

Assessments on the Water Conservation Practices and Wheat Adaptations to the Semiarid and Eroded Environments

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Abstract: The greatest fear of global climate changes is drought and water is the most important factor influencing crop growth. Soil and water conservation is necessary to sustain productivity and environmental quality in semiarid cropping systems. In the world, 61% of the country receives a rainfall of less than 550mm annually, domestication of wheat occurred in such a semiarid region of southwestern Asia, it originally came from dryland gardens. Wheat plants respond to drought through morphological, physiological, and metabolic modifications occurring in all plant organs. At the cellular level, plant responses to water deficit may result from cell damage, whereas other responses may correspond to adaptive processes. Although a large number of drought-induced genes have been identified in a wide range of wheat varieties, a molecular basis for wheat plant tolerance to water stress remains far from being completely understood. The rapid translocation of Abscisic Acid (ABA) in shoots via xylem flux and the increase of ABA concentration in wheat plant organs correlate with the major physiological changes that occur during plant response to drought. It is widely accepted that ABA mediates general adaptive responses to drought. However, there is evidence suggesting that additional signals be involved in this process. The drought resistance breeding showed that a high yield potential is negatively associated with certain drought adaptive traits in wheat. Such a negative association may put a limit on raising potential yield as means for improving actual yield under semiarid conditions. For a relatively determinate target stress environment and with stable genotype \times environment interaction, the probability for achieving progress is high. This approach will be possible only after we learn more about the physiology and genetics of wheat plant responses to water stress and their interactions. The difficulties encountered by molecular biologists in attempting to improve crop drought resistance are due to our ignorance in agronomy and crop physiology and not to lack of knowledge or technical expertise in molecular biology.

Keywords: semiarid conditions, wheat production, physiological adaptation, yield improvement

1 Soil and water conservation practices in dryland farming

Dryland farming, as at present understood, is the profitable production of useful crops, without irrigation, on lands that receives annually a rainfall of 500 mm or less. When the annual precipitation is under 500 mm, the methods of dryland farming are usually indispensable. Dryland farming, however, always implies farming under a relatively low annual rainfall (Monteith, 1990).

In arid and semiarid regions, the conservation of the natural water precipitation for crop production is of paramount importance. In these regions a major challenge is to manage water appropriately. The purpose of such management is to obtain water, conserve it, use it efficiently, and avoid damage to crops. Farm practices must conserve and utilize the available rainfall efficiently. To obtain maximum storage of moisture under any rainfall condition, the soil must absorb as much water as possible when it rains and losses due to evaporation or transpiration must be kept to a minimum. Dryland farming builds upon knowledge from general agriculture but carries out its practices in the light of the significant probability that this year or next will be a drought one. The following agricultural practices are discussed with this background.

1.1 Tillage

All tillage and plantings run across (or perpendicular to) the slope of the land. Such ridges will impede the downward movement of water. Water in the soil exists as a continuous film surrounding each grain. As water near the surface evaporates, water is drawn up from below to replace it, thinning the film. When it becomes too thin for plant roots to absorb, wilting occurs. Tillage creates a rough cloddy surface that lengthens the time necessary for the rain to break down the clods and seal the surface. For seed bed preparation in general, small seeds should have a finer bed than large seeds (Unger, 1992). After harvest, stubble mulch is created on the soil surface. Such material not only prevents raindrops from dropping directly on the soil, but also impedes the flow of water down the slope and thereby increases absorption time (Moldenhauer, 1959; Yadav, 1974; Ross *et al.*, 1985; Jama and Nair, 1996). In semiarid regions, the soil after harvest time is generally too dry for good plowing. Yet if the field is left uncultivated, this dry condition may become even worse and weeds will also grow and produce seeds. The field should be harrowed (or plowed without moldboard) and crop residues left to form a stubble mulch to absorb/retain moisture and soil until the rains return (Gregory *et al.*, 2000).

1.2 Mulch

Water easily enters porous soil and, as it seeps downward, becomes absorbed as films of water around the soil particles. These films form a continuous column of water to the surface of the soil. The film tends to remain at the same thickness around all the soil grains with which it is in contact. This film of water in the soil is known as the capillary water and it is the source of water for the plants (Moldenhauer, 1959). The sun, wind, and dry air will cause evaporation at the surface, thus reducing the thickness of the film at the surface. The thicker films in the subsoil will rise to equalize the distribution again. This will continue until the films are so thin that the plant roots can draw no further moisture from them. Stubble mulching aims at disrupting the soil drying process by protecting the soil surface at all times either with a growing crop or with crop residues left on the surface during fallow. The first benefit of the stubble mulch is that wind speed is reduced at the surface by up to 99% and, therefore, losses due to evaporation significantly reducing (Yadav, 1974). In addition, crop and weed residues can improve water penetration and decrease water runoff losses by 2 to 6 folds and reduce wind and water erosion by 4 to 8 folds relative to a bare fallow field. To obtain the benefit of mulching on soil structure without causing temporary de-nitrification, the mulch can be composted before adding it to the soil. Rapid bacterial action in the tropics makes composting less beneficial than in temperate climates but may still be worthwhile (Mandal and Ghosh, 1984; Ross *et al.*, 1985; Barros and Hanks, 1993; Jama and Nair, 1996). Stubble should not be immediately covered and incorporated in the soil unless rodent or insect infestation is heavy (and even then burning should be considered). It has been well demonstrated that it is normally impossible to raise the soil organic matter content in areas where temperatures are high for long periods. When moisture is present, the rates of oxidation are extremely high and incorporated organic matter is lost quickly. The benefits thus derived from decomposition, as it occurs in the more temperate regions, are not normally experienced. When left on the surface, however, organic matter does not decay so rapidly. Incorporation into the soils will tend to depress the levels of available nitrogen and, hence, it is detrimental to crops if soil nitrogen is low. If soil nitrogen levels are adequate, the incorporation of residues into the soil may be beneficial if done with spring plowing at the start of the rainy season.

