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Intercropping of *Cyphomandra betacea* with different ploidies of *Solanum* sect. *Solanum* (Solanaceae) wild vegetables increase their selenium uptakes

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Abstract: Selenium (Se) deficiency causes various diseases in human. Selenium is mainly obtained from fruits and vegetables. In this study, the fruit tree *Cyphomandra betacea* and three *Solanum* sect. *Solanum* (Solanaceae) wild vegetables [diploid (*S. photeinocarpum*), tetraploid (colchicine-induced *S. photeinocarpum*), and hexaploid (*S. nigrum*)] were intercropped, and Se uptake was determined by a pot experiment. Intercropping decreased the biomass, photosynthetic pigment contents and superoxide dismutase activity of *C. betacea*, but increased the peroxidase activity, catalase activity, and soluble protein content of *C. betacea.* These indicators of sect. *Solanum* increased after intercropping. Selenium contents increased in *C. betacea* and sect. *Solanum* plants after intercropping. *C. betacea* intercropped with diploid, tetraploid, and hexaploid exhibited increased shoot Se contents in *C. betacea* by 13.73, 17.49, and 26.50% relative to that of *C. betacea* monoculture. Intercropping of *C. betacea* with diploid, tetraploid, and hexaploid increased shoot Se contents in *C. betacea* by 35.22, 68.86, and 74.46% compared with their respective monocultures. The biomass and Se content of intercropped sect. *Solanum* showed linear relationships with the biomass and Se content of the monocultures. The biomass and Se content of intercropped *C. betacea* also exhibited linear relationships with that of sect. *Solanum* monocultures. Correlation and grey relational analyses revealed that CAT activity, POD activity, and soluble protein content were the top indicators closely associated with the *C. betacea* shoot Se content. The POD activity, soluble protein content, and translocation factor were the top four indicators closely associated with sect. *Solanum* shoot Se content. Therefore, intercropping promotes the Se uptake in *C. betacea* and sect. *Solanum* wild vegetables.

Keywords: *Cyphomandra betacea*; intercropping; *Solanum* sect. *Solanum*; selenium; antioxidant enzyme activity

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1. Introduction

Selenium (Se) is an essential trace element in humans. Humans obtain less than 40 μg d^{-1} of Se from the diet, and Se poisoning occurs after intake of concentration above 400 μg d^{-1} [1,2]. Se deficiency is associated with various human diseases such as heart disease, cancer, and reproductive disorders. High intake of Se in humans leads to loss of hair and nails and damage to the nervous and digestive systems [2]. The human body cannot synthesize Se so it is obtained through diet. Plant Se is the primary source of Se in humans [3,4]. Application of Se fertilization is a very common method for improving plant Se contents, but this approach is expensive with high environmental pollution risk [5]. Therefore, exploring effective and and eco-friendly methods to improve Se accumulation in crops is imperative.

Intercropping improves the rate of utilization of light, temperature, water, fertilizer and other resources by crops. Moreover, intercropping modulates crop root exudates, soil pH value, and soil enzyme activity, ultimately improving crop yield and quality [4,6]. Intercropping of maize with soybean is a typical representative of rational utilization of various resources for the production of crops [7]. Intercropping maize with legumes improves the absorption of nutrients and increases the yield of the two crops [8]. The hyperaccumulator *Thlaspi caerulescens* intercropped with the non-hyperaccumulator *Thlaspi arvense* under heavy metal contaminated condition promotes the growth of the two plants, increases zinc (Zn) accumulation in *T. caerulescens*, and decreases Zn uptake in *T. arvense* [9]. Intercropping cadmium (Cd)-hyperaccumulator *Solanum photeinocarpum* or its postgrafting generations with loquat seedlings promoted Cd accumulation and growth of the two plants [10]. In addition, intercropping of hyperaccumulator *Galinsoga parviflora* with the accumulator plants *Capsella bursa-pastoris*, *Cardamine hirsuta*, and *Galium aparine* exhibited different effects on Cd accumulation and growth of these plants, including promotion, inhibition, or no effects [11]. Three varieties (red, green, and black) of eggplant seedlings intercropped under Se-rich soil conditions showed increased Se accumulation and growth rate. Moreover, the three varieties exhibited increased photosynthetic pigment contents, antioxidant enzyme activities, and soluble protein contents [12]. Intercropping of three radish genotypes had various effects on their growth, physiology, and Se accumulation. Some intercropping combinations of radish promoted growth and Se accumulation of radish and improved their resistances to Se tress, whereas other intercropping combinations showed the opposite effects [13]. Intercropping of three genotypes of cherry tomato had various effects on the yield and quality of fruits, but all combinations showed increased Se contents in various organs [14]. These findings indicate that different intercropping combinations of crops may produce varying effects on their growth and Se accumulation, implying that appropriate intercropping combinations can promote Se accumulation in crops. Studies should explore suitable intercropping combinations to improve Se accumulation in crops.

Cyphomandra betacea is a perennial evergreen fruit tree with high edible and ornamental values [15,16]. The Se accumulation capacity of *C. betacea* is lower than that of other Se-rich vegetables and fruits [17]. *Solanum photeinocarpum* and *Solanum nigrum* are annual to perennial *Solanum* sect. *Solanum* wild vegetables with a high Se accumulation capacity [18-20]. *S. photeinocarpum* is a diploid plant, *S. nigrum* is a hexaploid plant, whereas *S. nigrum* was obtained from the breeding of *S. photeinocarpum* [21]. Intercropping *C. betacea* with *S. photeinocarpum* and *S. nigrum* may improve the Se accumulation capacities of these plants. Studies have not explored the effect of intercropping these plants on the Se accumulation capacities. Therefore, in this study, *C. betacea* was intercropped with *S. photeinocarpum* (diploid), colchicine-induced *S. photeinocarpum* (tetraploid), and *S. nigrum* (hexaploid), and the Se uptake in these plants was evaluated to determine the best combination of sect. *Solanum* and *C. betacea* for improving Se accumulation in these plants

2. Materials and Methods

2.1. Materials

The *C. betacea* seeds were collected from a five-year-old fruiting tree growing at the Chengdu Campus of Sichuan Agricultural University (30°42′N, 103°51′E) in September 2021. The seeds were air-dried. The seeds of *S. photeinocarpum* (diploid) and *S. nigrum* (hexaploid) were obtained from the farmlands around the Chengdu Campus in June 2021. The shoot tips of the diploid seedlings at the stage of unfolded cotyledons were treated with colchicine (0.3%) for 48 h, and the tetraploid was induced. Tetraploid seeds were obtained from the diploid plants treated with colchicine in September 2021. Diploid, tetraploid, and hexaploid seeds were air-dried. The seeds of four plants were planted in seedling trays filled with wet perlite in February 2022. Hoagland solutions were used to irrigate the seedlings every three days after emergence.

The soil used in this experiment was collected from the farmland around the Chengdu Campus. The soil ~~species~~ was fluvo-aquic soil, and the basic physicochemical properties of soil samples are presented in Table 1 [22].

Table 1. The basic chemical properties of soil.

