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Clean application of pistachio residues-based vermicompost with γ-aminobutyric acid can alleviate the negative effects of high soil pH on P uptake in saffron (*Crocus sativus* L.)

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ABSTRACT

In semiarid areas dominated by calcareous soils, a large portion of available P may be deformed into insoluble structures due to the chemical activity of carbonate compounds. This phenomenon, known as P deficiency stress, is considered one of the most important limiting factors for saffron (*Crocus sativus* L.) production. To avoid P limitation, the application of clean and practical techniques has been emphasized to improve saffron adaptability grown in P-deficient calcareous soils. Hence, field experiments were conducted based on a factorial randomized complete block design with three replicates during 2017–2018 and 2018–2019 (farm 1) and repeated during 2018–2019 and 2019–2020 growing seasons (farm 2). Four levels of γ-aminobutyric acid (GABA) (0, 0.5, 1, and 2 mg L^{-1}) and soil amendments (control, pistachio residues-based vermicompost (V_P: 10 t ha^{-1}; 50% in each growing season), sulfur (S: 100 kg ha^{-1}; 50% in each growing season), and V_P +S) were considered as experimental factors. From the results, application of V_P, S, and V_{P+S} decreased soil pH and increased Olsen-P, microbial biomass, and microbial respiration. Furthermore, the increase was observed for flower number, proline content and corm growth. Following GABA foliar application, flower number, proline content and P availability improved. Compared to control treatment, P concentration in large-sized daughter corms increased by 23.6, 16.8%, and 30.8%, following V_P, S, and V_P +S, respectively. Among the treatments, the highest P acquisition efficiency (39.2%) were recorded by applying V_P +S along with 2 mg L^{-1}. Overall, the results recommend the co-application of V_P with GABA foliar spray to improve saffron production grown in calcareous soils of semiarid regions.

1. Introduction

Saffron (*Crocus sativus* L.), a geophyte herbaceous plant from the Iridaceae family, is widely distributed in arid and semi-arid regions, especially northeastern Iran (Koocheki et al., 2014). Despite the relative adaptation of *Crocus* species to stressful conditions (Yarami and Sepaskhah, 2015), the shortage or low absorption of nutrients including P, Zn, and Fe, are considered as one of the main concerns for optimizing saffron production in these regions (Daneshmandi and Seyyedi, 2019).

Nutrient deficiency in plants grown under the arid and semi-arid areas, dominated by carbonate compounds, is predominantly due to high soil pH (Zaiter et al., 1993; Zhang et al., 2016). For instance, when soil chemical status is described by calcareous or alkaline compounds, available P can react with Ca and produce insoluble complexes (Sameni and Kasraian, 2004). Hence, by increasing the content of carbonate minerals, such as calcium carbonate, P solubility can be dramatically reduced (Mohammady Aria et al., 2010; Seyyedi et al., 2018).

While the clay-loam and well-drained soils containing high organic matter are recognized a suitable bed for saffron corm growth (Behnia et al., 1999), the low soil fertility resulting from poor organic carbon is known as another limiting factor against sustainable production (Seyyedi et al., 2018). The inadequate content of organic matter, a dominant phenomenon in calcareous soils (Clemente et al., 2006), is observed in many arid and semi-arid regions of the world (Barton et al., 2016), especially in the eastern, central, and southern regions of Iran (Fooladmand, 2008; Havaee et al., 2014). Furthermore, the life cycle of

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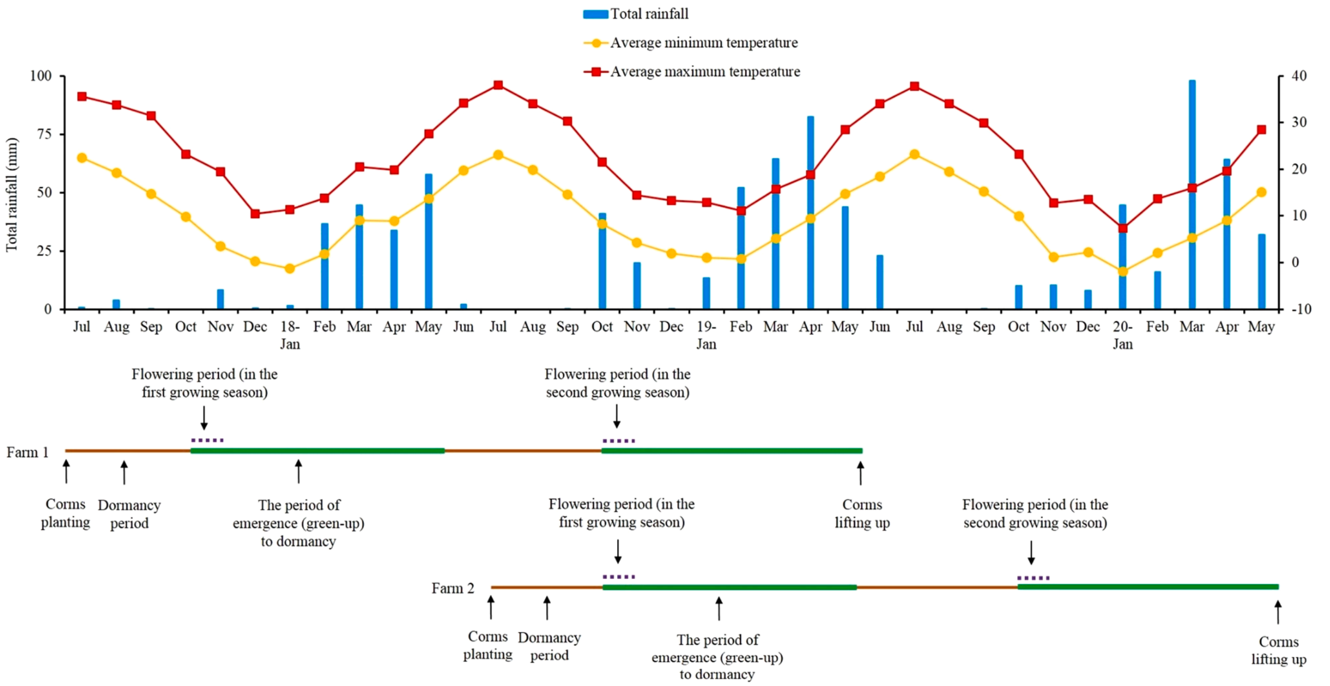

Fig. 1. Monthly rainfall and average temperature in Farm 1 (2017–2018 and 2018–2019) and Farm 2 (2018–2019 and 2019–2020). Both farms were located at the experimental station, Faculty of Agriculture, Ferdowsi University of Mashhad, Iran.

saffron, known as a perennial crop (Koocheki and Seyyedi, 2015), may negatively affect the soil physical and chemical parameters over the long term (Seyyedi et al., 2018). Accordingly, exposure to nutrient stress can be recognized as an inevitable consequence during the multi-life cycle of saffron.

