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Timing of systemic resistance induced by local exogenous ABA application within clonal network of stoloniferous herb *Centella asiatica* subjected to low water availability

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Resistance traits of plants can be activated both at the damaged site and undamaged parts. Systemic resistance induced by local exogenous abscisic acid (ABA) application alleviated negative effect of low water availability on growth performance of clonal plant. However, timing of systemic resistance was poorly understood. Timing of systemic resistance refers to its activation and decay time within clonal network. Clonal fragment of *Centella asiatica* with four successive ramets (including first-oldest, second-older, third-old and fourth-young ramets) subjected to low water availability (20% soil moisture content) was used to explore effects of local exogenous ABA application on the timing of resistance activation and decay. Systemic resistance activated by local exogenous ABA application after 4 days remained at least 28 days. Compared with control, biomass accumulation of whole clonal fragment, root biomass and ratio of belowground to aboveground biomass significantly increased by local exogenous ABA application after 28 days. It is suggested that rapid activation and delay of resistance response induced by local exogenous ABA application within clonal network may improve fitness of clonal plant subjected to abiotic stress.

KEYWORDS

clonal integration, resistance activation, resistance delay, chlorophyll fluorescence, photosynthetic parameters

1 Introduction

Non-resource substances (such as defense or stress signal) can be transmitted or shared between interconnected ramets of clonal plant as well as resource substances (Stuefer et al., 2005; Jelinkova et al., 2012; Liu et al., 2015). With the increase of foliar tannin content, growth performance of interconnected young ramets was improved by local herbivory on old ramets of stoloniferous herb *Trifolium repens* (Gomez et al., 2008). Similarly, damage of caterpillar *Gynaephora rnenyuanensis* herbivory on young ramets of rhizomatous sedge *Carex alrofusca* was significantly alleviated by local application of jasmonic-acid to interconnected old ramets (Chen et al., 2011). Systemic defense or resistance within clonal networks induced by transportation or sharing of non-resource substances (such as defense or stress signal) may be very important for improving fitness of clonal plant subjected to biotic or abiotic stress (Gomez et al., 2007; Koubek and Herben, 2007; Sharifi and Ryu, 2021).

Systemic defense of soybean (*Glycine max*) induced by Mexican bean beetle (*Epilachnavarivestis*) herbivory after damage by 3 days gradually decayed by 15 days after damage (Underwood, 1998). With enhanced expression of defense-related genes, phytohormone concentration of leaf tissue (such as jasmonic acid and linolenic acid) significantly increased when leaf of hybrid poplar saplings was exposed to volatile compounds (*cis*-3-hexenyl acetate) for 72-96 hours (Frost et al., 2008). Foliar palatability of stoloniferous herb *T. repens* decreased local herbivory attack of *Mamestra brassicae* larvae after damage by 38-51 hours, which lasted for 28 days at least among interconnected undamaged ramets (Gomez et al., 2010). Therefore, rapid activation and delay of systemic defense induced by local herbivory within clonal network may improve fitness of clonal plant subjected to abiotic stress.

Exposure to volatile organic compounds (bacterial volatile blends from *Bacillus subtilis* GB03 and *Bacillus amyloliquefaciens* IN937a) from rhizobacteria for as little as 4 days was sufficient to activate induced systemic resistance in *Arabidopsis* seedlings (Ryu et al., 2004). Melatonin application improved the activity of antioxidant enzymes [APX (ascorbate peroxidase), CAT (catalase), DHAR (dehydroascorbate reductase), GST (glutathione S-transferase), GR (glutathione reductase), MDHAR (monodehydroascorbate reductase), POD (peroxidase), and SOD (superoxide dismutase)] and their relative genes expression when tomato seedlings were subjected to drought stress (Altaf et al., 2022). With systemic resistance activation, oxidative stress ($O_2^{\bullet-}$ production rate and MDA content) in the leaf of the old,

mature and young ramets was significantly alleviated by exogenous ABA application to the oldest ramets of stoloniferous herb *C. asiatica* subjected to low water availability (Wei et al., 2019). However, timing of systemic resistance (activation and decay time) induced among interconnected ramets was poorly understood.

