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Original Research

Effect of Root Cortical Aerenchyma of Hybrid Corn (*Zea mays* L.) on Maize Resilience After Rehydration under Extreme Drought

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Abstract

Variation laws of growth conditions and root cortical aerenchyma (RCA) of 15 common maize hybrids (*Zea mays* L.) in Yunnan Province under simulated rare extreme drought and rehydration conditions were tested in this paper. The relationship between functions of root tissues in extreme drought process and resilience after rehydration was discussed. Results demonstrated: 1) in middle drought period, RCA area is closely related with drought resistance of varieties and 2) Varieties with large or small RCA area under drought stress have poor resilience after rehydration, while varieties with middle RCA area present strong resilience. We concluded that RCA area formed under drought stress will significantly influence recovery of root functions during rehydration. Large RCA area brings corn strong drought resistance, but it goes against recovery of root functions after rehydration. Small RCA area causes poor drought resistance of corn plants, which will induce serious damage to plants and make it difficult to recover root functions after rehydration. Moderate RCA area helps corn variety to develop certain drought resistance and recover functions of root tissues through further formation of RCA area by parenchymal cells in root cortical tissues. RCA area formed in corn roots can affect drought resistance significantly, and increased RCA area in root system after rehydration can enhance resilience of corn plants.

Keywords: corn, extreme drought, rehydration, RCA, resilience

Introduction

Recent studies have demonstrated that many ecosystems are vulnerable to extreme climatic events that will likely lead to profound ecological and social impacts on local to global scales [1]. Extreme drought occurs more frequently and strongly due to changes of atmospheric circulation and the hydrologic process, which has become a great threat to agricultural production with poor risk resistance [2]. By analyzing spatial-temporal distribution of drought events in China in the past five decades, southwest extreme droughts occur frequently in southwest China and have a large

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Table 1. Average aboveground biomass and stability during the simulated event.

Sample time	5.17 (1st-sample time)			6.17 (2nd-sample time)			7.27 (3rd-sample time)		
Maize hybrids (Abbr.)	Control (g)	Drought (g)	Resistance (%)	Control (g)	Drought (g)	Resistance (%)	Control (g)	Drought (g)	Resilience (%)
Yunrui999 (YR999)	2.25±0.258	0.88±0.063**	-61.11	12.30±2.256	6.48±2.238*	-47.35	39.67±2.077	24.65±3.281**	-37.87
Dedan3 (DD3)	2.05±0.466	0.93±0.165*	-54.88	19.93±0.587	9.18±2.571**	-53.95	45.72±3.781	33.62±5.283*	-26.46
Dedan5 (DD5)	2.35±0.173	0.53±0.189***	-77.66	15.08±0.440	8.47±1.929*	-43.78	40.25±4.588	29.45±9.567	-26.83
Yunrui2 (YR2)	2.13±0.457	0.58±0.137**	-72.94	14.68±1.112	6.97±0.275***	-52.47	38.82±5.406	29.97±5.769	-22.79
Yunrui21 (YR21)	1.10±0.104	0.59±0.297*	-46.59	17.08±1.227	8.23±0.579***	-51.83	47.27±1.753	53.80±11.427	13.80
Yunrui47 (YR47)	2.03±0.692	1.30±0.403	-35.96	16.55±1.797	3.66±0.390***	-77.87	39.55±6.704	22.20±1.779*	-43.87
Yunrui88 (YR88)	2.50±0.299	1.13±0.259*	-55.01	15.63±3.169	4.45±0.849*	-71.52	45.97±5.972	22.15±0.769**	-51.82
Yunrui6 (YR6)	2.88±0.256	1.03±0.275**	-64.35	17.15±1.598	5.82±2.549**	-66.03	38.97±1.583	23.87±4.153*	-38.74
Yunrui68 (YR68)	2.53±0.384	1.30±0.144*	-48.51	21.83±0.702	3.77±0.278***	-82.70	32.32±1.425	29.67±4.191	-8.20
Yunrui7 (YR7)	3.00±0.452	1.15±0.158**	-61.67	12.08±1.676	5.92±2.173**	-50.93	30.52±1.732	32.52±7.132	6.55
Yunrui8 (YR8)	2.05±0.379	1.30±0.371*	-36.59	15.73±1.060	6.20±1.569**	-60.57	31.20±0.491	31.97±5.663	2.48
Yunrui505 (YR505)	2.46±0.258	0.98±0.063**	-60.13	13.65±2.086	6.30±1.639*	-53.84	29.80±2.370	26.95±4.441	-9.56
Yunrui105 (YR105)	2.13±0.155	1.60±0.307*	-24.71	14.03±2.001	11.57±2.028	-17.53	30.60±1.565	30.00±10.281	-1.96
Yunrui10 (YR10)	2.65±0.071	1.23±0.350**	-53.77	14.55±0.470	3.60±0.155***	-75.25	29.85±2.447	21.17±1.584*	-29.06
Yunrui167 (YR167)	1.95±0.434	0.85±0.091*	-56.41	15.30±2.259	4.15±0.261**	-72.87	35.35±1.269	23.20±2.441**	-34.37

