

# Growth and changes of endogenous hormones of mulberry roots in a simulated rocky desertification area

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**Abstract** We studied the growth of roots of white mulberry (*Morus alba*) trees in response to different water and nutrient conditions in sets of three or five containers connected via small pipes and arranged so as to simulate the heterogeneous soil conditions associated with rocky desertification. The experiment was conducted to improve understanding of the adaptation of *M. alba* to this stressful environment. The trees were grown for a year under constant water and nutrient conditions in the soils within each container of any set of containers. Differences in root activity and endogenous hormones within root tips were measured at the end of the experiment. We compared four treatment groups: H (variable moisture among containers), F (variable nutrients among containers), HF (both moisture and nutrients varied among containers), and CK (non-varied control). Results showed the following: (1) Mulberry roots showed obvious hydrotropic and chemotropic growth patterns, but chemotropism did not occur in the condition of water shortage. (2) Measurement of growth indices (root surface area, total root length, number of root tips, root biomass) showed that growth status was best in group HF once the roots were able to access containers with

sufficient water and nutrients, followed by group H. The indices were significantly poorer in groups F and CK. (3) The content of auxin, cytokinin, and gibberellins in roots under soil drought conditions were lower than under wetter soil conditions. In contrast, abscisic acid content and root activity were higher under soil drought conditions than under wetter soil conditions. The results indicated that water is the key factor restricting growth of white mulberry trees in areas of rocky desertification but that the trees adjust endogenous hormones in their roots to promote tropic growth and obtain sufficient moisture and nutrients over the long term. Moreover, under long-term drought stress conditions, mulberry trees retained high root activity which appears to be adaptive in that all of the trees survived.

**Keywords** Rocky desertification · *Morus alba* · Hydrotropism · Chemotropism · Endogenous hormone

## Introduction

In areas of rocky desertification, bedrock is exposed at the surface, often with pockets of soil available for limited plant growth. In southwest China, these desertified areas have generally resulted from unsustainable human practices such as farming on slopes having insufficient soil cover (Wang et al. 2004). The total area of rocky desertification in the southwestern region is at least 13,000 km<sup>2</sup>, lying mostly, though not exclusively, within karst landforms (Wang et al. 2004; Ju and Dai 2005; Liu et al. 2008a). This rocky desertification has had severe effects on many local farming economies, and the problem is increasing in some regions due to additional unsuitable land having been brought into production (Wang et al. 2004; Ju and Dai 2005; Liu et al. 2008a). The need to restore ecological functions and services to these damaged

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areas is widely recognized (Tuyet 2001; Zhao et al. 2006; Du et al. 2014), as is selecting appropriate plant species for these purposes (Zhang et al. 2011; Shen 2001).

In recent years, interest has developed in the potential of mulberry (*Morus alba* L.) trees for ecological restoration in light of their adaptability to harsh natural environments, including tolerance of both drought and flooding (Liu and Willison 2013). Mulberry trees have been cultivated for thousands of years in China for many purposes including silk production, livestock forage, traditional medicines, and fruit (Huang et al. 2013; Liu and Willison 2013). For this reason, Chinese farmers readily adopt the species for agricultural use, which provides the potential for facilitating the restoration of ecological functions in areas of rocky desertification (Qin et al. 2010).

In karst landforms, many fissures exist in the bedrock due to its dissolution. Soil and water permeate through these fissures, providing opportunities for deep-rooted species to exploit these heterogeneous sites, but drought in surficial soil layers is a limiting factor for establishment of woody vegetation (Du et al. 2014; Jiang et al. 2014; Bakalowicz 2005; Nobel et al. 1992). Zhu and Yang (1987) examined the adaptation strategies of trees growing in water stressed karst areas in southwest China, and they found that the trees had large root systems that included many roots which grew into fissures in the bedrock where water and nutrients are available. The drought resistance of *M. alba* arises in part from its large root system which extends well beyond its canopy (Huang et al. 2013; Liu and Willison 2013; He et al. 2007; Chen et al. 2005). In heterogeneous habitats, plant roots have the capacity to grow spontaneously towards places having adequate moisture and nutrients, exhibiting the hydrotropism and chemotropism by which plants adapt to arid soil environments via root growth (Newcombe and Rhodes 1904; Jaffe et al. 1985; Takahashi 1997; Zhang et al. 2009; Farooq et al. 2009).

