Morphological plasticity of root growth under mild water stress increases water use efficiency without reducing yield in maize

Qian Cai[1, 2], Yulong Zhang[1*], Zhanxiang Sun[2*], Jiaming Zheng[2], Wei Bai[2], Yue Zhang[3], Yang Liu[2], Liangshan Feng[2], Chen Feng[2], Zhe Zhang[2], Ning Yang[2], Jochem B. Evers[4], Lizhen Zhang[3]

[1]College of Land and Environment, Shenyang Agricultural University, Shenyang, 110161, Liaoning, China;

[2]Tillage and Cultivation Research Institute, Liaoning Academy of Agricultural Sciences, Shenyang, 110161, Liaoning, China;

[3]College of Resources and Environmental Sciences, China Agricultural University, Beijing, 100193, China.

[4]Wageningen University, Centre for Crop Systems Analysis (CSA), Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands

First author

Qian Cai, Email: caiqian2005@163.com

***Corresponding author**

Yulong Zhang, Email: ylzsau@163.com;

Zhanxiang Sun, Email: sunzhanxiang@sohu.com

Abstract

Large yield gap exists in rain-fed maize (*Zea mays* L.) production in semi-arid regions, mainly caused by frequent droughts halfway the crop growing period due to uneven distribution of rainfall. It is questionable if irrigation systems are economically required in such a region since total amount of rainfall generally meet the crop requirement. This study aimed to quantitatively determine the effects of water stress during jointing to filling stages on root and shoot growth and the consequences for maize grain yield, above- and below-ground dry matter, water uptake (WU) and water use efficiency (WUE). Pot experiments were conducted in 2014 and 2015 with a mobile rain shelter. The experiments consisted of three treatments: (1) no water stress; (2) mild water stress; and (3) severe water stress. The cumulative frequency for no water stress (above 500 mm) during maize growing season was 69 % from 1965 to 2015, 28 % for mild water stress (350-450 mm) and 4 % for severe stress (200-300 mm). Maize yield in mild water stress across two year was not significantly affected, while severe stress reduced yield by 56 %. Water stress decreased root biomass slightly but shoot biomass substantially. Mild water stress decreased root length but increased root diameter, resulting a no effect on root surface area. Due to the morphological plasticity of root growth and the increase in root/shoot ratio, WU under water stress was decreased, and WUE for maize above-ground dry matter under mild water stress was increased by 20 % across two years, and 16 % for grain yield WUE. Our results demonstrates that well irrigation system using underground water in studied region might be not economically and ecologically necessary because the frequent occurred mild water stress did not reduce crop yield much. The study helps to understand crop responses to water stress during critical water-sensitive period (middle crop growing season) and to mitigate drought risk in

dry land agriculture.

Keywords: root diameter; root length; root surface area; root/shoot ratio; yield components; water utilization

1. Introduction

Maize (*Zea mays* L.) as one of the most important crops globally, is a major food crop in northeast China with an average yield around 5.3 t ha^{-1} (Dong et al., 2017). However, the yield gap to the potential of 10.9 t ha^{-1} is still large (Liu et al., 2012), mainly due to frequent summer droughts caused by an uneven distribution of rainfall during the crop growing season. As global warming causes high expected frequency of extreme climate events (IPCC, 2007), drought risk for agricultural production in this region is likely to increase (Song et al., 2014; Yu et al., 2014). Water stress changes crop responses in morphological and physiological traits (Pampino et al., 2006). Warming and dry trends under climate change would result deleterious effects on crop photosynthesis and yield (Richards, 2000).

Although the total amount of rainfall can meet the requirement of rain-fed maize in the semi-arid northeast China, the yearly and seasonal variations often cause a frequent drought (mostly mild water stress) during summer, resulting a high risk of yield loss. It can be questioned whether well irrigation systems using underground water are economically and ecologically required in this situation, since it is not quantitatively known how the crop yield and water use efficiency would be affected by drought stress during summer in this region.

Suppression of yield by water stress is caused by reducing crop growth (Payero et al., 2006), canopy height (Traore et al., 2000), leaf area index (NeSmith and Ritchie, 1992) and root growth (Gavloski et al., 1992). Crop shoot development and biomass accumulation are greatly reduced by soil water deficit at seeding stage (Kang et al., 2000). Short-duration water deficits during the rapid vegetative growth period causes around 30% loss in final dry matter (Cakir, 2004). The reduction of maize yield by water stress is caused by decreases in yield components such as ear density, number of kernels per ear and kernel weight (Ge et al., 2012), especially during or before maize silk and pollination period (Claassen and Shaw, 1970). The accumulative biomass and harvest index (the ratio of grain yield over total aboveground dry matter) are decreased under water stress during anthesis (Traore et al., 2000).

Water use efficiency (WUE, expressed in kg yield obtained per m^3 of water) is notably reduced by severe water stress especially at vegetative and reproductive stages. Interestingly a moderate water stress at V16 (with 16 fully expanded leaves) and R1 (silking) stages in maize increased WUE (Ge et al., 2012) because it did not significantly affected the ecophysiological characteristics during vegetative stages. The irrigation deficits before the maize tasseling stage are often used for improving WUE in regions with serious water scarcity, e.g. North China Plain (Qiu et al., 2008; Zhang et al., 2017). For example, in winter wheat WUE was increased continuously from 1987 to 2015 especially under water stress condition that was obtained from a increased harvest index and the reduced soil evaporation (Zhang et al., 2017). Under water stress, plant photosynthesis and transpiration decreases due to a decrease in stomata conductance (Killi et al., 2017) induced by increasing concentration of abscisic acid (ABA) in plant (Beis and Patakas, 2015). However, limited knowledge exists on how much the partitioning between shoot and root in maize is affected by water stress during middle and late growing stages, and if the root growth and morphology regulated by water stress could improve maize yielding and water use efficiency.

