REVIEW ARTICLE

Highly efficient use of limited water in wheat production of semiarid area*

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Abstract To obtain a greater yield per unit rainfall is one of the most important challenges in dryland wheat production. Highly efficient use of limited water may be one means of achieving this goal. This paper reviewed wheat physiological adaptation and benefits associated with water deficit and variable conditions. In addition, it reveals the compensatory effect of limited irrigation and fertilizer supplement on wheat water-use efficiency (WUE) and highlights the breeding of new varieties for high WUE that could improve wheat productivity under water-limited environments in the semiarid area. Considerable potential for further improvement in wheat productivity in semiarid area seems to depend on effective conservation of moisture and efficient use of this limited water. Different crops, soil and water management strategies should be adjusted according to the conditions that prevail in the various semiarid areas. By combining soil and water conservation approaches with regulating the cropping system by cultivating drought-tolerant and water-saving cultivars, the increase in wheat productivity could be achieved.

Keywords: semiarid area, dryland wheat, physiological adaptation, WUE improvement.

Global demand for wheat is growing faster than gains realized in genetic yield potential. Currently the gain increase is less than 1% per year in most regions[1]. To improve total production in China, attention has been focused on expansion in areas with low and medium yields in the semiarid area. This has required the development and dissemination of wheat production technologies that lead to sustainable and stable wheat yields in these areas[2].

Periods of drought alternating with short periods of available water are conditions common to many semiarid areas of the world[3]. The typical semiarid area in China, for instance, characterized by water shortage and low productivity, has special natural conditions and ecological environment. Annual precipitation in the area is about 350 ~ 550 mm and the percentages of its distribution in the spring, summer, autumn and winter are 12% ~ 15%, 46% ~ 65%, 20% ~35% and 1% ~3%, respectively. Rainfall, in the form of storms, occurs mainly in the period from July to September, characterized by irregular distribution and intensity[4]. Wheat response to this water deficit and variable environments is complex and uninsurable, because such conditions can cover different situations including variable frequency of drought and wet periods; variable degrees of drought; speed of onset of drought conditions; and varying patterns of soil water deficit and/or atmospheric water deficit.

Great yield potential of wheat production in semiarid area existed; to improve wheat yield, however, biggest challenge is effective conservation and efficient use of limited water resources. The objective of this paper is to view some benefit effects of wheat response to water deficit and variable conditions, discuss wheat water use efficiency (WUE) improvement and exploit drought-tolerant and water-saving potential of wheat for high efficient use of limited water resources in semiarid area of China.

1 Wheat adaptation to water deficit and variable conditions

Wheat drought tolerance is multi-routes, with all

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the mechanisms involved not clearly understood. Recent researches on the effects of water deficits on physiological processes at the molecular level show that some enzymatically mediated processes increase but others decrease[5]. Root/shoot communication is being increasingly studied at the molecular level[6~9]. A crop's sensitivity to drought varies during different stages of its life cycle. This provides the possibility to choose the crucial moments for watering the crop to reduce drought stress[10]. Also a crop's response to drought stress and the degree to which yield is reduced vary across the different growth stages of the crop, especially those closely related to yield formation. The order in which wheat physiological processes are serially affected by drought seems to be growth, stomatal movement, transpiration, photosynthesis and translocation[11~13]. These observations permit irrigation scheduling to be designed so as to minimize loss in wheat yield.

1.1 Wheat drought-tolerance during seedling establishment

Wheat seedling establishment under water deficit conditions has been widely studied[14,15] and how seedlings respond to stress signals and how stress affects regulation of gene expression have resulted in an understanding of these processes at the molecular level[16,17]. In particular, major results on hydrolysis in seed germination[18], anabolism during seedling establishment[19], plumule elongation growth[20], proteins and genes regulated by plant hormones[21], as well as water absorption mechanism during seedling establishment under water deficit conditions have all been reported[22,23].

It is generally accepted that crops are often less tolerant to drought during germination and seedling stages[24,25]. Deng et al.[12] showed that of all the stages of active axis extension, germination, plumule elongation and emergence of spring wheat, the plumule elongation stage is the most sensitive one to water deficit. Therefore, under water deficit conditions, the maintenance of anabolism and slow growth are greatly associated with ATP energy level in cells, as seedling establishment involves the energy-requiring metabolic reactions. Deng et al.[26] suggested that the mechanism of seedling drought tolerance seems to involve regulating ATP energy level to change the ratio of catabolism to anabolism in such a way that results in the accumulation of osmotic component and depression of osmotic potential in growing tissue. Under such conditions, the ability of seedling to uptake water is increased and slow seedling growth is maintained during water deficit.

