Physiological Responses of the Roots of 16 *Camellia Oleifera* Varieties to Aluminum Stress and Screening of Aluminum-tolerant Genotypes

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Abstract: *Targeting 16 varieties of Camellia oleifera planted in different regions, this paper explores the influence of aluminum (Al) stress over several physiological indices, namely, root activity, superoxide dismutase (SOD) activity, malondialdehyde (MDA) content, hydrogen peroxide (H_2O_2) content, proline content, and soluble sugar content and evaluates the overall Al tolerance of each variety. The purpose is to identify the difference between different C. oleifera varieties in physiological indices under Al stress, and to screen the varieties with relatively strong Al tolerance. The results show that: Al stress lowered the root activity and SOD activity, while enhancing MDA content, H_2O_2 content, proline content, soluble sugar content, and Al content. But the physiological indices of different C. oleifera varieties changed by vastly different amplitudes under Al stress. The variation amplitudes of root activity, MDA content, SOD activity, H_2O_2 content, proline content, soluble sugar content, and Al content were -47.06%~42.86%, 12.50%~133.33%,-8.33%%~26.28%, 11.11%~71.88%, 76.47%~420.00%, 4.97%~56.41%, and 23.43%~101.12%, respectively. Furthermore, the Al tolerance coefficients of the 16 C. oleifera varieties were analyzed comprehensively by membership functions. The results show that C. oleifera 'Huajin', C. oleifera 'Huashuo', and C. oleifera 'Huaxin' have relatively strong Al tolerance, while C. oleifera 'Ganyou No.2', C. oleifera 'Ganxing No.48', and C. oleifera 'Ganzhou No.70' have relatively weak Al tolerance.*

Keywords: *Camellia oleifera, Aluminum stress, Physiological response, Al tolerance screening.*

Introduction

Aluminum (Al), the most abundant metal in the Earth's crust, generally exists in the form of silicate or oxide. Due to its low solubility, Al is rarely absorbed by plants, and is thus not toxic to plants [8]. However, when the soil pH drops below 5, a large amount of Al dissolves into Al^{3+}. This ion can be easily absorbed by plants, causing great harms to plant growth and development.

More than 30% of the world's arable land is acid soil. The heavy presence of this type of soil, coupled with the frequent occurrence of acid rain and the intense application of physiologically acid salt fertilizers in recent years, makes Al toxicity an increasingly serious problem. Al hinders the root growth, and nutrient absorption of plants. Consequently, the internal physiological metabolism of crops becomes unbalanced, the synthesis of chlorophyll is blocked, and the enzymes that maintain the normal physiological activities of plants are denatured. All these lead to the eventual death of the plants [5].

The Al toxicity to plants varies with the varieties and genotypes. In recent years, extensive attention has been paid to the Al tolerance mechanism of plants, and the screening of Al-resistant germplasm resources. Some scholars screened a rice variety with relatively strong Al tolerance out of 45 varieties [9], identified three Al-resistant rapeseed varieties from 23 candidates [10], and determined two Al-resistant pea germplasm resources from 52 alternatives [1]. For the same crop, different genotypes respond very differently to Al toxicity. To explore the Al tolerance mechanism of a plant, it is very meaningful to screen the genotypes capable of withstanding Al toxicity.

Camellia oleifera is one of the four woody oil plants in the world, along with olive, oil palm, and coconut, and an important woody edible oil plant in the red acid soil regions of southern China. *C. oleifera* is widely distributed in Hunan, Jiangxi, Guangxi, Guangdong, and Hainan, covering an area of 4.5×10^6 hm^2. The rich genetic diversity and diverse growth environments lead to marked differences between *C. oleifera* germplasm resources in terms of Al tolerance. However, there is no report on the screening of Al-resistant *C. oleifera* varieties.

This paper mainly studies 16 *C. oleifera* varieties, which have been cultivated and widely grown in the main producing areas of *C. oleifera*, such as Hunan, Jiangxi, and Guangxi. The physiological response of each *C. oleifera* variety to Al stress was measured by indices like root activity, superoxide dismutase (SOD) activity, malondialdehyde (MDA) content, hydrogen peroxide (H_2O_2) content, proline content and soluble sugar. In addition, membership functions were adopted to screen the *C. oleifera* varieties with relatively strong Al tolerance. The research findings provide a reference for the seed selection of Al-resistant *C. oleifera*, and offer insights into the Al tolerance mechanism of *C. oleifera*.

Materials and methods

Test materials and cultivation conditions

Table 1 lists the 16 *C. oleifera* varieties being tested.

