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Effect of CO_2 Enrichment on Gas Exchanges, Biochemical Traits, and Minituber Yield in Potato (*Solanum tuberosum* L.) Cultivars

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ABSTRACT

Micro-propagated potato plantlets (*cvs.* Agria and Fontane) were grown in growth chambers under controlled conditions to determine the effect of different levels of CO_2 concentrations (400 *vs.* 800 μmol mol^{-1}) on physiological and biochemical traits and yield of minitubers, at the Ferdowsi University of Mashhad, in 2015. Irrespective of the cultivar, the elevated CO_2 significantly increased Net photosynthesis (Np) and leaf Dark Respiration (R_D) compared to the control at 34 and 57 days after transplanting. Higher *Np* under the elevated CO_2 resulted in a higher accumulation of leaflet starch and soluble sugar content. The elevated CO_2, compared to the ambient, induced allocation of more dry matter to the underground parts, especially tubers. CO_2 Enrichment did not significantly affect the number of tubers and mean tuber weight, however, the elevated CO_2 increased yield of Agria and Fontane by 17 and 39%, respectively. The yield of Fontane was increased more than Agria when exposed to elevated CO_2, mainly due to greater mean tuber weight than tuber number. The number of large size tubers increased under elevated CO_2. The results showed that the greater mean tuber weight might affect tuber yield more than the number of tubers. Our findings suggest that rising levels of CO_2 in minituber production systems could be beneficial to improve productivity and tuber yield.

Keywords: Carbohydrate, Dark respiration, Dry matter partitioning, Photosynthetic rate, Starch.

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INTRODUCTION

Potato (*Solanum tuberosum* L.), with annual production of 382 million tons and 20 t ha^{-1} yield, is ranked as the fourth important crop in the world (FAOSTAT, 2014). Potato is mostly propagated vegetatively through tubers, which decrease the seed quality by continued propagation mainly due to degradation in health status. Viral diseases are a major limiting factor in potato production. Virus free micro-propagated plantlets can produce disease-free seed potato, preventing yield losses (Struik and Wiersema, 2012). Minitubers are healthier potatoes with a faster multiplication rate for a greater tuber yield (Sharma and Pandey, 2013).

For many decades, extensive researches have been carried out on improvement of agronomic and physiological performance and, consequently, increasing crop yield (Ahmadi Lahijani *et al.*, 2018; Shahkoomahally and Shahkoomahally, 2017; Skraly *et al.*, 2018; Struik and Wiersema, 2012). Applying supplemental CO_2 to increase yields and quality of agricultural

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crops is becoming common among commercial growers (Li *et al.*, 2013). Due to the limitation of photosynthesis of C_3 plants under the present concentration of atmospheric CO_2, higher levels of CO_2 will increase both carbon fixation and plant biomass production (Aranjuelo *et al.*, 2005).

Increasing atmospheric CO_2 directly enhances photosynthesis in C_3 plants leading to increase in leaf sugar and starch content (Ainsworth and Lemonnier, 2018). Rising CO_2 concentration affects plants at the levels of molecular, developmental, and physiological functions. Changes in the plant functions may affect their ability to capture resources (e.g. leaf size or leaf number), and also alter the resource allocation among different parts, which may significantly influence yield and production (Gray and Brady, 2016).

Increased potato tuber yield due to elevated CO_2 has been reported in diverse studies (Finnan *et al.*, 2005; Högy and Fangmeier, 2009). Lawlor and Mitchell (1991) found that indeterminate crops like potato are supposed to respond more strongly to higher levels of CO_2 compared to determinate crops such as cereals. Potato and other crops with large belowground sinks for carbon and apoplastic mechanisms of phloem loading were suggested to highly respond to elevated CO_2 (Komor *et al.*, 1996). Finnan *et al.* (2005) attributed the increase in the tuber yield at elevated CO_2 to not only the higher tuber number and individual tuber weight but also a combination of both.