Soil type	pH value	Organic matter content (g kg^{-1})	Total N content (g kg^{-1})	Total P content (g kg^{-1})	Total K content (g kg^{-1})	Alkaline hydrolyzed N content (mg kg^{-1})	Available P content (mg kg^{-1})	Available K content (mg kg^{-1})	Total Se content (mg kg^{-1})
Fluvo-aquic	7.71	15.29	1.85	11.88	15.38	87.99	55.78	41.96	0.12

2.2. Experimental Design

The experiment was conducted in a greenhouse at the Chengdu Campus. The soil was treated in March 2022 according to Lin et al. (2020) [23]. Soil with 3.0 kg was placed in a plastic pot (21 cm diameter and 20 cm depth), and Na_2SeO_3 (analytical grade) was added to the soil to obtain 5 mg kg^{-1} Se concentration [24]. Then, the soil was watered to maintain the soil moisture content at 80% of the field capacity for one month. In April 2022, uniform seedlings ~~of plant seedlings~~ were transplanted in the pot. In each pot, four seedlings were planted with even distribution in all four directions. The experiment comprised seven treatments: *C. betacea* monoculture, diploid monoculture, tetraploid monoculture, hexaploid monoculture, *C. betacea* intercropped with diploid plants, *C. betacea* intercropped with tetraploid plants, and *C. betacea* intercropped with hexaploidy plants. Four seedlings of one plant species were planted in each pot for the monoculture treatments. Two seedlings of *C. betacea* and two seedlings each of diploid, tetraploid, or hexaploid were planted together in each pot for the intercropping treatments. Each treatment was conducted in triplicate (three pots) and a completely randomized design was used in the study. The plants were irrigated using tap water.

2.3. Determination of Indicators

Two months after plants transplanting, the third mature leaves of plants from top were collected to determine various parameters, including the contents of photosynthetic pigments (chlorophyll *a*, chlorophyll *b*, and carotenoid), activities of antioxidant enzyme [superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT)], and soluble protein content following the methods reported by Lin et al. (2020) [23] and Hao et al. (2004) [25]. Subsequently, the plants were harvested and treated as described by Li et al. (2022) [26]. The dry weights (biomass) of roots and shoots were measured using an electronic balance. The plant samples were dried, ground, and digested with nitric acid and perchloric acid. Further, the digestion solutions were reduced with withhydrochloric acid and determined the Se concentration using hydride generation-atomic fluorescence spectrometry (AFS-9700, Beijing Haiguang Instrument Co., Ltd., Beijing, China) [26]. The translocation factor (TF, Se content in shoots / Se content in roots) was calculated as described previously [27].

2.4. Statistical Analysis

The data were analyzed using SPSS 27.0 software (IBM, Chicago, IL, USA). Data were normalized and subjected to a homogeneity test. One-way analysis of variance was then conducted for comparison of the multiple groups, followed by Duncan's multiple range test for pairwise comparison ($P < 0.05$). Relationships of the biomass and Se content between the monoculture and intercropping treatments were evaluated using regression analysis. Pearson's correlation analysis was conducted to determine the correlations among the different indicators of each plant. Grey relational analysis was performed to explore the relationships of the different indicators with the shoot Se content of each plant as described by Wang (2019) [28] and Ma et al. (2022) [29].

3. Results

3.1. Biomass of Plants

The root and shoot biomass of *C. betacea* plants was lower than that of diploid, tetraploid, and hexaploid plants. The biomass order in different ploidies was diploid < tetraploid < hexaploid (Figure 1A, 1B). Compared with *C. betacea* monoculture, intercropped with diploid, tetraploid, and hexaploid decreased the root biomass of *C. betacea* by 6.07, 15.63, and 19.23%, respectively, and decreased the shoot biomass of *C. betacea* by 9.30, 20.15, and 23.13%, respectively. The root and shoot biomass of different ploidies intercropped with *C. betacea* was higher compared with that of their respective monoculture. In addition, the root biomass of plants intercropped with diploid, tetraploid, and hexaploid plants was linearly positively correlated with the root biomass of the respective monocultures (r = 0.704, N = 9, P = 0.034, Figure 2A). The root biomass of intercropped *C. betacea* was negatively correlated with the root biomass of monoculture diploid, tetraploid, and hexaploid plants (r = -0.896, N = 9, P = 0.001, Figure 2B). The shoot biomass of intercropped diploid, tetraploid, and hexaploid plants was positively related to the shoot biomass of the corresponding monocultures (r = 0.922, N = 9, P = 0.000, Figure 2C). The shoot biomass of intercropped *C. betacea* was linearly negatively correlated with the shoot biomass of monoculture diploid, tetraploid, and hexaploid plants (r = -0.796, N = 9, P = 0.010, Figure 2D).

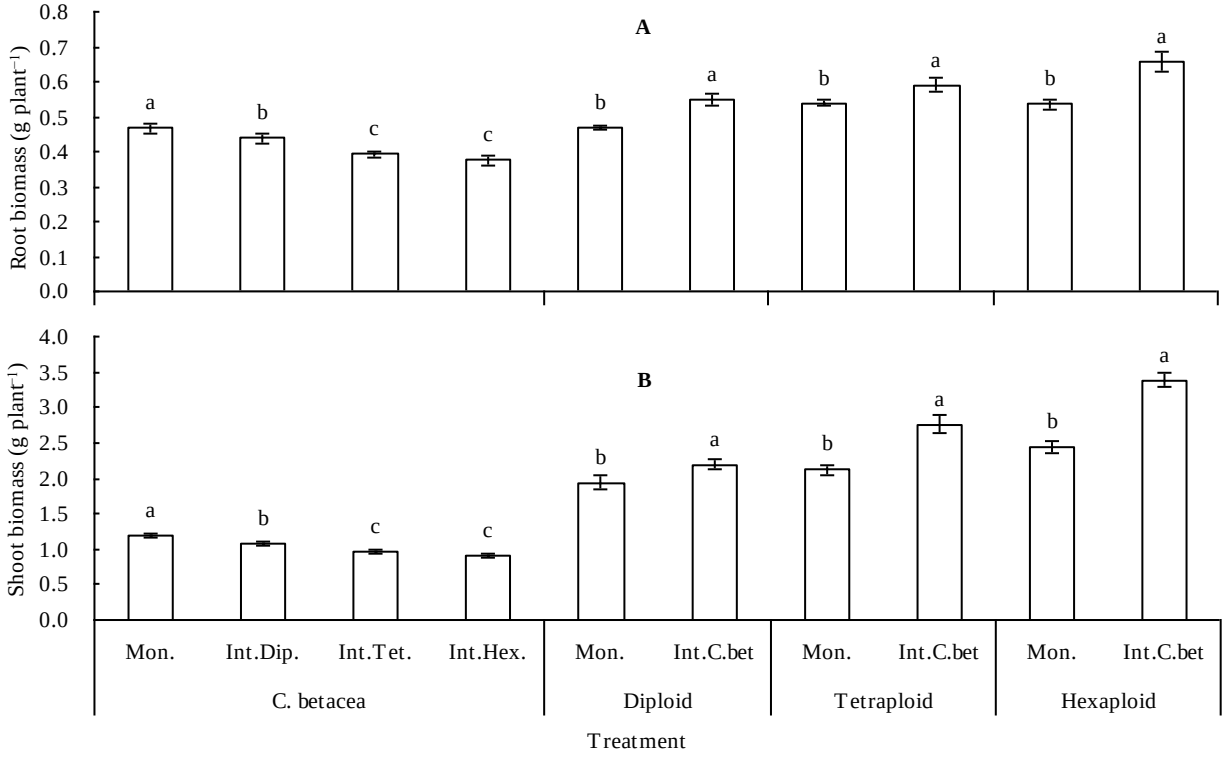


Figure 1. Biomass of plants. **A**: root biomass; **B**: shoot biomass. Values are means ± SD of three replicates. Different lowercase letters indicate significant differences among the treatments (Duncan's Multiple Range Test, P < 0.05). Mon. = monoculture; Int.Dip. = intercropped with diploid; Int.Tet. = intercropped with tetraploid; Int.Hex. = intercropped with hexaploid; Int.C.bet = intercropped with *C. betacea*.

