Cereal Research Communications 44(4), pp. 706–716 (2016)
DOI: 10.1556/0806.44.2016.026

Grain Yield of Durum Wheat as Affected by Waterlogging at Tillering

S. Pampana*, A. Masoni and I. Arduini

Department of Agriculture, Food and Environment, University of Pisa
Via del Borghetto 80, Pisa, Italy

(Received 4 January 2016; Accepted 1 March 2016;
Communicated by J. Kubat)

Waterlogging is one of the limiting factors influencing durum wheat (*Triticum durum* L.) production. In this paper we investigated the impact of seven waterlogging durations of 4, 8, 12, 16, 20, 40, and 60 days, imposed at 3-leaf and 4-leaf growth stages, on grain yield, grain yield components, straw and root dry weight and nitrogen concentration of grain, straw, and roots of two varieties of durum wheat. Grain yield of both varieties showed a significant reduction only when waterlogging was prolonged to more than 20 days, and 40-d and 60-d waterlogging reduced grain yield by 19% and 30%. Waterlogging depressed grain yield preventing many culms from producing spikes. It slowed down spikelet formation, consequently reducing the number of spikelets per spike, and reduced floret formation per spikelet, thus reducing the number of kernels per spike.

Keywords: durum wheat, roots, spikelet initiation, tillering, waterlogging

Introduction

Soil is considered waterlogged when excess water saturates the soil pores with either no layer of water or a very fine one on the soil surface. In agricultural soils, waterlogging is primarily caused by intense precipitation but also by inadequate soil drainage. Waterlogging affects approximately 10% of the global land area and about 10–15 million ha of the world's wheat growing areas are affected by waterlogging each year, which represents about 15–20% of the surface annually cultivated for wheat production (Hossain and Uddin 2011). As result of climate change, waterlogging risks will increase in the near future (Jiang et al. 2008).

Waterlogging inhibits the gas exchange between the roots and the atmosphere so that the oxygen concentration decreases rapidly, while carbon dioxide and ethylene concentrations increases in the root environment (Setter and Waters 2003). In winter cereals oxygen deficiency caused by waterlogging prematurely senesces leaves, reduces root growth, tillering, and dry matter accumulation, produces sterile florets, and lowers the number and weight of kernels as well as the grain yield (Sayre et al. 1994; Jiang et al. 2008; Hossain and Uddin 2011; Hossain et al. 2011). Waterlogging also causes nitrogen

---

*Corresponding author; E-mail: silvia.pampana@unipi.it

deficiency, by stimulating denitrification and leaching, and the accumulation of toxic substances, and favours development of soil-born pathogens.

Numerous studies have addressed the effect of waterlogging on common wheat yield but, to the best of our knowledge, no research was carried out to evaluate the effect of waterlogging duration on durum wheat. In common wheat plants waterlogged at the start of tillering, grain yield losses are mainly caused by a decrease in kernel number per plant (De San Celedonio et al. 2014), or in kernel weight per plant (Ghobadi et al. 2011), or by a combined reduction in kernel number per plant and the number of culms (Collaku and Harrison 2002). Common wheat tolerance to waterlogging is related to factors such as: i) the duration of the waterlogging event, ii) the crop development stage in which waterlogging occurs, and iii) the sensitivity of the species or variety (Belford 1981; Meyer and Barrs 1988; Brisson et al. 2002; Ghobadi and Ghobadi 2010; De San Celedonio et al. 2014).

In durum wheat, the grain yield per plant is the product of the number of kernels per plant and the mean kernel weight. The number of kernels per plant, in turn, is the product of the number of spikes per plant, the number of spikelets per spike, and the number of kernels per spikelet. In central Italy, where the study outlined in this paper was conducted, rainfall is concentrated from October to April, but waterlogging is more likely to occur during the winter months (January and February) due to lower transpiration and evaporation rates. Therefore, durum wheat is likely to experience waterlogging during the tillering stage, which is critical for crop establishment, tiller production and spikelet initiation. In durum wheat, the emergence of the first leaf tiller coincides with the appearance of the fourth leaf, and around the time that the main shoot apex reaches the terminal spikelet stage the tillers begin to die. Spikelet initiation starts during the emission of the fourth leaf (Brooking et al. 1995) and ends (terminal spikelet stage) when the leaf-sheaths become erect or when the first node is detectable (Kirby 1990). Therefore in durum wheat plants, the maximum number of spikes per plant, the number of spikelets per spike, and the number of grains per spikelet are established from the emission of the third-fourth leaf to the stage of first detectable node. These numbers may go down in the subsequent stages but never go up.