Elevated CO_2 stimulates the production of above- and belowground biomass, but their magnitude are varied with cultivar, plant species, growing condition, and agronomic practice (Finnan *et al.*, 2005; Reddy *et al.*, 2010). Several studies in potato reported that elevated CO_2 concentration enhanced greater dry matter partitioning in the tubers to aboveground parts. (Chen and Setter, 2012; Fleisher *et al.*, 2008a; Fleisher *et al.*, 2008b). Cell division and expansion of sink organs are highly responsive to the higher levels of CO_2 concentrations, hence, stronger sinks attract more assimilates and, consequently, enhance tuber size and tuber number (Chen and Setter, 2012).

Leaf dark respiration is a determinant factor controlling the growth and maintenance of plant tissues (Li *et al.*, 2013). However, the effect and mechanism of elevated CO_2 on the leaf dark respiration is not fully elucidated. Previous findings reported the effects of CO_2 elevation on respiration rate (Gomez-Casanovas *et al.*, 2007; Leakey *et al.*, 2009; Long *et al.*, 2004). Most of up- or down-regulation of respiration under elevated CO_2 conditions depends on developmental stage, plant species, growth conditions, and gas exchange measurement errors (Long *et al.*, 2004). Li *et al.* (2013) reported that higher dark respiration of tomato leaves under a higher concentration of CO_2 was due to greater content of proteins, carbohydrates, and transcripts involved in the glycolysis pathway, tricarboxylic acid cycle, and mitochondrial electron transport energy metabolism.

The number of tubers and mean tuber weight are of particular importance in minituber production systems. Although previous researches have reported the positive effects of elevated levels of CO_2 on photosynthetic rate, growth, and yield of potato plants, no reports documented the effect of elevated CO_2 concentrations on the respiratory pathway and its relationship with productivity and tuber yield of micro-propagated potato plantlets. The present work aimed to assay the potential positive effects of elevated level of CO_2 on physiological and biochemical traits, minituber production, and dry matter partitioning in two cultivars of potato plantlets (*cvs*. Agria and Fontane).

MATERIALS AND METHODS

Plant Materials and Growth Conditions

Uniform potato plantlets (*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) in the controlled environment chambers (Conviron, Winnipeg, Canada) at Ferdowsi University of Mashhad, in 2015. Plantlets were derived from *in vitro* micro-propagated shoot tips grown in agar culture plates containing the Murashige and Skoog medium supplemented with 3% sucrose at Yekta Seed Technology Company, Mashhad, Iran. The plantlets were grown inside the chambers at Photosynthetic Photon Flux Density (PPFD) of 400 µmol photons m^{-2} s^{-1} on the leaf surface supplied by fluorescent/incandescent lamps, photoperiod 12/12 (h) (day/night), day/night air temperature 24/16°C, and relative humidity of 50/60% (day/night). The plantlets were separated into two groups. Each group (including 9 pot per cultivar) were placed into a separate growth chamber deferring in CO_2 concentrations (400±10 and 800±10 µmol mol^{-1}) as "ambient" and "elevated" CO_2, respectively. The pots were subjected to CO_2 concentrations from the first day of transplanting. The CO_2-enriched air (a mixture of ambient air with commercial CO_2) from a compressed gas cylinder was injected into each chamber at a flow rate of one L min^{-1}, which was continuously monitored by a calibrated infrared gas analyzer (High-performance CO_2 meter, 77535, China). All plants were watered daily to prevent water stress and were fertilized with the standard Hoagland's solution every five days (Hoagland and Arnon, 1950).

Sampling

Gas exchange variables were measured from the third fully expanded upper leaves at 34 (stolonization stage) and 57 (tuberization stage) Days After Transplanting (DAT). The same leaves were collected for the metabolic assays at the same stages.

Measurements of Gas Exchange Variables

Fully expanded leaves were enclosed in a gas exchange leaf chamber using a portable photosynthesis system (HCM-1000, Waltz, Germany). Net photosynthesis was estimated at a PPFD of 1,500 µmol m^{-2} s^{-1} (Wang *et al.*, 2004). Leaves were equilibrated for 5 minutes at 1,500 µmol m^{-2} s^{-1} PPFD before each measurement. The leaf temperature, relative humidity inside the cuvette, and leaf-to-air vapor pressure deficit were set at 25°C, 50%, and 50 Pa kPa^{-1}, respectively. The leaf dark respiration was obtained through averaging three CO_2 efflux rates at zero PPFD for each plant at the end of the daily dark period from 05:00 to 07:00 hours. Three leaflets per replication were analyzed (n= 9).

