ADAPTATION OF BARLEY TO HARSH MEDITERRANEAN ENVIRONMENTS

CENTRALE LANDBOUWCATALOGUS
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Adaptation of barley to harsh Mediterranean environments

Aanpassing van gerst aan ongunstige Mediterrane milieu's

Proefschrift

ter verkrijging van de graad van
doctor in de landbouw- en milieuwetenschappen,
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BIBLIOTHEEK
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WAGENINGEN

NN 08201, 1579

1. De voorkeur van Syrische boeren voor zwartzadige gerst is een vorm van indirecte selectie voor opbrengststabiliteit.

2. Genen voor droogtetolerantie *per sé* bestaan niet.

3. Overvloedige irrigatie verhoogt in de toekomst de vraag naar droogtetolerante gerstcultivars.

4. Selectie van homozygote, homogene cultivars is nadelig voor de duurzaamheid van de landbouw in gebieden waar lage opbrengsten wél, maar de prevalente stress factoren niet voorspelbaar zijn.

5. Selectie voor opbrengstpotentie is nutteloos voor ongunstige milieu's, omdat het de beperkingen van het milieu niet in beschouwing neemt.
   (W. G. Jansen (1992). Bean production in fragile, unfavorable or marginal environments: overview and issues. In: O. Voysest (Ed.), Research Challenges for Improving Bean Production in Different Crop Growing Situations. CIAT, Cali, Colombia.)

6. Fysiologisch onderzoek naar droogtetolerantie is nutteloos als de fenologie van het gebruikte materiaal niet in beschouwing wordt genomen.

7. Een volledige misoogst van gerst komt in noord Syrië nooit voor.

8. Het feit dat 'university' in Syrië vaak wordt gespeld als 'univercity' suggereert dat daar ook op academisch niveau urbanisatie plaatsvindt.

9. In diverse islamitische landen leidt de vrouwenbeweging een 'undercover' bestaan.

10. Al vernieuwt men de atlas nog zo snel, nieuwe grenzen achterhalen hem wel.

Stellingen behorende bij het proefschrift "Adaptation of barley to harsh Mediterranean environments", publiekelijk te verdedigen door E. J. van Oosterom, woensdag 6 januari 1993 des namiddags te vier uur in de aula van de Landbouwuniversiteit te Wageningen.

to my wife BASMA

Contents

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INTRODUCTION

Growth of Barley in Syria

Barley (*Hordeum vulgare* L.) is an early maturing grain crop, which is especially grown in unfavourable environments. In northern Syria, it is the most important crop in areas receiving less than 300 mm annual precipitation. Yield is limited by low rainfall during the growing season (October-April), low winter temperatures, and high temperatures and hot dry winds during grain filling. Timing and intensity of these stresses, however, are highly variable, causing large fluctuations in grain yield between seasons and locations (Ceccarelli et al., 1991). Grain yield is often below 1 ton ha^{-1} and part of the yield is used for next years' crop (Somel et al., 1984). Under such conditions, a stable yield, which reduces the risk of no grain yield, is more important for local farmers than a high yield potential (Marshall, 1987).

In Syria, barley is sown in autumn, before the occurrence of the first rains (Somel et al., 1984). In the harshest environments, barley is part of a barley-livestock farming system, where it can only economically be grown, because of the need of straw for animal nutrition (Nordblom, 1983b). To maximize their income, farmers in those regions allow sheep to graze the crop. Although this affects crop yields, losses in barley yields are more than compensated for by the expected benefit from sheep growth (Nordblom, 1983a; Yau et al., 1989). At maturity, the crop will be grazed if the expected yields are so low, that direct grazing will be of more benefit than harvesting the crop (Nordblom, 1983b). In such farming systems, biomass production is as important as grain yield.

Strategies to Improve Selection Efficiency

Progress in breeding for harsh environments has been hampered by variable environmental conditions and the associated genotype × environment interactions. To improve the efficiency of selection, the interaction between performance in the testing environment and the target environment has to be minimized. Two possibilities to achieve this have been extensively investigated:

1. Identification of plant traits with a more stable performance across environments than yield. Such traits can serve as criteria for indirect selection for grain yield.
2. Identification of an optimal selection environment.

Indirect selection for grain yield

Selection for individual traits as a tool to improve grain yield has been done by plant breeders since the beginning of breeding. A well-known recent example is the use of Norin 10 dwarfing genes in wheat (Reitz & Salmon, 1968). However, Donald (1968) gave it a new dimension by his proposal of selection for a well-defined crop ideotype. Ideotype breeding has been defined by Rasmusson (1987) as "a method of breeding to enhance genetic yield potential based on modifying individual traits where the breeding goal for each trait is specified". Differences in grain yield are thus explained from an understanding of the traits relevant to the plant ideotype (Fischer, 1981). The major difference with traditional breeding is that for each trait the selection aim is defined, resulting in a model plant (Rasmusson, 1987).

Plant ideotypes have been identified for several crops, e.g., rice (Jennings, 1964), wheat (Donald, 1968), maize (Mock & Pearce, 1975), and barley (Rasmusson, 1987). However, most of these ideotypes have been proposed for favourable environments. The wheat ideotype proposed by Donald (1968), for example, had a short, strong stem; few, small, and erect leaves; a large and erect ear; a single culm. In favourable seasons, lines resembling this ideotype indeed performed better than control lines which produced tillers, but in unfavourable seasons, the difference was smaller (Donald, 1979). This suggests that ideotypes designed for favourable conditions, may not be suitable for unfavourable environments. Before an ideotype breeding program can be started, the target environment has to be well defined (Mock & Pearce, 1975).

Identification of an optimal selection environment

The choice of the optimal selection environment is one of the most controversial issues in plant breeding. Hamblin et al. (1980) listed four criteria a potential selection site must meet to be useful for selecting for high yield and wide adaptation:

1. Yield at the site must be representative of the complete range of target environments.
2. The site must discriminate well between genotypes.
3. Yield level must be high enough to ensure adequate supply of seeds.
4. Mean yields must be consistent across seasons.

Braun et al. (in press) identified irrigated, high-yielding environments as being efficient for selection for wide adaptation for wheat. Consistent increases in yield under drought following selection under near-optimum conditions have been reported (Pfeiffer, 1988). Nachit & Ouassou (1988) and Nachit (1989) proposed, for durum wheat in the Mediterranean region, simultaneous selection in favourable and unfavourable environments to combine yield potential with yield stability. Ceccarelli & Grando (1989) concluded for barley in northern Syria that the efficiency of direct selection for grain yield under stress was low, but still more than six times higher than indirect selection under non-stress. They therefore concluded that selection for low-input environments has to be done in the target environment (Ceccarelli & Grando, 1991a,b). This opinion is supported by numerical simulations of Simmonds (1991). Selection in unfavourable environments, however, does not ensure adequate seed supply and stable yields across seasons.

Research Objectives

The research was initiated with the following objectives:

1. The identification of a combination of morphological and phenological traits, or a plant ideotype, associated with higher yield in environments where both low winter temperatures and terminal drought stress are likely.

2. The assessment of the effect of plant ideotype on yield response.
3. The assessment of the influence of the environment of selection on the yield level and yield response of the selected genotypes.
4. The development of a more efficient selection procedure for breeding programs targeted at harsh Mediterranean environments.

The morphological and phenological basis for adaptation to Mediterranean environments is discussed in chapters 1 and 2. This results in the identification of contrasting plant ideotypes, adapted to terminal drought stressed Mediterranean environments experiencing either cold or mild winters. The effect of plant ideotype on yield and growth parameters is the subject of chapters 3 and 4. In chapter 3, the relation between plant ideotype and consistency in heading date is discussed and a simple model is introduced to assess the influence of plant ideotype on grain yield. Chapter 4 deals with the effect of ideotype on growth parameters (growth rate and leaf area). Chapters 5 and 6 focus on yield and yield response. Chapter 5 discusses the influence of rainfall and temperature on grain yield of two barley entries, both adapted to terminal drought, but representing contrasting plant ideotypes. In chapter 6, genotype × environment interactions for grain yield are analyzed. Chapter 7 finally integrates results of the previous chapters; the effect of plant ideotype on yield and yield response is discussed and recommendations for improving the efficiency of yield selection for harsh Mediterranean environments are made.

References

Braun, H.-J., W.H. Pfeiffer & W.G. Pollmer, In press. Environments for selecting widely adapted spring wheats. Crop Sci.

Ceccarelli, S., E. Acevedo & S. Grando, 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. Euphytica 56: 169-185.

Ceccarelli, S. & S. Grando, 1989. Efficiency of empirical selection under stress conditions in barley. J. Genet. and Breed. 43: 25-31.

Ceccarelli, S. & S. Grando, 1991a. Selection environment and environmental sensitivity in barley. Euphytica 57: 157-167.

Ceccarelli, S. & S. Grando, 1991b. Environment of selection and type of germplasm in barley breeding for low-yielding conditions. Euphytica 57: 207-219.

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

Donald, C.M., 1979. A barley breeding programme based on an ideotype. J. Agric. Sci., Camb. 93: 261-269.

Fischer, R.A., 1981. Optimizing the use of water and nitrogen through breeding of crops. In: J. Monteith & C. Webb (Eds.), Soil Water and Nitrogen in Mediterranean-type Environments, pp. 249-278. Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, Boston, London.

Hamblin, J., H.M. Fischer & H.I. Ridings, 1980. The choice of locality for plant breeding when selecting for high yield and general adaptation. Euphytica 29: 161-168.

Jennings, P.R., 1964. Plant type as a rice breeding objective. Crop Sci. 4: 13-15.

Marshall, D.R., 1987. Australian plant breeding strategies for rainfed areas. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 89-99. John Wiley & Sons Ltd., New York.

Mock, J.J. & R.B. Pearce, 1975. An ideotype of maize. Euphytica 24: 613-623.

Nachit, M.M., 1989. Moisture stress tolerance and yield stability in durum wheat (*Triticum durum* 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, Germany F.R. Th. Mann Publishers, Gelsenkirchen, Germany F.R.

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

Nordblom, T.L., 1983a. Livestock - crop interactions. The case of green stage grazing. ICARDA Disc. paper No. 9, Aleppo, Syria, 37 pp.

Nordblom, T.L., 1983b. Livestock - crop interactions. The decision to harvest or to graze a mature grain crop. ICARDA Disc. paper No. 10, Aleppo, Syria, 21 pp.

Pfeiffer, W.H., 1988. Drought tolerance in bread wheat - Analysis of yield improvement over the years in CIMMYT germplasm. In: A.R. Klatt (Ed.), Wheat Production Constraints in Tropical Environments, pp. 274-284. CIMMYT, Mexico D.F., Mexico.

Rasmusson, D.C., 1987. An evaluation of ideotype breeding. Crop Sci. 27: 1140-1146.

Reitz, L.P. & S.C. Salmon, 1968. Origin, history, and use of Norin 10 wheat. Crop Sci. 8: 686-689.

Simmonds, N.W., 1991. Selection for local adaptation in a plant breeding programme. Theor. Appl. Genet. 82: 363-367.

Somel, K., A. Mazid & M. Hallajian, 1984. Survey of barley producers; northern Syria 1981/1982. Volume III, Descriptive statistics. ICARDA Research Report No. 12, Aleppo, Syria, 75 pp.

Yau, S.K., M.S. Mekni, I. Naji & J.P. Srivastava, 1989. Effects of green-stage grazing on rainfed barley in northern Syria. II. Yield and economic returns. Expl. Agric. 25: 501-507.

CHAPTER 1

Adaptation of barley (Hordeum vulgare L.) to harsh Mediterranean environments. I. Morphological traits

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Euphytica (in press)

Key words: adaptation, barley, drought, *Hordeum vulgare*, indirect selection, morphology, plant ideotype

Summary

In the low-rainfall environments of the Middle East, genetic progress in grain yield through direct selection is slow. This study was conducted to identify a combination of traits (or plant ideotype) in barley (Hordeum vulgare L.), conducive to adaptation to terminal drought-stressed low-rainfall Mediterranean environments. Thirty-six two-row barley entries, ranging from local landraces and breeding lines to European cultivars, were grown at different sites in northern Syria. Observations were made on growth habit, plant colour, growth vigour, ground cover, cold tolerance, and heading date. Good ground cover and growth vigour in spring and early heading were related to higher yield under terminal drought. However, this good performance in spring was associated with two contrasting plant ideotypes in winter. The first ideotype, characteristic of landraces from Mediterranean environments with cold winters, was based on a moderate vernalization requirement. This assured appropriate cold tolerance, associated in winter with prostrate growth habit, dark plant colour, and poor early growth vigour. It enabled heading early enough to avoid terminal drought stress. The second ideotype was based on avoidance of terminal drought stress through early heading and good early growth vigour. The associated higher vulnerability to low-temperature stress was compensated by an ability to recover from cold damage. This ideotype was characteristic of entries from Mediterranean environments with mild winters. Since environmental stresses in the Middle East are variable, individual traits can only successfully be incorporated into a breeding program, if they are considered within the entire plant ideotype.

Introduction

Barley has been domesticated in the Middle East for at least 8000 years and was widely used as human food (Harlan, 1976). In classical times, wheat became more important as human food and barley was fed to the animals (Harlan, 1976). Barley is still an important feed for sheep; it can be grazed in the late tillering stage and at maturity, and both straw and grain are used for dry forage or grazing (Nordblom, 1983a,b).

In the low-rainfall areas (<250 mm annual precipitation) of the Middle East, barley is the predominant crop. It is usually planted dry, before the first rains in October (Keatinge et al., 1986) and harvested usually in May. The amount and distribution of rainfall, within and between seasons, are highly variable (Hadjichristodoulou, 1982; Ceccarelli et al., 1991). Also the timing of abiotic stresses, such as low temperatures, is unpredictable and therefore genotype × year × location interaction variance is high. Consequently, genetic gains with direct selection for grain yield are expected to be slow. Increasing the efficiency of traditional breeding is the justification for the use of an analytical approach when selecting for yield under dry conditions.

In the analytical approach, differences in grain yield are explained from an understanding of the traits relevant to the plant ideotype (Fischer, 1981). Such traits can only be of use to the breeder as indirect selection criteria if they meet certain criteria (Ceccarelli et al., 1991): 1) sufficient genetic variation must be available, 2) they must have a high heritability, 3) a good correlation with yield under drought must exist, and 4) they must be easy and inexpensive to screen.

Grain yield is a function of the crop's transpiration, transpiration efficiency, and harvest index (Passioura, 1977; Fischer & Turner, 1978). The transpiration of a crop in a given time interval is the amount of water used, which in turn is the precipitation minus net runoff, soil evaporation (E_s) and change in soil water in the root profile (Fischer & Turner, 1978). Since the actual E_s depends mainly upon the amount of radiation reaching the soil (Fischer & Turner, 1978; Richards, 1982), soil evaporation is in Syria a major source of water loss during winter, when the ground cover is incomplete and the soil surface wet. Cooper et al. (1983) found losses of up to 60% on a seasonal basis in dry environments of northern Syria. To reduce E_s, strategies must focus on early crop establishment and good ground cover in winter. Good early growth vigour, tillering capacity, cold tolerance, and prostrate growth habit are expected to increase the proportion of water available to the crop.

Transpiration efficiency (TE) is the amount of dry matter produced per unit water transpired by the crop. Because evaporative demands in the Middle East are lowest during the cool winter, an ability to maintain growth under low temperatures, i.e. good early growth vigour, will increase TE (Richards, 1987; Acevedo & Ceccarelli, 1989). Good early growth vigour, however, may lead to excessive water use early in the season if the vapour pressure deficit is high, and a trade-off between TE and harvest index may occur (Passioura, 1977). If this is the case, then poorer early growth vigour, with a prostrate growth habit to assure reasonable ground cover, might be a better strategy.

Another trait that may be associated with TE is plant colour (Fischer, 1981). Results reported by Acevedo & Ceccarelli (1989) indicated a relation of darker leaf colour with lower chlorophyll a/b ratio, but not with chlorophyll content per unit leaf area. Since photosystems in the leaves mainly contain chlorophyll a, the lower chlorophyll a/b ratio of darker leaves may indicate a higher content of antenna chlorophyll and hence a better interception of incoming radiation.

The harvest index can, in case of terminal drought stress, be manipulated by earlier heading (Passioura, 1977). In view of a decreased TE in spring, earliness is advantageous (Fischer, 1981). However, if terminal drought is combined with low winter temperatures, the crop must flower late enough to escape frost damage. Consequently, under those conditions an optimum anthesis date for attaining the highest grain yield is likely to exist (Ceccarelli et al., 1987).

Based upon the model of Passioura (1977) and Fischer & Turner (1978), morphological traits have been identified which are positively correlated with grain yield under drought, for example prostrate winter growth habit, good early ground cover, cold tolerance, vigorous seedling growth, light plant colour at anthesis, and early ear emergence (Fischer & Wood, 1979; Acevedo & Ceccarelli, 1989; Acevedo et al., 1991). Ceccarelli et al. (1991), however, concluded that for indirect selection a combination of traits rather than individual traits should be used. The aim of this study was the identification, based upon morpho-physiological traits, of plant ideotypes, adapted to Mediterranean environments experiencing terminal drought.

Materials and Methods

Locations and management

The experiments were conducted in 1987/88 and 1988/89. In 1987/88, three locations in northern Syria, differing in mean annual precipitation, were used: Tel Hadya (TH, 327 mm), Breda (BR, 262 mm), and Bouider (BO, 219 mm). In the second season, only the TH and BR sites were used. The individual site × year combinations (environments) will be referred to as TH8, BR8, and BO8 for 1987/88, and TH9 and BR9 for 1988/89. In 1990/91, three experiments differing in sowing date were conducted at TH to obtain additional data on plant colour. Emergence dates in 1987/88 and 1988/89 ranged from 4 November for TH8 to 13 December for BO8.

Experiments at TH were part of a barley-food legume rotation, those at BR and BO were in a barley-fallow rotation. The soil at TH was characterized as a vertic (calcic) luvisol, at BR as a calcic xerosol.

At TH, 40 kg N ha^{-1} (ammonium sulphate) and 60 kg P_2O_5 ha^{-1} (triple super phosphate) were applied before sowing and an additional top dressing of 40 kg N ha^{-1} was applied at the beginning of stem elongation. At BR and BO the two nitrogen applications were reduced to 20 kg ha^{-1}, while the phosphorus application was the same as at TH. Weeds and diseases, mainly powdery mildew, were controlled chemically. A severe infection of scald (*Rynchosporium secalis*) occurred at TH8 around heading and was not controlled. It affected yield at that site.

Plant material

Thirty-six two-row entries of barley (*Hordeum vulgare* L.), covering a wide range of genotypic diversity, were used in 1987/88. Their names, origins, pedigrees, and grouping are given in Table 1. Group A entries originated from the Waite Institute (WI) in Australia. Since large areas of Australia have a low-rainfall Mediterranean climate (Fischer & Turner, 1978; French & Schultz, 1984), WI entries may have adaptations to drought stress. Group B are cultivars with European origin and were therefore not expected to have any special adaptation to the Syrian environment. Group C entries are part of the barley breeding program at ICARDA and have a diverse origin. With the exception of Lignee 131, none of the above-mentioned entries required vernalization (ICARDA, 1989).

Groups D and E are mainly pure lines derived from landraces, collected in Jordan and Syria (Weltzien, 1988). However, Arabi Abiad and A. Aswad, two widely

Table 1. Entries used in the experiments. Groups are based on the origin of the entries.

Exp.[a]	Name	Origin	Pedigree
Group A: Entries from Waite Institute Australia (WI)			
1	WI 2198	Australia	-
1	WI 2269	Australia	-
1	WI 2291	Australia	-
1	WI 2291/WI 2269	Australia	-
2	WI 2291/BgS	Australia	ICB78-0672-6AP-0AP
2	WI 2291/EH 70-F3-AC	Australia, India	ICB78-0670-6AP-0AP
Group B: European Cultivars (EC)			
1	Alger/Union	Algeria/Germany	-
1	Atem	UK	-
2	Cytris	France	-
1	Lignee 131	France	-
2	Swanneck	UK/S. Africa	-
Group C: Locally Selected Entries (LS)			
1	ER/Apm	-	-
1	Roho	Egypt	-
2	A16//2728/Sv Mari	ICARDA	CMB77A-0897-2AP-0SH-2AP-1AP-0AP
2	Jerusalem a barbes lisses/CI10836P	ICARDA	ICB7-0319-1AP-0SH-2AP-1AP-0A
1	Harmal	ICARDA[b]	Union/CI03576//Coho Sel, 09L-12AP-0AP
1	Roho/Mazurka	ICARDA	ICB77-0170-4AP-1AP-3AP-1AP-0AP
1	Kervana/Mazurka	ICARDA	ICB77-0369-4AP-2AP-1AP-0AP
2	S BON 29[c]	ICARDA	WI 2291/4/11012-2/70-22425/3/APM/IB65//A16 ICB78-636-2AP-0AP
2	S BON 89	ICARDA	W.W. Wing/3/Bal.16//CM67 //Ds*2/Apro-3Y ICB78-1000-1AP-4AP-0AP
1	S BON 96	ICARDA	Pallidum 10342//CR115/ Por/3/Bahtim 9/4/Ds/ Apro/5/WI 2291 ICB78-0058-9A-4AP-0AP
1	BON 27	ICARDA	Kervana/Mazurka ICB77-0369-2AP-0AP
Group D: Jordanian Landraces (JLB 08)			
1	JLB 08-06	Wadi al Hassa	-
3	JLB 08-10	Wadi al Hassa	-
1	JLB 08-84	Wadi al Hassa	-
1	JLB 08-89	Wadi al Hassa	-

Table 1. Continued.

Exp.[a]	Name	Origin	Pedigree
Group E: Syrian Landraces (SLB)			
East Syria (SLB 03)			
3	SLB 03-23	Al Taibe (Palmyra)	-
1	SLB 03-77 (Tadmor)[d]	Al Taibe (Palmyra)	-
1	Arabi Aswad[e]	Al Taibe (Palmyra)	-
South Syria (SLB 39)			
1	SLB 39-43	Um-Zeitoun (Suweida)	-
3	SLB 39-58 (Arta)[f]	Um-Zeitoun (Suweida)	-
1	SLB 39-99	Um-Zeitoun (Suweida)	-
North East Syria (SLB 45)			
2	SLB 45-16	Wadi Hahmar	-
2	SLB 45-38	Wadi Hahmar	-
2	SLB 45-65	Wadi Hahmar	-
Mountains South West Syria (SLB 62)			
3	SLB 62-49	Sidnaya	-
1	SLB 62-68	Sidnaya	-
1	SLB 62-99	Sidnaya	-
Other Areas Syria			
1	Arabi Abiad[e]	Idlib	-
1	SLB 60-02	Sheikh Ali (Hama)	-
Group F: Crosses with Parents Adapted to Terminal Drought			
3	BIT 86-1084	ICARDA	Mo.BI337/WI 2291 ICB81-2606-2AP-4AP-0AP
3	BIT 86-7003	ICARDA	Bante025/Roho/3/ RM1508/Por//WI 2269 ICB82-0316-4AP-0SH-0AP
3	BIT 86-7073	ICARDA	5604/1025//A.Abiad/ 3/ER/Apm ICB82-0616-2AP-0SH-0AP
3	BIT 86-14136	ICARDA	WI 2269/A.Abiad ICB84-1698-0AP
3	BIT 86-17119	ICARDA	Roho/A.Abiad//A.Abiad ICB82-1293-4AP-0AP
3	BIT 86-22031-22033-22073-22112	ICARDA	Clipper/A.Abiad//A.Abiad ICB82-1002-(1AP/5AP/ 3AP/2AP)-0AP

[a]1: entry included in all experiments; 2: entry included in 1987/88 and in previous years; 3: entry included in 1988/89 only.
[b]ICARDA: International Center for Agricultural Research in the Dry Areas, Aleppo, Syria.
[c]Special Barley Observation Nursery.
[d]Pure line from A. Aswad.
[e]Commercially grown landrace, not a pure line.
[f]Pure line from A. Abiad, collected in a farmer's field near Suweida.

grown landraces in northern Syria, are not pure lines. The collection site of the landraces is indicated by the first number of the code; the second is arbitrary and refers to the ear collected. Syrian landraces had a moderate and Jordanian landraces a light vernalization requirement (ICARDA, 1989).

Based upon preliminary results obtained in 1985/86 and 1986/87, 20 entries apparently adapted to dry conditions and five poorly adapted (late heading) entries were selected for the 1988/89 experiments. In addition, 11 new entries were included, mainly local landraces and lines derived from promising crosses of the barley breeding program. All these entries had shown promising results under dry conditions in previous years.

Experimental design

In 1987/88, a randomized complete block design (RCB) with three replications was used. In 1988/89, a simple 6 × 6 lattice design was used at TH and a triple 6 × 6 lattice design at BR. Because in 1988/89 one entry had to be excluded from the analysis, these experiments were analyzed as an RCB design.

In all experiments the plot size was 2.4 × 5 m^2 with a 20 cm row spacing. The seed rate was 100 kg ha^{-1}, giving around 235 plants m^{-2}.

Field observations and statistical analysis

Observations on growth habit, plant colour, cold tolerance, growth vigour, and ground cover were made at two-weekly intervals, using the scales indicated in Table 2. Field observations from different dates were pooled and averaged for periods during which the expression of the trait concerned was stable, e.g., winter growth habit, winter plant colour, and spring plant colour. Growth vigour was divided into early and spring growth vigour. Early growth vigour represented the ability of the crop to grow under low temperatures early in the season, before cold damage occurred. Spring growth vigour represented the ability to grow under conditions of increasing temperature and moisture stress in spring, prior to heading. Date of heading was

Table 2. Scales used for the observations of five traits.

Trait	Scale	Plant expression	
		Low value	High value
Growth habit	1 - 3	Erect	Prostrate
Plant colour	1 - 3	Pale green	Dark green
Cold tolerance	1 - 5	No damage	Dead
Growth vigour	1 - 5	Poor	Good
Ground cover	1 - 10	10% cover	100% cover

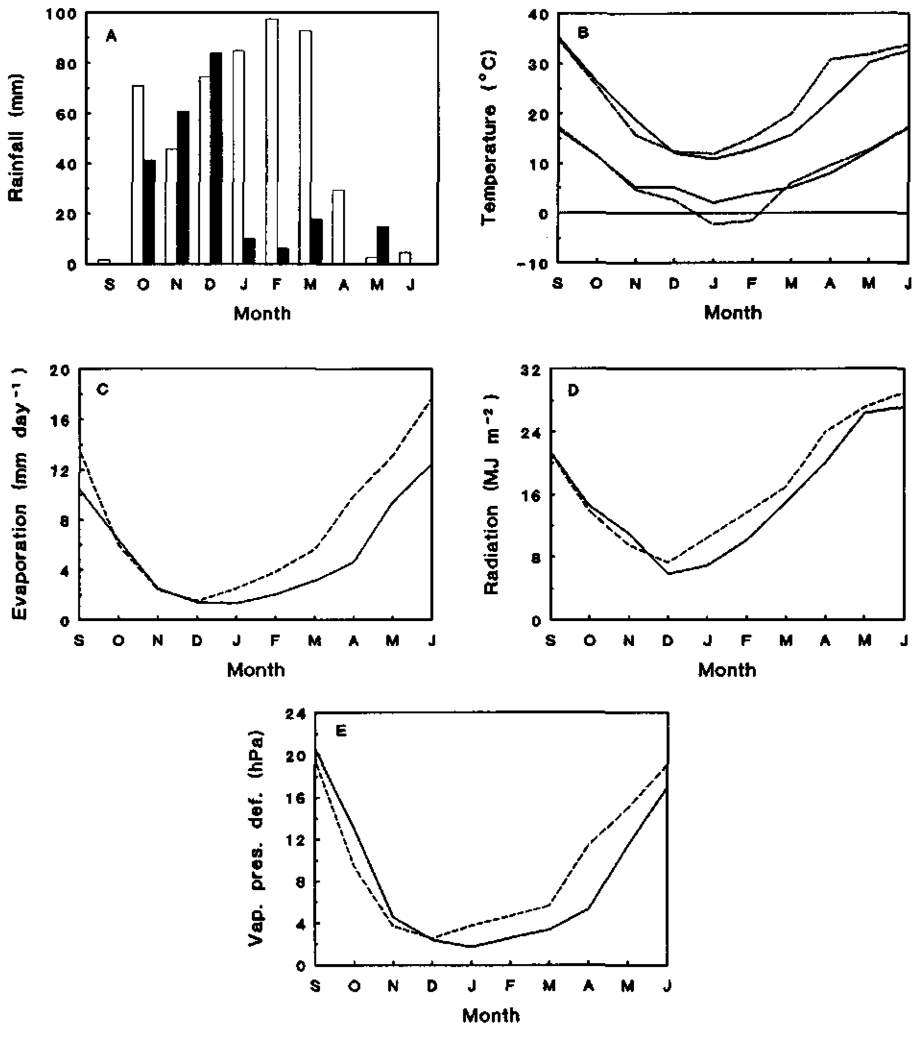

Fig. 1. Monthly averages for a) rainfall (mm), b) maximum and minimum air temperature (°C), c) class A pan evaporation (mm day^{-1}), d) solar radiation (MJ m^{-2}), and e) air vapour pressure deficit (hPa). Tel Hadya 1987/88 (□,——) and 1988/89 (■,-----).

scored as the date when 50% of the ears were extruded 50% from the boot. At the driest sites, it was scored if the tip of the awns from 50% of the ears was showing. Grain yield was obtained from a sample of 0.8 m^2 (four rows of 1 m) harvested by hand.

Statistical analyses were done by using the Statistical Analysis System (SAS, 1988), by applying the ANOVA, GLM, and TTEST procedures. Significance levels of differences between group means were calculated using Tukey's test for pairwise comparisons, assuming ten groups of entries.

Results

Meteorological data

The 1987/88 season was extremely wet (Fig. 1a), with above-average rainfall early in the season and in spring. Precipitation was 382 mm at BO, 408 mm at BR and 499 mm at TH. The winter was relatively mild: around 20 frost days were recorded at each site, but only in December did temperatures drop below -3 °C for some days. The 1988/89 season, in contrast, was wet until the beginning of January, but extremely dry afterwards: TH received 220 mm and BR 180 mm of precipitation. To alleviate drought stress at TH, an irrigation of 30 mm was applied on 10 February. Severe frost occurred in January and February (Fig. 1b); around 45 frost days were recorded after emergence at both TH and BR. Related to these differences between seasons were a higher class A pan evaporation, a higher solar radiation and higher vapour pressure deficit from January onward in 1988/89 (Figs. 1c,d,e).

Field observations

Results for most field observations are presented in Table 3 for two environments. Results from the other environments were similar and are not presented. Only for spring growth vigour did considerable differences between environments occur; these results are presented separately (Table 4).

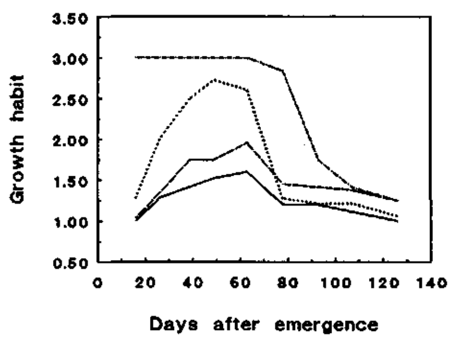

Fig. 2. Seasonal pattern for growth habit, averaged for two SLB 03 landraces (—·—), three JLB 08 landraces (·······), four European cultivars (-----), and six WI entries (——). Emergence was on 22/11/87. 1=erect, 3=prostrate. Breda 1987/88.

Table 3. Means for growth habit (GH), winter plant colour (WPLC), spring plant colour (SPLC), cold tolerance (CT), early growth vigour (EVIG) and days from emergence to heading (DH) for groups of entries at Bouider 1987/88 (BO8) and Tel Hadya 1988/89 (TH9). For details on entry groups, see Table 1.

Group	Entries[a]	GH	WPLC	SPLC	CT	EVIG	DH
BO8							
n[b]		3	3	2	2	1	
WI	3	1.40 a[c]	1.82 a	2.14 a	3.64 ab	1.50 ab	117.7 a
EC	4	1.36 a	1.92 ab	2.17 a	3.35 abc	1.46 ab	122.9 c
LS	11	1.68 ab	1.84 a	2.38 a	3.71 a	1.64 a	118.5 a
JLB 08	3	1.82 bc	2.33 b	1.17 b	3.16 bc	1.56 ab	117.6 a
SLB 39	2	2.14 c	2.28 ab	1.25 b	2.83 c	1.67 ab	118.3 ab
SLB 62	2	2.11 bc	2.33 b	1.42 b	3.33 abc	1.58 ab	118.2 ab
SLB 45	3	2.96 d	2.96 c	1.22 b	1.82 d	1.06 b	121.2 bc
SLB 03	2	2.92 d	3.00 c	1.17 b	1.90 d	1.50 ab	118.3 ab
TH9							
n[b]		4	5	2	3	3	
WI	4	1.30 a	1.50 a	1.63 ab	2.81 bc	3.10 a	123.0 a
Crosses	6	1.46 a	1.75 ab	1.75 ab	2.63 c	2.89 a	125.3 ab
EC	2	1.41 a	1.65 ab	1.75 ab	2.96 abc	2.21 bc	129.3 c
LS	7	1.51 a	1.53 a	1.79 a	3.20 a	2.70 ab	127.5 c
JLB 08	4	1.91 b	2.08 bc	1.25 c	3.19 ab	2.90 a	123.1 ab
SLB 39	3	2.04 b	2.27 bc	1.83 ab	2.14 d	2.56 abc	124.5 ab
SLB 62	3	2.44 c	2.47 cd	1.83 ab	2.11 d	2.78 ab	123.8 ab
SLB 03	3	3.00 d	2.97 d	1.42 bc	1.72 d	2.08 c	123.5 ab

[a] Number of entries per group. Lignee 131, A. Abiad and SLB 60-02 excluded.
[b] Number of observations per plot on which means are based.
[c] Means in the same column followed by the same letter are not significantly different ($P<0.05$) according to Tukey's test for pairwise comparisons.

Growth habit

Entries requiring vernalization, especially Lignee 131 and landraces from east and north east Syria and one from Hama, were most prostrate (Fig. 2, Table 3). Jordanian landraces were, within the landraces, least prostrate. WI entries were very erect.

Plant colour

Dark winter plant colour was highly positively correlated with prostrate winter growth habit ($r>0.50$, $P<0.001$ in four out of five environments). The prostrate entries, Lignee 131 and the landraces from east and north east Syria and Hama, had the darkest winter plant colour, while WI entries tended to be light green.

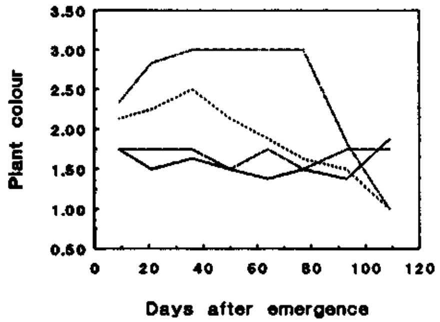

Fig. 3. Seasonal pattern for plant colour, averaged for three SLB 03 landraces (—·—), four JLB 08 landraces (······), two European cultivars (-----), and four WI entries (——). Emergence was on 22/11/88. 1=pale green, 3=dark green. Tel Hadya 1988/89.

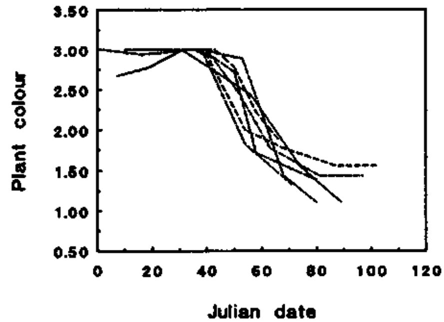

Fig. 4. Change in plant colour with time, averaged for three landraces from east Syria (Tadmor, A. Aswad, and SLB 03-23) in seven environments, ranging in emergence date from 4 November (Tel Hadya 1987/88) to 14 January (Tel Hadya 1990/91, late sowing).

At the end of the winter, the dark-coloured landraces changed rapidly from dark to pale green, and in spring they were lighter than most of the non-landraces (Fig. 3). The other landraces and dark-coloured non-landraces behaved similarly, but the effect was less pronounced. Small differences in timing occurred: landraces from north east Syria changed slightly later than those from east Syria, while the Jordanian landraces changed more gradually (Fig. 3).

Notwithstanding differences between entries in the timing of the change, and a range in emergence dates of two months, in most environments the plant colour of the landraces turned from dark to pale green during the second half of February (Fig. 4).

Cold tolerance

Despite the differences in minimum temperature between the two seasons, results for cold tolerance at BR8 and BO8 correlated well with those at TH9 and BR9. At TH8, however, differences between entries were not significant and neither were the correlations with the other environments.

A high level of cold tolerance was in most environments strongly positively correlated with both dark winter plant colour and growth habit. The correlation with plant colour remained significant within both independent groups of landraces and non-landraces. Syrian landraces were most cold tolerant, especially those from Hama and east and north east Syria (Table 3). Jordanian landraces were in general cold sensitive.

