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Relationship of fertilizer and periodic drought on biomass allocation in greenhouse-grown sunflower

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Abstract

The objective was to analyze organ plasticity in biomass allocation in response to limited resources and its influence on commercial traits of potted sunflower production. Although drought dramatically increased net photosynthetic rate and water-use efficiency, total leaf area, leaf dry mass, and total dry mass with drought stress decreased at rates of 20.9, 21.8, 23.0, and 9.9%, respectively. Irrigation positively affected specific leaf area, stem mass fraction, and root mass fraction. Adversely, fertilizer had a negative effect on stem mass fraction, root mass fraction, and root/shoot ratio. Interestingly, leaf mass fraction was not affected by them. Drought and greater fertilizer amount promoted flower yield and maintained leaf mass fraction stability at the expense of stem and root production. This induced plants to produce a thin stem, poor root system, and weak lodging resistance despite high flower production. This could have significant economic consequences for commercial potted flower production.

Keywords: Asteraceae; controlled environment agriculture; plant physiology; photosynthesis; tensiometer.

Introduction

Water and nutrients are two critical factors for plant growth and productivity, and there is an interaction effect between them (Yin *et al*. 2009). Water is required for the dissolution and absorption of nutrients. Meanwhile, the utilization of nutrients will affect the water-use efficiency of the plant (Hu *et al*. 2008, Song *et al*. 2010). Drought can interfere with various physiological and biochemical processes of a crop. The adverse effect of water deficit on plant growth and yield has led to considerable research focused on drought-induced photosynthetic damage and plant response mechanisms related to photochemical activity, stomatal regulation, and osmotic adjustment (Ahmad *et al*. 2014, Andrianasolo *et al*. 2016).

Research has shown that increasing fertilizer was effective and a practical way to alleviate the adverse effects of water deficits. Increasing nitrogen is correlated with greater concentrations of chlorophyll (Chl), upregulating the oxidative defense system, and greater net photosynthetic rates (Razzaq *et al*. 2017). Adequate potassium is essential to enhance drought resistance by increasing root elongation, reducing reactive oxygen species (ROS) production, and preventing oxidative degradation of Chl (Shehzad *et al*. 2020). The identification of foliar NK improved drought tolerance of sunflower (*Helianthus annuus* L.) by maintaining turgor and enhancing the accumulation of osmoprotectants and nutrient contents (Hussain *et al.* 2016).

However, a plant reaction to limited water and nutrients gradually exhibits a relatively retarded growth rate and loss of biomass production. Plants respond to abiotic stress by partitioning biomass among various plant organs to optimally capture the nutrients, light, water, and carbon dioxide to maximize its growth rate (Enquist and Niklas 2002, Achten *et al*. 2010). This developmentally explicit model of plasticity in biomass allocation in response to limited resources is described as optimal partitioning theory (OPT, Thornley 1972). Specifically, plants with a low nutrient supply beneficially allocate more biomass to roots to increase root mass fraction (RMF) and root/shoot ratio (R/S). If plants are grown at high densities, plants would show a clear increase in the stem fraction (SMF) (Poorter *et al*. 2012). To diminish plant root metabolism and oxygen demand, the root/shoot ratio can decline under saturated soil conditions (Chen *et al*. 2002). Quantitative biomass allocation has also depended on plant size and ontogeny besides limited resources (Smith-Martin *et al.*

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Abbreviations: E – transpiration rate; FMF – flower mass fraction; FUE – fertilizer-use efficiency; LDM – leaf dry mass; LMF – leaf mass fraction; OPT – optimal partitioning theory; P_N – net photosynthetic rate; RGR – relative growth rate; RMF – root mass fraction; R/S – root/shoot ratio; SLA – specific leaf area; SMF – stem mass fraction; TDM – total dry mass; TLA – total leaf area; ULR – unit leaf rate; WUE – water-use efficiency (= P_N/E).

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2019). Some studies have reported that adjustments in biomass allocation occur in response to nutrient limitation, but not necessarily in response to water, CO_2, and light availability (McConnaughay and Coleman 1999).