In recent years, there has been growing understanding of the inheritance and regulation of plant drought resistance (Bartels and Sunkar 2005) and specifically the roles played by endogenous hormones (Lenoble et al. 2004; Reynolds et al. 2005; Bartels and Sunkar 2005). Several endogenous hormones are involved and their interactions are complex. Endogenous hormones control the tropic movement of plants, as exemplified by the role of auxin (IAA) in phototropism and gravitropism (Blakeslee et al. 2007; Firm et al. 2000). In the case of the unusual gravitropic response of the elongating peanut gynophore, IAA, gibberellins (GA), and cytokinins (CTK) interact (Shushu and Cutter 1990; Moctezuma 1999). Abscisic acid (ABA) appears to adjust the transportation of IAA in hydrotropic root growth (Eapen et al. 2005). Root growth plays a critical role in the adaptation of plants to dry habitats (Ehlers et al. 1991; Jaffe et al. 1985), but the hydrotropic and chemotropic responses of roots are not yet fully understood (Eapen et al. 2005; Cassab et al. 2013).

For the reasons outlined above, we simulated soil and moisture conditions of heterogeneous habitats in rocky desertified areas and examined the growth of *M. alba* roots, as well as their associated endogenous hormones, in order to improve understanding of the adaptability of *M. alba* to drought in the context of efforts to counteract rocky desertification.

## Methods and materials

### Experimental materials and experimental design

The experiment was initiated on September 1, 2012, in a greenhouse at Southwest University, Chongqing, China. The mean annual temperature in the greenhouse was 21 °C (maximum 41 °C, minimum 6 °C), annual sunshine duration was 1400 h (in Chongqing, the sun is often obscured by cloud and fog), and no artificial light was used. Experiments were conducted using greenhouse-raised seedlings of the Guisangyuo 12 variety of white mulberry, *M. alba* L., each about 25 cm high and 3 mm stem diameter at base. Soil for the experiment was obtained from an area of rocky desertification in Beibei, Chongqing, and its nutrient condition is shown in Table 1. Open-topped styrofoam containers sized 30 cm×30 cm×30 cm were used for growing plants. To simulate fissures in karst bedrock, containers were connected together by drilling six holes (12 mm aperture) in the lower part of one or more sides of each container and soil-filled PVC pipes (5 cm length, 12 mm diameter) were inserted through adjacent holes to create connections from one container to the next in groups of three or five containers (Fig. 1). Each container was filled with 8 kg of well-mixed soil. There were four treatment groups: H (variable moisture), F (variable nutrients), HF (both moisture and nutrients varied), and CK (non-varied control). These were designed to simulate the heterogeneous soil conditions associated with rocky desertification, as detailed in Fig. 1. Each treatment group contained 10 replicates. We measured soil moisture in each container daily using an MP-406 analyzer (Nantong Inc. Jiangsu, China) and watered daily in order to control soil moisture in each container according to the experimental design (see Fig. 1 for details). Some containers within groups F and HF were irrigated with Hoagland's nutrient solution at three times during the experiment (November 1, 2012, March 1, 2013, and June 1, 2013) as detailed in Fig. 1. The nutrient solution was added to the soil evenly and periodically during each 1-day period based on the soil moisture content at the time, so that soil moisture content continued to meet the experimental design. After 1 year of treatment on September 1 and 2, 2013, we chose five plants randomly

**Table 1** Initial nutrient contents of the experimental soils

pH	Organic matter (g kg <sup>-1</sup> )	Alkali-hydrolysable N (mg kg <sup>-1</sup> )	Available P (mg kg <sup>-1</sup> )	Available K (mg kg <sup>-1</sup> )	Total N (g kg <sup>-1</sup> )	Total P (g kg <sup>-1</sup> )	Total K (g kg <sup>-1</sup> )
6.2	36.43	49.52	12.06	82.87	1.03	0.93	12.54

from each treatment and measured relevant indices as described below.

**Measurements**

*Root system growth*

Root morphology indices (root surface area, total root length, and number of root tips) were determined from scanned images using the WinRHIZO root analysis system (Regent Instruments, Quebec, Canada). After photography, roots were dried in an oven at 80 °C to constant weight and weighed with an analytical balance to determine biomass.

*Root activity*

The TTC (2,3,5-triphenyltetrazolium chloride) reduction method was used to determine root metabolic activity as described by Xiao and Wang (2005). Fresh non-woody root ends (excised to about 5 cm from the root tip) obtained from each container were bulked together and weighed. The material was then put into the TTC and phosphate buffer mixed solution and after 1 h of reaction were removed and ground with ethyl acetate to extract TPF (triphenyl formazan, the reduction product of TTC). Colorimetric absorbance was measured at 485 nm wavelength with a Shimadzu spectrophotometer. A blank reference test that was conducted at the same time as the test of the experimental material and TTC reducing capacity (root activity) was obtained from the standard curve.

