

Variations in internal water distribution and leaf anatomical structure in maize under persistently reduced soil water content and growth recovery after re-watering

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Abstract Episodes of regional drought are increasing and are frequently associated with increased duration and intensity. However, relatively little is known about effects of long-lasting drought on leaf microscopic structure and physiological metabolism of plants. In this study, we investigated internal water re-distribution and leaf anatomical structure of maize (*Zea mays* L.) grown under persistently reduced soil water content. Meanwhile, the threshold of soil water content at which maize cannot recover growth vitality after re-watering was determined. Our results showed that during persistent reductions in the field water capacity from 75 to 25 %, plant growth declined, while the water content in maize decreased following the order from the lower to upper leaves and their leaf sheathes to the stem and roots. At 20 % of field water capacity, the volume of bulliform cells declined, accompanied by an inward shrinkage of cell walls. Under field water capacity below 20 %, the number of chloroplasts in bundle-sheath cells decreased, chloroplasts in mesophyll cells deformed from oval to round, concomitant of a near to zero net photosynthetic rate. It was demonstrated that the growth vitality of maize plants could be recovered by re-watering even if field water capacity reduced to 15 %, but not to 10 %.

Keywords Internal water distribution · Leaf anatomical structure · Maize (*Zea mays* L.) · Persistent drought · Re-watering

Introduction

Drought is worldwide one of the major abiotic factors limiting plant growth and leading to crop-yield loss (Boyer 1982; Chaves et al. 2003; Oyekunle and Badu-Apraku 2014; Semenov et al. 2014). Under global climate changes, the duration and intensity of drought are predicted to increase over next decades (Overpeck and Cole 2006; IPCC 2010). Though there are mass data about drought effects on plant metabolism and growth (Foyer et al. 1998; Alvarez et al. 2008; Sicher and Barnaby 2012; Sun et al. 2015), however, response of plants to long-lasting drought and the lowest threshold of soil water content for plant survival remain poorly understood.

Water functioning as an important metabolite and metabolic medium is necessary to plant growth (Chaumont and Tyerman 2014). In general, plants absorb water from soil through enormous root system and transport it via the xylem to aboveground organs, subsequently, most of the water is lost into the atmosphere by leaf stomatal transpiration (Steudle 2001). Based on this translocation of water in the soil–plant–atmosphere continuum, plant growth and development is strongly dependent on the maintenance of a dynamic water balance (Lawlor and Cornic 2002; Lambers et al. 2008). Under water-limiting conditions, decreased water absorption by roots and increased water loss by leaf transpiration can break the balance, leading to metabolic disturbance and growth reduction or stop, and under extreme drought even resulting in plant death (Allen et al. 2010; Anjum et al. 2011; McDowell 2011; Farooq et al.

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2012; Sapeta et al. 2013). Hence, terrestrial plants are confronted with drought-induced potential stress and mortality due to water loss by transpiration (Claeys and Inzé 2013). In response to water deficit, plants can minimize transpirational water loss by decreasing leaf area and stomatal aperture (Chaves et al. 2009; Lopes et al. 2011; Hartmann et al. 2013; Sapeta et al. 2013). In addition, alterations in leaf anatomical structure in response to reduced environmental water availability are beneficial for the maintenance of a water balance (Ristic and Cass 1991; Al-Maskri et al. 2014). On the other hand, plants can allocate more internal assimilates (e.g., sugar) to roots and, thereby increasing water absorption from soil by stimulating adventitious root generation and root growth (Liu and Stützel 2004; Hummel et al. 2010). However, under severe or persistent drought, stomatal closure and damage of leaf microscopic structure can reduce leaf assimilative ability and inhibit assimilate translocation to roots, subsequently limiting the root ability to exploit and absorb soil water (Asch et al. 2005; Xu and Zhou 2005). Meanwhile, potential interactions between the utilization of stored energy for metabolism and defense, and the demand to maintain cell turgor will aggravate carbon competition. In this case, limited internal resource of water and assimilates is concentrated in the growing points of above- and underground organs to maintain the growth vitality. With further development of drought, finally, hydraulic failure and carbon starvation will lead to plant death (McDowell et al. 2008; McDowell 2011; Anderegg et al. 2012; Sevanto et al. 2014; Dickman et al. 2015). However, precise physiological mechanisms underlying plant mortality are still under discussion. For agricultural practice, it also is important to predict whether a re-watering of crops being exposed to lasting drought is still worthy.

In the present study, 2-week-old seedlings of maize (*Zea mays* L.) grown in pots were exposed to persistently reduced soil water content. The aims of this work were to determine (1) the variations in internal water distribution between different parts of plants and in leaf anatomical structure during persistent decrease in soil water content, (2) the threshold of soil water content at which maize plants cannot recover growth vitality after re-watering.

