Drought Resistance in Durum Wheat

Belay Simane

Promotores: dr. ir. P.C. Struik,
hoogleraar in de akkerbouw van de gematigde klimaatsgebieden

dr. ir. R. Rabbinge,
hoogleraar in de produktie-ecologie
met bijzondere aandacht voor de plantaardige produktie

Drought Resistance in Durum Wheat

Belay Simane

Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus
dr. C.M. Karssen
in het openbaar te verdedigen
op woensdag 20 oktober 1993
des namiddags te half twee in de Aula
van de Landbouwuniversiteit te Wageningen

CIP-GEGEVENS KONINKLIJKE BIBLIOTHEEK, DEN HAAG

Simane, Belay

Drought resistance in durum wheat / Belay Simane. -[S.l.:s.n.] - Ill.
Thesis Wageningen. -With ref. -With summary in Dutch.
ISBN 90-5485-162-7
Subject headings: durum wheat / drought resistance / water use efficiency.

STELLINGEN

1. The first step towards maximizing yield in dry-land agriculture is the matching of the phenology of cultivars to the water availability period of the target environment.

   This thesis

2. Yield stability and potential yields are equally important in dry-land farming systems.

   This thesis

3. In the semi-arid regions, plants with flexible relative growth rates have ecological advantage.

   This thesis

4. In Ethiopia, due to great geophysical diversity, specific adaptation is more appropriate than breeding for wide adaptation.

5. Ethiopian farmers rightly use mixtures of land races in order to cope with unpredictable weather.

6. The famine is Ethiopia is mainly man-made.

7. The use of genes from wild species to improve the possibilities of durum wheat cultivars to overcome drought periods is promising.

8. Breeding is a skill and an art.

9. Integrated pest management systems are better than conventional chemical control for both environmental and agricultural reasons.

Stellingen behorende bij het proefschrift van Belay Simane: "Drought resistance in durum wheat".

Wageningen, 20 oktober 1993

Abstract

Durum wheat is widely grown as a rainfed crop in the semi-arid tropics. Its production is low and variable from season to season due to frequent drought-stress. Characterization of target environment and employing both analytical and empirical breeding approaches would speed up progress in the development of cultivars with improved adaptation to the prevailing weather conditions.

Analysis of historical weather data and a crop growth model were used to predict the growing season and the optimum plant growth cycle in six different ecological regions of Ethiopia. The matching of crop development to the prevailing soil water availability patterns is considered as a major step towards sustainable durum wheat production.

High yield and yield stability are equally important breeding objectives under drought conditions. The cause-effect relationships of the duration of vegetative period, the duration of grain-filling period, yield components (number of spikes/m^2, kernels/spike, kernel weight) and grain yield revealed a complex pattern of relationships. Longer grain-filling period, increased number of kernels per spike and limited tillering were found to be associated with drought-resistance.

Increasing water use efficiency is the major focus of the dryland cropping system. The different definitions of water use efficiency are explained. Water use efficiency on the basis of grain yield proved the most valuable parameter. The ratios of water used before anthesis and after anthesis by drought-resistant and -susceptible cultivars were different.
Relative growth rate (RGR) and its components (leaf area ratio, LAR, and net assimilation rate, NAR) changed with growth stage and moisture availability. Drought-resistant cultivars were characterized by a fast growth rate in the beginning and slow growth later. Deep rooting and a low shoot:root ratio are effective components of drought-resistance.

Durum wheat straw is one of the major feed sources. The quality of straw varied among cultivars, but did not correlate with drought-resistance. Drought-stress considerably improved straw quality, due to reduced remobilization of assimilates.

The research showed that there is considerable potential to improve the current low and variable durum wheat production in the semi-arid regions.

Key words: agroclimatic analysis, crop growth model, drought-resistance, durum wheat, straw quality, water use efficiency

Acknowledgements

The research presented in this thesis was carried out at Debre Zeit, Alemaya University of Agriculture, Ethiopia; the International Centre for Agricultural Research in the Dry Areas (ICARDA), Syria and the Wageningen Agricultural University, the Netherlands. I thank these institutions for their financial and technical support. The technical assistance of the Durum Wheat Improvement Programme staffs of the Alemaya University of Agriculture (Ethiopia) and the Cereals Physiology staff of the International Centre for Agricultural Research in the Dry Areas (ICARDA) are gratefully acknowledged.

I am very much indebted to Professors P.C. Struik and R. Rabbinge who gave me this opportunity and whose interest in my work has been inspiring.

I take this opportunity to express my gratitude to Dr J.M. Peacock and Prof. H. van Keulen for their contribution in conducting the experiments and writing this thesis. I also thank Drs J. Hamblin, D. Makonnen, G. Makonnen, T. Mamo and T. Tesemma for their support in conducting the experiments.

Particular thanks are due to Prof. H. Lambers, Prof. J. Goudriaan, Drs I. Bos, B. Deinum, P. Dijkstra, J. Hamblin, H. Harris, G. Hof, S. Ketema, M.M. Nachit, A. van Schoonhoven, J. Schouls, E. Veneklaas, J. Vos and G. Walker for their critical comments on one or more chapters.

I also thank colleagues and friends in the Departments of Agronomy and Theoretical Production Ecology for their valuable advice and moral support. I thank G. van Laar for her advice on the final presentation of this thesis.

I thank the Stichting „Fonds Landbouw Export Bureau 1916/1918" for its financial support for the printing of this thesis.

Finally, I am sincerely grateful to my wife for her support and patience.

Contents

General introduction

Durum wheat in the semi-arid tropics

Durum wheat (*Triticum turgidum* L. var. *durum*) is one of the most important food crops in the semi-arid tropics (Nachit and Ouassou, 1988). Its primary centre of origin is the Mediterranean Centre (Simmonds, 1976; Zeven and De Wet, 1982). The secondary centre of genetic diversity developed after its introduction in Ethiopia (Zeven and De Wet, 1982). This region is known to have an amazing wealth of genetic diversity and has contributed a lot to the world durum wheat improvement programmes (Tesfaye, 1987). However, its production in the region is low and subject to more variation in both space and time than in humid and sub-humid regions (Parr *et al.*, 1990). This is because of several bio-physical and socio-economic constraints. Low and erratic rainfall, low soil fertility, low winter temperature and high temperature during grain filling, several pests and diseases and low inputs are among the prominent limiting factors (Harris *et al.*, 1989; Parr *et al.*, 1990; Elings, 1992).

The area suitable for agriculture in semi-arid tropics is small and fragile. Van Schoonhoven (1989) reported that, in West Asia and North Africa (WANA), only 128 million ha, which is 8% of the regions' 1.7 billion ha is suitable. He further noted that another 375 million ha (22%) are permanent pasture and perennial crops and forests. The remaining 70% is desert or semi-desert (steppe). Irrigated land is only 27% of the arable land (35 million ha).

Durum wheat is widely grown as a rainfed crop (Nachit and Ouassou, 1988). In the WANA region variation in annual rainfall has been reported to explain 75% of the variation in wheat yields (Blum and Pnuel, 1990). Singh and Bayerelee (1990) proved that low and erratic rainfall are the predominant factors influencing yield variability and thus the major climatic factors affecting crop production in dryland agriculture. The current increase in production is slow, only 1% per annum. In contrast population is growing at a very alarming rate (2.3% per annum). This is of serious concern, especially in the poorer countries of the region, such as Ethiopia, Sudan and Pakistan (Van Schoonhoven, 1989). Many of these dryland areas are characterized as a highly fragile natural resource base. Soils are often coarse-textured, sandy and inherently low in fertility, organic matter, and water holding capacity, and easily susceptible to wind and water erosion (Parr *et al.*, 1990). These trends of production and population growth pose critical challenges to the long-term sustainability of agriculture in the region. As the possibilities of expanding the cultivated area are limited and application of costly inputs such as irrigation is limited (Elings, 1992), development of drought-resistant cultivars should be given more emphasis to increase productivity.

Drought in agriculture occurs when the amount of rainfall is sufficiently low or its distribution highly erratic to cause a serious shortfall in crop yield. Although the Horn of

Africa has probably the longest recorded history, drought remains the single most important factor threatening the food security of the vast majority of the African and West and South Asian countries. The problem is becoming more serious mainly due to over-exploitation of the environment such as deforestation, cultivation of marginal lands, poor management practices, low input, *etc*. The growing concerns of food security and sustainability of agricultural resources underlie the urgency and importance of tackling drought by applying a systematic and integrated "resource-base" research. Development of a productive, profitable and environmentally sound agricultural production system has become a high priority in many countries. In the current economical and social context of many countries, the question "how to achieve such a region-specific agricultural system?" is not well understood. Currently, development of drought-resistant varieties is most important due to increased economic and environmental costs associated with irrigated agriculture.

Mechanisms of drought-resistance

Plants have a wide range of different response "strategies" to survive and reproduce under drought stress that occurs at various periods during the growth cycle. The mechanisms and physiology of drought resistance have been reviewed extensively (Blum, 1988; Levitt, 1980). It can be achieved by escape or tolerance. Drought escape usually involves early maturity to avoid the onset of stress. This is most important for conditions of late-season (terminal) drought stress. Drought tolerance involves either dehydration avoidance or desiccation tolerance. The basic mechanism of dehydration avoidance is by retaining a high level of tissue "hydration", in spite of drought. It could be achieved by maintaining water uptake (spenders) or reducing water loss (savers). Desiccation tolerance usually involves osmotic adjustment. Each mechanism includes several traits that can be used in breeding for drought-resistant cultivars. It may be conferred by any one or combination of the three mechanisms.

Breeding approach

Breeding wheat for drought resistance is a difficult, long term project (Winter *et al.*, 1988). Traditional (empirical) breeding methods have provided the main basis for yield improvement by yield testing in a range of environments. Blum (1988) emphasized the limited scope of further improvement due to the low heritability of grain yield such that non-genetic variations within and between environments are quite large, especially in drought affected (low-yielding) environments and response to selection is slow. Another approach to selection for drought resistance is an analytical approach which uses indirect selection for yield by using physiological attributes (Blum, 1988; Winter *et al.*, 1988). However, Fischer and Maurer (1978) reported that yield under drought stress is not only affected by the specific physiological responses to stress, but also by the yield potential of the genotype, which cannot be accounted for by physiological measurements of drought response.

Indirect selection traits for drought resistance

Breeding drought-resistant cultivars by selecting solely for grain yield is difficult as described earlier. Several morphological, physiological and metabolic traits that are claimed to be associated with or to confer drought resistance in crop plants have been suggested:

- Morphological traits: root development (Passioura, 1977); leaf area development, harvest index (Passioura, 1977); tillering habit (Donald, 1968), awns, glaucousness (Richards, 1983), etc.
- Physiological traits: leaf temperature (Blum *et al.*, 1989), osmotic adjustment (Morgan, 1983), carbon isotope fractionation (Farquhar and Richards, 1984), etc.
- Metabolic traits: abscisic acid accumulation (Blum, 1988); remobilization of stored assimilates (Blum *et al.*, 1983), etc.

The utility and implication of these and other potential techniques have been discussed in several reviews (Blum, 1988; Ludlow and Muchow, 1988). It is also worth mentioning that many soil and crop management factors, such as tillage and residue management, water harvesting techniques, weed control, optimum plant density, etc., can lead to efficient water use. The applications of such management factors are described in a number of reports (Bidinger and Johanson, 1988; Harris *et al.*, 1989; Singh *et al.*, 1990).

Research objectives and outlines

In view of the need to improve the productivity and stability of dryland farming systems for an expanding population of the region, the research was carried out in three phases with the following general objectives:

- to assess yield limiting weather conditions
- to evaluate the production potentials
- to examine the relative contributions of yield components under different drought stress conditions
- to examine the crop physiological response to drought and

- to identify indirect selection criteria for dryland durum wheat.

The thesis comprises of seven chapters. The first chapter deals with the agroclimatic analysis to support decision-making in agriculture. It addresses the question how to determine the growing period and how to fit crops and/or cultivars within the moisture available period. The second chapter focuses on the use of crop growth models to evaluate the production potential of various agro-ecological regions in Ethiopia. The third chapter provides the interrelationships of yield, yield components and duration of vegetative and grain-filling periods under different moisture stress conditions using path analysis. It also describes the importance of yield stability and yield potential. Chapter 4 explains the importance of water use, water use efficiency and harvest index in determining grain yield under drought conditions. In Chapter 5, drought-resistant and drought-susceptible cultivars are compared for some growth indices. The ecological advantages of slow-growing cultivars are explained. Chapter 6 describes whether leaf gas exchange parameters can be used as screening criteria for drought resistance. Chapter 7 presents the effect of cultivar and moisture stress on the quality of straw. It also examines the role of assimilate remobilization in drought-resistant cultivars. The application of the previous chapters are integrated in a general discussion.

References

Bidinger, F.F and Johansen, C., 1988. Drought research priorities for the dryland tropics. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, A.P. 502 324 India. 241 pp.

Blum, A., 1988. Plant breeding for stress environments. CRC press, Florida, 223 pp.

Blum, A. and Pnuel, Y., 1990. Physiological attributes associated with drought resistance of wheat cultivars in a Mediterranean environment. Aust. J. Agric. Res., 41: 799-810.

Blum, A., Poiarkova, H., Gozlan, G. and Mayer, J., 1983. Chemical desiccation of wheat plants as a simulator of post anthesis stress. 1. Effects of translocation and kernel growth. Field Crops Res., 6: 51-58.

Blum, A., Sphiler, L., Golan, G. and Mayer, J., 1989. Yield stability and canopy temperature of wheat genotypes under drought-stress. Field Crops Res., 22: 289-296.

Donald, C.M., 1968. The breeding of crop ideotypes. Euphytica, 17: 385-403.

Elings, A., 1992. The use of crop growth simulation in evaluation of large germplasm collections. Distribution, variation and evaluation of Syrian durum wheat landraces. Wageningen Agricultural University. Ph.D thesis. 183 pp.

Farquhar, G.D. and Richards, R.A., 1984. Isotopic composition of plant carbon correlates with water use efficiency for wheat genotypes. Aust. J. Plant Physiol., 11: 539-552.

Fischer, R.A. and Maurer, R., 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res., 29: 897-912.

Harris, H.C., Cooper, P.J.M. and Pala, M., 1989. Soil and crop management for improved water use efficiency in rainfed areas. International Centre for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria.

Levitt, J., 1980. Response of plants to environmental stresses. Water, radiation, salt and other stress. Academic Press, New York. 607 pp.

Ludlow, M.M. and Muchow, R.C., 1988. Critical evaluation of the possibilities of modifying crops for high production per unit of precipitation. *In*: Bidinger, F.F and Johansen, C. (Editors), Drought research priorities for the dryland tropics. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, A.P. 502 324 India. pp. 179-241.

Morgan, J.M., 1983. Osmoregulation as a selection criterion for drought tolerance in wheat. Aust. J. Agric. res., 334: 607-614.

Nachit, M.M. and Ouassou, A., 1988. Association of yield potential, drought tolerance and stability of yield in *Triticum turgidum* var. *durum*. *In*: Proceedings of the 7th International Wheat Genetics Symposium, Cambridge, UK, 10-13 July 1988. pp. 867-870.

Parr, J.F., Stewart, B.A., Hornick, S.B. and Singh, R.P., 1990. Improving the sustainability of dryland farming systems: a global perspective. *In*: Singh, R.P., Parr, J.F. and Stewart, B.A. (Editors), Dryland agriculture strategies for sustainability. Advances in Soil Sciences. Volume 13: 1-7.

Passioura, J.B., 1977. Grain yield, harvest index and water use efficiency. J. Aust. Inst. Agric. Sci., 43: 117-120.

Richards, R.A., 1987. Physiology and breeding of winter-grown cereals for dry areas. *In*: Srivastava, J.P., Porceddu E., Acevedo, E. and Varma, S. (Editors), Drought tolerance in winter cereals. John Wiley, UK, pp. 130-150.

Simmonds, N.W., 1976. Evolution of crop plants. Longman Group Ltd., London. 333 pp.

Singh, A.J. and Bayerelee, D., 1990. Relative variability in wheat yields across countries and over time. J. Agric. Econ., 41: 23-32.

Singh, R.P., Parr, J.F. and Stewart, B.A. (Editors), 1990. Dryland agriculture strategies for sustainability. Advances in Soil Sciences. Volume 13. pp. 373.

Tesfaye, T., 1987. Durum wheat breeding in Ethiopia. *In*: Van Jinkel, M. and Tanner, D.J. (Editors), Fifth regional wheat workshop for Eastern, Central and Southern Africa and the Indian Ocean. CIMMYT, Mexico. 18-22.

Van Schoonhoven, A., 1989. Soil and crop management for improved water use efficiency in dry areas: the challenge. *In*: Harris, H.C., Cooper, P.J.M. and Pala, M. (Editors), Soil and crop management for improved water use efficiency in rainfed areas. International Centre for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria. pp. 3-8.

Winter, S.R., Musick, J.T. and Porter, K.B., 1988. Evaluation of screening techniques for breeding drought-resistant winter wheat. Crop Sci., 28: 512-516.

Zeven, A.C. and De Wet, J.M.J., 1982. Dictionary of cultivated plants and their regions of diversity: Excluding most ornamental, forest trees and lower plants. Centre for Agricultural Publishing and Documentation (PUDOC), Wageningen, 263 pp.

Chapter 1

Agroclimatic analysis: a tool for planning sustainable durum wheat production in Ethiopia

B. Simane and P.C. Struik

Agriculture, Ecosystems & Environment (in press)

Abstract

Long-term weather data for six locations representing different eco-regions of Ethiopia were analysed to generate information for appropriate management practices and research priorities of durum wheat (*Triticum turgidum* L. var. *durum*) in Ethiopia. Among the weather elements examined, rainfall was variable and seasonal. The annual rainfall showed a random year-to-year variation both in space and time. Rainfall distribution during the growing period was much more variable than the seasonal total, resulting in a limited growing period. Dependable rainfall is much lower than the mean, particularly for the low-rainfall regions (Asmara, Metahara and Melkasa).

A close relationship between the amount of rainfall and the length of the growing season was observed. The beginning of the rainy season (planting time) ranged from early June to mid-July and the end of the growing season varied from early September to November. The growing season (moisture-available period) ranged from 60 (Metahara) to 140 days (Debre Markos). The results suggest that crop improvement strategies and cropping systems for sustainable durum wheat production should be designed for the different climatic-soil zones based on a realistic assessment of prevailing weather conditions.

Key words: agroclimate, dependable rainfall, drought, durum wheat, growing period, rainfall probability

Introduction

Wheat (*Triticum spp.*) is one of the five most important food crops in Ethiopia, occupying about 0.73 million hectares (CSO, 1987). Durum wheat (*Triticum turgidum* L. var. *durum*) occupies a significant portion of the total wheat area (60-70%) and has an amazing wealth of genetic diversity (Tesfaye, 1987). Farmers grow mixtures of landraces, which are adapted to the prevailing weather and low input conditions (Hailu *et al.*, 1987) in order to cope with unpredictable weather and poorly available resources. The average national yield (1.1 t/ha) is low compared to that (4 t/ha) reported from experimental fields and variable from season to season (Tesema and Mohammed, 1982; CSO, 1987).

Durum wheat is traditionally grown in the more marginal Central and Northern parts of the country under rainfed conditions. In these areas, like elsewhere in semi-arid regions, the start and distribution of rainfall during the growing season are highly variable (Virmani *et al.*, 1980). Farmers tend to plant late in the Northern regions waiting for dependable rainfall and in the Central regions to avoid water logging. As a result, durum wheat is usually exposed to terminal moisture stress during the grain filling period and yields are poor. The studies of Singh and Bayerlee (1990) in 57 countries, including Ethiopia, have also clearly demonstrated that rainfall is the predominant factor influencing yield variability and thus the major climatic factor affecting crop production in dryland agriculture.

In the semi-arid tropics, the distribution of rainfall during the growing season is more variable than the total seasonal amount. Therefore, recommendations of farm practices based on average data mask extremes of available soil moisture (Virmani *et al.*, 1980), and overestimate production potential. Planning of agricultural practices, therefore, should be based on dependable rainfall, which represents moisture availability in a more realistic manner (Hargreaves, 1975).

The important questions in planning dryland agriculture are the start and end of the rains and their distribution during the growing period (Stern *et al.*, 1982). Although defining the start of the growing season is not easy in the semi-arid tropics due to the erratic nature of rainfall and its variability from season to season, several attempts have been made. Stern et al. (1982) used the criterion of at least 20 mm of rain in two consecutive days with no 10-day dry spell in the next 30 days. Virmani (1975) used 20 mm of rain in one or two successive days. Davy *et al.* (1976) suggested 20 mm of rainfall over a 2-day period for millet planting. Kowal and Knabe (1972) defined the start as the first decade with more than 25 mm, provided the rainfall in the next decade exceeds half the potential evapotranspiration.

The criteria used to define the end of the growing season also vary depending on the particular application. Some authors used rainfall below a certain threshold amount (Walter, 1967; Gramzow and Henry, 1972). Stern *et al.* (1982) defined the end of the growing season more realistically as the first date on which available soil water is exhausted.

Detailed analysis of the expected amount of rainfall and its distribution may provide background information to both planning agronomic practices and adjusting crop growth cycles. Improved varieties may subsequently be developed that better fit the expected rainfall pattern. The challenge is to devise strategies to minimize the impact of weather-induced stress and variability on production. To achieve this, a detailed analysis of historical weather records can be used as a tool for strategic and tactical decisions (Dennett *et al.*, 1984; Stern *et al.*, 1982; Virmani *et al.*, 1982). However, such analyses, to support decision-making in production and set priorities for research, are not available in Ethiopia.

The objectives of this study were to generate information for strategic (selection of varieties, choice of land use and farming systems) and tactical (timing of cultural practices and application of chemicals) decisions as a basis for better management practices and appropriate research priorities to develop sustainable durum wheat production systems in different regions of Ethiopia.

Materials and methods

Six locations representing different ecoregions of Ethiopia (five major durum wheat areas: Asmara, Kombolcha, Debre Markos, Debre Zeit and Melkasa, and one arid lowland: Metahara) were included in the study (Table 1.1). Decadal values (10-day periods) (WMO, 1966) of rainfall, maximum and minimum temperature, potential evapotranspiration, relative

Table 1.1 Geographical attributes of the six locations representing various durum wheat growing regions in Ethiopia and the weather data base used in the study.

Location	Latitude (°N)	Longitude (°E)	Altitude (m)	Data base
Asmara	15.17	37.24	2355	1955-1988
Kombolcha	11.05	39.45	1903	1955-1989
Debre Markos	10.21	37.43	2440	1955-1988
Debre Zeit	8.44	39.02	1900	1955-1989
Melkasa	8.33	39.17	1622	1970-1989
Metahara	8.52	39.84	951	1955-1989

humidity, wind speed and sunshine hours were obtained from the various weather stations (Debre Markos and Debre Zeit) and from the National Meteorological Service. The analysis was based on decade values, assuming that plant water requirement over these periods usually is met by water stored in the soil, although short dry spells are common during the rainy season, particularly in the low-rainfall locations.

The trend in annual rainfall was determined using a 5-year moving average analysis. A normal year was defined as one with annual rainfall within one standard deviation of the average (X ± SD).

Dependable rainfall was defined as amount of rainfall received at 75% probability of a gamma distribution and was computed using the methods of Hargreaves (1975). The probabilities for 10, 20, 30, and 40 mm of rainfall in a decade were calculated using the Markov chain probability model (Robertson, 1976; Virmani *et al.*, 1982) to assess the pattern of rainfall distribution. A 75% probability level was chosen as a threshold value to mark the start and end of effective rainfall.

Soil water balance throughout the year was monitored using the water balance program WATBAL (Keig and McAlpine, 1974). The program takes into account the amount of rainfall, potential evapotranspiration (PET) and the potential water-holding capacity of the soil for each location. Potential available soil water content values were obtained from published and unpublished sources (Kamara and Haque, 1987; 1988). Where measured values were not available (Asmara and Metahara), they were determined according to Kramer (FAO, 1986). The change in available soil water content in a decade (SMOS) was computed as:

$$\text{SMOS} = \text{P} - \text{AE} - \text{R} \qquad (1.1)$$

in which P is rainfall in the decade; AE, actual evapotranspiration which is calculated from PET and R water loss (including surface runoff and deep drainage).

The beginning of the growing season was defined using the following criteria, to ensure stability and minimize the risk of false rainfall starts:

- 20 mm of dependable rainfall in a decade
- 30 mm of total rainfall in a decade provided it exceeds half the potential evapotranspiration in the previous decade and
- a period without dry spell (a decade receiving below 20 mm of dependable rainfall) for at least the next three decades based on the historical analysis.

End of growing season was defined as the first decade in which the available soil water content dropped below 20 mm and remained below that level until the following growing season.

The length of the growing season was derived from the calculated beginning and end of the growing season.

Results

Annual rainfall

Mean annual rainfall in the six regions varied from 542 to 1321 mm with considerable variability from year to year (Table 1.2). In agreement with the findings of Brown and Cochème (1969), the coefficient of variability was high in low annual rainfall areas (Asmara and Metahara), and decreased with increase in annual rainfall. The probability of years with above-average rainfall ranged from 6 (Debre Markos, Kombolcha) to 18% (Asmara) and that of below-average rainfall from 12 (Debre Zeit) to 18% (Asmara). However, the low-rainfall locations (Asmara, Metahara and Melkasa) are susceptible to drought even with small deviations from the mean, since mean rainfall is low and does not meet the evapotranspiration demand.

Analysis of the 5-year moving average of annual rainfall showed several periods of below- and above-average rainfall (Fig. 1.1). Time series analysis of annual rainfall did not show significant trends of dry and wet years for all the regions. However, the late 1960s, early 1970s and 1980s were dry in Asmara and Metahara. In Debre Markos and Melkasa annual rainfall showed a diminishing trend in recent years, whereas in Asmara the trend was increasing.

Table 1.2 Annual rainfall in six locations representing different ecoregions in Ethiopia for the period 1955-1989.

Location	X mm	SD mm	CV %	MAX mm	MIN mm	X+SD %	X-SD %
Asmara	542	171	31	991	209	18	18
Kombolcha	1013	167	16	1311	611	6	14
Debre Markos	1321	158	11	1768	1057	6	6
Debre Zeit	903	196	21	1462	401	12	12
Melkasa	808	158	19	1173	511	15	2
Metahara	582	147	25	898	320	12	15

X = mean annual rainfall.
SD= standard deviation.
CV= coefficient of variability.
MAX= maximum recorded value of annual rainfall.
MIN= minimum recorded value of annual rainfall.
X+SD= years with above-average annual rainfall.
X-SD= years with below-average annual rainfall.

Rainfall distribution

The distinctive characteristic of rainfall distribution in all the locations is its seasonality (Fig. 1.3). About 70% of total annual rainfall is concentrated in a 4-month periods, June to September in all locations.

Statistics of decade rainfall showed a very high coefficient of variability. In the dry decades it reached as high as 400%, whereas during the wet decades it ranged from 25 to 90%. In Kombolcha the distribution is bimodal, but the first rainy season (decades 9-13) is short and highly variable. The rainy season extends from decade 19-24 in Asmara, 19-28 in Kombolcha, 15-28 in Debre Markos, 17-26 in Debre Zeit, 18-26 in Melkasa and 19-25 in Metahara. In July and August, water logging and/or runoff may be a serious problem in high-rainfall areas (Debre Markos, Kombolcha and Debre Zeit), as a result of high rainfall intensity and the vertisolic nature of the soils.

Dependability of rainfall

Since the start and continuity of rainfall are not reliable in most regions, information on the

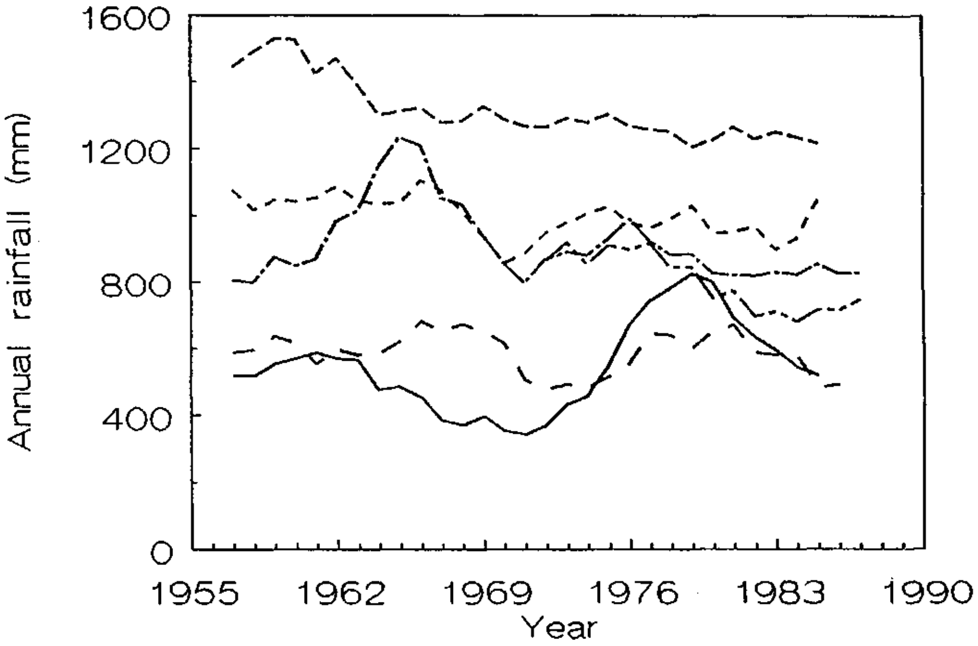


Fig. 1.1 Trend of annual rainfall using 5-year moving average values in six durum wheat growing locations in Ethiopia for the period 1955 - 1989. (symbols: —— Asmara, - - - Kombolcha,— —Debre Markos,— · —Debre Zeit,—··—Melkasa and — —Metahara).

probabilities of rainfall exceeding a certain amount is often more important than the average values. The probabilities of receiving 10, 20, 30 and 40 mm of rainfall in a decade are plotted in Fig. 1.2. For each location the various specified amounts of rainfall can be used as a threshold level for different crops and/or cultivars differing in drought tolerance or different soil types with different water-holding capacities. As expected, in all regions the smaller the threshold rainfall amount, the earlier the start of the rainy season and the longer the growing season (data not shown). Therefore, a very careful consideration of the target environment and kind of crop/cultivar should be given before applying this kind of analysis for agricultural planning. For durum wheat production, 20 mm of rainfall in a decade could serve as a reasonable threshold level. The number of consecutive decades with dependable rainfall exceeding 20 mm ranged from 5 (Asmara, Metahara) to 13 (Debre Markos). The start of the rainy season varied from decade 17 in Debre Markos to 20 in Metahara. These data could be used as a basis for identification of the growth duration of the target varieties and to plan moisture-sensitive farm operations (sowing, fertilizer and insecticide application, etc.).

Dependable annual rainfall is much lower than the mean value for all locations, 412 (76%), 886 (87%), 1209 (92%), 757 (84%), 691 (85%) and 473 (81%) for Asmara, Kombolcha, Debre Markos, Debre Zeit, Melkasa and Metahara, respectively (Table 1.3).

The number of decades with dependable rainfall varies depending on the selected threshold values. Debre Markos receives more than 20 mm of dependable rainfall for 11 consecutive decades followed by Kombolcha (8), Debre Zeit (7), Melkasa (6), Asmara (4) and Metahara (3).

Growing season

The application of Figure 1.3 illustrates rainfall and soil water balance analysis to define the growing season for different locations. Start of the growing season (sowing time) ranged from decade 17 (mid-June) in Debre Markos to decade 20 (mid-July) in Asmara and Metahara. End of growing season ranged from as early as decade 25 (beginning of September) in Asmara and Metahara to decade 33 (end of November) in Debre Markos. However, defining the start of the rain is at times difficult because of the intermittent and patchy nature of the rain and its variability from year to year.

In high rainfall locations, *viz.* Debre Markos, Kombolcha and Debre Zeit, once the criteron set to mark the beginning of the season is met, the occurrence of a dry spell during the first half of the growing season is unlikely. During this period there is usually sufficient rainfall to meet crop demands and replenish the soil to field capacity.

In Asmara dependable rainfall never exceeds potential evapotranspiration and hence, available soil moisture never reaches its maximum capacity. The soil moisture in the relatively low-rainfall locations (Asmara, Melkasa and Metahara) never reaches field capacity and the available soil water reserve is rapidly exhausted. As a result, the growing period is very short, a little over 2 months, compared to Debre Markos which is about 5 months.

In general, a close relationship between annual rainfall and the length of the growing season is observed (Fig. 1.4). In Debre Markos criteria for sowing are met before decade number 17 in 70% of the years, but in Melkasa sowing during decade 17 is possible only in 28% of the years (Fig. 1.4a). The difference in the end of the growing season is even more pronounced (Fig. 1.4b). In Debre Markos the growing season ends between decade 33 and 34 in 80% of the years. In Debre Zeit and Melkasa, the growing season terminates between decade 29 and 30 in 76% of the years. The frequency of occurrence of years without surplus rainfall above the potential evapotranspiration demand increases as annual rainfall decreases. Intermittent drought periods are also more frequent in Metahara, Asmara and Melkasa than in the other high-rainfall regions. For these ecoregions therefore more drought-tolerant cultivars are suitable.

A very low correlation (r = -0.019) was found between the start of the rainy season and end of growing season. Therefore, recommendations are complicated and need some flexibility. If rainfall starts early or on time at a given site, durum wheat cultivars with the recommended length of the growth cycle can be grown. However, if the onset is delayed

Table 1.3 Dependable precipitation (at 75% probability) using Gamma distribution (mm) in six durum wheat growing ecoregions for the period 1955-1989.

Decade	Asmara	Kombolcha	D. Markos	D. Zeit	Melkasa	Metahara
1	1	1	2	0	0	9
2	0	5	2	0	3	9
3	0	3	3	0	1	2
4	1	4	1	0	1	5
5	2	3	5	0	6	7
6	2	9	3	0	1	7
7	1	9	5	0	4	6
8	2	8	4	0	4	11
9	3	14	6	0	4	10
10	4	17	6	1	9	8
11	3	14	6	1	3	9
12	4	10	4	1	12	5
13	6	8	9	1	10	6
14	6	7	8	0	4	4
15	3	5	17	0	6	6
16	3	4	12	0	5	3
17	5	4	36	3	8	3
18	6	6	51	15	10	7
19	19	21	62	31	25	14
20	26	33	64	43	32	21
21	38	58	75	57	41	27
22	32	61	76	54	31	17
23	23	48	71	39	27	24
24	14	38	78	47	39	16
25	4	27	51	29	19	10
26	1	21	50	12	17	8
27	0	9	23	1	7	5
28	3	7	15	0	4	2
29	4	5	5	0	2	2
30	2	3	6	0	0	0
31	5	3	4	0	1	1
32	7	4	2	0	0	6
33	6	4	3	0	0	1
34	1	2	3	0	1	0
35	1	5	2	0	2	3
36	3	1	2	0	0	8
Annual	412	886	1209	757	691	473

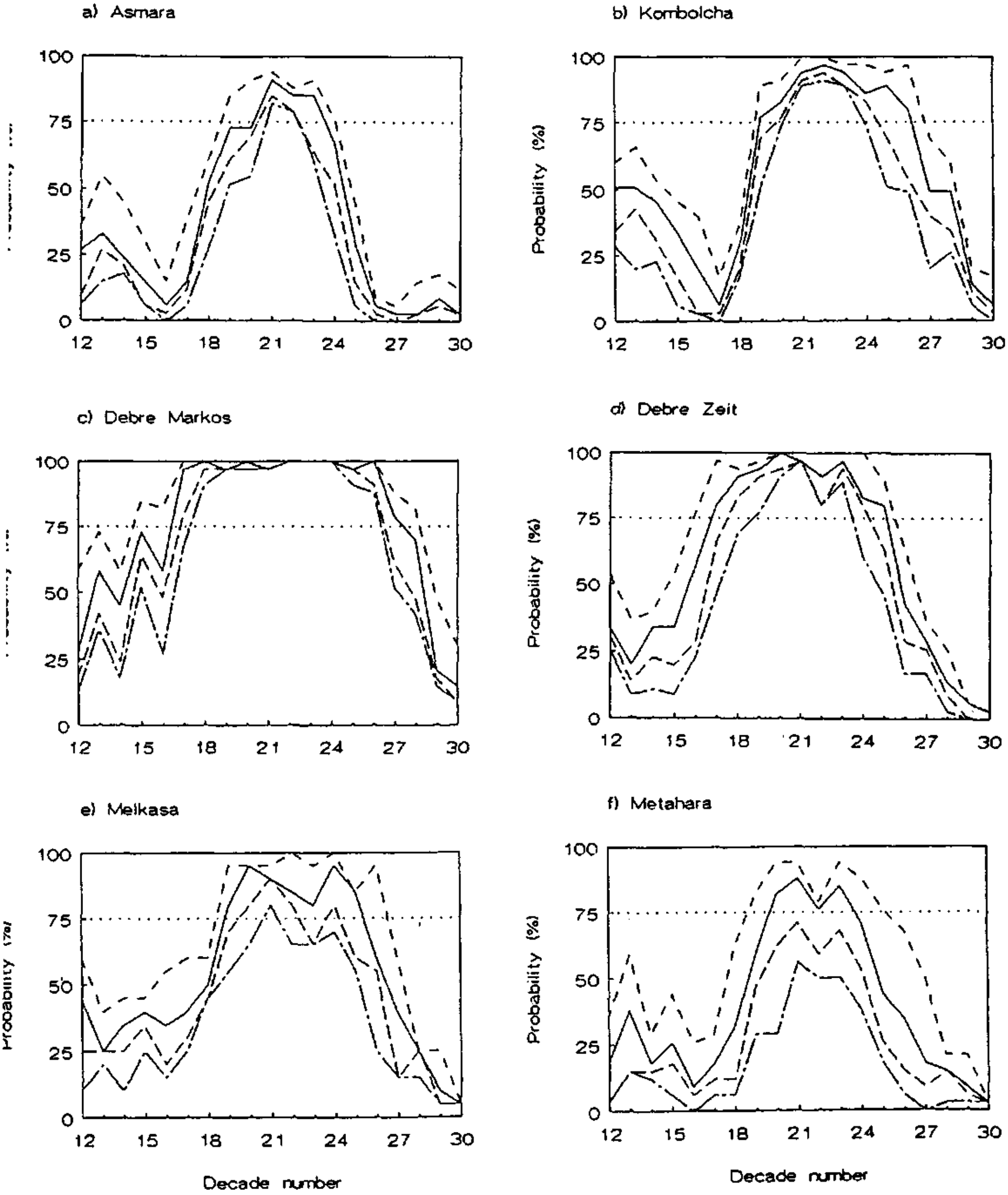


Fig. 1.2 Probabilities of receiving 10, 20, 30, 40 mm of rainfall per decade in six durum wheat growing locations in Ethiopia. (symbols: - - - 10 mm, —— 20 mm,— — 30 mm, —·— 40 mm, ... 75% probability line).

more than one decade beyond the average date, short-duration cultivars should be sown to ensure yield stability.

Other climatic elements

The thermal characteristics of the locations are of a typical tropical nature. The daily temperature amplitude is wide and the annual range is very narrow. Mean annual temperature is 15.5, 18.8, 15.6, 17.1, 21.1 and 23.9 °C in Asmara, Kombolcha, Debre Markos, Debre Zeit, Melkasa and Metahara, respectively. Relative humidity ranges between 40 and 85%. Average daily sunshine hours are between 6 and 10.5 throughout the year. These climatic elements are stable and predictable in all regions and suitable for cultivation of wheat varieties not requiring vernalization. Therefore, the detailed analysis of these weather elements is omitted in this paper.

Discussion

The implication of the present study is that current crop management practices and breeding goals may have to be modified, depending on the resources and resource-use research on the interactions of crop, weather and soil for sustainable wheat production. In all regions studied the rainfall distribution is seasonal and characterized by a very high coefficient of both inter- and intra-year variability. In such cases, a detailed analysis of historical weather data in combination with the soil characteristics, as presented in this paper, can be used to plan agricultural development (Dennet *et al.*, 1984; Peacock and Sivakumar, 1986; Virmani *et al.*, 1980) to select appropriate soil and water management practices to make the most efficient use of limited and variable rainfall. All field operations should be adapted where possible to the environmental variability of the target area, especially rainfall.