*Endogenous hormones of roots*

Detection of endogenous hormones was conducted using the method of Tong et al. (2009) with some modifications as follows. Non-woody ends of roots were excised to about 5 cm from the root tip. Root samples weighing about 1 g obtained from each container were accurately weighed and ground using a precooled mortar under low light and temperature conditions after addition of sodium diethyldithiocarbamate, quartz sand, and 5 ml of precooled 80 % methanol. The material was then stored in the dark at 4 °C overnight. Using vacuum filtration, the residue was washed three times with precooled 80 % methanol that included a drop of ammonia water. The total liquid was rotary evaporated to aqueous phase at 35 °C. Ten milliliters of double-distilled water was then used to wash the remnants. After three freeze-thaw cycles,

precipitations were removed by centrifugation (15,000×g, 5 min) and phenolic compounds were removed using a poly-vinyl pyrrolidone (PVP) column, eluted with double-distilled water. The solution was passed through a SepPak C18 cartridge (Waters, Milford, MA, USA), washed with 10 ml of water to collect CTK, passed through an acid SepPak C18 cartridge (balanced with 0.1 mM acetic acid), and washed with 10 ml of 0.1 mM acetic acid to collect GA, IAA, and ABA. These hormones were recovered by eluting with 10 ml of 60 % methanol and rotary evaporated to dryness. Following this, CTK was re-dissolved in 0.4 ml of 3 % acetonitrile/double-distilled water (pH=7.0). GA, IAA, and ABA were re-dissolved in 0.4 ml of 3 % acetonitrile (3 %)/acetic acid (0.1 mol l<sup>-1</sup>). Finally, samples were filtered through a 0.45-µm pore-size membrane filter and hormones were detected using an Agilent 1100 (Santa Clara, CA, USA) high-performance liquid chromatographic system (HPLC). IAA, GA, and ABA were detected at 210 nm wavelength, and CTK was detected at 265 nm wavelength. Sample size was 20 µl. The mobile phase consisted of three solvents (methanol, acetonitrile, phosphate buffer solution in the ratio 15:20:65). The column temperature was 35 °C, and the flow rate was 10 ml min<sup>-1</sup>.

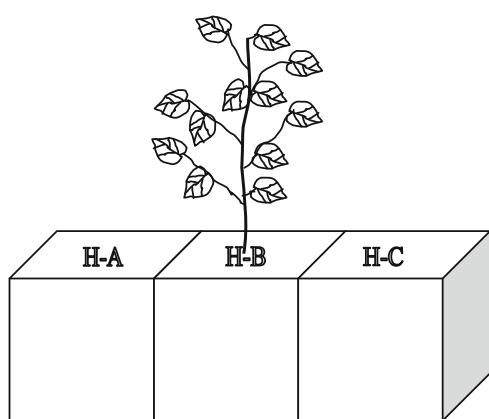
*Data processing*

Data were compiled and analyzed in Microsoft Excel. Two-way ANOVAs were conducted using SPSS 13.0 to test the significance of differences between the treatments in each group. Diagrams were created with OriginPro 7.5 (OriginLab Corp, Northampton, MA, USA).

**Results and analysis**

**Root growth and morphology**

The responses of mulberry roots to the various treatments are detailed in Table 2 and illustrated photographically by typical examples in Fig. 2. In group CK, under moderate drought stress condition for a year (having relative soil moisture held constant at 40–50 %), roots did not grow into or towards the adjoining containers having similar soil conditions. In group F, the soil moisture conditions of the three linked containers were like those in the control (CK), namely moderate drought, but the soil fertility differed among the containers. A mulberry

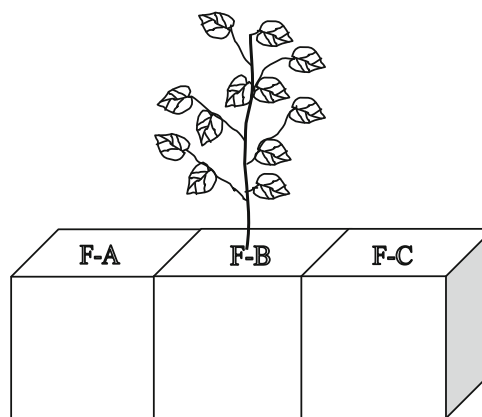


**Group H**

H-A: relative soil moisture held constant at 20-30%

H-B: relative soil moisture held constant at 40-50%

H-C: relative soil moisture held constant at 60-70%

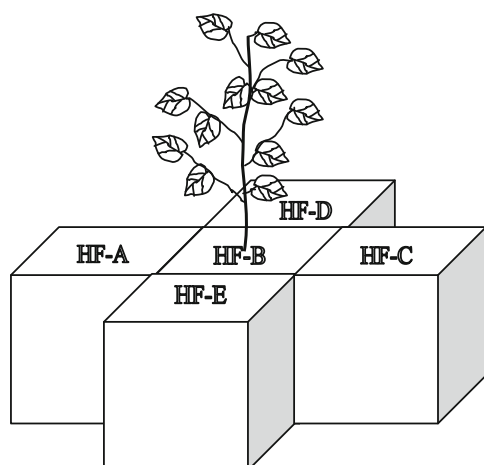


**Group F**

F-A: relative soil moisture held constant at 40-50%

F-B: relative soil moisture held constant at 40-50%, and 100 ml nutrient solution added at 3 scheduled times