Materials and methods

Plant material and treatments

Experiments were performed outdoors at the Institute of Water Saving Agriculture in Arid Areas, Northwest A&F University, Yangling, China (34°16'56" N, 108°4'28" E). Seeds of maize ('Zhengdan 958') were individually sown in pots (28 cm diameter, 30 cm depth, volume \approx 18.5 L)

filled with a mixture of local loess and vermiculite (2:1, v/v). After sowing, pots were watered to 75 ± 5 % of field water capacity to guarantee a normal germination and seedling growth. Two weeks after germination, when plants had four leaves, half of the seedlings were no longer watered, while the other half were grown continuously under non-limiting water condition (75 ± 5 % of field water capacity) as control. Soil water content in pots was controlled by weighing daily at dusk and, eventually, compensated with top water to maintain the uniformity of soil water content. A moveable transparent rainout shelter was used to avoid impact of rainfall on soil water content in pots. Six plants, respectively, grown under non-limiting water conditions and persistently reduced soil water content were harvested, when soil water content in the drying pots reduced from 75 ± 5 to 55 ± 5 , 35 ± 5 , 25 ± 5 , 20 ± 5 , 15 ± 5 , and 10 ± 5 % of field water capacity, respectively. One day before each harvest, diurnal variations in leaf net photosynthesis rate (P_n) were measured. Before each sampling, leaf thickness, plant height, total leaf area of individual plant, and leaf relative water content (RWC) were measured. Leaf thickness was measured using a micrometer ($n = 6$). Single leaf area was estimated using the formula: leaf area = leaf length \times leaf width \times 0.75 (Sanderson et al. 1981). Total leaf area of individual plants was the sum of all single leaf area. Meanwhile, pieces (2×3 mm²) from the middle of the third fully developed leaf from the apex were cut and immediately fixed in 0.1 M phosphate buffer solution (pH 7.0) containing 3 % glutaraldehyde to observe the variations in leaf anatomical structure. At harvest, different parts of plants including each leaf, sheath, stem, and roots were individually collected and weighed separately. Samples were dried at 80 °C to constant weight to determine biomass based on dry weight.

Determination of RWC

The third fully expanded leaf from the apex was used for determining RWC. Leaf RWC was calculated by the formula: $RWC (\%) = (FW - DW)/(TW - DW) \times 100$ %, where, FW and DW are fresh weight and dry weight, respectively, while TW is the saturated leaf weight which is obtained by immersing the leaf into distilled water at 4 °C for 48 h in the dark (Weatherley 1950).

Measurement of water content in different parts of plants

At each harvest, every leaf, sheath, stem, and roots of individual plants were collected separately. Fresh weight (FW) of the samples was immediately measured separately, while dry weight (DW) was determined after drying at

80 °C to constant weight. Water content of different parts of plants was calculated by the formula: $(FW - DW)/FW \times 100\%$ ($n = 6$) and imaged using the software Adobe Photoshop (version cs5, Adobe Systems Incorporated, CA, USA).

Determination of leaf anatomical structure

To observe the variations in leaf anatomical structure under persistently reduced soil water content, at each harvest, pieces ($2 \times 3 \text{ mm}^2$) from the middle of the third fully developed leaf from the apex were cut and immediately fixed in 0.1 M phosphate buffer solution (pH 7.0) containing 3 % glutaraldehyde at 4 °C for 8 h. After rinsing in phosphate buffer (pH 7.0), leaf pieces were post-fixed in 1 % osmium tetroxide at 4 °C for 2 h, subsequently, dehydrated through an ascending ethanol series (30, 50, 70, 80, 90, and 100 %). Samples were embedded in Epon 812 resin (Sigma, St. Louis, MO, USA) and cut into 10 μm using an ultramicrotome (Ultracut-UC7, Leica, Germany). Sections were stained with 1 % toluidine blue, then observed and photographed using a microscope (Leica-DMLB, Leica, Germany) (Dekov et al. 2000). The diameter of bundle-sheath cells in Kranz anatomy was determined randomly ($n = 30$). The area of bulliform cells was measured according to Zou et al. (2014).

Measurement of diurnal variations in P_n

On a cloudless day before each harvest, diurnal variations in leaf P_n of plants, respectively, grown under non-limiting water conditions and persistently reduced water content were measured on the third fully expanded leaf from the apex from 07:00 to 19:00 at 2-h intervals using a LI-COR 6400XT portable photosynthesis system (Li-COR Biosciences, Lincoln, Nebraska, USA). Light emitting diodes (LED) built into the LI-COR 6400 were used as light source at intensities of natural light radiation during the diurnal course (minimum $200 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 7:00, maximum $1800 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 13:00). The temperature inside the cuvette was also set to outside air temperatures during the diurnal course (minimum 26 °C at 7:00, maximum 34 °C at 13:00) (Liu et al. 2013).

