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RESEARCH ARTICLE

Growth and abscisic acid responses of *Medicago sativa* to water stress at different growth stages

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Abstract A pot experiment was conducted in a greenhouse with three alfalfa (*Medicago sativa*) cultivars, Aohan, Zhongmu No.1 and Sanditi, to examine the morphological and physiological responses of alfalfa to water stress. The response of alfalfa to water stress at different growth stages was generally similar, but varied among cultivars. At the branching, flowering and podding stages, the shoot biomasses of Aohan and Zhongmu No.1 were greatly affected by, and responded quickly to, water stress. The shoot biomass of Sanditi was not affected by mild water stress, but had a slight response to moderate and severe water stress. The root/shoot ratios in Aohan and Zhongmu No.1 were more sensitive to water stress than in Sanditi, with the root/shoot ratio in Aohan increasing most significantly. At flowering, the root/shoot ratio was the highest and the effect of water stress the greatest. The abscisic acid (ABA) concentration in the roots of Aohan and Zhongmu No.1 increased under water stress, while in Sanditi there was only a slight or delayed response of ABA concentration.

Keywords abscisic acid, alfalfa, drought response, growth stage, water deficit

1 Introduction

The morphological and physiological responses in plants to water stress vary at different stages of growth and are affected by hormones and their relative concentrations, leading to different outcomes for crop production[1,2]. Cereal crops harvested for grain suffer a more severe yield reduction from water stress during the reproductive stage than at the vegetative stage[1,2]. In contrast, forage crops, where the vegetative tissues are the harvested product, should be examined differently to cereal crops in experiments on the effect of water stress on production.

Abscisic acid (ABA) is one of the most important hormones related to plant physiological metabolism and is an important regulator of responses to water stress. ABA increases in leaves under water stress, resulting in partial closure of stomata thus reducing water loss. Water stress affects hormone equilibrium in plants; this affects plant morphology and physiology and ABA in particular can regulate leaf morphology. Its concentration is low at the vegetative stage, when plants grow vigorously, but ABA concentration increases at the reproductive stage as plants mature and then begin to senesce. The concentration of hormones varies at different growth stages. Few studies have investigated the response of ABA concentration to water stress in plants at different growth stage.

The regulatory effect of ABA on plant growth varies among species. For instance, an ABA concentration of 10 $\mu mol \cdot L^{-1}$ can depress the development of lateral roots in some plant species, however, it can increase the number of lateral roots in legume species, such as alfalfa[3]. Therefore, it is inferred that the role of ABA in the drought response of alfalfa may differ from that of other plant species. ABA is a hormone closely related to stresses and, therefore, can improve the tolerance of crops to various biotic and abiotic stresses. ABA accumulates in the leaves when plants are under water stress, and reduces stomata opening and water loss from stomata, thereby maintaining the balance of water uptake and loss in plants and increases the adaptation of plants to dry environments[4–8]. Previous studies on drought tolerance of alfalfa focused on responses of plant morphological traits[9], osmotic pressure regulatory substances[10] and peroxide scavenging systems[11]. The effect of water stress on ABA metabolism remains unclear. Han et al.[12] studied the hormone dynamics in the leaves of alfalfa cultivars with different drought tolerance using a weighing and water control method, but the research did not investigate the dynamics of ABA concentration in roots. Ren et al.[13] investigated ABA concentrations in the leaves and roots of alfalfa under water stress, but did not examine further the relationship

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between water stress and ABA concentration in the roots of alfalfa at different growth stages. Therefore, the objective of this study was to investigate the effect of water stress at different growth stages of alfalfa on growth and ABA concentration in roots, and to provide a better understanding of stress ecophysiology of alfalfa to assist in the selection of drought-tolerant cultivars.