Growth vigour

Early growth vigour was weakly correlated with the previous three traits (growth habit, plant colour, cold tolerance). The prostrate, cold-tolerant, dark-coloured entries had poor early growth vigour (Table 3). Apart from this, differences among groups were small and rarely significant. Landraces from Jordan and south Syria and Roho had the best early growth vigour; WI entries were vigorous, especially at TH.

Differences between seasons in spring growth vigour were observed. In 1987/88, it was negatively correlated with prostrate winter growth habit ($r=-0.57$, $P<0.001$ at TH8; $r=-0.39$, $P<0.01$ at BO8) and in 1988/89, positively correlated with high level of cold tolerance ($r=-0.38$, $P<0.05$ at TH9 and $r=-0.49$, $P<0.01$ at BR9; the negative sign is due to the scale used for cold tolerance, Table 1). At TH8 and BO8, non-landraces had a better spring growth vigour because of lodging of the landraces, while at TH9 and BR9 the landraces were more vigorous. A difference between landraces from Jordan and east Syria was that those from Jordan had good spring growth vigour in all environments (except TH8) while those from east Syria had very good spring growth vigour at the driest sites (BR7, B07, BR9), but only moderate spring growth vigour in the wet environments of 1987/88. At BO7, where crop failure was due to a combination of drought and cold, landraces from east and north east Syria had the best growth vigour in spring. Poor spring growth vigour was related to cold sensitivity, late heading, or both.

Table 4. Scores per group of entries for spring growth vigour at Breda 1987/88 (BR8, mean of three observations), Tel Hadya 1986/87 (TH7, mean of two observations), Breda 1988/89 (BR9, mean of three observations) and Bouider 1986/87 (BO7, one observation). Values in parentheses give the seasonal precipitation (mm). For details on entry groups, see Table 1.

BR8 (408)		TH7 (343)		BR9 (180)		BO7 (174)	
SLB 39	3.61 a[a]	JLB 08	3.89 a	SLB 03	4.07 a	SLB 03	2.17 a
JLB 08	3.44 ab	SLB 39	3.67 ab	JLB 08	3.90 ab	SLB 45	2.00 ab
SLB 62	3.39 abc	SLB 03	3.50 abc	SLB 62	3.85 abc	JLB 08	1.89 ab
SLB 45	3.30 abc	WI	3.42 bc	SLB 39	3.80 abc	SLB 62	1.67 abc
WI	3.27 abc	SLB 45	3.39 abc	Crosses	3.52 bcd	SLB 39	1.50 bc
SLB 03	3.22 abc	SLB 62	3.25 bc	WI	3.35 cde	WI	1.36 c
LS	3.18 bc	EC	3.23 bc	LS	3.23 de	LS	1.24 c
EC	3.03 c	LS	3.16 c	EC	2.89 e	EC	1.21 c

[a]Means in the same column followed by the same letter are not significantly different ($P<0.05$) according to Tukey's test for pairwise comparisons.

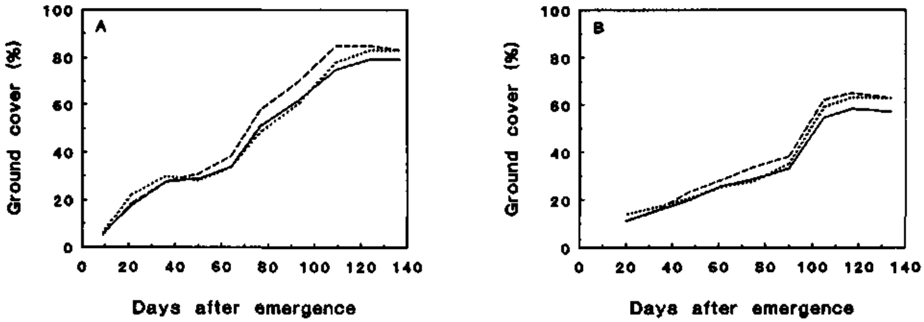

Fig. 5. Average ground cover during the 1988/89 season at a) Tel Hadya and b) Breda, averaged for three SLB 62 landraces (-----), four JLB 08 landraces (·······), and four WI entries (——).

Ground cover

Ground cover, measured in 1988/89 only, was strongly positively correlated with a high level of cold tolerance (r≈-0.6 to -0.7, P<0.001) at both sites during a major part of the growing season. In spring, it was positively correlated with spring growth vigour (r≈0.6 to 0.8, P<0.001). Syrian landraces tended to have the best ground cover, especially later in the season (Fig. 5). Jordanian landraces had better ground cover than WI entries after winter, about 90 days after emergence (Fig. 5). Apparently, these landraces recover well from cold damage. Poor ground cover was in general related to cold sensitivity or poor growth vigour.

The discontinuity in increase in ground cover at both TH9 and BR9 (Fig. 5) occurred during a period of low minimum temperatures (Fig. 1b). The discontinuity at TH9, 50 days after emergence, marks the beginning of this period; the increase at BR9 around 90 days after emergence marks the end of this period and the start in increase of growth rates.

Days to heading

The number of days to heading was consistently negatively related to growth vigour in spring (r≈-0.5 to -0.7, P<0.01), because of poor growth vigour of late entries. Correlations with other traits were absent.

Jordanian landraces and WI entries were in general the earliest (Table 3). In 1987/88, WI 2269, WI 2291/WI 2269, Harmal and S BON 96 (Pallidum 10342//CR115/Por/3/Bahtim 9/4/Ds/Apro/5/WI 2291) and in 1988/89, JLB 08-10 and JLB 08-89 were the earliest entries. The range in heading date within landraces was small (Table 3), but on average those from north east Syria and Hama were slightly later.

Table 5. Mean and range for growth habit (GH), winter plant colour (WPLC), spring plant colour (SPLC), cold tolerance (CT), early growth vigour (EVIG), spring growth vigour (SVIG), ground cover at the end of the winter (COV), days to heading (DH) and grain yield (GYM, g m^{-2}) for the 6 highest and lowest yielding entries in three contrasting environments.

Trait		BO8		TH9		BR9	
		High	Low	High	Low	High	Low
GH	mean	1.6	2.0	2.0	1.7	2.0	1.8
	range	1.3-2.3	1.2-3.0	1.2-3.0	1.1-3.0	1.3-3.0	1.3-3.0
WPLC	mean	2.0	2.5	2.3	1.6	2.1	1.6
	range	1.2-2.6	1.9-3.0	1.6-3.0	1.1-2.7	1.7-3.0	1.1-2.5
SPLC	mean	2.4*	1.8	1.8	1.9	1.3*	1.9
	range	2.2-2.5	1.0-2.3	1.3-2.0	1.3-3.0	1.2-1.3	1.3-2.7
CT	mean	3.6	2.9	2.1**	3.1	2.1	2.5
	range	3.1-3.9	1.7-3.4	1.6-2.7	2.1-3.7	1.6-2.6	2.0-3.1
EVIG	mean	1.5	1.4	2.6	2.4	2.6	2.5
	range	1.2-1.8	1.2-1.8	2.0-3.3	1.5-2.8	2.0-2.9	2.1-2.8
SVIG	mean	3.3*	3.0	4.2**	3.3	4.0***	2.9
	range	3.1-3.8	2.7-3.2	3.5-4.6	2.9-3.6	3.7-4.3	2.4-3.2
COV	mean	-	-	6.6*	5.6	3.7***	3.1
	range	-	-	5.5-7.3	4.8-6.5	3.5-4.0	2.8-3.3
DH	mean	116*	120	124*	129	126***	134
	range	114-121	118-124	122-127	125-133	123-130	130-137
GYM	mean	395***	170	336***	176	169***	76
	range	339-479	152-185	307-366	141-207	147-180	46- 96

*, ** and *** differences between top and bottom are significantly different at $P<0.05$, $P<0.01$ and $P<0.001$, respectively, based on a t-test, assuming unequal variances between groups and using Satterthwaite's approximation for calculating the effective degrees of freedom.

Relations with grain yield

High-yielding entries were significantly earlier in heading and had a better growth vigour and ground cover in spring than low-yielding entries in each of three contrasting environments (Table 5). Under drought, the negative correlation between days to heading and grain yield was due to a lower harvest index of the late entries ($r=-0.54$, $P<0.001$ at BR9). In addition, in dry environments a light spring plant colour was positively related to good yield, while at TH9, where severe cold damage occurred, high-yielding entries were significantly more cold tolerant than low-yielding entries. The other traits, however, were not related to grain yield; ranges of variation in high- and low-yielding entries generally overlapped (Table 5). Entries SLB 03-23 and JLB 08-89, both good performers at BR9, had, notwithstanding similar scores for traits measured in spring, contrasting expressions for traits measured in winter (Table 6). Lignee 131 and Atem were both low yielding because of their poor performance in spring. Lignee 131, however, had a winter plant ideotype comparable to SLB 03-23, while Atem was in winter comparable to JLB 08-89.

Discussion

The results for growth habit confirm previous findings of Ceccarelli et al. (1987) and Weltzien (1988) that landraces from east and north east Syria are more prostrate than those from Jordan and southern Syria. According to Weltzien (1988), this may reflect the more continental climate in eastern Syria. Ceccarelli et al. (1987) caution against relating plant ideotype to micro-climate of the collection site, because of frequent exchanges of seed between regions, especially after a dry year. The prostrate growth habit also may be an adaptive trait to green-stage grazing in east and north Syria. Under those conditions, prostrate entries are more productive because of a larger residual leaf area after defoliation (Rhodes, 1973).

Plant colour of spinach changes from dark to pale green as plants become reproductive (J.E. Parlevliet, personal communication). Such a relation between development and plant colour may explain the earlier onset of the change in plant colour for the Jordanian landraces (Fig. 3). Early in the season, they have a quicker apical development than the landraces from eastern Syria (van Oosterom & Acevedo, 1992).

The stability in timing of the change in plant colour of the Syrian landraces suggests a photoperiodic dependency. However, in both 1988/89 and 1990/91 the change coincided with a sharp rise in minimum screen air temperature. A relationship with temperature was also apparent in the 1990/91 early planting. In November,

Table 6. Values for grain yield (GYM, g m^{-2}), growth habit (GH), winter plant colour (WPLC), cold tolerance (CT), early growth vigour (EVIG), spring plant colour (SPLC), ground cover at the end of the winter (COV), spring growth vigour (SVIG), and days from emergence to heading (DH) for five contrasting entries at Breda 1988/89.

Trait	SLB 03-23	JLB 08-89	WI 2198	Lignee 131	Atem
GYM (g m^{-2})	161	178	116	57	46
Traits in winter					
GH	3.0	2.0	1.5	3.0	1.4
WPLC	3.0	2.0	1.0	2.5	1.4
CT	1.6	2.6	2.9	2.1	2.7
EVIG	2.0	2.6	3.1	2.3	2.8
Traits in spring					
SPLC	1.3	1.2	1.8	2.7	1.7
COV	3.8	3.5	3.0	3.0	3.0
SVIG	4.3	3.7	3.0	2.4	2.6
DH	130	127	129	137	135

when temperatures were high, these landraces had a light green colour, whereas in February, during a cold spell, they became darker. If sown in February and temperatures are high, they do not become dark at all (S. Ceccarelli, personal communication). Both temperature and a change to the reproductive stage result in higher leaf expansion rates (Peacock, 1976). An associated dilution of nutrients (nitrogen) may partly account for the lighter plant colour in spring. It is likely that the change to a lighter colour in spring depends on temperature, development, and photoperiodic response.

If the seasonal pattern in plant colour of the landraces reflects a pattern in efficiency of light interception, as suggested by Acevedo & Ceccarelli (1989), it might be a valuable adaptation to the prevailing radiation regime in northern Syria. During winter, when radiation is limiting photosynthesis (Fig. 1d), landraces are efficient because of their dark leaf colour and associated high content of antenna chlorophyll. In spring, radiation is supra-optimal for photosynthesis; the light colour and associated low content of antenna chlorophyll then may allow radiation shedding and prevent photo-inhibition. This mechanism is in accordance with the physical law that light-coloured bodies absorb less incoming energy than dark ones. The lower radiation load on the leaf causes a reduction in the leaf-to-air vapour pressure gradient, which in turn reduces the leaf temperature. A lower leaf temperature is a major factor influencing transpiration efficiency, especially when air temperature is supra-optimal for photosynthesis (Fischer, 1981).

The high level of cold tolerance in the landraces from east and north east Syria has been reported before (Ceccarelli et al., 1987). The cold sensitivity of the Jordanian landraces and of Roho, an Egyptian landrace, may be due to a low selection pressure for this trait in the original environment.

The consistent and highly significant mutual correlation between growth habit, plant colour, and cold tolerance is probably due to a vernalization requirement. When this requirement is not met, apical development is retarded (Porter et al., 1987). The apex remains vegetative and plants have a prostrate growth habit. However, the correlation between growth habit and vernalization requirement can be broken (Pugsley, 1971). A genetic linkage between cold tolerance and vernalization requirement has been found in barley (T. Blake, personal communication).

The consistently poor early growth vigour of landraces from east and north east Syria reflects their inability to grow under low-temperature conditions. In combination with good cold tolerance and tillering capacity they still have an adequate ground cover (e.g., SLB 03-23 and SLB 60-02). The good ground cover of the landraces, which developed during the second half of winter (Fig. 5), was related to a denser tillering (van Oosterom & Acevedo, unpublished data).

The absence of a correlation between heading date and growth habit, plant colour, or cold tolerance suggests that a vernalization requirement does not mean a late heading date. This is appealing, because a combination of slow early development with an early heading minimizes the effects of both low temperature and terminal drought stress. The earliness of the Jordanian landraces was reported before (Weltzien, 1988; Ceccarelli et al., 1991). The smaller-than-expected difference in heading date between the Jordanian and Syrian landraces at TH9 is most probably due to severe cold damage of the Jordanian landraces; at BR9 the difference between the Jordanian landraces and those from eastern Syria was more than three days (significant at $P<0.05$). If local landraces, as a result of natural and/or artificial selection, are adapted to the local environments, then the narrow range in heading dates represents a balance between avoidance of frost damage and terminal drought stress (Ceccarelli et al., 1987).

Traits which were measured in spring (ground cover, growth vigour, heading date) were consistently related to grain yield, except for spring plant colour, where the correlation depended upon the environment. The negative correlation between grain yield under drought and days to heading supports similar results obtained for spring wheat (Fischer & Maurer, 1978), barley (Hadjichristodoulou, 1981), and pearl millet (Bidinger et al., 1987a) and is due to a reduced harvest index (Passioura, 1977). The importance of light plant colour in spring in low-yielding environments (Table 5) supports data of Acevedo & Ceccarelli (1989). In a similar nursery, they found that light plant colour at anthesis was related to a drought resistance index (Bidinger et al., 1987b) that accounts for yield potential and heading date. The absence of a correlation between winter growth habit, winter plant colour, cold tolerance or early growth vigour, and grain yield, and the overlap in range of variation of high- and low-yielding entries, indicates that these traits are of little use as indirect selection criteria if they are considered as individual traits.

Good growth vigour and ground cover in spring and early heading can result from different combinations of traits (plant ideotypes) in winter. Landraces from east and north east Syria (SLB 03-23 in Table 6) meet these requirements by combining prostrate winter growth habit, dark winter plant colour, cold tolerance, and poor early growth vigour. Their prostrate growth habit, related to a vernalization requirement, is an adaptation to low winter temperatures, as indicated by the associated high level of cold tolerance. Poor growth vigour under low temperatures is often associated with cold tolerance. The poorer growth vigour in spring in more favourable environments (Table 4) indicates that this ideotype is especially useful in low-rainfall environments. However, it is not an assurance for good yield under those conditions if it is not combined with early heading (Lignee 131 in Table 6). The late heading of Lignee 131 is related to a high vernalization requirement (ICARDA, 1989). In spring, maximum temperatures, radiation and evaporation increase dramatically (Fig. 1) and if heading is late, the crop runs into water stress, as indicated by the negative correlation between days to heading and harvest index at BR9. The ideotype of landraces from east and north east Syria, based upon the combination of a moderate vernalization requirement with early heading, provides an adequate adaptation to low-rainfall Mediterranean environments with cold winters.

Jordanian landraces, Roho, and Australian entries ensure good performance in spring by good early growth vigour. Early growth is advantageous in terms of water use, because evaporative demands and air vapour pressure deficit are low during winter (Fig. 1e). However, it makes these entries more vulnerable to cold damage. Good growth vigour and ground cover in spring are assured by an ability to recover from this damage. With such an ideotype, prostrate growth habit is less important. The good spring growth vigour of these entries across a wide range of environments (Table 4) indicates that this ideotype may be more advantageous under favourable conditions than the one of the Syrian landraces. In environments where low winter temperatures are likely, however, it bears the risk of an insufficient recovery from cold damage. Even with an appropriate earliness, this will reduce grain yield (WI 2198 in Table 6). This ideotype is based on avoidance of terminal drought stress by good early growth vigour and early heading, an adaptation to low-rainfall Mediterranean environments with mild winters.

Good yields under terminal drought stress can arise from different combinations of traits. Since environmental variability in the Middle East is high and the occurrence of stresses is unpredictable, the identification of an optimum plant ideotype depends on the probability of adverse or favourable conditions. Population buffering through genetic heterogeneity has been proposed to increase yield stability (Ceccarelli et al., 1991). Under such conditions, use of individual traits as selection criteria in analytical breeding is virtually worthless. Our results support the conclusion of Ceccarelli et al. (1991) that these traits can only be incorporated successfully if they are considered as part of an entire plant ideotype.

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References

Acevedo, E. & S. Ceccarelli, 1989. Role of physiologist-breeder in a breeding program for drought resistance conditions. In: F.W.G. Baker (Ed.), Drought Resistance in Cereals, pp. 117-140. CAB International, Wallingford, UK.

Acevedo, E., P.Q. Craufurd, R.B. Austin & P. Pérez-Marco, 1991. Traits associated with high yield in barley in low-rainfall environments. J. Agric. Sci., Camb. 116: 23-36.

Bidinger, F.R., V. Mahalakshmi & G.D.P. Rao, 1987a. Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leeke]. I. Factors affecting yields under stress. Aust. J. Agric. Res. 38: 37-48.

Bidinger, F.R., V. Mahalakshmi & G.D.P. Rao, 1987b. Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leeke]. II. Estimation of genotype response to stress. Aust. J. Agric. Res. 38: 49-59.

Ceccarelli, S., E. Acevedo & S. Grando, 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. Euphytica 56: 169-185.

Ceccarelli, S., S. Grando & J.A.G. van Leur, 1987. Genetic diversity in barley landraces from Syria and Jordan. Euphytica 36: 389-405.

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

Fischer, R.A., 1981. Optimizing the use of water and nitrogen through breeding of crops. In: J. Monteith & C. Webb (Eds.), Soil Water and Nitrogen in Mediterranean-type Environments, pp. 249-278. Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, Boston, London.

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

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

Fischer, R.A. & J.T. Wood, 1979. Drought resistance in spring wheat cultivars. III. Yield associations with morphological traits. Aust. J. Agric. Res. 30: 1001-1020.

French, R.J. & J.E. Schultz, 1984. Water use efficiency of wheat in a Mediterranean-type environment. I. The relation between yield, water use and climate. Aust. J. Agric. Res. 35: 743-764.

Hadjichristodoulou, A., 1981. Aspects of barley breeding for dry Mediterranean regions. In: M.J.C. Ascher, R.P. Ellis, A.M. Hayter & R.N.H. Whitehouse (Eds.), Barley Genetics IV, pp. 383-388. Proc. 4th International Barley Genetics Symposium, Edinburgh, 22-29 July 1981.

Hadjichristodoulou, A., 1982. The effects of annual precipitation and its distribution on grain yield of dryland cereals. J. Agric. Sci., Camb. 99: 261-270.

Harlan, J.R., 1976. Barley. In: N.W. Simmonds (Ed.), Evolution of Crop Plants, pp. 93-98. Longman, London, New York.

ICARDA, 1989. Cereal Improvement Program: Annual Report 1988. International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria, 187 pp.

Keatinge, J.D.H., M.D. Dennett & J. Rodgers, 1986. The influence of precipitation regime on the crop management of dry areas in northern Syria. Field Crops Res. 13: 239-249.

Nordblom, T.L., 1983a. Livestock - crop interactions. The case of green stage grazing. ICARDA Disc. Paper No. 9, Aleppo, Syria, 37 pp.

Nordblom, T.L., 1983b. Livestock - crop interactions. The decision to harvest or to graze a mature grain crop. ICARDA Disc. Paper No. 10, Aleppo, Syria, 21 pp.

Oosterom, E.J. van & E. Acevedo, 1992. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. II. Apical development, leaf, and tiller appearance. Euphytica (in press).

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

Peacock, J.M., 1976. Temperature and leaf growth in four grass species. J. Appl. Ecol. 13: 225-232.

Porter, J.R., E.J.M. Kirby, W. Day, J.S. Adam, M. Appleyard, S. Ayling, C.K. Baker, P. Beale, R.K. Belford, P.V. Biscoe, A. Chapman, M.P. Fuller, J. Hampson, R.K.M. Hay, M.N. Hough, S. Matthews, W.J. Thompson, A.H. Weir, V.B.A. Willington & D.W. Wood, 1987. An analysis of morphological development stages in Avalon winter wheat crops with different sowing dates and at ten sites in England and Scotland. J. Agric. Sci., Camb. 109: 107-121.

Pugsley, A.T., 1971. A genetic analysis of spring-winter habit of growth in wheat. Aust. J. Agric. Res. 22: 21-31.

Rhodes, I., 1973. Relationship between canopy structure and productivity in herbage grasses and its implications for plant breeding. Herb. Abstr. 43: 129-133.

Richards, R.A., 1982. Breeding and selecting for drought resistance in wheat. In: Drought Resistance in Crops with Emphasis on Rice, pp. 303-316. IRRI, Los Banos, The Philippines.

Richards, R.A., 1987. Physiology and the breeding of winter-grown cereals for dry areas. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 133-150. John Wiley & Sons Ltd., New York.

SAS, 1988. SAS/STAT User's Guide, Release 6.03 Edition. Statistical Analysis System Institute Inc., Cary, NC, 1028 pp.

Weltzien. E., 1988. Evaluation of barley (*Hordeum vulgare* L.) landrace populations originating from different growing regions in the near east. Plant Breeding 101: 95-106.

CHAPTER 2

Adaptation of barley (Hordeum vulgare L.) to harsh Mediterranean environments. II. Apical development, leaf, and tiller appearance

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Euphytica (in press)

Key words: adaptation, apical development, barley, drought, *Hordeum vulgare* L., indirect selection, leaf appearance, leaf number, tiller appearance

Summary

Differences in development of the apex may be the reason for cultivar differences in adaptation of barley to terminal drought in Mediterranean environments. The present study was conducted to identify apical development patterns of barley adapted to terminal drought stressed Mediterranean environments and to determine plant characteristics which can be used as criteria to select for an adapted development. Thirty-five two-row barley (Hordeum vulgare L.) entries were grown at two sites in northern Syria (Tel Hadya and Breda) in 1988/89. Four apical development patterns were observed: slow or fast vegetative development, depending on the vernalization requirement, combined with slow or fast generative development, depending on the daylength response of the crop. Early heading was related to fast generative development. Leaf appearance rates on the main shoot were constant during a major part of the pre-anthesis period, but significant differences were observed among development patterns. Genotypic differences in main shoot tiller number were associated with differences in the onset of tiller appearance and not with differences in tiller appearance rate or final leaf number on the main shoot. Since vernalization requirements and daylength responses are largely independent of terminal drought stress, selection for an adapted phenology can be done in favourable environments. Morphological traits related to these responses (winter growth habit, cold tolerance, plant colour, growth vigour, heading date) can be used as criteria for selection for adaptation to low-rainfall Mediterranean environments.

Introduction

Barley (*Hordeum vulgare* L.) has its center of origin in the Middle East, where it has been cultivated for at least 8000 years (Harlan, 1976). In this area, barley landraces are still widely grown. The evaluation of landraces collected in Jordan and Syria has revealed a number of features which might be of adaptive significance to barley grown in low-rainfall Mediterranean environments (Ceccarelli et al., 1987; Weltzien, 1988). Although considerable variation is present within collection sites, significant differences in the average expression of morphological characteristics were found among sites. Landraces from the desert and steppe areas in east and north east Syria, where terminal drought stress occurs in combination with low winter temperatures, had a prostrate winter growth habit, dark winter plant colour, poor early growth vigour, and cold tolerance. Jordanian landraces, originating from areas characterized by mild winters and terminal drought stress, combined a more erect winter growth habit, light winter plant colour and good early growth vigour with cold sensitivity, but an ability to recover from cold damage (Ceccarelli et al., 1987; Weltzien, 1988; van Oosterom & Acevedo, 1992a). This plant ideotype resembled that of spring barleys from Australia and Egypt, where terminal drought stress is also combined with mild winters. In combination with an appropriate earliness, both ideotypes resulted in an adequate ground cover in spring, a key factor for attaining good yields in low-rainfall Mediterranean environments experiencing terminal drought stress (Fischer, 1981; Cooper et al., 1983; Acevedo & Ceccarelli, 1989; van Oosterom & Acevedo, 1992a).

An analysis of plant development is a prerequisite to understanding the importance of these ideotypes for low-rainfall Mediterranean regions. In the pre-anthesis development of the barley apex, two important stages can be distinguished. The first is the transition from initiation of leaf primordia to initiation of spikelet primordia. This marks the end of the vegetative phase of the apex and the beginning of the spike initiation phase. The transition is characterized by an increased rate of primordia initiation (Kirby, 1974; Gallagher, 1979; Baker & Gallagher, 1983b). The second stage occurs when the maximum number of primordia (MP) has been initiated and the meristematic dome has stopped initiating new primordia (Kirby & Appleyard, 1984). The spike initiation phase has finished and the spike growth phase, defined as the time from the MP stage to anthesis, has begun. Differences in duration of the three phases (vegetative, spike initiation, spike growth phase) may be the reason for the observed differences in plant ideotype between Syrian and Jordanian landraces.

Leaf and tiller appearance are expressions of growth of cereals. High leaf and tiller numbers can increase ground cover and thus the fraction of incoming radiation which is intercepted by the crop. This can reduce water losses by direct soil evaporation (Fischer & Turner, 1978; Cooper et al., 1983). The leaf appearance rate is a linear function of temperature, as long as temperatures do not fall below a base temperature of around 0 °C (Gallagher, 1979; Hay & Tunnicliffe Wilson, 1982; Kirby et al., 1985b). The tiller appearance rate is related to the leaf appearance rate (Friend, 1965; Jones & Allen, 1986). Significant genotypic differences in leaf appearance rate have been reported for barley and wheat (Syme, 1974; Kirby et al., 1985b; Kirby & Perry, 1987; Cao & Moss, 1989).

The two objectives of this study were: 1) identification of development patterns of barley adapted to Mediterranean environments, and 2) determination of plant characteristics, associated with development, which can be used as criteria for indirect selection of an adapted development.

Materials and Methods

Locations and environmental measurements

Experiments were conducted in 1988/89 at two locations in northern Syria, differing in their long-term average rainfall: Tel Hadya (TH, 327 mm, 36°10'N, 36°56'E) and Breda (BR, 262 mm, 35°56'N, 37°10'E). To prevent confounding effects of differences in daylength between the experiments, at both sites sowing was done on 9 November 1988. Emergence was on 22 November at TH and 24 November at BR. Preliminary observations were done in 1987/88 at Breda; emergence date of that experiment was 22 November 1987. The individual site × year combinations will be referred to as TH9 and BR9 for 1988/89 and BR8 for 1987/88. The soil at TH is classified as a vertic (calcic) luvisol and at BR as a calcic xerosol. To delay drought stress at TH9, an irrigation of 30 mm was applied on 10 February.

The soil water content was measured in 1988/89 every 10-15 days with a neutron probe in plots sown on the same day as the main experiment and adjacent to it. Measurements were taken at 15-cm intervals to a depth of 180 cm at TH and 150 cm at BR; soil water contents of the top 15 cm of the soil were measured gravimetrically. Measurements were done on eight plots: one fallow and seven with barley entries, landraces as well as non-landraces, six of which were included in the main experiments. Two access tubes per plot were installed at TH and one at BR.

The main purpose of measuring soil water was to characterize the environment of the growing season. Evapotranspiration was calculated as the difference between precipitation and change in total moisture content in the root profile. Runoff and drainage below the root profile did not occur.

Weather data were obtained from a meteorological station, located within 1 km of the experiments. Daily maximum and minimum screen air temperatures were used to calculate thermal units. Although the base temperature for development changes gradually during the life cycle of the plant (Wang, 1960; Angus et al., 1981; Porter et al., 1987), a base temperature of 0°C during the period from emergence to heading is widely used (e.g., Gallagher, 1979; Kirby & Ellis, 1980; Hay & Tunnicliffe Wilson, 1982). We also used 0°C as a base temperature for this period, and used 26°C as the optimum and 37°C as the maximum temperature (Weir et al., 1984). Adjustments for temperatures below 0°C or above 26°C were made, assuming a cosinusoidal variation in temperature between the daily minimum and maximum and a linear positive relationship between developmental rate and temperature between 0°C and 26°C and a linear negative relationship for temperatures between 26°C and 37°C (Weir et al., 1984).

Plant material

Thirty-five two-row barley entries and one six-row were included in the experiments. Among them were Syrian and Jordanian landraces, genotypes from the Waite Institute (WI) in South Australia, cultivars with European origin, and breeding lines from the barley breeding program at ICARDA. In 1987/88, observations were done on a subset of 25 entries. Details about the entries are given by Acevedo et al. (1991) and van Oosterom & Acevedo (1992a).

Experimental design

A simple 6 × 6 lattice design was used at TH9 and a triple 6 × 6 lattice design at BR9. Because the six-rowed entry was omitted from the analyses, the experiments were analyzed as a randomized complete block (RCB) design. In 1987/88, an RCB design with three replications was used.

In all experiments, the plot size was 2.4 × 5 m^2 with 20-cm row spacing, giving

12 rows per plot. The seed rate was 100 kg ha^{-1}, resulting in an average plant density of about 235 plants m^{-2}.

Sampling procedure

Samples of eight plants were taken from pre-determined rows of each plot at two-week intervals. Plant samples included part of the roots and were placed in polyethylene bags in a cooling box for transport to the laboratory. There, the soil was washed from the roots, whereafter each sample was wrapped in a wet tissue and a piece of cloth and stored in a polyethylene bag at 5°C. This method allowed satisfactory storage for up to one week, long enough to finish processing the samples. Four representative plants per sample were selected for measuring the apical development stage, the number of leaves on the main shoot and the number of main shoot tillers.

Apical development

A scale based on Kirby & Appleyard (1984) was used to describe the stages of development of the apex (Table 1). The duration of the vegetative phase was estimated as the thermal units from emergence to the appearance of the double ridges (DR), although it was realized that in cereals already half of the spikelet primordia have been initiated at this stage (Kirby, 1974, 1977; Baker & Gallagher, 1983a). For our purpose, to identify adapted development patterns, the DR stage gave an adequate estimate of early development. Thermal units from emergence to the DR and MP stage were estimated for each plot by interpolation of the fortnightly observations.

Table 1. Scale used to describe the successive development stages of the barley apex (Kirby & Appleyard, 1984).

Scale	Stage
1	Vegetative
2	Double ridge
3	Triple mound
4	Glume primordium
5	Lemma primordium
6	Stamen primordium
7	Awn primordium (max. number of primordia)
8	White anther
9	Green anther
10	Yellow anther

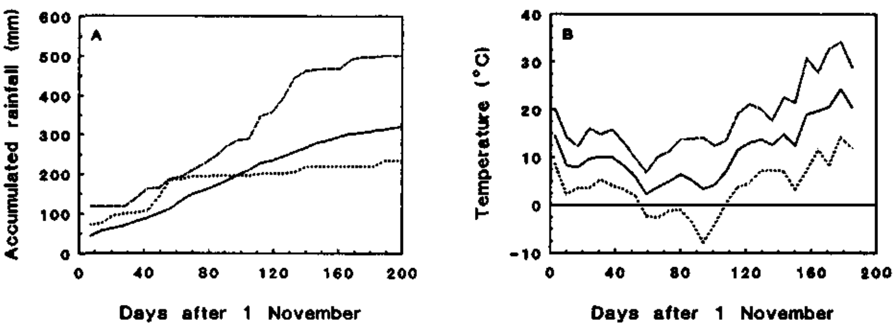

Fig. 1. Climatic data recorded at Tel Hadya: a) accumulated rainfall in 1987/88 (-----) and 1988/89 (·······), and long term average (——); b) weekly maximum (-----), minimum (·······), and average (——) air temperature in 1988/89.

Leaf and tiller number and appearance

The number of visible leaves and tillers on the main shoot was counted on the plants which were dissected for the analysis of apical development. A leaf was counted if its tip was visible above the ligule of the last expanded leaf; a tiller was counted as soon as its prophyll extended beyond the ligule of the subtending leaf (Baker & Gallagher, 1983a; Kirby et al., 1985c). In 1988/89, leaves were also counted on labelled plants in the field. Five plants per plot were labelled at TH9 and four at BR9. Countings were done at weekly intervals at TH9 and two-week intervals at BR9. When a main shoot was affected by frost, which happened often at TH9, a new plant was labelled. At the flag leaf stage, the date of full flag leaf expansion (ligule visible) was recorded for each plant (TH9 only), as well as the final number of leaves on the main shoot (TH9 and BR9).

The leaf appearance rate, or its inverse phyllochron interval (PI), was calculated for the laboratory and field measurements separately, using a least squares fit for the regression of leaf number on thermal units (Keuls & Garretsen, 1982). Significance levels of differences in PI between environments were calculated using a t-test (Gomez & Gomez, 1984).

Results

Environments

The 1987/88 season was extremely wet (Fig. 1a), with above-average early and spring rainfall. The 1988/89 season was similar until the beginning of January, but extremely dry afterwards. Drought was accompanied by a period with low minimum

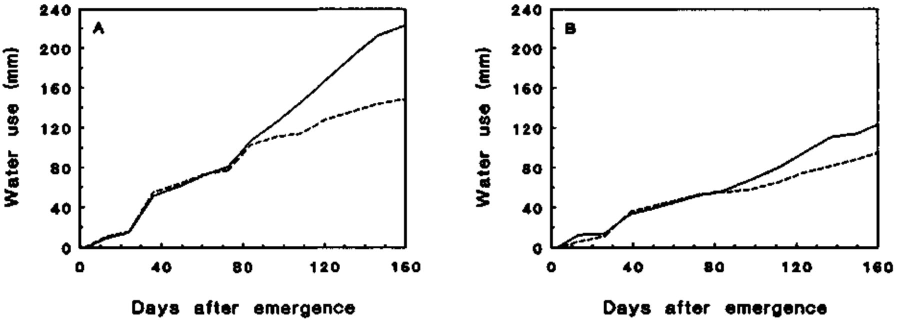

Fig. 2. Accumulated evapotranspiration (——) and bare soil evaporation (-----) at a) Tel Hadya 1988/89 and b) Breda 1988/89.

temperatures in winter and high maximum temperatures in spring (Fig. 1b). Only 1½ months elapsed between the time when minimum temperatures rose above 0 °C and maximum temperatures exceeded 25 °C.

Soils at TH had a greater water-holding capacity than those at BR. The depth to which water was extracted from the soil at TH by the crop increased gradually as the season progressed; by the end of the season, crops extracted water from a depth of 150 cm. Under fallow, losses due to direct soil evaporation were in general limited to the top 25 cm. At Breda, in contrast, the zone from which water was extracted was around 90 cm, slightly deeper than the depth to which water was lost due to soil evaporation.

Differences between the evapotranspiration under the barley crop (E_T) and the evaporation from uncropped soil (E_S) started to occur around 80-90 days after emergence at both TH9 and BR9 (Fig. 2). This was related to a rise in minimum temperatures (Fig. 1b). Differences between sites became apparent early in the season. At maturity, the accumulated E_T was 225 mm at TH9 and 123 mm at BR9, whereas the accumulated E_S was 152 mm at TH9 and 94 mm at BR9.

Apical development

In 1988/89, plants at TH and BR had comparable development patterns (Table 2). The slightly later heading at BR9 may have been due to an incomplete spike extrusion of droughted plants, causing a slight overestimation of the heading date. A comparison with the results of BR8 indicates that the main difference between the two seasons was a shorter spike growth phase in the dry season.

Four major patterns of development could be distinguished (Fig. 3):

A) Fast development before and intermediate rate of development after the DR

Table 2. Emergence date, seasonal precipitation (mm), and thermal units (°Cd) from emergence to three development stages at Tel Hadya 1988/89 (TH9), Breda 1988/89 (BR9), and Breda 1987/88 (BR8). Values are means of 35 entries (TH9, BR9) or 25 entries (BR8).

