CHAPTER 14

YIELD IMPROVEMENT ASSOCIATED WITH *Lr19* TRANSLOCATION IN WHEAT

Which plant attributes are modified?

D.J. MIRALLES[#,##], E. RESNICOFF[#] AND R. CARRETERO[#]

[#] *University of Buenos Aires, Department of Plant Production, Av. San Martin 4453 (C1417 DSE), Ciudad de Buenos Aires, Argentina.*
[##] *CONICET (National Council of Scientific and Technical Research).*
E-mail: miralles@agro.uba.ar

Abstract. Resistance to three rust pathogens (leaf rust, stripe rust and stem rust) is related to different resistance genes. Leaf-rust resistance gene *Lr19*, transferred to hexaploid wheat from *Agropyron elongatum*, appears to be a promising gene not only through the resistance to rust conferred by this gene, also because of yield increases produced in different backgrounds when alien chromatin carrying *Lr19* is introgressed in wheat. It was reported that *Lr19* was associated with increases in grain yield. Aerial biomass was also increased when *Lr19* was introgressed, although differences were not associated with improved light interception (indirectly measured) or radiation use efficiency (RUE). The physiological basis of the increased biomass and the mechanisms causing increased number of grains per spike, in terms of dynamic of floret development, are not completely understood.

The objective of this study was to determine the performance of a near-isogenic line (cv. Bourlaug) differing in *Lr19* in relation to: (i) the differences in grains per spike, by analysing the dynamics of floret primordia; and (ii) the dynamics of biomass partitioning between the spike and the rest of the vegetative organs pre- and post-anthesis.

Two field experiments were carried out during the 2001 and 2003 growing seasons; one near-isogenic line (cv. Bourlaug) was grown under potential conditions (i.e., without water and nutritional limitations). Also a check without *Lr19* was grown.

The results showed that *Lr19* was associated with increases in yield and a higher number of grains per unit area than the check. An increase in biomass was only observed in the 2003 growing season. Non-significant differences were observed in cumulative radiation intercepted between lines. Although RUE differed between growing seasons (i.e., 1.53 and 2.07 g MJ^{-1}), there was no significant difference between the *Lr19* and check genotype. In both years *Lr19* allocated more assimilates and nitrogen to the spike (14% and 50% more biomass and nitrogen, respectively), and this phenomenon was associated with more fertile florets per spike.

Summarizing the data, it can be concluded that the *Lr19* gene promotes the partitioning of assimilates to the reproductive organs and the nitrogen partitioning to the spike. This resulted in an increased number of fertile florets per spike and number of grains per unit area, without effecting number of spikes per unit area and crop development. Increases in biomass were not always evident.

J.H.J. Spiertz, P.C. Struik and H.H. van Laar (eds.), Scale and Complexity in Plant Systems Research: Gene-Plant-Crop Relations, 171–178.

INTRODUCTION

Different genes are known to confer resistance to three rust pathogens (leaf rust, stripe rust and stem rust). Leaf-rust resistance gene *Lr19*, transferred to hexaploid wheat from *Agropyron elongatum* by Sharma and Knott (1966), appeared to be promising also for yield and biomass increases (Singh et al. 1998). Reynolds et al. (2001; 2005) using isogenic lines with the 7DL.7Ag translocation (containing the *Lr19* gene) demonstrated increases in yield of ca 9% across different backgrounds, explained by increases in radiation use efficiency (RUE) during post-anthesis, which were related to improved number of grains per unit land area (Reynolds et al. 2005).

Increased yields in near-isogenic lines with the 7DL.7Ag translocation were associated with a more favourable partitioning of assimilates to the spike and as a consequence a larger number of grains per spike (Reynolds et al. 2001; 2005). However, the mechanisms associated with increased number of grains per spike, in terms of dynamics of floret development have not been analysed yet.

The objective of this study was to evaluate the performance of near-isogenic lines (cv. Bourlaug) differing in *Lr19* allelic form to determine the dynamics of floret primordia development together with that of biomass accumulation and partitioning.