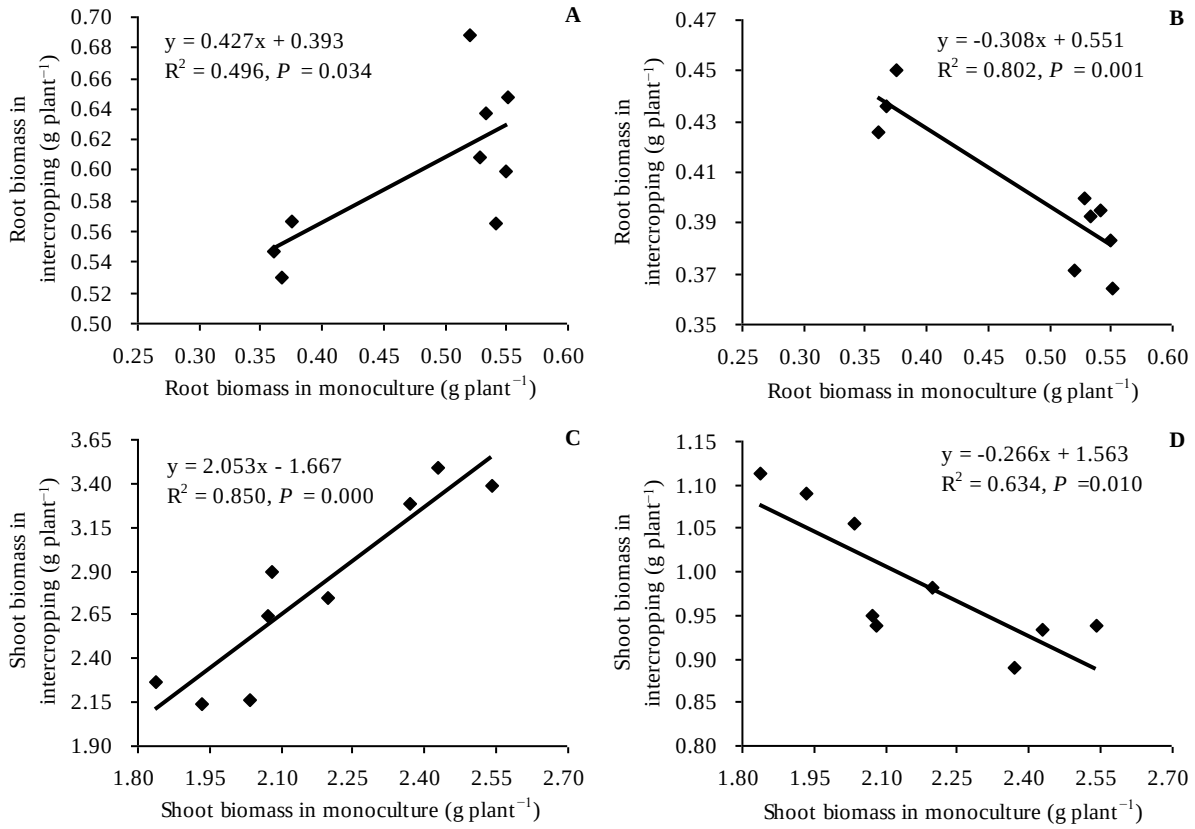


Figure 2. Linear regression relationships of plants' biomass. **A**: root biomass of diploid, tetraploid, and hexaploid in intercropping plotted against their root biomass in monoculture; **B**: root biomass of *C. betacea* in intercropping plotted against root biomass of diploid, tetraploid, and hexaploid in monoculture; **C**: shoot biomass of diploid, tetraploid, and hexaploid in intercropping plotted against their shoot biomass in monoculture; **D**: shoot biomass of *C. betacea* in intercropping plotted against shoot biomass of diploid, tetraploid, and hexaploid in monoculture.

3.2. Photosynthetic Pigment Contents in Plants

C. betacea plants intercropped with diploid, tetraploid, and hexaploid plants showed lower contents of chlorophyll *a*, chlorophyll *b*, and carotenoid compared with the levels in *C. betacea* monoculture. Notably, the contents of chlorophyll *a*/*b* of *C. betacea* monoculture were not significantly different compared with *C. betacea* plants intercropped with diploid, tetraploid, and hexaploid plants (Table 2). Diploids intercropped with *C. betacea* showed no significant differences in the contents of chlorophyll *a*, carotenoid relative to that of the monoculture of diploid. The content of chlorophyll *b* was higher in the diploids intercropped with *C. betacea*, and lower chlorophyll *a*/*b* compared with that of monoculture diploids. Tetraploids intercropped with *C. betacea* showed higher contents of chlorophyll *a*, chlorophyll *b*, and carotenoid relative to that of tetraploid monocultures, whereas there was no significant in chlorophyll *a*/*b* contents between tetraploid monocultures and intercropped tetraploids. Hexaploid intercropped with *C. betacea* exhibited higher levels of chlorophyll *a* and carotenoid compared with that in hexaploid monocultures. On the contrary, chlorophyll *b* content and chlorophyll *a*/*b* were not significantly different between hexaploid monocultures and intercropped hexaploid.

Table 2. Photosynthetic pigment contents in plants.

Treatment	Chlorophyll *a* content (mg g^{-1})	Chlorophyll *b* content (mg g^{-1})	Chlorophyll *a*/*b*	Carotenoid content (mg g^{-1})

C. betacea				
Mono.	1.014±0.047a	0.445±0.015a	2.281±0.147a	0.174±0.002a
Inter. diploid	0.896±0.031b	0.399±0.012b	2.243±0.018a	0.155±0.004b
Inter. tetraploid	0.790±0.022c	0.359±0.014c	2.203±0.059a	0.140±0.008c
Inter. hexaploid	0.789±0.018c	0.348±0.011c	2.265±0.023a	0.135±0.006c
Diploid				
Mono.	1.668±0.052a	0.680±0.030b	2.454±0.059a	0.285±0.012a
Inter. *C. betacea*	1.768±0.086a	0.773±0.035a	2.288±0.051b	0.302±0.013a
Tetraploid				
Mono.	1.873±0.055b	0.791±0.045b	2.372±0.078a	0.309±0.005b
Inter. *C. betacea*	2.056±0.067a	0.872±0.018a	2.358±0.097a	0.336±0.011a
Hexaploid				
Mono.	1.976±0.094b	0.857±0.039a	2.308±0.144a	0.322±0.016b
Inter. *C. betacea*	2.154±0.061a	0.876±0.023a	2.459±0.026a	0.355±0.010a

Values are means ± SD of three replicates. Different lowercase letters indicate significant differences among the treatments (Duncan's Multiple Range Test, $P < 0.05$). Mon. = monoculture; Inter. diploid = intercropped with diploid; Inter. tetraploid = intercropped with tetraploid; Inter. hexaploid = intercropped with hexaploid; Inter. *C. betacea* = intercropped with *C. betacea*.

