Wheat Special Report No. 25

Adaptation of Wheat to the Canopy Environment:

Physiological Evidence that Selection for Vigor or Random Selection May Reduce the Frequency of High-Yielding Genotypes

M.P. Reynolds, E. Acevedo,
K.D. Sayre, and R.A. Fischer

November 1993

CENTRO INTERNACIONAL DE MEJORAMIENTO DE MAIZ Y TRIGO
INTERNATIONAL MAIZE AND WHEAT IMPROVEMENT CENTER
Lisboa 27 Apartado Postal 6-641 06600 México, D.F. México

Wheat Special Report No. 25

Adaptation of Wheat to the Canopy Environment:

Physiological Evidence that Selection for Vigor or Random Selection May Reduce the Frequency of High-Yielding Genotypes

M.P. Reynolds, E. Acevedo,
K.D. Sayre, and R.A. Fischer

November 1993

Contents

iii Preface

1 Introduction

2 Materials and Methods
2 Manipulations in interplant competition
2 Measurements to explore mechanisms involved in interplant competition

4 Results
4 Manipulations in interplant competition
7 Experiments to explore mechanisms affecting interplant competition

7 Discussion
7 The interaction between genotype and interplant competition
10 Possible mechanisms affecting interplant competition
12 Implications for breeders

14 References

16 List of Wheat Special Reports

Note on Citing this Wheat Special Report
The information in this wheat special report is shared with the understanding that it is not published in the sense of a refereed journal. Therefore, this report should not be cited in other publications without the specific consent of E. Acevedo, CMP Subprogram Leader.

Correct Citation: Reynolds, M.P., E. Acevedo, K.D. Sayre, and R.A. Fischer. 1993. Adaptation of Wheat to the Canopy Environment: Physiological Evidence that Selection for Vigor or Random Selection May Reduce the Frequency of High-Yielding Genoptypes. Special Report No. 25. Mexico, D.F.: CIMMYT.

ISSN: 0187-7787
ISBN: 968-6923-15-2
AGROVOC descriptors: Wheats, canopy, adaptation, genotype environment interaction, yield factors, environmental factors.
AGRIS category codes: F30, F01, F60.
Dewey decimal classification: 631.523.

Preface

Increasing the potential yield of wheat is a major thrust of CIMMYT's Wheat Program. Farmer's wheat yields are linearly related to the yield potential of new varieties. At the same time, breeders should ideally be able to assess a new line's yield potential as early as possible after a cross has been made. Unfortunately, present breeding techniques do not allow confident assessment of grain yield in early generations.

The work covered in this Wheat Special Report is a contribution to our understanding of the factors limiting grain yield in wheat. It is also a test of Donald's ideas of adaptation to communal growth. We hope that the results and discussion shed some light on our main objectives, i.e., selecting high yielding wheats in early generations through a better physiological understanding and increasing the yield potential of wheat.

Edmundo Acevedo
Leader
Crop Management and Physiology
CIMMYT Wheat Program

Introduction

Spring wheat yields, even in favorable growing environments, fall well short of record yields (Boyer 1982). This would suggest that despite the gains in yield potential made by breeding, the crop is not optimally adapted to most of its growing environments, even under the best management. While it is believed by some that the limits of yield potential have been reached, others suggest that yield improvements will follow as we gain a more comprehensive understanding of the mechanisms limiting productivity (Evans 1991).

To understand how growth is determined in a field crop, it is necessary to consider its interaction with the micro- and the macro-environments. The micro-environment is a function of the interactions among individual plants in the crop community. In a typical crop stand, the relationship between plants will modify the availability of the key growth factors. For example, canopy architecture will modify the spatial distribution of incident radiation (Hawkins 1982). The intensity of root competition may effect the availability of water (Acevedo 1979), and there is evidence that plant density may affect the temporal availability of nitrogen, at least when it is a limiting factor (Reynolds et al. 1993).

The idea that yield is determined by the interaction between genotype and the communal way in which crops are cultivated was first discussed by Donald (1963). Developing this theme he hypothesized that one route to yield potential would be to have a "communal" ideotype (Donald 1968, 1981), defined as a sparsely tillering plant, with small erect leaves, performing relatively poorly at wide spacing. A crucial point of the hypothesis is that a "competitive" ideotype, e.g., one with taller stems and large overshadowing leaves, and not the communal ideotype, will be favored by both natural selection and breeder selection in segregating populations, while the communal ideotype will tend to be overlooked. Since that time, a number of experiments have tried to verify this ideotype in wheat, with emphasis on the morphological traits of the ideotype such as erect leaf angles (Araus et al. 1993, Trenbath and Angus 1975) and low tillering (Blum and Kraljevic-Balalic 1980, Saini and Nandi 1979). While these approaches have not endorsed the communal ideotype model under optimal conditions, experiments under water stress or in other crop species have lent support to the model (Sedgely 1991). However, such immediately obvious morphological traits are not the only ones that would be consistent with a communal ideotype. A lower investment in root growth, for example, would be consistent with the communal ideotype since it represents a less competitive growth habit, and favors a higher harvest index, assuming water and nutrient uptake is not limited. Similarly, the communal ideotype may be better adapted to the light environment of a crop canopy than the competitive ideotype whose growth habit is suited to intercepting its neighbors' potential light source. Neither of these traits are immediately apparent when observing a genotype.

This study was designed to examine the genetic variability that exists in spring wheats with respect to adaptation to the environment of the crop community, both above ground in the leaf canopy, and below ground in the rhizoshere. By manipulations of the crop canopy in field-grown plots, the level of interplant competition in the root zone and in the leaf canopy was decreased at different stages of development. By observing the interaction between genotype and changes in interplant competition for light and soil resources, we hoped to gain understanding on how yield improvement may have been--and may in the future be--related to the adaptation of genotypes to the levels of these resources in the crop community.

Materials and Methods

Manipulations in interplant competition

Four field experiments and one greenhouse experiment were conducted between June 1989 and April 1992 with CIMMYT spring bread wheat varieties, in two wheat growing environments in Mexico. Genotypes and environmental conditions are summarized in **Tables 1** and **2**. The first field experiment and the greenhouse experiment were conducted in central Mexico in a rainfed, temperate, spring wheat growing environment at CIMMYT's El Batan experiment station, at 19° 31' N; 98° 50' W, and 2249 masl. Three subsequent field experiments were conducted in northwestern Mexico in an irrigated, temperate, spring wheat growing environment at the CIANO (Centro de Investigaciones Agricolas del Noroeste) experimental station, at 27° 20' N; 109° 54' W; and 38 masl.

