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PHYSIOLOGICAL RESPONSES AND HEAT TOLERANCE EVALUATION OF TEN GROUND COVER PLANT SPECIES UNDER HEAT STRESS

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Abstract

To explore the heat tolerance capabilities of 10 ground cover plant species, treatments using maximum temperatures of 25°C (control), 30°C, 35°C, and 40°C were performed in growth chambers. Compared with the control group (25°C), under heat stress (30°C, 35°C, and 40°C), the largest reductions in root activity and transpiration rates occurred in *M. cordifolium* (86.04%) and *D. chinensis* (61.77%), respectively. Except for *P. lanceolata*, *V. hybrida*, and *D. chinensis*, the reduction in water content for the other seven species (including *C. roseus*) was less than 5%. Under 40°C stress, photosynthesis-related indicators such as relative chlorophyll content, net photosynthetic rate, and stomatal conductance decreased by 1.39%-67.29%, 7.75%-52.46%, and 1.09%-57.28% respectively, while intercellular CO_2 concentration increased by 12.08%-40.40% when compared to the control in the ten plant species. Under different temperature treatment conditions, superoxide dismutase (SOD) and peroxidase (POD) activities were highest in *C. roseus*, reaching 250.39 U/(g·min) and 3017.59 U/(g·min), respectively, while catalase (CAT) activity was highest in *P. lanceolata* at 152.73 U/(g·min). Malondialdehyde (MDA) content rose after increasing temperatures from 25°C to 35°C. However, the change trends of soluble protein, soluble sugar, and proline contents varied, ranging from -57.17% to 48.56%, -53.22% to 501.02%, and -47.66% to 227.34%, respectively. Principal component analysis showed that the first five principal components had a cumulative contribution rate of 83.162%. The membership function method combined with cluster analysis results allowed for the classification of these plants into three categories: strong heat tolerance (*C. roseus*, *P. lanceolata*, and *T. fournieri*, three species in total), moderate heat tolerance (*V. hybrida*, *A. hispida*, *M. cordifolium*, *P.* 'Cerveza'n Lime', and *C. scutellarioides*, five species in total), and weak heat tolerance (*D. chinensis* and *T. cerinthoides* 'Nanouk', two species in total). In summary, this study provides a physiological basis for selecting ground cover plant resources that could be used in areas with different temperatures.

Key words: Ground cover plants; Photosynthetic performance; Antioxidant capacity; Heat tolerance; Comprehensive evaluation

Introduction

The acceleration of China's urbanization process is linked with the development of eco-garden cities, leading to elevated standards for urban green space planning (Wang *et al*., 2008). With characteristics such as rapid growth, diverse morphology and flower colors, and strong ecological adaptability, ground cover plants can quickly form vegetation to increase green volume and optimize green space structure, enhancing community stability, regulating urban microclimate, creating colorful landscapes, and improving the comprehensive benefits of urban ecosystems. Therefore, ground cover plants play an important role in creating garden landscapes. However, global warming has led to frequent extreme high temperature events (Liu *et al*., 2022). Furthermore, heat stress has become a key abiotic stress factor limiting the growth, development, and distribution of these plants (Chen *et al*., 2023).

As 'producers' in ecosystems, plants respond sensitively to climate change. Under high temperature stress, their physiological processes are disturbed to varying degrees, sometimes leading to mortality (Zhao *et al*., 2024b). Research has shown that heat stress affects plant root activity, reducing roots' ability to absorb water and nutrients, thereby inhibiting growth (Xu *et al*., 2024). In addition, high temperatures also decrease chl content and photosynthetic capacity by affecting parameters such as photosynthetic rate, stomatal conductance, transpiration rate, and intercellular CO_2 concentration in *Erigeron breviscapus* and *Paeonia lactiflora* (Luo *et al*., 2025). Heat stress also disrupts the metabolic balance of reactive oxygen species (ROS) in plants and reduces antioxidant enzyme activity, leading to ROS accumulation (Li *et al*., 2025). Heat stress triggers membrane lipid peroxidation, increases cell membrane damage, and exacerbates electrolyte leakage (Li *et al*., 2024). Simultaneously, high temperatures accelerate water loss. To maintain cell turgor pressure and adapt to heat-stress environments, plants actively synthesize osmotic adjustment substances such as proline, soluble sugar, and soluble protein to maintain cell turgor pressure and adapt to heat-stress environments (Li *et al*., 2023; Lv *et al*., 2025).

In recent years, multivariate statistical methods have been widely applied for the comprehensive evaluation of plant heat tolerance (Zhang *et al*., 2023b). Some studies have evaluated the physiological mechanisms of heat

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tolerance in different varieties of certain ground cover plants (Wassie *et al.*, 2019), but comprehensive evaluations across different species have rarely been reported. Therefore, this study selected 10 common ground cover plant species for the treatment of heat stress conditions, measuring relevant physiological indicators. Furthermore, comprehensive evaluations using principal component analysis, membership function methods, and cluster analysis were conducted. Our study aims to reveal the physiological mechanisms of ground cover plants' responses to heat stress. Therefore, the results could provide a scientific basis for accurately selecting suitable ground cover plant resources according to local temperature conditions, thus enhancing the landscaping, beautification, and ecological effects of gardens.

Materials and Methods

Experimental materials and growth conditions: The 10 ground cover plant species used in this study were *Catharanthus roseus*, *Mesembryanthemum cordifolium*, *Pentas lanceolata*, *Acalypha hispida*, *Verbena hybrida*, *Plectranthus* 'Cerveza'n Lime', *Dianthus chinensis*, *Coleus scutellarioides*, *Torenia fournieri*, and *Tradescantia cerinthoides* 'Nanouk'. All plants were provided by Shanghai Yuanyi Seedling Co., Ltd.

The experiment was conducted in the plantation garden of Anhui Science and Technology University (longitude 117.56°E, latitude 32.87°N), beginning on March 19, 2024. Seedlings with consistent growth and vigor from each of the 10 ground cover plant species were selected and planted in plastic pots (21 cm diameter, 11 cm height), with 24 pots per species and 4 plants per pot. River sand was used as the cultivation substrate, and plants were grown under natural outdoor conditions. Plants were irrigated with Hoagland nutrient solution through consistent management (Zhao *et al.*, 2024a). On July 15, 2024, different temperature treatments were initiated.

Heat stress treatment: Potted plants were placed in growth chambers (Model GXL-P600B, Hefei Dascat Biological Technology Co., Ltd.) for 7 days of adaptive cultivation, with a photoperiod of 15 h/9 h (day–night), an illumination time from 7:00-22:00 (light intensity of 10,000 lx), and relative humidity maintained at 75%. Water management was consistent across treatments. On the 8th day, heat stress treatments were simulated with daily maximum temperatures set at 25°C (CK), 30°C, 35°C, and 40°C, for a total of four treatments. To avoid the effects of sudden temperature changes, a segmented temperature adjustment method was employed (Table 1). On the 10th day of treatment, leaves from the same position were selected for sampling, and relevant indicators were measured with three biological replicates.

Table 1. Temperature settings for different treatments (°C).

Treatment	7:00-10:00	10:00-16:00	16:00-22:00	22:00-7:00
CK	20	25	20	15
30	25	30	25	20
35	30	35	30	25
40	35	40	35	30

Physiological parameter measurement methods: Root activity was determined using the triphenyl tetrazolium chloride method. Water content was measured using the oven-drying method. Between 09:00 and 10:00, leaf transpiration rate, photosynthetic rate, stomatal conductance, and intercellular CO_2 concentration were measured using a portable photosynthesis system: TPS-2 (PP SYSTEMS, USA). SPAD values were determined using a SPAD-502 chlorophyll meter (Konica Minolta, Japan).

SOD activity was measured using the nitroblue tetrazolium method. POD activity was determined using the guaiacol method. CAT activity was assessed using the ultraviolet absorption method. Soluble sugar content was determined using the anthrone colorimetric method. Soluble protein content was measured using the Coomassie Brilliant Blue G-250 staining method. Free proline content was determined using the acid ninhydrin colorimetric method. MDA content was measured using the thiobarbituric acid colorimetric method. All methods were conducted according to Li Hesheng's protocols (Li, 2000). Each parameter was measured in triplicate, and the average values were used for analysis.