MATERIALS AND METHODS

Two field experiments were carried out during the 2001 and 2003 growing seasons at the experimental field of the Department of Plant Production, Faculty of Agronomy, University of Buenos Aires (35°35′ S, 59°29′ W; 25 m a.s.l.), Argentina. A pair of near-isogenic lines of cultivar Bourlaug (with and without the 7DL.7Ag translocation; from now on '+*Lr19*' and 'Check', respectively), kindly provided by Dr. M. Reynolds (CIMMYT), was sown on 29 June 2001 and 17 July 2003 at a density of 300 plants m^{-2} in plots of 9 rows, 0.15 m apart and 3 m long. Treatments were arranged in a randomized block design with three replicates. ANOVAs were performed in order to determine the impact of treatments, and significant differences among means were compared using least significant differences (LSD, $\alpha = 0.05$). The degree of association between variables was established by linear regressions.

Plots were irrigated to complement natural rainfall during the whole crop cycle maintaining soil near to field capacity. Urea was applied at sowing to reach a soil nitrogen availability of 150 kg N ha^{-1}. Phosphorus fertilizer was not applied as soil levels at sowing were higher than 20 mg kg^{-1}. Fungicides and insecticides were applied to prevent diseases and pest. Weeds were manually removed throughout the crop cycle.

Development stages at the beginning of stem elongation (DC30) and at anthesis (DC65) were determined. From emergence to anthesis, incident and transmitted global radiation were measured on clear days at noon. The percentage of intercepted radiation (IR%) was calculated considering the incident and transmitted radiation at ground level and the incident radiation measured over the crop canopy. The dynamics of IR% during crop growth was fitted by a sigmoid function. The

cumulative intercepted radiation was estimated from the fraction of daily intercepted radiation and daily total incident radiation over time. To determine the dynamics of dry-matter accumulation (in spike and vegetative organs) from emergence to anthesis at least six samples of 50 cm in a central row of aerial biomass were taken from each treatment. RUE during pre-flowering was calculated as the slope of the relationship between cumulative biomass and cumulative global radiation intercepted by the crop. At maturity plant samples of 1 m in a central row of each plot were taken and biomass, yield and its components were recorded.

In 2001, the dynamics of floret development was also followed. For that purpose, two plants per plot were randomly sampled twice weekly and their spikes were dissected and the total number of floret primordia counted. In each sample the score of each floret within basal, central and apical spikelet was assessed following the Waddington et al. (1983) scale.

RESULT AND DISCUSSION

Crop development

There was no effect of the 7DL.7Ag translocation on phenological development. In fact, flowering date for both lines was the same (10 and 24 October in 2001 and 2003, respectively) and timing of the occurrence of the different pre-flowering stages was also unaffected by treatments (data not shown). These data confirm those reported by Reynolds et al. (2001), who did not find differences in phenology between *+Lr19* and the Check line in different backgrounds. Final leaf number and phyllochron (120 °Cd per leaf) was also the same in both lines.

Biomass and its physiological components

No significant differences were observed in biomass at anthesis, or in its physiological determinants (Table 1). However, in 2003 the 7DL.7Ag translocation was significantly associated with higher biomass at harvest, indicating an improved post-anthesis growth because of the introgression.

Yield and its components

The 7DL.7Ag translocation increased grain yield (23 and 35% in 2001 and 2003, respectively) and increased the number of grains per unit area without significant effects on average grain weight (Table 2). Since there were no significant effects on the number of spikes per unit area (although during 2003 +Lr19 established 13% more spikes per m^2 than the Check) the main effect 7DL.7Ag translocation on grains per unit area was associated with changes in the number of grains per spike. Thus, the number of grains per spike was in both years increased by ca. 18% if the line carried the translocation (Table 2). The data obtained in this study showed a similar increase in grains per spike (in relative terms) to those reported for different backgrounds by Reynolds et al. (2001; 2005).

Although the increase in grains per spike associated with the 7DL.7Ag translocation was a consequence of the higher number of fertile florets per spike in both years, the differences were only significant in 2001. In 2003 a slight difference was observed between genotypes, suggesting that grain setting (i.e., the proportion of fertile florets (FF) that form grains) could also be responsible for the differences in grain number between *+Lr19* and the Check (Table 3).