As for faster-growing potted annuals, sunflowers are vulnerable to nutrients and water unavailability. Plasticity in biomass allocation patterns has inevitably caused morphological variation in terms of leaf size, leaf number, stem diameter and height, root structure, and flower and seed yield (Haworth *et al.* 2019, Kahrobaiyan *et al.* 2019). Remarkably, few studies have focused on the influence of biomass allocation patterns on ornamental characteristics of potted sunflower accounting for an optimal fertilizing and watering strategy. Our research was carried out to contribute to answering the following questions for potted sunflower production: (*1*) Whether the effects of water and nutrient availability are equal in regard to biomass partition to various organs? (*2*) Is it possible to characterize the phenotypic plasticity of potted sunflower to varying water and nutrient availability? (*3*) Can production quality be evaluated in relation to leaf size, flower yield, and stem support?

Materials and methods

Plant material: The project was performed in the Oklahoma State University Department of Horticulture and Landscape Architecture research greenhouses in Stillwater, OK, USA. The randomized design involved two irrigation levels and three fertilizer rate regimes resulting in six treatment combinations. Each treatment consisted of three replicates of eight uniform plants (experimental unit). Seeds of sunflower 'Choco Sun' (*Park Seed Wholesale Company*, Greenwood, SC) were sown in a commercial soilless media mix (*Metro-Mix-380*, *Sun Gro Horticulture*, Bellevue, WA). When the third pair of true leaves emerged, seedlings with uniform vigor were transplanted in 15-cm azalea pots. A week later, all seedlings were subjected to initial irrigation and fertilizer rates.

Under the conventional drought treatment, soil water content was controlled to maintain a stable water potential. In this research, drought was simulated as a natural drought by continuously decreasing water potential in the containers. Watering would start when soil water potential dropped at a threshold value. Drip emitters were applied to automatically control the irrigation with the use of an electronic tensiometer (*Irrometer*, Riverside, CA) set at –10 and –15 kPa representing normal and water deficit. Fertilizer treatments were applied with a controlled-release fertilizer (15 N–3.9 P–10 K) (*Osmocote® Plus*, *The Scotts Co.*, Marysville, OH) at three levels: 6, 12, or 18 g per pot. The temperature in the greenhouse was set at 21/18°C day/night and light intensity varied between 600 and 1,200 μmol(photon) m^{-2} s^{-1} on a clear sunny day.

Selection of testing samples: Ten samples were randomly marked from each treatment for biomass measurement and each plant had three replicate samples. All tested leaves were healthy, mature, and not shaded from the upper one-third of the canopy (Alkio *et al.* 2003). Three random samples from the ten marked plants in each treatment were used for the collection of the photosynthesis data.

Photosynthetic parameters: All data were collected at the transitional stage, which was about 23 d after the seedlings were transplanted in the pots. Photosynthetic activity, including net photosynthetic rate (P_N) and transpiration rate (E), were examined with a portable photosynthesis meter (*Li-6400*, *Li-COR*, Lincoln, NE, USA) at 8:30–11:00 and 15:00–17:00 h local time. All measurements were set at the consistent condition: a red-blue *6400-02B* light source was used and its intensity was set at 1,200 μmol(photon) m^{-2} s^{-1}. Carbon dioxide concentration in the 20 × 30 mm leaf chamber was controlled at 400 μmol mol^{-1} and the temperature was kept at 22°C. Water-use efficiency (WUE) was calculated by dividing P_N by E.

Leaf area, biomass, and growth rate: Each sample was harvested and separated by different organs. Every leaf of each sample was cut to be scanned by a leaf area meter (*LI-3100C*, *Li-COR*, Lincoln, NE, USA). The total leaf area (TLA) of a plant was summed by leaf area for each leaf within the plant. Subsequently, leaves, stems, flowers, and roots were dried at 80°C for a week. Total dry mass was calculated after weighing dry leaf mass, dry stem mass, dry flower mass, and dry root mass.