Statistical analysis

Excel was used for raw data processing. SPSS 27.0 was employed for analysis of variance, chart creation, principal component analysis, membership function analysis, and cluster analysis (Zhang *et al.*, 2024a). For positive indicators, the heat tolerance coefficient (*HTC*) = treatment group mean value/control group mean value; for negative indicators, *HTC* = control group mean value/treatment group mean value (Li *et al.*, 2021).

Results

Effects of heat stress on water status: Figure 1 shows that, except for *P.* 'Cerveza'n Lime' and *C. scutellarioides*, heat stress significantly reduced the root activity of the ground cover plant species following an increase in temperature. Compared with their respective controls, the magnitude of root activity reduction under 40°C stress ranked as follows, from largest to smallest: *M. cordifolium* > *T. cerinthoides* 'Nanouk' > *C. roseus* > *A. hispida* > *V. hybrida* > T. fournieri > *D. chinensis* > *C. scutellarioides* > *P. lanceolata* > *P.* 'Cerveza'n Lime'. The first three decreased by 86.04%, 83.45%, and 70.55%, respectively (Fig. 1A).

The water content of all tested plants exhibited an initial increase followed by a decrease when the temperature rose. Compared with their respective controls, only *M. cordifolium*, *A. hispida*, and *P.* 'Cerveza'n Lime' reached their maximum water content values at 30°C stress, with values of 96.77%, 74.17%, and 95.33%, respectively. The remaining seven species reached their maximum water content values at 35°C. Among these plants, *C. roseus* showed the highest increase compared with the control at 8.33%. Under different temperature treatments, *M. cordifolium*, *P.* 'Cerveza'n Lime', and *T. cerinthoides* 'Nanouk' maintained water content above 90%; *C. roseus*, *C. scutellarioides*, and *T. fournieri* had water content values between 80% and 90%; the remaining species all had water content values below 82.5% (Fig. 1B).

Under heat stress, the transpiration rate of the 10 ground cover species exhibited varying trends. *C. roseus*, *P. lanceolata*, *A. hispida*, *V. hybrida*, *P.* 'Cerveza'n Lime', *C. scutellarioides*, *T. fournieri*, and *T. cerinthoides* 'Nanouk' showed an initial increase followed by a decrease as temperature increased, all reaching maximum values at 30°C stress, with *C. scutellarioides* showing the highest growth rate of 81.39%. Only *M. cordifolium* and *D. chinensis* exhibited decreasing transpiration rate trends following temperature increases, and *D. chinensis* showed a substantial decrease of 61.77% (Fig. 1C).

Effects of heat stress on photosynthetic performance: The photosynthetic performance parameters of the 10 ground cover plant species displayed differential responses to temperature elevation (Fig. 2). Most plants exhibited an initial increase followed by a decrease in SPAD values, photosynthetic rate, and stomatal conductance, though the peak temperatures varied among the different species. Specifically, *P. lanceolata*, *A. hispida*, *V. hybrida*, and *C. scutellarioides* reached their peak SPAD values at 30°C stress, while *C. roseus*, *M. cordifolium*, and *T. fournieri* reached peak values at 35°C stress, with SPAD values of 38.33, 42.54, and 28.66, respectively. The SPAD values of these seven plant species exhibited unimodal curves following increasing temperature, whereas *P.* 'Cerveza'n Lime' and *T. cerinthoides* 'Nanouk' showed continuous declining trends (Fig. 2A).

The photosynthetic rate and stomatal conductance values of *C. roseus* and *P. lanceolata* reached their maximums at 35°C, where photosynthetic rate increased by 36.23% and 25.57% and stomatal conductance increased by 12.90% and 42.54%, respectively, compared with the controls. The stomatal conductance values of *P.* 'Cerveza'n Lime' and *D. chinensis* continuously decreased following increasing temperature, declining by 42.14% and 57.28%, respectively, under the 40°C treatment. The remaining six species exhibited their highest photosynthetic rate and stomatal conductance values at 30°C stress (Fig. 2B and 2D).

Intercellular CO_2 concentration exhibited two distinct trends. In *D. chinensis*, *C. scutellarioides*, and *T. cerinthoides* 'Nanouk', it showed continuous increases following temperature increases, with elevations of 21.44%, 18.15%, and 18.88%, respectively, at 40°C heat stress compared with the controls. However, the remaining seven species exhibited initial decreases followed by increases, with minimum values occurring at 30°C, and *V. hybrida* showed the largest decrease at 17.68% (Fig. 2C).

Effects of heat stress on antioxidant performance: Figure 3 shows the changes in three antioxidant enzyme activities and the membrane lipid peroxidation product MDA under different temperature treatments. Following heat stress, SOD activity increased in *C. roseus*, *P. lanceolata*, and *A. hispida* (Fig. 3A), reaching 250.39 U/g, 96.43 U/g, and 212.08 U/g, respectively, at 40°C stress. *M. cordifolium*, *V. hybrida*, *D. chinensis*, and *T. fournieri* exhibited an initial increase followed by a decrease, with peak values under the 30°C treatment at 28.66 U/g, 45.92 U/g, 35.45 U/g, and 58.01 U/g, respectively. In contrast, *P.* 'Cerveza'n Lime', *C. scutellarioides*, and *T. cerinthoides* 'Nanouk' showed decreasing SOD activity following increasing temperatures.

Changes in POD activity under heat stress were more complex among the tested ground cover plants (Fig. 3B). *A. hispida*, *C. roseus*, *P. lanceolata*, *P.* 'Cerveza'n Lime', *D. chinensis*, and *C. scutellarioides* demonstrated an initial increase followed by a decreasing trend. Among these plants, *A. hispida* reached its peak value at 30°C stress (a 57.42% increase compared with the control), while the other plants reached peak values at 35°C, with increases of 41.37%, 70.59%, 78.62%, 20.77%, and 29.39%, respectively. The POD activities of *M. cordifolium*, *V. hybrida*, and *T. fournieri* exhibited increasing trends, while *T. cerinthoides* 'Nanouk' showed a decreasing trend.

The changes in CAT activity are shown in Fig. 3C. Under the 30°C-40°C treatments, CAT activity decreased by 20.59%-39.08% and 52.06%-83.11% in *C. roseus* and *V. hybrida*, respectively, compared with the controls. *M. cordifolium* and *P.* 'Cerveza'n Lime' reached peak activity at 30°C stress, with values of 24.38 U/(g·min) and 15.17 U/(g·min), respectively. *P. lanceolata*, *A. hispida*, *C. scutellarioides*, and *T. cerinthoides* 'Nanouk' reached peak activity at 35°C stress, with values of 152.73 U/(g·min), 127.58 U/(g·min), 55.71 U/(g·min), and 24.15 U/(g·min), respectively. *D. chinensis* and *T. fournieri* exhibited increasing trends, with increases of 59.69% and 8.27% compared with the controls.

The MDA content of six plant species (*C. roseus*, *P. lanceolata*, *V. hybrida*, *P.* 'Cerveza'n Lime', *D. chinensis*, and *T. cerinthoides* 'Nanouk') generally demonstrated increasing trends in response to high temperatures (Fig. 3D). Among these plants, *P.* 'Cerveza'n Lime' showed the highest increase at 190.06%. The remaining four species exhibited an initial increase followed by a decrease, reaching maximum values at 35°C, of which *C. scutellarioides* showed the highest increase at 151.54%. *C. roseus*, *M. cordifolium*, *P.* 'Cerveza'n Lime', *C. scutellarioides*, and *T. cerinthoides* 'Nanouk' had significantly lower MDA contents than the other five ground cover plants.

