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Responses of Seedlings to Water Stress in Different Genotypes of Winter Wheat

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(With 3 figures)

1. Introduction

Water stress is one of the most important constraints to wheat yield (AUSTIN 1983, TURNER 1979). Drought occurs frequently during the growing season for wheat crops in many of the wheat areas in the world (HOUGH 1983). Stabilizing wheat production through better water management, especially irrigation, is a major objective in many wheat-growing regions (REITZ 1967). As a result, studies on physiological responses of this crop to drought stress and variations of drought tolerance amongst genotypes are emphasized (BEGG and TURNER 1976, JORDAN et al. 1983). Nevertheless, in the past, many of the varieties of wheat were enlisted into drought-tolerance groups by identification based merely upon drought-resistance indices (SUN 1983). FISCHER and MAURER (1978) examined a wide range of genotypes by imposing drought at various stages during pre-anthesis and detected that the most resistant were tall bread wheats and barleys, dwarf bread wheats were intermediate and durum wheats and triticales were most susceptible. Absolute yields of dwarf bread wheats were however higher than those of taller, more ‚drought-resistant' ones under water stress. MA and GREEN (1988) worked on the responses of two wheat sib-lines to water stress and also found that under drought conditions the yield of the dwarf cultivar was less reduced than that of the taller one. Actually, the above-mentioned findings questioned the validity of the classic concept of drought resistance. Therefore, our study was aimed at analyses of various physiological responses to water stress and variation of drought resistance of wheat seedlings amongst genotypes.

2. Material and Method

2.1 Material and treatment

The three winter wheat cultivars used in the experiment are HB7 (a1), HB25 (a2) and Yulinbai (a3). Both HB7 and HB25 are semi-dwarf, high-yielding varieties developed at the Hebei Institute of Cereal and Oil Crops. Yulinbai is a tall local race suitable for rainfed areas of Northern China (SUN 1983).

Two water supply treatments were favourable water conditions (b1) and water stress by withdrawal of water application after plant emergence (b2). The combination of variables is shown in table 1. The experiment was conducted with six replicates, in addition, two more blanks without seeds were added with two replicates for the determination of evaporation from the culture material surface.

2.2 Experimental methods

Polyethylene pots with a diameter of 8 cm and a depth of 8 cm were filled with vermiculite to a depth of 5 cm. Before seed planting, HOAGLAND and SNYDER (1933) solution was added to each pot up to a medium water content of 104,7 %. Thirty seeds were planted in each pot and then transferred to the growth chamber (type LH-200-RD Nippon Chemical Instruments Co. Ltd., Tokyo, Japan).

The temperature was kept at 25° C in the day and 15° C at night, with light (PAR: 250 μmol m^{-2} s^{-1}) and dark 12 hours each. The positions of pots were changed every day, to eliminate possible errors from the somewhat uneven light distribution within the growth chamber. After the emergence of plants, pots were thinned to twenty plants. The pots were weighed at 8—9 o'clock a.m. daily and rewatered to the original level for treatment b1 after sowing. For b2 the watering was the same as b1 before emergence of plants, but after emergence, irrigation was stopped until harvest. Plants were harvested on days 16—17 after emergence.

Table 1

Combination of treatment factors

Treatment	Cultivar	Water status
1	a1	b1
2	a1	b2
3	a2	b1
4	a2	b2
5	a3	b1
6	a3	b2
7		b1
8		b2

2.3 Physiological measurements

2.3.1 Leaf water potential

Leaf water potentials were taken three times after plant emergence with a pressure chamber (model ZLZ-4, Lanzhou University, China). Means for treatments were calculated from six readings.

2.3.2 Stomatal resistance and transpiration rate

Both parameters were taken twice from readouts of a Steady State Porometer (LI-1600, LI-COR, Lincoln, Nebraska, U.S.A.) on the second fully expanded leaves with six replicates for each treatment. For the measurement on September 18, some readings from the droughted plants were not available because of the serious wilting of leaves.

2.3.3 Fresh and dry weight of roots and shoots

At final harvest, the fresh weight of primary roots and shoots were determined from 15 plants per pot by immediate weighing after separation of roots from shoots. The dry weight data were obtained after 48 hours of oven drying at 80° C.

2.3.4 Daily evaporation and transpiration

Both parameters were calculated from the daily weighing data of the pots together with plants.