Assessment of growth recovery of drought-stressed plants after re-watering

When soil water content in the drying pots decreased to 25 ± 5 , 20 ± 5 , 15 ± 5 , and $10 \pm 5\%$ of field water capacity, respectively, six plants were harvested, while another six plants were re-watered to $75 \pm 5\%$ of field water capacity for a week. Growth vitality recovery of these plants after re-watering was visually observed and evaluated.

Statistical analyses

Significant difference in individual parameters between plants grown under non-limiting water conditions and persistently reduced soil water content was analyzed by one-way ANOVA tests using SPSS for Windows (version 17.0, SPSS Corp., Chicago, IL, USA). Difference was considered statistically significant at $P < 0.05$.

Results

Variations in leaf RWC under persistently reduced soil water content

Leaf RWC of maize grown under non-limiting soil water conditions remained at a relative stable level and tended to slightly increase with prolonged growth phases (Fig. 1a). When soil water content in the drying pots persistently reduced from 55 to 20 % of field water capacity, leaf RWC decreased only from about 80 to 60 % (Fig. 1b). The reduction amplitude inconsistency between the soil water content and leaf RWC demonstrates the ability of maize plants to regulate water balance of leaves. But if field water capacity further decreased to 15 and 10 %, leaf RWC fell dramatically to only 42 and 11 %, respectively. That may mean the loss of the ability regulating water balance.

Water distributions in different parts of plants under persistently reduced soil water content

Within individual plants grown under non-limiting water conditions, the highest water content was observed in leaf

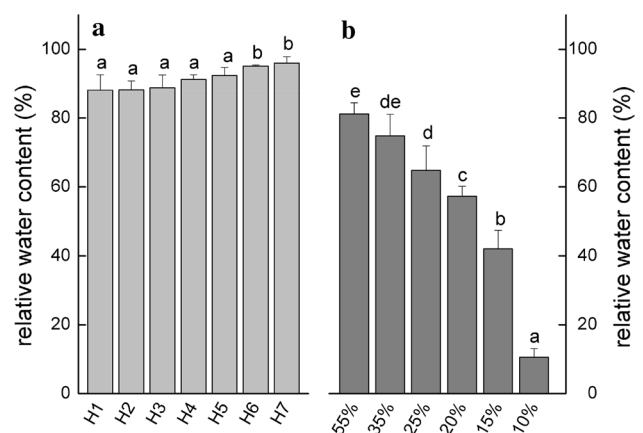
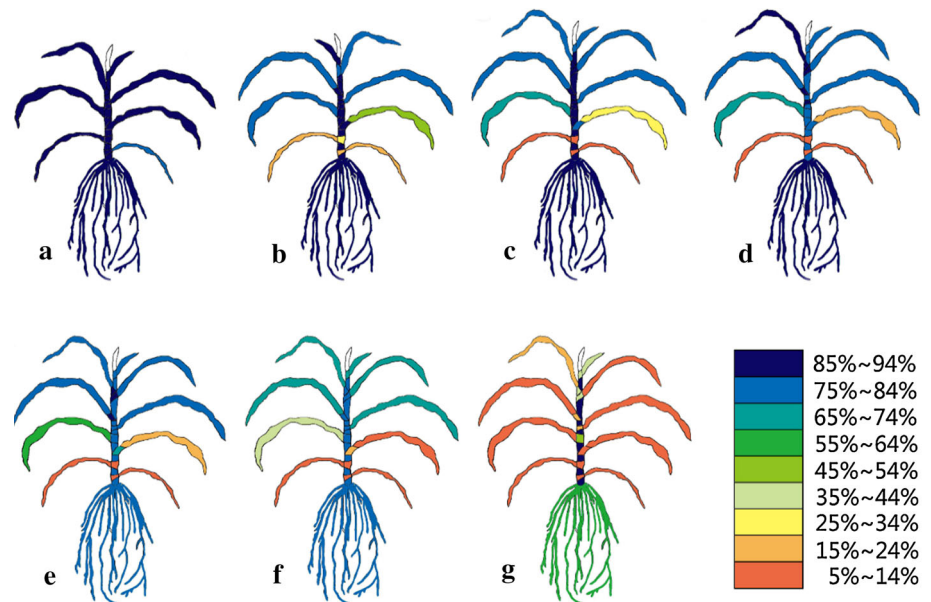


Fig. 1 Variations in leaf relative water content (RWC) of maize grown under non-limiting soil water conditions as control at seven harvests (H1–H7) (a) and under persistently reduced field water capacity (b, from 55 to 10 %). Different letters about columns indicate statistically significant difference at $P < 0.05$ (mean \pm SD, $n = 6$)