Effects of heat stress on organic osmotic adjustment substance content: Figure 4 reveals the changes in three organic osmotic adjustment substances in 10 ground cover plant species under heat stress. Compared with their respective controls, increased temperatures reduced soluble protein content in *C. roseus*, *P. lanceolata*, *V. hybrida*, and *T. cerinthoides* 'Nanouk' but increased soluble protein content in *P.* 'Cerveza'n Lime' and *D. chinensis*, with increases of 39.38% and 48.56%, respectively. The soluble protein content of *M. cordifolium* showed a slight initial increase and then a decrease following temperature increases, while the remaining three species exhibited an initial decrease followed by an increase (Fig. 4A). Of the species, *C. roseus*, *T. fournieri*, *P. lanceolata* (except under 40°C stress), and *V. hybrida* (except under 35°C and 40°C stresses) had significantly higher soluble protein contents than the other six species.

After heat treatment, the soluble sugar contents of *C. roseus*, *A. hispida*, *V. hybrida*, *T. fournieri*, and *T. cerinthoides* 'Nanouk' exhibited an initial decrease followed by an increase. *M. cordifolium* showed an increasing trend; *P. lanceolata* demonstrated a decreasing trend; and *P.* 'Cerveza'n Lime', *D. chinensis*, and *C. scutellarioides* exhibited initial increases followed by decreases. Under 35°C stress, the soluble sugar of *C. roseus* showed the largest decrease, with a 53.22% reduction compared with the control; however, it increased dramatically under 40°C stress, even surpassing the control by 5.81%. Among the tested ground cover plants, seven species (*C. roseus*, *P. lanceolata*, *A. hispida*, *V. hybrida*, *D. chinensis*, *C. scutellarioides*, and *T. fournieri*) had more soluble sugar content than the remaining three species (Fig. 4B).

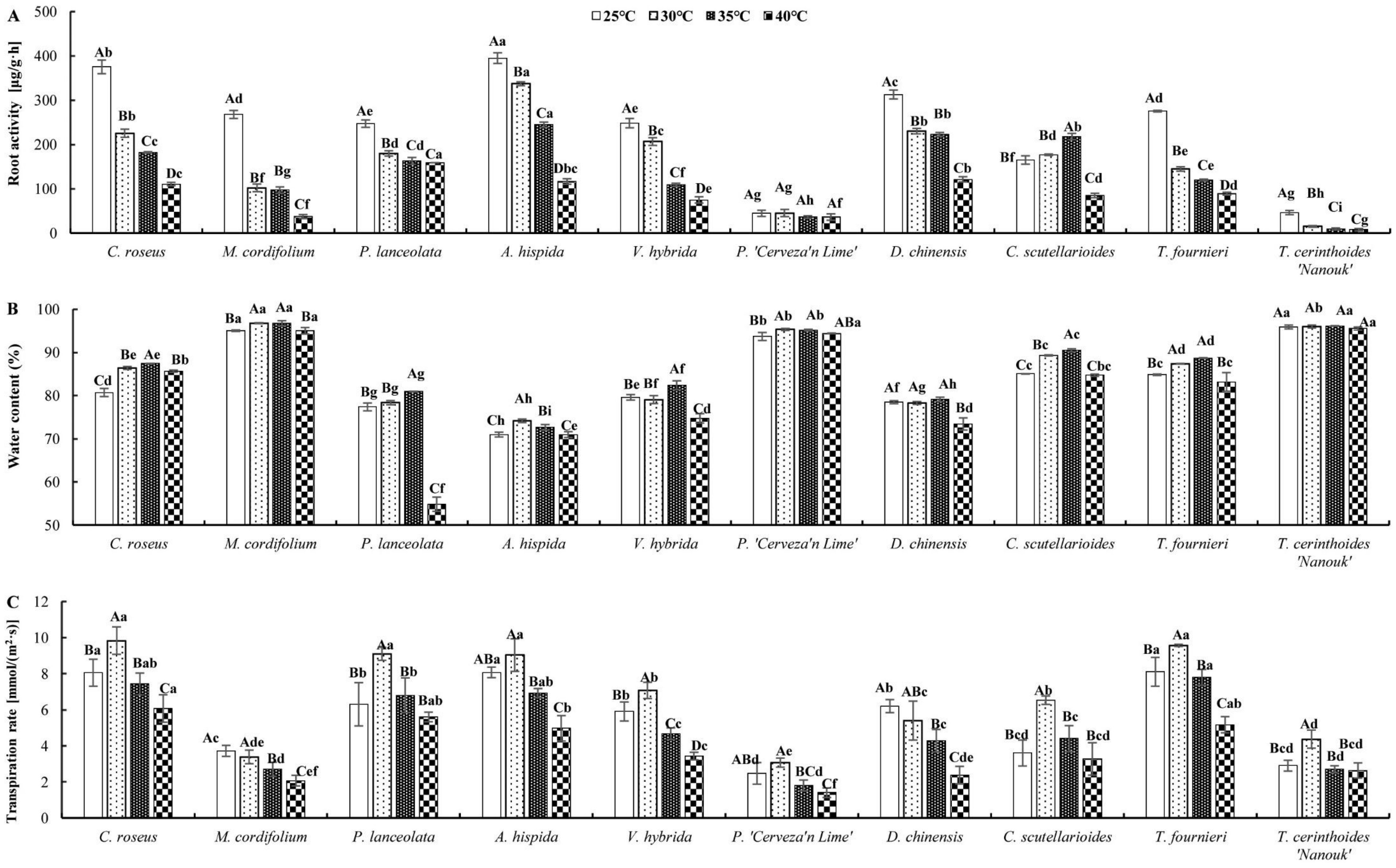


Fig. 1. Effects of heat stress on root activity (A), water content (B), and transpiration rate (C).

Note: Different uppercase letters indicate significant differences between treatments within the same species ($p<0.05$); different lowercase letters indicate significant differences between species under the same treatment ($p<0.05$). The same applies below.