Production of highly oxidizing ROS immediately affected photosynthesis when the plant was subjected to biotic or abiotic stress (Singh and Thakur, 2018; Qamer et al., 2021; Sachdev et al., 2021). Activation of MPK3/MPK6 can rapidly alter the expression of photosynthesis-related genes and inhibit photosynthesis when *Arabidopsis thaliana* was subjected to *Pseudomonas syringae* infection (Su et al., 2018). Young leaves of *A. thaliana* acclimate better to the onset of water deficit by dissipating the excess excitation energy by NPQ (Sperdouli and Moustakas, 2011). Therefore, plant subject to biotic or abiotic stress can also be evaluated by measuring photosynthetic efficiency such as maximum quantum yield of PSII (F_v/F_m), effective PSII quantum yield (Φ PSII), photochemical quenching (qP) and non-photochemical quenching (NPQ) (Corcuera et al., 2011; Lucas et al., 2014; Chen et al., 2016; He et al., 2018).

The phytohormone abscisic acid (ABA) is a key endogenous messenger in plants' responses to biotic and abiotic stresses such as various pathogens, heat, drought and high salinity (Yoshida et al., 2010; Osakabe et al., 2014; Lievens et al., 2017; Hu et al., 2018). It is rapid accumulation in response to stresses and mediation of many stress responses that help plant survival over the stresses (Sreenivasulu et al., 2012). Abscisic acid (ABA) as a stress hormone in plant responses to water shortage were well documented (Zhang et al., 2006; Zou et al., 2010; Yoshida et al., 2019). A greenhouse experiment with local application of exogenous ABA was conducted to investigate the timing of systematic resistance within clonal networks (Figure 1). We focused on (1) activation time of systemic resistance by local exogenous ABA application within clonal network of *C. asiatica*; (2) delay time of systemic resistance within clonal network after local exogenous ABA application. This research will help us to realize the mechanism for growth and fitness of clonal plant subjected to environmental stress.

2 Materials and methods

2.1 Plant material

As a perennial stoloniferous herb, *C. asiatica* was widely distributed in woodlands, forests edge, damp grass and roadsides

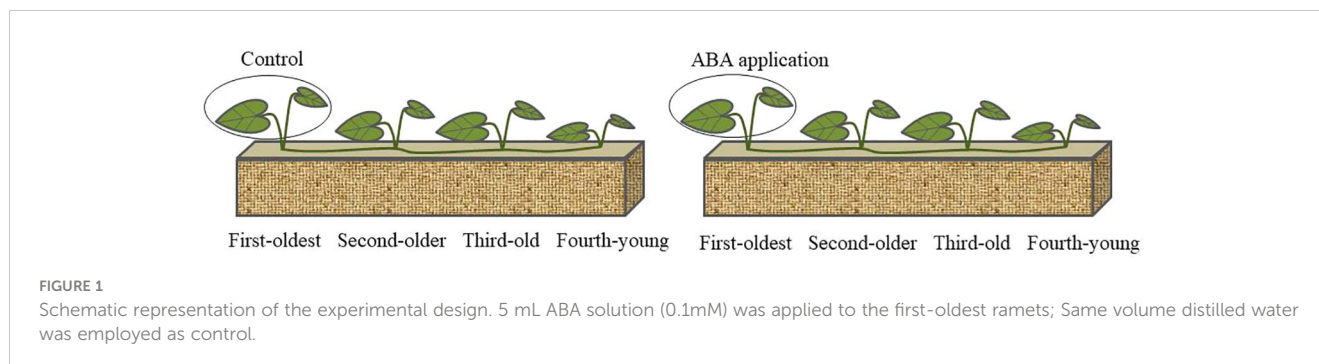


FIGURE 1

Schematic representation of the experimental design. 5 mL ABA solution (0.1mM) was applied to the first-oldest ramets; Same volume distilled water was employed as control.

or creeks. It usually takes root on each node of stolon when in contact with a moist substratum, forming a sympodial network above the ground (Li et al., 2018).