Since field water stress experiments were difficult to carry out in rain-fed agriculture, a large mobile rain shelter was often used in studies to control water stress (NeSmith and Ritchie 1992). The objective of this study was to quantify maize shoot and root growth, grain yield and WUE under different water stresses during middle crop growing season obtained by a well-controlled mobile rain shelter, to understand the crop response to water stress during critical water-sensitive period.

2. Materials and methods

2.1. Experimental design

The experiments were conducted at Shenyang (41°48′N, 123°23′E), Liaoning province, northeast China in 2014 and 2015. The experimental site is 45 m above sea level. On average from 1965 to 2015, annual potential evaporation is 1445 mm, total precipitation is 720 mm, and mean air temperature is 8 ^{o}C. The length of the frost-free period is 150-170 days. Average relative humidity is 63 %. Annual mean wind speed is 3.1 m s^{-1}. The climate is a typical continental monsoon climate with four distinct seasons, characterized as a hot summer and cold winter. The annual mean air temperature was 9.5 ^{o}C in 2014 and 9.1 ^{o}C in 2015. The mean air temperature during crop growing season (May to September) was 20.2 ^{o}C in 2014 and 19.4 ^{o}C in 2015 (Fig. 1).

Maize plants were grown in pots in three treatments: (1) no water stress; (2) mild water stress and (3) severe water stress (Table 1). The levels of water stresses were based on historical rainfall frequency analysis. The water supply was controlled by a mobile rain shelter with steel frame and transparent PVC cover. The mobile rain shelter is built on a mechanical movement track equipping with a electricity motor to move the shelter by a remote control. The shelter was moved away from the experimental plots in no rain days and covered before a rain came, therefore the effect of shelter on incoming radiation could be ignored. The mobile rain shelter is 9 m in width, 30 m in length and 4.5 m in height. The top and both sides of the shelter have PVC transparent boards to prevent outside rainfall. There is a water gutter at out side of movement track to drain the rain water. Therefore the rain water intrusion can be avoided. Water treatments began from maize jointing (V6, with 6 fully expended leaves) to filling stages (R3, milk) (Abendroth et al., 2011). Water treatments were conducted by supplying irrigations once per 5 days before starting water treatments with same amount for all pots, and once per 3 days during the period of water treatments. The detail amount of water supplied to each treatment was listed in Table 1. The experiments entailed a completely randomized block design with three replicates. Each treatment consisted of 12 pots (one plant per pot) and divided into 3 replicates (4 pots each). At each sampling time (totally sampling 4 times), one pot was used.

Each pot was 40 cm in diameter and 50 cm in height, filled with 40 kg naturally dried soil with a bulk density of 1.31 g cm^{-3}. Large size of pots in the experiments effectively avoided space effect of growing good maize. The soil was sandy loam with a pH of 6.15, total N of 1.46 g kg^{-1}, total of P 0.46 g kg^{-1} and total K of 12.96 g kg^{-1}. 46.5 g compound fertilizer (N 15 %, P_2O_5 15 % and K_2O 15 %) and 15.5 g diammonium phosphate (N 18 % and P_2O_5 46 %) were applied to each pot before sowing. There was no other fertilizer applied during maize growing season. Maize cultivar used in both years was Liaodan 565, a locally common used drought-resistant cultivar. One plant was grown in each pot. Maize was sown on 13 May and harvested on 30 Sept in both 2014 and 2015.

2.2 Dry matter and grain yield measurements

To determine maize dry matter, four plants were harvested on 49 (V6, jointing), 77 (VT, tasseling), 113 (R3, milk) and 141 (R5, dent) days after sowing (DAS) in 2014, and one sampling was done on 132 DAS in 2015. The samples were separated into root and shoot, and dried in an oven at 80 °C for 48 hours until reaching a constant weight. The shoot/root ratio was calculated using dry matters measured.

Grain yield was measured by harvesting all cobs in a pot in maize harvesting time. The grain was sundried with a water content of 15%. Yield components i.e. ear (cob) numbers per plant, kernel numbers per ear and thousand kernel weight were measured for all plots.

2.3 Root measurements

Root growth and morphological traits (root length, diameter and surface area) were measured four times during crop growing season on 49 , 77, 113, 141 DAS in 2014. The whole roots were collected per pot at the time of dry matter measurements. Root samples were carefully washed with tap water to remove impurities. The cleaned roots were placed on a glass plate of a root system scanner. Scanned root images were analyzed by a plant root image analyzer WinRHIZO PRO 2009 (Regent Instruments Inc., Canada) to quantify total root length (m), diameter (mm) and surface area (m^2) per plant (pot).

2.4 Measuring soil moisture content, water uptake and water use efficiency

Soil moisture contents were measured by a soil auger at sowing and harvesting times for each plot (3 replicates per treatment). Soil cores were taken from the middle of a pot for each 10 cm layer. After measuring fresh soil weight, soil samples were dried in an oven at 105 °C for around 48 hours until a constant weight was reached. The gravimetric soil moisture contents (%, g g^{-1}) measured by soil auger were calculated into volumetric soil moisture content (%, m^3 m^{-3}) by multiplying with soil bulk density.

Water uptake (WU) of maize was calculated using a simplified soil water balance equation (Kang et al., 2002). Because the experiments were sheltered, rainfall, drainage and capillary rise of water did not occur in this situation and therefore were not taken into account in the calculation of WU:

$$WU = I + \Delta S \quad (1)$$

where WU (mm) is crop water uptake (mm) during whole crop growing season, I is the amount of water supplied to each pot (mm). ΔS is the changes of soil water amount between sowing to harvesting dates.

Water use efficiency (WUE) was calculated by measured final yield or above-ground dry matter and total WU during crop growing season (Zhang et al., 2007).

$$WUE = Y/WU \quad (2)$$

where WUE (g m^{-2} mm^{-1} or kg m^{-3}) is water use efficiency expressed in gain yield WUE_Y or dry matter WUE_{DM}. Y (g m^{-2}) is grain yield or dry matter. WU (mm) is total water uptake during maize growing season.