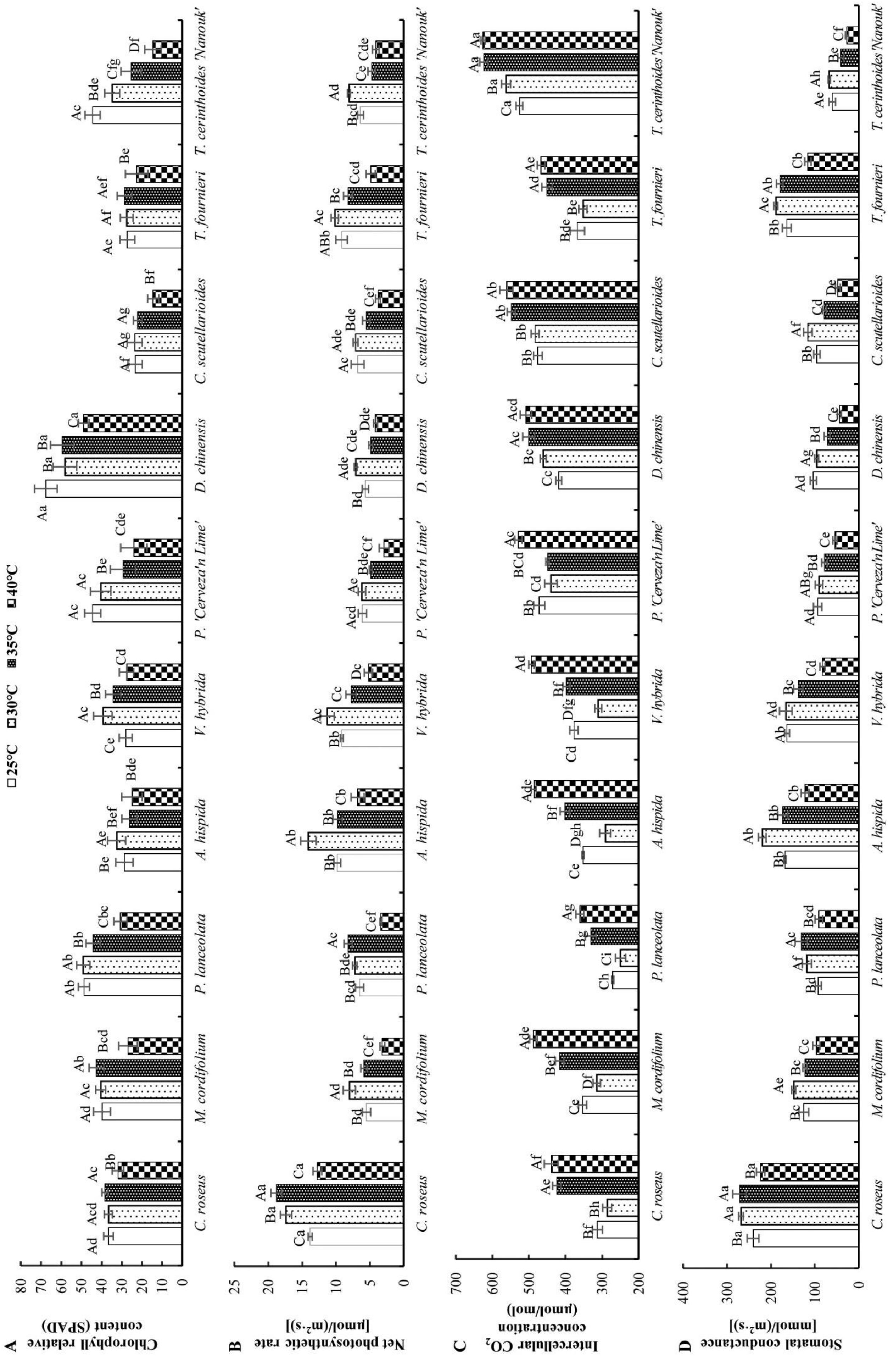


Fig. 2. The effect of high-temperature stress on SPAD values (A), photosynthetic rate (B), intercellular CO_2 concentration (C), and stomatal conductance (D).

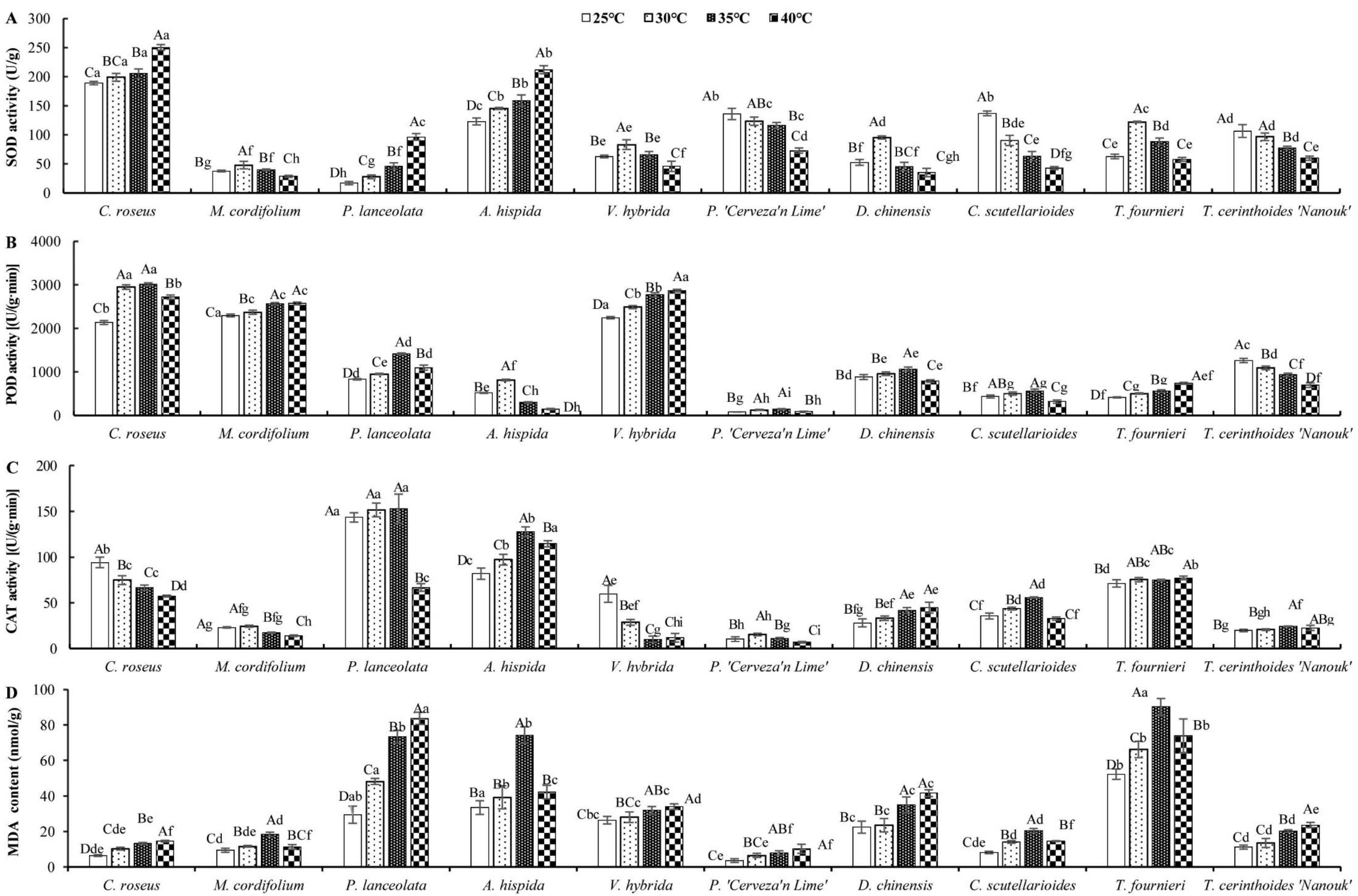


Fig. 3. The effect of high-temperature stress on the activities of SOD (A), POD (B), CAT (C), and MDA contents (D).