1.3 Planting density

Limited moisture dictates the necessity for wider row spacing and lower seeding rates (by one-half to two-thirds) than those used in moisture abundant areas. The resulting reduced plant population provides more moisture and nutrients per plant and thus enhances the possibility that the crop will reach maturity before the supplies are exhausted. Wheat should be planted 18 cm to 35 cm apart and crops such as millet, sorghum, sesame, safflower, etc. in rows 70 cm to 105 cm apart. In some cases, the practice of planting 2 or 4 rows and skipping one is successful in further increasing the efficiency of moisture

utilization. In general, with limited rain, higher seed rates produce more straw/stubble at the expense of grain production (Major *et al.*, 1991; Chauhan and Johansen, 1993; Reynolds *et al.*, 1999).

1.4 Crop rotation

One of the first principles of dry farming with regard to cropping practices is that crop rotation as practiced in more humid regions is not necessarily recommended in semiarid lands. The following constitutes the main differences. Only a limited number of crops are adapted to the climatic conditions and the farmer must sow the crop best suited to the moisture conditions encountered at that time. Moisture in some areas is so limiting, that “soil improving” crops are much less effective than in more humid areas.

1.5 Moisture conservation

Any system of crop rotation should be planned with moisture requirements as the main consideration. For a given set of climatic conditions, a crop may be described as either moisture dissipating or conserving. After harvest of a moisture-conserving crop, the soil contains more moisture than at planting. This conserved moisture can help guarantee the success of the succeeding crop. Crops which are sown in rows so that intertillage and dirt mulching can be practiced tend to be moisture conserving. Under sowing may also assist in conservation. Moisture may be insufficient to grow a crop and conserve enough water for the succeeding crop. In such a case, it is necessary to utilize the dirt and stubble mulched fallow in the rotation. If annual rainfall is 250 mm to 375 mm, this practice will be needed at least every other year; and if rainfall is 375 mm—500 mm, it will be needed at least one in every three years. Plants which are densely planted or which produce a dense ground cover tend to resist erosion much better than those which are intertilled or tend to be moisture conserving. Loss of soil due to erosion is a significant dry farming problem and erosion controlling crops should be included in a rotation, preferably in a strip cropping mode (Williams *et al.*, 1983).

1.6 Soil nutrients and structure

When related crops are successively planted specific soil minerals and nutrients are withdrawn faster than they can be replaced by decay or subsoil movement. This selective depletion causes a soil to be “worn out” quickly. Simple rotation of crops makes depletion more uniform so that soils “wear out” more slowly. The planting of legumes (such as gram or groundnut or alfalfa) with their nitrogen fixing capabilities tends to restore soil fertility. The use of green manure (plowing under of a green crop, such as alfalfa, rather than harvesting) can also improve soil fertility and texture but benefits may be short lived in the tropics and difficult for Third World farmers. The planting of any deep or extensively rooted plants (such as grasses, alfalfa, etc.) tends to improve soil structure and draw subsoil nutrients to the surface like a natural fallow and can increase pasturage during dry periods. Crops like cassava, which require relatively little soil nutrients may also be grown for rotation or when soil is almost worn out.

Rainfall after sowing equals the total rainfall accumulated after sowing for the indicated months. In general the amount of rainfall required at higher altitudes is slightly lower than indicated. The potential evapotranspiration does not change much during the rainy seasons for tropics and subtropics. After a dry season, sowing starts at there has been an accumulating more than 60 mm in less than 30 days. The maximum moisture storage within a soil at field capacity is approximately 100 mm—150 mm. When a crop is sown in a soil at field capacity, much less rainfall is required during the growing season. Rainfall in the month of flowering is for the 30 day period from 20 days before 50% flowering to 10 days after 50% flowering. If the crop is to be harvested by a combine, rainfall during harvest should be less than 120 mm/month (and much less than that if there is a heavy overcast and/or rains in the late morning).

2 Environmental limitation on wheat yield

Wheat is a common name for cereal grasses of a genus of the grass family, cultivated for food since

prehistoric times by the peoples of the temperate zones and now the most important grain crop of those regions. Wheat is a tall, annual plant attaining an average height of 1.2 m. The leaves, which resemble those of other grasses, appear early and are followed by slender stalks terminating in spikes, or so-called ears, of grain.

2.1 Wheat classification

Species of wheat are classified according to the number of chromosomes found in the vegetative cell. They are divided into three series: the diploid, or einkorn, containing 14 chromosomes; the tetraploid, or emmer, containing 28 chromosomes; and the hexaploid, containing 42 chromosomes (Gill *et al.*, 1991). Wheat species crossbreed relatively frequently in nature (Harris, 1990). Selection of the best varieties for domestication took place over many centuries in many regions (Li, 1970; Harlan, 1987). Today, only varieties of common, club, and durum wheats are of commercial importance, but other species are still grown to suit local conditions and provide essential stock for formal breeding programs (Talbert *et al.*, 1991). Remains of both emmer and einkorn wheats have been found by archaeologists working on sites in the Middle East dating from the 7th millennium BC. Emmer was grown in predynastic Egypt; in prehistoric Europe it was grown in association with barley and einkorn and club wheats. Bread wheat was identified at a 6th-millennium BC site in southern Turkestan, and a hexaploid wheat was found at Knossos in Crete (Harlan, 1987).

2.2 Wheat distribution and domestication

According to the regions in which they are grown, certain types of wheat are chosen for their adaptability to altitude, climate, and yield. The common wheats grown in China, United States, and Canada are spring and winter wheat, planted either in the spring for summer harvest or in the fall for spring harvest. The color of the grain varies from one type to another; white grains are mostly winter wheats, while red ones are spring wheats. Closely related to the common wheats are the club wheats, which have especially compact spikes, and spelta, in which the glumes (reduced, scale-like leaves) tightly enclose the grains. Durum wheat (Latin durum) is so called because of the hardness of the grain. It is grown in north-central regions of the United States.