Table 1. *C. oleifera* varieties being tested

Serial number	*C. oleifera* variety	Serial number	*C. oleifera* variety
1	*C. oleifera* ‘Xianglin No.1’	9	*C. oleifera* ‘Huajin’
2	*C. oleifera* ‘Xianglin No.27’	10	*C. oleifera* ‘Cenruan No.2’
3	*C. oleifera* ‘Xianglin No.210’	11	*C. oleifera* ‘Cenruan No.3’
4	*C. oleifera* ‘Changlin No.4’	12	*C. oleifera* ‘Gazhou No.70’
5	*C. oleifera* ‘Changlin No.40’	13	*C. oleifera* ‘Ganzhou Oil No.1’
6	*C. oleifera* ‘Changlin No.53’	14	*C. oleifera* ‘Ganzhou Oil No.2’
7	*C. oleifera* ‘Huashuo’	15	*C. oleifera* ‘Ganwu No.2’
8	*C. oleifera* ‘Huaxin’	16	*C. oleifera* ‘Ganxing No.48’

C. oleifera cuttings were selected for our experiments. During graftage, thick semi-lignified branches were adopted, and cut into 10 cm long scions, before being grafted onto the perlite seedbed. After being cultivated for 5 months, robust cuttings with consistent plant height and root growth were transplanted to 10×20 cm plastic flowerpots. Perlite and river sand were uniformly mixed at a volume ratio of 5:2 as the growth medium. Then, the cuttings were pre-cultured for 14 days. During this period, nutrient solution was poured every 2 days. The formula of the solution is ($mmol \cdot L^{-1}$):

$(NH_4)_2SO_4$ 0.713, NH_4NO_3 0.73, KH_2PO_4 0.1, K_2SO_4 0.46, $CaCl_2$ 0.5, $MgSO_4$ 0.41, Fe-EDTA 0.032, H_3BO_3 0.046, $CuSO_4$ 0.002, $MnSO_4$ 0.09, $Na_2MoO_4$0.0026, $ZnSO_4$ 0.0091, and the pH of the solution is 4.5 [3].

After the pre-culturing, $AlCl_3$ was added to the original formula to prepare a conditioning solution containing 3 $mmol \cdot L^{-1}$ Al^{3+}. Then, *C. oleifera* seedlings were treated with nutrient solutions containing 0 and 3 $mmol \cdot L^{-1}$ Al^{3+}. The treatment time under Al stress was 30 days.

Measurement of physiological indices

The physiological indices were measured by Gao's method [2]. After taking the healthy roots of robust plants, the root activity was measured by the triphenyltetrazolium chloride (TTC), the MDA content was measured by thiobarbituric acid method, the SOD activity was measured by nitroblue tetrazolium (NBT) method, and the H_2O_2 content was measured by titanium sulfate-concentrated ammonia development method. After the healthy roots were dried and ground, the proline content was measured by acid ninhydrin development method, and the soluble sugar content was measured by anthrone colorimetry. After the root powder was digested with nitric acid-hydrogen peroxide, the Al content was measured by an inductively coupled plasma-mass spectrometry (ICP-MS) analysis system.

Data analysis

Membership calculation

The specific membership values of each physiological index of *C. oleifera* root were calculated and accumulated to obtain the mean membership of Al tolerance. Then, the Al tolerance was evaluated for the 16 *C. oleifera* varieties. The Al tolerance of *C. oleifera* is positively correlated with root activity, SOD activity, proline content, and soluble sugar content: $X(\mu) = (X - X_{\min})/(X_{\max} - X_{\min})$, and negatively correlated with MDA content, H_2O_2 content, and Al content: $X(\mu) = 1 - (X - X_{\min})/(X_{\max} - X_{\min})$. Note that $X(\mu)$ is the membership of each index; $X_{\max}$ and $X_{\min}$ are the maximum and minimum of Al tolerance coefficient, respectively. The Al tolerance coefficient equals the ratio of index value under stress to the index value under no stress.

Data processing

The experimental data are the mean and standard error of 3 replicates. The data were processed on SPSS26.0, and subjected to t-test ($p < 0.05$). The relevant charts were plotted on Excel 2010.

Results and analysis

Physiological response

Influence of Al stress on root activity and MDA content

As shown in Fig. 1, compared to the control check (CK), the root activity of three *C. oleifera* varieties, namely, *C. oleifera* 'Huashuo', *C. oleifera* 'Huajin', and *C. oleifera* 'Huaxin', increased, while that of the other 13 *C. oleifera* varieties declined to different degrees.

Thus, the roots of the latter 13 *C. oleifera* varieties suffer different degrees of Al toxicity. The decrement of root activity reached statistically significant levels for the following *C. oleifera* varieties: *C. oleifera* ‘Xianglin No.1’, *C. oleifera* ‘Changlin No.40’, *C. oleifera* ‘Changlin No.53’, *C. oleifera* ‘Cenruan No.3’, *C. oleifera* ‘Ganzhou No. 70’, *C. oleifera* ‘Ganwu No.2’, and *C. oleifera* ‘Ganxing No.48’.