3.3. Antioxidant Enzyme Activities and Soluble Protein Contents in Plants

C. betacea intercropped with diploid and tetraploid did not exhibit significant differences in SOD activity compared with *C. betacea* monoculture (Table 3). *C. betacea* intercropped with hexaploid showed lower SOD activity than *C. betacea* monoculture (Table 3). *C. betacea* intercropped with diploid, tetraploid, and hexaploid showed higher POD activity, CAT activity, and soluble protein content compared with the monoculture of *C. betacea*. Diploid intercropped with *C. betacea* showed higher SOD activity, POD activity, CAT activity and soluble protein content compared with the monoculture of diploid. Tetraploid intercropped with *C. betacea* did not exhibit significant differences in SOD activity compared with the tetraploid monoculture. However, tetraploid intercropped with *C. betacea* had higher POD activity, CAT activity and soluble protein content relative to the tetraploid monoculture. Hexaploid intercropped with *C. betacea* did not exhibit significant differences in SOD activity and CAT activity relative to hexaploidy monoculture. Compared with the hexaploid monoculture, hexaploid intercropped with *C. betacea* had higher POD activity and soluble protein content.

Table 3. Antioxidant enzyme activities and soluble protein contents of plants.

Treatment	SOD activity ($U\ g^{-1}$)	POD activity ($U\ g^{-1}\ min^{-1}$)	CAT activity ($mg\ g^{-1}\ min^{-1}$)	Soluble protein content ($mg\ g^{-1}$)
C. betacea				
Mono.	361.1±16.43a	3889±48.82c	5.876±0.202c	12.21±0.56c
Inter. diploid	353.1±17.71ab	4397±91.16b	6.459±0.131b	13.26±0.47b
Inter. tetraploid	332.7±10.01ab	5410±79.98a	6.585±0.185b	13.91±0.52ab
Inter. hexaploid	327.6±13.71b	5426±58.01a	7.132±0.191a	14.56±0.49a
Diploid				
Mono.	235.1±8.67b	4666±87.25b	6.813±0.089b	10.70±0.20b
Inter. *C. betacea*	256.8±9.49a	5771±157.9a	7.064±0.078a	12.99±0.58a
Tetraploid				

Mono.	258.4±9.22a	5307±102.1b	7.112±0.095b	12.18±0.24b
Inter. *C. betacea*	268.1±5.44a	7334±316.9a	7.288±0.049a	15.94±0.14a
Hexaploid				
Mono.	272.3±7.78a	6811±225.3b	7.484±0.035a	13.52±0.49b
Inter. *C. betacea*	283.5±6.54a	8694±232.2a	7.542±0.054a	19.58±0.42a

Values are means ± SD of three replicates. Different lowercase letters indicate significant differences among the treatments (Duncan's Multiple Range Test, $P < 0.05$). Mon. = monoculture; Inter. diploid = intercropped with diploid; Inter. tetraploid = intercropped with tetraploid; Inter. hexaploid = intercropped with hexaploid; Inter. *C. betacea* = intercropped with *C. betacea*.

3.4. Se Content and Translocation Factor of Plants

C. betacea intercropped with diploid, tetraploid, and hexaploid exhibited higher root and shoot Se contents compared with that of their respective monoculture (Figure 3A, 3B). *C. betacea* intercropped with diploid, tetraploid, and hexaploid showed higher Se contents in shoots by 13.73%, 17.49%, and 26.50%, respectively, compared with *C. betacea* monoculture. Intercropping of different ploidies with *C. betacea* increased the shoot Se contents in diploid, tetraploid, and hexaploid plants by 35.22%, 68.86%, and 74.46%, respectively, compared with the diploid, tetraploid, and hexaploid monocultures. In addition, the root Se contents in *C. betacea* intercropped with diploid, tetraploid, and hexaploid were positively correlated with the root Se contents of the corresponding monocultures ($r = 0.760$, $N = 9$, $P = 0.018$, Figure 4A). Root Se contents in *C. betacea* intercropped with different ploidies were positively correlated with the root Se contents in corresponding diploid, tetraploid, and hexaploid monocultures ($r = 0.739$, $N = 9$, $P = 0.023$, Figure 4B). The shoot Se contents in *C. betacea* intercropped with diploid, tetraploid, and hexaploid plants were linearly positively correlated with shoot Se contents in the corresponding monocultures ($r = 0.927$, $N = 9$, $P = 0.000$, Figure 4C). The shoot Se contents in *C. betacea* intercropped with different ploidies were linearly positively correlated with the shoot Se contents in diploid, tetraploid, and hexaploid monocultures ($r = 0.958$, $N = 9$, $P = 0.000$, Figure 4D).

The findings showed that *C. betacea* intercropped with diploid had higher TF relative to the *C. betacea* monoculture. *C. betacea* intercropped with tetraploid showed no significant difference in TF, whereas *C. betacea* intercropped with hexaploid had lower TF compared with the *C. betacea* monoculture (Figure 3C). Diploid, tetraploid, and hexaploid plants intercropped with *C. betacea* exhibited higher TFs compared with the TF in diploid, tetraploid, and hexaploidy monocultures, respectively.