	TH9	BR9	BR8
Emergence	22/11/88	24/11/88	22/11/87
Precipitation (mm)	220+30[a]	180	408
Thermal units (°Cd) to			
Double ridge	321	321	-
Maximum no. primordia	729	727	708
Heading	1064	1116	1141

[a]Irrigation on 10 February during a period of drought.

stage, resulting in early heading; examples were WI 2269, WI 2291/WI 2269, Harmal, S BON 96 (Pallidum 10342//CR115/Por/3/Bahtim 9/4/Ds/Apro/5/WI 2291) and, to a lesser extent, WI 2291 and WI 2198.

B) Slow development before and fast development after the DR stage, resulting in a heading date not much later than pattern A. This pattern was characteristic of the SLB 03 landraces from east Syria, i.e., Arabi Aswad, Tadmor and SLB 03-23.

C) Intermediate rate of development before and slow development after the DR stage, resulting in late heading; examples were Atem, Alger/Union (both European cultivars), and two sister lines from the cross Kervana/Mazurka.

D) Slow development before and intermediate developmental rate after the DR stage, resulting in late heading; Lignee 131, a winter type barley, and to a lesser extent Roho/Mazurka, had this pattern.

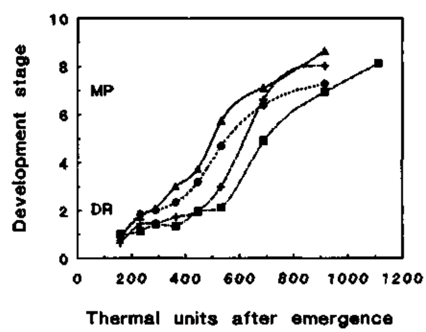

Fig. 3. Apical development as a function of accumulated thermal units (°Cd) after emergence for WI 2291/WI 2269 (▲——▲), Arabi Aswad (+——+), Atem (●······●), and Lignee 131 (■—·—■). DR = double ridge stage (stage 2), MP = maximum number of primordia stage (stage 7). Scale based on Kirby & Appleyard (1984).

Table 3. Mean phyllochron interval (PI), final number of leaves on the main shoot (FLMS) and days from emergence to complete flag leaf expansion (DFE) for four development patterns and three groups of landraces. Data are obtained from labelled plants in the field at Tel Hadya 1988/89.

Group	n[a]	PI		FLMS		DFE	
Pattern A[b]	6	104	a[c]	10.4	b	115.2	a
Pattern B	3	88	b	11.4	c	116.7	a
Pattern C	4	101	a	11.4	c	123.2	b
Pattern D	2	93	ab	12.6	d	127.1	c
JLB 08[d]	4	94	ab	10.8	abc	114.3	a
SLB 39[e]	3	96	ab	11.0	bc	116.9	a
SLB 62[f]	3	104	a	10.4	ab	116.0	a
Average	35	100		10.9		117.6	
ANOVA sum of squares							
Between groups	6	1599	**	19.6	***	788.2	***
Within groups	18	1309		3.5		204.5	**

[a]Number of entries per group. [b]For a definition of the development patterns, see text.
[c]Means followed by the same letter are not significantly ($P<0.05$) different based on Tukey's test for pairwise comparisons.
[d]Jordanian landraces. [e]Syrian landraces from Suweida (south Syria). [f]Syrian landraces from the mountains near Damascus.
** $P<0.01$; *** $P<0.001$.

The landraces other than those from east Syria had a development pattern which was intermediate between A and B. Jordanian landraces were on average most spring-type like, resulting in a slightly earlier attainment of full flag leaf expansion than the Syrian landraces (Table 3) and consequently an earlier heading date (van Oosterom & Acevedo, 1992a). A weak correlation between time to the DR stage and time to heading was found ($r=0.39$* at TH9 and $r=0.34$* at BR9), which was mainly due to Lignee 131; exclusion of this entry made the correlation coefficients non-significant ($r=0.17$ at TH9 and $r=0.03$ at BR9).

Main shoot leaf appearance and leaf number

The number of visible leaves on the main shoot was a linear function of accumulated thermal units during a major part of the pre-heading period (Figs. 4 and 5). At BR9, PI's were significantly longer ($P<0.01$ for both laboratory and field measurements) than at TH9 (Table 4).

Since there were no major differences in phenology between plants at TH9 and BR9 (Table 2), the shorter PI at TH9 resulted in a higher average leaf number on the main shoot (10.9 at TH9 versus 10.2 at BR9). The correlation coefficient between

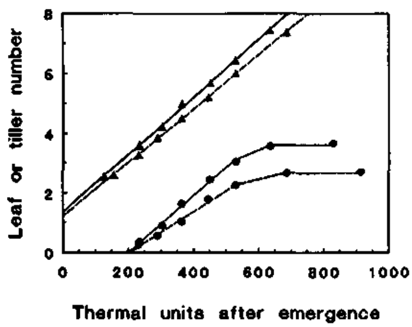

Fig. 4. Number of leaves on the main shoot (▲) and number of main shoot tillers (●) as a function of thermal units (°Cd) after emergence in 1988/89 at Tel Hadya (——) and Breda (----).

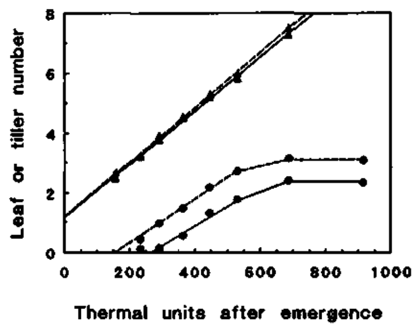

Fig. 5. Number of leaves on the main shoot (▲) and number of main shoot tillers (●) as a function of thermal units (°Cd) after emergence at Breda 1988/89, averaged for four WI entries (——) and three landraces from east Syria (----).

final leaf number at TH9 and BR9 was r=0.92. Entries having development pattern A had low leaf numbers and those with pattern B, C, or D had higher numbers. Leaf number was significantly correlated with thermal units to the DR stage (r=0.72*** at TH9 and r=0.57*** at BR9).

Significant differences in PI were found among development patterns (Table 3). At both TH9 and BR9, entries having development pattern B or D and three of the four Jordanian landraces had a short PI, whereas entries having development pattern

Table 4. Thermal units (°Cd) required for the appearance of one leaf or tiller, pooled for all entries measured in the laboratory or in the field at Tel Hadya and Breda in 1988/89. Intervals given are 95% confidence intervals.

Environment		Leaves[a]	Tillers[b]
Tel Hadya	Laboratory	103.7 ± 4.49 (7)[c]	106.5 ± 13.69 (5)
	Field	98.6 ± 2.75 (9)	-
Breda	Laboratory	110.8 ± 2.30 (7)	143.9 ± 24.93 (5)
	Field	107.3 ± 2.27 (5)	-

[a]All $r^2 \geq 0.999$.
[b]All $r^2 \geq 0.99$.
[c]Number of data points upon which the regression is based.

A or C had a long PI. These results confirmed those of BR8. The date of full flag leaf expansion was latest for entries having pattern C or D (Table 3). This was associated with a long PI (pattern C) or a high leaf number (pattern D). Jordanian landraces on average were early in reaching the stage of full flag leaf expansion, because of the combined effect of a quick leaf appearance and a low leaf number. An analysis of variance showed that, for a subset of 25 entries, the grouping explained a major part of the variance in PI, leaf number and days to full flag leaf expansion (Table 3).

The above results suggest an association between development and leaf appearance. The number of visible leaves on the main shoot at the double ridge (LNDR) or maximum number of primordia (LNMP) stage was strongly linearly related to final number of leaves on the main shoot (FLN) across the two environments (Fig. 6). The equations were:

$$LNDR = 0.60 * FLN - 2.30 \quad (r=0.74, n=70)$$
$$LNMP = 0.85 * FLN - 1.25 \quad (r=0.91, n=70)$$

Tiller appearance

The average number of main shoot tillers per plant was greater by one at TH9 than at BR9 (Fig. 4), owing to a lower tiller appearance rate at BR9. The overall tiller appearance rate was not significantly different from the overall leaf appearance rate at TH9, but at BR9 the difference was significant at $P<0.001$ (Table 4).

Landraces had a higher maximum number of main shoot tillers per plant than non-landraces (Fig. 5). This difference was due to an earlier onset of tiller appearance rather than to a higher number of main shoot leaves. At TH9, where the appearance rates for leaves and tillers were similar, tillers appeared about three phyllochron intervals after the appearance of the subtending leaf for landraces SLB

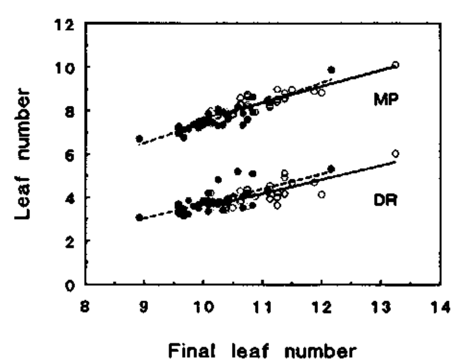

Fig. 6. Number of visible leaves at the double ridge (DR) or maximum number of primordia (MP) stage as a function of final leaf number at Tel Hadya 1988/89 (o) and Breda 1988/89 (•). Lines are regression lines for Tel Hadya (——) and Breda (-----).

Table 5. Correlation coefficients for 35 barley entries between thermal units (°Cd) to the double ridge stage or heading and morphological traits related to winter plant ideotype at Tel Hadya (TH) and Breda (BR) in 1988/89.

	Double ridge		Heading	
	TH	BR	TH	BR
Growth habit[a]	0.58***	0.60***	0.03	0.16
Winter plant colour[b]	0.52**	0.54***	-0.13	-0.01
Cold tolerance[c]	-0.45**	-0.36*	0.16	0.14
Early vigour[d]	-0.67***	-0.50**	-0.23	0.01

[a]1 = erect growth habit, 3 = prostrate growth habit. [b]1 = pale green colour, 3 = dark green colour. [c]1 = no damage, 5 = dead. [d]1 = poor vigour, 5 = good vigour.
* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

03 (east Syria) and SLB 62 (mountains near Damascus), whereas for WI entries (Australia) this period was around 3.6 phyllochron intervals. Landraces JLB 08 (Jordan) and SLB 39 (south Syria) had an intermediate behaviour.

Relationship of development with plant ideotype and yield

Traits associated with winter plant ideotype (winter growth habit, winter plant colour, cold tolerance, and early vigour) were strongly correlated with early development (Table 5). Entries with slow early development tended to have a prostrate winter growth habit, dark winter plant colour, cold tolerance, and poor early vigour. Correlations were only slightly weakened when Lignee 131, whose very slow early development might have biased the correlations, was excluded from the analysis.

Table 6. Correlation coefficients for 35 barley entries between phenological traits and grain yield at Tel Hadya 1988/89 (average yield = 254 g m^{-2}) and Breda 1988/89 (average yield = 125 g m^{-2}).

Trait	Grain yield	
	TH	BR
Time to double ridge (DR)	0.01	-0.07
Time to max. no. primordia (MP)	-0.33	-0.65***
Time to heading (HD)	-0.42*	-0.70***
Time from DR to MP	-0.32	-0.64***
Time from MP to HD	-0.10	-0.08

* $P<0.05$; *** $P<0.001$.

Correlations between these traits and thermal units to heading were absent, indicating that the plant ideotype that is associated with slow early development does not necessarily head late.

Under more stressed conditions, a strong negative correlation between days to heading and grain yield was observed (Table 6), but time to the DR stage was not associated with grain yield. At BR9, entries having development pattern C or D had on average a significantly lower yield than those having pattern A or B (Table 7). At TH9, differences were relatively smaller and not significant.

Grain yield at TH9 was significantly positively correlated with cold tolerance (van Oosterom & Acevedo, 1992a). Entries with slow early development tended to have higher grain yields than entries with quick early development but similar heading date: development pattern B gave higher average grain yields than pattern A and the same was found if pattern D was compared with pattern C and if landraces from southern Syria (SLB 39 or SLB 62) were compared with Jordanian landraces (JLB 08) (Table 7).

Discussion

Apical development

Anthesis of cereals has been shown to be hastened by two to four days under (mild) water stress (Angus & Moncur, 1977; Fischer & Maurer, 1978). In 1988/89, the rainfall pattern in Syria induced terminal drought stress, especially at BR. The present results indicate a hastening of heading at TH9, compared with the wet BR8 environment, of 80 °Cd, equivalent to about four days. Data obtained in 1985/86 also showed a tendency toward a faster development at the drier sites (E. Acevedo, unpublished data). The observed difference in heading date appeared to be due to a shorter spike growth period in the dry season.

The absence of any difference in development up to the stage of maximum primordia number between 1987/88 and 1988/89 is probably due to negligible water stress in 1988/89 until that stage. At both sites, the stage was reached on average at the beginning of March, around 725 °Cd (100 days) after emergence. This coincided with the start of depletion of water in the top 60 cm of the soil, and the onset of water extraction from deeper soil layers, especially at TH9. It was also three weeks after the time water losses under the barley crop started to exceed losses due to direct soil evaporation (Fig. 2). It is therefore likely that drought stress accumulated after the beginning of March, when water demands for the growing crop were high.

The slow early development of the Syrian landraces, especially those from eastern Syria (pattern B), and of Lignee 131 (pattern D), was due to a vernalization requirement (ICARDA, 1989), which lengthened the phase from emergence to the DR stage (Porter et al., 1987). The slower early development of Lignee 131, compared with the Syrian landraces, reflects the higher vernalization requirement of Lignee 131 (ICARDA, 1989). The increased cold tolerance of entries with a slow early development is related to a later induction and initiation of florals and an extended

Table 7. Mean grain yield (g m^{-2}) for four development patterns and three groups of landraces at Tel Hadya (TH) and Breda (BR) in 1988/89.

Group	n[a]	TH		BR	
Pattern A[b]	6	260	ab[c]	121	b
Pattern B	3	297	ab	143	ab
Pattern C	4	206	b	77	c
Pattern D	2	237	ab	76	c
JLB 08[d]	4	235	ab	161	a
SLB 39[e]	3	322	a	153	ab
SLB 62[f]	3	273	ab	137	ab
Average	35	254		125	
ANOVA sum of squares					
Between groups	6	61985	+	69118	***
Within groups	18	61687		20938	

[a]Number of entries per group. [b]For a definition of the development patterns, see text. [c]Means followed by the same letter are not significantly ($P<0.05$) different based on Tukey's test for pairwise comparisons. [d]Jordanian landraces. [e]Syrian landraces from Suweida (south Syria). [f]Syrian landraces from the mountains near Damascus.

+ $P<0.10$; *** $P<0.001$.

positioning of the apex below the soil surface (George, 1982; Kirby et al., 1985a). An additional advantage of this submerged apex position is a better survival of green stage grazing (Rhodes, 1975), a common farming practice in the dry areas of east and north east Syria (Nordblom, 1983).

The absence of a clear correlation between early development and heading date is in agreement with results of Kirby et al. (1985a) for barley and wheat. The strong correlation, under terminal drought, between heading date and grain yield, supports theoretical considerations of Passioura (1977) and has been observed for many crops, e.g., spring wheat (Fischer & Maurer, 1978), barley (Hadjichristodoulou, 1981), and pearl millet (Bidinger et al., 1987). Since this correlation is established during the spike initiation phase (Table 6), it can be concluded that a rapid development during this phase is a key factor for attaining good yields under low-rainfall Mediterranean environments. The cause of this rapid development therefore deserves further discussion.

The development of barley is controlled by vernalization, photoperiod, and temperature (Ellis et al., 1989). Because emergence dates of the experiments at TH9, BR8, and BR9 were similar and because the sites are only 40 km apart, variation in photoperiod could be ignored when comparing environments. Since a vernalization requirement does not influence the rate of development after the DR stage (Ellis et al., 1989) and since barley is a quantitative long-day plant, the rapid development after the DR stage of pattern B landraces suggests that they are very sensitive to longer days. This hypothesis is in agreement with the observation of Ellis et al. (1988) that, under controlled conditions, Arabi Abiad, a Syrian landrace, has a strong photoperiodic response, especially after the vernalization requirement has been met. The combination of a vernalization requirement, which delays the onset to the generative phase of the apex, with a rapid development after the DR stage, results in a relatively constant heading date across years, less sensitive to temperature fluctuations (van Oosterom & Acevedo, 1992b).

A stable heading date can be an important mechanism to reduce the risk of a crop failure in northern Syria, where grain yield can be reduced by both late frosts and terminal drought stress. Since timing and intensity of temperature and drought stress are unpredictable, pattern B allows a maximum probability of avoiding yield losses due to either of these stresses. Prices of cereals in developing countries increase sharply if yields are low (Marshall, 1987); consequently, a reduced risk of a crop failure has a high priority for local farmers. Pattern B is therefore particularly useful in Mediterranean environments were marginal yields are due to the combined effect of low winter temperatures and terminal drought stress.

Pattern A is based on a very rapid early development. This makes the crop vulnerable to cold damage (Table 5), but early heading ensures a good avoidance of terminal drought stress. This pattern is therefore preferable in Mediterranean environments where the risk of severe yield losses due to cold damage is low, such as the coastal areas of North Africa.

The slow development after the DR stage of pattern C indicates a low sensitivity to longer days. This is supported by the fact that all four entries having this response pattern had European improved cultivars in their pedigrees. Because this daylength response results in a late heading date in West Asia and North Africa, entries having this development pattern do not adequately avoid terminal drought stress in this region and hence are unadapted.

The late heading date of Lignee 131 (pattern D) was associated with a high vernalization requirement. Clearly, the balance between avoidance of both cold damage and terminal drought stress was gone, resulting in low yields if terminal drought stress increased (Table 7). The low yields of entries having development pattern C or D emphasize that photoperiodic response and level of vernalization requirement are key factors in the adaptation of barley to terminal drought stressed environments in West Asia and North Africa.

Main shoot leaf appearance and leaf number

Differences in final leaf number on the main shoot between TH9 and BR9 were most probably due to lower soil temperatures at BR9 during the period of leaf primordia initiation. The mean soil temperature at a depth of 5 cm during the six weeks after sowing was 7.2°C at BR9 compared with 10.6°C at TH9. An influence of soil temperature on leaf primordia initiation has been found by Cooper & Law (1978) for maize.

The linear relationship between leaf number and accumulated temperature is in accordance with results reported for wheat and barley (e.g., Syme, 1974; Gallagher, 1979; Hay & Tunnicliffe Wilson, 1982; Kirby et al., 1985b; Kirby & Perry, 1987). The observed differences in PI between development patterns also accord with results of Kirby et al. (1985b), who found for both barley and wheat that winter cultivars tended to have high leaf appearance rates (low PI), whereas a spring cultivar had the lowest rate in both species. The significant differences in PI between development patterns indicate an association between development and leaf appearance. The good correlation across environments between final leaf number on the main shoot and leaf number at the DR or MP stage indicates that this association is due to a similar reaction to environmental variables. Stapper (1984) reached the same conclusion for wheat grown across a range of environments in northern Syria. Craufurd et al. (1992) observed for sorghum that panicle development and leaf appearance had a comparable response to heat and drought stress.

Tiller appearance

Since tiller initiation is little affected by environmental conditions (Evans et al., 1964), the lower tiller appearance rate at BR9 must be due to the failure of tiller buds to expand. Klepper et al. (1982) found that adverse conditions can delay or suppress tiller production; assimilates are in that case apparently used for the growth or development of the main shoot (Friend, 1965). Lower temperatures and water-holding capacity of the soil at BR may have limited the supply of assimilates to the tillers.

Differences in main shoot tiller number within sites among entries were associated with a difference in the onset of tiller appearance (Fig. 5). The observed range in PI between the appearance of a leaf and its tiller (3-3½ PI at TH9) is in accordance with the period of around three PI's which has been observed for wheat and barley (Kirby & Riggs, 1978; Baker & Gallagher, 1983a; Kirby et al., 1985c). The number of PI's between the appearance of a leaf and its tiller is an indication of apical dominance (Friend, 1965). A short period (Syrian landraces in Fig. 5) indicates a low degree of apical dominance and a long period (WI entries in Fig. 5) a high degree. A relatively early emergence of tillers can be advantageous, as yield per tiller is directly related to age (Rawson, 1971). Another advantage of this earlier tillering is an improved ground cover. Van Oosterom & Acevedo (1992a) found that around 40 days after emergence, corresponding to around 300 °Cd, the ground cover of SLB 62 and SLB 03 landraces was superior to the ground cover of the WI entries. This coincided with the onset of tillering in the WI entries and with the moment the difference in number of main shoot tillers reached its maximum (Fig. 5). This demonstrates the direct influence of tillering upon ground cover.

Implications for breeding

Genotypic differences in apical development were due to different vernalization requirements and photoperiodic reactions. Selection of barley adapted to low-rainfall Mediterranean environments with cold winters is therefore primarily a matter of selecting the proper combination of vernalization requirement and daylength response. Time from emergence to the DR stage, and thus vernalization requirement, is strongly correlated with morphological traits in winter (growth habit, plant colour, cold tolerance, early vigour); the rate of development after the DR stage is strongly correlated with heading date. A combined selection for these morphological traits may therefore result in the selection of material with a development adapted to well-defined Mediterranean regions. Since both vernalization requirement and daylength response are largely independent of seasonal fluctuations, the expression of these traits is expected to be relatively stable across environments. This is confirmed by results of van Oosterom & Acevedo (1992a). Selection for these traits can in that case be done under favourable conditions and can be a useful indirect selection for grain yield in low-rainfall environments in northern Syria (van Oosterom & Acevedo, 1992b).

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References

Acevedo, E. & S. Ceccarelli, 1989. Role of physiologist-breeder in a breeding program for drought resistance conditions. In: F.W.G. Baker (Ed.), Drought Resistance in Cereals, pp. 117-140. CAB International, Wallingford, UK.

Acevedo, E., P.Q. Craufurd, R.B. Austin & P. Pérez-Marco, 1991. Traits associated with high yield in barley in low-rainfall environments. J. Agric. Sci., Camb. 116: 23-36.

Angus, J.F., D.H. Mackenzie, R. Morton & C.A. Schafer, 1981. Phasic development in field crops. II. Thermal and photoperiodic responses of winter wheat. Field Crops Res. 4: 269-283.

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

Baker, C.K. & J.N. Gallagher, 1983a. The development of winter wheat in the field. 1. Relation between apical development and plant morphology within and between seasons. J. Agric. Sci., Camb. 101: 327-335.

Baker, C.K. & J.N. Gallagher, 1983b. The development of winter wheat in the field. 2. The control of primordium initiation rate by temperature and photoperiod. J. Agric. Sci., Camb. 101: 337-344.

Bidinger, F.R., V. Mahalakshmi & G.D.P. Rao, 1987. Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leeke]. I. Factors affecting yields under stress. Aust. J. Agric. Res. 38: 37-48.

Cao, W. & D.N. Moss, 1989. Temperature effect on leaf emergence and phyllochron in wheat and barley. Crop Sci. 29: 1018-1021.

Ceccarelli, S., S. Grando & J.A.G. van Leur, 1987. Genetic diversity in barley landraces from Syria and Jordan. Euphytica 36: 389-405.

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

Cooper, P.J.M. & R. Law, 1978. Enhanced soil temperature during very early growth and its association with maize development and yield in the highlands of Kenya. J. Agric. Sci., Camb. 91: 569-577.

Craufurd, P.Q., D.J. Flower & J.M. Peacock, 1992. Effect of heat and drought stress on sorghum (*Sorghum bicolor* (L.) Moench). 1. Panicle development and leaf appearance. Expl. Agric. (in press).

Ellis, R.H., E.H. Roberts, R.J. Summerfield & J.P. Cooper, 1988. Environmental control of flowering in barley (*Hordeum vulgare* L.). II. Rate of development as a function of temperature and photoperiod and its modification by low-temperature vernalization. Ann. Bot. 62: 145-158.

Ellis, R.H., R.J. Summerfield, E.H. Roberts & J.P. Cooper, 1989. Environmental control of flowering in barley (*Hordeum vulgare*). III. Analysis of potential vernalization responses, and methods of screening germplasm for sensitivity to photoperiod and temperature. Ann. Bot. 63: 687-704.

Evans, L.T., I.F. Wardlaw & C.N. Williams, 1964. Environmental control of growth. In: C. Barnard (Ed.), Grasses and Grasslands, pp. 102-125. Macmillan & Co., Ltd., London.

Fischer, R.A., 1981. Optimizing the use of water and nitrogen through breeding of crops. In: J. Monteith & C. Webb (Eds.), Soil Water and Nitrogen in Mediterranean-type Environments, pp. 249-278. Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, Boston, London.

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

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

Friend, D.J.C., 1965. Tillering and leaf production in wheat as affected by temperature and light intensity. Can. J. Bot. 43: 1063-1076.

Gallagher, J.N., 1979. Field studies of cereal leaf growth. I. Initiation and expansion in relation to temperature and ontogeny. J. Exp. Bot. 30: 625-636.

George, D.W., 1982. The growing point of fall-sown wheat: a useful measure of physiological development. Crop Sci. 22: 235-239.

Gomez, K.A. & A.A. Gomez, 1984. Statistical Procedures for Agricultural Research, 2nd edition. John Wiley & Sons Ltd., New York.

Hadjichristodoulou, A., 1981. Aspects of barley breeding for dry Mediterranean regions. In: M.J.C. Ascher, R.P. Ellis, A.M. Hayter & R.N.H. Whitehouse (Eds.), Barley Genetics IV, pp. 383-388. Proc. 4th International Barley Genetics Symposium, Edinburgh, 22-29 July 1981.

Harlan, J.R., 1976. Barley. In: N.W. Simmonds (Ed.), Evolution of Crop Plants, pp. 93-98. Longman, London & New York.

Hay, R.K.M. & G. Tunnicliffe Wilson, 1982. Leaf appearance and extension in field-grown winter wheat plants: the importance of soil temperature during vegetative growth. J. Agric. Sci., Camb. 99: 403-410.

ICARDA, 1989. Cereal Improvement Program: Annual Report 1988. International Center for Agricultural Research in the Dry Areas, Aleppo, Syria, 187 pp.

Jones, J.L. & E.J. Allen, 1986. Development in barley (*Hordeum sativum*). J. Agric. Sci., Camb. 107: 187-213.

Keuls, M. & F. Garretsen, 1982. Statistical analysis of growth curves in plant breeding. Euphytica 31: 51-64.

Kirby, E.J.M., 1974. Ear development in spring wheat. J. Agric. Sci., Camb. 82: 437-447.

Kirby, E.J.M., 1977. The growth of the shoot apex and the apical dome during ear initiation. Ann. Bot.

41: 1297-1308.
Kirby, E.J.M. & M. Appleyard, 1984. Cereal Development Guide. NAC Cereal Unit, Stoneleigh, Warwickshire, U.K.
Kirby, E.J.M., M. Appleyard & G. Fellowes, 1985a. Variation in development of wheat and barley in response to sowing date and variety. J. Agric. Sci., Camb. 104: 383-396.
Kirby, E.J.M., M. Appleyard & G. Fellowes, 1985b. Effect of sowing date and variety on main shoot leaf emergence and number of leaves of barley and wheat. Agronomie 5: 117-126.
Kirby, E.J.M., M. Appleyard & G. Fellowes, 1985c. Leaf emergence and tillering in barley and wheat. Agronomie 5: 193-200.
Kirby, E.J.M. & R.P. Ellis, 1980. A comparison of spring barley grown in England and Scotland. 1. Shoot apex development. J. Agric. Sci., Camb. 95: 101-110.
Kirby, E.J.M. & M.W. Perry, 1987. Leaf emergence rates of wheat in a Mediterranean environment. Aust. J. Agric. Res. 38: 455-464.
Kirby, E.J.M. & T.J. Riggs, 1978. Developmental consequences of two-row and six-row ear type in spring barley. 2. Shoot apex, leaf and tiller development. J. Agric. Sci., Camb. 91: 207-216.
Klepper, B., R.W. Richman & C.M. Peterson, 1982. Quantitative characterization of vegetative development in small cereal grains. Agron. J. 74: 789-792.
Marshall, D.R., 1987. Australian plant breeding strategies for rainfed areas. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 171-189. John Wiley & Sons Ltd., New York.
Nordblom, T.L., 1983. Livestock - crop interactions. The case of green stage grazing. ICARDA Disc. Paper No. 9, Aleppo, Syria, 37 pp.
Oosterom, E.J. van & E. Acevedo, 1992a. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. I. Morphological traits. Euphytica (in press).
Oosterom, E.J. van & E. Acevedo, 1992b. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. III. Plant ideotype and grain yield. Euphytica (in press).
Passioura, J.B., 1977. Grain yield, harvest index, and water use of wheat. J. Aust. Inst. Agric. Sci. 43: 117-120.
Porter, J.R., E.J.M. Kirby, W. Day, J.S. Adam, M. Appleyard, S. Ayling, C.K. Baker, P. Beale, R.K. Belford, P.V. Biscoe, A. Chapman, M.P. Fuller, J. Hampson, R.K.M. Hay, M.N. Hough, S. Matthews, W.J. Thompson, A.H. Weir, V.B.A. Willington & D.W. Wood, 1987. An analysis of morphological development stages in Avalon winter wheat crops with different sowing dates and at ten sites in England and Scotland. J. Agric. Sci., Camb. 109: 107-121.
Rawson, H.M., 1971. Tillering patterns in wheat with special reference to the shoot at the coleoptile node. Aust. J. Biol. Sci. 24: 829-841.
Rhodes, I., 1975. The relationship between productivity and some components of canopy structure in ryegrass (*Lolium* spp.) IV. Canopy characters and their relationship with sward yields in some intra-population selections. J. Agric. Sci., Camb. 84: 345-351.
Stapper. M., 1984. Simulations assessing the productivity of wheat maturity types in a Mediterranean climate. Ph.D. dissertation, University of New England, Armidale, N.S.W., Australia, 313 pp.
Syme, J.R., 1974. Leaf appearance rate and associated characters in some Mexican and Australian wheats. Aust. J. Agric. Res. 25: 1-7.
Wang, J.Y., 1960. A critique of the heat unit approach to plant response studies. Ecology 41: 785-790.
Weir, A.H., P.L. Braggs, J.R. Porter & J.H. Rayner, 1984. A winter wheat crop simulation model without water or nutrient limitations. J. Agric. Sci., Camb. 102: 371-382.
Weltzien. E., 1988. Evaluation of barley (*Hordeum vulgare* L.) landrace populations originating from different growing regions in the near east. Plant Breeding 101: 95-106.

CHAPTER 3

Adaptation of barley (Hordeum vulgare L.) to harsh Mediterranean environments. III. Plant ideotype and grain yield

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Euphytica (in press)

Key words: adaptation, barley, drought, heading date, plant ideotype, principal component analysis, stability

Summary

Barley adapted to the combined stresses of low winter temperatures and terminal drought requires a medium early heading date, little affected by environmental fluctuations. Two plant ideotypes that are adapted to terminal drought in Mediterranean environments can be distinguished. The first combines early heading with good early growth vigour, erect winter growth habit, light plant colour, and ability to recover from cold damage. The second combines medium early heading, prostrate winter growth habit, dark winter plant colour which changes to pale green in spring, and cold tolerance. This study was conducted to determine the relationship between consistency in heading date and plant ideotype, and to identify the usefulness of earliness and plant ideotype as criteria for indirect selection for grain yield under drought. Thirty-six two-row entries of barley (Hordeum vulgare L.) were sown at 15 environments in northern Syria. Average grain yields ranged from 7 to 331 g m^{-2}; the range in average heading date was 20 days. Consistency in date of heading was related to the second ideotype through vernalization requirement. Early heading was positively correlated with grain yield in most of the environments, but especially in low-yielding environments. After eliminating the effect of heading date, the second plant ideotype was advantageous only under harsh conditions. In early generations, selection under favourable conditions for earliness, prostrate winter growth habit, dark winter plant colour, and cold tolerance is a useful alternative for yield testing, to identify material well adapted to environments experiencing low winter temperatures and terminal drought stress. Selection for the first plant ideotype is proposed for Mediterranean environments with mild winters.

Introduction

Under terminal stress, early heading in cereals is an important escape mechanism, and correlations between earliness and grain yield have been reported extensively, e.g., Fischer & Maurer (1978), Bidinger et al. (1987), Ceccarelli et al. (1987), van Oosterom & Acevedo (1992b). In the Mediterranean environments of northern Syria, frost also occurs, but timing and severity are highly unpredictable. The heading date must thus be early enough to enable adequate grain filling, but late enough to avoid cold damage. In environments with such a narrow optimum period for heading date, cultivars with heading dates less affected by environmental fluctuations are preferable.

Two plant ideotypes have been identified, which are adapted to terminal drought stress and which could be distinguished by the amount of vernalization required (van Oosterom & Acevedo, 1992a,b). The first ideotype was characteristic of spring-type barleys from Australia and of Jordanian landraces. Their ideotype is a combination of good early growth vigour, an erect growth habit and light plant colour in winter, an ability to recover from cold damage, and early heading. The second ideotype is characteristic of landraces from east and north east Syria. They have a prostrate winter growth habit with an early onset of tillering, a dark green plant colour in winter, changing to pale green in spring, a high level of cold tolerance, but poor early growth vigour; their heading date is medium early. Both ideotypes provided a good ground cover in spring (van Oosterom & Acevedo, 1992a), an important factor in reducing losses of water via direct soil evaporation (Cooper et al., 1983).

The heading date of entries requiring vernalization is less affected by temperature variations than the heading date of entries with a quick early development (Loss et al., 1990). This is related to the fact that the pre-spike initiation development of entries requiring vernalization is delayed under warm conditions. Entries having the second plant ideotype therefore might have a heading date that is less affected by seasonal fluctuations in emergence date or winter temperatures.

Controversy exists as to whether or not in a breeding program for dry areas yield testing has to be done under favourable or unfavourable conditions. Pfeiffer (1988) reported improved drought tolerance in bread wheat after yield selection in favourable environments. Ceccarelli (1987), however, argues that for barley in Mediterranean environments, segregating populations must be screened as early as possible in the dry target environment. This is to prevent losses of tolerant material, which could occur when selecting for some cycles in an optimum environment. However, in early generations, seed availability is limited, and yield is at best difficult to assess in a representative way (Weber, 1984). One reason is that single-row plots are less representative of farmers' fields than three- or six-row plots (Kramer et al., 1982; Spitters, 1984). This is especially so in dry environments, which also carry the risk of losing all material in very dry years. An early, indirect assessment of yield in a more favourable environment would therefore be of great use.

Many plant attributes of potential benefit to yield under drought have been identified in the literature, largely on theoretical grounds, e.g., ground cover, winter growth vigour, winter growth habit, plant colour, and reaction to cold (Fischer, 1981; Richards, 1982; Passioura, 1986; Acevedo, 1987; Richards, 1987; Acevedo & Ceccarelli, 1989). Unambiguous proof for their usefulness as indirect selection criteria, however, is scarce. This is not surprising, because Ceccarelli et al. (1991) and van Oosterom & Acevedo (1992a) showed that different combinations of relatively simple traits can give similar yields. Individual traits must therefore be considered as part of the entire plant ideotype.

The objective of this study was to determine the relationship between plant ideotype and stability in heading date, and to identify the usefulness of earliness and plant ideotype as possible criteria for indirect selection for yield in Mediterranean environments where both low-temperature stress and terminal-drought stress are likely to occur.

Table 1. Emergence date, average heading date, average grain yield (g m^{-2}) and precipitation (mm) for 15 experiments at four sites in northern Syria: Tel Hadya (TH), Breda (BR), Boulder (BO), and Jinderess (JI).

1985/86	TH6	BR6	BO6	JI6
Emergence date	02/01/86	06/01/86	04/01/86	05/01/86
Average heading date	08/04/86	04/04/86	02/04/86	30/03/86
Average grain yield (g m^{-2})	331	134	133	n.a.[a]
Precipitation (mm)	316	218	205	405
1986/87	TH7	BR7	BO7	
Emergence date	28/12/86	26/12/86	30/12/86	
Average heading date	15/04/87	15/04/87	*crop failure*	
Average grain yield (g m^{-2})	246	148	-	
Precipitation (mm)	343	245	174	
1987/88	TH8	BR8	BO8	
Emergence date	04/11/87	22/11/87	13/12/87	
Average heading date	29/03/88	04/04/88	11/04/88	
Average grain yield (g m^{-2})	296	n.a.	273	
Precipitation (mm)	499	408	382	
1988/89	TH9		BO9	
Emergence date	22/12/88		31/01/89	
Average heading date	n.a.		n.a.	
Average grain yield (g m^{-2})	89		7	
Precipitation (mm)	234		186	
1990/91	TH1 early	TH1 normal	TH1 late	
Emergence date	25/10/90	07/12/90	14/01/91	
Average heading date	27/03/91	04/04/91	14/04/91	
Average grain yield (g m^{-2})	n.a.	n.a.	n.a.	
Precipitation (mm)	294+100irr.[b]	294+65irr.	294+40irr.	

[a]Not available.
[b]Irrigation early in the season.

