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Yield Performance of Wheat Isolines With Different Dosages of the Short Arm of Rye  
Chromosome 1

A Thesis submitted in partial satisfaction  
of the requirements for the degree of

Master of Science

in

Plant Biology

by

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August 2013

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The Thesis of Dinusha C. Maheepala Mudalige is approved:

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Dinusha Maheepala

Riverside, CA

August 29, 2013.

## **Dedications**

To my loving parents

**Mr. Sumith Maheepala & Mrs. Kumudini Wickramarachchi**

&

My lovely fiancée

**Miss. Kathryn McGovern**

## ABSTRACT OF THE THESIS

### Yield Performance of Wheat Isolines With Different Dosages of the Short Arm of Rye Chromosome 1

by

Dinusha C. Maheepala Mudalige

Master of Science, Graduate Program in Plant Biology  
University of California, Riverside, August 2013  
Dr. Giles Waines, Chairperson

Translocations of the short arm of rye (*Secale cereale* L.) chromosome 1 (1RS) in wheat (*Triticum aestivum* L.) are known to increase root biomass. Such an increase enhances water and nutrient uptake and hence improves grain yield. Multiple doses of 1RS in wheat show an inversely proportional relationship with the metaxylem vessel diameter of wheat root. Previous research has shown that wheat genotypes with reduced metaxylem diameters perform better than those with larger metaxylem diameters under drought conditions. Therefore, a series of greenhouse and field experiments were carried out to evaluate phenotypic characters associated with varying dosages of 1RS including grain yield. The genotypes used were cv. Pavon 76 with zero dosages of 1RS ( $R_0$ ), Pavon 1RS.1AL with a single and double doses of 1RS ( $RA_1$  and  $RA_2$ ), Pavon 1RS.1DL ( $RD_2$ )

also with two doses of 1RS and Pavon 1RS.1AL-1RS.1DL (RAD<sub>4</sub>) with four dosages of 1RS.

Greenhouse experiments were carried out in 2012 and 2013 while a field experiment was conducted in 2013. The genotypes were grown under well-watered and terminal drought treatments. In the greenhouse, the five genotypes were grown in sand-tube experiments using a randomized complete block design (2012) under well-watered conditions or a factorial design under well-watered and droughted conditions in 2013. A split-plot design was used for the field experiment.

Results showed an increase in grain yield in response to an increase in root biomass up to two dosages of 1RS. Although the shoot and root biomass was further increased in the line with four 1RS translocations it had lowered grain yield compared to other genotypes because of the competition by roots for resource allocation leading to the abortion of embryos. Disomic translocation 1RS.1AL produced the highest grain yield under well-watered conditions while it was similar in performance to other genotypes under terminal drought conditions. Genotypes with 1RS translocations did not show greater grain yield under drought when compared to each other or the control. As the number of 1RS arms increased from 2 to 4 in RAD<sub>4</sub>, grain yield decreased in the well-watered treatment, but shoot and root biomass increased compared to other genotypes.

## TABLE OF CONTENTS

|                              |    |
|------------------------------|----|
| Acknowledgements.....        | iv |
| Dedications .....            | v  |
| Abstract of the Thesis ..... | vi |
| List of Tables .....         | ix |
| List of Figures.....         | x  |
|                              |    |
| Abstract.....                | 1  |
| Introduction.....            | 3  |
| Materials and Methods.....   | 8  |
| Results.....                 | 13 |
| Discussion.....              | 17 |
| Conclusion .....             | 21 |
| References.....              | 36 |



## LIST OF TABLES

|   |    |
|---|----|
| TABLE 1 MEAN VALUES OF DAYS TO BOOTING (DTB), DAYS TO HEADING (DTH), DAYS TO ANTHESIS (DTA), DAYS TO MATURITY (DTM), PLANT HEIGHT (PH), NUMBER OF TILLERS AND NUMBER OF SPIKES PER PLANT FOR PAVON 76 (R <sub>0</sub> ) AND ITS TRANSLOCATION LINES WITH ONE (RA <sub>1</sub> ), TWO (RA <sub>2</sub> AND RD <sub>2</sub> ), AND FOUR (RAD <sub>4</sub> ) 1RS GROWN IN A SAND-TUBE EXPERIMENT UNDER WELL-WATERED CONDITION IN GREENHOUSE IN 2012.....                                       | 22 |
| TABLE 2 MEAN VALUES OF DAYS TO BOOTING (DTB), DAYS TO HEADING (DTH), DAYS TO ANTHESIS (DTA), DAYS TO MATURITY (DTM), PLANT HEIGHT (PH), NUMBER OF TILLERS AND NUMBER OF SPIKES PER PLANT FOR PAVON 76 (R <sub>0</sub> ) AND ITS TRANSLOCATION LINES WITH ONE (RA <sub>1</sub> ), TWO (RA <sub>2</sub> AND RD <sub>2</sub> ), AND FOUR (RAD <sub>4</sub> ) 1RS GROWN IN A SAND-TUBE EXPERIMENT UNDER WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE IN 2013.....                 | 23 |
| TABLE 3 MEAN VALUES OF SHOOT BIOMASS (SBIO), LONGEST ROOT (LR), SHALLOW ROOT WEIGHT (SR), DEEP ROOT WEIGHT (DR), ROOT BIOMASS (RBIO), NUMBER OF GRAINS, GRAIN WEIGHT (GW) AND GRAIN YIELD (GY) PER PLANT FOR PAVON 76 (R <sub>0</sub> ) AND ITS TRANSLOCATION LINES WITH ONE (RA <sub>1</sub> ), TWO (RA <sub>2</sub> AND RD <sub>2</sub> ), AND FOUR (RAD <sub>4</sub> ) 1RS GROWN IN A SAND-TUBE EXPERIMENT UNDER WELL-WATERED CONDITION IN GREENHOUSE IN 2012.....                       | 24 |
| TABLE 4 MEAN VALUES OF SHOOT BIOMASS (SBIO), LONGEST ROOT (LR), SHALLOW-ROOT WEIGHT (SR), DEEP-ROOT WEIGHT (DR), ROOT BIOMASS (RBIO), GRAIN WEIGHT (GW), NUMBER OF GRAINS AND GRAIN YIELD (GY) PER PLANT FOR PAVON 76 (R <sub>0</sub> ) AND ITS TRANSLOCATION LINES WITH ONE (RA <sub>1</sub> ), TWO (RA <sub>2</sub> AND RD <sub>2</sub> ), AND FOUR (RAD <sub>4</sub> ) 1RS GROWN IN A SAND-TUBE EXPERIMENT UNDER WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE IN 2013..... | 25 |
| TABLE 5 MEAN VALUES OF PLANT HEIGHT (PH), NUMBER OF TILLERS AND NUMBER OF SPIKES, SHOOT BIOMASS (SBIO), GRAIN WEIGHT (GW), GRAIN YIELD (GY) AND HARVEST INDEX (HI) PER PLANT FOR PAVON 76 (R <sub>0</sub> ) AND ITS TRANSLOCATION LINES WITH ONE (RA <sub>1</sub> ), TWO (RA <sub>2</sub> AND RD <sub>2</sub> ), AND FOUR (RAD <sub>4</sub> ) 1RS GROWN IN A SPLIT-PLOT EXPERIMENT UNDER WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN THE FIELD IN 2013.....                             | 26 |

## LIST OF FIGURES

|   |    |
|---|----|
| FIGURE 1 MEAN SHOOT BIOMASS PER PLANT FOR PAVON 76 ( $R_0$ ) AND ITS TRANSLOCATION LINES WITH ONE ( $RA_1$ ), TWO ( $RA_2$ AND $RD_2$ ), AND FOUR ( $RAD_4$ ) 1RS GROWN IN SAND-TUBE EXPERIMENTS UNDER WELL-WATERED CONDITION IN GREENHOUSE IN 2012, AND WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE AND IN FIELD IN 2013. | 27 |
| FIGURE 2 MEAN SHALLOW ROOT WEIGHT PER PLANT FOR PAVON 76 ( $R_0$ ) AND ITS TRANSLOCATION LINES WITH ONE ( $RA_1$ ), TWO ( $RA_2$ AND $RD_2$ ), AND FOUR ( $RAD_4$ ) 1RS GROWN IN SAND-TUBE EXPERIMENTS UNDER WELL-WATERED CONDITION IN GREENHOUSE IN 2012, AND WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE IN 2013.        | 28 |
| FIGURE 3 MEAN DEEP ROOT WEIGHT PER PLANT FOR PAVON 76 ( $R_0$ ) AND ITS TRANSLOCATION LINES WITH ONE ( $RA_1$ ), TWO ( $RA_2$ AND $RD_2$ ), AND FOUR ( $RAD_4$ ) 1RS GROWN IN SAND-TUBE EXPERIMENTS UNDER WELL-WATERED CONDITION IN GREENHOUSE IN 2012, AND WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE IN 2013.           | 29 |
| FIGURE 4 MEAN GRAIN YIELD PER PLANT FOR PAVON 76 ( $R_0$ ) AND ITS TRANSLOCATION LINES WITH ONE ( $RA_1$ ), TWO ( $RA_2$ AND $RD_2$ ), AND FOUR ( $RAD_4$ ) 1RS GROWN IN SAND-TUBE EXPERIMENTS UNDER WELL-WATERED CONDITION IN GREENHOUSE IN 2012, AND WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE AND IN FIELD IN 2013.   | 30 |
| FIGURE 5 MEAN GRAIN NUMBER PER PLANT FOR PAVON 76 ( $R_0$ ) AND ITS TRANSLOCATION LINES WITH ONE ( $RA_1$ ), TWO ( $RA_2$ AND $RD_2$ ), AND FOUR ( $RAD_4$ ) 1RS GROWN IN SAND-TUBE EXPERIMENTS UNDER WELL-WATERED CONDITION IN GREENHOUSE IN 2012, AND WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE IN 2013.               | 31 |
| FIGURE 6 MEAN SINGLE GRAIN WEIGHT FOR PAVON 76 ( $R_0$ ) AND ITS TRANSLOCATION LINES WITH ONE ( $RA_1$ ), TWO ( $RA_2$ AND $RD_2$ ), AND FOUR ( $RAD_4$ ) 1RS GROWN IN SAND-TUBE EXPERIMENTS UNDER WELL-WATERED CONDITION IN GREENHOUSE IN 2012, AND WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE IN FIELD IN 2013.         | 32 |
| FIGURE 7 MEAN NUMBER OF SPIKELETS PER PLANT FOR PAVON 76 ( $R_0$ ) AND ITS TRANSLOCATION LINES WITH ONE ( $RA_1$ ), TWO ( $RA_2$ AND $RD_2$ ), AND FOUR ( $RAD_4$ ) 1RS GROWN IN SAND-TUBE EXPERIMENTS UNDER WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE IN 2013.  | 33 |