Treatments for reducing interplant light and root competition were applied in crop canopies using a replicated strip plot design. Wheat genotypes were sown as eight-row plots, 12 m long, with 20 cm between rows. At the requisite stage of development, treatments were applied as follows: reduced interplant competition for light (light treatment) was realized by bending the outer rows of the plot away from the inner two rows, allowing light to penetrate directly to the base of the remaining upright part of the canopy (the two border rows of the plot were uprooted first to remove any obstruction to bending). The remaining outer rows, which were held at an inclination away from the inner rows with cords, continued to grow to maturity. The treatment for reducing interplant root competition simultaneously with interplant competition for light (root/light treatment) was achieved simply by uprooting all but the inner 2 rows of the 8-row plot. All treatments were continuous until maturity.

Experimental units were 4 to 6 m in length. In experiment 1, the light treatment was applied at flag leaf ligule emergence (FLLE) for 20 genotypes. The light treatment was also applied to six of the genotypes at two successively later stages of development, anthesis, and 2 weeks after anthesis. The root/light treatment was started at FLLE for 14 genotypes. In experiment 2, the light and root/light treatments were applied at FLLE, and the light treatment 1 week after anthesis in all eight genotypes. In experiment 3, the light and root/light treatments were applied at FLLE in all 20 genotypes. In experiment 4, there was only 1 treatment--the root/light treatment applied at FLLE. In each experiment, control treatments consisted of undisturbed eight-row plots, where the inner six rows were used to estimate control yields. For all field experiments, management was optimal in terms of fertility, irrigation, and weed, pest, and disease control except when stated otherwise. Fertilizer was applied basally at the rates of 250:50:0 kg N:P:K/ha in the form of urea and triple super phosphate, respectively. All experiments were conducted on land that had previously supported a legume crop. Plots were irrigated when available soil water levels were 50% depleted, as determined by porometer readings at a depth of 40 cm (soil moisture probe, Soilmoisture Equipment Corp., Santa Barbara, CA)

Measurements to explore mechanisms involved in interplant competition

Additional measurements taken during the cycle in the experimental control plots included: 1) at FLLE, biomass and number of shoots/m^{2}; and 2) after heading, canopy light interception, canopy temperature depression, plant height, and dates of anthesis and maturity. Experiment 3 had a split plot factorial design whereby interplant competition treatments were nested within main plots differing in water management and fertility. There were two main plot treatments, a control (i.e., the optimal management described above), and a supraoptimal management treatment for fertilizer and irrigations. In terms of fertility, the supraoptimal treatments received a top dressing of 100:25:25 N:P:K/ha at

Table 1. Approximate mean maximum and minimum temperatures, and number of sun hours/day, for the growing cycles of four field experiments.

Expt.	Dates	Location	Tmax (°C)	Tmin (°C)	Sun h
1)	04/89-09/89	El Batan	24.1	10.2	6.0
2)	12/89-04/90	Obregon	25.0	8.0	-
3)	12/90-04/91	Obregon	25.5	10.0	8.1
4)	12/91-04/92	Obregon	24.5	11.0	7.1

Table 2. CIMMYT varieties and lines used in the experiments.

Genotype	Expt 1	Expt 2	Expt 3	Expt 4	Green-house
Aga/4*[illegible]r70//...				+	+
Atilla'S'			+	+	+
Atilla'S'			+		
Carrizo 89			+	+	+
Ciano 79	+	+	+	+	+
Ciano/Prl			+		
Cumpas 88		+	+		
Genaro 81	+		+		
Inia 66	+				
Hahn*2Prl'S'		+	+		
Jupateco	+				
Nacozari	+	+	+	+	+
Nainari 60	+				
Oasis 86				+	+
Opata 85	+		+		
Papago 76	+				
Parula'S'	+		+		
Pavon 76	+		+		
Penjamo 62	+		+		
Pitic 66	+		+	+	+
Seri 82	+	+	+	+	+
Ser*3//buc/bjy			+	+	+
Siete Cerros	+	+	+	+	+
Sonalika 68	+				
Sonora 64	+				
Super Kauz 88	+	+	+	+	+
Temporalera	+				
Tui'S'	+		+		
Weaver				+	+
Wuh1/glen/4..				+	+
Yecora	+	+	+	+	+

the irrigation prior to FLLE of the earliest varieties. In terms of irrigation, the supraoptimal plots received water at more frequent intervals than the controls, when moisture depletion had reached approximately 25% of available water.

One greenhouse trial was conducted in the summer of 1992 in El Batan using the same genotypes as those used in field experiment 4 (Table 2). Plants were grown, three to a pot, in plastic pots measuring 100 cm in length and 10 cm in diameter. The tubes were filled with a 3:1 sand soil mixture by adding 10 cm of mixture at a time and gently compacting it, so as to produce a relatively uniform soil compaction throughout the tubes length. Plants were fertilized basally and watered as necessary using 10% Hoagland's solution. The length of each plant's youngest leaf was measured on a daily basis between growth stages 30 and 40 (Zadoks et al. 1974), so as to estimate leaf elongation rates between irrigations. Plants were irrigated when soil water potential reached 50 mb at a depth of 30 cm, estimated porometrically (2900FI soil moisture probe, Soilmoisture Equipment Corp, Santa Barbara CA). At anthesis, the pots were split open, the roots cleaned, and oven-dried to ascertain root and shoot biomass.

Results

Manipulations in interplant competition

In all four field experiments, there was a clear response to the light and root/light treatments, when considering the main effect across all genotypes. The average yield response to reduced interplant competition for light from FLLE onwards was 1.4 t/ha over control yields. The root/light treatment, which reduced interplant root competition as well as interplant competition for light at the same stage (FLLE), gave an average yield increase of 2.6 t/ha. The increases in yield were due to an increase in all yield components (spikes/m^2, grains/spike, and TGW) in the case of light treatment, while all except TGW were increased in the root/light treatment (**Tables 3 and 4**). Changes in yield were accompanied by parallel changes in straw biomass, although harvest index went up by a small amount in some treatments.