F-C: relative soil moisture held constant at 40-50%, and 200 ml nutrient solution added at 3 scheduled times



**Group HF**

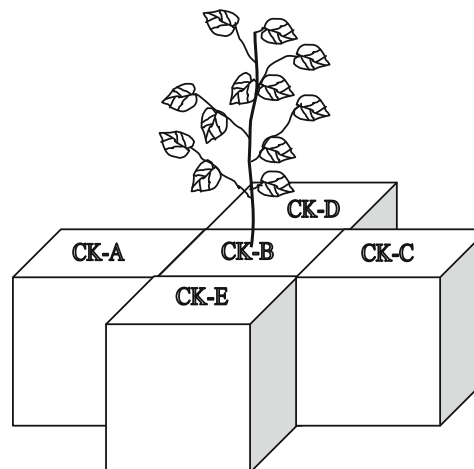
HF-A: relative soil moisture held constant at 60-70%

HF-B: relative soil moisture held constant at 40-50%, and 100 ml nutrient solution added at 3 scheduled times

HF-C: relative soil moisture held constant at 60-70%, and 200 ml nutrient solution added at 3 scheduled times

HF-D: relative soil moisture held constant at 20-30%

HF-E: relative soil moisture held constant at 20-30%, and 200 ml nutrient solution added at 3 scheduled times



**Group CK**

CK-A: relative soil moisture held constant at 40-50%

CK-B: relative soil moisture held constant at 40-50%

CK-C: relative soil moisture held constant at 40-50%

CK-D: relative soil moisture held constant at 40-50%

CK-E: relative soil moisture held constant at 40-50%

**Fig. 1** Schematic diagram of the experimental design. Groups H and F consisted of three containers; groups HF and CK consisted of five containers. Soil-filled PVC tubes (12 mm diameter) provided connections between adjacent containers and stabilized each group. A

mulberry seedling tree was planted in the middle container of each group. The other containers in each group simulated soil lying within cavities associated with rocky desertification

tree was planted in the medium fertility condition of each set, and 1 year later, no roots had grown to the adjacent containers

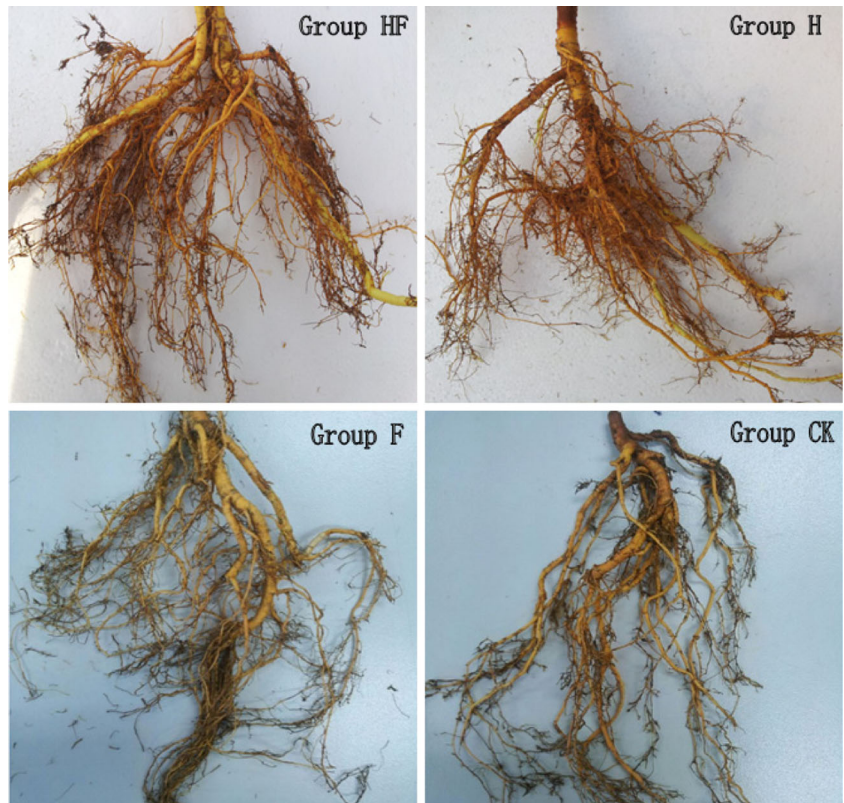
having either high or low fertility conditions. In group H, the soil moisture conditions of the three treatments were normal