Materials and Methods

Plant material and environments

Thirty-six two-row entries of barley (*Hordeum vulgare* L.), covering a wide range of genotypic variation, were sown for five seasons (1985/86 until 1990/91, except 1989/90) at one to four sites in northern Syria, differing in mean annual precipitation. The entries used in the experiments, the experimental design, and agronomical practices have been described (van Oosterom & Acevedo, 1992a). Briefly, the nursery contained Australian genotypes adapted to terminal drought stress, Syrian and Jordanian landraces, lines from the barley breeding program at ICARDA, and European cultivars. Details about the individual year × location combinations (environments) are given in Table 1.

Stability in heading date

Stability in heading date was calculated as the slope of the regression of heading date of each entry in each environment on the mean heading date of all entries in each environment (Finlay & Wilkinson, 1963). Since our main interest was in stability expressed in Julian dates, rather than in stability in the period from emergence to heading, days to heading was expressed as the number of days from 1 March on. An entry was regarded as having a stable date of heading if the among-environments variance, and thus the regression slope, was low (Finlay & Wilkinson, 1963). To investigate whether the linear regression explained a major part of the entry x environment interaction, a joint regression analysis of variance was performed as proposed by Perkins & Jinks (1968). The overall efficiency of the linear regression in accounting for the interaction was calculated as the linear proportion of the variance accounted for by the regression (Fripp & Caten, 1971): $100l\ (l + nl)^{-1}$, where l is the difference between the mean square of the heterogeneity of regression and the pooled residual mean square, and nl is the difference between the mean square of the deviations from regression and the pooled residual mean square.

Principal component analysis of plant ideotype

Because the two plant ideotypes mentioned above can be distinguished by their apical development pattern (van Oosterom & Acevedo, 1992b), some of the individual traits which make up the plant ideotype are causally related and consequently mutually correlated. It is therefore justified to describe the plant ideotype as one variable, being the first principal component (PC1) of a principal component analysis (PCA) with these mutually correlated traits as input variables. Data collected on growth habit, plant colour (expressed as the difference between winter and spring colour) and cold tolerance, obtained at three sites (Tel Hadya, Breda, and Bouider) in 1987/88 (van Oosterom & Acevedo, 1992a) were the input for the PCA. These traits were in general highly mutually correlated within locations, while a high correlation between the extremely wet 1987/88 season and the dry 1988/89 season suggested that the results of 1987/88 were representative for a wide range of environments. For each trait, one score per entry was obtained, being the mean of the scores in each of the three environments, which in turn were the mean values of two to six observations, taken at two-week intervals. Scores for cold tolerance at Tel Hadya, where only minor damage occurred, were not representative and therefore omitted as input values.

The theory of the PCA and the related matrix theory are described in detail in statistics handbooks, e.g., Pearce (1983), Anderson (1984), and Brook & Arnold (1985). In short, the PCA transforms a linear 'n'-dimensional model into a new model that contains 'n' orthogonal, uncorrelated principal components, each being a linear combination of the original variables. Since the eigenvalue of each principal component equals the variance of that component, the proportion of the variance of the original model explained by each principal component can be calculated as its eigenvalue, expressed as a fraction of the sum of all the eigenvalues. If the principal components are sorted according to a descending eigenvalue, the first principal components will have the largest variances and will give the best fit to the original data points. A PCA can therefore be used to reduce the number of variables in the model. In the present study, the PCA was performed on the correlation matrix of the three input variables (growth habit, plant colour, and cold tolerance).

Relation between plant ideotype, heading date, and grain yield

To investigate the direct influence of plant ideotype upon yield, a forward stepwise multiple regression analysis was performed with grain yield in each environment as the dependent variable and plant ideotype (represented by PC1) and heading date (days from 1 March to heading, averaged over 12 environments) as the independent variables. The low correlation between the two independent variables (r=0.15) justified the use of the multiple regression analysis.

Statistical analyses

The stability analysis was carried out in CRISP (Crop Research Integrated Statistical Package), a computer program available on the mainframe computer of ICARDA. All other computations were performed in SAS (1988); for the PCA the PRINCOMP-procedure was used and for the multiple regression analysis the REG-procedure.

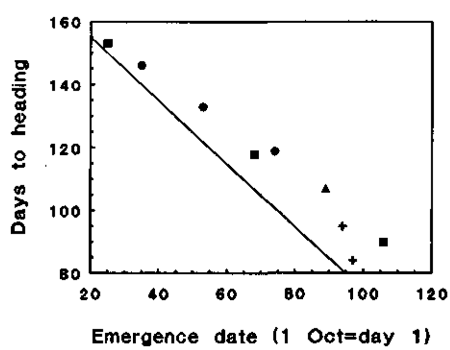

Fig. 1. Number of days from emergence to heading as a function of emergence date for barley in northern Syria in 1985/86 (+), 1986/87 (▲), 1987/88 (●), and 1990/91 (■). Only environments with an average yield level, high enough to assume a minor influence of drought stress on days to heading, are presented. The solid line represents the situation where delayed emergence will not delay heading.

Table 2. Joint regression analysis of variance for heading date for 36 barley entries grown in 12 environments in northern Syria.

Source	Degrees of freedom	Sum of squares	Mean square	F
Entries	35	4104.5	117.27	35.97[a]**
Environments	11	17563.5	1596.68	489.78
Entries x environments	385	1254.6	3.26	4.02[b]**
Heterogeneity of regressions	35	294.0	8.40	3.07[c]** 10.37[b]**
Deviations from regression	350	960.5	2.74	3.38[b]**
Rep (within environment)	24	343.9	14.33	
Error	840	684.1	0.81	

[a]Entries x environments MS used as denominator.
[b]Error MS used as denominator.
[c]Deviations from regression MS used as denominator.
** $P<0.01$.

Results

Stability in heading date

Although there was a range of 81 Julian days in emergence dates, the range in the average heading date for the experiments was only 19 days (Table 1). On average, 30 days delay in emergence resulted in seven days delay in heading (Fig. 1).

The entry x environment interaction for days to heading in the joint regression analysis of variance accounted for only 5% of the total sum of squares, compared with a contribution of 17% of the entries main effect (Table 2). Although the interaction was less important than the main effects, it was still highly significant. In the F-test for heterogeneity of regressions and for deviations from regression, the error mean square (MS) was used as the denominator (Freeman & Perkins, 1971; Freeman, 1973). The heterogeneity of regressions MS also was F-tested with the deviations MS, as suggested by Freeman (1973). The latter F-value was significant at $P<0.01$, indicating that the linear effect of environments accounted for a significant part of the observed interaction. The linear proportion of the variance in entry x environment interaction accounted for by the regressions was 80%. Deviations from linearity were significant at $P<0.05$ for 24 of the 36 entries; those with a late average heading date tended to have the highest deviation. Nevertheless, the correlations between the observed heading dates and those predicted by the model were high: the lowest correlation coefficient was $r=0.87$ for Lignee 131. The regression slopes were therefore considered to give an adequate estimate of the stability in heading date for each entry.

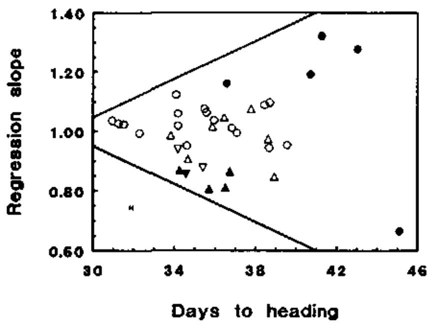

Fig. 2. Relationship of stability of heading date (linear regression slope) and mean number of days from 1 March to heading for Syrian landraces (△▲), Jordanian landraces (▽▼), and non-landraces (○●). Closed symbols represent entries with a slope significantly different from unity at P<0.05. Bar represents standard error of a genotype's heading date.

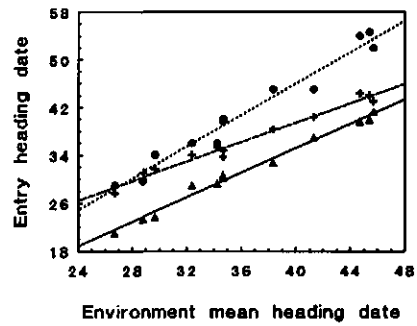

Fig. 3. Number of days from 1 March to heading as a function of the environmental mean number of days from 1 March to heading for WI 2291/WI 2269 (▲——▲), Arabi Aswad (+-----+), and BON 27 (●·······●).

The four earliest entries in the nursery had a slope close to unity (Fig. 2), indicating an early heading in all environments. The slopes of late entries tended to deviate from unity. Landraces had a range of only five days in average heading date. Their regression slopes were in general below average. The entry with the lowest slope was Lignee 131, a winter-type barley from France, which differed from the landraces by its much later heading. Using a one-sided t-test, six entries requiring vernalization (five landraces and Lignee 131) had a slope significantly lower than one; four entries, without vernalization requirement, had a slope significantly higher than one. There was no correlation between heading date and the regression slope (r=0.09).

The regression lines for three contrasting entries are shown in Fig. 3. If heading is early, Arabi Aswad, a landrace widely grown by the farmers in the drier areas of northern Syria, is as late as BON 27 (Kervana/Mazurka) and about one week later than WI 2291/WI 2269, an early spring-type barley from Australia. In years with late heading, A. Aswad is only about three days later than WI 2291/WI 2269 and about nine days earlier than BON 27.

Relationship between plant ideotype, heading date, and grain yield

The three input variables for the PCA (growth habit, change in plant colour, and cold tolerance) were strongly mutually correlated (r≥0.67 for all correlations). Consequently, the first principal component explained a major part, 81.5%, of the variation present in the original model and was hence considered to be representative of each of the three input variables.

The sign for a PC-axis is given arbitrarily. In our study, a high value for PC1 indicated a prostrate winter growth habit, a distinct change in plant colour from dark green in winter to pale green in spring, and cold tolerance; it represented a winter type of barley. A low value for PC1 represented spring types and indicated an erect growth habit, no change in plant colour, and cold sensitivity.

Results of the forward stepwise multiple regression analysis (Table 3) show that, across the range of environments, earliness is related to grain yield, earlier heading resulting in higher grain yields. After removal of the effect of earliness, PC1 did not explain a significant additional part of the variation in grain yield in the higher-yielding environments. The only exception was TH8, a very wet environment where PC1 was negatively correlated with grain yield, probably due to lodging of the landraces. Under low-yielding conditions, however, plant ideotype became more important, especially under the harsh conditions in 1988/89, when the crop received only 91 mm (TH9) and 23 mm (BO9) of precipitation after emergence.

The relationship between PC1 and average heading date is shown in Fig. 4. Note that the y-axis of this figure is similar to the x-axis of Fig. 2. Syrian landraces, especially those from east and north east Syria, SLB 03 and SLB 45 respectively, had high values for PC1, while the Jordanian landraces and the Syrian landraces collected in the mountains near Damascus, SLB 62, and in southern Syria, SLB 39, had values intermediate between the SLB 03 and SLB 45 landraces on the one hand and the earliest spring types on the other hand.

Although the earliest entries in the nursery were spring types, the high value for PC1 of some landraces and the related slow early development (van Oosterom & Acevedo, 1992b) did not necessarily imply lateness; PC1 was not correlated with

Table 3. Partial portion of the variation in grain yield (GY) per environment explained by average days from 1 March to heading (DH) and plant ideotype (PC1, representing growth habit, plant colour, and cold tolerance), using a forward stepwise multiple regression analysis.

	TH6[a]	TH8	BO8[a]	TH7	BR7[a]	BR6	BO6	TH9	BO9
GY (g m^{-2})	331	296	273	246	148	134	133	89	7
DH	0.16*	0.00	0.13*	0.41***	0.56***	0.36***	0.42***	0.50***	0.25**
PC1	0.02	0.13*[b]	0.08	0.01	0.10**	0.12**	0.01	0.20***	0.27***
Model	0.18*	0.13	0.21*	0.42***	0.66***	0.48***	0.43***	0.70***	0.52***

[a]TH6=Tel Hadya 1985/86, BR7=Breda 1986/87, BO8=Bouider 1987/88, etc.
[b]Due to a significant negative correlation between grain yield and PC1.
* P<0.05; ** P<0.01; *** P<0.001.

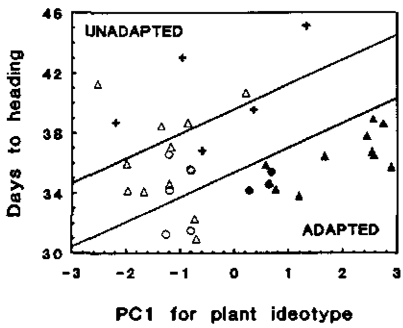

Fig. 4. Relationship between plant ideotype (expressed as principal component 1 (PC1) representing growth habit, plant colour, and cold tolerance) and mean number of days from 1 March to heading for European cultivars (+), lines from ICARDA's barley breeding program (▵), Australian entries (○), Jordanian landraces (●), and Syrian landraces (▲). Lines to separate entries which are adapted and unadapted to drought have been drawn arbitrarily.

days to heading (r=0.15). The correlation between PC1 and the regression slope in the stability analysis, in contrast, was highly significant (r=0.62, P<0.001).

A prostrate growth habit, combined with cold tolerance and a change in plant colour, becomes more advantageous under dry conditions as shown in Table 4, where yields of the four earliest entries (left corner, lower triangle, Fig. 4) and the six most prostrate landraces (upper corner, lower triangle, Fig. 4) across environments are compared. To enable a valid comparison between environments, the yields in each environment were standardized to a mean value of zero and a standard deviation of one. Although the early entries outyielded the prostrate entries in most of the environments, the difference progressively decreased and in BO9 the prostrate landraces outyielded the early entries. Entries without an early heading or appropriate plant ideotype (e.g., the seven entries in the upper triangle of Fig. 4) are unadapted to dry conditions, as can be seen from the increasing difference in standardized yield between these entries and the early or prostrate entries (Table 4).

Discussion

The highly significant correlation between stability in date of heading and plant ideotype, represented by PC1, was expected, since both characteristics are related to vernalization requirement. In case of an early emergence, the seedlings encounter high air temperatures. The mean daily screen air temperatures for the period between four days before emergence and 20 days after emergence were between 6.1 °C and 8.3 °C for emergence dates between 13 December and 14 January. Earlier emergence dates, however, showed progressively higher mean temperatures, up to 17.4 °C following emergence on 25 October. Since optimum vernalizing temperatures for cereals are in the range of 5 °C to 10 °C, the vernalization process

Table 4. Difference in standardized grain yield between groups of entries across a range of environments. Values presented a means of three successive environments after ranking for mean grain yield (see Table 3). The composition of groups is based upon Fig. 4.

Environments[a]	Contrast		
	Early (4)[b] vs prostrate (6)	Early (4) vs unadapted (7)	Prostrate (6) vs unadapted (7)
TH6 TH8 BO8	1.64[c]	1.18	-0.46
TH8 BO8 TH7	1.39	1.20	-0.19
BO8 TH7 BR7	1.09	1.67	0.58
TH7 BR7 BR6	0.71	1.86	1.15
BR7 BR6 BO6	0.77	2.00	1.23
BR6 BO6 TH9	0.78	2.17	1.39
BO6 TH9 BO9	0.41	2.08	1.67

[a]TH6=Tel Hadya 1985/86, BR7=Breda 1986/87, BO8=Bouider 1987/88, etc.
[b]Number of entries per group.
[c]A positive value indicates that the first group has the highest yield.

was retarded in case of an early emergence. This extended the photoperiod-insensitive vegetative phase of the apex and delayed heading (Porter et al., 1987; Ellis et al., 1988). The present results are in accordance with those reported by Loss et al. (1990), who found that the time of flowering of cultivars requiring vernalization, is less affected by fluctuations in temperature between environments than that of cultivars that do not require vernalization.

Time of heading is important for grain yield in environments where yield is limited by low winter temperatures, and terminal drought and heat stress. The narrow range in heading date of the landraces confirms data of Ceccarelli et al. (1987), who postulated that it represented an optimum balance between avoidance of both these stresses. Ellis et al. (1988) found, under controlled conditions, that Arabi Abiad, a popular landrace in northern Syria, is sensitive to photoperiod rather than to temperature after its vernalization requirement has been met. Results of van Oosterom & Acevedo (1992b) support this photoperiodic response of Syrian landraces. A certain vernalization requirement, a strong photoperiodic dependency, and hence insensitivity to effects of post-vernalization temperatures, are the major mechanisms through which the landraces assure a heading date within the narrow optimum range.

The control of heading date by the landraces makes their heading date less sensitive to delayed or early emergence. Little or no residual moisture is available in the soil at the end of the summer in the dry environments of northern Syria, and emergence therefore depends upon the occurrence of the first significant rainfall. A dry start of the season can, in combination with low temperatures early in the season, delay emergence. In the experiments of 1985/86 and 1987/88, for example, the range in sowing dates was 24 days (26 October-19 November), yet the range in emergence dates was 62 days (4 November-6 January). On the other hand, the stable heading date allows early emergence; the resulting better ground cover during the winter reduces water losses due to soil evaporation (Fischer & Turner, 1978; Richards, 1982; Cooper et al., 1983). The stable heading date of the local landraces therefore represents a good adaptation to local environmental conditions.

The two plant ideotypes discussed before, which are adapted to dry environments, are represented in Fig. 4 by the early spring types located in the left corner of the "adapted" triangle and by the medium early landraces with a high value for PC1 in the upper corner of the same triangle. The Jordanian landraces are located between these two groups, although their apical development pattern is closer to that of spring types (van Oosterom & Acevedo, 1992b). This discrepancy is due to the fact that PC1 is defined from observations made in 1987/88, when only minor cold damage occurred. The high level of cold sensitivity of the Jordanian landraces was apparently not fully expressed, which gave an overestimation of PC1. The fact that no entries appear in the lower right corner of Fig. 4 reflects, like the triangular shape of Fig. 2, the difficulty in combining vernalization requirement with earliness. However, the linkage between growth habit and vernalization requirement can be broken (Pugsley, 1971; Acevedo & Ceccarelli, 1989).

The positive effect on grain yield of a winter-type plant ideotype increased dramatically in low-yielding environments. This result agrees with the conclusion of Ceccarelli & Grando (1989) that in environments where drought is associated with low winter temperatures, earliness as an escape mechanism for terminal drought is not sufficient, but must be combined with a reasonable level of cold tolerance. Since growth habit, plant colour, and especially cold tolerance are highly correlated with ground cover throughout the season (van Oosterom & Acevedo, 1992a), the present results and those of Ceccarelli & Grando (1989) suggest that under harsh conditions good ground cover, and thus a reduction in the water losses due to soil evaporation (Fischer & Turner, 1978; Cooper et al., 1983), is important in attaining a reasonable grain yield.

In many parts of the Middle East, environmental and edaphic conditions are such that yields will rarely exceed 1.5-2 t ha^{-1}. For subsistence farmers without financial backing in such areas, a decrease in the risk of a crop failure is more important than increased yields in rare favourable years, since prices are high in years with a poor yield, while higher yields in good years are nearly worthless (Nix, 1982; Marshall, 1987). Although early spring entries outyielded the winter-type landraces in most environments, except BO9, the decrease in difference in standardized grain yield between the two groups when yield levels become lower (Table 4), suggests that the plant ideotype of the Syrian landraces may reduce the risk of a crop failure in those areas where low yields arise from a combination of both low winter temperatures and terminal drought stress.

The results of the stepwise regression analysis suggest scope for an indirect selection for grain yield under dry conditions by selecting for plant ideotype and earliness under more favourable conditions; the independent variables in the analysis were mainly obtained from high-yielding environments. Under favourable conditions, selection in early generations of bulks with early heading, a prostrate winter growth habit, a dark initial plant colour, changing to pale green in spring, and cold tolerance will result in the selection of lines adapted to environments where low winter temperatures and terminal drought stress occur frequently together. Emphasis on selection for earliness alone generally results in lines with good early growth vigour and erect winter growth habit. These lines are desirable in environments with mild winters. The proposed indirect selection procedure reduces the risk of losing, in early generations, material that is adapted to the target environment and is therefore a useful alternative for direct yield testing under harsh conditions in early generations.

Acknowledgements

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References

Acevedo, E., 1987. Assessing crop and plant attributes for cereal improvement in water-limited Mediterranean environments. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 303-320. John Wiley & Sons Ltd., New York.

Acevedo, E. & S. Ceccarelli, 1989. Role of physiologist-breeder in a breeding program for drought resistance conditions. In: F.W.G. Baker (Ed.), Drought Resistance in Cereals, pp. 117-140. CAB International, Wallingford, UK.

Anderson, T.W., 1984. An Introduction to Multivariate Statistical Analysis, 2nd edition. John Wiley & Sons Ltd., New York.

Bidinger, F.R., V. Mahalakshmi & G.D.P. Rao, 1987. Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leeke]. I. Factors affecting yields under stress. Aust. J. Agric. Res. 38: 37-48.

Brook, R.J. & G.C. Arnold, 1985. Applied Regression Analysis and Experimental Design. Statistics: Textbook and Monograph. Vol. 62. M. Dekker Inc., New York.

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

Ceccarelli, S., E. Acevedo & S. Grando, 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. Euphytica 56: 169-185.

Ceccarelli, S. & S. Grando, 1989. Efficiency of empirical selection under stress conditions in barley. J. Genet. and Breed. 43: 25-31.

Ceccarelli, S., S. Grando & J.A.G. van Leur, 1987. Genetic diversity in barley landraces from Syria and Jordan. Euphytica 36: 389-405.

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

Ellis, R.H., E.H. Roberts, R.J. Summerfield & J.P. Cooper, 1988. Environmental control of flowering in barley (*Hordeum vulgare* L.). II. Rate of development as a function of temperature and photoperiod and its modification by low-temperature vernalization. Ann. Bot. 62: 145-158.

Finlay, K.E. & G.N. Wilkinson, 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14: 742-754.

Fischer, R.A., 1981. Optimizing the use of water and nitrogen through breeding of crops. In: J. Monteith & C. Webb (Eds.), Soil Water and Nitrogen in Mediterranean-type Environments, pp. 249-278. Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, Boston, London.

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

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

Freeman, G.H., 1973. Statistical methods for the analysis of genotype-environment interactions. Heredity 31: 339-354.

Freeman, G.H. & J.M. Perkins, 1971. Environmental and genotype-environmental components of variability. VII. Relations between genotypes grown in different environments and measures of these environments. Heredity 27: 15-23.

Fripp, Y.J. & C.E. Caten, 1971. Genotype-environmental interactions in *Schizophyllum commune*. 1. Analysis and character. Heredity 27: 393-408.

Kramer, Th., J.W. van Ooyen & C.J.T. Spitters, 1982. Selection for yield in small plots of spring wheat. Euphytica 31: 549-564.

Loss, S.P., M.W. Perry & W.K. Anderson, 1990. Flowering times of wheats in South-Western Australia: a modelling approach. Aust. J. Agric. Res. 41: 213-223.

Marshall, D.R., 1987. Australian plant breeding strategies for rainfed areas. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 89-99. John Wiley & Sons Ltd., New York.

Nix, H.A., 1982. Aspects of drought from an agroclimatic perspective. In: Drought Resistance in Crops with Emphasis on Rice, pp. 3-15. IRRI, Los Banos, The Philippines.

Oosterom, E.J. van & E. Acevedo, 1992a. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. I. Morphological traits. Euphytica (in press).

Oosterom, E.J. van & E. Acevedo, 1992b. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. II. Apical development, leaf, and tiller appearance. Euphytica (in press).

Passioura, J.B., 1986. Resistance to drought and salinity: avenues for improvement. Aust. J. Plant Physiol. 13: 191-201.

Pearce, S.C., 1983. The Agricultural Field Experiment. A Statistical Examination of Theory and Practice. John Wiley & Sons Ltd., New York.

Perkins, J.M. & J.L. Jinks, 1968. Environmental and genotype-environmental components of variability. III. Multiple lines and crosses. Heredity 23: 339-356.

Pfeiffer, W.H., 1988. Drought tolerance in bread wheat - Analysis of yield improvement over the years in CIMMYT germplasm. In: A.R. Klatt (Ed.), Wheat Production Constraints in Tropical Environments, pp. 274-284. CIMMYT, Mexico DF, Mexico.

Porter, J.R., E.J.M. Kirby, W. Day, J.S. Adam, M. Appleyard, S. Ayling, C.K. Baker, P. Beale, R.K. Belford, P.V. Biscoe, A. Chapman, M.P. Fuller, J. Hampson, R.K.M. Hay, M.N. Hough, S. Matthews, W.J. Thompson, A.H. Weir, V.B.A. Willington & D.W. Wood, 1987. An analysis of morphological development stages in Avalon winter wheat crops with different sowing dates and at ten sites in England and Scotland. J. Agric. Sci., Camb. 109: 107-121.

Pugsley, A.T., 1971. A genetic analysis of spring-winter habit of growth in wheat. Aust. J. Agric. Res. 22: 21-31.

Richards, R.A., 1982. Breeding and selecting for drought resistance in wheat. In: Drought Resistance in Crops with Emphasis on Rice, pp. 303-316. IRRI, Los Banos, The Philippines.

Richards, R.A., 1987. Physiology and the breeding of winter-grown cereals for dry areas. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 133-150. John Wiley & Sons Ltd., New York.

SAS, 1988. SAS/STAT User's guide, Release 6.03 Edition. Statistical Analysis System Institute Inc., Cary, NC, 1028 pp.

Spitters, C.J.T., 1984. Effects of intergenotypic competition on selection. In: W. Lange, A.C. Zeven & N.G. Hogenboom (Eds.), Efficiency in Plant Breeding, pp. 13-27. Proc. 10th Congr. Europ. Ass. Res. Pl. Breed., EUCARPIA, Wageningen, The Netherlands, 19-24 June 1983. Pudoc, Wageningen, The Netherlands.

Weber, W.E., 1984. Selection in early generations. In: W. Lange, A.C. Zeven & N.G. Hogenboom (Eds.), Efficiency in Plant Breeding, pp. 72-81. Proc. 10th Congr. Europ. Ass. Res. Pl. Breed., EUCARPIA, Wageningen, The Netherlands, 19-24 June 1983. Pudoc, Wageningen, The Netherlands.

CHAPTER 4

Leaf area and crop growth in relation to phenology of barley in Mediterranean environments

E.J. van Oosterom & E. Acevedo

Plant and Soil (accepted)

Key words: adaptation, barley, growth rate, leaf area duration, phenology, specific leaf area, temperature, terminal drought

Summary

In a barley-livestock farming system of northern Syria, high biomass production in addition to high grain yield is desirable. The aim of this study was to assess the effect of environment and phenology on growth and yield of barley in northern Syria. Leaf area duration (LAD), specific leaf area (SLA), crop growth rate (CGR) on a thermal time basis, and biological and grain yields were compared for entries representing three contrasting development patterns: early heading spring types (pattern A), medium early heading winter types (pattern B), and late heading spring types (pattern C). The experiment was conducted in 1988/89 at two sites: Tel Hadya (TH, 250 mm precipitation) and Breda (BR, 180 mm). Cold damage occurred in winter and, especially at BR, drought stress developed in spring. At the two sites, development was similar, but yields at TH were twice those at BR. This was related to a longer LAD and a faster CGR in spring. Development pattern affected growth. A long vegetative phase (pattern B) resulted in small leaves with a low SLA in winter, probably due to a slow leaf extension rate. Since cold tolerance and profuse tillering compensated for the small leaf size, pattern B had on average a longer LAD than pattern A. Pattern C had a longer LAD than pattern A because of a longer crop duration. This long duration had a negative effect on yield, so LAD was poorly related to yield. Development in spring was associated with CGR. Pattern C had a slow CGR and low yields; pattern B had the fastest CGR, but the yield advantage over pattern A was not significant. These results suggest that early heading winter barley, which combines long LAD with fast spring CGR, may give the best performance in a barley-livestock farming system in northern Syria.

Introduction

In northern Syria, barley (*Hordeum vulgare* L.) is the predominant crop in areas receiving less than 300 mm annual precipitation. Grain yields average less than 1000 kg ha^{-1} (Somel et al., 1984). At such yield levels, there would be little interest in cultivating barley if straw and forage could not be used by livestock (Nordblom, 1983b).

Barley can be grazed at different stages of development. In north east Syria, grazing at the tillering stage is a common practice. Such grazing reduces both grain and straw yield, but this is more than compensated for by the revenues from forage (Nordblom, 1983a; Yau et al., 1989). After grazing, the crop is allowed to recover to produce grain. A mature crop, however, also can be grazed, depending on land tenure and the anticipated grain yield (Nordblom, 1983b). Even if the crop is harvested and the grain sold, the straw value can triple the net harvest benefits (Nordblom, 1983b). In such barley-livestock farming systems, biomass production is as important to farmers as grain yield.

Yield of barley in northern Syria is limited by low precipitation, low winter temperatures, and high temperatures and vapour pressure deficits in spring. Most precipitation falls during the cool winter months (Dennett et al., 1984) and little or no residual soil water is available after the hot and dry summer. Increasing the fraction of available water which is transpired by the crop and maximizing the water use efficiency (WUE), defined as the above-ground biomass produced per unit of evapotranspiration, are mechanisms to increase dry matter production under water-limited conditions (Fischer & Turner, 1978). In northern Syria, direct soil evaporation is a major source of water loss, and losses as high as 60% of the seasonal evapotranspiration have been reported (Cooper et al., 1983). These losses can be reduced by good early ground cover, which can be attained by a prostrate growth habit, ability to grow at low temperatures, and cold tolerance (Acevedo, 1987; Richards, 1987). A rapid early biomass accumulation is also advantageous in terms of WUE. In spring, when temperature, radiation, and vapour pressure deficit increase sharply in northern Syria, WUE decreases (Gregory, 1991). A high crop growth rate (CGR) when WUE is still high ought to give greater biomass production in water-limited environments.

Early in the season, CGR is linearly related to the radiation intercepted by the leaf surfaces (Shibles & Weber, 1966; Biscoe & Gallagher, 1977). The intercepted fraction of radiation, in turn, depends mainly on leaf area if the leaf area index (LAI), defined as leaf area per unit ground area, is below 3 (Shibles & Weber, 1965). A high leaf area early in the season may thus increase CGR early in the season, provided the crop has an adequate level of cold tolerance. Plants with narrow leaves probably suffer less frost damage in environments where radiation frosts can occur (Parkhurst & Loucks, 1972). In addition, they are expected to have a higher WUE in spring, when radiation levels in Syria are high and wind speeds increase, because they are better able to maintain a lower leaf temperature (Parkhurst & Loucks, 1972; Nobel, 1983). Production of many small and narrow leaves, rather than fewer large leaves, may be preferable for achieving a fast CGR and high biomass in northern Syria.

A major factor affecting growth rate is specific leaf area (SLA), defined as the leaf area per unit leaf dry weight (m^2 kg^{-1}). Poorter & Remkes (1990) found for 24 non-woody C_3-species, under optimum nutrient supply, that the relative growth rate was strongly correlated with SLA. Differences in SLA can be related to differences in leaf thickness, density, or both (Dornhoff & Shibles, 1976; Dijkstra, 1989; Witkowski & Lamont, 1991). A high SLA can maximize plant growth if water is not limiting, but in low-productivity environments a low SLA will probably enable better survival (Poorter, 1989).

This study addresses the effects of environment and phenology on leaf area, crop growth and biological yield and grain yield of two-row barley in northern Syria.

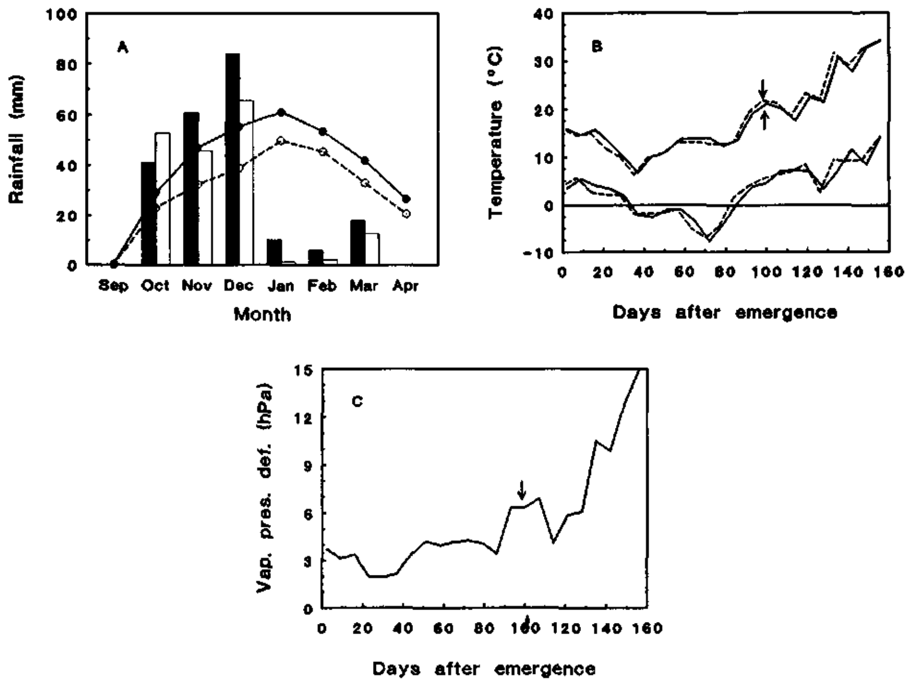

Fig. 1. a) Monthly precipitation (mm) in 1988/89 at Tel Hadya (■) and Breda (□) and long term average at Tel Hadya (●——●, 14 seasons) and Breda (o-----o, 12 seasons), b) weekly maximum and minimum temperature (°C) in 1988/89 at Tel Hadya (——) and Breda (-----), c) weekly vapour pressure deficit (hPa) in 1988/89 at Tel Hadya (——). Arrows indicates 700 °Cd after emergence.

Materials and Methods

Environments

The experiment was conducted in 1988/89 at two sites in northern Syria: Tel Hadya (TH, 36°01'N, 36°56'E) and Breda (BR, 35°56'N, 37°10'E). Sowing was on 9 November at both sites, at a rate of 100 kg ha^{-1}. Emergence was on 22 November at TH and 24 November at BR and final harvest in the first week of May.

Above-average rainfall was received until the end of December, but severe drought developed afterwards (Fig. 1a). Seasonal rainfall was 220 mm (34 mm after 1 January) at TH, and 180 mm (16 mm after 1 January) at BR. To delay terminal drought stress at TH, an irrigation of 30 mm was applied on 10 February (80 days after emergence, DAE). The drought was accompanied by low minimum temperatures in winter and high maximum temperatures and vapour pressure deficits in spring (Figs. 1b and 1c).

The design was a 6 x 6 simple lattice at TH and a 6 x 6 triple lattice at BR. Plots were 2.4 m wide (12 rows, 20 cm apart) and 5 m long. At TH, N (ammonium sulphate) was applied before sowing at 40 kg ha^{-1} and P (triple super phosphate) at 26.2 kg ha^{-1}; a top dressing of N (40 kg ha^{-1}) was applied at the beginning of stem elongation (*ca.* 75 DAE). At BR, the two nitrogen applications were reduced to 20 kg ha^{-1}, while phosphorus was the same as at TH. The experiment formed part of a barley-food legume rotation at TH and a barley-fallow rotation at BR. The soil was classified as a vertic (calcic) luvisol at TH and as a calcic xerosol at BR.

Plant material

Twenty-five two-row barley entries were evaluated, but the analyses concentrated on eight of them. These represented three contrasting patterns of apical development, discussed by van Oosterom & Acevedo (1992b). In short, the patterns are distinguished by their rate of development in winter, which depends on a vernalization requirement, and the rate of development after floral initiation, which appears to be photoperiod dependent. Pattern A constituted spring types with a rapid development, resulting in cold sensitivity and early heading. This pattern was represented by four entries: Harmal, S BON 96 (Pallidum 10342//CR 115/Por/3/Bahtim 9/4/Ds/Apro/5/WI 2291), WI 2269, and WI 2291/WI 2269. Pattern B was represented by two landraces from east Syria (Arabi Aswad and Tadmor), which were characterized by slow development in winter and rapid development in spring, resulting in cold tolerance and medium early heading. Pattern C constituted two entries of European origin: Atem and BON 27 (Kervana/Mazurka), both spring types with a slow development in spring. They were cold sensitive and headed late.

Leaf measurements

Sampling procedure and measurement of leaf area

For all 25 entries, eight random plants per plot were harvested from two predetermined rows at 2-week intervals from emergence until maturity. In the laboratory, samples were washed, wrapped in wet tissue and cloth and stored in a polyethylene bag at 5°C. This allowed a satisfactory storage for up to 1 week, time enough to finish processing the samples.

Green leaf area (only leaf laminae were considered) was measured with a Delta T area meter (Delta T Devices, Burwell, Cambridge, England) on four representative plants per sample during winter and three during spring. To quantify differences in tiller size, the area of leaves from the main shoot and tillers was measured separately. Leaf area index was estimated per plot by multiplying the average leaf area per plant by the average plant number per m^2 (mean of nine independent countings at TH and eight at BR).

Leaf area duration

The leaf area present during the season was calculated as the leaf area duration (LAD), defined as the integral of the LAI versus time curve (Hunt, 1982). To calculate LAD, a cubic spline was fitted through the means of the observed LAI values. The curve fitting program used (ICAGRAPH, available on the mainframe VAX computer of the International Center for Agricultural Research in the Dry Areas, ICARDA) calculated for each observation the parameter estimates of the derivatives of the fourth order polynomial function for LAI at that observation, what enabled calculation of the integral (LAD). For the three development patterns, average values over entries were used and curves were fitted for the complete crop and for the main shoots and tillers separately.