In this research we hypothesized that waterlogging during tillering reduces the grain yield of durum wheat (*Triticum durum* L.) reducing the culm and spikelet formation and that the amount of reductions is related to the length of waterlogging time. Thus, we investigated the impact of eight waterlogging durations imposed at 3-leaf and 4-leaf growth stages. Since the choice of cultivar may be a key factor influencing tolerance to waterlogging, we compared two varieties selected from those most commonly cultivated in central Italy.

Materials and Methods

The research was carried out in two consecutive growing seasons, 2011–2012 and 2012–2013, at the Research Centre of the Department of Agriculture, Food and Environment of the University of Pisa, Italy, which is located at approximately 5 km from the sea (43° 40′ N, 10° 19′ E) and 1 m above sea level. The climate of the area is hot-summer

Mediterranean (Csa) with mean annual maximum and minimum daily air temperatures of 20.2 and 9.5 °C, respectively, and a mean rainfall of 971 mm per year.

In each year, waterlogging treatments were imposed at 3-leaf and 4-leaf stages (Zadocks stages 13 and 14). At each growth stage, eight waterlogging treatments were imposed: one well-drained control and seven waterlogging durations of 4, 8, 12, 16, 20, 40, and 60 days. Claudio (Cimmyt35/Durango/IS1938/Grazia) and Svevo (Bittern/Yavaros79/Zenit) durum wheat varieties were used. For each year, a randomized complete block design was used, with treatments in a split-plot arrangement with three replications. Stages at the beginning of waterlogging were the main plots, waterlogging durations were allocated as sub-plots, and varieties as sub-sub-plots. For each year 96 pots were used (2 stages × 8 waterlogging durations × 2 varieties × 3 replications).

Plants were grown in 16-L pots made from polyvinyl chloride (PVC) tubes (80 cm long by 16 cm diameter) fitted with a PVC base, serving as a bottom, and filled with 12 kg of soil. A 30 mm diameter hole was drilled in the bottom of each pot. The soil main characteristics did not differ between years and were: 54.9% sand (2 mm > Ø > 0.05 mm), 33.5% silt (0.05 m > Ø > 0.002 mm), 11.6% clay (Ø < 0.002 mm), 7.7 pH, 0.7 g kg^{-1} total nitrogen (Kjeldahl method), 4.4 mg kg^{-1} available P (Olsen method), and 69.3 mg kg^{-1} available K ($BaCl_2$-TEA method).

Durum wheat was sown on 10 November 2011 and 9 November 2012. After emergence, the seedlings were thinned to eight plants per pot, corresponding to 400 plants m^{-2}. Phosphorus and potassium were applied pre-planting as triple mineral phosphate and potassium sulphate at the rate of 150 kg ha^{-1} of P_2O_5 and K_2O. Nitrogen was applied at the rate of 150 kg ha^{-1} and was split into three applications: at sowing and pseudo-stem erection, as ammonium sulphate, and at first node detectable as urea, in the following proportions: 30–60–60 kg N ha^{-1}.

Waterlogging was imposed on 13 December 2011 (3-leaf) and 27 December 2011 (4-leaf) and on 10 and 24 December 2012, by placing pots into containers (2 m × 1 m × 1 m) with a 1 cm layer of free water above the surface of the pots throughout the period of each waterlogging treatment (in this condition the soil in the pots was completely saturated by water). At the end of each waterlogging period, pots were taken out of the containers and left to drain freely, after which they were maintained near to field capacity until the plants reached maturity. Control pots were watered near to field capacity throughout the two growing seasons.

Weed control was performed throughout the two crop cycles by hand hoeing. The occurrence of diseases was checked weekly throughout the growth cycles. Waterlogging can favour disease development and give soil-born pathogens a greater opportunity to cause damage. However, in our research durum wheat plants remained almost disease-free throughout the experiment. Waterlogging probably did not increase the incidence of fungal diseases because of the low temperatures during the waterlogging period.

