



Aspects of Water Relations and Gas Exchange of Katsura and Tilia Seedlings Subjected to Wet-Dry Cycles: Indication of Strategies for Whole Plant Drought Tolerance

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Authors' contributions

This work was carried out in collaboration between all authors. Authors KHH, SOA and MH carried out Laboratory study, soil and plant measurements, statistical analysis. Authors KHH and SOA conceived the study and participated in its design and coordination and helped to draft the manuscript and performed the statistical analysis. Author RM participated in the design of the study and helped to draft the manuscript. All authors read and approved the final manuscript.

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ABSTRACT

This paper reports the effects of progressive drought and wet-dry cycles on water relations, stomatal conductance and photosynthetic carbon fixation of seedlings of two tree species adapted to temperate climate *Cercidiphyllum japonicum*, Sieb. & Zucc. (Katsura: Cerci) and *Tilia cordata* (Tilia) in the climate chamber of the Institute of Ecophysiology of Plants, Technical University, Munich (TUM), Freising, Germany. The watering regimes were applied in phases to simulate either well watered /hydration conditions, dry down/single drought phase and multiple/intermittent wet-dry cycle. The control plants were maintained under well-watered conditions dry-wet cycles (drought-

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rehydration phases) in phases. Plants in the multiple-drought treatment were subjected to two dry-wet phases while plants in the single-drought treatment were exposed to an initial drought phase followed by one hydration phase. In both *Cercidiphyllum japonicum* and *Tilia cordata*, drought induced leaf abscission and recovery (regrowth) were observed towards the end of the experiment. However, against expectation, although *Cerci* exhibited drought induced leaf abscission, but its water potential was kept below values obtained for *Tilia*. After relief from drought (post drought rewatering), leaf water potential and stomatal gas exchange recovered in magnitudes close to those of well watered control plants. As a result of increasing dehydration, water potential in *Tilia* declined sharply and one of the plants died off. It appeared that the magnitude of soil drought imposed was sufficient to initiate hydraulic failure in *Tilia*, an observation that can be attributed to a vulnerability to embolism. The water consumption measured via evaporative flux/weighing method and sap flow sensors), was higher for *Katsura* while its leaf water potential declined far more in *Cerci* relative to *Tilia* without causing noticeable damage. The respective pre-dawn and midday leaf water potentials were: *Tilia* (-0.88; -0.1250 MPa) and *Cerci* (-0.85; -0.104 MPa). It is concluded that both *Katsura* and *Tilia* are drought avoiders that abscise leaves to reduce transpirational water loss. The species are capable of regrowth and recovery of physiological functions after relief from drought, In order to maintain the greatest ornamental value in the landscape. *Katsura* and *Tilia* should be planted in areas that are not prone to drought.

Keywords: Drought; mortality; physiological; seedlings; sensitivities; species; temperate.

1. INTRODUCTION

Worldwide, massive mortality events have occurred recently across many tree species, often linked to severe drought and temperature, and are expected to increase with climate change in the next century [1,2]. Despite the prevalence and impact of these events, there is relatively little known about exactly how forests die from different episodes of drought in particular [1,3,4]. Thus, understanding the responses of forest tree species to drought would benefit local stakeholders. Such understanding will aid in projecting which regions, forest tree species, and forests could be most vulnerable to drought and changes in climate [5,6].

The distribution of species across regional landscapes affects how forest trees function and the services they provide to humans, such as timber, tourism, and wildlife habitat. Furthermore, forest diebacks can lead to dramatic decreases in forest uptake of carbon, resulting in a positive feedback to climate warming. Tree species distributions can shrink over time through reduced regeneration and subsequent adult mortality or they can expand via seedling establishment beyond current distribution boundaries [7]. Therefore, a critical component of our ability to predict future species distributions is an understanding of the mechanisms of seedling establishment, which requires a fundamental knowledge of seedling physiology [2,8,9].

Seedling establishment and survival is a determinant of species distribution. In order to

predict species distribution over landscapes, ecologies and climate, it is important to identify traits associated with seedling establishment and survival and tolerance of growing conditions such as climatic extremes of a given environment [4,10]. Plant water use (evapotranspiration), is an important component of ecosystem water balance and a part of the natural water cycle [5,11]. Multiple mechanisms may cause mortality during drought. A common mechanism for plants with isohydric regulation of water status results from avoidance of drought-induced hydraulic failure via stomatal closure, resulting in carbon starvation and a cascade of downstream effects such as a reduced resistance to biotic agents [12]. Isohydric species would experience mortality after prolonged periods of severely limited gas exchange as required to avoid hydraulic failure while anisohydric species would also avoid hydraulic failure, but sustain gas exchange due to its greater cavitation resistance [7]. Although anisohydric plants are relatively drought-tolerant, they are predisposed to hydraulic failure because they operate with narrower hydraulic safety margins during drought.

Soil moisture contents may vary considerably in natural and maintained landscapes, particularly as soil moisture changes in response to the seasonal wet-dry transitions [1,4]. Experiments simulating these conditions have been used to examine the physiological responses to drought stress trees subjected to cycles of drought and rehydration [4,8,11,13].

The genus *Cercidiphyllum* is endemic to Japan and China composed of two species native to eastern Asia. The common Katsura (*C. japonicum*) is native range China has diminished to the degree that it is now classified as uncommon [14]. As a landscape plant, Katsura is valued for its brilliant autumnal leaf color, picturesque form, slightly shaggy bark, and disease and pest resistance. The species gained celebrity by being named the Tree of the Year for 1997 by the International Dendrology Society [14]. The reputation of Katsura as a drought-intolerant tree may play a role in its limited usage. While experimental evidence pertaining to the drought intolerance of Katsura is inadequate. *Tilia* (*Tilia cordata*) is a common tree species across vegetation and landscapes in temperate climate of Europe. It is an imperative to improve understanding of how *Tilia* in the earliest phase of its growth can survive and tolerate drought conditions [15].

