INTERACTION OF LIGHT INTENSITY AND CO₂ CONCENTRATION ALTERS BIOMASS PARTITIONING IN CHRYSANTHEMUM

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ABSTRACT

Biomass partitioning is one of the pivotal determinants of crop growth management, which is influenced by environmental cues. Light and CO₂ are the main drivers of photosynthesis and biomass production in plants. In this study, the effects of CO₂ levels: ambient 400 ppm (a[CO₂]) and elevated to 1,000 ppm (e[CO₂]) and different light intensities (75, 150, 300, 600 μmol·m⁻²·s⁻¹ photosynthetic photon flux density – PPFD) were studied on the growth, yield, and biomass partitioning in chrysanthemum plants. The plants grown at higher light intensity had a higher dry weight (DW) of both the vegetative and floral organs. e[CO₂] diminished the stimulating effect of more intensive light on the DW of vegetative organs, although it positively influenced inflorescence DW. The flowering time in plants grown at e[CO₂] and light intensity of 600 μmol·m⁻²·s⁻¹ occurred earlier than that of plants grown at a[CO₂]. An increase in light intensity induced the allocation of biomass to inflorescence and e[CO₂] enhanced the increasing effect of light on the partitioning of biomass toward the inflorescence. In both CO₂ concentrations, the highest specific leaf area (SLA) was detected under the lowest light intensity, especially in plants grown at e[CO₂]. In conclusion, elevated light intensity and CO₂ direct the biomass toward inflorescence in chrysanthemum plants.

Key words: biomass allocation, dry weight, flowering time, inflorescence characteristic, water use efficiency

INTRODUCTION

Chrysanthemum is a short-day flowering plant belonging to the Asteraceae family (Arora 2012). It is one of the most popular ornamental plants and the second economically important cut flower in the world (Teixeira da Silva 2004). It is also used as potted and landscape plant (Liu et al. 2010). The production of chrysanthemum is one of the most intensive and controlled horticultural production systems, requiring the control of several growing conditions (Machin 1996; Carvalho & Heuvelink 2001).

There is ample evidence that the quality, intensity, and duration of light influence photosynthesis, biomass accumulation, flowering time, and the quality in many horticultural crops (Van Ieperen 2012; Demotes-Mainard et al. 2016; Zheng et al. 2019). The effect of light intensity and quality on chrysanthemum has also been shown in previous reports (Cockshull & Hughes 1971; Wang et al. 2009; Dierck et al. 2017; Kumar et al. 2017; Nissim-Levi et al. 2019).

Photosynthesis saturation of C3 plants requires 800–1,000 ppm CO₂ (Stitt 1991), while the ambient concentration (a[CO₂]) is about 400 ppm, therefore, commercial producers elevate the CO₂ level to improve crop biomass and productivity (Högy et al. 2009; Hasegawa et al. 2013) and to regulate the time of flowering (Reekie et al. 1994; López-Cubillos & Hughes 2016; Kobayasi et al. 2019). The elevation of CO₂ is defined as “CO₂ fertilization”; it has been shown to increase biomass by 50% in C3 plants (Prior et al. 2005), 35% in Crassulacean acid metabolism (CAM) plants (Drennan & Nobel 2000), and 12% in C4 plants (Poorter & Navas 2003). However, there are divergent reports on the effect of elevated CO₂ concentration (e[CO₂]) on different plant species (Croonenborghs et al. 2009). It was found that environmental factors, including nitrogen (Robinson et al. 2012) and other elements (De Graaff et al. 2006; Lotfiomran et al. 2016), temperature (Lee 2011; Madan et al. 2012; Kumari et al. 2019), water availability (Madhu & Hatfield 2015),

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air pollutants (Volin & Reich 1996), drought (Miranda-Apodaca et al. 2018), and light (Kerstiens 2001; Pérez-López et al. 2015) determine the magnitude of plant response to $e[\text{CO}_2]$. Naing et al. (2016) suggested an interaction between supplemental lighting and $e[\text{CO}_2]$ of the rose, and reported that the greatest increase in growth rate was achieved when $e[\text{CO}_2]$ was applied together with additional lightning (Naing et al. 2016). The same results were also obtained in the growth of seedlings and the yield of tomatoes and peppers by both $e[\text{CO}_2]$ and higher light intensity (Fierro et al. 1994). However, there is a lack of information regarding biomass partitioning under simultaneous increase in light intensity and CO_2 fertilization. Therefore, this research aimed to investigate the interactive effects of light intensity and $e[\text{CO}_2]$ on growth, flowering, and biomass partitioning of chrysanthemum to achieve high-quality flowering in a shorter time.