3. Results

3.1 Variation in evaporation and transpiration

3.1.1 Water extraction from the vermiculite substrate

The residual water changes during the treatment period are shown in fig. 1. In all of the control treatments of water status, water was daily restored to the original level. However, in the water stress treatments, withdrawal of water five days after planting allowed the available water to decrease gradually. In the blanks, where only evaporation but no transpiration occurred, water was lost linearly and least. It was found that under water stress conditions water was lost slowest in HB25 and fastest in Yulinbai, revealing a difference of water loss amongst genotypes. In addition, the most significant difference between genotypes in residual water occurred four to six days after emergence; from then on, the difference between genotypes became less and less.

3.1.2 Evapotranspiration

The evapotranspiration of plants under favourable water conditions increased gradually in accord with the growth of seedlings after the emergence of plants. In the water stress treatments, however, evapotranspiration originally increased and then turned to decrease sharply four days after emergence because of the

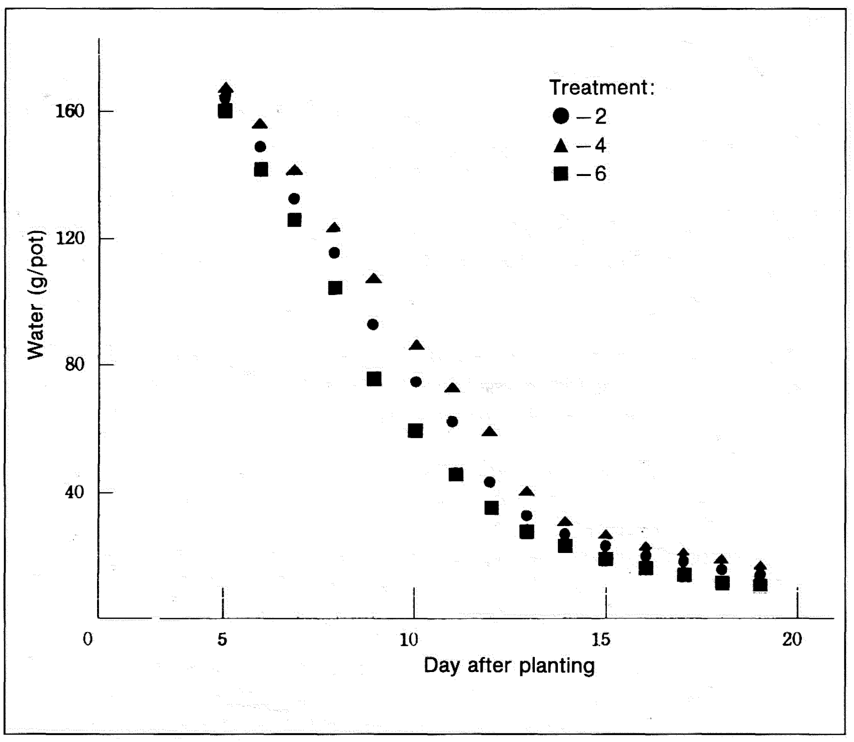


Fig. 1: Amount of Water in the Culture Medium