Under Al stress, the MDA content of the 16 *C. oleifera* varieties rose by different degrees (Fig. 2). Among them, *C. oleifera* ‘Xianglin No.27’, *C. oleifera* ‘Huaxin’, *C. oleifera* ‘Huajin’ and *C. oleifera* ‘Cenruan No.3’ root systems showed an increase in MDA content, but the difference was not significant compared with CK, indicating that the root cell membranes of these four *C. oleifera* varieties were less damaged under aluminum stress.

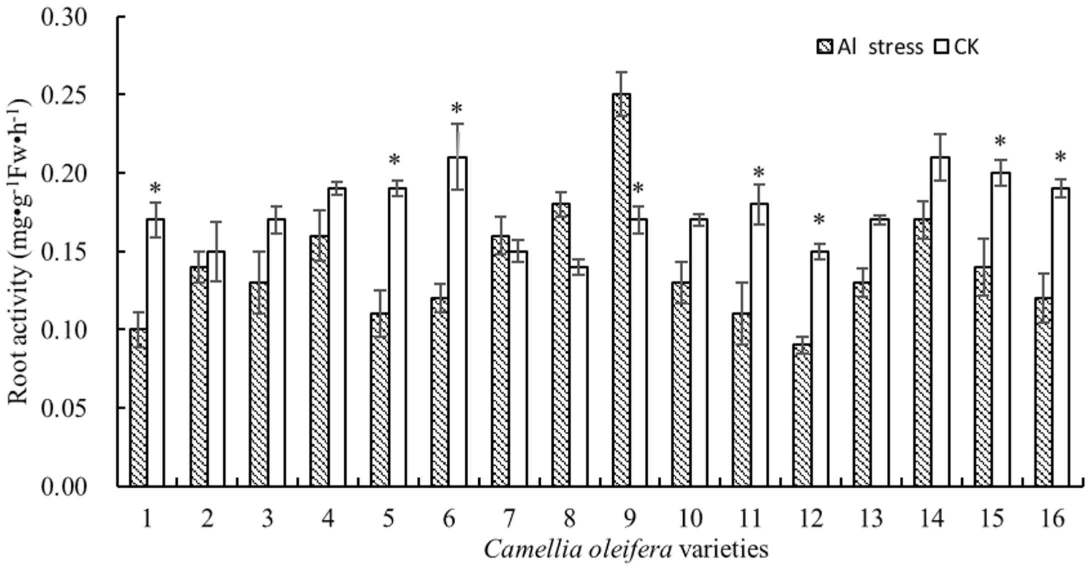

Fig. 1 Effects of Al stress on root activity of 16 *C. oleifera* varieties

Note: The ‘*’ on the bar chart indicates that the difference between Al treatment and CK of a certain grape germplasm is significant by *t* test (p < 0.05). The symbol ‘*’ keeps its meaning for the next figures as well.

