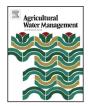
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Combined effects of high relative humidity and K⁺ supply mitigates damage caused by salt stress on growth, photosynthesis and ion homeostasis in *J. curcas* plants



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ABSTRACT

This study evaluated the capacity of high relative humidity associated with K⁺ supply in mitigating harmful effects caused by salt stress on physiological parameters of Jatropha curcas plants. The plants were subjected to four different treatments (K0Na0, K0Na1, K1Na0 and K1Na1) and two different levels of humidity, low (40%) and high (80%), in chamber growth conditions. The plants' growth was higher under conditions of high relative humidity when compared to low humidity in all the treatments studied. The CO₂ assimilation rate, transpiration and stomatal conductance were stimulated by high humidity independently of treatments of K⁺ and Na⁺. The Na⁺ concentration in the shoots was more elevated in plants treated with NaCl when compared to NaCl-free plants. On the other hand, the shoots' K⁺ concentration was highly stimulated in the presence of K⁺ ions, especially in combination with high relative humidity (RH). The shoots' Na⁺ transport rate was strongly stimulated by a combination of 50 mM NaCl+40% RH when compared to high humidity. Conversely, the shoots' K⁺ transport was significantly higher in plants when they were supplied with K⁺ and exposed to high relative humidity. In the roots, the transport rate of Na⁺ presented a similar pattern to that found in the shoot. However, surprisingly, K⁺ transport rate was increased in plants supplied with K⁺ and 40% RH in NaCl absence. The plants exposed to low relative humidity showed lower K*/Na* ratios than plants exposed to 80% RH both in shoots and roots. In addition, the shoots and roots selectivity (KNa) was strongly stimulated in plants exposed to high humidity when compared to low humidity. In conclusion, the combined effects of high relative humidity and a supply of K⁺ were able to improve the growth, the leaf gas exchange and ionic homeostasis of J. curcas plants.

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1. Introduction

Many physiological and morphological processes displayed by plants are affected by relative humidity (RH). It is well-documented that variations in RH exert influences on plant growth, leaf CO₂ assimilation rate, stomatal aperture, transpiration and nutrient uptake (Talbott et al., 2003; Cha-um et al., 2010). Some authors have reported that relative humidity between vapor pressure deficits (VPD) of 0.2 and 1.0 kPa had little effect on a plant's physiology

http://dx.doi.org/10.1016/j.agwat.2015.09.027 0378-3774/© 2015 Elsevier B.V. All rights reserved. (Wherley and Sinclair, 2009). However, VPD values lower than 0.2 kPa and higher than 1.0 kPa are frequently reached in controlled conditions such as in greenhouses.

High relative humidity may affect the salt tolerance of plants by decreasing transpiration (An et al., 2002, 2005). The improvement in growth under high RH conditions may be due to improvement in water status and/or reduction in salt accumulation in plant shoots (Salim, 1989; An et al., 2001). It has been reported that growth reduction in saline conditions was ameliorated by increasing RH in some species (An et al., 2002, 2005; Cha-um et al., 2010). However, other reports showed that humidity had no alleviation effect on the growth of plants (Torres-García et al., 2009). A previous study showed that increasing RH decreased Na⁺ and/or Cl⁻ uptake



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in plants cultivated in a greenhouse (Gislerod and Mortensen, 1990). Moreover, other studies showed that the salt tolerance was increased under conditions favoring higher transpiration (An et al., 2001, 2002, 2005).

It is well-known that ion uptake and transport in plants corresponds to the sum of two components; one metabolic energy ('active') component, and one 'non-active' component that is dependent on water flow (Salim, 1989). However, the relative contribution of each of the two components to the total ion uptake by a plant may be different in different plant species. In variable RH conditions, the ionic relationship may be affected so that relatively higher amounts of ions are taken up via non-active processes (Salim, 1989).

Generally, a RH of 75–85% accelerates the photosynthesis rate, though relative humidity may influence photosynthesis differently according to environmental changes. High RH of over 90% decreases the photosynthesis rate due to reduced stomata aperture. Under lower RH conditions, the photosynthesis tends to decrease due to water stress induced by excess transpiration (Kitaya, 2005). Accordingly, by lowering RH levels, rather than the general healing and acclimatization conditions in which RH is maintained as nearly saturated, this may promote photosynthesis by preventing the stomata apertures from closing.

An important approach about water use efficiency (WUE) indicate that the crop water use is limited when atmospheric vapor pressure deficit (VPD) is high allowing a large demand on the plants to transpire water (Sinclair et al., 2005; Fletcher et al., 2007; Kholova et al., 2010). This trait would be expressed as partial stomatal closure under high VPD, which may frequently occur around midday, and results in two benefits: First, it decreases the effective average daily VPD for transpiration allowing more efficient use of available water; second, water is conserved for use later in the growing season (Yang et al., 2012).