Since the 7DL.7Ag translocation did not modify crop development, the total number of spikelets was not affected. Thereby, differences in fertile florets per spike were mainly explained by changes in the number of FF per spikelet (2001) and by differences in the number of fertile spikelets per spike (2003). The difference in number of fertile florets per spikelet in the *+Lr19* respect to the Check observed in the 2001 growing season was evident in those spikelets placed in the central and apical position into the spike without significant differences in the basal spikelets (Figure 1).

Table 1. *Accumulated biomass (at flowering and at harvest) in main stems, tillers and total (main stems+tillers) and harvest index in both experimental years*
SE indicates the standard error of means

	Biomass at flowering ($g\ m^{-2}$)	Biomass at harvest ($g\ m^{-2}$)	Harvest index ($g\ g^{-1}$)
2001			
Check	627.2	754	0.34
+Lr19	712.9	774	0.40
SE	114.6	120.2	0.032
2003			
Check	812.9	934.4	0.47
+Lr19	844.7	1224.5	0.46
SE	113.8	119.4	0.0043

Table 2. *Plant height, grain yield and yield components*
SE indicates the standard error of means

	Height (cm)	Yield ($g\ m^{-2}$)	No. of grains (m^{-2})	Grain weight (mg)	No. of grains ($spike^{-1}$)	No. of spikes (m^{-2})
2001						
Check	62.3	248.8	7330	33.7	21.9	340
+Lr19	56.8	306.0	8383	36.5	26.0	342
SE	1.51	54.1	804.2	3.6	2.2	14.6
2003						
Check	84.5	424.3	11474	37.0	25.8	444
+Lr19	91.0	572.4	15186	37.5	30.3	502
SE	8.1	87.4	1826	1.6	2.4	17.5

Table 3. *Total and fertile spikelets per spike, fertile florets (FF) per spike and per spikelet for both genotypes (Check and* +Lr19*) in the 2001 and 2003 growing seasons*
SE indicates the standard error of means

	Number of spikelets		Fertile florets	
	Total	Fertile	spike^{-1}	spikelet^{-1}
2001				
Check	19.7	18.0	59.7	3.3
+*Lr19*	20.3	18.5	67.8	3.7
SE	0.7	0.6	4.7	0.1
2003				
Check	16.5	14.8	44.8	3.0
+*Lr19*	16.6	15.6	46.7	3.1
SE	0.8	1.1	4.1	0.3

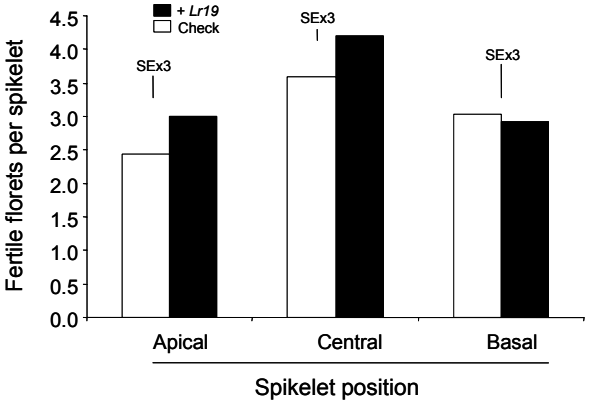

Figure 1*. Fertile florets per spikelet for different positions within the spike (apical, central and basal spikelets) in the* +Lr19 *(closed bars) and Check (open bars) lines. Vertical lines indicate three times the standard error. Data correspond to the 2001 growing season*

The analysis of the dynamics of floret primordia development showed that the increased spikelet fertility in the *+Lr19* was a consequence of a higher rate of development of the floret primordia (Figure 2). When floret development was plotted against thermal time, it could be observed that some florets at the same position on the spikelet progressed more in the *+Lr19* line than in the Check. For instance, considering the central spikelets into the spike, there was no difference in development for the first three floret primordia placed close to the rachis (F1 to F3), however, the 4th (F4) and 5th (F5) floret primordia reached a higher floret score in the *+Lr19* than in the Check (Figure 2).