The fact that some genotypes responded far more than others to the light and root/light treatments can be seen clearly in **Figure 1**. The differing responses of genotypes to treatments were verified by statistically significant interactions for yield and most yield components in all experiments. This was also reflected in the generally low genotype correlations observed among the treatments for yield and for yield components (**Table 5**).

Combined analyses over location/years were run for genotypes in common among the experiments (Table 1). For experiments 2 and 4 conducted in Obregon, the interaction between genotype and year was not significant. However, there was a significant interaction between genotype and location when comparing experiments 1 (El Batan) and 2 (Obregon).

In treatments where the extra light treatment was imposed at later stages of development (anthesis, and 1 or 2 weeks after anthesis), there was a sequential loss in the ability of yield components to respond to the extra light. In experiment 1, with the extra light treatment imposed at anthesis, there was an increase in spikes/m^2, and TGW, but not in grains/spike. When the extra light treatment was imposed 2 weeks after anthesis, there was no increase in grain number, only an increase in TGW giving a small but significant yield gain over the control (**Table 6**). The same was observed in experiment 2 where the light treatment was imposed 1 week after anthesis.

Table 3. Main effects of light and root/light treatments on mean yield and yield components of eight spring wheat genotypes grown under optimum management, CIANO, NW Mexico, 1989-90 (Experiment 2).

	Interplant competition treatments:			
	Control	Light	Root/light	standard error (6 df)
Yield (t/ha)	7.7	9.3	10.3	0.17
Biomass (t/ha)	18.7	21.2	23.6	0.38
Straw (t/ha)	11.0	11.9	13.3	0.26
HI	0.41	0.44	0.44	0.006
SP/m^2	469	496	516	10.1
GR/SP	47.0	54.7	57.0	1.0
GR/m^2 (x10^3)	21.6	27.0	29.3	0.47
TGW	34.5	35.6	34.4	0.44

HI=harvest index; SP/m^2=spikes/m^2; GR/SP=grains/spike; GR/m^2=grains/m2 (in thousands); TGW=weight of a thousand grains; df=degrees of freedom.

Table 4. Effects of light and root/light treatments on yield and yield components expressed as a percentage of the control treatment, and correlations (r) between yield and yield components within each treatment, for 14 genotypes grown under optimal management in El Batan, Mexico, 1989 (Experiment 1).

	Control value (SE*)	r with yield	Light % change	r with yield	Root/ light % change	r
Yield (t/ha)	5.4 (.19)	1.00	19%	1.00	37%	1.00
Biomass (t/ha)	15.8 (.54)	0.61	16%	0.30	36%	0.46
HI	0.34 (.006)	0.62	3%	0.60	3%	0.15
SP/m^2	616 (13.8)	0.53	5%	0.47	23%	0.15
GR/SP	26 (1.2)	0.65	8%	0.42	18%	0.50
TGW	36 (1.1)	0.10	6%	0.00	-3%	0.11
GR/m^2	15,700 (558)	0.76	7%	0.69	38%	0.80
Straw	10.4 (.41)	0.27	15%	0.00	36%	0.31

Correlations significant at 5% level with r>0.53. * Standard error for comparison of the three means.

Table 5. Correlation coefficients for growth parameters of genotypes compared among control, light, and root/light treatments, indicating the relative effects of treatments on genotypes (i.e., G*E), in Obregon and El Batan, Mexico, 1989-91.

Treatment	Yield	Biomass	Harvest Index	Grains /m^2	DF
Control v L/RT					
El Batan 1989 (Expt. 1)	0.30	0.18	0.41	-0.26	12
Obregon 1989 (Expt. 2)	-0.12	0.49	0.47	0.06	6
Obregon 1991 (Expt. 4)	-0.20	0.01	0.30	-0.23	12
Light v L/RT					
El Batan 1989 (Expt. 1)	0.46	0.35	0.29	-0.34	12
Obregon 1989 (Expt. 2)	0.58	0.67	0.69	0.81*	6
Control v Light					
El Batan 1989 (Expt. 1)	0.81*	0.70*	0.73*	0.95*	12
Obregon 1989 (Expt. 1)	-0.14	0.44	0.53	-0.16	6

* Statistically significant at P = 0.05.

Table 6. Main effects of light treatments imposed at three different stages of crop development on mean yield and yield components of six spring wheat genotypes grown under optimum management, El Batan, Mexico, 1989 (Experiment 1).

	Control	2 wks after anthesis	Anthesis	FLLE	SE (6 df)
Yield (t/ha)	5.1	5.3	6.3	7.2	0.05
Biomass (t/ha)	16.8	16.1	19.2	20.6	0.42
Straw	11.7	10.8	12.8	13.4	0.41
HI	0.30	0.33	0.33	0.35	0.007
GR/SP	28.9	30.1	31.0	33.6	1.54
SP/m^2	573	529	635	674	27.8
GR/m^2 ($x10^3$)	16.6	15.9	19.7	22.6	0.54
TGW	30.8	33.4	32.0	31.8	0.64

Experiments to explore mechanisms affecting interplant competition
Experiment 3 suffered poor stand establishment due to flooding during germination and from rat infestation during jointing. As a result, genotype comparisons were not possible but, using genotypes as additional repetitions for the other factors, the experiment was analyzed for the effect of management on light and root/light treatments. There was no interaction of yield between the management treatments (N-P-K and irrigation levels) and the light and root/light treatments. While the light and root/light treatments had similar effects on yield (**Table 7**) as those seen previously (Tables 3 and 4), the extra management had no apparent affect. It did, however, increase the number of spikes/m^2 in all treatments, and this was reflected by increased biomass and reduced harvest index in all treatments (Table 7).

Table 7. Main effects of extra irrigation and nutrients (EX) verus standard management on spring wheat, with and without reduced interplant competition for light and soil resources (Experiment 3).

	Interplant competition treatments:			
	Control	Light	Root/light	Standard error (6 df)
Yield (t/ha)	6.7	8.9	9.6[b]	0.09
Yield EX	6.8	8.9	9.4	
Biomass (t/ha)	16.6	20.8	23.1[b]	0.27
Biomass EX	17.4[a]	22.2	23.9	
Spikes/m^2	452	488	522[b]	8.9
Spikes/m^2 EX	477[a]	532	577	
HI	.41	.43	.42[b]	0.004
HI EX	.40[a]	.42	.39	
Grains/m^2 ($x10^3$)	12.5	15.6	16.3	0.20
Grains/m^2 EX	12.6	15.2	16.1	

[a] Differences between management treatments significant at >5%.
[b] Differences between competition treatments significant at >5%.
None of the interaction terms were significant.