The domestication of wheat occurred in the hilly region of southwestern Asia bordered on one side of the Tigris-Euphrates basin (ancient Mesopotamia) and on the other by the mountains of Iran, Turkey, Syria, and Jordan (Li, 1970). This region is usually referred to as the "Fertile Crescent". The earliest findings of the two species of cultivated wheat (*Triticum monococcum* L. and *T. turgidum* L. var. *dicoccoides*) were in deposits dated between 7,500 and 6,700 B.C. The cultivation of wheat dates back to the Indus valley civilization in the Indian subcontinent (about 300 B.C.). One of the wheats identified in the Mohenjodaro excavation was *T. aestivum* subspecies *sphaerococcum*, characterized by a dwarf plant habit and spherical grains. Cultivated as a food source for more than 9,000 years, wheat has undergone many changes in the process of its domestication. A likely ancestor to all cultivated wheats is wild einkorn, with small grains and long brittle stalks which typify early species such as einkorn, still cultivated as animal feed; wild emmer with slightly larger grains; and emmer, widely used by the Greeks and Romans and closely related to modern wheats. The strength and large grains of spelt wheat, a hybrid still grown in Europe, offered a radically high yield from fewer plants. Further modifications produced the large-grained durum wheat used to make most pasta, as well as bread wheat; high in gluten to make bread dough elastic and airy (Evans, 1976; Jennings and Cock, 1977).

Wheat is mostly grown in the temperate and subtropical zones of the world between 15 to 60°N and 25 to 40°S latitudes and at altitudes ranging from sea level to 3,000 m and with annual rainfall ranging from 250 to 2,000 mm per year. The optimum temperature for the wheat crop is about 20°C and any temperature above 35°C is not tolerated. The largest wheat-producing countries of the world are the United States, China and Russia; however, extensive wheat growing is also carried out in India, W Europe, Canada, Argentina and Australia. In the United States, the wheat belt covers the Ohio Valley, the prairie states, E Oregon, Kansas and Washington. Large-scale mechanized farming and the continuous planting of wheat without regard to crop rotation have exhausted the soil in many areas. High-yielding

wheat, one of the achievements of the Green Revolution, requires optimal growth conditions e.g. adequate irrigation and large amounts of fertilizer. New high-yielding wheats were developed in the 1960s for use in developing countries and research on them continued in the 1970s. Research programs have developed commercial wheat varieties for hardiness and disease resistance. In 1978, the identification of a drought-resistant and high-protein, ancestral species growing in the Middle East held promise for more improved wheat varieties (Kimber and Sears, 1987).

2.3 Wheat production in the world

Average wheat yields throughout the world approach only 30%—60% of maximum attainable yields. Water stresses are the major factors preventing the realization of maximum yield, with water-deficits and elevated temperatures causing the greatest reductions (Siddique *et al.*, 2000). Research has focused on the identification of genes involved in protecting plants when water is removed, the genetic diversity in rooting systems for water transport into the plant and the development of new irrigation technology (Fred, 1991). Global demand for wheat is growing faster than gains in genetic yield potential are being realized; currently a little under 1% per year in most regions. Improvement in yield of semidwarf wheat has generally been associated with increased harvest index (HI) and grain per square meter. For CIMMYT (International Maize and Wheat Improvement Center) varieties released between 1962 and 1988, yield increase was also associated with higher flag-leaf photosynthetic rate and related traits, but not higher biomass. Nevertheless, significantly higher biomass has been reported in more recent CIMMYT lines. Improved HI is associated with higher N use efficiency (yield per unit of available N) and improved yield of semidwarf lines is expressed at high and low levels of N input. Where interplant competition for light and soil factors are manipulated, yield improvement is associated with adaptation to high plant density (Reynolds *et al.*, 1999). Studies have confirmed that the juvenile spike growth phase is critical in determining both grain number and kernel weight (sink) potential. Improving assimilate availability during this stage, perhaps by lengthening its relative duration, may be one way to improve yield potential. Traits that could potentially be exploited for improving assimilate (source) capacity include early vigor, stay-green, leaf-angle and remobilization of stem reserves. Use of alien chromatin is a successful approach for introducing yield-enhancing genes into elite genetic backgrounds. Examples include the 1B/1R chromosome translocation from rye (*Secale cereale* L.) and more recently the LR19 segment from tall wheatgrass [*Agropyron elongatum* (Host) P. Beauv.]. Improving the efficiency of early-generation selection may be another strategy for raising yield potential by increasing the probability of identifying physiologically superior lines by techniques such as infrared thermometry and spectral reflectance.

2.4 Wheat adaptability to drought

In another aspect, the evaluation of crop genotypes for their adaptability is often performed by means of regression techniques of yields against some kind of an environmental index as independent variable. The weakness of these techniques lies in the lack of a direct assessment of a given environment by specific environmental factors. Karamanos and Papatheohari (1999) suggested a new index, the water potential index (WPI), as a measure of the total water stress experienced by any crop in a given environment for a specific time interval. Their results showed that the index is derived from the integral of the course of leaf water potential over time. Its usefulness is demonstrated in evaluations of field-grown bread wheat and faba bean genotypes of contrasting characteristics by yield vs. WPI linear regression analysis. In these regressions, the intercept represents the “potential” yield at no stress conditions and the slope represents the “adaptability” of each genotype. It was found that the dwarf wheat cultivars exhibited higher potential yields and lower adaptability in comparison with the tall cultivars. In faba beans, the smaller the seed size of a cultivar, the lower were the potential yield and the better the adaptability. On the basis of this regression analysis, different response scenarios of hypothetical crop genotypes are described. Furthermore, the “relative adaptability” concept is presented, in which the potential yield effect is removed from the adaptability of any genotype. Examples of the use of WPI for obtaining information on the involvement of water shortage in specific growth stages of the wheat crop or for assessing the sensitivity of faba bean yield components to water shortage are presented.

3 Water deficits on the wheat production

In order to understand how winter wheat growth and yield respond to soil moisture availability, one first needs to appreciate how wheat develops. The crop progresses through various developmental stages, each stage having its own unique consequences for the growth and yield potential of the stand. Once these stages and influence of the environment on them are understood, informed management and breeding strategies are possible. The following are some of the important developmental stages in winter wheat and the consequences for yield losses associated with severely limited soil water supplies.