From an agronomic viewpoint, Whan et al.[27], for example, suggested that indeterminate cultivars that have early and vigorous seedling establishment accumulated a relatively large amount of biomass by the beginning of the seed filling stage, and thus were able to remobilize accumulated photosynthate in response to declining soil moisture. Such cultivars were best adapted to drought conditions. Water stress inhibited plumule elongation and reduced seedling vigor, resulting in shorter coleoptiles, which leads to poor establishment and a reduced yield. To achieve better establishment and high yields under the water-limited conditions, longer coleoptile length probably is one of the approaches to this goal. Thus, long coleoptile wheat plants or lines can be further tested to select the desired seedling establishment. The availability of molecular markers for some coleoptile length genes in wheat can further enhance selection efficiency. High throughput markers are being developed for genes of interest and efficiency of implementation of these markers assessed and optimized in Australian CSIRO wheat breeding program[3].

1.2 WUE and root-shoot relations of wheat

While the current interest in research at the molecular level is important, it should accompany research on water relations at the whole plant level. The success of the wheat plant in producing yield depends primarily on the success of leaves in controlling water loss and the effectiveness of roots in taking up water when the soil water is limited. Tolerance of dehydration depends on characteristics at the molecular level, such as osmotic adjustment, the water transduction in tissues, and the manner in which water deficit affects enzyme-mediated processes. Clearly, both avoidance and tolerance of water deficit will contribute to successful wheat production under semiarid conditions. Avoidance of severe water deficit requires coordination at the whole plant level between the control of water loss from transpiring shoots and water absorption through root systems. With the methods of gas exchange and ^{13}C stable isotope, Zhang and Shan[28] demonstrated that sequence of WUE in modern wheat cultivars is irrigated varieties > varieties of both irrigated and dry land > dry land varieties. Zhang et al.[29] showed that in wheat evolution from $2n \rightarrow 6n$, WUE at whole plant level increases with the increase of ploidy chromosomes, root system size and root/shoot ratio of wheat decrease with the increase of ploidy chromosomes under drought and irrigated conditions. Root system growth has an adverse redundancy for WUE, and the root redundancy reduces with the increase of ploidy chromosomes, which results in the increase of wheat WUE at whole plant level. These results suggested that the use of genetic breeding to excavate water-saving potential of wheat is possible.

A deep root system is synonomous with more water uptake from the soil and better performance under drought. It may be, however, that the root systems of cultivars grown in a given region are already adequate and further improvement may not be required. Information on whether current cultivars absorb all the available soil water is required to establish this[30]. If soil water remains after harvest then a genetic improvement in rooting depth and/or distribution may be required. This trait is, of course, difficult to measure. The simplest way to increase rooting depth and root distribution of crops is to increase the duration of the vegetative period (i.e. the period up to anthesis). This may be achieved by sowing earlier or later flowering genotype if this is feasible. Greater osmotic adjustment may also result in more root growth and ability to uptake additional soil water. However, selection for osmotic adjustment is not easy at the present time, although a novel method of selection in the haploid stage in wheat has recently been demonstrated[31].

1.3 Photosynthetic characteristics of wheat under drought conditions

Under drought conditions, stomatal closure and inhibition of chloroplast activity reduce photosynthesis[32]. Stomatal closure increases the resistance to CO_2 diffusion into the leaf. Inhibition of chloroplast activity at low soil water potential decreases the capacity to fix available CO_2, and this cannot be overcome by increasing the concentration of CO_2[33]. Although stomatal closure generally occurs when plants are exposed to drought, in some cases photosynthesis may be more controlled by the chloroplast capacity to fix CO_2 than by the increased diffusive resistance[34]. However, how photosynthesis adapts to drought environments is not well understood.

In semiarid environments, photosynthesis is variable with different soil moisture contents[35]. Under gradual soil drying conditions, wheat exhibits a higher photosynthetic rate (Pn) than under fast soil drying conditions. In the former, osmotic adjustment increases to a certain extent while in the latter process it remains constant. Osmotic adjustment allows for maintenance of photosynthesis and growth by stomatal adjustment and photosynthetic adjustment[36, 37]. The reported evidence showed that under mild and/or moderate soil water deficit conditions, photosynthetic depression was caused by stomatal closure or stomatal limitation, but not by biochemical reactions. However, under severe soil water deficit conditions, non-stomatal factors including some limiting enzymes could have been responsible for the decline in photosynthetic capacity[38~40]. Midday declines in photosynthesis were mainly induced by severe vapor pressure deficit, and stomatal limitation was suggested as a major cause[41, 42]. Under natural semiarid conditions, however, this decline usually resulted from soil water deficit that induced a decrease in leaf water potential at midday. Deng et al.[13] reported that both soil water deficit and high vapor pressure deficit simultaneously induced the midday depression in photosynthesis, indicating that both stomatal and non-stomatal limitations were responsible for photosynthetic decline in spring wheat in the semiarid environment.