In the greenhouse experiment, root harvest indices measured at anthesis varied significantly between 9.3 and 13.3% of total plant biomass (**Table 8**). Leaf elongation rates also varied significantly among genotypes with values ranging from 3.3 to 5.0 mm elongation per day (Table 8).

Discussion

The interaction between genotype and interplant competition
The main hypothesis of this study is that high yield potential (HYP) genotypes owe, in part, their improved yield potential to an improved adaptation to the availability of light and soil resources experienced by the crop community. It is argued that these genotypes, as a consequence of their better adaptation to communal growth, are less responsive to a

Table 8. Root harvest index (HI) at anthesis, and mean leaf elongation rate between Zadoks stages 30-40, of 14 spring wheat genotypes grown in meter long pots under glasshouse conditions, El Batan, Mexico, 1992.

Genotype	Root HI %	Leaf elongation rate (mm/day)
Aga/4*yr70//...	12.0	4.9
Atilla 'S'	10.0	4.3
Carrizo 89	12.0	3.3
Ciano 79	13.3	3.9
Nacozari	11.5	4.7
Oasis 86	10.7	5.0
Pitic 66	13.3	3.7
Seri 82	12.2	4.3
Ser*3//buc/bjy	11.3	4.3
Siete Cerros	11.7	4.9
Super Kauz 88	11.7	4.8
Weaver	11.5	5.0
Wuh1/glen/4..	9.3	4.7
Yecora	11.0	5.0
se	0.01	0.41
df	39	39

decrease in interplant competition for growth factors than genotypes, which are normally more competitive. Essentially, a test of Donald's hypothesis that the ideal genotype for growth in monoculture would be one that outyields other genotypes communally, while being less well adapted to a more competitive niche (Donald and Hamblin 1968, Donald 1981). While HYP genotypes are by definition more efficient than low yield potential (LYP) genotypes, the physiological basis for the supposed synergy of communal growth is not well established. A previous study with a HYP spring wheat variety clearly demonstrated that there was interplant competition for light, which limited productivity, while there was no evidence for interplant root competition (Fischer and Laing 1975). This study demonstrated a clear tendency for HYP genotypes to be less responsive to reduced interplant light competition than LYP genotypes (Figure 1), suggesting that yield improvement has accompanied a reduced degree of interplant competition in the canopy. A similar and larger response to the simultaneous relief of above- and below-ground competition suggested that HYP genotypes were also less responsive to reduced interplant root competition than LYP genotypes, when interplant competition for light was also reduced. These data are supported by the consistently negative and generally significant correlations found between control yields and the yield increases caused by relief of interplant competition above- and below-ground (**Table 9**). The trend for LYP genotypes to respond more to the treatments than HYP genotypes is seen even more clearly if one considers the proportional increase in yield, resulting from relief of interplant competition, over the controls (**Figure 2**). While this trend was similar in both the light and root/light treatments, the magnitude of the response to the light treatment for any given genotype was not necessarily a good indicator of the magnitude of the response to the additional effect of relieving root competition (Figure 1). Furthermore, the genotypic correlations for yield between the light and root/light treatments were not significant (Table 5). These observations suggest that the response to interplant

Table 9. Correlation coefficients between control yields and yield increases caused by light and root treatments for varieties grown in Obregon and El Batan, Mexico, 1989-1991.

Control	Interplant competition treatments			df
	Light	Root/ yield	Root/ light[a]	
El Batan[b] (Expt. 1)	-0.53	-0.76	-0.65	12
Obregon 1989[c] (Expt. 2)	-0.65	-0.56	-0.30	6
Obregon 1991[b] (Expt. 4)	--	-0.84	--	12

[a] Correlation of yield with difference in yield between light and root treatment.
[b] Significant at 5% with r= 0.53.
[c] Significant at 5% with r= 0.71.

Table 10. Correlation coefficients (R) for the association between the change in yield component and the change in yield caused by light and root/light treatments across 14 genotypes, El Batan, Mexico, 1989.

Associated with change in yield component:	Effect of interplant competition treatments:		
	Light	Root/light	(Root/light)-(light)[a]
Biomass	0.38	0.53	0.31
HI	0.53	0.37	0.38
SP/m^2	-0.19	0.45	0.20
GR/SP	0.39	0.78	0.55
TGW	0.70	0.29	-0.39
GR/m^2	0.57	0.93	0.81
Straw	0.10	0.29	0.10

[a] Effect of root/light treatment with effect of light treatment subtracted from it.

Correlations significant at 5% level with r>0.53.

competition below- and above-ground were somewhat independent phenomena in a given genotype.

Flag leaf ligule emergence was chosen as the stage of development at which to impose most of the treatments for two reasons. First, it is an easily identifiable stage that approximately coincides with maximum canopy cover of all genotypes, in the well managed situation. Therefore, interplant competition, for light at least, is likely to be negligible before this stage of development. Second, under normal conditions, this stage would also coincide with maximum tiller number. Although the treatments did increase tiller survival, it was decided not to impose treatments at earlier stages to avoid the confounding effect of additional tillering, which does not normally occur after FLLE in well managed crops.

Possible mechanisms affecting interplant competition

The relationship between yield and yield components for each treatment (Table 4) and the change of yield associated with the change in yield components (**Table 10**) were studied to see if the response to treatments could be explained in terms of any particular compensating growth mechanism. Treatments appeared to result in an integrated response of all growth parameters, with the exception of increased TGW in the case of the root/light treatment. However, treatments applied at later stages of development showed more selective effects on growth parameters, corresponding to the potential of compensating yield mechanisms at different phenological stages. In experiment 2, the light treatment imposed 1 week after anthesis resulted in a high correlation (r=0.80) between yield increase and increase in TGW for the eight genotypes, while grain number was unaffected. The response of yield was also significantly negatively correlated (r=-0.85) with yield of control plots as was seen in the light treatments imposed at FLLE (Table 9).