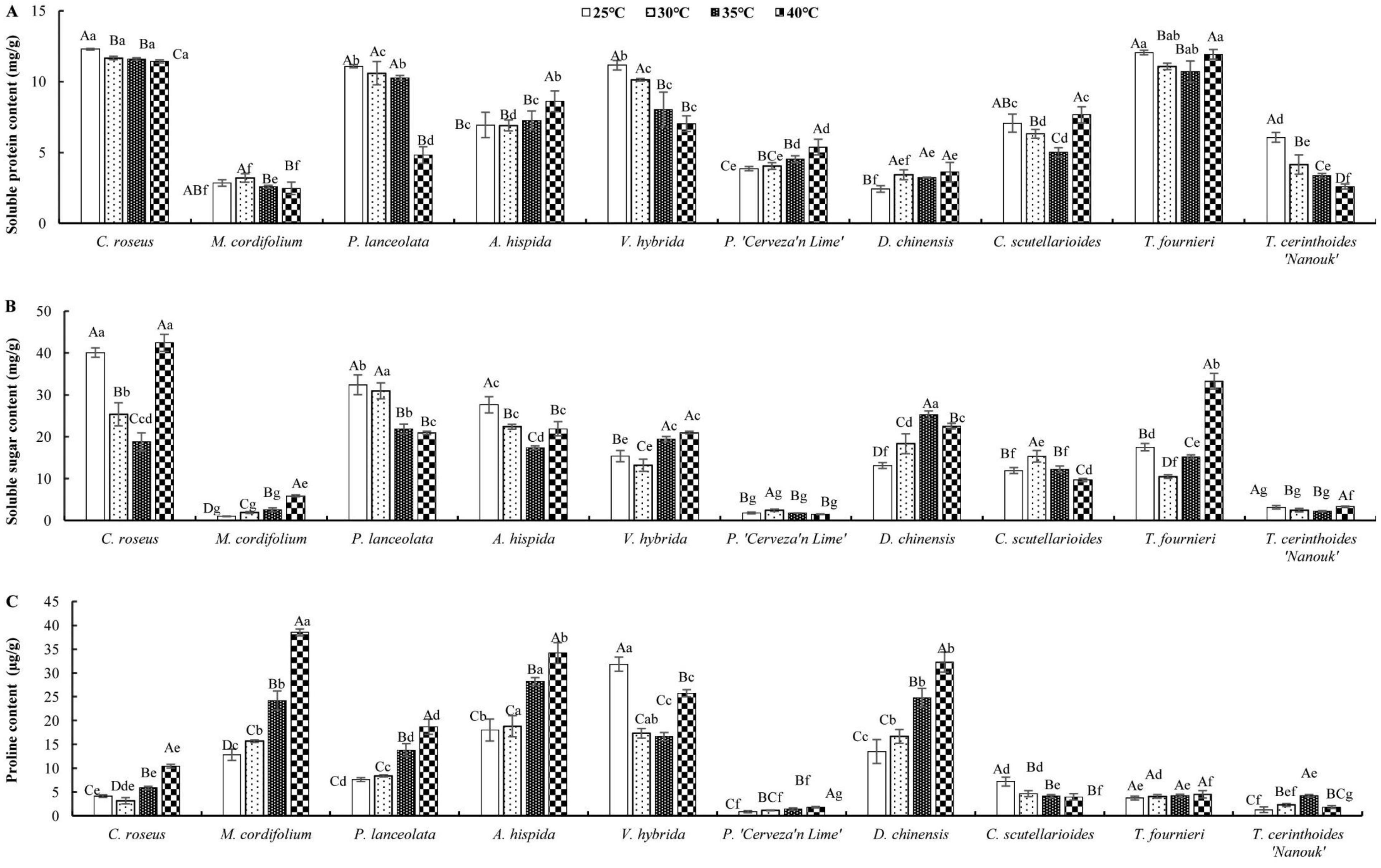
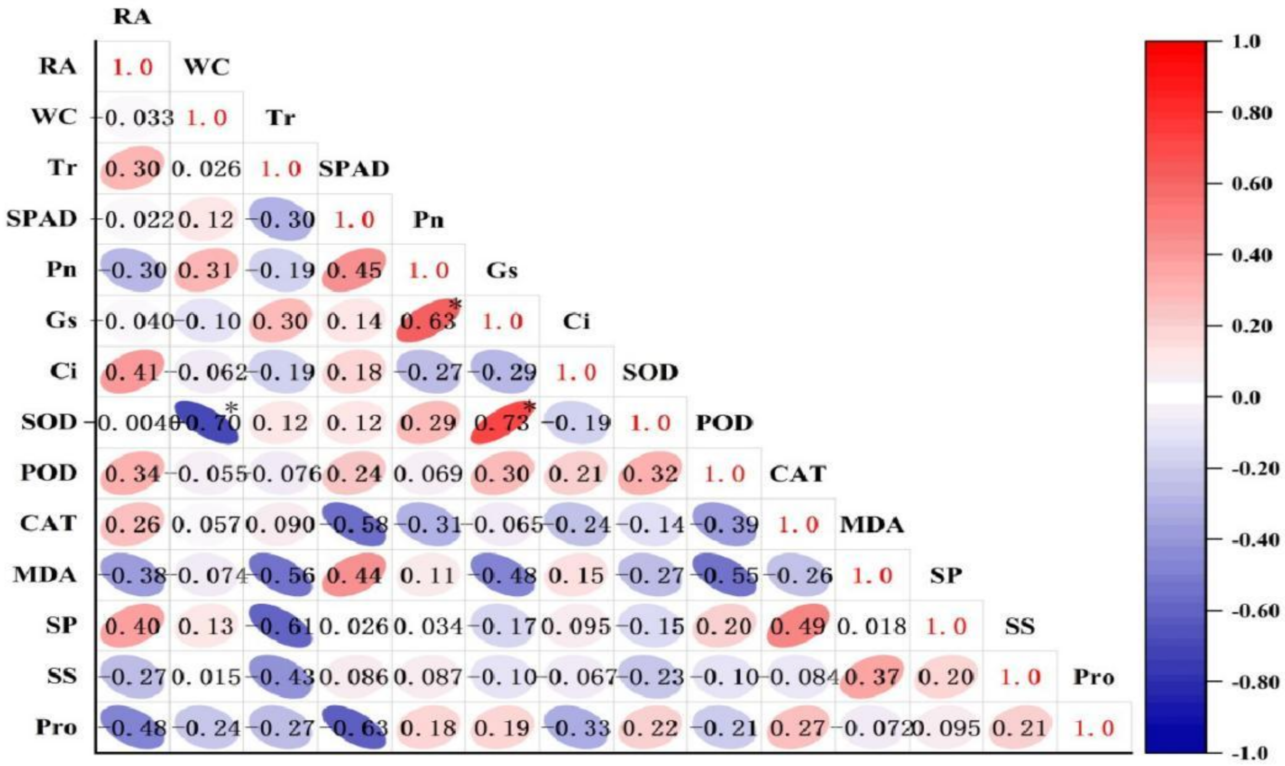


Fig. 4. The effect of high temperature stress on the content of soluble protein (A), soluble sugar (B), and proline content (C).

Table 2. *HTC* of the single indices of ten ground cover plant species.

Plant species	HTC													
	RA	WC	Tr	SPAD	Pn	Gs	Ci	SOD	POD	CAT	MDA	SP	SS	Pro
C. roseus	0.461	1.072	0.966	0.974	1.181	1.058	0.848	1.154	1.356	0.703	0.518	0.941	0.719	1.567
M. cordifolium	0.295	1.012	0.731	0.921	1.035	0.978	0.899	1.025	1.090	0.803	0.718	0.965	3.524	2.038
P. lanceolata	0.677	0.922	1.138	0.847	0.960	1.234	0.886	3.319	1.392	0.863	0.454	0.772	0.759	1.795
A. hispida	0.590	1.023	0.865	0.972	1.042	1.021	0.936	1.401	0.809	1.383	0.698	1.094	0.744	1.503
V. hybrida	0.525	0.989	0.806	1.203	0.886	0.688	0.976	1.037	1.206	0.282	0.848	0.752	1.164	0.625
P. 'Cerveza'n Lime'	0.882	1.014	0.846	0.705	0.801	0.793	1.005	0.767	1.517	1.072	0.445	1.206	1.015	1.663
D. chinensis	0.612	0.981	0.648	0.822	0.841	0.684	0.856	1.117	1.063	1.423	0.711	1.409	1.681	1.820
C. scutellarioides	0.968	1.037	1.315	0.856	0.806	0.847	0.900	0.479	1.061	1.240	0.511	0.896	1.382	0.591
T. fournieri	0.428	1.019	0.928	0.965	0.845	0.985	0.882	1.424	1.445	1.064	0.459	0.932	1.121	1.145
T. cerinthoides 'Nanouk'	0.232	1.000	1.115	0.559	0.787	0.748	0.873	0.732	0.718	1.138	0.617	0.556	0.854	2.161
Average	0.567	1.007	0.936	0.882	0.918	0.904	0.906	1.246	1.166	0.997	0.598	0.952	1.296	1.491
Standard deviation	0.222	0.037	0.193	0.164	0.125	0.171	0.049	0.745	0.254	0.328	0.133	0.229	0.798	0.516
Variable coefficient (%)	39.168	3.699	20.623	18.593	13.585	18.953	5.363	59.828	21.793	32.848	22.281	24.097	61.560	34.621

RA, Root activity; WC, Water content; *Tr*, Transpiration rate; *Pn*, Net photosynthetic rate; *Gs*, Stomatal conductance; *Ci*, Intercellular CO_2 concentration; SP, Soluble protein; SS, Soluble sugar; Pro, Proline



	RA	WC	Tr	SPAD	Pn	Gs	Ci	SOD	POD	CAT	MDA	SP	SS	Pro
RA	1.0													
WC	0.033	1.0												
Tr	0.30	0.026	1.0											
SPAD	0.022	0.12	-0.30	1.0										
Pn	-0.30	0.31	-0.19	0.45	1.0									
Gs	0.040	-0.10	0.30	0.14	0.63*	1.0								
Ci	0.41	-0.062	-0.19	0.18	-0.27	-0.29	1.0							
SOD	0.0040	-0.70*	0.12	0.12	0.29	0.73*	-0.19	1.0						
POD	0.34	-0.055	-0.076	0.24	0.069	0.30	0.21	0.32	1.0					
CAT	0.26	0.057	0.090	-0.58	-0.31	-0.065	-0.24	-0.14	-0.39	1.0				
MDA	-0.38	-0.074	-0.56	0.44	0.11	-0.48	0.15	-0.27	-0.55	-0.26	1.0			
SP	0.40	0.13	-0.61	0.026	0.034	-0.17	0.095	-0.15	0.20	0.49	0.018	1.0		
SS	-0.27	0.015	-0.43	0.086	0.087	-0.10	-0.067	-0.23	-0.10	-0.084	0.37	0.20	1.0	
Pro	-0.48	-0.24	-0.27	-0.63	0.18	0.19	-0.33	0.22	-0.21	0.27	-0.072	0.095	0.21	1.0

Fig. 5. Correlation analysis of heat resistance coefficients under high-temperature treatments.