Specific leaf area

After measuring the area, leaves were dried for at least 2 days at 75 °C. Specific leaf area was calculated for individual plants as green leaf area divided by green leaf dry weight (m^2 kg^{-1}).

Leaf laminae length and width

For each plant used for leaf area measurements, the length and width of the leaf lamina of the longest main shoot leaf was measured during winter; in addition, around heading, the length and width of the laminae of the main shoot flag leaf and penultimate leaf were measured.

To obtain additional data on leaf morphology, the length and width of successive main shoot leaf laminae were measured on labelled plants in a separate experiment at TH in 1990/91 for four entries: Harmal (Pattern A), Tadmor (Pattern B), Atem (Pattern C), and Lignee 131, a late-heading winter type with a high vernalization requirement. The experiment contained three replications and emergence was on 7 December 1990. Three plants per plot were labelled at random 1 week after emergence and the length and width of all main shoot leaf laminae, including the flag leaf, were measured. Plants having a main shoot killed by frost were discarded.

Dry matter accumulation

Sampling procedure

Samples for above-ground dry matter accumulation were taken for 25 entries from emergence until heading, along with the samples for leaf area. The sample size was 0.24 m^2 (30 cm of four predetermined rows). In the laboratory, the plants were counted, washed and the roots cut off. Samples were dried for 2 days at 75 °C.

Crop growth rate

Crop growth rate was defined as the rate of dry matter production per unit of time:

$$CGR = \Delta W / \Delta TU \quad (1)$$

where W represents dry matter (g m^{-2}) and TU thermal units (degree days, °Cd). Thermal units were calculated as the mean of the daily maximum and minimum screen air temperature, using a base temperature of 0°C (Gallagher, 1979; Kirby & Ellis, 1980). Adjustments if minimum temperatures fell below 0°C were made as described by Weir et al. (1984).

Estimates of CGR, prior to heading, were obtained from a polynomial function (Karimi & Siddique, 1991):

$$LN(W) = a + b*TU^{0.5} + c*TU + d*TU^2 \quad (2)$$

where the parameters a, b, c and d were estimated from a multiple regression (SAS, 1988). Curves were fitted for each site, each pattern × site combination (average over entries) and for the 25 individual entries at each site. The R^2, adjusted for degrees of freedom, was higher than 0.99 for each pattern × site combination, except for pattern C at TH, where it was 0.985. For individual entries, all adjusted R^2 values exceeded 0.965 ($P < 0.01$). Combining equations 1 and 2, CGR could thus

Table 1. Analysis of variance for thermal units (°Cd) from emergence to the appearance of double ridges, the maximum number of primordia stage, and heading and for biological yield (g m^{-2}) and grain yield (g m^{-2}) for three development patterns (PAT) at two locations in northern Syria in 1988/89.

	Thermal units to			Yield	
	Double ridges	Max. no. primordia	Heading	Biological	Grain
Tel Hadya (250 mm)					
PAT A[a]	279 a[b]	713 a	1045 a	819 a	269 ab
PAT B	391 c	740 a	1038 a	1042 a	310 a
PAT C	329 b	799 b	1134 b	769 a	173 b
Average (n=25)	318	737	1069	844	247
Breda (180 mm)					
PAT A	282 a	676 a	1073 a	370 a	122 a
PAT B	427 b	766 b	1098 a	418 a	133 a
PAT C	289 a	798 c	1197 b	207 b	60 b
Average (n=25)	317	731	1124	352	120

[a]For a description of development patterns, see text.
[b]Means followed by the same letter are not significantly (P<0.05) different according to Tukey's test for pairwise comparisons.
* P<0.05; ** P<0.01; *** P<0.001.

be estimated as

$$CGR = (0.5*b*TU^{-0.5} + c + 2*d*TU)e^{a + b*\sqrt{TU} + c*TU + d*TU*TU} \quad (3)$$

For each entry, CGR at 700°Cd after emergence (1 March at TH and 3 March at BR) was calculated to investigate whether a high growth rate in early spring is related to phenology and favours yield. Early March was two weeks after the end of a period with low winter temperatures (Fig. 1b) and one month before vapour pressure deficits increased sharply (Fig. 1c); it thus represented a period with relatively favourable growing conditions.

Final harvest

At maturity, a sample of 0.8 m^2 (4 rows, 1 m) was taken by cutting plants at soil level. After weighing field-dried samples for biological yield, a subsample was taken from which biological yield, grain yield, spike number and 1000-kernel weight were obtained.

Visual observations

Cold damage, plant colour, ground cover, and growth vigour were scored because these observations were expected to be related to differences in LAD and CGR. Observations were done at 2-week intervals. Cold damage was scored on a 1 (no damage) to 5 (dead) scale, and the average of three observations per plot was used. Plant colour was scored on a 1 (pale green) to 3 (dark green) scale; winter plant colour was obtained as the mean of five observations per plot. Ground cover was estimated using a scale of 1 (10% ground cover) to 10 (100% ground cover). Growth vigour was scored on a 1 (poor) to 5 (good) scale.

Results

Environmental effects

Phenology and yield

Differences in phenology between TH and BR were minor, but yields at BR were on average less than 50% of those at TH (Table 1). These differences were associated with differences in leaf area (LAI and LAD) and CGR.

Leaf area

Differences in LAI between TH and BR occurred by 30 DAE (Fig. 2). The increase in LAI at 80 DAE (mid-February) coincided with an increase in minimum temperatures (Fig. 1b). Maximum average LAI was 5.8 at TH and 1.9 at BR and occurred around 120 DAE, 1 week prior to heading. Complete leaf senescence occurred on average 155 DAE at TH and 147 DAE at BR. Total LAD at BR was about one-third of that at TH (Table 2). This was mainly due to a 75-80% reduction in tiller LAD (Table 2) and to smaller leaves; during winter, leaf length and width at BR were around 90% of TH,

Table 2. Leaf area duration (days) for crop, main shoots, and tillers during winter (0-85 days after emergence), early spring (85-125 DAE), and late spring (125 DAE - complete leaf senescence), averaged for 25 entries and for three development patterns for barley at two sites in northern Syria in 1988/89.

	Tel Hadya			Breda		
	Crop[a]	Main shoot	Tillers	Crop	Main shoot	Tillers
Average (n=25)						
Winter	57.1	32.9	13.8	28.4 (50)[b]	23.3 (71)	4.8 (35)
Early spring	162.6	37.0	121.5	64.7 (40)	25.3 (68)	38.3 (32)
Late spring	93.5	22.5	75.9	15.2 (16)	5.2 (23)	8.4 (11)
Total	*313.2*	*92.4*	*211.2*	*108.3 (35)*	*53.8 (58)*	*51.5 (24)*
Pattern A[c]						
Winter	41.1	33.3	8.2	27.2 (66)	25.0 (75)	2.1 (26)
Early spring	126.9	31.1	95.6	47.9 (38)	18.2 (59)	22.6 (24)
Late spring	67.5	15.4	52.0	13.5 (20)	4.5 (29)	8.4 (16)
Total	*235.6*	*79.8*	*155.8*	*88.6 (38)*	*47.7 (60)*	*33.0 (21)*
Pattern B						
Winter	52.8	30.4	23.1	23.1 (44)	17.7 (58)	5.5 (24)
Early spring	190.5	39.8	152.0	65.0 (34)	21.8 (55)	43.2 (28)
Late spring	83.1	17.5	68.2	19.6 (24)	6.4 (37)	13.4 (20)
Total	*326.3*	*87.7*	*243.4*	*107.6 (33)*	*45.9 (52)*	*62.1 (26)*
Pattern C						
Winter	45.1	33.7	11.7	24.8 (55)	22.0 (65)	2.6 (22)
Early spring	149.0	41.1	101.3	54.0 (36)	25.5 (62)	29.6 (29)
Late spring	109.5	31.0	78.3	26.2 (24)	11.3 (35)	13.3 (17)
Total	*303.7*	*106.6*	*191.3*	*105.0 (35)*	*58.8 (55)*	*45.5 (24)*

[a]Because of interpolations, the sum of main shoots and tillers does not exactly equal the complete crop.
[b]Percentage of value at TH.
[c]For a discussion of the development patterns, see text.

but that decreased to *ca.* 70% at the flag leaf stage.

The smaller leaves at BR were associated with a lower SLA (Fig. 3). Specific leaf area was greatest shortly after emergence and, in general, gradually declined throughout the life cycle of the plant. A small increase after 80 DAE coincided with the end of the cold period (Fig. 1b) and, at TH, with irrigation (applied 80 DAE). Increased differences in SLA before heading were associated with increasing differences in leaf size.

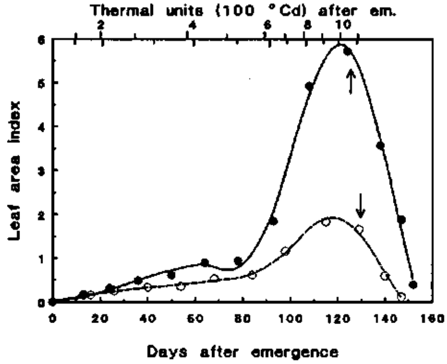

Fig. 2. Leaf area index as a function of time at Tel Hadya (●——●) and Breda (o-----o) in 1988/89, averaged over 25 entries. Curves are cubic spline interpolations. Arrows indicate average heading date. For thermal units, the upper axis refers to TH and the lower to BR.

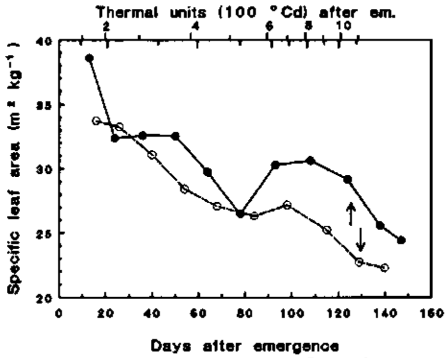

Fig. 3. Specific leaf area (m^2 kg^{-1}) at Tel Hadya (●——●) and Breda (o-----o) in 1988/89, averaged over 25 entries. Arrows indicate average heading date. For thermal units, the upper axis refers to TH and the lower one to BR.

Crop growth rate

The biomass at TH and BR was similar until 400°Cd after emergence (55-60 DAE) and CGRs were slow (Fig. 4). At TH, CGR increased gradually from this point to a maximum of 0.93 g m^{-2} °Cd^{-1} prior to heading. At BR, CGR remained slow until 700°Cd after emergence (100 DAE), but increased sharply afterwards, reaching

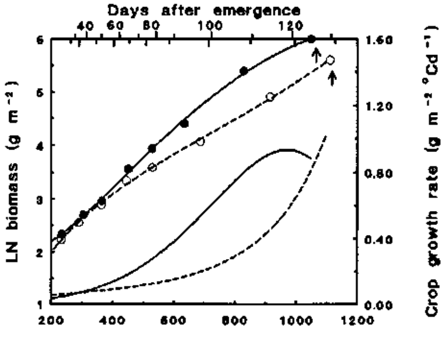

Fig. 4. Dependence of ln-transformed biomass (g m^{-2}) and crop growth rate (g m^{-2} °Cd^{-1}) on time after emergence at Tel Hadya (●——●) and Breda (o-----o) in 1988/89, averaged over 25 entries. Crop growth rates are estimated from third order polynomial functions for biomass. Arrows indicate average heading date. For days after emergence, the upper axis refers to TH and the lower one to BR.

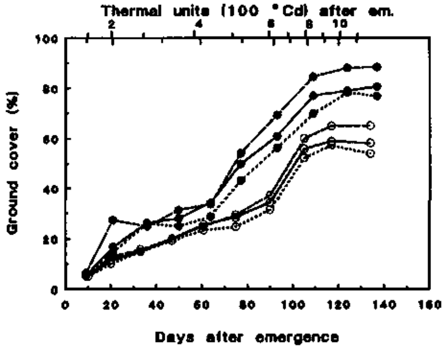

Fig. 5. Percentage ground cover during the season at Tel Hadya (•) and Breda (o) for development patterns A (——), B (-----), and C (·······). For thermal units, the upper axis refers to TH and the lower one to BR. For a discussion of the development patterns, see text.

values, prior to heading, comparable to TH. However, CGR around heading must be interpreted with care, since values at that stage are especially sensitive to errors in the last sample. The increase in CGR coincided at both sites with a period of increasing ground cover (Fig. 5).

Pattern effects

Phenology and yield

Pattern A and B had a similar heading date, but early development of pattern B was significantly slower (Table 1). Differences in yield between the two patterns were not significant, although pattern B tended to outyield pattern A at both locations, especially for biological yield. Heading date of pattern C was significantly later, mainly

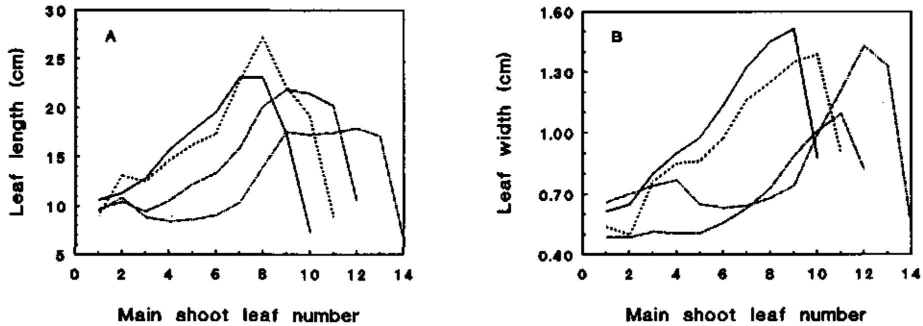

Fig. 6. a) Length and b) width of successive main shoot leaves for Harmal (——, development pattern A, n=4), Tadmor (-----, pattern B, n=7), Atem (·······, pattern C, n=4), and Lignee 131 (—·—, n=5) at Tel Hadya in 1990/91. For a discussion of development patterns, see text.

Table 3. Correlation coefficients of winter plant colour (WPLC) and cold damage (CD) with specific leaf area during the season at Tel Hadya and Breda in 1988/89 for 25 entries.

Tel Hadya			Breda		
DAE[a]	WPLC[b]	CD[c]	DAE[a]	WPLC[b]	CD[c]
13	-0.54 **	0.35 +	16	-0.81 ***	0.68 ***
24	-0.62 ***	0.68 ***	26	-0.67 ***	0.58 **
36	-0.45 *	0.41 *	40	-0.53 **	0.58 **
50	-0.28	0.41 *	54	-0.63 ***	0.59 **
64	-0.18	0.37 +	68	-0.50 *	0.46 *
78	-0.42 *	0.36 +	84	-0.48 *	0.53 *
93	-0.51 **	0.54 **	98	-0.49 *	0.43 *
108	-0.10	0.18	115	0.07	-0.02
124	-0.28	0.15	129	-0.03	0.04
138	0.14	-0.09	140	0.27	-0.25

[a]Days after emergence of specific leaf area measurement.
[b]1 = pale green; 3 = dark green; mean of five observations per plot.
[c]1 = no damage; 5 = dead; mean of three observations per plot.
+ $P<0.10$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

because of slow development after the double ridge stage. Yields of this pattern were significantly lower at BR than for the other patterns. At TH, differences were not significant, except for the difference in grain yield with pattern B.

Leaf area

Pattern A had the shortest total LAD at both locations, whereas pattern B and C had a similar LAD (Table 2). The difference between pattern A and B reflects the greater tillering of winter types. In contrast, the difference between pattern A and C was due to the longer crop duration of pattern C (Table 1).

The low LAD of the main shoot of pattern B during winter (0-85 DAE) at BR (Table 2) was associated with small leaves. Early in the season, the length and width of successive main shoot leaves increased at TH in 1990/91 for spring types (Harmal and Atem), whereas for winter types (Tadmor and Lignee 131, a late-heading winter type) leaf sizes were more uniform (Fig. 6). The proportionally smaller differences in LAD of the main shoots at TH in winter were caused by more severe cold damage, which especially affected spring types. During winter, cold damage at TH was positively correlated with the width of the longest main shoot leaf ($r \geq 0.41$, $P<0.05$, $n=25$, for four successive observations).

The small leaves of pattern B (winter type) in winter were associated with a low SLA compared with pattern A or C (spring types) at BR; Lignee 131 had the lowest SLA during winter (Fig. 7). The relationship between SLA and early development was

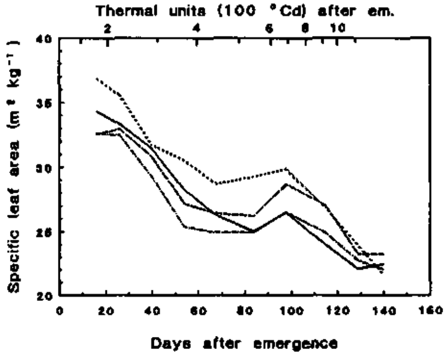

Fig. 7. Specific leaf area (m^2 kg^{-1}) for development pattern A (——), pattern B (-----), pattern C (·······), and Lignee 131 (—·—) at Breda in 1988/89. For a discussion of development patterns, see text.

reflected in consistent correlations of SLA with morphological traits associated with early development, e.g., winter plant colour and cold damage (Table 3). Tel Hadya showed similar trends. Around 70 DAE, correlations became weaker and disappeared completely around 100 DAE.

Total LAD was not related to either grain yield or biological yield at harvest. This was partly due to the late heading of pattern C, which had a negative effect on yield, especially at BR, whereas it favoured LAD. Pattern B, with on average a longer LAD than pattern A, outyielded pattern A for both grain and biological yield at both locations, although not significantly.

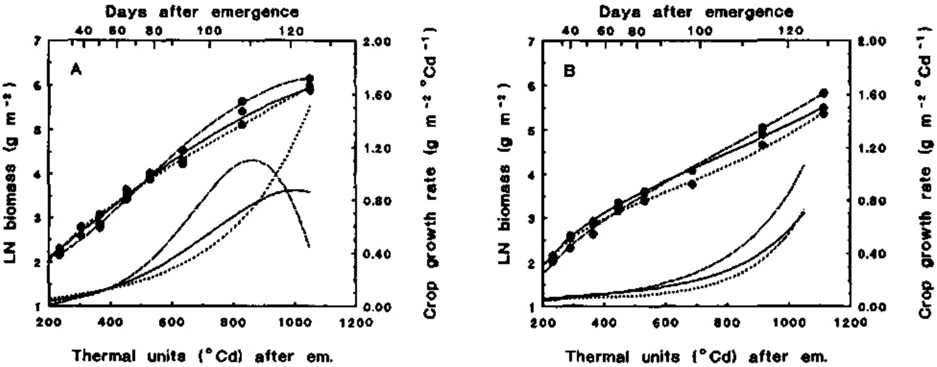

Fig. 8. Dependence of ln-transformed biomass and crop growth rate on accumulated thermal units after emergence at a) Tel Hadya and b) Breda in 1988/89 for development patterns A (——), B (-----), and C (·······). Crop growth rates are estimated from third order polynomial functions for biomass. For a discussion of development patterns, see text.

Table 4. Correlation coefficients of crop growth rate at 700°Cd after emergence (early spring) with phenological, morphological, and yield traits at Tel Hadya and Breda in 1988/89 for 25 entries.

	Tel Hadya	Breda
Phenological traits[a]		
Time (°Cd) to double ridge (DR) stage	-0.01	-0.01
Time (°Cd) to max. primordia (MP) stage	-0.47*	-0.39
Time (°Cd) from DR to MP	-0.52**	-0.51**
Time (°Cd) to heading	-0.43*	-0.49*
Morphological traits[b]		
Winter growth habit	0.38	0.49*
Winter plant colour	0.53**	0.53**
Cold tolerance	-0.69***	-0.64***
Early growth vigour[c]	-0.13	-0.18
Spring growth vigour	0.46*	0.66***
Spring ground cover	0.67***	0.69***
Yield traits[b]		
Shoot dry weight around heading	0.44*	0.79***
Biological yield at harvest	0.26	0.47*
Grain yield at harvest	0.57**	0.59**
Spike number per unit area at harvest	0.46*	0.53**
Kernel number per unit area at harvest	0.59**	0.55**
Kernel weight at harvest	0.05	0.42*

[a]Based on means, not adjusted for block effects in the lattice design.
[b]Based on means, adjusted for block effects in the lattice design.
[c]Scored prior to the occurrence of the first frost; mean of three observations per plot at Tel Hadya and two at Breda.
* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Crop growth rate

Consistent differences in CGR between patterns were found (Fig. 8). A faster CGR of pattern B became apparent at both locations at the end of the winter, and resulted in better ground cover (Fig. 5). Pattern C had the slowest CGR during the period 500-900°Cd after emergence and also had poor ground cover. A fast CGR at 700°Cd after emergence (early spring) was negatively correlated with the duration of the phase between the appearance of the double ridges and the maximum number of primordia and was consequently associated with early heading (Table 4).

At both locations, grain yield was strongly correlated with CGR at 700°Cd after emergence, but the association existed for biological yield only at BR (Table 4). The correlation with grain yield resulted from a correlation with kernel number rather than with kernel weight. All correlations reflected the relationship between CGR and earliness.

Discussion

Development pattern had its negative effect on yield mainly via heading date. A negative effect of late heading under terminal stress has been reported for spring wheat (Fischer & Maurer, 1978), barley (Hadjichristodoulou, 1981; Ceccarelli, 1987) and pearl millet (Bidinger et al., 1987). A significant effect of early development on yield under stress has been observed by van Oosterom & Acevedo (1992c) for barley in northern Syria. Across sites, development was similar, but yields varied greatly. The environmental effect on yield thus dominated the pattern effect. This is a common observation in the highly variable environments of the Mediterranean region (Yau et al., 1991; Nachit et al., 1992).

Environmental effects

The lower yields at BR were associated with a shorter LAD and a lower CGR in spring.

Early in the season, the shorter LAD at BR could be explained by lower soil temperatures. During the 6 weeks after sowing, the mean soil temperature at 5-cm depth was 7.2°C at BR and 10.6°C at TH. Gallagher & Biscoe (1979) observed for spring barley in England that early in the season the rate of leaf extension, and thus leaf size, was more closely related to soil than to air temperature. The lower leaf extension rate may also account for the lower SLA at BR, because a reduced extension rate results in smaller cells and hence denser leaves. Soil temperatures also influence the initiation of leaf primordia, and thus leaf number (Cooper & Law, 1978). Indeed, the final number of leaves on the main shoot was lower at BR than at TH (van Oosterom & Acevedo, 1992b).

The shorter LAD at BR later in the season may have resulted from drought stress. Cell growth is already reduced by small water deficits, causing a reduction in leaf area (Begg, 1980). A reduction in cell enlargement is supported by the slightly greater average length/width ratio of the main shoot flag leaf and penultimate leaf at TH compared with BR (10.5 versus 9.7 for the flag leaf and 14.6 versus 12.7 for the penultimate leaf). In addition, differences in SLA were most consistent after 80 DAE. A reduced SLA is a well-documented effect of adverse conditions (Fischer & Turner, 1978; Poorter, 1989; Witkowski & Lamont, 1991).

The shorter LAD at BR was associated with a lower ground cover and a slower CGR. A poor ground cover in spring is related to low grain yields (van Oosterom & Acevedo, 1992a), whereas a low CGR during spike initiation has been associated with low yields, mainly as a result of low kernel numbers per unit area (Biscoe & Gallagher, 1977; Brown et al., 1987). Yield differences between TH and BR thus appear to result from differences in growth rate in spring. Since CGR depends on the radiation intercepted by the leaves and thus, if LAI<3, on leaf area (Shibles &

Weber, 1965, 1966), the difference in spring CGR may be due to the difference in LAI early in the season. Environmental conditions early in the season may in that case be important factors determining the final yield.

Pattern effects

The consistent differences in leaf area and crop growth between development patterns suggest an association between development and growth. In winter, the short LAD of the main shoot of pattern B at BR was due to small leaves, which in turn were associated with a long vegetative period of the apex. During the pre-floral initiation stages, the leaf extension rate of grasses is slower than during the post-floral initiation stages, at similar temperatures (Peacock, 1976). The delayed increase in length and width of successive main shoot leaves of Tadmor (pattern B) and of Lignee 131 (Fig. 6) thus reflects the slow early development of these vernalization-requiring entries and may account for the observed differences in cold tolerance. The extended slow leaf extension rate of winter types results in dense leaves in winter and hence in a low SLA. The correlation, early in the season, between SLA and winter plant colour and cold damage confirms an association between SLA and early development. Poorter & Remkes (1990) observed a strong correlation between growth rate and SLA; fast-growing species had a higher SLA than slow-growing ones. The association between SLA and early development in our study thus reflects the poor early growth vigour which has been observed for winter types (van Oosterom & Acevedo, 1992a,b). Indeed, Fig. 8 suggests a low CGR of pattern B early in the season. In spring, consistent differences in CGR were associated with development pattern (Fig. 8). Karimi & Siddique (1991) reported, for wheat, a slower increase in CGR for a later cultivar. Parlevliet (1967) found that the CGR of spinach cultivars increased with increased rates of generative development. The early increase in CGR of pattern B (rapid development in spring) and the late increase of pattern C (slow development in spring) confirm these observations. The present results therefore indicate that development has a marked effect on growth.

The largest differences in CGR occurred in spring. As vapour pressures decline in spring, WUE decreases. A vigorous crop growth in that part of the season when water use is efficient will increase biomass production if water supply is limited (Fischer, 1981; Cooper et al., 1983; Richards, 1987). Pattern B, which had on average the fastest CGR in early spring, indeed outyielded pattern A in biological yield at both locations (although not significantly) whereas pattern C, with a late increase in CGR, had the lowest biological yield at harvest (Table 1). The significant correlations of CGR at 700 °Cd with heading date and both grain and biological yield, especially at BR, indicate that a fast CGR in early spring is important to achieve a good performance under harsh conditions.

The slow early development of pattern B, and the resulting prolonged positioning of the apex below the soil level, ensures a good survival of green-stage grazing (Rhodes, 1975). In addition, the presence of many small leaves and many tillers may result in a higher residual leaf area after grazing. Combined with the fast CGR in spring, this pattern is expected to perform well in a barley-livestock farming system in northern Syria.

Significant effects on yield of both early development and heading date have been reported for barley in environments in northern Syria where low winter temperatures and terminal drought are combined (van Oosterom & Acevedo, 1992c). The present results suggest that this may have been due to the combination of a rapid CGR in spring with a long LAD, characteristic of medium early heading winter barley.

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References

Acevedo, E., 1987. Assessing crop and plant attributes for cereal improvement in water-limited Mediterranean environments. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 303-320. John Wiley & Sons Ltd., New York.

Begg, J.E., 1980. Morphological adaptations of leaves to water stress. In: N.C. Turner & P.J. Kramer (Eds.), Adaptation of Plants to Water and High Temperature Stress, pp. 33-42. John Wiley & Sons, New York.

Bidinger, F.R., V. Mahalakshmi & G.D.P. Rao, 1987. Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leeke]. I. Factors affecting yields under stress. Aust. J. Agric. Res. 38: 37-48.

Biscoe, P.V. & J.N. Gallagher, 1977. Weather, dry matter production and yield. In: J.J. Landsberg & C.V. Cutting (Eds.), Environmental Effects on Crop Physiology, pp. 75-100. Academic Press, London.

Brown, S.C., J.D.H. Keatinge, P.J. Gregory & P.J.M. Cooper, 1987. Effects of fertilizer, variety and location on barley production under rainfed conditions in northern Syria. 1. Root and shoot growth. Field Crops Res. 16: 53-66.

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

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

Cooper, P.J.M. & R. Law, 1978. Enhanced soil temperature during very early growth and its association with maize development and yield in the highlands of Kenya. J. Agric. Sci., Camb. 91: 569-577.

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

Dijkstra, P., 1989. Cause and effect of differences in SLA. In: H. Lambers, M.L. Cambridge, H. Konings & T.L. Pons (Eds.), Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants, pp. 125-140. SPB Academic Publishing, The Hague, The Netherlands.

Dornhoff, G.M. & R. Shibles, 1976. Leaf morphology and anatomy in relation to CO_2-exchange rate of soybean leaves. Crop Sci. 16: 377-381.

Fischer, R.A., 1981. Optimizing the use of water and nitrogen through breeding of crops. In: J. Monteith & C. Webb (Eds.), Soil Water and Nitrogen in Mediterranean-type Environments, pp. 249-278. Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, Boston, London.

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

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

Gallagher, J.N., 1979. Field studies of cereal leaf growth. I. Initiation and expansion in relation to temperature and ontogeny. J. Exp. Bot. 30: 625-636.

Gallagher, J.N. & P.V. Biscoe, 1979. Field studies of cereal leaf growth. III. Barley leaf extension in relation to temperature, irradiance, and water potential. J. Exp. Bot. 30: 645-655.

Gregory, P.J., 1991. Concepts of water use efficiency. In: H.C. Harris, P.J.M. Cooper & M. Pala (Eds.), Soil and Crop Management for Improved Water Use Efficiency in Rainfed Areas, pp. 9-20. International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria.

Hadjichristodoulou, A., 1981. Aspects of barley breeding for dry Mediterranean regions. In: M.J.C. Ascher, R.P. Ellis, A.M. Hayter & R.N.H. Whitehouse (Eds.), Barley Genetics IV, pp. 383-388. Proc. 4th International Barley Genetics Symposium, Edinburgh, 22-29 July 1981.

Hunt, R., 1982. Plant Growth Curves. Edward Arnold, London, 248 pp.

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

Kirby, E.J.M. & R.P. Ellis, 1980. A comparison of spring barley grown in England and Scotland. 1. Shoot apex development. J. Agric. Sci., Camb. 95: 101-110.

Nachit, M.M., G. Nachit, H. Ketata, H.G. Gauch Jr & R.W. Zobel, 1992. Use of AMMI and linear regression models to analyze genotype-environment interaction in durum wheat. Theor. Appl. Genet. 83: 596-601.

Nobel, P.S., 1983. Biophysical Plant Physiology and Ecology. W.H. Freeman & Co., San Francisco, 608 pp.

Nordblom, T.L., 1983a. Livestock-crop interactions. The case of green stage grazing. ICARDA Disc. Paper No. 9, Aleppo, Syria, 37 pp.

Nordblom, T.L., 1983b. Livestock-crop interactions. The decision to harvest or to graze a mature grain crop. ICARDA Disc. Paper No. 10, Aleppo, Syria, 21 pp.

Oosterom, E.J. van & E. Acevedo, 1992a. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. I. Morphological traits. Euphytica (in press).

Oosterom, E.J. van & E. Acevedo, 1992b. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. II. Apical development, leaf, and tiller appearance. Euphytica (in press).

Oosterom, E.J. van & E. Acevedo, 1992c. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. III. Plant ideotype and grain yield. Euphytica (in press).

Parkhurst, D.F. & O.L. Loucks, 1972. Optimal leaf size in relation to environment. J. Ecol. 60: 505-537.

Parlevliet, J.E., 1967. The influence of external factors on the growth and development of spinach cultivars (*Spinacia oleracea* L.). Meded. Landbouwhogeschool Wageningen 67-2, 75 pp.

Peacock, J.M., 1976. Temperature and leaf growth in four grass species. J. Appl. Ecol. 13: 225-232.

Poorter, H., 1989. Interspecific variation in relative growth rate: On ecological causes and physiological consequences. In: H. Lambers, M.L. Cambridge, H. Konings & T.L. Pons (Eds.), Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants, pp. 45-68. SPB Academic Publishing, The Hague, The Netherlands.

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

Rhodes, I., 1975. The relationship between productivity and some components of canopy structure in ryegrass (*Lolium* spp.) IV. Canopy characters and their relationship with sward yields in some

intra-population selections. J. Agric. Sci., Camb. 84: 345-351.
Richards, R.A., 1987. Physiology and the breeding of winter-grown cereals for dry areas. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 133-150. John Wiley & Sons Ltd., New York.
SAS, 1988. SAS/STAT User's Guide, Release 6.03 Edition. Statistical Analysis System Institute Inc., Cary, NC, 1028 pp.
Shibles, R.M. & C.R. Weber, 1965. Leaf area, solar radiation interception and dry matter production by soybeans. Crop Sci. 5: 575-578.
Shibles, R.M. & C.R. Weber, 1966. Interception of solar radiation and dry matter production by various soybean planting patterns. Crop Sci. 6: 55-59.
Somel, K., A. Mazid & M. Hallajian, 1984. Survey of barley producers; northern Syria 1981/1982. Volume III, Descriptive statistics. ICARDA Research Report No. 12, Aleppo, Syria, 75 pp.
Weir, A.H., P.L. Braggs, J.R. Porter & J.H. Rayner, 1984. A winter wheat crop simulation model without water or nutrient limitations. J. Agric. Sci., Camb. 102: 371-382.
Witkowski, E.T.F. & B.B. Lamont, 1991. Leaf specific mass confounds leaf density and thickness. Oecologia 88: 486-493.
Yau, S.K., M.S. Mekni, I. Naji & J.P. Srivastava, 1989. Effects of green-stage grazing on rainfed barley in northern Syria. II. Yield and economic returns. Expl. Agric. 25: 501-507.
Yau, S.K., G. Ortiz-Ferrara & J.P. Srivastava, 1991. Classification of diverse bread wheat-growing environments based on differential yield responses. Crop Sci. 31: 571-576.

CHAPTER 5

Yield response of barley to rainfall and temperature in Mediterranean environments

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Summary

Grain yield of barley (Hordeum vulgare L.) in northern Syria is limited by water stress and extremes of temperature. The aim of the present study was to compare the yield response of two barley cultivars, Harmal (spring type, cold sensitive, early heading) and Arabi Aswad (winter type, cold tolerant, medium early heading), to rainfall and temperature. Grain yield was obtained from three sites in northern Syria for seven seasons, giving 18 environments. Multiple regression models, containing one rainfall and one temperature variable, were used to quantify yield responses to environmental fluctuations. Total seasonal rainfall was the variable most strongly correlated to the grain yield of Harmal, explaining 63.5% of the variation. For Arabi Aswad, rainfall from November to February gave the best fit (61.6%). December and January rainfall had the highest contribution to yield; contribution of March rainfall tended to be negative. The overall yield response to seasonal rainfall was 11.95 kg ha^{-1} mm^{-1} for Harmal and 8.57 for Arabi Aswad; the expected grain yield at the driest site was about 1270 kg ha^{-1} for both cultivars. The addition of a temperature variable gave a better fit, accounting for around 80% of the variation in grain yield for both cultivars if winter rainfall was combined with number of night frosts in spring. Based on these two variables, expected yields at the driest site were about 980 kg ha^{-1}. Arabi Aswad had a lower response to both rainfall and frost. In environments where low yields are due to both water and temperature stress, farmers should grow Arabi Aswad because its lower sensitivity to environmental fluctuations will ensure a better yield stability.

Introduction

Water and temperature stress are the major constraints to cereal production in the Middle East. Variation in annual rainfall has been reported to explain 75% of the variation in grain yield for wheat across 16 environments in this region, ranging in annual rainfall from 230 to 765 mm (Blum & Pnuel, 1990). Hadjichristodoulou (1982), however, found for cereals in Cyprus that the distribution of rainfall, rather than the seasonal total, was related to grain yield. Differences in temperature are also associated with differences in grain yield. Ceccarelli et al. (1991) reported average barley grain yields of 1562 kg ha^{-1} and 32 kg ha^{-1} from a single site in northern Syria in two seasons with comparable rainfall and rainfall distribution, but varying temperature. A reduced responsiveness to environmental fluctuations can reduce the risk of crop failure if marginal yields arise from adverse environmental conditions.

Two contrasting plant ideotypes for barley (*Hordeum vulgare* L.), both adapted to terminal drought-stressed Mediterranean environments, have been identified (van Oosterom & Acevedo, 1992a, b). The first ideotype was representative of spring-type barleys with a rapid seasonal development, resulting in a good early growth vigour and early heading on the one hand, but cold sensitivity on the other. The second ideotype was vernalization-dependent, with a poor early growth vigour, prostrate winter growth habit, cold tolerance, and medium early heading. Owing to the differences in development and growth, the second ideotype may give more stable yields in areas where both drought and cold stress are likely.

The aim of this study was to assess the influence of rainfall and temperature on grain yield of two barley cultivars, representing the above-mentioned two plant ideotypes, across a range of environments in northern Syria.

Materials and Methods

Plant material

The two barley (*H. vulgare*) cultivars, representing the above-mentioned ideotypes were Harmal, an early heading spring type, and Arabi Aswad, a Syrian landrace and medium early heading winter type. They are both two-row cultivars.

Table 1. Sites and years (environments) where experiments were conducted, including emergence date, seasonal rainfall (mm), number of night frosts after emergence and average grain yield (kg ha^{-1}) for two barley cultivars in each environment.