**Table 2** Root growth and morphological characteristics in each treatment group (mean ± SE)

Group	Treatment	Root surface area (cm <sup>2</sup> )	Total root length (cm)	Root tips	Root biomass (g)
CK	CK-A	—	—	—	—
	CK-B	263.97 ± 8.24	1716.15 ± 18.54	4577 ± 25.45	3.274 ± 0.44
	CK-C	—	—	—	—
	CK-D	—	—	—	—
	CK-E	—	—	—	—
	Totals	263.97 ± 15.24 A	1716.15 ± 18.54 A	4577 ± 25.45 A	3.274 ± 0.44 A
F	F-A	—	—	—	—
	F-B	332.17 ± 14.45	2220.39 ± 27.63	5133 ± 75.54	4.214 ± 0.61
	F-C	—	—	—	—
	Totals	332.17 ± 14.45 B	2220.39 ± 27.63 B	5133 ± 75.54 B	4.214 ± 0.61 B
H	H-A	—	—	—	—
	H-B	299.28 ± 17.21 a	1729.07 ± 32.59 a	4952 ± 41.47 a	6.108 ± 0.87 a
	H-C	165.09 ± 13.67 b	1036.17 ± 19.68 b	2399 ± 34.94 b	1.964 ± 0.53 b
	Totals	464.37 ± 24.78 C	2765.24 ± 40.34 C	7352 ± 44.52 C	8.072 ± 1.07 C
HF	HF-A	126.68 ± 8.65 a	834.69 ± 13.57 a	2150 ± 26.63 a	1.398 ± 0.47 a
	HF-B	382.77 ± 14.42 b	2093.44 ± 27.80 b	5330 ± 38.22 b	7.809 ± 0.12 b
	HF-C	166.13 ± 11.67 c	1593.29 ± 20.64 c	3212 ± 30.44 c	2.598 ± 0.52 c
	HF-D	—	—	—	—
	HF-E	—	—	—	—
	Totals	675.58 ± 20.08 D	4521.42 ± 32.30 D	10692.87 ± 85.35 D	11.805 ± 1.56 D

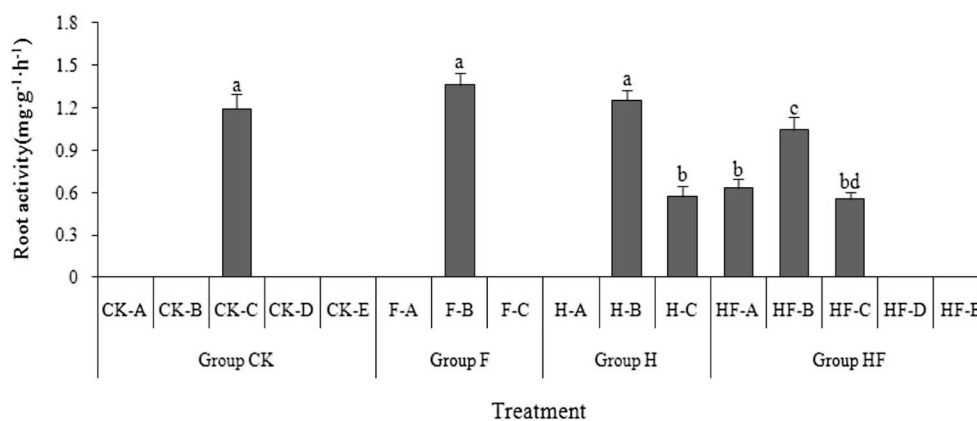
Notes: “—” refers to absence of roots from a container. Different lowercase letters indicate significant differences ( $P < 0.05$ ) between treatments within a group. Different capital letters indicate significant differences ( $P < 0.05$ ) among totals for any variable

**Fig. 2** Typical examples of the morphological characteristics of mulberry roots in each treatment group





**Fig. 3** Root metabolic activity, as measured by the TTC method, in the various treatment groups (mean  $\pm$  SE). Different letters indicate significant differences. Treatment classes without data had no roots



irrigation (having relative soil moisture held constant at 60–70 %), moderate drought (having relative soil moisture held constant at 40–50 %), and severe drought (having relative soil moisture held constant at 20–30 %). A mulberry tree was planted in the medium drought condition of each set of containers, and 1 year later, roots had grown towards and into the container that had been normally irrigated. In group HF, each mulberry tree was planted in the central container in which the soil was maintained with moderate drought and medium fertility and was surrounded by four containers having soil conditions that differed with respect to the availability of both water and nutrients. One year later, the roots had only grown towards two of the four soil conditions, namely normal irrigation combined with relatively high fertility and normal irrigation combined with relatively low fertility. All of the condition indicators of roots in normal irrigation and high fertility soil conditions were significantly higher than those in normal irrigation and low fertility soil conditions ( $P < 0.05$ ).