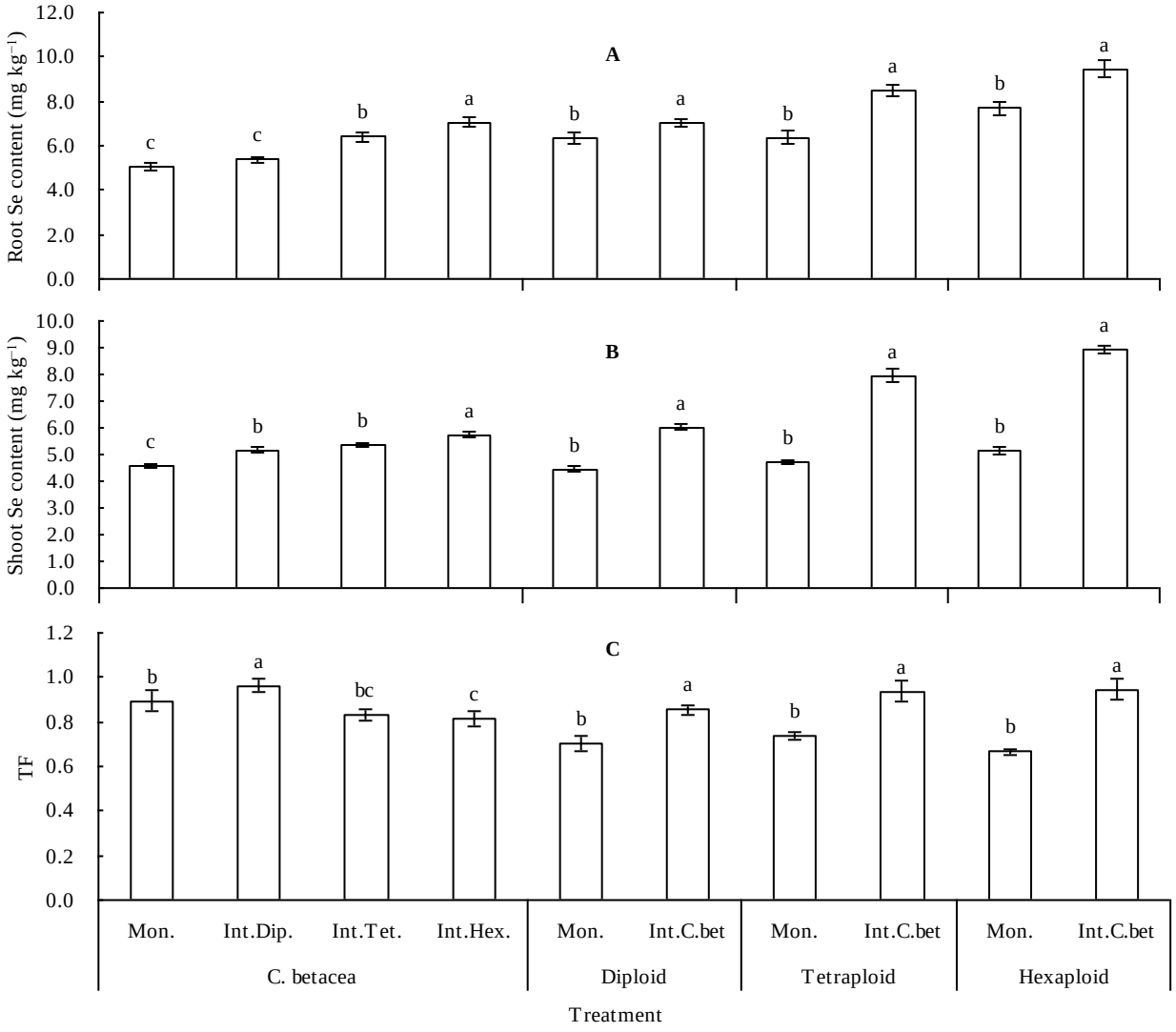


Figure 3. Se content and TF of plants. **A**: root Se content; **B**: shoot Se content; **C**: TF (translocation factor). Values are means ± SD of three replicates. Different lowercase letters indicate significant differences among the treatments (Duncan's Multiple Range Test, $P < 0.05$). Mon. = monoculture; Int.Dip. = intercropped with diploid; Int.Tet. = intercropped with tetraploid; Int.Hex. = intercropped with hexaploid; Int.C.bet = intercropped with *C. betacea*.

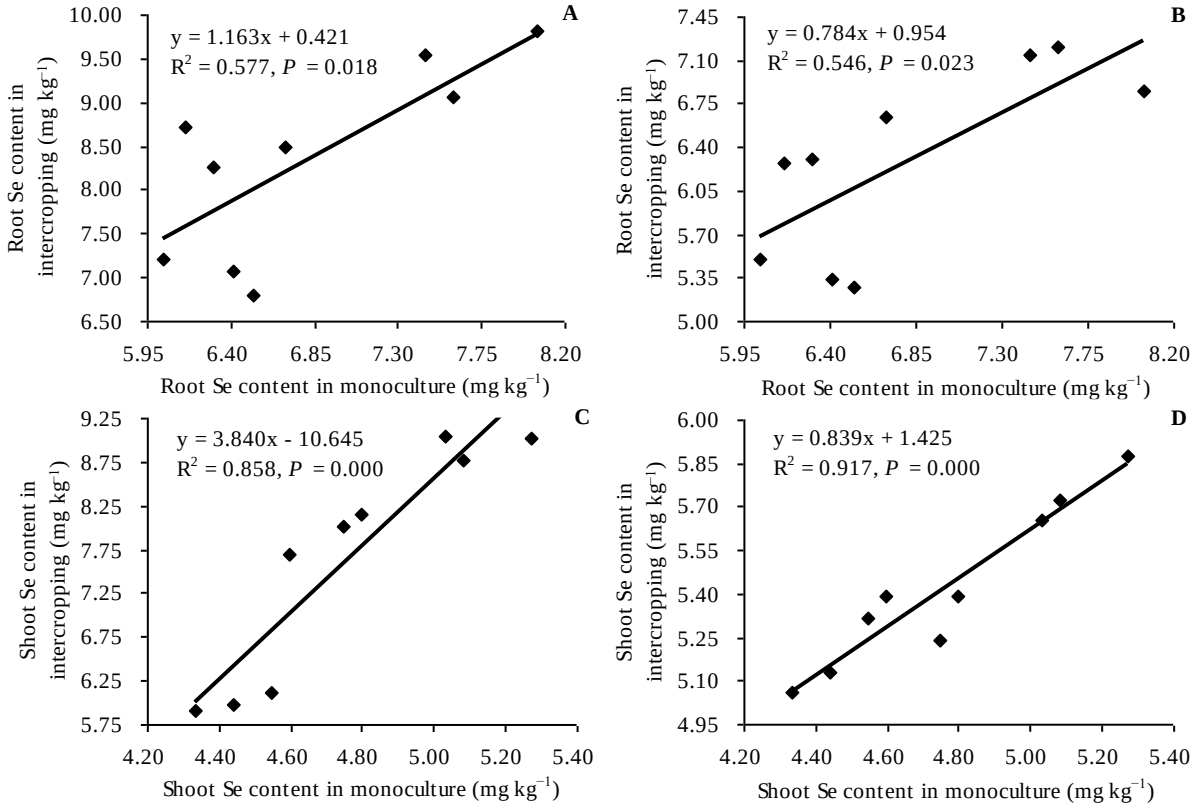


Figure 4. Linear regression relationships of Se contents in plants. **A**: root Se contents in diploid, tetraploid, and hexaploid in intercropping plotted against their root Se contents in monoculture; **B**: root Se contents in *C. betacea* in intercropping plotted against root Se contents in diploid, tetraploid, and hexaploid in monoculture; **C**: shoot Se contents in diploid, tetraploid, and hexaploid in intercropping plotted against their shoot Se contents in monoculture; **D**: shoot Se contents in *C. betacea* in intercropping plotted against shoot Se contents in diploid, tetraploid, and hexaploid in monoculture.

3.5. Relationship of Different Parameters in Plants

The root biomass and shoot biomass of *C. betacea* were highly significantly ($P < 0.01$) positively correlated with the chlorophyll *a* content, chlorophyll *b* content, carotenoid content, and SOD activity (Table 4). The root biomass and shoot biomass were highly significantly ($P < 0.01$) negatively correlated with the POD activity, CAT activity, and soluble protein content. The root Se content and shoot Se content were highly significantly ($P < 0.01$) positively correlated with the POD activity, CAT activity, and soluble protein content, and were highly significantly ($P < 0.01$) or significantly ($0.01 \le P < 0.05$) negatively correlated with the root biomass, shoot biomass, chlorophyll *a* content, chlorophyll *b* content, carotenoid content, and SOD activity. The root Se content was highly significantly ($P < 0.01$) positively correlated with the shoot Se content.

Table 4. Correlations among the different indicators of *C. betacea*.