FIGURE 8 MEAN FLAG LEAF AREA PER PLANT FOR PAVON 76 ( $R_0$ ) AND ITS TRANSLOCATION LINES WITH ONE ( $RA_1$ ), TWO ( $RA_2$  AND  $RD_2$ ), AND FOUR ( $RAD_4$ ) 1RS GROWN IN SAND-TUBE EXPERIMENTS UNDER WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE IN 2013. .... 34

FIGURE 9 MEAN PERCENT LOSS OF GRAIN YIELD PER PLANT FOR PAVON 76 ( $R_0$ ) AND ITS TRANSLOCATION LINES WITH ONE ( $RA_1$ ), TWO ( $RA_2$  AND  $RD_2$ ), AND FOUR ( $RAD_4$ ) 1RS GROWN UNDER WELL-WATERED AND TERMINAL DROUGHT CONDITIONS IN GREENHOUSE IN FIELD IN 2013. .... 35

## Abstract

It was reported that wheat cultivars with reduced metaxylem diameters in roots produced higher grain yields compared to those with larger metaxylem diameters under drought conditions, but not under well-watered conditions. Multiple dosages of rye 1RS translocations in wheat were reported to reduce root metaxylem diameter. The dosage number of 1RS translocations was inversely proportional to the root metaxylem diameter.

Two greenhouse experiments and a field experiment were carried out at University of California, Riverside in 2012 and 2013 under well-watered and terminal drought treatments to test whether translocation lines of wheat cv. Pavon 76 containing 1(RA<sub>1</sub>), 2 (RA<sub>2</sub> and RD<sub>2</sub>), and 4 dosages (RAD<sub>4</sub>) of 1RS produced higher grain yields than the control with zero dosage (R<sub>0</sub>) under terminal drought. Drought in the field experiment reduced grain yield significantly. Grain yield of RA<sub>2</sub> (23.9 g<sup>-1</sup>) was significantly greater than those of RD<sub>2</sub> (20.6 g<sup>-1</sup>) and RAD<sub>4</sub> (17.3 g<sup>-1</sup>) under well-watered field conditions. Also, grain yield of RAD<sub>4</sub> was significantly less than those of RA<sub>1</sub>, R<sub>0</sub>, and RD<sub>2</sub> under well-watered conditions. Under drought field conditions, only significant difference in grain yield was found between RA<sub>1</sub> (14.7 g<sup>-1</sup>) and RAD<sub>4</sub> (12.4 g<sup>-1</sup>). Harvest index was significantly greater in well watered (44.2%) than in droughted (34.6%) field conditions. On average, genotype R<sub>1</sub> (42.3%) and RA<sub>2</sub> (40.6%) had higher harvest index than RD<sub>2</sub> (38.3%) and DAR<sub>4</sub> (35.5%) in the field. Also, R<sub>0</sub> (40.2) and RD<sub>2</sub> (38.3) had higher harvest index than DAR<sub>4</sub>. In general, Pavon 1RS.1AL carrying double doses of 1RS showed higher grain yields under wet treatments. Pavon 1RS.1AL-1RS.1DL

carrying four doses of IRS produced largest shoot and root biomasses, but relatively had least grain yield. There was a negative correlation between the grain yield loss and metaxylem diameter in roots at mild stress levels (~36%).

## **Introduction**

The “Green Revolution” was the crowning plant-breeding achievement of 1960s and Norman Borlaug was the driving force behind it. This breakthrough radically increased the amount of grain yield of major cereal crops such as wheat. Dr. Borlaug received the Nobel Peace Prize as his initiatives dissipated the hunger crisis in developing countries such as India, Mexico and Pakistan. Nevertheless, barely half a century later, we have bounced back to the alarming situations that prevailed prior to the Green Revolution. However, it cannot be ruled out that the alarmist tone has more to do with fight for research funding than the actual or predicted food shortages.

The rate of contemporary human population increase has deemed it futile to consider feeding the world without sacrificing environmental sustenance. Although curbing our population explosion is beyond the scope of the current research, one cannot help but be optimistic about his or her future. Science, strengthened by the capability of genetic modifications in harmony with a combination of conventional and molecular plant breeding carry the promise of introducing new crop varieties that deliver harvests to battle hunger regardless of what unpredictable climate conditions the future holds.

Plant root system holds a great potential for crop improvement. Traditionally, all breeding is done based on the aboveground parts of plants; roots are ignored. In the decades following the Green Revolution, it has been shown that a larger root system is able to absorb more water and nutrients from the soil and thereby further amplify the

grain yield (Donald 1968). Therefore, it is vital to look at creative ways of improving the root system of wheat.

Transgenic wheats that carry translocations of the short arm of rye chromosome 1 (1RS) have been useful in breeding programs for many decades. Translocation 1RS.1BL introduced into wheat leaf rust, stem rust and powdery mildew resistance genes from rye (Graybosch et al. 1999) and it spread to commercial wheat the world over (Tang et al. 2009). However, even while pathogens evolved to overcome this resistance, the translocation still kept spreading, because it offered a measurable grain yield advantage. That yield advantage was associated with increased root biomass (Ehdaie et al. 2003).

On the basis of the original translocation 1RS.1BL, Lukaszewski (1997) developed a set of isogenic lines with translocations of the same 1RS to each of the three possible genomic locations in wheat: 1RS.1AL, 1RS.1BL and 1RS.1DL. The task was performed in cv. Pavon 76, a hexaploid commercial bread-wheat line developed by the International Maize and Wheat Improvement Center (CIMMYT), Mexico. These translocation lines showed increased root biomass in the ascending order of 1RS.1BL < 1RS.1DL < 1RS.1AL compared to Pavon 76. It was predicted that there were loci on 1RS that influence root characters under well watered and drought conditions (Ehdaie et al. 2003).

Increased root biomass has been experimentally shown to increase grain yield. This is probably because large root systems absorb nutrients and water more efficiently compared to plants with smaller root systems (Ehdaie et al. 2003). Better absorption by

the plant in turn reduces the amount of nitrogen leached into the soil, thereby diminishing a major factor of pollution by modern-day agriculture (Waines and Ehdaie 2007).

A remarkable characteristic pertaining to the centric 1RS translocations in Pavon 76 is that the seminal root length density, defined as the length of roots per unit volume of soil, is higher than many commercial bread wheat varieties in deep layers of soil. More deep roots in the subsoil layers increase a plant's ability to reach water deep in the ground. This trait is increasingly becoming crucial as the usable fresh water resources on Earth shrink. Several lines ranging from zero to four copies of 1RS translocations in a Pavon 76 genetic background (i.e. R<sub>0</sub>, RA<sub>1</sub>, RA<sub>2</sub>, RD<sub>2</sub> and RAD<sub>4</sub>) have been developed in Pavon 76 wheat. Sharma et al. (2010) have shown that the root system of wheat-rye translocation lines may be further developed via the increase in the dosage of 1RS. However, they did not measure the grain yield in their study.

Another crucial anatomical feature associated with the 1RS translocations in Pavon 76 wheat is that the number of metaxylem vessels and more importantly, the metaxylem vessel diameter of the seminal roots show a decreasing trend with increasing 1RS dosage (Sharma et al. 2010). To be elaborate, the mean metaxylem diameters were 58 µm, 58 µm, 54 µm, 45 µm and 42 µm for R<sub>0</sub>, RA<sub>1</sub>, RA<sub>2</sub>, RD<sub>2</sub> and RAD<sub>4</sub>, respectively (Sharma et al. 2010). The larger diameter of RA<sub>1</sub> may have been due to heterosis. Studies have shown that some Australian commercial wheats with reduced metaxylem diameters (less than 55 µm) produced better grain yields compared to wheat genotypes with larger metaxylem diameters (about 65 µm) under terminal drought conditions though there was



a yield reduction in all these genotypes compared to well-watered conditions. Furthermore, the grain yield of the above wheats was not different regardless of variations in metaxylem diameter under well-watered conditions (Richards and Passioura 1989).

It has been found that quantitative trait loci (QTL) for the metaxylem diameter are located on distal end of the long arm of rice (*Oryza sativa* L.) chromosome 10 (Uga et al. 2008). Rye 1RS is syntenic to rice chromosome 10 (Hackauf et al. 2009). Therefore, there is a chance that a QTL affecting the metaxylem diameter may also reside on 1RS.

Wheats with 1RS chromosome translocations do not produce dough with good bread-making qualities (Barbeau et al. 2003); the dough is overly sticky with reduced amount of gluten. Another reason for this poor quality of dough may be the presence of secalin proteins encoded by rye 1RS (Kim et al. 2005). Genes encoding gluten proteins in wheat are located, among others, on the short arm of wheat chromosome 1B, the arm replaced by 1RS in the most common wheat-rye translocation (Lukaszewski 2006). As a consequence, efforts have been made to engineer centric translocation 1RS so that gluten-producing loci would be added to 1RS so the lines would produce satisfactory bread. At the same time, genes responsible for the metaxylem diameter must be left intact in modified 1RS. This requires a good resolution genetic map of 1RS, one that depicts all genes responsible for the anatomical trait so that these loci can be preserved during the course of genetic selection (Sharma et al. 2011).

Global climate seems to be going through an era of drastic changes (Williams et al. 2007). The annual rainfall levels in most crop growing areas are either in decline or erratic. It is necessary to select for crop genotypes that do equally well under water-rich as well as drought conditions. It can be put forward, based upon the research mentioned thus far, that wheats with multiple copies of 1RS would be an ideal way of breeding such cultivars. These lines with large root system should be able to perform well under rainy spells while outperforming those genotypes with larger metaxylem diameters under drought conditions. Therefore, the dosage effect of the short arm of rye chromosome 1 provides a valuable opportunity for wheat breeders to produce wheat cultivars with improved performance under water deficits.