It is necessary to improve understanding the mechanisms of seedling establishment, growth and tolerance of climatic extremes and to model vegetation responses to climate change induced drought stress. This study will fill some gap in our knowledge about the fundamental physiological mechanisms of drought responses in tree species particular plant water use and adjustments under drought-induced soil moisture stress, and will contribute to modeling advances that can predict how temperate forest tree species will evolve as climate changes over the next years. Drought-related tree mortality occurs globally and may increase in the future. In view of climate change and the probability of extreme dry periods continuing, it is necessary to improve mechanistic understanding of drought induced tree mortality. Our results contributed to an improvement in understanding of the physiological mechanisms underlying mortality.

The survival, growth and physiology of growing seedlings of two species will be measured to assess desiccation tolerance and the impacts of drying on water relations and stomatal gas exchange including photosynthesis. The results from this research can be directly used in modeled predictions of vegetation responses to climate change because seedling survival is likely a primary determinant of species distributions. These findings will also be of interest to policy makers and land managers who are interested in potential drought impacts on productivity and distributions of certain species. It will also be of interest to tree and woody crop

breeders concerned with identifying traits associated with survival and productivity in given environments.

This study was designed to determine the effects of progressive drought and wet-dry cycles on water relations, stomatal conductance and photosynthetic carbon fixation of seedlings of two tree species (*Tilia cordata* and *Cercidiphyllum japonicum* (Katsura) adapted to temperate climate.

2. MATERIALS AND METHODS

Thirty potted seedlings each of fifteen year old *Cercidiphyllum japonicum*, Sieb. & Zucc. (Katsura: Cerci) and eight-year old *Tilia cordata* (*Tilia*) which were subjected to three watering regimes in the climate chamber of the Lehrstuhl fuer Oekophysiologie der Pflanzen, Wissenschaftszentrum Weihenstephan, TUM, D-85354 Freising, Germany.

The study consisted of three watering regimes were applied in phases to simulate either well watered /hydration conditions, dry down /single drought phase and multiple/intermittent wet-dry cycle. At the commencement of the study, Cerci and *Tilia* seedlings were well watered. The control plants were maintained under well-watered conditions while the dry-wet cycles (drought-rehydration phases) were applied in phases. Plants in the multiple-drought treatment were subjected to two dry-wet phases while plants in the single-drought treatment (long term dry down) were exposed to an initial drought phase followed by one hydration phase. The treatments were: (1) long term dry-down with rewatering to recover from drought intensities (2) multiple wet-dry cycles and (3) well watered plants with sustained watering levels in order to maintain constant root zone moisture. The plants in the drought treatments were subjected to multiple or single wet-dry conditions in phases.

Treatments were designated as: w: non-limiting water supply (hydrated throughout).

Treatment d: single drought cycle (long term dry down consisting of drought without watering for 35 days (24.07.2012 to 28.08.2012) followed by watering after drought had induced significant amount of leaf abscission. Treatment wd: the wet-drought cycle: where drought was interrupted by watering (two periods of wet-drought cycles).

The three watering strategies were employed each using a different cohort of plants. The period of the experiment in the climate chamber was from 20th June to 4th September, 2012. Each of the watering strategy used a different cohort of plants: (1) long term dry-down, (2) watering interrupted by two periods of wet-drought cycle) and (3) non-limiting water supply (hydrated throughout). The three watering strategies adopted aimed at investigating the limitations of physiological functions (rootzone moisture deficit-induced changes in leaf water potentials, sap fluxes and leaf gas exchange) by wet-dry cycles. The following measurements were made of Ceci and Tilia plants subjected to well hydrated and wet-dry cycle treatments:

- Determination of soil water content
- Measurement of water potential
- Determination of water consumption via the weighing of the potted plants via sustained watering levels by pot weight maintenance to examine daily water use and growth
- Determination of water consumption via the xylem sap flow
- Root zone moisture deficit induced responses of gas exchange using LiCor 6400

Pre-dawn and midday measurements of leaf water potential were made using a pressure chamber (Model 1002, PMS Instruments, Corvallis, OR, USA) and stomatal gas exchange measurements were made using a portable infrared gas analyser (IRGA) equipped with an artificial light source (Model LI-6400, Li-Cor Instruments). Sap fluxes will be measured using sap flow sensor (Heat ratio method; HRM: ICT, Australia) which derives sap mass flow from water velocity in the trunk by heat pulses [16]. Temperature sensors above and below the heater allow to assess water transport in both directions. Gas exchange parameters including synthetic carbon assimilation, stomatal conductance and transpiration were measured using a portable gas analyser (Li-6400; Licor, Lincoln, NE, USA), with a light intensity (photosynthetic photon flux density: PPF) at a constant of 1000 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ inside the chamber, and maintaining ambient CO_2 with a concentration at 350 $\mu\text{mol mol}^{-1}$ at a target air temperature of 20°C. Measurements were undertaken with a standard 20 × 30 mm leaf chamber equipped with blue-red light-emitting diodes mounted on the top of the chamber (Model 6400-02B). Five of the youngest fully

expanded leaves located within the lower crown of each sapling were recorded after A1500 and gs had stabilized (between 0.5 min and 2 min). To minimize the effects of time of measurement, a randomly chosen replicate from each treatment was measured. Gas exchange and leaf water potential (ψ_{leaf}) measurements were made on Tilia and Cerci plants subjected to watering regimes and measurements were restricted to few times to limit the amount of leaf material removed during ψ_{leaf} measurements. Whole-plant water loss was performed by weighing pots to an accuracy of ± 0.01 g (Mettler - Toledo) and values were calculated by the loss of weight of each plant between measurements. In the full droughted and intermittent drought-wet cycles, drought was imposed by withholding water followed by rewatering to observe growth (physiological function) recovery. Gas exchange and ψ_{leaf} measurements were made in plants subjected to the one drought cycle, but were restricted to three times during the growth of plants under sustained soil water deficit conditions to limit the amount of leaf material removed during ψ_{leaf} measurements so as to sustain dry-matter production.