In Ethiopia the most important and sensitive issue in planning agricultural production is accurate prediction of the start of the growing season. This will minimize the risk of crop failure due to false start of rainfall on the one hand and loss of rainfall before sowing on the other. Then, the criteria set to define the start of the growing season can be used with reasonable flexibility. Like several other authors working in the semi-arid tropics (Kassam, 1977; Kowel and Kassam, 1978; FAO, 1986), we have found that once decadal rainfall is above 30 mm and exceeds half the potential evapotranspiration (PET), it increases considerably. Therefore, this criteria could serve as a reliable threshold to start sowing. In Asmara, Kombolcha and Metahara this starts from decade 19; in Debre Markos from decade 15; in Debre Zeit from decade 17 and from decade 18 in Melkasa. These sowing

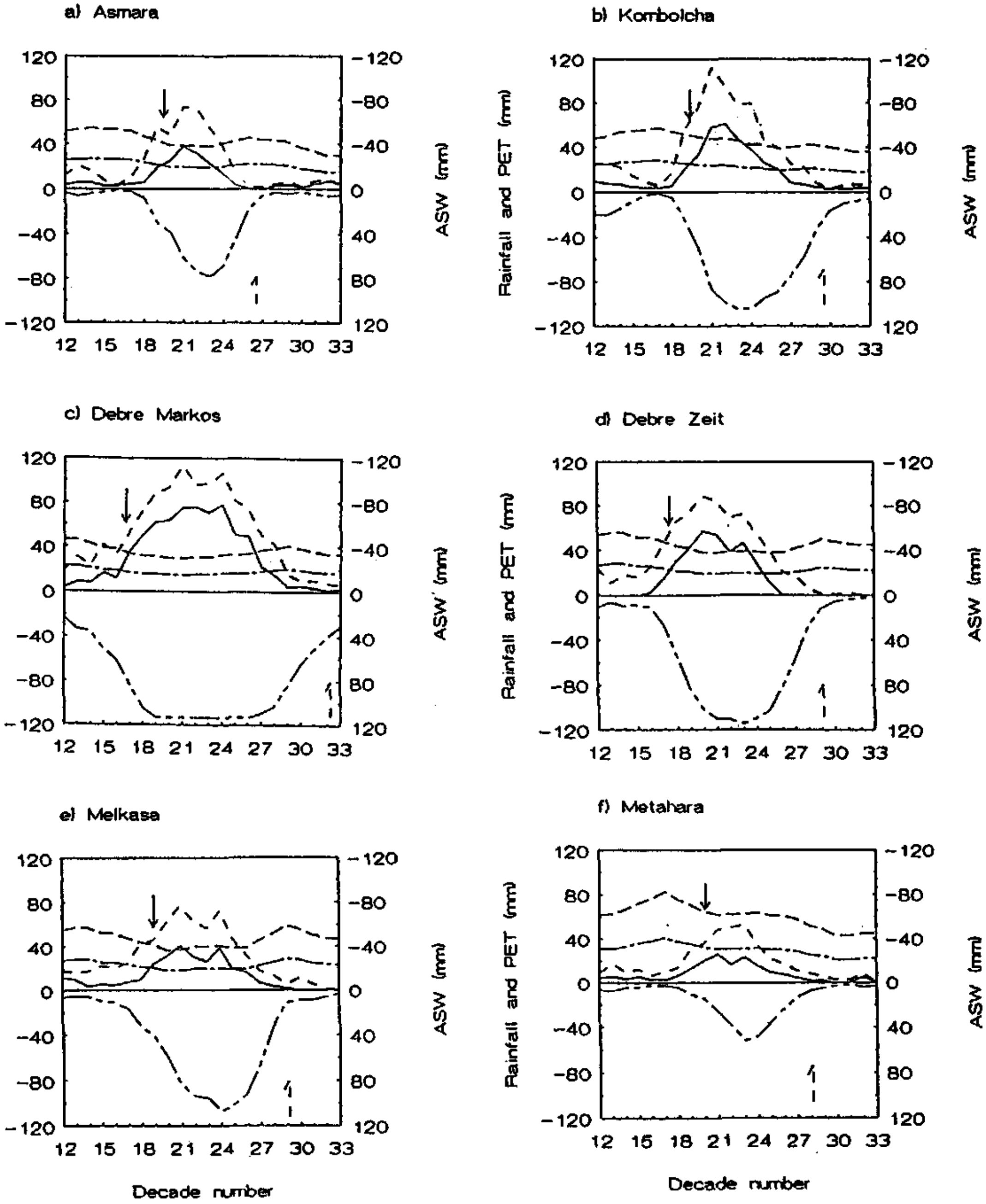


Fig. 1.3 Length of the growing period and soil water balance in six durum wheat growing locations of Ethiopia. (symbols: ↑ start of growing season, ↿ end of growing season, - - - mean rainfall, —— dependable rainfall,— —potential evapotranspiration,-.- 0.5 potential evapotranspiration,-..- available soil water content).

thresholds could be of considerable practical application if more reliable weather forecasts were available and farmers used them. For this to take place a monitoring and advisory service using these forecasts must also be operational.

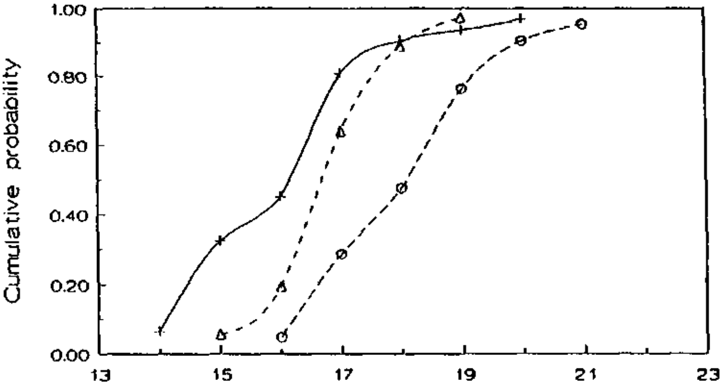
In low rainfall regions (Metahara, Asmara and Melkasa), due to the rapid exhaustion of the soil water reserve, the grain filling period for most of the available durum wheat cultivars extends beyond the period of moisture availability. Consequently, moisture stress during grain filling may result in premature drying of the leaves, with consequently reduced assimilatory capacity and lower grain yields, much below the potential yield of the improved cultivars.

In high rainfall regions like Debre Markos and Debre Zeit where waterlogging may be a problem at seedling establishment, other agronomic practices like raised beds (Broad Bed and Furrow) (Getachew Asamenew *et al.*, 1988) may be better than late planting. Soil conservation measures are also imperative in Debre Markos and Kombolcha, where water loss through surface run-off and deep drainage may exceed 45% of the annual rainfall. Therefore, a well-defined approach is needed to help farmers choose a planting schedule and to select the appropriate cultivars that fit their growing period. Breeders should also use this information for formulating their durum wheat breeding strategies under the respective environmental conditions.

Closer matching of phenology to rainfall regime appears to offer the best scope for improving and stabilizing durum wheat yields in Ethiopia. Rainfall pattern and soil moisture characteristics together determine timing and length of the growing season and thus dictate the choice of crops and cropping systems. It is therefore advisable to identify long-duration cultivars (120-140 days) for areas like Debre Markos, intermediate cultivars (90-110 days) for Debre Zeit and Kombolcha and short-duration cultivars (60-70 days) that are tolerant to intermittent drought for Asmara and Melkasa. It may be difficult and not worthwhile to develop a cultivar with a growth cycle of 60 days using presently available germplasm in the country. But such germplasm could be acquired from foreign sources like the International Centre for Agricultural Research in the Dry Areas (ICARDA). At Metahara, production of durum wheat is not recommended without supplementary irrigation.

In the context of current Ethiopian agriculture, selection of crop species and cultivars for drought-prone regions needs a very critical assessment, especially with respect to yield stability, so that farmers are guaranteed reasonable yields even in dry years. The use of mixtures of varieties with different maturity groups will be useful to consider as a strategy to minimize the risk of crop failures due to unfavourable weather conditions. Therefore, improvement of cultivars should focus on developing materials that are drought-tolerant and with the capacity to adapt to the prevailing variability of the weather.

a) start of growing



b) end of growing

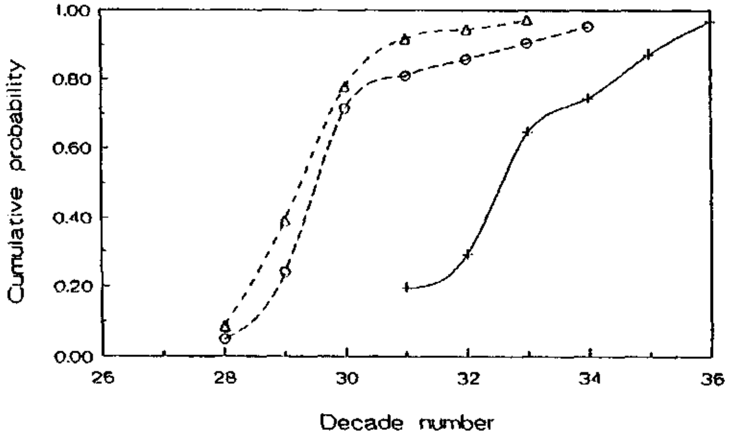


Fig. 1.4 Cumulative probability of the start (a) and end (b) of the growing period. (symbols: +—+Debre Markos, △- - △Debre Zeit ○- -○Melkasa).

References

Brown, L.H. and Cochème, J., 1969. A study of the agroclimatology of the highlands of Eastern Africa. FAO, Rome.

Central Statistics Office (CSO), 1987. Ethiopian Statistical Abstract. Time series data on area, production and yield of major crops of Ethiopia. Stat. Bull., 56.

Davy, E.G., Mattei, F. and Soloman, S.I., 1976. An evaluation of climatic and water resources for development of agriculture in the Sudano-Sahelian zone of West Africa. Special Environmental Rep. No. 9. WMO, Geneva, 289 pp.

Dennett, M.D., J.D.H. Keatinge and J.A. Rodgers, 1984. A comparison of rainfall regimes at six sites in northern Syria. Agric. For. Meteorol., 31: 319-328.

FAO (Food and Agriculture Organization), 1986. Early agrometeorological crop yield assessment. FAO plant *production* and *protection* paper. FAO, Rome.

Getachew Asamenew, Jutzi, S.C., Abate Tedla and McIntire, J., 1988. Economic evaluation of improved vertisol drainage for food production in the Ethiopian highlands. *In*: Jutzi, S.C., Haque, I., McIntire, J. and Stars, J.E.S. (Editors), Management of Vertisols in Sub-Saharan Africa. IAR, Addis Ababa, Ethiopia, pp. 263-283.

Gramzow, R.H. and Henry, W.K., 1972. The rainy pentads of Central America. J. Appl. Meteorol., 11: 637-642.

Hailu Gebre, Amsalu Tarekegn and Endale Asmare, 1987. Preliminary indications on the importance of yield limiting factors on wheat. Paper presented at the 5th Regional Wheat Workshop for Eastern, Central and Southern Africa and the Indian Ocean in Ansirabe, Madagascar, October 5 - 10, 1987.

Hargreaves, G.J., 1975. Water requirement manual for irrigated crops and rainfed agriculture. EMBRAPA and Utah State publication No. 75.d 158. EMBRAPA, Brasilia.

Kamara, C.S. and Haque, I., 1987. Characteristics of vertisols at ILCA research and outreach sites in Ethiopia. Working document. International Livestock Center for Africa (ILCA). Addis Ababa, Ethiopia.

Kamara, C.S. and Haque, I., 1988. Physical properties of Vertisols and their implications for management: a review. Working document. International Livestock Center for Africa (ILCA), Addis Ababa, Ethiopia.

Kassam, A.H., 1977. Agroclimatic suitability assessment of rainfed crops in Africa by growing period zones. FAO, Rome.

Keig, G., and McAlpine, J.R., 1974. WATBAL: a computer system for estimation and analysis of soil moisture from simple climatic data (2nd ed.). CSIRO Memo 74/7, Division of Land Research, Canberra, Australia, 45 pp.

Kowal, J.M., and Kassam, A.H., 1978. Agricultural Ecology of Savanna. Oxford University Press, Oxford, UK, 403 pp.

Kowal, J.M. and Knabe, D.T., 1972. An Agroclimatological Atlas of the Northern States of Nigeria. Ahmadu Bello University Press, Zaria.

Peacock, J.M. and Sivakumar, M.V.K., 1986. An environmental physiologist's approach to screening for drought resistance in sorghum with particular reference to Sub-Saharan Africa. In: Proceedings of an International Drought Symposium, 19 -23 May, 1986. Nairobi, Kenya. pp. 101 - 120.

Robertson, G.W., 1976. Dry and wet spells. UNDP (FAO), Tun Razak Agriculture Research Center. Sungh, Tekam, Malaysia, Project Field Report, Agrometeorology; a-6, 15 pp.

Singh, A.H. and Bayerlee, D., 1990. Relative variability in wheat yields across countries and over time. J. Agríc. Econ., 41: 23-32.

Stern, R.D., Dennett M.D. and Dale, I.C., 1982. Methods for analyzing daily rainfall measurement to give useful agronomic results. I. Direct methods. Exp. Agric. 18: 223-236.

Tesema, T. and Mohammed, J., 1982. Review of wheat breeding in Ethiopia. Eth. J. Agri. Sci. 1: 11 - 24.

Tesfaye T., 1987. Durum wheat breeding in Ethiopia. Paper presented at the 5th Regional Wheat Workshop for Eastern, Central and Southern Africa and the Indian Ocean in Ansirabe, Madagascar, October 5 - 10.

Virmani, S.M., 1975. The agricultural climate of the Hyderabad region in relation to crop planning (a sample analysis). International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, 502 324, India.

Virmani, S.M., Sivakumar, M.V.K. and Reddy, S.J., 1980. Climatological features of the semi-arid tropics in relation to the farming systems research program. In: Proceedings, International Workshop on the Agroclimatological Research needs of the semi-arid tropics. Nov., 1978. ICRISAT, Patancheru, A.P., India, pp. 22-24.

Virmani, S.M., Sivakumar, M.V.K. and Reddy, S.J., 1982. Rainfall probability estimates for selected locations in semi-arid India. Research Bulletin No. 1 (2nd enlarged edition). International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, 502 324, India, 170 pp.

Walter, M.W., 1967. Length of the rainy season in Nigeria. Nigerian Geog. J., 10: 123-128.

WMO (World Meteorological Organization), 1966. International Meteorological Vocabulary. WMO-No 182, TP.91. WMO, Geneva.

Chapter 2

Application of a crop growth model (SUCROS-87) to assess the effect of moisture stress on yield potential of durum wheat in Ethiopia

B. Simane, H. van Keulen, W. Stol and P.C. Struik

Agricultural Systems (in press)

Abstract

A spring wheat growth model (SUCROS-87) was used to identify moisture stress periods during the growing seasons and simulate yield potentials of durum wheat (*Triticum turgidum* L. var. *durum*) in six durum wheat growing regions of Ethiopia. The start of the rainy season and distribution of rainfall were erratic, particularly in the low-altitude regions. As a result, simulated dates of emergence varied from June to August. Moisture stresses of various intensities, at different growth stages of the plant, were limiting to durum wheat production in all the regions except Debre Markos. Terminal moisture stress was simulated in 7 out of 10 years in all locations except Debre Markos, whereas intermittent stress were simulated in 3 locations in 2 out of 10 years. In Metahara rain-fed durum wheat production is not feasible. Water-use efficiency decreased with decreasing rainfall but the transpiration coefficient increased. The average simulated potential grain yields at all the locations were high (6600 kg/ha) compared with the actual national average. Development of versatile and region-specific improvement strategies are emphasized to improve durum wheat production in the country.

Key words: crop growth model, durum wheat, moisture stress, water use efficiency, yield potential

Introduction

Durum wheat (*Triticum turgidum* L. var. *durum*) in Ethiopia occupies about 60-70% of the cultivated land devoted to wheat, and exhibits wide genetic variability (Tesfaye, 1987). It is cultivated in a range of environments, except in very arid and lowland regions. However, durum wheat is traditionally grown in the more marginal central and northern parts of the country, while bread wheat (*T. aestivum* L.) is grown in the more favourable, wetter central and southern parts.

Average national yields of both bread and durum wheats are low and variable, ranging from 1100 kg/ha for private farms to 2000 kg/ha for state farms (CSO, 1986). This is due to various technical and socio-economic constraints: lack of improved management practices, very low availability of commercial fertilizers (Dender, 1989), limited availability of improved varieties (only 10% of the total requirement; Tesfaye, 1987), considerable yield losses due to diseases (20-25%; Mengistu Huluka, pers. comm.), and weeds (as high as 36%; IAR, 1983).

The total amount of annual rainfall in many locations of the country is high, but its distribution is highly erratic (Simane and Struik, accepted). Each season has particular characteristics, such as the start of the main rainy season. The heavy black clay soils (Vertisols), where durum wheats are traditionally grown, easily crack on drying and are easily waterlogged during the rains (Tesfaye, 1987). In these regions like elsewhere in the semi-arid tropics a substantial proportion of the annual rainfall is lost by runoff (Perrier, 1988; Simane and Struik, accepted) and evaporation from the soil (van Keulen and Seligman, 1987; Unger *et al.*, 1988). To increase productivity in such environments a number of soil and crop management factors may be considered, such as: optimum plant density, early stand establishment, weed control, different tillage and residue management, water harvesting and moisture conservation measures to reduce evaporation and runoff. While these are important moisture conservation measures to increase actual yields, we felt that it is outside the scope of this paper and will be discussed separately.

Extrapolating results obtained under a particular set of conditions to other environments and generalizing over longer periods are both difficult and misleading in conditions like Ethiopia. This difficulty could be solved by using crop growth models (van Keulen and de Milliano, 1984; Grant, 1989; Whisler *et al.*, 1986). Several such models used over a wide range of environments applying the appropriate technology have shown increased opportunities in the determination of production constraints and yield potentials (van Keulen and Seligman, 1987; Whisler *et al.*, 1986), although they cannot replace field experiments as a final arbiter for practical application.

The objectives of this study were to identify moisture-related constraints of durum wheat production, and to assess yield potentials in six locations representing different durum wheat growing agro-ecological regions of Ethiopia, in order to plan improvement programmes. The results could serve as a yard-stick to study different moisture conservation measures described earlier.

Materials and methods

Effects of environment on yield potential of durum wheat were studied using the spring wheat version of the crop growth model SUCROS-87 (Simple and Universal CROp growth Simulator; Spitters *et al.*, 1989) for the years 1980 to 1989. The model simulates potential growth and yield of wheat under an optimum supply of nutrients in pest-, disease- and weed-free conditions under the prevailing weather conditions.

CO_2 assimilation is calculated as a function of radiation, temperature and crop characteristics. Maintenance and growth respiration are calculated as a function of crop dry weight and composition. Daily net assimilation is partitioned among roots, stems, leaves and storage organs using partitioning factors which are dependent on phenological development. Phenology is defined by the rate and order of appearance of vegetative and reproductive organs. Development stage is expressed as a dimensionless variable, being 0 at emergence, 1 at anthesis and 2 at physiological maturity. Intermediate values are calculated as the ratio between the current temperature sum, calculated as the integrated value of average daily temperature above a base temperature of 0°C and the temperature sum till anthesis or physiological maturity, respectively.

The soil moisture balance and moisture content were described for 10 soil layers, each

15 cm thick. A reduction factor for crop assimilation due to water stress was calculated as the ratio of actual to maximum transpiration. Moisture stress periods were marked as the periods when the reduction factor was less than 0.7.

Input data to run the model were site and cultivar characteristics. Six regions, representing different ecoregions (five major durum wheat growing areas, i.e. Asmara, Kombolcha, Debre Markos, Debre Zeit and Melkasa, and one arid-lowland region: Metahara) were included in the study (Table 2.1). The site-specific weather data consisted of daily rainfall and 10-day mean values of radiation, minimum and maximum temperature, vapor pressure and average wind speed. Soil physical characteristics (soil moisture content at various pF-values, texture) were derived from various working documents of the National Soil Service Laboratory of Ethiopia.

Plant input data were from field experiments of Boohai (improved and released durum wheat cultivar) in 1989 and 1990 at Debre Zeit Research Center. Temperature sums from emergence to heading and maturity were 1089 and 1764 °Cd, respectively (above a base temperature of 0°C). The fractions of dry matter allocated to different plant organs as a function of development stage is given in Table 2.2. Plant density was 220 plants/m^2 and maximum rooting depth was 150 cm.

Simulation started in May (well before germination), since early season rains are important for early stand establishment and final dry matter production. Emergence was assumed when soil water content of the upper 10 cm layer reached 30% of total available soil water (Virmani *et al.*, 1980).

Table 2.1 Geographical characteristics [latitude (LAT), longitude (LONG) and altitude (ALT)] and average annual daily sunshine hours (DSH), minimum temperature (MINT), maximum temperature (MAXT) and total annual rainfall (RFL) of six test locations in Ethiopia.

Location	LAT °N	LONG °E	ALT m	DSH h	MINT °C	MAXT °C	RFL mm
Asmara	15.17	37.24	2355	7.5	8.4	23.0	541.8
Kombolcha	11.05	37.24	1903	7.2	11.8	25.8	1012.9
D.Markos	10.21	37.43	2440	7.5	9.0	22.2	1320.9
D.Zeit	8.44	39.02	1900	8.0	14.2	28.0	903.2
Melkasa	8.33	39.17	1622	8.0	14.2	28.0	807.9
Metahara	8.52	39.84	951	8.5	18.3	29.6	581.7

Table 2.2 Fraction of dry-matter allocated to roots, leaves, stems and storage organs at different development stages (DVS) for the variety Boohai in Debre Zeit (1989 and 1990).

DVS	Roots	Leaves	Stem	Grain
0.10	0.50	0.32	0.18	0.00
0.25	0.35	0.45	0.20	0.00
0.50	0.15	0.43	0.42	0.00
0.70	0.10	0.14	0.76	0.00
1.00	0.00	0.00	0.05	0.95
1.10	0.00	0.00	0.00	1.00
2.00	0.00	0.00	0.00	1.00

Seasonal rainfall was defined as total rainfall between 20 days before emergence and physiological maturity. Water use efficiency (WUE) was calculated as the ratio of total above-ground biomass production to total amount of seasonal rainfall. Transpiration coefficient (TC) was calculated as the ratio of transpiration and total above-ground biomass production.

Results

The climate of durum wheat growing regions in the country is very diverse (Table 2.1). Daily radiation levels ranged from 7-8 KWh/m^2, for a period of 6-8 h/day during most of the year. Thermal characteristics of all the locations are of a typical tropical nature. Daily temperature amplitude is large and annual amplitude is very low (Fig. 2.1). Average annual temperature ranged from 15°C in Debre Markos to 24°C in Metahara. Consequently, the simulated length of the growth cycle from emergence to physiological maturity ranged from 82 days (Metahara) to 135 days (Debre Markos) (Table 2.3). Total annual rainfall and its distribution is variable both over space and time (Table 2.4). Distribution is unimodal except in Kombolcha where it is bimodal. Simulated yields significantly increased with increasing seasonal rainfall ($r = 0.86^{**}$), coinciding with higher annual rainfall and altitude.

Asmara

Asmara represents a semi-arid region with relatively low temperature (Table 2.1) and one

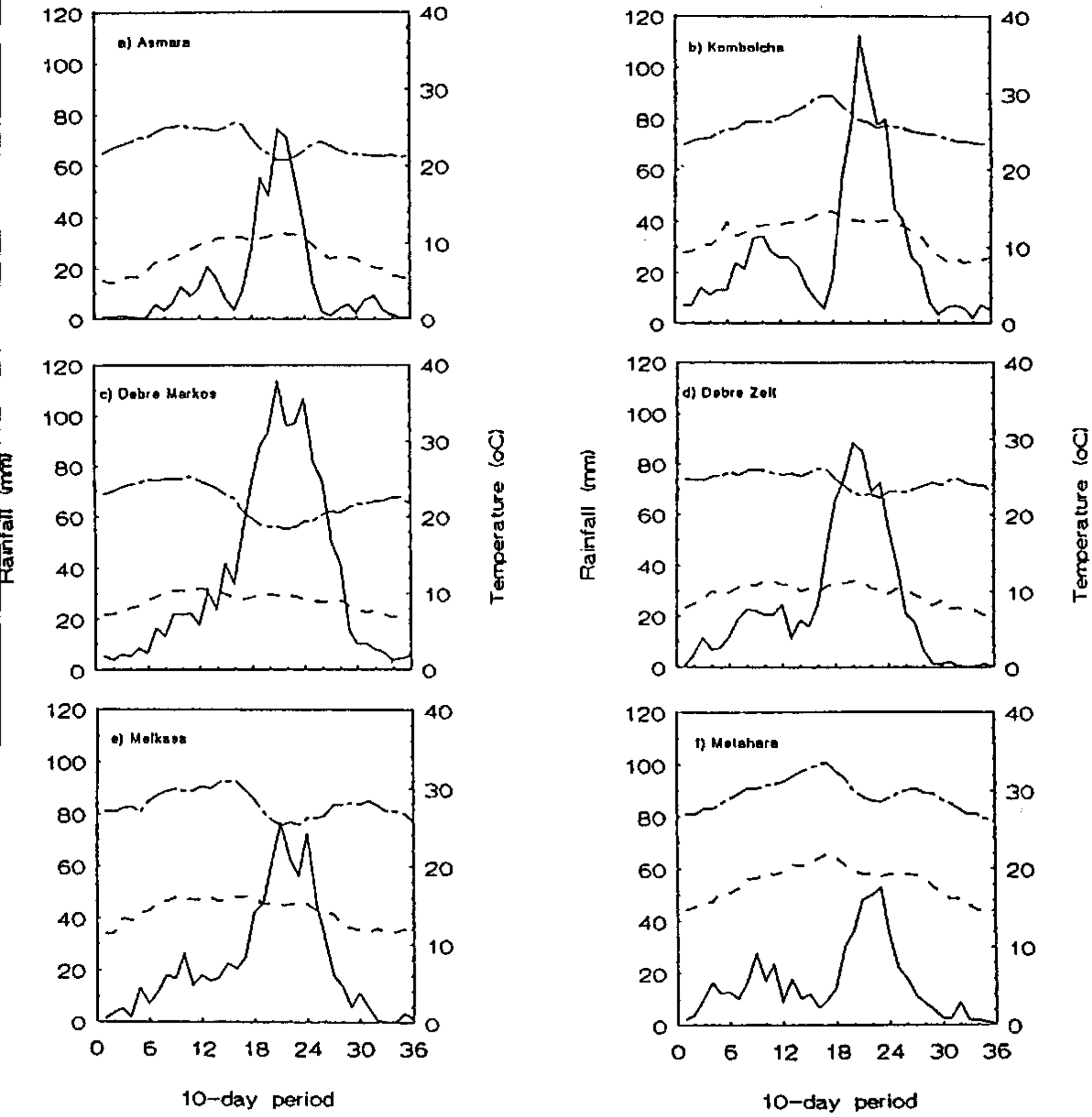


Fig. 2.1 Annual course of long-term average rainfall (——), maximum temperature (- - —) and minimum temperature (— · —) at the six test locations in Ethiopia.

short rainy season that allows cultivation of early maturing crops (Fig. 2.1). Seasonal rainfall was more stable (CV=24%) than annual rainfall (CV=31%) making up 62% of the annual total (Table 2.4). The date of the onset of rainfall was variable. Hence, simulated emergence date varied from mid-June to early August (Table 2.3). Early emergence gave good yields in the simulations. The growing season was relatively cool; therefore, the cultivar needed about 125 days to mature in the simulation. Terminal stress of variable intensity was simulated in 56% of the years starting early September, with no intermittent moisture stress (Table 2.5). This is a good indication that once rainfall starts it is reliable even though the rainy season is short.

Although highly variable, average simulated grain yield was high, 7000 kg/ha (Fig. 2.2), with a low harvest index (Table 2.6). Average simulated water use efficiency (WUE) was moderate, 50 kg ha^{-1} mm^{-1}, and transpiration coefficient (TC) was high, 0.0145 mm kg^{-1} ha (Table 2.7). In this region, moisture conservation management and use of early maturing varieties (2.5 - 3 months growth cycles) would result in better and more stable durum wheat production than the current farmers' yields.

Kombolcha

Kombolcha represents a warm, sub-humid region with two rainy seasons. The first is too short and unreliable for durum wheat production (Fig. 2.1). Although the first could be used for the production of green manure crops, it is only the second (main) rainy season that can reliably support a crop with a 3.0 - 3.5 month cycle to maturity.

Seasonal rainfall is much more variable than the annual total, ranging from 303 to 890 mm (Table 2.4). Simulated time of emergence varied between July 3 and 29, and an average of 104 days was required for maturity (Table 2.3). Short periods of intermittent drought were simulated in 2 out of 10 years, with mild terminal stress in 3 out of 10 years (Table 2.5). However, in 8 out of 10 years the rainfall in this region is high and could provide better growing conditions if simple and effective moisture conservation practices are applied. However, in 1984 and 1985 the seasonal rainfall was low, with no possibility for water conservation.

Simulated grain yields were consistently high, about 8500 kg/ha (Fig. 2.2) and harvest indices averaged 0.52. Water use efficiency was, however, low (only 44 kg ha^{-1} mm^{-1}) with a high transpiration coefficient of 0.0142 mm kg^{-1} ha (Table 2.7).

Debre Markos

Debre Markos represents a relatively cool and humid climate with one long dependable growth period (Fig. 2.1). This allows cultivation of a single crop with a growth cycle of

Table 2.3 Simulated emergence date (ED) and number of days from emergence to maturity (DM) for cultivar Boohai at six test locations in Ethiopia from 1980 to 1989.

Year	Asmara		Kombolcha		D. Markos		D. Zeit		Melkasa		Metahara	
	ED	DM	ED	DM	ED	DM	ED	DM	ED	DM	ED	DM
1980	Jul 04	125	Jul 11	104	Jun 26	135	Jul 03	119	Jul 17	96	CF	
1981	Jul 08	124	Jul 03	103	Jul 14	136	Jul 23	119	Jul 23	96	CF	
1982	Jul 05	124	Jul 30	109	Jun 22	135	Jul 04	119	Jul 23	96	Aug 09	83
1983	Jul 30	129	Jul 25	108	Jul 23	134	Jul 31	120	Jul 20	97	Jul 09	80
1984	Jul 04	125	Jul 09	103	Jun 23	135	Jul 12	119	Jul 02	97	Aug 01	81
1985	Jun 19	122	Jul 18	107	Jun 25	136	Jul 03	119	Jul 04	96	Jul 20	81
1986	Jun 29	123	Jul 28	101	Jun 22	136	Jul 01	118	Jul 10	96	CF	
1987	Aug 06	130	Jul 09	103	Jun 23	135	Jul 04	119	Jul 14	96	CF	
1988	Aug 01	129	Jul 29	112	Jun 09	136	Jul 13	120	Jul 14	95	Jul 14	81
1989	NA	NA	Jul 09	103	NA	NA	Jul 12	119	NA	NA	NA	
Avg.	Jun 26	125	Jul 18	104	Jun 26	135	Jul 09	119	Jul 15	96	Jul 23	82

NA= data not available.

CF= crop failure

up to 5 months. Average seasonal rainfall is 947 mm, higher than the annual total of the other locations except that of Kombolcha. Emergence was simulated in the last week of June except in three years and the average simulated length of the growing period was 135 days (Table 2.3) because of the cool temperatures. Moisture stress in this region is not a problem. Available moisture is not fully exploited by cultivars like Boohai, i.e. cultivars with longer growth cycles would give higher yields.

In this region the highest potential grain yields were consistently simulated (9750 kg/ha), more than double those in the low-rainfall areas (Fig. 2.2) associated with highest water use efficiency (58 kg ha^{-1} mm^{-1}) and lowest transpiration coefficient (0.0125 mm kg^{-1} ha) (Table 2.7). Hence, sustainable durum wheat production system may be practiced provided inputs are readily available.

Debre Zeit

Debre Zeit represents a warm and semi-arid climate with a rainy season of intermediate length (Fig. 2.1). Seasonal rainfall is 67% of the annual total but more variable (CV=27%) (Table 2.4). Simulated average time of emergence is the first week of July, ranging from July 1 to 31. On average, Boohai needs 119 days to mature (Table 2.3). In this region, terminal drought stress for this cultivar is common, but varies in intensity from year to year. Intermittent drought stress early in the season was simulated in 2 out of the 10 years (Table 2.5). Cultivars with a growth cycle of 3-3.5 months would be more suitable for this ecoregion.

Average simulated yield was 6700 kg/ha, but highly variable from year to year (Fig. 2.2), and the simulated harvest index was low (0.39). In 1987, the early vegetative period was dry (July 14 - August 5), which resulted in low simulated yield (1040 kg/ha). Simulated water use efficiency was low, only 35 kg ha^{-1} mm^{-1} with a high simulated transpiration coefficient (0.0190 mm kg^{-1} ha) (Table 2.7). Production may be improved by introducing varieties with shorter growth cycles and/or by early planting.

Melkasa

Melkasa represents a hot and semiarid climate, with a short but dependable rainy season (Fig. 2.1). Seasonal rainfall was about 70% of the annual total and more stable than at the other stations (Table 2.4). Simulated emergence was between the beginning and end of July. Terminal drought stress, of variable intensities was simulated in 9 out of 10 years and is a major problem for cultivars like Boohai (Table 2.5).

Simulated average potential grain yield was 5960 kg/ha (Fig. 2.2), but highly variable over years. Average simulated harvest index was 0.39 (Table 2.6). A very low water use

Table 2.4 Annual and seasonal rainfall (mm) at the six test locations in Ethiopia from 1980 to 1989

Year	Asmara		Kombolcha		Debre Markos		Debre Zeit		Melkasa		Metahara	
	A	S	A	S	A	S	A	S	A	S	A	S
1980	880	646	989	781	1302	1083	779	645	900	701	635	CF
1981	737	485	984	710	1152	933	921	483	783	571	348	CF
1982	689	506	1129	602	1367	1095	746	507	694	532	898	432
1983	445	306	1032	573	1249	1005	983	307	790	482	612	560
1984	425	337	610	303	1081	848	666	655	511	910	448	263
1985	685	441	1007	657	1406	1163	841	751	785	431	596	375
1986	488	378	1070	783	1079	884	883	529	626	436	351	CF
1987	555	348	780	441	1270	818	905	315	873	622	415	CF
1988	600	399	1193	890	1062	690	645	683	779	554	654	413
1989	NA	NA	1193	650	NA	NA	825	603	679	530	NA	NA
Average	688	427	998	647	1218	947	819	548	742	582	550	-
CV (%)	31	24.0	16	26.3	11	16.2	21	27.4	19	25.8	25	-

A = annual rainfall.

S = seasonal rainfall.

NA= data not available.

CF= no data as a result of crop failure.

efficiency (31 kg ha^{-1} mm^{-1}) and high transpiration coefficient (0.0238 mm kg^{-1} ha) were simulated. These were associated with the terminal drought stress and the high temperatures at this location. Short-duration cultivars (2.5-3.0 months) and moisture conservation measures could lead to stable durum wheat production system in this region.

Metahara

This region is characterised by hot and arid climate, with an extremely short and unreliable growing period (Fig. 2.1). In 50% of the years crop failure is simulated (Table 2.4) and in the remaining years yields are very low (Fig. 2.2). Durum wheat production is not feasible in this region unless supplemented with irrigation.

Discussion

In Debre Markos and Kombolcha the total rainfall is high and its distribution favourable, resulting in a long growing period. Debre Zeit and Melkasa receive moderate amounts of rainfall, with variable distribution, which results in a short growing period. In Asmara rainfall is low with variable distribution resulting in a very short growing period. In Metahara seasonal rainfall is very low and erratic. The onset of the rainy season, particularly in the low rainfall areas (Metahara and Asmara), is very variable. As a result, the simulated date of emergence was variable, ranging from June to August, and total crop failure was simulated repeatedly in Metahara (Table 2.3). Simulated time of emergence strongly influenced simulated final grain yield and biomass production in all the test locations.

Simulated growth rate and grain yield were adversely affected by both terminal and intermittent moisture stress (Table 2.3). However, terminal moisture stress of variable intensity, commencing after anthesis, was the major limiting factor, particularly in the low-rainfall and low-altitude locations. Simulations suggested that in 50% of the years, crop failure may result from moisture stress during the early vegetative period in Metahara whereas in Kombolcha and Debre Zeit moisture stress caused low yields.

In agreement with many reports on semi-arid dryland farming (van Keulen and Seligman, 1987; Blum and Pnuel, 1990; Buresh *et al.*, 1990; Singh and Byerelee, 1990; Chaves, 1991), variation in amount and distribution of seasonal rainfall was found to be the predominant factor affecting simulated grain yields and stability of durum wheat across regions and time. In high-rainfall areas, simulated grain yields were high and fairly stable, while in low-rainfall areas they were low and highly variable.

Table 2.5 Simulated periods of intermittent (IS) and terminal (TS) drought stress at six test locations in Ethiopia from 1980 to 1989

Year	Asmara		Kombolcha		D. Markos		D. Zeit		Melkasa		Metahara	
	IS	TS	IS	TS	IS	TS	IS	TS	IS	TS	IS	TS
1980	NS	NS	NS	NS	NS	NS	NS	9/22-E	NS	10/13-E	CF	
1981	NS	NS	NS	NS	NS	NS	8/11 -8/17	9/24-E	NS	9/21-E	CF	
1982	NS	NS	NS	NS	NS	NS	NS	9/18-E	NS	9/29-E	9/7- 10/15	10/23-E
1983	NS	10/3-E	NS	NS	NS	NS	NS	9/5-E	NS	9/15-E	NS	NS
1984	NS	9/9-E	7/24- 9/2	10/6-E	NS	9/30- E	NS	10/3-	NS	NS E	NS	8/14-E
1985	NS	NS	NS	9/15-E	NS	NS	NS	10/9-E	NS	9/4-E	NS	8/26-E
1986	NS	9/11-E	NS	NS	NS	NS	NS	10/1-E	NS	9/16-E	CF	
1987	NS	9/23-E	7/19- 8/5	10/14- E	NS	NS	7/14- 8/5	9/6-E	NS	10/16-	CF E	
1988	NS	9/29-E	NS	NS	NS	NS	NS E	10/16-E 9/15	NS	10/10-	8/20-	9/21-E
1989	NA	NA	NS	NS	NA	NA	NA	10/9-E	NS	10/2-E	NA	

NA= data not available.
NS= no stress.
E = until the end (i.e., harvest)
- = between these dates.
CF= crop failure.

Table 2.6 Simulated values of harvest index (HI) for durum wheat cv Boohai at the six test locations in Ethiopia from 1980 to 1989.

Year	Asmara	Kombolcha	D.Markos	D. Zeit	Melkasa	Metahara
1980	0.43	0.51	0.46	0.36	0.46	CF
1981	0.46	0.51	0.45	0.40	0.38	CF
1982	0.43	0.51	0.46	0.45	0.37	0.45
1983	0.18	0.49	0.45	0.59	0.28	0.45
1984	0.33	0.63	0.45	0.33	0.46	0.18
1985	0.47	0.50	0.46	0.42	0.32	0.14
1986	0.35	0.50	0.46	0.40	0.39	CF
1987	0.37	0.51	0.46	0.14	0.47	CF
1988	0.31	0.51	0.48	0.43	0.41	0.34
1989	NA	0.52	NA	0.39	0.40	NA
Average	0.37	0.52	0.46	0.39	0.39	0.30

NA= data not available

CF= crop failure

Average simulated grain yields for the various locations ranged from 1500 (Metahara) to 9700 kg/ha (Debre Markos) (Fig. 2.2). Simulated harvest index (HI) was low in areas experiencing terminal drought stress (Table 2.6). This is due to accelerated leaf senescence preventing photosynthesis and translocation of reserve assimilates to the grains. Where seasonal rainfall is low and erratic, sustainable production systems require cropping patterns that are sufficiently versatile to adjust to variable moisture availability. At Melkasa and Asmara, use of early maturing cultivars seems promising.

Simulated WUE ranged from 19 to 58 kg ha^{-1} mm^{-1} and TC from 0.0125 to 0.0257 mm kg^{-1} ha. This variation is due to the variable weather conditions affecting evapotranspirational demand during the growing period (Tanner and Sinclair, 1983). The decline in simulated WUE with decreasing seasonal rainfall suggests that the drier the site, the more water is used per unit of above-ground dry matter production. TC follows the reverse pattern, suggesting efficient water use in high seasonal rainfall locations. This is closely related to the substantial losses of moisture by direct soil surface evaporation (Cooper *et al.*, 1983; Tanner and Sinclair, 1983).

The cultivars currently under cultivation in Ethiopia appear not to be adapted to the prevailing climatic conditions, particularly to the period of moisture availability. This is illustrated by the long pre-anthesis (66 - 88 days) and short post-anthesis periods (41 - 57

Table 2.7 Water use efficiency, WUE (kg ha^{-1} mm^{-1}) and transpiration coefficient, TC (mm kg^{-1} ha) for durum wheat cv. Boohai at the six test locations in Ethiopia from 1980 to 1989.