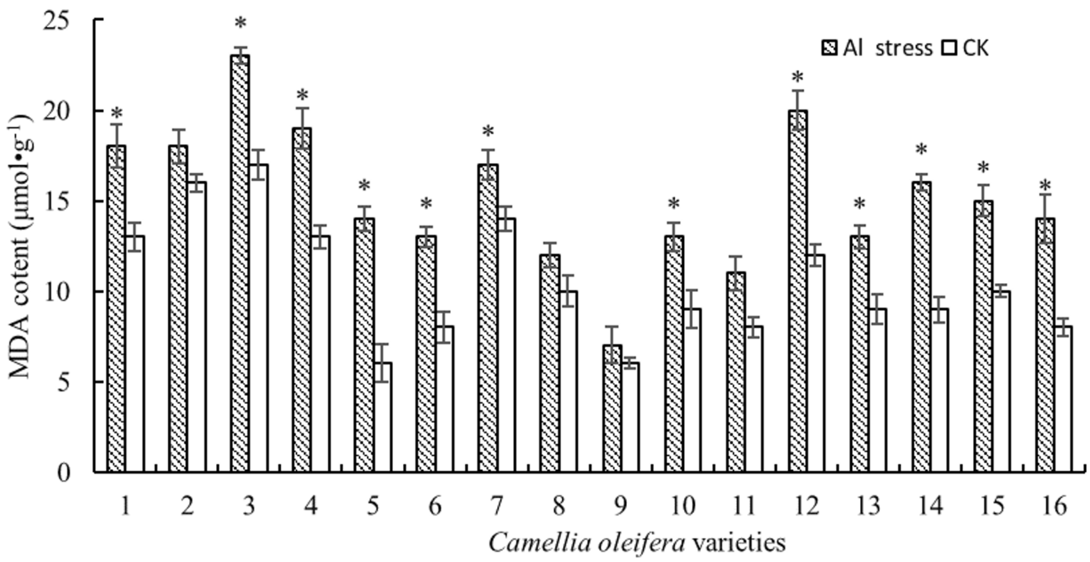

Fig. 2 Effects of Al stress on MDA content of 16 *C. oleifera* varieties

Influence of Al stress on SOD activity and H_2O_2 content

As shown in Fig. 3, compared with the CK, the SOD activity of *C. oleifera* ‘Huashuo’, *C. oleifera* ‘Huaxin’, and *C. oleifera* ‘Huajin’ increased slightly, while that of the other 13 *C. oleifera* varieties declined to different degrees. The largest decrease (26.28%) belongs to *C. oleifera* ‘Ganzhou Oil No.2’.

Under Al stress, the H_2O_2 content of the 16 *C. oleifera* varieties rose by different degrees (Fig. 4). The greatest increment (71.86%) was achieved by *C. oleifera* ‘Ganzhou No.70’, followed by *C. oleifera* ‘Ganxing No.48’ (65%), *C. oleifera* ‘Changlin No.40’ (62.50%), *C. oleifera* ‘Ganzhou Oil No.2’ (52.63%), and *C. oleifera* ‘Changlin No.4’ (50%).

Influence of Al stress on soluble sugar content, proline content, and Al content

Under Al stress, the soluble sugar content of the 16 *C. oleifera* varieties rose by different degrees (Fig. 5). Among them, the soluble sugar content of 12 *C. oleifera* varieties was significantly higher than that of the CK.