2 Materials and methods

2.1 Experimental design

The experiments were conducted at the Experimental Station of the Chinese Academy of Agricultural Sciences (CAAS), Langfang, Hebei Province, China. The three cultivars of alfalfa (*Medicago sativa*), Aohan, Zhongmu No.1 and Sanditi, used in the experiments were obtained from the Institute of Animal Science, CAAS. Seeds of alfalfa were surface-sterilized with 75% ethanol for 30 s and Hg solution (0.1%) for 3 min, then rinsed with distilled water three times before being transferred to wet filter paper in Petri dishes and germinated in the incubation chamber at 25°C. Four seedlings were transplanted to pots filled with culture medium (1:1 perlite:vermiculite). The pots were placed in the field and irrigated with tapwater for the first week after transplanting, and thereafter they were irrigated with 500 L water and nutrient solution alternately to avoid excess salinity. The pots were moved into a greenhouse when the plants reached specific growth stages, branching (2 months after seeding), flowering (80% of plants flowering) and podding, and water stress treatments applied 1 week later. Four water stress treatments were applied: well-watered control (90% to 95% field capacity), mild water stress (65% to 75% field capacity), moderate water stress (45% to 55% field capacity) and severe water stress (25% to 35% field capacity). Each treatment was replicated three times.

2.2 Sample analyses

The relative water content (RWC) was determined according to the protocol by Antolín[14] and calculated as follows:

$$RWC = (W_2 - W_1)/(W_2 - W_3)$$

where W_1 is leaf fresh weight, W_2 is the leaf turgid weight and W_3 is the leaf dry weight. The water potential of the upper fully expanded leaves was measured by Psypro water potential meter (Beijing Channel Scientific Instruments Co., Ltd., Beijing, China). Leaf stomatal conductance was measured by leaf pyrometer (Decagon Devices, Pullman, WA, USA). Plant biomass was dried initially in the oven at 110°C for 30 min and then at 65°C for 48 h to constant weight. Volumetric soil water content was measured by soil water meter (Delta-T Devices Ltd., Burwell, Cambridge, UK). Roots were collected from the pots, rinsed and dried with filter papers, then immediately frozen in liquid nitrogen and then stored at −80°C for further ABA analysis.

ABA in roots was measured by enzyme-linked immunosorbent assay. Samples (0.5 g) were ground in 4 mL of 80% methanol, and stored in centrifuge tubes for 4 h at 4°C. The extracts were centrifuged for 15 min at 4000 *g*. The ABA concentration in the extracts were determined by the ELISA method of Zhang et al.[15].

2.3 Statistical analyses

One-way analysis of variance followed by Duncan's multiple range test ($P < 0.05$) were performed using SAS 8.0.

3 Results

3.1 Effect of water stress on alfalfa at branching

Alfalfa plant growth was depressed by water stress with higher shoot biomass and lower root/shoot ratio in water stressed treatments compared to the control. The three cultivars responded similarly but varied in the extent to which plant growth was affected. Under mild water stress, the shoot biomass of Sanditi was barely affected, while that of Aohan and Zhongmu No.1 decreased significantly by 32.7% and 29.8%, respectively. Under moderate water stress, the shoot biomass of Aohan, Zhongmu No.1 and Sanditi decreased by 36.7%, 35.1% and 10.2%, respectively. Under severe water stress, the shoot biomass of Aohan, Zhongmu No.1 and Sanditi decreased by 44.9%, 38.6% and 24.5%, respectively. At branching, the shoot biomass differed significantly among cultivars with the highest biomass observed in Sanditi and the lowest biomass in Aohan.

The root/shoot ratio at branching increased in the three cultivars with increasing water stress. The root/shoot ratios in Aohan, Zhingmu No.1 and Sanditi were 0.74, 0.74 and 0.63, respectively, which were 1.64, 1.72 and 1.43 times the control, respectively, though the root/shoot ratio were not significantly different among the cultivars (Table 1).