At physiological maturity (19 June 2012 and 25 June 2013), plants from each pot were manually cut at ground level and partitioned into culms, leaves, chaff and grain, and weighed. The number of culms and spikes, the number of spikelets per spike, and mean kernel weight were determined. Roots were separated from the soil by gently washing with a low flow from sprinklers to minimize loss or damage. For dry weight determination, samples were oven dried at 65 °C to constant weight. The spike fertility index was calculated as the relation between the grain number and the dry weight of chaff representing the non-grain biomass of the spike (Abbate et al. 2013). The harvest index was calculated as the ratio between grain yield and total aboveground biomass. All plant parts were analysed for nitrogen concentration by the micro-Kjeldahl method. Nitrogen contents were obtained by multiplying N concentrations by dry matter. Leaf chlorophyll concentration was estimated at the beginning and the end of each waterlogging period using a SPAD meter (Model 502, Minolta Corp., Ramsey, N.J.). Measurements were taken on the last expanded leaf of each plant of the pot. Three readings were taken for each measurement, and the mean was used for the data analysis.

Daily weather data were recorded by an automatic meteorological station placed where the experiments were carried out. Between the two growing seasons, differences in temperature were relatively modest with very similar mean temperatures during the vegetative period (9.0 and 9.4 °C in 2011–2012 and 2012–2013, respectively). Rainfall varied considerably between years, with 2012–2013 being wetter (1,137 mm) than 2011–2012 (only 463 mm). Compared to the 25-year average, the first year was dry (–171 mm), while the second year was very wet (+503 mm). Rainfall distribution also differed between years: in 2011–2012 precipitation from sowing to flowering was 393 mm and only 70 mm fell from flowering to maturity. In 2012–2013 precipitation from sowing to flowering was 1,043 mm, and was 94 mm from flowering to maturity.

Results were subjected to analysis of variance. The experimental design was a split-plot with three replications: years were allocated as main plots, plant stages at waterlogging imposition as sub-plots, waterlogging durations as sub-sub-plots and cultivars as sub-sub-sub-plots. Significantly different means were separated at the 0.05 probability level by the least-significant difference test (Steel et al. 1997).

Results

The analysis of variance revealed significant differences between years and between varieties for some of the measured parameters but none of the interactions involving year or variety was statistically significant. No significant differences between the two stages (3-leaf and 4-leaf) of the plant development when waterlogging was imposed were detected, and none of the interactions involving stages was statistically significant.

Between the two years, only slight differences were detected in the length of the growth stages, and the duration of the growth cycle from sowing to physiological maturity was a few days longer in 2013 than 2012 for both varieties (Table 1). Waterlogging duration did not influence the phenological development of durum wheat and the first node detectable, flowering and maturity stages were reached at the same time in both the waterlogged and control plants (Table 1).

Analysis of variance showed statistically significant differences between years for grain, and straw biomass, which were 22% and 8% higher, respectively, in 2012 than in 2013 (Table 2). No significant differences were detected in root dry weight and spike

Table 1. Durum wheat major growth stages in the two growing seasons

Stage	Zadocks scale	Year	
		2012	2013
Sowing	0	10 Nov 2011	9 Nov 2012
3 leaves unfolded	13	13 Dec 2011	10 Dec 2012
4 leaves unfolded	14	27 Dec 2011	24 Dec 2012
Pseudo-stem erection	30	2 Mar 2012	28 Feb 2013
1st node detectable	31	20 Mar 2012	17 Mar 2013
Flowering	60	4 May 2012	2 May 2013
Maturity	92	19 June 2012	25 June 2013

number per plant. Thus, the higher grain yield in 2012 depended on kernel number per plant (+17%), which, in turn, depended on higher spike fertility (+12%). Nitrogen concentration and content of grain and straw were significantly higher in 2012 than in 2013, while root concentration and content did not vary between years (Table 2).