The data generated on the measured physiological variables of Tilia and Cerci were subjected to analysis of variance test and treatment means were separated using the Least Significance Difference (LSD) test at $P > 0.05$.

3. RESULTS AND DISCUSSION

The differential sensitivities of water relations, stomatal conductance and photosynthetic carbon fixation as mechanisms of survival and whole-plant drought tolerance using seedlings of *Cercidiphyllum japonicum* and *Tilia cordata*, both are temperate tree species. In the tested species, drought-induced leaf dieback while varied responses of leaf water potential and gas exchange were observed. In general, against expectation *Cercidiphyllum japonicum* exhibited higher drought stress tolerance than Tilia. The range of maximum leaf water potential (ψ_{leaf}) - 0.84 to -1.62 and -0.88 to -1.06 MPa for the respective droughted Cerci and Tilia (Twd and Td; Cwd and Cd) plants, brought about complete stomatal closure (below zero) (Table 1).

The effects of watering regimes on the temporal trends in water consumption in Tilia and Cerci are presented in Fig. 1a and b. Both species under drought and wet-dry cycle had low water use, substantial decreases in plant water use

was obtained for Cerci, especially the droughted and wet-dry cycle Cd and Cwd treatments (Fig. 1b). Across all sampling dates, water consumption, in spite of the progressive dehydration was comparatively higher in *Tilia cordata* especially under well watered and wet-dry cycles (Fig. 1a) than in *Cercidiphyllum japonicum* (Fig. 1b). In Fig. 2a and b, the temporal trends soil moisture contents in relation with leaf water potential are shown. Following water application to droughted plants, sharp recovery in plant water status (leaf water potential) was also observed (Fig. 2a and b).

The observed trends were similar in the responses of plant water relations to soil moisture status. Increases in soil wetness promoted favourable leaf water status (potential). The effects of watering strategies (wet, wet-dry and dry down) on soil moisture and leaf water potential for *Tilia* and *cerci* are presented in Fig. 3. Droughted plants (Td and Cd) had the lowest minimum leaf water potential, values were close for Tw and Twd and were relatively stable in *Cerci* across drought and wet dry cycles (Fig. 2a and b and Fig. 3).

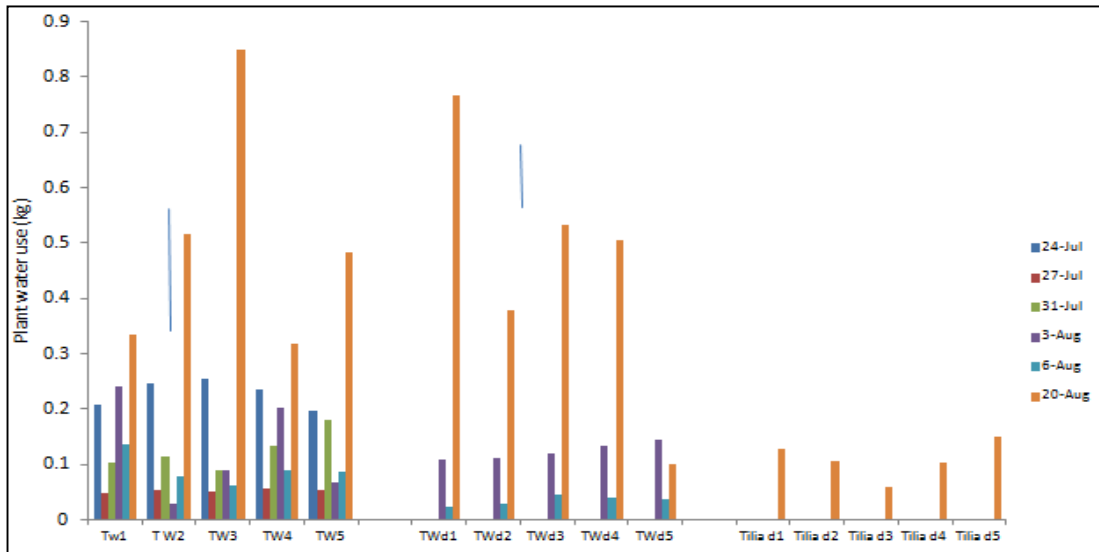


Fig. 1a. Temporal trends in plant water use in *Tilia* subjected to wet dry cycles. Tw (*Tilia* well watered); Twd (*Tilia* wet-dry cycle); Td (*Tilia* dry down). |LSD (error) bar

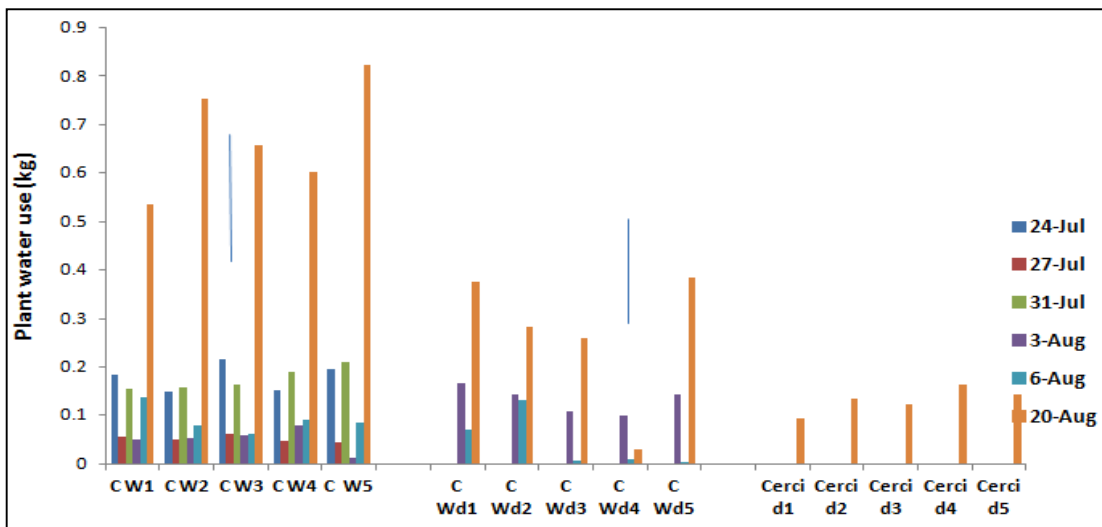


Fig. 1b. Temporal trends in plant water use in *Cerci* subjected to wet dry cycles. Cw (*Cerci* well watered); Cwd (*Cerci* wet-dry cycle); Cd (*Cerci* dry down). |LSD (error) bar