2.5. Statistical analysis

Analysis of variance on yield, WU, WUE, and dry matter for shoot and root were performed using General Linear Model of SPSS 20 (SPSS Inc., Chicago, USA). The differences between means were evaluated through LSD multiple comparison tests at a significant level of 0.05.

3. Results

3.1 Variation and frequency distribution of rainfall

The average rainfall during maize growing season (May to September) at experimental site from 1965 to 2015 was 531 mm with a standard deviation of 134 mm (Fig. 2 a). The cumulative frequency of rainfall above 500 mm was 69 % during past 51 years. The frequency with mild drought stress (350-450 mm) was 28 % and it with severe drought stress (200-300 mm) was 4 % (Fig. 2 b), indicating that the maize growing in this climate mainly suffered mild water stress.

3.2 Yield and yield components

Maize yield under mild water stress across two year was not significantly different with no stress control, while that in severe stress was 56 % lower (Table 2). The decrease of maize yield in severe water treatments was due to the decreases in ear number, kernel number and harvest index (HI). However, water stress did not affect kernel weight, while other yield components were decreased. Year effect was only significant for HI, which was likely caused by the variation in air temperature: the cooler weather in 2015 during maize growing season decreased HI comparing with a warmer year in 2014. There were no interactions between year and treatment.

3.3 Above- and below-ground dry matters

Mild water stress did not reduce root dry matter (Fig. 3 a, b), but greatly reduced shoot dry matter, especially at grain filling stage (113 DAS) (Fig. 3 c, d). The severe water stress decreased both root and shoot dry matter compared with no stress control, but the magnitude of the decrease in shoot was much larger than in root. At maize tasseling stage (77 DAS), as roots generally reached their maximum size, root dry matter under severe water stress was much lower than mild and no water stress treatments. However, it became less different later in the season, which indicated a strong complementarily growth of root system under water stress. Due to the different responses of shoot and root to water stress, the root/shoot ratios under water stress were increased (Fig. 3 e, f), especially during crop rapid growing period (77 to 113 DAS).

3.4 Root length, diameter and total surface area affected by water stresses

Root length per plant was much lower under severe water stress, especially at tasseling stage (77 DAS). Mild water stress during maize middle growing season also decreased root length, but the difference with no stress control was much smaller than severe stress (Fig. 4 a). Root diameters under both mild and severe water stress treatments were much higher than under no stress control (Fig. 4 b), especially at late growing season. Total root surface area was less changed (Fig. 4 c), especially during maize reproductive growth period (113 DAS).

3.5 Water uptake and use efficiency

Total water uptakes (WU) under water stress treatments were lower than under no stress control (Fig. 5). Water use efficiency for maize above-ground dry matter (WUE_{DM}) under water stresses was increased 30.3 % comparing with no stress control, across all years and treatments (Fig. 5 b). The WUE_{DM} in severe water stress was the highest. However, WUE for grain yield under severe water stress was not significantly different with that in the control, while that in mild water stress increased 15.7 % across two years (Fig. 5 c). The difference between WUE in dry matter and grain yield was due to a decrease in HI under severe water stress (Table 2).

4. Discussion and conclusions

Mild water stress during the middle growing period did not significantly reduce maize grain yield. It is different with previous report that maize yield is much more affected by water stress during flowering stage than other stages (Doorenbos et al., 1979). Our result differed with a previous study, which showed mild water stress seriously reduced crop production (Kang et al., 2000). This is likely due to our choice of a drought-resistant variety (Zhengdan 565) and the difference in ecological zones. Genotype-dependent relationships between yield and crop growth rate would be stronger under water stress than under no stress condition (Lake and Sadras, 2016).

Mild water stress during middle crop growing period can maintain maize yield but substantially reduces the water consumption at the same time in our study. Thus, the water use efficiency was increased (Liu et al., 2016). Mild water stress reduced total water uptake, resulting a 20 % higher WUE in dry matter and a 16% higher WUE in yield. The increase in WUE under mild water stress was from the responses of shoot and root growth to water stress, as an increase in root/shoot ratio. The water stress reduced root length growth, however, this reduction was compensated by an increase in root diameter. However, the maintenance of crop growth under water stress was limited by the severity of the stress. Under severe water stress, maize growth fails to be compensated by plant plasticity.

Severe water stress greatly reduced both shoot and root biomass. Large decreases in shoot growth, i.e. less biomass and leaf area, reduces the light interception and transpiration (Monteith, 1981). Under mild water stress during vegetative and tasselling stages, the shoot growth was not significantly reduced in this study but in previous report, e.g. plant height, leaf area development (Cakir, 2004). Mild soil water deficit may also reduce water loss from plants through physiological regulation (Davies and Zhang, 1991). A moderate soil drying at the vegetative stage encourages root growth and distributing in deep soil (Jupp and Newman, 1987; Zhang and Davies, 1989), which is consistent with our findings. Large root system with deep distribution is beneficial for water-limited agriculture (McIntyre et al., 1995). These mechanisms explained why maize yield under mild water stress was not decreased in our study.

We found an increase in root diameter under water stresses, although root length was decreased. This result indicated that the lateral roots under water stress were probably less than under no water stress. That may limit water absorption since the lateral roots is younger and more active in uptake function (Lynch, 1995). Average root diameters in all treatments decreased from 77 to 113 DAS, which was caused by highly emerged lateral roots after the main root system reached its maximum (VT stage). The higher average root diameter in water stress treatments than in the control at 141 DAS was probably due to a fast senescence of late developed lateral roots under water stress.