MATERIALS AND METHODS

Plant material and growth condition

Rooted cuttings (~9 cm stem length with 3–4 leaves) of cut chrysanthemum (*Chrysanthemum morifolium* ‘Zembla Lime’) (C.B.A, Deliflor, Dekker, Fides, Royal Van Zanten, and Yoder Bros. 2010, Germany) were planted in pots containing a mixture of cocopeat and perlite (1 : 1). Half strength of Hoagland solution was used for irrigation of the plants following transplanting cuttings to the pots. The plants were placed in eight growth chambers with different light intensities: 75, 150, 300, 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and CO_2 concentrations: ambient and elevated to 1,000 ppm. Each chamber was kept at $27 \pm 2^\circ\text{C}$ temperature and $50 \pm 5\%$ relative humidity. Each treatment consisted of six replications.

A combination of 3:1 red and blue light-emitting diodes (LEDs) with peaks at 600–685 nm for red and 415–500 nm for blue LEDs was used for application of different light intensities in the growth chambers. These LED light panels (24 W, Iran Grow Light) were used to limit the production of heat by the light sources. The same combination of red and blue LEDs was used in all the growth chambers, since based on

the previous reports they are the main light spectra for photosynthesis and growth of plants. The photoperiod was set at 12 h/12 h light/dark periods.

To supply high CO_2 concentration, a CO_2 cylinder that was equipped with a manometer, electric valve, and the digital timer was used. The cylinder outlet pressure was adjusted thrice using a pressure gauge connected to a timer resulting in injecting the CO_2 into the air every 2 min, and the CO_2 concentration was recorded using a CO_2 sensor equipped with a data logger (Trotec, BZ30, Germany).

Plant growth and morphology

After three months of plant growth at different light intensity and CO_2 concentration, growth and morphological characteristics, such as leaf and inflorescence number, fresh and dry weights (DWs) of above-ground parts and roots, were analyzed. The specific leaf area (SLA) of each plant was calculated using the following equation:

$$\text{SLA} = \frac{\text{leaf area (cm}^2\text{)}}{\text{leaf dry weight (g)}}$$

The flowering time was recorded based on the emergence of flower buds. The accumulation of biomass in the various plant organs was calculated by the DW measured at the end of the production cycle. To do so, plants were harvested, the different parts were separated, and, after measuring the fresh weight, their DWs were recorded after reaching a constant weight for 3 days at 80°C . Measurements included final dry weight of organs including leaf, stem, inflorescence, and root.

Water use efficiency

To determine the water use efficiency (WUE), the total amount of water consumed by the plants during the growth period was recorded. Under greenhouse conditions, the relationship between soil water evaporation and plant transpiration is inseparable (Ma et al. 2013). In our experiment, the total amount of water consumed by the plants was measured by subtracting the amount of water evaporated from the substrate in the absence of plants from the amount of water used for irrigation (Polley et al. 1996). To schedule the proper time and amount of water, irrigation was applied when 30% of water was taken from the pots.

This value was represented by “easily obtained water” (the amount of water retained by the fully irrigated substrate following 24 h). The soil was irrigated when the soil water content was lower than the amount of easily obtained water. WUE was calculated as the ratio of DW of the above-ground parts (including stem, leaf, inflorescence, and flowers) to the amount of water that was taken by the plants.

Statistical analysis

Six plants were used as six replicates in each treatment. Each plant was taken as an independent replicate. The data were subjected to two-way analysis of variance (ANOVA) and Duncan's test was used as a post-test; $p > 0.05$ was considered as not significant.

