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SOURCE–SINK RELATIONSHIPS AND GRAIN WEIGHT AT DIFFERENT POSITIONS WITHIN WHEAT SPIKE

ABSTRACT

The response in growth and final weight of grains from basal, middle and apical spikelets to increases in assimilate availability was studied by modifying source–sink relationships during the grain growth period in a wheat cultivar Lok–1. The source–sink relationship was altered in 1500 plants by removing spikelets in various positions i.e. either apical, middle or basal spikelets were pinched off on the day of anthesis. The final grain weight, grain growth rate and grain filling period (duration) was significantly affected by increasing the source capacity per grain by trimming i.e. removing some spikelets. The final grain weight was positively significantly correlated with grain growth rate while it was significantly but inversely correlated with grain filling duration. A clear effect of position of grain in spikelet and its (spikelet) position on the spike could be visualized. The results imply that there is a possibility that the availability of photosynthates is limiting and does not fully satisfy grain growth requirements. It is suggested that in this cultivar during post–anthesis period, grain yield is source limited.

Key words: grain growth rate grain filling duration, source–sink, *Triticum aestivum*

INTRODUCTION

Grain development in wheat is a complex process that responds to interactions among many primary genotypic factors and the environment. Both grain number and grain weight are influenced by many factors within a spike viz. spikelet location and position of each grain, as well as many anatomical factors. Grain number and weight are also influenced by environmental conditions, such as temperature, available light and nutrient supply, etc.

Some authors have concluded that wheat yields are source limited (Winzeler *et al.* 1989) whereas several reports emphasized simultaneous limitation by sink as well (Savin and Slafer 1991). According to Ma *et al.* (1990) cultivars responded differently to partial degraining; and reported that grain growth rate of some cultivars is source limited while other cultivars are not. There have been many studies on assimi–

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late partitioning and the interrelationships of source and sink activities. However we still lack understanding of genotypic response to assimilate accumulation by cereal grains following sink manipulations.

Grain development is determined by the availability of assimilates, the growth potential of the grain and the resistance within the pholem to the movement of assimilates to the grain (Bremner and Rawson 1978). Assimilate availability is determined in part by source–sink ratio and is one factor that may control grain growth rate and final weight. In fact before systematic increases in grain yield can be realized via selection for increased grain growth rate, duration of growth or weight, a better understanding is needed of the attainable limits for these parameters and the mechanisms that control their establishment.

Various researchers have used different means of increasing and decreasing the supply of photosynthates for eg. Fisher and Liang (1976) and Martinez–Carrasco and Thorne (1979) have used thinning as a technique for increasing photosynthate supply for developing grains and increasing grain weight while Winzeler *et al*. (1989) removed entire flag leaf or a portion of flag leaf to reduce the amount of photosynthate available to the developing grains. On the other hand, Slafer and Miralles (1992) did not find any change in the weight of comparable grains after removal of the upper half of the spikes. However, most of the available data on the effect of source–sink manipulation after anthesis indicates the effects on final grain weight i.e. averaged over the whole spike or the whole crop, with no indication of the effects on grain growth dynamics. There is also a lack of information about the effects on grains in different positions within the spike.

Decreasing the reproductive sink size by removal of wheat spikelets has provided a way to study source –sink relationships. Such manipulations enhanced the availability of assimilates to wheat spikes (Jenner 1980). In the present work we were interested in determining whether grain weight in wheat is source limited or sink limited under semi–arid environment. Such studies may provide knowledge about desirable source and sink traits for enhanced grain filling. In instituting this research, we hypothesized that increasing the supply of photosynthate to developing grains would cause a cultivar x treatment interaction if grain weight was restricted by sink capacity.

MATERIAL AND METHODS

A field experiment was conducted in a semi–arid region, Rajkot, Gujarat, India at the Department of Biosciences, in a farmer's field next to the university campus. Seeds of wheat (*Triticum aestivum* L.) cultivar Lok–1 were sown in black cotton soil (vertisol). The experimental plot was ploughed and layered with farmyard manure. At the time of sowing it was fertilized with diammonium phosphate as a basal dose (9 g × m^{-3}). Two times again, it was fertilized with urea (9 g × m^{-3}); the first after 40 days from sowing and second after another 30 days. There were prepared 25 rows, 20 m long and 0.3 m apart. After 15 days, the plants were thinned and a density of 50 plants × m^{-2} was maintained. Irrigation was done once a week from germination up to maturity. Weeding was done regularly and all unwanted plants were hand removed.

