



# Morphological and physiological plasticity of *Catalpa bungei* roots under partial root-zone drought as affected by nitrogen forms

Tiantian Sun<sup>1,2</sup> · Ruohan Ren<sup>1</sup> · Mingming Xing<sup>1</sup> · Qiuxiao Duan<sup>1</sup> · Lang Zhao<sup>1</sup> · Wenwen Yan<sup>1</sup> · Yang Fang<sup>1</sup> · Senyan Zhang<sup>1</sup> · Hao Dong<sup>1</sup> · Mengran Wang<sup>1</sup> · Qimeng Heng<sup>1</sup> · Wenyi Chen<sup>1</sup> · Ting Xu<sup>1</sup> · Lili Kou<sup>1</sup> · Kunpeng Li<sup>1</sup> · Junhui Wang<sup>3</sup> · Wenjun Ma<sup>3</sup> · Wangxiang Zhang<sup>2</sup> · Yinglong Chen<sup>4</sup> · Yizeng Lu<sup>5</sup> · Yi Zhang<sup>1</sup> 

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## Abstract

A greenhouse experiment was conducted to evaluate root plasticity and drought responses of *Catalpa bungei* under partial root-zone drought as affected by nitrogen (N) forms. A two-factor experimental design was used in which two nitrogen forms (ammonium nitrogen (AN) and nitrate nitrogen (NN)) were combined with four water treatments (well-watered condition (WW), vertical partial root-zone drought (V-PRD), horizontal partial root-zone drought (H-PRD), full root-zone drought (FRD)). Root parameters were inter-actively affected by water conditions and N forms. Root development was sharply inhibited by FRD, and nitrate (NN) was more beneficial than ammonium (AN) for lateral root elongation under FRD. Root responded to PRDs with changing of their morphological plasticity, depending on the supplied N forms. Moreover, root system exhibited contrasting strategy for water foraging under V-PRD and H-PRD. Under V-PRD, root forage for water by hydrotropism, which was indicated by active root proliferation in moist soil zone. This strategy contributed to the efficient carbohydrate production and dominant xylem development under V-PRD. In contrast, root forage for water under H-PRD by significant root proliferation in the drought soil zone. The absence of horizontal hydrotropism under H-PRD condition and the presence of vertical hydrotropism under V-PRD was related to the gravitropism action. Physiological plasticity under PRDs might be preliminary disclosed by the specific activation of antioxidant defense in the drought root zone. Specifically, APX, CAT and SOD were induced in the drought root zone (top zone) of V-PRD, and APX was induced in the drought root zone (right zone) of H-PRD. Root physiological plasticity under PRDs was related to N forms and it displayed contrasting patterns in NN and AN treatment.

**Keywords** Partial root-zone drought · *Catalpa bungei* · Drought tolerance · Morphological plasticity · Physiological plasticity

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Tiantian Sun, Ruohan Ren, Mingming Xing, and Qiuxiao Duan authors are equal contributors.

Extended author information available on the last page of the article

## Introduction

Soil drought is becoming a major environmental stress factor that seriously affects the development and distribution of plants (Luo et al. 2009; Shi et al. 2017; Zheng et al. 2017; Wang et al. 2021). Root system is critical for plants to absorb water and nutrients, and it is also the first sensitive part to receive drought signals (Pierik et al. 2014; Prince et al. 2015; Yildirm et al. 2018). Plants can adjust root morphological structure and configuration via signal transduction under drought stress and then initiate physiological and biochemical reactions to adapt environmental stress (Sannwald et al. 2011). High root plasticity and root activity under drought is listed as an indicator of strong drought resistance of plants (Kunert et al. 2016).

The spatial distribution of soil water is usually heterogeneous due to natural factors including precipitation, evaporation and human activity such as irrigation. This may result in partial root-zone drought (PRD), in which a part of roots is in moist soil zone while the other part is in dry soil zone (Dekker et al. 2001; Kang and Zhang 2001). PRD usually includes two typical types, horizontal PRD (H-PRD) and vertical PRD (V-PRD) (Wang et al. 2021). H-PRD is usually produced by alternate partial root-zone irrigation (PRI), a water-saving irrigation technology for crop plants and horticulture plants (Kang and Zhang 2001; Ghafair 2020). In comparison, the heterogenous distribution of soil moisture content in vertical orientation, i.e. V-PRD, occurs often in soil of arid and semi-arid regions (Wang et al. 2012; Schlesinger et al. 2015).

Previous studies have reported that water use efficiency in the agriculture and horticulture productions was improved by partial root-zone irrigation (PRI) as compared with conventional irrigation method (Iqbal and Raza 2019; Ahmad et al. 2020). For example, water-use efficiency was increased by PRI in *Triticum aestivum* (wheat) (Ahmad et al. 2020), *Gossypium* spp (cotton) (Iqbal and Raza 2019), *Zea mays* L (maize) (Kang et al. 2000), *Piper nigrum* L (pepper) (Kang et al. 2001) and *Pyrus* spp (pear) (Kang et al. 2002). Under PRD conditions, roots in drought zone can generate drought signals such as ABA, which can be transported to leaves via xylem and then stoma in the leaves will be regulated, thereby the damage caused by excessive transpiration would be mitigated (Schroeder et al. 2001; McLean 2011). In the meanwhile, roots in the moist soil zone can absorb water to maintain the water status and favor the growth of plants. By this process, plants can reduce water consumption and improve the water use efficiency (Verslues and Zhu 2005; Ghafari et al. 2020; Wang et al. 2021). In comparison with agriculture and horticulture soil, forest soil is usually far less irrigated. Consequently, both of H-PRD and V-PRD are common and significant for woody species. It is of great significance to evaluate the patterns of morphological and physiological plasticity of root systems in woody plants under differential root-zone drought.

Nitrogen (N) is a critical component of numerous metabolites such as proteins, vitamins, enzymes and phytohormones in plants (Shi et al. 2017; Song et al. 2019). Nitrogen forms and contents showed crucial effect on root growth, morphology and distribution (Kagenishi et al. 2016; Zou et al. 2020). Nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) are the primary inorganic N and they showed diverse effects on physiological regulation and lateral root development of plants (Yang et al. 2002; Alt et al. 2017). Previous studies demonstrated that nitrate application stimulated lateral root (LR) elongation and induced longer and thinner roots, and thus promote root biomass production (Remans et al. 2006; Gruber et al. 2013). In comparison, ammonium stimulated LR branching and primary root growth (Ravazzolo et al. 2020). Consequently, the root morphological plasticity under partial

root-zone drought may be differentially affected by nitrogen (N) forms. In addition, nitrate and ammonium may affect the content of various metabolites and the activity of enzymes (Escobar et al. 2010). Therefore, stress responses to PRDs including antioxidant defense and drought signaling activation may be also affected by nitrogen forms (Kagenishi et al. 2016; Trevisan et al. 2018). Although the effects of nitrogen forms on plant root development have been well studied, the patterns of how N forms impact morphological and physiological plasticity of roots under PRDs are known very little.