Leaf Soluble Carbohydrates and Starch Content

To assay the total Soluble Carbohydrates of leaves (SC), the method of Dubois *et al.* (1956) was used. A sample of 100 mg leaf fresh weight was homogenized in 70% methanol using a mortar and pestle. Total soluble carbohydrates content of leaflets were measured by a glucose standard curve. The method of Schlegel (1956) was applied to assay the Starch content of leaves (ST). Residuals of the soluble carbohydrates experiment were rinsed three times using perchloric acid. Absorbance was spectrophotometrically recorded at 485 nm. The starch content of leaves was determined through a glucose standard curve.

Crop Harvest and Growth Parameters

Plants were harvested 90 DAT, rinsed and separated into stems, leaves, roots, and tubers. Total green Leaf Number (LN), and number of tubers per plant (Katny *et al.*, 2005) were counted. Mean Tuber Weight (MTN) and tuber Yield per plant (Y) were also measured. The harvested tubers were classified based on smaller diameter in three size categories (< 15, 15-25, and > 25 mm). The above- and below-ground parts of the plants were weighted and then dried out at 75 °C until constant mass and weighed. The total plant DM was calculated by adding the values obtained for roots, shoots, and tubers. Dry matter partitioning among the plant parts was calculated as a percentage of DM accumulated in the leaves, stems, roots, and tubers to the total plant DM. Leaf Area (LA) was measured using an automatic leaf area meter (Li-3100, LI-COR, Lincoln, NE).

Statistical Analysis

The experimental design was a completely randomized design in a factorial (two cultivars and two CO_2 concentrations) scheme with three replications. Data were presented as the mean ± standard deviation. Statistical analyses were performed by Analysis Of Variance (ANOVA) in SAS software. Differences between treatment means were determined by Fisher's Least Significant Differences (LSD) test at 0.05 probability level.

RESULTS

Gas Exchange Variables

Elevated CO_2 concentration increased *Np* and R_D of cultivars at stolonization and tuberization stages (Table 1). A greater *Np* at 34 DAT compared with 57 DAT was recorded, but R_D was greater at 57 DAT in both cultivars (Table 2). Net photosynthesis rate of Agria increased more than Fontane at both measurement dates when exposed to the elevated CO_2. Elevated CO_2 increased *Np* of Agria by 104 and 84% at 34 and 57 DAT, respectively, while the increases in Fontane were 51 and 12% at similar stages, respectively, compared with the ambient (Table 2).

There was no significant difference in R_D between cultivars at 34 or 57 DAT, but elevated CO_2 significantly influenced R_D at both stages (Table 1). Elevated CO_2 increased R_D of Agria at 34 and 57 DAT by 177 and 5%, respectively, while, these were 192 and 8% in Fontane at the same stages, respectively. Both at ambient and elevated CO_2, Agria showed a higher R_D at 34 DAT than 57 DAT. This superiority reversed in Fontane, with higher R_D under both CO_2 conditions at 57 DAT. (Table 2).

Leaf Soluble Carbohydrates and Starch Content

There were no significant differences between the cultivars in SC either at 34 or 57 DAT (Table 1). Despite producing higher values of SC at elevated CO_2, no statistical difference was observed between the CO_2 treatments (Table 3). Exposure to elevated CO_2 increased ST of Agria at both measurement times more than Fontane. Elevated CO_2 increased ST of Agria by 37 and 78% at 34 and 57 DAT, respectively,

Table 1. ANOVA results of gas exchange and chemical parameters at 34 and 57 days after transplanting.

Variables	Cultivar (V)	CO_2 concentration (C)	V×C	r^2	*CV*
34 DAT[a]					
Leaf Soluble sugars (SC)	NS	NS	NS	0.48	8.1
Leaf Starch content (ST)	NS	*	NS	0.68	13.2
Net photosynthetic rate (Np)	**	**	**	0.96	11.2
Dark Respiration (R_D)	NS	**	NS	0.61	16.4
57 DAT[a]					
Leaf Soluble sugars (SC)	NS	NS	NS	0.29	10.6
Leaf Starch content (ST)	**	**	*	0.96	7.7
Net photosynthetic rate (Np)	**	**	NS	0.94	9.8
Dark respiration (R_D)	NS	**	NS	0.81	16.4

* Significant at $P< 0.05$, ** Significant at $P< 0.01$, NS: Not Significant, LSD test. [a] DAT: Day After Transplanting, 34 DAT (Stolonization stage), 57 DAT (Tuberization stage).