Biomass allocation showed the distribution of different organ yields. Six indexes were used to measure the proportion of organ production to total biomass. The specific leaf area (SLA) was calculated as the leaf area divided by dry leaf mass. Leaf mass fraction (LMF) was equal to LDM divided by TDM. The stem mass fraction (SMF), flower mass fraction (FMF), and root mass fraction (RMF) were determined by a ratio of DSM to TDM, DFM to TDM, and DRM to TDM separately. Root/shoot ratio (R/S) was calculated as dry root mass divided by dry aboveground biomass.

Unit leaf rate (ULR) indicates an increase in total plant dry mass per leaf area each day (g m^{-2} d^{-1}). The relative growth rate (RGR) is an increase in plant mass as a unit of plant mass per day. The relative growth rate (RGR) of the plants is then given by the product of the above three traits (Evans 1972). It was measured as RGR = ULR × SLA × LMF.

Fertilizer-use efficiency (FUE) is described as the decreasing percentage of total dry mass with increasing fertilizer per gram. It was determined as: $FUE = [(TDM_D - TDM_N)/TDM_N]/\text{fertilizer amount}$. TDM_N represented total dry biomass under normal watering with the same fertilizer rate, whereas TDM_D meant total dry mass at drought conditions.

Data analysis: The significance of irrigation, fertilizer, and their interactions on each growth index and photosynthetic parameters were conducted by analyses of variance (*ANOVA*) using *EXCEL* (*Microsoft Company*, USA). In the case of significance tests of difference, data were analyzed using an *ANOVA* and *Fisher*'s LSD test at a significance level of 5% (p=0.05). To discern the variance contribution of different organ mass fraction and assess the influence of phenotypic development, principal component analysis (PCA) was used to assess their variation (LMF, SMF, FMF, RMF, and R/S) based on *SPSS 17.0* (*SPSS Inc*., Chicago, IL, USA).

Results

Photosynthetic activity, biomass, and growth rate: Fertilizer rate and irrigation level significantly affected the performance of P_N, E, and WUE. Drought dramatically increased P_N and WUE. The greater P_N usually appeared in the groups with more fertilizer at –15 kPa with 21.40 µmol m^{-2} s^{-1} (–15 kPa/12 g) and 20.34 µmol m^{-2} s^{-1} (–15 kPa/18 g). Fertilizer had a positive relationship with P_N but negative with WUE. WUE attained the greatest value at –15 kPa/12 g (8.87 µmol mol^{-1}) (Fig. 1*B*). Drought and limited nutrients also resulted in a reduction of leaf area and biomass. Three variables (TLA, LDM, and TDM) were significantly affected by watering, fertilizing, and their interaction. The average TLA at –10 kPa was 1,268.26 cm^2, which was 276.52 cm^2 larger than that at –15 kPa. The 18 g per pot treatment had the greatest TLA with 1,317.45 cm^2 (Table 1). For LDM and TDM, there was no significant difference between the high rate (18 g per pot) and medium rate (12 g per pot) of fertilizer, although each was greater than that at the 6 g per pot treatment. Maximum TDM was observed in the –10 kPa/12 g treatment (44.3 5 g) and the minimum was in –15 kPa/6 g (34.08 g) (Fig. 1*E*). Drought reduced TDM in the 6, 12, and 18 g per pot by 1.2, 18.1, and 8.3%, respectively. Drought reduced FUE by 0.2% for the 6 g per pot treatment, which was 0.3% greater than that at the 18 g per pot. Smallest FUE happened at the moderate fertilizer