Mean ± standard deviation; *, **, *** Significant at levels of 0.05, 0.01 and 0.001. Differences between treated and control plants are compared at each sampling date.

scope of influence [3]. Therefore, improving drought resistance of crops becomes one of the key agricultural bottlenecks that must be solved in southwestern China.

Extreme drought will cause low nutrient availability and inhibit microbial activity, thus influencing nutrient cycling. However, nutrient availability increases quickly during rehydration [4]. Recovery of nutrient uptake and recovery degree of plant root system from water are one of the important functions that determines resilience and further reproduction at the end of drought stress. Nevertheless, there has been no thorough study on the role of plant root system in resilience after rehydration has been reported. RCA formation in corn plant during drought stress is an irreversible process. RCA area and quantity not only affect root functions under drought stress [5], but exert important impacts on recovery of root functions after rehydration. Existing research on RCA mainly concentrates on RCA content under stress conditions as well as its effects on water and nutrient use efficiency [6-7]. Effects of RCA on root function recovery and resilience of plants after rehydration have not been studied.

In this paper, changes of RCA in root system of corn plants in extreme drought and rehydration processes were discussed, and resilience of corn plants after rehydration was analyzed, aiming to provide theoretical references to make field management measures of corn plants with reference to extreme conditions. Several scientific hypothesis were made: RCA area in root system of different hybrid corn varieties, which is formed during extreme drought stress, will influence maize resilience after rehydration. Although hybrid corn plants with larger RCA area in root system will develop stronger drought resistance of hybrid corn plants, it may not achieve resilience after rehydration. Hybrid corn plants with moderate RCA area can form new RCA area from parenchymal cells in root cortical tissues, which will further improve maize resilience after rehydration.

Experimental

Test Materials

Common 15 hybrid corn varieties in Yunnan Province were chosen as test materials (Table 1).

Experiment

Based on observation data in five meteorological stations (Yuxi, Chuxiong, Qujing, Dali, and Kunming) in the center of Yunnan Province, China, a rare extreme drought event (once in 50 years) was set [4]. Data were collected from the China Meteorological Data Sharing Service System. Drought condition was realized by transparent agricultural film. Height of rain shelter was set at 250 cm to ensure near-surface ventilation. Moreover, average precipitation was set as the reference level of precipitation, which was realized by artificial rainfall in a rain shelter. Rainfall capacity applied every week was the mean of the corresponding period in 50 years (1964-2013). Duration of typical drought event during the vegetative period (April-June) of corn plants were selected from source data as simulation days of drought period. Average precipitation in the corresponding period was used as the rainfall capacity during rehydration. In this experiment, the extreme drought events started from April 17 to June 17, 1986. According to the results, an extreme drought event is 60 consecutive days with precipitation of less than 0.1 mm in the study. Thus, a drought period of 60 days was applied by intercepting precipitation from 29 July to 16 August, 2015. The average precipitation from June 18 to September 30 in 50 years (1964-2013) was used as the rainfall capacity during rehydration (from June 18 to September 30, 2015; Fig. 1).