Clonal fragments of *C. asiatica* were collected from a forest edge, located in Chengdu, Sichuan province, China (30°05'~31°26' N; 102°54'~104°53' E). Each clonal fragment comprises four rooted ramets with different age (first-oldest, second-older, third-old and fourth-young ramets).

2.2 Experimental design

The container (dimensions: 10 cm × 8.5 cm × 15 cm) separated into 4 equal pots was used for the experiment. On 18 October 2021, four successive ramets of each clonal fragment were planted into the pots respectively. The pots were filled with substrate in a 3:1 mixture of humus soil and sand. 0.2 g Peters Professional (20% N, 20% P, 20% K; The Scotts Company, LLC., Marysville, OH, USA) was added to each pot at the beginning of experiment. The volumetric soil moisture content of each pot was maintained at 20% (volume of water present/the total volume). In the everyday morning (9:00-11:00 h), all pots were measured with a portable soil moisture meter (TDR-300, Spectrum, USA) and watered to maintain corresponding soil moisture. During the experiment, the mean temperature was $28.5 \pm 1.4^\circ\text{C}$, and light intensity was equivalent to approx. 90% of full daylight outside the greenhouse (minimum and maximum photosynthetic photon flux density in the greenhouse was 136.2 and $325.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively).

In the experiment, 5 ml of 0.1 mM ABA solution was applied to fully unfolded leaves of the first-oldest ramets and the same volume of distilled water was used as control. ABA dosage was based on a previous study (Wei et al., 2019). Neighboring sibling ramets were shielded from spray with a piece of plastic. Then, the first-oldest ramets were sealed in a transparent plastic bag until dry. The chlorophyll fluorescence parameters and photosynthetic parameters were measured at 1, 4, 7 and 14 days after ABA application. The experiment lasted for 28 days. There were seven replicates for per treatment.

2.3 Measurement of chlorophyll fluorescence parameters

Chlorophyll fluorescence measurements were carried out using a portable, modulated fluorescence monitoring system (FMS-2, Hansatech Instruments Ltd., UK) on fully expanded leaves. The minimum fluorescence (F_0) was determined using a measuring beam of $0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ intensity after 30 min of dark adaptation. Following a dark-adapted state, a saturation pulse (1 s white light of $7,500 \mu\text{mol m}^{-2} \text{s}^{-1}$ intensity) was used to obtain the maximum fluorescence (F_m). Light-induced changes in chlorophyll fluorescence following actinic illumination ($300 \mu\text{mol m}^{-2} \text{s}^{-1}$) were recorded prior to the measurement of F'_o (minimum fluorescence in light-saturated state), F'_m (maximum fluorescence in light-saturated state) and F_s (steady-state fluorescence in the light-saturated state). The maximum quantum yield of PSII (F_v/F_m), the effective PSII quantum yield (ΦPSII), the photochemical quenching (qP) and non-photochemical quenching (NPQ) were

calculated using $(F_m - F_0)/F_m$, $(F'_m - F_s)/F'_m$ (Genty et al., 1989), $(F'_m - F_s)/(F'_m - F'_o)$ and $(F_m - F'_m)/F'_m$ respectively (Turan and Ekmekçi, 2010).

2.4 Measurement of photosynthetic parameters

Photosynthetic parameters were made by a portable photosynthesis system GFS-3000 (Heinz Walz GmbH, Effeltrich, Germany). The measurement was conducted on the fully expanded mature leaves at a temperature of 25°C , photosynthetic photon flux density of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ and CO_2 concentration of $400 \mu\text{mol mol}^{-1}$. Net photosynthetic rate (P_n) and stomatal conductance (G_s) were recorded when gas exchange had equilibrated (taken to be when the coefficient of variation for external CO_2 partial pressure between the sample and reference analysis was below 0.3%).