The aim of the research described here was to test the hypothesis that increasing dosage of 1RS translocations in wheat increases root biomass and consequently grain yield under well-watered and drought conditions. Two greenhouse experiments and a field experiment were performed to test this hypothesis.

## Materials and Methods

Plant material for this study consisted of the following lines: cv. Pavon 76, as control, zero doses of rye chromosome arm 1RS; Pavon 1RS.1AL and Pavon 1RS.1DL were both disomic for respective translocations. Pavon 1RS.1AL-1RS.1DL combined the two translocations in one line, which, therefore, carried four doses of 1RS. A cross between standard Pavon 76 and Pavon 1RS.1AL created a line with a single dose of 1RS. The cross was done by hand, on greenhouse-grown plants.

### Greenhouse Experiments

Two greenhouse experiments were conducted at the University of California at Riverside starting early January in 2012 and in 2013 using a randomized complete block designs with six replicates. In the first year, the five genotypes were grown only under well-watered conditions. The second year experiment included both well-watered (wet) and terminal drought (dry) treatments. A factorial design with 10 treatments (5 genotypes  $\times$  2 irrigation regimes) was used.

The sand-tube technique of growing plants described by Ehdaie and Waines (2006) was used to measure root system and shoot traits. Seeds from the five genotypes were germinated in Petri dishes and five-day old seedlings were transplanted into clear plastic sleeves, filled with 8.5 kg of industrial grade #30 silica sand enclosed in a 0.80 m tall polyvinyl chloride (PVC) tube that was 0.10 m in diameter. One seedling was planted per sleeve. The bottom of each plastic sleeve had two holes for drainage and covered with

a filter paper to prevent sand loss with drain water. Prior to planting, the plastic sleeves were brought to the water holding capacity by supplying the amount of water equal to 24% of the weight of sand in each tube on two consecutive days.

After planting, each tube was given 100 mL of half-strength Hoagland solution each day. The amount of water was gradually increased in accordance with the growth and development of wheat plant. At late booting, the amount of water given to the drought treatment was reduced to 60 % of that in the wet treatment. From that point on, the volume of water given to the dry treatment was constantly reduced until terminal drought in the grain-filling stage. Watering was stopped for plants undergoing wet treatment when each plant reached physiological maturity.

Days to booting, heading, anthesis and maturity were counted from the germination date. A plant was considered to be at physiological maturity when its main tiller turned yellow. Plant height, length of the flag leaf and the width of the flag leaf were measured. Numbers of tillers and spikes per plant were counted.

Plants were kept in the greenhouse after reaching physiological maturity. Then the spikes of each plant were harvested into separate paper bags and the remaining aboveground portions of each plant were harvested from the sand surface. All this material was stored in an air-drying oven at 80 °C for 48 hours and weighed. Spikes of each plant were threshed, numbers of seeds per plant were counted and the grain yield was weighed.

The sand filled plastic sleeves containing the root systems were taken out of the PVC tubes and washed in a water-filled basin. The length of the deepest root was measured before dividing the whole root system into two segments at 0.30 m from the base of the stem. The resulting two segments of the root system was air dried in the glasshouse and further drying was done in an air-drying oven at 80 °C for 48 hours. Afterwards, the weight of the shallow roots, from the base of the stem to 0.30 m in length and the weight of the deep roots, the portion deeper than 0.30 m, were measured.

#### Field Experiment

A split-plot design with six replications was used for the field experiment. The planting was done on January 27<sup>th</sup>, 2013 at the Agricultural Operations field station in Riverside, California. An N-P-K fertilizer was added to the soil prior to planting. The field soil type was a sandy loam. Two irrigation treatments, namely well-watered and terminal drought, were used.

The main plots consisted of the two irrigation regimes and the split-plots consisted of the genotypes. Each plot was a raised bed containing three 4.0 m rows. The distance between the rows was 0.13 m and between the plants in a row was 0.05 m. An unplanted bed was left between two adjacent main plots.

Seeds were hand-sown into the soil. Germination was close to 100 percent. After seeding, a drip irrigation system was installed with two drip lines per bed placed on either side of the middle row. The flow rate in a drip line was 0.056 liters per minute per meter of drip tube.

All plots were watered for an hour three days a week. When plants reached late booting stage in half of plots in dry treatments, irrigation time for the dry treatment was reduced from an hour to half an hour. Two weeks later, irrigation was terminated for the plots under drought treatment, whereas plots under well-watered treatment were continuously watered for an hour until plants in more than fifty percent of the plots reached maturity. After maturity, three readings of plant height from soil surface to the tip of the main spike, excluding the awns, in the middle row were taken. A length of 0.50 m of a row without any gaps was selected in the middle row of each bed and the number of tillers and spikes were counted. In each plot, plants on 0.50 m of each side of the middle row were discarded. Then the remaining plants in the middle row were harvested by hand from the soil surface, put in a plastic bag and placed in a large dryer for a week before shoot biomass was measured. Afterwards, the material was mechanically threshed and seed was collected and further cleaned by hand. Finally, the total grain yield as well as the weight of 100 grains of each genotype was measured.

## Calculations and Data Analysis

The average of the three readings of plant height per each row was calculated to obtain mean plant height for each plot. The mean of the 100 grain weight was used to calculate mean seed weight. Using the number of plants on the middle row, shoot biomass, grain yield, number of tillers and spikes were calculated on plant basis. Harvest index was calculated as the ratio of grain yield to shoot biomass. The data obtained or calculated was subjected to analysis of variance (ANOVA) for each year (Steel et al. 1997). Means were compared using LSD (0.05 or 0.10). Correlation analysis was used to quantify relationship between traits.

## Results

### Greenhouse Studies

In 2012, the main effect of genotype was significant for days to booting, heading, anthesis, maturity, shoot biomass, shallow root weight and root biomass. In 2013, the main effect of irrigation regime was significant for days to anthesis, maturity, plant height, flag leaf width, flag leaf area, number of tillers, number of spikes, shoot biomass, grain yield, number of grains, grain weight, shallow root weight, deep root weight and root biomass. Moreover, the main effect of genotype was significant for days to booting, heading, anthesis, maturity, plant height, flag leaf width, flag leaf area, number of tillers, number of spikelets, shoot biomass, grain yield, number of grains, shallow root weight, deep root weight and root biomass. The number of tillers, shoot biomass, shallow root weight, deep root weight and root biomass significant genotype  $\times$  irrigation interaction at  $P = 0.05$ . Genotype RAD<sub>4</sub> always was late to reach each phenological stage compared with other genotypes. It was followed by RA<sub>2</sub>, RD<sub>2</sub>, RA<sub>1</sub> and R<sub>0</sub> in descending order in terms of the number of days to reach each stage regardless of the year and treatment.

### Wet treatments

All genotypes in 2013 in the wet treatment showed a significant increase in shoot biomass, shallow root weight, deep root weight, grain yield and number of grains compared to those in 2012. The time differences to reach booting, heading, anthesis and maturity between RAD<sub>4</sub> and R<sub>0</sub> were 12, 14, 14, 16 and 4 days. In 2013, the time



differences were 9, 10, 9, and 4 days, respectively. Plant height ranged from about 73 cm to 85 cm (Tables 1 and 2). There was an increase and more variation in the number of tillers per plant for each genotype in 2013 compared to 2012. Genotype RAD<sub>4</sub> had the highest shoot biomass for both years in the wet treatment (Figure 1). Genotype RA<sub>2</sub> was also in the same category as RAD<sub>4</sub> in terms of shoot biomass in 2013.

Shallow root weight of RAD<sub>4</sub> was significantly larger than the other genotypes in the wet treatment in both years. R<sub>0</sub> had the smallest shallow root weight (Figure 2). Genotype RAD<sub>4</sub> had a significantly larger deep root weight in 2013 wet treatment (Figure 3). Although RAD<sub>4</sub> also had the largest deep root weight in the 2012 wet treatment, the differences among genotypes were not as pronounced as in 2013. Genotype RA<sub>2</sub> had the largest grain yield compared to the rest of the genotypes (Tables 3, 4 and Figure 4). Genotype RA<sub>1</sub> had the highest number of grains in 2012 while RA<sub>2</sub> had the highest number of grains per plant in 2013 in the wet treatment. However, there was no significant difference between these two genotypes in either year (Figure 5). Genotype RD<sub>2</sub> had the lowest number of grains per plant in 2012. Both RD<sub>2</sub> and RAD<sub>4</sub> had the lowest number of grains in 2013 and these were significantly lower than the remaining genotypes. There were no significant differences in grain weight among the genotypes in either year (Figure 6).

The number of spikelets was the lowest in R<sub>0</sub> in both years. This number was significantly lower than that for RA<sub>2</sub> in the wet treatment in 2013 (Figure 7). The number of spikelets in the wet treatment in 2013 for genotypes RA<sub>1</sub>, RD<sub>2</sub> and RAD<sub>4</sub> was not

significantly different from RA<sub>2</sub>. The flag leaf area for R<sub>0</sub> was significantly higher than that for RA<sub>2</sub> in the wet treatment in 2013. This character ranged between R<sub>0</sub> and RA<sub>2</sub> in the remaining genotypes (Figure 8). There were no significant differences in the percent loss of grain yield for any of the genotypes in the wet treatment in 2013 (Figure 9). It was the lowest in R<sub>0</sub> and highest in RD<sub>2</sub>.

#### Dry treatment

The time differences to reach booting, heading, anthesis and maturity between RAD<sub>4</sub> and R<sub>0</sub> were 7, 8, 3 and 4 days, respectively. Plant height ranged from 68 cm to 74 cm (Tables 1 and 2). It was significantly lower in RAD<sub>4</sub> compared to other genotypes. None of the remaining phenotypic characters were significantly different among the genotypes in the dry treatment.