Year	Asmara		Kombolcha		D. Markos		D. Zeit		Melkasa		Metahara	
	WUE	TC	WUE	TC	WUE	TC	WUE	TC	WUE	TC	WUE	TC
1980	51	0.0140	45	0.0144	59	0.0125	38	0.0186	32	0.0230	CF	
1981	57	0.0137	50	0.0146	55	0.0125	42	0.0188	32	0.0239	CF	
1982	55	0.0137	52	0.0133	59	0.0125	41	0.0187	40	0.0257	18	0.0267
1983	43	0.0148	48	0.0138	56	0.0127	27	0.0217	27	0.0250	20	0.0272
1984	52	0.0142	41	0.0139	58	0.0125	32	0.0189	24	0.0249	12	0.0300
1985	59	0.0139	43	0.0144	57	0.0125	38	0.0184	34	0.0228	22	0.0167
1986	51	0.0141	45	0.0152	56	0.0125	36	0.0183	30	0.0226	CF	
1987	50	0.0135	30	0.0137	57	0.0125	24	0.0187	33	0.0227	CF	
1988	40	0.0184	47	0.0146	62	0.0126	35	0.0188	31	0.0233	24	0.0281
1989	NA	NA	40	0.0146	NA	NA	35	0.0189	30	0.0238	NA	NA
Average	50	0.0145	44	0.0142	58	0.0125	35	0.0190	31	0.0238	19	0.0257

NA= data not available.

CF= crop failure.

days) of the cultivar Boohai, resulting in low harvest indices and grain yields. Therefore, the results of the present study must be considered by breeders and agronomists to fully exploit the length of the period with dependable moisture supply to produce higher grain yields. Simulation showed that at all locations, except Debre Markos and Kombolcha available moisture is exhausted by the beginning of October. In combination with the cracking nature of the soils, the desiccating winds and the relatively high temperatures during the grain-filling period leads to rapid leaf senescence. This prevents complete translocation of the reserve assimilates, accompanied by premature drying of the spikes. It is, therefore, very important to identify different cultivars with suitable phenological characteristics for the prevailing weather conditions for each of the target areas and to understand the physiological mechanisms of adaptation of the plant to moisture stress. Appropriate soil and crop managements to conserve rainfall and supplementary irrigation could be also considered as options to improve water use efficiency.

The results of the present study illustrate the overriding influence of moisture in determining yield potential and variability across agro-ecological environments. The high simulated yields across locations clearly indicate the scope for durum wheat improvement in the country on one hand and the challenges to realize this level on the other.

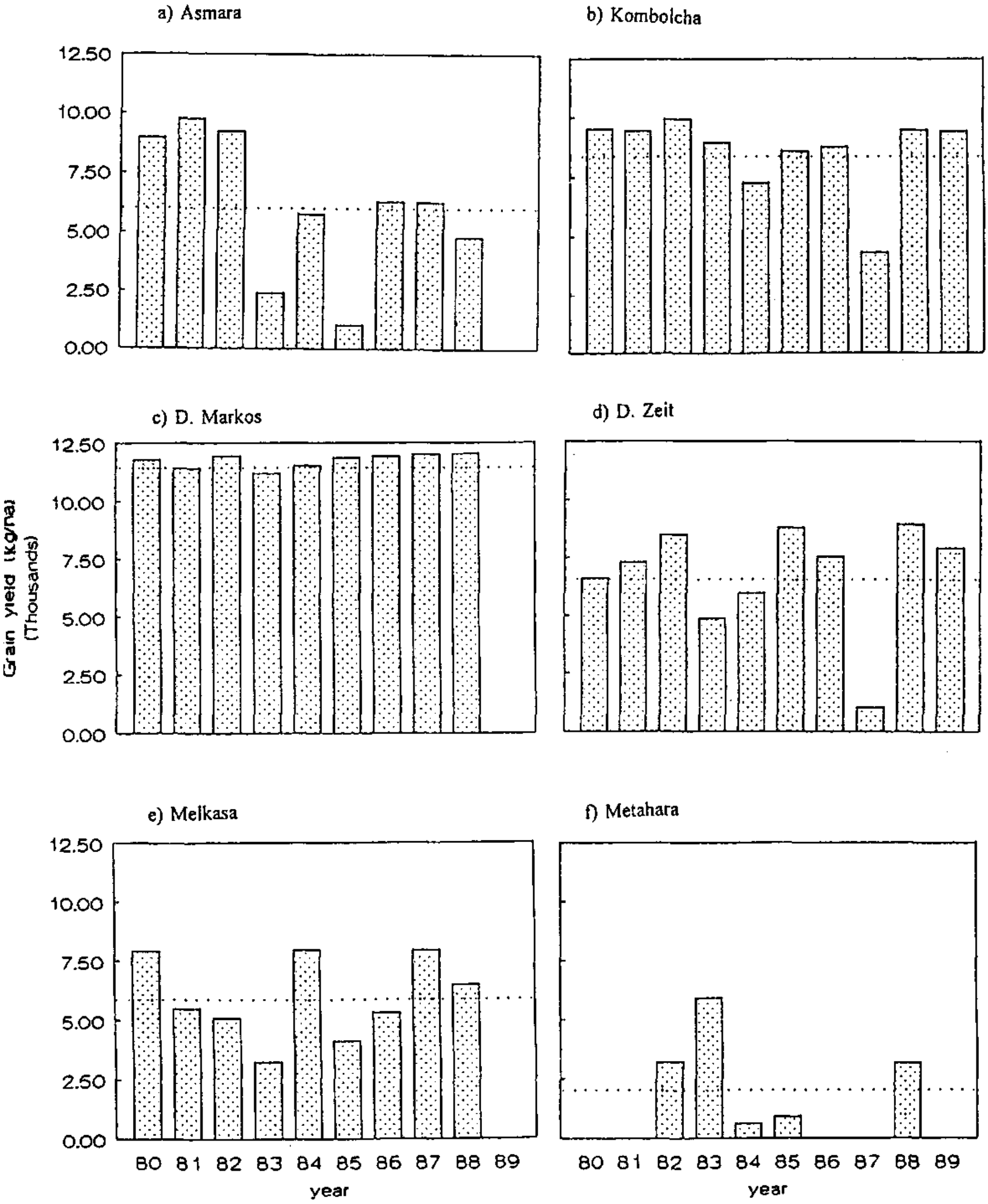
Conclusions

Analysis of historical weather data (such as onset and cessation of rainfall) and soil physical properties to predict probability of water shortage in relation to crop phenology, are important in planning activities.

Versatile cropping patterns and moisture conservation practices should be developed for each ecoregion, including the use of region-specific cultivars of different maturity groups, which can easily be adjusted to the specific moisture regime of the season.

Durum wheat is subjected to temporally and spatially variable moisture stresses. Therefore, to analyse crop response under different conditions, it is imperative to quantify the effect of different timing and degree of moisture stress on crop growth and development. Development of drought-tolerant cultivars should be for particular environments, rather than for wide adaptation.

The wide gap between the current actual farmers' yields and simulated potential yields in Ethiopia suggests that there is a considerable scope for increasing durum wheat yields. Effective soil moisture conservation systems and variety selection may offer some opportunities for the future.



a) Asmara

b) Kombolcha

c) D. Markos

d) D. Zeit

e) Melkasa

f) Metahara

Fig. 2.2 Simulated grain yields of durum wheat for the years 1980 to 1989 at the six test locations in Ethiopia. Dotted lines indicate average grain yields.

References

Blum, A. and Pnuel, Y., 1990. Physiological attributes associated with drought resistance of wheat cultivars in Mediterranean environments. Australian Journal of Agricultural Research 41, 799 - 810.

Buresh, R.J., Vlek P.L.G. and Harmsen K., 1990. Fate of fertilizer nitrogen applied to wheat under simulated Mediterranean environmental conditions. Fertiliser Research 23, 25 - 36.

Chaves, M.M., 1991. Effect of water deficit on carbon assimilation. Journal of Experimental Botany 42, 1 - 16.

Cooper, P.J.M., Keatinge J.D.H. and Hughes, G., 1983. Crop evapotranspiration- a technique for calculation of its components by field measurements. Field Crops Research 7, 299-312.

CSO 1986. Ethiopian statistical abstract. Central Statistical Office, Addis Ababa, Ethiopia.

Dender W.M., 1989. Food policy objectives in the ten year perspective plan. Paper presented at the National Conference on a Disaster prevention and preparedness strategy for Ehiopia, Addis Ababa, 4-5 December 1988.

Grant, R.F., 1989. Simulation of carbon assimilation and partitioning in maize. Agronomy Journal 81, 563-571.

IAR, 1983. Crop Protection Department Progress Report 1977/78. Institute of Agricultural Research, Addis Ababa, Ethiopia. 128 pp.

Perrier, E.R., 1988. Opportunities for the productive use of rainfall normally lost to cropping for temporal or spatial reasons. *In*: Bidinger, F.R. and Johansen, C. (Editors.), Drought research priorities for the dryland tropics. ICRISAT, Patancheru, AP 502324, India, pp. 113-129.

Simane, B. and Struik, P.C., 1993. Agroclimatic analysis: a tool for planning sustainable durum wheat (*Triticum turgidum* L. var. *durum*) production in Ethiopia. Agriculture, Ecosystem and Environment, in press.

Singh, A. J. and Byerelee, D., 1990. Relative variability in wheat yields across countries and over time. Journal of Agricultural Economics 41, 23 - 32.

Spitters, C.J.T., van Keulen, H. and van Kraalingen, D.W.G., 1989. A simple and universal crop growth simulator: SUCROS 87. *In*: Rabbinge, R., Ward, S.A. and van Laar, H.H (Editors), Simulation and Systems Management in Crop Protection. Simulation Monograph no. 32, Pudoc, Wageningen, pp. 147-181.

Tanner, C.B. and Sinclair, T.R., 1983. Efficient water use in crop production: Research or Re-search. *In*: Taylor, H.M., Jordan, W.R. & Sinclair, T.R. (Editors), Limitations to Efficient Water Use in Crop Production. ASA-CSSA-SSSA, Madison, WI, USA, pp. 1-26.

Tesfaye T., 1987. Durum wheat breeding in Ethiopia. In: van Ginkel, M. & Tanner, G.J. (Eds.), Fifth Regional Wheat Workshop for Eastern, Central & Southern Africa & the Indian Ocean. CIMMYT, Mexico, pp. 18-22.

Unger, P.W., Jones, O.R. and Steiner, J.L., 1988. Principles of crop and soil management procedures for maximizing production per unit rainfall. *In*: Bidinger, F.R. and Johansen, C. (Editors), Drought research priorities for the dryland tropics. ICRISAT, Patancheru, AP 502324, India, pp. 97-112.

van Keulen, H. and de Milliano, W.A.J., 1984. Potential wheat yields in Zambia: a simulation approach. Agricultural Systems 14, 171-192.

van Keulen, H. and Seligman, N.G., 1987. Simulation of water use, nitrogen nutrition and growth of a spring wheat crop. Simulation Monographs. Pudoc, Wageningen. 310 pp.

Virmani, S.M., Sivakumar, M.V.K., and Reddy, S.J., 1980. Climatological features of the semi-arid tropics in relation to Farming Systems Research Program. *In*: Proceedings of the International Workshop of the Agroclimatological Research Needs of the Semi-Arid Tropics, 22-24 Nov. 1978, ICRISAT, Hyderabad, India, pp. 5-16.

Whisler, F.D., Acock, B., Baker, D.N., Fye, R.Y., Hodges, H.F., Lambert, J.R., Lemmon, H.E., McKinion, J.M. and Reddy, V.R., 1986. Crop simulation models in agronomic systems. Advances in Agronomy 40, 141-208.

Chapter 3

Ontogenetic analysis of yield components and yield stability of durum wheat in water-limited environments.

B. Simane, P.C. Struik, M.M. Nachit and J.M. Peacock

Euphytica (submitted)

Abstract

One main reason for the slow improvement of durum wheat in water-limited environments is the lack of clear understanding of the interrelationships of yield components and their compensatory growth under low and/or erratic moisture availability. Five cultivars, varying in many physiological attributes, were tested under different moisture stress conditions in field and greenhouse experiments. The cause-effect relationships of duration of vegetative period, duration of grain filling period, number of spikes/m^2, kernels/spike, kernel weight and grain yield were assessed. Further, yield stability was evaluated. Yield reduction was largest under mid-season stress (58%) followed by terminal-stress (30%) and early-stress (22%). Cultivar Po was very sensitive to terminal stress.

Path-coefficient analysis revealed a complex pattern of relationships among the six variables. An increase in vegetative period reduced the grain filling period under all conditions. It increased number of kernels per spike under non-stress conditions. The direct effect of spikes per m^2 on grain yield was significantly positive. However, more spikes per m^2 resulted in fewer kernels per spike and low kernel weight and, as a result, a negative relationship with grain yield under early stress. Grain filling period had a strong influence on grain yield *via* kernel weight. Kernels per spike had the largest direct effect on grain yield. However, it was negatively correlated with kernel weight, especially under terminal stress. Grain yield heavily depended on kernels per spike under early stress and grain filling period and kernels per spike under terminal stress.

Variation in drought susceptibility index among cultivars was significant under early and terminal stress conditions, but not under mid-stress conditions. Yield potential and stability were not correlated for the different moisture-stress conditions.

Longer grain filling period, increased kernels per spike and limited spike number per m^2 can be used as selection criteria for sustainable yield in water-limited environments.

Key words: drought susceptibility index, moisture stress, path analysis, *Triticum turgidum* L. var. *durum*, yield components, yield potential.

Introduction

Durum wheat (*Triticum turgidum* L. var. *durum*) is extensively grown throughout the dry areas of North Africa and the Middle East (Nachit and Ouassou, 1988). Its production is low and subject to substantial year-to-year fluctuation because of low and erratic distribution of rainfall (Simane *et al.*, 1993[a]). In these regions, variation in annual rainfall has been reported to explain 75% of the variations in wheat yield (Blum and Pnuel, 1990).

Grain yield can be analyzed in terms of three yield components (number of spikes per unit area of land, number of kernels per spike and mean kernel weight). These components develop sequentially, with later-developing components under control of earlier-developing ones (Dofing and Knight, 1992), and interact in compensatory patterns, particularly under stress environments (Garcia del Moral *et al.*, 1991). Tillering occurs during early growth and depends on many factors such as availability of water, nitrogen and spacing.

Development of floral organs occurs during the time of rapid vegetative growth. Competition for limiting resources between vegetative organs and floral organs may occur (Austin *et al.*, 1980). Most of the proteins and carbohydrates during grain growth are derived from senescing leaves and stems, particularly under water and nitrogen shortage.

Compensation of yield components occurs as a result of competition for limiting resources. Simple correlations with grain yield may not provide a complete picture of the importance of each component in determining grain yield (Garcia del Moral *et al.*, 1991). Selecting for grain yield under variable moisture availability is difficult, particularly in the harsh Mediterranean climate where drought of different severity may occur any time of the growing period. Path analysis of yield components and the duration of the vegetative and grain-filling period, as described by Li (1956), allows the separation of direct influence of each yield component on grain yield from the indirect influence caused *via* mutual relationships among yield components.

In semi-arid conditions, where the rainfall distribution is highly variable from season-to-season, the potential yield under stress is not the best indicator for drought resistance (Simane and Struik, 1993). Yield stability, the extent of variation in yield between stress and non-stress conditions, is widely accepted as a better indicator of genotypic response to stress (Fischer and Maurer, 1978; Blum, 1988; Blum *et al.*, 1989).

The objectives of the research described in the present paper were: 1) to investigate the relationships among yield, yield components and duration of vegetative and grain-filling periods and to separate the direct effect on grain yield from the indirect influence *via* the mutual relationships under different time and intensity of moisture stress, and 2) to study the relationship between yield potential and yield stability of durum wheat cultivars. In the experiments five cultivars, contrasting in many physiological parameters (related to drought-resistance) such as: growth rate and shoot:root ratio (Simane *et al.*, 1993[b]), water use and water use efficiency (Simane *et al.*, submitted), were used.

Materials and methods

Detailed information on cultivars, methodology and environmental conditions used in this report has been given elsewhere (Simane *et al.*, 1993[b]). Only a brief summary of the relevant experimental details is presented here.

Five durum wheat (*T. turgidum* L. var. *durum*) cultivars bred in Ethiopia and Syria were tested under field and greenhouse conditions. The cultivars represent different levels of drought resistance under field conditions of Mediterranean regions. Three cultivars (Tob-2, DZ (900-4DZ) and Boohai) were bred in Ethiopia. The selection was made under terminal moisture stress conditions. Omrabi-5 was bred from a landrace adapted to drought (Haurani) and a high yielding variety (Jori C69). It was selected under dry, cold, and hot conditions. In contrast, Po was developed for high input conditions and selected under non-stress conditions.

Two field experiments were conducted during 1990-91 at Debre Zeit Agricultural Research Centre (8°44'N, 39°02'E), Alemaya University of Agriculture, Ethiopia. Plot size was 7 rows of 2 m long (0.2 m between rows with a density of 220 plants/m^2). The greenhouse experiment was conducted in 1991/92 at ICARDA, Tel Hadya, Syria (36°10'N, 36°56'E). Three plants were grown per 5 kg dry soil capacity pot. Plant density based on pot surface area and its spacing was equivalent to 220 plants/m^2. Eight pots were used for each treatment. A randomized complete block design with four replications was used in both field and greenhouse experiments.

Four moisture treatments were applied: stress induced a) early (at tillering), b) mid season (at flowering), c) late season (grain filling) and d) control (no stress). Soil moisture status in the field experiments was monitored using the modified Penman-Monteith method (FAO, 1984). In the non-stressed treatments, a measured quantity of water was replenished whenever 30% of the available soil water was depleted. A buffer channel of 0,5 m wide separated each plot. Soil moisture status in the pot experiment was determined gravimetrically by weighing each pot every other day.

Path coefficient analysis was carried out to partition the correlation coefficients, r_{ij}, into direct and indirect effects using the SAS (PROC CALIS) computer programme. The characters used were: (1) duration of vegetative period, (2) number of spikes per square meter, (3) duration of grain-filling period, (4) number of kernels per spike (5) individual kernel weight and (6) grain yield per square meter. Path coefficient can also be calculated using the following four sets of simultaneous equations (Gebeyehou *et al.*, 1982; Garcia del Moral *et al.*, 1991).

$$\begin{aligned} r_{26} &= P_{26} + r_{24}P_{46} + r_{25}P_{56} \\ r_{46} &= r_{24}P_{26} + P_{46} + r_{45}P_{56} \\ r_{56} &= r_{25}P_{26} + r_{45}P_{46} + P_{56} \end{aligned} \tag{3.1}$$

$$\begin{aligned} r_{25} &= P_{25} + r_{23}P_{35} + r_{24}P_{45} \\ r_{35} &= r_{23}P_{25} + P_{35} + r_{34}P_{45} \\ r_{45} &= r_{24}P_{25} + r_{34}P_{35} + P_{45} \end{aligned} \tag{3.2}$$

$$\begin{aligned} r_{14} &= P_{14} + r_{12}P_{24} + r_{13}P_{34} \\ r_{24} &= r_{12}P_{14} + P_{24} + r_{23}P_{34} \\ r_{34} &= r_{13}P_{14} + r_{23}P_{24} + P_{34} \end{aligned} \tag{3.3}$$

$$\begin{aligned} r_{13} &= \quad P_{13} + r_{12}P_{23} \\ r_{23} &= r_{12}P_{13} + \quad P_{23} \end{aligned} \tag{3.4}$$

where, P_{ij} (with subscripts indicating the six characters) is the path coefficient.

The cause and effect system was based on the ontogeny of durum wheat as shown in Fig. 3.2. In the equation $r_{13} = P_{13} + r_{12}P_{23}$, P_{13} is the path coefficient (direct effect) of character 1 on 3, while $r_{12}P_{23}$ is the indirect effect of character 1 on 3 via 2.

The drought susceptibility index (DSI) was calculated for each cultivar and moisture regime using the following formula (Fischer and Maurer, 1978; Blum *et al.*, 1989).

$$DSI = (1 - Y/Y_p) / (1 - X/X_p) \tag{3.5}$$

where Y is the yield of a certain cultivar under stress, Y_p is the yield of the same cultivar without stress and X and X_p represents average yields across all cultivars under stress and non-stress conditions respectively.

Results

Minimum, maximum and mean values and standard deviations of duration of vegetative period (VP) number of spikes per m^2 (S/m^2), grain-filling period (GFP), number of kernels per spike (K/S) and kernel weight (KW)) and grain yield (GY) are given in Table 3.1. Analysis of variance revealed that significant differences existed both among cultivars and moisture treatments for all variables except KW. S/m^2 and K/S are the yield components which varied most in response to different times and intensities of moisture stress. Moisture stress, no matter its timing, reduced potential grain yield (Fig. 3.1). Yield reductions averaged over cultivars were 22%, 58% and 30% under early, mid-season and terminal moisture stresses respectively. The yield potentials of ICARDA cultivars (Omrabi-5 and Po) were higher than those of cultivars from Ethiopia. However, the mean grain yield of Po under the stress environments was substantially less than of all other cultivars.

The relative influences of the five characters on grain yield and their mutual relationships were different under different moisture stress treatments (Table 3.2). GY was significantly correlated with K/S under early stress, with GFP and K/S under terminal stress and with S/m^2, GFP and K/S under non-stressed conditions. The negative relationship between VP and GFP was significant under all moisture stress treatments. Similarly, S/m^2 was negatively related with K/S, except in the control. KW positively correlated with GY, but not significantly under all conditions.

Table 3.1 Statistics of the duration of the vegetative period (VP), no of spikes per m^2 (S/m^2), duration of grain-filling period (GFP), no. of kernels per spike (K/S), kernel weight (KW) and grain yield (GY) in Ethiopia and Syria (ICARDA).

	Minimum	Maximum	Mean	SD
1) VP (days)	46.0	84.0	65.5	9.7
2) S/m^2 (no/m^2)	252.0	1066.6	584.3	168.5
3) GFP (days)	25.0	70.0	46.8	10.1
4) K/S (no/spike)	6.6	68.6	28.2	12.3
5) KW (mg)	24.2	55.4	47.3	5.7
6) GY (g/m^2)	229.6	1264.0	763.7	273.8

Results of the path coefficient analysis across cultivars for the different moisture treatments are given in Fig. 3.2. Correlation coefficients among the six parameters were separated into direct and indirect effects as described in Eqs. 3.1-3.4 using values from Table 3.2 and Fig. 3.2. This is illustrated in Table 3 using the data from terminal stress, which is most important in the North African and West Asian regions. All direct effects of yield components were positive, suggesting that when other yield components are held constant, each direct effect results in increased yield. K/S had the most significant direct effect on yield, followed by S/m^2 under all stress conditions. KW did not influence GY except under mid-season stress. All the indirect effects of S/m^2 via K/S and KW were negative. A greater S/m^2 resulted in smaller K/S and KW. GFP had a positive direct effect on KW. An increase in K/S resulted in a significantly lower KW under all moisture conditions. VP had a highly significant negative influence on GFP. It is also worth noting that GFP had a strong effect on GY via KW, except under early stress. The direct effects obtained suggested that GY is heavily dependent upon S/m^2 and K/S.

Drought susceptibility index (DSI) calculated from the mean values of GY ranged from 0.64 to 2.06 (Fig. 3.3). Mean S values averaged over all moisture stress conditions were 1.03, 0.94, 1.01, 0.70 and 1.39 for Tob-2, DZ, Boohai, Omrabi-5 and Po respectively. Since smaller values of DSI indicate yield stability (drought resistance), Omrabi-5 is the most stable cultivar followed in order by DZ, Boohai, Tob-2 and Po. However, cultivars responded differently to different timing of stress. Stress intensity (the term "$1 - X/X_p$" of Eq . 3.5) was 0.24, 0.59 and 0.29 for early, mid-season and terminal stress. There were no cultivar differences in S under mid-stress. This underlines that moisture stress during anthesis has the most detrimental effect on grain yield. Grain yield stability (DSI value) and yield potential (yield under non-stressed condition) of cultivars did not correlate.

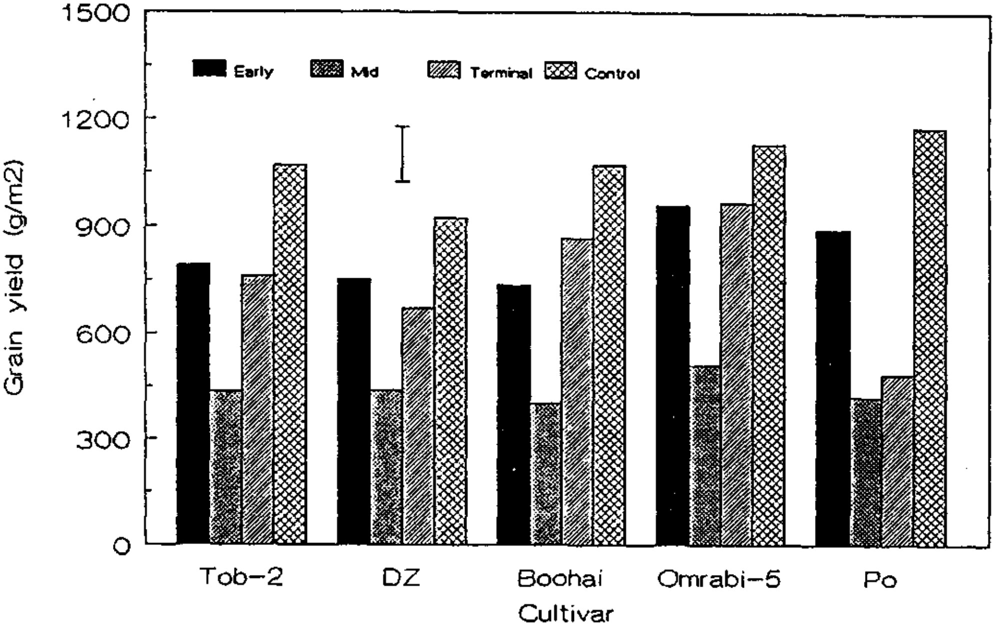


Fig. 3.1 Mean grain yield of five durum wheat cultivars grown under different stress conditions. Vertical bar indicates LSD (0.05) value.

Discussion

The time and intensity of moisture stresses imposed in this study were those commonly encountered by rain-fed cereals in the semi-arid tropics, particularly in East African highlands (Simane and Struik, 1993). A substantial reduction of yield potential and high coefficient of variability of yield components under different episodes of moisture stress illustrated the overriding influence of moisture stress in the agricultural system of the semi-arid tropics. This is in accord with previous results (Simane *et al.*, 1993^a).

The maximum expression of each yield component was determined sequentially according to the order of their development. Earlier-developing yield components could affect later-developing ones in compensatory patterns during development, particularly when there is shortage of resources (such as water) (Fischer, 1985; Blum, 1983). The adaptive responses vary according to different timing of drought. In general variation in grain yield among cultivars and moisture treatments was associated with GFP, S/m^2 and K/S. This result agrees with previous reports under water-limited conditions (Fischer and Maurer, 1978; Garcia del Moral *et al.*, 1991). KW was highly stable, possibly due to the high proportion of translocated stored pre-anthesis reserves as a source for grain filling when the photosynthetic source is limited by stress (Austin *et al.*, 1980; Blum, 1983).

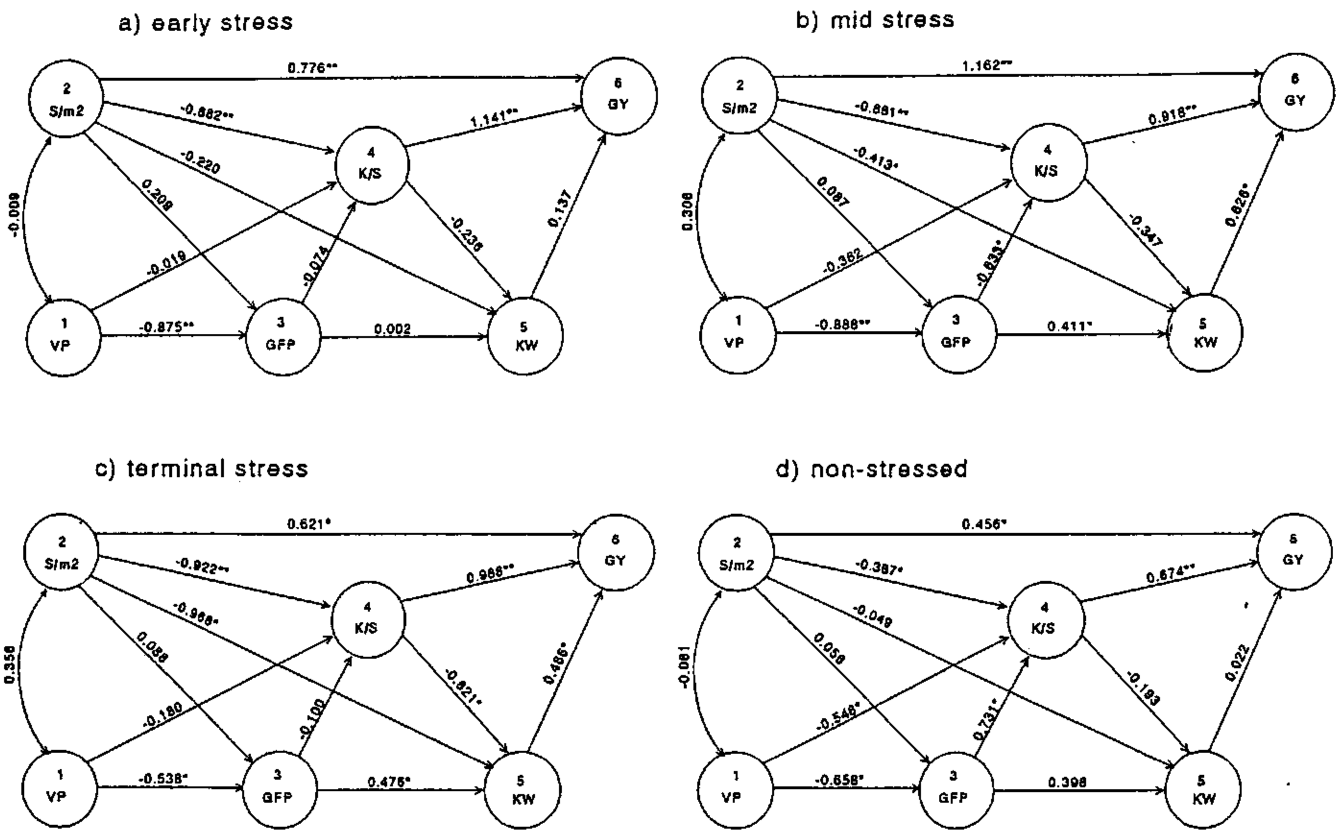


Fig. 3.2 Path coefficient diagrams showing the interrelationships among 1) duration of vegetative period (VP), 2) numbers of spikes per m^2 (S/m^2), 3) duration of grain-filling period (GFP), 4) number of kernels per spike (K/S), 5) kernel weight and 6) grain yield (GY). The single-headed arrows indicate path coefficients and double-arrows indicate simple correlation coefficients. * and **, indicate significance at P< 0.05 and P< 0.01 respectively.

Table 3.2 Pooled linear correlation coefficients among vegetative period (VP), spikes/m^2 (S/m^2), grain-filling period (GFP), kernels/spike (K/S), kernel weight (KW) and grain yield (GY).

	VP	S/m^2	GFP	K/S	KW
		a) early stress			
S/m^2	-0.009				
GFP	-0.877**	0.218			
K/S	-0.122	-0.896**	-0.095		
KW	-0.170	-0.009	-0.023	-0.039	
GY	-0.182	-0.247	0.115	0.440*	0.086
		b) mid stress			
S/m^2	0.306				
GFP	-0.861**	-0.185			
K/S	-0.025	-0.674**	-0.195		
KW	-0.503*	-0.256	0.555**	-0.148	
GY	-0.079	0.383	0.036	0.042	0.193
		c) terminal stress			
S/m^2	-0.356				
GFP	-0.569**	0.280			
K/S	0.091	-0.763**	-0.055		
KW	-0.241	-0.153	0.250	0.044	
GY	-0.397	-0.270	0.552**	0.452*	0.327
		d) control			
S/m^2	-0.061				
GFP	-0.662**	-0.096			
K/S	-0.088	-0.350	0.278		
KW	0.591**	0.020	0.467*	0.308	
GY	0.229	0.423*	0.516*	0.563**	0.379

* P< 0.05 and ** P< 0.01

Vegetative period had a significant negative effect on GFP and subsequently on GY, particularly under terminal moisture stress. This confirms earlier reports (Fischer and Maurer, 1978; Garcia del Moral *et al.*, 1991). It is mainly due to the depletion of soil water which in turn reduces photosynthesis during GFP. In agreement with others (Gebeyehou *et al.*, 1982; Garcia del Moral *et al.*, 1991), GFP has a significant direct effect on KW except under early stress, due to a possible increased transient photosynthetic source in addition to the translocated stored stem reserves for the same sink size (Blum, 1983; Van Oosterom and Acevedo, 1992).

Number of spikes per m^2 had a significantly positive direct effect on GY. The indirect effects *via* K/S and KW are significantly negative which is in accord with previous reports (Garcia del Moral *et al.*, 1991; Dofing and Knight, 1992). The negative direct effect of S/m^2 on K/S and KW suggests a compensatory effect between tillering and apical growth (Garcia del Moral *et al.*, 1991). The importance of tillering as a selection index is still unresolved, especially under water-limited environments. Hadjichristodoulou (1985) advocated profuse tillering capacity, whereas, others (Islam and Sedgley, 1981; Dofing and Karlsson, 1993) advocated 'uniculm ideotypes' for water-limited environments. The present result and our previous results on growth rate and water use efficiency of the same cultivars clearly proved that cultivars with high tillering capacity show increased vegetative growth. This exhausts the limited available soil water and reduces the source:sink ratio during the grain-filling period and will result in low harvest index (Simane *et al.*, 1993[a,b]). Therefore in agreement with Common and Klink (1981), limited numbers of tillers i.e. genotypes having two or three tillers will do better under water-limited conditions. However, under non-stress conditions increased tillering capacity will produce higher yields if adequate amounts of nutrients are applied. The number of kernels per spike is predominantly related to grain yield under all timings of moisture stress. This is in agreement with several reports (Fischer, 1985; Garcia del Moral *et al.*, 1991; Dofing and Knight, 1992). The physiological reason for this is that wheat yield is normally sink-limited during grain filling period (Fischer, 1985; Slafer and Andrade, 1991). This close association suggests that increased K/S could be used as a selection criterion under water-limited environments.

Yield stability is of prime importance and accepted as a more useful indicator of cultivar response to variable moisture availability (Fischer and Maurer, 1978; Blum, 1988; Simane and Struik, 1993). In agreement with previous findings (Edhaie *et al.*, 1988; Winter *et al.*, 1988; Blum, 1988), yield stability and potential yield of cultivars were not correlated (data not shown). This leads to the conclusion that yield potential and stability are independent parameters that contribute to adaptation to water-limited environments. Using this criterion cv. Omrabi-5 has both a high yield potential and high stability, confirming the appropriateness of the selection strategy used to breed it (Nachit and Ouassou, 1988). Po

Table 3.3 Path coefficient (P) analysis of grain yield of five durum wheat cultivars grown under terminal moisture stress conditions. (See text for further explanation.)

Pathway	
S/m^2 vs. GY:	
Direct effect (P_{26})	0.621*
Indirect effect *via*	
K/S ($r_{24}P_{46}$)	-0.751
KW ($r_{25}P_{56}$)	-0.071
Correlation (r_{26})	-0.270
K/S vs. GY)	
Direct effect (P_{46})	0.988**
Indirect effect *via*	
S/m^2 ($r_{24}P_{26}$)	-0.467
KW ($r_{45}P_{56}$)	-0.021
Correlation (r_{46})	0.452
KW vs GY	
Direct effect (P_{56})	0.466*
Indirect effect *via*	
S/m^2 ($r_{25}P_{26}$)	-0.095
K/S ($r_{45}P_{46}$)	-0.043
Correlation (r_{56})	0.327
Residual (U)	0.678

has the highest yield potential but is the most drought-susceptible. In contrast Ethiopian cultivars are relatively drought-resistant but have low yield potentials.

The data presented here show that i) selection of cultivars for water-limited environments should critically assess high yield potential and stability ii) limited S/m^2, longer GFP and increased K/S can be used as selection criteria in developing drought-resistant cultivars.

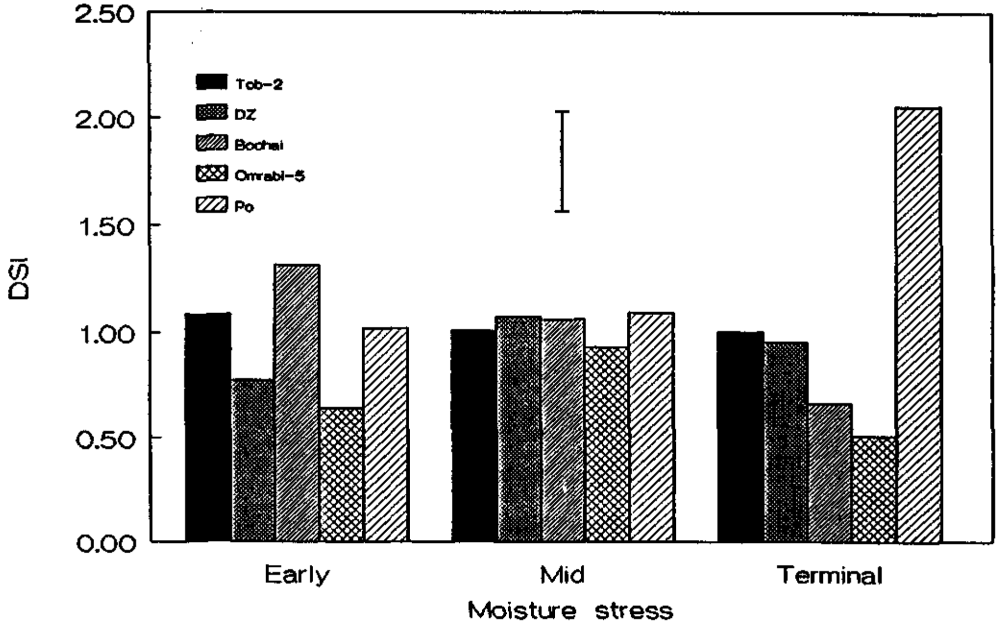


Fig. 3.3 Mean drought susceptibility index (DSI) of five durum wheat cultivars grown under different drought stress conditions. Vertical bar indicates LSD (0.05) value.

References

Austin, R.B., Morgan, C.L., Ford, M.A. and Blackwell, R.D., 1980. Contribution to grain yield from pre-anthesis assimilation in tall and dwarf barley phenotypes in two contrasting seasons. Annals of Botany, 45: 309-319.

Blum, A., 1983. Genetic and physiological relationships in plant breeding for drought resistance. Agric. Water Mng. 7, 195-205.

Blum, A., 1988. Plant breeding for stress environments. CRC Press, Florida, 223 pp.

Blum, A. and Pnuel, Y., 1990. Physiological attributes associated with drought resistance of wheat cultivars in a Mediterranean environment. Aust. J. Agric. Res., 41: 799-810.

Blum, A., Sphiler, L., Golan, G. and Mayer, J., 1989. Yield stability and canopy temperature of wheat genotypes under drought-stress. Field Crops Res., 22: 289-296.

Common, J.C. and Klink, H.R., 1981. Sequence and synchrony of culm development: implication in breeding for limited tillering barleys. *In*: Barley Genetics IV. Proc. 4th Int. Barley Genet. Symp., Edinburgh, Scotland. Edinburgh Univ. Press. 533-536.

Dofing, S.M. and Karlsson, M.J., 1993. Growth and development of uniculm and conventional-tillering barley lines. Agron. J., 85: 58-61.

Dofing, S.M. and Knight, C.W., 1992. Alternative model for path analysis of small-grain yield. Crop Sci., 32: 487-489.

Ehdaie, B. Waines, J.G. and Hall, A.E., 1988. Differential responses of landrace and improved spring wheat genotypes to stress environments. Crop Sci., 28: 838-842.

FAO, 1984. Crop water requirement. FAO bul. No 24, pp. 15-30.

Fischer, R.A., 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. J. Agric. Sci., 105, 447-461.

Fisher, R.A. and Maurer, R., 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res., 29: 897-912.

Garcia del Moral, L.F., Ramos, J.M., Garcia del Moral, M.B. and Jimenez-Tejada, M.P., 1991. Ontogenetic approach to grain production in spring barley based on path-coefficient analysis. Crop Sci., 31: 1179-1185.

Gebeyehou, G., Knott, D.R. and Baker, B.J., 1982. Relationships among duration of vegetative and grain filling phases, yield components and grain yield in durum wheat cultivars. Crop Sci., 22: 287-290.

Hadjichristodoulou, A., 1985. The stability of the number of tillers of barley genotypes and its relation with consistency of performance under semi-arid conditions. Euphytica, 34: 641-649.

Islam, T.M. and Sedgley, R.H., 1981. Evidence for a 'uniculm effect' in spring wheat (*Triticum aestivum* L.) in a Mediterranean environment. Euphytica, 30: 277-283.