2.5 Measurement of biomass characteristics of whole clonal fragment

Clonal fragments were separated into root, leaf and stolon and oven-dried to constant weight at 70°C for 72 h. Leaf and stolon biomass, root biomass, and biomass accumulation of whole clonal fragment were determined. Ratio of belowground to aboveground biomass was counted in whole clonal fragments (He et al., 2021).

2.6 Statistical analysis

The chlorophyll fluorescence parameters and photosynthetic parameters were analyzed by two-way repeated-measures (ANOVA). Two-way analysis of variance (ANOVA) was employed to investigate the leaf and stolon biomass, root biomass, ratio of belowground to aboveground biomass and biomass accumulation of whole clonal fragment. All analyses were conducted with SPSS 24.0 software (SPSS Inc.).

3 Result

3.1 Chlorophyll fluorescence parameters

Compared with control, NPQ of four interconnected ramets was decreased by local exogenous ABA application after 1 day (Table 1, Figure 2). Opposite pattern was observed in ΦPSII , F_v/F_m and qP (Table 1, Figure 2). After 4 days, significant difference was not observed between ΦPSII , F_v/F_m , qP and NPQ of four interconnected ramets subjected to local exogenous ABA application and those of control (Table 1, Figure 2). After 7 and 14 days, ΦPSII , F_v/F_m , and qP of four interconnected ramets subjected to local exogenous ABA application were significantly greater than those of control as well as significant decrease of NPQ (Table 1, Figure 2). From 7 to 14 days, significant effects of local exogenous ABA application on ΦPSII of four interconnected ramets

were detected. However, significant effects of local exogenous ABA application on F_v/F_m , qP and NPQ of four interconnected ramets were not detected (Table 1, Figure 2).

3.2 Photosynthetic parameters

Compared with control, P_n and G_s of four interconnected ramets were significantly decreased by local exogenous ABA application after 1 day (Table 1, Figure 3). After 4 days, significant difference was not observed between P_n and G_s of four interconnected ramets subjected

to local exogenous ABA application and those of control (Table 1, Figure 3). After 7 and 14 days, P_n and G_s of four interconnected ramets subjected to local exogenous ABA application were significantly greater than those of control (Table 1, Figure 3). G_s of fourth-young ramets was significantly greater than second-older ramets by local exogenous ABA applications after 14 days (Table 1, Figure 3). Meanwhile, P_n of fourth-young ramets was significantly greater than those of the first-oldest and third-older ramets (Table 1, Figure 3). From 7 to 14 days, significant effects of local exogenous ABA application on P_n and G_s of four interconnected ramets were detected (Table 1, Figure 3).

TABLE 1 Results of two-way repeated-measures analysis of variance, with 'exogenous ABA application' and 'ramet age' as between-subject effects for differences in chlorophyll fluorescence parameters and photosynthetic parameters among interconnected ramets.

Effects	df	Φ PSII		qP		NPQ		F_v/F_m		Stomatal conductance		Photosynthesis	
		F	P	F	P	F	P	F	P	F	P	F	P
Between-subject effects													
Exogenous ABA application (A)	1	738.284	0.001	171.218	0.001	208.048	0.001	171.218	0.001	342.657	0.001	398.312	0.001
Ramet age (R)	3	4.11	0.017	3.479	0.032	0.644	0.582	3.479	0.032	1.596	0.23	3.455	0.042
A × R	3	4.964	0.008	0.667	0.58	2.726	<i>0.066</i>	0.667	0.58	2.273	0.119	2.622	<i>0.068</i>
Within subject effects													
Time (T)	3	9.438	0.001	12.033	0.001	21.315	0.001	12.033	0.001	116.92	0.001	317.862	0.001
T × A	3	542.905	0.001	37.357	0.001	204.263	0.001	37.357	0.001	228.454	0.001	612.769	0.001
T × R	9	2.391	0.02	2.807	<i>0.07</i>	2.55	0.013	2.807	0.007	0.905	<i>0.0529</i>	3.77	0.001
T × A × R	9	1.446	0.185	3.73	0.001	2.634	0.011	3.73	0.001	1.198	0.0318	2.534	0.018

Values are in bold when $P < 0.05$, and in italic when $0.05 < P < 0.1$.