A number of hypotheses were tested to account for the differential response of genotypes to the light and root/light treatments. In the case of the light treatment, two hypotheses were proposed. One was that HYP genotypes were more determinate, partitioning less assimilates to the growth of nonproductive tillers in the vegetative phase than LYP genotypes. Consequently, the LYP genotypes would respond more to the light treatment at FLLE because they had more redundant tillers than the HYP genotypes. This hypothesis was tested in experiments 2 and 4 by counting the number of shoots in each genotype at FLLE and by comparing this to the number of spikes at maturity in all treatments. There was no relationship between the number of tillers aborted between FLLE and maturity and yield of any of the treatments--nor was there any relationship between absolute number of tillers/m^2 at FLLE and yield in any treatment. It has been suggested that more determinate tillering would be consistent with the high yielding, communal ideotype (Donald 1981), but this as well as a number of other experiments have failed to verify the idea (Sedgely 1991).

Another hypothesis proposed was that the canopies of HYP genotypes experienced a more optimal light distribution profile than LYP genotypes, therefore, the relative response to reduced interplant competition for light favored the LYP genotypes. Differences in light use efficiency of the canopy could theoretically be a function of canopy architecture or improved photosynthetic efficiency of the component leaves in the canopy. Collaborative studies comparing canopy architecture in the Obregon environment have not revealed significant differences in light use efficiency, at least when comparing genotypes with contrasting leaf angles (Araus et al. 1993). With regard to the photosynthetic rate, eight of the same genotypes as used in experiment 4 have been investigated for their rate of net carbon fixation of flag leaves in direct sunlight (1500-1800 $\mu E/m^2/s$). The study revealed a significant correlation between yield of varieties

and photosynthetic rate in both preheading (r=0.71), and postheading (r=0.89) stages, under well managed conditions (Rees et al. 1993). This could be considered as an adaptation to communal growth if, for example, the HYP genotypes have a higher potential rate of photosynthesis in their flag leaves at the expense of the photosynthetic capacity of their lower leaves. However, no further evidence is available.

Interpretation of the response to the root/light treatment is more complex since the treatment confounds the effect of interplant competition above- and below-ground. Nonetheless, as already discussed, the data indicate that the above- and below-ground effects were somewhat independent and three hypothesis were tested involving interplant root competition. One was that HYP genotypes might be better adapted than the LYP genotypes to the canopy situation, in terms of utilizing nutrients and water, and consequently derive relatively less benefit when interplant root competition was decreased. This hypothesis was tested in experiment 3 by supplying higher than normal levels of nutrients and water to a range of genotypes, with and without reduced interplant root competition. Despite the fact that it was not possible to make comparisons among genotypes in this experiment, it was clear from the main effects that the effect of extra nutrients and water on plants subjected to the light treatment did not parallel the effect of reduced root competition (Table 7). The result indicated that the immediate availability of nutrients and water in the soil was not causal in the observed response to reduced root competition.

A second hypothesis was tested based on the phenomenon of root signals, whereby roots respond to dry soil profiles by sending signals to the shoots to slow down cell expansion rates (Davies and Zhang 1991). It was hypothesized that if this phenomenon shows genotypic variability in wheat, then reduced sensitivity to drying soils would confer a yield advantage since plants would not experience reduced cell expansion rates during the relatively dry period prior to irrigation. Consequently, HYP varieties would lose their yield advantage under the root/light treatment because under reduced plant density, the decreased rate of soil drying would reduce the likelihood of root signalling for all genotypes. Fourteen varieties were grown in 1-m long pots in the greenhouse, and leaf elongation rates were measured as the soil dried between irrigations to 60 mb, at 30 cm depth. Although there were significant differences among genotypes in leaf elongation rate, there was no interaction between genotype and soil water potential nor was there any correlation of leaf elongation rate with control yields of field grown varieties or their responses to root/light treatment. Additional evidence refuting the involvement of soil water potential in the response to treatments already comes from experiment 3 (Table 7). Incidentally, however, leaf expansion rate in pots did show a significant correlation (r=0.62) with biomass and straw biomass for the control plots of the same genotypes when grown in the field (experiment 4).

A third hypothesis is that HYP genotypes invested relatively more assimilates in seed than root growth in comparison to the LYP genotypes. Implicit to this hypothesis is the idea that the lower investment in root growth of the HYP genotype is an adaptation to the communal, canopy environment. Conversely, the LYP genotype, investing more resources in root growth, would be better adapted to a more competitive niche. This is consistent with the proposal by Donald (1981) that the competition ideotype would have a greater investment of dry matter in structure at the expense of seed. Specifically, he argued that the competitive ideotype would tend towards a low HI while the communal or crop ideotype would have minimal resources invested in structure, and hence a higher HI. The greenhouse study revealed a relationship between the root biomass (expressed as a percentage of total plant biomass at anthesis), and several of the growth parameters of the field grown plots subjected to the root/light treatment, namely grains/m^2 (r=0.50), total biomass (0.60), and straw biomass (0.60). In addition, the % root biomass in pots

was also correlated with the increase in the number of grains/m^2 (0.60), and increase in biomass (0.40) caused by the root/light treatment. There was also a low, but negative (-0.30) correlation between % root biomass and yield of field grown control plots (yield potential). The correlations ($r >= 0.53$ significant at the 5% level) lend support to the hypothesis that yield potential may be related to reduced partitioning to root growth, bearing in mind that the root effect was confounded with the light effect in this experiment. This being the case, the greater investment in root growth by LYP genotypes may have enabled them to support greater shoot growth than HYP genotypes after interplant competition was relieved experimentally. The physiological basis for this response is not clear since root competition effects were not apparently related to nutrient or water deficits (Table 7), as already discussed. However, one might speculate that soil oxygen concentrations were, in fact, the limiting factor to root activity in the communal (control) situation. This is speculative, but since nutrients and water were apparently not limiting to root systems of well managed plots, there may have been root competition for oxygen. If the root/light treatment relieved competition for oxygen, the advantage may have gone to the LYP genotypes simply because they had more roots to utilize the higher oxygen levels.

It should be noted that responses to light and root/light treatments did not show systematic relationships with any of the additional parameters measured in control plots, namely phenology, mature plant height, biomass at FLLE, crop canopy temperature, or total light interception after anthesis.