Table 1 Effect of drought on wheat growth and yield consequences*

	Effect of Drought	Yield Consequences
Seed	Germination reduced & delayed	Altered yield components. Reduced yield if less than ca. 1,000 plants/m ²
Seedling	Increased tiller	Reduced spikes/m ² and yield
	Reduced N uptake	Accelerated senescence
Tillering, Spike Initiation	Death of young florets	Reduced grain set and yield
	Reduced stem elongation	
Stem Elongation & Spike Growth		Greater accumulation of soluble stem carbohydrates, partially buffers plant against loss of photosynthesis during grain filling
Anthesis (flowering)	Accelerated senescence	Reduced mean grain size
Maturity		

*After Lafond and Baker, 1986; Navari-Izzo *et al.*, 1989; Deng *et al.*, 1990; Pecetti *et al.*, 1992)

In the past, wheat yield increase has invariably resulted from increased kernel number per unit area with little change in kernel weight (Feil, 1992). Fischer (1985) proposed that kernel number is the resultant of spike dry weight at anthesis (g per unit area), which has increased through breeding, and kernels per unit spike weight, which is unchanged. Spike weight in turn is the product of duration of spike growth phase, crop growth rate and partitioning of dry matter into spike during this phase. Another way to view the effects of water stress on wheat yield potential is to understand yield as a function of its yield components, as follows:

Yield Component	Important Developmental Stages
Spike Number	Seed-Tillering
Number of Grains per Spike	Tillering-Early Grain Filling
Grain Weight	Anthesis-Maturity

Many plant traits have been related to drought resistance. The following are some of the most commonly-reported (from Ludlow and Muchow, 1990; Blum *et al.*, 1991):

Grain Yield	Leaf/Spike Pubescence
Grain Yield Stability	Leaf Rolling
Early Maturity	Leaf Senescence
Early Vigor	Leaf Size
Extensive Root System	Leaf Orientation
Plant/Growth Recovery	Leaf Elongation Rate
Awns	Epicuticular Wax
Tiller Death	Cell Membrane Stability

Stomatal Resistance
 Leaf Water Retention
 Carbon Translocation
 Carbon Discrimination

Osmotic Adjustment
 Canopy Temperature
 Water Use Efficiency
 Accumulation of ABA, Pro., Asp

Despite considerable efforts of plant scientists to understand plant drought responses, little progress has been made in programs specifically designed to improve wheat drought resistance through breeding of traits other than those directly related to yield. Drought resistance is a complex phenomenon with diverse plant traits (above) having varying consequences on plant yield in different environments. The greatest progress has been in breeding strategies that involve simple genetics such as early maturity and more efficient carbon translocation (semi-dwarfs). The introduction of dwarfing genes was not a drought resistance strategy, although it appears to benefit wheat yields in all but specifically in the most severe drought-prone environments.

3.1 Physiological adaptations to water stress

Wheat plants close their stomata in response to low soil water potential. Closure of stomata greatly reduces the flux of CO₂ into the leaf and of water out of the leaf (Deng *et al.*, 2000). This can quickly stress the wheat crop in several ways. Water transpiring through the plant's stomata provides a means of cooling the plant and thereby avoiding temperature stress (Ludlow, 1980; Jones, 1998). Carbon from CO₂ is the ultimate electron acceptor in photosynthesis. In the presence of light, Photosystem I (PSI) continues to operate resulting in the production of the reducing compound NADPH. Plants have a very limited capacity to store NADPH. The light reactions involve the splitting of water to produce protons and oxygen free radicals (O₂[•]), hydroxyl radicals (OH[•]) and singlet oxygen, highly reactive, unstable molecules with unpaired electrons in the outer shell. These can destroy membrane lipids, chlorophyll and proteins unless a receptor (NADP⁺) for the increased reducing power is present. Evans (1993) noted that photorespiration may be adaptive for plants growing under water stress by regulating reductant and avoiding photochemical damage. Thus efforts to improve crops by eliminating photorespiration might make them less tolerant to water stress and, hence, less adapted to dry regions. Polyamine metabolic level also was linked with water stress (Reggiani *et al.*, 1993).

3.2 Morphological adaptations to water stress

In order to cope with prolonged stomatal closure, many wheat varieties have adaptations that function to reduce R(n), the amount of absorbed radiation reaching the photosynthetic tissues, thus alleviating the problems of heat load and the adverse affects of photochemical damage. Interception of solar radiation is reduced by several drought adaptations. Increasing reflectance by the presence of a dense covering of light-colored trichomes (hairs) on the leaf surface, resinous coatings on the foliage, or thick waxy cuticles. A thick cuticle has added advantages, it absorbs ultraviolet radiation, greatly reduces cuticular transpiration and increases disease resistance (by imposing a barrier to fungal and bacterial pathogens). Evans (1993) noted that increased glaucousness (waxy surface) in wheat and barley can increase yields in dryland environments by lowering leaf temperatures and improving water-use efficiency. Some wheat varieties have a high leaf density resulting from production of fibers, sclerenchyma, thick cell walls or the accumulation of silica. Such drought inducible traits is helpful for protecting insects (Philippe *et al.*, 2000). These adaptations favor survival of plants during drought but are associated with reduced photosynthetic rates (Fischer and Turner, 1978; Fitter and Hay, 1987).

These morphological adaptations to dry conditions clearly involve tradeoffs. That is, increased light reflectance and increased resistance to H₂O diffusion become constraints to photosynthesis and growth when water is readily available. Thus such adaptations would not be beneficial for wheat selected for high yields in more favorable environments (Blum, 1985). It is often suggested that the yields of conventional wheat in dry areas can be improved by introducing "genes for drought tolerance" from its relative species. Crop characteristics like drought-tolerance are a likely focus of the new technologies. The adaptations that allow some plants to lose very little water through their leaves in transpiration, transferred to more

widely grown crops, could reduce irrigation needs. This strategy of bioengineering drought tolerance into wheat is likely to fail if the trade-offs inherent in many adaptations to drought are not taken into account.