Under water deficit conditions, the crop is able to synthesize abscisic acid (ABA) by its root system. ABA is then transported through the xylem to leaves, causing regulation of several ion channels in guard cells which triggering stomatal closure[43, 44]. This may be linked to the role of farnesylations that have been connected with ABA signal conduction[45, 46]. With regard to chloroplast capacity to fix CO_2, the evidence shows that the Rubisco holoenzyme is assembled in a catalytically inactive form and is activated by Rubisco activase (RCA)[47, 48].

Deng et al.[49] indicated that the notable midday decline in stomatal conductance that was parallel to photosynthetic rate depression resulted from severe vapor pressure deficit at midday. The deviation of stomatal conductance between the control and soil moisture deficit treatments was closely related to the leaf water status that was obviously affected by the prevailing soil moisture deficit. The hypothesis was, therefore, proposed that molecular mechanism of stomatal conductance variation and intercellular CO_2 concentration oscillation is closely linked with ABA-reduced stomatal response and activation status of the enzyme Rubisco affected by circadian oscillation of RCA.

2 Compensatory effect of limited irrigation in wheat

Loomis and Connor[50] suggested that there are three strategies available to improve the water use of crops in dry areas. The first is to maximize crop evapotranspiration (ET). The second is to maximize crop transpiration (*Tr*), as a fraction of total evapotranspiration. And the third is to maximize crop WUE. Consistent with these strategies and water limited conditions, Deng et al.[51] proposed that 200 mm of supplemental water is needed to achieve the maximum grain yield; 100 mm of supplemental water is necessary to get the greatest WUE; and 60 mm of supplemental water is indispensable for the highest irrigated WUE. In semiarid areas of North China, the critical water quantum for limited irrigation of spring wheat is 60 mm.

Many studies[52,53] have looked at the yield losses associated with drought at different stages of plant development. Villareal et al.[54] showed that crown root initiation and anthesis are the two stages at which yield losses from drought stress can be most critical to wheat. Current research[55] is aimed at identifying different plant traits that would allow wheat varieties to withstand the different types of drought that occur in the developing world.

Liang et al.[56] demonstrated that the drying-rewatering alternation had a significant compensatory effect that could reduce transpiration and keep wheat growing and WUE significantly increasing under drought conditions. Deng et al.[51] showed that, in the Guyan County of the Ningxia Hui Autonomous Region of China, where the annual precipitation is about 450 mm and the annual mean temperature is 6.5 ℃, a single irrigation of 600 m^3/ha applied at the jointing stage (equivalent to 30% of irrigated volume of water for a full cropping season with the highest yield) yields up to 75% of the highest yield. This amounts to a 2.8 kg increase in grain yield per cubic meter of water. The optimum time for limited irritation in spring wheat is the jointing stage and the water deficit critical period and the optimum irrigation time in wheat are not at the same growth stage. It seems essential to make a distinction between the critical growth stage at which yield is greatly reduced by drought from that one at which supplemental irrigation results in the highest yield.

3 Effect of soil fertilization on wheat WUE

Drought and poor soil fertility are the main restrictive factors for the production of dryland wheat in the semiarid and eroded areas of China. Because poor soil fertility results from severe water loss and soil erosion, supplying the nutrient needs of the wheat plant is essential for increasing grain production in the low yielding areas of semiarid area. This can be achieved through the use of organic fertilizers, for example by applying animal manure, incorporating crop residues and including legumes in rotation[4]. Chemical fertilizers are also used to increase grain production and fulfill the crop's nutrient needs. Under rainfed conditions, application of nitrogen and phosphorous fertilizers could considerably improve wheat yields. Rainfall variability greatly increases the risk of using fertilizer in dryland environments. However, estimates from farmers' fields and experimental stations indicated that the wheat crop usually recovers only 30% ~ 50% of the nitrogen that farmers apply[57]. The rest is lost, either dissipated into the atmosphere or leached down the soil profile or into ground water[58].