Implications for breeders

These results lend support to the hypothesis of Donald (1963) that the so-called "weak competitor" characteristic of genotypes does confer a yield advantage to spring bread wheat in a high yield environment. Although previous work has lent partial support to the hypothesis in water-limited conditions for cereals (Jones and Kirby 1977, Islam and Sedgely 1985) and without water limitation for soybean (Beuerlein 1971), no previous study has verified the hypothesis for wheat in a high yielding environment. It is apparent from the review of Sedgely (1991) that the ramifications of the hypothesis have had some influence on breeding strategies over the last 2 to 3 decades. However, a lack of experimental support for the hypothesis has left others skeptical (Marshall 1991).

The rebuttal of Donald's ideas may well have limited genetic progress in yield improvement (Sedgely 1991). While a large body of evidence has shown early generation selection strategies to have been ineffective (Bhatt 1980), natural selection in segregating populations may, in fact, be detrimental (Donald 1968). The unavoidable effect of natural selection in segregating populations will favor the predominance of competitive ideotypes (Donald 1962, Donald and Hamblin 1983), whether deliberate selections are made in early generations or not. Wheat, like grasses in general, has evolved as a primary colonizer and, as such, tends towards a competitive rather than communal behavior. The wholesale presence of a negative yield trait in a crop species, even after decades of breeding effort, is not without precedent. In tropical maize, a trait that effects yield by determining the relative partitioning of assimilates to the development of the female and male flowers can only be effectively selected for under drought, and has therefore remained largely unselected for in breeding populations for high yield (Bolaños and Edmeades 1993).

Despite the difficulties associated with selection for communal genotypes, there is evidence that the trait has been incorporated into high-yielding genotypes, albeit unconsciously. Changes in morphological traits consistent with the communal ideotype, such as increased harvest index and smaller leaves, have accompanied higher yields in many crops (Donald and Hamblin 1983, Siddique et al. 1989). This may be due, in part,

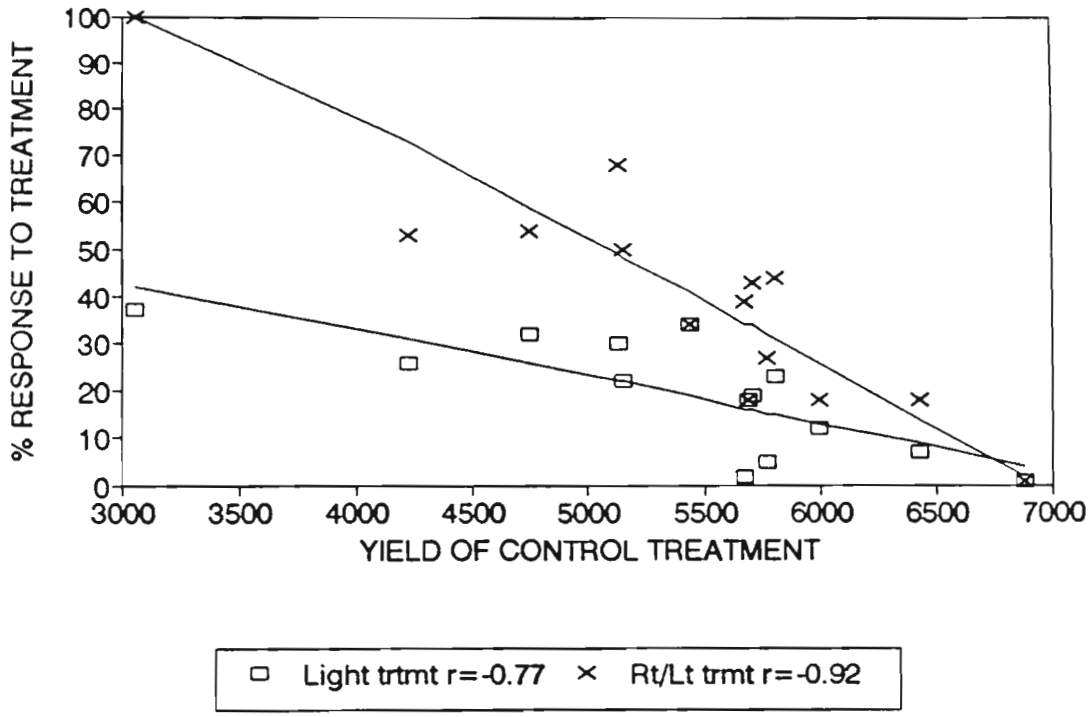

Figure 1. Yields of 14 wheat genotypes in conventional plant stands (control), with reduced interplant competition for light (light treatment) and with reduced interplant competition for soil resources and light (root/light treatment), under optimal management, El Batan, Mexico, 1989 (Experiment 1).

