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Research article

Variations in assimilation rate, photoassimilate translocation, and cellular fine structure of potato cultivars (*Solanum Tuberosum* L.) exposed to elevated CO₂



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ABSTRACT

Rising atmospheric CO₂ concentrations are expected to impact the productivity of plants. Cultivars demonstrate different responses to CO₂ levels, hence, screening and recognizing the cultivars with a higher capacity for translocation of photoassimilates would certainly be beneficiary. To investigate the interactive impact of enhancing CO₂ on physiology, cellular fine structure and photoassimilate translocation of micro-propagated potato plantlets, plantlets (cvs. Agria and Fontane) were grown under ambient (400 ppm) or elevated (800 ppm) CO2 concentrations in controlled environments. These high-yielding cultivars are widely cultivated in Iran and have a wide range of consumption as fresh marketing, French fries, and chips industry. Transmission electron micrographs showed an increase in the length, width, and area of chloroplasts. The number of chloroplasts per cell area was significantly increased in Agria at elevated CO2. Also, there was an increase in mitochondria number in Agria and Fontane. Chloroplast number and Np were increased by a similar magnitude at doubled CO₂, while, mitochondria number was increased greater than the leaf Rd enhancement at elevated CO₂. Elevated CO₂ increased net photosynthesis, dark respiration (Rd), and starch concentration in leaves. However, there was no dramatic change in the leaf soluble carbohydrate content in the plants grown at elevated CO₂, apart from at 75 days after transplant (DAT) in Agria. Net photosynthesis remained relatively unchanged for each cultivar throughout the growing season at elevated CO₂, which demonstrated more efficient CO₂ assimilation to ambient CO2. The greatest starch content was measured at 55 DAT that was accompanied by lower Np and higher Rd. The diminished starch content of leaves was contributed to a lower leaf dry matter as well as a greater tuber dry matter in Fontane. Our results highlighted a variation in photoassimilate translocation between these cultivars, in which Fontane demonstrated a more efficient photoassimilate translocation system at the elevated CO2.

1. Introduction

Several studies have revealed that photosynthesis and sink utilization of carbohydrates are highly coordinated (Ainsworth and Bush, 2011; Kaschuk et al., 2010; Paul and Foyer, 2001). It has been reported that 50–80% of the photoassimilates are transported from a mature leaf to fulfill demands of the non-photosynthetic organs of plants (Kalt-Torres et al., 1987). Elevated CO_2 effectively increases carbohydrate accumulation in leaves and influences biomass partitioning between the source and sink organs depending on plant species (Makino and Mae,

1999).

Elevated CO₂ has been proven that directly enhances photosynthesis of C₃ plants, which leads to increase carbohydrate production and respiratory pathway, plant growth, biomass, and yield (Ainsworth and Long, 2005; Hao et al., 2013; Reddy et al., 2010). The magnitude of stimulation of photosynthesis by CO₂ enrichment depends on environmental, experimental, and genetic factors, and vary with crops, cultivars and their developmental stages (Leakey et al., 2009). The yield of tuberous and root crops are amongst the most responsive species to elevated CO₂ (Kimball et al., 2002; Miglietta et al., 2000). Such

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indeterminate crops as potato (*Solanum tuberosum* L.) are expected to respond more strongly to higher levels of CO_2 than determinate crops such as cereals (Lawlor and Mitchell, 1991). Potato and other crops with large below ground sinks for carbon and apoplastic mechanisms of phloem loading are suggested to respond best to elevated CO_2 (Komor et al., 1996). Apoplastic loaders had more flexibility. Given that carbohydrate export was being managed with adjusting by membranebound certain transfer proteins (Amiard et al., 2005). Acclimation and up-regulation of photosynthetic capacity under a changing environment were confirmed in pea (*Pisum sativum*), spinach (*Spinacia oleracea*), and *Arabidopsis*, species with apoplastic loading (Adams et al., 2007).

A rise in the atmospheric CO₂ concentration stimulates carbohydrate production, phloem transport, as well as the growth of C₃ plants due to the limitation of the photosynthetic rate under the current level of atmospheric CO₂ (Lemoine et al., 2013). Although elevated CO₂ stimulates photoassimilation rate for a short period of time, long-term exposure to higher CO₂ levels has been reported to suppress photosynthesis by a greater accumulation of photoassimilates (Cheng et al., 1998). Plant grown at elevated CO₂ initially shows stimulated photosynthesis, but this enhancement often does not maintain due to photosynthesis acclimations to the new environment. In spite of the greater buildup of photoassimilates in leaves, e.g. soluble carbohydrates and starch, studies have also suggested that the translocation and utilization of photoassimilates could be promoted at elevated CO₂ (Grimmer and Komor, 1999; Teng et al., 2006). Chloroplasts temporarily accumulate excess photoassimilates as starch grains at elevated CO₂ (Wolfe et al., 1998), therefore, a balanced synthesis and translocation of photoassimilates is important if plant growth and yield is to be enhanced by higher CO₂ concentrations.

Elevated CO_2 can alter the structure of chloroplast and mitochondria (Griffin et al., 2001; Sharma et al., 2014; Sun et al., 2011; Wang et al., 2004). In general, a greater number and size of chloroplast, as the primary site for conversion of CO_2 into photoassimilates, have been reported in different plant species as a result of exposure to higher atmospheric CO_2 concentrations (Sinha et al., 2009; Wang et al., 2004). Wang et al. (2004) found that chloroplast number and photosynthetic rate were increased by a similar magnitude under elevated CO_2 in *Nicotiana sylvestris*, but, by doubling mitochondria number under such conditions, dark respiration increased only by 48%. Less increase in dark respiration compared with mitochondrion numbers have been also reported in earlier studies (Griffin et al., 2001; Wang and Curtis, 2002).