Table 2. Effects of CO_2 levels on photosynthetic rate and dark respiration of potato cultivars at 34 and 57 days after transplanting.[a]

Treatment	*Np* (µmol m^{-2} s^{-1})		R_D (µmol m^{-2} s^{-1})	
	34 DAT	57 DAT	34 DAT	57 DAT
C1 AM	17.95±2.53	13.85±3.79	0.63±0.79	3.19±0.06
C1 EL	36.68±1.50	25.5±1.26	1.75±0.27	3.34±1.33
C2 AM	13.89±1.38	14.1±3.14	0.53±0.33	4.11±0.12
C2 EL	21±1.35	15.85±1.75	1.55±0.67	4.46±0.88

[a] Values are mean±*SD* of three replicates (n= 9). C1; Agria, C2; Fontane, AM; Ambient CO_2, EL; Elevated CO_2, *Np*; Net photosynthesis rate, R_D; Dark Respiration, DAT; Day After Transplanting, 34 DAT (Stolonization stage), 57 DAT (Tuberization stage).

Table 3. Effects of CO_2 treatments on leaf soluble sugar and starch content of potato cultivars at 34 and 57 days after transplanting.[a]

Treatment	Soluble carbohydrates (mg g^{-1} FW)		Starch (mg g^{-1} FW)	
	34 DAT	57 DAT	34 DAT	57 DAT
C1 AM	24.1±1.67	35.2±0.79	109.5±5.73	135.8±6.61
C1 EL	25.2±2.11	32.4±1.16	151.1±9.33	242.8±18.5
C2 AM	23.0±2.07	33.4±1.49	110.8±7.05	109.4±10.07
C2 EL	25.7±2.42	34.5±3.47	137.1±4.88	171.8±19.1

[a] Values are mean±*SD* of three replicates (n= 9). Symbols as defined under Table 2.

while the increases in Fontane were 24 and 57% at the similar stages, respectively, compared with the ambient.

Growth Parameters and Dry Matter Partitioning

Leaf, stem, and total dry matter of the potato plants were influenced by either cultivar or CO_2 concentration (Table 4). Plants grown at elevated CO_2 produced 33, 42, and 35% greater leaf, stem, and total shoot DM, respectively, compared with ambient CO_2 conditions (Table 5). Dry matter partitioning to different parts of the plants was influenced by cultivar and CO_2 (Table 4). Carbon dioxide enrichment enhanced allocation of DM to the underground parts, especially tubers, and decreased it to the aerial parts of the plants (Table 5 and Figure 1).

The increase in shoot DM of Fontane was greater than Agria at elevated CO_2, and Agria also gained more tuber DM (Table 5). While Fontane allocated more biomass to the roots at elevated CO_2, Agria greatly allocated biomass to the tubers (Table 5). Tuber DM was greatly increased in Agria and Fontane under elevated CO_2 compared with the control. However, Fontane produced greater tuber dry matter than Agria either at ambient or elevated CO_2 (Table 5). Exposure to elevated CO_2 decreased shoot DM allocation in Agria and Fontane by 17 and 12%, respectively, compared to the ambient. In contrast, DM of the underground parts of Agria and Fontane increased by 13 and 7%, respectively (Figure 1).

The analysis of leaf area per plants revealed that there was a significant increase in the leaf area associated with higher level of CO_2 (Table 4). Leaf areas of Fontane and Agria increased by 31% and 12%, respectively, at elevated CO_2 compared to

Table 4. ANOVA results of growth parameters of potato cultivars.