Our results on root morphological plasticity affected by mild water deficit provided another evidence for enhancing WUE and maintaining yielding. However, the mechanism that determines crop response to water stress may also involve other processes, e.g. intercellular CO_2, stomatal conductance, photosynthetic rate, oxidative stress, sugar signaling, membrane stability and root chemical signals (Xue et al., 2006; Dodd, 2009). The relationship between carbon assimilation and water stress have been widely explored to understand the physiological mechanism for improving WUE (Ennahli and Earl, 2005; Xue et al., 2006; Zhang et al., 2013). The abscisic acid (ABA)-based drought stress chemical signals regulates crop vegetative and reproductive development and contributes to crop drought adaptation (Killi et al., 2017). Increased concentration of ABA in the root induced by soil drying may maintain root growth and increase root hydraulic conductivity, thus increases crop water uptake and thereby postpone the development of water deficit in the shoot (Liu et al., 2005). The increase of ABA can also induce stomatal closure and reduces crop transpiration (Haworth et al. 2016), net photosynthesis and crop growth (Killi et al., 2017).

The maize yield in 2015 was much lower than in 2014 independent of water stress. That might be caused by a higher maximum air temperature in 2015 (32.0 ^{o}C) than in 2014 (29.1 ^{o}C) during flowering period. High air temperature would reduce maize pollination (Muller and Rieu, 2016) and directly affected yield formation and HI.

This study clearly demonstrates that the maize yield under mild water stress during summer does not decrease but the water use efficiency increases due to changes in root and shoot growth. A higher root/shoot ratio under mild water stress allows plant efficiently use limited soil water. In studied region (Liaoning province), maize mainly grows in rain-fed condition (2.4 million ha), covering 73 % of total area for grain crops. To reduce the possible effect of drought on maize production, the wells system piping underground water to irrigate crop is planned recently. The wells need to be 60 to 70 m deep with an average cost of 12,000 Yuan for each. Each well can only irrigate 9 to 10 ha of maize. According to our results, only severe water stress significantly reduces maize yield (up to 50%), which occurs less than 5 % during 1965 to 2015. Mild water stress occurs much frequently (28% of years), however, it does not affect maize yield significantly. Our study suggested that the well system in this region might not be economically and ecologically necessary. Other agronomy practices such as intercropping maize with crops requiring less water (e.g. peanut), cultivar selection, adjusting sowing windows (Liu et al., 2013; Lu et al., 2017) and ridge-furrow with plastic film (Dong et al., 2017) are more applicable in optimizing crop yield and regional sustainability. Our study provides more evidences to understand crop responses to water stress, especially in relation to root morphological plasticity in a drought environment. The results can be further applied combining with crop model (Mao et al., 2015) to mitigate climate risk in dry land agriculture.

Author contribution

Z. Sun, Y. Zhang, J. Zheng and Q. Cai conceived and designed the experiments. Q. Cai, W. Bai, Y Zhang, Y. Liu, L. Feng, C. Feng, Z. Zhang and N. Yang performed the experiments. L. Zhang, Q. Cai and J.B. Evers analyzed the data and wrote the paper.

Competing interests

The authors declare that they have no conflict of interest.

Special issue statement

Special issue: Ecosystem processes and functioning across current and future dryness gradients in arid and semi-arid lands.

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References

Abendroth, L.J., Elmore, R.W., Boyer, M.J., Marlay, S.K., 2011. Corn Growth and Development. PMR 1009. Iowa State University Extension, Ames, Iowa, USA. https://store.extension.iastate.edu/Product/Corn-Growth-and-Development (accessed in 8 June 2017).

Beis, A., Patakas, A., 2015. Differential physiological and biochemical responses to drought in grapevines subjected to partial root drying and deficit irrigation. Eur. J. Agron. 62, 90-97.

Cakir, R., 2004. Effect of water stress at different development stages on vegetative and reproductive growth of corn. Field Crop Res. 89, 1-16.

Claassen, M.M., Shaw, R.H., 1970. Water deficit effects on corn. II. Grain components. Agron. J. 62, 652-655.

Davies, W.J., Zhang, J., 1991. Root signals and the regulation of growth and development of plants in drying soil. Ann. Rev. Plant Physiol. Plant Mol. Biol. 42, 55-76.

Dodd, I.C., 2009. Ehizosphere manipulations to maximize crop per drop during deficit irrigation. J. Exp. Bot. 60, 2454-2459.

Dong, W., Zhang, L., Duan, Y., Sun, L., Zhao, P., van der Werf, W., Evers, J.B., Wang, Q., Wang, R., Sun, Z., 2017. Ridge and furrow systems with film cover increase maize yields and mitigate climate risks of cold and drought stress in continental climates. Field Crops Res. Doi:10.1016/j.fcr.2017.03.003.

Doorenbos, J., Kassam, A.H., Bentvelsen, C., Uittenbogaard, G., 1979. Yield response to water. FAO Irrigation and Drainage Paper No. 33, FAO, Rome, Italy. pp.193.

Ennahli, S., Earl, H.J., 2005. Physiological limitations to photosynthetic carbon assimilation in cotton under water stress. Crop Sci. 45, 2374-2382.

Gavloski, J.E., Whitfield, G.H., Ellis, C.R., 1992. Effect of restricted watering on sap flow and growth in corn (*Zea mays* L.). Can. J. Plant Sci. 72, 361-368.

Ge, T., Sui, F., Bai, L., Tong, C. and Sun, N., 2012. Effects of water stress on growth, biomass partitioning, and water-use efficiency in summer maize (*Zea mays* L.) throughout the growth cycle. Acta Physiol. Plant. 34(3), 1043-1053.

Haworth, M., Cosentino, S.L., Marino, G., Brunetti, C., Scordia, D., Testa, G., Riggi, E., Avola, G., Loreto, F., Centritto, M., 2016. Physiological responses of *Arundo donax* ecotypes to drought: a common garden study. Glob. Change Biol. Bioenergy. Doi:10.1111/gcbb.12348.