Li, C.C., 1956. The concept of path coefficient and its impact on population genetics. Biometrics, 12: 190-210.

Nachit, M.M. and Ouassou, A., 1988. Association of yield potential, drought tolerance and stability of yield in *Triticum turgidum* var. *durum*. *In*: Proceedings of the 7th International Wheat Genetics Symposium, Cambridge, UK, 10-13 July 1988, pp. 867-870.

Simane, B. Peacock, J.M. and Struik, P.C., 1993^b. Differences in developmental plasticity and growth rate among drought resistant and susceptible genotypes of durum wheat (*Triticum turgidum* L. var. *durum*). Plant and Soil, in press.

Simane, B. and Struik, P.C., 1993. Agroclimatic analysis; a tool for planning sustainable durum wheat (*Triticum turgidum* L var. *durum*) production in Ethiopia. Agriculture Ecosystem and Environment, in press.

Simane, B., Struik, P.C. and Peacock, J.M. Water use efficiency of durum wheat genotypes differing in drought resistance grown under different moisture regimes. Plant and Soil, submitted.

Simane, B., Van Keulen, H., Stol, W. and Struik, P.C., 1993^a. Application of crop growth model (SUCROS-87) to assess the effect of moisture stress on yield potential of durum wheat in Ethiopia. Agricultural Systems, in press.

Slafer, G.A. and Andrade, F.H., 1991. Changes in physiological attributes of the dry matter economy of bread wheat (*Triticum aestivum*) through genetic improvement of grain yield potential at different regions of the world. Euphytica 58: 37-49.

Van Oosterom, E. J. and Acevedo, E., 1992. Adaptation of barley (*Hordium vulgare* L.) to harsh Mediterranean environments. I. Morphological traits. Euphytica 62: 1-14.

Winter, S.R., Musick, J.T. and Porter, K.B., 1988. Evaluation of screening techniques for breeding drought-resistant winter wheat. Crop Sci., 28: 512-516.

Chapter 4

Water use efficiency of durum wheat cultivars differing in drought resistance grown under different moisture regimes

B. Simane, P.C. Struik and J.M.Peacock

Plant and Soil (submitted)

Abstract

Field and greenhouse experiments were conducted to study water use efficiency (WUE) of contrasting durum wheat (*Triticum turgidum* L. var. *durum*) cultivars grown under different moisture regimes and to identify associated characters. Total water use (W) by drought-resistant and -susceptible cultivars was similar whereas WUE and harvest index (HI) were different. WUE was defined in different ways. Values of water use efficiency based on grain yield (WUE_g) are the best characteristics in defining drought resistance in the context relevant to plant breeders and farmers in water-limited environments. Drought-resistant cultivars used a larger proportion of the total water used in the post-anthesis period. The ratio of pre- and post-anthesis water use (ET_{ba}:ET_{pa}) was negatively related with WUE_g and HI. Carbon isotope fractionation of grain ($^{13}\delta$) varied among cultivars and moisture treatments, and was significantly correlated with ET_{ba}:ET_{pa}, WUE_g and HI. Relative growth rate (RGR) and shoot:root ratio were positively correlated with water use efficiency based on total dry matter (WUE_t) and based on above ground dry matter (WUE_s) but not with WUE_g. Differences in total leaf water potential among drought-resistant and drought-susceptible cultivars were not found.

We conclude that selection for increased WUE_g and HI would increase production in water-limited environments. ET_{ba}:ET_{pa} and $^{13}\delta$ could be used as indirect screening tools for WUE_g and HI, whereas shoot:root ratio and RGR could be used for increased WUE_s.

Key words: carbon isotope fractionation, harvest index, transpiration efficiency, water potential, water stress

Introduction

Durum wheat (*Triticum turgidum* L. var. *durum*) in the semi-arid tropics is grown mainly in marginal environments. In these areas, water shortage resulting from low and erratic rainfall is the most important production constraint (Simane et al., 1993[a]). Yield (Y_s) under such condition is a product of amount of usable water (W) by the crop and water use efficiency (WUE) (Richards, 1987). WUE is defined in various ways (Tanner and Sinclair, 1983; Gregory, 1989), but most often as:

$$WUE = Y/W \quad (g\ kg^{-1}) \tag{4.1}$$

where Y is yield per unit area and W is water used to produce that yield.

If grain yield (GY) is the important economic product, then yield is expressed as a product of W, WUE and harvest index (HI) (Passioura, 1977; Blum, 1988).

$$GY = W * WUE * HI \qquad (g\ m^{-2}) \tag{4.2}$$

Yield may be expressed in various ways, *viz.*; total dry matter including roots or above ground dry matter or grain yield. The quantity of water used may also be expressed in different ways, *viz.*; the total water input (evaporation + transpiration) or, as in many agronomic studies, the transpiration component only.

Genetic variation in WUE among wheat cultivars has been reported (Fischer and Turner, 1978; Siddique *et al.*, 1990). Different explanations have been given for these genetic variations: differences in leaf thickness and/or shoot:root ratio (Passioura, 1977); differences in relative growth rate, time of flowering, canopy structure, harvest index (Cooper *et al.*, 1987; Siddique *et al.*, 1990), differences in photosynthetic path-ways, and composition of dry matter (Tanner and Sinclair, 1983; Gregory, 1989).

Carbon isotope fractionation ($^{13}\delta$) has been proposed as an indirect measure of WUE (Farquhar and Richards, 1984). Genotypic variation in $^{13}\delta$ inversely relating with variation in WUE has been reported for many crops and the method has been advocated as a precise selection technique under water-limited conditions in wheat (Farquhar and Richards, 1984; Condon *et al.*, 1990), potato (Vos and Groenwold, 1989), tomato (Martin and Thorstenson, 1988) and peanut (Hubick *et al.*, 1986).

Crop improvement programmes in water-limited environments do not generally emphasize WUE, because of lack of clear definition and simple and reliable screening criteria for increased WUE. The aims of this study, therefore, were to investigate differences in WUE among drought-resistant and drought-susceptible cultivars and to identify characters contributing to an increased WUE.

Materials and methods

Field and greenhouse experiments were carried out to study the effect of moisture stress on WUE. Five durum wheat (*T. turgidum* L var. *durum*) cultivars developed in Ethiopia and at the International Centre for Agricultural Research in the Dry Areas (ICARDA), which are different in their levels of drought resistance, were used (for descriptions see: Simane *et al.*, 1993[b]). Three cultivars (Tob-2, DZ, Boohai) were bred in Ethiopia for different agro-ecological zones; Omrabi-5 is drought-resistant and grown extensively in Mediterranean regions, while Po was developed for high input areas and is drought-susceptible.

The field experiment was conducted during 1990-91 at Debre Zeit Agricultural Research Centre (8°44'N, 39°02'E), Alemaya University of Agriculture, Ethiopia. Plot size was 7 rows of 2 m long (0.2 m between rows with a plant density of 220/m^2). A pot experiment was conducted in 1991/92 in a controlled environment greenhouse, at ICARDA, Tel Hadya, Syria (36°10'N, 36°56'E). The night/day temperature was 15/20°C. Three plants were grown per 5 kg dry soil capacity pot which is equivalent to 220 plants/m^2. A randomized complete block design with four replications was used in both field and greenhouse experiments.

Table 4.1. Soil moisture regimes applied during the field and greenhouse experiments

Treatment	Time of stress	Range of ASWC*
1) Early-stress	at tillering for 15 days	10 - 20%
2) Mid-season stress	at flowering for 15 days	10 - 20%
3) Late-season stress	at grain filling till harvest	10 - 20%
4) Control	no stress	70 - 100%

* lower and upper limit of Available Soil Water Content

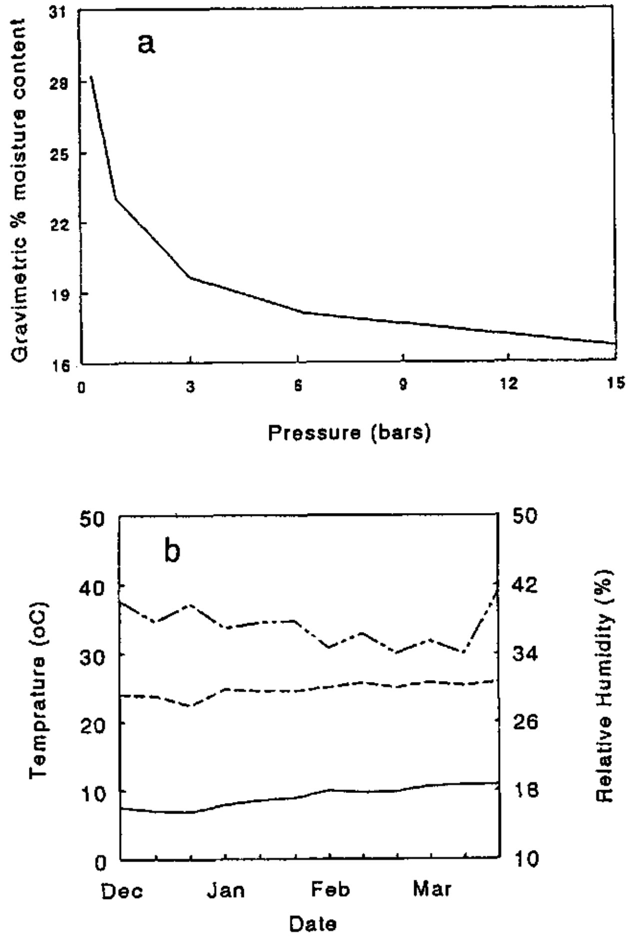


Fig. 4.1 a) The soil moisture characteristics curve b) minimum temperature (——), maximum temperature (- - -) and relative humidity (-·-) of the field experiment at Debre Zeit Agricultural Research Centre in Ethiopia.

Four moisture treatments were applied in both experiments (Table 4.1). Soil moisture characteristics and weather conditions of the field experiment are given in Fig. 4.1. Soil moisture status in the field experiment was monitored using the modified Penman-Monteith method (FAO, 1984). In the non-stressed treatments, a measured quantity of water was replenished whenever 30% of the available soil water (ASW) was depleted. A buffer channel of 0,5 m wide separated each plot.

Soil moisture status in the pot experiment was determined gravimetrically by weighing each pot every other day. Whenever the soil had dried out beyond the pre-set limit, water was added to bring the soil moisture content back to the pre-determined level given in Table 4.1. Four bare soil treatments per replicate were placed between plants to estimate soil evaporation. Daily values of transpiration were calculated as the differences in water applied and bare soil evaporation.

A pressure chamber (Soil Moisture Equipment Corp. Santa Barbara, CA. 93105 USA. model 3005) was used to measure leaf water potential. The upper fully expanded leaf on the main stem was cut adjacent to the ligule for each measurement, and was then enclosed in a plastic wrap impermeable to water and placed in an ice-box to minimize tissue water loss until measurement. Two leaves from two plants per plot were used each time.

At harvest plants were separated into above ground dry matter and roots. Weights of all parts were determined after oven-drying at 75°C for 48 hours. Harvest index (HI) was calculated as the ratio of grain yield to above ground dry matter.

For clarity, we use the terms water use efficiency (WUE) and transpiration efficiency (TE) for yield per unit total water applied (ET) and yield per unit transpiration (T) respectively. Both parameters are defined in three different ways:

$$WUE_t = TDM/ET \qquad (g\ kg^{-1}) \tag{4.3}$$
$$WUE_s = ADM/ET \qquad (g\ kg^{-1}) \tag{4.4}$$
$$WUE_g = GY/ET \qquad (g\ kg^{-1}) \tag{4.5}$$

where WUE_t is water use efficiency based on total biomass, including roots, WUE_s is based on shoot biomass and WUE_g is based on grain, TDM is total dry matter weight, ADM is above ground dry matter weight, GY is grain weight and ET is amount of water used for evaporation and transpiration.

$$TE_t = TDM/T \qquad (g\ kg^{-1}) \tag{4.6}$$
$$TE_s = ADM/T \qquad (g\ kg^{-1}) \tag{4.7}$$
$$TE_g = GY/T \qquad (g\ kg^{-1}) \tag{4.8}$$

where TE_t is transpiration efficiency based on total biomass, including roots, TE_s is based on shoot biomass, TE_g is based on grain and T is amount of water used for transpiration.

The stable carbon isotope composition of the grains was determined using an automated N/C analyzer-mass spectrometer (ANC-IRMS, Europe Scientific, Crewe, UK). About 3.5 mg of oven-dried (80°C) and finely ground grain samples were used. The results were expressed in terms of the standard Pee Dee Belemnite (PDB) defined as:

$$^{13}\delta = (^{13}R_p/^{13}R_{PDB} - 1) * 1000 \qquad (^0/_{00}) \qquad (4.9)$$

Where $^{13}\delta$ is carbon isotope composition of the sample, $^{13}R_p$ and $^{13}R_{PDB}$ are the molar abundance ratios of $^{13}C/^{12}C$ of the sample and the standard, PDB, respectively (Farquhar *et al.*, 1982).

RESULTS

Water use (W)

Cumulative water use over the entire growth period (till physiological maturity) was similar for all cultivars both in the field and in the greenhouse (Table 4.2). A marked reduction in total water use was observed with time and magnitude of moisture stress. However, the relatively high water use recorded in the early stressed treatments is the result of delayed flowering (data not presented).

A significant variation in the ratio of pre- to post-anthesis water use (ET_{ba}:ET_{pa}) was recorded among varieties and moisture treatments, ranging from 0.46 to 2.73 under field conditions and from 0.44 to 3.80 under greenhouse conditions. Pre-anthesis water use (ET_{ba}) of the drought-susceptible cultivar (Po) was substantially higher than drought-resistant cultivars. ET_{ba}:ET_{pa} was negatively correlated with WUE_g, TE_g and HI (Table 4.8). In contrast a significant positive relationship was obtained between ET_{ba}:ET_{pa} and $^{13}\delta$ (Fig. 4.2).

Water use efficiency (WUE)

A significant difference in the average values of WUE was obtained depending on the definition of yield in Equation 4.1 (Table 4.3). Comparative values of WUE in the field were lower than in the greenhouse. In the case of terminal stress, the values of WUE in the field experiment were higher.

WUE_t ranged from 4.37 to 6.57 g/kg. In general, the ICARDA cultivars (Po and Omrabi-5) showed higher WUE_t than the cultivars from Ethiopia (Tob-2, DZ and Boohai).

Table 4.2 Pre-anthesis (ET_{ba}), post-anthesis (ET_{pa}) and ratio of pre- to post-anthesis water use (ET_{ba}:ET_{pa}) of 5 durum wheat cultivars grown under field (1990/91) and greenhouse (1991/92).

Variety	stresss	Field (l/m^2)			Greenhouse (g/plant)		
		ET_{ba}	ET_{pa}	ET_{ba}:ET_{pa}	ET_{ba}	ET_{pa}	ET_{ba}:ET_{pa}
Tob-2	1	170	370	0.46	758	1696	0.44
	2	300	110	2.73	1448	478	3.03
	3	300	180	0.60	1448	917	1.58
	4	300	340	0.88	1448	1428	1.04
DZ	1	170	380	0.45	759	1600	0.47
	2	300	120	2.50	1448	563	2.57
	3	300	190	1.58	1448	895	1.62
	4	300	350	0.86	1448	1574	0.92
Boohai	1	170	350	0.49	742	1607	0.46
	2	320	130	2.46	1388	526	2.64
	3	320	190	1.68	1388	826	1.68
	4	320	310	1.03	1388	1464	0.95
Omrabi-5	1	-	-	-	788	1806	0.44
	2	-	-	-	1404	526	2.67
	3	-	-	-	1404	903	1.55
	4	-	-	-	1404	1659	0.85
Po	1	-	-	-	1490	1088	1.34
	2	-	-	-	1988	532	3.74
	3	-	-	-	1988	523	3.80
	4	-	-	-	1988	1073	1.85
Mean		273	253	1.37	1378	1084	1.68
LSD (P<0.5)		11.54	99.84	0.36	54.4	176.5	0.41
CV (%)		2.12	19.85	13.1	2.9	11.8	17.49

However, the differences were not significant.

Significant differences in WUE$_s$ among cultivars and moisture treatments were recorded both under field and greenhouse conditions. ICARDA cultivars had a higherWUE$_s$ than

Table 4.3 Water use efficiency (g kg^{-1}) for total dry matter (WUE_t), above ground dry matter (WUE_s) and grain (WUE_g) of 5 durum wheat cultivars grown under field (1990/91) and greenhouse (1991/92)

Variety	Stress	Field		Greenhouse		
		WUE_s	WUE_g	WUE_t	WUE_s	WUE_g
Tob-2	1	2.73	1.17	5.18	4.55	1.97
	2	3.54	1.04	5.03	4.01	1.23
	3	2.78	1.52	5.28	4.36	1.55
	4	3.79	1.67	5.17	4.43	1.98
DZ	1	3.70	1.10	5.85	5.04	1.93
	2	4.29	1.12	4.78	3.84	1.11
	3	4.21	1.57	5.18	4.15	1.40
	4	3.76	1.45	5.01	4.15	1.61
Boohai	1	3.60	0.95	5.28	4.70	2.02
	2	5.05	0.92	4.74	3.78	1.12
	3	5.20	1.85	6.27	4.72	1.97
	4	4.34	1.72	5.68	4.48	1.97
Omrabi-5	1	-	-	6.19	5.02	1.85
	2	-	-	5.80	4.39	1.33
	3	-	-	6.27	4.64	2.09
	4	-	-	5.57	4.50	1.85
Po	1	-	-	6.57	5.54	1.73
	2	-	-	4.37	3.85	0.83
	3	-	-	6.30	4.98	0.97
	4	-	-	5.95	4.86	1.92
Mean		3.91	1.34	5.53	4.50	1.60
LSD ($P<0.5$)		0.92	0.31	0.62	0.34	0.27
CV (%)		11.73	11.68	8.07	5.54	12.06

those from Ethiopia. Among the cultivars, pooled over moisture treatments, the drought-susceptible cultivar (Po) had the highest value (4.81) followed by the drought-resistant cultivar, Omrabi-5, (4.64) and Boohai (4.42). Among the moisture treatments, early stress resulted in the highest value (4.97) followed by terminal stress (4.64) and control (4.48).

Difference in WUE_g between resistant and susceptible cultivars were significant, ranging from 1.78 (Omrabi-5) to 1.28 (Po). Average values pooled over varieties show that under terminal stress varieties used water more efficiently than under other stress conditions under the field condition. In the greenhouse, early stress was the best followed by the control and terminal stress. The ranking of cultivars in their WUE_g coincided with the level of drought resistance. The cultivar x moisture stress interaction was also statistically significant. Boohai had the highest WUE_g under early stress condition, whereas Omrabi-5 had the highest values under mid-season and terminal stress conditions.

Transpiration efficiency (TE)

Average values of transpiration efficiency over cultivar and moisture treatments were 10.61 for TE_t, 8.65 for TE_s and 3.07 for TE_g (Table 4.4). TE_t pooled over cultivars ranged from 11.77 (Tob-2) to 9.46 (DZ) and over moisture treatments from 11.12 (early stress) to 10.32 (stress during anthesis). However, the differences in both situations were not significant.

Average TE_s for cultivars ranged from 9.87 (Tob-2) to 7.81 (DZ) and moisture treatments ranged from 9.56 (early stress) to 8.29 (stress during anthesis). The difference in both situations was significant. The drought-susceptible cultivar (Po) used water more efficiently to produce above ground dry matter than the drought-resistant cultivars. TE_s positively correlated with RGR (not shown) whereas a negative relationship was observed with ET_{ba}:ET_{pa}, $^{13}\delta$ and shoot:root ratio (Table 4.7).

The differences in TE_g means over varieties and moisture treatments were statistically significant (Table 4.4). Average values for varieties ranged from 1.78 (Omrabi-5, drought-resistant) to 1.28 (Po, drought-susceptible). The ranking agreed with the drought-resistance level used by plant breeders and farmers in the region.

Harvest index (HI)

A significant variation in HI was exhibited both among cultivars and moisture stress treatments, ranging from 0.19 to 0.45 (Table 4.5). Among the varieties, pooled over moisture treatments, the lowest HI was recorded for the drought-susceptible variety (Po) and the highest HI was recorded for drought-resistant cultivars (Boohai, Omrabi-5 and Tob-2). Among moisture stress treatments, pooled over varieties, the control treatment (4) had the highest HI followed by early stress (1) and terminal stress (3). Stress at flowering (2) caused the lowest HI for all cultivars with the exception of Po. HI negatively correlated with ET_{ba}:ET_{pa} (Fig. 4.2b) and $^{13}\delta$ (Fig. 4.3b). In contrast HI positively correlated with WUEg, TEg and grain yield (Table 4.8).

Table 4.4 Transpiration efficiency (g kg^{-1}) for total dry matter (TE_t), above ground dry matter (TE_s) and grain (TE_g) of 5 durum wheat cultivars grown at different moisture regimes in the greenhouse

Variety	stress	TE_t	TE_s	TE_g
Tob-2	1	9.64	8.47	3.67
	2	10.73	8.55	2.62
	3	14.00	11.56	4.11
	4	12.69	10.88	4.87
DZ	1	11.57	9.96	3.82
	2	9.72	7.81	2.26
	3	8.34	6.69	2.25
	4	8.19	6.78	2.63
Boohai	1	10.23	9.09	3.91
	2	10.25	8.15	2.42
	3	10.51	7.91	3.33
	4	9.43	7.59	3.34
Omrabi-5	1	11.01	8.93	3.28
	2	12.34	9.34	2.82
	3	10.21	7.56	3.41
	4	9.26	7.28	2.99
Po	1	13.48	11.34	3.54
	2	8.58	7.56	1.63
	3	11.31	8.94	1.73
	4	10.56	8.64	3.40
Mean		10.61	8.65	3.07
LSD (P<0.5)		0.99	0.60	0.75
CV%		9.36	6.89	17.68

Carbon isotope fractionation ($^{13}\delta$)

Carbon isotope fractionation ($^{13}\delta$) of the grain varied significantly among cultivars and moisture treatments (Table 4.6). It ranged from -23.79 (Po, early stress) to -25.69 $^{0}/_{00}$(Tob-2, control). The ranking of the average value over varieties corresponded with TE_g. A significant positive relationship was observed between $^{13}\delta$ and ET_{ba}:ET_{pa} (Fig. 4.3a), whereas the relationship with WUEg was negative (Fig. 4.2d).

Table 4.5 Harvest Index (HI) of 5 durum wheat cultivars grown at different moisture regimes in the greenhouse (1991/92)

Variety	stress				
	early stress	mid stress	late stress	control	Mean
Tob-2	0.432	0.306	0.355	0.448	0.385
DZ	0.384	0.290	0.337	0.389	0.350
Boohai	0.430	0.297	0.417	0.439	0.396
Omrabi-5	0.368	0.302	0.451	0.410	0.383
Po	0.312	0.216	0.194	0.391	0.278
Mean	0.385	0.285	0.356	0.415	0.358

LSD ($P < 0.05$) = 0.057
CV% = 11.58

Water potential

Mid-day total leaf water potential values of stressed and well-watered (control) plants at different time of moisture stress is given in Table 4.7. The values ranged from -18.9 to -24.8 bars under stress conditions and from -7.6 to -19.8 bars under well watered conditions. However, the values obtained did not show any trend or explain differences in levels of drought resistance.

Discussion

In the semi-arid and arid tropics, where water supply is often limiting due to low and erratic rainfall, agronomic practices should aim at increasing water use efficiency. Several agronomic practices have been proposed to reduce soil evaporation, thus increasing water use efficiency (Fischer and Turner, 1978; Tanner and Sinclair, 1983; Cooper *et al.*, 1987; Gregory, 1989). However, transpiration efficiency may not be improved since it is a measure of crop/cultivar performance (Tanner and Sinclair, 1983). Since the major environmental variable affecting TE is air saturation deficit, data from pot experiments may be used as a valid determination of TE (Van Keulen, 1975; Fischer and Turner, 1978; Tanner and Sinclair, 1983).

Table 4.6 Carbon isotope fractionation of the grain ($^{13}\delta$, $^{0}/_{00}$) of 5 durum wheat cultivars grown at different moisture regimes in the greenhouse (1991/92)

Variety	stress				
	early stress	mid stress	late stress	control	Mean
Tob-2	-25.30	-24.18	-24.75	-25.69	-24.98
DZ	-24.99	-24.01	-25.06	-25.32	-24.85
Boohai	-24.62	-24.27	-24.47	-25.05	-24.60
Omrabi-5	-24.35	-24.46	-24.23	-25.16	-24.55
Po	-23.89	-23.79	-24.20	-24.17	-24.01
Mean	-24.63	-24.14	-24.54	-25.08	-24.60

LSD ($P < 0.05$) = 0.409
CV% = 1.21

Water use efficiency can be defined on the basis of either total evapotranspiration (ET) (Equations 4.3 - 4.5) or transpiration (T) only (Equations 4.6 - 4.8). The difference is important since water loss through soil evaporation may be substantial (Fischer and Turner, 1978, Cooper *et al.*, 1987). The magnitude of evaporation depends on crop cover, moisture content of the soil, its texture, etc. Genetic manipulation that reaches full ground cover quickly (early vigour) could minimize soil evaporation and crops may extract as much water as possible (Fisher and Turner, 1978; Tanner and Sinclair, 1983; Ludlow and Muchow, 1988). However, there are high risks associated with this strategy in environments with an erratic rainfall distribution because the crop will exhaust the available soil water before maturity. Particularly in areas where terminal moisture stress is the predominant constraint, a more conservative strategy is preferred to complete grain filling.

The amount of water (ET) used per plant in the field experiment was different from that in the greenhouse. This may be because of the differences in evaporation as a result of the different exposures and energy balances of the two environments. However, the ratio of pre- and post-anthesis water use (ET_{ba}:ET_{pa}) was almost equal in both conditions.

Water use efficiency should be explicitly defined for its proper application in plant breeding. Although cereal straw is an important animal feed in the semi-arid tropics, grains are usually the sole marketable commodity for the farmers (Gregory, 1989). Surprisingly, the drought-susceptible cultivar (Po) was the best in WUE_s, whereas the drought-resistant

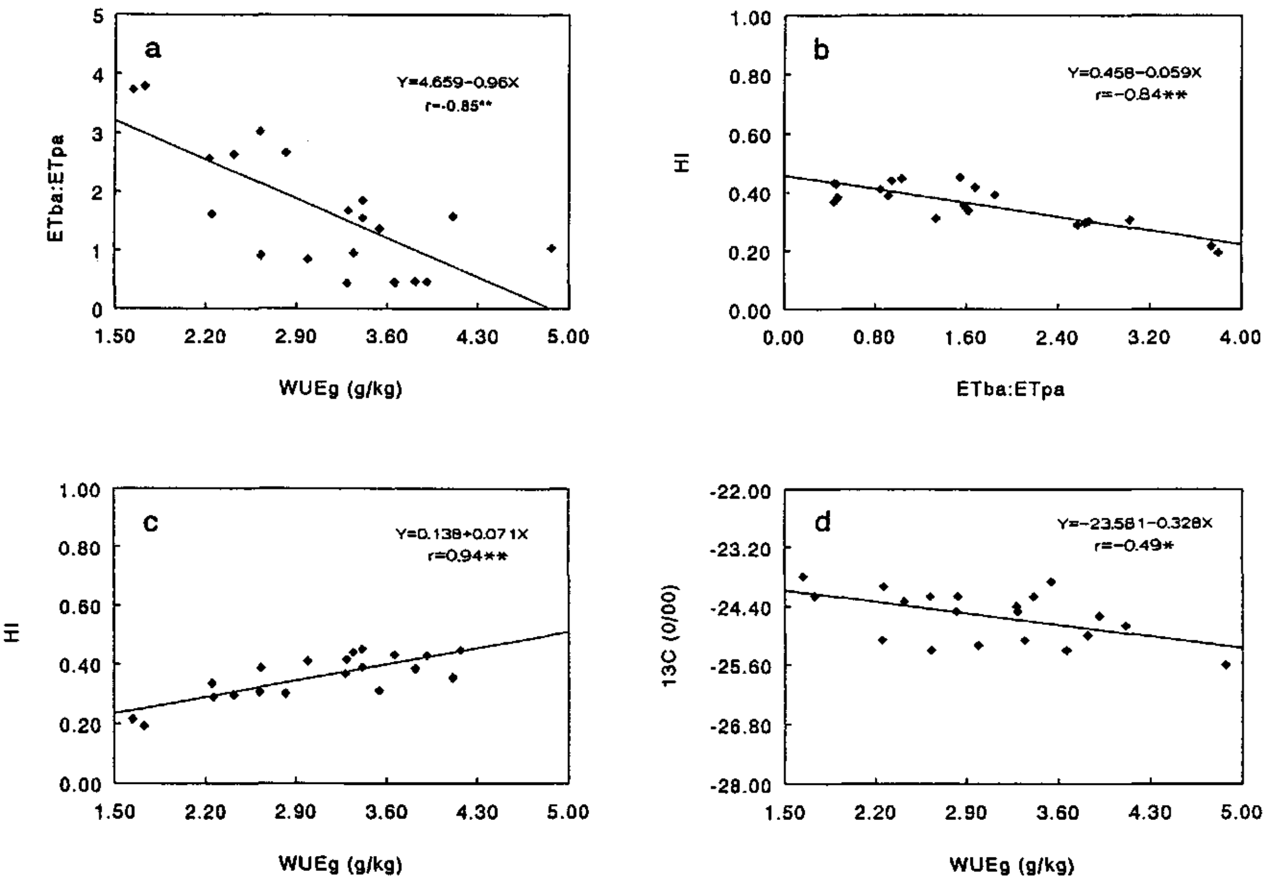


Fig. 4.2 Relationship between a) pre-anthesis:post-anthesis water use (ET_{ba}:ET_{pa}) and water use efficiency based on grain (WUE_g) b) pre-anthesis:post-anthesis water use (ET_{ba}:ET_{pa}) and harvest index (HI) c) water use efficiency based on grain (WUE_g) and harvest index d) water use efficiency based on grain (WUE_g) and grain carbon isotope fraction (^{13}C).

Table 4.7 Mid-day leaf water potential (-bars) of 5 durum wheat cultivars grown under different moisture regimes in the greenhouse.

Variety	Leaf Water Potential				
	early-season		mid-season		10 days after the start of terminal stress
	mid	end	mid	end	
		Stressed			
Tob-2	27.1	32.8	21.3	27.0	16.9
DZ	21.9	24.2	22.4	24.3	16.3
Boohai	27.3	27.6	19.4	28.3	14.4
Omrabi-5	27.2	31.9	24.2	29.5	15.1
Po	20.7	28.3	28.9	31.9	31.9
Mean	24.8	29.0	23.2	28.2	18.9
		Control			
Tob-2	13.1	6.9	14.3	13.5	19.8
DZ	12.2	7.4	13.8	14.3	18.8
Boohai	11.4	9.6	15.7	16.2	16.9
Omrabi-5	12.6	8.1	18.3	19.3	17.8
Po	12.4	6.0	18.5	20.5	24.1
Mean	12.3	7.6	16.1	16.8	19.5
Mean	15.5	12.9	19.8	20.1	19.5
SD	1.1	1.3	1.8	1.8	2.0

cultivar (Omrabi-5) was best in WUE_g. Efficient water use may be defined as the improvement of economic return for the investment of water (Tanner and Sinclair, 1983). It is therefore logical and sensible to breeders and farmers to consider WUE based on grain and/or above ground dry matter and harvest index together.

The significant negative relationships between $ET_{ba}:ET_{pa}$ and WUE_g (Fig. 4.2a) obtained in this experiment suggest that grain yield was strongly influenced by the post-anthesis water supply confirming the results of Fischer and Turner (1978). The negative correlation

Table 4.8 Correlation coefficients among water use efficiency for total dry matter (WUE_t), above ground dry matter (WUE_s) and grain (WUE_g), transpiration efficiency for total dry matter (TE_t), above ground dry matter (TE_s) and grain (TE_g), ratio of pre- to post-anthesis water use (ET_{ba}:ET_{pa}), carbon isotope fractionation of the grain ($^{13}\delta$), harvest index (HI), grain yield (GY) and above ground dry matter (AGDM) (11)

	WUE_t	WUE_s	WUE_g	TE_t	TE_s	TE_g	ET_{ba}:ET_{pa}	$^{13}\delta$	HI	GY
WUE_s	0.88^{**}									
WUE_g	0.48^{*}	0.55^{*}								
TE_t	0.43	0.49^{*}	0.13							
TE_s	0.27	0.49^{*}	0.16	0.95^{**}						
TE_g	0.27	0.44	0.82^{**}	0.55^{*}	0.62^{*}					
ET_{ba}:ET_{pa}	-0.24	-0.42	-0.87^{**}	-0.02	-0.13	-0.73^{**}				
$^{13}\delta$	0.14	0.04	-0.49^{*}	0.11	0.03	-0.50^{*}	0.65^{*}			
HI	0.21	0.23	0.94^{**}	-0.04	-0.02	0.77^{**}	-0.84^{**}	-0.63^{*}		
GY	0.41	0.52^{*}	0.91^{**}	0.03	0.08	0.71^{**}	-0.82^{**}	-0.56^{*}	0.85^{**}	
AGDM	0.57^{*}	0.74^{**}	0.58^{*}	0.13	0.20	0.40	-0.50^{*}	-0.27	0.38	0.80^{**}

* $P < 0.05$ and ** $P < 0.01$

between HI and ET_{ba}:ET_{pa} (Fig. 4.2b) shows that HI is a function of how much of the total water supply is available to the crop after anthesis, and thus suggesting that the grain yield is strongly dependent on biomass accumulation after anthesis in water limited environments. This agrees with Passioura (1977), Fisher and Turner (1978), Tanner and Sinclair (1983), Ludlow and Muchow (1988). Genetic variation in HI under adequate water supply and water-limited conditions will offer a good opportunity for increasing WUE_g and grain yield. In agreement with other findings (Fischer and Turner, 1978; Siddique *et al.*, 1991), the results led us to conclude that ET_{ba}:ET_{pa} could be a good selection criterion to screen cultivars for increased grain yield potential.

Substantial variation in $^{13}\delta$ among cultivars (Table 4.6), and its significant negative correlations with WUE_g (Fig. 4.2d), HI (Fig. 4.3b) and positive correlation with ET_{ba}:ET_{pa} (Fig. 4.3a) in the present study, suggest as in many other works (Farquhar *et al.*, 1982; Farquhar and Richard, 1984; Hubick *et al.*, 1986; Martin et al, 1988, Vos and Groenwold, 1989 and Condon *et al.*, 1987; 1990), that it may be possible to use it as a screening tool for improved water use efficiency and grain yield. The absence of a significant relationship between $^{13}\delta$ of the grain and the biological yield in the present study, may explain which plant organ should be used in the analysis that corresponds to the definition of yield in Equations 4.3 - 4.8.

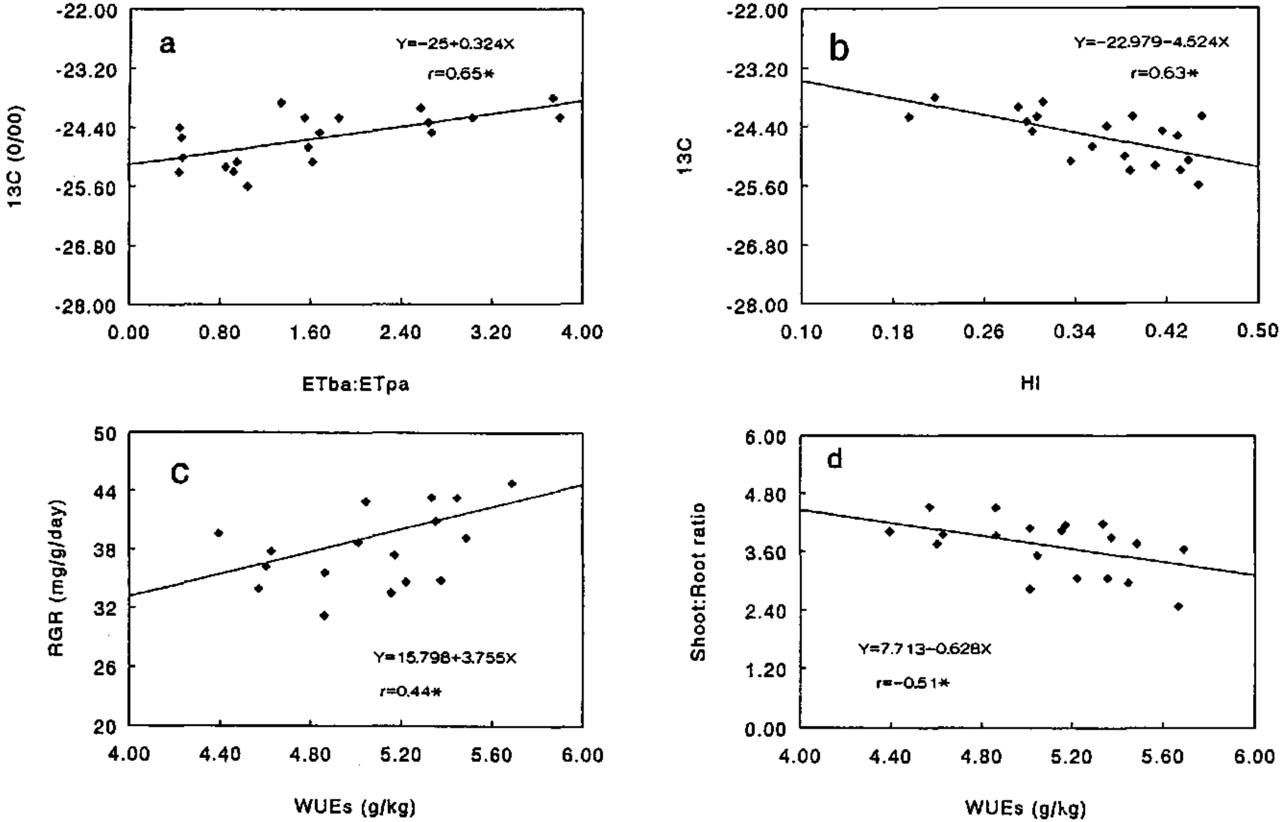


Fig. 4.3 Relationship between a) pre-anthesis:post-anthesis water use (ET_{ba}:ET_{pa}) and grain carbon isotope fraction (^{13}C) b) harvest index (HI) and grain carbon isotope fraction (^{13}C) c) above ground dry matter water use efficiency (WUE_s) and relative growth rate (RGR) d) above ground dry matter water use efficiency (WUE_s) and shoot:root ratio.

Genotypic variation in RGR among the five cultivars has been reported (Simane *et al.*, 1993^b) and its components have been proposed as a selection criteria under sub-optimal conditions (Lambers and Poorter, 1992). RGR and shoot:root ratio significantly correlated with WUE_s (Figs. 4.3c and 4.3d) confirming the earlier suggestions. However, both RGR and shoot:root ratio did not correlate with WUE_g, emphasizing the need for a clear definition of WUE.

Values of total leaf water potential between stressed and well watered treatments were easily measured. However, differences among cultivars were not consistent. Although total leaf water potential has been used as a selection criterion in dry environments (Blum, 1988; Siddique *et al.*, 1990), in agreement with other findings (Turner, 1981; Van Keulen, 1975) we conclude that total leaf water potential is not a useful criterion to select genotypes for increased water use efficiency.

This study has demonstrated that under water-limited environments, yield of durum wheat could be increased by improving the relative proportion of post-anthesis water use, WUE and HI. The genetic variation in ET_{ba}:ET_{pa}, $^{13}\delta$, RGR, shoot:root ratio, HI could be used as good selection criteria to screen genotypes for increased WUE or production in water-limited environments.

References

Blum, A., 1988. Plant breeding for stress environments. CRC Press, Florida. 223 pp.

Condon, A.G., Richards, R.A. and Farquhar, G.D., 1987. Carbon isotope discrimination is positively correlated with grain yield and dry matter production in field-grown wheat. Crop Sci., 27: 996-1001.

Condon, A.G., Farquhar, G.D. and Richards, R.A., 1990. Genotypic variation in carbon isotope discrimination and transpiration efficiency in wheat. Leaf gas exchange and whole plant studies. Aust. J. Plant Physiol., 17: 9-22.

Cooper, P.J.M., Gregory, P.J., Tully, D. and Harris, H.C., 1987. Improving water use efficiency of annual crops in the rainfed farming systems of West Asia and North Africa. Exp. Agric. 23, 113-158.

FAO, 1984. Crop water requirement. FAO Bull. No - 24, 15-30.

Farquhar, G.D., O'Leary, M.H. and Berry, J.A., 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol., 9: 121-137.

Farquhar, G.D. and Richards, R.A., 1984. Isotopic composition of plant carbon correlates with water use efficiency of wheat genotypes. Aust. J. Plant Physiol., 11: 539-552.