Variables	Cultivar (V)	CO_2 concentration (C)	V×C	r^2	*CV*
Leaf Dry Matter (LDM)	**	**	NS	0.85	10.4
Stem Dry Matter (SDM)	NS	**	NS	0.74	14.4
Total Shoot Dry Matter (SHDM)	**	**	NS	0.89	8.5
Root Dry Matter (RDM)	**	*	NS	0.80	25.5
Tuber Dry Matter (TDM)	NS	**	NS	0.75	22.5
Total Dry Matter (TDM)	**	**	NS	0.85	15.2
Leaf Area (LA)	**	**	NS	0.88	9.1
Leaf Number (LN)	**	**	NS	0.95	5.1
Tuber Yield (Y)	NS	**	NS	0.80	18.5
Tuber number (TN)	NS	NS	NS	0.74	15.1
Mean Tuber Weight (MTW)	NS	NS	NS	0.71	24.5
Small tuber (< 15 mm)	NS	NS	NS	0.40	26.7
Average tuber (15-25 mm)	NS	NS	NS	0.52	19.4
Large tuber (> 25 mm)	NS	**	NS	0.68	14.1

*Significant at $P< 0.05$, ** Significant at $P< 0.01$, NS: Not Significant, LSD test.

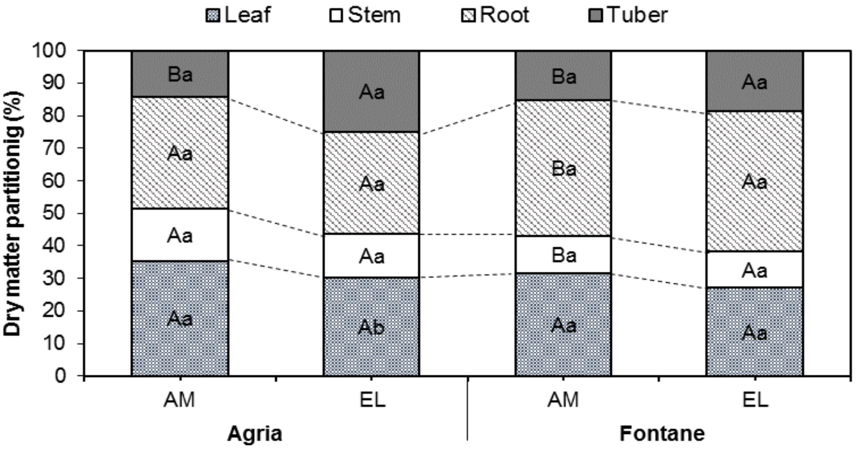

Figure 1. Effect of elevated CO_2 on dry matter partitioning of potato cultivars. AM: 400 ppm, EL: 800 ppm. Different lowercase letters indicate a significant difference between CO_2 levels for the same cultivar, whereas different uppercase letters indicate a significant difference between cultivars at the same CO_2 level, at P< 0.05, according to LSD test.

Table 5. Effects of CO_2 treatments on growth parameters of potato cultivars.[a]

Treatment	LDM (g plant^{-1})	SDM (g plant^{-1})	SHDM (g plant^{-1})	RDM (g plant^{-1})	TUDM (g plant^{-1})	TDM (g plant^{-1})
C1 AM	1.59±0.27	0.71±0.17	2.31±0.34	1.55±0.52	0.64±0.16	4.51±0.74
C1 EL	2.05±0.06	0.91±0.13	2.96±0.18	2.12±0.65	1.70±0.47	6.78±1.17
C2 AM	2.08±0.33	0.74±0.11	2.82±0.34	2.73±0.63	1.10±0.09	6.56±0.81
C2 EL	2.84±0.06	1.15±0.06	4.00±0.01	4.5±0.91	1.95±0.51	10.46±1.42

[a] The measurements were carried out when the plants were 90 days old. Values are mean±*SD* of three replicates (n=9). C1; Agria, C2; Fontane, AM; Ambient CO_2, EL; Elevated CO_2, LDM; Leaf Dry Matter, SDM; Stem Dry Matter, SHDM; Shoot Dry Matter, RDM; Root Dry Matter, TUDM; Tuber Dry Matter, TDM; Total Dry Matter.

the ambient (Table 6). The plants grown under elevated CO_2 conditions produced a higher number of leaves (Table 4). Fontane had a greater LN under both conditions, but elevated CO_2 increased LN of Agria greatly (Table 6).