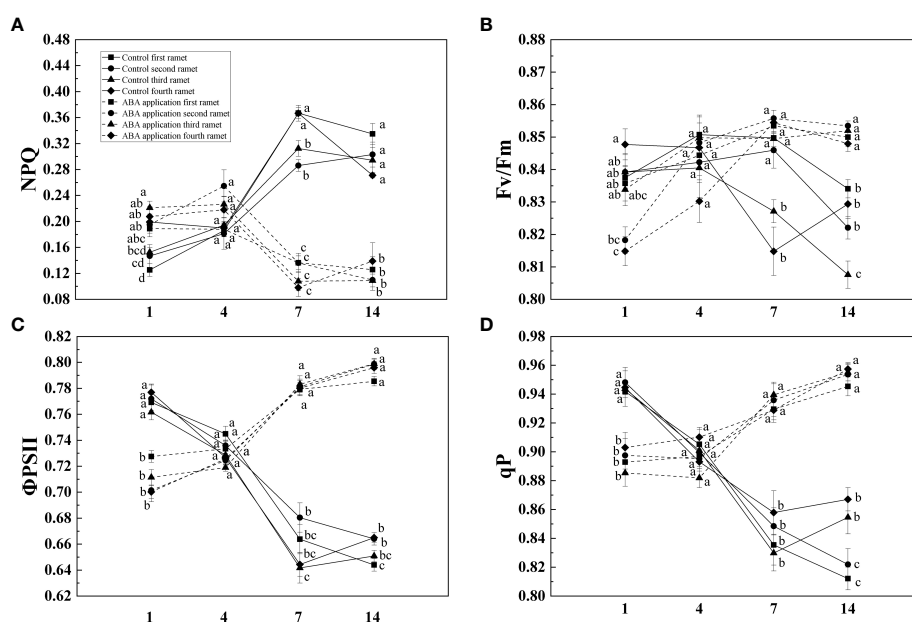


FIGURE 2 NPQ (A), F_v/F_m (B), Φ PSII (C) and qP (D) of interconnected ramets (including first-oldest, second-older, third-older and fourth-young ramet) 1, 4, 7 and 14 days after local exogenous ABA application. Same letters (at the same day) mean that they are not significantly different ($P > 0.05$).

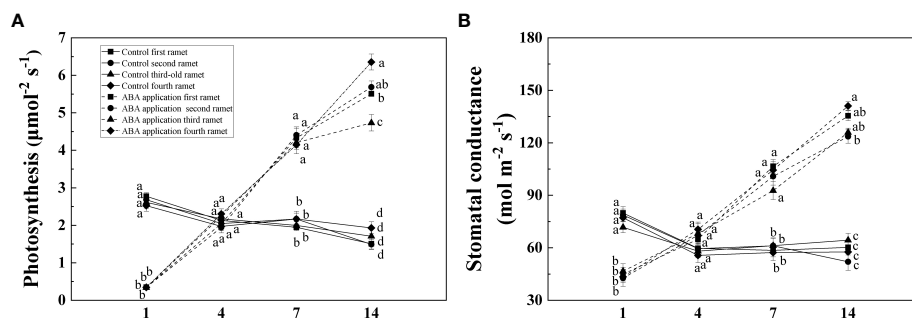


FIGURE 3 Net photosynthetic rate (A) and stomatal conductance (B) of interconnected ramets (including first-oldest, second-older, third-older and fourth-young ramet) 1, 4, 7 and 14 days after local exogenous ABA application. Same letters (at the same day) mean that they are not significantly different ($P > 0.05$).