Fischer, R.A. and Turner, N.C., 1978. Plant productivity in the arid and semi-arid zones. Ann. Rev. Plant. Physiol., 29: 277-317.

Gregory, P.J., 1989. Concepts of water use efficiency. *In*: H.C. Harris, P.J.M. Cooper and M. Pala, M. (Eds.), Soil and crop management for improved water use efficiency in rainfed areas. ICARDA, Aleppo, Syria. pp. 9-20.

Hubick, K.T., Farquhar, G.D. and Shorter, R., 1986. Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germplasm. Aust. J. Plant Physiol., 13: 803-816.

Lambers, H. and Poorter, H., 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Advances in Ecological Research, 23: 187-261.

Ludlow, M.M and Muchow, R.C., 1988. Critical evaluation of the possibilities for modifying crops to high production per unit of precipitation. *In*: Bidinger, F.R. and Johansen, C. (Editors), Drought research priorities for the dryland tropics. ICRISAT, Patancheru, A.P. 502 324, India. pp. 179-211.

Martin, B. and Thorstenson, Y.R., 1988. Stable carbon isotope composition ($\delta^{13}C$), water use efficiency, and biomass productivity of *Lycopersicon esculentum, Lycopersicon pennelli*, and the F1 hybrid. Plant Physiol., 88: 213-217.

Passioura, J.B., 1977. Grain yield, harvest index and water use of wheat. J. Aust. Inst. Agric. Sci., 43: 117-120.

Richards, R.A., 1987. Physiology and the breeding of winter-grown cereals for dry areas. *In*: Srivastava, J.P., Porceddu, E., Acevedo, E. and Varma, S. (Editors), Drought tolerance in winter cereals. Cambridge University Press, UK. pp. 133-150.

Siddique, K.H.M., Tennant, D., Perry, M.W. and Belford, R.K., 1990. Water use and water use efficiency of old and modern wheat cultivars in a Mediterranean-type environment. Aust. J. Agric. Res. 41, 431-447.

Simane, B. Peacock, J.M. and Struik, P.C., 1993^b. Differences in developmental plasticity and growth rate among drought-resistant and -susceptible cultivars of durum wheat (*Triticum turgidum* L. var. *durum*). Plant and Soil, in press.

Simane, B., van Keulen, H., Stol, W. and Struik, P.C., 1993^a. Application of crop growth model (SUCROS-87) to assess the effect of moisture stress on yield potential of durum wheat in Ethiopia. Agricultural Systems, in press.

Tanner, C.B. and Sinclair, T.R., 1983. Efficient water use in crop production: research or re-search?. *In*: Taylor, H.M., Jordan, W.R. and Sinclair, T.R. (Editors), Limitations to efficient water use in crop production. ASA, CSSA, SSSA, 1-27.

Turner, N.C., 1981. Techniques and experimental approaches for the measurement of plant water status. Plant and Soil, 58: 339-366.

Van Keulen, H., 1975. Simulation of water use and herbage growth in arid regions. Simulation Monographs, Pudoc, Wageningen. 175 pp.

Vos, J. and Groenwold, J., 1989. Genetic differences in water-use efficiency, stomatal conductance and carbon isotope fractionation in potato. Potato Res., 32: 113-121.

Chapter 5

Differences in developmental plasticity and growth rate among drought-resistant and susceptible cultivars of durum wheat

B. Simane, J.M. Peacock and P.C. Struik
Plant and Soil (in press)

Abstract

Understanding how growth and development of durum wheat cultivars respond to drought could provide a basis to develop crop improvement programmes in drought-affected tropical and subtropical countries. A greenhouse experiment was conducted to study the responses of five durum wheat cultivars to moisture stress at different developmental phases. Phenology, total dry matter (TDM), relative growth rate (RGR), leaf area ratio (LAR), net assimilation rate (NAR), leaf weight ratio (LWR), specific leaf area (SLA) and shoot:root ratio were compared.

Pre-anthesis moisture stress delayed phenological development, whereas post-anthesis moisture stress accelerated it. TDM accumulation rate was different between drought-resistant and susceptible cultivars. RGR and its components changed with age and moisture availability. Drought-resistant cultivars had a high RGR in favourable periods of the growing season and a low RGR during moisture stress. In contrast, the drought-susceptible cultivar (Po) showed an opposite trend. LAR explained the differences in RGR ($r=0.788$) best, whereas the relationship between NAR and RGR was not significant. Even though both LWR and SLA were important factors determining the potential growth rate, LWR was of major importance to describe cultivar differences in LAR, and consequently in RGR. The drought-resistant cultivars Omrabi-5 and Boohai showed vigorous root development and/or a low shoot:root ratio. It is concluded that biomass allocation is the major factor explaining variation in RGR among the investigated durum wheat cultivars.

Key words: durum wheat, leaf area ratio, net assimilation rate, developmental plasticity, moisture stress, relative growth rate, shoot:root ratio

Introduction

Durum wheat (*Triticum turgidum* L. var. *durum*) is traditionally grown under rainfed conditions in marginal environments of the semi-arid tropics. In these regions, water limitation is the most important production constraint (Simane and Struik, 1993), although nutrient (N and P) shortages play an important role as well. Water limitation affects growth and phenology of wheat depending on its timing, duration and intensity. Phenological development may be accelerated or slowed down. This adaptive response may be the result of periodic changes in growth rate and has been referred to as developmental plasticity or ontogenetic flexibility (Van Andel and Jager, 1981).

Plants with a high relative growth rate (RGR) have the opportunity to acquire a larger share of the limiting resources like moisture than slow-growing ones (Poorter, 1989). Due to their low RGR slow-growing plants have low demands for resources and consequently are less likely to exhaust the limiting resources, thus saving for later growth (Chapin, 1980; Poorter and Lambers, 1986). Selection for low RGR *per se* in breeding programmes is complex; rather one of the components of RGR should be the target of selection (Chapin, 1980; Dijkstra and Lambers, 1989). It is still questionable which factors determine growth rate under dry conditions, and selection for growth parameters is far from being applied in plant breeding. Therefore, an analysis of the relative growth rate (RGR), and its components (net assimilation rate (NAR), leaf area ratio (LAR), leaf weight ratio (LWR) and specific leaf area (SLA)), can help to understand variation in growth and development (Lambers *et al.*, 1989). Root development and shoot:root ratio are also very important parameters to explain performance of crops under harsh environments (Passioura, 1977). For a number of species such growth analyses have been carried out (Dijkstra and Lambers, 1989; Poorter, 1989; Karimi and Siddique, 1991). However, information on the physiological differences among durum wheat cultivars differing in drought-resistance is scarce.

The objectives of this paper, therefore, are to examine the effect of moisture stress on growth and development of durum wheat cultivars and to identify the factors determining their RGR.

Materials and methods

Experimental design

A greenhouse experiment was conducted, at the International Centre for Agricultural Research in the Dry Areas (ICARDA) at Tel Hadya (36°10'N, 36°56'E; Syria) in 1991/92. The night/day temperature regime was 15/20°C. Three plants were grown in a 5 kg capacity pot. Plant density based on pot surface area and pot spacing was equivalent to 220 plants/m². A randomized complete block design with four replicates was used. Eight pots were used for each treatment. Measurements were made in additional pots that received all the required treatments up to measurement date.

Cultivars

Five durum wheat (*T. turgidum* L. var. *durum*) cultivars developed in Ethiopia and at ICARDA were used (Table 5.1), representing different levels of drought-resistance and phasic development under field conditions of Mediterranean regions*. The first three cultivars (Tob-2, DZ (900-4DZ) and Boohai) were bred in Ethiopia for different agro-ecological zones. Omrabi-5 is drought-resistant and grown extensively in Mediterranean regions, while Po was developed for high input areas and is drought-susceptible.

Moisture regime

Four moisture treatments: Stress induced a) early (at tillering), b) mid season (at flowering) or c) terminal (grain filling) and d) control (no stress) were applied (Table 5.2). Soil moisture status was determined gravimetrically by weighing each pot every other day. The

* Nachit, unpublished data (ICARDA); Simane and Demmissie, unpublished data (Ethiopia)

Table 5.1 Durum wheat genotypes used in the experiment and average duration of development stages in days after sowing (Growing degree days (GDD) after sowing are shown in parentheses).

Cultivar	SAT	DSI	DRC	DA	DM
Tob-2	Ethiopia	0.96	resistant to early drought	75 (1274)	120 (2220)
DZ	Ethiopia	0.91	moderately resistant	79 (1355)	130 (2417)
Boohai	Ethiopia	0.67	resistant to terminal stress	75 (1274)	121 (2241)
Omrabi-5	ICARDA	0.51	resistant	77 (1314)	128 (2379)
Po	ICARDA	2.06	susceptible	92 (1664)	135 (2524)

SAT - source and test place under field conditions
DSI - drought susceptibility index as described by Fischer and Maurer (1978)
DRC - drought resistance classification by breeders
DA - days to anthesis
DM - days to maturity

lower and upper limits of soil water were 10 and 20% of the available soil water content respectively for stressed treatments and 70 and 100% for the control. Whenever the soil haddried out beyond the limit, water was added to restore the soil moisture content back to the predetermined level.

Sampling

Sampling was carried out nine times, at the beginning, middle and end of each moisture treatment. At each sampling, plants were separated into roots, stems (with sheaths), green leaf blades, dead leaf blades and heads (spikes) when appropriate. Weights were determined after drying each sample at 75 °C for 48 hours. The green leaf area of individual plants was measured using a LI-3100 (LI-COR, Lincoln, Nebraska, USA) leaf area meter.

Growth indices

Because of the differences in developmental pattern and maturity among the cultivars used (Table 5.1), a regression technique, logistic growth curve, was applied to calculate dry-matter accumulation at uniform time intervals.

Table 5.2 Soil moisture regimes applied during the experiment

Treatment	Time of stress	Range of ASWC (lower - upper)
1) Early stress	at tillering for 15 days	10 - 20%
2) Mid-season stress	at flowering for 15 days	10 - 20%
3) Terminal stress	at grain filling till harvest	10 - 20%
4) Control	no stress	70 - 100%

ASWC - Available Soil Water Content

$$DM = A + C/(1+EXP(-B*(X-M))) \quad (5.1)$$

where DM is dry matter in g, A lower asymptote, M point of inflection, B slope parameter and C upper asymptote. The percentages of variances (R^2) accounted for by the fitted curves were greater than 97 ($P< 0.001$) for all cultivars and treatments. Relative growth rate and its components were calculated using the following equations (Watson, 1952; Hunt, 1982):

$$RGR = (1/DM) * (dDM/dT) \quad (5.2)$$

where RGR is the relative growth rate (mg g^{-1} day^{-1}), dDM is dry weight increment (mg) for the interval dT (days).

Leaf area ratio (LAR in m^2 kg^{-1}) was calculated as the green leaf area (LA in m^2) divided by total dry matter (DM in kg):

$$LAR = LA/DM \quad (5.3)$$

Net assimilation rate, NAR (g m^{-2} day^{-1}), was calculated as:

$$NAR = (1/LA) * (dDM/dT) \quad (5.4)$$

Leaf weight ratio, LWR, (g g^{-1}) was calculated as the green leaf weight, LW (g) divided by total dry matter (DM in g):

$$LWR = LW/DM \tag{5.5}$$

Specific leaf area ($m^2\ kg^{-1}$) was computed as green leaf area (LA in m^2) divided by green leaf weight (LW in kg):

$$SLA = LA/LW \tag{5.6}$$

Relative growth rate can also be calculated as the product of LAR and NAR:

$$RGR = LAR * NAR \tag{5.7}$$

Similarly, LAR can also be calculated as the product of LWR and SLA:

$$LAR = LWR * SLA \tag{5.8}$$

Results

Phenology

Timing of moisture stress affected the duration of various development stages differently (Table 5.3). Early season stress delayed time of anthesis and physiological maturity. Mid and terminal moisture stresses did not affect the time to anthesis but shortened the grain filling period by 10 and 11 days, respectively. The developmental retardation was more marked in the tillers than in the main stem (data not shown). Drought- resistant cultivars reached anthesis and physiological maturity earlier than the susceptible one, but had a longer grain-filling period. The three Ethiopian cultivars reached anthesis 5 days earlier than Omrabi-5, the ICARDA cultivar.

Total dry matter accumulation (TDM)

Differences in dry matter accumulation rate were observed between drought-resistant and susceptible cultivars and among moisture treatments (Fig. 5.1). Resistant cultivars were characterized by fast growth during early season and a lower rate in dry-matter accumulation later in the season. In contrast, the drought-susceptible cultivar (Po) accumulated dry-matter more slowly in the early growth stages (till the 4-tiller stage) but consistently continued accumulation in the later stages. Regardless of its timing, moisture stress resulted in low dry-matter accumulation compared to the control. In terms of total dry -matter gain, mid-season stress caused greater reduction than early and terminal stresses.

Table 5.3 The effect of different times of moisture stress on days to anthesis and physiological maturity in main stems.

Stress	Days from emergence to		Days from anthesis to physiol. maturity
	Anthesis	Physiol. maturity	
early	81	131	50
mid-season	78	116	38
terminal	78	115	37
control	79	127	48
LSD ($P<0.05$)	4	5	6

Relative growth rate (RGR)

Relative growth rate declined throughout the season in all treatments (Fig. 5.2). Cultivars differed significantly in mean values of RGR during the entire growth cycle under all moisture treatments. Variation in RGR among cultivars with age and occurrence of moisture stress reflected their differences in drought-resistance. The drought-resistant cultivars (Omrabi-5 and Boohai) had a higher RGR during the first half of the season, when water was abundant and declined sharply during the second half of the season in contrast to that of the drought-susceptible cultivar. All water-limited treatments led to a lower RGR than that of the controls.

Values of LAR and NAR, the principal components of RGR, varied among cultivars and moisture treatments. As a result, the relationships between RGR and LAR (Fig. 5.3) and between RGR and NAR (data not shown) also differed for the various moisture treatments and cultivars. There was a significant positive correlation between RGR and LAR (the morphological component) ($r=0.788$) (Table 5.4). In contrast, the correlation between RGR and NAR was not significant ($r=-0.176$). This illustrates that dry-matter allocation among different organs is an important factor explaining the variation in RGR.

In all moisture treatments LAR was the main factor explaining the variation in RGR. The average value of LAR over different moisture treatments varied significantly among genotypes, ranging from 9.4 m^2 kg^{-1} for Ethiopian cultivars to 18.1 m^2 kg^{-1} for the drought-susceptible ICARDA cultivar (Fig. 5.4). A significant difference was also observed among moisture treatments ranging from 9.1 m^2 kg^{-1} (early stress) to 15.1 m^2 kg^{-1} (control).

Leaf area ratio is determined partly by biomass allocation (LWR) and partly by leaf morphology (SLA). Both LWR and SLA showed a significant positive correlation with

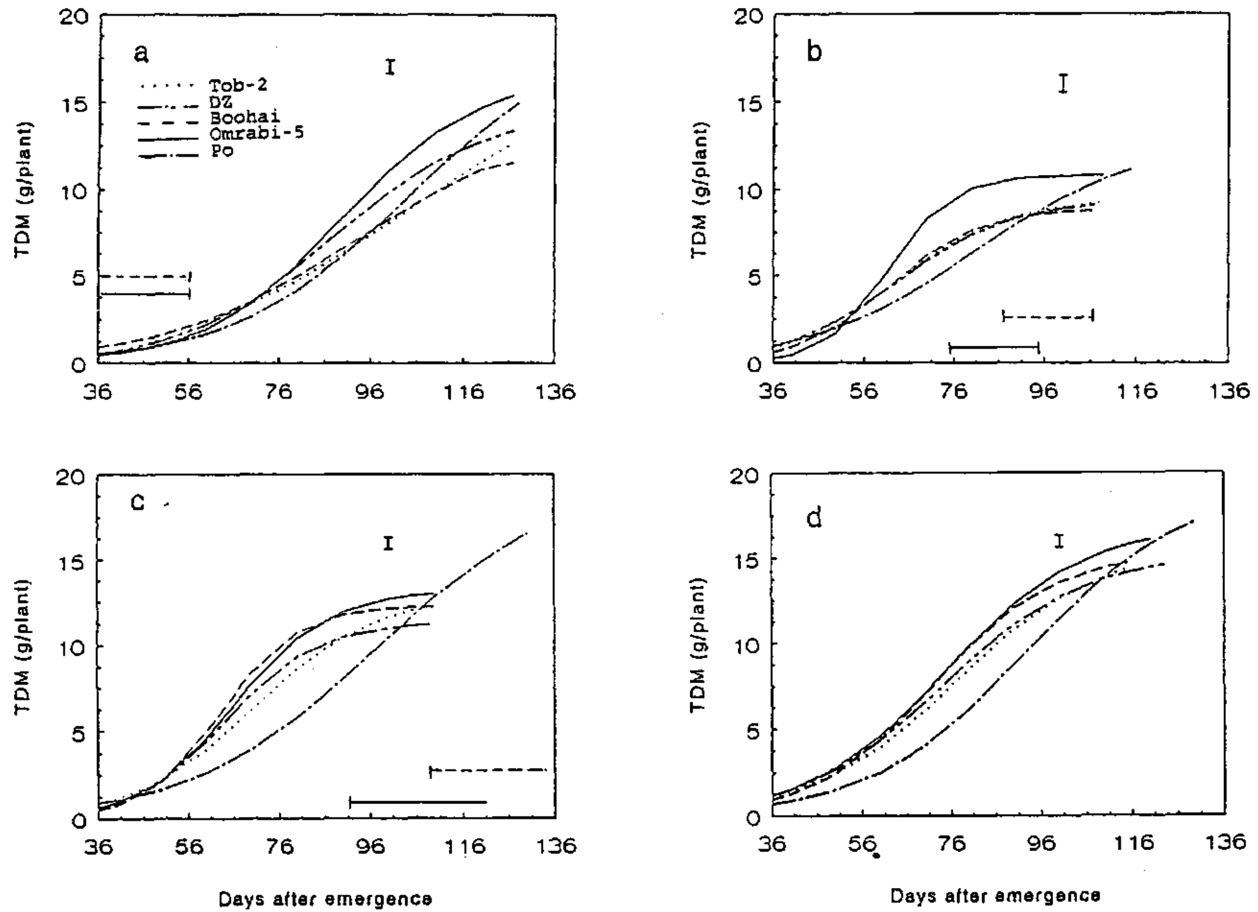


Fig. 5.1 Effect of moisture stress on total dry-matter accumulation (TDM) of durum wheat genotypes from tillering to physiological maturity. a) early-season stress, b) mid-season stress, c) late-season (terminal) stress and d) control (no stress). Solid bars indicate time of moisture stress for the first four genotypes and broken bars for Po. Vertical bars indicate LSD (0.05) values.

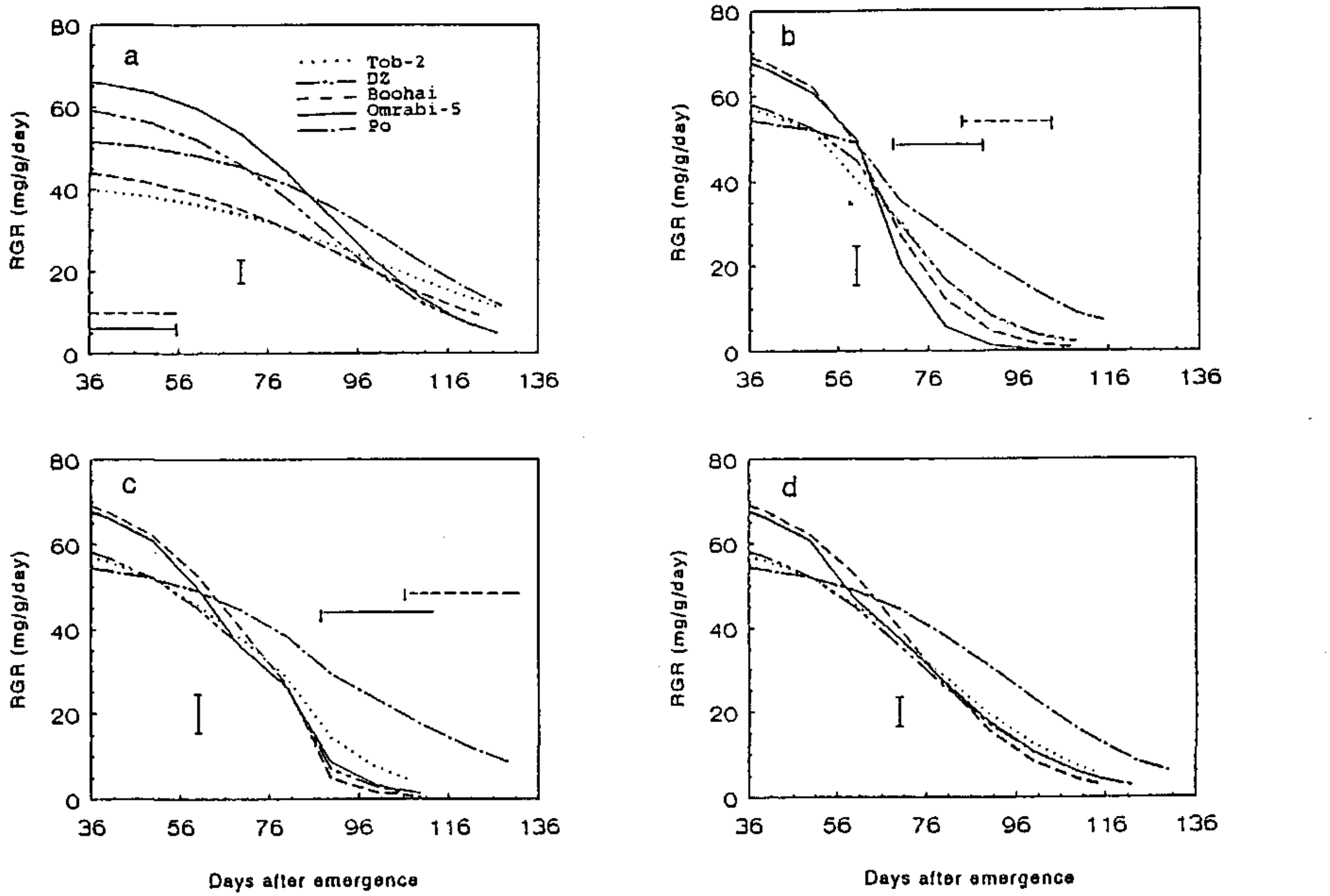


Fig. 5.2 Effect of moisture stress on relative growth rate (RGR) of durum wheat genotypes from tillering to physiological maturity. a) early-season stress, b) mid-season stress, c) late- season (terminal) stress and d) control (no stress). Solid bars indicate the time of moisture stress for the first four genotypes and broken bars for Po. Vertical bars indicate LSD (0.05) values.

LAR and consequently with RGR (Table 5.4). Comparing the two, LWR was the factor that correlated best with LAR (r=0.727) and most likely the predominant factor explaining the variations in LAR and RGR (Table 5.4).

Irrespective of moisture treatment, LWR of the susceptible cultivars was significantly higher than that of the drought-resistant one (Fig. 5.5).

Root development

The proportion of biomass allocated to the root under moisture stress conditions was higher than in the control, except under early moisture stress. Differences among cultivars in root growth were observed in all moisture treatments (Fig. 5.6). Under late stress conditions, drought-resistant and susceptible cultivars behaved differently. Omrabi-5 had prolific root growth in all treatments except in early moisture stress conditions. The cv. Po showed poor root development in all conditions.

Shoot:root ratio was closely associated with drought-resistance (Fig. 5.7). Regardless of the time of moisture stress, drought-resistant cultivars had lower shoot:root ratios than the drought-susceptible cultivar.

Discussion

Timing, intensity and duration of moisture stress in dryland environments vary. Very different developmental processes occur during the various stages, so that apart from anything else, durations of stages can hardly be expected to vary in the same way for the same stimulus. Therefore, traits which are appropriate for one environment may be inappropriate for another.

The results of the current experiment show that phenological development is affected differently by different timing of moisture stress. Pre-anthesis moisture stress delayed development, whereas moisture stress during grain filling hastened development, in agreement with the result of Angus and Moncur (1977). Different mechanisms have been suggested to explain this phenomenon. The delayed development during pre-anthesis moisture stress may be associated with reduced leaf expansion and/or increased assimilate partitioning to the roots. During terminal stress, increased leaf temperature may speed up development analogous to ambient temperature (Angus and Moncur, 1977; Donatelli *et al.*, 1992). The importance of this kind of developmental plasticity in crop improvement, therefore, could be seen in two different ways. Late flowering under early stress conditions has the advantage of delayed differentiation which subsequently enables plants to have a higher number of grains per grain mass (Blum *et al.*, 1990), provided there is enough moisture late in the season. However, this condition cannot be met in many semi-arid

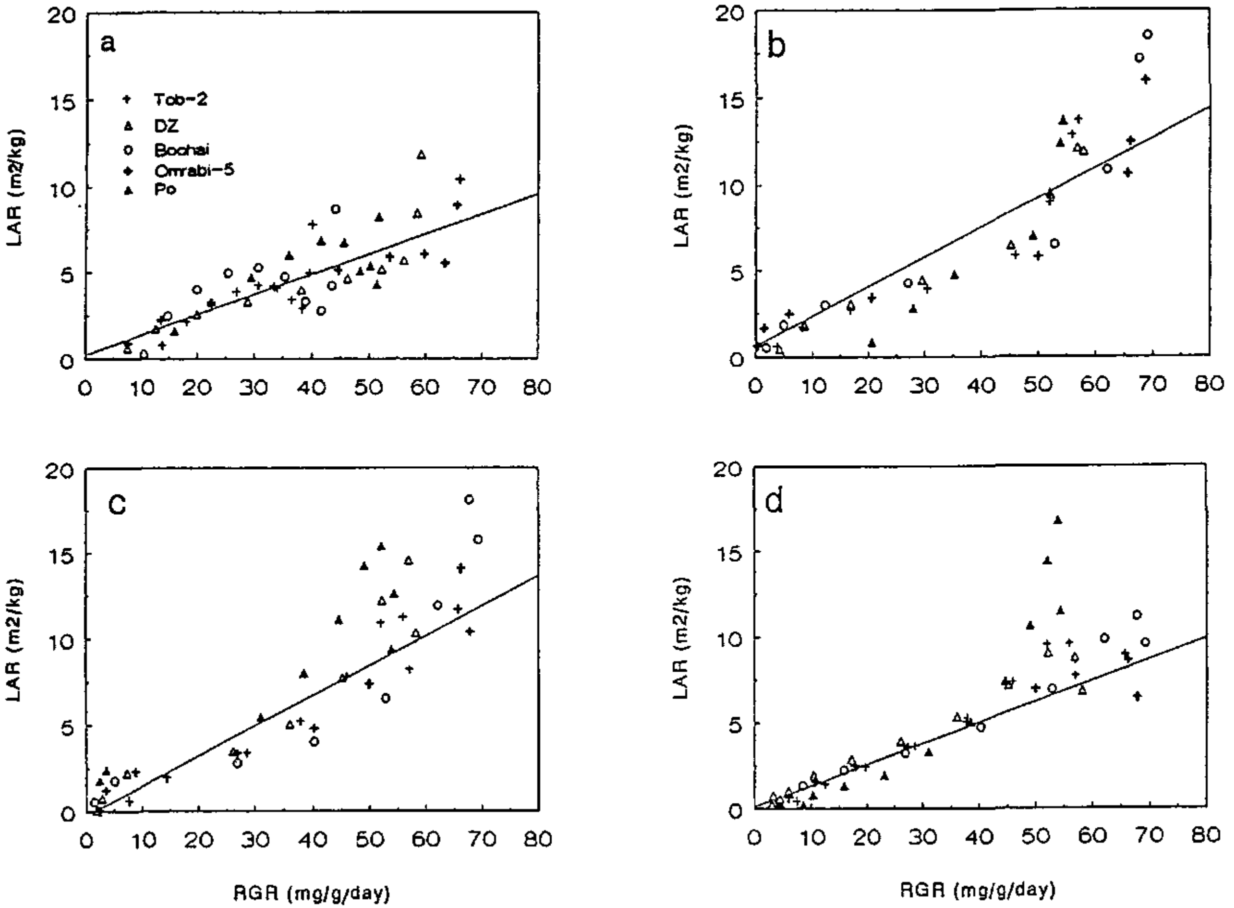


Fig. 5.3 The relationship between relative growth rate (RGR) and leaf area ratio (LAR) under different timing of moisture stress for five durum wheat genotypes from tillering to physiological maturity. a) early-season stress, b) mid-season stress, c) late- season (terminal) stress and d) control (no stress).

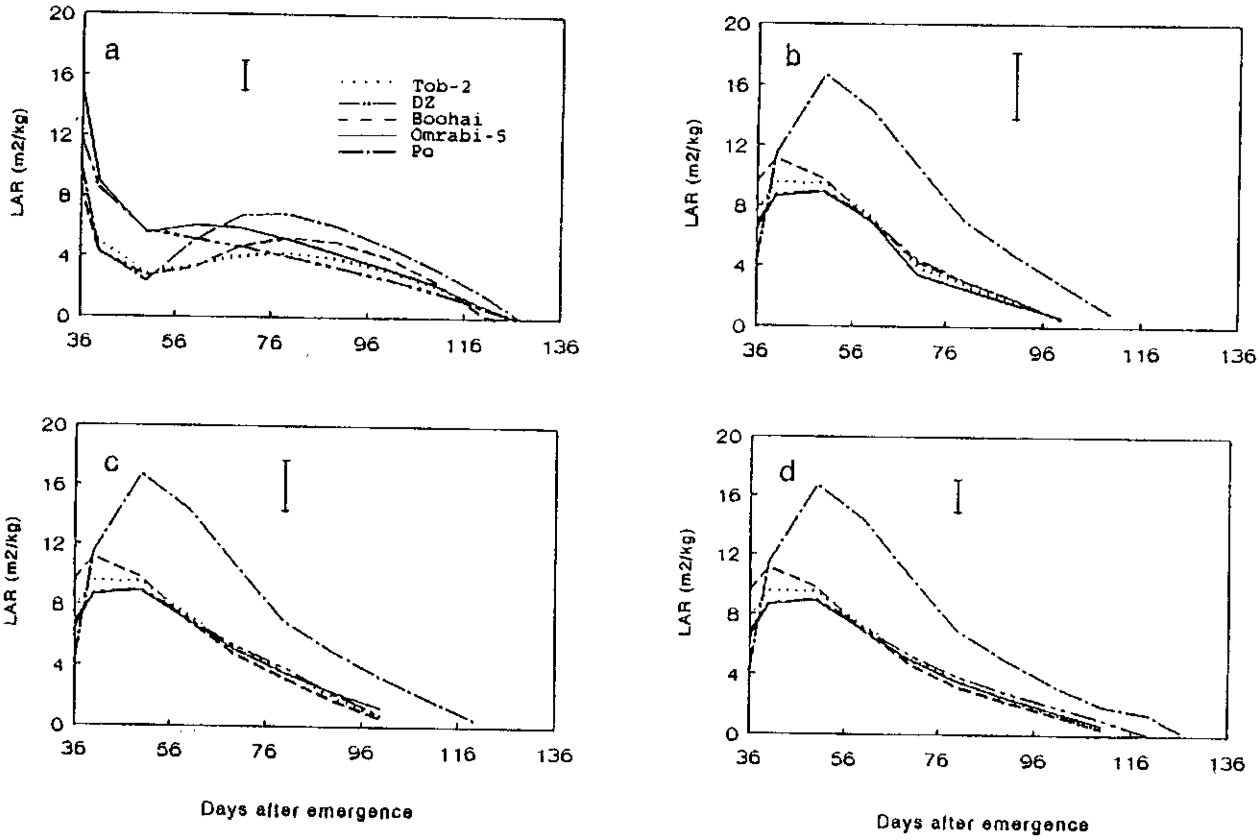


Fig. 5.4 Effect of moisture stress on leaf area ratio (LAR) of durum wheat genotypes from tillering to physiological maturity. a) early-season stress, b) mid-season stress, c) terminal stress and d) control (no stress). Vertical bars indicate LSD (0.05) values.

Table 5.4 Pooled[1] correlation among RGR and component characteristics of five durum wheat genotypes grown under different moisture treatments at ICARDA.

	LA	LW	LAR	NAR	SLA	LWR
LW	0.945**					
LAR	-0.033	0.100				
NAR	-0.233	-0.189	-0.540**			
SLA	-0.480**	-0.537**	0.425*	-0.036		
LWR	0.281	0.311	0.727**	-0.493**	0.082	
RGR	0.223	-0.274	0.788**	-0.176	0.558**	0.561**

* $P < 0.05$ and ** $P < 0.01$

[1] - values averaged over cultivars and moisture stresses

environments (Simane and Struik, 1993). In contrast, cultivars that mature early may escape terminal moisture stress (Fischer and Maurer, 1978).

Different trends in RGR in relation to moisture treatments and cultivars were observed, confirming earlier findings (Van Andel and Jager, 1981). Moisture stress, irrespective of its time of occurrence, resulted in lower rates of dry-matter accumulation (Fig. 5.1). This was mainly due to accelerated leaf senescence and hence decreased photosynthetic area, which is an acclimation mechanism to survive moisture stress by reducing transpiration. The drought-resistant cultivars, compared with the susceptible one, were characterized by a higher RGR and DM accumulation during the early vegetative period and a rapid decline during the later stages. Under early stress all drought-resistant cultivars exhibited a high RGR except Tob-2. This may be due to the fact that Omrabi-5 and Boohai were selected in environments characterized by terminal stress whereas Tob-2 was selected in environments with intermittent drought-conditions. However, terminal moisture stress is of major concern, since it is the predominant problem in North Africa and the Middle East.

The advantage of cultivars with a low RGR in harsh environments is that they have low demands and therefore will not exhaust the limited soil water reserve (Chapin, 1980; Poorter, 1989). In environments with variable water availability, cultivars with high physiological and/or morphological plasticity with respect to RGR are better adapted (Poorter and Lambers, 1986). This kind of adaptation is of particular significance for crops grown in the semi-arid tropics.

Lambers and Dijkstra (1987) recommend that the components of RGR rather than RGR *per se*, are the target for selection under harsh environments. Therefore, it is important to

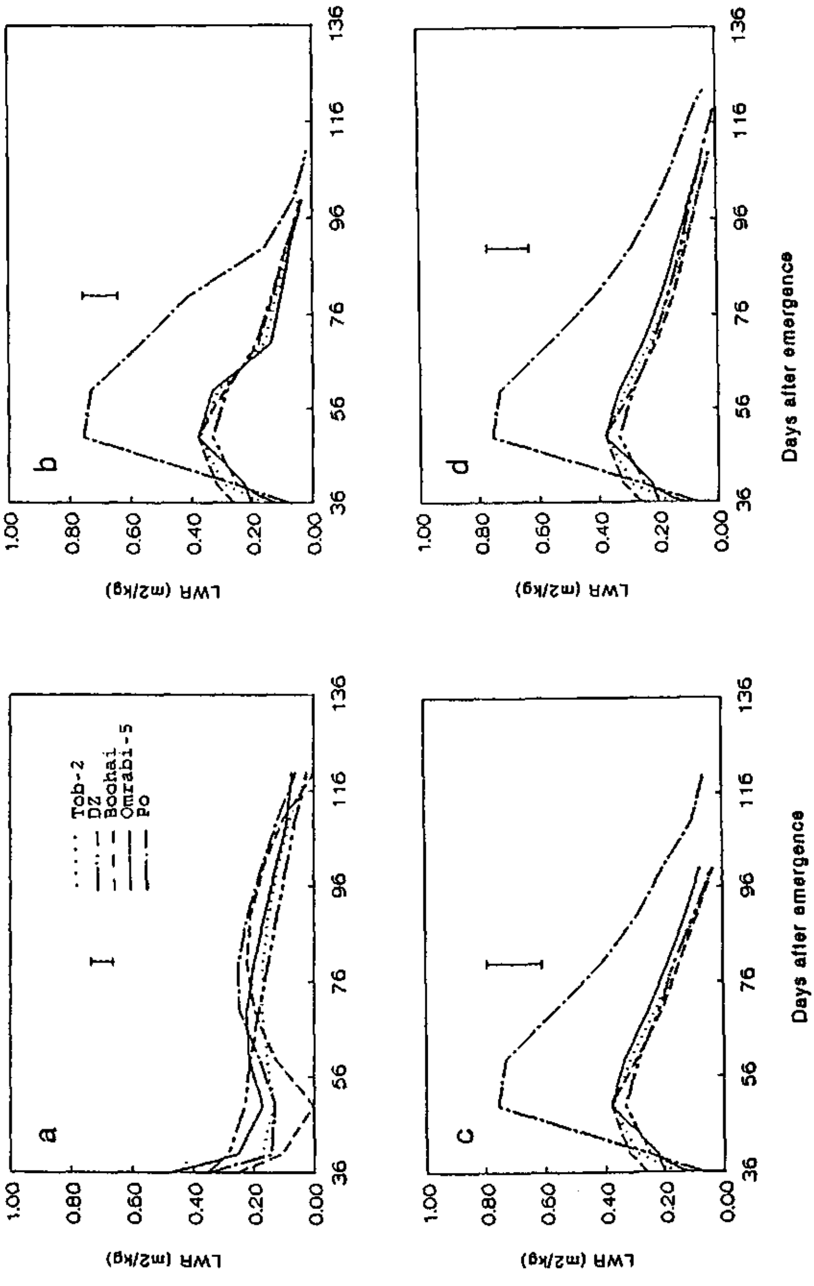


Fig. 5.5 Effect of moisture stress on leaf weight ratio (LWR) of durum wheat genotypes from tillering to physiological maturity. a) early-season stress, b) mid season-stress, c) terminal stress and d) control (no stress). Vertical bars indicate LSD (0.05) values.

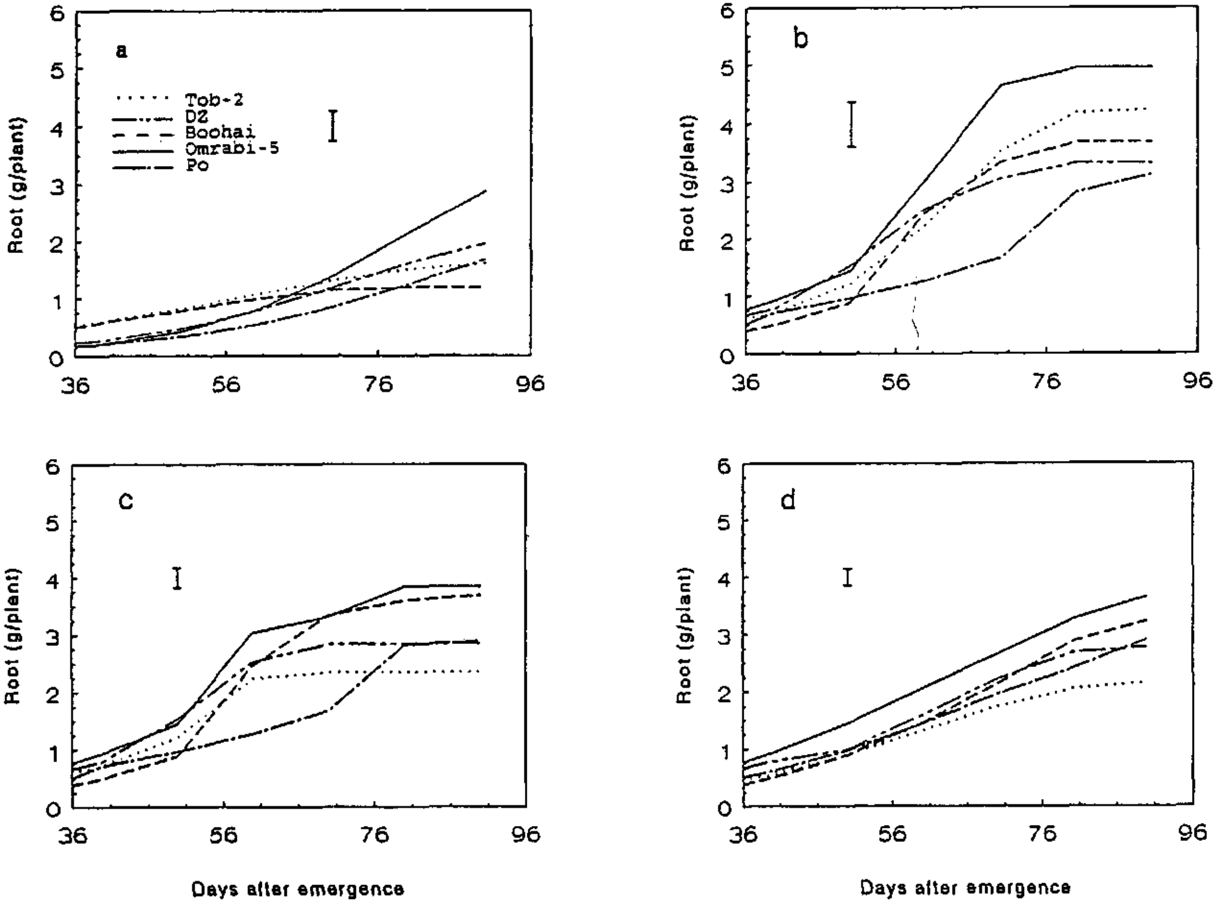


Fig. 5.6 Effect of moisture stress on root development of durum wheat genotypes). a) early-season stress, b) mid-season stress, c) late-season (terminal) stress and d) control (no stress). Vertical bars indicate LSD (0.05) values.