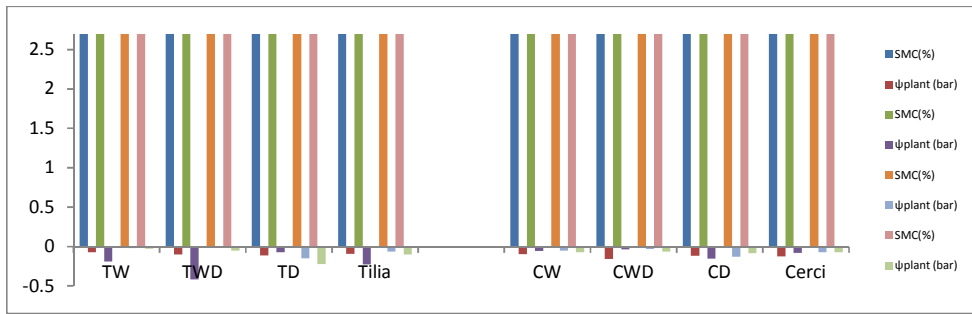


Fig. 2a. Temporal trends in soil moisture content and leaf water potential in Tilia and Cerci subjected to wet dry cycles

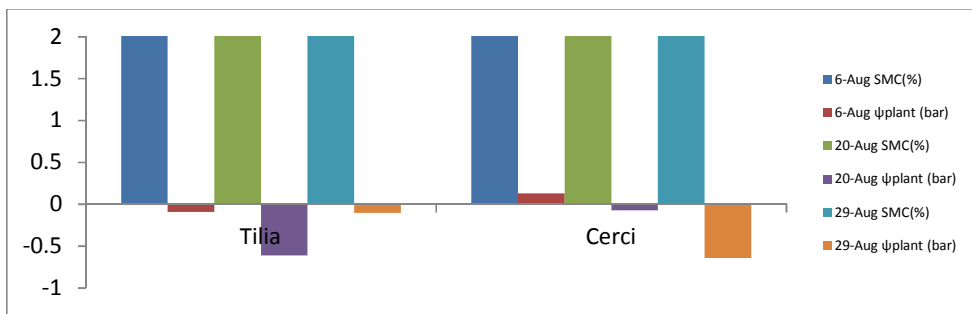


Fig. 2b. The temporal trends of soil moisture contents and leaf water potential of Tilia and Cerci

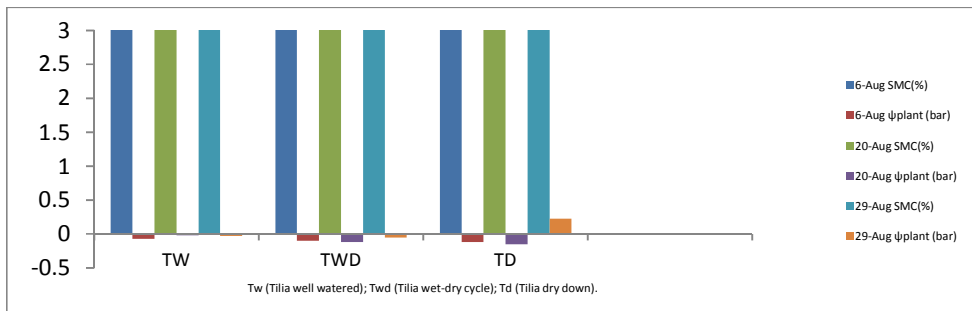


Fig. 2c. Effects of watering regimes on the temporal trends of soil moisture contents and leaf water potential of Tilia

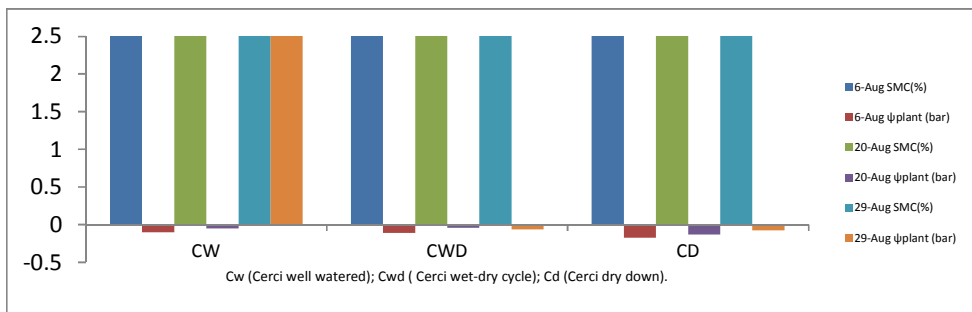


Fig. 2d. Effects of watering regimes on the temporal trends of soil moisture contents and leaf water potential of Cerci

For plants subjected to soil drought, limited gas exchange would be required to avoid hydraulic failure, Cerci sustained favourable leaf water potential and gas exchange longer than Tilia. In droughted and wet-drought cycle treatments (Twd and Td; Cwd and Cd) post-stress rewatering provoked recovery from losses incurred in plant water status and stomatal gas exchange. Both species avoided hydraulic failure, but safety margins from critical ψ_{leaf} were much smaller in Tilia under drought, this species would have experienced chronically low hydraulic conductance [7,17].

