

Original article

Variation in relative water content, proline accumulation and stress gene expression in two cowpea landraces under drought



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ABSTRACT

Many landraces of cowpea [*Vigna unguiculata* (L.) Walp.] are adapted to particular geographical and climatic conditions. Here we describe two landraces grown respectively in arid and temperate areas of Algeria and assess their physiological and molecular responses to drought stress. As expected, when deprived of water cowpea plants lose water over time with a gradual reduction in transpiration rate. The landraces differed in their relative water content (RWC) and whole plant transpiration rate. The landrace from Menia, an arid area, retained more water in adult leaves. Both landraces responded to drought stress at the molecular level by increasing expression of stress-related genes in aerial parts, including proline metabolism genes. Expression of gene(s) encoding proline synthesis enzyme P5CS was up regulated and gene expression of ProDH, a proline catabolism enzyme, was down regulated. Relatively low amounts of proline accumulated in adult leaves with slight differences between the two landraces. During drought stress the most apical part of plants stayed relatively turgid with a high RWC compared to distal parts that wilted. Expression of key stress genes was higher and more proline accumulated at the apex than in distal leaves indicating that cowpea has a non-uniform stress response at the whole plant level. Our study reveals a developmental control of water stress through preferential proline accumulation in the upper tier of the cowpea plant. We also conclude that cowpea landraces display physiological adaptations to water stress suited to the arid and temperate climates in which they are cultivated.

1. Introduction

Cowpea, the domesticated subspecies of *Vigna unguiculata* [*Vigna unguiculata* (L.) Walp.], is an important crop in semi-arid regions (Pasquet, 1993; Pasquet, 1999; Ba et al., 2004). Cowpea originates from the wild *V. unguiculata spontanea* and within the *V. unguiculata* subspecies, cultivated genotypes have been distinguished based on anatomical characteristics, and isozyme and DNA markers (Pasquet, 1993; Pasquet, 1999; Ba et al., 2004). Hundreds of cowpea genotypes currently cultivated worldwide are curated in seed banks (Egbadzor et al., 2014; Ba et al., 2004).

African cowpea landrace diversity has been assessed using anatomical and developmental characteristics and molecular genotyping (Egbadzor et al., 2014; Ghalmi et al., 2009). Genetically close African cowpea landraces (20 Algerian or 113 Ghana) often have similar features including seed-coat colour, ranging from black to red, mottled or cream (Egbadzor et al., 2014; Ghalmi et al., 2010). However,

geographically and genetically distant landraces with different adaptations may have similar features, for example, by having the same seed-coat colour (Ghalmi et al., 2009; Muchero et al., 2009; Huynh et al., 2016).

Compared to other leguminous plants, cowpea is considered to be drought resistant (Belko et al., 2013). Yield, photosynthesis, water content, transpiration and water potential of local cowpea landraces have been compared showing that the ability to withstand drought varies according to the genotype (Singh et al., 2010; Singh and Raja Reddy, 2011). A subset of especially drought resistant cowpea landraces have been identified as possible progenitors for breeding improved cowpea varieties (Hall, 2012).

When cowpea responds to drought stress stomata close rapidly and leaf transpiration is reduced (Hall and Schulze, 1980; Belko et al., 2013). ABA and lipid signalling and lipid enzyme activity have been correlated to stomatal closure and drought resistance in cowpea (Iuchi et al., 2000; Torres-Franklin et al., 2007; Singh and Raja Reddy, 2011).

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Stress and ABA also induce the expression of stress-related transcription factors, such as DREB2A, which in turn induce a variety of stress-responsive genes (Sadhukhan et al., 2014a).

During water stress, plant mitochondria and chloroplasts accumulate reactive oxygen species (ROS) as by-products of respiration and photosynthesis respectively (Mittler, 2002). A variety of enzymatic or non-enzymatic mechanisms or the induction of alternative electron transport may limit the amount of ROS that accumulates during stress. For example, mitochondrial alternative oxidase (AOX) isoforms can be induced by drought in plants, including cowpea, to limit mitochondrial ROS production (Vanlerberghe et al., 2016; Costa et al., 2010; Wang and Vanlerberghe, 2013). The plastid terminal oxidase PTOX, a chloroplast homologue of AOX, is induced in some plant species to limit excess electron transfer in the chloroplast during stress (Laureau et al., 2013; Johnson and Stepien, 2016).

Another characteristic of stress response in plants is the synthesis of osmolytes, small molecules, such as sugar and the amino acid proline (Szabados and Savaouré, 2010). These molecules allow dehydrated plant cells to withstand dehydration by maintaining turgor, buffering against ROS and maintaining redox homeostasis (Szabados and Savaouré, 2010).

Proline accumulates when it is synthesised from glutamate at the same time as its catabolism is repressed. Drought stress induces expression of the biosynthetic gene *P5CS*, which encodes bi-functional pyrroline-5-carboxylate synthase (EC 2.7.2.11/1.2.1.41) (Pérez-Arellano et al., 2010), and represses *ProDH*, which encodes proline dehydrogenase (EC 1.5.5.2) (Peng et al., 1996; Verslues and Sharma, 2010). Different signals induce proline biosynthesis in plants. ABA signalling induces *P5CS* (Savaouré et al., 1997; Strizhov et al., 1997) and lipid signalling, through the action of phosphatidic acid and ROS produced by NADPH oxidases, can modulate *P5CS* and *ProDH* gene expression (Ghars et al., 2012; Ben Rejeb et al., 2015).