*Catalpa bungei* is a high-quality and precious timber tree species, which showed strong adaptability and large economic value (Zheng et al. 2017; Shi et al. 2017). *C. bungei* is mainly distributed in northern regions of China where drought stress and nitrogen deficiency are major limiting factors for tree growth and forest productivity (Zheng et al. 2017). In this study, we conducted a greenhouse experiment to address the following hypotheses: (i) the water foraging strategy of morphological and physiological plasticity of *C. bungei* root may be different under partial root-zone drought in vertical direction (V-PRD) and horizontal direction (H-PRD); (ii) nitrogen forms (nitrate or ammonium) may influence morphological and physiological plasticity of *C. bungei* roots under differential root-zone drought. These studies would provide a theoretical basis and guideline for forest management and breeding of *C. bungei* under drought conditions.

## Materials and methods

### Plant material and experimental design

A greenhouse experiment was conducted during the 2018 growing season. A clone of *C. bungei* (clone ID, 2) was used as the plant material which was derived from a crossbreeding program of *C. bungei*. The plantlets were prepared by micropropagation and then cultivated in a climate chamber for 25 days (average temperature, 25 °C; relative humidity, 50–60%; light, 14 h per day). The seedlings were then transplanted into the pots and cultivated in a greenhouse (nature light, day/night 26 °C/20 °C, 50–60% relative humidity), which located in the Northwest Agriculture and Forestry University. The pots were filled with 8 L mixture of sand and soil (sand: peat soil, 2:1, v/v), and the diameter and height of pot were 35 cm and 40 cm, respectively.

Two nitrogen treatment (nitrate and ammonium) were combined with four water treatments for experimental design, giving a combination of 8 treatments. The growth of seedlings was more sensitive to water stress but was less sensitive to nitrogen applications. Therefore, the nitrogen application was started on the 20<sup>th</sup> day of seedling transplant and it was lasted for two-month before water treatment was started, to ensure the effect of contrasting N condition on drought responses of seedlings. In total the nitrogen treatment was lasted for 90 days until harvest. For nitrate and ammonium treatment, 2.0 mM Ca (NO<sub>3</sub>)<sub>2</sub> (the final pH was 5.5) and 4.0 mM NH<sub>4</sub>HCO<sub>3</sub> (the final pH was 5.8) were applied, respectively. The NH<sub>4</sub><sup>+</sup> are not migrated easily in soil but can be transformed into nitrate. However, the nitrate nitrogen in soil is difficult to be transformed into other forms of nitrogen. Therefore, in this experiment, the small amount of nutrient solutions were applied slightly and frequently (50 ml per pot and once every three days) to ensure that most of them can be absorbed by plants and to avoid NH<sub>4</sub><sup>+</sup> being transformed to nitrate in the soil. The drip irrigation equipment was used in the experiment to ensure the nutrient solution and water can drip slowly, periodically and

quantitatively. In addition to N nutrition, the modified LA solution was applied, which contained 0.5 mM KCl, 0.3 mM  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ , 0.6 mM  $\text{KH}_2\text{PO}_4$ , 0.042 mM  $\text{K}_2\text{HPO}_4$ , 0.9 mM  $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$ , 2  $\mu\text{M}$   $\text{MnSO}_4 \cdot 4\text{H}_2\text{O}$ , 10  $\mu\text{M}$   $\text{H}_3\text{BO}_3$ , 7  $\mu\text{M}$   $\text{Na}_2\text{MoO}_4$ , 0.05  $\mu\text{M}$   $\text{CoSO}_4$ , 0.2  $\mu\text{M}$   $\text{ZnSO}_4$ , 0.2  $\mu\text{M}$   $\text{CuSO}_4$ , 0.01 mM Fe-EDTA. After the transplanting of seedlings, 150 ml Longashton (LA) nutrient solution was supplied once every three days.

Water treatment was started on the 60th day of nitrogen treatments and it was lasted for 30 days until harvest. The four water treatments were well-watered (WW,  $70 \pm 5\%$  field capacity), full root-zone drought (FRD,  $45 \pm 5\%$  field capacity), partial root-zone drought in the horizontal orientation (H-PRD,  $45 \pm 5\%$  field capacity in the right zone, and  $70 \pm 5\%$  field capacity in the left zone), and partial root-zone drought in the vertical orientation (V-PRD,  $45 \pm 5\%$  field capacity in the top zone, and  $70 \pm 5\%$  field capacity in the bottom zone). The pot experiment was separated into two sub-groups, in which the first sub-group consist of WW, V-PRD, and FRD, and the second sub-group consist of WW, H-PRD, and FRD. For both of WW and FRD treatment, there were three replicated pots in each of the two sub-groups respectively. As a result, there were three replicated pots (H-PRD and V-PRD treatment) or six replicated pots (WW and FRD treatment) in total. To maintain the specific threshold of water content in different soil area of V-PRD condition, two independent droppers were placed in the top zone and bottom zone. Similarly, two separate droppers were placed in the right zone and left zone to maintain the specific threshold of water content in H-PRD condition. The water content of different soil regions was monitored by a time-domain reflection (TDR) instrument (TRD300), which was measured every 2–3 days during the treatment.

### Harvest of plant material and measurement of root parameters

On the 30<sup>th</sup> day of water treatment, root material was harvested. For seedlings in the first sub-group (WW, V-PRD and FRD), the pot was cut into two halves transversely at the middle point, and the roots were evenly separated into the top zone and bottom zone. For seedlings in the second sub-group (WW, H-PRD and FRD), the pot was cut into two halves horizontally at the middle point, and the roots were evenly separated into the left zone and right zone. Roots in each zone were harvested separately, and the harvested roots were rinsed with water immediately and thereafter scanned by a root scanner and analyzed by Win/MacRHIZO software (Régent Instruments, Quebec, Canada). During the scanning process, roots in the top zone and in the bottom zone of V-PRD were scanned respectively. Similarly, roots in the left zone and in the right zone of H-PRD were scanned respectively. The root parameters including root length (RL), the number of root tips (RT), root average diameter (RAD) and fine root length (FRL) were analyzed, and root parameters from the same root zone of different water treatment were compared.

Subsequently, one part of the roots was frozen in liquid  $\text{N}_2$  before they were stored at  $-80^\circ\text{C}$  for the determination of physiological indexes. The other part of the roots was dried at  $60^\circ\text{C}$  until the weight remained constant. In the process of indexes measurement, the roots in the same root zone were compared separately for the different irrigation treatments (one is for roots in V-PRD compared with WW and FRD, and another is for roots in H-PRD compared with WW and FRD), which was consistent with the analysis and comparison method of the root parameters described above. All physiological indexes were calculated based on dry weight unless indicated otherwise.

## Analysis of free proline and antioxidant enzyme activities

The frozen samples were ground into fine powders in liquid N<sub>2</sub> and were used for the determination. The concentration of free proline was measured according to the method provided by Shi et al. (2017). The analyzed antioxidant enzymes included ascorbate peroxidase (APX; EC 1.11.1.11), catalase (CAT; E.C.1.11.1.6) and superoxide dismutase (SOD; EC 1.15.1.1). Among them, APX was analyzed according to the methods of Chen et al. (2011). The activity of SOD was measured spectrophotometrically at 550 nm by the method according to Cao et al. (2014), and CAT was evaluated spectrophotometrically at the wavelength of 240 nm as described previously (He et al. 2011). One unit of APX was defined as the quantity of enzyme that decomposed 1 nmol ascorbic acid min<sup>-1</sup> mg<sup>-1</sup> of protein at 290 nm using a spectrophotometer. One unit of SOD was defined as the quantity of enzyme that catalyzed 50% SOD-inhibiting nitroblue tetrazolium. One unit of CAT was defined as the quantity of enzyme that broke down 1 mmol H<sub>2</sub>O<sub>2</sub> per minute at 25 °C.

