



The interaction between drought and elevated CO₂ in water relations in two grassland species is species-specific

Jon Miranda-Apodaca^{a,*}, Usue Pérez-López^a, Maite Lacuesta^b, Amaia Mena-Petite^a, Alberto Muñoz-Rueda^a

^a Departamento de Biología Vegetal y Ecología, Facultad de Ciencia y Tecnología, Universidad del País Vasco, UPV/EHU, Apdo. 644, E-48080 Bilbao, Spain

^b Departamento de Biología Vegetal y Ecología, Facultad de Farmacia, Universidad del País Vasco, UPV/EHU, P^o de la Universidad 7, 01006 Vitoria-Gasteiz, Spain

ARTICLE INFO

Keywords:

Agrostis capillaris
Carbon dioxide
Climate change
Trifolium pratense
Water stress

ABSTRACT

Climate change can have major consequences for grassland communities since the different species of the community utilize different mechanisms for adaptation to drought and elevated CO₂ levels. In addition, contradictory data exist when the combined effects of elevated CO₂ and drought are analyzed because the soil water content is not usually similar between CO₂ concentrations. Thus, the objectives of this work have been to examine the effect of water stress on plant water relations in two grassland species (*Trifolium pratense* and *Agrostis capillaris*), analyzing the possible differences between the two species when soil water content is equal in all treatments, and to elucidate if development under elevated CO₂ increases drought tolerance and if so, which are the underlying mechanisms. At ambient CO₂, when soil volumetric water content was 15%, both species decreased their water potential in order to continue taking up water. *Trifolium pratense* performed osmotic adjustment, while *Agrostis capillaris* decreased the rigidity of its cell wall; moreover, both species increased the root to shoot ratio and decreased leaf area. However, these mechanisms were not sufficient to maintain cell turgor. Elevated CO₂ partially mitigated the negative impact of drought on turgor potential in *Trifolium pratense* through a higher osmotic adjustment and root to shoot ratio and in *Agrostis capillaris* through a higher leaf relative water content caused by higher hydraulic conductance, but the impact of drought was not mitigated in either species by higher soil water conservation.

1. Introduction

The atmospheric CO₂ concentration has increased since the beginning of the industrial revolution, from a concentration of 280 μmol mol⁻¹ to the current concentration of 400 μmol mol⁻¹ (Stocker et al., 2011), mainly due to anthropogenic causes. Recently, the IPCC (2014) stated that the atmospheric concentration of CO₂ increases at an average rate of 2.0 ± 0.1 μmol mol⁻¹ year⁻¹, the largest average increase since direct CO₂ concentration measurements began in 1958. On this basis, the IPCC (2014) has predicted several scenarios regarding the future climate conditions; in this respect, the average estimate for the concentration of CO₂ in the atmosphere at the end of the century would be approximately 700 μmol mol⁻¹, i.e., twice that registered at the beginning of the same century.

In addition to increasing the concentration of CO₂, climate change is expected to provoke a change in the amount of rainfall, increasing in some areas and significantly decreasing in others. In addition, due to the change in the distribution of rainfall, extreme events of drought and flooding are expected to increase (IPCC, 2014). These global climatic changes can have major consequences for terrestrial vegetation, including short-term physiological responses in crop plants and long-term changes in the structure and function of ecosystems (Mooney et al., 1991; Smith et al., 2005; Naudts et al., 2011, 2013; Peñuelas et al., 2013; Xu et al., 2014).

Water is the most limiting resource for plant growth (Boyer, 1982; Chaves et al., 2003), and its scarcity jeopardizes the productivity of crops and grasslands. Drought alters the aeration and hydraulic conductance of the soil, causing a decrease in soil water potential (Rozema,

Abbreviations: Ac, *Agrostis capillaris*; DH, dehydration; DW, dry weight; FW, fresh weight; HC, hydraulic conductance; Ψ_{opd}, leaf predawn osmotic potential; Ψ_{ppd}, leaf predawn turgor potential; Ψ_{wpd}, leaf predawn water potential; Ψ_{omd}, leaf midday osmotic potential; Ψ_{pmd}, leaf midday turgor potential; Ψ_{wmd}, leaf midday water potential; Ψ_o¹⁰⁰, leaf osmotic potential at full turgor; OA, osmotic adjustment; Ψ_o, osmotic potential; RWC, relative water content; θ_v, soil volumetric water content; Tp, *Trifolium pratense*; TW, turgid weight; Ψ_p, turgor potential; ε, volumetric elasticity modulus; Ψ_w, water potential

* Corresponding author.