Site	Year[a]	Emergence	Rainfall Oct-April	Night frosts	Grain yield Harmal	A. Aswad
Tel Hadya	1985	n.a.[b]	369.5	41[c]	3804	3951
Breda	1985	22/11/84	268.5	37	933	1570
Bouider	1985	22/11/84	171.0	n.a.	687	1563
Tel Hadya	1986	02/01/86	287.5	9	4142	3000
Breda	1986	06/01/86	207.9	16	1688	1154
Bouider	1986	04/01/86	198.4[d]	13	1471	1475
Tel Hadya	1987	28/11/86	340.3	31	1987	1981
Breda	1987	18/11/86	244.6	40	757	644
Bouider	1987	18/11/86	174.0	46	163	83
Tel Hadya	1988	29/11/87	495.2	19	4286	3307
Bouider	1988	21/11/87	376.1	20	3586	2226
Tel Hadya	1989	05/12/88	219.5	45	2774	2802
Breda	1989	24/11/88	179.6	44	1198	1335
Bouider	1989	24/11/88	184.0	53	821	1023
Tel Hadya	1990	13/12/89	227.0	46	943	863
Breda	1990	07/12/89	177.6	41	649	525
Breda	1991	09/01/91	209.7	21	1145	970
Bouider	1991	02/01/91	196.8	24	1265	1185

[a]Year of harvest.
[b]Not available.
[c]Assuming an emergence before 30/11/1984.
[d]Rainfall October (20.6 mm) estimated from rainfall at Breda.

Environments

The data were obtained from yield trials conducted in northern Syria at 18 environments, representing seven growing seasons and three locations (Table 1): Tel Hadya (36°10'N, 36°56'E), Breda (35°56'N, 37°10'E) and Bouider (35°40'N, 37°10'E). The mean annual rainfall ranges from 327 mm at Tel Hadya (mean of 13 seasons) to 262 mm at Breda (mean of 11 seasons) and 219 mm at Bouider (mean of 6 seasons). Bouider, the driest site, also tends to have the highest number of night frosts (Table 1). For 14 environments, grain yield data were obtained from trials of ICARDA's barley breeding project. Depending on the number of lines tested, each yield trial was split into at least 11 experiments. Each experiment was a simple lattice at Tel Hadya and Breda and a triple lattice at Bouider. Plots were 1.8 m wide (6 rows at 30 cm distance) and 2.5 or 5 m long. The seed rate was 120 kg ha^{-1}. The central four rows of each plot were harvested. Harmal and Arabi Aswad were included as check in each experiment. Average yield per environment for these two cultivars was calculated as the average of the adjusted means for each experiment and was thus based on at least 22 plots.

Additionally, we used yield data from four of ICARDA's cereal physiology experiments, carried out at all three sites in 1985/86 and at Breda in 1988/89. In 1985/86, the experimental design was a randomized complete block with three replications; in 1988/89, a triple lattice was used. Plots were 2.4 m wide (12 rows at 20 cm distance) and 5 m long, with a seed rate of 100 kg ha^{-1}. Grain yield was based on a hand-harvested sample of 0.8 m^2 (4 rows of 1 m).

Experiments were sown between 23 October and 29 November. Emergence dates, however, ranged from 18 November to 9 January (Table 1). The late emergence in 1985/86 and 1990/91 was associated with low rainfall in October and November. Harvest was usually in May.

Statistical analysis

Meteorological variables, which were expected *a priori* to influence grain yield and which were related to either rainfall or temperature, were used in the analysis (Table 2). To investigate which of these variables had to be incorporated in the multiple linear regression model, simple correlations and a forward multiple regression were performed, using the yields of the individual cultivars as dependent variables and meteorological variables as independent variables. To prevent too low a number of degrees of freedom for the error in the model, only multiple regressions with two independent variables, one related to rainfall and one to temperature, were considered. The only exception was a multiple regression with the monthly rainfall from November to April as independent variables. Because temperature data were not available for Bouider 1985, only 17 environments were used for the multiple regressions. The coefficient of determination (R^2), adjusted for degrees of freedom (SAS, 1988), was used to assess the goodness of fit of the model.

Table 2. Mean, coefficient of variation (CV), and minimum and maximum value for each meteorological variable used in the analysis, plus the simple correlation with grain yield (kg ha^{-1}) of Harmal and Arabi Aswad across 18 environments in northern Syria.

	Mean	CV(%)	Min.	Max.	Correlation with yield Harmal	A. Aswad
Rainfall (mm)						
October	27.3	72.5	4.4	71.0	0.63**	0.54*
November	35.8	70.7	3.8	98.0	0.29	0.42
December	40.8	53.5	12.4	83.9	0.41	0.34
January	56.5	57.0	1.2	126.3	0.49*	0.52*
February	42.0	66.1	0.4	97.4	0.66**	0.52*
March	32.7	71.5	8.4	92.6	0.35	0.24
April	16.4	65.9	0.0	35.2	0.18	0.10
Oct-Nov	63.1	56.9	20.2	126.2	0.55*	0.59**
Nov-Jan	133.2	32.6	86.9	246.3	0.73***	0.80***
Nov-Feb	175.1	36.0	108.0	307.6	0.80***	0.78***
Nov-March	207.8	35.7	126.8	394.8	0.79***	0.74***
Nov-April	224.2	34.7	126.8	424.2	0.77***	0.72***
Oct-April	251.5	35.7	171.0	495.2	0.81***	0.74***
March-April	49.1	61.7	11.4	122.0	0.34	0.22
Night frosts						
After emergence	31.6	44.5	9	53	-0.60*[a]	-0.47[a]
March-April	4.8	79.1	1	12	-0.19[b]	-0.05[b]
Absolute minimum temperature (°C)						
After emergence	-7.8	26.9	-11.5	-4.0	-0.00[b]	-0.09[b]
March-April	-4.1	75.9	-9.6	-0.8	0.24[b]	0.08[b]
Average minimum temperature (°C)						
January	1.1	230.6	-2.9	4.1	0.32[a]	0.29[a]
February	2.0	103.2	-2.1	4.4	0.25[b]	0.05[b]

[a]n=16; Bouider 1985 and Bouider 1986 missing.
[b]n=17; Bouider 1985 missing.
* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Results

Meteorological variables

About 95% of the rain in northern Syria falls between October and April. Rainfall was highly variable within and between seasons (Table 1). In both 1984/85 and 1986/87, rainfall at Tel Hadya, the wettest site, was about twice as high as at Bouider, the driest site. On the other hand, rainfall in 1987/88 was more than twice the rainfall in

1988/89 at Tel Hadya and more than twice the rainfall in 1984/85 at Bouider. Consequently, the coefficient of variation for the rainfall variables was high, and in all cases the range exceeded the mean (Table 2).

The number of night frosts varied mainly between seasons (Table 1). It was low following late emergence in 1985/86 and 1990/91 and in the wet 1987/88 season, but high in the dry 1988/89 season and in 1986/87. The highest coefficient of variation was found for number of night frosts in March and April (Table 2).

Influence of rainfall on grain yield

Seasonal rainfall (October - April) was significantly and positively associated with grain yield (Table 2). The regression explained 63.5% of the variation in grain yield for Harmal and 51.7% for Arabi Aswad. The equations were:

Harmal GY (kg ha^{-1}) = 11.95 PREC (mm) -1211

Arabi Aswad GY (kg ha^{-1}) = 8.57 PREC (mm) - 507

This indicates a crossover in expected grain yield at a seasonal rainfall of 208 mm. The responses to rainfall of 12.0 $\pm$ 2.16 kg ha^{-1} mm^{-1} for Harmal and 8.6 $\pm$ 1.96 kg ha^{-1} mm^{-1} for Arabi Aswad were significantly different at $P<0.15$. For Arabi Aswad, a better fit was obtained if rainfall from November to January was considered (adjusted R^2=0.616).

The proportion of the variation in grain yield explained by rainfall increased to 71.8% for Arabi Aswad when a multiple regression with monthly rainfall from November to April was used (Table 3). In the case of Harmal, the multiple regression was only slightly more efficient than the simple regression with total seasonal rainfall; the fit increased from 63.5% to 67.3%. December rainfall had the highest effect on grain yield, around 50 kg ha^{-1} mm^{-1}, followed by January rainfall. The effect of rainfall gradually decreased as the season progressed and tended to be negative, although

Table 3. Effect on grain yield and contribution to grain yield of monthly rainfall for Harmal and Arabi Aswad across 18 environments in northern Syria. Standard error included in parentheses.

	Effect (kg ha^{-1} mm^{-1})		Contribution (%)	
	Harmal	A. Aswad	Harmal	A. Aswad
Adjusted R^2	0.673	0.718		
November	8.7 (8.63)	11.6 (6.29)+	6.7	9.9
December	53.7 (15.20)**	50.1 (11.08)***	47.0	49.0
January	28.3 (12.66)*	37.2 (9.22)**	34.3	50.4
February	2.7 (13.10)	-15.7 (9.55)	2.4	-15.8
March	-10.0 (11.32)	-16.7 (8.25)+	-7.0	-13.1
April	47.1 (31.21)	49.9 (22.76)+	16.6	19.6

+ P<0.10; * P<0.05; ** P<0.01; *** P<0.001.

Table 4. Percentage of variation of grain yield of Harmal and Arabi Aswad, explained by individual meteorological variables or combinations of them, across 17 environments in northern Syria.

	Harmal	Arabi Aswad
Rain (Nov-Jan)	48.5**	65.7***
Rain (Nov-Jan) + frost (March-April)	68.8**[a]	77.0*[a]
Rain (Nov-Feb)	59.1***	61.2***
Rain (Nov-Feb) + frost (March-April)	82.3***[a]	71.1*[a]
Rain (Oct-April)	61.8***	53.9***
Rain (Oct-April) + frost (March-April)	67.6*[a]	52.4[a]
Rain (Nov-April)	55.6***	50.0***
Monthly rain Nov-April	65.2**	71.9**

[a]Level of significance refers to contribution of frost only.
* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

not significantly, in March (Table 3). In April, the effect became positive again, but, because of the high variability, this effect was not significant. If the response of grain yield to rainfall was multiplied by the average monthly rainfall, December rainfall contributed about 50% to the final grain yield (Table 3). January rainfall contributed about 50% for Arabi Aswad but only 34% for Harmal; this difference was related to different contributions of February rainfall.

Influence of rainfall and temperature on grain yield

Temperature-related variables, e.g., minimum temperature and number of night frosts, were not correlated with grain yield, except for the number of night frosts after emergence, which had a weak negative correlation (Table 2). However, temperature was significantly correlated with rainfall. In winter, mean minimum temperature was positively correlated with rainfall ($r=0.89$, $P<0.001$ for January; $r=0.66$, $P<0.01$ for February), whereas in spring, mean maximum temperature was negatively correlated with rainfall ($r=-0.55$, $P<0.05$ for March; $r=-0.62$, $P<0.01$ for April).

When a multiple regression with one rainfall and one temperature variable was used, the best-fit model for Harmal included rainfall from November to February and number of night frosts in March and April (Table 4). This model improved the fit to 82.3%. For Arabi Aswad, the best fit was obtained if rainfall from November to January was used in conjunction with number of night frosts in March and April, explaining 77.0% of the variation in grain yield (Table 4).

Arabi Aswad had a lower yield response to additional rainfall, but its yield was also less affected by late frosts (Table 5). On average, grain yield of Arabi Aswad increased 500 kg ha^{-1} when 32.2 mm additional rainfall was received, but five night frosts in March and April would neutralize that effect. For Harmal, an increased yield of 500 kg ha^{-1}, due to 24.9 mm of rainfall, was nullified by three night frosts in March and April.

Discussion

Grain yield is primarily influenced by rainfall, but the multiple regression analysis showed that it can also be greatly affected by temperature. A similar result was obtained by Erskine & El Ashkar (in press), who found for lentil across 13 experiments in northwest Syria that total seasonal rainfall explained 78.6% of the variation in grain yield, but that addition of the number of night frosts improved the fit to 84.4%. Their results, however, also showed that the effect of winter temperature varied across regions.

Several studies have related grain yield of cereals in the east Mediterranean region to seasonal rainfall. For a six-rowed barley, grown in Cyprus, Hadjichristodoulou (1982) reported a yield response to seasonal rainfall of 8.12 kg ha^{-1} mm^{-1} across 34 environments with a range in seasonal rainfall similar to our study, but a slightly higher average (307 mm). For wheat, grown in slightly wetter environments, the response ranged from 6.42 to 16.92 kg ha^{-1} mm^{-1}. Blum & Pnuel (1990) found an average response of 7.4 kg ha^{-1} mm^{-1} for wheat grown across 16 environments with a mean seasonal rainfall of 485 mm. Ketata (1987) reported for barley and wheat in Syria responses of 11-19 kg ha^{-1} mm^{-1}. The present results, 12.0 ± 2.16 kg ha^{-1} mm^{-1} for Harmal and 8.6 ± 1.96 kg ha^{-1} mm^{-1} for Arabi Aswad, fall well within the range of reported responses in the east Mediterranean region.

Table 5. Parameter estimates for the multiple regression of rainfall during November-February and number of night frosts in March and April on grain yield (kg ha^{-1}) of Harmal and Arabi Aswad, grown across 17 environments in northern Syria. Standard errors included in parentheses.

	Harmal			Arabi Aswad		
Intercept	-882	(422.6)	+	-644	(434.4)	
Rain (Nov-Feb) (mm)	20.1	(2.35)	***	15.5	(2.42)	***
Night Frosts (March-April)	-179.7	(39.44)	***	-100.7	(40.54)	*

+ $P<0.10$; * $P<0.05$; *** $P<0.001$.

Table 6. Monthly rainfall, class A pan evaporation and the ratio of rainfall and evaporation, averaged over 17 environments in northern Syria.

	Rainfall (mm month^{-1})	Evaporation (mm day^{-1})	Ratio (day month^{-1})
November	37.7	2.6	14.5
December	41.0	1.5	27.3
January	56.6	1.5	37.7
February	42.2	2.6	16.2
March	33.4	4.1	8.1
April	16.1	6.7	2.4

Rainfall had the highest contribution to grain yield during winter. Temperature, radiation, and evaporation in northern Syria are low during this period and rainfall exceeds evaporation (Table 6) and the water needs of the crop (Cooper et al., 1983). Maximum water storage under a wheat crop at Tel Hadya occurred at the end of March in the wet 1987/88 season, in mid-February in 1986/87, but in mid-January in 1988/89, when nearly no rain fell after 1 January (ICARDA, 1990, p. 151). The steady decrease, during winter, in the effect of rainfall on grain yield thus indicates the accumulation of stored moisture in the soil profile. The significant positive correlation of January and February rainfall with grain yield (Table 2) reflects the significant positive correlation between rainfall and minimum temperature in these months, and thus a reduced effect of frost damage in wet winters. The tendency toward a negative effect of March rainfall may be explained by the negative correlation in spring between rainfall and maximum temperature. Average heading date of barley in northern Syria is around the beginning of April, and higher temperatures in March can increase the growth rate during the period preceding heading. A high growth rate during this period is positively correlated to kernel number per unit area at harvest (Biscoe & Gallagher, 1977; Brown et al., 1987), which in turn is strongly associated with grain yield (Gallagher et al., 1975). In April, during the grain filling period, rainy weather is associated with lower temperatures. Together, these factors can delay senescence, extend the grain filling period, and thus result in increased kernel weights (Erskine & El Ashkar, in press). However, rainfall in spring provides only a fraction of the evaporative demands (Table 6) and is thus of limited value to relieve terminal drought stress. This indicates that the intensity of terminal drought stress, a limiting factor for grain yield in the Middle East, does not depend upon erratic rainfall late in the season, but rather on an adequate recharge of the soil profile during winter.

If temperature was also considered, the best-fit model incorporated rainfall in winter and number of night frosts in spring. The negative effect of frost in spring was substantial (Table 5). During the period 1979/80 to 1991/92, in five out of the 13 seasons the number of night frosts in March and April at Tel Hadya exceeded five. According to Table 5, this implies that more than once every three years spring frost reduces yield by more than 500 kg ha^{-1} for Arabi Aswad and more than 900 kg ha^{-1} for Harmal. In the drier regions of northern Syria, where yields above 2500 kg ha^{-1} are rare, losses of 500-900 kg ha^{-1} are considerable. This can be seen if the expected grain yield at Bouider, based on seven seasons of meteorological data (for one season, temperature data were not available, and number of night frosts for Breda was used) are calculated. If only seasonal rainfall (October-April) is considered, the expected grain yield was 1272 kg ha^{-1} for Harmal and 1274 kg ha^{-1} for Arabi Aswad. Based on a model including winter rainfall (November-February) and spring frost (March-April), however, the expected grain yield for Harmal was 983 kg ha^{-1} and for Arabi Aswad 981 kg ha^{-1}, a reduction of 23%. Our results indicate that if rainfall in winter has been adequate, the occurrence of spring frost is a major environmental factor limiting grain yield.

The higher level of frost resistance of Arabi Aswad was related to its vernalization requirement. This requirement causes a delay in the development of the apex (van Oosterom & Acevedo, 1992b), which reduces the probability of frost damage of the developing spikes later in the season. Decreased levels of foliar damage, following frost in mid-March, for winter-type lines compared with spring-type lines, have been found within the progeny of a winter - spring barley cross (ICARDA, 1991, p. 125).

In subsistence agriculture of less-developed countries with small local markets, avoidance of a crop failure is critically important (Marshall, 1987). Prices of barley in developing countries increase dramatically in low-yielding seasons, but are low in high-yielding seasons (Marshall, 1987). An improved yield stability is thus likely to increase benefits to the farmer, even if the average grain yield does not increase. In northern Syria, the gradient in rainfall from northwest to southeast is steep (Dennett et al., 1984). Since the driest testing site, Bouider, also tends to have the highest occurrence of frost (Table 1), the relative reduction in grain yield due to spring frost is highest in the drier areas. Because frost can severely affect the crop, farmers tend to be biased toward frost avoidance (Nix, 1982). The very high coefficient of variation for night frosts in March and April (Table 2) indeed suggests that cold tolerance can be an important tool in improving yield stability.

The plant ideotype represented by Harmal only avoids terminal drought stress, whereas the plant ideotype represented by Arabi Aswad avoids both terminal drought stress and cold damage; the latter ideotype will therefore give a better yield stability in the dry areas in northern Syria where cold damage is likely. Although the lower response to rainfall of Arabi Aswad is a disadvantage in an extremely wet season (Bouider 1988, Table 1), a trade-off between yield stability and yield potential can be expected because the genetic correlation between tolerance to stress and yield in favourable environments is in general negative (Rosielle & Hamblin, 1981; Ceccarelli et al., in press). In environments like Bouider, where the expected grain yield is below 1000 kg ha^{-1}, improved genotypes will only be adopted by the farmers if they combine higher yields with better yield stability. This can be achieved through avoidance of terminal drought stress and tolerance to cold damage.

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References

Biscoe, P.V. & J.N. Gallagher, 1979. Weather, dry matter production and yield. In: J.J. Landsberg & C.V. Cutting (Eds.), Environmental Effects on Crop Physiology, pp. 75-100. Academic Press, London.

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

Brown, S.C., J.D.H. Keatinge, P.J. Gregory & P.J.M. Cooper, 1987. Effects of fertilizer, variety and location on barley production under rainfed conditions in northern Syria. 1. Root and shoot growth. Field Crops Res. 16: 53-66.

Ceccarelli, S., E. Acevedo & S. Grando, 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. Euphytica 56: 169-185.

Ceccarelli, S., S. Grando & J. Hamblin, in press. Relationship between barley grain yield measured in low- and high-yielding environments. Euphytica.

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

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

Erskine, W. & F. El Ashkar, in press. Rainfall and temperature effects on lentil seed yield in a Mediterranean environment. Expl. Agric.

Gallagher, J.N., P.V. Biscoe & R.K. Scott, 1975. Barley and its environment. V. Stability of grain weight. J. Appl. Ecology 12: 319-336.

Hadjichristodoulou, A., 1982. The effects of annual precipitation and its distribution on grain yield of dryland cereals. J. Agric. Sci., Camb., 99: 261-270.

ICARDA, 1990. Farm Resource Management Program: Annual Report 1989. International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria, 372 pp.

ICARDA, 1991. Cereal Improvement Program: Annual Report 1990. International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria, 210 pp.

Ketata, H., 1987. Actual and potential yields of cereal crops in moisture-limited environments. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 55-62. John Wiley & Sons Ltd., New York.

Marshall, D.R., 1987. Australian plant breeding strategies for rainfed areas. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 89-99. John Wiley & Sons Ltd., New York.

Nix, H.A., 1982. Aspects of drought from an agroclimatic perspective. In: Drought Resistance in Crops with Emphasis on Rice, pp. 3-15. IRRI, Los Banos, The Philippines.

Oosterom, E.J. van & E. Acevedo, 1992a. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. I. Morphological traits. Euphytica (in press).

Oosterom, E.J. van & E. Acevedo, 1992b. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. II. Apical development, leaf, and tiller appearance. Euphytica (in press).

Rosielle, A.A. & J. Hamblin, 1981. Theoretical aspects of selection for yield in stress and non-stress environments. Crop Sci. 21: 943-946.

SAS, 1988. SAS/STAT User's Guide, Release 6.03 Edition. Statistical Analysis System Institute Inc, Cary, NC, 1028 pp.

CHAPTER 6

Genotype × environment interactions of barley in the Mediterranean region

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Crop Science (submitted)

Summary

In the Mediterranean region, progress in selection for yield in harsh environments is hampered by large environmental variation between seasons and locations. This study analyzes the genotype × environment interaction of 36 two-row genotypes of barley (Hordeum vulgare L.), grown in 14 environments in Syria and North Africa, and assesses the influence of yield selection in contrasting environments on the yield response of the selected genotypes. Average grain yield per environment ranged from 7 to 513 g m^{-2}. Genotypes and environments were classified by a cluster analysis and the interaction was analyzed with an additive main effects and multiplicative interaction (AMMI) model. Genotypes were classified into four clusters, related to their growth type (winter or spring type) and earliness of heading. Environments were clustered in a high-yielding (HY) and low-yielding (LY) group; this classification was related to seasonal rainfall. Medium early heading winter types had a positive interaction with LY environments and a negative interaction with HY environments. Late heading genotypes (spring and winter types) had the opposite interaction pattern. Early heading spring types had above-average mean yields; the highest-yielding among them tended to have a low interaction with environments. Selection for yield in HY environments resulted in selection of both early heading genotypes with high yields under stress and late heading genotypes with low yields under stress. This shows that for a breeding program aimed at improving yield in regions where favourable conditions are rare, selection for yield should be done in the target environment.

Introduction

In the east Mediterranean region, seasonal rainfall, rainfall distribution, and temperature are the major abiotic factors limiting grain yield (Hadjichristodoulou, 1982; Ceccarelli et al., 1991). Ceccarelli et al. (1991) reported for barley in northern Syria average yields of 1562 kg ha^{-1} and 32 kg ha^{-1} from the same site in two successive seasons with minor differences in total rainfall. The crop failure was due to the combined effect of low temperatures and moisture stress. Under such variable conditions, genotype × environment (G×E) interactions are expected to be large.

To analyze G×E interaction, genotypes with similar response patterns can be grouped in clusters, such that the interaction within each cluster is minimized. An advantage of clustering is that the relative relationship between genotypes is independent of the data set used (Lin et al., 1986). A disadvantage, however, is that clustering gives no insight into the yield response of genotypes across environments.

To interpret G×E interactions more directly, Finlay & Wilkinson (1963) used a linear regression model where the yield of each genotype in an environment was regressed upon an environmental index, usually the average yield of all genotypes in that environment. This method has several limitations. The model is useless in case of low linearity; in addition, the main effects are generally confounded with the interaction (Byth et al., 1976; Zobel et al., 1988). An improved model was developed by Gauch (1988), who combined the analysis of main effects and interaction in an additive main effects and multiplicative interaction (AMMI) model. Main effects are accounted for by an analysis of variance, while interactions are analyzed by a principal component analysis (Gauch, 1988; Gauch & Zobel, 1988). The AMMI model is in general more effective in explaining G×E interactions than the linear regression model (Zobel et al., 1988; Nachit et al., 1992).

Genotype × environment interactions can reduce the progress of a breeding program if the test environment is not representative of the target environment. Hamblin et al. (1980), listing the criteria that useful selection sites must meet, posed the question whether selection for yield under stress has to be done under stress or non-stress conditions. Pfeiffer (1988) believes that high yield potential and a response to input can be combined with drought tolerance in bread wheat. He argued that because genetic advance in non-stress conditions may be higher than in stress conditions, initial selection is preferably done under non-stress conditions. Recently, Braun et al. (in press) concluded that irrigated, high-yielding (HY) environments have the highest screening ability for selection of widely adapted spring bread wheat cultivars. Ceccarelli (1987) and Ceccarelli & Grando (1989, 1991b), in contrast, concluded for barley, grown in unfavourable environments in Syria where high yields are rare, that selection for yield under stress has to be done in representative stress environments. This is in agreement with findings of Rosielle & Hamblin (1981) and of Simmonds (1981, 1991) that selection for yield potential tends to reduce tolerance to stress. Nachit & Ouassou (1988) and Nachit (1989) suggested for durum wheat, grown in more favourable Mediterranean environments where high and low yielding seasons are alternating, a synthetic approach with simultaneous selection in low-yielding (LY) and HY environments, to combine yield potential with stress tolerance.

The objectives of the present study were first to classify barley genotypes on the basis of their yield response across Mediterranean environments, and second to determine the influence of yield selection in contrasting environments on the yield response of the selected genotypes.

Materials and Methods

Plant material and environments

Thirty-six two-row genotypes of barley were grown in 14 environments (location × year combinations), nine in Syria and five in North Africa. Details of the genotypes are given in Table 1. Most of the genotypes referred to as landraces are pure lines extracted from Syrian or Jordanian landraces; only Arabi Abiad and Arabi Aswad, the two barley landraces widely grown in Syria, are mixtures. The word genotypes is thus used for convenience and does not imply homozygosity of all material used.

In Syria, experiments were carried out at three locations: Tel Hadya, Breda, and Bouider (Table 2), ranging in mean annual rainfall from 327 mm at Tel Hadya to 262 mm at Breda and 219 mm at Bouider. The north african environments in this study in general had higher amounts of rainfall, especially in March and April (Table 2).

Table 1. Name, origin, mean grain yield (g m^{-2}), growth type, heading date, and classification in the cluster analysis of the genotypes used in the analysis.

Name	Origin	Mean yield[a]	Growth type[b]	Heading date[c]	Cluster
Entries from Waite Institute Australia (WI)					
WI 2198	Australia	235.1	S	34.2	1
WI 2269	Australia	274.8	S	31.3	1
WI 2291	Australia	253.8	S	35.6	1
WI 2291/WI 2269	Australia	254.9	S	31.5	1
WI 2291/BgS	Australia	238.6	S	35.5	1
WI 2291/EH 70-F3-AC	Australia India	215.7	S	36.6	3
Improved Cultivars (IC)					
Alger/Union	Algeria/Germany	188.5	S	39.5	3
Atem	UK	221.5	S	43.0	3
Cytris	France	233.4	S	38.7	3
Lignee 131	France	226.1	W	45.1	4
Swanneck	UK/S. Africa	195.0	S	36.8	3
Genotypes from ICARDA breeding program					
ER/Apm	-	272.1	S	34.6	1
Roho	Egypt	261.0	S	34.2	1
A16//2728/Sv Mari	ICARDA	237.7	S	35.9	1
Jerusalem a barbes lisses/CI10836	ICARDA	230.7	S	37.1	1
Harmal	ICARDA	280.2	S	30.9	1
Roho/Mazurka	ICARDA	283.3	S	38.7	1
Kervana/Mazurka	ICARDA	205.5	S	38.4	3
S BON 29	ICARDA	241.4	S	34.1	1
S BON 89	ICARDA	203.8	S	40.7	3
S BON 96	ICARDA	252.6	S	32.3	1
BON 27	ICARDA	214.7	S	41.3	1
Landraces					
JLB 08-06	Jordan	207.4	W	34.6	2
JLB 08-84	Jordan	206.1	W	34.2	1
JLB 08-89	Jordan	210.6	W	35.4	1
SLB 03-77 (Tadmor)	East Syria	199.8	W	35.7	2
SLB 39-43	South Syria	205.5	W	35.9	2
SLB 39-99	South Syria	230.6	W	33.8	1
SLB 45-16	North east Syria	176.9	W	38.6	2
SLB 45-38	North east Syria	190.9	W	36.7	2
SLB 45-65	North east Syria	198.6	W	38.9	2
SLB 60-02	North west Syria	227.8	W	37.8	1
SLB 62-68	South west Syria	178.6	W	34.7	2
SLB 62-99	South west Syria	192.7	W	34.3	2
Arabi Abiad	North west Syria	231.8	W	36.4	1
Arabi Aswad	East Syria	187.0	W	36.5	2

[a]Grand mean grain yield: 224.0 g m^{-2}.
[b]S = spring type; W = winter type.
[c]Days from 1 March to heading; average of 12 experiments. Average days to heading: 36.4.

Table 2. Latitude, mean barley grain yield (g m^{-2}), seasonal precipitation and classification in the cluster analysis of 14 Mediterranean environments (site × year combinations).

Year	Site	Latitude	Yield (g m^{-2})	Precipitation (mm)[a] O-A	Precipitation (mm)[a] M-A	Cluster
	Syria					
1985/86	Tel Hadya (TH6)	36°01	331	287.5	48.1	A
	Breda (BR6)	35°56	134	207.9	34.0	B
	Bouider (BO6)	35°40	133	177.8[b]	42.0	B
1986/87	Tel Hadya (TH7)	36°01	246	340.3	76.1	B
	Breda (BR7)	35°56	148	244.6	64.6	B
1987/88	Tel Hadya (TH8)	36°01	296	495.2	122.0	A
	Bouider (BO8)	35°40	273	376.0	66.4	A
1988/89	Tel Hadya (TH9)	36°01	89	219.5	17.8	B
	Bouider (BO9)	35°40	7	184.0	26.7	B
	Morocco					
1987/88	Annoceur (AN8)	33°50	200	462.3	64.0	A
1988/89	Annoceur (AN9)	33°50	286	364.7	193.3	A
	Jemaa Shiam (JS9)	32°40	226	408.0[b]	133.0	A
	Sidi El Aidi (SA9)	33°10	254	406.4	134.0	A
	Algeria					
1988/89	Khroub (KH9)	36°25	513	326.8	99.7	A

[a]O-A October-April; M-A March-April.
[b]Excluding October.

Although frost occurs, winters in North Africa tend to be milder than in Syria, with higher absolute minimum temperatures. Latitudes in Morocco were comparable to those of south Syria.

The experimental design was a randomized complete block with three replications. Plots were 2.4 m wide (12 rows, 20 cm apart) and 5 m long. Emergence dates ranged from early November to late January. Grain yield was obtained from a hand-harvested sample of 0.8 m^2; for environment Khroub 1989, combine-harvested yields were used. Average grain yields ranged from 7 g m^{-2} at Bouider 1989 to 513 g m^{-2} at Khroub 1989. The very low yields at Tel Hadya and Bouider in 1989 were due to the combination of a late emergence and a very dry spring; plants were mainly growing on stored moisture.

Classification of genotypes and environments

To group genotypes, a cluster analysis was used. The similarity between two genotypes was expressed as the squared euclidean distance. To adjust for differences in yield level between environments, data for each environment were standardized to a mean of zero and a standard deviation of one (Fox & Rosielle, 1982). The clustering method employed was the average linkage method, which estimates the distance between two clusters as the average distance between pairs of genotypes, one in each cluster (SAS, 1988). A large distance between the last few clustering steps was an indicator of truncation of the clustering.

Environments were grouped similarly, using the same data set, standardized per environment.

Genotype × environment interaction

To analyze the G×E interaction, the AMMI model was used (Gauch, 1988; Nachit et al., 1992). The equation of this model is:

$$Y_{ge} = \mu + \alpha_g + \beta_e + \sum_{n=1}^{N} \lambda_n \gamma_{gn} \delta_{en} + \theta_{ge} + \epsilon_{ge}$$

where Y_{ge} is the yield of genotype g in environment e; μ is the grand mean yield; α_g is the genotype mean deviation; β_e is the environment mean deviation; λ_n is the eigenvalue of the n^{th} principal component; γ_{gn} and δ_{en} are the genotype and environment scores for the n^{th} principal component; θ_{ge} is the residual and ϵ_{ge} is the random error (Gauch, 1988; Zobel et al., 1988). The additive part of the AMMI model (μ, α_g, and β_e) is estimated from an analysis of variance and the multiplicative part (λ_n, γ_{gn}, and δ_{en}) from a principal component analysis (PCA). If most of the G×E interaction sum of squares (SS) can be captured in the first N PCA axes, a reduced AMMI model, incorporating only the first N axes, can be used. The interaction between any genotype and environment can be estimated by multiplying the interaction PCA (IPCA) score of a genotype ($\lambda_n^{0.5} * \gamma_{gn}$) by an environment IPCA score ($\lambda_n^{0.5} * \delta_{en}$). Provided the first IPCA (IPCA1) explains at least 50% of the interaction SS, the interaction can be depicted in a biplot, where the main effects of treatments are shown on the x-axis and their scores for IPCA1 on the y-axis.

Yield selection in contrasting environments

If the G×E interaction is significant, individual environments must have a different pattern of contributions to the classification of genotypes. Environmental contributions to the major fusion points in the genotype clustering (Fig. 1) were calculated as the squared difference in each environment between the mean standardized yields of the two groups clustered (Shorter et al., 1977).

To study the effect of yield selection in contrasting environments on the yield response of the selected genotypes, 12 genotypes with the highest average standardized grain yield in the six highest-yielding or five lowest-yielding environments were compared for their yield in LY and HY environments.

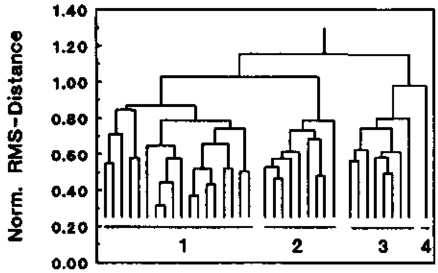

Fig. 1. Dendrogram from average linkage cluster analysis of standardized grain yield of 36 two-row barley genotypes grown in 14 environments in Syria and North Africa. Distances between clusters are expressed as root mean square (RMS) distances. Values below each cluster represent the cluster number.

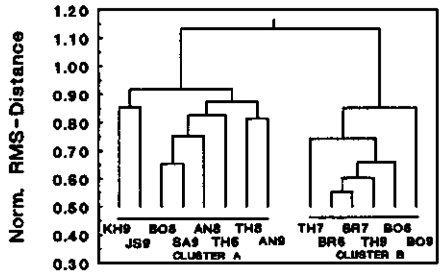

Fig. 2. Dendrogram from average linkage cluster analysis of standardized barley grain yield of 14 environments in Syria and North Africa. Yield level of each environment is given in Table 1. Distances between clusters are expressed as root mean square (RMS) distances.

Results

Genotype and environment classification

The classification of genotypes was truncated at the four-group level (Fig. 1). Differences between clusters explained 63.0% of the genotype SS (Table 3). The first cluster contained 18 genotypes: 5 out of 6 Australian genotypes, 8 out of 11 genotypes from the barley breeding program at ICARDA, and 5 out of 14 landraces (Table 1). All but two of these genotypes had an above average mean grain yield and, with two exceptions, headed earlier than average. Apart from the five landraces, these genotypes were spring types. Cluster 2 contained the remaining nine landraces (Table 1). All of them were winter types, with a below-average mean grain yield and heading close to the average. The third cluster included one Australian genotype, three genotypes from ICARDA's barley breeding program and four improved cultivars (Table 1). These genotypes were all spring types, characterized by a below average mean grain yield (except genotype Cytris) and late heading. The fourth cluster contained only Lignee 131, a winter type with late heading but an average grain yield close to the grand mean (Table 1).

The classification of environments was truncated at the two-group level (Fig. 2); this division explained 51.4% of the SS for environments (Table 3). The two clusters had significantly different average grain yields ($P<0.001$ for a t-test), despite standardization of the data. Environments with yield levels of 200 g m^{-2} and above were grouped in cluster A and those with yield levels below 200 g m^{-2} in cluster B.

Table 3. Analysis of variance plus the partitioning of the sum of squares into among- and within-group components for grain yield of 36 two-row barley genotypes across 14 environments in Syria and North Africa.

Source	df	SS	MS	
Total	1511	30728338	20336	**
Treatments	503	26583859	52851	**
Genotypes (G)	35	1249076	35868	**
Among clusters (C_g)	3	786914	262304	**
Within clusters ($G(C_g)$)	32	462161	14443	**
Environments (E)	13	21158336	1627564	**
Among clusters (C_e)	1	10878246	10878246	**
Within clusters ($E(C_e)$)	12	10280090	856674	**
G × E	455	4176447	9179	**
$C_g \times E$	39	1758060	45078	**
$G(C_g) \times E$	416	2418387	5813	**
$G \times C_e$	35	1110592	31731	**
$G \times E(C_e)$	420	3065855	7300	**
$C_g \times C_e$	3	734613	244871	**
Residual	452	3441834	7615	**
Rep(env)	28	488050	17430	**
Error	980	3656505	3731	

** $P<0.01$.

An exception was Tel Hadya 1987 (average yield of 246 g m^{-2}), which was clustered with the LY environments. High-yielding environments (HY) were in general wetter than LY ones (Table 2).