IPCC Climate change, 2007. The physical science basis. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L., (Eds). Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge. pp. 996.

Jupp, A.P., Newman, E.I., 1987. Morphological and anatomical effects of severe drought on the roots of *Lolium perenne* L. New Phytol. 105, 393-402.

Kang, S.Z., Shi, W.J , Zhang, J.H, 2000. An improved water-use efficiency for maize grown under regulated deficit irrigation. Field Crops Res. 67, 207-214

Kang, S.Z., Zhang, L., Liang, Y.L., Hu, X.T., Cai, H.J., Gu, B.J., 2002. Effects of limited irrigation on yield and water use efficiency of winter wheat in the Loess Plateau of China. Agric. Water Manage. 55, 203-216.

Killi, D., Bussotti, F., Raschi A., Haworth, M., 2017. Adaptation to high temperature mitigates the impact of water deficit during combined heat and drought stress in C3 sunflower and C4 maize varieties with contrasting drought tolerance. Physiol. Plant. 159, 130-147.

Lake, L., Sadras, V.O., 2016. Screening chickpea for adaptation to water stress: Associations between yield and crop growth rate. Eur. J. Agron. 81, 86-91.

Liu, E.K., Mei, X.R., Yan, C.R., Gong, D.Z., Zhang, Y.Q., 2016. Effects of water stress on photosynthetic characteristics, dry matter translocation and WUE in two winter wheat genotypes. Agric. Water Manage. 167, 75-85.

Liu, F., Jensen, C.R., Andersen, M.N., 2005. A review of drought adaptation in crop plants: changes in vegetative and reproductive physiology induced by ABA-based chemical signals. Australian J. Agric. Res. 56(11), 1245-1252.

Liu, Z.J., Hubbard, K.G., Lin, X.M., Yang, X.G., 2013. Negative effects of climate warming on maize yield are reversed by the changing of sowing date and cultivar selection in Northeast China. Glob. Chang. Biol. 19, 3481-3492.

Liu, Z.J., Yang, X.G., Hubbard, K.G., Lin, X.M., 2012. Maize potential yields and yield gaps in the changing climate of northeast China. Glob. Chang. Biol. 18, 3441-3454.

Lu, H., Xue, J., Guo, D., 2017. Efficacy of planting date adjustment as a cultivation strategy to cope with drought stress and increase rainfed maize yield and water-use efficiency. Agric. Water Manage. 179, 227-235.

Lynch, J.P., 1995. Root architecture and plant productivity. Plant Physiol.109, 7-13.

Mao, L., Zhang, L., Evers, J. B., van der Werf, W., Wang, J., Sun, H., Su, Z., Spiertz, H., 2015. Resource use, sustainability and ecological intensification of intercropping systems. J. Integr. Agr. 14(8), 1442-1550.

McIntyre, B.D., Riha, S.J., Flower, D.J., 1995. Water uptake by pearl millet in a semiarid environment. Field Crops Res. 43, 67-76

Monteith, J.L., 1981. Coupling of plants to the atmosphere. In: Grace, J., Ford, E.D., Jarvis, P.G., (Eds.). Plants and their Atmospheric Environment. Blackwell, Oxford. pp. 1-29.

Muller, F., Rieu, I., 2016. Acclimation to high temperature during pollen development. Plant Reprod. 29(102), 107-118.

NeSmith, D.S., Ritchie, J.T., 1992. Short- and long-term responses of corn to pre-anthesis soil water deficit. Agron. J. 84, 107-113.

Payero, J.O., Melvin, S.R., Irmak, S., Tarkalson, D., 2006. Yield response of corn to deficit irrigation in a semiarid climate. Agric. Water Manage. 84, 101-112.

Qiu, G.Y., Wang, L.M., He, X.H., Zhang, X.Y., Chen, S.Y., Chen, J., Yang, Y.H., 2008. Water use efficiency and evapotranspiration of winter wheat and its response to irrigation regime in the north China plain. Agric. For. Meteorol. 148,1848-1859.

Rampino, P., Pataleo, S., Gerardi, C., Mita, G., Perrotta, C., 2006. Drought stress response in wheat: physiological and molecular analysis of resistant and sensitive genotypes. Plant Cell Environ. 29, 2143-2152.

Richards, A., 2000. Selectable traits to increase crop photosynthesis and yield of grain crops. J. Exp. Bot. 51, 447-458.

Song, X.Y., Li, L.J., Fu, G.B., Li, J.Y., Zhang, A.J., Liu, W.B., Zhang, K., 2014. Spatial-temporal variations of spring drought based on spring-composite index values for the Songnen Plain, Northeast China. Theor. Appl. Climatol. 116, 371-384.

Traore, S.B., Carlson, R.E., Pilcher, C.D., Rice, M.E., 2000. Bt and Non-Bt maize growth and development as affected by temperature and drought stress. Agron. J. 92, 1027-1035.

Xue, Q.W., Zhu, Z.X., Musick, J.T., Stewart, B.A., Dusek, D.A., 2006. Physiological mechanisms contributing to the increased water-use efficiency in winter wheat under deficit irrigation. J. Plant Physiol. 163, 154-164.

Yu, X.Y., He, X.Y., Zheng, H.F., Guo, R.C., Ren, Z.B., Zhang, D., Lin, J.X., 2014. Spatial and temporal analysis of drought risk during the crop-growing season over northeast China. Nat. Hazards 71, 275-289.

Zhang, J., Davies, W.J., 1989. Abscisic acid produced in dehydrating roots may enable the plant to measure the water status of the soil. Plant Cell Environ. 12, 73-81.

Zhang, J., Sun, J.S., Duan, A., Wang, J.L., Shen, X.J., Liu, X.F., 2007. Effects of different planting patterns on water use and yield performance of winter wheat in the Huang-Huai-Hai plain of China. Agric. Water Manage. 92, 41-47.