## Analysis of phytohormone concentration

Phytohormones including gibberellic acid (GA<sub>3</sub>), salicylic acid (SA), and indole acetic acid (IAA) were measured by the standard system of extraction and purification. Firstly, 4 ml extracting solution which contained 80% methanol, 0.2 g/L butylated hydroxytoluene (BHT) and 0.5 g/L citric acid monohydrate (CAM) were mixed with 500 mg ground materials. The samples were extracted by shaking at 4 °C overnight. Thereafter, they were centrifuged at 4 °C, 10,000 g for 15 min before the supernatant was collected. The precipitate was extracted twice for one hour and then all the supernatants were combined. The supernatants were dried by N<sub>2</sub> at 33 °C. Finally, the samples were dissolved in 0.8 mL 100% methanol solution and filtered by 0.22 μm filter membrane before measurement. The phytohormones were determined by the Ultra Performance Liquid Chromatography (UPLC). GA<sub>3</sub> (G7645), SA (S7401) and IAA (I2886) were purchased from Sigma for the preparation of standard curves to quantify hormone concentrations in the samples.

## Statistical analysis

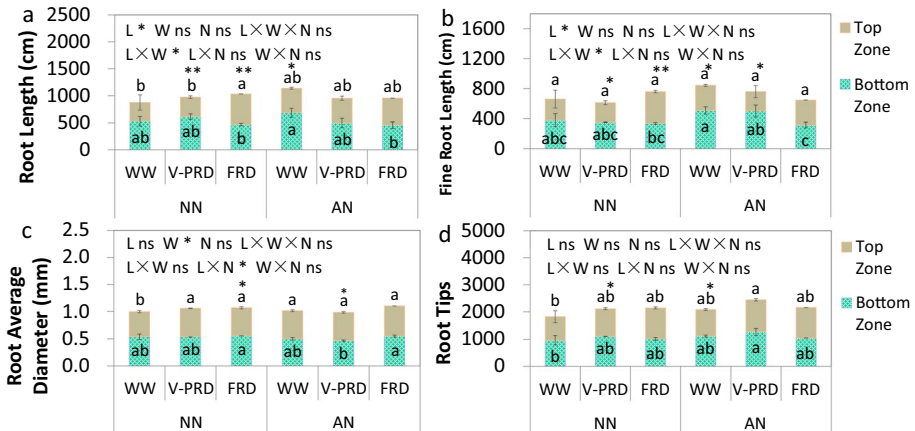
Statistical analysis was conducted by SAS software, and the UNIVARIATE program in SAS software was used to test the normality of all data (SAS Institute, Cary, NC; 1996). To detect the differences and interactions of nitrogen forms and water treatments and different root-zones for experimental variables, three-way ANOVAs were applied. To investigate the effects of nitrogen, watering and the interactive effects of nitrogen × watering, multiple mean comparisons (Fisher's LSD test) were applied on all variables. The paired T-test was employed to compare the differences in root parameters between the two root zones (left and right, or top and bottom) under the same combined condition of water and N forms. Another T-test was employed to compare the differences in physiological parameters between the two N forms. Differences were considered significant at  $P \leq 0.05$ . After data were standardized, the principal component analysis (PCA) was performed by the command `prcomp()` in R (<http://www.rproject.org/>) as described previously (Zheng et al. 2017).

## Results

### Root parameters in vertically partial root-zone as affected by nitrogen forms

In NN treatment, root length and fine root length both were unaltered by V-RPD regardless of N forms and root zones. Root length in the top zone was increased by FRD as it was 55.32% and 62.61% larger in FRD than that in V-PRD and WW condition (Fig. 1a) respectively, while the inhibition was not present in the bottom root zone. Root average diameter was 13.95% larger in the top zone of V-PRD and 11.67% larger in FRD than that of WW (Fig. 1c). In AN treatment, both of root length (33.03%) and fine root length (37.92%) in the bottom zone of FRD was smaller than that of WW (Fig. 1b). Root average diameter in the bottom zone of FRD was 17.85% larger than that of V-PRD (Fig. 1c). There were no differences in root tip number between the three water treatments or the two N treatments (Fig. 1d).

In NN treatment, root length, fine root length and root tip number all were dominant in the bottom root zone (moist zone) as compared with the top root zone under V-PRD condition (Fig. 1a and b), indicating the significant root plasticity and hydrotropism in NN treatment. In comparison, only fine root length was dominant in the bottom zone of V-PRD in AN treatment (Fig. 1b). Under FRD condition of NN treatment, root average diameter was 7.44% smaller in the top zone than that in the bottom zone (Fig. 1c). Under V-PRD condition of AN treatment, root average diameter was 10.26% larger in the top zone than that in the bottom zone (Fig. 1c). Under FRD condition in NN

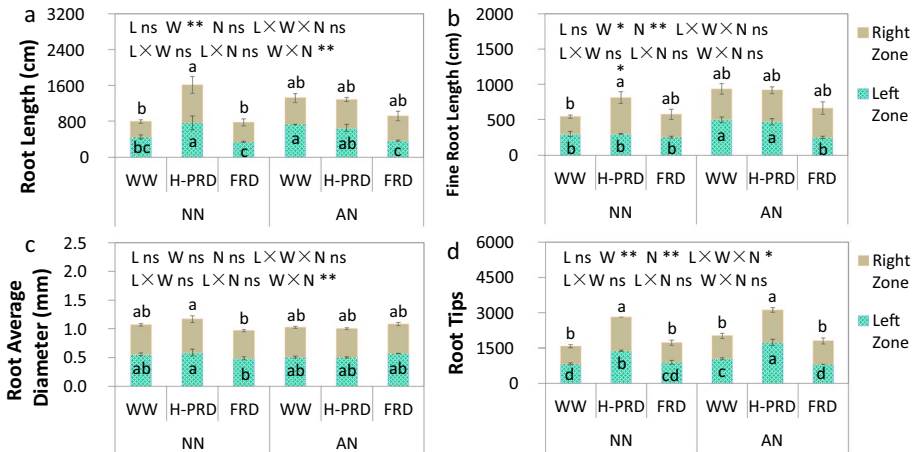


**Fig. 1** Root length (a), fine root length (b), root diameter (c), root tips (d) of *Catalpa bungei* seedlings under different water and nitrogen forms. WW, well-watered condition; V-PRD, vertically partial root-zone drought condition ( $45 \pm 5\%$  field capacity in the top zone, and  $70 \pm 5\%$  field capacity in the bottom zone); FRD, full root-zone drought condition ( $45 \pm 5\%$  field capacity in whole soil profile). NN, nitrate nitrate ( $\text{NO}_3^-$ ); AN, ammonium ( $\text{NH}_4^+$ ). The bar indicates mean  $\pm$  SE ( $n=4$ ). *P*-values obtained from the three-way ANOVAs for nitrogen forms (N), water treatments (W), root-zone locations (L) and their interactions ( $N \times W$ ,  $N \times L$ ,  $W \times L$ ,  $N \times W \times L$ ) are labelled as: \* $P < 0.05$ ; \*\* $P < 0.01$ ; ns, not significant. The results of multiple mean comparisons between each combined treatment of N and water were indicated by letters around error bars, and bars with different letters indicate significant differences ( $P < 0.05$ ). The results of T-test that discerning difference between the two root-zones was labelled by ‘\*’ ( $P < 0.05$ ) and ‘\*\*’ ( $P < 0.01$ ) above the letters

treatment, root length (19.42%) and fine root length (24.90%) both were larger in the top zone than that in the bottom zone.