Tuber Yield

Elevated CO_2 significantly stimulated the tuber yield per plant (Table 4). Fontane produced a greater tuber yield than Agria when exposed to elevated CO_2 (Table 6). Elevated CO_2 increased the yield of Agria and Fontane by 21 and 65%, respectively. There was no significant effect of higher CO_2 concentration on the TN and MTW of the plants (Table 4). Although insignificantly, a greater MTW was recorded at elevated CO_2 in Fontane compared with the ambient conditions (Table 6). Tuber number of Agria was increased (26%) more than Fontane (4%) under elevated CO_2 conditions, however, the change was not significant (Table 4). CO_2 enrichment significantly increased the proportion of large size tubers (> 25 mm) of the plants compared with the ambient conditions (Table 4). The percent distribution of medium size tubers (15-25 mm) was also higher in Agria at elevated CO_2 compared with the ambient conditions, although, the effect was not significant (Figure 2).

DISCUSSION

Photosynthesis of C_3 plants is not fully saturated at the current atmospheric levels of CO_2. Rising atmospheric CO_2 concentration has been elucidated to enhance the rate of photosynthesis and influences the growth and yield of C_3 plants (Reddy *et al.*, 2010). Our results revealed that *Np* was significantly stimulated in both cultivars of potato. Chen and Setter (2012) suggested that the availability of sufficient sink is important to increase the photosynthetic response of C_3 plants at elevated CO_2. Although there was no significant effect of elevated CO_2 on the number of tubers and mean tuber weight, the plants grown at elevated CO_2 produced slightly more tuber number and mean tuber weight, which could serve as a greater sink strength. The greater number of tubers increase sink strength, thereby, reducing the feedback inhibition of starch build-up on the photosynthetic rate. Finnan *et al.* (2005) stated that the tuberization process would be stimulated under elevated CO_2 conditions, and a greater number of tubers would increase the sink strength to attract more assimilates. Aien *et al.* (2014) also reported that the photosynthetic rate of two potato cultivars increased at 30 and 60 DAT under elevated levels of CO_2. They concluded that increase in the rate of photosynthesis under elevated CO_2 might be attributed to the higher number of tubers under such conditions.

Table 6. Effects of CO_2 treatments on yield, yield component, leaf area, and leaf number per plant of potato cultivars.[a]

Treatment	Yield (g plant^{-1})	Mean tuber weight (g)	Tuber number (plant^{-1})	Leaf area (cm^{-2} plant^{-1})	Leaf number
C1 AM	10.0±1.87	3.8±1.00	2.6±0.57	399±49.4	15.7±0.75
C1 EL	12.1±3.12	3.7±1.28	3.3±0.32	449±15.2	17.7±0.39
C2 AM	9.3±1.33	3.7±0.24	2.5±0.40	510±8.66	22.4±0.80
C2 EL	15.4±2.01	5.9±1.32	2.6±0.35	671±10.6	26.1±0.23

[a] The measurements were carried out when the plants were 90 days old. Each value represents the mean±SD. C1; Agria, C2; Fontane, AM; Ambient CO2, EL; Elevated CO2.

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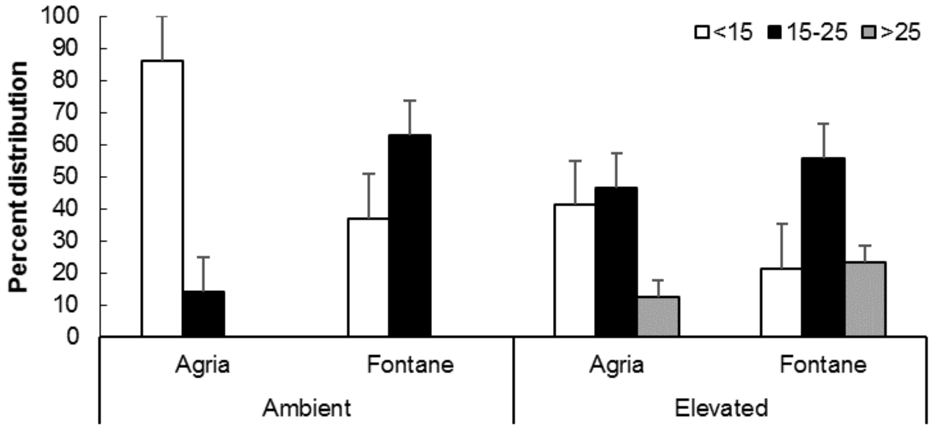

Figure 2. Percentage of the number of tubers produced per size category for different cultivars under ambient and elevated CO_2 conditions. Ambient; 400 µmol mol^{-1}, Elevated; 800 µmol mol^{-1}, Size category (mm). Vertical bar shows Standard Error of the difference (SE).