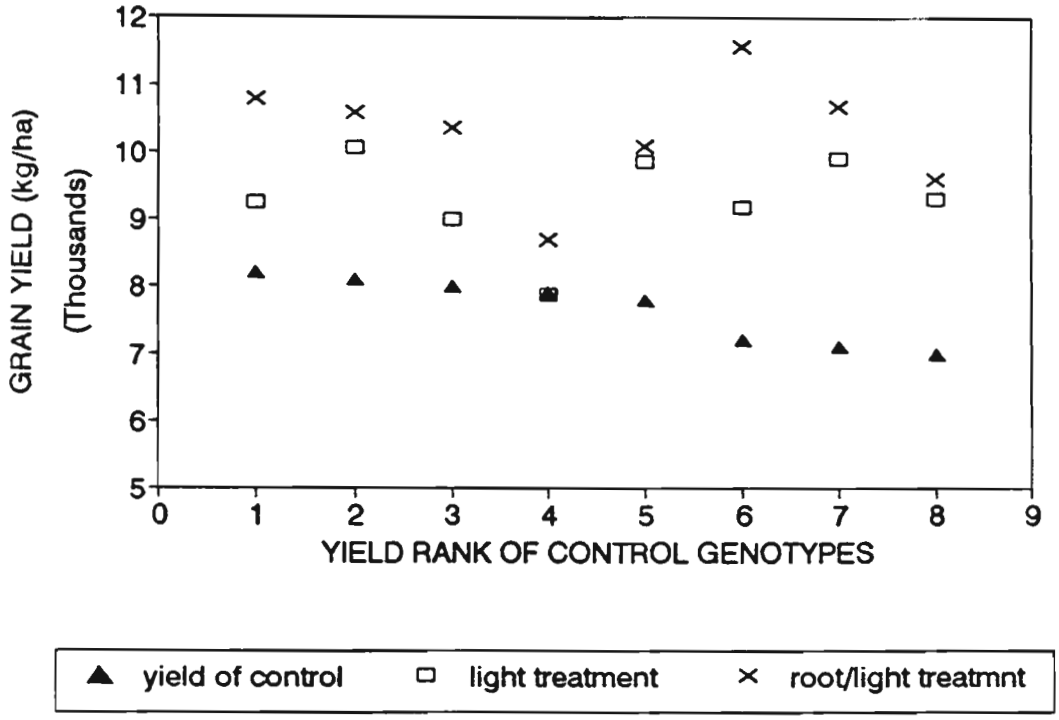

Figure 2. Relationship between control yield of spring wheat, and the response of eight genotypes to two treatments, reduced interplant competition for light (light treatment) and reduced interplant competition for soil resources and light (root/light treatment), under optimal management, Cd. Obregon, Mexico, 1989-90 (Experiment 2).

to the fact that some traits show a plastic response to their environment, depending for example on planting density (Soetono and Donald 1980). The emphasis on traits that complement communal growth is the key to the ideotype approach to breeding. This is especially true in early generations when the overall performance of the communal genotypes will be at a disadvantage in comparison to that of competitive genotypes in a segregating population, or even in isolation. Our increased understanding of the interactions between genotype and the communal environment will help us to identify communal-adaptive traits, which can be adopted more widely in breeding programs.

References

Acevedo, E. 1979. Interacciones suelo-agua-raíz en el proceso de absorción de agua por las plantas. Bol. Tec. 44:17-25. Fac. Agron. Univ.. Chile.

Araus, J.L., M.P. Reynolds, and E. Acevedo. 1993. Influence of leaf posture on grain yield and its components, crop growth pattern, leaf structure and carbon isotope discrimination in wheat. Crop Sci. (in press).

Beuerlein, J.E., J.W. Pendleton, M.E. Bauer, and S.R. Ghorashy. 1971. Effect of branch removal and plant population at equidistant spacings on yield and light use efficiency of soybean canopies. Agron. J. 36:317-319.

Bhatt, G.M. 1980. Early generation selection criteria for yield in wheat. J. Aust. Inst. Agric. Sci. 46:14-22.

Blum, A., and M. Kraljevic-Balalic. 1980. Productivity of single-culm and multi-culm plants of winter wheat cultivars in field conditions. Euphytica 29:7705-713.

Bolaños, J., and G. Edmeades. 1993. Eight cycles of selection for drought in tropical maize. II. Response in reproductive behaviour. Field Crops Research 31:253-268.

Boyer, J.S. 1982. Plant productivity and environment. Science 218:443-448.

Davies, W.J., and Zhang. 1991. Root signals and the regulation of growth and development in drying soil. Annu. Rev. Plant Physiol. Mol. Biol. 42:55-76.

Donald, C.M. 1962. In search of yield. J. Aust. Inst. Agrc. Sci. 238:171-178.

Donald, C.M. 1963. Competition among crop and pasture plants. Adv. Agron. 15:1-118.

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

Donald, C.M. 1981. Competitive plants, communal plats, and yield in wheat crops. In L.T. Evans and W.J. Peacock, eds., Wheat Science--Today and Tomorrow.

Donald, C.M., and J. Hamblin. 1983. The convergent evolution of annual seed crops in agriculture. Adv. Agron. 36:97-143.

Evans, L.T. 1991. Proceedings of the International Conference on Determination of Yield in Crop Plants, Gainsville, Florida (in press).

Fischer, R.A., and D.R. Laing. 1976. Yield potential in a dwarf spring wheat and response to crop thinning. J. Agric. Sci. Camb. 87:113-122.

Hawkins, A.F. 1982. Light interception, photosynthesis and crop productivity. Outlook Agr. 11:104-113.

Islam, T.M.T., and R.H. Sedgely. 1985. Evidence for a "uniculum effect" in spring wheat (*Triticum aestivum* L.) in a Mediterranean environment. Euphytica 30:277-282.

Jones, H.G., and E.J.M. Kirby. 1977. Effects of manipulation of number of tillers and water supply on grain yield in barley. J. Agric. Sci. (Camb.), 88:391-397.

Marshall, D.R. 1991. Alternative approaches and perspectives in breeding for higher yield. Field Crops Research 26:171-190.

Rees, D., K.D. Sayre, E. Acevedo, T. Nava Sanchez, Z. Lu, E. Zeiger, and A. Limon. 1993. Canopy Temperatures of Wheat: Relationship with Yield and Potential as a Technique for Early Generation Selection. Wheat Special Report No. 10. Mexico, D.F.: CIMMYT.

Reynolds, M.P., K.D. Sayre, and H.E. Vivar. 1993. Intercropping cereals with N-fixing legume species: a method for conserving soil resources in low input systems. J. Agr. Sci., Camb., U.K. (submitted).

Saini, A.D., and R. Nandi. 1979. The effect of culm number on yield in wheat (*T. aestivum* L.). Indian J. Plant Physiol. 22:97-101.

Sedgely, R.H. 1991. An appraisal of the Donald ideotype after 21 years. Field Crop Res. 26:93-112.

Siddique, K.H.M., E.J.M. Kirby, and M.W. Perry. 1989. Ear stem ratio in old and modern wheat varieties: Relationship with improvement in number of grains per ear and yield. Field Crops Res. 21:59-78.

Soetono and C.M. Donald. 1980. Emergence, growth and dominance in drilled and square-planted barley crops. Aust. J. Agric. Res. 31:455-470.

Trenbath, B.R., and J.F. Angus. 1975. Leaf inclination and crop production. Field Crop Abstracts 28(5). Farnham Royal, U.K.

Zadoks, J.C., T.T. Chang, and C.F. Konzak. 1974. A decimal code for the growth stages of cereals. Weed Res. 14:415-421.

CIMMYT Wheat Special Reports Completed or In Press
(As of Nov. 10, 1993)

Wheat Special Report No. 1. Burnett, P.A., J. Robinson, B. Skovmand, A. Mujeeb-Kazi, and G.P. Hettel. 1991. Russian Wheat Aphid Research at CIMMYT: Current Status and Future Goals. 27 pages.