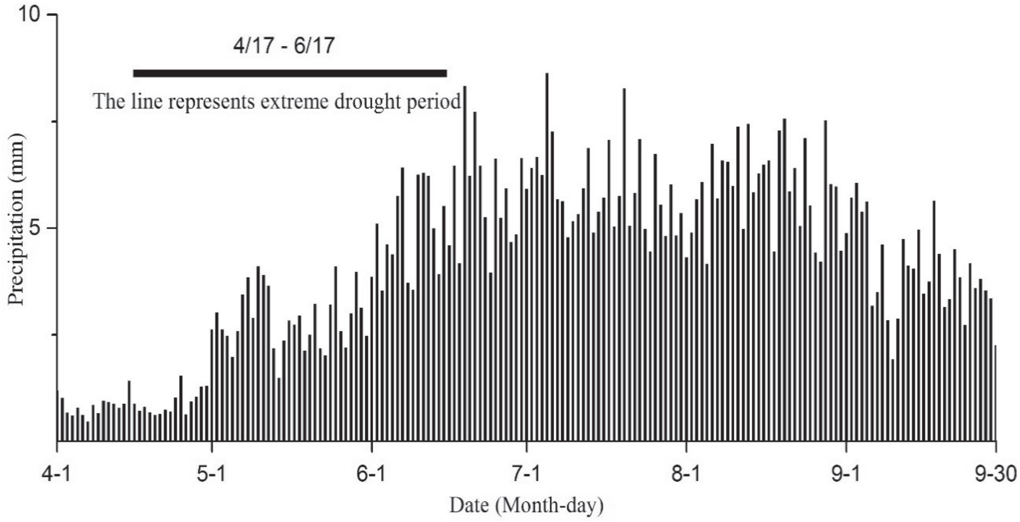

Fig. 1. Daily mean precipitation from April 1 to September 30, 1964-2013.

Temperature and Humidity Monitoring in Soil Environment

Soil water content and temperature were monitored by a HOBO weather station. Test depth was set 10 cm below the earth surface. Humidity and temperature were tested every 30 min.

Plant Biomass Test

Above- and underground standing crop biomasses of different corn varieties were tested by harvest and root washing method in middle period of extreme drought (May 17, 2015, 1st sample time), late period of extreme drought (June 17, 2015, 2nd sample time), and middle period of rehydration (July 25, 2015, 3rd sample time). Samples were dried to constant weight in a constant-temperature drying oven (65ºC) and then weighed.

RCA Area Test

RCA area was expressed by percentage of cortex that is aerenchyma in root section. RCA of corn root system was sampled for three times in the study period. Sample time was the same with the test time of biomass. The root section (8 cm) that can represent the average RCA area of the whole root, that is, the middle position at first and second-whorl crown roots, was cut [8]. The root section was fixed in FAA stationary liquid for 24 h and then stored in 70% ethyl alcohol after gradient dehydration by ethyl alcohol. Next, it was cut into sheets by a double-edge blade under 110 magnifications of a stereoscopic microscope (Olympus-16, Tokyo, Japan) and then observed and shot under LCD (Olympus-DP7, Tokyo, Japan) optical microscope (Olympus- BX51, Tokyo, Japan). Finally, RCA area in the root section was calculated by Rootscan software (Version 2.0, Penn State University, PA, USA).

Calculating Crop Stability

Crop stability was evaluated by way of the McNaughton method [9]. It includes drought resistance and resilience. The index between extreme drought group and historical control group in the extreme drought process was used as drought resistance, while the index between two groups after rehydration was used as resilience. The numerical difference between two groups in the same sample period was used as crop stability, i.e.: Resistance = % change from control = (treatment-control /control) × 100%.

Statistical Analysis

Biomass differences of different varieties under extreme drought and historical control conditions were tested by T-test. RCA area difference was tested by one-way analysis of variance. SAS9.0 was used for statistical analysis. Statistical analysis on overall stability and RCA area of different hybrid corn varieties was implemented by Canoco 4.50, and principal component analysis (PCA) in linear model of non-constraint scheduling was used as the analysis model.

Results

Effects of Extreme Drought and Rehydration on Soil Water and Temperature

Extreme drought group can reduce volumetric water content in soil significantly. The volumetric water content in soil was decreased by 82.28% at the end of

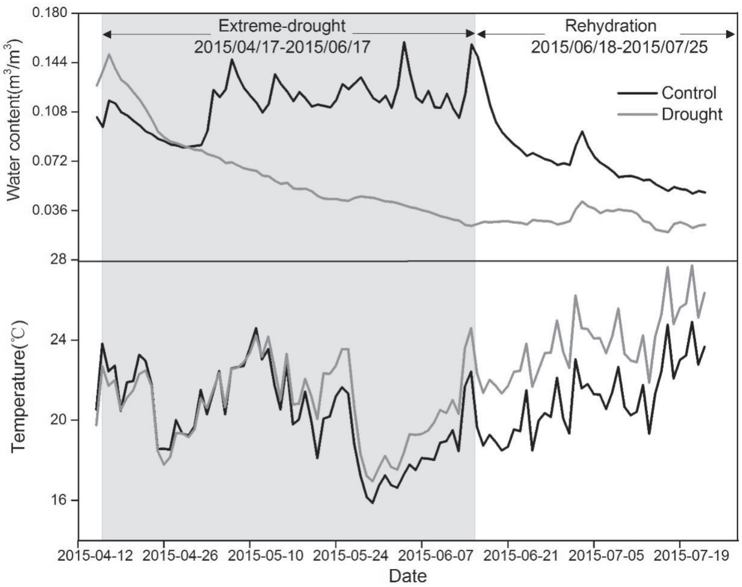

Fig. 2. Daily soil water content and temperature (0–10 cm) under simulated treatments.