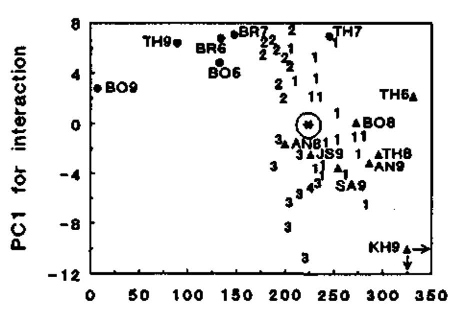

Fig. 3. Biplot of the AMMI model for 36 two-row barley genotypes, grown in 14 environments in Syria and North Africa. Genotypes are represented by the number of the cluster in which they are grouped (Fig. 1). Environments are represented by ▲ (cluster A) and ● (cluster B). Environment Khroub 1988/89 (KH9) fell outside the range of the figure. Encircled star represents grand mean yield.

Table 4. AMMI partitioning of the genotype × environment interaction for grain yield of 36 barley genotypes, grown in 14 Mediterranean environments.

Source	df	SS	MS	
Treatments	503	26583859	52851	**
Genotypes (G)	35	1249076	35688	**
Environments (E)	13	21158336	1627564	**
GE interaction	455	4176447	9179	**
IPCA1	47	2105759	44803	**
IPCA2	45	602238	13383	**
IPCA3	43	411031	9559	**
IPCA4	41	331427	8084	**
IPCA5	39	226174	5799	*
Residual	240	499816	2083	
Rep(env)	28	488050	17430	**
Error	980	3656505	3731	

* $P<0.05$; ** $P<0.01$.

Genotype × environment interaction

The G×E interaction was highly significant (Table 3). The interaction between the genotype classification and environments explained 42.1% of the G×E interaction SS, using only 8.6% of the interaction degrees of freedom (df). The interaction between genotype classification and environment classification still captured 17.6% of the G×E interaction SS, using less than 1% of the interaction df (Table 3).

In the AMMI model, IPCA1 explained 50.4% of the interaction SS, using 10.1% of the interaction df (Table 4). The first five IPCA's were significant. However, the noise in the interaction could be estimated as 455 (interaction df) * 3731 (error MS) = 1697605. Discarding a residual of this amount suggests that IPCA3 and higher are mainly noise, IPCA1 most probably has a predictive value, whereas IPCA2 is transitional.

A biplot of the results of the AMMI model is given in Fig. 3. For both genotypes and environments, clusters in the biplot were well-separated, except for the separation of cluster 3 from cluster 4. The landraces of cluster 2 had a positive interaction with all the environments of cluster B, including the higher yielding environment Tel Hadya 1987. Their interaction with cluster A environments was negative or close to zero, except with Tel Hadya 1986. Genotypes of clusters 3 and 4 had average grain yields comparable to those of cluster 2, but an opposite response pattern, with a negative interaction with LY environments and a positive interaction with HY environments. Genotypes of cluster 1 had a wide range in response patterns; however, the highest yielding genotypes had, with two exceptions, a low interaction with environments, as their IPCA1 was close to zero.

Yield selection in contrasting environments

Environments of cluster B (LY environments) had a high contribution to the separation of genotype clusters 1 and 2 from clusters 3 and 4 (Table 5). This was due to the low grain yield of genotypes of clusters 3 and 4 in these environments. Environments of cluster A (HY environments), in contrast, discriminated genotype cluster 1 from cluster 2, due to the low yield potential of cluster 2 genotypes. In general, they also separated cluster 3 better from cluster 4 than did LY environments.

Since HY environments did not separate clusters 3 and 4 well from clusters 1 and 2, they did not discriminate well among genotypes with good and poor yield in LY environments. This poor discrimination of HY environments is illustrated by the selection of the 12 genotypes with the highest average (standardized) yield in the six highest and five lowest yielding environments. The two groups had five genotypes

Table 5. Contribution of each environment to the three major fusions in the cluster analysis for genotypes. Contributions are expressed as the squared difference between the mean standardized yields of the two groups of genotypes clustered.

Environment	Grain yield ($g\ m^{-2}$)	Fusion 1[a]	2[b]	3[c]
Cluster A				
Khroub 1989	513	1.270	1.376	0.004
Tel Hadya 1986	331	0.885	1.316	3.698
Tel Hadya 1988	296	0.095	1.199	2.415
Annoceur 19898	286	0.301	1.073	2.554
Bouider 1988	273	0.356	2.611	1.447
Sidi El Aidi 1989	254	0.038	3.419	1.997
Jemaa Shiam 1989	226	0.023	0.760	7.054
Annoceur 1988	200	0.003	2.176	0.001
Cluster B				
Tel Hadya 1987	246	2.170	0.364	0.046
Breda 1987	148	3.698	0.010	0.001
Breda 1986	134	3.056	0.015	1.042
Bouider 1986	133	2.307	0.099	0.524
Tel Hadya 1989	89	2.641	0.017	0.019
Bouider 1989	7	1.893	0.945	0.071

[a]Separation of clusters 1 and 2 from clusters 3 and 4.
[b]Separation of cluster 1 from cluster 2.
[c]Separation of cluster 3 from cluster 4.

Table 6. Average grain yield (g m^{-2}) in high-yielding (HY), low-yielding (LY), and intermediate-yielding environments for 36 barley genotypes and for genotypes selected for grain yield in both HY and LY environments (HY/LY) and in only HY or LY environments.

	Mean n=36	HY/LY n=5	HY n=7	LY n=7
HY environments				
KH9	513	556 ab[a]	591 a	404 b
TH6	331	393 a	379 ab	330 b
TH8	296	369 a	341 a	249 b
AN9	286	347 a	336 a	229 b
BO8	273	360 a	345 a	237 b
SA9	254	295 a	302 a	211 b
Average	326	387	382	277
LY environments				
BR7	148	184 a	140 b	167 a
BR6	134	174 a	120 b	169 a
BO6	133	170 a	121 b	158 a
TH9	89	124 a	71 b	115 a
BO9	7	9 a	5 a	11 a
Average	102	132	91	124
Intermediate environments (not used for selection)				
TH9[b]	254	271 a	218 a	292 a
TH7	246	271 a	249 a	270 a
JS9	226	233 a	262 a	198 a
AN8	200	223 a	232 a	160 b
Average	232	250	240	230

[a]Values in the same row followed by a different letter differ significantly at $P<0.05$ according to a t-test.
[b]Experiment with a slightly different nursery; for HY/LY: n=5, for LY: n=6, and for HY: n=4.

in common, all of cluster 1 and characterized by early heading. The seven remaining genotypes selected in only LY environments were all landraces (two of cluster 1, five of cluster 2) with a positive interaction with LY environments. Genotypes selected in only HY environments (five of cluster 1, one of cluster 3, one of cluster 4) all had a strong negative interaction with LY environments or an interaction close to zero. In HY environments, genotypes selected in only LY environments had significantly lower average yields than the other two groups (Table 6). In LY environments, in contrast, genotypes selected in only HY environments had significantly lower average yields.

In four environments with an intermediate yield level, not used for selection, differences in grain yield between the groups decreased to non-significant levels.

Discussion

The G×E interaction accounted for 16% of the treatments SS. This low percentage was due to the high SS of environments, which in turn resulted from the wide range in environmental mean yields. Compared with the genotypes SS, however, the interaction SS was a factor 3.3 higher. This is slightly higher than found by Byth et al. (1976) for an international wheat yield trial and by Zobel et al. (1988) for soybean in New York. Nachit et al. (1992) found for durum wheat in Mediterranean environments even a factor of 21.1. This shows the importance of G×E interaction in the Mediterranean region.

The classification of genotypes was related to heading date and growth type: late heading genotypes were grouped in clusters 3 and 4, whereas most winter types were grouped in clusters 2 and 4. Early heading spring types were thus grouped in cluster 1, medium early heading winter types in cluster 2, late heading spring types in cluster 3, and late heading winter types in cluster 4. Different combinations of growth type and earliness are associated with differences in apical development pattern (van Oosterom & Acevedo, 1992a). The classification of genotypes therefore strongly suggests that development pattern has a marked effect on yield response across environments and thus on yield stability.

The five landraces that were grouped in cluster 1 all had a high average grain yield compared with the other landraces (Table 1). This was due to a better performance in HY environments than the other landraces. The landrace with the highest average yield in HY environments was Arabi Abiad, which is widely grown by farmers in the more favourable environments of northern Syria. Among the four other landraces grouped in cluster 1 were SLB 60-02, collected from an area with good fertility and high expected yield (Weltzien & Fischbeck, 1988; Weltzien, 1989), one landrace from southern Syria, and two Jordanian landraces. Compared with Syrian landraces, those from Jordan have a more rapid development early in the season and earlier heading (van Oosterom & Acevedo, 1992a). They thus resemble early heading spring types of cluster 1 more than the Syrian landraces.

The classification of environments was mainly based on environmental mean yield, despite standardization of the data. Low-yielding environments had yield levels up to 200 to 250 g m^{-2}, while HY environments had yield levels of 200 to 250 g m^{-2} and higher. This is in close agreement with Ceccarelli (1989), who defined for barley in Mediterranean environments 250 g m^{-2} as the lower yield limit for non-stress environments. Determining factors for the relation between yield level and classification can be the amount of rainfall and the temperature. High-yielding environments all had high seasonal or spring rainfall (Table 2). This may lengthen the growing season, which is especially beneficial for late heading genotypes of clusters 3 and 4. The clustering of Tel Hadya 1987 with the LY environments can be explained by a temperature effect. In 1986/87, a period with below-zero minimum temperatures occurred in spring. Such low temperatures late in the season affect yields of early heading spring types (cluster 1) more adversely than of medium early heading winter types of cluster 2 (van Oosterom et al., in press). Indeed, the high value for IPCA1 of both 1987 environments (Fig. 3) suggests a positive interaction of genotypes of cluster 2 with environments experiencing late frost. Tel Hadya 1987 was thus more unfavourable than expected based on rainfall alone. Yau et al. (1991) found for standardized grain yields of bread wheat in Mediterranean environments a classification of environments that was also determined by moisture supply and winter temperatures. If rainfall and temperature are the two major criteria for the classification of environments, the weak clustering of especially the four Tel Hadya environments in Fig. 2 shows high inter-seasonal fluctuations for these variables in Syria.

The clustering of environments into LY and HY groups strongly suggests that HY environments were not representative of LY ones. The major drawback of yield selection in HY environments was that it did not discriminate well against genotypes that were poorly adapted to LY conditions. This was related to a weaker correlation between heading date and grain yield in HY than in LY environments (van Oosterom & Acevedo, 1992b). Therefore, selection on the basis of yield potential can result in the selection of late genotypes that do not adequately avoid terminal drought stress in LY environments. In addition, selection for yield potential may discard genotypes with good performance under stress but low yield potential. A trade-off between yield potential and tolerance to stress has been predicted on theoretical grounds by Rosielle & Hamblin (1981) and confirmed experimentally by Ceccarelli & Grando (1991a). Our results suggest that for barley, grown in unfavourable Mediterranean environments with low expected yields, selection for yield has to be done in representative LY environments.

In environments with yield levels around 200 to 250 g m^{-2}, differences in grain yield between the groups of selected genotypes were non-significant (Table 6). This supports results of Simmonds (1991) that environments with an intermediate yield level are not suitable as selection sites for extreme environments, either LY or HY.

The selection, in both HY and LY environments, of early heading genotypes suggests that high yield potential and tolerance to stress can be combined by selection for earliness along with yield potential. However, these early genotypes are less adapted to (late) frost than genotypes of cluster 2, as shown by the high values for IPCA1 for both 1987 environments (Fig. 3). Consequently, they will have a lower yield stability than landraces in environments where low yields arise from both low winter temperatures and terminal drought stress. In areas where barley is the dominant crop, expected yields are below 1 ton ha^{-1} (Somel et al., 1984). At such yield levels, yield stability rather than yield potential is of primary concern to the farmers.

In conclusion, the present results show that the response pattern of barley across Mediterranean environments is associated with apical development pattern. Therefore, selection for development pattern can be a useful tool for indirect selection for yield in LY environments. Due to genotypic differences in yield response pattern, HY environments are not representative of LY environments. Selection for grain yield in environments where high yields are rare therefore has to be done in LY environments.

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References

Braun, H.-J, W.H. Pfeiffer & W.G. Pollmer, in press. Environments for selecting widely adapted spring wheats. Crop Sci.

Byth, D.E., R.L. Eisemann & I.H. De Lacy, 1976. Two-way pattern analysis of a large data set to evaluate genotypic adaptation. Heredity 37: 215-230.

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

Ceccarelli, S., 1989. Wide adaptation: how wide? Euphytica 40: 197-205.

Ceccarelli, S., E. Acevedo & S. Grando, 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. Euphytica 56: 169-186.

Ceccarelli, S. & S. Grando, 1989. Efficiency of empirical selection under stress conditions in barley. J. Genet. and Breed. 43: 25-31.

Ceccarelli, S. & S. Grando, 1991a. Selection environment and environmental sensitivity in barley. Euphytica 57: 157-167.

Ceccarelli, S. & S. Grando, 1991b. Environment of selection and type of germplasm in barley breeding for low-yielding conditions. Euphytica 57: 207-219.

Finlay, K.E. & G.N. Wilkinson, 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14: 742-754.

Fox, P.N. & A.A. Rosielle, 1982. Reducing the influence of environmental main-effects on pattern analysis of plant breeding environments. Euphytica 31: 645-656.

Gauch Jr., H.G., 1988. Model selection and validation for yield trials with interaction. Biometrics 44: 705-715.

Gauch Jr., H.G. & R.W. Zobel, 1988. Predictive and postdictive success of statistical analyses of yield trials. Theor. Appl. Genet. 76: 1-10.

Hadjichristodoulou, A., 1982. The effects of annual precipitation and its distribution on grain yield of dryland cereals. J. Agric. Sci., Camb. 99: 261-270.

Hamblin, J., H.M. Fischer & H.I. Ridings, 1980. The choice of locality for plant breeding when selecting for high yield and general adaptation. Euphytica 29: 161-168.

Lin, C.S., M.R. Binns & L.P. Lefkovitch, 1986. Stability analysis: where do we stand? Crop Sci. 26: 894-900.

Nachit, M.M., 1989. Moisture stress tolerance and yield stability in durum wheat (*Triticum durum* 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, Germany F.R. Th. Mann Publishers, Gelsenkirchen, Germany F.R.

Nachit, M.M., G. Nachit, H. Ketata, H.G. Gauch Jr. & R.W. Zobel, 1992. Use of AMMI and linear regression models to analyze genotype-environment interaction in durum wheat. Theor. Appl.

Gent. 83: 597-601.

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

Oosterom, E.J. van & E. Acevedo, 1992a. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. II. Apical development, leaf, and tiller appearance. Euphytica (in press).

Oosterom, E.J. van & E. Acevedo, 1992b. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. III. Plant ideotype and grain yield. Euphytica (in press).

Oosterom, E.J. van, S. Ceccarelli & J.M. Peacock, in press. Yield response of barley to rainfall and temperature in Mediterranean environments. J. Agric. Sci., Camb.

Pfeiffer, W.H., 1988. Drought tolerance in bread wheat - Analysis of yield improvement over the years in CIMMYT germplasm. In: A.R. Klatt (Ed.), Wheat Production Constraints in Tropical Environments, pp. 274-278. CIMMYT, Mexico DF, Mexico.

Rosielle, A.A. & J. Hamblin, 1981. Theoretical aspects of selection for yield in stress and non-stress environments. Crop Sci. 21: 943-946.

SAS, 1988. SAS/STAT User's guide, Release 6.03 Edition. Statistical Analysis System Institute Inc., Cary, NC, 1028 pp.

Shorter, R., D.E. Byth & V.E. Mungomery, 1977. Genotype × environment interactions and environmental adaptation. II. Assessment of environmental contributions. Aust. J. Agric. Res. 28: 223-235.

Simmonds, N.W., 1981. Genotype (*G*), environment (*E*) and *GE* components of crop yields. Expl. Agric. 17: 355-362.

Simmonds, N.W., 1991. Selection for local adaptation in a plant breeding programme. Theor. Appl. Genet. 82: 363-367.

Somel, K., A. Mazid & M. Hallajian, 1984. Survey of barley producers; northern Syria 1981/1982. Volume III, Descriptive Statistics. ICARDA Research Report No. 12, Aleppo, Syria, 75 pp.

Weltzien, E., 1989. Differentiation among barley landrace populations from the Near East. Euphytica 43: 29-39.

Weltzien, E. & G. Fischbeck. 1988. Genotypic variability and productivity of local barley landraces under marginal growing conditions in Syria. In: E.E. Whitehead, C.F. Hutchinson, B.N. Timmermann & R.G. Varady (Eds.), Arid Lands: Today and Tomorrow, pp. 511-522. Proc. International Research and Development Conference, Tucson, AZ, USA, 20-25 October 1985. Westview/Cress, Boulder, CO, USA.

Yau, S.K., G. Ortiz-Ferrara & J.P. Srivastava, 1991. Classification of bread wheat-growing environments based on differential yield responses. Crop Sci. 31: 571-576.

Zobel, R.W., M.J. Wright & H.G. Gauch Jr., 1988. Statistical analysis of a yield trial. Agron. J. 80: 388-393.

CHAPTER 7

Plant ideotype as a tool for indirect selection for grain yield of barley in harsh Mediterranean environments

E.J. van Oosterom & S. Ceccarelli

Summary

Adaptation of barley to Mediterranean environments is related to development. The aim of this study was to assess whether, plant traits related to development in winter or spring can be used in favourable environments as criteria for indirect selection for grain yield in environments where low winter temperatures and terminal drought stress occur. Thirty-six two-row barley (Hordeum vulgare L.) genotypes were grown in 15 Mediterranean environments. Winter development was represented by winter plant ideotype (WPI), a principal component of winter growth habit, winter plant colour, and cold tolerance. Winter type barley had high values for WPI; spring type barley had low values. Spring development was represented by days from 1 March to heading. Data for all four traits were obtained from three favourable environments. Grain yield under favourable and unfavourable conditions was represented by average standardized grain yields in six high-yielding (HY) and five low-yielding (LY) environments respectively. Yield response was expressed as the first interaction principal component of the AMMI model and as the slope of the linear regression model. Effects of WPI and heading date on yield and yield response were calculated with a path analysis. The effect of WPI on yield was significantly positive in LY environments, but negative in HY environments. The effect of late heading was significantly negative in LY environments, but absent in HY environments. Consequently, both traits had a significant effect on yield response. The results suggest that selection for WPI and heading date in HY environments can have a significant positive effect on yield under stress and yield response. A procedure is proposed, in which ideotype selection in early generations under favourable conditions is combined with empirical yield selection in later generations under stress.

Introduction

The impact of plant breeding on agriculture in low-input environments has been modest during the last decades. One of the reasons is that breeding progress for these environments has been hampered by unpredictable timing and intensity of stresses. In northern Syria, seasonal rainfall is highly variable between locations and seasons (van Oosterom et al., in press a); variable winter temperatures increase the environmental variability (Ceccarelli et al., 1991). Under such circumstances, breeding efficiency can be improved if plant traits can be identified which are associated with yield under stress, but have a higher heritability than yield itself, and hence a more stable expression across environments.

A multitude of traits has been associated with grain yield under stress, ranging from morpho-phenological traits like growth habit, growth vigour, ground cover, and heading date (Fischer & Wood, 1979; Acevedo, 1987; Richards, 1987) to physiological ones like leaf water potential (Blum et al., 1981) and carbon isotope discrimination (Farquhar & Richards, 1984). Among those traits, the morpho-phenological ones are in general most attractive to breeders, because they are rapid and inexpensive to screen. Notwithstanding ample theoretical evidence for the relation of these traits to yield under stress, experimental evidence for their usefulness as indirect selection tools is scarce. This is partly due to the fact that these traits are often considered individually by using simple correlations with yield (Fischer & Wood, 1979; Acevedo et al., 1991). However, morpho-phenological traits also are mutually correlated (Rasmusson, 1987; Ceccarelli et al., 1991; van Oosterom & Acevedo, 1992a). Consequently, direct effects on yield under stress may in the simple correlation be masked by indirect effects, of opposite sign, via correlated traits. The conclusion of Ceccarelli et al. (1991) and van Oosterom & Acevedo (1992a) that combinations of traits, rather than single traits, constitute adaptation to stress, may reflect the role of indirect effects.

In an attempt to integrate single traits, van Oosterom & Acevedo (1992b) identified in barley morphological traits related to apical development pattern, which have a key adaptive role for stress in the Mediterranean region. Four contrasting development patterns were distinguished, which differed in their rate of development in winter and spring. Development in winter was associated with a vernalization requirement; vernalization slowed apical development and resulted in cold tolerance. Development in spring was associated with a photoperiodic response; rapid apical development resulted in early heading and hence avoidance of terminal drought stress. In a subsequent study (van Oosterom & Acevedo, 1992c), evidence was found that after removal of the effect of heading date on grain yield under stress, traits related to development explained a significant additional part of the variation in yield. However, no clear distinction was made between traits related to development in winter or spring, whereas heading date was obtained from both favourable and unfavourable environments. The yield response of barley across Mediterranean environments also appears to be associated with development pattern (van Oosterom et al., in press b).

The aim of the present study was to assess for barley in Mediterranean environments the direct effects of morphological and phenological traits, related to development in either winter or spring and obtained from high-yielding (HY) environments, on yield in low-yielding (LY) and HY environments and on yield response by using a path coefficient analysis. The implication of the results for a breeding program aimed at improving yield in LY environments are discussed.

Materials and Methods

Plant material and environments

Details about the plant material and environments are given by van Oosterom et al. (in press b). In short, 36 two-row barley genotypes were grown across 15 environments (location × year combinations) in Syria and North Africa. The genotypes constituted both winter and spring types and the range in genotypic mean heading date within environments was about two weeks. Grain yield was obtained from 14 environments, nine in Syria and five in North Africa. The environmental mean grain yield ranged from 7 to 514 g m^{-2}.

The experimental design was a randomized complete block with three replications.

Winter plant ideotype

Early development of barley is significantly correlated with winter growth habit, winter plant colour, and cold damage (van Oosterom & Acevedo, 1992b). Since these three variables are also highly mutually correlated, early development can be represented by the first principal component of an analysis with these variables as input.

Observations on winter growth habit, winter plant colour and cold damage were made at three locations in northern Syria (Tel Hadya, Breda, and Bouider) in 1987/88. This was an extremely wet season with a mild winter (one cold spell occurred) and favourable growing conditions. No yield data were obtained from Breda. Observations were made at two-week intervals from December till early February. For each trait, between two and six observations were made per location. Growth habit was rated from 1 (erect) to 3 (prostrate), plant colour was rated from 1 (pale green) to 3 (dark green), and cold damage from 1 (no damage) to 5 (dead). Averages per genotype were calculated for each trait at each location, and the averages of the location means were used as input in the principal component analysis. For cold damage, the average of Breda and Bouider was used, since only minor damage occurred at Tel Hadya. The principal component analysis was performed on the correlation matrix of the three input variables.

The first principal component explained 79.2% of the variation present in the three input variables and was thus considered to represent winter plant ideotype (WPI) adequately. Winter type barley (prostrate winter growth habit, dark winter plant colour, cold tolerant) had high values for WPI and spring type barley low values.

Heading date

Development in spring is significantly correlated with heading date (van Oosterom & Acevedo, 1992b). Heading date was scored as the date when 50% of the ears had emerged from the boot for 50% of the plants. It was expressed as the number of days from 1 March to heading, averaged over the same three favourable environments as used for the calculation of WPI. The interaction between emergence date and heading date (van Oosterom & Acevedo, 1992c) was accounted for by the range in emergence dates from 4 November at Tel Hadya to 22 November at Breda to 13 December at Bouider.

Yield and yield response

The average performance in LY environments was calculated as the mean yield in the five lowest yielding environments, after standardization per environment to a mean yield of zero and a standard deviation of one. Yield in HY environments was calculated similarly from the six highest yielding environments. High- and low-yielding environments have contrasting genotypic yield responses (van Oosterom et al., in press b).

Yield response across environments was expressed in two ways: 1) as the first interaction principal component (IPCA1) of the additive main effects and multiplicative interaction (AMMI) model and 2) as the slope of the linear regression, after log-10 transformation, of genotypic mean yield per environment on environmental mean yield (Finlay & Wilkinson, 1963). The AMMI model has been described in detail by Gauch (1988) and Zobel et al. (1988). In the present data set, IPCA1 explained 50.4% of the genotype × environment (G×E) interaction (van Oosterom et al., in press b). In the linear regression model, the slopes accounted for 71.6% of the variation. This high percentage was due to the high contribution, after transformation, of the lowest yielding environment. However, omitting this environment did not affect the results.

A mathematical relationship exists between IPCA1 of the AMMI analysis and the linear regression slope (Gauch, 1988). Indeed, the two parameters were significantly correlated ($r=-0.77$, $P<0.001$). In our study, a high value for IPCA1 indicated a positive interaction with LY and a negative interaction with HY environments, whereas a low value for IPCA1 indicates the opposite response pattern (van Oosterom et al., in press b). A high linear regression slope indicates better performance in HY environments. The effect of WPI and heading date was assessed on both IPCA1 and the linear regression slope because 1) both parameters explain only part of the G×E interaction and 2) similar results may indicate absence of bias due to outliers.

Path analysis

The direct effect of WPI and heading date on yield and yield response was calculated from a path-coefficient analysis. We assumed WPI to have a direct effect on yield and yield response, but also an indirect effect via an effect on heading date (Figs. 1 and 2). Similarly, heading date was assumed to have a direct effect on yield and yield response plus an indirect effect via the effect of WPI. Direct and indirect effects together make up the simple correlation

$$r_{13} = P_{13} + r_{12}P_{23}$$
$$r_{23} = r_{12}P_{13} + P_{23}$$

In the first equation, r_{13} represents the simple correlation between WPI (character 1) and yield or yield response (character 3), P_{13} the direct effect of WPI on yield or yield response and $r_{12}P_{23}$ the indirect effect of WPI on yield or yield response via heading date (character 2). The direct effects were calculated as

$$P_{13} = b_1(\sigma_1/\sigma_3)$$
$$P_{23} = b_2(\sigma_2/\sigma_3)$$

with b_1 and b_2 being the parameter estimates in the multiple regression of WPI and heading date on yield or yield response, and σ_1, σ_2, and σ_3 the respective standard deviations (Li, 1975).

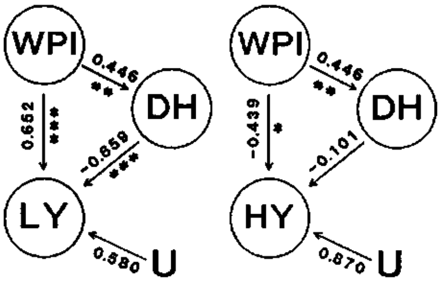

Fig. 1. Path coefficient diagram showing the relationship between winter plant ideotype (WPI), the number of days from 1 March to heading (DH) and average standardized grain yield in five low-yielding (LY) or six high-yielding (HY) Mediterranean environments. WPI and DH were obtained from three HY environments. Arrows indicate direct effects. U = unexplained residual.

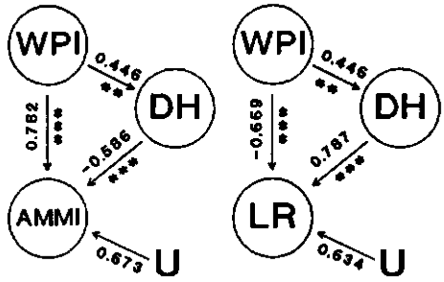

Fig. 2. Path coefficient diagram showing the relationship between winter plant ideotype (WPI), the number of days from 1 March to heading (DH) and yield response across 14 Mediterranean environments, expressed as either the first interaction principal component in the AMMI model or the slope of the linear regression (LR) model. WPI and DH were obtained from three HY environments. Arrows indicate direct effects. U = unexplained residual.

Results and Discussion

Simple correlations showed that either WPI or heading date was correlated with yield or yield response, but never both variables together (Table 1). Yield in LY environments was correlated with heading date, but yield in HY environments with WPI. Correlations with yield response gave inconsistent results; WPI was correlated only with IPCA1 of the AMMI model, while heading date was correlated only with the linear regression slope. In the multiple regressions, the correlations increased significantly, except for yield in HY environments. This increase reflects the fact that, except for yield in HY environments, the direct effects of WPI and heading date on yield or yield response were partly nullified by indirect effects of opposite sign, resulting from the correlation between WPI and heading date (Figs. 1 and 2).

In LY environments, a high value for WPI (winter types) had a significantly positive effect on yield (Fig. 1). However, this did not result in good yields if it was not combined with an appropriate heading date. In LY environments where both low winter temperatures and terminal drought stress are likely, early heading winter types are expected to perform best. This is in agreement with the conclusion of Ortiz-Ferrara et al. (1991) for bread wheat that in cold and dry Mediterranean areas genotypes with a long vegetative period and a short grain filling period are desirable. Our results suggest that selection for WPI and heading date in favourable environments can have a significant impact on yield under stress, as long as these

Table 1. Simple and multiple correlation coefficients of winter plant ideotype (WPI) and days from 1 March to heading (DH) with standardized grain yield, averaged over six high-yielding (HY) Mediterranean environments or five low-yielding (LY) environments, and with the first interaction principal component in an AMMI analysis (14 environments) and the slope of the linear regression (LR) across 14 environments.

	HY	LY	AMMI	LR
WPI[a]	-0.484 **	0.269	0.520 **	-0.318
DH[b]	-0.297	-0.568 ***	-0.237	0.489 **
WPI+DH	0.492 *	0.815 ***	0.773 ***	0.739 ***

[a]Winter types have a high value, spring types a low value. Based on observations in three favourable environments; for calculation, see text.
[b]Averaged over three favourable environments.

traits are considered together and not individually.

In HY environments, in contrast, the effect of a high value for WPI on yield was weakly negative, whereas heading date had no effect (Fig. 1). Consequently, the unexplained part of the variation in yield was large. The difference with LY environments in the effect of WPI and heading date on yield is due to the fact that HY environments are wetter (Table 2). During winter, rainfall is positively correlated with the average daily minimum temperature (van Oosterom et al., in press a); the wetter HY environments thus tend to have milder winters than LY environments, reducing the advantage of winter types. Figure 1 even suggests that spring-types are higher yielding. The higher rainfall in HY environments also reduces terminal drought stress and thus the need for early heading. This agrees with observations for spring wheat (Fischer & Maurer, 1978), pearl millet (Bidinger et al., 1987), and barley (Ceccarelli, 1987) that early heading becomes more important as terminal drought stress increases. The difference between HY and LY environments in direct effect of

Table 2. Mean and standard deviation for rainfall from October to February (O-F) and from March to April (M-A) and for grain yield (g m^{-2}) for six high-yielding (HY) and five low-yielding (LY) environments.

Environment	Rainfall (mm)		Grain yield
	O-F	M-A	(g m^{-2})
High-yielding	376 ± 71.4	111 ± 52.0	326 ± 95.4
Low-yielding	207 ± 27.2	37 ± 17.8	102 ± 57.7

WPI and heading date on yield indicates that different ideotypes are required for optimum performance in different environments. This supports the conclusion of Ceccarelli et al. (in press) that the alleles controlling yield in both environments are not entirely similar.

As a result of the differences between LY and HY environments, both WPI and heading date had a significant direct effect on yield response (Fig. 2). Path analyses for the two yield response parameters gave rather similar results. Early heading winter types, represented by Syrian landraces, had a high value for IPCA1 of the AMMI model and a low regression slope. This confirms their relatively better performance in LY environments and thus their poor response to inputs. A low yield potential of landraces was also reported by Ceccarelli et al. (1991) for barley and by Nachit & Ketata (1986) for durum wheat. Results of Fig. 2 suggest that WPI and heading date, and thus development pattern, strongly affect yield response.

The question of whether or not selection for yield in LY environments has to be done in favourable or unfavourable environments has been addressed by many papers and remains controversial. Braun et al. (in press) concluded for bread wheat that selection is preferably done in favourable environments. Ceccarelli (1987), in contrast, concluded for barley in Syria that, in order to prevent losses of germplasm adapted to stress, segregating populations must be screened as early as possible in the target environment. Nachit (1989) proposed for durum wheat in Mediterranean environments a synthetic approach, with selection in both LY and HY environments. Several disadvantages are associated with yield testing in early generations under adverse conditions. Because of limited seed availability, breeders are confined to small plots, which are less representative of farmers' fields than larger plots (Kramer et al., 1982; Spitters, 1984). In addition, harsh environments carry the risk of losing all the material in adverse seasons. If adaptation to stress can be adequately assessed in early generations under favourable conditions with a minimum risk of losing adapted germplasm, the efficiency of selection for yield under stress can be improved.

The present results suggest that a simultaneous selection for winter plant ideotype and heading date can be used as a tool for indirect selection for grain yield in LY environments and yield response. To obtain the desired variation in germplasm, targeted crosses with adapted germplasm can be made. Nachit & Ketata (1986) concluded for durum wheat that high yield in LY environments can be combined with good yield potential. Recent results obtained for barley in northern Syria (ICARDA, 1992, p. 24-30) suggest that significant differences in combining ability exist between genotypes. We propose that in early generations (F_3 - F_4), selection must focus on the identification of plant ideotypes, adapted to the LY target environments. For environments where both low winter temperatures and terminal drought stress are likely, like those in north and east Syria, this may include simultaneous selection for prostrate winter growth habit, dark winter plant colour, cold tolerance, and early heading. All these traits are easy and rapid to screen and their expression is not affected by the yield level of the selection site. The present results, where WPI and heading date were based on observations done in favourable environments, indicate that such a selection, even if done in favourable environments, can have a significant impact on yield under stress. Once a pool of adapted germplasm has been created and sufficient seed is available, yield testing can be done in LY target environments. Ceccarelli & Grando (1989) concluded for barley in Syria that empirical yield selection for LY environments is most efficient if selection is done in a representative environment using adapted germplasm. The proposed selection scheme thus combines ideotype breeding in early generations under favourable conditions with a relatively efficient empirical selection for yield under stress in later generations.

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References

Acevedo, E., 1987. Assessing crop and plant attributes for cereal improvement in water-limited Mediterranean environments. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 303-320. John Wiley & Sons Ltd., New York.

Acevedo, E., P.Q. Craufurd, R.B. Austin & P. Pérez-Marco, 1991. Traits associated with high yield in barley in low-rainfall environments. J. Agric. Sci., Camb. 116: 23-36.

Bidinger, F.R., V. Mahalakshmi & G.D.P. Rao, 1987. Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leeke]. I. Factors affecting yields under stress. Aust. J. Agric. Res. 38: 37-48.

Blum, A., G. Gozlan & J. Mayer, 1981. The manifestation of dehydration avoidance in wheat. Crop Sci. 21: 495-499.

Braun, H.-J., W.H. Pfeiffer & W.G. Pollmer, in press. Environments for selecting widely adapted spring wheats. Crop Sci.

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

Ceccarelli, S., E. Acevedo & S. Grando, 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. Euphytica 56: 169-185.

Ceccarelli, S. & S. Grando, 1989. Efficiency of empirical selection under stress conditions in barley. J. Genet. and Breed. 43: 25-31.

Ceccarelli, S., S. Grando & J. Hamblin, in press. Relationship between barley grain yield measured in low- and high-yielding environments. Euphytica.

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

Finlay, K.E. & G.N. Wilkinson, 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14: 742-754.

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

Fischer, R.A. & J.T. Wood, 1979. Drought resistance in spring wheat cultivars. III. Yield associated with morpho-physiological traits. Aust. J. Agric. Res. 30: 1001-1020.

Gauch Jr., H.G., 1988. Model selection and validation for yield trials with interaction. Biometrics 44: 705-715.

ICARDA, 1992. Cereal Improvement Program: Annual Report 1991. International Center for Agricultural Research in the Dry Areas, Aleppo, Syria, 241 pp.

Kramer, Th., J.W. van Ooyen & C.J.T. Spitters, 1982. Selection for yield in small plots of spring wheat. Euphytica 31: 549-564.

Li, C.C., 1975. Path Analysis - A Primer. The Boxwood Press, Pacific Grove, CA, USA, 347 pp.

Nachit, M.M., 1989. Moisture stress tolerance and yield stability in durum wheat (*Triticum durum* 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, Germany F.R.

Nachit, M.M. & H. Ketata, 1986. Breeding strategy for improving durum wheat in Mediterranean rainfed areas. In: Proc. of the International Wheat Conference, Rabat, Morocco, 2-5 May 1986.

Oosterom, E.J. van & E. Acevedo, 1992a. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. I. Morphological traits. Euphytica (in press).

Oosterom, E.J. van & E. Acevedo, 1992b. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. II. Apical development, leaf, and tiller appearance. Euphytica (in press).