Wheat Special Report No. 2. He Zhonghu and Chen Tianyou. 1991. Wheat and Wheat Breeding in China. 14 pages.

Wheat Special Report No. 3. Meisner, C.A. 1992. Impact of Crop Management Research in Bangladesh: Implications of CIMMYT's Involvement Since 1983. 15 pages.

Wheat Special Report No. 4. Skovmand, B. 1994. Wheat Cultivar Abbreviations. Paper and diskette versions. In press.

Wheat Special Report No. 5. Rajaram, S., and M. van Ginkel. 1993 (rev.). A Guide to the CIMMYT Bread Wheat Section. 52 pages.

Wheat Special Report No. 6. Meisner, C.A., E. Acevedo, D. Flores, K. Sayre, I. Ortiz-Monasterio, and D. Byerlee. 1992. Wheat Production and Grower Practices in the Yaqui Valley, Sonora, Mexico. 75 pages.

Wheat Special Report No. 7a. Fuentes-Davila, G. and G.P. Hettel, eds. 1992. Update on Karnal Bunt Research in Mexico. 38 pages.

Reporte Especial de Trigo No. 7b. Fuentes-Davila, G., y G.P. Hettel, eds. 1992. Estado actual de la investigación sobre el carbón parcial en México. 41 pages.

Wheat Special Report No. 8. Fox, P.N., and G.P. Hettel, eds. 1992. Management and Use of International Trial Data for Improving Breeding Efficiency. 100 pages.

Wheat Special Report No. 9. Rajaram, S., E.E. Saari, and G.P. Hettel, eds. 1992. Durum Wheats: Challenges and Opportunities. 190 pages.

Wheat Special Report No. 10. Rees, D., K. Sayre, E. Acevedo, T. Nava Sanchez, Z. Lu, E. Zeiger, and A. Limon. 1993. Canopy Temperatures of Wheat: Relationship with Yield and Potential as a Technique for Early Generation Selection. 32 pages.

Wheat Special Report No. 11. Mann, C.E., and B. Rerkasem, eds. 1992. Boron deficiency in Wheat. 132 pages.

Wheat Special Report No. 12. Acevedo, E. 1992. Developing the Yield Potential of Irrigated Bread Wheat: Basis for Physiological Research at CIMMYT. 18 pages.

Wheat Special Report No. 13. Morgunov, A.I. 1992. Wheat Breeding in the Former USSR. 34 pages.

Wheat Special Report No. 14. Reynolds, M., E. Acevedo, O.A.A. Ageeb, S. Ahmed, L.J.C.B. Carvalho, M. Balata, R.A. Fischer, E. Ghanem, R.R. Hanchinal, C.E. Mann, L. Okuyama, L.B. Olegbemi, G. Ortiz-Ferrara, M.A. Razzaque, and J.P. Tandon. 1992. Results of the 1st International Heat Stress Genotype Experiment. 19 pages.

Wheat Special Report No. 15. Bertschinger, L. 1993. Research on BYD Viruses: A Brief State of the Art of CIMMYT's Program on BYD and Its Future Research Guidelines. In press.

Wheat Special Report No. 16. Acevedo, E., and G.P. Hettel, eds. A Guide to the CIMMYT Wheat Crop Management & Physiology Subprogram. 161 pages.

Wheat Special Report No. 17. Huerta, J., and A.P. Roelfs. 1993. The Virulence Analysis of Wheat Leaf and Stem Rust on a Worldwide Basis. In press.

Wheat Special Report No. 18. Bell, M.A., and R.A. Fischer. 1993. Guide to Soil Measurements for Agronomic and Physiological Research in Small Grain Cereals. 40 pages.

Wheat Special Report No. 19. Woolston, J.E. 1993. Wheat, Barley, and Triticale Cultivars: A List of Publications in Which National Cereal Breeders Have Noted the Cooperation or Germplasm They Received from CIMMYT. 68 pages

Wheat Special Report No. 20. Balota, M., I. Amani, M.P. Reynolds, and E. Acevedo. 1993. An Evaluation of Membrane Thermostability and Canopy Temperature Depression as Screening Traits for Heat Tolerance in Wheat. 26 pages.

Reporte Especial de Trigo No. 21a. Moreno, J.I., y L. Gilchrist S. 1993. La roña o tizón la espicga del trigo. In press.

Wheat Special Report No. 21b. Moreno, J.I., and L. Gilchrist S. 1993. Fusarium head blight of wheat. In press.

Wheat Special Report No. 22. Stefany, P. 1993. Vernalization Requirement and Response to Day Length in Guiding Development in Wheat. 39 pages.

Wheat Special Report No. 23a (short version). Dhillon, S.S., and I. Ortiz-Monasterio R. 1993. Effects of Date of Sowing on the Yield and Yield Components of Spring Wheat and Their Relationships with Solar Radiation and Temperature at Ludhiana (Punjab), India. 33 pages.

Wheat Special Report No. 23b (long version). Dhillon, S.S., and I. Ortiz-Monasterio R. 1993. Effects of Date of Sowing on the Yield and Yield Components of Spring Wheat and Their Relationships with Solar Radiation and Temperature at Ludhiana (Punjab), India. 83 pages.

Wheat Special Report No. 24. Saari, E.E., and G.P. Hettel, eds. 1993. Guide to the CIMMYT Wheat Crop Protection Subprogram. In press.

Wheat Special Report No. 25. Reynolds, M.P., E. Acevedo, K.D. Sayre, and R.A. Fischer. 1993. Adaptation of Wheat to the Canopy Environment: Physiological Evidence that Selection for Vigor or Random Selection May Reduce the Frequency of High Yielding Genotypes. 17 pages.

Wheat Special Report No. 26. Reynolds, M.P., K.D. Sayre, and H.E. Vivar. 1993. Intercropping Cereals with N-Fixing Legume Species: A Method for Conserving Soil Resources in Low-Input Systems. 14 pages.

CENTRO INTERNACIONAL DE MEJORAMIENTO DE MAIZ Y TRIGO
INTERNATIONAL MAIZE AND WHEAT IMPROVEMENT CENTER
Lisboa 27 Apartado Postal 6-641 06600 México, D.F. México