Indicator	Root biomass	Shoot biomass	Chlorophyll *a* content	Chlorophyll *b* content	Chlorophyll *a*/*b*	Carotenoid content	SOD activity	POD activity	CAT activity	Soluble protein content	Root Se content	Shoot Se content	TF
Root biomass													

Shoot biomass	0.922**											
Chlorophyll *a* content	0.880**	0.953**										
Chlorophyll *b* content	0.923**	0.926**	0.949**									
Chlorophyll *a*/*b*	0.094	0.315	0.397	0.090								
Carotenoid content	0.893**	0.942**	0.918**	0.952**	0.129							
SOD activity	0.709**	0.776**	0.649*	0.747**	-0.107	0.787**						
POD activity	-0.956**	-0.957**	-0.928**	-0.935**	-0.217	-0.923**	-0.738**					
CAT activity	-0.874**	-0.838**	-0.824**	-0.912**	0.061	-0.914**	-0.685*	0.833**				
Soluble protein content	-0.779**	-0.894**	-0.804**	-0.830**	-0.110	-0.858**	-0.759**	0.783**	0.749**			
Root Se content	-0.912**	-0.930**	-0.866**	-0.865**	-0.208	-0.841**	-0.694*	0.933**	0.823**	0.794**		
Shoot Se content	-0.922**	-0.930**	-0.898**	-0.931**	-0.127	-0.916**	-0.733**	0.881**	0.936**	0.855**	0.870**	
TF	0.128	0.231	0.254	0.145	0.403	0.246	0.042	-0.236	-0.141	-0.082	-0.190	-0.212

N = 12. **: Correlation is significant at the 0.01 level (two-tailed test). *: Correlation is significant at the 0.05 level (two-tailed test). TF = translocation factor.

The root biomass of diploid plants was highly significantly ($P < 0.01$) or significantly ($0.01 \le P < 0.05$) positively correlated with the POD activity, CAT activity, soluble protein content, and TF (Table 5). The shoot biomass was highly significantly ($P < 0.01$) or significantly ($0.01 \le P < 0.05$) positively correlated with the CAT activity, soluble protein content, and TF. The root Se content was highly significantly ($P < 0.01$) or significantly ($0.01 \le P < 0.05$) positively correlated with the root biomass, carotenoid content, POD activity, and soluble protein content. The shoot Se content was highly significantly ($P < 0.01$) or significantly ($0.01 \le P < 0.05$) positively correlated with the root biomass, shoot biomass, chlorophyll *b* content, POD activity, CAT activity, soluble protein content, and TF, and was significantly ($0.01 \le P < 0.05$) negatively correlated with the content of chlorophyll *a*/*b*. The

root Se content was highly significantly ($P < 0.01$) positively correlated with the shoot Se content.

Table 5. Correlations among the different indicators of diploid.

Indicator	Root biomass	Shoot biomass	Chlorophyll *a* content	Chlorophyll *b* content	Chlorophyll *a*/*b*	Carotenoid content	SOD activity	POD activity	CAT activity	Soluble protein content	Root Se content	Shoot Se content	TF
Root biomass													
Shoot biomass	0.813*												
Chlorophyll *a* content	0.691	0.531											
Chlorophyll *b* content	0.810	0.739	0.892*										
Chlorophyll *a*/*b*	-0.733	-0.779	-0.537	-0.859*									
Carotenoid content	0.705	0.322	0.662	0.706	-0.592								
SOD activity	0.691	0.672	0.332	0.655	-0.827*	0.315							
POD activity	0.976**	0.784	0.692	0.869*	-0.841*	0.765	0.772						
CAT activity	0.909*	0.883*	0.422	0.582	-0.609	0.401	0.651	0.836*					
Soluble protein content	0.939**	0.813*	0.830*	0.942**	-0.816*	0.662	0.759	0.954**	0.783				
Root Se content	0.888*	0.552	0.601	0.772	-0.767	0.881*	0.699	0.945**	0.675	0.840*			
Shoot Se content	0.961**	0.864*	0.727	0.913*	-0.883*	0.692	0.788	0.984**	0.842*	0.975**	0.881*		
TF	0.896*	0.955**	0.711	0.893*	-0.860*	0.501	0.759	0.899*	0.849*	0.945**	0.713	0.960**	

N = 6. **: Correlation is significant at the 0.01 level (two-tailed test). *: Correlation is significant at the 0.05 level (two-tailed test). TF = translocation factor.

The root biomass of tetraploid plants was significantly ($0.01 \le P < 0.05$) positively correlated with the chlorophyll *a* content, chlorophyll *b* content, carotenoid content, CAT activity, and soluble protein content (Table 6). The shoot biomass was highly significantly ($P < 0.01$) or significantly ($0.01 \le P < 0.05$) positively correlated with the chlorophyll *b* content, POD activity, soluble protein content, and TF. The root Se content and shoot Se content were highly significantly ($P < 0.01$) or significantly ($0.01 \le P < 0.05$) positively correlated with the root biomass, shoot biomass, chlorophyll *a* content, chlorophyll *b* content, carotenoid content, POD activity, CAT activity, soluble protein content, and TF. The root

Se content was highly significantly ($P < 0.01$) positively correlated with the shoot Se content.

Table 6. Correlations among the different indicators of tetraploid.

Indicator	Root biomass	Shoot biomass	Chlorophyll *a* content	Chlorophyll *b* content	Chlorophyll *a*/*b*	Carotenoid content	SOD activity	POD activity	CAT activity	Soluble protein content	Root Se content	Shoot Se content	TF
Root biomass													
Shoot biomass	0.876*												
Chlorophyll *a* content	0.823*	0.784											
Chlorophyll *b* content	0.902*	0.867*	0.854*										
Chlorophyll *a*/*b*	-0.333	-0.326	0.038	-0.487									
Carotenoid content	0.874*	0.788	0.963**	0.788	0.114								
SOD activity	0.563	0.613	0.308	0.298	-0.011	0.492							
POD activity	0.787	0.968**	0.803	0.769	-0.105	0.807	0.596						
CAT activity	0.865*	0.739	0.946**	0.847*	-0.037	0.929**	0.209	0.734					
Soluble protein content	0.835*	0.958**	0.855*	0.782	-0.043	0.881*	0.646	0.987**	0.780				
Root Se content	0.937**	0.960**	0.880*	0.873*	-0.178	0.907*	0.566	0.945**	0.880*	0.963**			
Shoot Se content	0.863*	0.948**	0.913*	0.832*	-0.047	0.922**	0.571	0.972**	0.849*	0.992**	0.975**		
TF	0.736	0.888*	0.895*	0.747	0.082	0.882*	0.545	0.950**	0.766	0.969**	0.897*	0.972**	

N = 6. **: Correlation is significant at the 0.01 level (two-tailed test). *: Correlation is significant at the 0.05 level (two-tailed test). TF = translocation factor.

The root biomass of hexaploid plants was highly significantly ($P < 0.01$) or significantly ($0.01 \le P < 0.05$) positively correlated with the chlorophyll *a* content, SOD activity, POD activity, soluble protein content, and TF (Table 7). The shoot biomass was highly significantly ($P < 0.01$) positively correlated with the POD activity, soluble protein content, and TF. The root Se content was highly significantly ($P < 0.01$) or significantly ($0.01 \le P < 0.05$) positively correlated with the root biomass, shoot biomass, carotenoid content, POD activity, and soluble protein content, and TF. The shoot Se content was highly significantly ($P < 0.01$) or significantly ($0.01 \le P < 0.05$) positively correlated with the root biomass, shoot

biomass, chlorophyll *a* content, carotenoid content, POD activity, soluble protein content, and TF. The root Se content was highly significantly ($P < 0.01$) positively correlated with the shoot Se content.

Table 7. Correlations among the different indicators of hexaploid.