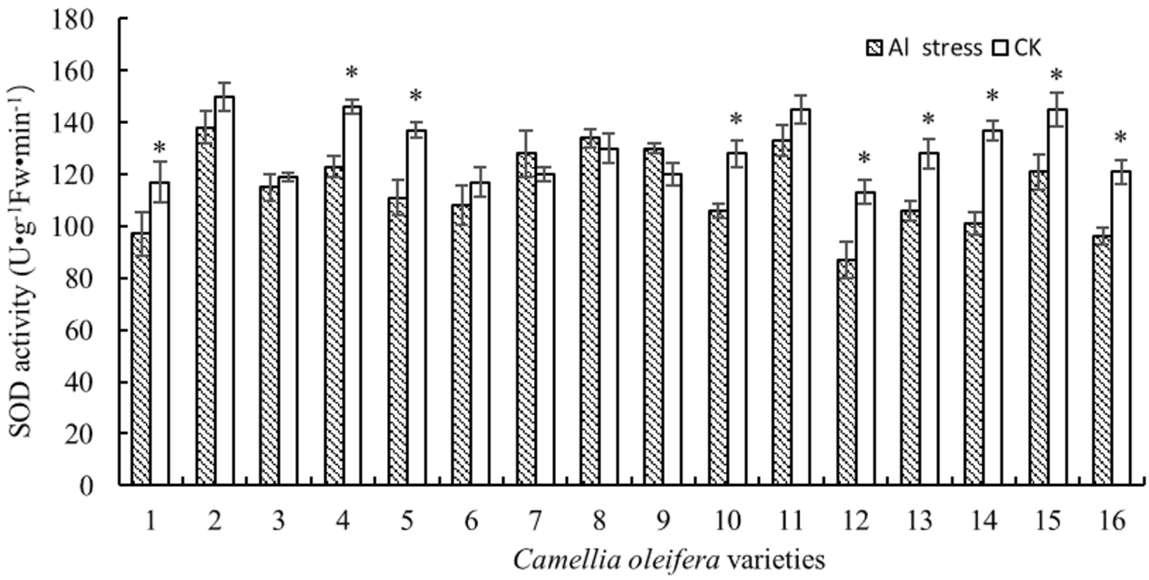

Fig. 3 Effects of Al stress on SOD activity of 16 *C. oleifera* varieties

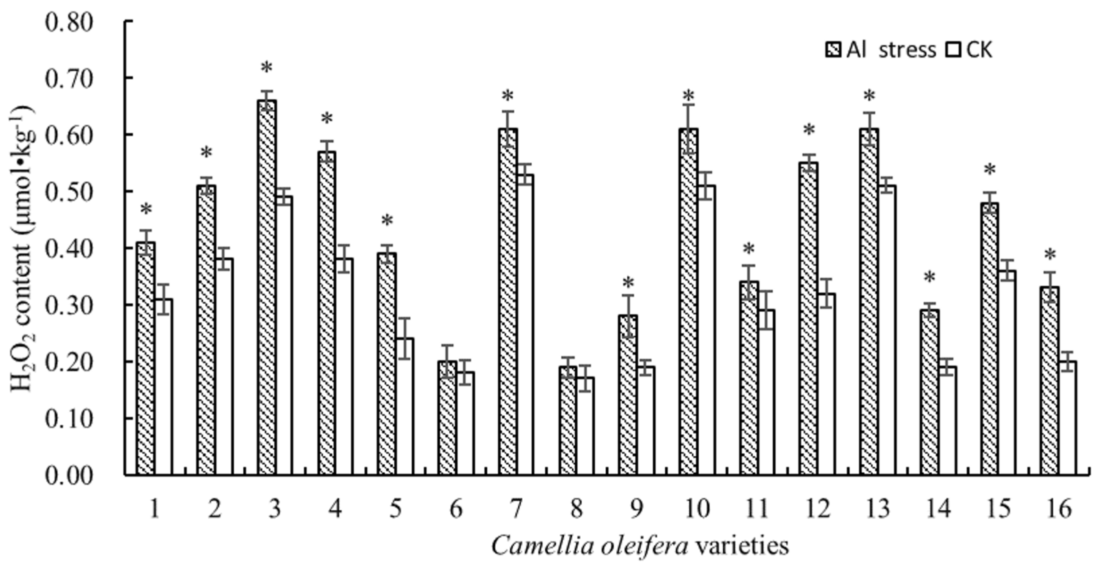

Fig. 4 Effects of Al stress on H_2O_2 content of 16 *C. oleifera* varieties

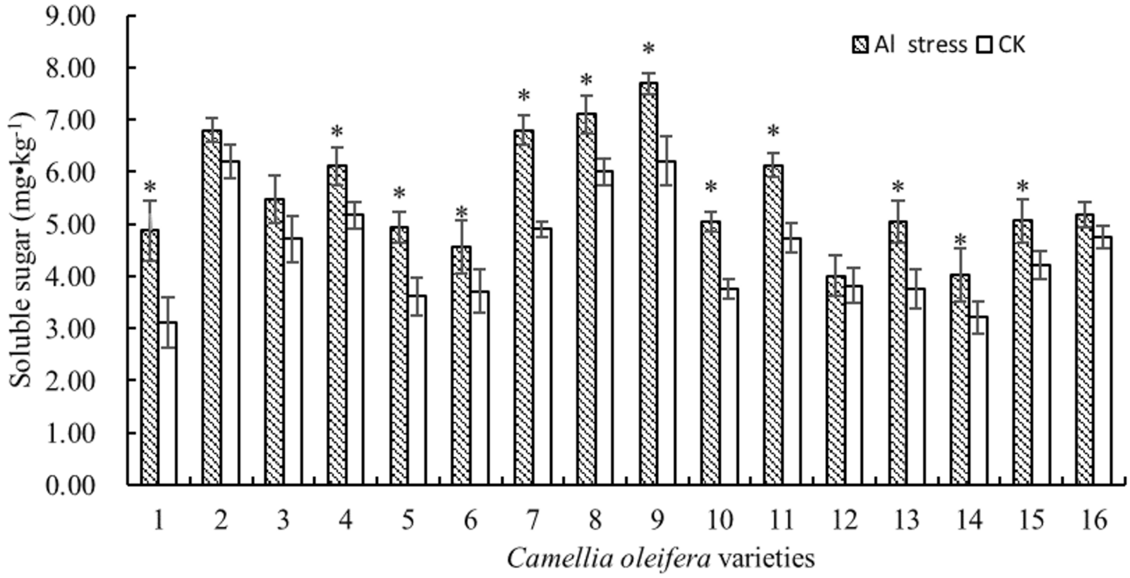

Fig 5. Effects of Al stress on soluble sugar of 16 *C. oleifera* varieties

As shown in Figs. 6 and 7, compared to the CK, the proline content and Al content of the 16 *C. oleifera* varieties increased significantly under Al stress. Among them, the proline content of 12 *C. oleifera* varieties was more than twice that of the CK. The greatest increment was achieved by *C. oleifera* 'Huajin', whose proline content was 5.2 times that of the CK.

The greatest increase in aluminum content of *C. oleifera* root system was *C. oleifera* 'Xianglin No.27' reaching 101.12%, and the least increase was *C. oleifera* 'Changlin No.40' which was only 23.43%. Under the same treatment conditions, the large difference in Al content between *C. oleifera* varieties may be attributed to the selective absorption by the root. Thus, different *C. oleifera* varieties vary in Al tolerance.