Table 2. Dry weight, nitrogen concentration and content of grain yield, straw and root and grain yield components of the two varieties in well-drained condition and year mean effect

Parameters	Variety in well-drained conditions		Year mean effect	
	Claudio	Svevo	2012	2013
Grain yield (g plant^{-1})	2.6 a	2.4 b	2.6 a	2.1 b
Spike number (n plant^{-1})	2.0 a	1.6 b	1.8 a	1.7 a
Number of spikelet per spike	18.2 a	14.7 b	16.5 a	15.5 b
Number of kernels per spikelet	1.7 a	2.1 b	1.9 a	1.9 a
Number of kernels per spike	30.8 a	31.2 a	30.6 a	28.8 b
Number of kernels per plant	60.1 a	50.7 b	56.2 a	47.9 b
Mean kernel weight (mg)	43.5 a	46.6 a	45.9 a	44.1 a
Spike fertility (n g^{-1})	61.9 a	66.3 b	61.0 a	54.6 b
Straw dry weight (g plant^{-1})	4.4 a	3.7 b	4.0 a	3.8 b
Root dry weight (g plant^{-1})	1.0 a	0.9 a	0.9 a	0.8 b
Harvest index (%)	0.37 a	0.39 a	39.0 a	36.0 b
Grain N concentration (mg g^{-1})	17.3 a	18.1 a	19.4 a	18.5 b
Straw N concentration (mg g^{-1})	5.3 a	5.5 a	6.1 a	5.5 b
Root N concentration (mg g^{-1})	5.0 a	5.1 a	5.6 a	5.4 a
Grain N content (mg plant^{-1})	45.3 a	42.7 a	50.1 a	39.0 b
Straw N content (mg plant^{-1})	23.4 a	20.2 a	24.6 a	20.7 b
Root N content (mg plant^{-1})	4.8 a	4.4 a	4.9 a	4.5 b

For each treatment values followed by different letters within lines are significantly different ($P<0.05$).

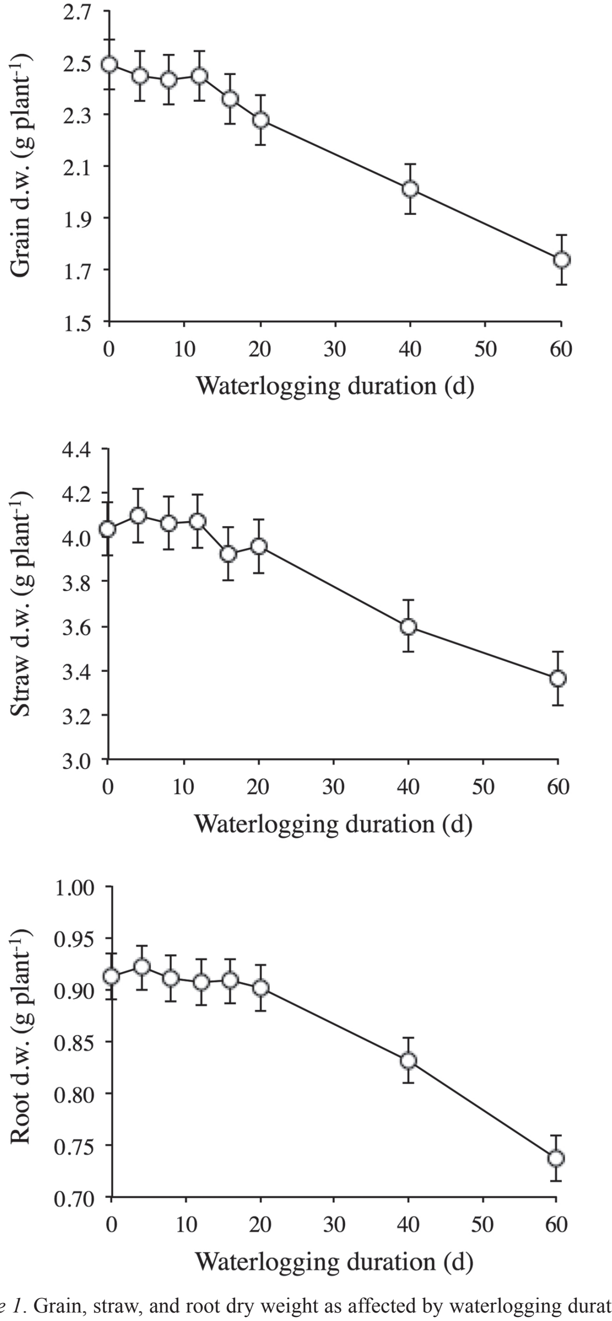

Figure 1. Grain, straw, and root dry weight as affected by waterlogging duration. Vertical bars represent LSD at $P < 0.05$