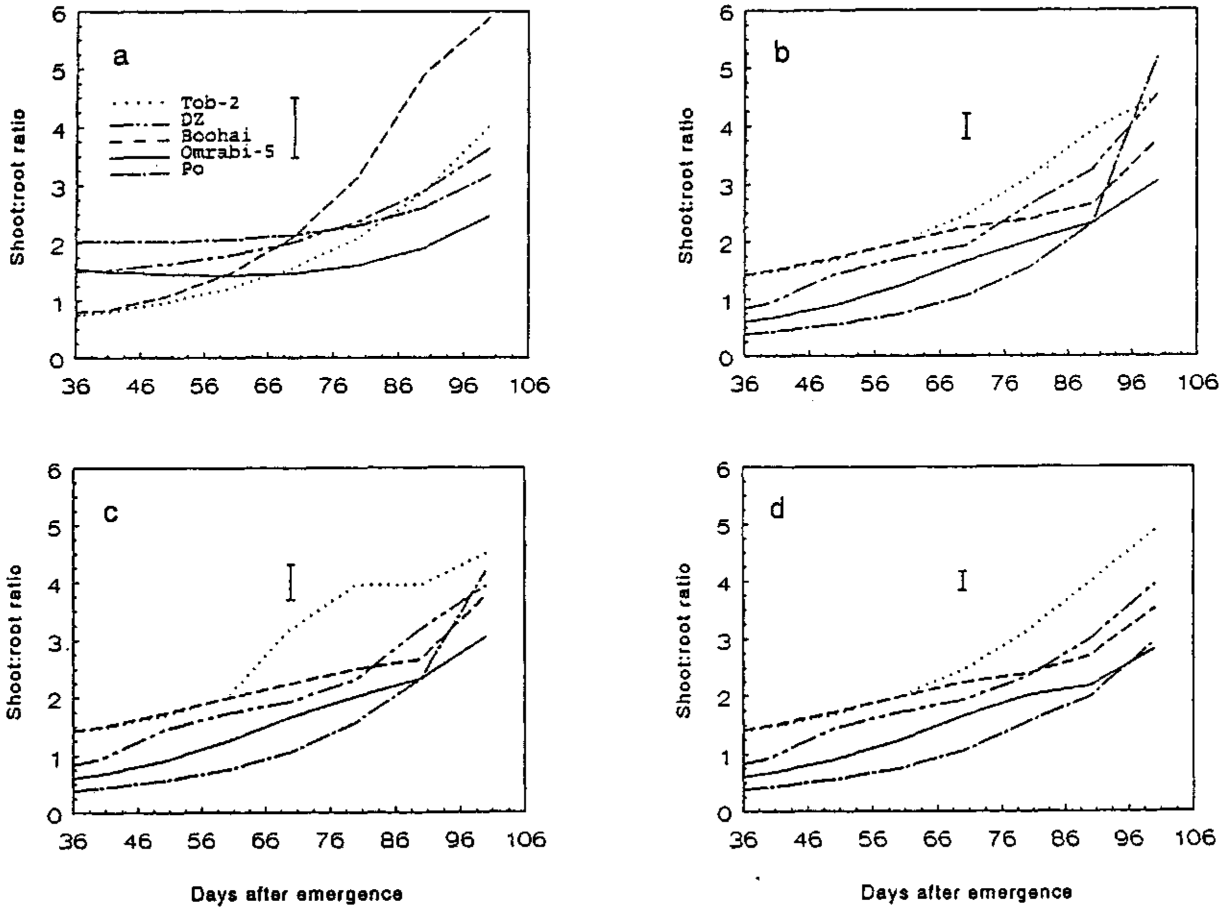


Fig. 5.7 Effect of moisture stress on shoot:root ratio of durum wheat genotypes). a) early-season stress b) mid-season stress c) late-season (terminal) stress and d) control (no stress). Vertical bars indicate LSD (0.05) values.

identify the association of morphological and physiological components of RGR that can easily be used in plant breeding programmes. The values of LAR and NAR varied among cultivars and moisture treatments confirming the results of Konings (1989). The results clearly demonstrated that there is a close correlation between RGR and LAR (r=0.788), whereas the correlation between RGR and NAR is not significant. This is in agreement with previous reports (Poorter and Remkes, 1990). One possible reason could be that the balance between the amount of roots and leaf area may influence the water status of the leaves and as a result photosynthesis. Another explanation could be that an increase in LAR may require increased rates of photosynthesis, which can be realized by additional investment in the photosynthetic apparatus, thus decreasing SLA (Konings, 1989; Poorter, 1989). Unlike Poorter (1989), we found that NAR is negatively correlated with both SLA and LWR. Therefore, both SLA and LWR could contribute to the negative correlation between NAR and LAR. Under moisture stress, the usefulness of NAR as an expression of the balance between carbon gain (photosynthesis) and carbon losses (respiration) is limited, because photosynthesis is not restricted to the leaf, but also occurs in other green parts including the awns.

Under moisture stress conditions, irrespective of its timing, biomass allocation to the roots was higher, in accordance with the results of Konings (1989). Prolific root growth and/or low shoot:root ratios were associated with drought-resistance (Figs 5.6 and 5.7). Vigorous roots can penetrate as far as the wetting front and extract all available soil water (Passioura, 1977) to support the transpiring above ground biomass. The ratio of root weight to shoot weight and leaf area to shoot weight may influence the water status of the leaves and as a result photosynthesis and transpiration.

From the results we conclude that dry-matter allocation (LAR and its components and shoot:root ratio) is the prime factor determining genotypic variation in RGR of durum wheat under drought conditions.

References

Angus, J.F. and Moncur, M.W., 1977. Water stress and phenology in wheat. Aust. J. Agric. Res., 28: 177-181.

Blum, A., Ramaiah, S., Kanemasu, E.T. and Paulsen, G.M., 1990. Wheat recovery from drought stress at the tillering stage of development. Field Crops Res., 24: 67-85.

Chapin, F.S., 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Sys., 11: 233-260.

Dijkstra, P. and Lambers, H., 1989. A physiological analysis of genetic variation in relative growth within *Plantago major* L. Functional Ecology, 3: 577-587.

Donatelli, M., Hammer, G.L. and Vanderlip, R.L., 1992. Genotype and water limitation effects on phenology, growth and transpiration efficiency in grain sorghum. Crop Sci., 32: 781-786.

Fischer, R.A. and Maurer, R., 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res., 29: 897-912.

Hunt, R.,1982. Plant growth curves. The functional approach to growth analysis. Edward Arnol. London.

Karimi, M. and Siddique, H.M., 1991. Crop growth and relative growth rates of old and modern wheat cultivars, Aust. J. Agric. Res., 42: 13-20.

Konings, H., 1989. Physiological and morphological differences between plants with high NAR or high LAR as related to environmental conditions. *In*: H. Lambers, M.L. Cambridge, H. Konings and T.L. Pons (Editors), Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague, 101-123

Lambers, H. and Dijkstra, P., 1987. A physiological analysis of genotypic variation in relative growth rate: can growth rate confer ecological advantage? *In*: J Van Andel *et al.* (Editors), Disturbance in Grasslands. Junk, Dordrecht, 237-252.

Lambers, H., Freijsen, N., Poorter, H., Hirose, T. and Van der Werf, A., 1989. Analysis of growth based on net assimilation rate and nitrogen productivity. Their physiological background. *In*: H. Lambers, M.L. Cambridge, H. Konings and T.L. Pons (Editors), Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague, 1-17.

Passioura, J.B., 1977. Grain yield, harvest index and water use of wheat. J. Aust. Inst. of Agric. Sci., 43: 117-120.

Poorter, H., 1989. Interspecific variation in relative growth rate: on ecological causes and physiological consequences. *In*: H. Lambers, M.L. Cambridge, H. Konings and T.L. Pons (Editors), Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague, 45-68.

Poorter, H. and Lambers, H., 1986. Growth and competitive ability of a higher plastic and marginally plastic genotype of *Plantago major* L. in fluctuating environment. Physiol. Plant., 67: 217-222.

Poorter, H. and Remkes, C., 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia, 83: 553-559.

Simane, B. and Struik, P.C., 1993. Agroclimatic analysis: a tool for planning sustainable durum wheat (*Triticum turgidum* L. var. *durum*) production in Ethiopia. Agriculture, Ecosystem and Environment, in press.

Van Andel, J. and Jager, J.C., 1981. Analysis of growth and nutrition of six plant species of woodland clearings. Journal of Ecology, 69: 871-882.

Watson, D.J., 1952. The physiological basis of variation in yield. Advances in Agron. Vol. IV: 101-145.

Chapter 6

Leaf gas exchange and leaf area of durum wheat cultivars differing in drought-resistance

B. Simane, P.C. Struik and J.M. Peacock

Plant and Soil (submitted)

Abstract

It is still unclear whether leaf gas exchange traits can be used as criteria for selecting drought-resistant cultivars in water-limited environments. Leaf gas exchange traits of drought-resistant and drought-susceptible cultivars of durum wheat grown under different moisture regimes were compared in a greenhouse experiment. Mid-day stomatal conductance, photosynthesis, transpiration rate per unit leaf area and assimilation:transpiration ratio decreased sharply under stress regardless of its timing. The drought-resistant and drought-susceptible cultivars responded similarly under stressed and non-stressed conditions. The ratio of intercellular to ambient CO_2 concentration was constant under all moisture treatments. Leaf area development, however, differed significantly among cultivars. The drought-susceptible cv. Po had a very slow leaf area development till the three tiller stage but much higher in later stages. It is concluded that instantaneous leaf gas exchange measurements do not adequately represent the whole canopy assimilation rate and cannot be used as selection criteria to breed for high yields in water-limited environments.

Key words: assimilation:transpiration ratio, drought, photosynthesis, stomatal conductance, transpiration

Introduction

Crop production in water-limited environments is reduced by the integrated effects of water stress at various levels of plant organization (Blum, 1985). Efficient water use is an ecologically important factor influencing adaptation of crop species to water-limited environments. Genetic variation among wheat cultivars has been reported (Richards, 1987; Cooper *et al.*, 1987). However, it is difficult to measure water use efficiency (WUE) in the field, since it is difficult to separate soil evaporation from transpiration (Van Keulen, 1975; Cooper *et al.*, 1987). A physiologically-based indirect means to evaluate WUE will greatly help plant breeding programmes in large segregating populations (Blum, 1985; Winter *et al.* 1988).

The cellular implications of water deficits, as the underlying reasons for the effects observed at higher levels of plant organization, are still unclear. Genetic variation in photosynthetic rate and stomatal conductance have been reported for wheat (Austin, 1989; Johnson *et al.*, 1987; Morgan and LeCain, 1991) and sorghum (Kreig, 1983; Peng and Kreig, 1992). These traits might be used to select cultivars with increased WUE. Many factors, such as N content (Poorter *et al.*, 1990), leaf age (Rawson *et al.*, 1983), leaf water status (Johnson *et al.*, 1984) and temperature (Blum *et al.*, 1989) have been reported to affect gas exchange. The application of such physiological measures in crop improvement requires the establishment of significant association between the various physiological traits and drought-resistance.

In this study we examined whether there are differential responses to drought in leaf gas exchange rates among drought-resistant and drought-susceptible cultivars. We measured leaf gas exchange rates of uppermost fully expanded leaves of drought-resistant and drought-susceptible durum wheat cultivars exposed to moisture stress at different growth stages.

Materials and methods

A greenhouse experiment was conducted at the International Centre for Agricultural Research in the Dry Areas, Northern Syria (ICARDA) at Tel Hadya (36°10'N, 36°56'E). The night/day temperature was 15/20°C. Three plants per 5 kg pot were grown. Plant density based on surface area of the pots and their spacing was equivalent to 220 plants/m^2. A randomized complete block design with four replications was used. Eight pots were used for each treatment.

Five durum wheat (*Triticum turgidum* L. var. *durum*) cultivars developed in Ethiopia and at ICARDA were used (for details see Simane *et al.*, 1993). These cultivars represent different levels of drought-resistance under field conditions (Nachit, unpublished data; Simane and Demmissie, unpublished data) and differ in phenological development (Fig. 6.1). Three of the cultivars (Tob-2, DZ, Boohai) were bred in Ethiopia for different agro-ecological zones. Omrabi-5 is drought-resistant and grown extensively in Mediterranean regions, while Po was developed for high input areas and is drought-susceptible.

Four moisture treatments: *viz.* 1) stress at tillering (22 Zadoks scale) for 15 days; 2) stress at boot stage (49 Zadoks scale) for 15 days; 3) terminal stress 10 days after anthesis (73 Zadoks scale) and 4) control (no stress), were applied (for details see Simane *et al.*, in press). Soil moisture status was determined gravimetrically by weighing each pot every other day. Whenever the weight indicated that the soil had dried out beyond the limit (70% of the available soil water (ASW) for the control and stressed treatments were maintained at 10-30% ASW), water was added to restore soil moisture content to the predetermined level.

Single leaf gas exchange rate was determined between 1000 and 1300 h on fully expanded uppermost leaves using the ADC steady state gas-exchange system (Analytical Development Co., Hoddeson, England) with the model PLC(N) leaf chamber, LCA2 infrared gas analyzer and ASU(MF) air supply unit. To minimize fluctuations in CO_2 concentration, air was drawn through a sampling mast from 3 m above the pots. About 30 seconds were required to obtain a steady-state reading. Measurements were made seven times from Zadoks scale 22 to 75 (3 during early, 3 during mid-season and 1 during terminal stress) on three separate leaves for each replication. Assimilation:transpiration ratio (AER) was calculated as the ratio between photosynthesis and transpiration rates.

Green leaf area of individual plants was measured eight times during the season using a LI-3100 (LI-COR, Lincoln, Nebraska, USA) leaf area meter.

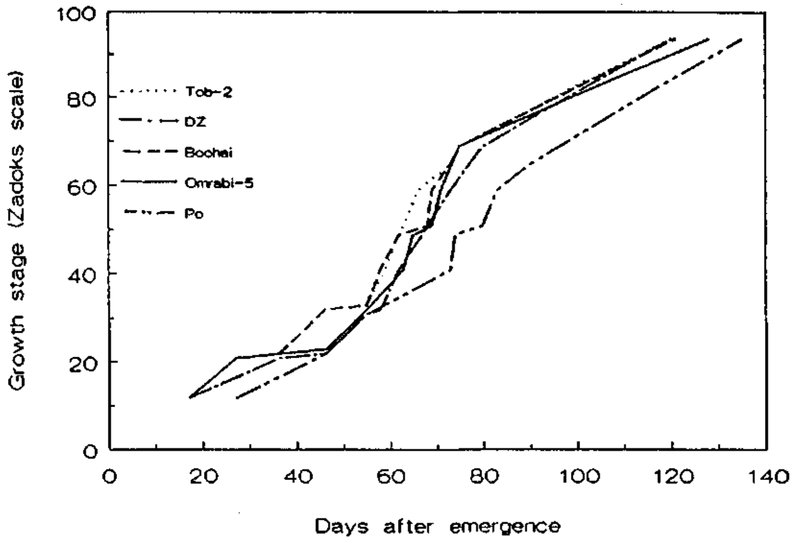


Fig. 6.1 Phenology of the five durum wheat cultivars used in the experiment under non stressed condition.

The significance of cultivar differences in gas exchange traits and leaf area was determined by analysis of variance. Data were analyzed by ANOVA using a completely randomized design. A least significant difference test was used to separate the cultivar means.

Results

Leaf gas exchange

The effect of moisture stress on leaf gas exchange traits *viz.*: transpiration (E), stomatal conductance (g), photosynthesis (A) and assimilation:transpiration ratio (AER) is shown in Fig. 6.2. Regardless of the timing of stress a significant reduction in E, g, and A rates was observed similarly for all cultivars when stressed. Since the impact of moisture stress on A and E was proportional, the response of AER to moisture stress was also similar to the effect on A and g with no significant difference among cultivars (Fig. 6.2d).

Ratio of intercellular to ambient CO_2 concentration (C_i:C_a) was not affected by moisture stress conditions and was maintained almost constant (Fig. 6.3).

Since both E and A are depending on g, they were affected proportionally irrespective of the timing of moisture stress. As a result, the regression coefficients for the relationship of g and A were not significant also (Fig. 6.4).

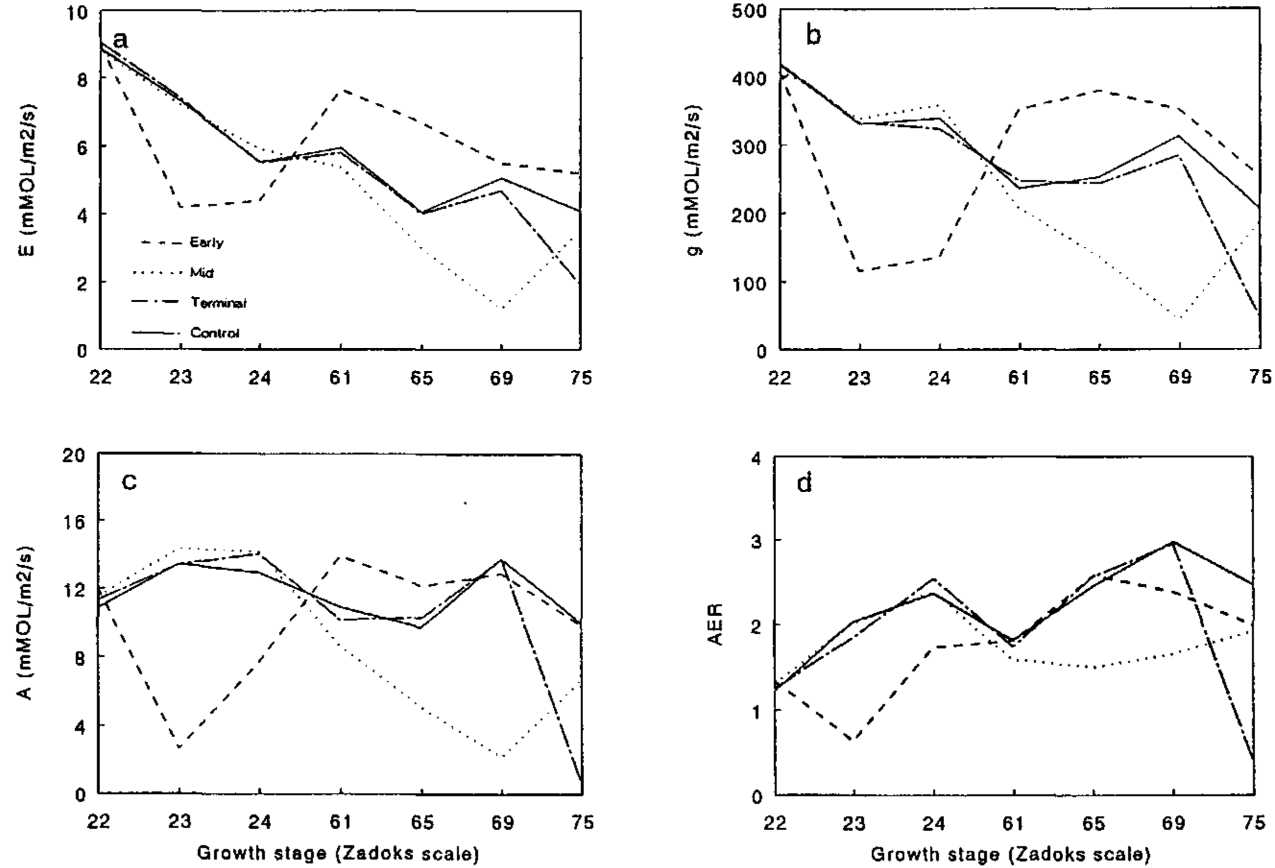


Fig. 6.2 Effect of different timing of moisture stress on leaf gas exchange rate of five durum wheat cultivars differing in drought resistance. a) transpiration (E), b) stomatal conductance (g), c) photosynthesis (A) and d) assimilation:transpiration ratio (AER).

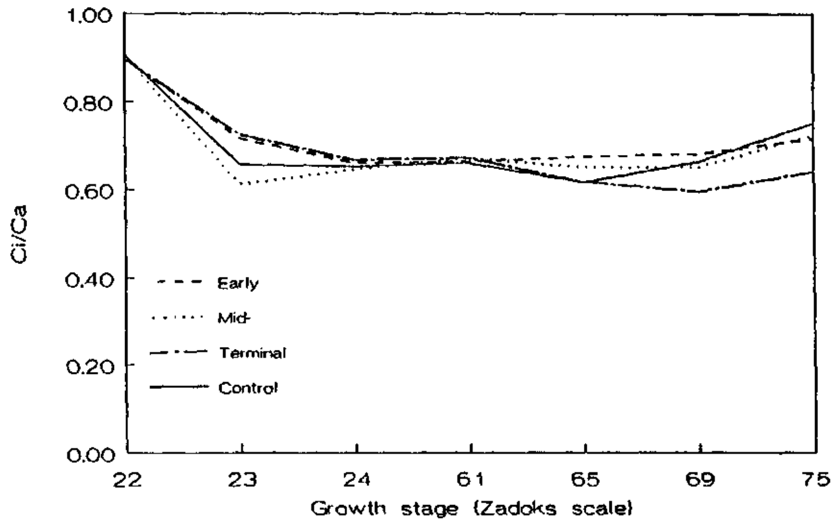


Fig. 6.3 Effect of different timing of moisture stress on the ratio of internal to ambient CO_2 concentration (Ci/Ca) of five durum wheat cultivars differing in drought resistance.

Data of all leaf gas exchange traits were analyzed separately for each measuring date. However, no differential response was observed at any measuring date. Therefore, to examine whether cultivars differ in their response to moisture stress, cultivar means averaged across the seven measuring dates have been analyzed (Tables 6.1-6.4). Significant differences among cultivars were found only in g under mid-season stress, A under early-season stress and AER under early and mid-season stress conditions only. Cultivars differing significantly are marked with different superscript letters. However, these differences did not allow to rank cultivars in terms of any leaf gas exchange traits and to draw a physiologically based conclusion about drought-resistance.

Leaf area

Leaf area development in all cultivars was very sensitive to moisture stress (Fig. 6.5). Significant differences in leaf area among cultivars and moisture treatments were observed. The drought-susceptible cv., Po, had a very slow rate of leaf area development until 23 Zadoks scale, but subsequently showed a rapid rate of development resulting in the largest leaf area per plant. Leaf area development for the other four cultivars was similar. However, under early stress conditions Tob-2 and Boohai exhibited a slower development resulting in the lowest average leaf area per plant.

Table 6.1 Average values of transpiration rate (mMOL/m^2/s) for five durum wheat cultivars grown under different moisture regimes.

Variety	Moisture stress				
	1) early	2) mid	3) terminal	4) control	Mean
Tob-2	5.80	4.80	5.31	5.59	5.38
DZ	6.19	5.49	5.68	6.17	5.88
Boohai	5.36	5.00	5.32	5.51	5.30
Omrabi-5	5.61	5.21	5.96	5.89	5.50
Po	6.10	4.59	5.94	6.15	5.70
Mean	5.81	5.02	5.51	5.86	5.55
LSD (< 0.05)	1.12	0.98	0.90	1.00	1.00

Discussion

Leaf gas exchange rates and leaf area exhibited a significant response to moisture stress. In agreement with a number of reports (Vos and Groenwold, 1989; Condon *et al.*, 1990), the changes in E, g and A in response to moisture stress were highly correlated. As a result, the time course of AER was similar to that of A.

The ratio of intercellular to ambient CO_2 (C_i:C_a) depends on the balance between photosynthetic capacity and stomatal conductance (Condon *et al.*, 1987). In the present study, since both g and A were affected proportionally, C_i:C_a remained constant under all moisture treatments (Fig. 6.5).

In earlier experiments with the same cultivars a significant difference in relative growth rate (RGR) and its components (Simane *et al.*, 1993) and in water use, water use efficiency (WUE) and dry-matter partitioning (Simane *et al.*, submitted) have been reported. However, in spite of the differences in RGR and WUE, the responses of mid-day instantaneous leaf gas exchange of all cultivars to different timing of moisture stress were similar. This result agrees with the conclusions of Dijkstra and Lambers (1989) and Poorter *et al.*, (1990) that fast and slow-growing species of similar life forms have similar rates of photosynthesis per unit leaf area. On the other hand, genotypic variation in leaf gas exchange traits in response to moisture stress has been reported for a number of crops (wheat by Ritchie *et al.*, 1990; Morgan and LeCain, 1991; sorghum by Peng and Krieg, 1992; potato by Vos and

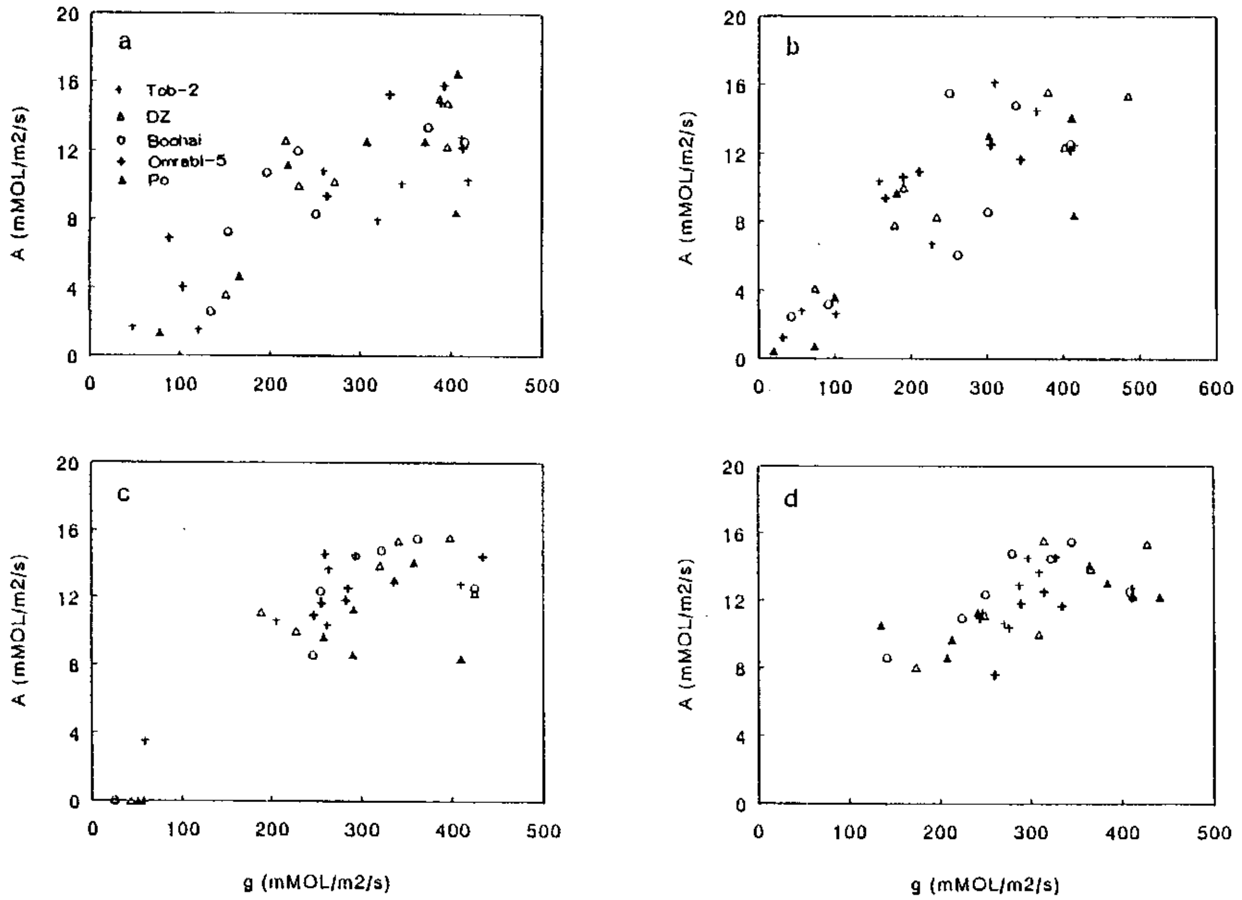


Fig. 6.4 The relationship between stomatal conductance (g) and photosynthesis (A) under different timing of moisture stress. a) early stress, b) mid-season stress, c) terminal stress, d) control.

Table 6.2 Average values of stomatal conductance rate (mMOL/m^2/s) for five durum wheat cultivars grown under different moisture regimes.

Variety	Moisture stress				
	1) early	2) mid	3) terminal	4) control	Mean
Tob-2	274.86	233.36^{AB}	261.29	300.80	267.58
DZ	293.21	277.93^{A}	277.57	321.79	292.63
Boohai	250.86	242.50^{AB}	275.64	281.86	262.70
Omrabi-5	283.14	237.14^{AB}	260.14	311.77	273.05
Po	279.21	214.64^{B}	285.00	284.07	265.73
Mean	276.26	241.00	271.92	299.91	272.27
LSD (< 0.05)	67.73	71.69	41.97	60.18	60.39

Groenwold, 1989). However, their conclusions were based on experiments either in growth chambers only for a short period of the vegetative period or based on whole plant level and did not give information on moisture levels which makes it difficult to draw any conclusion as to why our results differ from theirs.

Possible reasons for the absence of genotypic differences among drought-resistant and drought-susceptible cultivars, *i.e.* on the use of instantaneous leaf gas exchange traits as a physiological index in water-limited environments, are the following.

First, whole plant growth is a function of source activity and sink activity (Kreig, 1983). Very significant cultivar differences in green leaf area were observed (Fig. 6. 5). Canopy CO_2 assimilation, therefore, may vary as a result of differences in leaf area and duration of growth (Rawson et al, 1983; Morgan and LeCain, 1991). However, the variation in CO_2 assimilation is not proportional to that of leaf area (Penning de Vries *et al.*, 1989; Morgan and LeCain, 1991). The difference in RGR and WUE at plant level could be the result of differences in leaf area. In water-limited environments, reduced leaf area tends to restrict water losses through reduced transpiration, but then also restricts photosynthesis as a result of reduced radiation interception. If leaf area is reduced too much, there may be either insufficient pre-anthesis growth to establish adequate yielding capacity and root growth to extract all available soil water or excessive soil surface evaporation at the expense of transpiration. Therefore, leaf area during vegetative growth should be manipulated judiciously. Under terminal stress conditions, where crops depend on water stored in the soil, reduced leaf area will conserve water for the grain filling period, thus increasing harvest

Table 6.3 Average values of photosynthesis rate (mMOL/m^2/s) for five durum wheat cultivars grown under different moisture regimes.

Variety	Moisture stress				
	1) early	2) mid	3) terminal	4) control	Mean
Tob-2	8.27^{C}	8.91	10.82	11.70	9.93
DZ	11.12^{AB}	10.11	11.17	13.55	11.49
Boohai	9.69^{BC}	9.27	10.10	11.66	10.18
Omrabi-5	12.04^{A}	9.61	10.99	12.18	11.21
Po	9.88^{BC}	7.04	9.72	11.24	9.47
Mean	10.20	8.99	10.56	12.07	10.45
LSD (< 0.05)	2.31	3.04	2.77	3.26	2.85

index (Richards, 1987).

Secondly, integration of instantaneous measurements of leaf gas exchange into daily or seasonal values requires several additional assumptions. Most important is the variation in daily time course of weather parameters affecting leaf gas exchange, such as light intensity, temperature, relative humidity, etc. Therefore, mid-day instantaneous measurements of leaf gas exchange may not be representative for the diurnal course of leaf conductance and photosynthesis. The occurrence of mid-day depressions in water-stressed plants will further complicate the interpretation. Diurnal course of leaf gas exchange traits could be calculated as described by Goudriaan (1986) using a Gaussian integration method of instantaneous rate of leaf photosynthesis in time and space.

Thirdly, under water-limited conditions, the system is complicated due to the presence of different sources of assimilates such as awns, green stems and spikes. It has been clearly demonstrated by Evans *et al.* (1972) and Johnson *et al.* (1974) that the photosynthetic capacity of awned spikes was higher than that of awnless cultivars of barley and wheat during water stress.

Fourthly, final dry matter production of plants is not only determined by gross photosynthesis, as approximately 30-40% of the carbon fixed per day is respired (Lambers *et al.*, 1989). In previous experiments, we found these cultivars to have different dry-matter accumulation rates and relative growth rates particularly during the second half of the growing period (Simane *et al.*, 1993). Therefore, there may be differences in respiratory costs that eventually have caused differences in WUE.

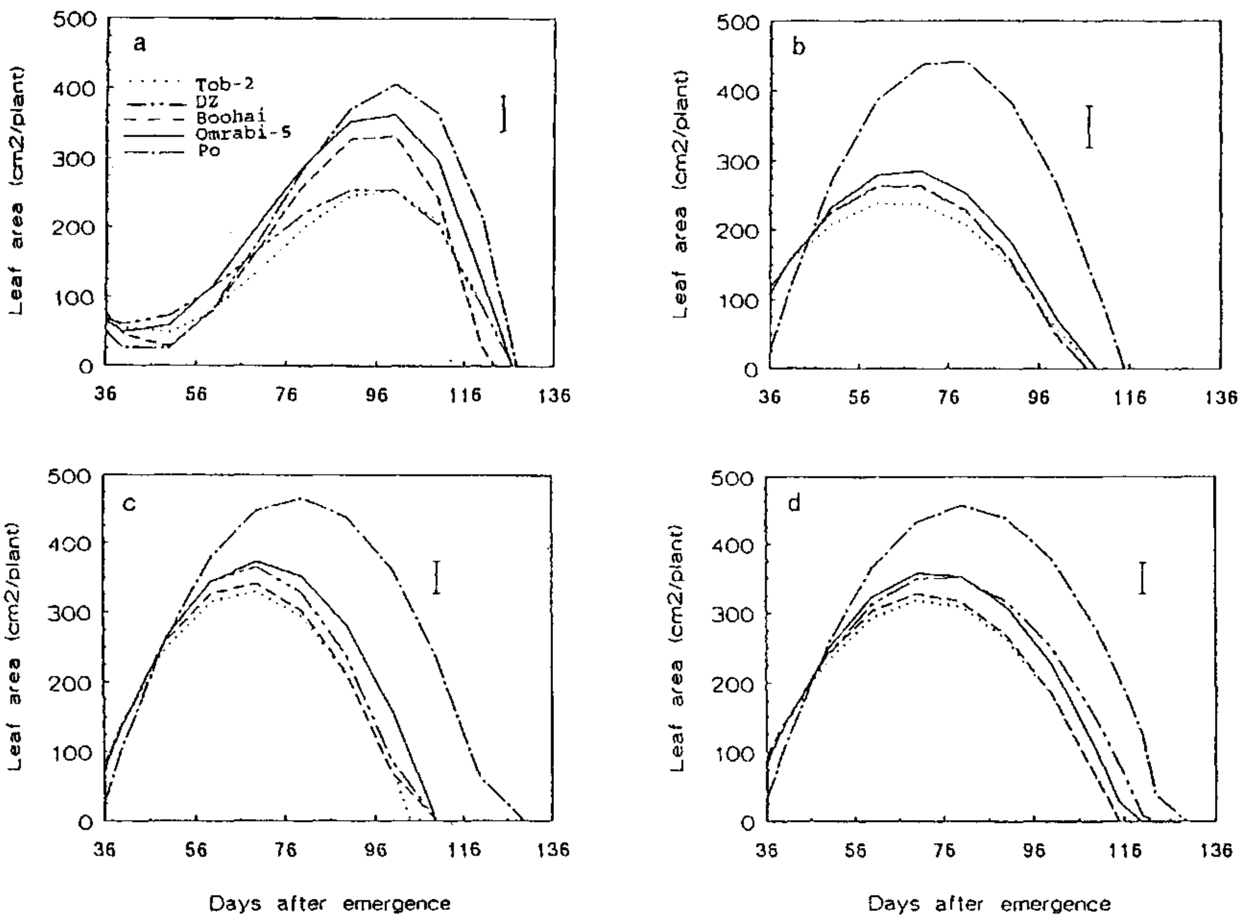


Fig. 6.5 Time course of leaf area development as affected by timing of moisture stress. a) early stress b) mid-season stress c) terminal stress d) control. Vertical bars indicate LSD (<0.05) values.

Table 6.4 Average values of assimilation:transpiration ratio (AER) for five durum wheat cultivars grown under different moisture regimes.

Variety		Moisture stress			
	1) early	2) mid	3) terminal	4) control	Mean
Tob-2	1.40^{C}	1.79	2.11	2.21	1.87
DZ	1.90^{AB}	1.89	1.93	2.04	2.42
Boohai	1.88^{AB}	1.87	1.77	2.37	1.97
Omrabi-5	2.18^{A}	1.97	2.04	2.27	2.12
Po	1.56^{BC}	1.37	1.04	1.96	1.48
Mean	1.79	1.78	1.91	2.20	1.92
LSD (< 0.05)	0.44	0.63	0.73	0.66	0.61

Another important issue in breeding programmes of agricultural crops is that yield is often considered to be only part of the biomass which is economically important. Therefore, much emphasis is given to variations in the allocation of dry matter (harvest index, shoot:root ratio) which may obscure the physiology and dry matter production (Poorter *et al.*, 1990).

The absence of differences in leaf gas exchange traits among drought-resistant and drought-susceptible cultivars in the present study, contrasts to our previous findings where we reported significant differences in RGR and WUE. We, therefore, conclude that diurnal and seasonal course of whole canopy physiology must be given serious attention to develop physiologically based selection criteria in breeding programmes for water-limited environments.

References

Austin, R.B., 1989. Genetic variation in photosynthesis (review). J. Agric. Sci. Camb., 112: 287-294.

Blum, A., 1985. Breeding crop varieties for stress environments. CRC Crit. Rev. Plant Sci., 2: 199-239.

Blum, A., Golan, S.G. and Mayer, J., 1989. Yield stability and canopy temperature of wheat genotypes under drought-stress. Field Crops Res., 22: 289-296.

Condon, A.G., Richards, R.A. and Farquhar, G.D., 1987. Carbon isotope discrimination is positively correlated with grain yield and dry matter production in field-grown wheat. Aust. J. Plant Physiol., 27: 996-1001.

Condon, A.G., Farquhar, G.D. and Richards, R.A., 1990. Genotypic variation in carbon isotope discrimination and transpiration efficiency in wheat. Leaf gas exchange and whole plant studies. Aust. J. Plant Physiol., 17: 9-22.

Cooper, P.J.M., Gregory, P.J., Tully, D. and Harris, H.C., 1987. Improving water use efficiency of annual crops in the rainfed farming systems of West Asia and North Africa. Exp. Agric., 23: 113-158.

Dijkstra, P. and Lambers, H., 1989. Analysis of specific leaf area and photosynthesis of two inbred lines of *Plantago major* differing in relative growth rate. New Phytol., 113: 283-290.

Evans, L.T., Bingham, J., Jackson, P. and Sutherland, J., 1972. Effect of awns and drought on the supply of photosynthate and its distribution within wheat ears. Ann. Appl. Biol., 70: 67-76.

Goudriaan, J., 1986. A simple and fast numerical method for the computation of daily totals of crop photosynthesis. Agric. and Forest Meteorol., 38: 249-254.

Johnson, R.R., Frey, N.M. and Moss, D.N., 1974. Effect of water stress on photosynthesis and transpiration of flag leaves and spikes of barley and wheat. Crop Sci., 14: 728-731.

Johnson, R.C., Kebede, H., Mornhinweg, D.W., Craver, B.F., Rayburn, A.L. and Nguyen, H.T., 1987. Photosynthetic differences among *Triticum* accessions at tillering. Crop Sci., 27: 1046-1050.

Johnson, R.C., Nguyen, H.T.and Croy, L.I., 1984. Osmotic adjustment and solute accumulation in two wheat genotypes differing in drought resistance. Crop Sci., 24: 978-962.

Kreig, D.R., 1983. Photosynthetic activity during stress. Agric. Water Mngmt., 7: 249-263.

Lambers, H., Freijsen, N., Poorter, H., Hirose, T. and Van der Werf, A., 1989. Analysis of growth based on net assimilation rate and nitrogen productivity. Their physiological backgrounds. *In*: Lambers, H. Cambridge, M.L., Konings, H. and Pons, T.L. (Editors), Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague. pp. 1-17.

Morgan, J.A. and LeCain, D.R., 1991. Leaf gas exchange and related leaf traits among 15 winter wheat genotypes. Crop Sci., 31: 443-448.

Peng, S. and Kreig, D.R., 1992. Gas exchange traits and their relationship to water use efficiency of grain sorghum. Crop Sci., 32: 386-391.