The dry-down and recovery (after rewatering) of root zone soil moisture spanned leaf water potentials ranging from -0.88; -0.125MPa: -0.85; -0.104 MPa for the respective pre-dawn and midday (ψ_{PD} and ψ_{MD}) in Cerci and Tilia. In Tilia and Cerci subjected to soil water stress, it appears that the imposed rootzone moisture stress was below the threshold of ψ_{PD} that could provoke visible leaf damage and loss of functionality of stomatal systems. The effect of watering strategies on the pre-dawn and midday leaf water potentials of well watered and droughted Tilia and Cerci are shown in Fig. 4.

Droughted Cerci even under the most severe soil water deficit (Cd) maintained relatively stable for the respective pre-dawn and midday ψ_{PD} and ψ_{MD} (Fig. 4).

The well watered treatments had higher values of the measured physiological indicators based on results of the temporal trends in stomatal gas exchange characters and sap fluxes in Tilia and Cerci (Fig. 5a). The time-dynamics of stomatal gas exchange (stomatal conductance and transpiration rates) and photosynthesis of well watered and droughted Tilia and Cerci (Fig. 5b). Droughted Cerci sustained stomatal gas exchange (transpiration and photosynthesis) even under the most severe soil water deficit (dry down treatment) (Fig. 6). More than 50% of droughted Tilia had below zero stomatal conductance (gs) while few droughted Cerci had. Across the drought and wet-dry cycle treatments, transpiration was higher for Tila while the magnitudes of transpiration rates and stomatal conductance, photosynthesis and sap flow were higher for Cerci seedlings (Fig. 6). The decreasing order of magnitude in the values of photosynthesis were wet > wet-dry > droughted cycle (Fig. 7d).

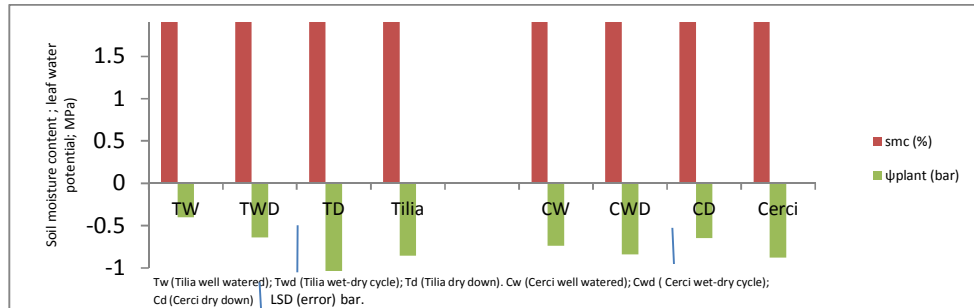


Fig. 3. Effects of watering strategies (wet-dry cycles) on soil moisture contents and leaf water potential of Tilia and Cerci

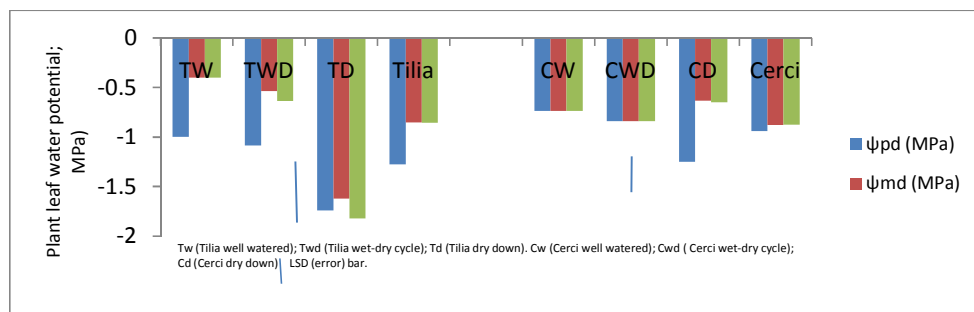


Fig. 4. Effects of watering regimes on pre-dawn and midday leaf water potential of Tilia and Cerci

Table 1. The effects of watering strategies on the measured physiological variables of *Tilia cordata* and *Cercidiphyllum japonicum*

| Treatments | Water use (Evaporative flux) (kg/day) | Pre-dawn leaf potential ψ_{md} (MPa) | Midday leaf potential ψ_{md} (MPa) | Stomatal conductance (mmol/cm ² /s) | Transpiration rate (mmol/cm ² /s) | Photosynthesis rate (mmol/cm ² /s) | Sap flow (kg/day) | Xylem hydraulic conductance (g/MPa/s) |
|-----------------------|--|---|---|---|---|--|----------------------|---|
| Tilia W | 0.573 | -0.99 | -0.41 | 0.114 | 1.72 | 5.06 | 0.32 | 0.0144 |
| Tilia Wd | 0.564 | -1.09 | -0.54 | 0.095 | 1.34 | 4.09 | 0.30 | 0.0137 |
| Tili D | 0.511 | -1.74 | -1.62 | 0.103 | 1.23 | 6.42 | 0.26 | 0.0091 |
| Tilia | 0.550 | -1.27 | -0.85 | 0.104 | 1.43 | 5.45 | 0.29 | 0.0119 |
| Cerci W | 0.764 | -0.74 | -0.74 | 0.135 | 1.51 | 6.85 | 0.41 | 0.0346 |
| Cerci Wd | 0.393 | -0.84 | -0.84 | 0.140 | 1.37 | 5.52 | 0.30 | 0.0254 |
| Cerci D | 0.431 | -1.25 | -1.06 | 0.103 | 1.01 | 5.04 | 0.27 | 0.0096 |
| Cerci | 0.530 | -0.94 | -0.88 | 0.125 | 1.32 | 5.80 | 0.33 | 0.0169 |
| LSD _(0.05) | 0.142 | -0.29 | -0.32 | 0.022 | 0.031 | 0.83 | 0.03 | 0.004 |