### Root parameters in horizontally partial root-zone as affected by nitrogen forms

In NN treatment, root length in the left zone (moist zone) and right zone (drought zone) of H-PRD both were 69.13% larger in the left zone and 150.16% larger in the right zone than that of WW and it was also 122.29% larger in the left zone and 98.27% larger in the right zone than that of FRD conditions (Fig. 2a), indicating significant root plasticity in both moist and drought root zone. Fine root length in the right zone of H-PRD was 112.05% larger than that of WW condition (Fig. 2b). In AN treatment, root length and fine root length were smaller in the left zone of FRD than that of WW (Fig. 2a and b). Root average diameter in both zones of H-PRD was 19.60% larger in the right zone and 22.56% larger in the left zone than that of FRD in NN treatment, while the difference was not observed in AN treatment (Fig. 2c). Root tip number in the both zones of H-PRD was 67.37% larger in the moist zone and 91.38% larger in the drought zone than that of WW in NN treatment. It was also 54.24% larger in the moist zone and 74.22% larger in the drought zone than that of FRD in NN treatment. In AN treatment, root tip number in the both zones of H-PRD was 63.28% larger in the moist zone and 45.43% larger in the drought zone than that of WW. It was also 112.16% larger in the moist zone and 40.98% larger in the drought zone than that of FRD conditions, respectively (Fig. 2d).



**Fig. 2** Root length (a), fine root length (b), root diameter (c), root tips (d) of *C. bungei* seedlings under different water and nitrogen forms. WW, well-watered condition; H-PRD, horizontally partial root-zone drought condition (45 ± 5% field capacity in the right zone, and 70 ± 5% field capacity in the left zone); FRD, full root-zone drought condition (45 ± 5% field capacity in whole soil profile). NN, nitrate nitrate (NO<sub>3</sub><sup>-</sup>); AN, ammonium (NH<sub>4</sub><sup>+</sup>). The bar indicates mean ± SE (n=4). *P*-values obtained from the three-way ANOVAs for nitrogen forms (N), water treatments (W) and their interactions (N×W, N×L, W×L, N×W×L) are labelled as: \**P* < 0.05; \*\**P* < 0.01; ns, not significant. The results of multiple mean comparisons between each combined treatment of N and water were indicated by letters around error bars, and bars with different letters indicate significant differences (*P* < 0.05). The results of T-test that discerning difference between the two root-zones was labelled by ‘\*’ (*P* < 0.05) and ‘\*\*’ (*P* < 0.01) above the letters

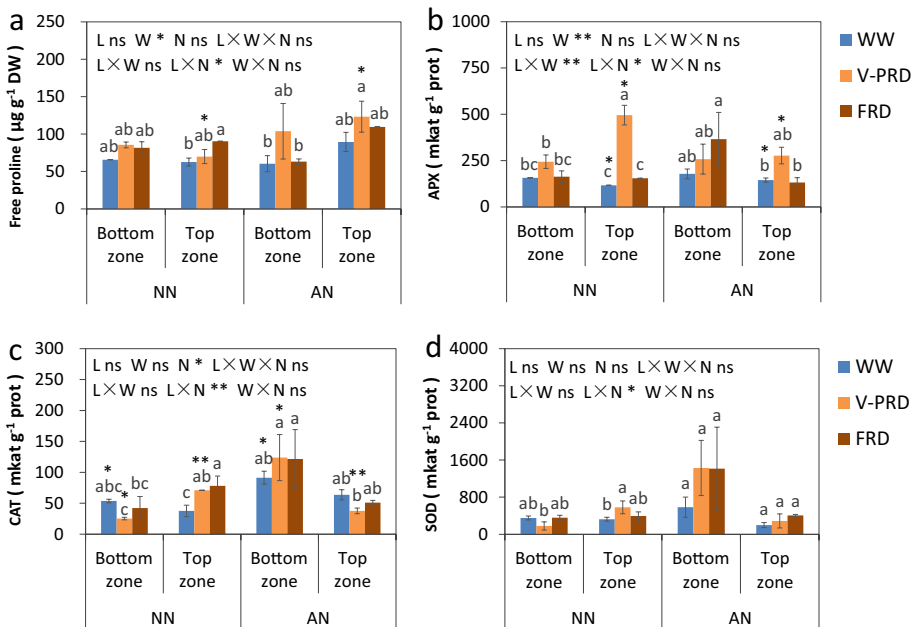


Under H-PRD condition of NN treatment, fine root length was 68.08% larger in the right zone (drought zone) than that in the left zone (moist zone), indicated that morphological root plasticity as indicated by active root proliferation was opposite to the direction of hydrotropism (Fig. 2b). In comparison, root plasticity under H-PRD were not observed in AN treatment as root parameters have no differences between the two root zones (Fig. 2b).

### The level of antioxidants in vertically partial root-zone as affected by N forms

In AN treatment, the activity of APX was higher in the top zone of V-PRD (drought zone) than that of WW and FRD (Fig. 3b). In NN treatment, the activity of SOD was 78.50% higher in the top root zone of V-PRD condition than that of WW condition (Fig. 3d). The level of free proline and CAT was 44.37% and 108.19% higher in the top zone of FRD than that of WW condition, while the difference was not observed in AN treatment (Fig. 3a and c). In AN treatment, CAT activity was 69.59% lower in the top zone of V-PRD than that in the bottom zone (Fig. 3c).

In the top zone of V-PRD condition, the level of free proline in NN treatment was 43.26% lower than that in AN treatment (Fig. 3a), while APX and CAT activity was



**Fig. 3** Contents of root free proline (a), APX (b), CAT (c), SOD (d) activity in roots of *C. bungei* seedlings under different water conditions and nitrogen forms. WW, well-watered condition; V-PRD, vertically partial root-zone drought condition ( $45 \pm 5\%$  field capacity in the top zone, and  $70 \pm 5\%$  field capacity in the bottom zone); FRD, full root-zone drought condition ( $45 \pm 5\%$  field capacity in whole soil profile). NN, nitrate nitrate ( $\text{NO}_3^-$ ); AN, ammonium ( $\text{NH}_4^+$ ). The bars indicates mean  $\pm$  SE ( $n=4$ ).  $P$ -values obtained from the three-way ANOVAs on nitrogen forms (N), water treatments (W), root-zone locations (L) and their interactions ( $N \times W$ ,  $N \times L$ ,  $W \times L$ ,  $N \times W \times L$ ) are labelled as: \* $P < 0.05$ ; \*\* $P < 0.01$ ; ns, not significant. The results of multiple mean comparisons between the six columns (combinations of three water treatments and two root zones) within each N treatment were indicated by letters around error bars, and bars with different letters indicate significant differences ( $P < 0.05$ )