Penning de Vries, F.W.T., Jansen, D.M., Ten Berge, H.F.M and Bakema, A., 1989. Simulation of ecophysiological processes of growth in several annual crops. Simulation Monographs 29, Pudoc, Wageningen. 270 pp.

Poorter, H., Remkes, C. and Lambers, H., 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. Plant Physiol., 94: 621-627.

Rawson, H.M., Hindmarsh, J.H., Fischer, R.A. and Stockman, Y.M., 1983. Changes in leaf photosynthesis with plant ontogeny and relationships with yield per ear in wheat cultivars and 120 progenies. Aust. J. Plant Physiol., 10: 503-514.

Richards, R.A., 1987. Physiology and the breeding of winter-grown cereals for dry areas. *In*: Srivastava, J.P., Porcedu, E., Acevedo, E. and Varma, S. (Editors), Drought tolerance in winter cereals. Cambridge University Press, UK. pp. 133-150.

Ritchie, S.W., Nguyen, H.T. and Holaday, A.S., 1990. Leaf water content and gas-exchange parameters of two wheat genotypes differing in drought resistance. Crop Sci., 30: 105-111.

Simane, B., Peacock, J.M. and Struik, P.C., 1993. Differences in developmental plasticity and growth rate among drought resistant and susceptible cultivars of durum wheat (*Triticum turgidum* var. *durum*). Plant and Soil, in press.

Simane, B., Struik, P.C. and Peacock, J.M. Water use efficiency of durum wheat differing in drought resistance grown under different moisture regimes. Plant and Soil, submitted.

Van Keulen, H., 1975. Simulation of water use and herbage growth in arid regions. Simulation Monographs, Pudoc, Wageningen. 175 pp.

Vos, J. and Groenwold, J., 1989. Characteristics of photosynthesis and conductance of potato canopies and the effect of cultivar and transient drought. Field Crops Res., 20: 237-250.

Winter, S.R., Musick, J.T. and Porter, K.B., 1988. Evaluation of screening techniques for breeding drought-resistant winter wheat. Crop Sci., 28: 512-516.

Chapter 7

Effect of drought stress and nitrogen on straw and grain quality of durum wheat cultivars differing in drought resistance

B. Simane, P.C. Struik, T. Goodchild and J.M. Peacock

Animal Feed Science and Technology (submitted)

Abstract

In addition to grain yield, quality and quantity of straw are important characteristics for farmers to accept new cultivars. Five durum wheat cultivars, differing in drought resistance, were grown under different moisture and nitrogen regimes in two greenhouse experiments. Ash, nitrogen (N), neutral-detergent fibre (NDF), acid-detergent fibre (ADF) and in-vitro digestibility of organic matter (DOMD) of the different morphological fractions of straw (stem, leaf and chaff) and harvest index (HI) and grain:straw nitrogen ratio (NR) were measured.

Yield of straw varied among cultivars and was reduced by drought stress in all cases. The different morphological components, i.e. stem, leaf and chaff, varied significantly in relative proportions, chemical composition and digestibility. Stem fraction made up the largest proportion, but leaf fraction was highest in most quality components. Relative proportions of morphological fractions were similar for all cultivars, but different times of drought stresses affected the relative proportions of stem:leaf:chaff differently. Quality of straw varied among cultivars and drought treatments with hardly any significant interactions. Straw quality of the drought-susceptible (Po) and the drought-resistant (Omrabi-5) cultivars was higher than that of cultivars from Ethiopia. Mid and terminal drought stress considerably improved straw quality, whereas early stress hardly affected it. HI and NR varied among cultivars and drought treatments. The drought susceptible cultivar (Po) had the lowest HI and NR. Drought stress reduced harvest index. Cultivar and drought stress, however, did not affect grain N% and NDF%. Nitrogen fertilizer treatments did not affect the quality of straw.

Variation in straw quality was strongly associated with HI and NR, but they did not correlate with either yield potential or with drought susceptibility. Therefore, there is scope to improve straw quality without affecting grain yield.

Key words: acid-detergent fibre, drought-resistance, grain:straw nitrogen ratio, in-vitro digestibility of organic matter, harvest index, neutral-detergent fibre

Introduction

North Africa and the Middle East are deficit areas in all important food commodities and animal feeds (Van Schoonhoven, 1989). This is partly due to low rainfall which is highly erratic in both space and time ranging from 50 to 1200 mm per year (Harris, 1989). Durum wheat (*Triticum turgidum* L. var. *durum*), an important crop in the region, is a dual-purpose crop, since both grain and straw are used (Nachit and Ouassou, 1988). Thus, the economic return from durum wheat includes the combined value of grain and straw. The grains are used for human consumption and straw is a major feed source for ruminants and is more important than special forage crops because of competition for land with crops for human consumption (Van Soest, 1988). Many cereal breeding programmes are focused on increasing grain yield and grain quality only. Quality and quantity of cereal straws, however, are becoming important criteria in the farmers' decision to accept new cultivars (Capper, 1986).

In some years drought stress is such that grain yields are small and the economic value of the straw may exceed that of grain (Capper, 1986). Under such conditions, the quality of straw and the overall biological yield become important characteristics for selecting wheat genotypes. The feeding value of straw can be improved by chemical treatment, but genetic improvement of straw quality would be cheaper and more logical if it is not at the expense of the agronomic and grain yield attributes (Deinum, 1988).

Cultivar differences in straw quality have been reported for a number of cereals (White *et al.*, 1981; Tuah *et al.*, 1986; Capper, 1988; Orskov, 1988; Ramanzin *et al.*, 1991). Effects of drought stress on straw quality has been also reported (Wilson, 1982, Capper, 1988). However, information on the effects of cultivars that are different in drought-resistance and different timings of drought stress on the quality of durum wheat straw is limited.

The objectives of this study were to examine 1) the differences in nutritive value among drought-resistant and -susceptible cultivars 2) the effect of drought-stress on quality and quantity of durum wheat straw, and 3) the effect of nitrogen fertilizer on quality and quantity of straw. This paper deals with five durum wheat cultivars which are different in growth rate, water use efficiency and drought-resistance and is a sequel to earlier reports (Simane *et al.*, 1993; submitted[1]). Nutritive value of straw is compared primarily based on its digestibility, nitrogen and cell wall content.

Materials and methods

The straw and grain yield quality of five durum wheat (*T. turgidum* L. var. *durum*) cultivars grown under different drought regimes were analyzed in the laboratories of the International Centre for Agricultural Research in the Dry Areas (ICARDA) Aleppo, Syria and the Department of Agronomy, Wageningen Agricultural University, The Netherlands. The cultivars are different in relative growth rate, water use efficiency, drought-resistance and potential yield (for details see Simane *et al.*, 1993). Omrabi-5 is drought-resistant with a high yield potential and Po is the most drought-susceptible with a high yielding potential and a highest relative growth rate (RGR). The other three cultivars (Tob-2, Boohai and DZ) which are bred in Ethiopia are nearly similar and are lower in yield potential but medium in drought-resistance.

Two experiments were conducted in 1991 and 1992 in a controlled environment (greenhouse) at ICARDA, Tel Hadya, Syria (36°10'N, 36°56'E). Three plants were grown per 5 kg dry soil capacity pot. Plant density based on pot surface area and its spacing was equivalent to 220 plants/m^2. A randomized complete block design with four replications was used in both experiments.

In the first experiment four moisture treatments: stress induced a) early (at tillering), b) mid season (at flowering) or c) late season (grain filling) and d) control (no stress) were applied. In the second experiment only a) early, c) terminal and d) control were applied. Soil moisture status was determined gravimetrically by weighing each pot every other day.

Nitrogen fertilizer as ammonium nitrate (NH_4NO_3) was varied in the second experiment and given in Table 7.1.

At physiological maturity of each treatment the biomass was separated manually into stem (including leaf sheaths), leaf, chaff and grain. Weights were determined after drying each sample at 75 °C for 48 hours. Harvest index (HI) was calculated by dividing grain yield by total biomass.

Morphological fractions were ground to pass a 0.5 mm mesh separately and used for chemical analysis. All the morphological fractions were analyzed for concentrations of ash and Kjeldahl N and for neutral-detergent fibre (NDF), acid-detergent fibre (ADF) (Goering and Van Soest, 1970) and in-vitro digestibility of organic dry matter (Tilley and Terry, 1963). Grain:straw ratio of nitrogen (NR) was determined by dividing the amount of N in the grain by the amount of N in the straw (all morphological fractions).

The least significant difference at the 5% probability level was used to evaluate differences among genotypic and drought treatment means when the F test proved significant effects.

Results

Experiment 1

The quantity of the different morphological fractions of the straw (stem, leaves and chaff) of all cultivars is presented in Table 7.2. The proportions of these fractions were almost

Table 7.1 Nitrogen treatments (kg/ha) used in experiment 2.

Treatment	Time of application		Total
	at planting	stem elongation	
1) low-early	35	-	35
2) medium-early	70	-	70
3) medium-late	-	70	70
4) medium (0.5:0.5)	35	35	70
5) high-early	140	-	140
6) high-late	-	140	140
7) high (0.5:0.5)	70	70	140

Table 7.2 Yields of morphological fractions (g/m^2) in the straw and harvest index (HI) of five durum wheat cultivars grown under different moisture regimes in Exp. 1.

	Stem	Leaf	Chaff	HI
Cultivar				
Tob-2	817 ± 134	243 ± 40	200 ± 39	0.39 ± 0.07
DZ	852 ± 172	233 ± 33	248 ± 67	0.35 ± 0.05
Boohai	824 ± 150	246 ± 34	212 ± 63	0.40 ± 0.07
Omrabi-5	963 ± 155	295 ± 39	249 ± 67	0.38 ± 0.06
Po	1153 ± 173	355 ± 36	304 ± 85	0.29 ± 0.09
Sign.	**	**	**	**
LSD	71	22	23	0.06
Moisture stress				
Early	968 ± 185	242 ± 59	302 ± 77	0.38 ± 0.05
Mid	722 ± 140	281 ± 57	164 ± 36	0.28 ± 0.04
Terminal	953 ± 164	283 ± 50	239 ± 22	0.36 ± 0.10
control	1044 ± 155	291 ± 57	266 ± 64	0.42 ± 0.03
Sign.	**	**	**	**
LSD	63	20	21	0.06
Mean	922 ± 200	274 ± 58	243 ± 74	0.36 ± 0.07

*, ** significant at $P < 0.05$ and $P < 0.01$ respectively.

similar (1 : 0.30 : 0.26). Stem, including the leaf sheath, made up the highest proportion. Total straw mass varied significantly both among cultivars and drought treatments. Cultivar Po had the highest straw mass followed by Omrabi-5. All Ethiopian cultivars had comparable straw yields. Cultivars varied significantly in harvest index (HI), ranging from 0.29 (Po) to 0.40 (Boohai).

Different times of drought stress considerably reduced the mass of the different fractions and affected relative proportions of straw components differently (Table 7.2). The reduction in whole straw mass was 6%, 27% and 8% for early, mid- and terminal stress respectively. Early stress decreased the relative proportion of the leaves but increased that of the chaff. In contrast mid-stress increased leaf proportion and decreased chaff proportion. It also reduced HI significantly. The reduction was most severe under mid-season stress (14%) followed by terminal stress (6%).

Table 7.3 Ash, nitrogen (N), neutral-detergent fiber (NDF), acid-detergent fiber (ADF) and in-vitro digestibility of organic matter (DOMD) contents in dry matter for five durum wheat cultivars in Exp. 1.

	Ash%	N%	NDF%	ADF%	DOMD%
Stem					
Tob-2	7.16 ±0.7	0.37 ±0.2	66.0 ±4.2	39.8 ±3.4	43.3 ±4.2
DZ	5.51 ±0.8	0.33 ±0.1	60.8 ±4.0	35.9 ±3.0	50.0 ±4.1
Boohai	6.63 ±0.8	0.36 ±0.1	66.3 ±2.9	39.4 ±2.1	45.5 ±2.6
Omrabi	5.15 ±0.8	0.39 ±0.1	61.5 ±5.4	36.2 ±3.2	52.1 ±4.7
Po	5.17 ±0.5	0.45 ±0.2	58.9 ±5.6	33.3 ±2.9	54.5 ±3.8
Mean	5.92 ±1.1	0.38 ±0.1	62.7 ±5.2	36.9 ±3.8	49.1 ±5.6
Sign.	**	NS	**	**	**
LSD	0.53	-	3.83	2.35	2.87
Leaf					
Tob-2	14.94 ±1.5	0.80 ±0.2	47.3 ±2.3	28.3 ±1.3	60.9 ±1.9
DZ	13.71 ±1.4	0.74 ±0.1	46.5 ±2.5	27.6 ±2.0	62.5 ±3.2
Boohai	14.42 ±1.9	0.71 ±0.1	48.1 ±2.4	28.8 ±1.4	61.8 ±2.1
Omrabi	13.66 ±1.6	0.65 ±0.2	49.5 ±1.5	29.0 ±1.4	64.5 ±2.0
Po	12.87 ±0.5	0.81 ±0.1	53.2 ±1.3	30.4 ±1.6	63.6 ±1.1
Mean	13.92 ±1.5	0.74 ±0.2	48.9 ±3.1	28.8 ±1.8	62.6 ±2.4
Sign.	*	NS	**	**	**
LSD	1.25	-	1.39	1.26	2.03
Chaff					
Tob-2	10.37 ±2.8	0.57 ±0.3	70.1 ±1.8	34.6 ±3.3	38.9 ±8.4
DZ	8.20 ±1.9	0.49 ±0.1	70.9 ±1.7	35.3 ±2.7	42.4 ±7.2
Boohai	9.43 ±2.5	0.54 ±0.2	71.1 ±1.3	35.2 ±1.9	42.2 ±9.0
Omrabi	7.94 ±2.2	0.66 ±0.3	69.4 ±2.6	32.6 ±2.8	51.5 ±8.0
Po	5.43 ±1.3	0.70 ±0.3	71.7 ±2.5	35.5 ±2.1	52.4 ±8.6
Mean	8.27 ±2.7	0.59 ±0.2	70.6 ±2.1	34.7 ±2.7	45.5 ±9.6
Sign.	**	**	NS	**	**
LSD	1.09	0.10	-	1.49	3.01

NS, non significant; * and ** significant at $P < 0.05$ and $P < 0.01$ respectively

The different morphological fractions varied considerably in chemical composition and in-vitro digestibility (Tables 7.3 and 7.4). In almost all varieties and drought treatments, leaf showed higher ash and N contents, lower cell wall content and better in-vitro digestibility than the chaff and stem fractions.

Cultivars differed in quality of all morphological components (Table 7.3). Stem and leaf fractions showed cultivar differences in all parameters except for N%. The chaff fraction showed differences among cultivars for all parameters, except NDF%. The drought-susceptible cultivar, Po, was lowest in ash, highest in N concentration, lowest in NDF and ADF and highest in DOMD. The drought-resistant cultivar, Omrabi-5, was second best next to Po in stem fraction. All Ethiopian cultivars had relatively higher concentrations in ash, NDF, ADF and lower concentrations in N and DOMD.

The quality of all morphological components was strongly influenced by drought stress (Table 7.4). Early stress had no significant effect on stem quality and the values were similar to that of non-stressed treatments. Stem N% and DOMD% were increased and NDF% and ADF% slightly decreased by mid- and terminal stresses. In the leaf N contents increased under early and mid-stresses. Terminal stress showed the highest leaf DOMD. In the chaff, ash, NDF and ADF contents were substantially decreased and N and DOMD increased by mid- and terminal stresses whereas early stress only reduced ash content and increased DOMD.

Experiment 2

Nitrogen treatments affected significantly only N content of the stem, cell wall contents of the leaf and chaff, and digestibility of the leaf (Table 7.5). Additional N increased the N content of the stem and the NDF% in the leaf and chaff, especially when applied early. In contrast, its effects on DOMD of leaf were less systematic. Effect of drought stress were similar as in Experiment 1 (Table 7.6). Early stress increased N% of stem and leaf, but did not affect the NDF% of any fraction. It only improved DOMD% of the chaff fraction significantly. Terminal stress slightly improved N% in all fractions and reduced the NDF% in stem and chaff. It strongly increased the DOMD% of stem and chaff.

The correlation coefficients among the parameters examined to study the quality of the different morphological components of straw are presented in Table 7.7. Ash concentration had a very strong negative association with DOMD in all fractions and with the dry weight of the stem and chaff. DOMD was negatively associated with NDF in the stem fraction, but not in the leaf. Increased N concentration in the stem and chaff increased DOMD, by decreasing NDF and ADF. In the chaff, N had also a negative relationship with ash content and chaff mass.

In the grains, N content ranged from 2.27 to 2.42% and NDF ranged from 10.05 to 11.31%. There were no cultivar differences in grain N and cell-wall content (data not shown). Drought stress slightly increased the N content, but did not affect cell-wall content of the grain (data not shown).

Grain:straw nitrogen ratio (NR) varied among cultivars and drought stresses, ranging from 0.9 (Po, mid- stress) to 5.0 (Boohai, early stress) (Fig. 7.1). Comparing the average cultivar values, the drought susceptible cultivar Po had the lowest value (1.84) whereas the

Table 7.4 Ash, nitrogen (N), neutral-detergent fiber (NDF), acid-detergent fiber (ADF) and in-vitro digestibility of organic matter (DOMD) contents for four moisture stress treatments in Exp.1.

Stress	Ash%	N%	NDF%	ADF%	DOMD%
Stem					
Early	5.47 ±1.0	0.27 ±0.1	65.3 ±4.9	39.3 ±3.7	47.2 ±5.4
Mid	6.84 ±0.9	0.55 ±0.1	62.6 ±5.7	36.2 ±3.1	49.8 ±4.7
Terminal	5.47 ±0.9	0.43 ±0.1	59.9 ±6.1	34.5 ±4.3	53.2 ±6.1
Control	5.92 ±1.1	0.28 ±0.1	63.0 ±3.1	37.8 ±2.3	46.1 ±3.8
Mean	5.93 ±1.1	0.38 ±0.1	62.7 ±5.2	36.9 ±3.8	49.1 ±5.6
Sign.	**	**	*	**	**
LSD	0.48	0.08	3.42	2.09	2.57
Leaf					
Early	14.75 ±1.8	0.78 ±0.1	47.7 ±3.1	28.0 ±1.5	61.6 ±2.6
Mid	14.84 ±1.1	0.82 ±0.3	51.4 ±1.9	30.3 ±1.5	61.8 ±1.4
Terminal	12.56 ±0.6	0.73 ±0.1	47.6 ±3.4	27.7 ±1.8	64.5 ±2.0
Control	13.54 ±1.2	0.65 ±0.1	49.1 ±2.5	29.2 ±1.0	62.6 ±2.7
Mean	13.92 ±1.5	0.74 ±0.2	48.9 ±3.1	28.8 ±1.8	62.6 ±2.4
Sign.	**	*	**	**	**
LSD	1.25	0.13	1.39	1.26	2.03
Chaff					
Early	9.52 ±2.9	0.43 ±0.1	71.7 ±1.7	36.6 ±1.4	41.2 ±7.9
Mid	7.15 ±1.6	0.88 ±0.2	69.8 ±1.8	31.7 ±2.0	53.6 ±5.3
Terminal	5.89 ±1.1	0.65 ±0.1	69.9 ±2.3	33.9 ±2.3	51.4 ±6.1
Control	10.53 ±2.0	0.41 ±0.1	71.2 ±2.2	36.4 ±1.5	35.6 ±5.2
Mean	8.28 ±2.7	0.59 ±0.2	70.6 ±2.1	34.7 ±2.7	45.5 ±9.6
Sign.	**	**	*	**	**
LSD	0.98	0.09	1.15	1.33	2.69

* , ** significant at $P < 0.05$ and $P < 0.01$ respectively

others had more than 3 units. Drought stress had a large impact on NR. Reductions were 7.7%, 50.1% and 30.0% under early, mid and terminal stresses respectively. Cultivar X drought stress interaction was significant ($P<0.05$).

The relationship of HI with some straw feeding value parameters is given in Fig. 7.2. N and DOMD of the stem and chaff were negatively related with HI. Even though the relations were not significant, similar trends were observed for the leaf. In contrast, NR was

Table 7.5 Effect of nitrogen fertilizer on quality parameters of durum wheat (cv. Boohai) straw in Exp. 2.

Treat. code	Stem			Leaf			Chaff		
	N%	NDF%	DOMD%	N%	NDF%	DOMD%	N%	NDF%	DOMD%
1	0.42	70.7	41.9	0.33	45.7	50.9	0.35	66.4	30.2
2	0.51	72.4	41.8	0.55	47.2	52.4	0.30	68.5	27.9
3	0.47	71.6	41.4	0.43	47.6	53.9	0.34	67.0	30.1
4	0.48	72.1	41.2	0.64	47.0	51.4	0.34	66.5	29.4
5	0.55	72.2	41.4	0.42	50.1	52.8	0.35	69.6	27.4
6	0.46	73.6	38.9	0.47	46.7	51.7	0.33	67.5	32.4
7	0.51	72.3	41.9	0.53	49.2	53.7	0.34	67.8	30.6
Mean	0.49	72.1	41.2	0.48	47.6	52.4	0.34	67.6	29.7
Sign.	**	NS	NS	NS	**	*	NS	*	NS
LSD	0.04	-	-	-	1.8	2.0	-	2.1	-

NS, non significant; * and ** significant at $P < 0.05$ and $P < 0.01$ respectively

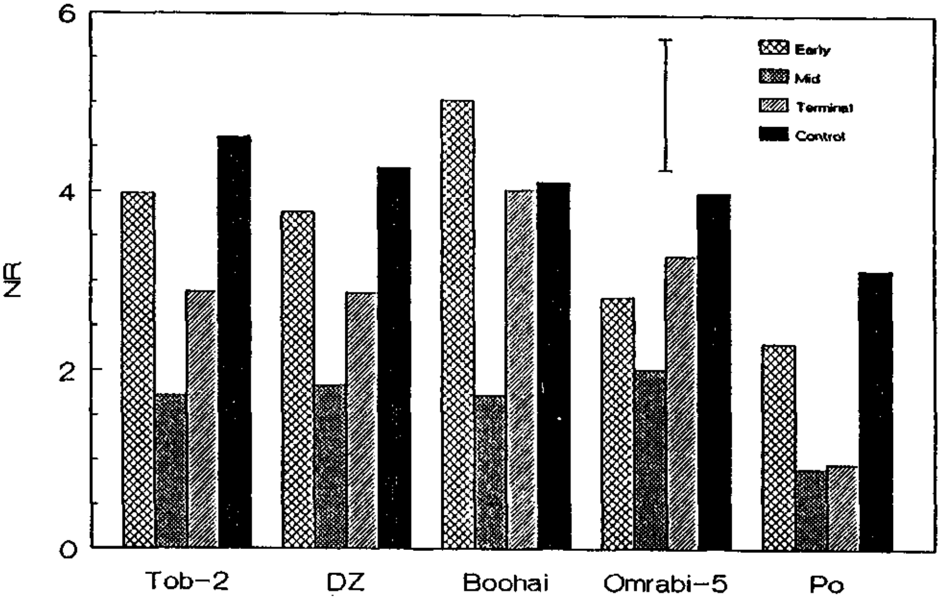


Fig. 7.1 Effect of moisture stress on the grain:straw nitrogen ratio (NR) of five durum wheat cultivars (Exp. 1). Vertical bar indicates LSD (0.05) value.

Table 7.6 Effect of drought stress on contents of nitrogen (N), neutral-detergent fiber (NDF), in-vitro digestibility of organic matter (DOMD) of durum wheat straw (cv. Boohai) in Exp. 2.

Stress	Stem			Leaf			Chaff		
	N%	NDF%	DOMD%	N%	NDF%	DOMD%	N%	NDF%	DOMD%
Early	0.57	74.1	39.4	0.28	46.4	52.8	0.33	68.9	30.1
Terminal	0.45	68.8	44.8	0.28	48.5	52.2	0.36	65.0	34.6
Control	0.45	73.5	39.4	0.25	47.9	52.2	0.32	69.1	25.7
Mean	0.49	72.1	41.2	0.27	47.6	52.4	0.33	67.6	29.7
Sign.	**	**	**	NS	*	NS	NS	**	**
LSD	0.05	2.5	3.1	-	0.3	-	-	2.5	6.2

NS, non significant; * and ** significant at $P < 0.05$ and $P < 0.01$ respectively

positively associated with HI (Fig. 7.3) and its relationship with DOMD% was similar to that of HI (data not shown).

Discussion

The different morphological fractions, i.e., stem, leaf and chaff, varied considerably in nutritive value. This is in agreement with many other reports (Tuah *et al.*, 1986; Capper, 1988; Orskov, 1988; Ramanzin *et al.*, 1991). The leaf fraction contained more ash and N, much less cell-wall component and much more digestible organic matter than stem and chaff. Thus, the ratio of the leaf at harvesting may considerably change the quality of straw.Cultivar differences in the relative proportions of the morphological fractions, however, were not found. Moreover, the stem fraction comprises a much larger proportion of straw than leaves and chaff and much of the leaves and chaff material is lost during harvesting and threshing. The real straw offered to animals contains a larger proportion of stem than indicated in Table 7.1. Therefore, greater emphasis must be given to the stem fraction.

ICARDA bred cultivars Po and Omrabi-5 have higher grain yield potentials than the Ethiopian cultivars Tob-2, DZ and Boohai (Simane *et al.*, submitted). Similarly, straw yield was also better. In agreement with previous reports cultivars varied in straw quality components (White, *et al.*, 1981; Erickson *et al.*, 1982; Capper, 1988). The straw quality of Po (which is the most drought-susceptible one) and Omrabi-5 (which is the most drought

Table 7.7 Correlation matrix among ash, nitrogen (N), neutral-detergent fiber (NDF), acid-detergent fiber (ADF), in-vitro digestibility of organic matter (DOMD) and the dry weight of morphological fractions of durum wheat straw.

	Ash%	N%	NDF%	ADF%	DOMD%
stem					
N%	0.29				
NDF%	0.45*	-0.40			
ADF%	0.39	-0.57**	0.90**		
DOMD%	-0.56**	0.51*	-0.85**	-0.94**	
Stem wt.	-0.72**	-0.32	-0.38	-0.34	0.37
leaf					
N%	0.20				
NDF%	-0.10	0.22			
ADF%	-0.05	-0.15	0.84**		
DOMD%	-0.84**	-0.20	0.10	-0.02	
Leaf wt.	-0.57**	0.06	0.80**	0.61**	0.54*
chaff					
N%	-0.65**				
NDF%	0.16	-0.52*			
ADF%	0.46*	-0.84**	0.73**		
DOMD%	-0.89**	0.85**	-0.34	-0.70**	
Chaff wt.	-0.10	-0.51*	0.51*	0.58**	-0.17

*, ** significant at $P < 0.05$ and $P < 0.01$ respectively.

-resistant), wascomparable and better than the straw quality of cultivars from Ethiopia. This agrees with their lower HI and NR, especially when exposed to early or terminal stress (Table 7.2 and Fig. 7.1). Variation in straw quality, however, did not consistently associate either with yield potential or with drought susceptibility, confirming earlier reports (Capper, 1988; Tuah *et al.*, 1986). Omrabi-5 showed good quality straw and is the most drought-resistant cultivar (Simane *et al.*, submitted[2]). This could be attributed to its high yield potential, root:shoot ratio, optimum leaf area, and phenological plasticity. The difference in straw quality without affecting the grain yield provides a scope to improve the feeding value of wheat straw through breeding.

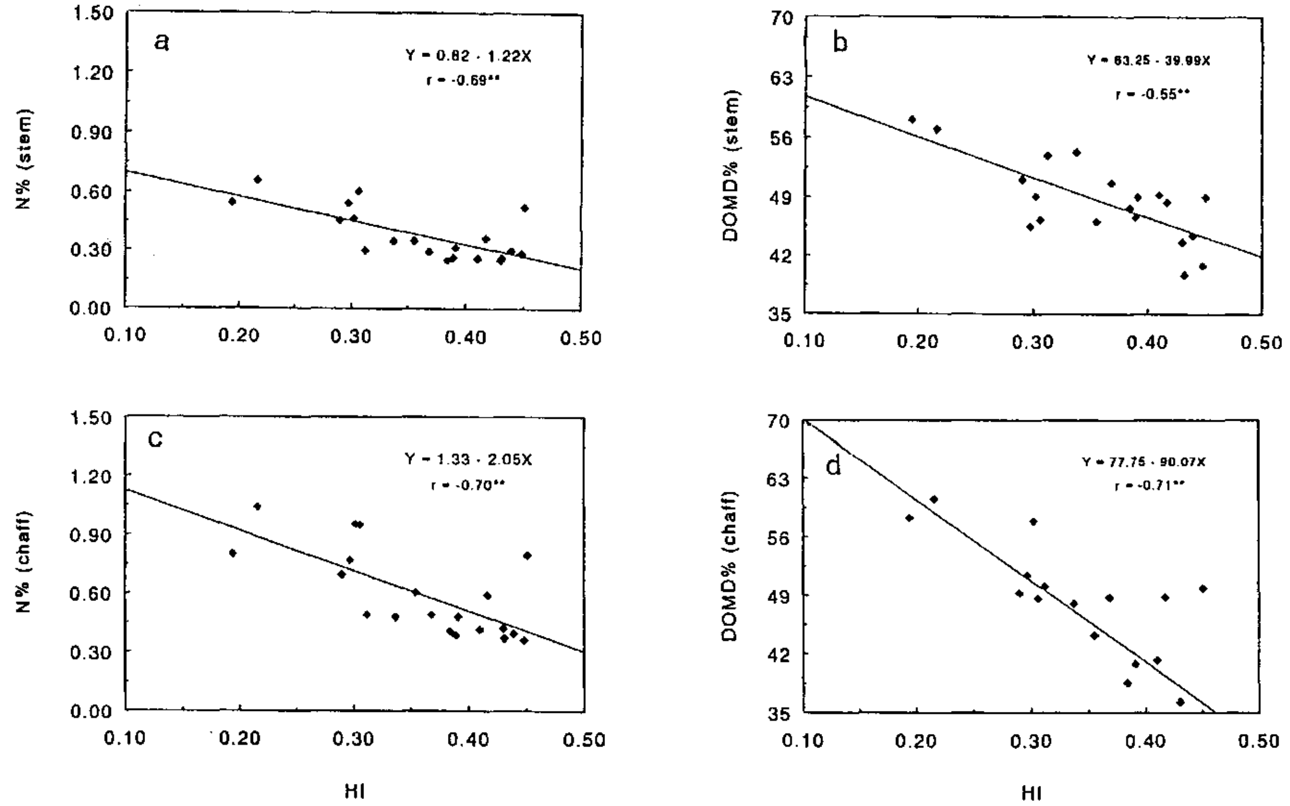


Fig. 7.2 The relationship between harvest index (HI) and some important straw quality parameters of five durum wheat cultivars grown under different drought regimes (Exp. 1). a) nitrogen content of the stem (N% stem), b) in-vitro digestibility of stem (DOMD%), c) nitrogen content of chaff (N% chaff) and d) in-vitro digestibility of chaff (DOMD% chaff).

Drought stress, in agreement with previous reports (Wilson, 1982; Capper, 1988), changed the morphological composition and improved the quality of the fractions, but reduced the biomass per unit area. Early stress retarded the development of leaf, whereas mid-stress reduced stem and chaff fractions. Terminal stress affected the chaff fraction most. The improved quality of the straw when stressed can be explained by the reduced development of organs to a later stage, especially reduced seed development. This allows much of the resources required for grain growth (like nitrogenous compounds and water soluble carbohydrates) to remain in the leaves and stems, promoting higher nutritive value (Van Soest, 1988). This is clearly demonstrated by low values of HI (Table 7.2) and NR (Fig. 7.1) of stressed treatments and the negative relationships of N and DOMD with HI (Fig. 7.2). Moreover, the mass of ash and some organic matter components per unit area were similar for stressed and non-stressed treatments. The low biomass yield per unit area under stress, therefore, may lead to increased concentration in N and other important minerals that can contribute to improve quality of straw.

The positive relationship of N with DOMD is a rumen related factor and confirms other previous reports (Tuah *et al.*, 1986; Orskov, 1987; Ramanzin *et al.*, 1991). N is the major factor in determining the activities of rumen microbes, thus it enhances rate and extent of fermentation. The negative relationship of ash content and NDF with DOMD is probably due to the effects of components like silica and lignin on the digestibility of the straw (Akin, 1982).

The correlation between post-anthesis water use and harvest index reported previously (Simane *et al.*, submitted^2), suggests that grain yield is highly dependent on biomass accumulation after anthesis. However, the low HI and NR of the drought-susceptible cultivar (Po) confirmed that remobilization of pre-anthesis-assimilates is one plant response to drought (particularly under terminal drought). This is in accord with the findings of Bidinger *et al.* (1977), Blum *et al.* (1983) and Ludlow and Muchow (1988). Bidinger *et al.* (1977) reported that up to 20% of the grain yield can be due to pre-anthesis assimilates in drought-stressed wheat. The high transfer of assimilates to the grain reduced straw quality (Fig. 7.2) and increased HI (Fig. 7.3). However, it is very likely that variation in the digestibility of the non-soluble fraction of the straw contributed to the quality differences observed. Especially the differences between cultivars may be partly due to differences in cell-wall digestibility as in many other crops (Deinum and Bakker, 1981; Deinum, 1988).

The result, presence of cultivar differences in straw quality, yield potential and drought-resistance, indicate the possibility to select durum wheat cultivars, with adequate nutritive value of straw without affecting grain yields and drought-resistance.

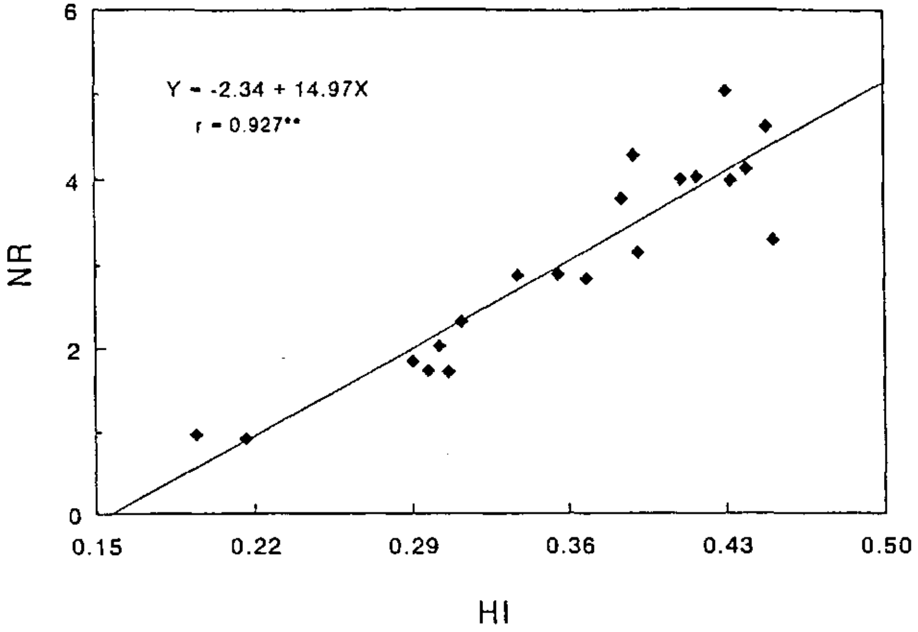


Fig. 7.3 The relationship between harvest index (HI) and grain:straw nitrogen ratio (NR) of five durum wheat cultivars grown under four different drought regimes.

References

Akin, D.A., 1982. Microbial breakdown of feed in the digestive tract. *In*: Hacker, J.B.H. (Editor), Nutritional limits to animal production from pastures. St. Luica, Queensland, Australia (August 24th-28th, 1981). Commonwealth Agricultural Bureaux, Farnham House, Slough, SL2 3BN, UK. pp 201-223.

Bidinger, F.F., Musgrave, R.B. and Fischer, R.A., 1977. Contribution of stored pre-anthesis assimilates to grain yield in wheat and barley. Nature, 270: 431-433.

Blum, A., Poiarkova, H., Gozlan, G. and Mayer, J., 1983. Chemical desiccation of wheat plants as a simulator of post anthesis stress. 1. Effects of translocation and kernel growth. Field Crops Res., 6: 51-58.

Capper, B.S., 1986. The feeding value of straw from different genotypes of barley when given to Awassi sheep. Anim. Prod., 42: 337-342.

Capper, B.S., 1988. Genetic variation in the feeding value of cereal straw. Anim. Feed Sci. and Technol., 21: 127-140.

Deinum, B., 1988. Cereal breeding, A ruminant nutrition point of view. *In*: Singh, K. and Schiere, J.B. (Editors), Fibrous crop residues as animal feed. Indian Council of Agricultural Research (ICAR), New Delhi, India. pp. 143-150.

Deinum, B. and Bakker, J.J., 1981. Genetic differences in digestibility of forage maize hybrids. Neth. J. Agric. Sci., 29: 93-98.

Erickson, D.O., Mayer, D.W. and Foster, A.C., 1982. The effects of genotypes on the feed value of barley straw. J. Anim. Sci., 55: 1015-1026.

Goering, H.K. and Van Soest, P.J., 1970. Forage fiber analysis (Apparatus, Reagents, Procedures, and some Applications). Agricultural Handbook No. 379, Agricultural Research Service, U.S.D.A., 20 pp.

Harris, H.C., 1989. Implication of climatic variability. *In*: Harris, H.C., Cooper, P.J.M. and Pala, M. (Editors). Soil and crop management for improved water use efficiency in rainfed areas. International Centre for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria. pp. 21-34.

Ludlow, M.M. and Murchow, R.C., 1988. Critical evaluation of the possibilities of modifying crops for higher production per unit precipitation. *In*: Bidinger, F.R. and Johansen, C. (Editors), Drought research priorities for the dry land tropics. International Crop Research Institute for the Semi-Arid Tropics (ICRISAT). Patancheru, A.P. 505 324, India. pp. 179-211.

Nachit, M.M. and Ouassou, A., 1988. Association of yield potential, drought tolerance and stability of yield in *Triticum turgidum* var. *durum*. *In*: Proceedings of the 7th International Wheat Genetics Symposium, Cambridge, UK, 10-13 July 1988. pp. 867-870.

Orskov, E.R., 1988. Consistency of differences in nutritive value of straw from different varieties in different seasons. *In*: Reed, J.D.; Capper, B.S. and Neate, P.J.H. (Editors), Plant breeding and the nutritive value of crop residues. International Livestock Centre for Africa (ILCA), Addis Ababa, Ethiopia. pp. 163 - 173.

Ramanzin, M., Bailoni, L. and Beni, G., 1991. Varietal differences in rumen degradation of barley, wheat and hard wheat straws. Anim. Prod.,.53: 143-150.

Simane, B. Peacock, J.M. and Struik, P.C., 1993. Differences in developmental plasticity and growth rate among drought resistant and susceptible genotypes of durum wheat (*Triticum turgidum* var. durum). Plant and Soil, in press.

Simane, B., Struik, P.C., Nachit, M.M. and Peacock, J.M. Ontogenetic analysis of yield components and yield stability of durum wheat in water-limited environments. Euphytica, submitted[2].

Simane, B., Struik, P.C. and Peacock, J.M. Water use efficiency of durum wheat genotypes differing in drought grown under different moisture regimes. Plant and Soil, submitted[1].

Tilley, J.M.A. and Terry, R.A., 1963. A two stage technique for the in vitro digestion of forage crops. J. Br. Grassl. Soc., 18: 104-111.

Tuah, A.K., Lufadeju, E. and Orskov, E.R., 1986. Rumen degradation of straw. 1. Untreated and ammonia-treated barley, oat and wheat straw varieties and triticale straw. Anim. Prod., 43: 261-269.

Van Schoonhoven, A., 1989. Soil and crop management for improved water use efficiency in dry areas: the challenge. *In*: Harris, H.C., Cooper, P.J.M. and Pala, M. (Editors). Soil and crop management for improved water use efficiency in rainfed areas. International Centre for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria. pp. 3-8.

Van Soest, P.N., 1988. Effect of environment and quality of fibre on the nutritive value of crop residues. *In*: Reed, J.D., Capper, B.S. and Neate, P.J.H. (Editors), Plant breeding and the nutritive value of crop residues. International Livestock Centre for Africa (ILCA), Addis Ababa, Ethiopia. pp. 71-94.

White, L.M., Hartman, G.P. and Bergman, J.W., 1981. In vitro digestibility, crude protein and phosphorus content of straw of winter wheat, spring wheat, barley and oat cultivars in Eastern Montana. Agron. J., 73: 117-121.

Wilson, J.R., 1982. Environmental and nutritional factors affecting herbage quality. *In*: Hacker, J.B.H. (Editor), Nutritional limits to animal production from pastures. St. Luica, Queensland, Australia (August 24th-28th, 1981). Commonwealth Agricultural Bureaux, Farmham House, Slough, SL2 3BN, UK. pp. 111-131.

