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Water relations, short-chain oligosaccharides and rheological properties in lettuces subjected to limited water supply and low temperature stress

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ABSTRACT

Reducing water consumption and increasing the quality of vegetables is a particularly high priority in agricultural production. Thus, we set out to analyze the effect of restricting the water supply on water relations, rheological properties, and the accumulation of solutes and protective fructooligosaccharides (FOS) and raffinose family compounds (RFOs) in lettuces grown under controlled greenhouse conditions. In addition, we analyzed whether water restriction can prevent senescence-related changes and overcome the stress imposed by subsequent exposure to low temperature. Lettuces var. Maravilla de Verano were grown under three different water supply regimes, well-watered (WW), moderate water deficit (MWD) and severe water deficit (SWD). Our results indicate that accumulated transpiration (AT) was higher in WW plants than in lettuces subjected to water deficit. The relative water content (RWC) was significantly influenced by a restricted water supply but not by additional low temperature stress. Water deficit caused a significant decrease in the amount of unfreezable water (Uw), determined calorimetrically, in association with a significant decrease in total water content (T_W). After the additional low temperature stress, there was no further drop in Tw, although a significant decrease in Uw was evident, mainly in SWD lettuces. A moderate water deficit enhanced nystose and kestopentaose accumulation. After imposing low temperature stress, MWD lettuces had a lower apparent viscosity, concomitant with an increase in firmness, fewer senescence-related changes and a sharp increase in raffinose. We conclude that moderate water limitation, improving the endogenous levels of FOS and reducing the cleavage of wall polysaccharides backbones, thus reducing viscosity and increasing firmness, could be useful to retain water inside cells, avoiding quality loss and increasing the capacity of the lettuce to resist low non-freezing temperatures.

1. Introduction

Water is a limited natural resource and consequently, there is increased pressure to optimize the efficiency of crop water use. Therefore, reduce water consumption in lettuces during growing is a challenge of special relevance (Gallardo et al., 1996; Tsabedze and Wahome, 2010). Apart from the implication of water supply on processes related to growth, productivity and biomass water plays a relevant role on the quality of horticultural crops (Jones and Tardieu, 1998) mainly in the case of lettuce, with 95% of water (Kim et al., 2016). Indeed, irrigation deficit preserved postharvest quality and shelf-life of fresh cut lettuces (Luna et al., 2012; Vickers et al., 2015). Thus, better insight into the impact of deficient irrigation on the water relations in growing lettuces in terms of water status, osmoprotection and rheological properties is needed. Furthermore, the fact that cold hardiness of a plant seems to be related to its ability to modify the amount and physical state of water (Yoshida et al., 1997) has prompted us to analyze the combined effects of a limited water supply and low temperature stress on water status in growing lettuces. So, an accurate measurement of water status is essential, and a considerable work has been done in this direction (Vertucci and Stushnoff, 1992; Wolfe et al., 2002; Romero and Botía, 2006; Singh et al., 2006; Barg et al., 2009). Indeed, we previously determined water status of fruit tissues and the properties of oligomers relating to water in terms of thermal analysis by differential scanning calorimetry (Goñi et al., 2011; Blanch et al., 2012). We reported that the content of unfreezable water, sometimes called "bound", meaning the amount of water in a system which does not freeze out as ice at subfreezing temperatures, decreased in fruit tissues during postharvest storage at severe low temperature. However, further work is needed to determine the relationships among water status, accumulation of hydrophilic compounds such as carbohydrates and structural changes in growing lettuces in response to limited water supply and low

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temperature stress.

Various molecular networks, signal pathways and biochemical processes are involved in drought and cold stress (Shinozaki and Yamaguchi-Shinozaki, 2000; Mahajan and Tuteja, 2005; Khan et al., 2016), some of which are involved with the accumulation of osmolytes. Osmoregulation is an important mechanism in plants to decrease the osmotic potential of their tissues through the active accumulation of organic ions or solutes, thereby maintaining a favorable water flow gradient from the soil into the roots under conditions of water deficit. Carbohydrates play important roles in osmoregulation, and FOS and raffinose-oligosaccharides (RFOs) have been associated with plant protection against several stresses, including water deficit (Pilon-Smits et al., 1999; Livingston et al., 2009; Oliveira et al., 2013; ElSayed et al., 2014; Sengupta et al., 2015). Moreover, these carbohydrates are functional food ingredients (Mussatto and Mancilha, 2007) and short-chain FOS with a low degree of polymerization (DP) have a higher water binding capacity in comparison with other sugars (Furuki, 2002; Blanch et al., 2012). However, FOS compounds are complex mixtures of isomers with different bonds between the monomeric sugar units and with different degree of polymerization that make difficult their characterization and quantification accurately. In the present work we have employed mass spectrometry (MS) to identify and analyze the accumulation of raffinose and short-chain FOS (DP3, DP4 and DP5) in lettuces. Furthermore, the relationship between stress protection and changes in the concentrations of low DP oligosaccharides or of specific isomers remains unclear. It was found that only 1-kestose significantly accumulated in response to low temperature in two cultivars of timothy, while neokestose, 6-kestose, nystose and raffinose did not accumulate in response to low temperature treatments in neither cultivar (Thorsteinsson et al., 2002). 1-Kestose, 6-kestose and 6G-kestose are the templates for further elongation that give rise to inulins, levans and neo-series fructans, respectively. We previously reported increased levels of inulin fructans (DP $<$ 6) in strawberries and table grape fruit subjected to beneficial high CO_2 treatment that prevents the structural changes induced by storage at suboptimal low temperatures, while neo-series were not involved (Blanch et al., 2011, 2012). With respect to RFOs, galactinol is the galactosyl-donor exclusive to raffinose synthesis and it increased in association with cold tolerance (Davik et al., 2013). However, no data are available on the behavior of galactinol, and raffinose in lettuce at different levels of water stress with or without further low temperature stress. Lettuce (*Lactuca sativa* L.) is one of the most popular cultivated vegetables in Spain, and the cultivar Maravilla de Verano belonging to the variety *capitata* is cultivated extensively in greenhouses. This lettuce is well appreciated and commercialized for consumption in salads, its crispness being one of the most desired sensory characteristics. Thus, textural and rheological properties of this variety acquire special relevance to determine its deterioration during growing. Furthermore, nutritional value of lettuces can be enhanced by manipulating growing conditions (Baslam and Goicoechea, 2012; Baslam et al., 2013), but the effect of water reduction supply on FOS, oligomers with benefits for plants and humans (Ritsema and Smeekens, 2003), is still unknown.

