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Research article

Differential physiological and molecular response of barley genotypes to water deficit



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A R T I C L E I N F O

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ABSTRACT

Changes in physiological parameters (relative water content (RWC), biomass, water use efficiency (WUE), net photosynthetic yield (P_N) and quantum yield of PSII (F_v/F_m)), in proline and sugar content, and expression profile of genes reported to be associated with the barley response to water deficit, including LEA genes, NHX1, Hsdr4, BLT101 and genes encoding transcription factors (HvDREB1, HvABF1, HvABI5 and HvZIP1), were analyzed in seedlings of nine barley genotypes subjected to a progressive increase in water deficit. Seedlings of all genotypes wilted when the soil water content (SWC) declined from 65% (control conditions) to 10% (severe drought conditions), but recovered turgor within a few hours of re-watering. However, when severe drought conditions were prolonged for a week, large differences in survival characteristics were observed between genotypes after re-watering. Multivariate analysis of the changes in physiological and molecular characteristics allowed several different homogenous groups within the genotypes to be distinguished, depending on stress intensity. Furthermore, integration between the stress-response traits was found and was shown to vary depending on the genotype and the stress level. Based on analysis of physiological traits and survival characteristics, two barley genotypes with high adaptability to the stress conditions (cv. Saida and breeding line Cam/B1), and two with low adaptability (cv. Express and breeding line Harmal), were identified. In addition, only changes in expression of the genes HvZIP1, encoding a b-ZIP-type transcription factor, and Hsdr4, encoding a protein of unknown function, were shown to be linked with adaptability of barley to water deficit. In summary, physiological and molecular data revealed large, stress-level-dependent differences between the barley cultivars and breeding lines tested in their response to water deficit.

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1. Introduction

Plants often experience periods of soil and atmospheric water deficit during their life cycle that impair morphological, physiological, biochemical and molecular processes resulting in growth inhibition. Fluctuations in water availability affect the cultivation of most crop plants causing yield instability and loss. It is thought that about 28% of the Earth's land is too dry for crop production (Bray, 2004). To be able to cultivate such land, development of crop plants with higher tolerance to drought and better adaptation to drought-prone environments, or plants with increased water use efficiency, is needed. This represents a significant challenge for

plant breeders and researchers, but will be required in the face of increasing pressure on food resources (Ceccarelli et al., 2010).

Plants have evolved many strategies to maintain growth when water availability is restricted or unpredictable. One adaptive strategy to water scarcity is the improvement of water uptake. Accumulation of compatible solutes and mineral nutrients in plants during water-deficit stress helps to maintain turgor, metabolic activity and water uptake under conditions of decreasing soil water potential (Hummel et al., 2010).

Stomatal closure is part of an early response to drought that reduces water loss: leaf water status is dependent on stomatal conductance and transpiration. It is noteworthy that stomata are able to close in response to drought before any change in leaf potential or relative water content is detectable (Flexas and Medrano, 2002; Chaves et al., 2003). In addition, stomatal regulation responds to a complex interaction of internal and external factors



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(Brodribb and Holbrook, 2003; Lazaridou and Noitsakis, 2005) and is also accompanied by a consequent reduction of photosynthetic rate. The effects of water deficit on photosynthesis are either direct, resulting in diffusion limitations through the stomata and the mesophyll, and in alterations in photosynthetic metabolism, or secondary, such as the oxidative stress arising from the superimposition of multiple stresses (Flexas and Medrano, 2002; Chaves et al., 2009; Lawlor and Cornic, 2002). A decline in PSII quantum yield during leaf drying occurs at a lower water potential than stomatal closure (Brodribb and Holbrook, 2003; Lawlor and Cornic, 2002).

The relationship between above-ground dry matter and water used during the growth period, including water lost through transpiration and evaporation from the soil, defines water use efficiency (WUE) (Hatfield et al., 2001; Howell, 2001; Rytter, 2005), and is a measure of potential yield under restricted or unpredictable water availability (Blum and Gerig, 2005). However, other plant characteristics, such as leaf size, structure and orientation may also affect WUE. In addition, climatic factors such as rainfall distribution, vapor pressure deficit of the air, and CO₂ concentration (Nielsen et al., 2005; Da Costa and Huang, 2006), together with soil factors such as soil water content, infiltration rates, soil surface features, water movement, SWC availability, impedance of root penetration and nutrient status, also contribute to WUE values (Johnson and Asay, 1993; Yu et al., 2005).