Zhang, X., Qin, W., Chen, S., Shao, L., Sun, H., 2017. Responses of yield and WUE of winter wheat to water stress during the past three decades—A case study in the North China Plain. Agric. Water Mange. 179, 47-54.

Zhang, X., Wang, Y., Sun, H., Chen, S., Shao, L., 2013. Optimizing the yield of winter wheat by regulating water consumption during vegetative and reproductive stages under limited water supply. Irrig. Sci. 31, 1103-1112.

Table 1 Water treatments during crop growing seasons in 2014 to 2015.

Year	Water treatment	Initial volumetric soil moisture content (%)	Actual water supply at three growing periods (mm)			
			Early (16-29 DAS[1])	Middle (30-102 DAS)	Late (103-121 DAS)	Total
2014	No stress	24.4	11.9	478	56	545
	Mild stress	24.8	11.9	299	56	366
	Severe stress	24.9	11.9	122	56	190
2015	No stress	25.3	11.9	510	32	553
	Mild stress	25.3	11.9	334	32	378
	Severe stress	24.4	11.9	159	32	203

[1]DAS refers days after maize sowing.

Table 2 Yield and yield components affected by different water stresses in 2014 to 2015

Year	Water treatment	Ear number	Kernel number	Thousand kernel weight	Yield per plant	Harvest index
		ears plant^{-1}	kernels ear^{-1}	g	g plant^{-1}	g g^{-1}
2014	No stress	2.0±0.0a	354±32a	440±6.8a	301±33a	0.36±0.01a
	Mild stress	2.0±0.0a	350±16a	416±1.2b	276±14a	0.37±0.01a
	Severe stress	2.0±0.0a	245±35b	412±3.7b	166±25b	0.27±0.02b
2015	No stress	2.0±0.0a	341±67a	426±12a	240±60a	0.29±0.04a
	Mild stress	2.0±0.0a	244±53a	427±22a	168±42ab	0.25±0.03a
	Severe stress	1.3±0.3b	172±46a	412±16a	81±22b	0.17±0.04a
mean	No stress	2.0±0.2a	347±38a	432±7.5a	266±36a	0.32±0.03a
	Mild stress	2.0±0.0a	289±36ab	422±12a	214±32a	0.30±0.03ab
	Severe stress	1.6±0.0b	203±31b	412±8.5a	118±23b	0.21±0.03b
P	Treatment	0.021	0.003	0.556	0.005	0.013
	Year	0.184	0.514	0.889	0.237	0.039
	Treat×Year	0.111	0.664	0.555	0.835	0.758

Same small letters indicate no significant difference between water treatment within same year at *a*=0.05.

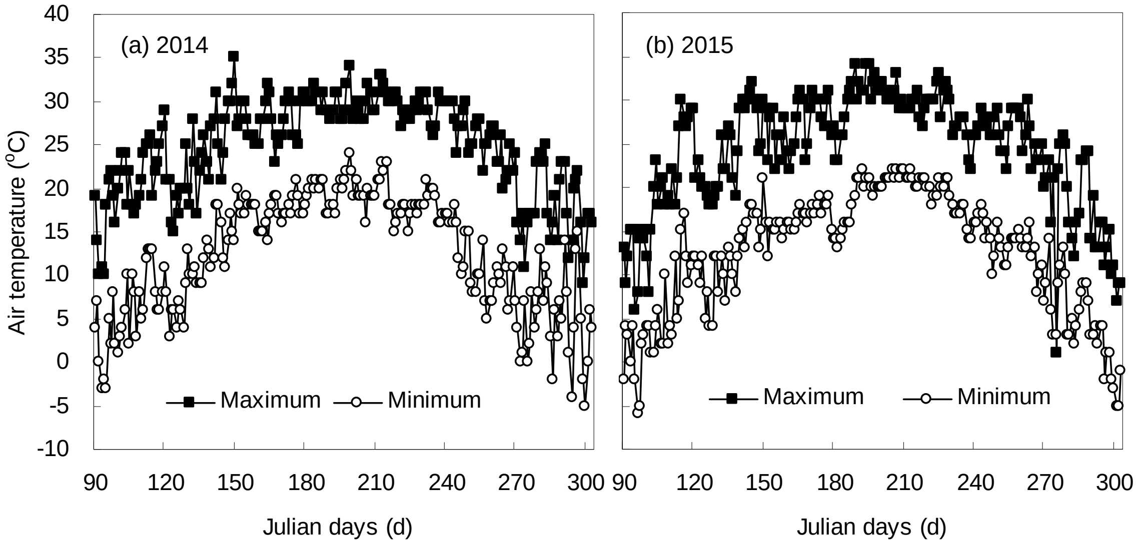


Fig. 1 Daily maximum and minimum air temperatures in 2014 and 2015 in Shengyang, Liaoning, China