3.3 Biomass accumulation

Root biomass, ratio of belowground to aboveground biomass and biomass accumulation of whole clonal fragments were significantly increased by local exogenous ABA application after 28 days (Table 2, Figures 4B, 5A, B). However, similar patterns were not observed in leaf and stolon biomass (Table 2, Figure 4A).

4 Discussion

Stomatal closure resulting from exogenous ABA application reduced water loss of wheat (Travaglia et al., 2010). In this study, with the stomatal closure, foliar net photosynthetic rate of four interconnected ramets significantly decreased by local exogenous ABA application after 1 day. By altering the kinetics of de-epoxidation of the xanthophyll cycle, exogenous ABA application incurred increase of NPQ in cabbage (*Brassica campestris*) and rice (*Oryza sativa* L) (Zhu et al., 2011). With its inhibition on photochemical activity, increase of NPQ implied that more light energy was used for heat dissipation to avoid damage to photosystem II of four interconnected ramets (Wilson and Ruban, 2020). Meanwhile, photoinhibition (decrease of F_v/F_m , Φ PSII and qP) was induced by abscisic acid (ABA) application after 1 day when clonal fragments of *C. asiatica* subjected to low water availability. Similar patterns were observed in the study that exogenous ABA application

resulted in decrease of F_v/F_m , Φ PSII and qP of maize subjected high light intensity ($1500 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Jia and Lu, 2003).

Φ PSII and qP of sugarcane subjected to drought treatment were increased by the exogenous ABA application after 3 days and remained at least 7 days (Srivastava et al., 2009). Selenium (Se) application can alleviate oxidative stress in the chloroplasts to increase F_v/F_m when potato (*Solanum tuberosum* L.) was subjected to photooxidative stress (Turakainen et al., 2008). In this study, chlorophyll fluorescence and photosynthesis of four interconnected ramets were restored by local exogenous ABA application after 4 days. Altogether, the recovery of chlorophyll fluorescence and photosynthesis capacity are interpreted as activation of systemic resistance. With the exogenous ABA application, root growth was improved when *Arabidopsis* seedlings was subjected to low water availability (Miao et al., 2021). Exogenous ABA application significantly increased root/shoot ratio of *Malus sieversii* and *Malus hupehensis* seedlings subjected to low water availability. Similar pattern was observed in our experiment (Ma et al., 2008). Biomass accumulation significantly increased by local exogenous ABA application when wheat was subjected to low water availability (Kaur and Asthir, 2020). The positive effects on growth performance of whole clonal fragments were observed by local exogenous ABA application after 28 days. We tentatively suggested that defense induction persisted for at least 28 days.

Systemic resistance may give priority to protection of youngest tissues (Chen et al., 2011). Young ramets were the most valuable

TABLE 2 Two-way analysis of variance (ANOVA) for effects of ABA application, ramet age and their interaction on leaf and stolon biomass, root biomass, biomass accumulation of whole clonal fragments and ratio of belowground to aboveground biomass.

Effects	df	leaf and stolon biomass		root biomass		biomass accumulation of whole clonal fragments		ratio of belowground to aboveground biomass	
		F	P	F	P	F	P	F	P
Exogenous ABA application (A)	1	1.829	0.189	38.731	0.000	11.914	0.002	53.017	0.000
Ramet age (R)	3	1.461	0.250	1.205	0.329	0.206	0.891	8.628	0.000
A×R	3	0.623	0.607	1.710	0.192	1.117	0.362	0.792	0.511

Values are in bold when $P < 0.05$, and in italic when $0.05 < P < 0.1$.

