be explained by Pimentel (2004), who states that decreases in the water content of the cell result in cell wall distortions and the rupture and lysis of plasma membranes, chloroplasts, mitochondria, and other organelles, which can lead to the collapse of the intercellular spaces and cell lysis. According to the same author, when de-compartmentation of the cells and paralysis of the physiological events occur, such as with photosynthesis and respiration, the water deficiency becomes lethal and there is no possibility of recovery.

The results obtained in our study emphasize the importance of identifying the differences among species in terms of water demand, especially for those species that are used most in environmental and commercial spheres, to ensure efficient planning strategies and successful plantations. It was observed that *E. saligna* was more sensitive than *C. fissilis* to reduced water availability in the soil, which resulted in the death of all plants in the most severe treatments (HR1-7/14-21 and HR7) at 14 DAT. Studies that aim to determine the performance of forest species under climate change scenarios are critical for maintaining existing communities as well as for defining new management strategies and more appropriate cropping areas. Since future simulations indicate significant increases in air temperature, changes in the distribution of precipitation, and a reduction in rainfall in South America (Chou et al. 2014), additional studies, such as this one, are needed.

Conclusion

Eucalyptus saligna, with emphasis on the clone studied, is highly susceptible to seedling mortality when there is a 60% reduction in field capacity during the initial post-transplanting phase. In contrast, when maintained at this field capacity, *E. saligna* presented a higher growth potential than that of *Cedrela fissilis*. After a short period of water restriction, rehydration allows for a rapid recovery of young *C. fissilis* plants, indicating good physiological plasticity of this species when submitted to non-severe stress levels. Thus, intermittent irrigation is recommended for the best performance of this plant. Young *C. fissilis* seedlings had greater resistance to water stress than those of *E. saligna* and may present better performance in regions prone to drought.

Acknowledgements We gratefully acknowledge the National Council for Scientific and Technological Development (CNPq) and Coordination for the Improvement of Higher Education Personnel (Capes) for granting scholarships.

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