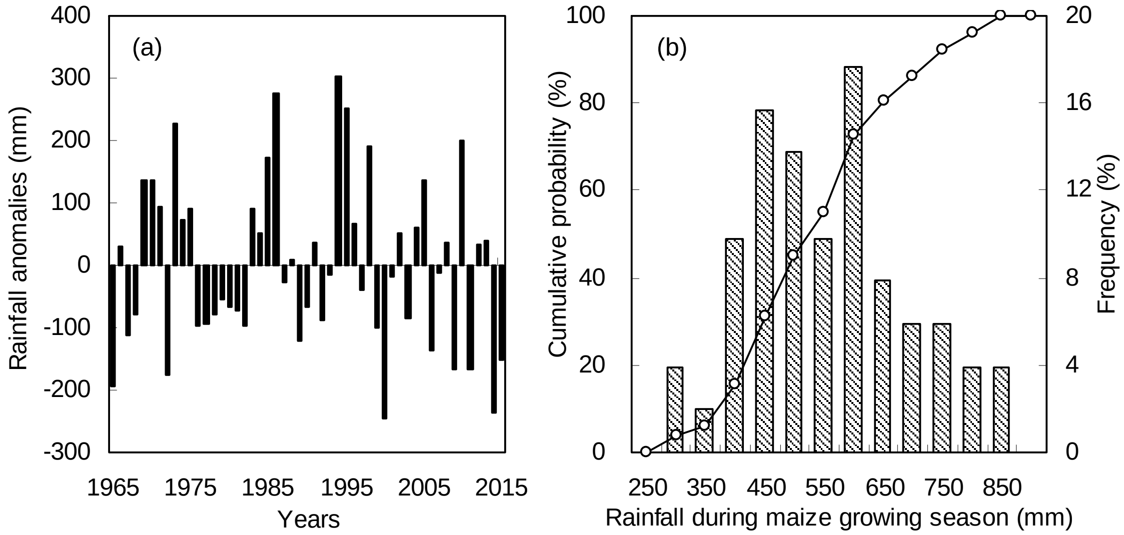
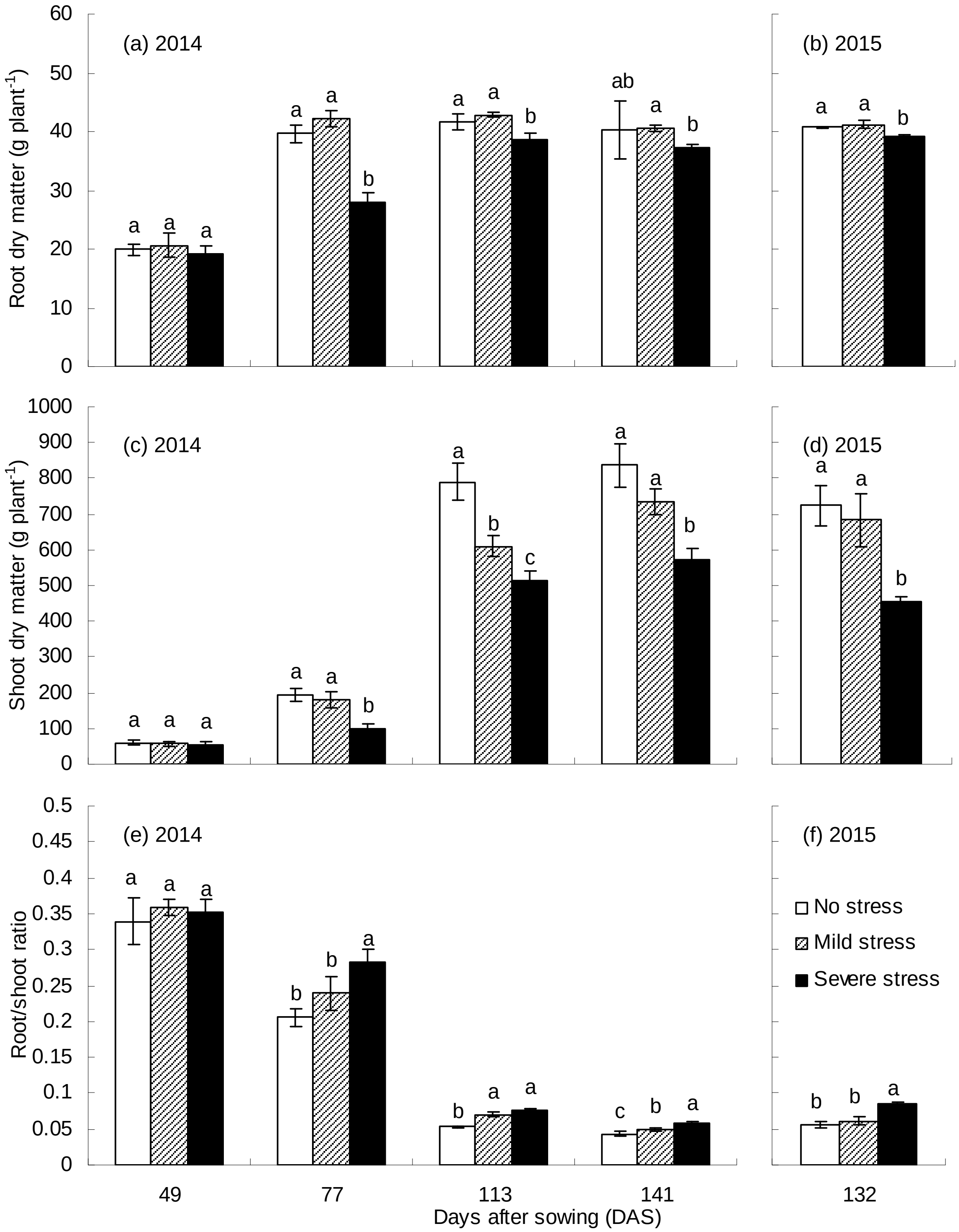
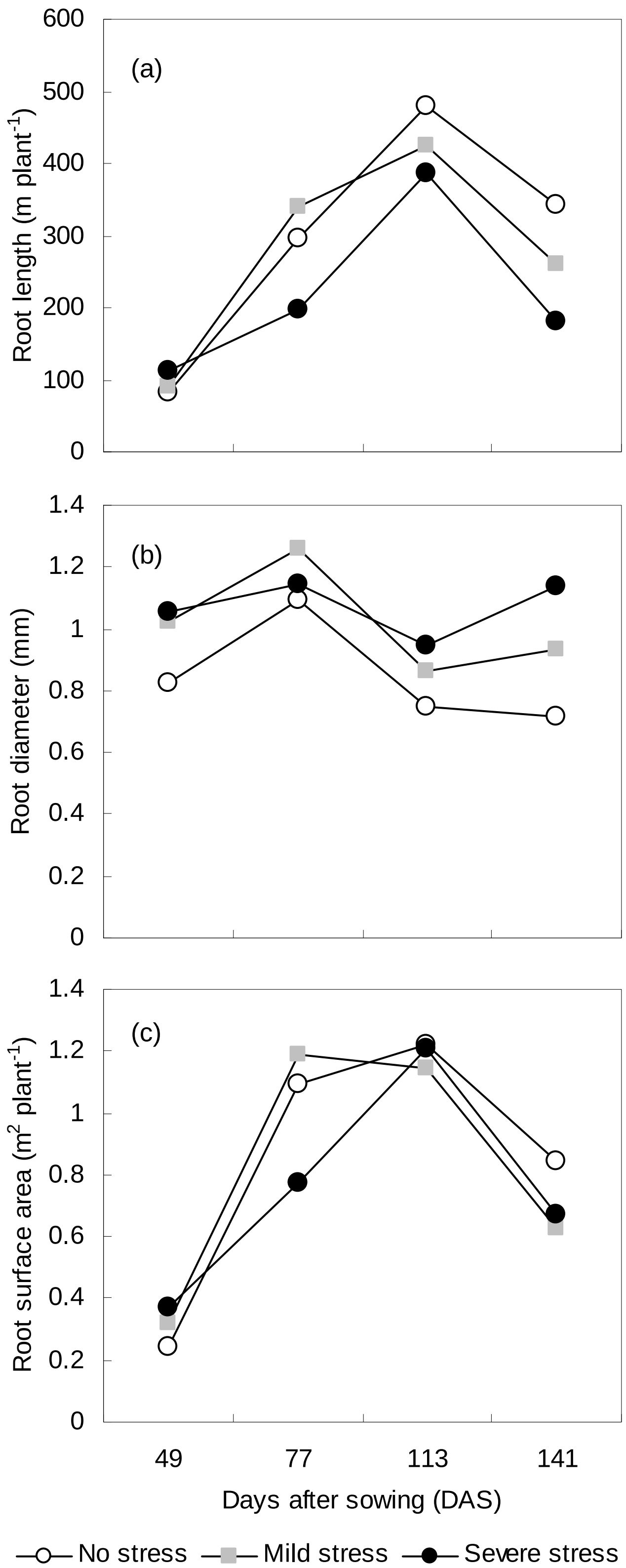