The nutrients that are found to be most limiting in the loess hilly region of China are N and P[4]. Most of the soils in the loess region of China are calcareous and these soils are particularly distributed on the eroded hilly tops. The deficiency is really a problem of runoff[59]. The yield and WUE increase from added N were observed in several dryland areas where crops were grown on the same land for several years[11]. Liu et al.[60] indicated that maximum yield and highest WUE were achieved under the optimum fertilizer input of 90 kg N and 135 kg P_2O_5 per ha in the semiarid field conditions of loess hilly area in Ningxia. Increase in soil fertilization was positively correlated with grain yield and WUE in spring wheat, with a correlation coefficient of 0.959 and 0.894, respectively. Increasing fertilizer level significantly increased fertile spikelet number, kernels per spike and kernel weight. Fertile spikelet number was sensitive to fertilization, whereas kernel number and weight was mainly affected by plant density. Fertilization applied in spring wheat improved root system development and especially enhanced roots growth in the cultivated soil layer of 0 ~ 20 cm. Ameliorated root system was able to improve crop water use and nutrient absorption and hence, crop yield and WUE was increased. Their study highlighted the compensatory effects of improving inorganic nutrition on the highly efficient use of limited water in dry land wheat production.

4 Ecophysiological approaches for wheat WUE improvement

To achieve a greater yield per unit rainfall is one of the most important challenges in dryland wheat. WUE represents a given level of biomass or grain yield per unit of water used by the crop. With increasing concern about the availability of water resources in both irrigated and dryland agriculture, there is renewed interest in trying to develop an understanding of how WUE can be improved and how farming systems can be modified to be more efficient in water use[61]. Maximizing WUE may be more suitable in areas where water, not land, is the most limiting factor[62]. There is a need for accurately understanding of wheat response to water deficit conditions on real-time. Consequently, it is possible to combine knowledge of crop adaptation and water use with the available technology to control the efficient use of limited water resources.

The effective use of precipitation and optimization of WUE are critical for promoting wheat yield in dryland farming systems[63]. These can be summarized in Figure 1.

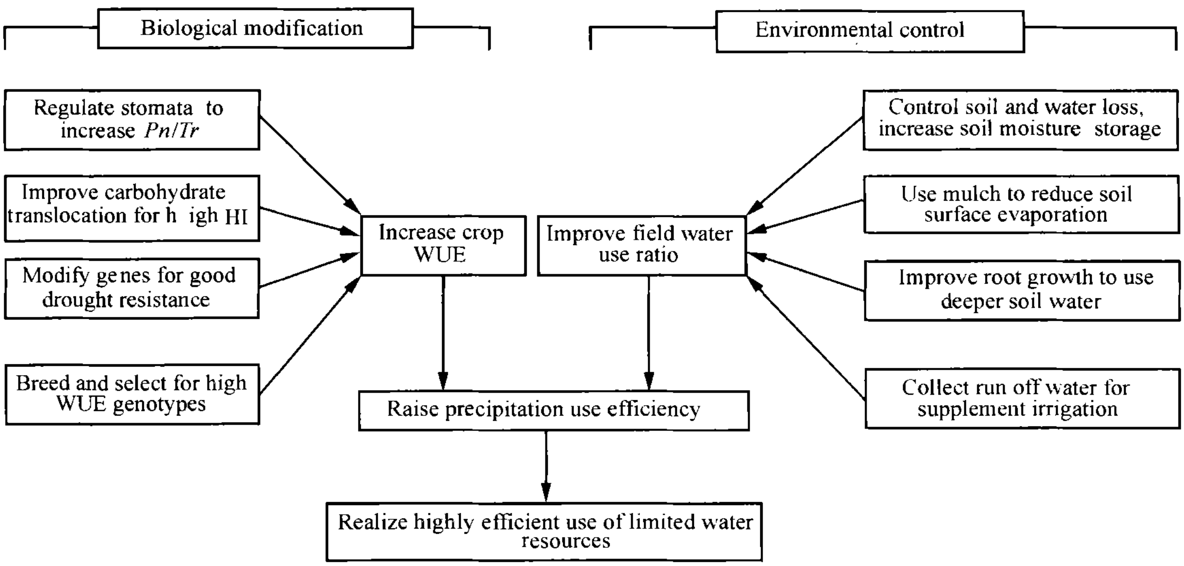

Fig. 1. Comprehensive technical approaches to improving crop production in semiarid regions with eroded environments (HI: harvest index).

The water deficit and variable conditions in semiarid environments are the major issues influencing wheat growth. Water-saving agricultural practice must, therefore, be designed and utilized. Central to such research should be the relationship between the effect of drought stress on crop physiological processes and the yield formation ability.