The following growth indices of the roots were measured in the four treatment groups: root surface area, total root length, number of root tips, and root biomass (Table 2). These indices showed that the growth status of mulberry trees in group HF was most vigorous, followed by those in group H. The indicators were significantly poorer in groups F and CK. As illustrated in Fig. 2, roots of group HF tended to bifurcate with a taproot and lateral roots growing laterally towards the containers having relatively well-irrigated soils of both higher and lower fertility. Roots of group H tended to have obvious directional growth with many lateral roots growing towards the soil container having more abundant water (a hydrotropic response). The morphological characteristics of roots in groups F and CK were similar, generally growing downwards but having neither taproot bifurcation nor laterally oriented growth.

### Root activity

As shown in Fig. 3, the measurement of root metabolic activity revealed differences among the treatments. In four

moderate drought treatments (CK-C, F-B, H-B, and HF-B), the roots demonstrated significantly higher ( $P < 0.05$ ) activity than in three normal irrigation treatments (H-C, HF-A, and HF-C). Root activities in all cases within group HF were significantly lower than those in group CK ( $P < 0.05$ ).

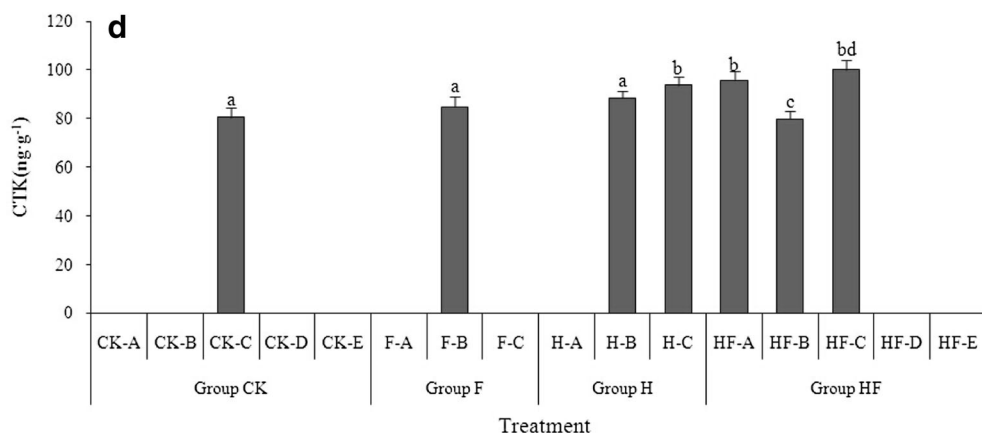
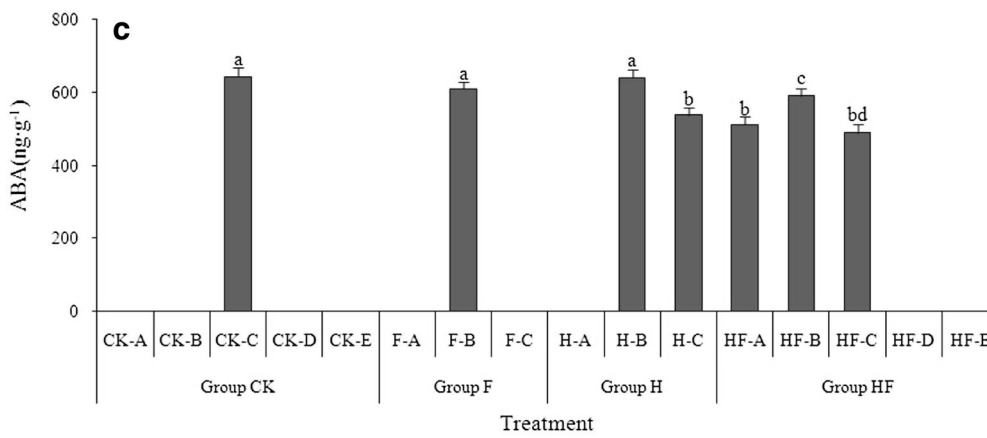
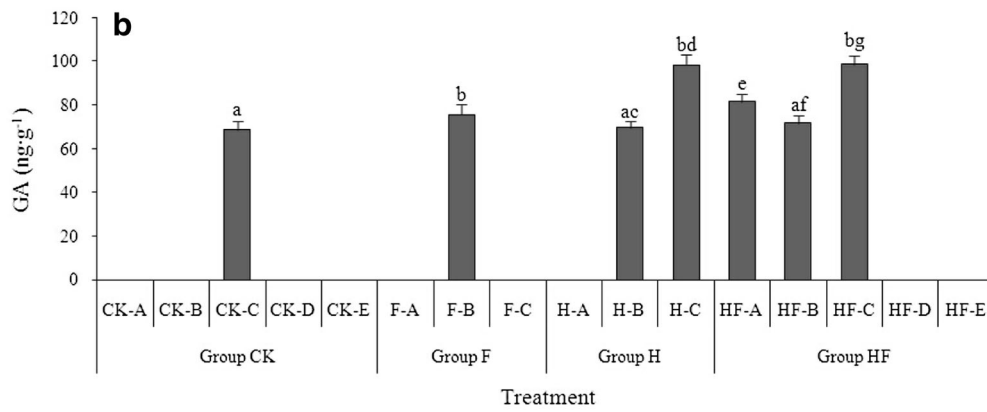
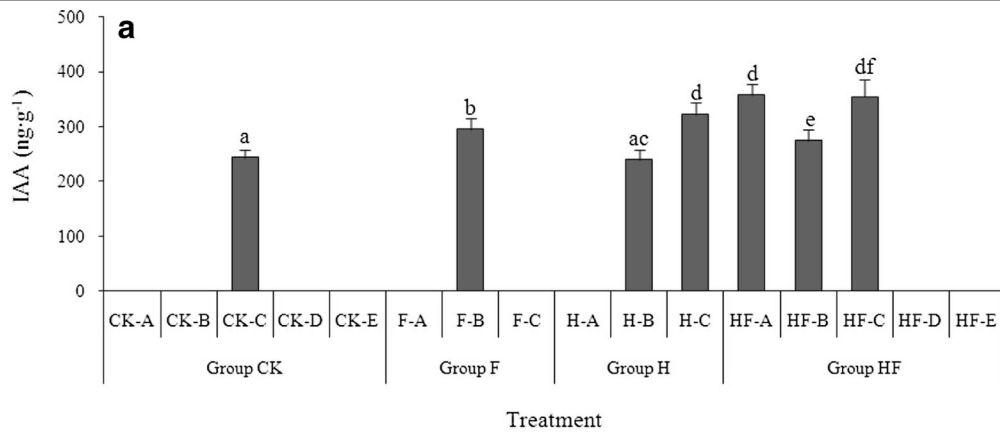
### Endogenous hormones