General discussion

Characterization of the target environment

Agroclimatic analysis

In the semi-arid and arid tropics, rainfall variability is the major climatic factor affecting crop yields. The effective cropping season in the semi-arid environments is restricted by the rainfall amount and distribution, thereby setting limits on choice of crops, cultivars and cropping systems. Matching the phenology of the cultivars to the expected water supply is, therefore, the most important approach to dryland farming (Ludlow and Muchow, 1988). Quantitative descriptions of the patterns and the probabilities of water availability in the target environment are required before starting a breeding programme for drought-tolerance. Important aspects of the environment in relation to dryland farming are discussed in Chapter 1. Relevant historical weather data (rainfall, evapotranspiration, temperature, day length) and soil characteristics of six different locations in Ethiopia were analyzed using different models. This revealed that rainfall (especially its distribution) is the most important yield limiting factor. In Ethiopia, as it is a highland country, temperature is not limiting production.

Markov chain procedure (rainfall distributions at different probability levels) were used to define the dependability of rainfall that helps in developing alternate production strategies. A method to determine the start and the end of the growing season has been described using the weather data and soil characteristics. Early onset of rainfall indicates increased probabilities of more rainfall, so longer season cultivars, increased population density and fertilizers should be used. Conversely, if the start is late different sets of decisions are important. The results suggest that the crop maturity group and cropping systems should be planned separately for the different agroclimatic-soil regions. The final decision on the optimum growth period has to consider additional factors such as disease and insect incidence.

Another important factor, which is overlooked in the country, is the high rate of soil degradation due to water erosion. Although rainfall shortages limit production in many dryland regions, the highland parts of Ethiopia are highly susceptible to water erosion. Up to 50% of the total annual rainfall is lost as run-off. This is mainly due to the high-intensity rain storms and cultivation of sloping lands. This calls for effective soil conservation measures to arrest soil degradation.

Use of crop growth models

In the semi-arid tropics factors influencing production such as weather condition, soil type, and agricultural practices are enormous and variable. Field experiments in all desirable situations are impossible (Van Keulen and Seligman, 1987; Penning de Vries *et al.*, 1992). Under such conditions dynamic crop growth models to plan optimum plant type and productivity in the target environment are useful tools. A broad overview of crop growth models and their application is presented elsewhere (Rabbinge *et al.*, 1989; Penning de Vries *et al.*, 1992). SUCROS-87 (a spring wheat growth model) was used to estimate potential durum wheat production for different agro-ecological regions to provide perspectives and goals for plant breeders and management advice (Chapter 2). Durum wheat in many regions is subjected to temporally and spatially variable drought stress. The cultivars, which are currently under production appeared not to be adapted to the prevailing weather conditions (moisture availability period).

The simulated potential yields are much higher than the actual farmers' yields. This suggests the enormous possibility of increasing production on one hand and the challenge to achieve this attainable yield on the other. Similar approaches have shown considerable scope for evaluating crops, crop varieties and cropping systems in many semi-arid and arid regions: wheat in Syria (Harris *et al.*, 1987), Zambia (Van Keulen and De Milliano, 1984) and South East Asia (Aggarwal and Penning de Vries, 1988); maize in North China plane (Wu *et al.*, 1989); yield levels of various food crops on a regional scale (Van Keulen and Wolf, 1986).

Several soil and crop management factors, such as plant density, fertilizer application, fungicide application, irrigation schedule, etc., may be addressed using sufficiently powerful models (Rabbinge *et al.*, 1989).

Potential yield and yield stability

The main objective of any breeding program is obviously the yield potential. However, yield stability is of prime interest to farmers in regions where moisture availability is highly variable from season-to-season. Three major breeding strategies have been proposed regarding yield potential and stability. Several plant breeders believe that a variety with superior yields under optimal conditions will also yield well under drought conditions, since yield performance of a genotype under stress is a reflection of both its potential yield level and its yield response to the stress (Johnson and Geadelman, 1989; Whitehead and Allen, 1990). Others reported that under drought-stress, potential yields are irrelevant, because optimal growing conditions never exist and varieties with superior drought resistance should be developed under representative conditions (Ceccarelli, 1987; Ceccarelli and Grando, 1991; Simmonds, 1991). The argument given in this strategy was that selection for yield potential reduces tolerance to stress. A third alternative strategy is that yield potential and stability are independent of each other, and can be combined (Ceccarelli et al., 1992; Ud-Din *et al.*, 1992). Nachit (1989) proved this by applying a synthetic approach with simultaneous selection in low-yielding and high-yielding environments to combine yield potential with drought-resistance.

In environments with variable rainfall pattern both yield stability and potential yields are equally important. In the present study, a direct relationship between yield potential and yield stability under water-limited environments was not found (Chapter 3). This suggests that both parameters are controlled independently and can be combined. One of the drought resistant cultivars, Omrabi-5, is highly stable under drought and potentially high yielding under optimum conditions. This suggests that the genetic control of both parameters is independent and that both parameters can be combined in a favourable way as used by Nachit (1989).

Ontogenetic analysis of yield components

The plant architecture approach has been the subject of many breeders since the "ideotype concept" by Donald (1968). Selection is based on yield components rather than on yield *per se*. However, it has not made much impact under drought-stress conditions. This is because yield components are determined at different stages and an early-developing yield component is affecting the later-developing ones in compensatory patterns, particularly when there is shortage of resources (such as water, N) (Fischer, 1985; Blum, 1983). A method to study the cause-effect relationships of duration of vegetative period (VP) and grain-filling period (GFP), yield components (number of spikes per m^2 (S/m^2), number of kernels per spike (K/S) and individual kernel weight (KW) and grain yield (GY) was presented in Chapter 3.

The duration of vegetative period had a significant negative effect on GFP and subsequently on GY, particularly under terminal moisture stress. This effect is mainly due to the depletion of soil water which in turn reduces photosynthesis during grain filling period, in accord to other reports (Garcia del Moral *et al.*, 1991).

Number of spikes per m^2 had a significantly positive direct effect on GY. The negative direct effect of S/m^2 on K/S and KW suggests a compensatory effect between tillering and apical growth. The importance of tillering as a selection index is still unresolved, especially under water-limited environments. Hadjichristodoulou (1985) advocated profuse tillering capacity, whereas others (Islam and Sedgley, 1981; Dofing and Karlsson, 1993) advocated 'uniculm ideotypes' for water-limited environments. Cultivars with high tillering capacity are associated with increased vegetative growth. This exhausts the limited available soil water and affects the source:sink ratio during the grain filling period and will result in low harvest index. Limited numbers of tillers, *i.e.* genotypes having two or three tillers will do better under water-limited conditions (Common and Klink, 1981). However, the heritability of tillering should be further investigated.

Number of kernels per spike has got a positive direct effect on grain yield under all conditions. Increased K/S could be used as a selection criterion under water-limited environments. Wheat production is normally sink-limited during the grain-filling period (Fischer, 1985; Slafer and Andrade, 1991).

Individual kernel weight was highly stable, possibly due to the high proportion of remobilization of pre-anthesis reserves as a source for grain filling when the photosynthetic source is limited by stress (Austin *et al.*, 1980; Blum, 1983).

Under water-limited conditions characters associated with drought-resistance are GFP, S/m^2 and K/S. Genetic variation for all these characters was available and these can be used as selection criteria to improve drought-resistance.

Physiology of drought-resistance

Drought resistance does not exist as a unique heritable plant attribute and research should aim at understanding the specific components of physiological responses of plants to water stress and their association with grain yield. The major focus of dryland cropping systems is increasing the efficiency of water use. Grain yield (GY) under water-limited conditions is the product of water used (T), water use efficiency (WUE) and harvest index (HI) (Passioura, 1977). The application of this model in plant breeding has been extensively discussed by Fischer and Turner (1978) and Richards (1987). The components are largely independent of each other and focus directly on the processes that affect productivity in dryland farming.

Water use

Total water use (ET) was not significantly different between drought-resistant and -susceptible cultivars. However, the ratio of pre-anthesis to post-anthesis water use (ET_{ba}:ET_{pa}) was different among cultivars. Drought-resistant cultivars used much more water during grain filling than the drought-susceptible cultivar. In contrast, the drought-susceptible cultivar used relatively more water during its vegetative period. The negative relationship of ET_{ba}:ET_{pa} with HI and WUE based on grain yield (WUE_g) showed that grain yield is influenced by the post-anthesis water supply, confirming the results of Fischer and Turner (1978).

Water use efficiency (WUE)

Efficient water use may be defined as the improvement of economic return for the investment of water (Tanner and Sinclair, 1983). The term water use efficiency has been defined differently, ranging from gas exchange rates by individual leaves for a few minutes to grain yield response for an entire season (Tanner and Sinclair, 1983; Gregory, 1989).

This brought a great confusion over its use. The definition of WUE from the agronomy point of view and its proper application in plant breeding is explicitly defined in Chapter 4. Although cereal straw is an important animal feed in the semi-arid tropics, grains are usually the sole marketable commodity for the farmers (Gregory, 1989). The results indicated that defining WUE based on grain yield and/or above ground dry matter and harvest index together is more logical and appropriate to breeders and farmers.

The quantity of water may be expressed in total water use (evaporation + transpiration, ET) or transpiration component only. In the agronomic sense, the transpiration component is more important. However, separating evaporation from transpiration is difficult under field conditions (Van Keulen, 1975; Cooper *et al.*, 1987).

The magnitude of evaporation depends on crop cover, moisture content of the soil, its texture, *etc.* Selection of cultivars that reaches full ground cover quickly (early vigour) could minimize soil evaporation and crops may extract as much water as possible (Fisher and Turner, 1978; Tanner and Sinclair, 1983; Ludlow and Muchow, 1988). However, there are high risks associated with this strategy in environments with an erratic rainfall distribution because the crop will exhaust the available soil water before maturity. Particularly in areas where terminal moisture stress is the predominant constraint, a more conservative strategy is preferred to complete grain filling.

Carbon isotope fractionation ($^{13}\delta$)

The use of stable isotopes is increasing to understand the physiological ecology especially in studies on water use efficiency. During the assimilation of carbon, the naturally occurring isotope ^{13}C is discriminated against ^{12}C because of its greater molecular weight (Farquhar and Richard, 1984). The discrimination will be least in plants that assimilate the greatest amount of carbon per unit of water transpired (drought-resistant). Substantial variation in $^{13}\delta$ among genotypes was found (Chapter 4). The negative correlations of $^{13}\delta$ with WUE_g, HI and positive correlation with $ET_{ba}:ET_{pa}$ confirmed the usefulness of the method as a screening tool for improved water use efficiency in agreement with Farquhar and Richard (1984) and Condon *et al.* (1990).

Measurement of $^{13}\delta$ to estimate WUE has many attractive features: 1) it can be determined on fresh or stored, immature or mature parts of any morphological fraction. 2) very small samples are required, 3) it can be automated using ratio mass spectrometer (Richards, 1987).

Water potential

Total leaf water potential has been suggested as a selection criterion to identify cultivars with a dehydration avoidance strategy in dry environments (Blum, 1988; Siddique *et al.*, 1990). Values of total leaf water potential between stressed and well watered treatments were easily measured. However, differences among genotypes were not consistent. In agreement with other reports (Turner, 1981; Van Keulen, 1975), the present result showed that total leaf water potential is not a useful criterion to select genotypes for increased water use efficiency.

Increased osmoregulation is another way of increasing soil water extraction (Blum, 1988). The role of osmotic adjustment and desiccation postponement must be given due emphasis in future research.

Growth analysis

Crop species/cultivars vary in their growth potential. The ecological advantage of slow-growing plants is their low demands of resources (Lambers and Poorter, 1992). Slow growth exhausts the limiting factors (water) slowly, thus saves for later growth. Growth analysis of durum wheat cultivars in terms of relative growth rate (RGR) and its components (leaf area ratio (LAR), leaf weight ratio (LWR)) revealed that there is sufficient difference among drought-resistant and -susceptible cultivars (Chapter 5) that can be used in breeding for water-limited regions. In many semi-arid tropics, rainfall distribution during the crop growth cycle is different, a cultivar with high RGR during the favourable periods and low during moisture stress periods is more drought-resistant. The higher RGR of drought-resistant cultivars in the early growing season reduces surface water evaporation (E) relative to transpiration (T). Estimates of E as a proportion of evapotranspiration (ET) in Syria ranged from 32% (in fertilized wheat) where ET was 370 mm to 62% (unfertilized barley) where ET was 220 mm (Cooper *et al.*, 1983). The considerable genetic variation in growth rate (rate at which ground cover is achieved) can be used in breeding programmes (Richards, 1987). As measuring RGR is difficult for routine breeding programme, the use of one of its components (LAR) is proven to be satisfactory (Lambers and Poorter, 1992).

Root development

One way of increasing soil water extraction is by increasing root depth (Passioura, 1983). Significant differences in root development and shoot:root ratio among drought-resistant and drought-susceptible cultivars exist, especially after the imposition of drought stress (Chapter 5). Thus, it appears that the potential expression of root growth of cultivars may be influenced by the availability of soil moisture (Miam *et al.*, 1993). The shoot:root ratio decreased largely because shoot growth was inhibited relatively more than root growth under drought stress. Selection for better root development and low shoot:root ratio should be given a high priority in developing drought-resistant cultivars. However, the current available root measurement procedures are difficult to apply in extensive breeding programmes.

Leaf gas exchange

Leaf gas exchange parameters (stomatal conductance, photosynthesis, transpiration and intercellular CO_2 concentration) were examined to study the cellular implications of water deficit and find physiologically-based indirect measures of WUE. However, drought-resistant and drought-susceptible cultivars responded similarly under water stress (Chapter 6). Some authors reported that genetic variation among wheat cultivars exists for these parameters (Richards, 1987). However, instantaneous leaf gas exchange parameters were poor indicators of the plant performance. Therefore, future research should emphasize on whole plant gas exchange rates and leaf area development.

Leaf area

In dryland farming transpiration is linearly related to leaf area up to a leaf area index (LAI) of about 3 (Richards, 1987). Therefore WUE is directly related to leaf area throughout the season and a reduced leaf area development will conserve water for grain filling. Significant cultivar differences were found between drought-resistant and -susceptible cultivars with growth stage in the rate of leaf area development. Drought-resistant cultivars had a faster leaf area development early in the season and a very slow one after stem elongation. In contrast the drought-susceptible cultivars showed a very slow leaf area development initially and a very fast one late in the season.

Harvest Index (HI)

Harvest index is determined by the proportion of the total water supply that is available to the crop after anthesis, *i.e.* the balance between dry matter produced before and after anthesis and the amount of remobilized pre-anthesis assimilates. HI is much below the potential under drought conditions. Variation among cultivars and moisture treatments were found (Chapters 4 and 7). Under the prevailing weather conditions of the West Asia and North Africa (WANA) region, HI can be increased if 1) leaf area is reduced 2) flowering is early and 3) tillering is reduced (Richards, 1987). If a crop exhausts most of the soil water before anthesis, little will be left for grain filling. This results in a low HI (Richards, 1987; Ludlow and Muchow, 1988). A strong positive correlation between ET_{pa} (post-anthesis water use) and HI was found. This shows that grain yield is highly dependent on biomass accumulation after anthesis.

Straw quality and assimilate remobilization

Straw quality and quantity are additional important factors in WANA. Straw quality differed among cultivars. The different morphological components, i.e. stem, leaf and chaff, varied significantly in yields, chemical composition and digestibility. Relative proportions of morphological fractions were similar for all cultivars, but different times of drought stresses affected the relative proportions of stem:leaf:chaff differently. Straw quality of the drought-susceptible (Po) and the drought-resistant (Omrabi-5) cultivars, was higher in feed quality than those of cultivars from Ethiopia. Drought stress considerably improved straw quality.

Remobilization of pre-anthesis assimilates is one plant response to drought, especially under terminal drought (Blum and Pnuel, 1990; Ludlow and Muchow, 1988). Grain:straw nitrogen ratio (NR) varied among cultivars and drought treatments. The drought-susceptible cultivar (Po) had the lowest rate of N remobilization from straw to the grains.

Application

It has been noted that breeding for drought resistance is complex and that no selection index can be used singly for achieving progress. A successful dryland improvement programme should involve integration of several drought-related criteria in a system approach. Matching the phenology of the crop to the expected water supply is the most important approach (Ludlow and Muchow, 1988). Analysis of historical weather data and regionally adapted crop growth models as used in this report could be used to define strategic and tactical decisions.

Much of the selection of wheat has been done under optimal and uniform growing conditions with subsequent testing in drought-stressed environments using an empirical approach only. However, using both an analytical approach (which uses indirect selection for yield by selecting for physiological parameters) in early generations and an empirical approach in the final stage will be much more effective (Blum, 1988). A number of traits that can be used are suggested. The application of particular indirect screening techniques for a practical breeding program depends on:

- the availability of genetic variation
- the heritability of the character
- whether the character can be easily recognised and/or measured.

Other important considerations are the cost and time effectiveness of using a particular trait.

Besides genetic improvement, methods of soil and crop management to increase efficiency of water use should be explored. Crop management, such as narrow spacing and nitrogen fertilizer application at planting have increased the rates of ground cover and consequently reduced the evaporation (E) from the soil (Richards, 1987). Several agronomic practices have been proposed to reduce soil evaporation, thus increasing water use efficiency (Fischer and Turner, 1978; Tanner and Sinclair, 1983; Cooper *et al.*, 1987; Gregory, 1989).

The results indicate that there are possibilities to improve the current low and variable durum wheat production in the semi-arid regions. This can be achieved by integrating all possible ways, from defining the target environment to the utilization of morphological, physiological and metabolic indirect selection traits in conjunction with yield testing, into a coherent system approach for the different target ecoregions. The research has shown the potentials of agronomic and breeding activities to improve water use efficiency in the semi-arid regions and the information will be valuable as a guidance for future research in water-limited environments.

References

Aggarwal, P.K. and Penning de Vries, F.W.T., 1989. Potential production of wheat in Southeast Asia. Agricultural Systems, 30: 49-69.

Austin, R.B., Morgan, C. L., Ford, M.A. and Blackwell, R.D., 1980. Contribution to grain yield from pre-anthesis assimilation in tall and dwarf barley phenotypes in two contrasting seasons. Annals of Botany 45: 309-319.

Blum, A., 1983. Genetic and physiological relationships in plant breeding for drought resistance. Agric. Water Mng., 7: 195-205.

Blum, A., 1988. Plant breeding for stress environments. CRC Press, Florida, 223 pp.

Blum, A. and Pnuel,Y., 1990. Physiological attributes associated with drought resistance of wheat cultivars in a Mediterranean environment. Aust. J. Agric. Res., 41: 799-810.

Ceccarelli, S. 1987. Yield potential and drought tolerance of segregating populations of barley in contrasting environments. Euphytica, 36: 265-273.

Ceccarelli, S. and Grando, S., 1991. Environment of selection and type of germplasm in barley breeding for low-yielding conditions. Euphytica, 57: 157-167.

Ceccarelli, S., Valkoun, J., Erskine, S., Weigand, S. Miller, R. and Van Leur, J.A.G., 1992. Plant genetic resources and plant improvement as tools to develop sustainable agriculture. Expl. Agric., 28: 89-98.

Common, J.C. and Klink, H.R., 1981. Sequence and synchrony of culm development: implication in breeding for limited tillering barleys. *In*: Barley Genetics IV. Proc. 4th Int. Barley Genet. Symp., Edinburgh, Scotland. Edinburgh Univ. Press. pp. 533-536.

Condon, A.G., Farquhar, G.D. and Richards, R.A., 1990. Genotypic variation in carbon isotope discrimination and transpiration efficiency in wheat. Leaf gas exchange and whole plant studies. Aust. J. Plant Physiol., 17: 9 - 22.

Cooper, P.J.M., Gregory, P.J., Tully, D. and Harris, H.C., 1987. Improving water use efficiency of annual crops in the rainfed farming systems of West Asia and North Africa. Exp. Agric., 23: 113-158.

Dofing, S.M. and Karlsson, M.J., 1993. Growth and development of uniculm and conventional-tillering barley lines. Agron. J., 85: 58-61.

Donald, C.M., 1968. The breeding of crop ideotypes. Euphytica, 17: 385-403.

Farquhar, G.D. and Richards, R.A., 1984. Isotopic composition of plant carbon correlates with water use efficiency of wheat genotypes. Aust. J. Plant Physiol., 11, 539 - 552.

Fischer, R.A., 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. J. Agric. Sci., 105: 447-461.

Fischer, R.A. and Maurer, R., 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res., 29: 897-912.

Fischer, R.A. and Turner, N.C., 1978. Plant productivity in the arid and semi-arid zones. Ann. Rev. Plant. Physiol., 29: 277-317.

Garcia del Moral, L.F., J.M. Ramos, M.B. Garcia del Moral, M.B. & Jimenez-Tejada, M.P., 1991. Ontogenetic approach to grain production in spring barley based on path-coefficient analysis. Crop Sci., 31: 1179-1185.

Gregory, P.J., 1989. Concepts of water use efficiency. *In:* Harris, H.C., Cooper P.J.M. and Pala, M. (Editors), Soil and crop management for improved water use efficiency in rainfed areas. ICARDA, Aleppo, Syria. pp. 9-20.

Hadjichristodoulou, A., 1985. The stability of the number of tillers of barley genotypes and its relation with consistency of performance under semi-arid conditions. Euphytica, 34: 641-649.

Harris, H.C., Goebel, W. and Cooper, P.J.M., 1987. Crop genotype-environment interaction. *In:* Srivastava, J.P., Porceddu, E., Acevedo, E. and Varma, S. (Editors), Drought tolerance in winter cereals. Cambridge University Press, UK. pp. 37-50.

Islam, T.M. and Sedgley, R.H., 1981. Evidence for a 'uniculm effect' in spring wheat (*Triticum aestivum* L.) in a Mediterranean environment. Euphytica, 30: 277-283.

Johnson, S.S. and Geadelman, J.L., 1989. Influence of water stress on grain yield response to current selection in maize. Crop Sci., 29: 558-564.

Lambers, H. and Poorter, H., 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Advances in Ecological Research, 23: 187-261.

Ludlow, M.M and Muchow, R.C., 1988. Critical evaluation of the possibilities for modifying crops to high production per unit of precipitation. *In:* Bidinger, F.R. and Johansen, C. (Editors), Drought research priorities for the dryland tropics. ICRISAT, Patancheru, A.P.502 324 India. pp. 179-211.

Miam, M.A.R., Nafziger, E.D., Kolb, F.L. and Tayker, R.H., 1993. Root growth of wheat genotypes in hydroponic culture and in the greenhouse under different soil moisture regimes. Crop Sci., 32: 283-286.

Nachit, M.M., 1989. Moisture stress tolerance and yield stability in durum wheat (*Triticum turgidum* L. var. *durum*) under Mediterranean dryland conditions. *In:* Science for Plant Breeding, Book of Poster Abstracts Part II, Poster Groups 16-33, Abstract 23-2. XII EUCARPIA Congress, 27 February - 4 March 1989, Göttingen, F.R. Germany, The Mann Publishers, Gelsenkirchen, F.R. Germany.

Passioura, J.B., 1977. Grain yield, harvest index and water use of wheat. J. Aust. Inst. Agric. Sci. 43, 117-120.

Penning de Vries, F.W.T., Jansen, D.M., ten Berg, H.F.M. and Bakema, A., 1992. Simulation of ecophysiological processes and growth in several annual crops. Simulation Monographs 29. IRRI, Los Banos, PUDOC, Wageningen.

Rabbinge, R., Ward, S.A. and Laar, H.H. van, 1989. Simulation and systems management in crop protection. Simulation Monographs 32. PUDOC, Wageningen.

Richards, R.A., 1987. Physiology and the breeding of winter-grown cereals for dry areas. *In:* Srivastava, J.P., Porceddu, E., Acevedo, E. and Varma, S. (Editors), Drought tolerance in winter cereals. Cambridge

University Press, UK. pp. 133-150.

Siddique, K.H.M., Tennant, D., Perry, M.W. and Belford, R.K., 1990. Water use and water use efficiency of old and modern wheat cultivars in a Mediterranean-type environment. Aust. J. Agric. Res., 41: 431-447.

Simmonds, N.W., 1991. Selection for local adaptation in a plant breeding program. Theor. Appl. Agric., 17: 363-367.

Slafer, G.A. and Andrade, F.H., 1991. Changes in physiological attributes of the dry matter economy of bread wheat (*Triticum aestivum)* through genetic improvement of grain yield potential at different regions of the world. Euphytica, 58: 37-49.

Tanner, C.B. and Sinclair, T.R., 1983. Efficient water use in crop production: research or re-search?. *In*: Taylor, H.M., Jordan, W.R. and Sinclair, T.R. (Editors), Limitations to efficient water use in crop production. ASA, CSSA, SSSA, pp. 1-27.

Turner, N.C., 1981. Techniques and experimental approaches for the measurement of plant water status. Plant and Soil, 58: 339-366.

Ud-Din, N., Carver, B.F. and Clutter, A.C., 1992. Genetic analysis and selection for wheat yield in drought-stressed and irrigated environments. Euphytica, 62: 89-96.

Van Keulen, H., 1975. Simulation of water use and herbage growth in arid regions. Simulation Monographs. Pudoc, Wageningen.

Van Keulen, H and de Milliano, W.A.J., 1984. Potential wheat yields in Zambia: a simulation approach. Agric. Systems, 14: 171-192.

Van Keulen, H. and Seligman, N.G., 1987. Simulation of water use, nitrogen nutrition and growth of spring wheat crop. Simulation Monographs. Pudoc, Wageningen.

Van Keulen, H. and Wolf, J., 1986. Modelling of agricultural production: weather, soils and crops. Simulation Monographs. Pudoc, Wageningen.

Whitehead, W.F. and Allen, F.L., 1990. High- vs. low-stress yield test environments for selecting superior soybean lines. Crop Sci., 30: 912-918.

Wu, Y., Sakamoto, C.M. and Botner, D.M., 1989. On the application of the CERES-Maize model to the North China Plain. Agric. For. Meteorol., 49: 9-22.

Summary

Drought is the major factor limiting crop production of dryland farming systems in the semi-arid and arid regions of the world. In these regions durum wheat production is low and variable due to low and erratic rainfall. The goal of the research discussed was to assess a system approach to improve drought tolerance of durum wheat.

The first step in planning the ideal plant type for a particular environment is defining the target environment. Different climatic models were used to examine historical weather data for six locations representing different ecoregions of Ethiopia. Among the weather elements examined, rainfall was highly variable and seasonal, limiting durum wheat production. The historical weather data and soil parameters were used to set criteria to mark the beginning and the end of the growing season. The result emphasized that the matching of the phenology of the crop or cultivar to the prevailing weather conditions. Moreover soil erosion should be taken into consideration in planning improvement strategies in the country.

A dynamic crop growth model was used as a next step to define the most appropriate phenology and yield potentials for the different agro-ecological zones. Although intermittent drought stresses of different magnitude were identified, terminal drought was predominant, occurring in 7 out of 10 years in most locations. The average simulated potential grain yields at all locations were high compared with the actual national average, indicating the scope of improving durum wheat productivity. Developments of versatile and region-specific improvement strategies are suggested to improve durum wheat production. The results revealed that many of the durum wheat cultivars are not adapted to the prevailing rainfall pattern of different regions in Ethiopia where they are grown.

Field and greenhouse experiments were conducted to understand the different morphological, physiological and metabolic traits that confer drought-resistance in durum wheat. Five cultivars, differing in drought-resistance, were used in evaluating indirect selection criteria. Plants were grown under four drought-stress conditions, differing in timing and intensity.

The study on the cause-effect relationships of duration of vegetative period, duration of grain filling period, number of spikes/m^2, number of kernels/spike, kernel weight and grain yield revealed a complex pattern of relationships under drought conditions. An increase in the duration of the vegetative period shortened the grain-filling period. The duration of the grain-filling period had a strong influence on grain yield *via* kernel weight. Drought-resistant cultivars were characterized by early flowering and a longer grain-filling period than the drought-susceptible one. More tillering resulted in fewer kernels per spike and low kernel weight and as a result a negative relationship with grain yield under drought. Number of kernels per spike, grain-filling period and tillering had the largest direct effects on grain yield.

Variation in drought-susceptibility among cultivars was significant under early and terminal-stress conditions. Yield potential and stability were not correlated for the different moisture-stress conditions, suggesting the possibility of breeding for a high potential and stable cultivar.

Total water uses (W) by drought-resistant and -susceptible cultivars were similar whereas water use efficiency (WUE) and harvest index (HI) were different. Drought-resistant cultivars used a larger proportion of the total water used in the post-anthesis period. Values of water use efficiency based on grain yield (WUE_g) defined drought-resistance best in the context used for plant breeders and farmers in water-limited environments. Carbon isotope fractionation of grain ($^{13}\delta$) varied among cultivars and moisture treatments, and correlated with WUE and HI. Differences in total leaf water potential among drought-resistant and drought-susceptible cultivars were not found.

Relative growth rate (RGR) and its components (leaf area ratio, LAR, and net assimilation rate, NAR) changed with age and moisture availability. Drought-resistant cultivars had a high RGR in early growth stages and a low RGR after tillering. In contrast, the drought-susceptible cultivar showed an opposite trend. LAR explained the differences in RGR best, whereas the relationship between NAR and RGR was not significant. Though both LWR and SLA were relevant factors determining the potential growth rate, LWR was important to describe cultivar differences in LAR, and consequently in RGR.

Deep rooting (if the soil moisture is not limiting at deeper soil horizons) and low shoot:root ratio are effective components of drought-resistance. The drought-resistant cultivars had vigorous root development and/or a low shoot:root ratio.

Leaf gas exchange traits of drought-resistant and drought-susceptible cultivars of durum wheat grown under different moisture regimes were compared in a greenhouse experiment. Mid-day stomatal conductance, photosynthesis, transpiration rate per unit leaf area and assimilation/transpiration ratio decreased sharply under stress irrespective of its timing. However, there was no cultivar difference. Leaf area development followed the trend of RGR. The drought-susceptible cultivar had very slow leaf area development until the three tiller stage but much faster in later stages. Reduced leaf area is one way of drought avoidance by reducing the amount of water lost through transpiration.

Quantity and quality of straw differed among cultivars. The different morphological components, i.e. stem, leaf and chaff, varied significantly in amounts, chemical composition and digestibility. Straw quality of the drought-susceptible (Po) and the drought-resistant (Omrabi-5) cultivars, was comparable. This suggests the possibility of incorporating both drought-resistance and better straw quality in a cultivar. Drought stress considerably improved straw quality, but decreased grain yield. Remobilization of assimilates is another important way of increasing harvest index under terminal drought-stress, and consequently drought-resistance. Grain:straw nitrogen ratio (NR) was used as an index to evaluate remobilization of assimilates from the vegetative part to the grain. NR varied among cultivars and drought treatments. The drought susceptible cultivar (Po) had the lowest rate of N remobilization from straw to the grain.

The results indicate that there are potentials to improve the current low and variable durum wheat production in the semi-arid regions. These can be achieved by integrating all possible ways, from defining target environment to the utilization of morphological, physiological and metabolic indirect selection traits in conjunction with yield testing, into a coherent holistic system for the different target ecoregions. It is believed that the information will be valuable as a guidance for future research in water-limited environments.

Samenvatting

Droogte is de belangrijkste opbrengstlimiterende factor in de regenafhankelijke landbouwsystemen van de (semi-) aride gebieden. De opbrengst van durumtarwe (*Triticum turgidum* L. var. *durum*) in deze streken is laag en de oogstzekerheid is gering vanwege de lage en variabele neerslaghoeveelheden. Het in dit proefschrift beschreven onderzoek had als doel de verschillende aspekten van droogtetolerantie en watergebruikseffici ëntie bij durumtarwe te analyseren.

De eerste stap naar het definiëren van een planttype dat ideaal is voor een bepaalde teeltsituatie, is het nauwkeurig beschrijven van het beoogde milieu. Verschillende klimaatsmodellen werden gebruikt om de historische weersgegevens voor zes verschillende locaties, die representatief zijn voor de verschillende ecologische zones van Ethiopië, te bestuderen en te evalueren. Van de onderzochte weersgegevens bleek vooral de zeer variabele en seizoensgebonden regenval de opbrengst van durumtarwe sterk te beperken. Op basis van weersgegevens en bodemeigenschappen werden criteria opgesteld waarmee het begin en het eind van het groeiseizoen konden worden vastgesteld. Deze analyse maakte duidelijk dat het zeer belangrijk is om de ontwikkeling van een gewas (of van een ras) nauw te laten aansluiten bij het overheersende weertype. Bovendien werd duidelijk dat het risico van bodemerosie in de beschouwingen dient te worden betrokken.

Als volgende stap werd met behulp van een dynamisch model dat de gewasgroei beschrijft de optimale gewasontwikkeling en de potentiële produktie voor de verschillende agro-ecologische zones benaderd. Daarbij bleek dat er weliswaar kortdurende opbrengstbeperkende droogteperiodes tijdens het groeiseizoen voorkwamen, maar dat een terminale droogtestress het belangrijkst was. Een dergelijke stress kwam op de meeste onderzochte locaties in 7 van de 10 jaar voor.

De groeisimulaties leverden gemiddelde opbrengsten op die veel hoger waren dan de gemiddelde actuele opbrengsten. Er is kennelijk nog veel ruimte voor opbrengststijgingen. De meeste gangbare durumrassen bleken ook niet erg goed aan de heersende omstandigheden te zijn aangepast. De strategieën om via teeltmaatregelen en veredeling de opbrengsten te verbeteren moeten evenwel regio-specifiek en flexibiel zijn.

In veld- en kasproeven werden de verschillende morfologische en fysiologische aspekten van droogteresistentie onderzocht. Hierbij werden de reacties van vijf rassen, die varieerden in droogtegevoeligheid, op watertekorten onderzocht. De toegepaste vochtregimes verschilden daarbij in het tijdstip en de mate van droogtestress.

In de studie naar de oorzakelijke verbanden tussen de duur van de vegetatieve fase, de korrelvullingsduur, het aantal aren per m^2, het aantal korrels per aar en het individueel korrelgewicht enerzijds en de korrelopbrengst per m^2 anderzijds kwamen bij droogte-stress complexe relaties aan het licht. Een verlenging van de vegetatieve groei leidde tot een kortere korrelvullingsfase. De duur van de korrelvulling beïnvloedde de korrelopbrengst sterk vanwege het effect op het korrelgewicht. Droogteresistente rassen bloeiden eerder en hadden een langere korrelvulingsperiode dan het droogtegevoelige ras. Meer uitstoeling leidde tot minder korrels per aar en een lager korrelgewicht, resulterend in een lagere korrelopbrengst per m^2 bij droogte. Het aantal korrels per aar, de korrelvullingsduur en de mate van uitstoeling hadden de grootste directe effecten op de korrelopbrengst.

Er was sprake van significante verschillen tussen rassen in de droogtegevoeligheid, zowel bij vroege droogtestress als bij terminale droogtestress. Potentiële opbrengst en opbrengststabiliteit waren echter niet gecorreleerd voor de verschillende droogte-stress condities zodat het mogelijk lijkt om tegelijkertijd op beide eigenschappen te veredelen.

Het totale waterverbruik was voor droogteresistente en droogtegevoelige rassen niet onderscheidend, maar er werden wel verschillen gevonden in watergebruiksefficiëntie en in oogstindex. De droogteresistente rassen gebruikten relatief meer water tijdens de korrelvullingsfase. Droogteresistente rassen waren daardoor het best te karakteriseren met behulp van de watergebruiksefficiëntie op basis van korrelopbrengst. De koolstof isotoop fractionering (volgens de zogenaamde C^{13} methode) verschilde voor de verschillende rassen en droogtebehandelingen en bleek goed gecorreleerd te zijn met de watergebruiksefficiëntie en de oogstindex. Droogtegevoelige en droogteresistente rassen bleken echter niet te verschillen in de waterpotentiaal van het blad.

De relatieve groeisnelheid (RGR) en zijn componenten (leaf area ratio (LAR) en net assimilation rate (NAR)) veranderden in de tijd en werden tevens beïnvloed door de droogtebehandelingen. Droogteresistente rassen hadden een hoge RGR vroeg in het groeiseizoen, maar een lage RGR na het uitstoelen. Daarentegen bleek het droogtegevoelige ras een omgekeerde trend te vertonen. De LAR verklaarde de verschillen in RGR het beste, terwijl de correlatie tussen RGR en NAR niet significant bleek. Hoewel zowel de LWR (leaf weight ratio) en de SLA (specific leaf area) beide een grote invloed op de potentiële groeisnelheid hadden, bleek de LWR de rasverschillen in LAR (en dus in RGR) het beste te verklaren.

Een diep wortelstelsel (vooropgesteld dat er voldoende vocht in de diepere bodemlagen aanwezig is) en een lage spruit-wortel verhouding zijn belangrijk voor de mate van droogteresistentie. Inderdaad bleken de droogteresistente rassen een sterk ontwikkeld wortelstelsel en een lage spruit-wortelverhouding te hebben.

In een kasproef werden de gasuitwisselingskarakteristieken van de verschillende droogteresistente en droogtegevoelige durumtarwe rassen bij verschillende vochtregimes gemeten en vergeleken. De huidmondjesgeleiding gedurende het midden van de dag, de fotosynthese, de transpiratiesnelheid per eenheid bladoppervlak en de verhouding tussen assimilatie en transpiratie bleken alle sterk te dalen als gevolg van stress. Dit effect werd bij alle begintijdstippen van de stress gevonden. De trend van de ontwikkeling in de tijd van het bladoppervlak was vergelijkbaar met de ontwikkeling van de RGR. Er werd echter geen verschil in respons tussen de rassen gevonden. Het droogtegevoelige ras vertoonde een zeer langzame ontwikkeling van het bladoppervlak totdat het stadium waarin drie zijspruiten gevormd waren, bereikt was. De bladontwikkeling was echter veel sneller na dit stadium. Door deze tragere bladontwikkeling kan droogte worden vermeden omdat immers de hoeveelheid water die door transpiratie verloren gaat, verminderd wordt.

Er werden ook rasverschillen waargenomen in hoeveelheid en kwaliteit van het stro. De hoeveelheden van de verschillende morfologische stro-componenten, t.w. stengel, blad en kaf, alsmede hun chemische samenstelling en verteerbaarheid varieerden. De stro-kwaliteit van het droogtegevoelige ras en de droogteresistente rassen was vergelijkbaar. Het lijkt derhalve mogelijk te selecteren op droogteresistentie zonder de strokwaliteit negatief te beïnvloeden. Droogte-stress had zelfs een positief effect op strokwaliteit, maar een negatief effect op de korrelopbrengst. De redistributie van assimilaten van het stro naar de korrels bleek een belangrijke rol te spelen. Deze redistributie verhoogt de oogstindex bij terminale droogte- stress en draagt daarmee bij aan een verhoogde droogte- resistentie. De verhouding tussen de hoeveelheid stikstof in de korrel en die in het stro (NR) werd gebruikt als index om aan te duiden hoe sterk de redistributie was. De NR bleek sterk te variëren, zowel tussen rassen als tussen droogtebehandelingen. Het droogtegevoelige ras had de laagste snelheid van redistributie van assimilaten van stro naar de korrels.

Op basis van dit onderzoek kan worden geconcludeerd dat er zeker mogelijkheden bestaan om de huidige lage en variabele opbrengsten van durumtarwe in de semi-aride gebieden te verbeteren. Daarbij dient gebruik te worden gemaakt van alle beschikbare middelen: van een juiste definitie van de teeltomgeving tot aan de benutting van indirecte morfologische en fysiologische selectiecriteria in veredelingsprogramma's, opdat een coherente systeembenadering een regio-specifieke uitwerking van de optimale teeltsituatie mogelijk maakt. Moge deze studie daaraan een eerste bijdrage zijn.

Curriculum vitae

Belay Simane was born on 14 July 1957 in Debre Markos, Ethiopia. He finished his high school education in 1975 and received a diploma in Agriculture from the Awassa College of Agriculture, Addis Ababa University, in 1980. In the period between 1980 and 1982, he worked as a researcher in the Ministry of State Farms in Ethiopia. In 1986 he took a master's degree in agronomy from the Timeriazev Agricultural Academy of Moscow. From 1986 to 1989 he worked as a lecturer in the Alemaya University of Agriculture, Ethiopia. From 1989 to 1990 he worked as a research fellow in agroclimatology in the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India.

Since February 1990 he has worked on his doctoral thesis at the Departments of Agronomy and Theoretical Production Ecology, Wageningen Agricultural University under the supervision of Profs P.C. Struik and R. Rabbinge. The field and greenhouse experiments have been done at Debre Zeit, Alemaya University of Agriculture (AUA), Ethiopia, and the International Centre for Agricultural Research in the Dry Areas (ICARDA), Syria. He has been financially supported by the Wageningen Agricultural University, ICARDA and the Alemaya University of Agriculture.