Fig. 2 Water distributions in different parts of maize plants when field water capacity persistently reduced from $75 \pm 5\%$ (a), to $55 \pm 5\%$ (b), $35 \pm 5\%$ (c), $25 \pm 5\%$ (d), $20 \pm 5\%$ (e), $15 \pm 5\%$ (f), and $10 \pm 5\%$ (g), respectively ($n = 6$). Variations in the color from dark blue to orange indicate decreasing water content. Data of water content in different parts of plants were imaged using the software Adobe Photoshop (version cs5, Adobe Systems Incorporated, CA, USA)



sheathes, followed by stem and roots, and the water content of leaves was lowest (Fig. 2a). Among the leaves, the water content of upper leaves was higher than lower old leaves. During the reduction in the field water capacity from 75 to 35 %, the water content in lower old leaves and their leaf sheathes decreased significantly, but in upper leaves, stem, and roots was not obviously affected (Fig. 2a–c). At field water capacity lower than 25 %, water content of upper leaves, stem, and roots decreased significantly (Fig. 2d–f). Once the field water capacity further decreased to 10 %, the limited internal water resource mainly concentrated in the stem and roots (Fig. 2g).

Variations in leaf anatomical structure under persistently reduced soil water content

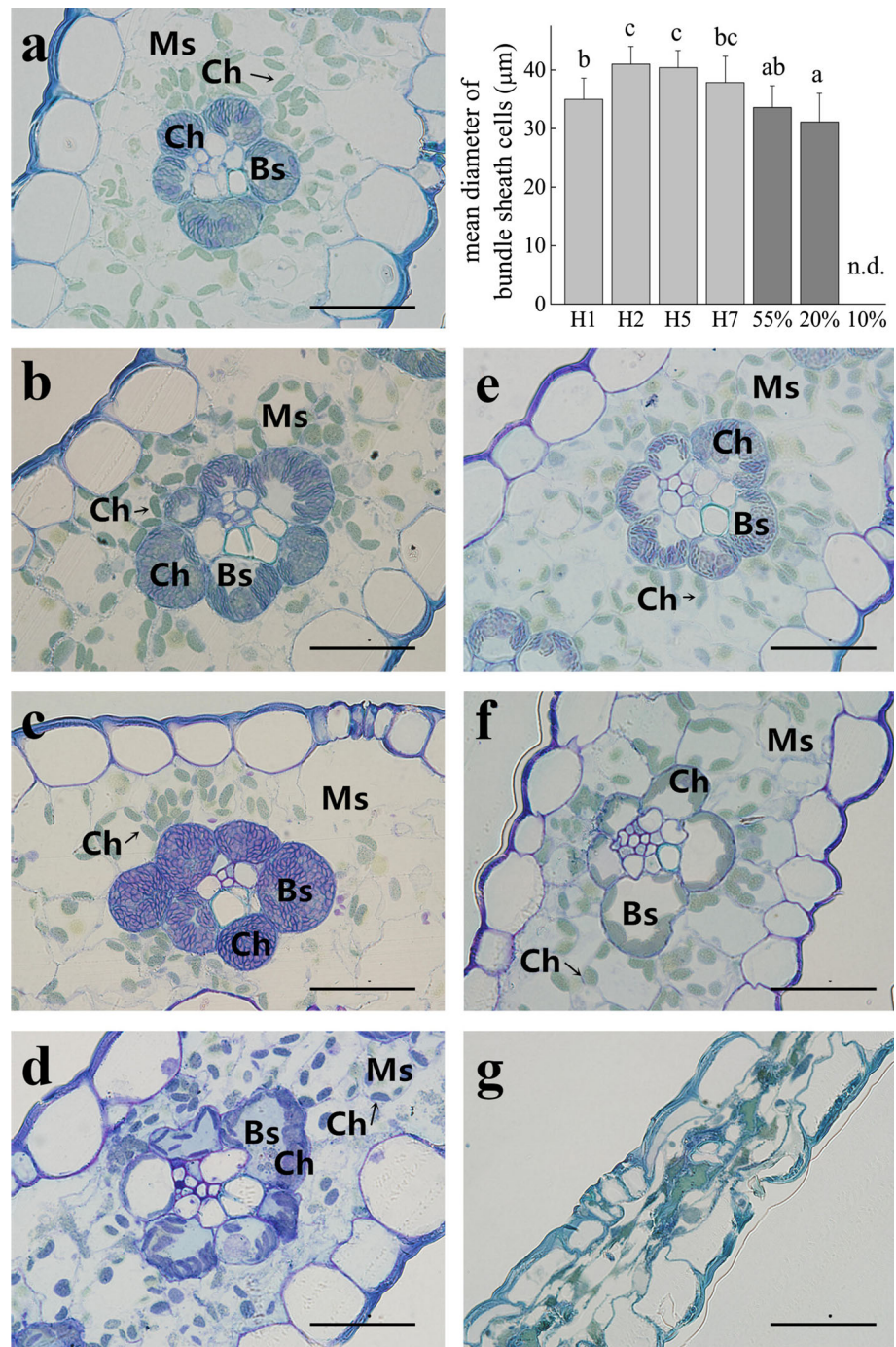
Under non-limiting water conditions, bundle-sheath cells of maize leaves were fully filled with plenty of chloroplasts possessing only stroma lamella but no grana lamella, and the number of chloroplasts in the bundle-sheath cells tended to decrease with the prolongation of developmental phases (Fig. 3a–d). However, as soil water content in the drying pots decreased from 75 to 55 and 20 % of field water capacity, the volume of Kranz anatomy shrank, the diameter of bundle-sheath cells and the number of chloroplasts in the bundle-sheath cells declined, and, the chloroplasts in the bundle-sheath cells moved towards the cell edge (Fig. 3e, f). At 20 % of field water capacity, the shape of chloroplasts in mesophyll cells changed from oval to round (Fig. 3f), whereas at 10 % of field water capacity, Kranz anatomy in leaves was already not visible due to complete wreck of leaf anatomical structure (Fig. 3g).