The proline contents of *C. roseus* and *V. hybrida* exhibited an initial decrease and then an increase following increasing temperatures. However, the proline contents of *M. cordifolium*, *P. lanceolata*, *A. hispida*, *P.* 'Cerveza'n Lime', *D. chinensis*, and *T. fournieri* showed consistently increasing trends. *C. scutellarioides* demonstrated a decreasing trend, while *T. cerinthoides* 'Nanouk' exhibited an initial increase followed by a decrease. Under 40°C, *M. cordifolium* had the highest proline content, with a 200.31% increase compared with the control (Fig. 4C).

Comprehensive evaluation of heat tolerance

***HTC* and correlation analysis:** The *HTC* values of 14 physiological indicators for the 10 ground cover plant species (Table 2) exhibited substantial variation, with some ratios >1, and coefficients of variation ranging from 3.699% to 61.560%.

Correlation analysis revealed varying degrees of correlation between the *HTC* values (Fig. 5). For instance, photosynthetic rate showed significant positive correlation with stomatal conductance, while stomatal conductance showed significant positive correlation with photosynthetic rate and SOD. SOD exhibited significant positive correlation with stomatal conductance and significant negative correlation with water content. Evidently, certain correlations exist between the *HTC* values of various indicators, suggesting information overlap among individual parameters. Since heat tolerance in ground cover plants is a complex and comprehensive trait, the *HTC* of a single indicator cannot objectively be used to evaluate plant heat tolerance. Therefore, principal component analysis, membership function analysis, and other analytical methods were employed for comprehensive evaluation.

Principal component analysis of HTCs: As shown in Table 3, principal component analysis was performed using the *HTC*s of various indicators. Following the principle of eigenvalues > 1, the first five principal components were extracted, with a cumulative contribution rate of 83.162%, explaining the majority of information from the 14 indicators. The loading matrix (Table 3) reflects the main information represented by each principal component; higher loading on a principal component indicates a greater contribution to that component. Principal component (PC) 1 primarily reflects information from four indicators, including stomatal conductance, SOD, transpiration rate, and MDA. Principal component 2 mainly reflects information from three indicators, including relative SPAD, photosynthetic rate , and CAT. Principal component 3 primarily reflects information from four indicators, including root activity, intercellular CO_2 concentration, POD, and proline. Principal component 4 mainly reflects information from soluble protein, and principal component 5 primarily reflects information from water content.

Using the SPSS 27.0 software, standardized processing was performed on the HTCs of the 14 indicators to obtain standardized values (Z_1, Z_2, ..., Z_{14}) and eigenvectors (Table 4). The product of these two values yielded the comprehensive indicator scores for the 10 ground cover plant species. For example, $CI_1 = 0.016Z_1 + 0.234Z_2 - 0.107Z_3 - 0.039Z_4 + 0.081Z_5 + 0.260Z_6 - 0.095Z_7 + 0.254Z_8 + 0.118Z_9 - 0.039Z_{10} - 0.216Z_{11} - 0.142Z_{12} - 0.151Z_{13} + 0.043Z_{14}$. Similar calculations were performed for the CI_2, CI_3, CI_4, and CI_5 comprehensive indicator values (Table 5).

Table 3. Loading matrix and proportion of comprehensive indicators.

Index	PC 1	PC 2	PC 3	PC 4	PC 5
RA	0.049	-0.553	0.643	0.287	0.015
WC	-0.332	0.049	0.098	-0.041	0.911
Tr	0.728	-0.269	0.060	-0.577	0.164
SPAD	-0.120	0.750	0.557	0.068	0.056
Pn	0.251	0.747	-0.161	0.273	0.410
Gs	0.807	0.307	-0.083	0.329	0.182
Ci	-0.295	-0.119	0.631	-0.049	-0.346
SOD	0.787	0.231	-0.038	0.282	-0.434
POD	0.365	0.049	0.594	0.461	-0.046
CAT	-0.121	-0.698	-0.412	0.307	0.181
MDA	-0.670	0.527	-0.126	-0.232	-0.297
SP	-0.440	-0.218	0.067	0.841	0.055
SS	-0.468	0.344	-0.292	0.262	-0.148
Pro	0.134	-0.053	-0.830	0.272	-0.194
Eigen value	3.103	2.599	2.487	1.898	1.555
Contribution ratio (%)	22.164	18.563	17.768	13.559	11.109
Cumulative contribution ratio (%)	22.164	40.727	58.495	72.053	83.162

Table 4. Eigenvectors of each comprehensive index.

Index	PC 1	PC 2	PC 3	PC 4	PC 5
RA	0.016	-0.213	0.259	0.151	0.009
WC	-0.107	0.019	0.039	-0.022	0.586
Tr	0.234	-0.104	0.024	-0.304	0.105
SPAD	-0.039	0.289	0.224	0.036	0.036
Pn	0.081	0.287	-0.065	0.144	0.263
Gs	0.260	0.118	-0.033	0.173	0.117
Ci	-0.095	-0.046	0.254	-0.026	-0.222
SOD	0.254	0.089	-0.015	0.149	-0.279
POD	0.118	0.019	0.239	0.243	-0.030
CAT	-0.039	-0.269	-0.166	0.162	0.116
MDA	-0.216	0.203	-0.051	-0.122	-0.191
SP	-0.142	-0.084	0.027	0.443	0.035
SS	-0.151	0.132	-0.117	0.138	-0.095
Pro	0.043	-0.020	-0.334	0.143	-0.125

Membership function comprehensive analysis: Based on the comprehensive indicator values (Table 5), corresponding membership function (*U*) values were calculated. Combined with the weights (Table 6), comprehensive evaluation (*D*) values were determined (Table 6). According to the *D* values, the heat tolerance of the 10 ground cover plant species ranked as follows, from strongest to weakest: *C. roseus* > *P. lanceolata* > *T. fournieri* > *V. hybrida* > *A. hispida* > *M. cordifolium* > *C. scutellarioides* > *P.* 'Cerveza'n Lime' > *D. chinensis* > *T. cerinthoides* 'Nanouk'.

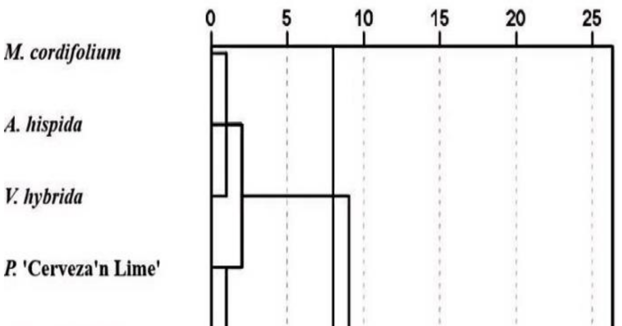


Fig. 6. Cluster analysis of the heat tolerance of ten ground cover plant species.

Table 5. Comprehensive index values of ten ground cover plant species.