Measurement of the leaf dark respiration revealed that the respiratory metabolism was up-regulated under elevated CO_2. The metabolic analysis showed that starch and soluble carbohydrates content increased under elevated CO_2. Because of the enhanced photosynthetic rate at elevated CO_2, higher accumulation of carbohydrates might be a consequence of higher substrate availability to stimulate the respiratory pathway (Aranjuelo *et al.*, 2011; Aranjuelo *et al.*, 2006). Energy demand and substrate supply are able to control respiration rates, which indicates that plants regulate carbon and nutrients allocation to increase photosynthesis and growth (Gonzàlez-Meler *et al.*, 2009). A common consequence of growing plants at elevated CO_2 is a higher production of photoassimilates and a higher concentration of carbohydrates in the plant tissues (Kimball *et al.*, 2002). Li *et al.* (2013) also reported a significant increase in the leaf carbohydrate content and dark respiration in tomato plants when exposed to elevated CO_2. Higher leaf dark respiration because of greater leaf carbohydrate and starch content helps plants to meet energy demand for growth and maintenance. Carbohydrates play a vital role in starch biosynthesis and tuber growth and are known as the stimulators of tuber initiation (Ramawat and Merillon, 2013). An increase in carbohydrates content activate a number of genes involved in starch biosynthesis and increase the tubers capacity for storing more photoassimilates (Kloosterman *et al.*, 2005).

This study showed greater tuber yield in the plants grown under elevated CO_2 conditions. This is consistent with Fleisher *et al.* (2013) who found substantial stimulation in the tuber yield of potato exposed to elevated CO_2. Lawson *et al.* (2001), however, reported no significant effect of such conditions on the tuber yield. Numerous studies on the effect of elevated CO_2 on potato yield have reported an increase in the tuber number associated with a greater tuber yield (Aien *et al.*, 2014). However, in spite of increase in tuber yield, a decrease in the tuber number was also reported under higher CO_2 concentration (Finnan *et al.*, 2005; Finnan *et al.*, 2002). The results of the CHIP project showed that the increase in potato tuber number under elevated CO_2 was insufficient to quantify the tuber yield, therefore, mean tuber weight also contributes to increasing yield (Craigon *et al.*, 2002). In agreement with this, it was

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observed that the mean tuber weight was more stimulated than the tuber number when plants were exposed to a higher level of CO_2.

The results of our study showed that elevated CO_2 concentration increased the percent distribution of medium and large size tubers compared with the ambient conditions (Figure 2). The results are in agreement with Högy and Fangmeier (2009) who reported an increase in the size of individual tubers under elevated CO_2. They concluded that the stimulation of potato tuber yield in response to CO_2 enrichment was mainly due to increased growth of the formerly initiated tubers than an increase in the number of tubers. During the tuber formation stage, numerous potential tubers initiate on potato plants, but some of them do not develop due to limited assimilate flow toward the tubers (Struik, 2007). We observed that elevated CO_2 increased leaf area and leaf number of the plants. Therefore, it is possible that competition between the newly developing leaves with the tubers resulted in a lower positive effect of greater assimilate production on the mean tuber weight and the tuber number of plants under elevated CO_2 concentrations.

Despite higher *Np* in Agria under both CO_2 levels, the tuber yield of Fontane increased more than Agria under elevated CO_2. The higher tuber yield of Fontane was closely associated with the greater photosynthetic units (LA and LN) than *Np* on the leaf area basis. Additionally, the lower leaf starch content and the higher tuber dry matter of Fontane compared with Agria likely indicated the better translocation of photoassimilates to underground parts in this cultivar. Fleisher *et al.* (2008a) observed no significant changes in leaf area of potato plants at higher CO_2 concentration. They concluded that higher productivity of the potato plants was due to higher assimilation rate under such conditions. However, Finnan *et al.* (2005) concluded that the increase in potato tuber yield under elevated CO_2 could be a result of either a higher photosynthetic rate per leaf area unit or an increase in leaf area, and likely a combination of both.