The application of sulfur (S) and its oxidation by *Thiobacillus* bacteria, especially *T. thiooxidans* (T), can increase P solubility in the rhizosphere by producing sulfuric acid (Daneshmandi and Seyyedi, 2019; Sameni and Kasraian, 2004). Furthermore, increasing the availability of nutrients through applying organic wastes (Leytem et al., 2011; Sileshi et al., 2019), such as pistachio residues-based vermicompost (V_P) (Esmaeili et al., 2020), is another approach for improving plant production. In this regard, pistachio wastes are produced at a rate of 2000 t yr^{-1} in Feyzabad region, northeastern Iran (Agricultural statistics, 2019), which can be subjected to composting and vermicomposting processes (Jalili et al., 2019). However, there is still no comprehensive study to evaluate flower yield and P uptake in saffron affected by the interaction between S and V_P.

Besides improving soil fertility, the exogenous application of protective osmolytes such as γ-Aminobutyric acid (GABA) can play a special role in increasing plant physiological resistance against adverse environmental factors (Li et al., 2016; Rezaei-Chiyaneh et al., 2018). GABA, acting as an endogenous signal molecule, is a well-known plant growth regulator in response to environmental stresses to optimize osmotic potential and stabilize cell membrane (Kinnersley and Turano, 2000; Soleimani Aghdam et al., 2016). The positive role of exogenous GABA in increasing white clover (Yong et al., 2019), black cumin (Rezaei--Chiyaneh et al., 2018), and medicinal pumpkin (Tavakkol Afshari and Seyyedi, 2020) tolerance against drought conditions have been reported. The improved adaptability of plants to chilling (Wang et al., 2014), oxidative (Song et al., 2010), and salinity (Jin et al., 2019) stresses caused by GABA application have also been observed. However, the effect of GABA on adjusting nutrient uptake is still not well known. In addition, it is relatively unclear what interaction may be established between the application of V_P and GABA in plants under P-deficient calcareous soils.

The current study was aimed to evaluate how soil amendments and GABA affect flower yield and daughter corms growth in saffron. To better understand this effect, the changes in chemical and biological indices of soil were also examined during the growing season.

2. Material and methods

2.1. Site description

The experiment was conducted during 2017–2018 and 2018–2019 (farm 1) and repeated during 2018–2019 and 2019–2020 growing seasons (farm 2) at the experimental station, Faculty of Agriculture, Ferdowsi University of Mashhad, Iran (latitude: 36°15′ N; longitude: 59°28′E; elevation: 985 m asl). Monthly rainfall and average temperature during the experiment are presented in Fig. 1.

The selected farms were adjacent to each other and had the same soil texture. Some soil physical and chemical properties of sites (0–30 cm depth) before the experiment were as follows:

Farm 1: clay, sand, and silt 41.30%, 26.11%, and 32.59%, respectively; OC 0.43%; available N, P, and K 13.26, 7.73, and 189.19 mg kg^{-1}, respectively; pH 8.36; EC 1.39 dS m^{-1}; $CaCO_3$ 18.66%.

Farm 2: clay, sand, and silt 42.48%, 28.92%, and 28.60%, respectively; OC 0.47%; available N, P, and K 12.56, 8.33, and 201.21 mg kg^{-1}, respectively; pH 8.28; EC 1.26 dS m^{-1}; $CaCO_3$ 15.80%.

2.2. Experimental design

The study was carried out based on a factorial randomized complete block design with three replicates. Four levels of GABA (0, 0.5, 1, and 2 mg L^{-1}) and soil amendments (control, V_P, S, and V_P +S) were considered as the first and the second experimental factors, respectively.

2.3. Agronomic practices

According to the local practice for saffron production, the planting bed was prepared by applying plow, disk, and leveler and then plots (2.5 m long × 1.5 m width) were designed. Between plots and blocks, 1 and 2 m alley were kept as buffer zone, respectively.

Table 1
Irrigation schemes for saffron in farm 1 and 2 at the experimental station, Ferdowsi University of Mashhad, Iran.

Farm 1		Farm 2	
2017–2018	2018–2019	2018–2019	2019–2020
20 August 2017	23 August 2018	18 August 2018	21 August 2019
21 September 2017	21 September 2018	22 September 2018	23 September 2019
10 November 2017	9 November 2018	12 November 2018	11 November 2019
15 March 2018	17 March 2019	18 March 2019	16 March 2020
10 April 2018	12 April 2019	8 April 2019	11 April 2020

pistachio residues-based vermicompost was produced by the activity of earthworms on organic wastes: 90% pistachio residues (produced after peeling operation) + 10% cow manure. The operating period of vermicomposting was set for 60 days, during which the environment was controlled in terms of temperature (24–27 °C), humidity 35–40%) and light conditions. The chemical analysis of the final product was as follow: OM 36.72%; pH 7.94; EC 12.55 dS m^{-1}. Due to soil infertility in farm 1, caused by low OC (0.43%) and high pH (8.36), V_P and S were applied on 4 September 2017 and 8 September 2018. The application method was 50% of V_P (5 t ha^{-1}) and 50% of S (100 kg ha^{-1}) in each growing season. Along with S application, T (10 L ha^{-1}) was incorporated into the soil as recommended by the company that produced it. (Dayan Company, Iran) Similarly, V_P, S, and T was applied in farm 2 (8 September 2018 and 11 September 2019).

According to the basin method, 10–12 g corms were planted (100 corms m^{-2}) at 15 cm depth with 25 cm distance between rows on 4 July 2017 (farm 1) and 8 July 2018 (farm 2). Irrigation scheme (Table 1) was performed separately for each plot using polyethylene pipe network equipped with the valve and counter. In Farm 1, GABA (Sigma-Aldrich company; Linear Formula: $NH_2(CH_2)_3COOH$; CAS No.: 56–12–2; MW: 103.12 g mol^{-1}) foliar spraying was performed according to the treatments after flower picking on 14 November (In 2-leaf stage with an average leaf length of 8 cm) 2017 and 13 November 2018 (In 3-leaf stage with an average leaf length of 10 cm). The same spraying in the farm 2 was done on 16 November 2018 and 15 November, 2019. In both farms, no chemicals (insecticide, herbicide or fungicide) were applied and weeds were controlled by hand-removal.

2.4. Measurements

All samples were taken from central part of each plot (2 m long × 1 m width) to eliminate the effects of lateral treatments.

2.4.1. Soil-related measurements

In farm 1, Olsen-P (Olsen (1954), pH (using a JENWAY 3510 pH meter), microbial biomass (Jenkinson and Powlson, 1976), and microbial respiration (Black and Stotzky, 1965) were determined at four times: 14 November 2017 (after flowering in the first growing seasons), 27 May 2018 (at the end of the first growing season), 13 November 2018 (after flowering in the second growing seasons), 28 May 2019 (at the end of the second growing season). In farm 2, all traits were similarly determined on 16 November 2018, 28 May 2019, 15 November 2019, and 30 May 2020.