#### Field Study

The main effect of irrigation regime was significant for grain weight, shoot biomass, grain yield, and harvest index, but not for plant height, number of tillers and spikes per plant. The main effect of genotype was significant only for grain yield and harvest index. Only grain yield showed significant genotype × irrigation interaction at  $P = 0.08$ . Considering both treatment, plant height showed small variation ranging from 75 to 78 cm. Little variation was found for number of tillers per plant ranging from 3 to 4 and for number of spikes per plant ranging from 2 to 3 (Table 5). Seed weight was significantly higher in well-watered (44.4 mg) than in drought (29.8 mg) treatment.

However, the differences among the genotypes for seed weight were not significant in both treatments. Similar trends were found for shoot biomass per plant (Table 5).

Grain yield per plant was significantly higher in well-watered (20.9 g) than in drought (13.4 g) treatment. Grain yield of RA<sub>2</sub> (23.9 g) was significantly greater than those of RD<sub>2</sub> (20.6 g) and RAD<sub>4</sub> (17.3 g) under well-watered field conditions (Table 5). Also, grain yield of RAD<sub>4</sub> was significantly less than those of RA<sub>1</sub>, R<sub>0</sub>, and RD<sub>2</sub> under well-watered conditions. Under drought field conditions, only significant difference in grain yield per plant was found between RA<sub>1</sub> (14.7 g) and RAD<sub>4</sub> (12.4 g). Harvest index was significantly greater in well watered (44.2%) than in droughted (34.6%) field conditions. On average, genotype R<sub>1</sub> (42.3%) and RA<sub>2</sub> (40.6%) had higher harvest index than RD<sub>2</sub> (38.3%) and DAR<sub>4</sub> (35.5%) in the field (Table 5). Also, R<sub>0</sub> (40.2) and RD<sub>2</sub> (38.3) had higher harvest index than DAR<sub>4</sub>. The percent loss of grain yield in the field experiment showed significant differences (Figure 9). Genotypes R<sub>0</sub> and RA<sub>2</sub> underwent the largest loss of grain yield while RAD<sub>4</sub> contained the lowest reduction in grain yield.

## Discussion

The increased dosages of 1RS contributed to lateness. The mean grain yield from the 2013 wet treatment in the sand-tube greenhouse experiment was 89 % higher compared to that from 2012 (Figure 4). This indicates year-to-year variation of environmental conditions such as temperature, relative humidity, and light intensity for this quantitative trait.

In the well-watered treatments, RA<sub>2</sub> produced higher grain yields compared to other genotypes grown in the greenhouse. There were no significant differences in grain yield among the genotypes under drought conditions. It appeared that RA<sub>2</sub>, a translocation of Pavon 76 with two copies of 1RS (1RS.1AL) stands as the genotype that will provide satisfactory grain yields under a variety of environmental conditions.

Previous studies have shown a positive correlation between grain yield and root biomass (Ehdaie et al. 2010). In the current study, this relationship held true for up to the two doses of 1RS translocations in Pavon 76. Combinations with one (RA<sub>1</sub>), and two (RA<sub>2</sub> and RD<sub>2</sub>) doses showed increases in shallow root weight over Pavon 76 (R<sub>0</sub>) along with corresponding increases in grain yield (Figures 2 and 3). Shoot biomass also showed an incremental increase with the number of dosages of 1RS translocations (Figure 1).

The grain yield of RAD<sub>4</sub> was lower despite an increase in root biomass over the genotypes containing lower dosages of 1RS. Perhaps this is a reflection of competition by an excessively growing roots in this genotype for assimilate allocation, which leaves less

assimilate for grain filling that results in abortion of embryos and thus less grain number. Higher allocations of assimilates to the root reduced the resource availability for grains (Ehdaie et al. 2008; Ehdaie and Waines 2012). It also shows that larger root systems do not necessarily translate into higher grain yields. The number of grains per plant of genotype RAD<sub>4</sub> does showed a reduction in the wet treatments (Figure 5). The single grain weight of RAD<sub>4</sub> was not different from other genotypes (Figure 6) suggesting that it was the low number of grains not a decrease in grain weight that led to a decrease in grain yield in this genotype.

None of the lines from the present study with multiple dosages of 1RS translocations produced higher grain yields under drought conditions than genotypes with zero or one dosage of 1RS. There was no clear relationship between percent losses of grain yield (Figure 9) in the greenhouse where RD<sub>2</sub> underwent the greatest loss (79%) and R<sub>0</sub> the lowest (29%). On the other hand, there seemed to be a general pattern in the field where the yield loss of RA<sub>1</sub>, RD<sub>2</sub> and RAD<sub>4</sub> in the dry treatment compared to the wet treatment was significantly lower than the rest (data not shown). Genotypes RA<sub>2</sub> (43%) and R<sub>0</sub> (41%) suffered the highest grain yield losses while RAD<sub>4</sub> suffered the lowest (28.68%). It is possible that such a pattern did not show up in the greenhouse experiment due to very high levels of stress (78%) compared to the field experiment (36%).

Repeated field experiments with wheat lines isogenic for various 1RS translocations, both centric (whole arm) or recombinants of small segments, tend to

produce unpredictable results with strong positive responses only in some seasons, when apparently the stress pressure is applied at the sensitive window (C. Hohn, A.J. Lukaszewski, personal communication). Unlike the commercial wheat cultivars used by Richards and Passioura in 1989, the genotypes of the present study did not produce equal amounts of grain yields under well-watered conditions. It may be that genetic factors such as the dosage of IRS and the physiological phenomena such as resource depletion by the excessive growth of root system determine the grain yield for these genotypes at plentiful water supply. Nevertheless, at mild stress levels (~36%) it may be the case that the diameter of root metaxylems influences grain yield since RAD<sub>4</sub> only had a 29% yield loss compared to the other four lines that averaged at 38%. The fact that the yield loss is the least for the genotype with the smallest metaxylem diameter in the root means that the root metaxylem diameter acts to lessen the negative effect of yield loss rather than to act directly on increasing grain yield.

A possible reason for wheat genotypes with reduced metaxylem diameters to perform better under drought situations might be their ability to conserve subsoil water (Richards and Passioura 1989). Since the hydraulic conductivity of a vessel element is proportional to the fourth power of its diameter, smaller xylem diameters provide more resistance towards water transportation upwards through the plant compared to larger xylem diameters (Evert et al. 2006). As a consequence water may be used up more slowly by the genotypes with smaller metaxylem diameters.

The wider metaxylem vessels also face a heightened challenge of embolisms caused by relatively large air bubbles, which are harder to dissolve. Moreover, metaxylem vessel elements with larger diameters tend to be longer compared to narrower metaxylem vessels (Evert et al. 2006). As a result, such plants with wider metaxylem diameters transport larger volumes of water through their conduits and stand the risk of losing a considerable proportion of water carrying capacity owing to embolisms. Such is also the case with roots as they generally have wider metaxylem vessels. Therefore, genotypes with narrow metaxylem vessels in the roots have a reduced risk of water loss due to blockage, which may have contributed to the reduction in loss of grain yield in these lines.

## **Conclusion**

Pavon 1RS.1AL (RA<sub>2</sub>) translocation line produced the highest grain yields under well-watered conditions and it did not perform any worse than the rest of the genotypes under drought conditions. As a whole, these qualities make the 1RS.1AL translocation the most suitable one in Pavon 76.

No significant relationship between grain yield and root biomass was observed in this study. Grain yield in RAD<sub>4</sub> was relatively lower than other genotypes. This may be due to competition between heavy root system produced in this genotype and grain production for assimilates, which leads to the abortion of embryos when drought was initiated at late booting stages (Ehdaie and Waines 2012). It would be reasonable to test various doses of non-centric 1RS translocations in wheat. Moreover, test of lines with six doses of 1RS would probably be informative. Last but not least, smaller metaxylem vessel diameters in roots decreased the grain yield loss under mild stress conditions.



**Table 1** Mean values of days to booting (DTB), days to heading (DTH), days to anthesis (DTA), days to maturity (DTM), plant height (PH), number of tillers and number of spikes per plant for Pavon 76 (R<sub>0</sub>) and its translocation lines with one (RA<sub>1</sub>), two (RA<sub>2</sub> and RD<sub>2</sub>), and four (RAD<sub>4</sub>) IRS grown in a sand-tube experiment under well-watered condition in greenhouse in 2012.

| Genotype         | DTB  | DTH   | DTA  | DTM    | PH (cm) | # Tillers | # Spikes |
|------------------|------|-------|------|--------|---------|-----------|----------|
| R <sub>0</sub>   | 49 d | 58 d  | 64 b | 112 d  | 82 a    | 8 b       | 8 b      |
| RA <sub>1</sub>  | 59 b | 68 b  | 76 a | 114 b  | 83 a    | 10 a      | 10 a     |
| RA <sub>2</sub>  | 50 d | 60 cd | 65 b | 112 cd | 78 a    | 10 ab     | 10 ab    |
| RD <sub>2</sub>  | 54 c | 62 c  | 69 b | 113 bc | 80 a    | 8 ab      | 8 ab     |
| RAD <sub>4</sub> | 63 a | 72 a  | 80 a | 116 a  | 81 a    | 8 b       | 8 b      |

Values within each column followed by the same lower case letter are not significantly different ( $P = 0.05$ ) according to LSD test.