4 Water stress cellular and molecular biology on wheat

Wheat plants respond to drought through morphological, physiological, and metabolic modifications occurring in all plant organs. At the cellular level, plant responses to water deficit may result from cell damage, whereas other responses may correspond to adaptive processes. Although a large number of drought-induced genes have been identified in a wide range of wheat varieties, a molecular basis for wheat plant tolerance to water stress remains far from being completely understood (Ingram and Bartels, 1996). The rapid translocation of ABA in shoots via xylem flux and the increase of ABA concentration in wheat plant organs correlate with the major physiological changes that occur during plant response to drought (Zeevaert and Creelman, 1988). It is widely accepted that ABA mediates general adaptive responses to drought. However, there is evidence suggesting that additional signals be involved in this process (Munns and King, 1988; Davies and Zhang, 1991; Munns *et al.*, 1993; Griffiths and Bray, 1996).

Six cDNAs corresponding to transcripts up-regulated by water stress were isolated previously from a drought-tolerant sunflower (*Helianthus annuus* L.) line, R1 (Ouvrard *et al.*, 1996). Comparison of the steady-state level of transcripts between the R1 line and a closely related drought-sensitive line, S1 has shown that three of those transcripts (HaElip1, HaDhn1 and HaDhn2) were differently accumulated in tolerant compared with sensitive plants during water deficit. In response to exogenous ABA in leaves of the R1 genotype, HaDhn1 and HaDhn2 transcripts were up-regulated and the steady-state level of HaElip1 transcripts was not modified (Ouvrard *et al.*, 1996). HaDhn1- and HaDhn2-deduced proteins belong to the dehydrin family, and HaElip1 is a related homolog of early-light-induced protein (ELIP).

Among the water-stress-induced proteins so far identified, dehydrins and the D-11 subgroup of late-embryogenesis-abundant (LEA) proteins (Dure *et al.*, 1989) are frequently observed, and more than 65 plant dehydrin sequences are available (Close, 1997). Dehydrins are highly abundant in desiccation-tolerant seed embryos and accumulate during periods of water deficit in vegetative tissues. These proteins display particular structural features such as the highly conserved Lys-rich domain predicted to be involved in hydrophobic interaction leading to macromolecule stabilization (Close, 1996).

Very little is known about dehydrin functions in plant. Studies have established correlations between drought adaptation and dehydrin accumulation in wheat and poplar (Labhili *et al.*, 1995; Pelah *et al.*, 1997). Positive correlations were also reported for species tolerant to stresses that have a dehydrative component such as salt stress (Galvez *et al.*, 1993; Moons *et al.*, 1995) and freezing and cold stress (Arora and Wisniewski, 1994; Close, 1996; Artlip *et al.*, 1997). Physiological observations associated with the varietal difference in tolerance have been reported (Moons *et al.*, 1995; Pelah *et al.*, 1997). In most of the published studies, gene expression was described as a function of time after the stress was applied rather than as a function of parameters describing the plant's water status. Therefore, it is difficult to determine from these data precise relationships between plant physiological responses to drought and drought-induced gene expression.

5 Wheat yield improvement in the semiarid area

Evidence in drought resistance breeding showed that a high yield potential is negatively associated with certain drought adaptive traits in wheat (Blum, 1993). Such a negative association may put a limit on raising potential yield as means for improving actual yield under semiarid conditions. For a relatively determinate target stress environment and with stable genotypex environment interaction, the probability of achieving progress is high. This approach will be possible only after we learn more about the physiology and genetics of wheat plant responses to water stress and their interactions. The difficulties encountered by molecular biologists in attempting to improve crop drought resistance are due to our ignorance in agronomy and crop physiology and not to lack of knowledge or technical expertise in molecular biology.

Recent advances in crop management have enabled the production of winter wheat in most of the Canadian (Entz and Fowler, 1991). They comparatively studied the agronomic performance of dominant

hard red winter and high-quality hard red spring wheat cultivars in semiarid and dry subhumid regions of Saskatchewan. Their results showed that in 15 trials, winter wheat (WW) over yielded spring wheat (SW) by an average of 36%; and in three trials, 'Norstar' WW yielded 26% higher than the high-yielding semidwarf SW, 'RY 320.' Protein yield was higher for WW in two of 15 trials and protein concentration was always higher for SW. Higher grain yield of WW was attributed mainly to the production of a higher kernel number per square meter (KNO). Crop development rate, aerial dry matter production, evapotranspiration (ET), and water use efficiency (WUE), were measured for Norstar WW and 'Katepwa' SW in six trials grown between 1986 and 1988. The period between Zadoks growth stage (ZGS) 21 and 65 was 4 to 14 d longer for Norstar than for Katepwa. Average daily air temperature between ZGS 21 and 65 was 2.6 °C higher for Katepwa, and daily air temperature during this period was negatively correlated with KNO in both cultivars. Early season dry matter production was highest for Norstar. These early season cultivar differences gradually disappeared and, with the exception of two trials, total dry matter was similar by crop maturity. Harvest index was significantly higher for Norstar in five of six trials. Seasonal ET patterns were similar for Norstar and Katepwa, except in three out of six trials where ET in early May was significantly higher for the WW cultivar. The WUE for dry matter production, grain yield and grain protein yield was consistently higher for Norstar.

Long-term N fertilizer trials for dryland wheat are frequently confounded by large year-to-year variability in yields resulting from moisture stress fluctuations. To account for this variability, Korentajer and Berliner (1988) conducted a N fertilizer study in which the magnitude of moisture stress was monitored. Their experiment was carried out on a loamy fine sand soil, with wheat (cv. Betta), using a completely randomized block design with four replicates and five of N fertilizer levels: 0 kg • N • ha⁻¹, 30 kg • N • ha⁻¹, 60 kg • N • ha⁻¹, 90 kg • N • ha⁻¹, and 120 kg • N • ha⁻¹. The seasonal moisture stress index, S, was estimated from a weighted product of ET/ET(p) ratios (actual to potential evapotranspiration) obtained for the different phenological wheat growing periods. The ET was estimated from soil moisture (monitored by means of a neutron moisture meter), whereas ET(p) was calculated from meteorological measurements using Penman's equation. The response to N in both relatively dry and wet years was significant with mean yields of 3.18 ton • ha⁻¹ and 1.7 ton • ha⁻¹, respectively. The data were statistically analyzed by means of a postulated multiple regression model with N and S levels as the explanatory variables. The model was validated using yield and meteorological data from several other 2-yr N response studies. A good correlation ($R^2 = 0.63$, standard error of the estimate = 0.27 ton • ha⁻¹) was obtained between the predicted and the observed yields. Their results highlight the need for moisture stress measurements to be included in fertilizer trials conducted in areas of large seasonal rainfall variability.