2.4.2. Flower-, leaf-, and corm-related measurements

In the both farms, flowers were manually picked up daily during October-November. The stigma was separated from the flower and dried in an oven at 30 °C for 24 h (Gresta et al., 2009).

Concurrent with maximum vegetative growth stage in each season (farm 1: 4 April 2018 and 6 April 2019; farm 2: 3 April 2019 and 6 April 2020), three fresh leaves were randomly selected and proline content was measured as suggested by Bates et al. (1973). Moreover, average leaf length (ALL_{max}) and leaf area index (LAI_{max}) were estimated non-destructively (Kumar, 2009):

$ILA = 191.33\, e^{(L)\, 0.0037}$ (Eq. 1).

ILA: individual leaf area (mm^2), L: leaf length (mm),

$LAP = ILA_1 + ILA_2 + ILA_3 + \ldots$ (Eq. 2).

LAP: leaf area $plant^{-1}$.

At the end of second growing season (farm 1: 28 May 2019; farm 2: 30 May 2020), daughter corms were lifted up and related indices were recorded in three separate groups: < 5 g or small sized, 5.0–10 g or mid-sized and > 10 g or large-sized. Then, P concentration in daughter corms and aerial part were measured according to Murphy and Riley (1962) method.

As suggested by Koocheki and Seyyedi (2015), P acquisition efficiency (PAE) was calculated using Eq. (3−4):

$P_T = P_P + P_O$ (Eq. 3).

PAE (%) $= (P_P / P_T) \times 100$ (Eq. 4).

Table 2
Some soil characteristics as affected by farm type, soil amendments, GABA application, and sampling rounds.

Treatments	Soil pH	Olsen-P (mg kg^{-1})	Microbial biomass (mg 100 g^{-1})	Microbial respiration (mg CO_2 g^{-1} soil)
Farm (F)				
Farm 1 (2017–2018 and 2018–2019)	7.99 a	18.69 b	52.72 a	0.0459 a
Farm 2 (2018–2019 and 2019–2020)	7.87 b	19.22 a	55.53 a	0.0463 a
Soil amendments (A)				
Control	8.24 a	9.33 d	18.31 d	0.0281 d
Pistachio residues-based vermicompost (V_P)	7.94 b	23.98 b	70.36 b	0.0516 b
Sulfur (S)	7.80c	17.11c	46.17c	0.0468c
V_P + S	7.74 d	25.41 a	81.66 a	0.0580 a
GABA application (G)				
0 mg L^{-1}	7.93 a	18.91 a	51.65 a	0.0455 a
0.5 mg L^{-1}	7.94 a	18.95 a	55.19 a	0.0459 a
1 mg L^{-1}	7.93 a	18.86 a	54.35 a	0.0463 a
2 mg L^{-1}	7.93 a	19.09 a	55.30 a	0.0464 a
Sampling rounds (R)				
First	8.21 a	14.47 d	43.27c	0.0426c
Second	7.92 b	18.18c	50.05 b	0.0453 b
Third	7.85c	20.89 b	59.88 a	0.0476 a
fourth	7.74 d	22.28 a	63.30 a	0.0489 a
Sources of variations				
F	* *	* *	*	*NS*
A	* *	* *	* *	* *
G	*NS*	*NS*	*NS*	*NS*
AG	*NS*	*NS*	*NS*	*NS*
FA	* *	* *	*NS*	*NS*
FG	*NS*	*NS*	*NS*	*NS*
FAG	*NS*	*NS*	*NS*	*NS*
R	* *	* *	* *	* *
AR	* *	* *	* *	*
GR	*NS*	*NS*	*NS*	*NS*
FR	* *	* *	*NS*	*NS*
FAR	* *	*	*NS*	*NS*
FGR	*NS*	*NS*	*NS*	*NS*
AGR	*NS*	*	*NS*	*NS*
FAGR	*NS*	*NS*	*NS*	*NS*

* *: significant at $P \leq 0.01$; *: significant at $0.01 < P \leq 0.05$; NS: non-significant ($0.05 < P$).
Value followed by the same letter are not significantly different (Duncan's multiple range test at 5% level).