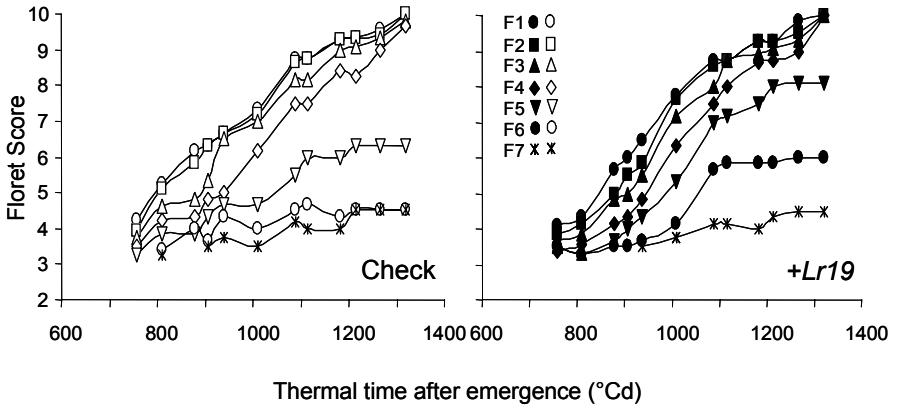

Figure 2. *Development of all florets primordia within the central spikelets in the* +Lr19 *and Check genotype in the 2001 growing season. Floret positions are indicated from F1 to F7, F1 being the floret closest to the rachis*

Reynolds et al. (2001) found that 7DL.7Ag translocation increased assimilate partitioning with ca. 13% to the spike. The results of this study showed that the dynamics of spike growth (mainly in 2001) were different between *+Lr19* and Check. The rate of biomass accumulation in the *+Lr19* was significantly higher than that observed in the Check between booting and flowering, resulting in a higher spike dry weight at anthesis (Figure 3). On the other hand, no significant differences were evident in the dynamics of shoot (stem+leaves) growth among genotypes.

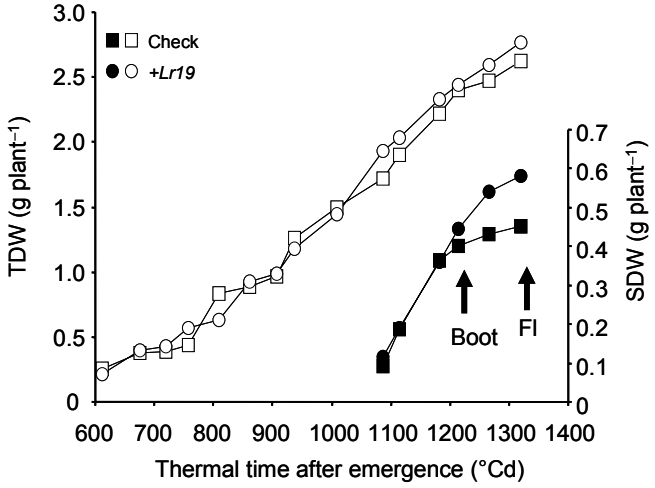

Figure 3. *Dynamics of total (TDW, open symbols) and spike (SDW, closed symbols) dry weight per plant in the* +Lr19 *and Check genotypes in the 2001 growing season. Black arrows indicate the stages of booting (Boot) and flowering (Fl)*

When the number of grains per unit area was plotted against the spike dry weight at flowering a positive association was found in both genotypes. However, the slope of the linear regressions was higher in the *+Lr19* (84 grains g^{-1}) than in the Check (66 grains g^{-1}), suggesting a more efficient investment of spike dry weight to produce grains in the *+Lr19* than in the Check.

In 2001, the spike nitrogen concentration was measured at anthesis. The data showed that, as was observed for spike biomass at anthesis, *+Lr19* also increased the nitrogen concentration in the spike. The percentages of N content in the spike at anthesis were 1.54 and 1.09% for the *+Lr19* and Check, respectively. Abbate et al. (1995) suggested a direct effect of nitrogen concentration on the number of grains per spike. Thus, the higher number of grains per spike observed in the *+Lr19* could be associated with either (i) an improved assimilates partitioning to the spike at anthesis or (ii) a more favourable nitrogen partitioning to the spike.