**Table 2** Mean values of days to booting (DTB), days to heading (DTH), days to anthesis (DTA), days to maturity (DTM), plant height (PH), number of tillers and number of spikes per plant for Pavon 76 (R0) and its translocation lines with one (RA1), two (RA2 and RD2), and four (RAD4) IRS grown in a sand-tube experiment under well-watered and terminal drought conditions in greenhouse in 2013.

| Genotype/treatment   | DTB    | DTH    | DTA    | DTM    | PH (cm) | # Tillers | # Spikes |
|----------------------|--------|--------|--------|--------|---------|-----------|----------|
| R <sub>0</sub> wet   | 59 f   | 68 e   | 73 d   | 114 c  | 84 a    | 11 d      | 9 a      |
| RA <sub>1</sub> wet  | 62 def | 70 de  | 75 cd  | 115 bc | 83 a    | 15 bc     | 9 a      |
| RA <sub>2</sub> wet  | 64 cde | 74 bc  | 78 bc  | 117 ab | 84 a    | 17 b      | 9 a      |
| RD <sub>2</sub> wet  | 62 def | 72 bcd | 76 cd  | 113 c  | 85 a    | 16 b      | 9 a      |
| RAD <sub>4</sub> wet | 68 a   | 78 a   | 82 ab  | 118 a  | 78 b    | 23 a      | 9 a      |
| R <sub>0</sub> dry   | 60 f   | 70 de  | 79 abc | 101 e  | 73 bc   | 10 d      | 7 b      |
| RA <sub>1</sub> dry  | 61 ef  | 71 cd  | 77 cd  | 102 e  | 74 bc   | 11 d      | 6 b      |
| RA <sub>2</sub> dry  | 64 bc  | 75 ab  | 82 a   | 104 d  | 73 cd   | 11 d      | 6 b      |
| RD <sub>2</sub> dry  | 64 cd  | 73 bc  | 77 cd  | 101 e  | 77 bc   | 13 cd     | 6 b      |
| RAD <sub>4</sub> dry | 67 ab  | 78 a   | 82 a   | 105 c  | 68 d    | 11 d      | 7 b      |

Values within each column followed by the same lower case letter are not significantly different (P = 0.05) according to LSD test

**Table 3** Mean values of shoot biomass (SBio), longest root (LR), shallow root weight (SR), deep root weight (DR), root biomass (RBio), number of grains, grain weight (GW) and grain yield (GY) per plant for Pavon 76 (R0) and its translocation lines with one (RA1), two (RA2 and RD2), and four (RAD4) 1RS grown in a sand-tube experiment under well-watered condition in greenhouse in 2012.

| Genotype         | SBio<br>(g/plant) | LR (cm) | SR (g/plant) | DR (g/plant) | RBio<br>(g/plant) | # Grains | GW (mg) | GY (g/plant) |
|------------------|-------------------|---------|--------------|--------------|-------------------|----------|---------|--------------|
| R <sub>0</sub>   | 22.2 c            | 77 a    | 1.16 d       | 0.30 c       | 1.46 d            | 266 ab   | 42.7 a  | 11.4 b       |
| RA <sub>1</sub>  | 29.1 a            | 86 a    | 2.00 b       | 0.44 ab      | 2.43 b            | 320 a    | 44.8 a  | 14.3 a       |
| RA <sub>2</sub>  | 24.0 bc           | 82 a    | 1.41 cd      | 0.34 bc      | 1.75 cd           | 289 ab   | 43.1 a  | 12.4 ab      |
| RD <sub>2</sub>  | 22.7 c            | 82 a    | 1.54 c       | 0.38 abc     | 1.92 c            | 249 b    | 45.3 a  | 11.2 b       |
| RAD <sub>4</sub> | 28.2 ab           | 81 a    | 2.45 a       | 0.47 a       | 2.92 a            | 270 ab   | 48.0 a  | 12.4 ab      |

Values within each column followed by the same lower case letter are not significantly different (P = 0.05) according to LSD test.

**Table 4** Mean values of shoot biomass (SBio), longest root (LR), shallow-root weight (SR), deep-root weight (DR), root biomass (RBio), grain weight (GW), number of grains and grain yield (GY) per plant for Pavon 76 (R<sub>0</sub>) and its translocation lines with one (RA<sub>1</sub>), two (RA<sub>2</sub> and RD<sub>2</sub>), and four (RAD<sub>4</sub>) 1RS grown in a sand-tube experiment under well-watered and terminal drought conditions in greenhouse in 2013.

| Genotype/treatment   | SBio<br>(g/plant) | LR (cm) | SR (g/plant) | DR<br>(g/plant) | RBio<br>(g/plant) | # Grains | GW (mg) | GY<br>(g/plant) |
|----------------------|-------------------|---------|--------------|-----------------|-------------------|----------|---------|-----------------|
| R <sub>0</sub> wet   | 46.0 b            | 101 a   | 4.49 c       | 1.84 bc         | 6.33 b            | 483 a    | 49.9 ab | 24.1 a          |
| RA <sub>1</sub> wet  | 48.3 b            | 102 a   | 4.68 bc      | 1.87 b          | 6.55 b            | 486 a    | 49.2 b  | 23.9 a          |
| RA <sub>2</sub> wet  | 52.8 a            | 100 a   | 4.72 bc      | 1.86 bc         | 6.58 b            | 503 a    | 51.6 ab | 26.0 a          |
| RD <sub>2</sub> wet  | 48.1 b            | 104 a   | 5.46 b       | 1.75 bc         | 7.21 b            | 412 b    | 52.6 a  | 21.7 b          |
| RAD <sub>4</sub> wet | 52.2 a            | 104 a   | 6.47 a       | 3.84 a          | 10.32 a           | 420 b    | 50.2 ab | 21.1 b          |
| R <sub>0</sub> dry   | 17.7 c            | 102 a   | 1.84 d       | 1.47 bc         | 3.30 c            | 230 c    | 26.3 c  | 6.0 c           |
| RA <sub>1</sub> dry  | 17.2 c            | 100 a   | 2.26 d       | 1.20 c          | 3.46 c            | 219 c    | 25.4 c  | 5.5 c           |
| RA <sub>2</sub> dry  | 17.5 c            | 104 a   | 2.00 d       | 1.52 bc         | 3.52 c            | 219 c    | 24.7 c  | 5.4 c           |
| RD <sub>2</sub> dry  | 17.6 c            | 103 a   | 2.46 d       | 1.22 bc         | 3.67 c            | 184 c    | 23.8 c  | 4.4 c           |
| RAD <sub>4</sub> dry | 17.6 c            | 104 a   | 2.09 d       | 1.72 bc         | 3.81 c            | 193 c    | 23.5 c  | 4.4 c           |

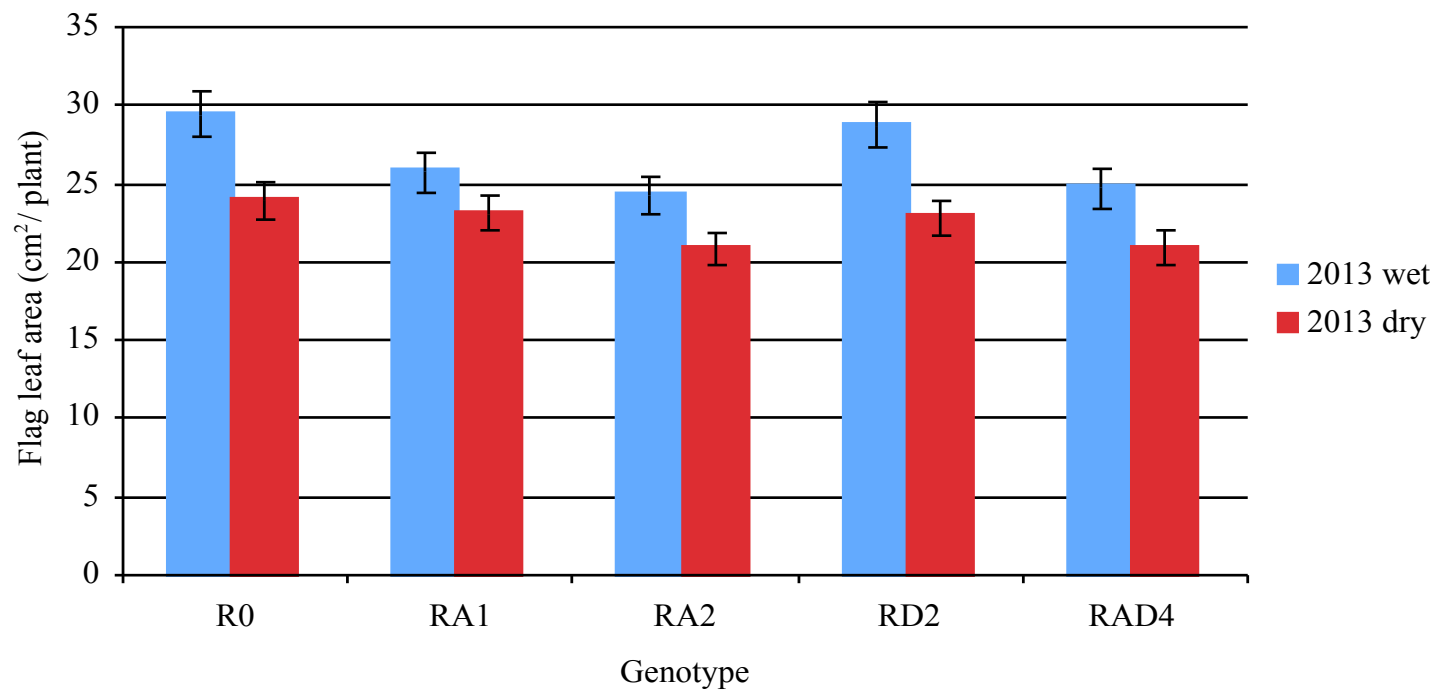
Values within each column followed by the same lower case letter are not significantly different (P = 0.05) according to LSD test.

**Table 5** Mean values of plant height (PH), number of tillers and number of spikes, shoot biomass (SBio), grain weight (GW), grain yield (GY) and harvest index (HI) per plant for Pavon 76 (R<sub>0</sub>) and its translocation lines with one (RA<sub>1</sub>), two (RA<sub>2</sub> and RD<sub>2</sub>), and four (RAD<sub>4</sub>) IRS grown in a split-plot experiment under well-watered and terminal drought conditions in the field in 2013.