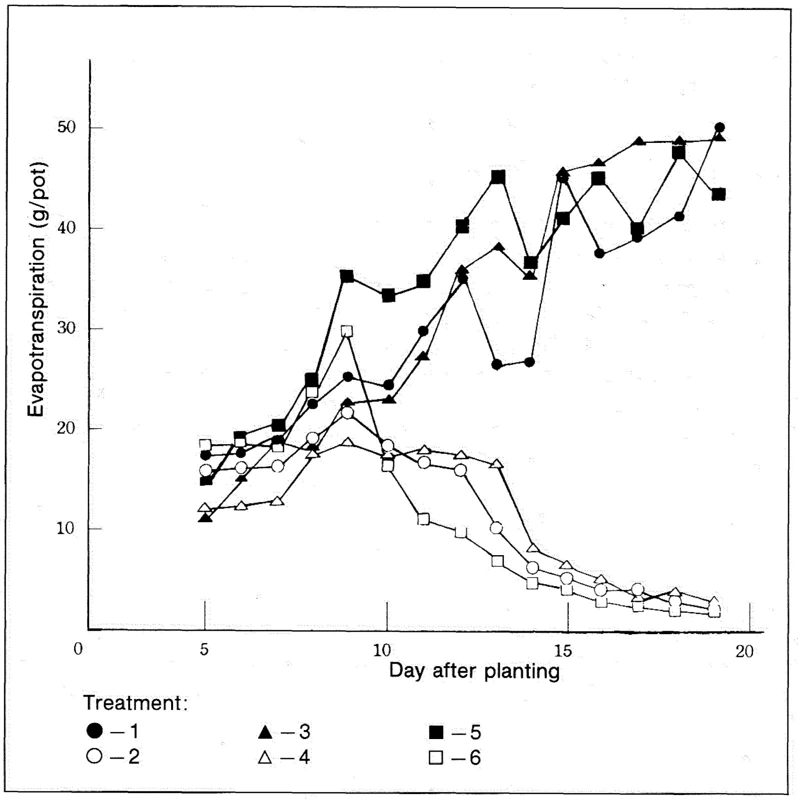


Fig. 2: Daily Evapotranspiration Rate

reduced availability of water in the pot (fig. 2). The total evapotranspiration accumulated for HB7, HB25 and Yulinbai correspondingly were 516.9, 545.0 and 585.4 ml/pot in the well-watered controls. Under water stress conditions, there was no large variation of evapotranspiration (231.5, 221.0 and 228.2 ml/pot for the three cultivars in the order mentioned above), due possibly to the severe deficits of water supply during the late period of the experiment (fig. 1).

3.1.3 Transpiration

In this study, the amount of water transpired was calculated from the total water lost by evapotranspiration minus the evaporation in the corresponding unplanted blanks. This resulted in negative values for the transpiration of severely stressed plants.

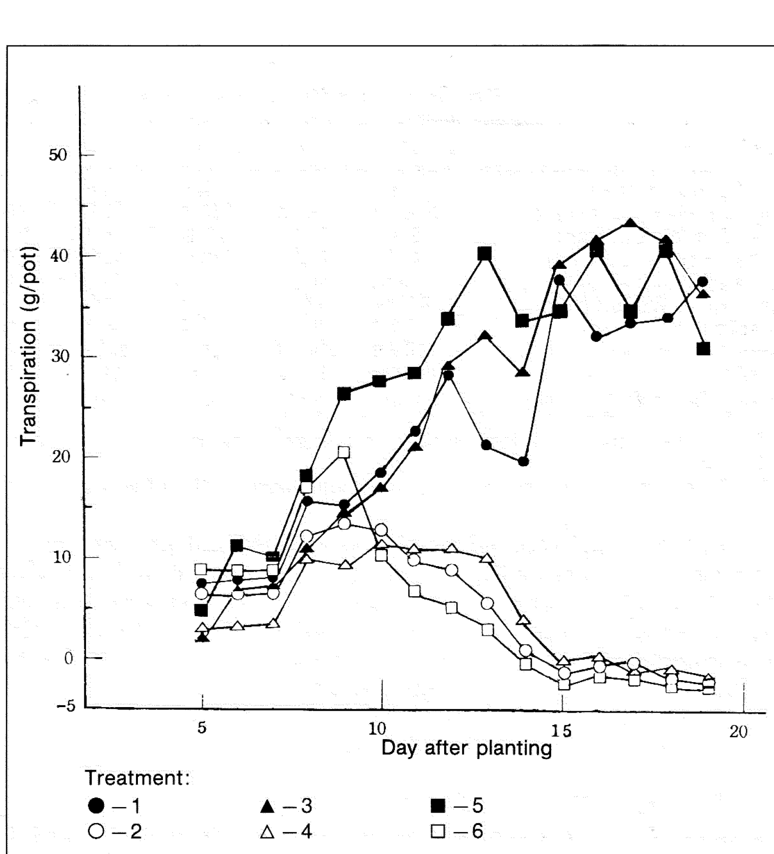
There might be two kinds of errors for this kind of calculation:

a) it was difficult to evaluate the influence of the plant canopy on the evaporation from the culture surface;

b) the considerable divergence of the available water between the water stress treatments and the blank over the late phase of the experiment resulted possibly in the negative value. Nevertheless, we thought the data to be still valuable for the analysis.