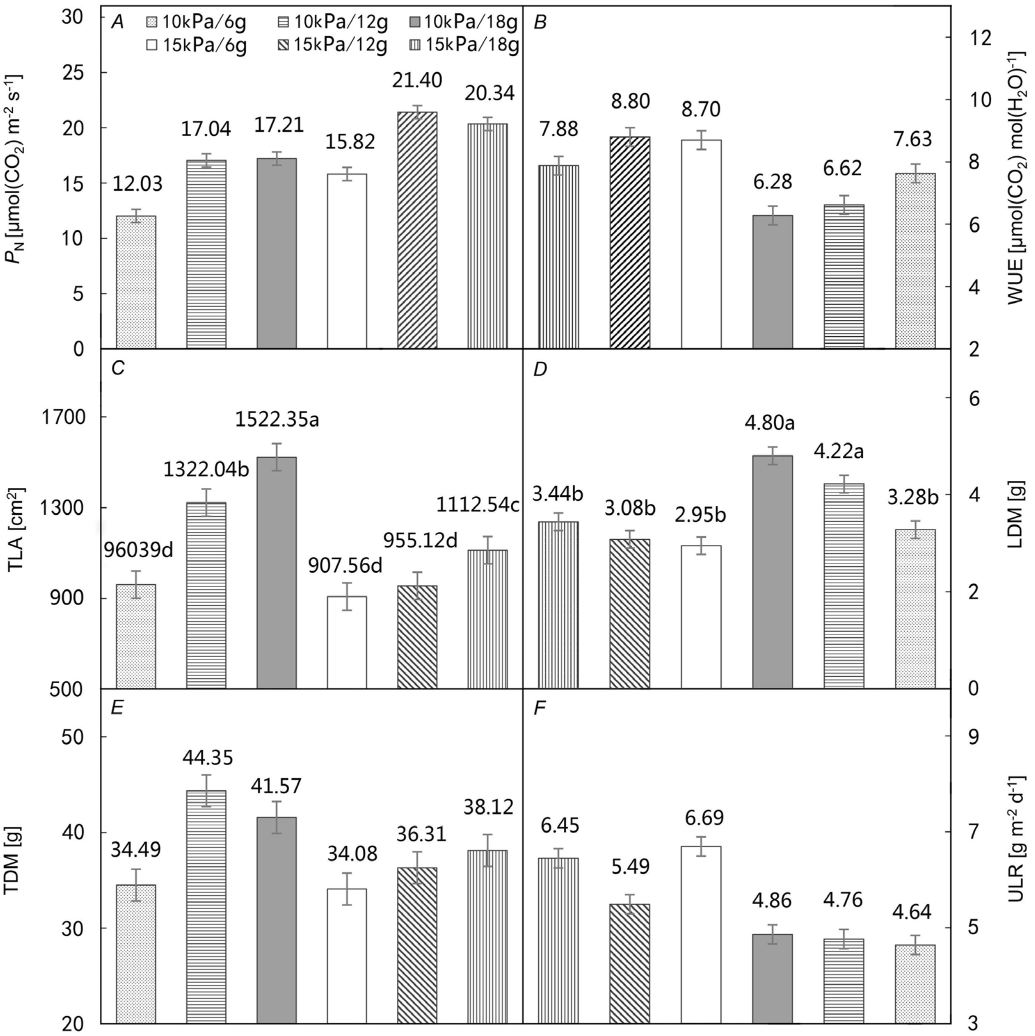

Fig. 1. Photosynthetic activity, leaf area, and biomass of sunflower 'Choco Sun' leaves exposed to the different combination of fertilizer and irrigation rates. (*A*) Net photosynthetic rate, P_N; (*B*) water-use efficiency, WUE; (*C*) total leaf area, TLA; (*D*) leaf dry mass, LDM; (*E*) total dry mass, TDM; (*F*) unit leaf rate, ULR. *Different lowercase letters* indicated significantly different means (two-way *ANOVA*, $P \leq 0.05$).

rate (12 g per pot) with the highest decreasing percentage of 1.5%.

ULR was affected by irrigation but not a fertilizer or the two-way interaction. Drought promoted ULR which was 1.46 g m^{-2} d^{-1} greater than that under normal conditions (4.75 g m^{-2} d^{-1}). The treatment –15 kPa/6 g had the greatest ULR value of 6.69 g m^{-2} d^{-1}, but it showed no significant difference with other rates. The results also indicated that RGR was 11.63 mg g^{-1} d^{-1} and kept constant in all six treatments.