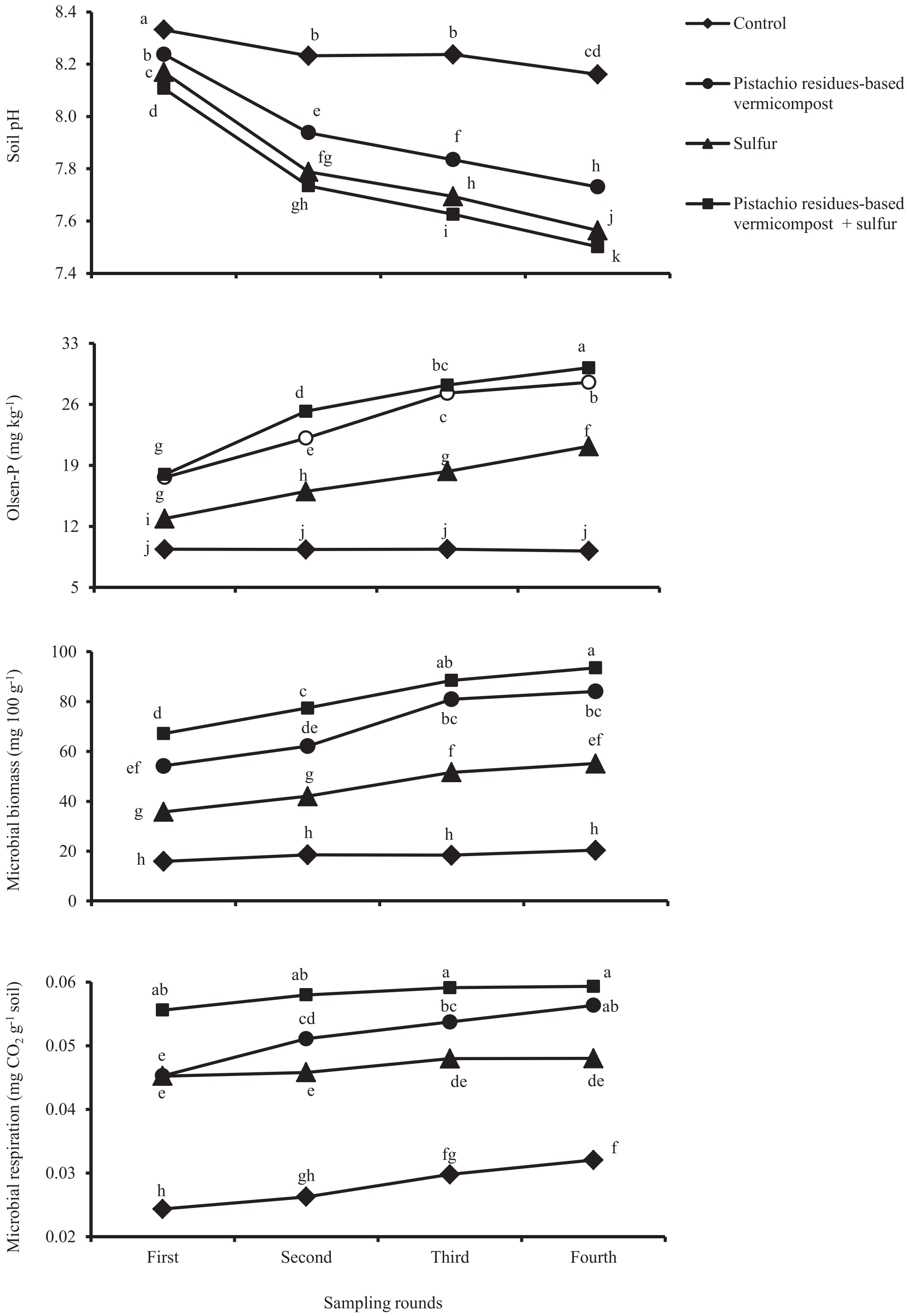

Fig. 2. Interaction effects of soil amendments and sampling rounds on soil pH, Olsen-P, microbial biomass, and microbial respiration. Value followed by the same letter are not significantly different (Duncan's multiple range test at 5% level).

P_P: P content (g m^{-2}) in plant (aerial part + daughter corms), P_O: Olsen-P (g m^{-2}) at the end of second growing season (based on soil bulk density at the depth of 25 cm), P_T: Total available P (g m^{-2}) added to the soil as a result of fertilizer inputs.

2.5. Statistical analysis

All the data were analyzed according to combined analyses as follows:

Flower- and leaf-related traits: A randomized complete block design arranged in factorial-split including 16 main plots (soil amendments × GABA application) and 2 sub-plots (two samples).

Soil-related traits: A randomized complete block design arranged in factorial-split including 16 main plots (soil amendments × GABA application) and 2 sub-plots (four samples).

Corm-related traits: A randomized complete block design arranged in factorial (soil amendments and GABA application as the first and the second experimental factors, respectively).

The analysis of variance and Duncan's multiple range test ($P \leq 0.05$) were performed using SAS 9.3 software (SAS, 2011).

3. Results

This experiment was considered to be too complex due to the high

Table 3
Flower and leaf traits of saffron as affected by farm type, soil amendments, GABA application, and sampling rounds.

Treatments	Flower number (m^2)	Dried stigma yield (kg ha^{-1})	ALL (mm $plant^{-1}$)	LAI	Proline (μg g^{-1} FW)
Farm type (F)					
Farm 1 (2017–2018 and 2018–2019)	139 a	4.497 b	286.8 b	0.87 b	15.61 a
Farm 2 (2018–2019 and 2019–2020)	144 a	4.776 a	313.3 a	0.95 a	16.14 a
Soil amendments (A)					
Control	115c	3.728c	268.6c	0.52c	13.27 b
Pistachio residues-based vermicompost (V_P)	156 a	5.122 a	314.5 a	1.13 a	16.19 a
Sulfur (S)	133 b	4.350 b	291.7 b	0.80 b	15.72 a
V_P + S	162 a	5.347 a	325.3 a	1.20 a	16.48 a
GABA application (G)					
0 mg L^{-1}	132c	4.327 b	276.8c	0.74c	13.89c
0.5 mg L^{-1}	139 BCE	4.558 ab	297.5 b	0.90 b	15.62 b
1 mg L^{-1}	146 ab	4.784 a	311.1 ab	0.99 ab	16.81 ab
2 mg L^{-1}	148 a	4.878 a	314.7 a	1.03 a	17.18 a
Sampling rounds (R)					
First	83 b	2.706 b	237.8 b	0.35 b	14.94 b
Second	200 a	6.567 a	362.2 a	1.48 a	16.80 a
Sources of variations					
F	*NS*	* *	* *	* *	*NS*
A	* *	* *	* *	* *	*
G	* *	* *	* *	*	* *
AG	*NS*	*NS*	*NS*	*NS*	*NS*
FA	*NS*	*NS*	*NS*	*NS*	*NS*
FG	*NS*	*NS*	*NS*	*NS*	*NS*
FAG	*NS*	*NS*	*NS*	*NS*	*NS*
R	* *	* *	* *	* *	*NS*
AR	* *	* *	* *	*	*NS*
GR	* *	* *	*	* *	*NS*
FR	*NS*	*NS*	*NS*	*NS*	*NS*
FAR	*NS*	*NS*	*NS*	*NS*	*NS*
FGR	*NS*	*NS*	*NS*	*NS*	*NS*
AGR	*NS*	*NS*	*NS*	*NS*	*NS*
FAGR	*NS*	*NS*	*NS*	*NS*	*NS*

* *: significant at $P \leq 0.01$; * : significant at $0.01 < P \leq 0.05$; NS: non-significant ($0.05 < P$).
Value followed by the same letter are not significantly different (Duncan's multiple range test at 5% level).
ALL_{max} and LAI_{max}: average leaf length and leaf area index, respectively, when recorded at maximum values during the growing season.

number of treatments. Hence, the results related to the farm effect and its interaction were omitted.

3.1. Soil-related traits

Soil pH and Olsen-P were significantly affected by the individual and interaction effects of soil amendments (A) and sampling rounds (R). However, the individual effects of GABA and interaction GABA × A or GABA × R were not significant (Table 2).

When control treatment (no fertilizer application) was tested, the maximum soil pH was recorded, while the application of soil amendments exacerbated the decrease in soil pH index, compared with control conditions. For example, soil pH was recorded as 7.50 by applying V_P +S at the end of the growing season (Fig. 2). At the same time, this value was found to be 8.16 in the control treatment (Fig. 2).

Concurrent with soil pH reduction, P solubility significantly increased during the growing season. Considering the interaction of A and R, the maximum Olsen-P (30.21 mg kg^{-1}) was recorded as a result of V_P +S in the fourth stage (Fig. 2). Similar results were found for microbial biomass and microbial respiration (Fig. 2).

3.2. Flower- and leaf-related traits

According to the results, V_P played a significant role in increasing flower number, dried stigma yield, ALL, LAI, and proline content. On the other hand, there was no significant difference between V_P and V_P +S in terms of these traits. In addition, all traits were significantly higher in the second sampling than in the first sampling (Table 3). Based on the interaction of A and R, the maximum flower number, dried stigma yield, ALL, and LAI were observed in the second sampling after applying V_P +S (Fig. 3).

With increasing the concentration of GABA application, a significant upward trend was observed in flower number, dried stigma yield, ALL, LAI, and proline content (Table 3). Moreover, all traits were significantly affected by G × R except for proline content. the maximum values were obtained in the second sampling after 2 mg L^{-1} GABA (Fig. 4).