When well-drained, cv. Claudio had a higher grain yield (+11%) and straw dry weight (+20%) than cv. Svevo (Table 2). This higher grain yield of cv. Claudio was due to the higher number of spikes per plant (+20%) and number of spikelets per spike (+24%). The higher straw dry weight was due to the higher number of culms per plant (+20%). Nitrogen concentrations and contents of grain, straw and roots were similar in the two cultivars.

Chlorosis and early senescence of leaves were observed with waterlogging periods of longer than 20 days in both varieties. Chlorophyll concentration of the last expanded leaf, estimated with SPAD measures, tended to decrease with waterlogging duration, and after 60-d waterlogging the value was 41% lower than the control (data not shown).

The response of the two durum wheat varieties to waterlogging at tillering was similar and both genotypes showed a significant reduction in grain yield, straw and root dry weight, number of spikes as well as other grain yield components. Waterlogging for 40 and 60 days depressed grain yield by 19% and 30%, respectively (Fig. 1), primarily as a consequence of less kernels per plant, which was the most affected grain yield component (Table 3).

Waterlogging did not affect the number of culms per plant while it significantly decreased the number of spikes per plant at maturity after 40 and 60 days of waterlogging (–8% and –11%) (Table 3). The decrease in spike number did not go with that in culm number likely because many tillers failed to produce spikes due to waterlogging stress.

The number of spikelets per spike was unchanged by 20 days of waterlogging, while it significantly decreased with 40 and 60 days although the reduction was limited to 5% and 9% of the control (Table 3). The number of kernels per spikelet was reduced significantly only by 60 days of waterlogging (–13%) compared to the control (Table 3). The spike fertility was reduced with 40 and 60 days of waterlogging (–12% and –21%). Finally, the mean kernel weight was the unique yield component insensitive to waterlogging. Grain

Table 3. Spike number per plant, grain dry weight per spike, spike fertility, number of spikelets per spike, number of kernels per spikelet, number of kernels per plant, and number of kernels per spike as affected by waterlogging duration

Waterlogging duration (d)	Spike number per plant	Grain d.w. per spike (g)	Spike fertility (n g^{-1})	Spikelet number per spike	Kernel number		
					per plant	per spike	per spikelet
0	1.8 a	1.4 a	63.6 a	16.4 a	55.2 a	30.9 a	1.88 a
4	1.8 a	1.4 a	59.3 b	16.4 a	54.8 a	30.5 a	1.86 a
8	1.8 a	1.4 a	60.6 ab	16.3 ab	54.2 a	30.2 a	1.85 ab
12	1.8 a	1.4 a	61.1 ab	16.3 ab	54.1 a	30.2 a	1.85 ab
16	1.8 a	1.3 ab	58.3 bc	16.2 ab	52.4 a	29.7 ab	1.83 ab
20	1.8 a	1.3 ab	58.8 b	16.0 b	50.6 a	28.7 ab	1.80 b
40	1.6 b	1.2 bc	55.7 c	15.6 c	44.6 b	27.2 b	1.74 c
60	1.6 b	1.1 c	50.7 d	14.9 d	38.5 c	24.3 c	1.63 d

Values followed by different letters within columns are significantly different ($P < 0.05$).