Biomass allocation to the different organs: Four indexes were influenced by fertilizer and irrigation main effects (Table 2). Irrigation had a positive relationship with SLA, SMF, RMF, R/S but negative with FMF. Drought reduced SMF, R/S, and RMF by 30, 29, and 24%, respectively. In contrast, fertilizer had a positive effect on FMF. Limited nutrients (6 g per pot) greatly enhanced SMF, RMF, and R/S by 9, 35, and 3%, respectively, compared to the 12 g treatment. Nevertheless, the greater fertilizer amount (18 g) did not improve the mass distribution from leaf to stem and root on account of showing no significant difference with 12 g per pot. The specific leaf area (SLA) dramatically decreased by 35.36 cm^{2} g^{-1} under drought stress compared to –10kPa treatment. Interestingly, LMF did not respond to drought and fertilizer.

Data revealed that limited nutrients promoted more biomass partition to roots for greater SMF, RMF, and R/S. Drought inhibited the biomass allocation to stems and roots but increased it to flowers, which did not correspond with optimal partitioning theory. However, water deficit and greater fertilizer rates were beneficial to a greater FMF. The greatest value of FMF was shown in the –15 kPa/12 g treatment with 0.65 g g^{-1} (Fig. 2). Only R/S was greatly influenced by the interaction of irrigation and fertilizer.

Variance contribution revealed the influence of phenotypic plasticity: By extracting initial eigenvalues, principle component analysis (PCA) showed that components 1 and 2 could explain 99.44% of the total variance, in which component 1 accounted for 78.6% (Table 3). FMF, SMF, and RMF were listed as three of the prominent variance contributors in component 1, reaching 18.4, 17.9, and 17.7%, respectively. The sequence of the accumulative contribution of components 1 and 2 was arranged as followed: R/S (21.1%), RMF (21.0%), SMF (20.3%), LMF (18.5%), and FMF (18.5%). The contribution clearly distinguished the effects of irrigation and fertilizer on different organ plasticity.

Table 1. *ANOVA* results of irrigation regimes, fertilizer rates, and interaction between them on sunflower 'Choco Sun' photosynthetic activity, leaf area, biomass, and growth rate. LSD$_{0.05}$ means the least squared difference at the $P \leq 0.05$. X, Y – means within the same column followed by *different lowercase letters* are significantly different at 0.05 level of single-factor *ANOVA*. P_N – net photosynthetic rate; E – transpiration rate; WUE – water-use efficiency; TLA – total leaf area; LDM – leaf dry mass; TDM – total dry mass; ULR – unit leaf rate; FUE – fertilizer-use efficiency [g g^{-1} g^{-1}].

Factor	Treatment	P_N [µmol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	WUE [µmol mol^{-1}]	TLA [cm^{2}]	LDM [g]	TDM [g]	ULR [g m^{-2} d^{-1}]	FUE [g g^{-1} g^{-1}]
Irrigation	–10 kPa	15.43^{bX}	2.30	6.85^{b}	$1,268.26^{a}$	4.10^{a}	40.14^{a}	4.75^{b}	-
	–15 kPa	19.19^{a}	2.28	8.47^{a}	991.74^{b}	3.16^{b}	36.17^{b}	6.21^{a}	-
LSD$_{0.05}$		3.09	0.36	0.76	121.80	0.37	2.71	0.77	-
Fertilizer	6 g	13.92^{bY}	1.70^{b}	8.17^{a}	933.97^{c}	3.12^{b}	34.29^{b}	5.67	0.20
	12 g	19.22^{a}	2.50^{a}	7.75^{a}	$1,138.58^{b}$	3.65^{a}	40.33^{a}	5.13	1.51
	18 g	18.77^{a}	2.66^{a}	7.06^{b}	$1,317.45^{a}$	4.12^{a}	39.84^{a}	5.65	0.46
LSD$_{0.05}$		2.06	0.24	0.51	99.45	0.30	2.22	0.63	-