The results of this study showed that exposure to elevated CO_2 altered dry matter allocation to the tubers. This is in agreement with the results of previous studies that reported a greater increase in mean tuber weight and tuber number of potato plants (Fleisher *et al.*, 2008b; Högy and Fangmeier, 2009). Studies on the effect of higher CO_2 concentration on the growth and productivity of tomato (Cong and Tanksley, 2006) and Arabidopsis (Horiguchi *et al.*, 2006) indicated that cell proliferation and expansion in the sink organs are important factors for developing sink capacity. Higher levels of CO_2 concentration shift partitioning of photoassimilates toward the tubers. Since cell division in the sinks is highly responsive to elevated CO_2, it results in producing larger sinks to store more assimilates (Chen and Setter, 2012). However, Chen and Setter (2012) reported that a greater potato tuber growth under elevated CO_2 is more related to stimulated tuber cell proliferation than cell expansion.

CONCLUSIONS

Elevated CO_2 concentration increased dry matter partitioning toward the underground parts of the plants, especially tubers. There was a significant increase in the tuber yield of both cultivars. However, no significant increase in the number of tubers or mean tuber weight of cultivars was observed at elevated CO_2. It seems that a slight increase in either tuber number or individual tuber weight potentially contributed to increase in tuber yield under elevated CO_2. The increase in tuber yield of Fontane seemed to be more associated with mean tuber weight, while, in Agria, it was more associated with the number of tubers under elevated CO_2. Additionally, Elevated level of CO_2 significantly increased the number of large size tubers as a portion of total tuber numbers, which would be beneficial for a better establishment of plants in the field.

Our results demonstrated that the higher level of CO_2 concentration stimulated leaf soluble carbohydrates and starch content of both cultivars, which could serve as a greater substrate for increasing the leaf dark respiration. Overall, these results suggest that raising the levels of CO_2 in minituber production systems could be beneficial to stimulate the productivity and tuber yield.

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تاثیر افزایش دی‌اکسیدکربن بر تبادل گازی، ویژگی‌های بیوشیمیایی و عملکرد ریزغده‌های سیب‌زمینی (*Solanum tuberosum* L.)

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چکیده

به منظور بررسی اثر سطوح مختلف دی‌اکسیدکربن (۴۰۰ و ۸۰۰ میکرومول بر مول) بر ویژگی‌های بیوشیمیایی و فیزیولوژیک و عملکرد ریزغده، گیاهچه‌های ریزازدیاد شده سیب‌زمینی (رقم آگریا و فونتانه) در شرایط کنترل‌شده در دانشگاه فردوسی مشهد در سال ۱۳۹۴ کشت شدند. بدون توجه به رقم، افزایش دی‌اکسیدکربن موجب افزایش معنی‌دار فتوسنتز و تنفس تاریکی در ۳۴ و ۵۷ روز پس از کاشت در مقایسه با شاهد شد. فتوسنتز بیشتر تحت تاثیر افزایش دی‌اکسیدکربن منجر به تجمع بیشتر نشاسته و کربوهیدارت محلول در برگ شد. افزایش دی‌اکسیدکربن منجر به تسهیم ماده خشک بیشتر به سمت اندام‌های زیرزمینی به ویژه ریزغده‌ها شد. افزایش دی‌اکسیدکربن تاثیر معنی‌داری بر تعداد و میانگین وزن ریزغده نداشت، اما بهرحال، افزایش دی‌اکسیدکربن باعث افزایش عملکرد غده آگریا و فونتانه به ترتیب به میزان ۱۷ و ۳۹ درصد شد. عملکرد فونتانه بیش از آگریا در اثر افزایش دی‌اکسیدکربن افزایش یافت که عمدتا به دلیل میانگین وزن غده بیشتر بود. نتایج نشان داد که میانگین وزن غده بیش از تعداد غده عملکرد را تحت تاثیر قرار می‌دهد. با توجه به نتایج، به نظر می‌رسد که افزایش غلظت دی‌اکسیدکربن در سیستم‌های تولید ریزغده سیب‌زمینی می‌تواند برای بهبود تولیدکنندگی و عملکرد ریزغده سودمند باشد.

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