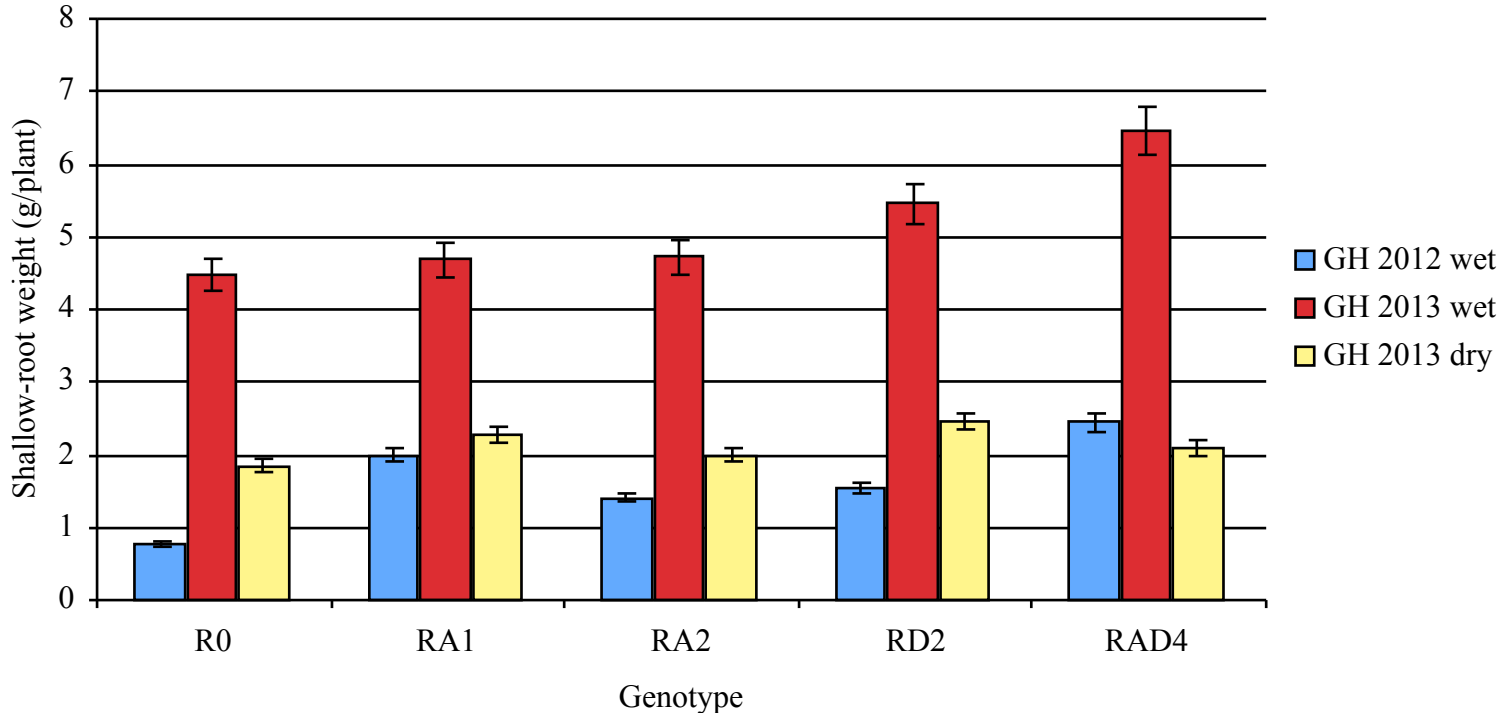
| Genotype/treatment   | PH (cm) | # Tillers | # Spikes | SBio (g/plant) | GW (mg) | GY (g/plant) | HI (%)  |
|----------------------|---------|-----------|----------|----------------|---------|--------------|---------|
| R <sub>0</sub> wet   | 78 a    | 4 ab      | 3 a      | 47.4 ab        | 44.8 a  | 21.58 ab     | 45.7 ab |
| RA <sub>1</sub> wet  | 78 a    | 4 ab      | 2 b      | 47.5 ab        | 45.3 a  | 21.94 ab     | 46.7 a  |
| RA <sub>2</sub> wet  | 76 a    | 4 ab      | 3 a      | 50.7 a         | 44.8 a  | 23.19 a      | 46.3 a  |
| RD <sub>2</sub> wet  | 76 a    | 4 ab      | 2 ab     | 48.2 ab        | 44.5 a  | 20.59 b      | 42.8 b  |
| RAD <sub>4</sub> wet | 76 a    | 4 a       | 2 ab     | 43.6 bc        | 42.8 a  | 17.32 c      | 39.5 c  |
| R <sub>0</sub> dry   | 78 a    | 3 b       | 2 b      | 37.4 c         | 30.0 b  | 12.76 d      | 34.7 ef |
| RA <sub>1</sub> dry  | 78 a    | 3 ab      | 2 b      | 38.9 c         | 29.7 b  | 14.65 cd     | 38.0 cd |
| RA <sub>2</sub> dry  | 75 a    | 4 ab      | 2 ab     | 38.9 c         | 28.6 b  | 13.29 cd     | 34.8 de |
| RD <sub>2</sub> dry  | 76 a    | 4 ab      | 2 ab     | 42.1 bc        | 29.7 b  | 13.91 cd     | 33.8 ef |
| RAD <sub>4</sub> dry | 76 a    | 4 ab      | 3 a      | 39.4 c         | 31.1 b  | 12.35 d      | 31.5 f  |

Values within each column followed by the same lower case letter are not significantly different ( $P = 0.05$ ) according to LSD test.

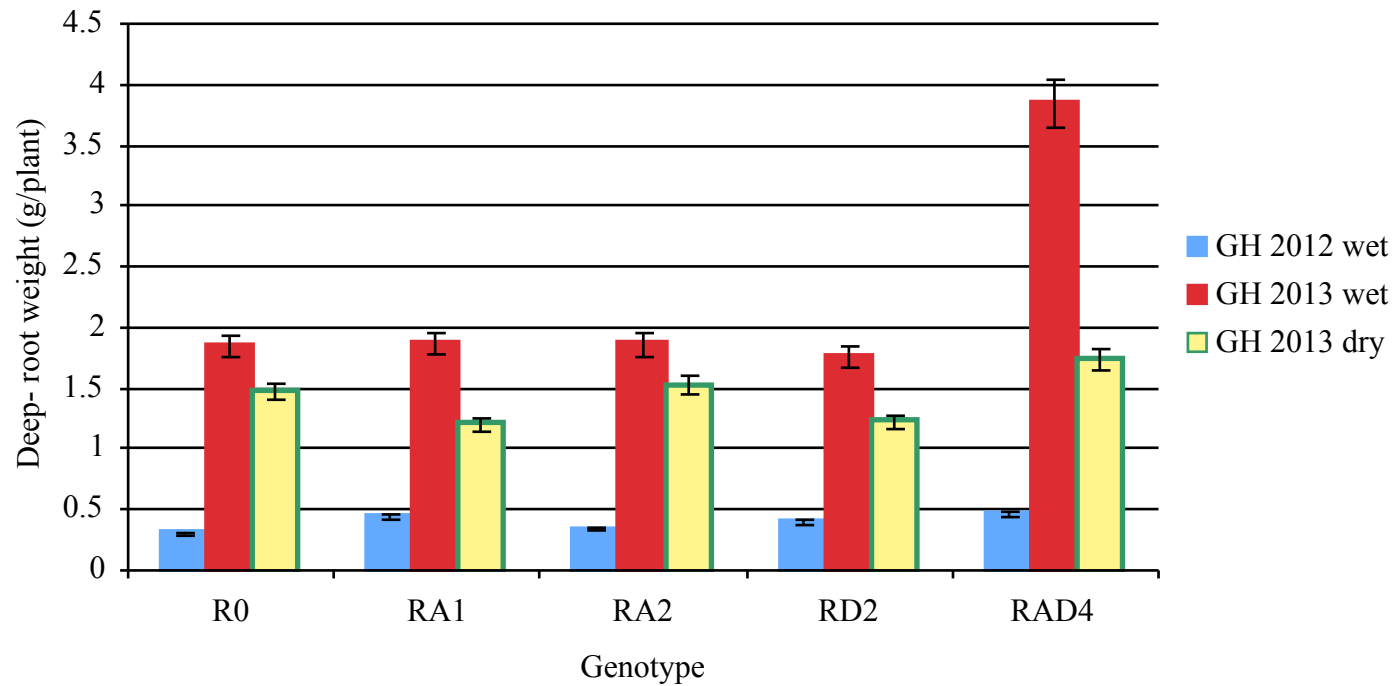
**Figure 1** Mean shoot biomass per plant for Pavon 76 (R<sub>0</sub>) and its translocation lines with one (RA<sub>1</sub>), two (RA<sub>2</sub> and RD<sub>2</sub>), and four (RAD<sub>4</sub>) 1RS grown in sand-tube experiments under well-watered condition in greenhouse in 2012, and well-watered and terminal drought conditions in greenhouse and in field in 2013.



**Figure 2** Mean shallow root weight per plant for Pavon 76 ( $R_0$ ) and its translocation lines with one ( $RA_1$ ), two ( $RA_2$  and  $RD_2$ ), and four ( $RAD_4$ ) 1RS grown in sand-tube experiments under well-watered condition in greenhouse in 2012, and well-watered and terminal drought conditions in greenhouse in 2013.