In the molecular physiology aspect, Loggini *et al.* (1999) analyzed antioxidative defenses, photosynthesis, and pigments (especially xanthophyll-cycle components) in two wheat (*Triticum durum* Desf.) cultivars, Adamello and Ofanto, during dehydration and rehydration to determine the difference in their sensitivities to drought and to elucidate the role of different protective mechanisms against oxidative stress. Drought caused a more pronounced inhibition in growth and photosynthetic rates of the more sensitive cv Adamello compared with the relatively tolerant cv Ofanto. During dehydration the glutathione content decreased in both wheat cultivars, but only cv Adamello showed a significant increase in glutathione reductase and hydrogen peroxide-glutathione peroxidase activities. The activation states of two sulfhydryl-containing chloroplast enzymes, NADP⁺-dependent glyceraldehyde-3-phosphate dehydrogenase and fructose-1,6-bisphosphatase, were maintained at control levels during dehydration and rehydration in both cultivars. This indicates that the defense systems involved are efficient in the protection of sulfhydryl groups against oxidation. Drought did not cause significant effects on lipid peroxidation. Upon dehydration, a decline in chlorophyll a, lutein, neoxanthin, and β -carotene contents, and an increase in the pool of de-epoxidized xanthophyll-cycle components (i.e. zeaxanthin and antheraxanthin), were evident only in cv Adamello. Accordingly, after exposure to drought, cv Adamello showed a larger reduction in the actual photosystem II photochemical efficiency and a higher increase in nonradiative energy dissipation than cv Ofanto. Although differences in zeaxanthin content were not sufficient to explain the difference in drought tolerance between the two cultivars, zeaxanthin formation may be relevant in avoiding irreversible damage to photosystem II in the more sensitive cultivar.

6 Conclusions and perspectives

(1) It is clear that the greatest fear of global climate changes is drought. Even today, water is the most important factor influencing crop growth. In the world, 61% of the country receives a rainfall of less than 500mm annually, which is considered the minimum for successful dryland farming, but more highly populated, industrial and mining centers of the country. This is rapidly becoming less feasible, however, and greater attention should be paid to the management of demand and more efficient use of water. Undertaking dryland cropping in areas of the country where the long term annual rainfall is equal to or less than the minimum required to successfully sustain such activities will inevitably lead to drought, and this is more an indication of unwise farming rather than unusual weather.

The agricultural industry often equates conservation programs with arable land reductions and increased production costs. Conservation production represents a opportunity to combine both increased agricultural productivity and resource conservation. Conservation production embraces the philosophies of profitable conservation farming by providing the opportunity for:

- Improved control of soil erosion.
- More efficient crop moisture utilization.
- Higher crop productivity.
- Longer crop rotations without summer fallow.
- Reduced tillage.
- Improved water use efficiency.

(2) The domestication of wheat occurred in the semiarid region of southwestern Asia bordered on one side by the Tigris-Euphrates basin (ancient Mesopotamia) and on the other by the mountains of Iran, Turkey, Syria, and Jordan. This region is usually referred to as the "Fertile Crescent". The earliest findings of the two species of cultivated wheat (*Triticum monococcum* L. and *T. turgidum* L. var. *dicoccoides*) were in deposits dated between 7,500 and 6,700 B.C. The cultivation of wheat dates back to the Indus valley civilization in the Indian subcontinent (about 300 B.C.). One of the wheats identified in the Mohenjodaro excavation was *T. aestivum* subspecies *sphaerococcum* characterized by a dwarf plant habit and spherical grains. Cultivated as a food source for more than 9,000 years, wheat has undergone many changes in the process of its domestication. A likely ancestor to all cultivated wheats is wild einkorn, the small grains and long, brittle stalks of which typify early species such as einkorn, still cultivated as animal feed. Wild emmer with slightly larger grains, widely used by the Greeks and Romans and closely related to the modern wheats cultivated at present. The strength and large grains of spelt wheat, a hybrid still grown in Europe, offered a remarkable high yield from fewer plants. Further modifications produced the large-grained durum wheat used to make most pasta, as well as bread wheat with high in gluten content that makes bread dough elastic and airy. It seems that these foods originally came from dryland gardens.

(3) One of the wheat physiological adaptations to water stress is the closure their stomata in response to low soil water potential. Closure of stomata greatly reduces the flux of CO₂ into the leaf and of water out of the leaf. This can quickly stress the wheat crop in several ways. Water transpiring through the plant's stomata provides a means of cooling the plant and thereby, avoiding temperature stress. Carbon from CO₂ is the ultimate electron acceptor in photosynthesis. In the presence of light, Photosystem I (PSI) continues to operate resulting in the production of the reducing compound NADPH. Wheat plants have a very limited capacity to store NADPH. Photorespiration may be adaptable for wheat plants growing under water stress by regulating reductant and avoiding photochemical damage. Thus, efforts to improve crops by eliminating photorespiration might make them less tolerant of water stress and, hence, less adapted to dry regions. In the aspect of morphological adaptations to water stress, many wheat varieties have adaptations that function to reduce R(n), the amount of absorbed radiation reaching the photosynthetic tissues, thus alleviating the problems of heat load and the adverse affects of photochemical damage. Interception of solar radiation is reduced by several drought adaptations. Increasing reflectance by the presence of a dense covering of light-colored trichomes (hairs) on the leaf surface, resinous coatings on the foliage, or thick waxy cuticles. A thick cuticle has added advantages as it absorbs ultraviolet radiation and greatly reduces cuticular transpiration. Increased glaucousness (waxy surface) in wheat and barley can increase yields in dryland environments by lowering leaf temperatures and

improving water-use efficiency. Some wheat varieties have a high leaf density resulting from production of fibers, sclerenchyma, thick cell walls, or the accumulation of silica. These adaptations favor survival of plants during drought but are associated with reduced photosynthetic rates.