ABA concentration increased to various degrees under water stress compared to the control. Under mild water stress, ABA concentration increased slightly. Under moderate water stress, ABA concentration was not significantly different ($P > 0.05$) from the control in both Aohan and Zhongmu No.1. However, ABA concentration under severe water stress was significantly different ($P < 0.05$) from to the control. ABA concentration in the root of Zhongmu No.1 was significantly higher than in Aohan and Sanditi ($P < 0.05$). ABA concentration

Table 1 Effect of water stress on shoot biomass, root/shoot ratio and root ABA concentration of alfalfa at branching

Cultivar	Water stress	Shoot biomass/($g \cdot m^{-2}$)	Root/shoot ratio	ABA concentration/($ng \cdot g^{-1}$ DW)
Aohan	Control	0.49±0.02a	0.45±0.03b	57.9±3.4c
	Mild	0.33±0.01b	0.64±0.03a	60.3±4.2bc
	Moderate	0.31±0.02bc	0.66±0.04a	74.4±7.7ab
	Severe	0.27±0.02c	0.74±0.05a	88.7±12.7a
Zhongmu No.1	Control	0.57±0.08a	0.43±0.02b	86.1±7.3b
	Mild	0.40±0.03b	0.63±0.03b	93.5±4.2ab
	Moderate	0.37±0.02b	0.66±0.05ab	88.7±6. 0b
	Severe	0.35±0.04b	0.74±0.05a	113.4±20.6a
Sanditi	Control	0.49±0.06a	0.44±0.01b	60.4±11.5b
	Mild	0.49±0.01a	0.64±0.03a	65.0±8.1ab
	Moderate	0.44±0.05a	0.68±0.03a	83.1±20.1ab
	Severe	0.37±0.00a	0.63±0.02a	94.5±21.9a

Note: Means of each cultivar within the same column followed by the same letters are not significantly different ($P > 0.05$).

significantly differed between cultivars ($P < 0.05$), with the highest being Zhongmu No.1 and Aohan the lowest.

The leaf water potential of alfalfa under water stress is shown in Fig. 1. Leaf water potential decreased with increasing water stress. Nevertheless, mild water stress did not affect leaf water potential in Aohan and Sanditi. Under moderate and severe water stress, leaf water potential significantly decreased by 42% and 62% for Aohan, 33% and 72% for Sanditi compared to the control ($P < 0.05$). Leaf water potential of Zhongmu No.1 decreased by 16%, 52% and 67% under mild, moderate and severe water stress, respectively, compared to the control ($P < 0.05$).

A comparison of RWC among cultivars is shown in Fig. 2. RWC decreased with the increasing water stress. RWC was not affected by mild water stress. Under moderate water stress, RWC of Zhongmu No.1 decreased significantly ($P < 0.05$), while RWC of Zhongmu No.1 and Sanditi was not affected or significantly different ($P > 0.05$) from the control. Under severe water stress, Zhongmu No.1 had the lowest RWC and Aohan had the highest RWC. RWCs of Zhongmu No.1 and Sanditi were significantly lower than the control ($P < 0.05$), while RWC of Aohan was similar to the control.

3.2 Effect of water stress on alfalfa at flowering

The effect of water stress on alfalfa growth at flowering was similar to that at branching. The shoot biomass of

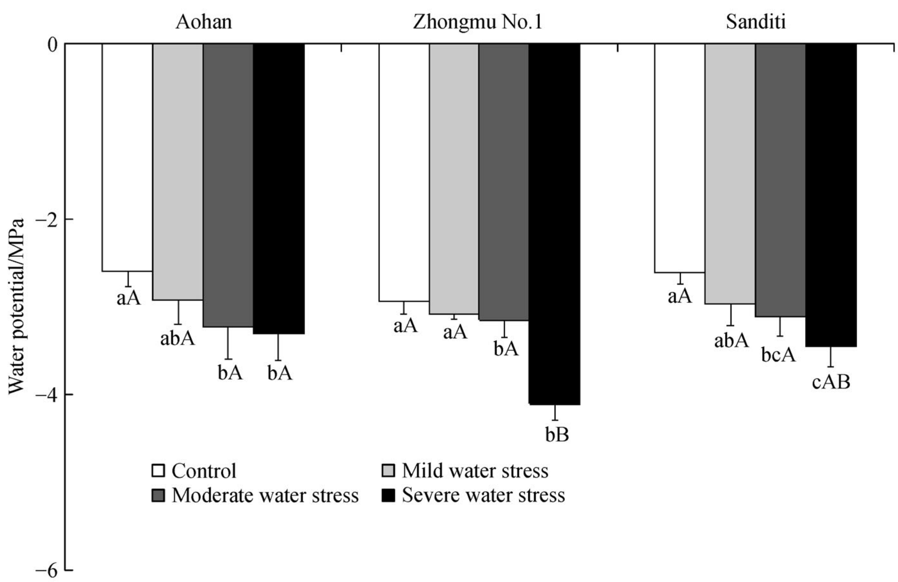

Fig. 1 Effect of water stress on leaf water potential of alfalfa plants. Means with the same lowercase or uppercase letters are not significantly different ($P > 0.05$ or $P > 0.01$), respectively.