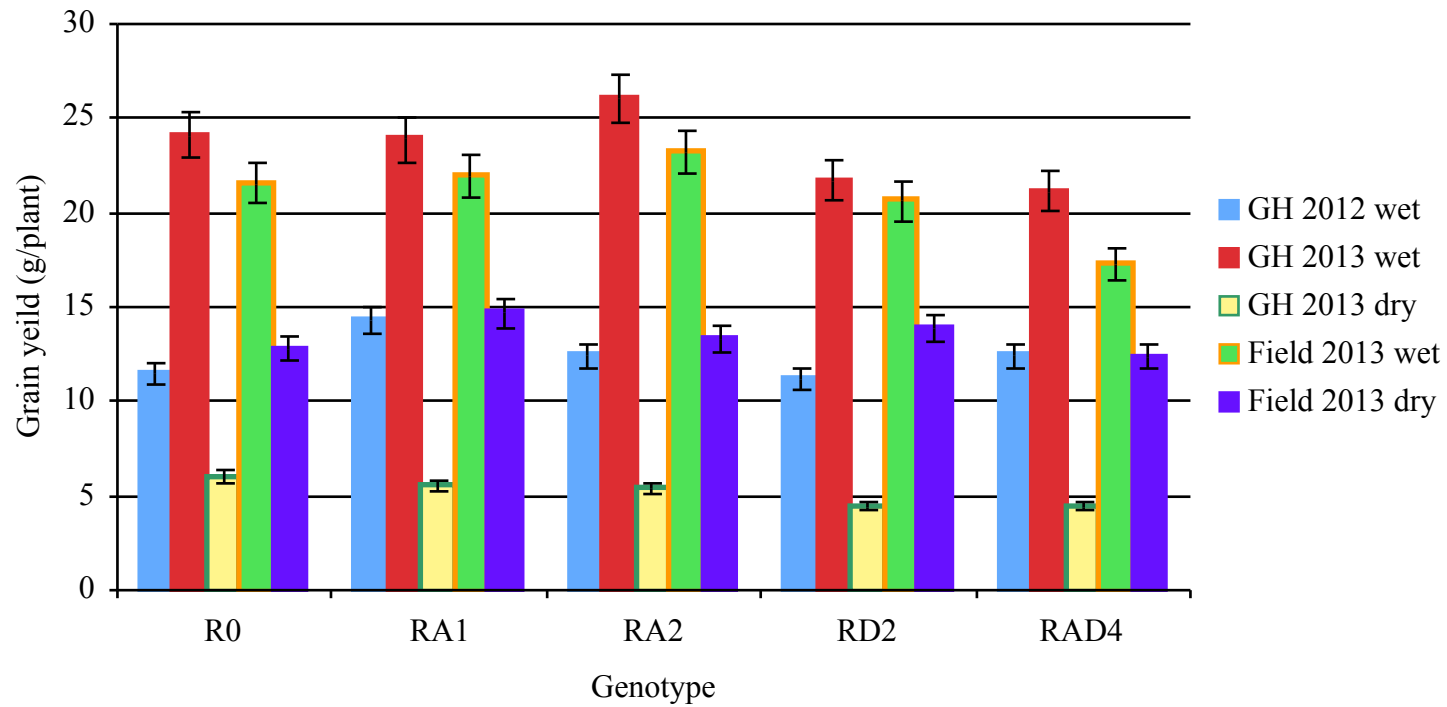


**Figure 3** Mean deep root weight per plant for Pavon 76 ( $R_0$ ) and its translocation lines with one ( $RA_1$ ), two ( $RA_2$  and  $RD_2$ ), and four ( $RAD_4$ ) IRS grown in sand-tube experiments under well-watered condition in greenhouse in 2012, and well-watered and terminal drought conditions in greenhouse in 2013.

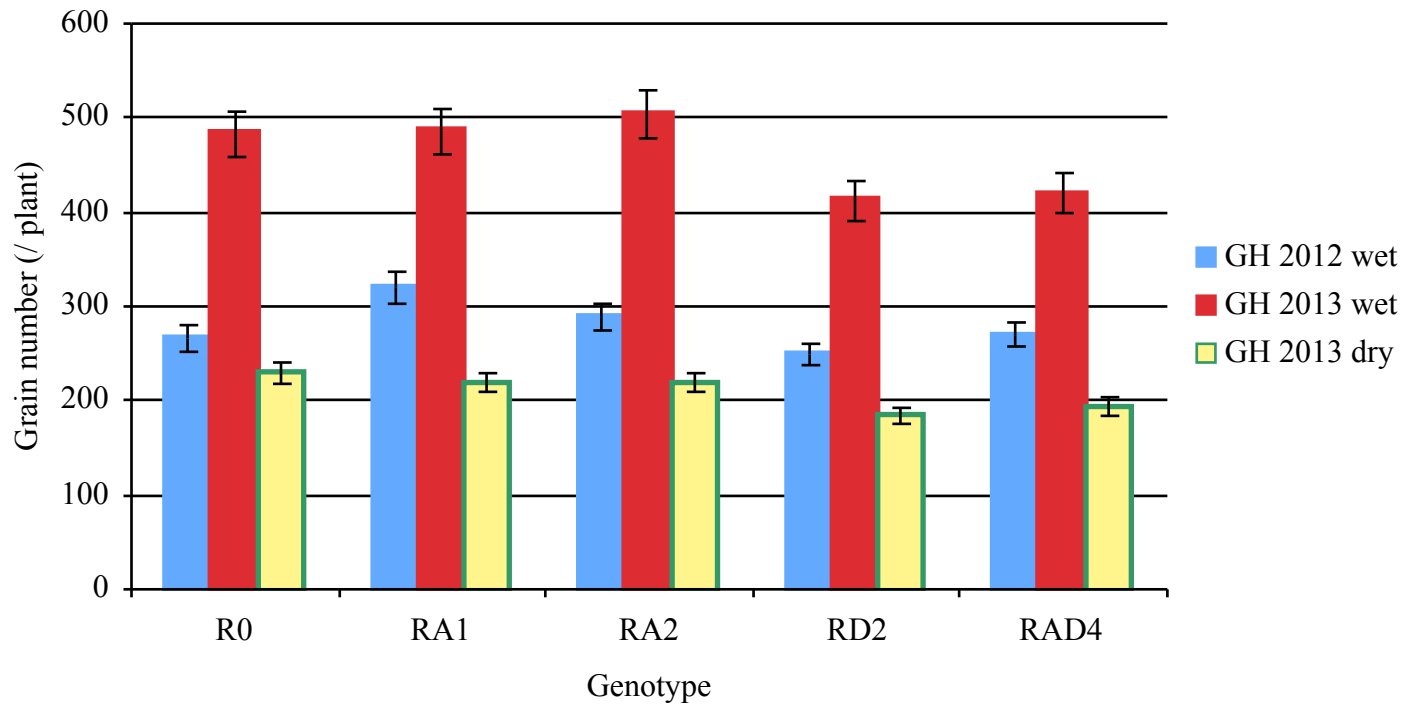




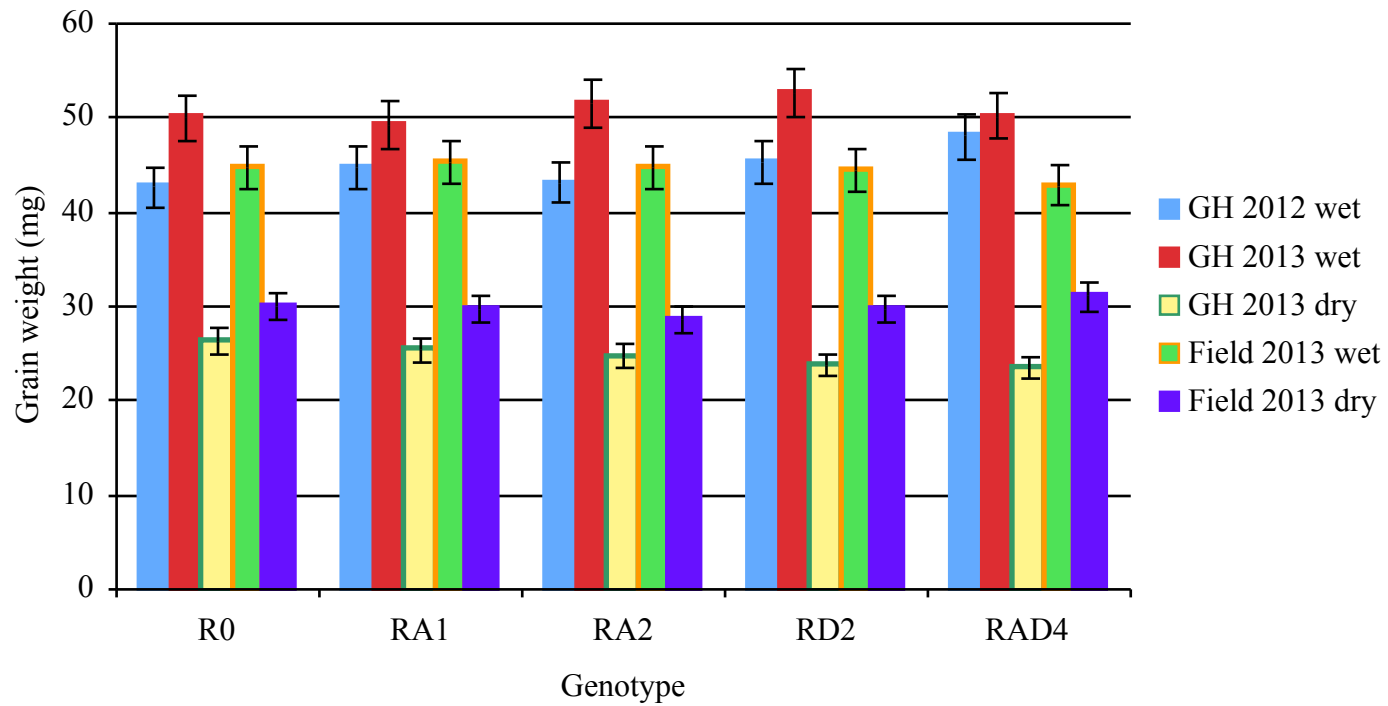
**Figure 4** Mean grain yield per plant for Pavon 76 ( $R_0$ ) and its translocation lines with one ( $RA_1$ ), two ( $RA_2$  and  $RD_2$ ), and four ( $RAD_4$ ) 1RS grown in sand-tube experiments under well-watered condition in greenhouse in 2012, and well-watered and terminal drought conditions in greenhouse and in field in 2013.