Bulliform cells located on the upper epidermis of maize leaves, are large parenchyma cells containing a large vacuole. They are considered one of the components involved in the regulation of leaf shriveling and spreading through quick water loss and acquisition (Zhang et al. 2015). Under non-limiting water conditions, the volume of bulliform cells tended to decrease with developmental phase of maize (Fig. 4a–d). Reducing soil water content led to a significant decline in the volume and an inward shrinkage of cell walls of bulliform cells (Fig. 4e, f). Once the field water capacity reduced to the level of 10 %, bulliform cells collapsed as leaf anatomical structure was damaged seriously (Fig. 4g).

Effects of persistently reduced soil water content on plant growth

During the reduction in the field water capacity from 75 to 35 %, maize plants still showed an obvious increase in height, leaf area, and total biomass based on dry weight (Fig. 5a–c). Even if the field water capacity decreased further to 25 %, leaf area did not expand further, but plant height and biomass still tended to increase. However, under soil water content below 25 % field water capacity, not only plant growth stopped completely, but also the height and biomass tended to decrease, likely due to drought-induced shrinkage and respiration consumption of plant organs. Also leaf thickness decreased significantly with persistent reduction in soil water content (Fig. 5d).

Fig. 3 Variations in leaf Kranz anatomy with the development of maize grown under non-limiting water conditions (from **a** and **b** to **c** and **d**) and when field water capacity reduced to $55 \pm 5\%$ (**e**), $20 \pm 5\%$ (**f**), and $10 \pm 5\%$ (**g**), and variations in the diameter of bundle-sheath cells of maize grown under non-limiting water condition (from *H1* and *H2* to *H5* and *H7*) and when field water capacity reduced to $55 \pm 5\%$ and $20 \pm 5\%$ (*n. d.* not determined), respectively. *Ch* chloroplast, *Bs* bundle-sheath cells, *Ms* mesophyll cells. Bar 100 μm