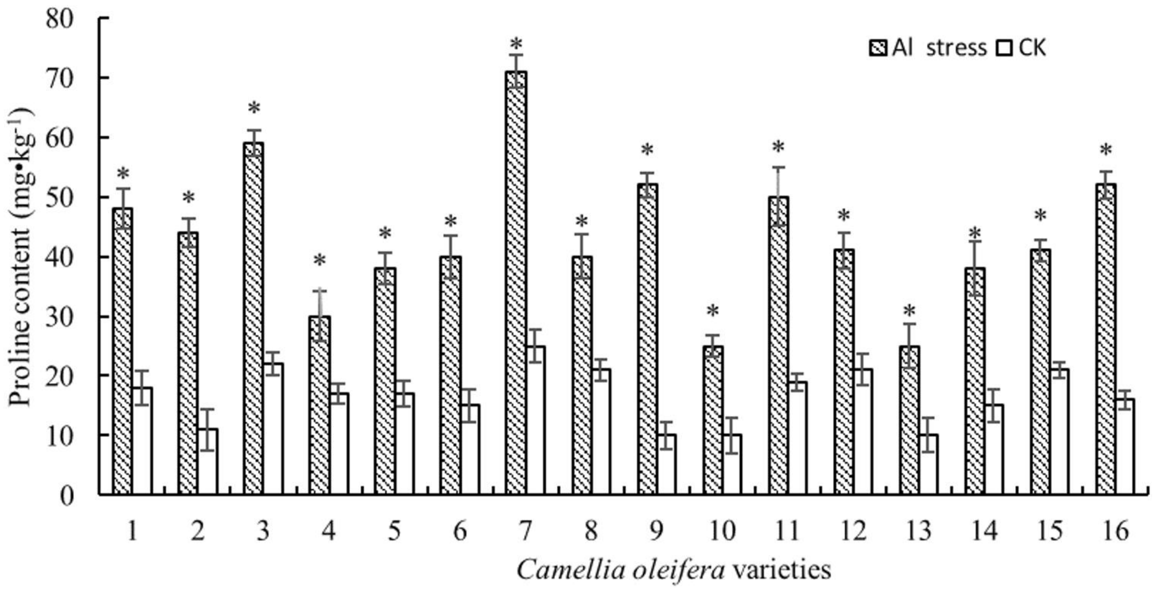

Fig. 6 Effects of Al stress on Proline content of 16 *C. oleifera* varieties

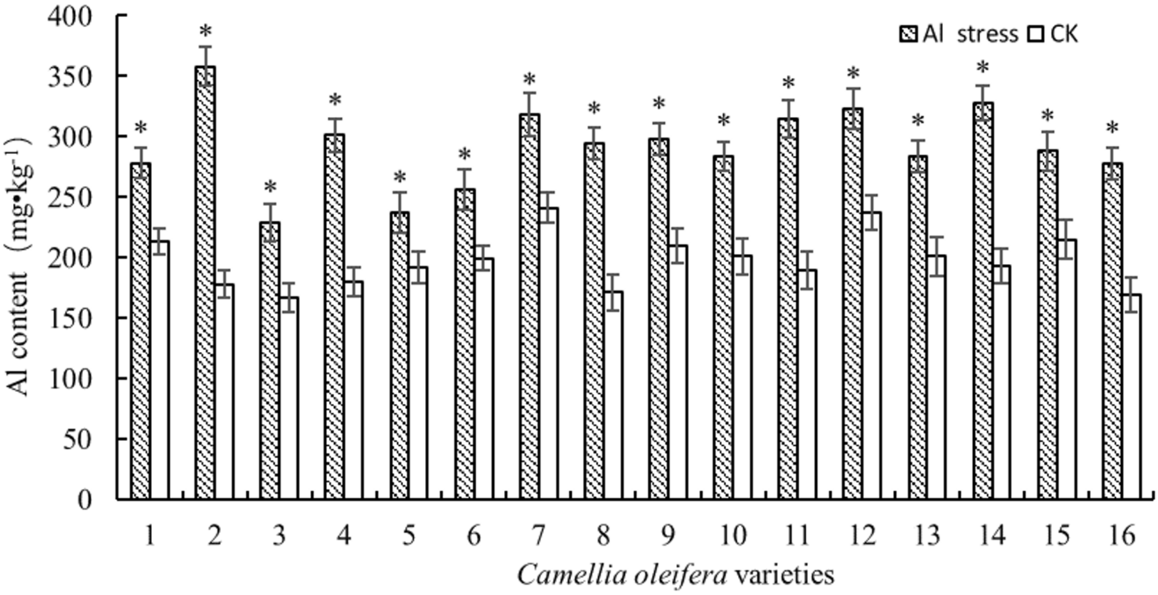

Fig. 7 Effects of Al stress on Al content of 16 *C. oleifera* varieties

Magnitude of change of each index

The magnitude of change in each index of the 16 *C. oleifera* varieties were calculated based on the measured results on these varieties under Al stress and the CK. The variation amplitudes of root activity, MDA content, SOD activity, H_2O_2 content, proline content, soluble sugar content, and Al content were -47.06%~42.86%, 12.50%~133.33%, -8.33% ~26.28%, 11.11%~71.88%, 76.47%~420.00%, 4.97%~56.41%, and 23.44%~101.12%, respectively.