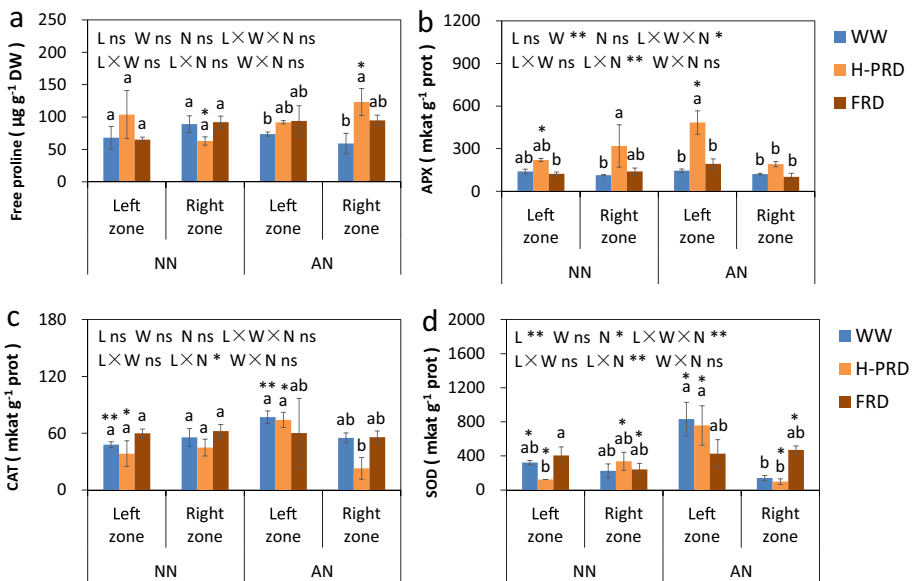


78.86% and 88.44% higher than that in AN treatment (Fig. 3b and c). In the bottom zone of V-PRD and WW conditions, CAT activity was 79.66% and 41.26% lower in V-PRD and WW of NN treatment than that of AN treatment (Fig. 3c). There were no differences in SOD activity between the two N forms (Fig. 3d).

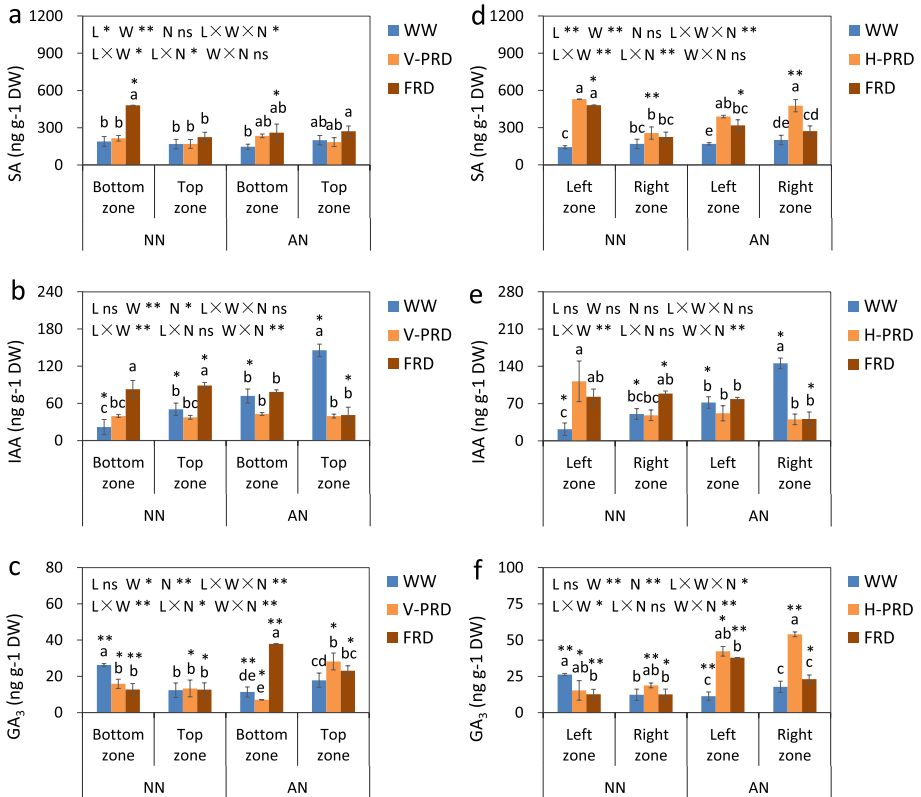
### The level of antioxidants in horizontally partial root-zone as affected by N forms

In AN treatment, the level of free proline was 108.48% higher in the right zone (drought zone) of H-PRD than that of WW, while this pattern was absent in NN treatment (Fig. 4a). APX activity was 182.36% larger in the right zone of H-PRD than that of WW in NN treatment (Fig. 4b). In AN treatment, APX activity was 87.37% and 58.19% larger in the left zone of H-PRD than that of FRD and WW conditions in AN treatment (Fig. 4b). SOD activity was 230.55% larger in the left zone of FRD than that of H-PRD in NN treatment (Fig. 4d). In AN treatment, SOD activity was 671.73% larger in the left zone of H-PRD and 494.63% larger in WW than that in the right zone (Fig. 4d).

In the right zone of H-PRD condition, free proline content was 48.88% lower in NN treatment than that in AN treatment (Fig. 4a). In the left zone of H-PRD condition, the activity of APX (54.44%), CAT (48.11%) and SOD (83.78%) were lower in NN treatment than that in AN treatment (Fig. 4b, c and d). In the right zone of H-PRD, SOD activity was



**Fig. 4** Contents of free proline (a), APX (b), CAT (c), SOD (d) activity in roots of *C. bungei* seedlings under different water conditions and nitrogen forms. WW, well-watered condition; H-PRD, horizontally partial root-zone drought condition (45 ± 5% field capacity in the right zone, and 70 ± 5% field capacity in the left zone); FRD, full root-zone drought condition (45 ± 5% field capacity in whole soil profile). NN, nitrate nitrate (NO<sub>3</sub><sup>-</sup>); AN, ammonium (NH<sub>4</sub><sup>+</sup>). The bars indicates mean ± SE (n=4). *P*-values obtained from the three-way ANOVAs on nitrogen forms (N), water treatments (W), root-zone locations (L) and their interactions (N × W, N × L, W × L, N × W × L) are labelled as: \**P* < 0.05; \*\**P* < 0.01; ns, not significant. The results of multiple mean comparisons between the six columns (combinations of three water treatments and two root zones) within each N treatment were indicated by letters around error bars, and bars with different letters indicate significant differences (*P* < 0.05)



**Fig. 5** Content of SA (a, d), IAA (b, e), GA (c, f) of *C. bungei* roots under different water and nitrogen forms. WW, well-watered condition; V-PRD, vertically partial root-zone drought condition ( $45 \pm 5\%$  field capacity in the top zone, and  $70 \pm 5\%$  field capacity in the bottom zone); H-PRD, horizontally partial root-zone drought condition ( $45 \pm 5\%$  field capacity in the right zone, and  $70 \pm 5\%$  field capacity in the left zone); FRD, full root-zone drought condition ( $45 \pm 5\%$  field capacity in whole soil profile). NN, nitrate nitrate ( $\text{NO}_3^-$ ); AN, ammonium ( $\text{NH}_4^+$ ). SA, salicylic acid. IAA, indole acetic acid.  $\text{GA}_3$ , gibberellic acid. The bars indicates mean  $\pm$  SE ( $n=4$ ). *P*-values obtained from the three-way ANOVAs on nitrogen (N), water treatments (W), root-zone locations (L) and their interactions ( $N \times W$ ,  $N \times L$ ,  $W \times L$ ,  $N \times W \times L$ ) are labelled as: \* $P < 0.05$ ; \*\* $P < 0.01$ ; ns, not significant. The results of multiple mean comparisons between the six columns (combinations of three water treatments and two root zones) within each N treatment were indicated by letters around error bars, and bars with different letters indicate significant differences ( $P < 0.05$ )

243.60% larger in NN treatment than that in AN treatment (Fig. 4d). In the left zone WW condition, CAT (37.87%) and SOD (61.35%) activity were lower in NN treatment than that in AN treatment (Fig. 4c and d).