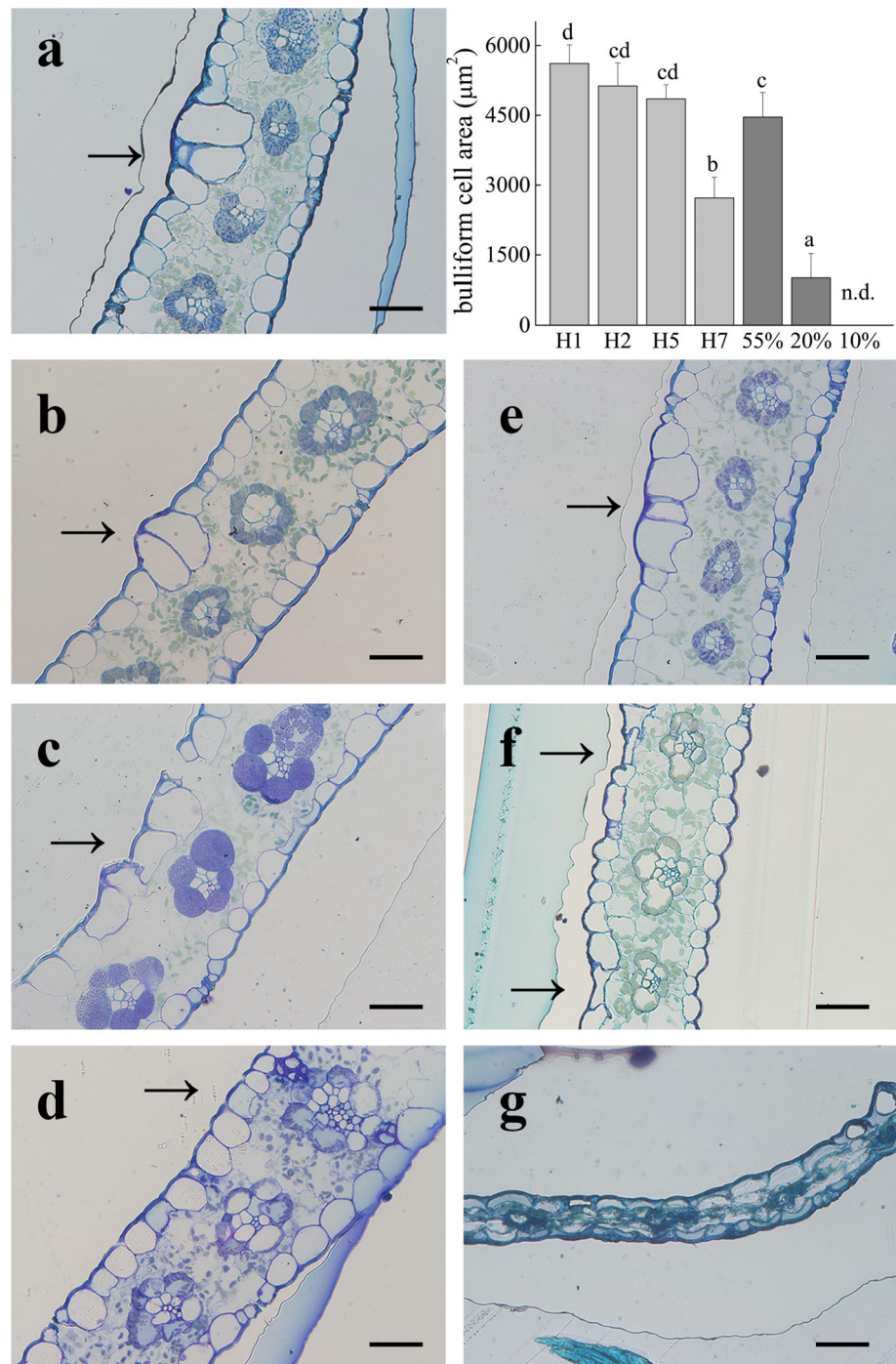


Effects of persistently reduced soil water content on diurnal variations in P_n

P_n of plants grown at 55 % field water capacity did not differ from plants grown under non-limiting water conditions, but at 35 % field water capacity, P_n decreased significantly from 9:00 to 19:00 compared to control (Fig. 6a). In plants grown

at field water capacity reduced to 25 and 20 %, P_n showed a relative high level only in the early morning, then decreased significantly through the rest of the day (Fig. 6b). Once the field water capacity further decreased to 15 %, P_n was near to zero in the whole day (Fig. 6b), and was undeterminable at 10 % field water capacity, that means a complete loss of leaf photosynthetic ability.

Fig. 4 Morphological variations in leaf bulliform cells with the development of maize grown under non-limiting water content (from **a** and **b** to **c** and **d**) and when field water capacity reduced to 55 ± 5 % (**e**), 20 ± 5 % (**f**), and 10 ± 5 % (**g**), and variations in the area of leaf bulliform cells of maize grown under non-limiting water conditions (from *H1* and *H2* to *H5* and *H7*) and when field water capacity reduced to 55 ± 5 and 20 ± 5 % (*n. d.* not determined), respectively. Bar $100 \mu\text{m}$



Observation of growth vitality recovery of drought-stressed plants after re-watering

Morphological observations showed that as soon as the field water capacity decreased to 35 %, leaves began to shrink and curl. But despite the leaf shrinkage and curling, spatial configuration of plants remained as it was before, even if field water capacity decreased to 25 and 10 % (Fig. 7a–d). Results of re-watering experiments

demonstrated that plants which had been suffered the persistent reduction to 25, 20, and 15 % of field water capacity, after re-watering, could quickly absorb water and recover growth vitality within few hours, which was reflected by leaf spreading and increasing in leaf water content (Fig. 7e–h). However, plants which had been exposed to a persistent reduction in field water capacity to 10 %, could not recover their growth vitality until a week after re-watering.