Oosterom, E.J. van & E. Acevedo, 1992c. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. III. Plant ideotype and grain yield. Euphytica (in press).

Oosterom, E.J. van, S. Ceccarelli & J.M. Peacock, in press a. Yield response of barley to rainfall and temperature in Mediterranean environments. J. Agric. Sci., Camb.

Oosterom, E.J. van, D. Kleijn & S. Ceccarelli, in press b. Genotype × environment interactions of barley in the Mediterranean region. Crop Sci.

Ortiz-Ferrara, G., S.K. Yau & M. Assad Moussa, 1991. Identification of agronomic traits associated with yield under stress conditions. In: E. Acevedo, A.P. Conesa, P. Monneveux & J.P. Srivastava (Eds.), Physiology-Breeding of Winter Cereals for Stressed Mediterranean Environments, pp. 67-88. Proc. of the International Symposium 'Physiology-Breeding of Winter Cereals for Stressed Mediterranean Environments', Montpellier, France, 3-6 July 1989. INRA, Paris, France.

Rasmusson, D.C., 1987. An evaluation of ideotype breeding. Crop Sci. 27: 1140-1146.

Richards, R.A., 1987. Physiology and the breeding of winter-grown cereals for dry areas. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought Tolerance in Winter Cereals, pp. 133-150. John Wiley & Sons Ltd., New York.

Spitters, C.J.T. 1984. Effects of intergenotypic competition on selection. In: W. Lange, A.C. Zeven & N.G. Hogenboom (Eds.), Efficiency in Plant Breeding, pp. 13-27. Proc 10th Congr. Europ. Ass. Res. Pl. Breed., EUCARPIA. Pudoc, Wageningen, The Netherlands.

Zobel, R.W., M.J. Wright & H.G. Gauch Jr., 1988. Statistical analysis of a yield trial. Agron. J. 80: 388-393.

DISCUSSION

Summary Chapter 1 to 7

Potential traits to be used as indirect selection criteria in a breeding program were identified (chapter 1). Spring ground cover, spring growth vigour, and early heading were consistently associated with grain yield, but good performance in spring was associated with two contrasting plant ideotypes in winter: 1) erect growth habit and good early growth vigour, combined with light plant colour and cold sensitivity, and 2) prostrate growth habit and poor early growth vigour, combined with dark winter plant colour and cold tolerance. However, a similar morphology in winter did not necessarily result in a similar performance in spring. For a successful incorporation of morphological and physiological traits in a breeding program, potential traits must therefore be considered within the entire plant ideotype, rather than as individual traits.

Differences in plant ideotype were related to differences in apical development pattern (chapter 2), which in turn were related to differences in vernalization requirement and photoperiodic response. The development pattern of the apex thus was a key in the identification of plant ideotypes, adapted to Mediterranean environments.

Since dissections of the apex are too laborious in a breeding program, morphological traits, associated with development pattern, were selected in chapter 3 to assess the influence of plant ideotype on grain yield. Early heading was strongly positively correlated with grain yield under harsh conditions, but morphological traits associated with development (winter growth habit, plant colour, and cold tolerance) explained a significant additional part of the variation in grain yield in these environments.

The relation between development pattern and some growth parameters was studied in chapter 4. A rapid development during spike initiation was associated with a fast growth rate in early spring, which in turn was correlated with early heading and high yield, especially under harsh conditions. Development patterns differed in their leaf area duration, but a long duration did not result in high yield if it resulted from a long crop duration. Good yields under stress appeared to be associated with the combination of rapid crop growth rate in spring and long leaf area duration.

Yield responses across environments were discussed in chapters 5 and 6. The grain yield of a medium early heading winter barley, adapted to low winter temperatures and terminal drought stress, had a lower response to both frost and rainfall than the yield of an early heading spring barley, adapted to only terminal drought stress (chapter 5). Although average grain yields of the two entries were similar in low-yielding (LY) environments, the results suggest that the winter type will have a more stable yield across seasons. This was confirmed in chapter 6, where the results suggested that apical development pattern affects yield response. This chapter also gave evidence that for barley in the Mediterranean region high-yielding (HY) environments are not representative of LY environments. The results of chapters 1 to 6 were integrated in chapter 7. Indirect selection for pattern of development through selection, in favourable environments, for morphological and phenological traits related to development can have a marked effect on yield in unfavourable conditions. A selection procedure for barley in Mediterranean environments is proposed, where ideotype selection in favourable environments in early generations is combined with empirical yield selection under representative stress conditions in later generations.

Ideotype Identification

A first step in an ideotype breeding approach involves a definition of the target environment to identify expressions of the traits which are adapted to the target environment (Mock & Pearce, 1975). In the present study, the identification of ideotypes was based on the development pattern of the apex. Since this pattern depends on vernalization requirement and daylength response (chapter 2), ideotypes have been identified based on their adaptation to environmental conditions.

Two development patterns, both adapted to terminal drought stress but differing in their cold tolerance, were distinguished. Pattern A was characterized by rapid development throughout the life cycle. Early in the season, this was associated with good growth vigour, erect growth habit, and cold sensitivity. In spring, growth vigour and ground cover were good and heading was early. It was postulated in chapter 2 that this development pattern is very useful in Mediterranean environments where terminal drought stress is combined with a low risk of cold damage. Pattern B, in contrast, was characterized by slow development in winter, but very rapid development in spring, due to the combination of a mild vernalization requirement with an appropriate photoperiodic response. The vernalization requirement resulted in a prostrate winter growth habit, dark winter plant colour, cold resistance, but poor early vigour (chapters 1 and 2). The rapid development in spring was associated with a fast growth rate in early spring, which in turn was correlated with good growth vigour and ground cover in spring and with early heading (chapter 4). In addition, these entries have a short grain filling period. Pattern B is especially adapted to terminal drought stressed environments with low winter temperatures. This result supports the conclusion of Ortiz-Ferrara et al. (1991) for bread wheat that genotypes with a long vegetative period and a short grain filling period will be more desirable for cold and dry areas in the Mediterranean region. In addition, two development patterns were identified, which were not adapted to Mediterranean environments, due to a late heading. Pattern C was cold sensitive and did not avoid terminal drought stress, presumably because the absence of a vernalization requirement was combined with a low sensitivity to longer photoperiods (chapter 2). Pattern D, finally, had a too high vernalization requirement, delaying development to such an extent that heading was too late to avoid terminal drought stress. It was concluded in chapter 2 that a fine-tuned balance between temperature and daylength response is required to ensure optimal adaptation to the variable environmental conditions of northern Syria.

To improve the efficiency of empirical selection for grain yield, plant ideotypes have been identified for several crops, e.g., rice (Jennings, 1964), wheat (Donald, 1968), maize (Mock & Pearce, 1975), and barley (Rasmusson, 1987). The ideotypes proposed were all designed to improve yields in HY, high input environments. In traditional agriculture in the Middle East, in contrast, use of fertilizer is limited (Brown et al., 1987) and efficient use of potentially environmentally hazardous resources (fertilizer, water) is critical (Ceccarelli et al., 1992). Contrary to the ideotypes suggested before, those presented here are not aimed at increasing yield *per sé*, but rather at improving adaptation to a well-defined target environment. This is important, because use of adapted germplasm can increase selection efficiency for harsh Mediterranean environments (Ceccarelli & Grando, 1989, 1991b).

Plant Ideotype and Yield Response

In subsistence agriculture, stable yields are important (Marshall, 1987). Farmers lacking adequate financial reserves cannot afford a high risk of low or no grain yields. A first reason is that part of the grain yield is used as seed source for the next cropping season, e.g., in northern Syria (Somel et al., 1984). A second reason is the increase of prices in unfavourable years, but a decrease in case of good yields (Marshall, 1987). Since frost damage can severely affect crop yields (chapter 5), farmers are strongly biased toward avoidance of frost damage to improve yield stability (Nix, 1982). In view of a sustainable agriculture, yield stability is important, because stable yields can relieve the grazing pressure on non-arable and erodible soils (Ceccarelli et al., 1992). New cultivars therefore can only successfully be introduced, if they combine cold tolerance with a low probability of no grain yield. This shows the importance of the relation between plant ideotype and yield response.

Plant ideotype was in the present study significantly related to yield response (chapter 7). Early heading winter types had the lowest yield response to more favourable conditions (low linear regression slope), a positive interaction with LY environments and a negative interaction with HY environments. Early heading is often associated with good early growth vigour, erect growth habit, and cold sensitivity (Ceccarelli et al., 1991; chapter 7) and hence with rapid early development (chapter 2). However, Syrian landraces show that slow early development can be combined with medium early heading, if the vernalization requirement and photoperiodic response are properly balanced.

It can be argued that the low yield response of landraces in chapters 5 and 6 was obtained across a wide range of yield levels, whereas Syrian farmers are more interested in stability within LY environments. To estimate yield stability in LY environments, the coefficient of variation (CV) for grain yield in BR6, BR7, BR9, and BO6 can be calculated. These four environments had slightly different seasonal precipitation (180-245 mm), very different number of frost events after emergence (14-44), but similar grain yields (129-148 g m^{-2}). The four environments had 25 entries in common. The correlation between the CV within four LY environments and yield response across HY and LY environments was highly significant ($r=0.62$, $P=0.001$ for the linear regression slope; $r=-0.56$, $P<0.01$ for IPCA1 of the AMMI model). This suggests good agreement between stability across HY and LY environments and within LY environments.

Although plant ideotype is highly related to yield stability, it remains questionable whether one single genotype can result in maximum yield stability in environments as variable as those in Syria. Much evidence is present that landraces are mixtures of genotypes (e.g., Ceccarelli et al., 1987; van Leur et al., 1989; Weltzien, 1989). This genetic heterogeneity allows population buffering, a mechanism where different genotypes in the population are best adapted to different environmental extremes (Ceccarelli et al., 1987). This compensation and interaction between different genotypes can result in yield stability, in addition to yield stability due to individual buffering (Allard & Bradshaw, 1964). Since millennia of semi-natural selection for barley in the Middle East has not resulted in the selection of one single genotype, associated with optimum yield stability under harsh conditions, population buffering may be a valuable tool to stabilize yield (Ceccarelli et al., 1991, 1992). Indeed, evidence exists for cereals that heterogeneous populations have a higher yield stability than homozygous populations (Simmonds, 1979). A combination of several genotypes, all expressing a certain desired plant ideotype, though with small but subtle differences, may ultimately result in the best long-term yield stability. To exploit yield stability resulting from population buffering, breeding programs at ICARDA (e.g., barley and lentil) bulk progenies of single plant selections to maintain limited heterogeneity within the selected material (Ceccarelli et al., 1992).

Identification of an Optimal Selection Environment

Selection during the last decades for high yield in favourable environments has for several crops resulted in an unconscious selection for cultivars with a high environmental response (Simmonds, 1981). Experiments where simultaneous selection in HY and LY environments was done gave similar results (Jinks & Connolly, 1973, 1975; Ceccarelli & Grando, 1991a; Simmonds, 1991). Results presented in chapter 6 confirm these observations. A higher environmental responsiveness of cultivars with a higher yield potential has been reported frequently (Eberhart & Russell, 1966; Laing & Fischer, 1977; Fischer & Maurer, 1978; Brennan & Byth, 1979). Rosielle & Hamblin (1981) concluded on theoretical grounds that stress tolerance and mean yield have a negative genetic correlation if the genetic variance under stress is less than under non-stress conditions.

Notwithstanding this agreement in results, the interpretation has been contradictory. Ceccarelli & Grando (1989) and Simmonds (1981, 1991) conclude that selection for high yield under stress has to be done in unfavourable environments. Ceccarelli et al. (in press) reported a negative association between the genetic correlation coefficients between yields in LY and HY environments and yield in the HY environment. Pfeiffer (1988) and recently Braun et al. (in press), in contrast, concluded for bread wheat that favourable environments are more efficient than unfavourable environments in selecting widely adapted genotypes which combine yield potential with tolerance to stress. Their conclusion is based on the observation that cultivars with a higher yield potential maintain their yield advantage under stress, and are even in the lowest yielding environments on average not worse than varieties with a better yield stability (e.g., Laing & Fischer, 1977). Nachit & Ouassou (1988) and Nachit (1989) proposed for durum wheat a synthetic approach in regions where favourable and unfavourable seasons are alternating. The controversy in the choice of the selection site is due to a difference in the level of stress (severe or mild) and to a different selection aim.

Ceccarelli (1989) defined for barley in Syria the upper limit for stress environments at a yield level of 2.5 ton ha^{-1}. As pointed out by the same author, the stress environments in the studies of Rajaram et al. (1984) and Pfeiffer (1988) yielded around 4 ton ha^{-1}, well within the range of non-stress environments according to Ceccarelli's (1989) definition. Fischer & Maurer (1978) concluded that modern dwarf bread wheats, bred under irrigation, performed better than old tall cultivars which are mainly bred under rainfed conditions. Indeed, under favourable conditions, dwarf cultivars (n=23) on average outyielded the tall cultivars (n=8) (5540 kg ha^{-1} versus 4470 kg ha^{-1}), whereas under unfavourable conditions average yields were nearly similar (2320 kg ha^{-1} versus 2250 kg ha^{-1}). However, the average yield of bread wheat in ICARDA's on-farm verification trials in Syria during the period 1982/83-1990/91 (66 experiments) was only 1796 kg ha^{-1} (ICARDA, 1992). This average had even an upward bias due to the extremely wet 1987/88 season, when the average yield was 3493 kg ha^{-1} (the average yield in the second-highest yielding season was 2115 kg ha^{-1}); exclusion of 1987/88 reduced the average yield to 1527 kg ha^{-1}. Extrapolation of the data of Fischer & Maurer (1978) to those yield levels suggests that the old taller cultivars are expected to give higher average yields than the modern dwarf ones. A reappraisal of these data within the context of Syrian agriculture will thus lead to the same conclusion as Ceccarelli & Grando (1989, 1991a) for barley in Syria, namely that development of cultivars for environments yielding on average 1-2 ton ha^{-1} has to be done under LY conditions.

It has been argued that selection for yield potential can be important for LY environments, because high yields in favourable years contribute most to the long-term average yield (Richards, 1982). If stress is unpredictable and favourable and unfavourable seasons occur both, as is the case for durum wheat in the Mediterranean region, selection for yield potential is useful. However, barley is in the Mediterranean region grown in the most unfavourable areas, where the probability of high yields is small. At Khanassar, a site comparable to Bouider, the driest experimental site used, the probability of seasonal rainfall exceeding 285 mm is around 5% (Dennett et al., 1984). According to chapter 5, this suggests that, based on rainfall only, the probability of yields exceeding 2 ton ha^{-1} is about 5% at that site; inclusion of the number of frost events will reduce this probability. High yields are thus unlikely, but a crop failure, in terms of grain yield, not. However, grain yield in even the worst seasons is very important. Farmers thus accept low risk levels, even if this will reduce the long-term average yield (Nix, 1982). Ceccarelli & Grando (1991a), using a safety-first index, showed that the probability of no grain yield was between 1.8 and 2.7 times higher for genotypes selected for grain yield in HY environments, compared with genotypes selected for grain yield in LY environments. The strong association between plant ideotype and yield response (chapter 7) makes it unlikely that factors contributing to plant survival in the harshest environments will favour higher yields in favourable environments. The decision to select for either yield stability or yield potential will hence not only affect the choice of the targeted plant ideotype, but also of the required selection environment.

Barley production in areas where the expected grain yield is around 1 ton ha^{-1} may be irrelevant to the production of food on a world scale. However, only very little barley appears on the world market, and the majority is consumed locally (Harlan, 1976). This is obvious for northern Syria, where grazing is a common farming practice (Nordblom, 1983a,b; Yau et al., 1989). Khaldi (1984) concluded that the gap between production and requirements of coarse grains, mainly barley, is expected to increase rapidly in West Asia and North Africa, and may reach 36 million tons (2/3 of the region's gap in staple food) in the year 2000. Yield stability, in terms of grain as well as biomass, is a key to a sustainable agriculture in a region where much barley is grown by subsistence farmers.

Impact of Results on a Breeding Program

The impact of plant breeding on agriculture in harsh environments has been very modest during the last decades. A possible explanation for this lack of success is the attempt by many breeders to introduce cultivars with a high yield potential into these farming systems, ignoring the trade-off between yield potential and stability (Ceccarelli & Grando, 1991b). In addition, it should be realized that the major gains in productivity during the last century in HY environments have been achieved by increasing grain yield through increasing harvest index, rather than increasing total biomass (Austin et al., 1989). In subsistence agriculture, where the total biomass is important (Nordblom, 1983a,b), changes in dry matter distribution alone will have only a minor impact on agriculture. The results of the previous chapters, however, offer scope for yield improvements in those environments.

A selection procedure for LY environments is suggested, where ideotype breeding in early generations under favourable conditions (to obtain a pool of adapted germplasm) and empirical yield selection in later generations under unfavourable conditions complement each other to achieve maximum breeding efficiency. Within the adapted gene pool, a further selection for traits desirable under drought (e.g., plant height) can be done. If a mixture of genotypes is desired, elite lines with small but subtle differences in morphology can be pooled to improve yield stability of the "cultivar"; avoidance of genetic drift in this mixture, however, may be a concern. The ideotype breeding is based on the observation that adaptation to stress is related to development pattern. Although the present results are based on a case study of barley in the Mediterranean region, the proposed selection procedure may have wider application to other crops and environments. Essential is, prior to yield testing, the identification of a plant ideotype that is specifically adapted to the target environment. Locally adapted germplasm, e.g., landraces, may be valuable in developing such a desired plant ideotype.

References

Allard, R.W.& A.D. Bradshaw, 1964. Implications of genotype-environment interaction in applied plant breeding. Crop Sci. 4: 503-508.

Austin, R.B., M.A. Ford & C.L. Morgan, 1989. Genetic improvement in the yield of winter wheat: a further evaluation. J. Agric. Sci., Camb. 112: 295-301.

Braun, H.-J., W.H. Pfeiffer & W.G. Pollmer, in press. Environments for selecting widely adapted spring wheats. Crop Sci.

Brennan, P.S. & D.E. Byth, 1979. Genotype × environmental interactions for wheat yields and selection for widely adapted wheat genotypes. Aust. J. Agric. Res. 30: 221-232.

Brown, S.C., J.D.H. Keatinge, P.J. Gregory & P.J.M. Cooper, 1987. Effects of fertilizer, variety and location on barley production under rainfed conditions in northern Syria. 1. Root and shoot growth. Field Crops Res. 16: 53-66.

Ceccarelli, S., 1989. Wide adaptation: how wide? Euphytica 40: 197-205.

Ceccarelli, S., E. Acevedo & S. Grando, 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. Euphytica 56: 169-185.

Ceccarelli, S. & S. Grando, 1989. Efficiency of empirical selection under stress conditions in barley. J. Genet. and Breed. 43: 25-31.

Ceccarelli, S. & S. Grando, 1991a. Selection environment and environmental sensitivity in barley. Euphytica 57: 157-167.

Ceccarelli, S. & S. Grando, 1991b. Environment of selection and type of germplasm in barley breeding for low-yielding conditions. Euphytica 57: 207-219.

Ceccarelli, S., S. Grando & J. Hamblin, in press. Relationship between barley grain yield measured in low- and high-yielding environments. Euphytica.

Ceccarelli, S., S. Grando & J.A.G. van Leur, 1987. Genetic diversity in barley landraces from Syria and Jordan. Euphytica 36: 389-405.

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

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

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

Eberhart, S.A. & W.A. Russell, 1966. Stability parameters for comparing varieties. Crop Sci. 6: 36-40.

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

Harlan, J.R., 1976. Barley. In: N.W. Simmonds (Ed.), Evolution of Crop Plants, pp. 93-98. Longman, London & New York.

ICARDA, 1992. Cereal Improvement Program: Annual Report 1991. International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria, 241 pp.

Jennings, P.R., 1964. Plant type as a rice breeding objective. Crop Sci. 4: 13-15.

Jinks, J.L. and V. Connolly, 1973. Selection for specific and general response to environmental differences. Heredity 30: 33-40.

Jinks, J.L. and V. Connolly, 1975. Determination of the environmental sensitivity of selection lines by the selection environment. Heredity 34: 401-406.

Khaldi, N., 1984. Evolving food gaps in the Middle East/North Africa: Prospects and policy implications. IFPRI Research Report 47, Washington D.C.

Laing, D.R. & R.A. Fischer, 1977. Adaptation of semi-dwarf wheat cultivars to rainfed conditions.

Euphytica 26: 129-139.
Leur, J.A.G. van, S. Ceccarelli & S. Grando, 1989. Diversity for disease resistance in barley landraces from Syria and Jordan. Plant Breeding 103: 324-335.
Marshall, D.R., 1987. Australian plant breeding strategies for rainfed areas. In: J.P. Srivastava, E. Porceddu, E. Acevedo & S. Varma (Eds.), Drought tolerance in winter cereals, pp. 89-99. John Wiley & Sons Ltd., New York.
Mock, J.J. & R.B. Pearce, 1975. An ideotype of maize. Euphytica 24: 613-623.
Nachit, M.M., 1989. Moisture stress tolerance and yield stability in durum wheat (*Triticum durum* 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, Germany F.R. Th. Mann Publishers, Gelsenkirchen, Germany F.R.
Nachit, M.M. & A. Ouassou, 1988. Association of yield potential, drought tolerance and stability of yield in *Triticum durum* L. var. *durum*. In: Proceedings of the 7th International Wheat Genetics Symposium, pp. 867-870. Cambridge, UK, 10-13 July 1988. Institute of Plant Science Research, Cambridge, UK.
Nix, H.A., 1982. Aspects of drought from an agroclimatic perspective. In: Drought Resistance in Crops with Emphasis on Rice, pp. 3-15. IRRI, Los Banos, The Philippines.
Nordblom, T.L., 1983a. Livestock - crop interactions. The case of green stage grazing. ICARDA Disc. Paper No. 9, Aleppo, Syria, 37 pp.
Nordblom, T.L., 1983b. Livestock - crop interactions. The decision to harvest or to graze a mature grain crop. ICARDA Disc. Paper No. 10, Aleppo, Syria, 21 pp.
Ortiz-Ferrara, G., S.K. Yau & M. Assad Moussa, 1991. Identification of agronomic traits associated with yield under stress conditions. In: E. Acevedo, A.P. Conesa, P. Monneveux & J.P. Srivastava (Eds.), Physiology-Breeding of Winter Cereals for Stressed Mediterranean Environments. Proc. of the International Symposium 'Physiology-Breeding of Winter Cereals for Stressed Mediterranean Environments', Montpellier, France, 3-6 July 1989, pp. 67-88. INRA, Paris, France.
Pfeiffer, W.H., 1988. Drought tolerance in bread wheat - Analysis of yield improvement over the years in CIMMYT germplasm. In: A.R. Klatt (Ed.), Wheat Production Constraints in Tropical Environments, pp. 274-284. CIMMYT, Mexico DF, Mexico.
Rajaram, S., B. Skovmand & B.C. Curtis, 1984. Philosophy and methodology of an international wheat breeding program. In: J.P. Gustafson (Ed.), Gene Manipulation in Plant Improvement, pp. 33-60. Plenum Press, New York.
Rasmusson, D.C., 1987. An evaluation of ideotype breeding. Crop Sci. 27: 1140-1146.
Richards, R.A., 1982. Breeding and selecting for drought resistance in wheat. In: Drought Resistance in Crops with Emphasis on Rice, pp. 303-316. IRRI, Los Banos, The Philippines.
Rosielle, A.A. & J. Hamblin, 1981. Theoretical aspects of selection for yield in stress and non-stress environments. Crop Sci. 21: 943-946.
Simmonds, N.W., 1979. Principles of Crop Improvement. Longman, London.
Simmonds, N.W., 1981. Genotype (G), environment (*E*) and *GE* components of crop yields. Expl. Agric. 17: 355-362.
Simmonds, N.W., 1991. Selection for local adaptation in a plant breeding programme. Theor. Appl. Genet. 82: 363-367.
Somel, K., A. Mazid & M. Hallajian, 1984. Survey of barley producers; northern Syria 1981/1982. Volume III, Descriptive statistics. ICARDA Research Report No. 12, Aleppo, Syria, 75 pp.
Weltzien, E., 1989. Differentiation among barley landrace populations from the Near East. Euphytica 43: 29-39.
Yau, S.K., M.S. Mekni, I. Naji & J.P. Srivastava, 1989. Effects of green-stage grazing on rainfed barley in northern Syria. II. Yield and economic returns. Expl. Agric. 25: 501-507.

Summary
Research Objectives

Barley is in Syria the dominant crop in areas receiving less than 300 mm annual precipitation. Grain yield is often below 1 ton ha^{-1}, and is reduced by low temperatures in winter and terminal drought stress in spring. Variation in the timing and intensity of the stresses, however, can cause considerable fluctuations in yield between both locations and seasons. For environments where low yields are predictable, but not the stresses causing these low yields, selection for a stable yield across years and a reduced risk of no grain yield, is more important than selection for yield potential. Breeding targeted at these environments, however, is hampered by genotype × environment interactions.

This thesis had several aims. The first was the identification of a combination of morphological and physiological traits, or a plant ideotype, related to adaptation of barley to environments where both low temperatures early in the season and high temperatures and drought during grain filling (terminal drought) are likely. A next step was assessing the effect of plant ideotype on yield in contrasting environments and the identification of the most appropriate environment to select for plant ideotype and yield under stress. These results together culminated in the development of a selection procedure for breeding programs targeted at harsh Mediterranean environments.

Results

Adaptation of barley to Mediterranean environments depends on the development pattern of the apex. Within a group of 36 cultivars, four contrasting development patterns were distinguished, of which two were adapted. The first pattern constituted early heading spring types: they did not have a vernalization requirement, were cold sensitive, but avoided terminal drought stress. This pattern is especially adapted to Mediterranean environments with mild winters and terminal drought, like those in Jordan and North Africa. The second pattern represented medium early heading winter types. They had a mild vernalization requirement, a very rapid development in spring and are especially adapted to Mediterranean environments where both cold winters and terminal drought are likely, e.g., those in northern Syria. Two other development patterns, late heading spring types and late heading winter types, are unadapted to Mediterranean environments, because of an inadequate avoidance of terminal drought stress: the former group had a too slow development in spring, whereas in the second group development was delayed too much by a too high vernalization requirement. The development pattern of the apex thus depended on the vernalization requirement in winter and the response to photoperiod in spring.

To select indirectly for development pattern, morphological traits were identified, which are related to the rate of development in winter or spring. In winter, a slow development was strongly associated with a plant ideotype, which could be described by a prostrate growth habit, dark plant colour, and cold tolerance. This ideotype was characteristic of winter types. In spring, a rapid development resulted in an early heading. Selection for these traits together thus enabled selection for an appropriate development pattern. The results indicate that it is the combination of traits, rather than an individual trait, which determines adaptation of barley to Mediterranean environments.

Plant ideotype in winter and heading date both influence yield. Cold tolerance and a prostrate growth habit and dark plant colour in winter had a positive effect on yield in low-yielding (LY) environments, but a weakly negative effect in high-yielding (HY) environments. Early heading was very important in LY environments, but of minor importance in HY environments, apparently because terminal drought stress was less important in those environments. Early heading winter types thus had the highest yield in LY environments. This was caused by a fast crop growth rate in early spring, combined with a long green leaf area duration. In addition, the yield of early heading winter types was little affected by frost, what improved yield stability. The differences between HY and LY environments, concerning the effect of plant ideotype and heading date on yield, show that HY environments are not representative of LY environments. Selection for yield in HY environments has the risk of selection for a plant ideotype which is not adapted to LY environments.

Implications for Plant Breeding

Yield selection in early generations is difficult, especially under harsh conditions. Based on the results presented in this thesis, a selection procedure can be proposed, where ideotype breeding and empirical yield selection complement each other. In early generations (F_3 - F_4), selection must focus on the identification of ideotypes which are adapted to the LY target environment. This can be done in HY environments by selection for plant ideotype in winter and heading date in spring. In later generations, the adapted material can be tested for yield in the LY target environment; in addition, selection for other desirable traits can be done. Since empirical selection for yield in LY Mediterranean environments is most efficient if selection is carried out in representative LY environments, using adapted germplasm, the proposed combination of ideotype breeding and empirical yield selection seems to be efficient: it combines a low risk of losses of adapted germplasm in early generations with a relatively efficient empirical selection in later generations.

The proposed selection procedure is easily applicable and can be used for many crops and types of stress environments. Essential is, before yield testing, the identification of a plant ideotype which is adapted to the dominant stresses in the LY target environment. Because landraces are often adapted to the local environment, landraces may be very useful in this identification.

Samenvatting
Doel van het Onderzoek

Gerst is in Syriё het belangrijkste gewas in gebieden met minder dan 300 mm neerslag per jaar. De korrel opbrengst is vaak minder dan 1 ton ha^{-1}, en wordt beperkt door lage temperaturen in de winter en terminale droogte stress in het voorjaar. Variatie in het moment waarop en de intensiteit waarmee stress optreedt, kan echter aanzienlijke variatie in opbrengst veroorzaken, zowel tussen locaties als seizoenen. Voor milieu's waar lage opbrengsten voorspelbaar zijn, maar niet de stress factoren die tot die lage opbrengsten leiden, is selectie voor een stabiele opbrengst over jaren en een verminderd risico van een gewas zonder korrel opbrengst belangrijker dan selectie voor opbrengst potentie. Veredeling voor zulke milieu's wordt echter bemoeilijkt door genotype × milieu interacties.

Dit proefschrift had verschillende doelen. Het eerste was de identificatie van een combinatie van morfologische en fysiologische eigenschappen, ofwel een plant ideotype, gerelateerd aan aanpassing van gerst aan teelt gebieden waar zowel lage temperaturen vroeg in het seizoen als hoge temperaturen en droogte gedurende de korrel vulling (terminale droogte) voor kunnen komen. Een volgende stap was het vaststellen van het effect van plant ideotype op opbrengst in contrasterende milieu's en het identificeren van het meest geschikte milieu om voor plant ideotype en opbrengst onder stress te selecteren. Deze resultaten samen leidden tenslotte tot de ontwikkeling van een selectie procedure die is gericht op ongunstige Mediterrane milieu's.

Resultaten

Aanpassing van gerst aan Mediterrane milieu's hangt af van het ontwikkelings patroon van het groeipunt. Binnen een groep van 36 gerst cultivars werden vier contrasterende ontwikkelings patronen onderscheiden, waarvan er twee waren aangepast. Het eerste patroon omvatte vroeg in aar komende zomer types: deze hadden geen vernalizatie behoefte, waren koude gevoelig, maar vermijdden terminale droogte. Dit patroon is vooral aangepast aan Mediterrane milieu's met milde winters en terminale droogte, zoals die in Jordaniё en Noord Afrika. Het tweede patroon omvatte vroeg in aar komende winter types. Deze hadden een milde vernalizatie behoefte, een erg snelle ontwikkeling in het voorjaar, en zijn vooral aangepast aan Mediterrane milieu's waar koude winters en terminale droogte allebei voor kunnen komen, zoals die in noord Syriё. Twee andere ontwikkelings patronen, laat bloeiende zomer types en laat bloeiende winter types, zijn niet aangepast aan Mediterrane milieu's, omdat ze terminale droogte stress onvoldoende vermijden: de eerste groep had een te langzame ontwikkeling in het voorjaar, terwijl in de tweede groep de ontwikkeling te veel werd vertraagd door een te sterke vernalizatie behoefte. Het ontwikkelings patroon van het groeipunt hangt dus af van de vernalizatie behoefte in de winter en de daglengte reactie in het voorjaar.

Om indirect voor ontwikkelings patroon te kunnen selecteren, werden morfologische eigenschappen onderscheiden, die zijn gerelateerd aan de snelheid van ontwikkeling in de winter of het voorjaar. In de winter was een langzame ontwikkeling sterk geassocieerd met een plant ideotype, dat kon worden beschreven met een kruipende groeiwijze, een donker groene plant kleur, en koude tolerantie. Dit ideotype was karakteristiek voor winter types. In het voorjaar resulteerde een vlotte ontwikkeling in een vroeg in aar komen. Selectie voor deze eigenschappen samen maakt dus een selectie voor het juiste ontwikkelings patroon mogelijk. De resultaten laten zien dat het vooral de combinatie van eigenschappen is, en niet zozeer een individuele eigenschap, die de aanpassing van gerst aan Mediterrane milieu's bepaalt.

Plant ideotype in de winter en datum van in aar komen hebben allebei invloed op de opbrengst. Koude tolerantie en een kruipende groeiwijze en donker groene plant kleur in de winter hadden een positief effect op opbrengst in laag-opbrengende (LO) milieu's, maar een zwak negatief effect in hoog-opbrengende (HO) milieu's. Vroeg in aar komen was erg belangrijk in LO milieu's, maar van weinig belang in HO milieu's, kennelijk omdat terminale droogte stress daar minder belangrijk was. Vroeg in aar komende winter types hadden dus de hoogste opbrengst in LO milieu's. Dit was het gevolg van een vlotte groei snelheid vroeg in het voorjaar, gecombineerd met de aanwezigheid van een groot groen blad oppervlak gedurende langere tijd. De opbrengst van vroeg in aar komende winter types had bovendien relatief weinig te lijden van vorst, wat de opbrengst stabiliteit bevorderde. De verschillen tussen LO en HO milieu's, betreffende het effect van plant ideotype en datum van in aar komen op opbrengst, laten zien dat HO milieu's niet representatief zijn voor LO milieu's. Selectie voor opbrengst in HO milieu's heeft het risico van selectie van een plant ideotype dat niet is aangepast aan LO milieu's.

Gevolgen voor Plantenveredeling

Opbrengst selectie in vroege generaties is moeilijk, vooral onder ongunstige omstandigheden. Gebaseerd op de resultaten die in dit proefschrift zijn gepresenteerd, kan een selectie procedure worden voorgesteld, waar ideotype selectie en empirische opbrengst selectie elkaar aanvullen. In vroege generaties (F_3 - F_4) moet selectie worden gericht op de identificatie van ideotypes die zijn aangepast aan het beoogde LO milieu. Dit kan in HO milieu's worden gedaan, door selectie voor plant ideotype in de winter en datum van in aar komen in het voorjaar. In latere generaties kan het aangepaste materiaal worden getest voor opbrengst in het beoogde LO milieu, terwijl dan bovendien voor andere gewenste eigenschappen kan worden geselecteerd. Aangezien empirische selectie voor opbrengst in LO Mediterrane milieu's het meest efficiënt is als de selectie wordt gedaan in representatieve LO milieu's, gebruik makend van aangepast materiaal, lijkt de voorgestelde combinatie van ideotype selectie en empirische opbrengst selectie erg efficiënt: het combineert een laag risico van verlies van aangepast materiaal in vroege generaties met een relatief efficiënte empirische selectie in latere generaties.

De voorgestelde selectie procedure is makkelijk toepasbaar en kan voor diverse gewassen en types stress milieu's worden gebruikt. Essentieel is, voorafgaand aan opbrengst proeven, de identificatie van een plant ideotype dat is aangepast aan de meest voorkomende stress in het beoogde LO milieu. Omdat landrassen vaak aan het locale milieu zijn aangepast, kunnen landrassen erg bruikbaar zijn bij deze identificatie.

Curriculum Vitae

Erik van Oosterom werd op 30 januari 1962 in Velp, Gelderland, geboren. Nadat hij in 1980 het VWO diploma aan het Christelijk Lyceum te Arnhem had behaald, ging hij in Wageningen plantenveredeling studeren. De Kandidaats fase werd in 1984 *cum laude* afgerond. De praktijktijd bracht hij door op het Rijksstation voor Plantenveredeling in Merelbeke (België), waar hij vier maanden in het grassen veredelings programma meewerkte, en op het Kweekbedrijf Zelder B.V. te Ottersum, waar hij drie maanden in het blauwmaanzaad veredelings programma werkte. In de Doctoraal fase was het hoofdvak plantenveredeling. Hij deed een studie naar de invloed van het selectie milieu op de opbrengst eigenschappen van de geselecteerde populatie bij zomergerst, en een literatuur onderzoek naar de bruikbaarheid van primitieve knoldragende aardappels als bron van genetische variatie in de aardappel veredeling. Als verzwaard bijvak deed hij fytopathologie, waarbij hij onderzoek deed naar de fysiologische achtergrond van de waardplant-pathogeen relatie bij de tomaat-*Cladosporium fulvum* interactie. Een tweede bijvak deed hij op de vakgroep landbouwplantenteelt, waar hij een gewas analyse deed aan twee morfine-rijke blauwmaanzaad selecties. Het Doctoraal examen werd in juni 1987 *cum laude* behaald.

In juli 1987 begon hij met zijn promotie onderzoek, dat gesubsidieerd werd door de Stichting voor Wetenschappelijk Onderzoek van de Tropen (WOTRO). Het onderzoek werd uitgevoerd op het International Center for Agricultural Research in the Dry Areas (ICARDA) in Syrië. In september 1987 vertrok hij naar het ICARDA en bleef daar tot december 1992 om het proefschrift af te ronden.