Table 2. Average underground biomass and stability during the simulated event.

Sample time	5.17 (1st-sample time)			6.17 (2nd-sample time)			7.27 (3rd-sample time)		
Maize hybrids	Control (g)	Drought (g)	Resistance (%)	Control (g)	Drought (g)	Resistance (%)	Control (g)	Drought (g)	Resilience (%)
YR999	1.55±0.248	1.07±0.125*	-30.64	4.22±1.318	1.60±0.178*	-62.13	5.32±0.976	0.97±0.578***	-81.69
DD3	1.30±0.312	1.25±0.158	-3.85	4.15±0.210	1.60±0.187***	-61.44	3.10±0.944	2.35±0.863	-24.19
DD5	1.05±0.178	1.12±0.131	6.67	3.27±0.286	1.65±0.239**	-49.61	3.72±1.329	1.72±0.625	-53.69
YR2	1.32±0.063	1.02±0.266	-22.64	4.07±0.386	1.47±0.347**	-63.8	2.35±1.220	2.57±0.863	9.57
YR21	1.10±0.132	1.10±0.278	0.00	4.40±0.868	1.57±0.390***	-64.2	3.37±0.427	5.40±1.438	60.00
YR47	1.42±0.025	1.35±0.122	-5.26	4.27±0.886	0.95±0.218***	-77.78	2.30±0.763	0.72±0.342*	-68.48
YR88	1.00±0.225	1.32±0.103	32.00	3.67±0.943	0.87±0.209**	-76.19	4.00±1.163	0.55±0.210**	-86.25
YR6	1.30±0.240	1.67±0.287	28.46	4.60±0.682	1.25±0.206***	-72.83	3.17±0.759	0.37±0.085**	-88.19
YR68	1.65±0.187	1.40±0.104	-15.15	5.32±0.545	0.95±0.104***	-82.16	2.82±0.295	1.92±0.638	-31.85
YR7	1.52±0.175	1.12±0.025*	-26.23	3.55±0.695	1.22±0.292**	-65.49	1.55±0.491	2.65±1.462	70.97
YR8	1.42±0.287	1.10±0.064	-22.81	5.42±0.981	1.23±0.165***	-77.42	2.00±0.441	2.22±0.893	11.25
YR505	1.45±0.147	0.77±0.075**	-46.55	3.75±1.437	1.90±0.571	-49.33	1.82±0.433	1.00±0.636	-45.21
YR105	1.40±0.132	1.12±0.025*	-20.00	3.87±0.824	1.62±0.197*	-58.06	1.90±0.505	1.17±0.175	-38.16
YR10	1.47±0.110	1.55±0.178	5.42	5.42±0.772	1.27±0.188***	-76.49	4.05±0.497	0.50±0.308***	-87.65
YR167	1.37±0.085	0.70±0.064***	-49.09	4.42±0.359	1.17±0.103***	-73.44	2.95±0.194	0.65±0.340***	-77.97

Mean ± standard deviation; *, **, *** Significant at levels of 0.05, 0.01 and 0.001. Differences between treated and control plants are compared at each sampling date.

