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ScienceDirect

Environmental and Experimental Botany 60 (2007) 484–494

Environmental and Experimental Botany

www.elsevier.com/locate/envexpbot

Effect and after-effect of water stress on the distribution of newly-fixed ^{14}C-photoassimilate in micropropagated apple plants

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Received 14 March 2006; received in revised form 20 December 2006; accepted 2 February 2007

Abstract

The effect and after-effect of water stress on the distribution of photoassimilate, fixed at different times during and after water stress, were investigated in one-year-old micropropagated 'Gala' apple plants (*Malus domestica* Borkh.) by feeding mature leaves with $^{14}CO_2$. Plants grown in Hoagland's nutrition solution were subjected either to water stress at moderate intensity, induced by polyethylene glycol (PEG6000), for 15 days (prolonged water stress, PWS) or for 3 days, and then transferred to the solution without PEG for a recovery of 12 days (rewatering after water stress, RAWS), compared with plants under normal water conditions (CK). Three parameters were used to quantify the ^{14}C-photoassimilate distribution: specific radioactivity (SRA), which gives a measure of the actual amount of photoassimilates obtained by organs; the proportion distribution value, which reflects the relative distribution pattern among different organs within a given plant; the distribution coefficient (K), which gives an indication of the competitive sink strength, respectively. The carbon fixation rate and export capacity of source leaves were significantly reduced 24 h after initiating water stress, while the strength of sink organs (K) was increased in roots but decreased in other organs (shoot apex, phloem, xylem) with different response velocities. For the first 5 days of water stress, the enhanced sink strength of fine roots in PWS plants compensated for the reduced carbon availability due to the decreased total carbon fixation. As a result, fine roots obtained the same or even greater amounts of ^{14}C-photoassimilates (SRA) than those of CK plants, but the compensatory effect became insufficient as water stress continued. The rapid decrease in the distribution parameters of shoot apexes under water stress indicates that shoot apexes are highly sensitive to water stress. The shift of ^{14}C-photoassimilates from above-ground to the roots, caused by the sensitivity of shoot apexes and the enhanced sink strength of roots under water stress, should be advantageous to maintaining root growth and tolerance to water stress. Upon rewatering, 5- and 3-day lags occurred for the carbon fixation rate and export capacity, respectively, in order to complete recovery to pre-stress levels after removing water stress. In contrast, the percentage distribution values and SRA of ^{14}C-photoassimilates obtained by fine roots in RAWS plants did not return to the pre-stress levels, but instead remained at higher levels than those of CK plants during the rewatering stage. This greater investment of photoassimilate into the roots during the rewatering period might provide abundant carbon substrates and energy for the restoration of the metabolic activity of the roots. Apparently, there was also an after-effect of water stress on the other organ sink strengths, as revealed by the delayed recovery of SRA, the proportion distribution value and K in RAWS plants, depending on organ sensitivities to water stress. On the other hand, the percentage of ^{14}C-photoassimilate distributed to the phloem declined linearly with the increased retention in the labeled leaf, confirming that the phloem was just a pathway for transporting photoassimilate, and the higher K revealed during water stress did not signify a stronger sink strength of water-stressed phloem.

Keywords: After-effect; Apple; ^{14}C-Photoassimilate distribution; Rewatering; Source and sink; Water stress

1. Introduction

Photoassimilate is one of the major substrates for plant metabolism, and most of the biomass of fruit trees is derived from photosynthetically-fixed carbon (Jackson, 2003). The transport and distribution of photoassimilate between source and sink organs play an important role in vegetative growth, yield and fruit quality (Gifford et al., 1984; Li et al., 2001; Wu et al., 2002). Photoassimilates obtained by any particular sink organ depend on both source capability and competitive sink strength (Kozlowski, 1992; Marcelis, 1996; Minchin and Thorpe, 1996; Hellmann et al., 2000). The source and sink activities can be affected by many environmental factors, including water deficit (Davidson, 1969). Moreover, the response patterns of source or sink activities under water stress, up- or down-regulation, are associated

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doi:10.1016/j.envexpbot.2007.02.001