In the southern hilly area of Ningxia Hui Autonomous Region of China, with about 450 mm of annual precipitation from 1980 to 1994, the spring wheat yield was 0.75 ~ 2.25 tones/ha, with average water consumption of 280 mm, which is about 62% of the annual rainfall[11]. The above figure shows that there is still a considerable potential for further improvement in the use of rainfall received. To raise rainfall utilization rate, a comprehensive approach including prevention of water loss and soil erosion, elimination of topsoil evaporation, extraction of water stored in deeper layers and steady heightening of the absorbable share of water by crops must be adopted. In the semiarid Loess Plateau, for instance, the water-saving drive is to raise the rainfall utilization ratio by the construction of high-yield farmlands through the building of leveled terraces, the utilization of harvested rainwater for limited irrigation, the use of tillage practice that conserves water and soil, the introduction of drought-tolerant varieties and the application of manure and fertilizer. Especially, for the low yielding of dryland wheat production, the wide use of chemical fertilizer has played a major role in this aspect[2,49]. In a 10-year period (1980 to 1990), dryland wheat production in this area doubled its annual output. The major contributing factor to the change was the use of chemical fertilizer[4].

Changes in soil management practice to reduce evaporation from the soil surface have been successful in some location[64]. It is possible to increase WUE by 25% to 40% through soil management practice that involves tillage. Li and Xiao[65] demonstrated that the use of a mulch crop to cover fields with green manure plants, crop residue, or plastic film protecting the soil from moisture loss by evaporation, reduces soil erosion and thus, improves soil fertility and conserves water. These changes result in an increased wheat yield and WUE in the low yielding areas examined. Xu[66] showed that mulching significantly improved water conservation and soil fertility and resulted in a large increase in wheat yield in dryland areas. When 30 tones/ha of green manure was used on fallow land, about 50 mm of water could be conserved, soil organic matter and nutrients simultaneously enhanced, yield increased by 2.25 tones/ha and WUE increased by 23%. Numerous results in different regions agree that straw mulching significantly improves the field ability of natural rainfall restoring, soil water supplying, and soil evaporation restricting[67~69]. To recognize the water and fertility shortage in semiarid areas, these measures of straw mulching are important to economize the limited water resources, as well as avoid over uptake of soil nutrients. It should be emphasized that straw mulching makes no change of crop gross water consumption against control one, but it changes the portion between soil evaporation and plant transpiration. This means that straw mulching improved use efficiency of limited water resources, and in turn improved wheat productivity.

Genetic advances in grain yield under rainfed conditions have been achieved by empirical breeding methods. Progress is slowed, however, by the interaction between a large genotype and season, and location arising from unpredictable rainfalls, which is a feature of drought environments. A good understanding of factors limiting and/or regulating yield now provides us with an opportunity to identify and then select for physiological and morphological traits that increase the efficiency of water use and yield under rainfed conditions[3].

WUE is broader in scope than most agronomic applications and must be considered on a watershed, basin, irrigation district, or catchment scale. The main pathways for high WUE in limited irrigation are to increase the output per unit of water (engineering and agronomic management aspects), reduce losses of water to unusable sinks, reduce water degradation (environmental aspects), and reallocate water to higher priority uses (societal aspects)[70].

5 Perspectives

In the last decade, our understanding of the processes underlying wheat response to drought, at the molecular and whole-plant levels, has rapidly progressed. Knowledge of these processes is necessary to improve crop management and breeding techniques. Hundreds of genes that are induced under drought have been identified[71]. A range of tools, from gene expression patterns to the use of transgenic wheat plants, is being used to study the specific function of those genes and their roles in wheat plants adaptation to water deficit and WUE improvement[72]. However, because wheat responses to drought are cascaded, the functions of many of the genes are still unknown. The new tools that operate at molecular, whole-plant and ecosystem levels are revolutionizing our understanding of wheat plant response to drought, and our ability to monitor it. For example, carbon isotope discrimination ($\Delta^{13}C$) is a measure of the $^{13}C/^{12}C$ ratio in plant material relative to the value the same ratio in the air on which wheat plants fed. The $\Delta^{13}C$ is positively related to the ratio of the intercellular CO_2 concentration and the atmospheric CO_2 concentration. Therefore $\Delta^{13}C$ correlates with WUE of wheat. Consequently, $\Delta^{13}C$, due to its convenience and a relatively low cost, has become a useful indicator of differences in WUE. Recently this method has been used for high WUE breeding in wheat[73]. Other techniques such as genome-wide tools and thermal or fluorescence imaging may allow the genotype-phenotype gap to be bridged, which is essential for faster progress in high WUE research.

A possible means of realizing high WUE of wheat in semiarid area is to manage transpiration so that relatively more water is used, since highly efficient use of limited water is determined by both crop water use and WUE. The increase in transpiration efficiency may result both from an increase in *Pn* and a decrease in stomatal conductance. Wheat under drought stress has self-regulatory processes for enduring the adversity. These range from metabolic adaptation to reduced growth. If the drought does not damage the crop beyond a critical threshold, then some physiological compensation will take place as soon as the water supply is resumed, thus minimizing the impact of the water deficit on wheat growth, and often yield[35, 63]. Often the highest efficiency in farmland irrigation is achieved with moderate, compared with abundant water supply[51, 74, 75]. Limited irrigation refers to a system of crop management in which dryland cultivation is integrated with limited water supply in an irrigation network, as in a water-deficient area, for example, when an irrigation network is only able to supply part of the water needed for wheat growth[76].