RESULTS

Vegetative growth influenced by light intensity and CO₂ concentration

The DW of the above-ground parts increased gradually with increasing the light intensity in plants grown at a[CO₂]. Plants grown at 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ showed the maximum DW of above-ground parts. These plants had four times higher DW of above-ground parts than those obtained in plants grown at 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 1A). In e[CO₂], there was a more than twofold increase in DW of above-ground parts of plants grown at 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ compared to DW of above-ground parts of the plants grown at lower light intensity.

Increase in light intensity resulted in a gradual increase in leaf DW and in the number of leaves only in plants grown at a[CO₂]. The maximum leaf DW and the number of leaves were obtained in plants grown at 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. In these plants, there were three times higher leaf DW and five times more leaves than those in plants grown at 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. However, e[CO₂] eliminated the stimulating effect of increasing light intensity on the studied parameters (Fig. 1B–C).

The SLA of plants grown at 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and exposed to e[CO₂] was significantly higher than SLA of plants exposed to higher light intensities irrespective of CO₂ level (Fig. 1D). At light intensities higher than 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, there was no significant difference among the light intensity or CO₂ level.

Root growth enhanced by increase in light intensity

A drastic increase in the DW of the roots was observed with the increase in the light intensity from 75 to 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The DW of the roots of plants grown at 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was more than 13 times higher than those grown at 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a[CO₂] and 5 times higher at e[CO₂]. Also, a drastic reduction in the DW of the roots was observed in plants grown at intensity of 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and e[CO₂] comparing with plants grown at a[CO₂] (Figs. 2A and 3).

Generative growth influenced by interaction of light intensity and CO₂ concentration

The inflorescence DW increased with increasing light intensity; although at a[CO₂], no differences were found between 75 and 150 as well as between 300 and 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. At e[CO₂], plants grown at 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ had the highest DW of inflorescence. The DW inflorescence of these plants was 14 times higher than the inflorescence DW of plants grown at 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and in e[CO₂] and 35 times higher when the plants were grown in a[CO₂] (Fig. 2B). In plants grown at 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, exposure to e[CO₂] resulted in approximately three times higher inflorescence DW than in the plants grown at a[CO₂].

The number of inflorescences increased with increasing light intensity; this effect was more visible at a[CO₂]. In plants grown at e[CO₂], there was no significant difference between the number of inflorescences at 75, 150, and 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, while e[CO₂] doubled the number of inflorescences in plants grown at 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 2C and 4).

The time of flowering was positively influenced by both the light intensity and the level of CO₂. The number of days to flowering decreased gradually with increasing light intensity (Fig. 2D). The transition to the generative phase was accelerated (45% earlier) by increasing the light intensity from 75 to 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in plants grown under a[CO₂]. Enrichment with CO₂ caused the further acceleration of flowering (53% earlier than at a[CO₂]), by increasing the light intensity from 75 to 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Figs. 2D and 4).

Figure 1. Interaction effects of light intensity and concentration of CO₂ on (A) DW of above-ground parts, (B) leaf DW, (C) total number of leaves, and (D) SLA of chrysanthemum. Plants were exposed to different concentrations of CO₂ (400 ppm – black columns and 1,000 ppm – gray columns) and different light intensities (75, 150, 300, and 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD). Bars are mean value $\pm$ SEM and when the letters above the bars are similar, it means that they are not significantly different according to the ANOVA test at $p \leq 0.05$; ANOVA – analysis of variance; DW – dry weight; PPFD – photosynthetic photon flux density; SLA – specific leaf area

Figure 2. Interaction effects of light intensity and concentration of CO₂ on (A) root DW, (B) inflorescence DW, (C) number of inflorescences, and (D) the time of flowering of chrysanthemum. Plants were exposed to different concentrations of CO₂ (400 ppm – black columns and 1,000 ppm – gray columns) and different light intensities (75, 150, 300, and 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD). Note: See Figure 1

Figure 3. Root system of chrysanthemum affected by light intensity and CO₂ concentration. The plants were exposed to different concentrations of CO₂ [400 ppm as ambient CO₂ (a[CO₂]) and 1,000 ppm as elevated CO₂ (e[CO₂])] and light intensities (75, 150, 300, and 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD)

Note: See Figure 1

Figure 4. Interaction effect of light intensity and concentration of CO₂ on the flowering of chrysanthemum. Plants were exposed to different concentrations of CO₂ [400 ppm as ambient CO₂ (a[CO₂]) and 1,000 ppm as elevated CO₂ (e[CO₂])] and light intensities (75, 150, 300, and 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD)