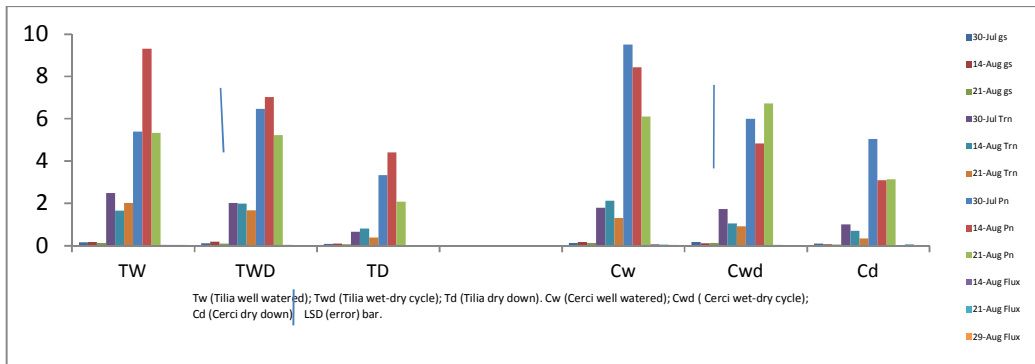


Fig 5a. Effects of watering strategies on the temporal trends of stomatal gas exchange characters and stem sap fluxes in *Tilia* and *Cerci*

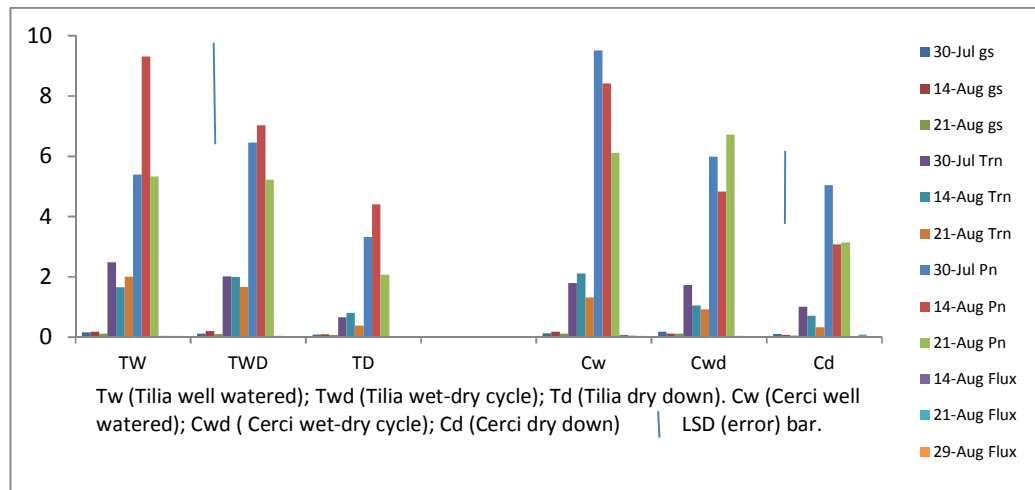


Fig. 5b. Temporal trends in stomatal conductance and transpiration rates in *Tilia* and *Cerci*

In both the long term dry-down and intermittent drought and rewatering cycle were aimed at investigating the ability of the species to recover from the drought intensities and the possible limitations of plant hydraulics on leaf gas exchange. Leaves on trees subjected to drought stress often become scorched and after prolonged periods senesced and abscised (data not shown). While drought may induce a significant amount of leaf abscission, refoliation after water becomes available was observed (data not shown). As a result of increasing dehydration, water potential in *Tilia cordata* declined sharply and one of the plants died off about period of near-zero gas exchange. This observation can be attributed to a vulnerability to embolism. It appeared that the magnitude of soil drought imposed was sufficient to initiate hydraulic failure in *Tilia* [12,18]. It is suggested that very low plant hydraulic (xylem water transport characteristics) would have limited gas

exchange and promoted drought-related mortality in *Tilia* tree seedlings [6]. Hydraulic limits to gas exchange and its promotion of drought-related mortality are widely reported in literature [4,7,20].

Leaf water potential of *Cercidiphyllum japonicum* declined far more relative to that of *Tilia* without causing noticeable damage. Leaf dieback is known to occur which suggests the sacrificial death of more disposable plant regions in order to improve the hydraulic conductance and water status to remaining foliage [1,10]. This phenomenon has been reported as a last resort mechanism to avoid whole-plant mortality and aid long-term survival by protecting vital plant parts such as stems and nodal regions [12,15,18,19]. Induction of hydraulic and stomatal dysfunction by water stress has been reported for both herbaceous (Maize: [21], Rice, [22]) and woody plants [9,23].

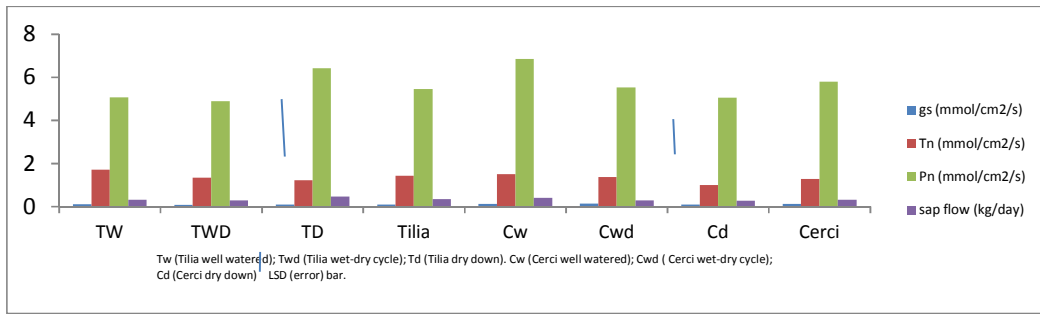


Fig. 6. Effects of watering strategies on stomatal gas exchange parameters and sap flow in Tilia and Cerci subjected to wet-dry cycles