To better characterise cowpea adaptation, we measured variations of key physiological indicators and gene expression in response to drought stress in two cowpea landraces originating from regions of Algeria with either temperate or arid climates. Relative water content (RWC) was measured to better characterize water deficit. The landrace originating from the arid area maintained a higher RWC over the duration of the drought stress and transpired less than the landrace from the temperate area. In both landraces, proline biosynthesis genes are regulated by drought stress but surprisingly, more proline accumulates in the upper tier of the plant compared to older leaves suggesting developmental control of water stress responses.

2. Materials and methods

2.1. Plant material and growth

Cowpea [*Vigna unguiculata* (L.) Walp.] landraces were provided by local Algerian farmers. Landrace Bejaia (named B in this work) is grown in Bejaia in north-east Algeria, an area with a sub-humid climate. Landrace Menia (named M in this work) is grown in Menia in central Algeria, a relatively hot and arid region (according to Emberger classification) (Emberger, 1955; Peel et al., 2007) (Table 1).

Seeds of landrace Bejaia (B) are black, while seeds from landrace Menia (M) are pale or deep golden in colour (Supp. Fig. 1A). The mean 100-seed weight is 7.06 g for Landrace B and 6.91 g for landrace M ($p < 0.001$ using a Mann-Whitney test with $n = 10$ samples) (Supp. Fig. 1B).

Seeds were surface sterilized, imbibed on moist filter paper overnight at 4 °C, and left to germinate at room temperature. Germinated seeds were transplanted into 1800 cm³ plastic containers containing 60 g of a peat-perlite-vermiculite mixture (2:1:1, v/v/v). The peat (reference V1 mix, Jiffy Products International BV, The Netherlands) is a mix of white and black peat with added fertilizer NFU42001 giving NPK content of 17, 10 and 4 kg/m³ respectively.

Plants were grown at 22 °C in long-day conditions (16 h light) in a

Table 1
Characteristics of geographical origin of cowpea landraces used in this study. T°: temperature.

Landrace	Bejaia (B)	Menia (M)
Area of origin	Bejaia (North-East Algeria)	Menia (Central Algeria)
Geographical location	36°45'N, 5°05'E	30°35'N, 2°51'E
Elevation above sea level	86 m	387 m
Climate (Emberger) (Emberger, 1955)	Sub humid	Hot arid
Climate (Köppen-Geiger) (Peel et al., 2007)	Csa	BWh
Average Temperature	17.6 °C	21.9 °C
Annual Rainfall	834 mm	34 mm

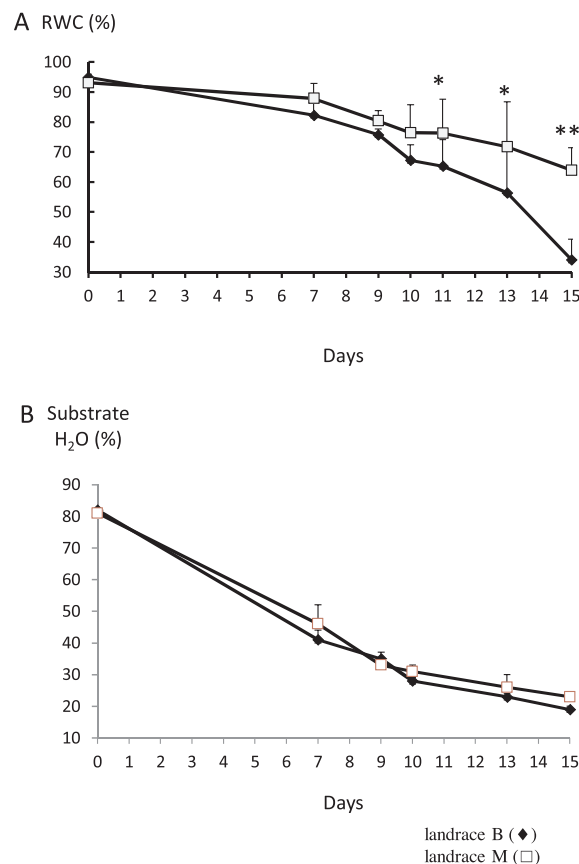


Fig. 1. Decrease in relative water content in cowpea landraces.

A, Relative water content (RWC) of first trifoliolate leaves and B, soil humidity during water deprivation of landrace B (◆) and landrace M (□). Measurements were done daily after soil was watered to saturation on Day 0. Significant differences between landraces ($n = 8$) are indicated by * for $p < 0.05$ and ** for $p < 0.01$ in Mann-Whitney tests. Error bars represent standard deviation.

temperate glasshouse under natural light supplemented with sodium lamps with photosynthetically active radiation (PAR) averaging 90 $\mu\text{moles photons m}^{-2} \text{s}^{-1}$. Total PAR was estimated between 90–500 $\mu\text{moles photons m}^{-2} \text{s}^{-1}$, a makeshift shutter system cutting-off excess light.

2.2. Imposition of drought stress, measuring relative water content and transpiration

Prior to drought the experiment, plants were grown for seven days until the first trifoliolate leaves (TFL1) had fully developed, at which time a watering of the soil to saturation was conducted. To impose drought stress, watering was stopped. Relative water content (RWC) was

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