Table 3. Average biomass and stability during the simulated event

Sample time	5.17 (1st-sample time)			6.17 (2nd-sample time)			7.27 (3rd-sample time)		
Maize hybrids	Control (g)	Drought (g)	Resistance (%)	Control (g)	Drought (g)	Resistance (%)	Control (g)	Drought (g)	Resilience (%)
YR999	3.80±0.253	1.95±0.099*	-48.68	16.53±3.550	8.07±2.128**	-51.09	44.99±1.623	25.6±2.356***	-43.05
DD3	3.35±0.397	2.18±0.162*	-34.93	24.07±0.743	10.77±2.634***	-55.23	48.82±2.756	35.97±3.785**	-26.32
DD5	3.40±0.176	1.65±0.163***	-51.47	18.35±0.677	10.12±2.168**	-44.85	43.97±3.378	31.17±6.779*	-29.11
YR2	3.45±0.326	1.6±0.212***	-53.62	18.75±0.901	8.45±0.372***	-54.99	41.17±3.919	32.54±4.125	-20.96
YR21	2.2±0.119	1.69±0.288	-23.18	21.47±1.475	9.80±0.864***	-54.38	50.64±1.276	59.20±8.144	16.90
YR47	3.45±0.49	2.65±0.298	-23.19	20.82±1.070	4.61±0.462***	-77.86	41.85±4.771	22.92±1.281*	-45.23
YR88	3.5±0.265	2.45±0.197**	-30.00	19.30±2.700	5.32±0.802***	-72.44	49.97±4.302	22.7±0.564***	-54.57
YR6	4.18±0.248	2.70±0.281**	-35.41	21.75±1.968	7.07±2.377***	-67.49	42.14±1.241	24.24±2.937**	-42.48
YR68	4.18±0.302	2.70±0.126**	-35.33	27.15±0.979	4.72±0.263***	-82.62	35.14±1.029	31.59±2.998	-10.10
YR7	4.52±0.343	2.27±0.113**	-49.78	15.62±1.429	7.15±2.164**	-54.32	32.07±1.273	35.17±5.148	9.67
YR8	3.47±0.336	2.4±0.266*	-30.84	21.15±0.901	7.42±1.427***	-64.87	33.20±0.467	34.19±4.054	2.98
YR505	3.91±0.21	1.75±0.069***	-55.24	17.40±2.656	8.20±1.357***	-52.87	31.62±1.704	27.95±3.172	-11.61
YR105	3.53±0.144	2.72±0.218	-22.95	17.90±2.812	13.20±2.183*	-26.31	32.50±1.163	31.17±7.271	-4.09
YR10	4.12±0.093	2.78±0.278***	-32.52	19.97±0.676	4.87±0.335***	-75.61	33.90±1.766	21.67±1.141**	-36.08
YR167	3.32±0.313	1.55±0.079**	-53.31	19.72±2.419	5.32±0.301***	-73.02	38.30±0.908	23.85±1.743	-37.73

Mean ± standard deviation; *, **, *** Significant at levels of 0.05, 0.01 and 0.001. Differences between treated and control plants are compared at each sampling date.