Note: See Figure 1

Dry matter accumulation and biomass partitioning

The accumulation of biomass (stem, leaf, flower, and root) increased in proportion to the increasing light intensity. Comparison of biomass production under each of the light intensity showed that $e[\text{CO}_2]$ diminish the accumulation of biomass compared with $a[\text{CO}_2]$. This effect was more pronounced with an increase in the light intensity from 75 to $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which resulted in a 9% and 69% reduction in biomass of plants grown at 75 and $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively (Fig. 5). These results indicate that plants grown under low light intensities respond better to $e[\text{CO}_2]$ and an increase in light intensity reduces the stimulating effect of CO_2 , which indicates resistance to the physiological effect of light on the accumulation of biomass (Fig. 5).

Both the increase in the light intensity and the CO_2 level increased the share of biomass of inflorescence at the expense of the amount of leaf biomass (Fig. 6). As the light intensity increased, a gradual increase in the inflorescence was observed. The biomass of inflorescence of plants grown at $600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was about five times higher than that of plants grown at $75 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. In addition, the root biomass also increased with the increase in

light intensity and the maximum root biomass was observed in plants grown at $600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, showing a twice higher biomass accumulation compared with plants grown at $75 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and at $a[\text{CO}_2]$. In contrast, a downward trend in the leaves biomass was observed with increasing light intensity, which shows a reduction of leaf biomass by 47.35% in plants grown at $600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ compared with those at $75 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 6). The biomass of inflorescence at the highest light intensity was three times greater than that of plants grown at $75 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which is less than five times the increase at $a[\text{CO}_2]$ at the same light intensities (Fig. 6). An increase in root biomass in response to the increase in light intensity was not observed in plants grown at $e[\text{CO}_2]$ (Fig. 6). Moreover, at $e[\text{CO}_2]$, a drastic reduction of the leaf biomass of plants at $75 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ compared to plants grown at $600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, was observed, showing a stronger reduction compared to the reduction of leaf biomass at the same light intensity and at $a[\text{CO}_2]$ (Fig. 6). Considering the influence of $e[\text{CO}_2]$ on the allocation of biomass at each light intensity, the biomass of inflorescences increased, and the biomass of leaves decreased with increasing CO_2 concentration (Fig. 6).

Figure 5. Diminishing effect of elevated CO_2 (calculated as reduction in biomass accumulation in plants under $e[\text{CO}_2]$ compared to $a[\text{CO}_2]$) on total biomass of chrysanthemum plants grown under different light intensities

Water use efficiency

Different light intensities and CO₂ concentrations significantly affected WUE (Fig. 7). The WUE value increased 5 times and 4.7 times under a[CO₂] and e[CO₂], respectively, when light intensity

increased from 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Considering the impact of CO₂ concentration regardless of light intensity, e[CO₂] reduced the WUE value the strongest at 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ compared to other light intensities (Fig. 7).

Figure 6. Allocation of biomass (DW) to different organs in response to CO₂ concentrations and light intensities. Plants were exposed to different concentrations of CO₂ [400 ppm as ambient CO₂ (a[CO₂]) and 1,000 ppm as elevated CO₂ (e[CO₂])] and light intensities (75, 150, 300, and 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD)

Note: See Figure 1

Figure 7. Interaction effect of light intensity and concentration of CO₂ on water use efficiency (WUE) of chrysanthemum. Plants were exposed to different concentration of CO₂ (400 ppm – black columns and 1,000 ppm – gray columns) and different light intensities (75, 150, 300, and 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD)

Note: See Figure 1

DISCUSSION

In the present study, a positive effect of light intensity and increased level of CO₂ on the dry weight of inflorescences was observed. This finding is in agreement with the results of a previous study on rose plants that showed an increase in fresh weight of inflorescences when the plants are exposed to a combination of e[CO₂] and additional lighting (Naing et al. 2016). These authors postulated that an increase in water use efficiency enhanced the photosynthesis rate in the modified atmosphere and led to the provision of more carbohydrates utilized in flowering and flower development. Moreover, supplementary lighting increases the fresh weight of flowers by reducing the number of blind flowers in *Rosa hybrida* 'Frisco' (Van Labeke et al. 2000).