E-mail addresses: jon.miranda@ehu.es (J. Miranda-Apodaca), usue.perez@ehu.es (U. Pérez-López), maite.lacuesta@ehu.es (M. Lacuesta), amaia.mena@ehu.es (A. Mena-Petite), a.munoz-rueda@ehu.es (A. Muñoz-Rueda).

<https://doi.org/10.1016/j.jplph.2017.11.006>

Received 26 July 2017; Received in revised form 14 November 2017; Accepted 15 November 2017

Available online 23 November 2017

0176-1617/ © 2017 Elsevier GmbH. All rights reserved.

1993), which complicates water uptake. Therefore, plants must be able to tolerate or adapt to drought as a mechanism to sustain their development and productivity. Drought tolerance is a complex trait involving multiple adaptations. The key to this is that the plant must have the ability to maintain water uptake in increasingly dry soil while minimizing water loss through its leaves. Moreover, differences among species are also observed, as each species has different mechanisms for adaptation to drought (Xu et al., 2014; AbdElgawad et al., 2015).

Plants achieve this tolerance by means of morphological adaptations such as the development of more numerous and/or longer roots or alterations in leaf morphology, reducing their size and/or increasing the cuticle, and by physiological and biochemical adaptations such as stomatal closure to prevent water loss, and decreasing water potential (Ψ_w) to maintain water uptake. Thus, several authors have described that some plants are able to maintain water uptake by actively decreasing Ψ_w through the lowering of osmotic potential (Ψ_o). Ψ_o is determined by the concentration of osmotically active substances, especially in the vacuole, and depends on the degree of hydration, the absolute amount of osmolytes, and the relative distribution of water between the symplast and apoplast fractions (Girma and Krieg, 1992; Sánchez-Blanco et al., 1998). A decrease in Ψ_o may occur either by dehydration (DH), which causes a passive increase in the concentration of osmolytes, or by active synthesis of osmolytes, which is known as osmotic adjustment (OA) (Martínez et al., 2004; Martínez et al., 2007; Pérez-López et al., 2010). OA includes the active accumulation of organic and inorganic solutes in the cell, thereby achieving a reduction of Ψ_o and an increase in the inflow of water to the cell, maintaining turgor pressure (Sánchez et al., 2004).

Nevertheless, the usefulness of OA as a mechanism of drought tolerance is controversial. Some authors have suggested that OA is a result of reduced growth by drought (Munns, 1988). Others have suggested that OA only operates under severe water deficit, when the plant's survival is threatened (Serraj and Sinclair, 2002).

In the case that dehydration occurs, this cellular water loss may result in a loss of turgor. To maintain turgor despite the lower water content, plant adjusts their cell wall elasticity, making it more elastic (Saito and Terashima, 2004). However, the opposite trend has also been observed, i.e., the plant decreases the elasticity, making it more rigid (Martínez et al., 2007) to reduce Ψ_w with minimal loss of leaf water and, therefore, maintain water uptake. Both strategies are considered advantageous for the plant (Schulte, 1992; Saito and Terashima, 2004).

As mentioned above, another mechanism for tolerating drought is to diminish water loss. To achieve this goal and, therefore, maintain a better water status, plants tend to reduce transpiration by stomatal closure, by reducing hydraulic conductance and/or by decreasing leaf area (Sadras et al., 1993; Liu and Stützel, 2002; Robredo et al., 2007).

In addition to increased soil drought, as aforementioned, the future climatic conditions are expected to provoke an increase in the atmospheric concentration of CO_2 , which under well-watered conditions has not generally affected water relations (De Luis et al., 1999; Robredo et al., 2007; Perry et al., 2013). However, when the increase in the concentration of CO_2 acts together with drought, interactive effects have been detected in the response of different morphological, physiological and biochemical parameters (Xu et al., 2013 and references therein). Regarding water relations, several studies have shown that plants have a better water status than at ambient CO_2 due to reduced transpiration rate as a result of the stomatal closure associated with increased CO_2 (Robredo et al., 2007; Leakey et al., 2009; Morgan et al., 2011; Miranda-Apodaca et al., 2015). Conversely, other studies have not observed differences between CO_2 concentrations (Ferris and Taylor, 1994; Manderscheid et al., 2014), and in some studies, the effect of increased CO_2 concentration on water status is even negative (Centritto et al., 1999; De Luis et al., 1999; Zeppel et al., 2012). Furthermore, Samarakoon and Gifford (1995) established that the response of transpiration to the combined effects of elevated CO_2 and drought is determined by the relationship between the increase in leaf area and