Species	Comprehensive indicator value (*CI*)				
	CI_1	CI_2	CI_3	CI_4	CI_5
C. roseus	0.675	0.995	0.004	0.282	1.951
M. cordifolium	-0.748	1.363	-1.039	0.609	-0.253
P. lanceolata	2.327	0.107	-0.013	0.407	-1.388
A. hispida	-0.238	0.191	-0.242	0.331	0.476
V. hybrida	-0.853	1.319	1.561	-1.280	-1.068
P. 'Cerveza'n Lime'	-0.356	-1.464	1.002	0.841	-0.370
D. chinensis	-1.185	-0.538	-0.806	1.240	-0.644
C. scutellarioides	-0.157	-1.115	0.869	-0.654	1.033
T. fournieri	0.473	-0.027	0.363	0.205	0.434
T. cerinthoides 'Nanouk'	0.063	-0.831	-1.699	-1.981	-0.172

Table 6. Membership function value (*U*), weight, comprehensive evaluation (*D*) value, and ranking of ten ground cover plant species.

Species	Membership function value					*D* value	Ranking
	U_1	U_2	U_3	U_4	U_5		
C. roseus	0.530	0.870	0.522	0.703	1.000	0.695	1
M. cordifolium	0.125	1.000	0.203	0.804	0.340	0.476	6
P. lanceolata	1.000	0.556	0.517	0.741	0.000	0.622	2
A. hispida	0.270	0.586	0.447	0.718	0.558	0.490	5
V. hybrida	0.095	0.985	1.000	0.218	0.096	0.507	4
P. ‘Cerveza’n Lime’	0.236	0.000	0.828	0.876	0.305	0.423	8
D. chinensis	0.000	0.328	0.274	1.000	0.223	0.324	9
C. scutellarioides	0.293	0.124	0.788	0.412	0.725	0.438	7
T. fournieri	0.472	0.508	0.633	0.679	0.545	0.558	3
T. cerinthoides ‘Nanouk’	0.356	0.224	0.000	0.000	0.364	0.193	10
Index weight	0.267	0.223	0.214	0.163	0.134	-	-

Cluster analysis: Using the square Euclidean distance method, cluster analysis was performed on the *D* values (Fig. 6). At a Euclidean distance of 8, the species were divided into three categories. Category 1, with strong heat tolerance, included *C. roseus*, *P. lanceolata*, and *T. fournieri*; Category 2, with moderate heat tolerance, included *V. hybrida*, *A. hispida*, *M. cordifolium*, *P.* 'Cerveza'n Lime', and *C. scutellarioides*; Category 3, with weak heat tolerance, included *D. chinensis* and *T. cerinthoides* 'Nanouk'.

Discussion

Water metabolism under heat stress: Root activity reflects the active capacity of plants for water and mineral nutrient absorption. Plants with stronger root activity exhibit enhanced active absorption and stress resistance abilities (Zhang *et al*., 2024b). This study found that heat stress caused significant decreases in root activity in nine ground cover plant species (with the exception of *P.* 'Cerveza'n Lime'), indicating a reduction in their active water absorption capacity, which aligns with the research conclusions of a previous study (Cao *et al*., 2008). Compared with the controls, under 40°C stress, *C. roseus*, *P. lanceolata*, and *T. fournieri* exhibited greater decreases in root activity than *P.* 'Cerveza'n Lime'. Meanwhile, in the comprehensive heat tolerance evaluation, the *D* values of *C. roseus*, *P. lanceolata*, and *T. fournieri* were higher than those of *P.* 'Cerveza'n Lime'. This result differs from a previous study, in which the heat-sensitive tall fescue (*Festuca arundinacea*) exhibited more significant decreases in root activity than the heat-tolerant type (Zhao *et al*., 2015). Therefore, evaluating the heat tolerance of different plants based on a single indicator is not objective.

Water content is an important indicator reflecting water status, and to some extent, the magnitude of its changes reflects a plant's ability to adapt to stress conditions (Xu *et al*., 2023). In this experiment, the water content and its reduction magnitude under heat stress varied between the 10 ground cover plant species, indicating differences in their adaptability to heat stress. Comparing water content with *D* values (comprehensive heat tolerance evaluation values), we found that *C. roseus* had moderate water content but the highest *D* value, while *T. cerinthoides* 'Nanouk' had high water content but the lowest *D* value. This is inconsistent with Wassie et al.'s conclusion that ‘more resistant alfalfa (*Medicago sativa*) typically maintains higher water content under adverse conditions’(Wassie *et al*., 2019). This suggests that water content and the magnitude of its changes exhibit interspecific differences.

Transpiration rate is a primary indicator characterizing the rate of water loss in plants and can also reflect root water absorption and transportation-driving capabilities. Transpiration rate responds sensitively to changes in temperature and moisture within a certain range in the environment (Wang, 2020). This study found that under heat stress, *M. cordifolium* and *D. chinensis* showed a continuous decline in transpiration rate with increasing temperature, consistent with research conclusions on dahlia (*Dahlia pinnata*) (Liu *et al*., 2023). The remaining eight ground cover plant species exhibited an initial increase followed by a decrease in transpiration rate, aligning with a previous report (Sun *et al*., 2008). Therefore, the differences in transpiration rate among these 10 ground cover plant species reflect varying degrees of sensitivity to water loss caused by heat stress, as well as interspecific differences in water absorption efficiency and water transport driving forces.

Water is an essential component for maintaining normal physiological functions in plants, and water metabolism status reflects their ability to adapt to adverse conditions (Wang *et al*., 2017). Comprehensive analysis of indicators such as root activity, water content, and transpiration rate in this experiment indicated that under different heat stress conditions, the 10 ground cover plant species exhibited varying capacities for water absorption, retention, and loss. In other words, the mechanisms for maintaining water homeostasis differ both between temperature treatments and species. Therefore, it is difficult to objectively reflect their heat tolerance strength based solely on water metabolism status.

Photosynthetic performance under heat stress: Chlorophylls play a role in absorbing, transmitting, and converting light energy. The SPAD value represents the relative chl content, and to some extent, its magnitude can reflect a plant's photosynthetic potential and heat tolerance capacity (Hu *et al*., 2020; Huang *et al*., 2021). In this experiment, the peak SPAD values of the 10 ground cover plant species occurred between 25°C and 35°C, indicating that different plants have different optimal temperatures for maintaining chl homeostasis. Under 40°C, all ground cover plants showed decreased SPAD values, which were similar to research results for summer maize (Zhang *et al*., 2023a). The reduction of chlorophyll content under high temperature may be primarily due to two aspects. On one hand, high temperatures inhibit the activity of enzymes related to chlorophyll biosynthesis, reducing its synthesis rate and leading to decreased production. On the other hand, chlorophyll molecules are unstable, and high temperatures destroy their molecular structure, accelerating their degradation.

Photosynthesis is a physiological process that is very sensitive to temperature changes (Sun *et al*., 2023). This study found that high temperatures inhibit photosynthetic rate; higher temperatures induce higher decreases in photosynthetic rate, which is consistent with research on early rice (*Oryza sativa*) (Yang *et al*., 2024). In this study, *C. roseus* had significantly lower SPAD values and significantly higher photosynthetic rate than *D. chinensis*, indicating that high SPAD values do not necessarily correspond to strong photosynthetic rate. Therefore, to some extent, the strength of photosynthetic rate is not only correlated with chlorophyll content but also with factors such as stomatal conductance and intercellular CO_2 concentration.

The effects of heat stress on photosynthetic rate include both stomatal and non-stomatal factors (Xu *et al*., 2011). High temperatures inhibit stomatal opening and reduce CO_2 entry, decreasing both stomatal conductance and intercellular CO_2 concentration and leading to reduced photosynthetic rate. A decrease in stomatal conductance is accompanied by an increase in intercellular CO_2 concentration, which damages the structure and function of photosystem II because of high temperatures, leading to decreased photosynthetic rate. This can be attributed to non-stomatal factors. Our experiment found that when *C. roseus* and *P. lanceolata* were under stress temperatures ≤35°C, photosynthetic rate and stomatal conductance continued to increase, indicating that their photosynthetic tolerance thresholds were significantly higher than those of the other eight ground cover plant species. When *C. roseus* and *P. lanceolata* were under stress temperatures >35°C, and the remaining six ground cover plant species (*M. cordifolium*, *A. hispida*, *V. hybrida*, *C. scutellarioides*, *T. fournieri*, and *T. cerinthoides* 'Nanouk') were under stress temperatures >30°C, their stomatal conductance and photosynthetic rate decreased synchronously, but intercellular CO_2 concentration increased, attributable to non-stomatal factor regulation.