Besides an increase in the number of cellular fine structures, the size of these organelles has also been reported to be affected by elevated CO_2 concentrations (Teng et al., 2006). Xu et al. (2012) concluded that an increase in chloroplast size had been mostly attributed to an increase in the chloroplast width than the length. This increment has been reported to be as a result of larger starch grains accumulated in chloroplast at elevated CO_2 (Madsen, 1971; Teng et al., 2006). However, an increase in both length and width of chloroplast in *Brassica juncea* and *Solanum tuberosum* grown at elevated CO_2 have also reported (Sun et al., 2011; Uprety et al., 2001). An increase in the number and size of starch grains in chloroplast of cucumber (Wei et al., 2002), *Arabidopsis thaliana* (Duan et al., 2014; Teng et al., 2009), *Nicotiana sylvestris* (Wang et al., 2004), and other plants grown at elevated CO_2 have also reported (Hao et al., 2013; Sinha et al., 2009).

Given that applying higher levels of CO_2 to increase yield and quality of agricultural crops has received much attention amongst commercial growers (Li et al., 2013), identifying the sensitive physiological and biochemical processes of plants to elevated atmospheric CO_2 is critical. Agria and Fontane have been widely consumed and are among the most grown cultivars in Iran. A great tuber dry matter of these high-yielding cultivars makes them valuable for industrial consumption, such as French fries and chips production. Understanding how elevated CO_2 affects minituber production would generate valuable information for commercial growers to choose cultivars better responses to such conditions. There may be some experimental evidence to assess the genetic variation available for improving responsiveness to elevated CO_2 (Ainsworth et al., 2008). Plant species and genotypes significantly vary in the response to environmental conditions, external treatments, and elevated CO_2 (Ahmadi Lahijani et al., 2018; Tang et al., 2013). Enriched CO_2 tends to enhance plant growth and reproduction, though, recognizing intraspecific variation in response to elevated CO_2 can lead to identify the cultivars better respond to such conditions (Lindroth et al., 2001). Manipulation of the existing species, e.g. overexpression of *Suc* transporters in sink cell, would enhance sink demand and photoassimilates export (Ainsworth and Bush, 2011). However, screening and recognizing the cultivars with a higher capacity for translocation of photoassimilates would certainly be simpler and cost-effective.

Given that earlier research have discovered a dramatic rise of mitochondrion numbers in an extensive variety of species at elevated CO₂ (Griffin et al., 2001; Robertson and Leech, 1995), we hypothesized that elevated CO₂ could further rise mitochondrion number in Agria and Fontane leaves. Dark respiration is an important component of the carbon cycle, hence, it is significant to a better understanding of respiratory response to elevated CO₂ and how this is related to cellular fine structural changes at elevated CO₂ (Schimel, 1995). Yet, there is no research concerning the effect of elevated CO₂ on the leaf photosynthetic physiology, biochemistry and ultra-structure, and their relationship with growth and dry matter partitioning in micro-propagated potato plantlets. This study evaluated differences between photosynthetic efficiency and the amount of starch accumulated in chloroplasts of potato cultivars, Agria and Fontane, at elevated CO₂. We also examine the simultaneous trend in chloroplast numbers and photosynthetic rates in addition to mitochondrion numbers and leaf dark respiration rates in response to increased CO₂. In addition, whether there are differences between the cultivars in term of translocation of photoassimilates out of leaves were also evaluated.

2. Materials and methods

2.1. Plant materials and growth conditions

Virus-free potato plantlets (Solanum tuberosum L. cvs. Agria and Fontane) were transplanted in a sterile medium containing a mixture of perlite-coco peat (1:1, v:v) in plastic pots (diameter, 15 cm; depth, 30 cm; one per pot). The plantlets were derived from micro-propagated shoot tips grown in agar culture plates containing the Murashige and Skoog medium supplement with 3% sucrose (Yekta Seed Technology Company). The environmental conditions inside the chambers (Conviron, Winnipeg, Canada) were as follow: 400 μmol photons m^{-2} s^{-1} photosynthetic photon flux density (PPFD) on the leaf surface supplied by fluorescent/incandescent lamps, 12h photoperiod, 24/ 16 °C day/night air temperature, and 50 \pm 5% relative humidity. Nine uniform single plantlets of each cultivar (five cm in shoot length) from the first day of transplanting were subjected to 400 \pm 10 µmol mol⁻¹ or 800 \pm 10 µmol mol⁻¹ as ambient and elevated CO₂, respectively. The CO_2 -enriched air (a mixture of ambient air with commercial CO_2) from a compressed gas cylinder was injected into the chamber at a flow rate of $1 \, l \, min^{-1}$, which was continuously monitored by a calibrated infrared gas analyzer (High-performance CO₂ meter, 77535, China). All plants were watered daily to prevent water stress and fertilized with the standard Hoagland's solution in five-day intervals (Hoagland and Arnon, 1950). The experiment was carried out as a completely randomized design in a factorial (two cultivars and two CO₂ concentrations) scheme with three replications.

2.2. Gas exchange measurements

Net photosynthetic rate (Np) and leaf dark respiration (Rd) were measured using a portable photosynthesis system (HCM-1000, Waltz, Germany) on the youngest mature leaves of each plant at 35, 55, and 75 Download English Version:

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