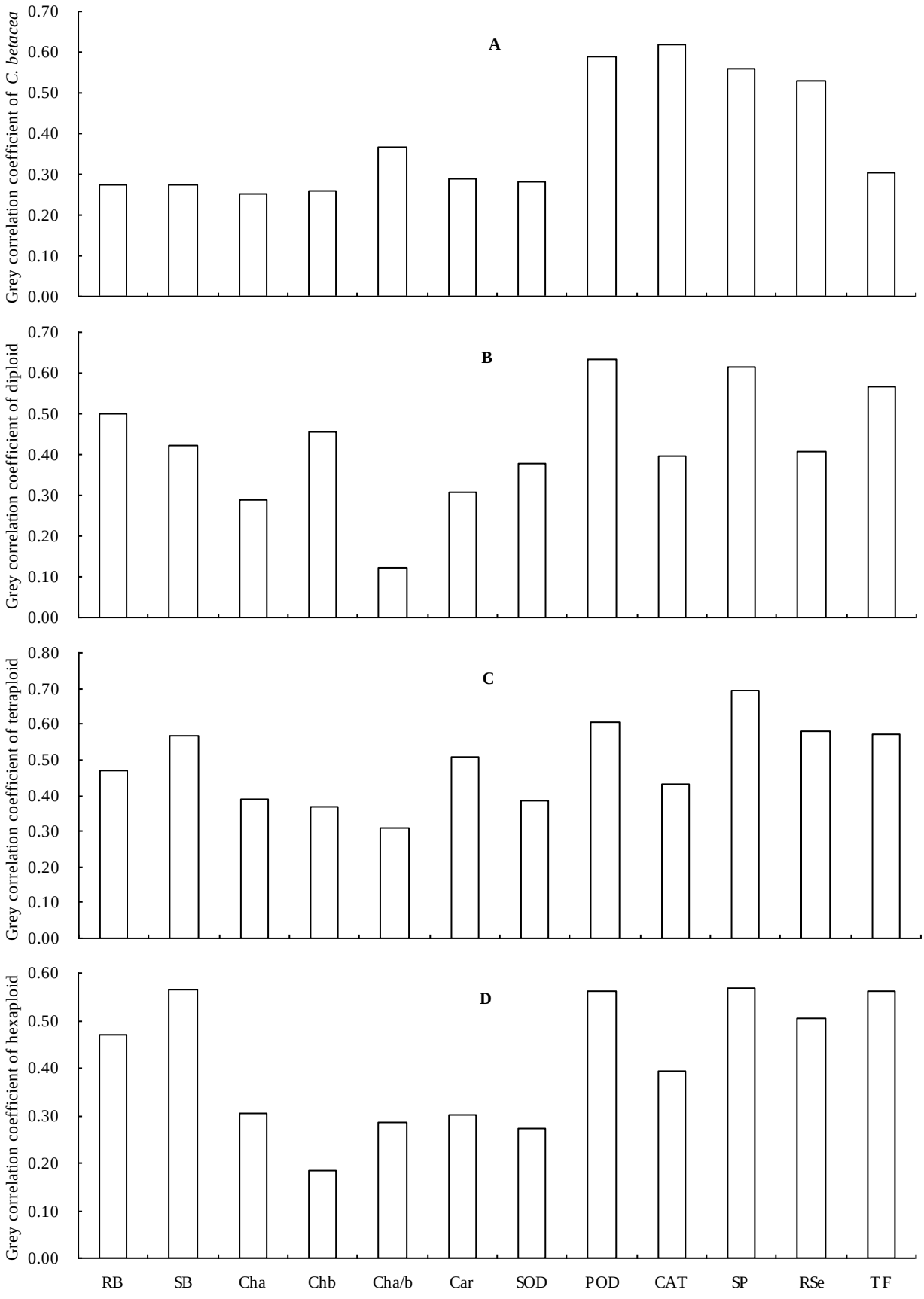
Indicator	Root biomass	Shoot biomass	Chlorophyll *a* content	Chlorophyll *b* content	Chlorophyll *a*/*b*	Carotenoid content	SOD activity	POD activity	CAT activity	Soluble protein content	Root Se content	Shoot Se content	TF
Root biomass													
Shoot biomass	0.932**												
Chlorophyll *a* content	0.870*	0.805											
Chlorophyll *b* content	0.534	0.359	0.463										
Chlorophyll *a*/*b*	0.597	0.646	0.793	-0.172									
Carotenoid content	0.770	0.764	0.484	-0.008	0.540								
SOD activity	0.815*	0.683	0.972**	0.598	0.669	0.345							
POD activity	0.891*	0.968**	0.726	0.155	0.699	0.883*	0.572						
CAT activity	0.456	0.586	0.312	-0.377	0.607	0.756	0.128	0.723					
Soluble protein content	0.957**	0.991**	0.803	0.374	0.634	0.810	0.691	0.969**	0.626				
Root Se content	0.939**	0.893*	0.784	0.234	0.707	0.921**	0.681	0.939**	0.656	0.929**			
Shoot Se content	0.957**	0.983**	0.824*	0.317	0.695	0.839*	0.706	0.980**	0.597	0.985**	0.956**		
TF	0.921**	0.994**	0.811	0.337	0.668	0.754	0.686	0.964**	0.543	0.975**	0.886*	0.983**	

N = 6. **: Correlation is significant at the 0.01 level (two-tailed test). *: Correlation is significant at the 0.05 level (two-tailed test). TF = translocation factor.

3.6. Grey Relational Analysis

The grey relationships of different indicators with the shoot Se content were evaluated and the results showed that all indicators were correlated with the shoot Se content (Figure 6). The top four indicators in *C. betacea* with the highest grey correlation coefficients were CAT activity, POD activity, soluble protein content, and root Se content (Figure 6A). The top indicators with the highest grey correlation coefficients in diploid plants were POD activity, soluble protein content, TF, and root biomass (Figure 6B). The top

indicators for tetraploid plants were soluble protein content, POD activity, root Se content, and TF (Figure 6C), and the top indicators for hexaploid plants were soluble protein content, shoot biomass, TF, and POD activity (Figure 6D).


A
Grey correlation coefficient of C. betacea
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
B
Grey correlation coefficient of diploid
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
C
Grey correlation coefficient of tetraploid
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
D
Grey correlation coefficient of hexaploid
0.60
0.50
0.40
0.30
0.20
0.10
0.00
RB
SB
Cha
Chb
Cha/b
Car
SOD
POD
CAT
SP
RSe
TF

315

Figure 6. Grey correlation coefficients of the different indicators with the shoot Se content. **A**: *C. betacea*; **B**: diploid; **C**: tetraploid; **D**: hexaploid. RB = root biomass; SB = shoot biomass; Cha = chlorophyll *a* content; Chb = chlorophyll *b* content; Cha/b = chlorophyll *a/b*; Car = carotenoid content; SOD = SOD activity; POD = POD activity; CAT = CAT activity; SP = soluble protein content; RSe = root Se content; TF = translocation factor.