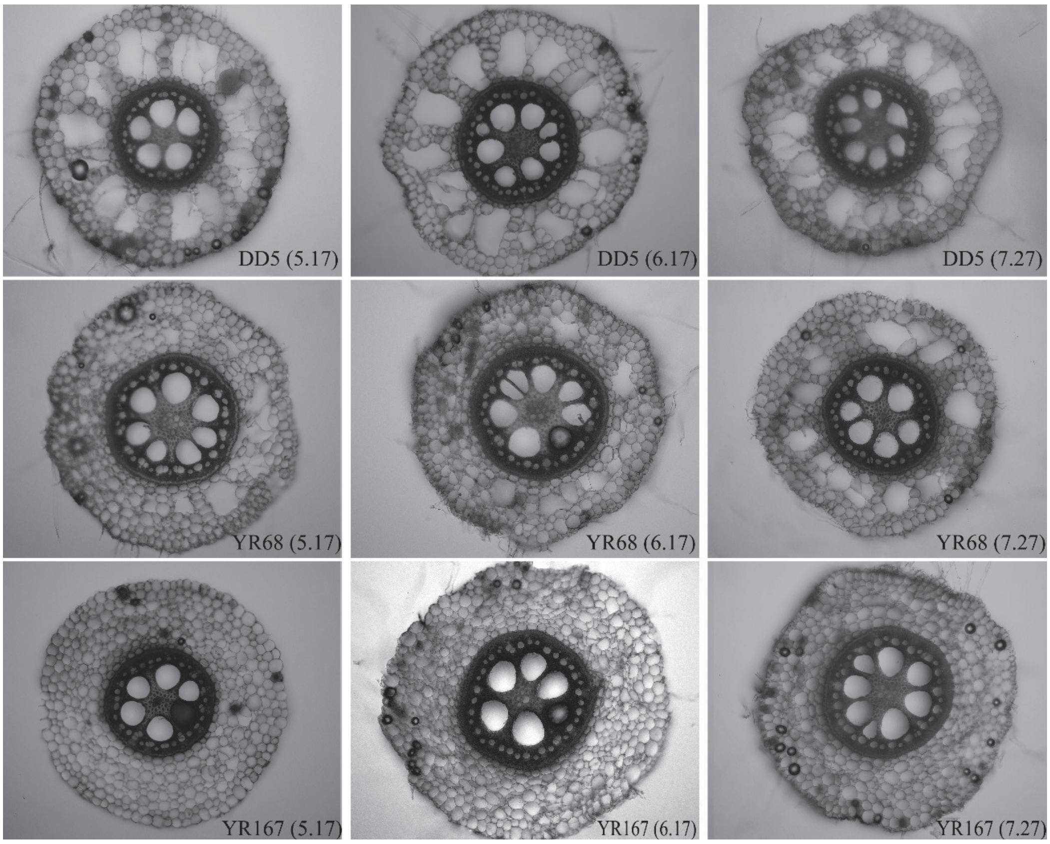

Fig. 3. Root sections of hybrid corn with various degrees of RCA area under the simulated event.

drought stress compared to the initial value. The average reduction of volumetric water content in soil during the extreme drought process was 43.79%. In the middle and late period of extreme drought, soil temperature was slightly higher than that in the control group. In the rehydration period, volumetric water content in soil didn't increase to the level of historical control group, and soil temperature was little higher than that of the control group (Fig. 2).

Effects of Extreme Drought and Rehydration on Aboveground Biomass as well as Aboveground Drought Resistance and Resilience

Moderate water stress caused certain aboveground biomass reductions in the 1st sample time, and was particularly more significant in the 2nd sample time under severe water deficit. Such changes varied among different hybrid corn varieties. All hybrid varieties achieved resilience to different extents in the 3rd sample time (Table 1). Most of them can recover to the level of control.

Effects of Extreme Drought and Rehydration on Underground Biomass as Well as Underground Drought Resistance and Root Function Recovery

Dry weight of underground biomass changed slightly in the 1st sample time compared to dry weight of aboveground biomass, but it changed significantly in the 2nd sample time. Such change was different among different hybrid corn varieties. All hybrid varieties achieved resilience to different extents in the 3rd sample time (Table 2). Some varieties can recover to the level of the control group.

Effects of Extreme Drought and Rehydration on Overall Biomass as well as Overall Drought Resistance and Resilience

Table 3 shows that the overall biomass in the 2nd sample time was slightly lower than that in the 1st sample time. The resilience of all hybrid corn varieties enhanced in the 3rd sample time and all varieties can recover to the level of the control group.

Effects of Extreme Drought and Rehydration on RCA Area

YR999 and YR167 formed the smallest RCA area in the 1st sample time, and maintained a small RCA area in the 2nd and 3rd sample times. On the contrary, DD5, YR88, YR6, and YR10 formed large RCA area in the early period of extreme drought, but maintained the same or smaller RCA area in the late period of extreme drought and rehydration period (Table 4). Rest varieties formed moderate RCA area in the middle part of the extreme period, but larger RCA area in the

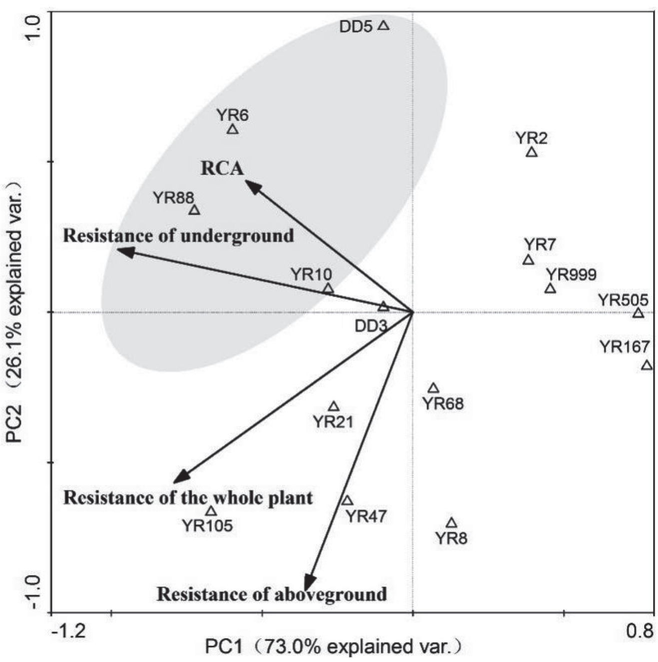

Fig. 4. Principal component analysis of the stability and RCA area of different hybrid corn varieties in middle period of extreme drought.

late period of extreme drought and rehydration period (Fig. 3).