the decrease in transpiration per area induced by stomatal closure. Thus, if the decrease in transpiration per area is greater than the increase in leaf area, the total transpiration will be reduced; however, if the increase in leaf area is greater the total transpiration will increase.

In addition, some authors have argued that, under elevated CO_2 , the increased CO_2 assimilation rate would permit the plant to have more carbon skeletons to perform OA (Wall et al., 2006; Chen et al., 2015); however, other authors have observed that due to the higher growth rate at elevated CO_2 the concentration of solutes in the leaf could decrease, turning Ψ_o less negative and observing a minor OA (Tschaplinski et al., 1993; 1995). Furthermore, some authors have affirmed that elevated CO_2 would permit the plant to increase the fine roots and, in general, the root biomass, raising the root to shoot ratio, boosting drought tolerance (Xu et al., 2013). Thus, there is not a general consensus regarding how the interaction between drought and elevated CO_2 affects water relations and associated tolerance mechanisms; probably because in the aforementioned studies the water content of the soil was not always similar between CO_2 treatments, which could be masking direct and specific effects of elevated CO_2 .

Grasslands are one of the largest ecosystems, covering approximately 25% of land cover (FAO, 2010) and constituting approximately 40% of the potential agricultural area in Western Europe (Peeters, 2004). Furthermore, due to its wide occurrence, it is argued that the grassland ecosystem is of great importance as a potential mitigating factor for climate change through underground carbon sequestration; FAO (2010) established that the total carbon sequestration by grasslands is 50% higher than that by woods.

With all this in mind, the objectives of this work have been to examine the effect of water stress on plant water relations in two grassland species (*Trifolium pratense* and *Agrostis capillaris*), analyzing the possible differences between the two species when soil water content is equal in all treatments and to elucidate whether development under elevated CO_2 increases drought tolerance and if so, which are the underlying mechanisms. With these objectives, the hypotheses were 1) when all treatments have the same amount of water in the soil, the species that can develop more efficient mechanisms of drought tolerance will present greater turgor potential and leaf water content; 2) under combined environmental conditions, the elevated CO_2 will partially mitigate the negative effect of drought, through higher root to shoot ratio and osmotic adjustment as a consequence of the increased availability of carbon skeletons for use in the synthesis of compatible osmolytes, and not through higher soil water conservation.

2. Materials and methods

2.1. Plant material and experimental design

Two grassland species were used: *Agrostis capillaris* L. (Ac; grass) and *Trifolium pratense* L. (Tp; legume). Seedlings were grown in a mixture of peat/vermiculite (1/1 v/v) in 6 L pots. Thirty-six seeds were sown in each pot and were watered every other day with deionized water for 4 days till the plants germinated. Fourteen days after sowing, the twelve more uniform plants were selected, reaching a final density of 315 plant m^{-2} . After emergence and for 24 days, the seedlings were watered two days a week with 250 mL of Hoagland's solution, and in order to reach field capacity, the plants were also watered with deionized water between each application of Hoagland's solution.

Plants were grown in a Conviron PGR15 controlled environment growth chamber (Conviron, Manitoba, Canada) with a daily 14 h light regime, an average day/night temperature of 24/20 °C, and a relative day/night humidity of 70/80%. During the light period, the photosynthetic photon flux density in the chamber was 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Light was provided by a combination of incandescent bulbs and warm-white fluorescent lamps.

The CO_2 treatments were 400 $\mu\text{mol mol}^{-1}$ (ambient CO_2) and 700 $\mu\text{mol mol}^{-1}$ (elevated CO_2). The growth chamber atmosphere was

Download English Version:

<https://daneshyari.com/en/article/8387051>

Download Persian Version:

<https://daneshyari.com/article/8387051>

[Daneshyari.com](https://daneshyari.com)