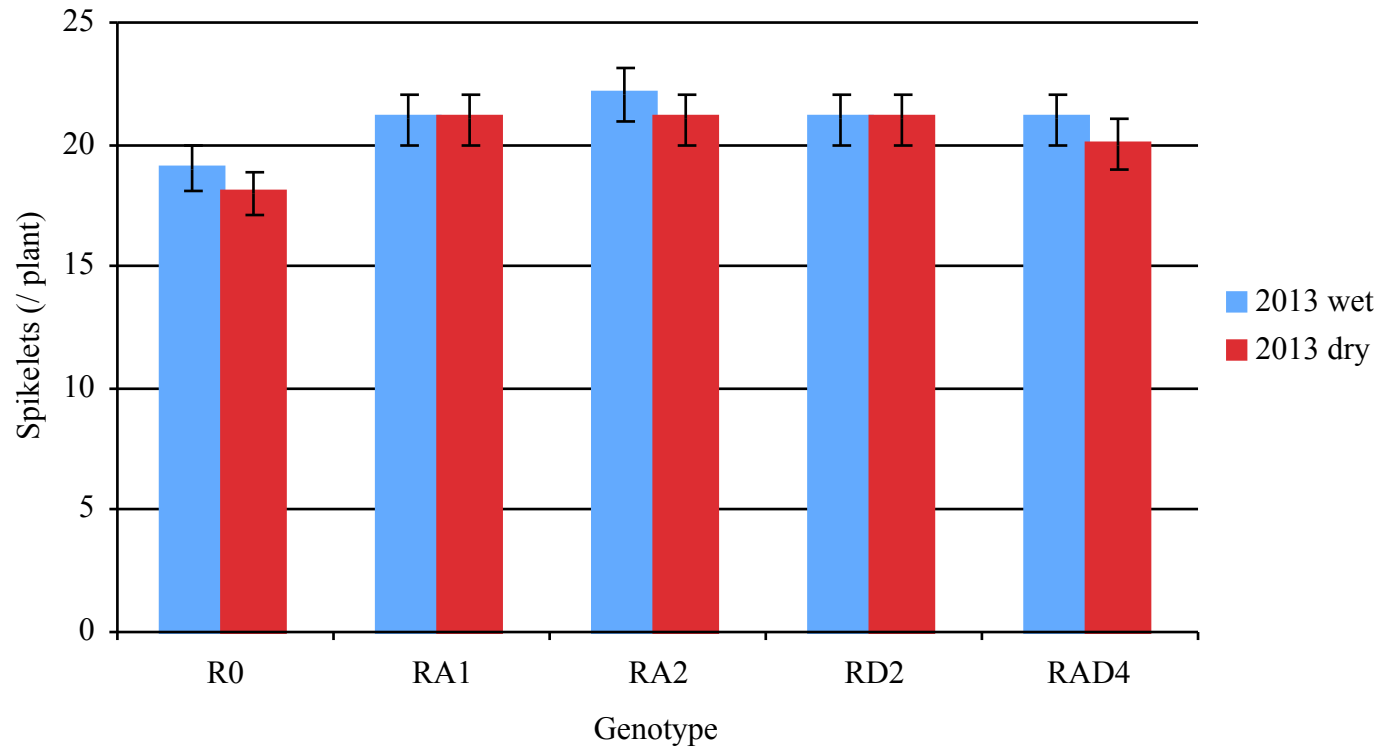
**Figure 5** Mean grain number per plant for Pavon 76 ( $R_0$ ) and its translocation lines with one ( $RA_1$ ), two ( $RA_2$  and  $RD_2$ ), and four ( $RAD_4$ ) 1RS grown in sand-tube experiments under well-watered condition in greenhouse in 2012, and well-watered and terminal drought conditions in greenhouse in 2013.



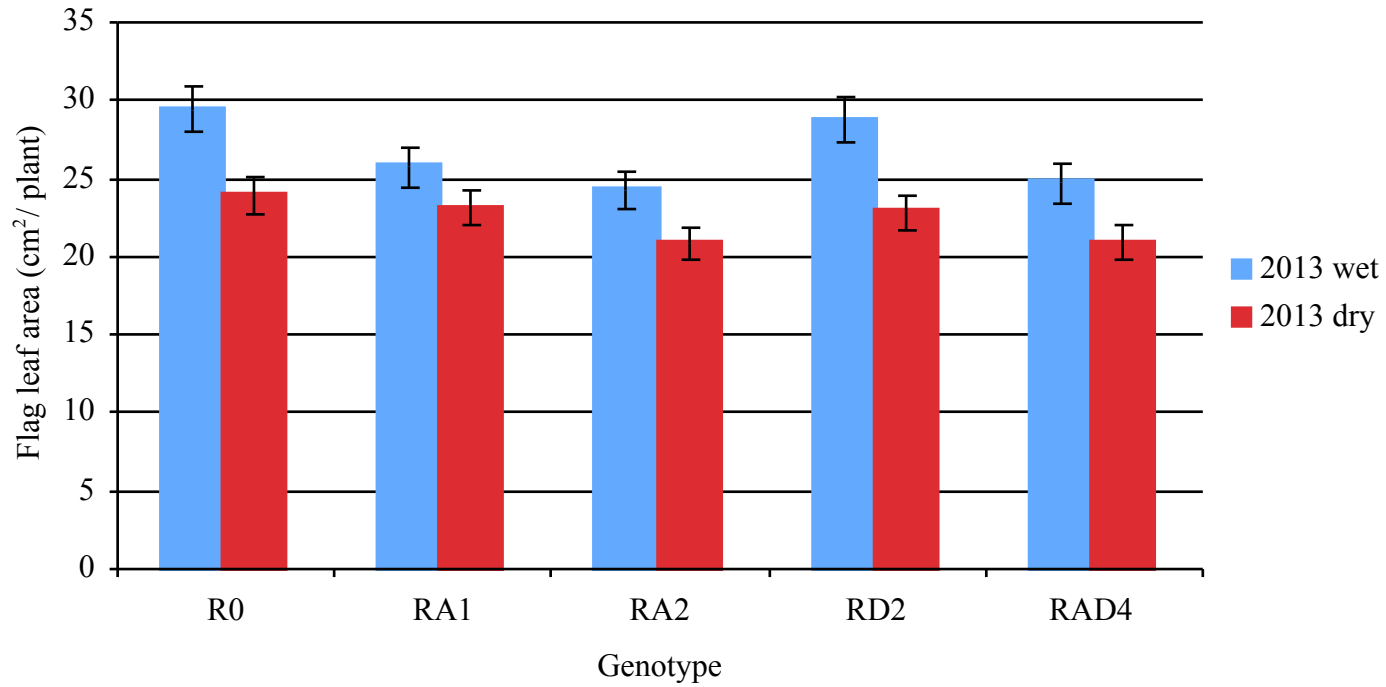
**Figure 6** Mean single grain weight for Pavon 76 ( $R_0$ ) and its translocation lines with one ( $RA_1$ ), two ( $RA_2$  and  $RD_2$ ), and four ( $RAD_4$ ) 1RS grown in sand-tube experiments under well-watered condition in greenhouse in 2012, and well-watered and terminal drought conditions in greenhouse in field in 2013.



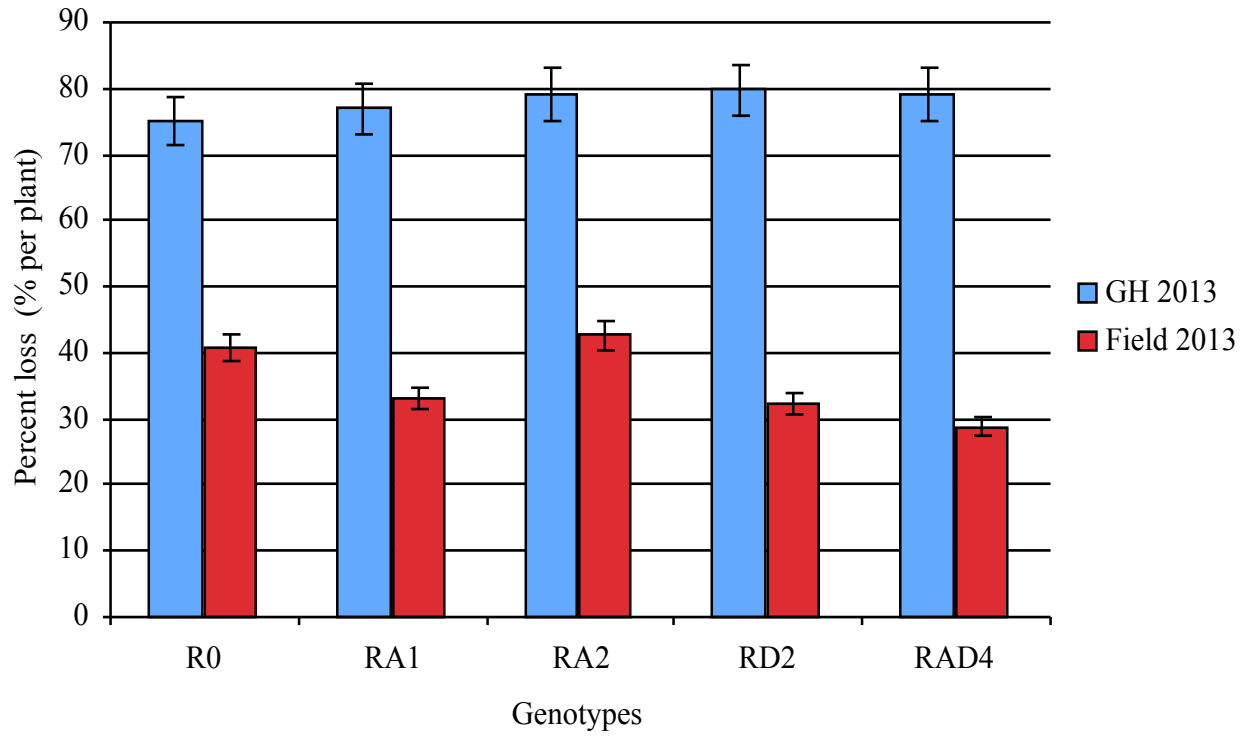
**Figure 7** Mean number of spikelets per plant for Pavon 76 ( $R_0$ ) and its translocation lines with one ( $RA_1$ ), two ( $RA_2$  and  $RD_2$ ), and four ( $RAD_4$ ) 1RS grown in sand-tube experiments under well-watered and terminal drought conditions in greenhouse in 2013.



**Figure 8** Mean flag leaf area per plant for Pavon 76 ( $R_0$ ) and its translocation lines with one ( $RA_1$ ), two ( $RA_2$  and  $RD_2$ ), and four ( $RAD_4$ ) IRS grown in sand-tube experiments under well-watered and terminal drought conditions in greenhouse in 2013.



**Figure 9** Mean percent loss of grain yield per plant for Pavon 76 ( $R_0$ ) and its translocation lines with one ( $RA_1$ ), two ( $RA_2$  and  $RD_2$ ), and four ( $RAD_4$ ) 1RS grown under well-watered and terminal drought conditions in greenhouse in field in 2013.



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