Changes of transpiration in different cultivars under varying water status are shown in figure 3. The transpiration under favourable water conditions increased with the wheat growth. The total water transpired over the experimental period by HB7, HB25 and Yulinbai was 342.5, 373.7 and 408.6 ml/pot. Early in

Fig. 3: Daily Transpiration Rate



the water stress treatments, no clear depressions were revealed and the highest transpiration occurred in Yulinbai. With increasing severity of drought, the availability of water from the vermiculite could not meet the requirement of plants, which induced a depression of transpiration, and, finally, the plant wilted. It is easily seen in figure 3 that under water stress conditions, Yulinbai lost water fastest and water deficit occurred earliest (when 40 % of water remained in the pot 9 days from planting). The plants were severely wilted and nearly dead before harvest. But for HB7, when the water content was 40 % in the culture medium (10 days after planting), the transpiration rate began to decrease only slowly, only at 23 % water content a swift reduction set in. For HB25, there was no large shift when the water content of the culture changed from 68 % to 20 %, and also the water was consumed very slowly; therefore, some water was still available for the growth of the crop till very late and wilting was delayed, particularly in comparison with variety Yulinbai.

3.2 Variation in plant traits and water use efficiency

3.2.1 Number and weight of primary roots

There was a consistent tendency among the three varieties that water stress influenced adversely the development of roots. HB25 showed comparatively more negative effects than the others, but it had more roots in absolute numbers under water stress (table 2).

Table 2

*Plant traits in different treatments**

Treatment	1	2	3	4	5	6
No. of Primary Roots	4.3	3.9	4.9	4.4	4.1	4.0
Shoot Fresh Weight (mg)	336.1 b	58.5 d	390.9 a	71.9 d	297.3 c	47.6 d
Shoot Dry Weight (mg)	32.9 b	17.1 c	43.2 a	18.9 c	31.3 b	13.5 d
Root Fresh Weight (mg)	137.5 b	41.1 d	188.6 a	44.0d	93.8 c	34.7 d
Root Dry Weight (mg)	8.6 a	6.1 c	10.5 a	7.0 b	5.9 c	5.1 c
Total Fresh Weight (mg)	473.6	99.6	579.5	115.9	391.1	72.3
Total Dry Weight (mg)	41.5	23.2	53.7	25.9	37.2	18.6
Water lost (ml/pot)	516.9 a	231.5 b	545.0a	221.0b	585.4 a	228.2 b
WUE**	8.03	10.02	9.85	11.70	6.35	8.15
Ratio of Shoot and Root	3.83	2.80	4.11	2.70	5.31	2.65

* The same letter in a line denotes no significant difference between treatments at P = 0.05 level.
** WUE, Water Use Efficiency as a percentage based on the total dry matter.

Water stress affected adversely both fresh and dry weights, especially the fresh weight, indicating the fact that severe dehydration had occurred at harvest when the available water in the vermiculite was nearly used up. Moreover, there was a significant difference in root weight between cultivars: HB25 showed the highest under both water regimes, and Yulinbai the lowest. Relatively speaking, the ratio of root weight of drought treatment and control was superficially highest in Yulinbai; however, this was due to a very low weight of the control roots and not to good root growth under stress.

3.2.2 Biomass and shoot/root ratio

It could be found from both above ground dry matter and total dry matter including roots that there was a significant difference between varieties and water treatments (table 2). Absolute values of HB25 were the highest under both water regimes, which indicated that cultivars like HB25 may possess not only superb productivity under favourable environmental conditions, but also a better ability for drought tolerance and a wider adaption to the environment.

There was a converse trend between water treatments in the shoot/root ratio. The highest ratio ocurred in Yulinbai when the plant was well-watered, but when droughted, Yulinbai was the lowest (although there was only a small difference in varieties). This would reveal that the constraint of water stress in Yulinbai on canopy growth was relatively heavier than on the root system.

3.2.3 Water use efficiency

Droughted wheat seedlings showed a higher water use efficiency (WUE). The WUE of HB25 was remarkably higher than that of Yulinbai.

3.3 Variation of plant water potential and stomatal resistance

3.3.1 Plant water potential

„Plant water potential depression" is defined as the difference of potentials between predawn and mid-day. Measurements at three different times showed that the predawn plant water potential became remarkably reduced when the availability of water in the stress treatments declined (fig. 1). There was a consistency in the differences between the plant water potentials of varieties and the amount of residual water in the medium in the stress treatments (as shown in figure 1 and table 3). Therefore, it may be inferred that differences between varieties or treatments would be readily confused when the tests for drought resistance were done under excessively severe drought conditions. In general, under water stress conditions, HB25 maintained a higher mid-day plant water potential and a lower "plant water potential depression", especially when the plants were already severely droughted.