### The level of phytohormones in vertically partial root-zone as affected by N forms

In NN treatment, SA (153.66%) and IAA (279.70%) in the bottom root zone was higher in FRD than that in WW condition (Fig. 5a and b), IAA content in the top root zone was 75.76% higher in FRD than that in WW, while  $\text{GA}_3$  content in the bottom root zone was 39.43% lower in V-PRD and 51.56% lower in FRD than that in WW (Fig. 5c). In AN

treatment, IAA level in the top root zone was 72.85% lower in V-PRD and 71.73% lower in FRD than that in WW (Fig. 5b).  $GA_3$  level in the top root zone was 58.40% higher in V-PRD than that in WW (Fig. 5c), while  $GA_3$  in the bottom root zone was 232.69% and 433.25% higher in FRD than that in WW and V-PRD (Fig. 5c).

In the bottom zone of FRD condition, SA level was 84.33% higher in NN treatment than that in AN treatment (Fig. 5a). In both root zones of WW condition, IAA level was 69.71% lower in the bottom zone and 65.32% lower in the top zone of NN treatment than that of AN treatment, while IAA in the top zone of FRD condition was 115.63% higher in NN than that in AN (Fig. 5b). In the top zone of V-PRD and FRD,  $GA_3$  was 52.78% lower in V-PRD and 45.22% lower in FRD of NN treatment than that of AN treatment (Fig. 5c). In the bottom zone of V-PRD and WW conditions,  $GA_3$  was 130.59% and 123.88% higher in NN than that in AN treatment, respectively.

### The level of phytohormones in horizontally partial root-zone as affected by N forms

In NN treatment, SA (270.88%) and IAA (412.92%) level in the left root zone (moist zone) were higher in H-PRD than those in WW. SA (237.10) and IAA (279.70%) level in the left root zone were also higher in FRD than that in WW (Fig. 5d and e).  $GA_3$  level in the left root zone of was 51.56% lower in FRD than that in WW (Fig. 5f). In AN treatment, SA level in the right zone (drought zone) was 137.95% and 75.23% higher in H-PRD than that in WW and FRD, while SA in the left zone was 130.16% higher in H-PRD and 87.95% higher in FRD than that in WW (Fig. 5d). In AN treatment, IAA in the right zone of WW was 260.50% and 253.70% higher than H-PRD and FRD (Fig. 5e).  $GA_3$  level was 271.88% higher in the left zone of H-PRD and 232.69% higher in FRD than that in WW, while  $GA_3$  in the right zone of H-PRD was 203.50% higher in WW and 134.28% higher in FRD treatment (Fig. 5f).

In the right zone of H-PRD, SA (86.07%) and  $GA_3$  (187.49%) level was higher in AN treatment than that in NN treatment (Fig. 5d and f). In the left zone of H-PRD, SA was 35.78% higher in NN treatment (Fig. 5d). In the right zone of WW, IAA was 65.32% lower in NN treatment (Fig. 5e). In the left zone of H-PRD and FRD,  $GA_3$  was 63.72% lower in H-PRD and 66.43% lower in FRD NN treatment than that in AN treatment (Fig. 5f).

### Principle component analysis (PCA) of root physiological parameters on the combination of drought and N forms

To test if the composition of root physiological parameters differed between water treatments and between N forms, PCA were performed based on free proline, antioxidant enzymes and phytohormones (Fig. 6). PC1 and PC2 accounted for 26.06% and 18.32% of the total variation, respectively (Fig. 6a). The samples under two N form treatments were nearly separated into two clusters. Further analysis showed that CAT, APX, SOD and IAA of bottom zone, APX and  $GA_3$  of top zone under V-PRD had the greatest influence on the clustering of the two N forms (Table S1). Moreover, the samples of V-PRD and WW were completely separated into two parts under both NN and AN treatments (Fig. 6a).

PC1 and PC2 accounted for 33.29% and 18.12% of the total variation, respectively (Fig. 6b). Free proline, CAT, SOD, SA and  $GA_3$  of right zone, APX, SOD and SA of left zone under H-PRD are the main contributors on the clustering of two N forms (Table S<sub>2</sub>). Interestingly, when left and right zones were considered, NN and AN did not form

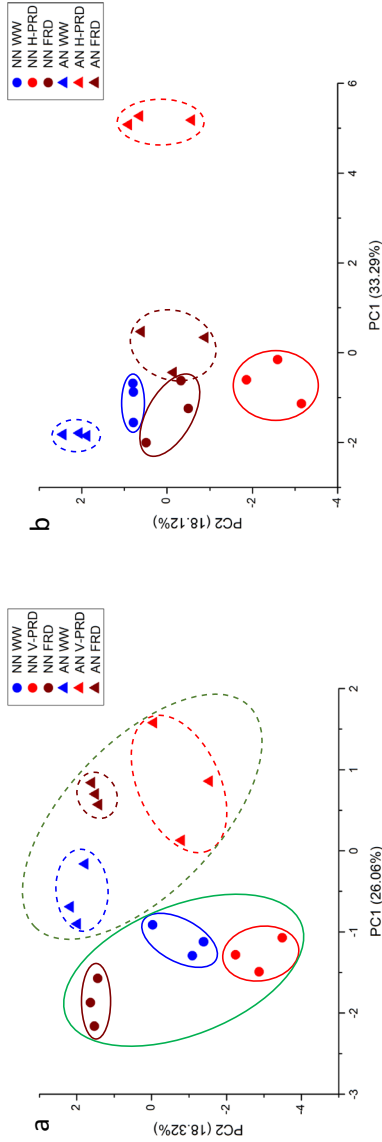
individual clusters if the root physiological parameters were studied. Under both NN and AN treatments, samples of WW, H-PRD and FRD were separated into individual clusters except between NN FRD and AN FRD.

## Discussion

### Root morphological plasticity under PRDs and FRD as affected by N forms

The present study demonstrated that the influence of soil water on root development was related to both of drought types and N forms. As compared with WW condition, root length increased in the top zone of FRD in NN treatment but it decreased in the bottom zone of FRD in AN treatment, indicating that nitrate nitrogen (NN) was more beneficial than ammonium nitrogen (AN) for root elongation under FRD. It was reported that ammonium promotes lateral root initiation and root branching but hardly stimulates lateral root elongation, whereas the elongation of lateral roots is stimulated mainly by nitrate (Remans et al. 2006; Lima et al. 2010; Ravazzolo et al. 2020). Although some woody plants prefer ammonium to nitrate N sources due to the energy-consuming processes of  $\text{NO}_3^-$  reduction (Luo et al. 2009). However, ammonium may cause toxicity to root due to the excessive accumulation of extracellular  $\text{H}^+$  that damages cell membranes and cell walls (Ravazzolo et al. 2020). This may partially explain the preference of nitrate nitrogen (NN) for root elongation under FRD in the present study.