Source–sink manipulations were done by modifying spikelet number. At anthesis, main shoots of all the plants in the entire area (having an identical number of spikelets per spike; in this case it is 12) were tagged. The spikelets were numbered from base to tip of the spike; 1 being the lower most spikelet at the base and 12^{th} spikelet being the apical most at the tip. The entire spike was divided into 3 parts. The basal part consisting of 1 to 4 spikelets, middle part consisting of 5 to 8 spikelets and apical part consisting of 9 to 12 spikelets. In all, 4 sub–plots were prepared each of 5 rows. 1^{st} plot was control where all spikelets were left intact. In the other 3 plots, partial degraining was done by removing spikelets at various positions.

In 2^{nd} plot, the spikelets of lower region i.e. 1–4 spikelets were kept intact and others were pinched off by hand. In 3^{rd} plot, only middle region spikelets i.e. 5–8 spikelets were kept intact and other spikelets i.e. below and above the middle region were pinched off. In the 4^{th} plot, only upper spikelets i.e. 9–12 spikelets were kept intact and all the others were pinched off. All pinching off was done by hand taking care that other spikelets are not damaged.

At an interval of 5–6 days, 10 spikes from each plot were harvested and brought to the laboratory. Each individual grain from respective spikelet was separated and then oven dried at 65°C to a constant weight. Then the dry weight was measured. All the grains from each spikelet in control and treated plants were analyzed but the data of a single representative spikelet is given. One spikelet from each region of the spike i.e. from the lower region (3^{rd} spikelet), from the middle region (7^{th} spikelet) and from the upper region (11^{th} spikelet) was selected. Each spikelet had 2 basal and 1 apical grains (except 11^{th} and 12^{th} spikelets; where apical grains were absent). The basal grains of 3rd spikelet are named as 3 and 3B and apical grain as 3A. Similarly, the basal grains of 7^{th} spikelet are named as 7 and 7B and apical grain as 7A. 11^{th} spikelet had only basal grains hence they are named as 11 and 11B. The entire experiment was repeated twice.

Statistical Analysis

Seed dry weight data is fitted to polynomial equation of the type

$$Y = a^0 + bx + cx^2 + dx^3$$

where Y is grain dry weight,
x is a number of days after anthesis
and

a, b, c and d are regression coefficients.

The best fit curve was cubic polynomial which was determined statistically. Duration of the grain filling was calculated using the formula:

Maximum weight of the grain was calculated by substituting x (x = duration from the above) in cubic polynomial equation. Average

$$Duration = \frac{C''' \times c^2 - 3bd}{3d}$$

rate of grain filling per day is calculated by dividing maximum weight by duration.

RESULTS AND DISCUSSION

In this study, source–sink relationships were modified by manipulating spikelet number. Sink strength was reduced through removal of entire spikelets. Trimming the spike at various positions did not result in further floret development nor it increased grain set in the remaining spikelets. Therefore it reduced the number of grains per spike, and effectively increased the potential source availability for each grain.

Table 1

Maximum grain dry weight, grain growth rate and grain filling duration of a single grain of representative spikelets of control and treated plants

Number of the grain	Maxmimum weight [mg]		Rate [mg increase per day]		Duration [days]	
	Control	Treated	Control	Treated	Control	Treated
3	53.72	63.44	1.0095	1.4152	53.22	44.83
3A	30.80	47.29	0.5543	1.0736	56.58	44.05
3B	49.42	64.54	0.9235	1.5873	53.52	40.66
7	67.93	74.91	1.4505	1.7134	46.83	44.30
7A	54.15	64.13	1.0893	1.3903	49.71	46.13
7B	66.83	73.30	1.3997	1.6453	47.75	44.55
11	62.05	66.26	1.3278	1.5058	46.73	44.00
11B	60.66	66.46	1.2710	1.5418	47.72	43.10