Fig. 5 Effects of persistently reduced soil water content on plant height (a), total leaf area of individual plant (b), biomass (c), and leaf thickness (d) of maize (*n. d.* not determined). Different letters about columns indicate statistically significant difference at $P < 0.05$ (mean \pm SD, $n = 6$)

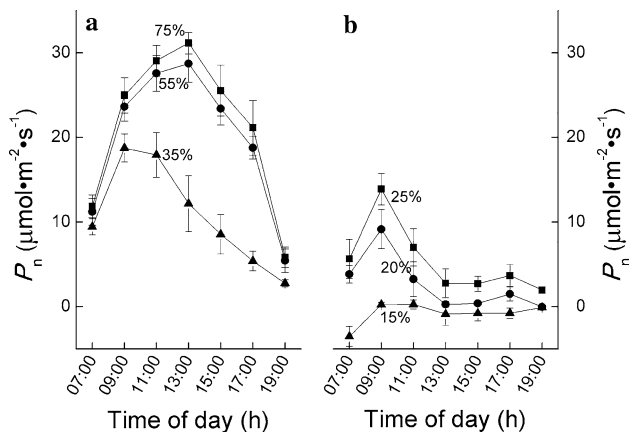
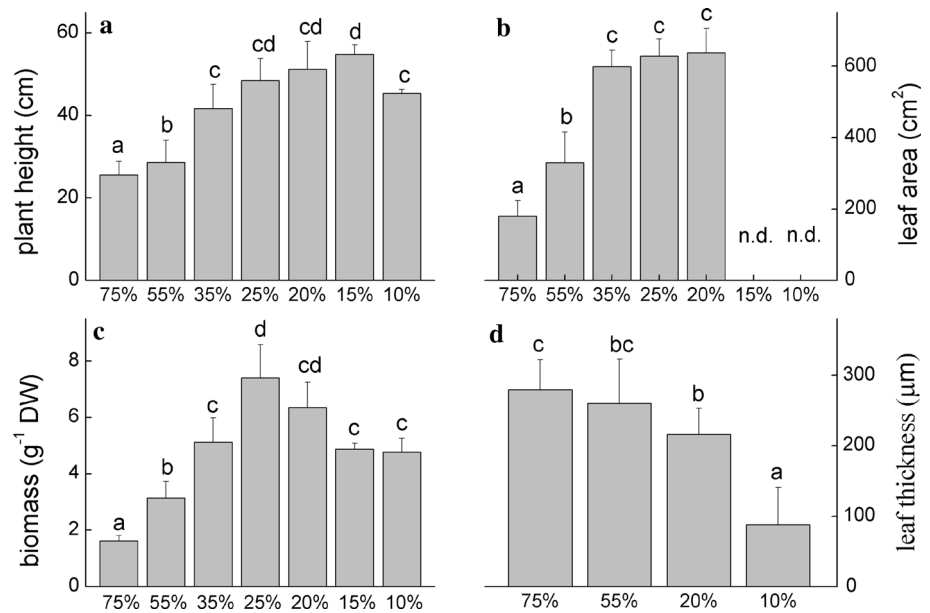


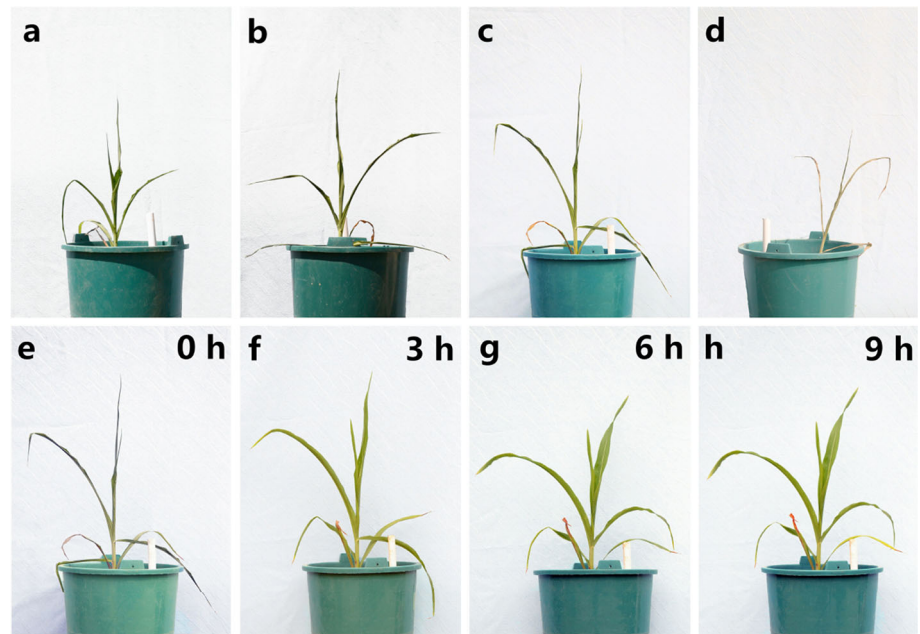
Fig. 6 Diurnal variations in net photosynthetic rate (P_n) of maize leaves when field water capacity persistently reduced from 75 ± 5 to 55 ± 5 %, 35 ± 5 % (a), 25 ± 5 %, 20 ± 5 %, and 15 ± 5 % (b), respectively (mean \pm SD, $n = 6$)

Discussion

During the past decades, much progress in plant science has been made toward understanding plant drought-resistant mechanism. However, in the face of the challenge of increasing drought frequency and duration, our understanding of crop response to both durable drought and repeated drought is relatively poor, and the mechanism of plant death induced by drought remain still in discussion (Sperry et al. 1988; McDowell et al. 2008; Anderegge et al. 2012). For agricultural practice, the knowledge about whether plants which have been exposed to a long-lasting drought can recover growth after re-watering is also important.