(4) Wheat plants respond to drought through morphological, physiological, and metabolic modifications occurring in all plant organs. At the cellular level, plant responses to water deficit may result from cell damage, whereas other responses may correspond to adaptive processes. Although a large number of drought-induced genes have been identified in a wide range of wheat varieties, a molecular basis for wheat plant tolerance to water stress remains far from being completely understood. The rapid translocation of ABA in shoots via xylem flux and the increase of ABA concentration in wheat plant organs correlate with the major physiological changes that occur during plant response to drought. It is widely accepted that ABA mediates general adaptive responses to drought. However, there is evidence suggesting that additional signals are involved in this process.

(5) Evidence in drought resistance breeding showed that a high yield potential is negatively associated with certain drought adaptive traits in wheat. Such a negative association may put a limit on raising potential yield as means for improving actual yield under semiarid conditions. For a relatively determinate target stress environment and with stable genotypex environment interaction, the probability for achieving progress is high. This approach will be possible only after we learn more about the physiology and genetics of wheat plant responses to water stress and their interactions. The difficulties encountered by molecular biologists in attempting to improve crop drought resistance are due to our ignorance in agronomy and crop physiology and not to lack of knowledge or technical expertise in molecular biology.

References

- Arora R, Wisniewski ME (1994) Cold acclimation in genetically related (sibling) deciduous and evergreen peach (*Prunus persica* L. Batsch). II. A 60-kilodalton bark protein in cold-acclimated tissues of peach is heat stable and related to the dehydrin family of proteins. *Plant Physiology*. **105**, 95-101.
- Artlip TS, Callahan AM, Bassett CL, Wisniewski ME (1997) Seasonal expression of a dehydrin gene in sibling deciduous and evergreen genotypes of peach (*Prunus persica* L. Batsch). *Plant Molecular Biology* **33**, 61-70.
- Barros LCG, Hanks RJ (1993) Evapotranspiration and yield as affected by mulch and irrigation. *Agronomy Journal* **85**, 692-697.
- Blum A (1985) Breeding crop varieties for stress environments. *Critical Reviews in Plant Sciences* **2**, 199-238.
- Blum A (1993) Selection for sustained production in water deficit environments. In 'International crop science I' (Eds DR Buxton, R Shibles.) pp. 343-347. (Wisconsin, Crop science of America)
- Blum A, Shpiler L, Golan G, Meyer J, Sinmena B (1991) Mass selection of wheat for grain filling without transient photosynthesis. *Euphytica* **54**, 111-116.
- Brengle KG (1982) 'Principles and practices of dryland farming.' (Boulder, Colorado Associated University Press)
- Chauhan YS, Johansen C, Singh L (1993) Adaptation of extra short duration pigeonpea to rainfed semi-arid environments. *Experimental agriculture* **29**, 233-243.
- Close TJ (1996) Dehydrins: emergence of a biochemical role of a family of plant dehydration proteins. *Physiol. Plant* **97**, 795-803.
- Close TJ (1997) Dehydrins: a commonality in the response of plants to dehydration and low temperature. *Physiol. Plant* **100**, 291-296.
- Davies WJ, Zhang J (1991) Root signals and the regulation of growth and development of plants in drying soil. *Annual Review in Plant Physiology and Plant Molecular Biology* **42**, 55-76.
- Deng XP, Shan L, Inanaga S (1990) Relationship between osmotic adjustment and energy metabolism during plumule elongation of spring wheat. *Acta Phytophysiological Sinica* **16**, 373-379.
- Deng XP, Shan L, Ma YQ, Inanaga S (2000) Diurnal oscillation in the intercellular CO₂ concentration of Spring Wheat under the Semiarid Conditions, *Photosynthetica* **38**, 187-192.

- Dennis P, Fry GLA (1992) Field margins: can they enhance natural enemy population densities and general arthropod diversity on farmland. *Agriculture, Ecosystems, and Environment* **40**, 95-115.
- Dure LM, Crouch M, Harada J, Ho T-HD, Mundy J, Quatrano R, Thomas T, Sung ZR (1989) Common amino acid sequence domains among the LEA proteins of higher plants. *Plant Molecular Biology* **12**, 475-486.
- Entz MH, Fowler DB (1991) Agronomic performance of winter versus spring wheat. *Agronomy Journal* **83**, 527-532.
- Evans LT (1993) 'Crop evolution, adaptation and yield.' (Cambridge, Cambridge University Press)
- Feil B (1992) Breeding progress in small grain cereals: A comparison of old and modern cultivars. *Plant Breeding* **108**, 1-11.
- Fischer RA (1985) Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science* **105**, 447-461.
- Fischer RA, Turner NC (1978) Plant productivity in the arid and semiarid zones. *Annual Review in Plant Physiology* **29**, 277-317.
- Fitter AH, Hay RKM (1987) 'Environmental physiology of plants.' (London, Academic Press)
- Galvez AF, Gulick PJ, Dvorak J (1993) Characterization of the early stages of genetic salt-stress responses in salt-tolerant *Lophopyrum elongatum*, salt-sensitive wheat, and their amphiploid. *Plant Physiology* **103**, 257-265.
- Gamo M (1999) Classification of arid regions by climate and vegetation. *Journal of Arid Land Studies* **1**, 9-17.
- Gregory S M, Robert MA, David CN (2000) Optimizing Wheat Harvest Cutting Height for Harvest Efficiency and Soil and Water Conservation. *Agronomy Journal* **92**, 1104-1107.
- Griffiths A, Bray EA (1996) Shoot induction of ABA-requiring genes in response to soil drying. *Journal of Experimental Botany* **47**, 1525-1531.
- Ingram J, Bartels D (1996) The molecular basis of dehydration tolerance in plants. *Annual Review in Plant Physiology and Plant Molecular Biology* **47**, 377-403.
- Jama BA, Nair PK (1996) Decomposition and nitrogen-mineralization patterns of *Leucaena leucocephala* and *Cassia siamea* mulch under tropical semiarid conditions in Kenya. *Plant and Soils* **179**, 275-285.
- Jones HG (1998) Stomatal control of photosynthesis and transpiration. *Journal of Experimental Botany* **49**, 387-398.
- Karamanos AJ, Papatheohari AY (1999) Assessment of Drought Resistance of Crop Genotypes by Means of the Water Potential Index. *Crop Science* **39**, 1792-1797.
- Korentajer L, Berliner PR (1988) Effects of moisture stress on nitrogen fertilizer response in dryland wheat. *Agronomy Journal* **80**, 977-981.
- Labhili M, Joudrier P, Gautier MF (1995) Characterization of cDNAs encoding *Triticum durum* dehydrins and their expression patterns in cultivars that differ in drought tolerance. *Plant Science* **112**, 219-230.
- Lafond GP, Baker RJ (1986) Effect of temperature, moisture stress, and seed size on germination of nine spring wheat cultivars. *Crop Science* **26**, 563-567.
- Loggini B, Scartazza BA, Navari-Izzo EF (1999) Antioxidative Defense System, Pigment Composition, and Photosynthetic Efficiency in Two Wheat Cultivars Subjected to Drought. *Plant Physiology* **119**, 1091-1100.
- Ludlow MM (1980) Adaptive significance of stomatal responses to water stress. In 'Adaptation of Plants to water and High Temperature Stress' (Eds NC Turner, PJ Kramer) pp.16-47. (Persimmon Press, Oxford)
- Ludlow MM, Muchow RC (1990) A critical evaluation of traits for improving crop yields in water-limited environments. *Advantages in Agronomy* **43**, 107-152.
- Major DJ, Morrison RJ, Blackshaw RE, Roth BT (1991) Agronomy of dryland corn production at the northern fringe of the Great Plains. *Journal of production agriculture* **4**, 606-613.
- Mandal BK, Ghosh TK (1984) Efficacy of mulches in the reduction of irrigation requirement of groundnut. *The Indian journal of agricultural sciences* **54**, 446-449.
- Moldenhauer WC (1959) Establishment of Grasses on Sandy Soil of the Southern High Plains of Texas Using a Mulch and Simulated Moisture Levels. *Agronomy Journal* **51**, 39-41.