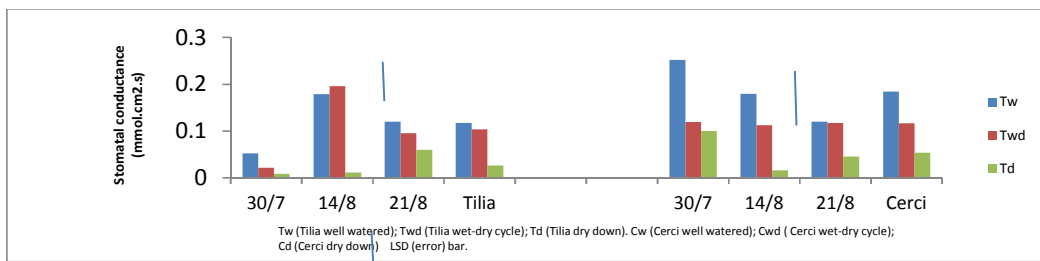


Fig. 7a. Temporal trends in stomatal conductance in Tilia and Cerci subjected to wet dry cycles

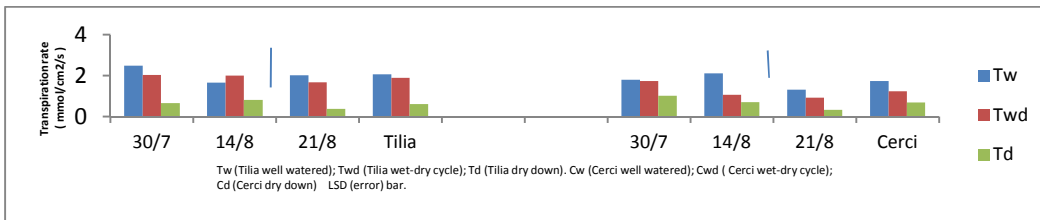


Fig. 7b. Temporal trends in transpiration rates in Tilia and Cerci subjected to wet dry cycles

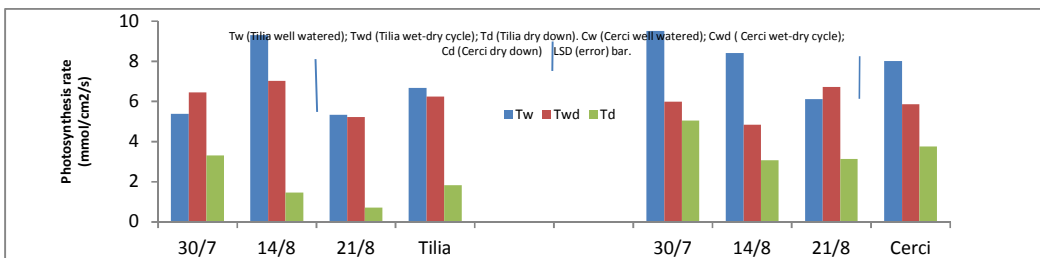


Fig. 7c. Temporal trends in photosynthesis rates in Tilia and Cerci subjected to wet dry cycles

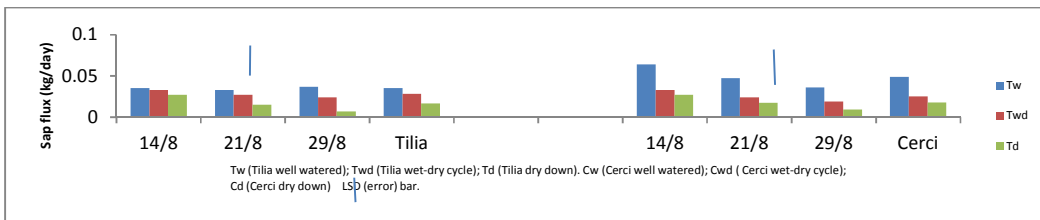


Fig. 7d. Temporal trends in stem sap flow rates in Tilia and Cerci subjected to wet dry cycles

Tilia also experienced chronically low hydraulic conductance and more defoliation and even mortality, the limited gas exchange and xylem hydraulic conductance required to avoid hydraulic failure. It appeared that the soil drought imposed was sufficient to initiate hydraulic failure in species [9]. The defining characteristic of *Tilia* was high near-zero gas exchange. After 2 months of observation, two of the droughted *Tilia* plants died while no seedling mortality occurred in *Cerci*. Water stress-induced hydraulic dysfunction presents a problem not only for long-term survival during severe drought events, but also for daily productivity during short-term fluctuations in soil water availability [8,24, 25].

The drought treatments imposed were effective for some aspects of understanding of tree mortality mechanisms. Perhaps the most critical value of this study is that some of the *Tilia* trees in the drought treatment died; very few studies of drought effects arrive at that endpoint. Such an end-point is important to infer mortality mechanisms [24,26]. Plaut et al. [7] reported that an improvement in xylem hydraulics provides a greater buffering capacity of ψ_{leaf} and hence gas exchange equivalent of the stomatal safety margin displayed in drought-tolerant plants.

Isohydic species would experience mortality after prolonged periods of severely limited gas exchange as required to avoid hydraulic failure while anisohydic species would avoid hydraulic failure, but sustain gas exchange due to its greater cavitation resistance [20,25].

In the single drought and multiple drought-wet cycles, drought induced leaf abscission, however, droughted plants resuscitated by refoliation after drought stress effects was alleviated by rewatering (data not shown). *Tilia* is presumed to follow an isohydic strategy so that upon stomatal closure under incipient drought growth is limited by reduced carbon uptake whereas *Cerci* appeared to have followed an anisohydic strategy so that advanced drought does not limit stomatal functions as such growth may be limited by hydraulic failure. The findings from this study will enhance mechanistic understanding of the growth-limiting processes caused by soil drought on two tree species with contrasting drought stress strategies. The results obtained on the measured physiological characters of *Tilia* and *Cerci* across the imposed watering regimes will improve knowledge of strategies of whole plant drought tolerance, this

has implications for the habitat requirements of *Cercidiphyllum japonicum* and *Tilia cordata*.