Table 2. Effect of irrigation and fertilizer (15 N–3.9 P–10 K) on biomass allocation of sunflower 'Choco Sun' grown in a greenhouse in Stillwater, OK in 2018. SLA – specific leaf area [cm^{2} g^{-1}]; LMF – leaf mass fraction [g g^{-1}]; SMF – stem mass fraction [g g^{-1}]; FMF – flower mass fraction [g g^{-1}]; RMF – root mass fraction [g g^{-1}]; R/S – root/shoot ratio [g g^{-1}]. LSD$_{0.05}$ means the least squared difference at the $P \leq 0.05$. X, Y – means within the same column followed by *different lowercase letters* are significantly different at 0.05 level of single-factor *ANOVA*.

Factor	Treatment	SLA [cm^{2} g^{-1}]	LMF [g g^{-1}]	SMF [g g^{-1}]	FMF [g g^{-1}]	RMF [g g^{-1}]	R/S [g g^{-1}]
Irrigation	–10 kPa	254.45^{aX}	0.098	0.13^{a}	0.52^{b}	0.25^{a}	0.34^{a}
	–15 kPa	219.09^{b}	0.090	0.10^{b}	0.62^{a}	0.19^{b}	0.24^{b}
LSD$_{0.05}$		27.24	0.011	0.01	0.03	0.03	0.05
Fertilizer	6 g	241.35	0.091	0.12^{aY}	0.52^{b}	0.27^{a}	0.3^{8}a
	12 g	244.08	0.095	0.11^{b}	0.60^{a}	0.20^{b}	0.26^{b}
	18 g	224.88	0.096	0.11^{b}	0.60^{a}	0.19^{b}	0.24^{b}
LSD$_{0.05}$		18.16	0.007	0.01	0.02	0.02	0.04