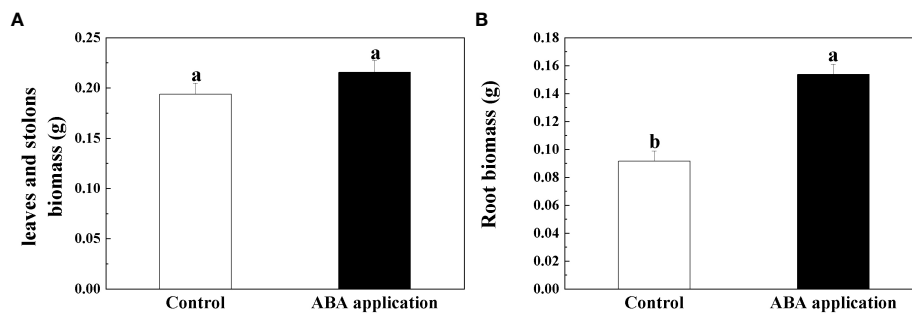


FIGURE 4

Leaf and stolon biomass (A) and Root biomass (B) of interconnected ramets after 28 days; Open bars, control; closed bars, exogenous ABA application. Error bars indicate \pm s.e. for 10 replicates. Bars with the same lower case letters are not significantly different ($P > 0.05$).

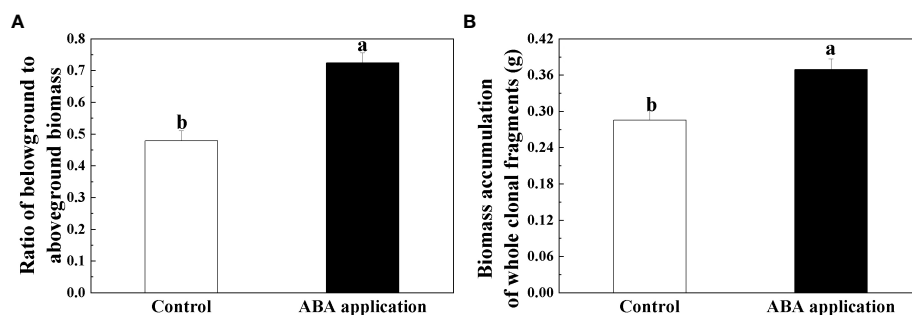


FIGURE 5

Ratio of belowground to aboveground biomass (A) and Biomass accumulation of whole clonal fragments (B) after 28 days; Open bars, control; closed bars, exogenous ABA application. Error bars indicate \pm s.e. for 10 replicates. Bars with the same lower case letters are not significantly different ($P > 0.05$).

tissues for growth and fitness within clonal networks (Stuefer et al., 2005; Gomez and Stuefer, 2006). The optimal defense theory predicts that plant tissues with a high contribution to fitness should be better protected than other plant tissues (Hunziker et al., 2021). In the experiment, our study was consistent with previous study that compared with the old and mature ramets, foliar antioxidant capacity of young ramets was significantly higher and oxidative stress was significantly lower when exogenous ABA application to the oldest ramets (Wei et al., 2019). It is suggested that the protection of young ramets may confer clonal plants with considerable benefits in adapting to environmental stress.

Our study implies that rapid activation and delay of resistance response induced by local exogenous ABA application within clonal network may improve fitness of clonal plant subjected to abiotic stress. Benefit of systemic resistance will depend on the absence or presence of subsequent environmental stress (van Hulst et al., 2006). In the future, more studies are needed to understand the generality and ecological advantages afforded by systematic resistance within clonal network.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

Author contributions

S-JD: Writing – original draft, Data curation, Investigation, Methodology, Conceptualization, Formal Analysis, Software, Validation, Visualization. G-JS: Data curation, Methodology, Investigation, Formal Analysis, Writing – original draft. YD: Investigation, Methodology, Data curation, Writing – original draft. JD: Methodology, Data curation, Investigation, Writing – original draft. D-WY: Methodology, Data curation, Writing – original draft. QW: Methodology, Data curation, Writing – original draft. C-FC: Investigation, Writing – original draft. JJ: Investigation, Writing – original draft. X-MW: Investigation, Writing – original draft. T-JR: Investigation, Writing – original draft. Y-ML: Writing – review & editing, Supervision, Validation. J-SC: Writing – review & editing, Supervision, Validation.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer ZY declared a shared affiliation with the author(s) GS and YL to the handling editor at the time of review.

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