This is consistent with a previous study showing that increased intercellular CO_2 concentration may be due to reduced photosynthetic utilization or enhanced respiratory activities (Zhao *et al*., 2013); the increase in intercellular CO_2 concentration may be due to reduced photosynthetic utilization or enhanced respiratory activity. Only *P.* 'Cerveza'n Lime' and *D. chinensis* showed decreases in stomatal conductance with increasing stress temperature, indicating that their optimal temperatures for stomatal opening are lower than those of the remaining eight ground cover plant species. Evidently, when facing different degrees of heat stress, different plant species have different photosynthetic capacities, and the response mechanisms of the various components constituting their photosynthetic performance differ.

Antioxidant performance under heat stress: Under appropriate conditions, plants can maintain a dynamic balance between the generation and elimination of ROS. Under adverse conditions such as heat stress, this dynamic balance can be disrupted, leading to excessive ROS accumulation, membrane lipid peroxidation, protein denaturation, oxidative damage, the disruption of normal physiological metabolism, and even plant death. Plants with stronger resistance rapidly initiate stress responses, inducing the expression of antioxidant enzymes SOD, POD, and CAT and accelerating the synthesis of antioxidant substances. These antioxidant components work together to effectively eliminate excess ROS and resist adverse damage (Lu *et al*., 2022). Among these antioxidant enzymes, SOD primarily eliminates superoxide anion free radicals O_2^-; POD catalyzes the decomposition of peroxides, producing H_2O_2 and O_2; and CAT catalyzes H_2O_2 into H_2O and O_2. These three enzymes work synergistically to efficiently eliminate ROS and mitigate the chain reactions triggered by ROS. MDA is the main final product of lipid peroxidation reactions in plants, and its concentration can reflect the severity of adverse stress (Sun *et al*., 2019).

In this study, *C. roseus* and *A. hispida* showed a stronger SOD capacity for eliminating $O_2^{\cdot-}$ under heat stress than the other eight ground cover plant species. *C. roseus*, *M. cordifolium*, and *V. hybrida* showed stronger POD capacity for eliminating peroxides than the other seven species. *P. lanceolata* and *A. hispida* exhibited stronger CAT capacity for eliminating H_2O_2 than the other eight species. Comprehensive analysis of the *D* values and changes in the three antioxidant enzyme activities of the 10 species under heat stress revealed three results. First, the main antioxidant enzymes for eliminating ROS differ between plants. Second, the stress response capabilities of these three enzymes for heat stress vary among different plants. Third, *C. roseus* had the highest *D* value, primarily relying on SOD and POD to eliminate ROS, resulting in a mild degree of membrane peroxidation that was consistent with Wu et al.'s (Wu *et al*., 2016) study of *P. lactiflora* under high temperature stress. However, *P. lanceolata*, which ranked second in *D* value, did not show strong SOD or POD activities but had strong CAT activity. Therefore, it is difficult to eliminate ROS by solely relying on CAT. Consequently, evaluating the tolerance or resistance of a plant to adverse conditions based solely on antioxidant capacity is also difficult or inaccurate.

The accumulation of organic small-molecule osmotic adjustment substances under heat stress: Under heat stress, plants actively synthesize organic small-molecule osmotic adjustment substances such as soluble protein, soluble sugar, and proline to maintain their water homeostasis and cell turgor pressure (Bu *et al*., 2024). This is an important physiological mechanism for osmotic adjustment in response to adverse conditions. Based on the D values and changes in the soluble sugar and soluble protein content of the 10 ground cover plant species, we speculate that different plants have different capacities and mechanisms for accumulating soluble protein and soluble sugar in response to heat stress, which may be related to differences in their own water content, osmotic adjustment capacity, and heat tolerance. Under heat stress, the top three species in terms of *D* values, *C. roseus*, *P. lanceolata*, and *T. fournieri*, had higher soluble protein levels than the other seven species. The top five species in terms of *D* values, *C. roseus*, *P. lanceolata*, *T. fournieri*, *V. hybrida*, and *A. hispida*, had higher soluble sugar contents than *M. cordifolium*, *P.* 'Cerveza'n Lime', and *T. cerinthoides* 'Nanouk', indicating that a stronger osmotic adjustment capacity relies on soluble protein and soluble sugar. Additionally, previous studies have shown that plants with higher soluble sugar and soluble protein contents under heat stress often have less lipid peroxidation and membrane damage, reducing heat injuries (Zhang *et al*., 2023b). However, given the results of this study, further investigation into whether soluble sugar and soluble protein participate in reducing membrane damage is required.

Under appropriate conditions, plants maintain proline at relatively low levels, whereas heat stress induces the accumulation of large quantities of proline to enhance stress resistance (Bu *et al*., 2024). In this study, the proline content and its trends and change magnitudes varied between the 10 species under different temperature stresses. Moreover, *C. roseus* and *T. fournieri* (high *D* values) and *T. cerinthoides* 'Nanouk' (low *D* value) had significantly lower proline content than *M. cordifolium*, *A. hispida*, and *V. hybrida* (moderate *D* values). Given these results, first, different plants have different mechanisms for proline accumulation in response to heat stress; second, there is a weak correlation between proline content and heat tolerance strength in different plants; third, proline content is far lower than soluble protein and soluble sugar contents, indicating that the osmotic adjustment capacity of proline is far lower than that of soluble protein and soluble sugar.

Comprehensive evaluation of heat tolerance in 10 ground cover plant species: As a whole organism, the plant body exhibits complex responses to heat stress related to multiple physiological and biochemical indicators (Li *et al*., 2021). Changes in a single or certain aspect of physiological and biochemical indicators are inadequate for comprehensively reflecting the strength of heat tolerance. Multivariate statistical methods based on principal component analysis combined with membership function analysis can reduce the dimensionality of multiple physiological and biochemical indicators. This approach is increasingly valued in plant stress resistance evaluation. Related studies have shown that multivariate statistical analysis methods have been used to evaluate and classify the heat tolerance of 140 peony varieties and to select heat-tolerant varieties based on heat tolerance evaluation D values (Hou *et al*., 2023). In one study, 12 heat tolerance-related indicators were transformed into three comprehensive indicators through multivariate statistical methods, deriving the D value of heat tolerance in cucumber (*Cucumis sativus*) (Fu *et al*., 2020). These studies all focused on the comprehensive evaluation of different varieties of the same plant species. In this study, multivariate statistical methods combining principal component analysis with membership function analysis were applied to comprehensively evaluate the heat tolerance of 10 different ground cover plant species from four perspectives, including water metabolism, photosynthetic performance, antioxidant capacity, and osmotic adjustment capacity. This approach effectively eliminated interference from interspecific differences and objectively evaluated heat tolerance differences among the 10 species.

Conclusion

Within the temperature range of 25°C-40°C, as temperature increased, the trends and magnitudes of changes in 14 physiological indicators of 10 ground cover plant species reflected their varying capacities in terms of physiological responses, including water metabolism, photosynthetic performance, antioxidant capacity, and osmotic regulation. A comprehensive evaluation revealed the following: *C. roseus*, *P. lanceolata*, and *T. fournieri* demonstrated strong heat tolerance; *V. hybrida*, *A. hispida*, *M. cordifolium*, *P.* 'Cerveza'n Lime', and *C. scutellarioides* showed moderate heat tolerance; and *D. chinensis* and *T. cerinthoides* 'Nanouk' showed weak heat tolerance. Therefore, according to our results, appropriate ground cover plant resources can be selected based on local temperature conditions and the plants' tolerance to high temperatures for use in landscape gardening.

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