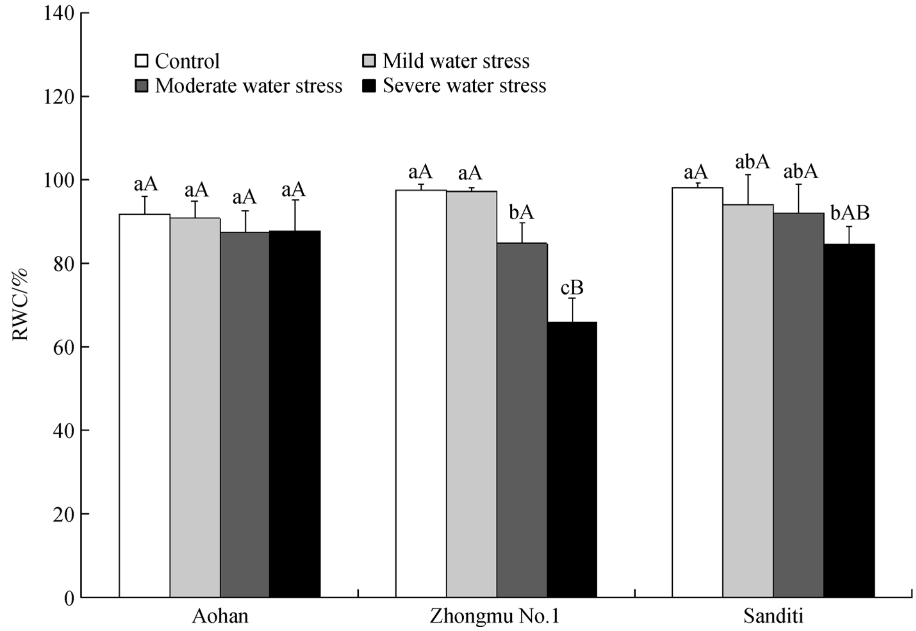

Fig. 2 Effect of water stress on relative leaf water content (RWC) of alfalfa plants. Means with the same lowercase or uppercase letters are not significantly different ($P > 0.05$ or $P > 0.01$), respectively.

Aohan and Zongmu No.1 decreased, while that of Sanditi increased, with increasing water stress. Severe water stress significantly decreased shoot biomass ($P < 0.05$). The shoot biomass of Aohan and Zhongmu No.1 decreased 39.5% and 47.4%, respectively. The shoot biomass change of Sanditi was more complicated: first increasing and decreasing with increasing water stress, with the shoot biomass being the highest under mild water stress, and then decreasing under moderate and severe water stress. The shoot biomass differed significantly among cultivars ($P < 0.05$), with Sanditi being the highest Zhongmu No.1 and Aohan the lowest (Table 2).

The root/shoot ratio increased with increasing water stress. Under severe water stress, the root/shoot ratios for Aohan, Zhongmu No.1 and Sanditi were 2.63, 2.45 and 2.73, which were 1.8, 1.49 and 1.41 times the control, respectively, but the root/shoot ratio was similar among cultivars.

ABA concentration in the roots increased with increasing water stress in Aohan and Zhongmu No.1, but was lower in Sanditi compared to the control. ABA concentration differed significantly among cultivars at flowering with the highest ABA concentration in Sanditi and the lowest in Aohan.

3.3 Effect of water stress on alfalfa at podding

At podding, the shoot biomass under mild water stress was higher than the control. The shoot biomass of Sanditi decreased with increasing water stress, while the change in shoot biomass for Zhongmu No.1 at podding was similar to those at flowering and branching. The shoot biomass at podding differed significantly among cultivars ($P < 0.05$), with the highest in Sanditi and the lowest in Aohan.