Table 4. Nitrogen concentration and content of grain, straw, and roots as affected by waterlogging duration

Waterlogging duration (d)	Nitrogen concentration (mg g^{-1})			Nitrogen content (mg $plant^{-1}$)		
	Grain	Straw	Roots	Grain	Straw	Roots
0	17.7 a	5.4 a	5.1 a	44.0 a	21.8 a	4.6 a
4	17.5 a	5.5 a	5.2 a	42.9 a	22.5 a	4.8 a
8	17.6 a	5.5 a	5.2 a	42.8 a	22.5 a	4.7 a
12	17.7 a	5.3 a	5.1 a	43.4 a	21.5 a	4.6 a
16	17.7 a	5.6 a	5.3 a	41.8 a	22.0 a	4.8 a
20	18.3 a	5.7 a	5.6 a	41.6 a	22.6 a	5.0 a
40	21.3 b	6.3 b	6.1 b	42.8 a	22.6 a	5.0 a
60	23.5 c	7.0 c	6.8 c	40.9 a	23.5 a	5.0 a

Values followed by different letters within columns are significantly different ($P < 0.05$)

yield per plant was more affected than that per spike (21% vs. 30%) thus confirming that the main effect of waterlogging was a heavy reduced production of kernels by the plants.

Straw and root dry weights decreased only when waterlogging was longer than 20 days. Straw decreased by 11% after 40 d of waterlogging and by 17% after 60 d and roots by 9 and 19% (Fig. 1). As a result of the different levels of reduction in reproductive and vegetative plant parts, the harvest index decreased from 0.38 of the control to 0.34 of plants that were 60-d waterlogged.

Waterlogging duration did not affect the nitrogen concentration of any of the plant parts up to 20 days of waterlogging (Table 4). Thereafter, 40 and 60 days of waterlogging progressively increased the N concentration of grain and straw and root by about 20% and 30% in relative value. Increased nitrogen concentrations by waterlogging compensated the reductions in dry weights so that N contents of grain, straw and root did not statistically change among waterlogging treatments (Table 4).

Discussion

We hypothesised that waterlogging duration during tillering affects the grain yield of durum wheat due to a reduced formation of culms and spikes per plant and of spikelets per spike, and that the reduction could also be affected by the stage at which submersion begins. However, in both years and varieties no statistical differences in measured parameters were found between the two beginning stages of waterlogging, and the hypothesis that waterlogging at 3-leaf and 4-leaf growth stages could affect the grain yield of durum wheat differently was not supported by this experiment.

Grain yield of both varieties showed a significant reduction only when waterlogging was prolonged to more than 20 days, and 40 and 60-d waterlogging reduced grain yield by 19% and 30% (Fig. 1). To the best of our knowledge, no research was carried out to evaluate the effect of waterlogging duration on durum wheat. However, results of research with waterlogging imposed at tillering displayed great differences in common wheat yield losses related to waterlogging duration. Dickin et al. (2009) reported a reduction in grain yield of only 9%, Cannell et al. (1984) by 24%, and Musgrave (1994), Musgrave and Ding (1998), and Ghobadi et al. (2011) reported a reduction of about 40%.

As mentioned above, in durum wheat plants the maximum number of spikes per plant, number of spikelets per spike, and number of grains per spikelet are established from the emission of the fourth leaf to the stage of first node detectable and none of these parameters can be increased after the beginning of stem elongation. In our research, waterlogging decreased spike number per plant (Table 3), but not culm number. This indicates that prolonged waterlogging prompted many culms to fail in producing spikes, thus limiting the final grain yield.

The number of kernels per spike is associated with the number of spikelets per spike and the number of florets per spikelet. Spikelets and florets of a durum wheat crop are initiated consecutively. Spikelet initiation starts during the emission of the fourth leaf and ends when leaf-sheaths become erect or in correspondence to the stage of first node detectable. In our study, the number of spikelets per spike decreased with waterlogging duration of higher than 20 days (Table 3). This thus indicates that waterlogging from double ridge to terminal spikelet stage reduced the rate of spikelet initiation and formation, and that the subsequent period between the end of waterlogging and the beginning of stem elongation is not sufficient to compensate for the reduction. The number of fertile florets is defined between terminal spikelet stage and anthesis (Kirby 1990), and only florets that develop all floral organs by the time of spike emergence continue to develop further (Sinclair and Jamieson 2006). The number of kernels per spikelet was reduced by waterlogging but only when prolonged for 60 days (Table 3). According to Whingwiri and Stern (1982), treatments that reduced the number of kernels per spikelet did so by reducing the number of florets initiated by terminal spikelet rather than by increasing floret survival at a later stage. In our research the spike fertility decreased with longer periods of waterlogging, thus waterlogging duration decreased floret formation rather than increasing floral sterility (Table 3). Finally, the mean kernel weight, which is determined after anthesis, was unaffected by waterlogging at tillering.