Fig. 2 Anomalies and cumulative frequency of rainfall during maize growing season (May to September) from 1965 to 2015 at Shengyang, Liaoning.



480 **Fig. 3** Root and shoot dry matters of maize under water stress at different growing
481 periods in 2014-2015.



483 **Fig. 4** Total root length, average diameter and total surface area per plant affected by

484 water stress in 2014

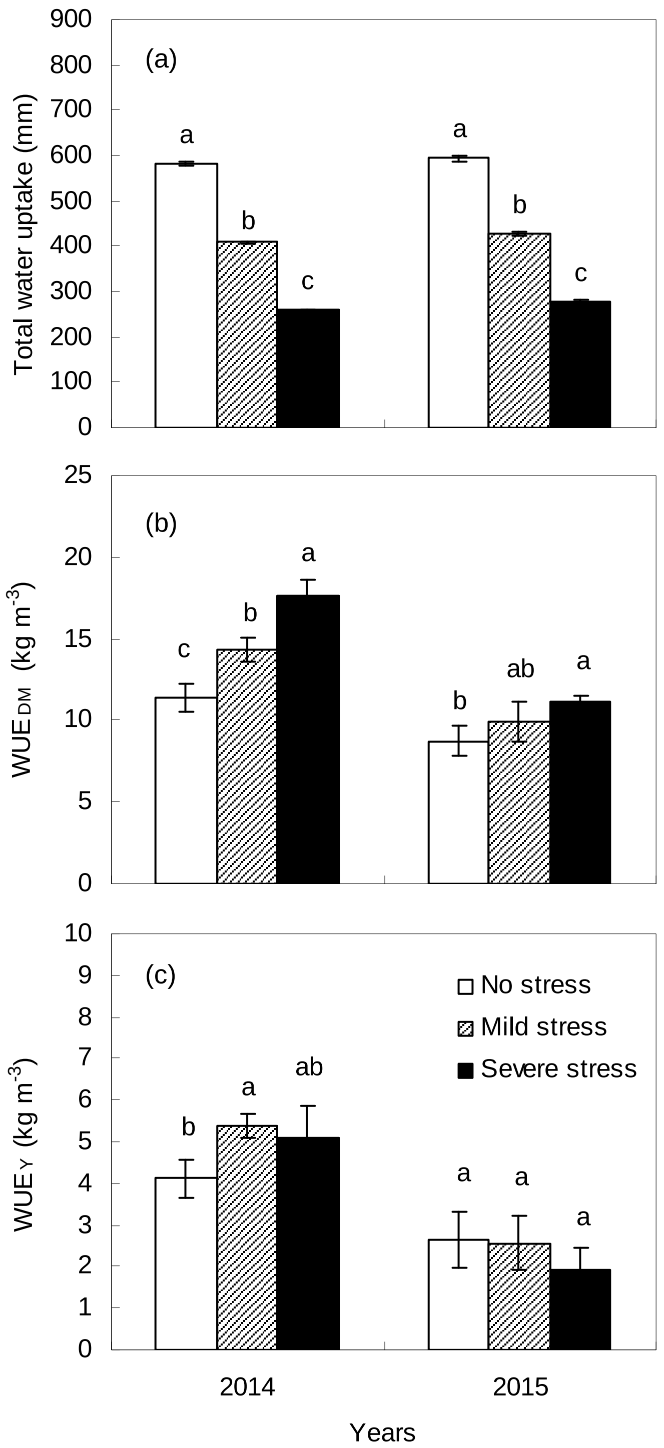


Fig. 5 Total water uptake (WU) during crop growing season and water use efficiency for above-ground dry matter (WUE_{DM}) and grain yield (WUE_Y) under water stress in 2014-2015