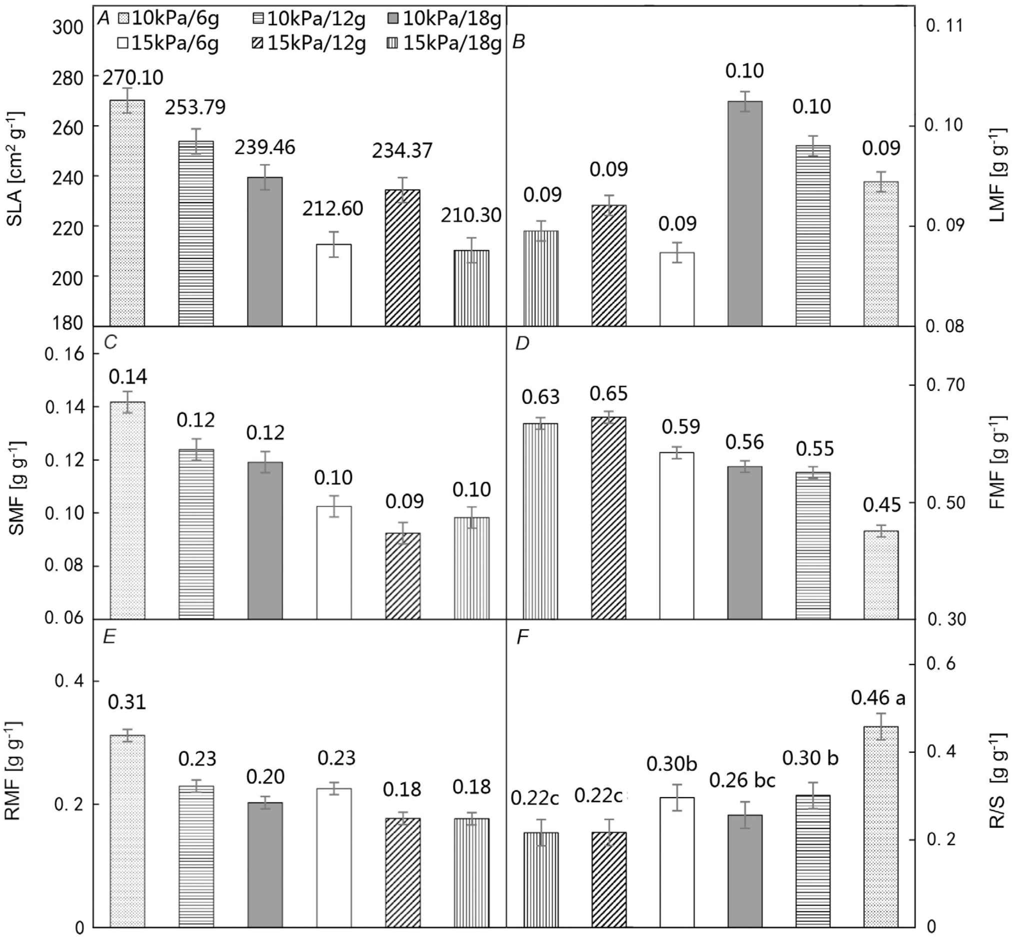

Fig. 2. Effect of biomass allocation on leaf development and root growth of sunflower exposed to the different combination of fertilizer and irrigation. (*A*) Specific leaf area, SLA; (*B*) leaf mass fraction, LMF; (*C*) stem mass fraction, SMF; (*D*) flower mass fraction, FMF; (*E*) root mass fraction, RMF; (*F*) root/shoot ratio, R/S. *Different lowercase letters* indicated significantly different means (two-way *ANOVA*, *P*≤0.05).

Table 3. The total cumulative contribution of components 1 and 2 of five biomass parameters of potted sunflower 'Choco Sun'. FMF – flower mass fraction; LMF – leaf mass fraction; RMF – root mass fraction; R/S – root/shoot ratio; SMF – stem mass fraction.

	Component 1		Component 2		Total cumulative variance [%]
	Extacted eigenvalues	Variance [%]	Extacted eigenvalues	Variance [%]	
LMF	0.384	7.06	0.922	11.45	18.51
SMF	0.974	17.91	0.193	2.40	20.31
FMF	–0.998	18.36	0.007	0.09	18.45
RMF	0.961	17.67	–0.271	3.36	21.03
R/S	0.956	17.58	–0.287	3.56	21.14
Total	4.273	78.58	1.680	20.86	99.44

Biomass allocation on commercial traits of potted flower: Low fertilizer amount (6 g per pot) generated a greater SMF, R/S, and RMF but a small FMF and TLA. If potted sunflower was grown in this condition, it would have good support at the expense of ornamental value including poor flowering performance.

Discussion

Optimal partitioning theory (OPT) was developed to predict how plants should optimally allot their metabolic production between leaves, stems, and roots in a limiting resource environment (McCarthy and Enquist 2007).

If the variation in organ mass allocation demonstrates an optimal partitioning model, it could be predicted that plants allocate more biomass to the organ that is closest to the limiting resource. Plants supplied with low nutrition would decrease the nutrient uptake and respiration consumption per unit root mass (van Wijk *et al.* 2003). Theoretically, the increased allocation to roots was observed for improving R/S, RMF, and decreasing LMF (Evans 1996, McConnaughay and Coleman 1999) in case of limited nutrients. Generally, plants will trade the greater carbon cost of root production to increase water acquisition capacity when water is limited (Smith-Martin *et al.* 2019). Therefore, there will be beneficial carbohydrate transportation from leaves to roots.