Considerable potential for further improvement in wheat productivity in semiarid environments seems to depend on effective conservation of moisture and efficient use of this limited water[77]. Different crop, soil and water management strategies should be adjusted according to the conditions that prevail in the various semiarid areas. By combining soil and water conservation practices with adjusting the cropping system by cultivating drought-tolerant varieties, the increase in wheat productivity could be achieved.

References

1 Reynolds, M. P. et al. Avenues for genetic modification of radiation use efficiency in wheat. Journal of Experimental Botany, 2000, 51: 459.

2 Shan, L. Development of tendency on dry land farming technologies. Agricultural Sciences in China, 2002, 1(8): 934.

3 Richards, R. A. et al. Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. Crop Science, 2002, 42: 111.

4 Shan, L. et al. The Principle and Practices of Dry Land Farming on the Loess Plateau (in Chinese). Beijing: Chinese Academic Press, 1993.

5 Loggini, B. et al. Antioxidative defense system, pigment composition, and photosynthetic efficiency in two wheat cultivars subjected to drought. Plant Physiology, 1999, 119: 1091.

6 Davies, W. J. et al. Root signals and the regulation of growth and development of plants in drying soil. Annual Reviews of Plant Physiology and Plant Molecular Biology, 1991, 42: 55.

7 Chandler, P.M. et al. Gene expression regulated by abscisic acid and its relation to stress tolerance. Annual Reviews of Plant Physiology and Plant Molecular Biology, 1994, 45: 113.

8 Giraudat, J. et al. Current advances in abscisic acid action and signalling. Plant Molecular Biology, 1994, 26: 1557.

9 Griffiths, A. et al. Shoot induction of ABA-requiring genes in response to soil drying. Journal of Experimental Botany, 1996, 47: 1525.

10 Blum, A. Crop responses to drought and the interpretation of adaptation. Plant Growth Regulation, 1996, 20: 135.

11 Shan L. et al. Eco-Physiological Bases of Dryland Farming (in Chinese). Beijing: Chinese Academic Press, 1998.

12 Deng, X. P. et al. Effect of water stress on the seedling establishment of spring wheat. In: Innovation of Agricultural Engineering Technologies for the 21st Century, Proceedings of International Conference on Agriculture Engineering. Beijing: China Agricultural University Press, 1999, 12.

13 Deng, X. P. et al. Effect of drought environments on the photosynthesis of spring wheat in the semi-arid area of Loess Plateau, China. In: Soil Erosion & Dryland Farming (eds Laflen, J. M. et al.), New York: CRC Press, 2000.

14 Bray, E. A. Plant responses to water deficit. Trends Plant Science, 1997, 2: 48.

15 Singh, S. et al. Role of calcium in regulation of proteolysis during early mung bean growth. Journal of Plant Physiology, 1997, 114: 291.

16 Chrispeels, M. J. et al. Aquaporins: The molecular basis of facilitated water movement through living plant cells. Plant Physiology, 1994, 105: 9.

17 Alejandra, M. R. et al. Quantification of GA-regulated mRNA abundance in individual tomato seeds using tissue printing. Journal of Plant Physiology, 1997, 114: 292.

18 Banik, M. et al. Molecular cloning of cDNAs encoding (14)—xylan endohydrolases from the aleurone layer of germinated barley (*Hordeum vulgare*). Plant Molecular Biology, 1996, 31: 1163.

19 Toyomasu, T. et al. Phytochrome Regulates Gibberellin Biosynthesis during Germination of Photoblastic Lettuce Seeds. Plant Physiology, 1998, 118: 1517.

20 Collett, C. E. et al. Hormonal interactions in the control of Arabidopsis hypocotyl elongation. Plant Physiology, 2000, 124: 553.

21 McCourt, P. Genetic analysis of hormone signaling. Annual Reviews of Plant Physiology and Plant Molecular Biology, 1999, 50: 219.

22 Maurel, C. Aquaporins and water permeability of plant membranes. Annual Reviews of Plant Physiology and Plant Molecular Biology, 1997, 48: 399.

23 Johansson, I. et al. Water transport activity of the plasma membrane aquaporin PM28A is regulated by phosphorylation. Plant Cell, 1998, 10: 451.