Analysis of Overall Stability and RCA Area of Different Hybrid Corn Varieties

Based on PCA (Fig. 4), the proportion of interpretable principal component axes in the first and second ordination axes reached 98.1%. RCA formation in the middle period of extreme drought can enhance drought resistance of underground parts. Besides, drought resistance of underground and aboveground parts make basically equal contributions to the overall drought resistance of the plant in this period. Tables 1 and 2 revealed that the drought resistance of underground parts is stronger than that of aboveground parts during the middle period of extreme drought.

According to the PCA results (Fig. 5), the proportion of interpretable principal component axes in the first and second ordination axes reached 98.7%. RCA

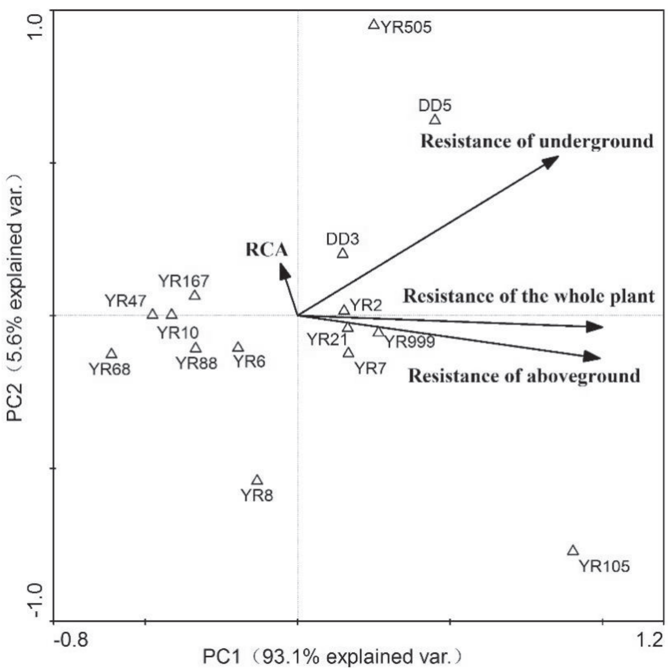

Fig. 5. Principal component analysis of the stability and RCA area of different hybrid corn varieties in late period of extreme drought.

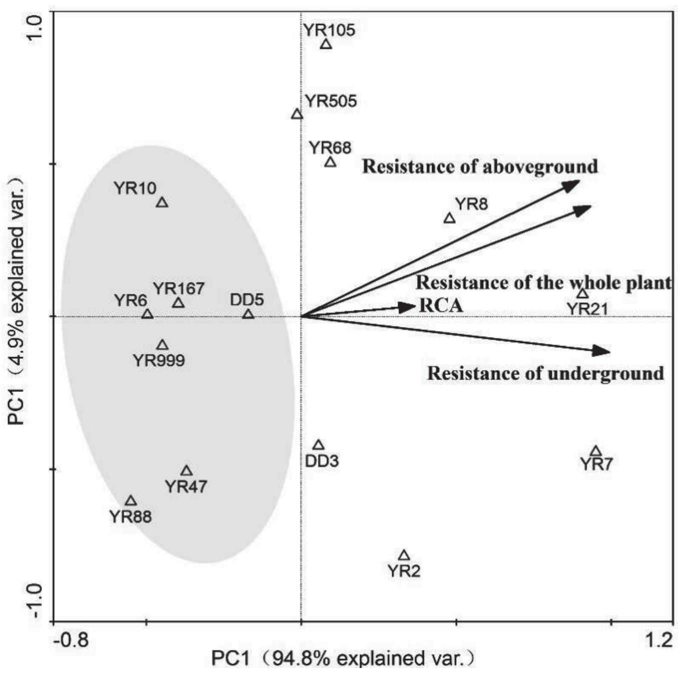

Fig. 6. Principal component analysis of the stability and RCA area of different hybrid corn varieties in middle period of rehydration.

area influences drought resistance of crops slightly in the late period of extreme drought. Based on Tables 1 and 2, we found that drought resistance of aboveground parts makes greater contributions to the overall drought resistance of crops in the late period of extreme drought.

The PCA reported (Fig. 6) that the proportion of interpretable principal component axes in the first and second ordination axes reached 99.7%. RCA formation after rehydration can enhance recovery of root functions. By combining Table 4, hybrid corn varieties with large or small RCA area in the middle period of extreme drought have weaker resilience after rehydration, while hybrid corn varieties with moderate RCA area gain certain resilience.