Figure 4 shows that there were some significant differences in the quantities of phytohormones (IAA, GA, and CTK) extracted from the ends of roots in the various treatments. In the four treatments (CK-C, F-B, H-B, and HF-B) in which the mulberry seedlings were grown in moderate soil drought conditions, IAA, GA, and CTK were all relatively low. However, in all normal irrigation conditions (H-C, HF-A, and HF-C), the content of these three hormones was significantly higher ( $P < 0.05$ ). By contrast, ABA content under drought soil condition was relatively high and significantly lower under normal irrigation ( $P < 0.05$ ). Analysis of correlations (Table 3) revealed that IAA, GA, and CTK were positively correlated with each other, but ABA was negatively correlated with the other hormones. The negative correlation between IAA and ABA was particularly strong ( $P < 0.01$ ).

### Discussion and conclusions

Hydrotropic and chemotropic bending of primary roots of *Lupinus albus* and chemotropic proliferation of young roots of *Raphanus sativus* were reported long ago in experiments conducted in vitro by Newcombe and Rhodes (1904). The physiological mechanisms of plant root tropisms like these have been subjects of intense interest since then, and the hormonal signals originating in the root cap that drive tropic responses are now better understood as a result of carefully

**Fig. 4 a–d** Content of endogenous hormones of root tips in the various treatment groups (mean  $\pm$  SE). Different letters indicate significant differences



**Table 3** Correlation coefficients of four endogenous hormones of mulberry roots

	IAA	GA	CTK	ABA
IAA	1	0.795*	0.815*	-0.964**
GA		1	0.819*	-0.852*
CTK			1	-0.843*
ABA				1

\* $P < 0.05$ ; \*\* $P < 0.01$ 

controlled laboratory experiments on model systems such as seedling roots of *Arabidopsis* (Eapen et al. 2005; Paciorek and Friml 2006; Blakeslee et al. 2007). In the case of hydrotropism, root tips send signals to the plant as a whole in response to changes in the water status of the surrounding soil environment and these signals result in the hydrotropic response (Eapen et al. 2005) and play an important role in the development of the plant root system as a whole (Tsutsumi et al. 2003).

While the fundamental physiological mechanisms of plant tropisms are now better understood, Cassab et al. (2013) noted that little work has been conducted on root tropisms of plants growing in soil in long-term drought-stressed conditions. Even less work has been conducted on drought-hardy perennial woody plants such as *M. alba*. We grew *M. alba* for a year under constant stress and we found that (1) *M. alba* roots showed no tropic movement beyond normal geotropism when there were uniform conditions in the surrounding soil; (2) roots demonstrated no chemotropic responses when the surrounding soil had variable nutrients but were subjected to drought; (3) roots clearly responded in a hydrotropic manner when the soil that surrounded the plant had variable moisture conditions, but similar nutrient conditions; (4) when surrounded by soils with both variable nutrients and variable water, roots grew to soil with sufficient water regardless of its fertility; and (5) when water was sufficient, roots were significantly more abundant in high fertility soil than in low fertility soil. These results show that the roots of mulberry trees are capable of hydrotropic and chemotropic responses when situated in heterogeneous habitats that simulate rocky desertification conditions.