4. Discussion

Root exudates of intercropped plants diffuse into the rhizosphere soil resulting in a change in the physical and chemical properties of rhizosphere soil. Intercropping changes soil organic acid content, soil pH value, soil nutrient availability, and soil enzyme activity, ultimately affecting the nutrient uptake and growth of plants [30]. In addition, intercropping system results in competition between plants, which may inhibit the growth of the plants [31]. Different species of intercropped eggplants exhibited an increase in the biomass of their seedlings under Se-rich soil conditions [12], whereas intercropping of white radish with the green radish resulted in an increase in the biomass of white radish and a decrease in the biomass of green radish [13]. In the current study, *C. betacea* intercropped with sect. *Solanum* showed a decrease in the biomass of *C. betacea* and an increase in the biomass of sect. *Solanum*. This result is consistent with the findings from previous studies [13, 14], but different from results from some studies [9,10,12]. This finding indicates competition for growth resources between *C. betacea* and sect. *Solanum*. The biomass of sect. *Solanum* was higher than that of *C. betacea* in the present study. Sect. *Solanum* are herbs, and their growth rate are higher than that of the seedlings of *C. betacea*, a woody plant. Therefore, sect. *Solanum* had a faster growth than *C. betacea*, inhibiting the growth of *C. betacea*. The biomass order of sect. *Solanum* was diploid < tetraploid < hexaploidy. Intercropping of *C. betacea* with sect. *Solanum* showed that the biomass order was diploid < tetraploid < hexaploid. This finding implies that sect. *Solanum* competed and inhibited the growth of *C. betacea*. The biomass of intercropped sect. *Solanum* showed a positive linear relationship with the respective monocultures. The biomass of intercropped *C. betacea* exhibited a linear negative relationship with that of the sect. *Solanum* monocultures. This result further indicates the growth competition between *C. betacea* and sect. *Solanum.* Further studies should be conducted to explore the competition mechanism between the two species.

The content of photosynthetic pigments in plants reflects the photosynthetic capacity [32]. Eggplant intercropped with the cadmium-hyperaccumulator *S. nigrum* exhibited a decrease in the photosynthetic pigment content in eggplant planted in cadmium-contaminated soil. Tomato intercropped with *S. nigrum* under the same conditions showed an increase in the photosynthetic pigment content [32]. Grape seedlings intercropped with *S. nigrum* planted in cadmium contamination soil showed increased chlorophyll a and total chlorophyll contents [24]. Maize intercropped with peanut and maize intercropped with soybean showed increased chlorophyll content [7, 33]. In the current study, intercropping of *C. betacea* with sect. *Solanum* exhibited a decrease in the photosynthetic pigment content in *C. betacea* and an increase in the photosynthetic pigment content in sect. *Solanum*. These results indicate that the competition between *C. betacea* and sect. *Solanum* inhibited synthesis of photosynthetic pigments in *C. betacea*, and promoted the synthesis of photosynthetic pigments in sect. *Solanum*, which may be related to the competition for light, nutrients, and water resources.

High concentrations of Se in plants promote the production of reactive oxygen species (ROS) and induce oxidative stress in plants [34]. Plant defense mechanisms to alleviate Se stress include activating different antioxidant enzymes such as SOD, POD and CAT [34,35]. Soluble protein is an essential osmotic regulator of plant cells and is implicated in plant stress resistance [36]. Eggplant intercropped with *S. nigrum* in cadmium-contaminated soils showed increased antioxidant enzyme activity and soluble protein content [37]. Lettuce intercropped with the cadmium-hyperaccumulator *Galinsoga parviflora* exhibited increased antioxidant enzyme activity and soluble protein content [38]. In the

present study, intercropping of *C. betacea* with diploid and tetraploid plants had no significant effects on the SOD activity of *C. betacea*, whereas intercropping of *C. betacea* with hexaploid plants decreased SOD activity. Intercropping *C. betacea* with diploid, tetraploid, and hexaploid increased the POD activity, CAT activity, and soluble protein content of *C. betacea*. Intercropping sect. *Solanum* with *C. betacea* increased the antioxidant enzyme activity and soluble protein content of sect. *Solanum*. These results indicate that intercropping of *C. betacea* with sect. *Solanum* can improve the resistance of the two plants to cadmium stress, consistent with findings from previous studies [10,12]. Moreover, *C. betacea* intercropped with sect. *Solanum* may promote "rhizosphere dialogue", resulting in the transfer of the active compounds to each other to mutually improve their resistance to heavy metal stress [39].

The uptake of Se by plants is modulated by various factors such as soil pH value, soil redox conditions, and soil selenium state [4]. Se has a strong metalloid property and exists in inorganic forms with different oxidation states. The different soil oxidation states modulate the various valence states of Se [40,41]. The pathway for absorption of selenite by plants is similar to the absorption pathway for phosphate. Absorption of selenite by plants mainly occurs through the root system [42,43]. Intercropping improves the absorption of nutrients such as nitrogen, phosphorus, and potassium in maize and legumes [7,8,44]. Intercropping of heavy metal hyperaccumulator with non-heavy metal hyperaccumulator increases heavy metal uptake in hyperaccumulator but decreases heavy metal uptake in non-hyperaccumulator [9,45]. Intercropping of different genotypes of tomato, eggplant, and radish with themselves exhibits a decrease or increase in Se uptake [12-14]. In the current study, intercropping of *C. betacea* with sect. *Solanum* increased Se uptake in the two plants, consistent with findings on the other plants planted in cadmium-contaminated soils [10]. These findings are consistent with results on the uptake level of Se in tomato, eggplant, and radish reported in previous studies [14-14]. The Se content of intercropped sect. *Solanum* exhibited a positive linear relationship with the Se content of the monocultures. The Se content of intercropped *C. betacea* showed a linear negative relationship with the Se content in sect. *Solanum* monocultures. These results indicate that intercropping promoted Se uptake in *C. betacea* and sect. *Solanum* further confirming the "rhizosphere dialogue" [39] between *C. betacea* and sect. *Solanum*. Several active compounds may be exchanged between *C. betacea* and sect. *Solanum* to improve the Se accumulation capacity of the two plants. Intercropped of *C. betacea* with diploid increased the TF of *C. betacea*, intercropping with tetraploid had no significant effect on the TF of *C. betacea*, whereas intercropping with hexaploid decreased the TF of *C. betacea*. However, intercropping of sect. *Solanum* with *C. betacea* increased the TFs of sect. *Solanum*. These results indicate that *C. betacea* intercropped with sect. *Solanum* had significant Se effects on sect. *Solanum* than *C. betacea*. This finding explains the higher percentage of shoot Se content in sect. *Solanum* than in *C. betacea*. Correlation and grey relational analyses revealed that CAT activity, POD activity, and soluble protein content were the top three indicators significantly associated with *C. betacea* shoot Se content. In contrast, POD activity, soluble protein content, and translocation factor were the top four indicators markedly associated with sect. *Solanum* shoot Se content. These results further imply that intercropping promoted Se absorption by increasing the resistance of the two plants to Se, and their action mechanisms should be explored further.

5. CONCLUSIONS

Intercropping of *C. betacea* with sect. *Solanum* inhibited the growth of *C. betacea* and promoted the growth of sect. *Solanum* as indicated by decrease or increase in their biomass and photosynthetic pigment contents. In addition, intercropping *C. betacea* with sect. *Solanum* improved their resistances to cadmium by increasing the levels of antioxidant enzyme activities and soluble protein contents in the two plants. Moreover, intercropping of the two plants increased the shoot Se contents in *C. betacea* and sect. *Solanum*. The biomass and Se content of intercropped sect. *Solanum* exhibited linear relationships with that of the

monocultures, and the biomass and Se content of intercropped *C. betacea* showed linear relationships with that of sect. *Solanum* monocultures. CAT activity, POD activity, and soluble protein content were the top three indicators highly associated with the Se content in *C. betacea* shoots. The POD activity, soluble protein content, and translocation factor were the top four indicators significantly associated with the Se content in sect. *Solanum* shoots. Further studies should be conducted under field conditions to verify these findings. Furthermore, the effects of Se uptake in *C. betacea* fruits should be evaluated.

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