4. CONCLUSION

In both *Cercidiphyllum japonicum* and *Tilia cordata*, drought induced leaf abscission and recovery (regrowth) were observed, in addition, following relief from drought (post drought rewatering), leaf water potential and stomatal gas exchange recovered and in magnitudes close to those of well watered control plants. Increasing dehydration brought about sharp declines in leaf water potential in *Tilia* and one of the plants died off. However, against expectation, *Cerci* exhibited drought induced leaf abscission but its water potential was kept below values obtained for *Tilia*. It is concluded that both *Katsura* and *Tilia* are drought avoider that abscise leaves to reduce transpirational water loss. The species are capable of regrowth and recovery of physiological functions after relief from drought. In order to maintain the greatest ornamental value in the landscape, *Katsura* and *Tilia* should be planted in areas that are not prone to drought. The information generated from this study is useful in modeling and predictions of vegetation responses to climate change. The findings are also useful to policy makers and land managers interested in potential drought impacts on productivity and distributions of species, and to tree breeders concerned with identifying traits associated with survival and productivity in species in the frame of changing environmental conditions.

COMPETING INTERESTS

Authors have declared that no competing interests exist

REFERENCES

1. McDowell N, Pockman WT, Allen CD. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*. 2008;178:719–739.
2. Adams HD, Guardiola-Claramonte M, Barron-Gafford GA. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences USA*. 2009;106:7063–7066.

3. Rehfeldt GE, Ferguson DE, Crookston NL. Aspen, climate and sudden decline in western USA. *Forest Ecology and Management*. 2009;258:2353–2364.
4. Holloway-Phillips MM, Brodribb TJ. Minimum hydraulic safety leads to maximum water-use efficiency in a forage grass. *Plant, Cell & Environment*. 2011; 34:302–313.
DOI: 10.1111
5. Phillips OL, Aragão LEOC, Lewis SL. Drought sensitivity of the Amazon rainforest. *Science*. 2009;323:1344–1347.
6. Van Mantgem PJ, Stephenson NL, Byrne JC. Widespread increase of tree mortality rates in the Western United States. *Science*. 2009;323:521–524.
7. Plaut JA, Yepetz A, Hill EA, Pangle J, Sperry JS, Pockman WT, McDowell NG. Hydraulic limits preceding mortality in a piñon–juniper woodland under experimental drought. *Plant, Cell & Environment*. 2012;35:1601–1617.
8. Brodribb TJ, Bowman DJM, Nichols S, Delzon S, Burrell R. Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytologist*. 2010;188:533–542.
9. Berger JD, Ludwig C. Contrasting adaptive strategies to terminal drought-stress gradients in Mediterranean legumes: Phenology, productivity and water relations in wild and domesticated. *Journal of Experimental Botany*. 2014;65(21):6219–6229.
10. Brodribb TJ, Cochard H. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology*. 2009;149:575–584.
11. Breshears DD, Cobb NS, Rich PM. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences USA*. 2005;102:15144–15148.
12. Michaelian M, Hogg EH, Hall RJ, Arsenault E. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*. 2011;17:2084–2094.
13. Royer PD, Cobb NS, Clifford MJ, Huang C, Breshears DD, Adams HD, Villegas JC. Extreme climatic event-triggered overstorey vegetation loss increases understorey solar input regionally: Primary and secondary ecological implications. *Journal of Ecology*. 2011;99:714–723.
14. Andrews S. Tree of the year: *Cercidiphyllum japonicum*. *International Dendrology Society Year Book*. 1998;1997:17-46.
15. Dosmann MS, Iles JK, Graves WR. Drought avoidance in Katsura by drought-induced leaf abscission and rapid refoliation. *Hort Science*. 1999;34(5):871–874.
16. Burgess SSO, Adams MA, Turner NC, Beverly CR, Ong CK, Khan AAH, Bleby TM. An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiol*. 2001;21: 589–598.
17. Addington RN, Donovan LA, Mitchell RJ, Vose JM, Pecot SD, Jack SB, Hacke UG, Sperry JS, Oren R. Adjustments in hydraulic architecture to wet-dry cycle maintain similar stomatal conductance in xeric and mesic habitats. *Plant Cell & Environment*. 2006;29:535-545.
18. Davis SD, Ewers FW, Sperry JS, Portwood KA, Crocker MC, Adams GC. Shoot dieback during prolonged drought in *Ceanothus* (Rhamnaceae) chaparral of California: A possible case of hydraulic failure. *American Journal of Botany*. 2002; 89:820–828.
19. Porter L, McDonald I, Alarcon A, Fichtler E, Licona JC, Pena-Claros M, Sterck F, Villegas Z, Sass-Klaassen U. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist*. 2010;185:481–492.
20. Sala A, Piper F, Hoch G. Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist*. 2010;186:274–281.
21. Cochard H. Xylem embolism and drought-induced stomatal closure in maize. *Planta*. 2002;215:466–471.
22. Stiller V, Lafitt HR, Sperry JS. Hydraulic properties of rice (*Oryza sativa* L.) and the response of gas exchange to water stress. *Plant Physiology*. 2003;132:1698-1706.
23. Brodribb TJ, Holbrook NM. Declining hydraulic efficiency as transpiring leaves desiccate: Two types of response. *Plant, Cell & Environment*. 2006;29:2205–2215
24. McDowell NG, Sevanto S. The mechanisms of carbon starvation: How, when, or does it even occur at all. *New Phytologist*. 2010;86:264-266

25. Suarez ML, Ghermandi L, Kitzberger T. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. *Journal of Ecology*. 2004;92:954–966.
26. McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution*. 2011;26:523–532.

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