Mineral nutrition is transmitted to, and absorbed by, plants when dissolved in water. Thus, when there is a deficit of soil water, chemotropism is potentially inhibited due to lack of transmission of any chemotropic signal through the soil. This may have contributed to the lack of any visible chemotropic response in group F (variable fertility, moderate drought) in our experiment.

We measured root metabolic activity using the TTC reduction method which mainly indicates succinic dehydrogenase activity associated with respiration (Roberts 1951; Yang and Wang 1989). In some plants, drought stress raises the

respiration rate of roots, but this adaptive response is variable depending on species, stress levels, and other environmental conditions (Farooq et al. 2009). We found that root activity in *M. alba* was significantly higher under soil drought conditions than when water was sufficient. For example, root activities in the control (CK, constant moderate drought) were significantly higher than those in group HF (variable water and nutrients). This suggests that when *M. alba* roots are subjected to drought stress, the plant has the capacity to respond by raising its respiration rate and other relevant physiological activities, thereby improving the capacity of roots to find and absorb water. In group HF, roots which had responded hydrotropically and extended to soil with more water had significantly lower root activity, suggesting that the drought stress had been relieved. These observations contrast with the findings of Liu et al. (2008b) who examined the interaction between short-term drought stress and soil fertility in cotton (*Gossypium hirsutum*) plants growing in pots. They found that root activity declined significantly when water was withheld for 8 days but was enhanced above pre-drought levels following re-watering. This suggests that the adaptive responses of woody plants to short-term drought and long-term drought may be quite different.

Interaction between environmental factors and endogenous hormones of plants affect the growth and development of roots (Casimiro et al. 2003; Lopez-Bucio et al. 2003; Malamy 2005), and endogenous hormones regulate stress adaptation under soil drought conditions (Comstock 2002; Pustovoitova et al. 2004; Lenoble et al. 2004). IAA, GA, and CTK act synergistically to promote cell division and determine the spatial formation of root systems (Binns 1994; Laskowski et al. 1995; Woodward and Bartel 2005; Fukaki and Tasaka 2009). ABA, on the other hand, is antagonistic with the other hormones, tending to inhibit cell division and root formation (De Smet et al. 2006). It plays important roles in drought resistance of plants, such as by promoting dormancy and closing stomata (Xiong and Zhu 2003; Farooq et al. 2009; Bano et al. 2012; Wilkinson et al. 2012). We also found that the content of ABA in mulberry roots was significantly higher under drought conditions and negatively correlated with the other phytohormones, which is consistent with expectations (Wilkinson et al. 2012). It is considered that the antagonistic effect of ABA protects plants by weakening certain metabolic activities and thereby preventing stress-related damage (Farooq et al. 2009; Wilkinson et al. 2012). We found that *M. alba* roots which had extended to soil with sufficient water and nutrients (group HF-C) had significantly lower levels of ABA and significantly higher levels of IAA, GA, and CTK. These roots had lower root activity but grew better (more mass, length, and root tips). Drought stress was relieved in these plants as shown by increased leaf size and stem length (data not shown). We tentatively conclude that the capacity of mulberry roots to synthesize ABA in response to soil drought



signals reduces water loss by adjusting physiological activities in the above-ground parts of the tree while also regulating root growth via control of the growth-promoting hormones (IAA, GA, and CTK) that ultimately permit the hydrotropic response. The high level of root activity under long-term drought stress indicates that the response to drought, while effective, is metabolically expensive. Given its hardiness to many stresses and ease of cultivation (Liu and Willison 2013), *M. alba* may be a useful model for learning more about the hydrotropic and chemotropic physiological behavior of deep-rooted woody plants.

Ehlers et al. (1991) concluded that the rate of water absorption for agricultural crops relies mostly on root depth in soil. Drought-hardy varieties of wheat, for example, have more extensive root systems than drought-sensitive varieties (Hurd 1974). Access to water is clearly a key limiting factor for mulberry trees growing in a desertified area, but our results indicate that the trees can adjust root growth under the influence of endogenous hormones and obtain sufficient moisture and nutrients. Under long-term drought stress conditions, mulberry trees retained high root activity and had elevated levels of ABA. These results underscore the value of mulberry as a hardy perennial woody plant suitable for restoring ecosystem services to rocky desertified areas while also having the potential to provide agricultural benefits for farmers.

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