Stomatal response is considered to be related to the hydraulic dynamics in the plant (Torres-Ruiz et al., 2015). High water vapor loss from guard cells and/or a shortage of water supply to the epidermal cells, including the guard cells in particular, can result in decreased turgor pressure and cause partial stomata closure (Eamus et al., 2008). Transpiration restriction by stomata at high VPD appears to result from limiting hydraulic conductance in the plant, which constrains the flow of water from roots to transpiration sites in the leaf surface (Brodribb and Jordan, 2008; Sinclair et al., 2008; Sadok and Sinclair, 2010). A substantial portion of the hydraulic resistance can be located in the leaf, especially the extravascular component (Matzner and Comstock, 2001; Cochard et al., 2004; Mott, 2007). There is also evidence of resistance residing in roots (Parent et al., 2009).

In addition to the effects of relative humidity on the metabolism of the plants already mentioned above it has been widely reported that elevated levels of K⁺ in the external medium exert beneficial effects on plants exposed to high levels of Na⁺, thus, restricting salt toxicity (Rodrigues et al., 2012, 2013). Moreover, the maintenance of a high cytosolic K⁺/Na⁺ ratio is a key feature of salt tolerance. In fact this K⁺/Na⁺ ratio has been utilized as a physiological marker for the selection of salt-tolerant cultivars for some species (Dasgan et al., 2002; Maathuis and Amtmann, 1999; Flowers, 2004; Tammam et al., 2008). Under optimal conditions, the cytosolic K⁺ content is estimated to be about 150 mM with a negligible Na⁺ content (Carden et al., 2003). However, due to excessive Na⁺ accumulation in the cytosol associated with salt-induced K⁺ efflux, the cytosolic K⁺/Na⁺ ratio falls dramatically under saline conditions (Shabala et al., 2003). This salinity-induced K⁺ loss from cells is a result of NaCl-induced membrane depolarization, leading to the activation of depolarization-activated outward-rectifying K⁺ channels (Cuin et al., 2008).

Jatropha curcas grows in marginal areas where important crop species are not able to survive (Silva et al., 2010). Furthermore, it presents high economic potential due to its seed oil quality, which can be converted into biodiesel by industrial processes (Kheira and Atta, 2009). Recent studies have demonstrated that *J. curcas* plants display a strong antagonism between K⁺ and Na⁺ in terms of transport and partitioning (Rodrigues et al., 2013). Moreover, this study also showed that this species has a higher affinity for K⁺ over Na⁺ in all organs.

Although previous studies have shown that satisfactory yields of *J. curcas* can be obtained under constraining conditions of semiarid regions such as during drought and at high temperatures (Silva et al., 2010, 2012), the knowledge on the combined effects of high relative humidity and K^+ supply on the growth, photosynthesis, ion uptake, transport and selectivity under salt stress are scarce. To date, there are no reports in the literature that address in detail the beneficial effects of high relative humidity and K^+ on all the processes mentioned above under salt-stressed plants. Thus, the present study was carried out to test the hypothesis that high relative humidity combined with an adequate K^+ supply mitigates the effects caused by salinity in *J. curcas* plants.

2. Materials and methods

2.1. Plant growth conditions and treatments

The experiment was carried out in a greenhouse under natural conditions; the mean air temperature varied between 24 °C (minimum) and 36 °C (maximum) with a mean temperature of 29 °C, a mean air relative humidity of 65%, a mean maximum photosynthetic photon flux density (PPFD) of 700 μ mol m⁻² s⁻¹ and a photoperiod of approximately 12 h. In Fig. 1 were indicated the environmental conditions during the experimental period in greenhouse. These data were extracted from Data loggers (model HOBO U12-012 onset). J. curcas seeds, cultivar FT1, supplied by Tamadua Institute (Brazil), were previously selected for size (from 1.5 cm to 2.0 cm) and weight (from 600 mg to 900 mg), surface-sterilized with a 5% sodium hypochlorite solution, germinated in sand and irrigated daily with 500 mL of distilled water. Eight days after sowing, seedlings were transferred to plastic pots (2L) containing one-fourth strength Hoagland and Arnon (1950) nutrient solution during the first week and one-half strength thereafter. The solution was changed every week, and the pH was adjusted to 6.0 ± 0.5 every two days with 1 M NaOH or 1 M HCl. To 23 days old, the treatments containing KCl and NaCl were applied to plants via a nutrient solution. Four treatments were then performed: (1) without K⁺ and Na⁺ (KONa0); (2) without K⁺ and 50 mM NaCl (KONa1); (3) 10 mM KCl and NaCl-free (K1Na0); and (4) 10 mM KCl and 50 mM NaCl (K1Na1). The K1Na0 treatment was adopted as a control. Afterwards, the plants were transferred from the greenhouse to two growth chambers with two different relative humidity values (low humidity, 40%, and high humidity, 80%). Both growth chambers had controlled environmental conditions, with a PPFD of 400 μ mol m⁻² s⁻¹, an air temperature of 27 °C, and a photoperiod of 12 h. The plants remained in these conditions for 48 h. At the end of the experiment, the plants were harvested, and leaves and stems (shoots) and roots were separated and dried in an oven at 75 °C for 48 h for further chemical analyses as previously done by Rodrigues et al. (2013).

2.2. Determination of concentration and transport rates of Na⁺ and K⁺ and selectivity of K⁺ in relation to Na⁺ ($S_{K,Na}$) in the shoots and roots

The Na⁺ and K⁺ contents in plant tissues (shoots and roots) were measured by flame photometry, as previously described (Rodrigues Download English Version:

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