3.3. Daughter corms-related traits

The individual and interaction effects of A and GABA had significant effects on daughter corms number and weight (Table 4). Irrespective of GABA, the maximum number and weight of small-sized (<5 g) daughter corms were obtained in control treatment. Nonetheless, the number of small-sized daughter corms decreased significantly when V_P or S was applied. In terms of large-sized (> 10.0 g) daughter corms, the best results were recorded in V_P +S treatment (Table 4).

Following GABA foliar application, the number and weight of small-sized daughter corms decreased, while the number and weight of middle- and large-sized daughter corms significantly increased (Table 4). The maximum values were observed after applying 2 mg L^{-1} GABA concurrent with V_P +S application (Table 5).

3.4. P uptake-related traits

All calcareous soil amendments showed a significant effect on P concentration in daughter corms and aerial part (Table 6). For example, after the application of V_P treatment, P concentration in large-sized daughter corms increased by 23.6% compared to control treatment. Similar results were observed following S (16.8%) and V_P +S (30.8%) (Table 6).

From the results, GABA foliar spray alleviated the adverse effect of P deficiency on daughter corms (Table 6). For instance, when the non-fertilizer treatment was considered, 2 mg L^{-1} GABA increased P concentration in large-sized daughter corms by 10.3% compared to control (no foliar spray). Under similar conditions, PAE increased up to 29.7%. Among the treatments, the highest P concentration in large-sized daughter corms (3.22 g kg^{-1}) and PAE (39.21%) were recorded by applying V_P +S along with 2 mg L^{-1} GABA (Fig. 5).

4. Discussion

4.1. Soil-related traits

As mentioned before, saffron is known as a relatively adapted plant to arid and semi-arid environments (Koocheki et al., 2014). However, low organic matter content occurring in parallel with the deficiency of available nutrients, especially P, are the main limiting factors for saffron

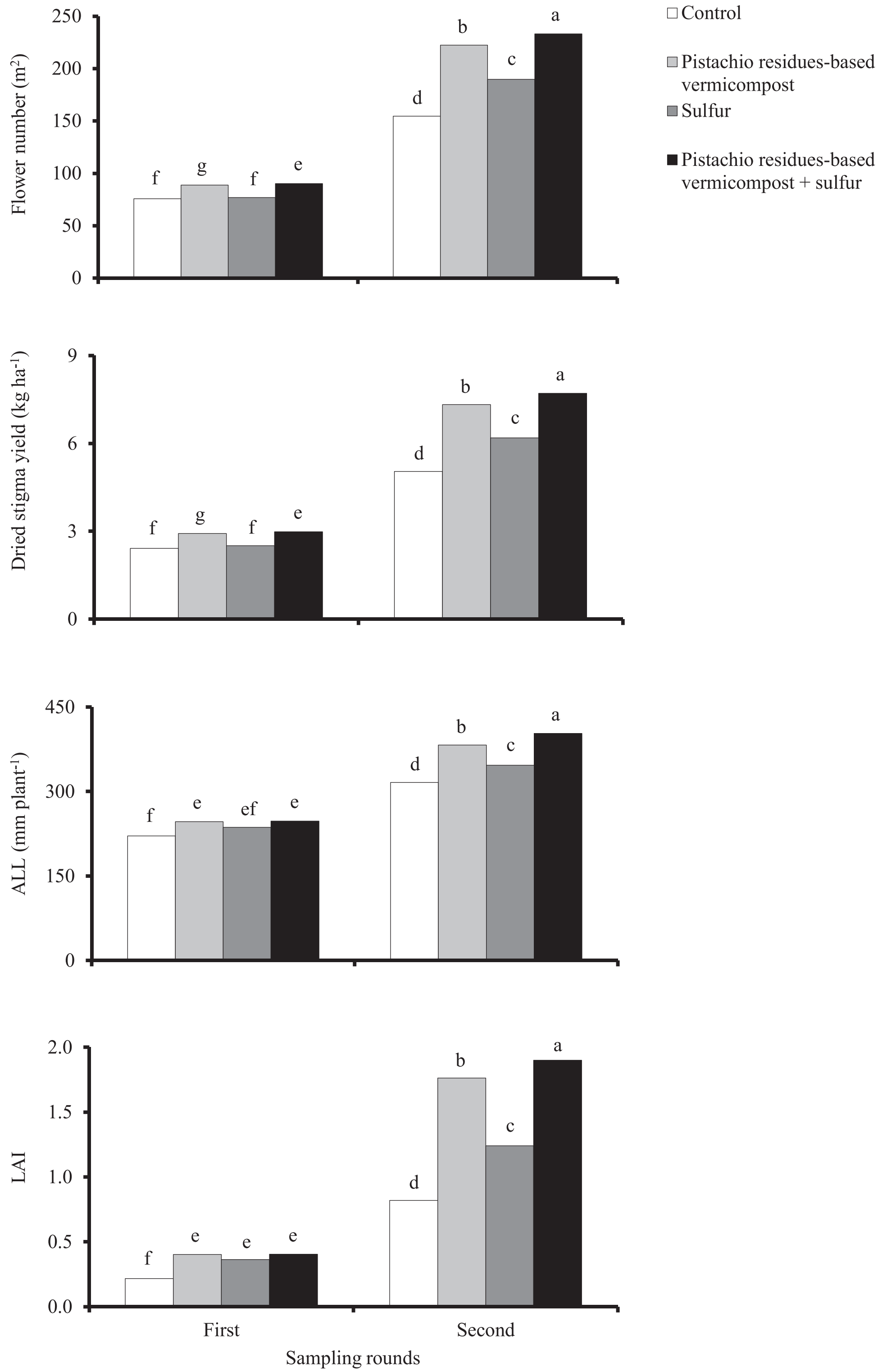

Fig. 3. Interaction effects of soil amendments and sampling rounds on flower number, dried stigma yield, ALL, and LAI. Value followed by the same letter are not significantly different (Duncan's multiple range test at 5% level).

production in these regions (Daneshmandi and Seyyedi, 2019).

Under calcareous soils, typically found in semi-arid areas, limited P uptake is usually not attributed to low soil P content (Khanmirzaei et al., 2009). In other words, the plant exposure to P deficiency stress may occur by transforming a large portion of available P to insoluble complexes (Sameni and Kasraian, 2004).