The root/shoot ratio increased with increasing water stress. Under severe water stress, the root/shoot ratios for Aohan, Zhongmu No.1 and Sanditi were 1.68, 1.36 and 0.97, which were 1.3, 1.3 and 1.14 times the control, respectively. The root/shoot ratio differed significantly among cultivars ($P < 0.05$), with the highest in Aohan and the lowest in Sanditi (Table 3). ABA concentration in the roots increased with increased water stress in Aohan and Zhongmu No.1, while the change in ABA concentration in Sanditi was similar to that at flowering: it was lower than the control under mild water stress and then increased with increasing water stress. ABA concentration at podding was not significantly different among cultivars ($P > 0.05$).

4 Discussion

Stomatal conductance, water physiology, biomass, shoot/root ratio and root ABA concentration were investigated in this study. Biomass accumulates through photosynthesis, and therefore the effect of water stress on photosynthesis is reflected in the change in plant biomass. In this study, the shoot biomass under water stress was higher than the control during flowering and podding. There may be two possible reasons for this result. Firstly, a mild water stress may have enhanced plant growth given the fact that alfalfa plants favors a slightly drier environment. Secondly, the growth of plants in the control was restricted by some

Table 2 Effect of water stress on shoot biomass, R/S and root ABA concentration of alfalfa at flowering

Cultivar	Water stress	Shoot biomass/(g per plant)	Root/shoot ratio	ABA concentration/($ng \cdot g^{-1}$ DW)
Aohan	Control	2.66±0.18a	1.44±0.13d	368±11.6b
	Mild	2.06±0.55ab	2.08±0.16bc	893±125.0a
	Moderate	2.08±0.19ab	2.09±0.36b	718±0.0ab
	Severe	1.61±0.08b	2.64±0.14a	564±204.9ab
Zhongmu No.1	Control	3.63±0.33a	1.64±0.13b	442±129.5a
	Mild	2.87±0.44ab	2.01±0.21ab	504±34.3a
	Moderate	2.13±0.10b	2.42±0.11a	685±139.8a
	Severe	1.91±0.48b	2.45±0.19a	511±164.0a
Sanditi	Control	2.51±0.25b	1.94±0.13b	1227±94.9a
	Mild	3.94±0.36a	2.18±0.13b	700±246.6b
	Moderate	3.33±0.09a	1.82±0.08b	641±4.4b
	Severe	2.21±0.08b	2.73±0.12a	579±49.3b

Note: Means of each cultivar within the same column followed by the same letters are not significantly different ($P > 0.05$).

Table 3 Effect of water stress on shoot biomass, R/S and root ABA concentration of alfalfa at podding

Cultivar	Water stress	Shoot biomass/(g per plant)	Root/shoot ratio	ABA concentration/($ng \cdot g^{-1}$ DW)
Aohan	Control	3.82±0.36ab	1.29±0.12b	318±38.8a
	Mild	4.27±0.29a	1.18±0.05b	340±49.5a
	Moderate	3.43±0.35ab	1.48±0.15ab	463±71.0a
	Severe	2.94±0.28b	1.68±0.12a	335±49.9a
Zhongmu No.1	Control	5.42±1.05a	1.05±0.08b	294±31.2a
	Mild	3.92±0.55a	1.15±0.11a	337±97.2a
	Moderate	3.23±1.03a	1.52±0.21a	425±73.7a
	Severe	3.00±0.26b	1.36±0.05a	586±152.5a
Sanditi	Control	7.74±0.39a	0.85±0.05a	482±108.8ab
	Mild	7.28±0.25a	0.85±0.04a	263±20.8b
	Moderate	5.57±0.71a	1.12±0.09a	389±65.1ab
	Severe	6.75±2.24a	0.97±0.14a	599±99.3a

Note: Means of each cultivar within the same column followed by the same letters are not significantly different ($P > 0.05$).

unknown environmental factors which had an effect greater than that of the treatment, leading to a lower biomass in the control. Overall, shoot biomass decreased with increasing water stress, though there was variation among cultivars. The shoot biomass was affected more in Sanditi than in Aohan and Zhongmu No.1. The shoot biomass differed among cultivars, with the greatest shoot biomass in Sanditi and the lowest in Aohan.