Accordingly, the aims of this work were: 1) to analyze the impact of water deficit, as well as the combination of water deficit and low temperature stress, on water relations and how this relates to the rheological properties and accumulation of organic osmolytes, including FOS, raffinose and galactinol 2) to analyze whether the responses triggered by water deficit are enhanced or diminished when growing lettuces were subjected to additional low temperature stress. With respect to water relations we assessed the accumulated transpiration, relative water content (RWC), unfreezable and freezable water (Uw and Fw) content. The FOS with different DPs, and raffinose and galactinol, were characterized and quantified in lettuce by mass spectrometry. Rheological properties, chromatic characteristics and changes in chlorophylls and carotenoids in Maravilla de Verano lettuces were also determined.

2. Materials and methods

2.1. Plant material

Seeds of Maravilla de verano (*Lactuca sativa* L. var. *capitata*) were sown in Petri dishes and maintained under conditions of darkness for 8 days. The seedlings were then planted in 1 L plastic pots (40 cm top diameter, 15 cm of bottom diameter and 20 cm high), containing a mixture of peat/perlite (blond peat 45%, black peat 50% and perlite 5%). Three days after sowing (DAS), the pots were restricted to only one lettuce plant, that which exhibited the best physical appearance. Plants were watered every two days until the 17th DAS when the imposition of water deficit experiments started. As such, the same amount of water was given to each pot (0.5 L per pot) and after 45 min, when all the water had percolated, this process was repeated twice. Lettuces were grown in a greenhouse at 20 °C day/night temperature and 60–85% relative humidity, and received natural day light supplemented with irradiation from fluorescent lamps (Philips Master TL-D 58W, Holland) that provided a 12060 Lux luminous flux during a 16 h photoperiod. To minimize the effects of intra-chamber environmental gradients, the pots were repositioned randomly on the benches every watering day. Water deficit was imposed by ceasing irrigation in two lots of twelve plants each. Three different conditions were imposed: the controls were kept as well-watered (WW) and they were watered to field capacity, according to the water loss by plant transpiration (determined gravimetrically) until the end of experiment; for moderate water deficits (MWD), the pots were not watered for 9 days to achieve 69–70% of the initial pot weight; severe water deficit (SWD) was established by not watering the pots for 16 days, reaching 64–65% of the initial pot weight. The additional low temperature stress was imposed in six pots for each water supply condition by storage in a cold chamber for 7 days at 0 °C $\pm$ 0.5 °C. Each pot was put in individual 20 L capacity cabinets that permit a relative humidity of 95–98% to be reached and they were not watered throughout the low temperature stress experiment. Six plants per treatment were sampled on each day. In total, 6 different treatments were employed: control, WW and WW combined with low temperature (WW + LT); MWD and MWD combined with low temperature (MWD + LT); and SWD and SWD combined with low temperature (SWD +LT). At the end of each individual treatment and after the combined experiment, all the leaves were collected. The measurements of RWC, Uw and texture were performed always on the third leaf sampled from the rosette and for each sampling day and treatment, 18 leaves from 6 different pots were used. The rest of the leaves were divided into two groups, a part of the fresh material was pressed to obtain raw lettuce juice and used to determine viscosity, total soluble solids (TSS) and color. The remaining leaves material was frozen in liquid nitrogen and stored at −80 °C until use.

2.2. Water status determination

The total water (Tw), expressed relative to the dry weight, was determined as:

$$Tw\ (\%) = 100\ [(PF\text{-}PS)/(PS)]$$

The relative water content (RWC) was determined by gravimetric methods, according to the equation:

$$RWC\ (\%) = 100\ [(PF\text{-}PS)/(PT\text{-}PS)]$$

where PF = fresh weight of the sample; PS = dry weight of the sample and PT = turgid weight.

Once cut and weighed, the leaf was split and placed for 24 h into a plastic tube with deionized water at 4 °C in a dark chamber. After 24 h, the leaf was weighed again to obtain the turgid weight and the dry weight of the leaf was then obtained after 48 h in an oven at 80 °C.

The accumulated transpiration (AT) per pot was calculated by

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