It was reported that V-PRD and H-PRD both inhibited above-ground growth of *C. bungei* in a less extent than that of FRD (Wang et al. 2021). In the present study, root parameters including root length, fine root length and root tip numbers all were inhibited by FRD but unaltered by V-PRD and H-PRD. Plants have to forage soil for water and nutrients via morphological and physiological plasticity, as the spatial distribution of these resources is often patchy and dynamic (Paz et al. 2015; Cantó et al. 2020). We observed root morphological plasticity under V-PRD and H-PRD conditions, the patterns of which were related to both of N forms and drought types. Under V-PRD, morphological plasticity was presented in the form of hydrotropism, which was indicated by the dominant root proliferation in the bottom root zone (moist zone). Hydrotropism allows roots to grow actively towards water sources that are heterogeneously located in any direction, and subsequently increase the acquirement of water sources (Nakajima et al. 2017; Dietrich 2018). Root system respond to moisture gradient via lateral root initiation and/or root elongation, the patterns of which may differ between species (Miyazawa et al. 2008; Dietrich et al. 2017; Nakajima et al. 2017). The present results demonstrated that the patterns of hydrotropism differ between N forms. Both initiation and elongation of lateral roots were involved in the hydrotropism response in NN treatment, since root length, fine root length and root tip number all were dominant in the moist zone. In contrast, only root elongation participated in hydrotropism response in AN treatment as fine root length was dominant in the moist root zone. This result can be partially explained as, ammonium led to excess iron accumulation in the apoplast of phloem as compared with nitrate, which lead to massive callose deposition in the phloem and thus attenuates primary root initiation from phloem (Liu et al. 2022). Additionally, ammonium in most soils is highly adsorbed to the negatively charged residues of the soil matrix and is less soluble compared to nitrate, so the diffusion distances from the lateral roots to ammonium sources were limited (Miller et al. 2007; Lima et al. 2010). In contrast, nitrate has strong mobility so it can be efficiently transported and



**Fig. 6** PCA of physiological indicators in roots of *C. bungei* under combined conditions of N forms and water conditions. The results of V-PRD (a) and H-PRD (b) are analyzed separately. WW, well-watered condition; V-PRD, vertically partial root-zone drought condition; H-PRD, horizontally partial root-zone drought condition; FRD, full root-zone drought condition. NN, nitrate nitrogen; AN, ammonium nitrogen

exploited by lateral roots at different distances (Miller et al. 2007; Ravazzolo et al. 2020). These results were consistent with our initial hypothesis that nitrogen forms may influence morphological and physiological plasticity of *C. bungei* roots under differential root-zone drought.

In comparison with V-PRD, root hydrotropism was not presented in H-PRD treatment. Interestingly, vigorous root elongation in the drought soil zone was observed in AN treatment, as indicated by greater FRL in the drought soil zone (right side) than that in the moist soil zone (left side). These results indicated that the roots of *C. bungei* exhibited contrasting strategy for water foraging when PRDs occurred in vertical/horizontal orientation. Since fine roots are crucial for plants to absorb water, the obvious proliferation of fine roots in drought zone may help the root system to absorb the limited water in drought zone. In contrast, the active hydrotropism under V-PRD condition promoted the total water absorption and thus contributed to the efficient carbohydrate production and dominant xylem development under V-PRD condition as observed in our previous investigation (Wang et al. 2021). It was reported that gravity plays a critical role in root hydrotropism (Li et al. 2020). When the heterogeneous distribution of water is in the oblique orientation to the gravity vector, the gravitropism action may inhibit root hydrotropism and the acquisition of heterogeneous water (Morohashi et al. 2017; Li et al. 2020). In contrast, when the orientation of heterogeneous water distribution is parallel to the gravity vector, the gravitropism action promotes root growth in a straight downward direction and thus facilitates root hydrotropism in the vertical direction (Morohashi et al. 2017; Li et al. 2020). Taken together with the present results, we propose that the gravitropism action impedes hydrotropism in the horizontal direction under H-PRD condition while it promotes hydrotropism in the vertical direction under V-PRD condition.

### Root drought physiology under PRDs and FRD as affected by N forms

Root system usually respond to drought stress via producing free proline and antioxidant enzymes (Albert et al. 2012; Cao et al. 2014; Song et al. 2019). SOD formed the primary enzymatic pathway of scavenging ROS via catalyzing the dismutation of superoxide radicals ( $O_2^{\cdot-}$ ) to oxygen ( $O_2$ ) and hydrogen peroxide ( $H_2O_2$ ) (Sarma and Saikia 2014). APX and CAT were responsible for the elimination of  $H_2O_2$  (Kaushik and Aryadeep 2014). The present study showed that diverse antioxidant enzymes were induced by different types of drought conditions. CAT contributed to antioxidant defense under FRD, while APX, SOD and CAT were activated by V-PRD, and APX and free proline were induced by H-PRD. Interestingly, APX was induced by H-PRD and V-PRD but not by FRD, indicating that APX played a critical role in antioxidant defense under partial root-zone drought but not full root-zone drought.

In NN treatment, APX, CAT and SOD activity all elevated in drought root zone (top zone) but not in moist root zone of V-PRD. Similarly, APX activity elevated in drought root zone (right zone) but not in moist root zone of H-PRD. Therefore, physiological plasticity, i.e. the local inducement of antioxidant defense in drought root zone, may be critical for drought acclimation of root systems under partial root-zone drought. Moreover, we found that physiological plasticity was related to N forms, as these specific inducements of antioxidants in drought root zone was observed in NN but not in AN treatment. It was demonstrated that the production of various metabolites is affected by N forms (Guo et al. 2005; Escobar et al. 2010). Root system plasticity is regulated by  $NO_3^-$  via a tight interplay with auxin (Müller 2020; Song et al. 2020; Xu et al. 2020). Further analysis is still needed to address the mechanistic connection of nitrate and root physiological plasticity under drought stress.