Straw and root dry weight of both varieties decreased only when waterlogging was prolonged for more than 20 days, and for both parameters the reduction was only 19% after 60-d waterlogging. Malik et al. (2002) and Dickin et al. (2009) have reported a high reduction in dry weight and nitrogen concentration of shoots and roots of common wheat during winter waterlogging. We measured the dry weight of shoots or roots at maturity and did not know the amount of plant growth reduction at the end of waterlogging. However, chlorosis, early senescence of leaves, and reduction in the chlorophyll concentration of leaves observed during and at the end of longer waterlogging periods led us to hypothesise that the plant growth had been slowed down by prolonged water excess. This result is in accordance with Collaku and Harrison (2002) who attributed chlorosis and premature senescence of the leaves of common wheat waterlogged plants to the mobilization and redistribution of nitrogen from older to younger leaves. We also collected the plants at grain maturity, approximately four months after the end of the longer waterlogging period, and considerable compensatory growth can occur in this period. Their winter growth gives the durum wheat plants plenty of time to recover from any sub-lethal winter stress when rapid growth is resumed in spring. Huang and Johnson (1995) reported that 21-d waterlogging imposed 14 days after planting markedly reduced the dry weight of common wheat roots, which was restored to the control value in only seven days after the end of waterlogging.

Waterlogging duration longer than 20 days increased the nitrogen concentration of the grain, straw, and roots (Table 4). With the same soil and N fertilization level, the N concentration of durum wheat plant parts declines with the increase in biomass (dilution effect). Waterlogging reduced plant growth, thus increasing the nitrogen available per unit of biomass. The increased nitrogen concentrations by waterlogging compensated for the reductions in dry weight so that N contents of grain, straw and root did not statistically change among waterlogging treatments. In our research, topdressing nitrogen fertilization was split at pseudo-stem erection and first node detectable, which both took place after waterlogging had ended. In common wheat the application of nitrogen fertilizer at the end of waterlogging was shown to compensate, either partially or fully, for reduction growth due to waterlogging treatments (Robertson et al. 2009; Rasaei et al. 2012). This may also explain the difference between the two years observed in our research. The higher rainfall in 2013 than in 2012 between the pseudo-stem erection stage and maturity may have increased nitrogen leaching, thus reducing the N available for the plants and subsequently depressing plant growth.

Waterlogging depressed grain yield of durum wheat in three ways: i) preventing many culms from producing spikes; ii) slowing down spikelet formation and consequently reducing the number of spikelets per spike; and iii) reducing floret formation per spikelet, thus reducing the number of kernels per spike. However, waterlogging for up to 20 days did not affect the durum wheat grain yield in any of the varieties, and only when prolonged for 40 and 60 days did it depress their production. The two most prolonged waterlogging durations were selected as the most extreme field conditions in central Italy and are not very likely to occur. Therefore in usual weather conditions (less than 20 d of waterlogging) waterlogging at tillering did not produce significant reductions in the grain yield of durum wheat.

References

Abbate, P.E., Pontaroli, A.C., Làzaro, L., Gutheim, F. 2013. A method of screening for spike fertility in wheat. J. Agr. Sci. **151:**322–330.

Belford, R.K. 1981. Response of winter wheat to prolonged waterlogging under outdoor conditions. J. Agric. Sci. **97**:557–568.

Brisson, N., Rebiere, B., Zimmer, D., Renault, P. 2002. Response of the root system of a winter wheat crop to waterlogging. Plant Soil **243**:43–55.

Brooking, I.R., Jamieson, P.D., Porter, J.R. 1995. The influence of daylength on final leaf number in spring wheat. Field Crop. Res. **41**:155–165.

Cannell, R.Q., Belford, R.K., Gales, K., Dennis, C.W., Prew, R.D. 1980. Effect of waterlogging at different stages of development on the growth and yield of winter wheat. J. Sci. Food Agric. **31**:117–132.