3.3.2 Stomatal resistance

Stomatal resistances were forced to increase markedly by water stresses (table 4). For the first measurements on day 14 after planting (DAP), stomatal resistances were higher in HB7 and HB25 than in Yulinbai under both water regimes. For the second measurement, the reading in HB25 was lower than in HB7 in agreement with the larger water residue in the pot (fig. 1); no reasonable readings could be obtained from the severely wilted Yulinbai.

Table 3

Plant water potential (-MPa)

DAP	Time	Treatment 1	2	3	4	5	6
14	Pre-dawn	0.32	0.52	0.22	0.40	0.27	0.87
	Mid-day	0.14	0.99	0.16	0.65	0.14	1.16
16	Pre-dawn	0.18	1.27	0.21	1.06	0.14	1.34
	Mid-day	0.41	1.47	0.46	1.64	0.30	1.67
18	Pre-dawn	0.25	1.46	0.22	1.76	0.16	2.15
	Mid-day	0.44	2.79	0.20	2.42	0.35	3.07

Table 4

Stomatal resistance (S. cm-1)

DAP	Treatment 1	2	3	4	5	6
14	3.19	9.46	3.25	12.17	2.88	5.79
18	1.91	19.44	1.98	14.02	0.99	*

* No datum available

Discussion

The drought resistance in plants may be classified into three types, ie., drought escape, drought avoidance and drought tolerance, each of which is characterized by different responses of morphological and physiological traits (Turner 1979, Jordan et al. 1983, Ma 1986). In terms of cultivation for human consumption, the drought trait needed is a higher performance under water stress rather than survival of the drought to avoid elimination in competition. In this sense, a drought resistance test should be closely related to productivity. Nevertheless, there is always a discrepancy between results of relative yield (that is the index of drought resistance) and absolute yield (Fischer and Maurer 1978, Ma and Green 1988). Thus, it would be possible to conclude that some genotypes possessing physiological traits for both drought resistance and high performance under favourable water status should be classified as susceptible to drought, if the comparison were made by the index of drought resistance only without consideration of the absolute yield under drought. For instance, in this experiment, there is a significant difference in plant biomass under good water supply. In terms of index of drought resistance, HB7 was higher than HB25 and Yulinbai which were similar. Actually, absolute biomass of HB25 subjected to drought was highest, showing the consistency between drought resistance and physiological responses.

Drought avoidance is defined as the tolerance of drought by maintaining a high tissue water potential (Turner 1979, Jordan et al. 1983). Higher plant water potential was kept continually in droughted HB25 (table 3) and was closely related to the more developed roots. Therefore, HB25 could best survive the increasing drought (fig. 1).

Seedlings of genotypes differed in adaptive strategy towards the gradually intensified drought (fig. 3). HB25 seems to respond quickly to water stress by a sharp decrease in transpiration rate when water supply is only slightly reduced. Moreover, HB25 could maintain a steady and lower transpiration and assimilation within a larger range of soil water content. A sharp decrease in transpiration occurred only when a threshold of water deficit was reached. Thus HB25 followed an adaptive pattern different from cultivar Yulinbai. Yulinbai in the beginning did not respond to drought imposition with a reduced water loss, however, transpiration rate decreased considerably when a certain value of water shortage was reached (approximately 40 % of water content in this experiment). Combining all results, it seems that the first strategy of adaptation to drought was more beneficial in terms of agriculture. HB7 seems to be an intermediate type when we integrate all traits measured. Of course, the hypothesis remains to be verified by experiments under field conditions.

Summary

The responses of different genotypes in winter wheat to drought stress were studied with wheat seedlings grown in vermiculite culture in a growth chamber. The stressed plants were kept without water from seedling emergence on, while the control plants were kept under favourable water conditions by weighing and watering to the original level every day. Water loss, leaf water potential, leaf stomatal resistance and transpiration, and root and shoot dry matter were measured. It was found that water stress considerably affected the growth of roots and shoots, due to reduced leaf water potential, increased stomatal resistance, and reduced transpiration. It seems, however, that water use efficiency (WUE) increased somewhat under stress. It was shown by the physiological measurements that the cultivars used responded differently to water supply. HB 25 showed both a higher production potential and higher WUE under favourable water supply. In terms of absolute values, but not relative values of biomass, WUE, transpiration rate, leaf water potential and stomatal resistance, HB 25 is superior to the native Yulinbai, an assumed drought-tolerant variety. Therefore, it is suggested that a re-appraisal of the so-called 'drought tolerant' varieties, especially local ones, would be worthwhile.