Some natural processes have a positive role in reducing soil pH. For instance, carbon dioxide (CO_2), produced by root respiration or bacterial activity, can slightly reduce soil pH by converting to carbonic acid (H_2CO_3) (Kuzyakov, 2006). As previously state, V_P contains a balanced amount of organic carbon. During organic matter decomposition, the production of organic acids can considerably reduce soil pH and simultaneously increase the conversion rate of insoluble P to soluble form (Adi and Noor, 2009; Parastesh et al., 2019). These changes may be

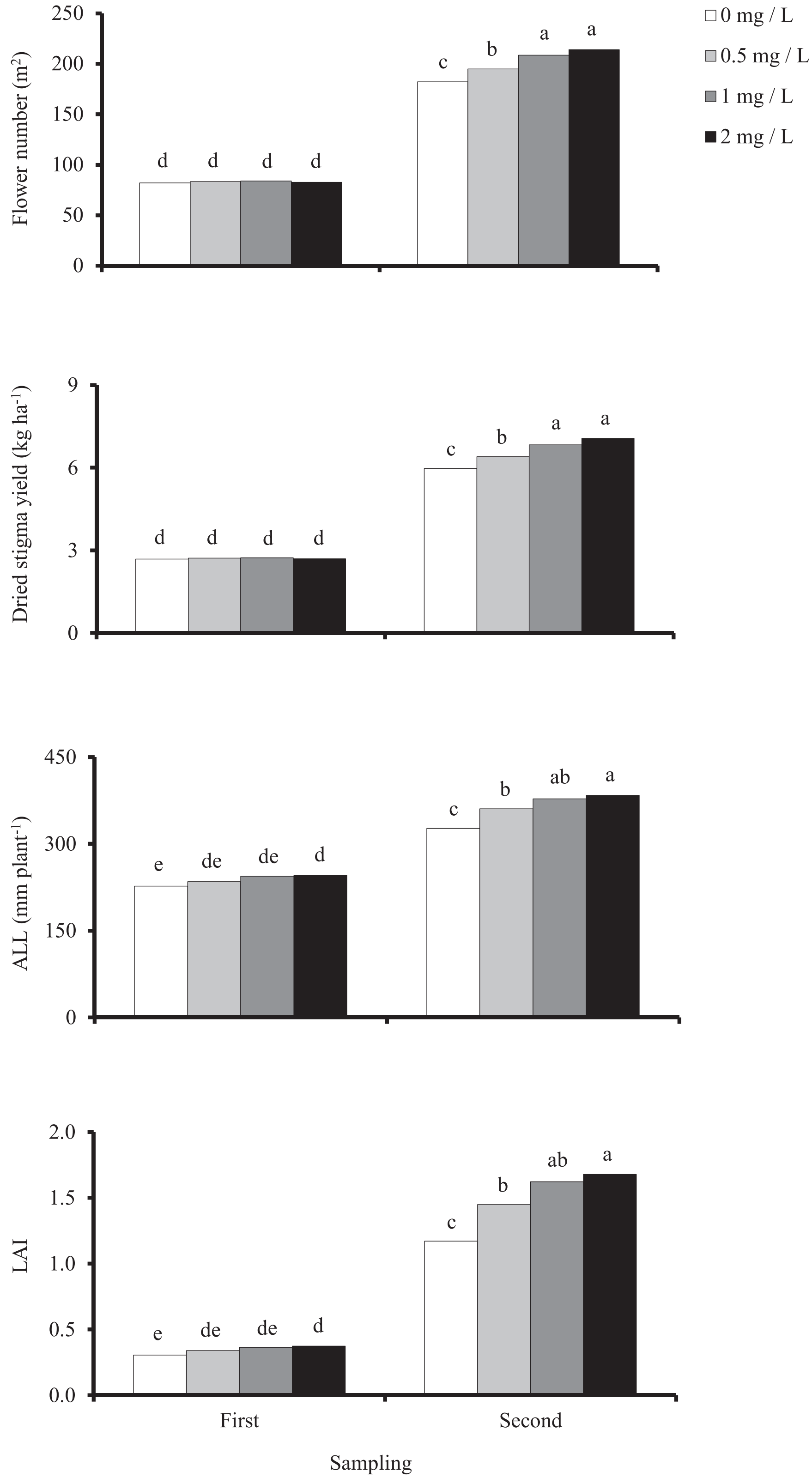

Fig. 4. Interaction effects of GABA application and sampling rounds on flower number, dried stigma yield, ALL, and LAI. Value followed by the same letter are not significantly different (Duncan's multiple range test at 5% level).

a justification for increased soil respiration and P solubility due to V_P application.

Sulfuric acid (H_2SO_4) production, resulting from biological S oxidation, is considered another effective approach to decline soil pH, dissolve calcium phosphate and finally augment P availability (Pith Otero et al., 1995). In this regard, *T. thiooxidans* is one of the best known S-oxidizing bacteria in arid and semi-arid areas (Ansari et al., 2017; Seyyedi et al., 2015). Applying organic inputs commonly leads to a positive effect in terms of accelerating S oxidation, because the main source of energy needed for these microorganisms can be derived from

Table 4
Number and weight of saffron daughter corms as affected by farm type, soil amendments, GABA application, and sampling rounds.

Treatments	< 5.0 g		5.0–10.0 g		> 10.0 g	
	Number (m^2)	Weight (g m^2)	Number (m^2)	Weight (g m^2)	Number (m^2)	Weight (g m^2)
Farm (F)						
Farm 1 (2017–2018 and 2018–2019)	241.25 (51.61) a	509.29 a	138.56 (29.64) a	1130.02 a	87.63 (18.75) a	1182.78 a
Farm 2 (2018–2019 and 2019–2020)	235.38 (50.33) a	491.34 a	141.15 (30.18) a	1164.25 a	91.10 (19.48) a	1210.97 a
Soil amendments (A)						
Control	416.58 (82.78) a	812.29 a	58.25 (11.57) d	374.14 d	28.42 (5.65) d	316.63 d
Pistachio residues-based vermicompost (V_P)	151.75 (33.31) c	353.84c	172.29 (37.81) b	1487.39 b	131.58 (28.88) b	1772.78 b
Sulfur (S)	273.00 (58.60) b	552.02 b	137.54 (29.52) c	1104.71c	55.33 (11.88) c	658.47c
V_P + S	123.92 (27.09) d	311.10 d	191.33 (41.83) a	1682.32 a	142.13 (31.07) a	1999.63 a
GABA application (G)						
0 mg L^{-1}	280.42 (58.32) a	563.38 a	126.63 (26.34) c	1005.13c	73.79 (15.35) c	936.41c
0.5 mg L^{-1}	256.00 (53.69) b	524.93 b	136.75 (28.68) b	1131.28 b	84.04 (17.63) b	1096.79 b
1 mg L^{-1}	220.46 (47.45) c	476.48c	146.79 (31.59) a	1240.82 a	97.38 (20.96) a	1325.20 a
2 mg L^{-1}	208.38 (45.31) c	464.46c	149.25 (32.45) a	1271.32 a	102.25 (22.23) a	1389.11 a
Sources of variations						
F	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
A	* *	* *	* *	* *	* *	* *
G	* *	* *	* *	* *	* *	* *
AG	* *	* *	*	*	*	* *
FA	*NS*	*NS*	* *	* *	*NS*	*NS*
FG	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
FAG	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*

* *: significant at $P \leq 0.01$; * : significant at $0.01 < P \leq 0.05$; NS: non-significant ($0.05 < P$).
Value followed by the same letter are not significantly different (Duncan's multiple range test at 5% level).
Numbers in parentheses show the percentage of daughter corms from total daughter corms.