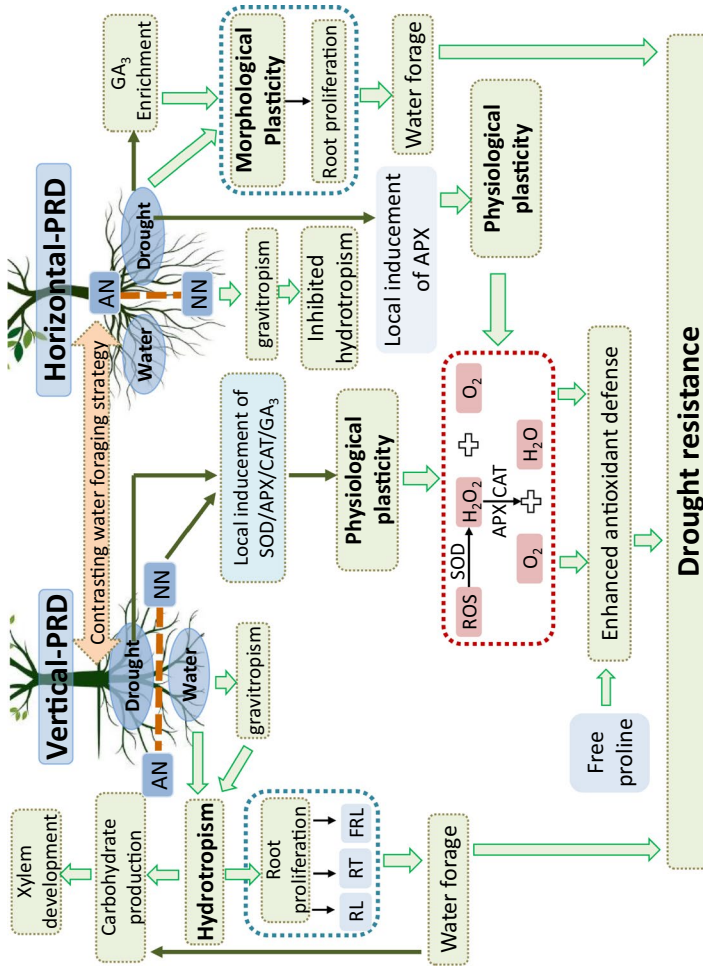
Various phytohormones interactively modulate morphological and physiological response of plants to drought stress, which reduce adverse effect caused by stress (Roychoudhury and Aftab 2021). Our previous study found that the N-stimulated ABA production under H-PRD may negatively impact photosynthesis efficiency and thus lead to a lower  $WUE_i$  and less active xylem development under H-PRD condition. In contrast, only IAA was up-regulated by N application under V-PRD (Wang et al. 2021). In the AN treatment of the present study, SA and  $GA_3$  signals were synchronously induced in the drought root zone in H-PRD, while the inducement was present in a lower extent in the moist root zone. This pattern is another evidence for physiological plasticity under PRDs. SA enhance drought tolerance via triggering antioxidant defenses and relieving oxidative damage (Horváth et al. 2007), while GA regulates both cell division in the meristematic zone and cell elongation in the elongation zone of root (Rizza et al. 2021), and B-type gibberellin (GA) receptor  $GID1s$  participated in root elongation under stress (Hideki et al. 2018). In the present study, the specific inducement of SA in drought root zone lead to physiological plasticity and enhanced drought tolerance of roots together with free proline. Synchronously,  $GA_3$  was also induced in drought root zone, which lead to root morphological plasticity and resulted in greater FRL in the drought soil zone. Interestingly, these patterns were present in AN but not in NN treatment. Further analysis at physiological and molecular levels are needed to elucidate the mechanisms underlying the roles of N forms in cross-talk between phytohormones.

IAA is critical for cell growth and adventitious roots formation (Zhao et al. 2012; Cheng et al. 2020). In response to drought stress, IAA act as a regulator contributes to root development and shows crucial roles in water transport (Cheng et al. 2020; Demirkol et al. 2021). Moreover, IAA synthesis should be in a dynamic balance level with plant growth under drought stress (Pustovoitova et al. 2003; Lecube et al. 2014). In NN treatment of the present study, IAA level in both of the bottom and the top root zone increased upon FRD, while this pattern was not observed in AN treatment. The nitrate-dependent inducement of IAA production should have contributed to the larger root length in the top root zone of FRD as compared with WW and V-PRD. It was reported that a partner protein for high-affinity nitrate transport, *OsNAR2.2* was involved in the root growth in a nitrate-dependent manner in rice, which was closely associated with auxin (Xu et al. 2020; Song et al. 2020). The involvement of high-affinity nitrate transport in nitrate-dependent IAA inducement and root development under drought condition should be addressed in the future investigation.

## Conclusion

The schematic model of root morphological plasticity and physiological responses of *C.bungei* under PRDs as affected by N forms were displayed (Fig. 7). Root system exhibited contrasting strategy for water foraging when PRDs occurred in vertical/horizontal orientation. Under V-PRD condition, root forage for water via hydrotropism in vertical direction, which benefited water absorption and contributed to the dominant xylem development. Under H-PRD, root forage for water by vigorous root proliferation in the drought soil zone. Physiological plasticity, as indicated by the local inducement of antioxidants production in the drought root-zone, contributed to drought acclimation under both V-PRD and H-PRD. Both of the lateral root initiation and elongation were involved in the hydrotropism response in NN treatment, while only root elongation was involved in AN





**Fig. 7** The schematic model of root morphological plasticity and physiological responses of *C. bungei* under PRDs and FRD as affected by N forms. The roots of *C. bungei* exhibited contrasting strategy for water foraging when PRDs occurred in vertical/horizontal orientation. Under V-PRD condition, root forage for water via hydrotropism in vertical direction, which contributed to the efficient carbohydrate production and dominant xylem development. Under H-PRD, root forage for water by vigorous root proliferation in the drought soil zone. The local enrichment of GA<sub>3</sub> contributed to root morphological plasticity and lead to root proliferation in the drought soil zone of H-PRD. Gravitropism action impeded hydrotropism in the horizontal direction under H-PRD condition, while it promoted hydrotropism in the vertical direction under V-PRD condition. Physiological plasticity, which was indicated by the local induction of antioxidants production in the drought root-zone, contributed to drought acclimation of root systems under both V-PRD and H-PRD

treatment, indicating that the patterns of hydrotropism differ between N forms. The specific inducements of antioxidants in drought root zone was observed in NN but not in AN treatment. The specific inducement of SA enhanced drought tolerance together with free proline, while the specific inducement of GA<sub>3</sub> in drought zoot zone contributed to root morphological plasticity. Interestingly, these patterns were present in AN but not in NN treatment, supporting our initial assumption that N forms may influence morphological and physiological plasticity of *C. bungei* roots under differential root-zone drought.

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## Authors and Affiliations

Tiantian Sun<sup>1,2</sup> · Ruohan Ren<sup>1</sup> · Mingming Xing<sup>1</sup> · Qixiao Duan<sup>1</sup> · Lang Zhao<sup>1</sup> · Wenwen Yan<sup>1</sup> · Yang Fang<sup>1</sup> · Senyan Zhang<sup>1</sup> · Hao Dong<sup>1</sup> · Mengran Wang<sup>1</sup> · Qimeng Heng<sup>1</sup> · Wenyi Chen<sup>1</sup> · Ting Xu<sup>1</sup> · Lili Kou<sup>1</sup> · Kunpeng Li<sup>1</sup> · Junhui Wang<sup>3</sup> · Wenjun Ma<sup>3</sup> · Wangxiang Zhang<sup>2</sup> · Yinglong Chen<sup>4</sup> · Yizeng Lu<sup>5</sup> · Yi Zhang<sup>1</sup> 

✉ Junhui Wang  
wangjh808@sina.com

✉ Wangxiang Zhang  
malus2011@163.com

✉ Yi Zhang  
zhangyi.1978@163.com

<sup>1</sup> Key Laboratory of Silviculture On the Loess Plateau State Forestry Administration, College of Forestry, Northwest A&F University, Yangling, Shaanxi 712100, People's Republic of China

<sup>2</sup> College of Forestry, Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing 210037, People's Republic of China

<sup>3</sup> Key Laboratory of Tree Genetics and Breeding, Key Laboratory of Tree Breeding and Cultivation of State Forestry Administration, Beijing 100091, People's Republic of China

<sup>4</sup> The UWA Institute of Agriculture, The University of Western Australia, Perth, WA 6001, Australia

<sup>5</sup> Shandong Provincial Center of Forest and Grass Germplasm Resources, Jinan 250102, People's Republic of China