It can be seen that the physiological indices of the 16 *C. oleifera* varieties respond very differently to Al stress. A single index is insufficient to fully reflect the strength of Al tolerance. The results obtained from the judgment of aluminum tolerance of each varieties need to be integrated to be more reliable.

Membership of Al tolerance

On the basis of calculating the aluminum tolerance coefficient of each physiological index (Table 2), calculate its membership value, and finally obtain a comprehensive ranking (Table 3). After considering all the indices, the top 3 varieties in terms of Al tolerance are *C. oleifera* 'Huajin', *C. oleifera* 'Huashuo', and *C. oleifera* 'Huaxin' (Table 3).

Overall, the Hua series *C. oleifera* varieties from Hunan have much higher Al tolerance than the other varieties, while the Gan series *C. oleifera* varieties from Jiangxi have relatively poor Al tolerance. The bottom three varieties all belong to the Gan series, namely, *C. oleifera* 'Ganzhou Oil No.2', *C. oleifera* 'Ganxing No.48', and *C. oleifera* 'GanZhou No.70'. The Qinruan series from Guangxi, Xianglin series from Hunan, and Changlin series from Jiangxi have moderate Al tolerance.

Table 2. Al tolerance coefficient of 16 *C. oleifera* varieties

Varieties	**Root activity**	**MDA content**	**SOD activity**	**H_2O_2 content**	**Proline content**	**Soluble sugar content**	**Al content**
C. oleifera 'Xianglin No.1'	0.59	1.38	0.83	1.32	2.67	1.56	1.31
C. oleifera 'Xianglin No.27'	0.93	1.13	0.92	1.34	4.00	1.10	2.01
C. oleifera 'Xianglin No.210'	0.76	1.35	0.97	1.35	2.68	1.16	1.37
C. oleifera 'Changlin No.4'	0.84	1.46	0.84	1.50	1.76	1.18	1.67
C. oleifera 'Changlin No.40'	0.58	2.33	0.81	1.63	2.24	1.37	1.23
C. oleifera 'Changlin No.53'	0.57	1.63	0.92	1.11	2.67	1.23	1.29
C. oleifera 'Huashuo'	1.07	1.21	1.07	1.15	2.84	1.39	1.32
C. oleifera 'Huaxin'	1.29	1.20	1.03	1.12	1.90	1.18	1.72
C. oleifera 'Huajin'	1.47	1.17	1.08	1.47	5.20	1.24	1.42
C. oleifera 'Cenruan No.2'	0.76	1.44	0.83	1.20	2.50	1.34	1.41
C. oleifera 'Cenruan No.3'	0.61	1.38	0.92	1.17	2.63	1.29	1.67
C. oleifera 'Ganzhou No.70'	0.60	1.67	0.77	1.72	1.95	1.05	1.36
C. oleifera 'Ganzhou Oil No.1'	0.76	1.44	0.83	1.20	2.50	1.34	1.41
C. oleifera 'Ganzhou Oil No.2'	0.81	1.78	0.74	1.53	2.53	1.26	1.70
C. oleifera 'Ganwu No.2'	0.70	1.50	0.83	1.33	1.95	1.20	1.34
C. oleifera 'Ganxing No.48'	0.63	1.75	0.79	1.65	3.25	1.09	1.64

Table 3. Affiliation values of aluminum tolerance index of 16 *C. oleifera* varieties

Varieties	Root activity	MDA content	SOD activity	H_2O_2 content	Proline content	Soluble sugar content	Al content	Average of SF	Rate of aluminum resistant
C. oleifera 'Xianglin No.1'	0.02	0.79	0.25	0.65	0.26	1.01	0.90	0.56	4
C. oleifera 'Xianglin No.27'	0.40	1.00	0.51	0.62	0.65	0.09	0.00	0.47	10
C. oleifera 'Xianglin No.210'	0.22	0.82	0.65	0.61	0.27	0.22	0.82	0.51	8
C. oleifera 'Changlin No.4'	0.30	0.73	0.29	0.36	0.00	0.26	0.43	0.34	12
C. oleifera 'Changlin No.40'	0.01	0.01	0.20	0.16	0.14	0.62	0.99	0.30	13
C. oleifera 'Changlin No.53'	0.00	0.59	0.52	1.00	0.26	0.35	0.93	0.52	5
C. oleifera 'Huashuo'	0.55	0.93	0.93	0.93	0.31	0.66	0.89	0.74	2
C. oleifera 'Huaxin'	0.80	0.94	0.83	0.99	0.04	0.26	0.37	0.60	3
C. oleifera 'Huajin'	1.00	0.97	0.98	0.40	1.00	0.38	0.76	0.78	1
C. oleifera 'Cenruan No.2'	0.22	0.74	0.25	0.86	0.22	0.57	0.77	0.52	6
C. oleifera 'Cenruan No.3'	0.05	0.80	0.51	0.90	0.25	0.48	0.44	0.49	9
C. oleifera 'Ganzhou No.70'	0.03	0.56	0.09	0.00	0.06	0.00	0.83	0.22	16
C. oleifera 'Ganzhou Oil No.1'	0.22	0.74	0.25	0.86	0.22	0.57	0.77	0.52	6
C. oleifera 'Ganzhou Oil No.2'	0.27	0.46	0.00	0.32	0.22	0.40	0.40	0.30	14
C. oleifera 'Ganwu No.2'	0.14	0.69	0.27	0.63	0.06	0.30	0.86	0.42	11
C. oleifera 'Ganxing No.48'	0.07	0.49	0.15	0.11	0.43	0.08	0.47	0.26	15