Table 5
Interaction effects of soil amendments and GABA application on number and weight of saffron daughter corms.

Soil amendments	GABA application (mg L^{-1})	< 5.0 g		5.0–10.0 g		> 10.0 g	
		Number (m^2)	Weight (g m^2)	Number (m^2)	Weight (g m^2)	Number (m^2)	Weight (g m^2)
Control	0	469.7 (87.76) a	881.9 a	46.67 (8.72) i	246.2 g	18.83 (3.52) k	193.3 k
	0.5	451.8 (85.04) a	864.4 a	55.17 (10.38) hi	338.1 g	24.33 (4.58) jk	258.8 jk
	1	387.5 (79.84) b	783.9 b	64.83 (13.36) gh	445.6 f	33.00 (6.80) j	376.7 ijk
	2	357.3 (77.48) c	719.0c	66.33 (14.38) g	466.6 f	37.50 (8.13) ij	437.8 hij
Pistachio residues-based vermicompost (V_P)	0	177.2 (40.31) f	390.5 g	154.7 (35.19) e	1279.5 d	107.7 (24.50) f	1358.1 f
	0.5	159.0 (34.85) fg	363.4 gh	171.3 (37.54) d	1475.4c	126.0 (27.61) de	1691.6 e
	1	142.5 (30.65) gh	333.8 gh	179.8 (38.67) cd	1569.3 BCE	142.7 (30.69) bc	1967.5 cd
	2	128.3 (27.79) hi	327.7 gh	183.3 (39.71) c	1625.3 b	150.0 (32.50) ab	2073.9 BCE
Sulfur (S)	0	332.3 (65.85) c	648.8c	125.3 (24.83) f	973.8 e	47.00 (9.31) hi	563.0 ghi
	0.5	285.2 (60.98) d	572.1 e	132.5 (28.33) f	1050.5 e	50.00 (10.69) hi	609.1 gh
	1	237.5 (53.69) e	489.1 f	144.5 (32.67) e	1183.6 d	60.33 (13.64) gh	716.9 g
	2	237.0 (52.81) e	498.0 f	147.8 (32.93) e	1211.0 d	64.00 (14.26) g	744.8 g
V_P + S	0	142.5 (32.09) gh	332.4 gh	179.8 (40.50) cd	1521.0c	121.7 (27.41) e	1631.2 e
	0.5	128.0 (28.33) hi	299.7 h	188.0 (41.61) bc	1661.1 b	135.8 (30.06) cd	1827.6 de
	1	114.3 (24.54) hi	299.1 h	198.0 (42.51) ab	1764.8 a	153.5 (32.95) ab	2239.7 ab
	2	110.8 (23.69) i	313.1 h	199.5 (42.65) a	1782.3 a	157.5 (33.67) a	2300.0 a

Value followed by the same letter are not significantly different (Duncan's multiple range test at 5% level).
Numbers in parentheses show the percentage of daughter corms from total daughter corms.

oxidizable inorganic and organic S compounds (Mohammady Aria et al., 2010; Vidyalakshmi, 2009). This can be a reason for further reduction of soil pH in V_P +S compared to S treatment, followed by a higher increase in microbial biomass and microbial respiration.

Table 6
P uptake-related traits of saffron as affected by farm type, soil amendments, and GABA application.

Experimental treatments	P concentration ($g\ kg^{-1}$)				P acquisition efficiency (%)
	Daughter corms			Aerial part	
	< 5.0 g	5.0–10.0 g	> 10.0 g		
Farm (F)					
Farm 1 (2017–2018 and 2018–2019)	1.65 a	1.91 a	2.82 a	1.45 a	32.48 a
Farm 2 (2018–2019 and 2019–2020)	1.46 b	1.86 b	2.76 b	1.44 a	29.96 b
Soil amendments (A)					
Control	1.26c	1.49 d	2.37 d	1.21 b	29.27c
Pistachio residues-based vermicompost (V_P)	1.69 a	2.03 b	2.93 b	1.54 a	33.23 b
Sulfur (S)	1.55 b	1.88c	2.77c	1.49 a	26.78 d
V_P + S	1.73 a	2.13 a	3.10 a	1.57 a	35.60 a
GABA application (G)					
0 mg L^{-1}	1.44 d	1.70c	2.67c	1.36 b	26.75c
0.5 mg L^{-1}	1.55c	1.87 b	2.77 b	1.43 ab	30.15 b
1 mg L^{-1}	1.60 b	1.96 a	2.84 a	1.50 a	33.45 a
2 mg L^{-1}	1.64 a	2.00 a	2.88 a	1.53 a	34.53 a
Sources of variations					
F	* *	* *	* *	*NS*	* *
A	* *	* *	* *	* *	* *
G	* *	* *	* *	* *	* *
AG	*NS*	*NS*	*	*NS*	*
FA	* *	* *	* *	*NS*	* *
FG	*NS*	*NS*	*	*NS*	*NS*
FAG	*NS*	*NS*	*	*NS*	*NS*

* *: significant at $P \leq 0.01$; *: significant at $0.01 < P \leq 0.05$; NS: non-significant ($0.05 < P$).
Value followed by the same letter are not significantly different (Duncan's multiple range test at 5% level).

4.2. Flower-, leaf-, and daughter corms-related traits

The primary growth of saffron is mainly dependent on the size or nutrient reserves of mother corms (Seyyedi et al., 2018). Corm adaptability against environmental stresses is also directly related to the quality of nutrient reserves (Gresta et al., 2009). Moreover, each "daughter corm" which is formed at the end of the first growing season, can be considered like a "mother corm" at the beginning of the second growing season (Gresta et al., 2008). Therefore, the balanced availability of organic matter and mineral nutrients probably increase flower yield in the next year by enhancing the growth and quality of daughter corms.

Considering the adverse effects associated with chemical fertilizers (Maeda et al., 2003; Yoshinaga et al., 2007), the application of clean amendments is a well-known and reliable method for producing saffron under nutrient-deficient conditions (Daneshmandi and Seyyedi, 2019). In this regard, V_P has been recognized as a stabilized organic fertilizer with high porosity and water holding capacity that can improve rhizosphere wettability, balance soil ventilation, and stimulate microbial activity in P-deficient calcareous soils (Esmaeili et al., 2020; Golchin et al., 2006). Supplying mineral nutrients and thereby increasing soil fertility for daughter corm growth (Daneshmandi and Seyyedi, 2019) may be considered as other reasons.

The life cycle of plants grown in semi-arid regions is often exposed to various environmental stresses (Sepaskhah and Yarami, 2009). The biochemical consequences regarding P deficiency, one of the most prevalent stresses in these areas (Shariatmadari et al., 2006), can accelerate oxidative damage and impair cellular function (Bargaz et al., 2013). Under these conditions, self-adaptive mechanisms can be induced through endogenous signals to alleviate oxidative injury and stabilize cellular function (Koocheki and Seyyedi, 2019). The efficiency of these mechanisms is affected by nutrient mobilization; so a higher reserve utilization intensifies the possibility of more effective physiological induction (Kumar et al., 2009). However, with increasing P stress, biochemical induction of defense mechanisms can be impaired, ultimately leading to cellular degradation (Bargaz et al., 2013; Mroczek-Zdyrska et al., 2017).