Although various studies highlighted the impact of assimilates availability during pre-anthesis on the number of fertile florets (e.g., Fischer and Stockman 1980; Fischer 1985; Reynolds et al. 2001), none of them have studied floret development. The results of this study show that the increased number of fertile florets associated with the 7DL.7Ag translocation was a result of a continued development of distal floret primordia within the spikelets, probably associated with a more favourable carbohydrate and nitrogen acquisition by the spikes at anthesis. It is important to highlight that even when a more favourable partitioning to the spike could be produced by different ways, as, for example: dwarfing-genes introgression (Miralles et al. 1998); altering the duration of the spike growth period (Miralles et al. 2000; Slafer et al. 2001; González et al. 2003b; 2003a); and introgression of alien chromatin carrying *Lr19* (Reynolds et al. 2001), the consequence on the number of fertile florets is exactly the same, i.e. increasing spike fertility. All this evidence suggest that independently of the mechanism involved, promoting a higher spike growth during pre-anthesis appears to be the common strategy to increase fertile-floret survival and thereby increase the number of grains per unit area and yield (Slafer et al. 2005).

REFERENCES

Abbate, P.E., Andrade, F.H. and Culot, J.P., 1995. The effects of radiation and nitrogen on number of grains in wheat. *Journal of Agricultural Science,* 124 (3), 351-360.

Fischer, R.A., 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science,* 105 (2), 447-461.

Fischer, R.A. and Stockman, Y.M., 1980. Kernel number per spike in wheat (*Triticum aestivum* L.): responses to preanthesis shading. *Australian Journal of Plant Physiology,* 7 (2), 169-180.

González, F.G., Slafer, G.A. and Miralles, D.J., 2003a. Floret development and spike growth as affected by photoperiod during stem elongation in wheat. *Field Crops Research,* 81 (1), 29-38.

González, F.G., Slafer, G.A. and Miralles, D.J., 2003b. Grain and floret number in response to photoperiod during stem elongation in fully and slightly vernalized wheats. *Field Crops Research,* 81 (1), 17-27.

Miralles, D.J., Katz, S.D., Colloca, A., et al., 1998. Floret development in near isogenic wheat lines differing in plant height. *Field Crops Research,* 59 (1), 21-30.

Miralles, D.J., Richards, R.A. and Slafer, G.A., 2000. Duration of the stem elongation period influences the number of fertile florets in wheat and barley. *Australian Journal of Plant Physiology,* 27 (10), 931-940.

Reynolds, M.P., Calderini, D.F., Condon, A.G., et al., 2001. Physiological basis of yield gains in wheat associated with the *LR19* translocation from *Agropyron elongatum*. *Euphytica,* 119 (1/2), 137-141.

Reynolds, M.P., Pellegrineschi, A. and Skovmand, B., 2005. Sink-limitation to yield and biomass: a summary of some investigations in spring wheat. *Annals of Applied Biology,* 146 (1), 39-49.

Sharma, D. and Knott, D.R., 1966. The transfer of leaf-rust resistance from *Agropyron* to *Triticum* by irradiation. *Canadian Journal of Genetics and Cytology,* 8 (1), 137-143.

Singh, R.P., Huerta-Espino, J., Rajaram, S., et al., 1998. Agronomic effects from chromosome translocations 7DL.7Ag and 1BL.1RS in spring wheat. *Crop Science,* 38 (1), 27-33.

Slafer, G.A., Abeledo, L.G., Miralles, D.J., et al., 2001. Photoperiod sensitivity during stem elongation as an avenue to raise potential yield in wheat. *Euphytica,* 119 (1/2), 191-197.

Slafer, G.A., Araus, J.L., Royo, C., et al., 2005. Promising eco-physiological traits for genetic improvement of cereal yields in Mediterranean environments. *Annals of Applied Biology,* 146 (1), 61-70.

Waddington, S.R., Cartwright, P.M. and Wall, P.C., 1983. A quantitative scale of spike initial and pistil development in barley and wheat. *Annals of Botany,* 51 (1), 119-130.