Discussion and conclusions

The worsening of soil acidification amplifies the problem of Al toxicity in soil. This problem can be solved quickly by screening Al-resistant varieties [7]. Different plants or different varieties of the same plant vary significantly in the sensitivity to Al stress, laying the basis for screening of Al tolerant varieties. The previous studies have shown that, under Al stress, the varieties with strong root activity are superior in Al tolerance than those with weak root activity. Our research finds that, under Al stress, the three *C. oleifera* varieties of the Hua series, namely, *C. oleifera* 'Huashuo', *C. oleifera* 'Huashuo', and *C. oleifera* 'Huaxin', saw enhanced root activity; By contrast, the root activity of the remaining 13 *C. oleifera* varieties decreased to different degrees.

The Al stress induces plant cells to generate lots of H_2O_2 reactive oxygen species (ROS). The accumulation of ROS would cause oxidative damage to the cells. The MDA is the product of lipid peroxidation of cell membrane. The growing contents of H_2O_2 and MDA mean the falling anti-oxidant capacity of the plants, leading to poor Al tolerance [4]. This is consistent with our research results. Under Al stress, the H_2O_2 and MDA contents of *C. oleifera* roots increased by different degrees, indicating that Al tolerance is affected by Al stress, yet the effect varies with germplasms. The change amplitudes of H_2O_2 and MDA were 11%~72%, and 13%~133%, respectively. SOD antioxidant enzymes can scavenge the ROS in plants under stress, and improve the Al tolerance of plants. Our research finds that the SOD activity of three *C. oleifera* varieties increased, namely, *C. oleifera* 'Huashuo', *C. oleifera* 'Huaxin', and *C. oleifera* 'Huajin', but that of the other 13 *C. oleifera* varieties dropped to different degrees. Hence, the Hua series *C. oleifera* varieties boast relatively good anti-oxidant capability, and a strong resistance to Al stress.

Under Al stress, the accumulation of osmo-regulatory substances in plants is closely related to the degree of exposure to Al toxicity. In general, the higher the content of osmo-regulatory substances, the stronger the Al tolerance [6]. Under Al stress, proline accumulates in large quantities, which reduces the damages of cell membrane. In our study, the Al stress pushed up the proline content significantly in all *C. oleifera* varieties, which agrees with the phenomena of Al tolerance of grapes [11]. However, different *C. oleifera* varieties differed significantly in proline content growth. The highest proline content belongs to *C. oleifera* 'Huajin, which is 5.2 times that of the CK; the lowest proline content belongs to *C. oleifera* 'Changlin No.4', which is only 1.7 times that of the CK. Soluble sugar can maintain the basic structure of plant cells after dehydration, and thus reduce damage to the cells. Under Al stress, the roots of all 16 *C. oleifera* varieties accumulated lots of soluble sugar. Among them, the soluble sugar content of 12 varieties was significantly higher than that of CK. But the increment varied significantly between varieties, falling between 5% and 56%.

Through comprehensive analysis on the membership functions of the composite Al tolerance coefficients of the 16 *C. oleifera* varieties, it was learned that *C. oleifera* 'Huajin', *C. oleifera* 'Huashuo', and *C. oleifera* 'Huaxin' have relatively strong Al tolerance, while *C. oleifera* 'Ganyou No.2', *C. oleifera* 'Ganxing No.48', and *C. oleifera* 'Ganzhou No.70' have relatively weak Al tolerance. Overall, the Hua series *C. oleifera* varieties from Hunan have much higher Al tolerance than the other varieties, while the Gan series *C. oleifera* varieties from Jiangxi have relatively poor Al tolerance. The Qinruan series from Guangxi, Xianglin series from Hunan, and Changlin series from Jiangxi have moderate Al tolerance.

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