The exogenous application of bioactive compounds such as GABA has been suggested as an effective and practical technique to maintain cell stability under stressful environments (Song et al., 2010; Hu et al., 2015). It can support self-compatible mechanisms to establish an enhanced response (Cheng et al., 2018). The observed results also support this hypothesis when the proline content, flower number, LAI, and daughter corms increased after GABA treatment. Similarly, increased leaf area, reduced oxidative damage, and improved nutrient uptake have been found as positive effects of GABA foliar application (Cheng et al., 2018; Rezaei-Chiyaneh et al., 2018).

4.3. P uptake-related traits

As mentioned earlier, the maximum P concentration in saffron organs was observed by spraying 2 mg L^{-1} GABA on plants treated with V_P +S. Improved corm growth and increased leaf area in V_P and V_P +S treatments, compared with control treatment, may indicate the plant's ability to absorb more P from the soil. Similar results have been observed by others (Koocheki and Seyyedi, 2015; Seyyedi et al., 2018). Moreover, expanding leaf area and increasing proline content due to GABA application can increase plant tolerance to P deficiency stress. These findings are in accordance with Xiang et al. (2016) who reported that GABA application increased leaf area and protected chloroplast structure under salinity-alkalinity stress.

PAE in plants may reduce by increasing the application of fertilizer inputs (Fageria and Filho, 2007; Wang et al., 2010). A similar trend has been reported in lentil (Singh et al., 2005) and flax (Xie et al., 2016). The decrease in PAE as a result of S treatment compared with control treatment is in agreement with this hypothesis. However, it was interesting that the application of V_P and V_P +S resulted in more PAE than control treatment. The reason for this increase can be justified according to Eq. (3−4). In fact, although there is a negative relationship between PAE and P_T (total amount of P added to the soil due to fertilizer inputs), the increase in P_P (total amount of P absorbed by the plant) may offset the decreasing effect of P_T on PAE. Hence, improving plant potential to absorb more P from the soil may increase P_P to P_T ratio in V_P or V_P +S treatment, compared with control treatment.

5. Conclusion

The reduced ability of the root system to absorb P from the soil, resulting from the chemical reaction of carbonate compounds with soluble P, is considered one of the major consequences of saffron cultivation in calcareous soils. Although increasing P stress significantly decreased flower yield and LAI, GABA application attenuated these negative effects. Moreover, with improving P solubility following V_P or V_P +S treatments, microbial respiration, flower number, proline content, and PAE increased. Such results can be a logical confirmation of the hypothesis expressed in the experiment; because a positive correlation was recorded between the application of vermicompost and GABA to improve quantitative and qualitative performance. Overall, the results suggest the co-application of V_P (10 t ha^{-1}) with GABA foliar spray (2 mg L^{-1}) to mitigate the adverse effects of high soil pH.

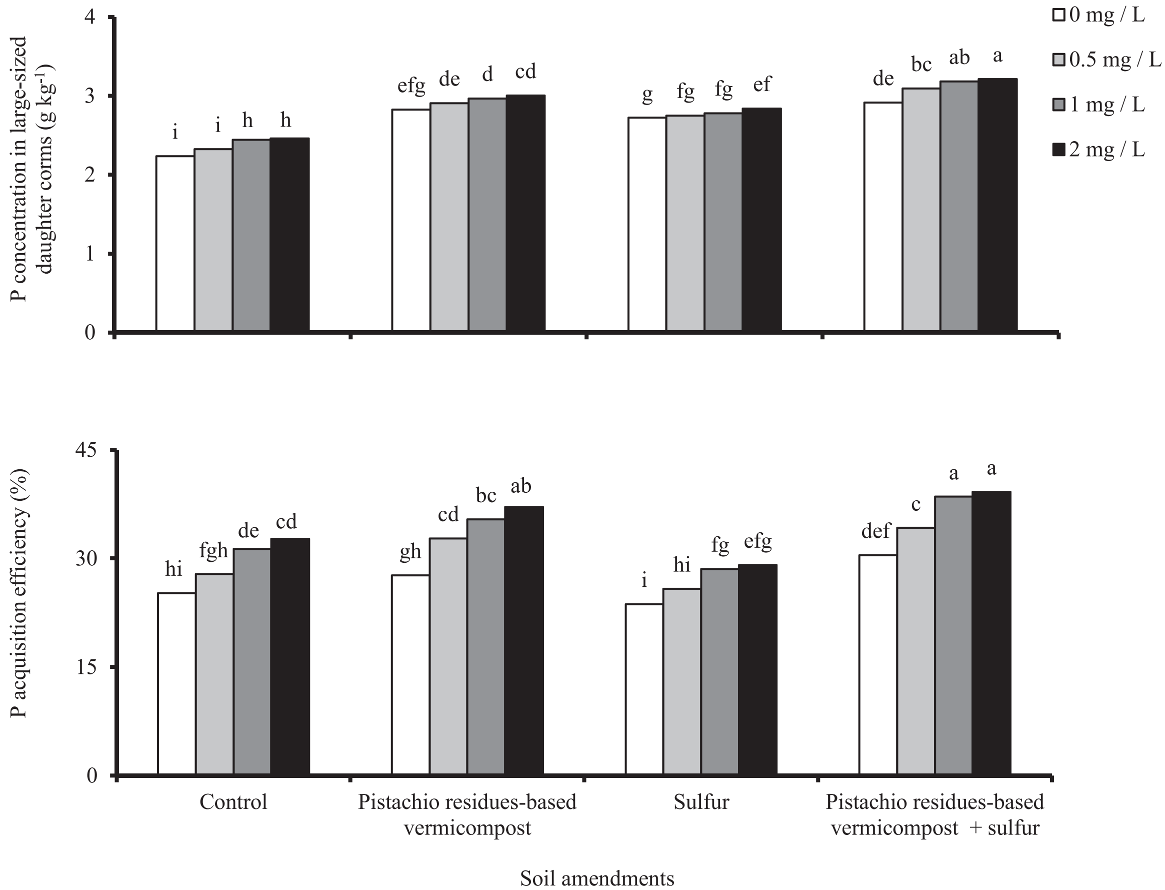

Fig. 5. Interaction effects of soil amendments and GABA application on P concentration in large-sized daughter corms and P acquisition efficiency. Value followed by the same letter are not significantly different (Duncan's multiple range test at 5% level).

CRediT authorship contribution statement

R. Tavakkol Afshari: Conceptualization, Writing – review & editing. **S.M. Seyyedi**: Investigation, Writing – review & editing. **S.M. Mirmiran**: Experimental measurement, Data analysis, Writing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

No data was used for the research described in the article.

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