The response to drought conditions is highly complex and is the result of the coordination of molecular, physiological, biochemical and metabolic adjustments at the cellular and whole plant levels. which enable survival under stress conditions. Plants have evolved both mechanisms to perceive environmental stress signals and also signal transduction pathways that induce transcriptional regulatory networks. In turn, these networks trigger expression of appropriate genes, the protein products of which lead to the development of protective and adaptive mechanisms (Bartels and Sunkar, 2005). Many drought-inducible genes with various functions have been identified by molecular and genomic analyses in Arabidopsis, rice, and other plant species, including genes encoding signal transduction and transcriptional regulatory components. For example, members of the DREB/CBF, MYB, bZIP, and zinc-finger families of transcription factors have well-characterized roles in the regulation of plant stress responses (Bartels and Sunkar, 2005; Hu et al., 2010; Yamaguchi-Shinozaki and Shinozaki, 2006; Nakashima and Yamaguchi-Shinozaki, 2006; Umezawa et al., 2006; Shinozaki and Yamaguchi-Shinozaki, 2007). Furthermore, many genes encoding proteins with a putative role in drought tolerance, such as ion transport (uptake, extrusion and sequestration) and membrane stabilization, or governing the accumulation of osmoprotectants (proline, glycine betaine, sugars), have been identified recently (Hummel et al., 2010; Bartels and Sunkar, 2005; Bray, 2002; Guo et al., 2009; Verslues and Bray, 2006). The contributions of some of these genes – encoding LEA proteins, enzymes for osmolyte biosynthesis and detoxification enzymes - to drought tolerance have been demonstrated by manipulating their expression in transgenic plants (Umezawa et al., 2006; Xu et al., 1996; Cushman and Bohnert, 2000; Laporte et al., 2002; Abebe et al., 2003; Zhang et al., 2004; Brini et al., 2007).

Barley is a one of most important cereal crops grown in Europe, the Middle East, North and South Africa and Asia, where it often experiences seasonal water deprivation or permanent drought conditions that affect yield productivity (Ceccarelli et al., 2007). As reported (Shakhatreh et al., 2001; Ceccarelli et al., 2004), the final yield of barley productivity is dependent on water supply, and it is more adversely affected when drought is imposed at the pollination and flowering stages, rather than at the vegetative or seed filling stages (Ceccarelli et al., 2007). Increasing drought tolerance and yield stability during water scarcity is therefore an important aim for barley breeders, and an understanding of drought-tolerance genes should enable the use of genetic and genomic approaches towards this goal. High-throughput screening techniques such as microarray analysis have been used to identify the genes that respond to drought and other stresses in barley (Talamè et al., 2007: Ozturk et al., 2002: Ueda et al., 2004: Walia et al., 2006: Guo et al., 2007a), for example, after imposing a short period of dehydration shock (Ozturk et al., 2002; Ueda et al., 2004), or after a longer period of water stress that corresponds more closely to field conditions, where the effects on both seedling (Talamè et al., 2007) and reproductive development (Guo et al., 2009, 2007b) have been examined. However, with high-throughput screening data from only a single genotype, it is difficult to separate drought tolerance from drought-responsive genes. The situation is clearer when two barley genotypes differing in drought tolerance are compared, allowing seventeen genes that are more abundantly expressed in the drought-tolerant genotype to be identified in one study (Guo et al., 2009). Indeed, Baum et al. (Baum et al., 2007) reported that natural genetic variations in drought tolerance in barley species and cultivars may contribute to increased yield and yield stability under drought conditions, and that these genetic variations could be introgressed into improved varieties.

The impact of the various physiological, metabolic and biochemical characteristics on drought tolerance differs from species to species and depends on the developmental phase of the life cycle, and on the stress intensity and its duration (Szira et al., 2008). It is therefore difficult to select characteristics that unequivocally define plant drought tolerance, and which result in yield stability under drought conditions. Nevertheless, a detailed comparison of relevant characteristics under drought conditions among a number of closely related genotypes, during both vegetative and generative stages of development, should reveal crucial relationships between physiological traits and the level of drought tolerance and adaptive ability to the stress.

In the study presented here, we investigated physiological and metabolic changes, together with the expression profile of genes reported to be associated with the barley response to water deficit (LEA genes, NHX1, Hsdr4, BLT101 and genes encoding transcription factors HvDREB1, HvABF1, HvABI5 and HvZIP1) in seedlings of nine barley genotypes (representing European and Syrian cultivars and breeding lines) experiencing progressive increase of soil-water deficit. After analysis using two-factor variance performed independently or jointly for the different characteristics, our data revealed that the genotypes exhibit individual responses to the stress, but that a few different homogenous groups can be distinguished at different levels of stress factor intensity, and that the composition of these groups depends on SWC. Two-factor analysis of variance of RWC, F_V/F_m and P_N performed jointly revealed interaction between the traits, and that the interaction changes according to the level of stress intensity. Overall, the data obtained allowed us to distinguish which barley genotypes showed higher or lower ability to adapt to the stress conditions imposed.

2. Materials and methods

2.1. Plant materials and growth conditions

Seeds of European barley cultivar (*Hordeum vulgare* L) varieties Georgie, Lubuski, Maresi, and Sebastian, Syrian cultivars Express and Saida, and breeding lines Cam/B1//CI 08887/CI 05761, Harmal-02//Esp/1808-4L and M. Dingo/Deir Alla 106, were surfacesterilized in 1.5% Javel for 5 min, and then rinsed with sterile water. Sterilized seeds were sown in sterile soil (sourced from an arable field and supplemented with $0.5 \times$ Murashine and Skoog Download English Version:

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