Cannell, R.Q., Belford, R.K., Gales, K., Thomson, R.J., Webster, C.P. 1984. Effects of waterlogging and drought on winter wheat and winter barley grown on a clay and a sandy loam soil. Plant Soil **80**:53–66.

Collaku, A., Harrison, S.A. 2002. Losses in wheat due to waterlogging. Crop Sci. **42**:444–450.

De San Celedonio, R.P., Abeledo, L.G, Miralles, D.J. 2014. Identifying the critical period for waterlogging on yield and its components in wheat and barley. Plant Soil **378**:265–277.

Dickin, E., Bennett, S., Wright, D. 2009. Growth and yield responses of UK wheat cultivars to winter waterlogging. J. Agr. Sci. **147**:127–140.

Ghobadi, M.E., Ghobadi, M. 2010. Effect of anoxia on root growth and grain yield of wheat cultivars. World Acad. Sci. Eng. Technol. **70**:85–88.

Ghobadi, M.E., Ghobadi, M., Zebarjadi, A. 2011. The response of winter wheat to flooding. World Acad. of Sci., Engineering and Technol. **78**:440–442.

Hossain, M.A., Uddin, S.N. 2011. Mechanisms of waterlogging tolerance in wheat: Morphological and metabolic adaptations under hypoxia or anoxia. Aust. J. Crop Sci. **5**:1094–1101.

Hossain, M.A., Araki, H., Takahashi, T. 2011. Poor grain filling induced by waterlogging is similar to that in abnormal early ripening in wheat in Western Japan. Field Crop Res. **123**:100–108.

Huang, B., Johnson, J.W. 1995. Root respiration and carbohydrate status of two wheat genotypes in response to hypoxia. Ann. Bot. **75**:427–432.

Jiang, D., Fan, X., Dai, T., Cao, W. 2008. Nitrogen fertiliser rate and post-anthesis waterlogging effects on carbohydrate and nitrogen dynamics in wheat. Plant Soil **304**:301–314.

Kirby, E.J.M. 1990. Co-ordination of leaf emergence and leaf and spikelet primordium initiation in wheat. Field Crops Res. **25**:253–264.

Malik, A.I., Colmer, T.D., Lambers, H., Setter, T.L., Schortemeyer, M. 2002. Short-term waterlogging has long-term effects on the growth and physiology of wheat. New Phytol. **153**:225–236.

Meyer, W.S., Barrs, H.D. 1988. Response of wheat to single short-term waterlogging during and after stem elongation. Aust. J. Agric. Res. **39**:11–20.

Musgrave, M.E. 1994. Waterlogging effects on yield and photosynthesis in eight winter wheat cultivars. Crop Sci. **34**:1314–1318.

Musgrave, M.E., Ding, N. 1998. Evaluating wheat cultivars for waterlogging tolerance. Crop Sci. **38**:90–97.

Rasaei, A., Ghobadi, M.E., Jalali-Honarmand, S., Ghobadi, M., Saeidi, M. 2012. Impacts of waterlogging on shoot apex development and recovery effects of nitrogen on grain yield of wheat. Eur. J. Exp. Bio. **2**:1000–1007.

Robertson, D., Zhang, H., Palta, J.A., Colmer, T., Turner, N.C. 2009. Waterlogging affects the growth, development of tillers, and yield of wheat through a severe, but transient, N deficiency. Crop Pasture Sci. **60**:578–586.

Sayre, K.D., Van Ginkel, M., Rajaram, S., Ortiz-Monasterio, I. 1994. Tolerance to waterlogging losses in spring bread wheat: effect of time of onset on expression. Annu. Wheat Newslet. **40**:165–171.

Setter, T.L., Waters, I. 2003. Review of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. Plant and Soil **253**:1–34.

Sinclair, T.R., Jamieson, P.D. 2006. Grain number, wheat yield, and bottling beer: An analysis. Field Crop Res. **98**:60–67.

Steel, R.G.D., Torrie, J.H., Dickey, D.A. 1997. Principles and procedures of statistics: A biometrical approach. 3rd Ed. McGraw-Hill. New York, USA.

Whingwiri, E.E., Stern, W.R. 1982. Floret survival in wheat: Significance of the time of floret initiation relative to terminal spikelet formation. J. Agric. Sci. **98**:257–268.