Grain yield is the most important indicator for evaluating drought tolerance of cereal crops as grain production is the main purpose in growing these crops. However, unlike cereal crops, in forage crops higher vegetative dry matter yield is the main purpose of production. Also, for perennial forage species, the stability and persistence of production are also important factors to be considered. Therefore, in addition to shoot biomass, other parameters, such as root/shoot ratio, are also important

Under water stress, the shoot and root biomass are generally affected differently[16], and changes in root/shoot ratio are caused by the change in allocation of assimilates[17]. In our study, the root/shoot ratio did not change under mild and moderate water stress, while it increased under severe water stress, which is consist with the results of Erice et al.[18]. It has been reported that root/shoot ratio tended to increase under water stress and higher root/shoot ratio represented higher drought tolerance[19,20]. A larger root system provides a greater ability to absorb water from the soil, while smaller shoot biomass means there is less moisture loss from transpiration, which thereby decreases water stress. In our study, the root/shoot ratio for Aohan and Zhongmu was always greater than Sanditi under water stress, with the root/shoot ratio of Aohan and Sanditi under severe water stress at flowering being 1.8 and 1.4 times higher, respectively, than the control, indicating higher drought tolerance of Aohan than Sanditi.

It is widely thought that under water stress, ABA production in roots increases and is transported to the shoot through the xylem, however some studies have shown that this is not always the case and that ABA concentration can increase under water stress. Jeschke et al.[21] found that leaf and xylem ABA concentrations increased significantly under low soil phosphorus, while root ABA did not increase substantially under the same conditions. This result led to the conclusion that newly-produced ABA in the roots is quickly transferred to leaves and other above-ground parts of the plant through the xylem. In our study, root ABA concentration did not significantly increased under mild and moderate water stress at branching in any of the cultivars, which is consistent with the results of Jeschke et al.[21]. As ABA concentrations in the xylem and leaves were not tested, further research is needed to better understand the mechanism of ABA dynamics in roots. Severe water stress increased root ABA significantly, and this could be caused by air in the vascular bundle, which blocked the transport of root ABA to the shoot. Jeschke et al.[21] and Brodersen et al.[22] reported the complexity of root ABA dynamics under water stress. In our study, root ABA concentration in Aohan responded quickly to water stress and remained high at flowering and podding. The root ABA in Zhongmu No.1 also increased with increasing water stress. However, unlike the other cultivars, the root ABA concentration in Sanditi did not increase under mild and moderate water stress, while it increased only under severe water stress. The above results suggest that root ABA production was more responsive to water stress in Aohan and Zhongmu No.1 than in Sanditi. However, root ABA concentration alone cannot verify this suggestion, and further studies on protein and gene expression are required. In addition, root ABA concentration in Zhongmu No.1 and Sanditi was always higher than in Aohan, which might reflect genetic variation and variable sensitivity to ABA among cultivars.

5 Conclusions

The responses of alfalfa cultivars to water stress at different growth stages were similar, but there were differences between cultivars. At the three growth stages, the shoot biomass of Aohan and Zhongmu No.1 was affected significantly by water stress, indicating a more rapid response of these cultivars to stress. The shoot biomass of Sanditi did not respond significantly to mild water stress, and was significantly affected under moderate and severe water stress. The root/shoot ratios of Aohan and Zhongmu No.1 were more sensitive to water stress than that of Sanditi, with Aohan having the greatest increase in root/shoot ratio. The root/shoot ratio, and its increase, were higher at flowering than at branching and flowering in the three cultivars. Under water stress, root ABA increased in Aohan and Zhongmu No.1, while there was only a weak or delayed response in root ABA concentration in Sanditi.

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Compliance with ethics guidelines Yue Li, Liqiang Wan, Yufei Wang, and Xianglin Li declare they have no conflicts of interest or financial conflicts to disclose.

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