24 Nielsen, D. C. et al. Black bean sensitivity to water stress at various growth stages. Crop Science, 1998, 38: 422.

25 Desclaux, D. et al. Identification of soybean plant characteristics that indicate the timing of drought stress. Crop Science, 2000, 40: 716.

26 Deng, X. P. et al. Sensitivity and resistance of seedling establishment to water stress in spring wheat. Cereal Research Communications, 2002, 30: 125.

27 Whan, B. R. et al. Integration of breeding and physioloy: lessons from a water-limited environment. In: International Crop Science I. (eds Buxton, D. R. & Shibles, R.), Wisconsin: Crop Science Society of America, 1993.

28 Zhang, Z. B. et al. Comparison study on water use efficiency of wheat flag leaf. Chinese Science Bulletin, 1998, 43(14): 1205.

29 Zhang, S. Q. et al. Change of water use efficiency and its relation with root system growth in wheat evolution. Chinese Science Bulletin, 2002, 47(22): 1879.

30 Angus, J.F. et al. Increasing water use and water use efficiency in dryland wheat. Agronomy Journal, 2001, 93: 290.

31 Morgan, J. M. Pollen grain expression of a gene controlling differences in osmoregulation in wheat leaves: a simple breeding method. Australian Journal of Agricultural Research, 1999, 50: 953.

32 Farquhar, G.D. et al. Stomatal conductance and photosynthesis. Annual Reviews of Plant Physiology, 1982, 33: 317.

33 Boese, S. R. et al. Elevated CO_2 mitigates chilling-induced water stress and photosynthetic reduction during chilling. Plant Cell & Environments, 1997, 20: 625.

34 Faver, K. L. et al. Late season water stress in cotton: II. Leaf gas exchange and assimilation capacity. Crop Science, 1996, 36: 922.

35 Deng, X. P. et al. Daily photosynthetic characteristics of spring wheat in four growth stages on the Loess Plateau of China. In: Proceedings of the 2nd Asian Crop Science Conference, Tokyo, Asian Crop Science Society, 1996.