3 and 3B are basal grains and 3A apical grain of 3rd spikelet
7 and 7B are basal grains and 7A apical grain of 7th spikelet
11 and 11B are basal grains of 11th spikelet

Spikelet removal at different positions resulted in differential effect on grain, depending upon its position in spikelet as well as position of spikelet on the spike. This sink manipulations not only affected final grain weight but also affected grain growth rate and effective grain filling period as shown in Table 1. Comparison of maximum grain dry weight of control and treated plants revealed that maximum increase was in the grains of lower spikelet and minimum increase in the upper spikelet. It indicates that thought the possibility of increasing the dry weight of all the grains exists, potentiality exists more for grains of lower spikelet than for the grains of other two spikelets. When you compare the basal and apical grains, the increase was more in the apical grains i.e. grains which were smaller in size (less weight) showed maximum response. In other words maximum increase in weight was noted.

Grain weight is a component of grain yield and duration of grain filling is a component of maturity. Both are important traits in applied plant breeding and both depend upon the grain filling process. In the present work, when you compare the duration of grain dry weight increase, again marked differences were observed, depending upon the position of the grains on the spike. Duration of grain filling of all the grains of control plants was distinctly more than that of treated plants. Here also the apical grains of the control plants took longer duration than the basal grains.

Many researchers have reported a positive correlation between duration of grain filling and final grain weight in wheat (Sofield *et al*. 1977, Gebeyehou *et al*. 1982) indicating that increasing grain weight could result in longer durations of grain filling. But our results do not support this conclusion. Here, the control plants exhibited a longer duration but resulted in lesser maximum grain weight (Table 1). In fact, final grain weight and duration showed a significant but inverse correlation. Gebeyehou *et al*. (1982) found little genetic association between rate and duration of grain filling and suggested that it should be possible for increased rate of filling and grain weight without increasing duration.

The relationship among rate and duration of grain filling and final grain weight are also important. Bruckner and Frohberg (1982) estimated average grain filling rate as the ratio of maximum weight to duration, both estimated from quadratic polynomial curves. Here a similar approach was followed to estimate maximum final weight, duration and average grain filling rate per day but the polynomial curves were cubic in nature. All the grains of treated plants had higher rate of dry matter accumulation irrespective of their position on the spike. The rate of grain filling of apical grains was slightly less than the basal grains. There was a significant positive correlation between maximum weight and rate of grain filling (Table 2). Further the differences were found within the spikelets and also the position effect could be visualized. A partial correlation was worked out between maximum weight and rate or duration. This analysis revealed that both rate and duration are significantly correlated (linearly and inversely respectively) and both are independent (Table 2).

Table 2

Values of partial correlation coefficients where grain growth rate ($r_{12.3}$) or grain filling duration ($r_{13.2}$) has been held constant and linear correlation coefficients between dependent variable maximum weight and duration (r_{12}) or rate (r_{13})

Partial correlation coefficients	Linear correlation coefficients
$r_{12.3} = -0.855$	$r_{12} = 0.731$
$r_{13.2} = +0.982$	$r_{13} = 0.968$

All values significant at $\alpha < 0.001$

Thus in this cultivar (at least) it appears that yield might be source limited (because removing of some spikelets resulted in increasing the grain weight of the remaining grains) as has been reported by other au–thors (Martinez–Carrasco *et al*. 1988, Grabau *et al*. 1990, Ma *et al*. 1990). However the effect of reducing number of grains at a particular position had different effect on different spikelets. When the number of grains were reduced, individual grain weight increased maximum in grain of lower spikelet. This may be because on decreasing the number of grains, each of the remainder grains had a greater amount of assimi–lates available which increased the individual grain weight and sug–gests that these particular grains were growing under a source limited condition. When the same condition was applied to the grains of upper spikelet, the increase in weight was considerably less. This implies that their potential demand for assimilates was satisfied independently of the total number of grains on the spike; since these grains have lower weight potential, and these grains did not experience any additional growth as a consequence of a smaller sink–source ratio. Similar results were reported by Fischer and HilleRis Lambers (1978) and Ledent and Stoy (1985).

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