Plants growing in changing environment always maintain a dynamic water balance by regulating the relationship between the acquirement by roots from soil, leaf transpirative loss, and metabolic use. When soil water deficit occurs, roots firstly sense the reduction in soil water content and generate a series of hydraulic and/or chemical signals, that induce metabolic changes to stimulate water absorption by roots and reduce leaf transpiration and plant growth (Davies and Zhang 1991; Davies et al. 2002; Alvarez et al. 2008; McDowell et al. 2008; Baluška 2013; Yao et al. 2013). But if soil water availability is too low that acquired water by roots cannot compensate leaf transpirative loss, internal re-distribution of limited water resource between different parts of plants is very important in response to drought. Results of the present study showed that during persistent reduction in field water capacity from 75 to 20 %, maize plant growth decreased, while water content declined first in lower old leaves and their leaf sheathes, subsequently in upper leaves and leaf sheathes, and then in stem and roots. But even at 20 % field water capacity, the water content of upper leaves remained still at the level of 60 %, and the leaves possessed the photosynthetic ability in the early morning. The reduction amplitude inconsistency between soil water content and leaf water content demonstrates the ability of maize plants to regulate water balance of leaves by the internal water re-distribution. The programmed reduction in water content and the heterogeneity of water distribution between the different parts of the plants may be an effective mechanism for maintaining the ability of carbon assimilation of upper leaves and the vitality of growing points of above and underground organs (Lawlor and Cornic 2002; Lambers

Fig. 7 Morphological variations of maize exposed to persistent reduction in field water capacity from $25 \pm 5\%$ (a), to $20 \pm 5\%$ (b), $15 \pm 5\%$ (c), and $10 \pm 5\%$ (d), and growth vitality recovery of plants which had exposed to a persistent reduction in field water capacity until to $15 \pm 5\%$ after re-watering (e–h)



et al. 2008; Randriamanana et al. 2012; Van den Bilcke et al. 2013; Nada and Abogadallah 2014).

However, if drought developed further the role of internal water re-distribution apparently was limited and the regulation was not enough to help plants to survive, because of drought-induced damage to leaf microscopic structure, especially photosynthetic machine. At 20 % field water capacity, in this study, a decline in the volume and an inward shrinkage of bulliform cells could prevent leaf dehydration (Clarke 1986; Ristic and Cass 1991; Al-Maskri et al. 2014), but on the other hand also means the loss of the ability of the leaves for hydraulic fine regulation. Under lower field water capacity than 20 %, the number of chloroplasts in bundle-sheath cells decreased, and chloroplasts in mesophyll cells deformed, similar to previous studies (Dekov et al. 2000; Yamane et al. 2003; Chen et al. 2004; Grigorova et al. 2012), concomitant of a complete loss in carbon assimilation ability of the leaves, reflected by P_n close to zero. In this case, carbon starvation will occur and, under further development of drought, lead to plant death (McDowell et al. 2008; McDowell 2011; Anderegge et al. 2012; Sevanto et al. 2014; Dickman et al. 2015). In the present study, maize plants did not die quickly, even if the field water capacity reduced further to 15 %, as after a timely soil water compensation, maize plants could recover growth vitality within few hours. Only under field water capacity lower than 15 %, the re-watering was useless. In agricultural practice, this is important for crops which are exposed to persistent drought.

In conclusion, under persistent reduction in soil water content, maize growth decreased, while water content declined along the sequence of lower old leaves and their leaf

sheathes, upper leaves and leaf sheathes, stem and roots, to keep the ability of carbon assimilation of upper leaves and the vitality of growing points of above and underground organs. Soil water content below 20 % field water capacity led to a severe damage of leaf anatomical structure, concomitant of a P_n close to zero and of growth stop. Maize plants could recover growth vitality after re-watering even if field water capacity persistently reduced to 15 % but not to 10 %.

Author contribution statement Xiping Liu and Chunmei Gong contributed to the conception of the study. Yonglin Sun performed the experiments, analyzed the data and wrote the manuscript. Hongyue Wang and Hao Sheng helped perform the analysis with constructive discussions. Yaqin Yao approved the final version.

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Compliance with ethical standards

Conflicts of interest The authors of the paper declare that they have no conflict of interest.

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