Our findings showed that R/S, RMF, and SMF decreased under drought. The performance of roots and stems in response to nutrient availability was in a manner compatible with optimal partitioning theory. But drought did not follow this rule. Presumably, sunflowers sustained a high WUE (8.47 μmol mol^{-1}) under drought to reduce the stress of roots on water absorption. Moreover, low water availability led to a reduction in water and nutrient uptake per unit root mass, which theoretically promoted a shift of more mass allocation from leaves to roots. However, water shortage simultaneously decreased the photosynthetic products because of a smaller leaf area and impaired the mass flow to roots. ULR and FMF revealed that drought enhanced the biomass allocation to leaves and flowers in favor of maintaining a high P_N of 19.19 μmol m^{-2} s^{-1} and reproductive growth. In other words, sunflower leaves and flowers inevitably increased competition in assimilation products and hampered its allocation to roots. Reduced photosynthesis also inhibited the shoot growth to the same extent. In short, drought caused more biomass allocation to the aboveground tissues of potted sunflowers and generated a low RMF, R/S, and SMF.

The biomass allocation strategy is various among plant life-forms among various organs. Poorter and Nagel (2000) concluded the averaged biomass allocation values of nearly 500 herbaceous plants. R/S attained 0.43. FMF, SMF, and RMF reached 0.46, 0.24, and 0.30 separately. They found that four parameters were extremely affected by nutrients and significant by water except for SMF. Changes in allocation patterns were relatively strong with nutrient supply and modest in the case of varying water supply (Müller *et al.* 2000). Roots, stems, flowers, and leaves of sunflower had distinctive response mechanisms to resource availability. Using PCA, the study showed that the root phenotype of potted sunflower exhibited greater variation in response to nutrients and water than stems, whereas leaf and flower plasticity showed greater stability.

LMF remained relatively constant and did not remarkably alter with water stress or fertilizer rate, which suggested that sunflowers invested more resources in the leaves. Some reported that the fraction of whole-plant mass represented by leaves (LMF) increased strongly with nutrients (Poorter *et al.* 2012). Alternatively, SLA responded to water rather than nutrients gradient and did not perform as OPT predicted. Previous studies indicated that lianas (*Distictis lactiflora* (Vahl) DC) allocate more biomass to leaves while trees allocate more to stems in response to water stress (Müller *et al.* 2000, Cai *et al.* 2007, van der Heijden *et al.* 2015).

More evidence showed that the reason why the plasticity in biomass allocation patterns was partially consistent with OPT could attribute to various responses to ontogenetical constraints, especially for rapidly growing annual species (McConnaughay and Coleman 1999). Presumably, adjustments in biomass allocation patterns of sunflower leaves partially depended on its ontogeny. In most comparisons across environmental factors, the variation in LMF is less than that in other components of the growth analysis equation: the leaf area (TLA) and SLA (Poorter *et al.* 2012). Our results also supported their findings. Any consequent increases in allocation to leaves proved to have a more rapid turnover time compared to other tissues (Powers *et al.* 2009). This may be an adaptative strategy for those plants grown with limited resources.

It was believed that increasing fertilizer rates under drought conditions could alleviate yield reduction and adverse effects in arid regions (Zhou *et al* 2011). Generally, biomass reduction caused a changeable morphological structure due to limited mass partitioning. Some crops were found to decline in plant height, tiller number, and leaf area index in saline soil (Semiz *et al.* 2012, Baath *et al.* 2017, Jafari *et al.* 2019).

For commercial quality, potted flowers require strong stem support to improve lodging-resistant capability. R/S could sustain the container stability by keeping a balance between aboveground and belowground parts. Therefore, SMF and R/S were two critical variables used to assess this quality. Meanwhile, reproductive biomass (FMF) represented the potential characters of flower numbers, flower size, and duration.

Our results revealed that increasing fertilizer under drought dramatically promoted flower yield and maintained LMF stability at the expense of stem and root production but impaired its flower production. If SMF, R/S, and FMF under medium rate with normal watering (–10 kPa/12 g) were taken as the reference frame, drought decreased SMF, TLA, and R/S but increased FMF. Potted sunflowers grown under these conditions tend to have a typical phenotype with small leaf size, slim stem, poor root system, weak lodging-resistance despite greater flower production. In our research, a high fertilizer rate produced a low FUE although increasing fertilizer could prevent a sharp reduction in yield, but this comes at a greater economic cost in greenhouse production.

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