In our experiment, the number of inflorescences increased with increasing light intensity under ambient CO₂ level but CO₂ elevation diminished the effect of higher light intensity. These results are in agreement with another study that showed the effect of e[CO₂] and light intensity on the production and quality of flower stems in *Alstroemeria* (Van Labeke & Dambre 1998).

In our research, an increase in light intensity and CO₂ concentration accelerated flowering. In contrast, e[CO₂] was reported to delay flowering in four short-day species, however, in long-day species flower bud initiation was promoted in response to e[CO₂] (Reekie et al. 1994).

Leaf DW was affected by both CO₂ concentration and light intensity, so that the leaf DW increased with increasing light intensity in plants that were exposed to a[CO₂], while under e[CO₂] the positive effect of light intensity was eliminated. There is controversy with previous reports investigating the effects of e[CO₂] on the growth of different plant species. For instance, the treatment of lettuce with e[CO₂] reduced fresh weight, while application of e[CO₂] together with complementary nutrients led to an increase in fresh weight compared to control plants (Croonenborghs et al. 2009; Miyagi et al. 2017).

The number of leaves per plant increased significantly by exposure to higher light intensities under a[CO₂], while e[CO₂] antagonistically interacted with light intensity in this regard. Notably, under e[CO₂], no significant difference was observed in the number of leaves depending on light intensities.

This suggests that e[CO₂] inhibits the positive effect of high light intensity on leaf production. In line with our results, a 23% reduction in the number of leaves have been reported in soybean; however, the effect of e[CO₂] on the number of leaves depended on the plant growth stage (Madhu & Hatfield 2015).

SLA value increased at e[CO₂] and 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, but no significant effect was detected under higher light intensities. It has been reported that SLA decreased in response to e[CO₂] in the four dominant *Quercus* species (Chae et al. 2016) as well as in other species (Poorter & Navas 2003; Ainsworth & Long 2005), while the positive effect of e[CO₂] and the temperature on the leaf area was recorded in *Rosa hybrida* (Pandey et al. 2010). This contradiction allowed us to postulate that the effect of e[CO₂] on plants could be modified by other factors including, temperature, growth habit, and light intensity.

At both CO₂ concentrations, higher light intensities increased the root DW, but the enhancing effect of light intensity on roots decreased at elevation of CO₂ level. Similarly, a positive effect of light intensity on root growth was demonstrated in *Nicotiana tabacum* (Nagel et al. 2006). Moreover, in studies on onion, it was observed that the root growth rate increased with increasing light intensity and slows down with low light intensity. Therefore, at a low light intensity, the root growth was reduced at the expense of above-ground parts to widen the area of light capturing (Son et al. 1989). In plants grown at 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a[CO₂], less biomass was allocated to the roots compared to the same light intensity but at e[CO₂]. At higher light intensities, the allocation of biomass to the roots was higher with e[CO₂]. Earlier studies have also shown that e[CO₂] increases the root/shoot ratio by 35% in *Picea sitchensis*; however, this effect was not observed in the third growing season (Murray et al. 1996).

In contrast, increasing CO₂ has been reported to reduce root/shoot ratio in *Gerbera jamesonii* (Xu et al. 2014). However, it was expected that due to the increasing photoassimilation as a result of e[CO₂], the root/shoot ratio increased to support the supply of adequate water and nutrient levels for the photosynthetic organs (Norisada et al. 2006). Rogers et al. (1996) reviewed the available literature and summarized that in response to e[CO₂], the root/shoot ratio was greater in 59.5%, lower in 37.5%, and remained unchanged in 3% of the crop species tested.