Growth period of corn will encounter different degrees of drought stress. The compensatory effect after the drought is a positive regulatory mechanism of crops, which is significant for their stress resistance [10]. Drought stress decreases plant growth rate significantly and can lead to the inhibition of plant growth and biomass reduction [11]. Plants can recover growth quickly under rehydration conditions and eliminate growth inhibition immediately. Sometimes, it will generate super compensation effect and offset plant loss caused by drought [12-13]. Therefore, drought resistance and resilience are of equal importance to plant growth under drought environment. Quick resilience after rehydration might be more important to crop production and it also can minimize the effect of drought stress on growth. The super compensatory effect can offset losses of crop output caused by previous drought stress and even can increase crop output [14].

Some researchers have proven that drought resistance and resilience can be measured by plant biomass under drought stress [4]. Drought resistance is the final consequence of the influence of drought stress on crops. It reflects sensitivity of crop varieties to drought stress and is a reliable index for drought resistance assessment. Resilience is an important evaluation index of growth recovery after drought stress is eliminated. In this paper, drought resistance and resilience of different hybrid corn varieties were evaluated by biomass coefficient.

Under extreme drought conditions, root cortex will make great changes. Crops can resist drought stress by reducing material consumption based on the formation of RCA. In addition, crops can develop drought resistance by dehydration-induced deformation of cortex parenchyma cells, which shrink cell volume and change resistance against radial water transportation [15]. However, such drought resistance can easily cause damage to the root system by inhibiting plant growth [16]. In this paper, hybrid corn varieties with large RCA area didn’t show strong resilience, but those with moderate RCA achieved certain resilience. This indicates that the RCA area formed in the root system under drought stress plays an important role in recovery of crops. These hybrid varieties with moderate RCA under drought stress can also form a certain RCA area after rehydration. The RCA area formed under drought stress is mainly for reducing material consumption of plant roots and promoting root growth to increase drought resistance of the plant [17]. The RCA area formed under rehydration conditions can further promote growth of root system and soil nutrient absorption and use efficiency, thus improving resilience of plants [7, 18].

Table 4. Percentage of cortex that is aerenchyma under the simulated event (%).

Sample time	5.17 (1st-sample time)			6.17 (2nd-sample time)			7.27 (3rd-sample time)		
YR999	3.76±0.455	fg	DE	5.45±1.249	cd	CD	4.99±0.953	e	D
DD3	6.61±2.376	def	BCDE	6.47±1.158	bcd	BCD	8.68±2.544	bcde	BCD
DD5	14.30±3.970	ab	A	13.78±2.621	a	A	10.79±1.660	abcde	ABCD
YR2	5.13±1.321	efg	CDE	7.21±0.735	bcd	BCD	13.40±2.147	ab	AB
YR21	5.77±1.657	defg	CDE	5.53±1.078	cd	BCD	7.28±1.677	cde	BCD
YR47	9.14±0.804	bcde	ABCD	10.6±1.642	abc	ABC	13.90±2.899	ab	AB
YR88	12.25±2.472	abc	AB	10.63±4.762	abc	ABC	8.61±1.608	bcde	BCD
YR6	10.48±1.957	abcd	ABC	5.90±0.818	cd	BCD	7.25±1.947	cde	BCD
YR68	6.90±1.392	def	BCD	7.39±2.408	bcd	BCD	16.04±3.262	a	A
YR7	9.96±1.829	abcde	ABC	9.64±2.732	abc	ABC	12.39±3.505	abc	ABC
YR8	5.03±0.178	efg	CDE	9.50±1.741	abc	ABC	13.43±3.914	ab	AB
YR505	8.90±1.014	cdef	ABCD	7.62±1.364	bcd	BCD	11.47±2.181	abcd	ABCD
YR105	8.19±2.628	cdef	BCD	7.02±1.124	bcd	BCD	10.36±1.880	abcde	ABCD
YR10	14.80±3.701	a	A	11.56±2.639	ab	AB	8.84±2.327	bcde	BCD
YR167	0.72±0.206	g	E	3.11±0.596	d	D	5.40±1.390	de	CD

Mean ± standard deviation. Different letters show significant difference among the means (The capital letters indicate; the significant difference at1% level; the lower-case letters indicate the significant difference at 5% level.)

Conclusions

In conclusion, different corn varieties show different drought resistance and resilience after rehydration. Previous researchers have pointed out that RCA can enhance resistance to both drought stress and waterlogging stress. However, whether RCA can promote late resilience has not yet been studied. Our results show the important role of RCA in both drought resistance during extreme drought and resilience after rehydration.

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Conflict of Interest

The authors declare no conflict of interest.

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