36 Turner, N.C. Crop water deficits: a decade of progress. Advances in Agronomy, 1986, 39: 1.
37 Shangguan, Z.P. et al. Interaction of osmotic adjustment and photosynthesis in winter wheat under soil drought. Journal of Plant Physiology, 1999, 154: 753.
38 Kalt-Torres, W. et al. Diurnal changes in maize leaf photosynthesis: Carbon exchange rate, assimilate export rate, and enzyme activities. Plant Physiology, 1987, 83: 283.
39 Du, Y.C. et al. Effects of water stress on carbon exchange rate and activities of photosynthetic enzymes in leaves of sugarcane (Saccharum sp.). Australian Journal of Plant Physiology, 1996, 23: 719.
40 Du, Y.C. et al. Responses to water stress of enzyme activities and metabolite levels in relation to surcrose and starch synthesis, the Calvin cycle and C4 pathway in sugarcane (Saccharum sp.) leaves. Australian Journal of Plant Physiology, 1998, 25: 253.
41 Schulze, E.D. Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. Annual Reviews of Plant Physiology, 1986, 73: 247.
42 Xu, D.Q. et al. Diurnal variations in the photosynthetic efficiency in plants. Acta Phytophysiologica Sinica, 1997, 23: 410.
43 Slovik, S. et al. Compartmental distribution and redistribution of abscisic acid in intact leaves. III. Analysis of the stress signal chain. Planta, 1992, 187: 37.
44 Schulze, E.D. Flux Control in Biological Systems: From Enzymes to Populations and Ecosystems. New York: Academic Press, 1994.
45 Grill, E. et al. A plants dilemma. Science, 1998, 282: 252.
46 Pei, Z.M. et al. Role of Farnesyltransferase in ABA regulation of guard cell anion channels and plant water loss. Science, 1998, 282: 287.
47 Portis, A.R. Regulation of ribulose-1, 5-bisphosphate carboxylase-oxygenase activity. Annual Reviews of Plant Physiology and Plant Molecular Biology, 1992, 34: 415.
48 Mott, K.A. et al. Kinetics of rubisco activation as determined from gas-exchange measurements in antisense plants Arabidopsis thaliana containing reduced levels of rubisco activase. Australian Journal of Plant Physiology, 1997, 24: 811.
49 Deng, X.P. et al. Diurnal oscillation in the intercellular CO_2 concentration of Spring Wheat under the Semiarid Conditions. Photosynthetica, 2000, 38: 187.
50 Loomis, R.S. et al. Crop ecology. Cambridge: Cambridge University Press, 1992.
51 Deng, X.P. et al. High efficient use of limited supplemental water by dryland spring wheat. Transactions of the CSAE, 2002, 18 (5): 84.
52 Mary, J.G. et al. Relative sensitivity of spring wheat grain yield and quality parameters to moisture deficit. Crop Science, 2001, 41: 327.
53 James, R.F. et al. Drought-stress effects on branch and main stem seed yield and yield components of determinate soybean. Crop Science, 2001, 41: 759.
54 Villareal, R.L. et al. Exploiting synthetic hexaploids for abiotic stress tolerance in wheat. In: Regional Wheat Workshop for Eastern, Central and Southern Africa, 10. CIMMYT; Addis Ababa, Ethiopia, University of Stellenbosch, 1999.
55 Trethowan, R.M. et al. Challenges and future strategies in breeding wheat for adaptation to drought stressed environments. In: Molecular Approaches for the Genetic Improvement of Cereals for Stable Production in Water-Limited Environments (ed. Ribaut, J. M & Poland, D.). Texcoco: CIMMYT, 2002.
56 Liang Z.S. et al. The relations of stomatal conductance, water consumption, growth rate to leaf water potential during soil drying and rewatering cycle of wheat. Botanical Bulletin of Academia Sinica, 2002, 43: 187
57 Raun, W.R. et al. Improving nitrogen use efficiency for cereal production. Agronomy Journal, 1999, 91: 357.
58 Harmsen, K. et al. Crop response to nitrogen and phosphorus in rainfed agriculture. In: Proceedings of the 17th Colloquium of the International Potash Institute. Rabat and Marrakech, Morroco, 1983.
59 Wei, X.P. et al. The Loss of soil nutrients on Loess Plateau affected by precipitation. In: Soil Erosion & Dryland Farming (eds Laflen, J.M et al.), New York: CRC Press, 2000.
60 Liu, Z.M. et al. Effects of fertilizer and plant density on the yields, root system and water use of spring wheat. Research of Soil and Water Conservation (in Chinese), 1998, 5(1): 70.
61 Hatfield, J.L. et al. Managing soils to achieve greater water use efficiency. Agronomy Journal, 2001, 93: 271.
62 Oweis, T. et al. Water use efficiency of rainfed and irrigated bread wheat in a Mediterranean environment. Agronomy Journal, 2000, 92: 231.
63 Shan, L. Research and practice of water-saving agriculture. Bulletin of the Chinese Academy of Sciences, 1998, 112: 42.
64 Gregory, P.J. et al. Soil type, climatic regime, and the response of water use efficiency to crop management. Agronomy Journal, 2000, 92: 814.
65 Li, S.X. et al. Distribution and management of dryland in the People's Republic of China. Advances in Soil Sciences, 1992, 18: 147.
66 Xu, Z. A study of mulching cultivation technique with green manure on wheat in the hilly area. In: Advances Wheat Cultivation Researches in China (in Chinese) (ed Lu, L.S.), Beijing: Chinese Agricultural Publishing House, 1992.
67 Zhang B.J. et al. Preliminary opinions on the theory-studied and practice-applied of wheat plastic film mulching cultivation in China (in Chinese). Research of Soil and Water Conservation, 2000, 17 (1): 54.
68 Wang Y.H. et al. Effect of stubble and straw mulch on soil and water erosion on loess slope land. Agricultural Research in the Arid Area (in Chinese), 2002, 20(4): 109.
69 Xu, C.P. et al. Effects of straw mulch on water consumption and water use efficiency in winter wheat. Irrigation and Drainage (in Chinese), 2002, 21(3): 24.
70 Howell, T.A. Enhancing water use efficiency in irrigated agriculture. Agronomy Journal, 2001, 93: 281.
71 Chaves, M.M. et al. Understanding plant responses to drought: from genes to the whole plant. Functional Plant Biology, 2003, 30 (3): 239.
72 Sivamani, E., A. et al. Improved biomass productivity and water use efficiency under water deficit conditions in transgenic wheat constitutively expressing the barley HVA 1 gene. Plant Science, 2000, 155: 1.
73 Condon, A.G. et al. Improving intrinsic water use efficiency and crop yield. Crop Science, 2002, 42: 122.
74 Stewart, B.A. et al. Yield and water use efficiency of grain sorghum in limited irrigation-dryland farming. Agronomy Journal, 1983, 75: 629.
75 Turner, N.C. Plant water relations and irrigation management. Agricultural Water Management, 1990, 17: 59.
76 Kang, S.Z. et al. Effects of limited irrigation on yield and water use efficiency of winter wheat in the Loess Plateau of China. Agricultural Water Management, 2002, 55: 203.
77 Shan, L. et al. Current situation and perspective of agricultural water used in semiarid area of China. Journal of Hydraulic Engineering (in Chinese), 2002, 9: 27.