The results of our study showed that with increasing light intensity, the DW of the above-ground parts increased at both a[CO₂] and e[CO₂] levels, but at all light intensities, lower values of DW were obtained at higher CO₂ level. The positive effect of e[CO₂] on the above-ground biomass production and its negative effect on the grain yield were reported in wheat (Högy et al. 2009). Dry matter accumulation was increased by exposure to higher light intensity in either a[CO₂] or e[CO₂], but higher total biomass production in a[CO₂] indicates a repressive effect of e[CO₂] on dry matter accumulation. It has been shown that e[CO₂] increases biomass production of rye, wheat, *Brassica napus*, and *Arabidopsis thaliana*, suggesting that increase in biomass provides an active absorber under conditions where the photosynthetic substrates (e.g., CO₂) are greater than the required level (Dahal et al. 2014). Similar results were obtained for other plant species (Ainsworth 2008; Xu et al. 2014; Kumari et al. 2019). Moreover, the low intensity of irradiation reduced biomass accumulation in *Grindelia chiloensis* (Zavala & Ravetta 2001). In the case of duckweed, the increase in irradiation from 20 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to 110 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ increased biomass but a further increase in the irradiation value to 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was not effective (Yin et al. 2015).

The biomass partitioning to different plant organs depends on species, ontogeny, and the environment surrounding the plant (Poorter & Nagel 2000). Our study showed that distribution of biomass to different plant parts depends on light intensity and CO₂ concentrations. In the perennial herb, *Plantago lanceolata*, the allocation of biomass to inflorescences in a[CO₂] was twice as high as in e[CO₂] (Fajer et al. 1991). It was contrary to results of our experiment, where e[CO₂]. It can be conceived from our data that increase in CO₂ concentration shifted the biomass from the leaves to the inflorescence. Similar to the effect of e[CO₂] on allocation of biomass to inflorescence, increase in light intensity also directed the biomass toward the root and inflorescence organs, which occurred at the expense of reduction in biomass partitioning into the leaves. The light intensity-dependent increase in biomass allocation to inflorescence was higher in plants grown under e[CO₂]. It has been reported that a high carbon-to-nitrogen ratio is one of the determinants for induction of flowering

and inhibition of vegetative growth in various plant species (Chao et al. 2017). Both e[CO₂] and increase in light intensity elevate the C/N ratio (Esmaili et al. 2020). In cucumber grown with optimal nitrogen fertilization, the allocation of biomass to the generative organs increased at the expense of the reduction of leaf biomass. The allocation of more biomass to the generative organs was due to the long exposure to e[CO₂] (Dong et al. 2016). The decrease in biomass allocation to leaves by the increase in light intensity that was observed in this study could be due to an optimization strategy that guarantees optimal photosynthesis; in other words, under low light levels, plants invest more biomass on photosynthetic organs rather than in high light conditions (Patty et al. 2010), which is confirmed by a higher share of biomass in leaves at 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ than at 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

WUE was also affected by both CO₂ concentration and the light intensity. By increasing light intensity, WUE increased more in plants grown at a[CO₂], showing that CO₂ enrichment and higher light intensity have a synergistic effect on WUE. The enhancing effect of increased light intensity on WUE was also demonstrated in pepper (Pan et al. 2020), lettuce (Esmaili et al. 2020), and wheat (Yi et al. 2020). In the case of lettuce, there was also an improvement in WUE by exposing the plants to a higher light intensity and enriching CO₂ up to threshold levels (Esmaili et al. 2020). However, the declining impact of CO₂ on WUE is in contradiction with previous reports on pigeon pea (Sreeharsha et al. 2015; Zhang et al. 2018). These contradictions in describing the interaction effect of light intensity and e[CO₂] require further investigation.

CONCLUSION

Light intensity and concentration of CO₂ had considerable effect on the growth and reproduction of chrysanthemum. The plants grown at higher light intensities and ambient CO₂ were characterized with higher dry weight of vegetative organs and total biomass while having a lower dry weight of the inflorescences. The CO₂ increased to 1,000 ppm reduced the positive effect of light on the dry weight of vegetative organs; however, its opposite effect was observed on dry weight of inflorescence, suggesting that at a higher CO₂ level, biomass tends to be shifted toward inflorescence compared to vegetative organs.

In addition, flowering was accelerated at higher CO₂ and higher light intensities. The increase in light intensity favors the allocation of biomass to the inflorescence and elevation of CO₂, enhancing the increasing effect of light on partitioning of biomass to the inflorescence. Overall, our study provides insight into the role of light intensity and CO₂ concentration on vegetative and generative growth of chrysanthemum.

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