with the specific organs due to their different sensitivities to water stress (Hsiao and Xu, 2000). For the source leaves, water stress can lead to a reduced carbon fixation rate and eventually result in source limitation to plant growth (Kaiser, 1987). Previous results obtained with ^{14}C radioactive labeling techniques showed that the rate and relative amount of ^{14}C-photoassimilate exported out of source leaves decreased under water stress in apple (Li et al., 2003), cacao (Deng et al., 1990a, 1990b) and grapevine (Bota et al., 2004), but increased in maize (Trouverie and Prioul, 2006). Kinetic analysis showed that the amount of photoassimilates exported out of labeled source leaves was relatively constant as of 48 h after the photoassimilate was fixed, under water stress and well water conditions (Liu, 1997). As regards sink organs, the distribution pattern under water stress was reported to be typical of investing more photoassimilates into the trunk and roots but less into new shoots, young leaves, flowers and fruits, whereas the precise pattern depended on their relative competitive strengths (Westgate and Boyer, 1985; Staveley and Wolsteaholme, 1990; Steinberg et al., 1990; Daie, 1996). Since both source and sink activities dynamically change with the development of water stress, the distribution of photoassimilate fixed under different source activities might differ from one time to the next. However, most of the previous studies only concerned the distribution of photoassimilates fixed at a particular stage of water stress and gave no indication of the response sequence of newly-fixed photoassimilates in relation to developing water stress. The distribution pattern of newly-fixed photoassimilates as a function of the duration of water stress is still less clear, particularly regarding perennial fruit trees (Xu et al., 2003; Chai et al., 2004). Therefore, it would be of particular interest to understand the dynamic effect of water stress on the distribution of newly-fixed photoassimilates during a drought cycle.

The effect of water stress on photoassimilate distribution may persist for some time after water stress has been eliminated (i.e., after-effect of water stress), and the capacity of plant recovery from water stress has a substantial impact on plant survival and acclimation to water stress (Quick et al., 1992; Roe et al., 1995; DaCosta and Huang, 2006). However, very few experiments have been conducted on ^{14}C-photoassimilate distributions after removing water stress, and the available studies were confined to the redistribution of photoassimilate pre-fixed during water stress (Hall et al., 1988; Nandwal et al., 1996). In addition to the photoassimilates reserved during water stress (Hall et al., 1988; Nandwal et al., 1996; DaCosta and Huang, 2006), the photoassimilates fixed during rewatering might also be important in supplying substrates and energy to restored metabolism. Photosynthesis of source leaves returns to pre-stress levels, but the speed and degree of the recovery vary with plant species and the degree of water stress (Angelopoulos et al., 1996; Miyashita et al., 2005). Furthermore, the physiological status of source leaves, such as photosynthesis rate and sucrose accumulation concentration, that can be affected by water stress (Lo Bianco et al., 2000; Cui et al., 2004; Li and Li, 2005) has an important effect on the export rate of newly-fixed carbon (Fader and Koller, 1983; Leonardos et al., 1996; Grodzinski et al., 1998). The speed and degree of the recovery of carbon fixation by the source leaf might thereby also affect the photoassimilate distribution during rewatering. Hence, investigation of the recovery of source activities and the distribution of newly-fixed photoassimilates after water stress has been eliminated would help to clarify the after-effect of water stress on the growth of different organs and the relative importance of the newly-fixed photoassimilates in regulating the response of different sink organs after the elimination of water stress.

The effect of water stress on field-grown trees might be confused with other environmental factors such as high irradiance and high temperature (Beppu et al., 2003; Pastenes et al., 2005). Furthermore, field-grown fruit trees are often large-sized, making it difficult to experimentally manipulate large plants to obtain varying levels of water stress. This problem could be solved by using micropropagated virus-free plants with the same genetic background and uniform growth, grown in environmentally controlled plant growth chambers. Moreover, a well-controlled water stress environment can be obtained by using polyethylene glycol (PEG6000) to simulate water deficit in hydroponic systems (Lagerwerff et al., 1961; Li and Li, 2005). In the present study, we investigated the effect and after-effect of water stress on the distribution of photoassimilates that were fixed at different times during water stress and after water stress was eliminated. We hypothesized that the export from source leaves and the distribution among sink organs of the newly-fixed photoassimilates would vary in relation to the duration of water stress and rewatering due to the different responses of source and sink activities, shedding light on the role of photoassimilates in regulating the response sensitivity and growth of different sink organs of fruit trees under water stress and subsequent rewatering.

2. Materials and methods

2.1. Plant material and water treatments

One-year-old micropropagated ‘Gala’ apple (*Malus domestica* Borkh.) plants were pre-cultured hydroponically in plastic pots with 1/2-strength Hoagland’s nutrient solution for approximately 20 days to make sure that plant growth was restored and that new roots were formed, and then in full-strength Hoagland’s solution in an environmentally-controlled growth chamber. Nine aquarium pumps were used to provide sufficient oxygen to the nutrient solution and a black plastic film was used to cover the pots to prevent the exposure of roots to light. Water was added daily to compensate for solution loss through transpiration. The solution was completely changed at 3-day intervals throughout the experiments. The growing conditions in the chamber were as follows: a light intensity of 400 μmol m^{-2} s^{-1} at the top of the plants, provided by cool-white fluorescent lamps (14 h light/10 h dark), and 25 °C/20 °C (light/dark).

Plants with uniform vegetative growth were selected for the study, and the experiment was initiated when plants were about 25 cm in height. Two water stress treatments, prolonged water stress (PWS) and rewatering after water stress (RAWS), were performed by regulating the osmotic potential of the solution using PEG6000 (18% w/v) at moderate stress, compared with the control under normal water conditions (CK). Plants