Reaktion von Sämlingen auf Wasserstreß bei verschiedenen Genotypen von Winterweizen

Zusammenfassung

In einer Klimakammer wurde an Sämlingen in Vermiculit-Kultur die Reaktion verschiedener Genotypen des Winterweizens auf Trockenstreß untersucht. Die Versuchspflanzen wurden nach dem Auflaufen unbewässert gelassen, der

Wassergehalt der Kontrolltöpfe wurde nach täglicher Wägung bis zum ursprünglichen Niveau ergänzt. Erfaßt wurden der Wasserverlust, das Blattwasserpotential, der stomatäre Widerstand und die Transpiration der Pflanze sowie die Trokkenmasse von Wurzel und Sproß. Es zeigte sich, daß der Wasserstreß das Wachstum von Wurzel und Sproß stark beeinträchtigte, was auf das negativere Blattwasserpotential, die erhöhten stomatären Widerstände und die verringerte Transpiration zurückgeführt werden kann. Der Wasserausnützungskoeffizient (WUE) scheint jedoch unter Streß etwas anzusteigen. Die physiologischen Messungen zeigten, daß die untersuchten Sorten auf die Wasserversorgung verschieden reagierten. HB25 zeigte bei günstiger Wasserversorgung sowohl höhere Biomasseproduktion als auch höhere WUE. Nach absoluten (aber nicht relativen) Werten der Biomasse, der WUE, der Transpirationsrate, des Blattwasserpotentials und der stomatären Leitfähigkeit ist HB25 der Lokalrasse Yulinbai, einer als trockenresistent angesehenen Sorte, überlegen. Es wird daher vorgeschlagen, die sogenannten „trockenresistenten" Sorten, besonders die lokalen, neu zu bewerten.

Acknowledgement

We wish to acknowledge the support from the National Scientific Foundation of China for research funds. Thanks to Dr. Hanno Richter for the technical support on the use of the pressure chamber and careful correction of the manuscript.

References

Austin, R. B.: Variety, environment and the yield of cereals. In: Factors Affecting the Accumulation of Exploitable Reserves in the Cereal Plant. Agronomy Conference Newmarket — May 1983 (MAFF) Her Majesty's Stationery Office, 1—13, London 1983.

Begg, J. E. and N. C. Turner: Crop water deficits. In: Advances in Agronomy *28*, 161—218. Academic Press, New York 1976.

Fischer, R. A. and R. Maurer: Drought resistance in spring wheat cultivars. I. grain yield response. Australian Journal of Agricultural Research *29*, 897—912, 1978.

Hoagland, D. R. and W. C. Snyder: Nutrition of Strawberry plant under controlled conditions. Proc. Amer. Society hort. Sci. *30*, 288—294, 1933.

Hough, M. N.: The influence of weather on cereal yields. In: Factors Affecting the Accumulation of Exploitable Reserves in the Cereal Plant. Agronomy Conference Newmarket-May 1983 (MAFF) Her Majesty's Stationery Office, 27—51, London 1983.

Jordan, W. R., W. A. Dugas Jr. and P. J. Shouse: Strategies for crop improvement for drought-prone regions. In: Plant Production and Management under Drought Conditions (Stone and Wills eds.). Elsevier Science Publishers B. V. Amsterdam 281—299, 1983.

Ma, R. K.: A review on the agronomic and physiologic studies on water stress and drought resistance in wheat crops. Bulletin of Field Crop Research n. 4, 11—16, 1986.

Ma, R. K. and C. F. Green: An analysis on the effect of water stress on the yield, soil and plant water relations of winter wheat. National Conference on Crop Physiology of China. Vol. 1, Taiyuan 1988.

Reitz, L. P.: Chapter 1. World distribution and importance of wheat. In: Wheat and Wheat Improvement (Quisenberry and Reitz eds.). American Society of Agronomy Inc., (Publisher) Madison, USA, 1—17, 1967.

Sun, F. R.: Historic Records of Wheat Varieties in Hebei Province. Hebei Academy of Agricultural and Forestry Sciences, Institute of Crops, 125, 1983.

Turner, N. C.: Drought resistance and adaption to water deficits in crop plants. In: Stress Physiology in Crop Plants (Mussell and Staples eds.), John Wiley and Sons, New York, 343—372, 1979.

(Manuskript eingelangt am 25. April 1991, angenommen am 20. August 1991)

Anschrift der Verfasser:

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