- Monteith JL (1990) Steps in crop climatology. *In* 'Challenges in dryland agriculture, a global perspective: proceedings of the International Conference on Dryland Farming.' pp. 273-282. Amarillo/Bushland, TX, USA.
- Moons A, Bauw G, Prinsen E, Van Montagu M, Van Der Straeten D (1995) Molecular and physiological responses to abscisic acid and salts in roots of salt-sensitive and salt-tolerant indicator rice varieties. *Plant Physiology* **107**, 177-186.
- Munns R, King RW (1988) Abscisic acid is not the only stomatal inhibitor in the transpiration stream of wheat plants. *Plant Physiology* **88**, 703-708.
- Munns R, Passioura JB, Milborrow BV, James RA, Close TJ (1993) Stored xylem sap from wheat and barley in drying soil contains a transpiration inhibitor with a large molecular size. *Plant Cell & Environment* **16**, 867-872.
- Navari-Izzo F, Guartacci MF, Izzo R (1989) Lipid changes in Maize seedlings in response to field water deficits. *Journal of Experimental Botany* **40**, 675-680.
- Ouvrard O, Cellier F, Ferrare K, Tusch D, Lamaze T, Dupuis JM, Casse-Delbart F (1996) Identification and expression of water stress- and abscisic acid-regulated genes in a drought-tolerant sunflower genotype. *Plant Molecular Biology* **31**, 819-829.
- Parr JF, Stewart BA, Hornick SB, Singh RP (1990) 'Improving the sustain-ability of dryland farming systems: a global perspective.' (New York, Springer-Verlag)
- Pecetti L, Damania AB, Kashour G (1992) Geographic variation for spike and grain characteristics in durum wheat germplasm adapted to dryland conditions. *Genetic resources and crop evolution* **39**, 97-105.
- Pelah D, Wang W, Altman A, Shoseyov O, Bartels D (1997) Differential accumulation of water stress-related proteins, sucrose synthase and soluble sugars in *Populus* species that differ in their water stress response. *Physiol. Plant*, **99**, 153-159.
- Philippe R, Hans W, Martine D, and Edward EF (2000) Differential Gene Expression in Response to Mechanical Wounding and Insect Feeding in *Arabidopsis*. *Plant Cell* **12**, 707-720.
- Reggiani R, Aurisano N, Mattano M, Bertani A (1993) Influence of K⁺ ions on polyamine level in wheat seedlings. *Journal of Plant Physiology* **141**, 136-140.
- Reynolds MP, Rajaram S, Sayre KD (1999) Physiological and Genetic Changes of Irrigated Wheat in the Post-Green Revolution Period and Approaches for Meeting Projected Global Demand. *Crop Science* **39**, 1611-1621.
- Ross PJ, Williams J, McCown RL (1985) Soil temperature and the energy balance of vegetative mulch in the semi-arid tropics. Static analysis of the radiation balance. *Australian. Journal of Soil Research* **23**, 493-514.
- Schillinger WF, Cook RJ, Papendick RI (1999) Increased Dryland Cropping Intensity with No-Till Barley. *Agronomy Journal* **91**, 744-752.
- Siddique MRB, Hamid A, Islam MS (2000) Drought stress effects on water relations of wheat. *Botanical Bulletin of Academia Sinica* **41**, 35-39.
- Stewart BA (1988) Dryland Farming: the North American experience. Proceedings on International Conference of Dryland Farming. 54-59. Bushland, Texas, USA.
- UNEP (1997) World atlas of desertification. United Nations Environmental Programme, 1-182.
- Unger PW (1992) Infiltration of simulated rainfall: tillage system and crop residue effects. *Soil Science Society of American Journal* **56**, 283-289.
- Yadav RC (1974) Note on the effect of mulches on the conservation of soil moisture and on maize yield under semi-arid conditions. *Indian Journal of Agricultural Sciences* **44**, 241-242.
- Zeevaart JAD, Creelman RA (1988) Metabolism and physiology of abscisic acid. *Annual Review in Plant Physiology* **39**, 439-473.