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Waterlogging at jointing and/or after anthesis in wheat induces early leaf senescence and impairs grain filling

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ABSTRACT

Waterlogging may be involved in the grain-filling disorder known as 'abnormal early ripening' (AER) in wheat (*Triticum aestivum*) in western Japan. This study carried out over two consecutive cropping seasons (2009/10 and 2010/11), examines whether or not wheat plants exposed to waterlogging at jointing exhibit early leaf senescence during grain filling. The effects of a single waterlogging at jointing (WL_{joint}) or after anthesis (WL_{anthe}), and of a double waterlogging at the same two stages (WW) were compared in three Japanese wheat cultivars. Waterlogging for 21 days was imposed in all cases except for after anthesis in 2010/11 when the treatment was for only 11 days. In both cropping seasons, grain yield in the WL_{joint} plants was 10–15% lower than that in the well-drained plants. The lower yields were due to smaller grain weights, rather than to decreases in spike number or grain number per spike. The WL_{anthe} treatment also reduced yield by 15%, although the duration of stress in the WL_{anthe} plots was 10 days shorter than in the WL_{joint} plots. This indicates that the WL_{anthe} treatment had a more negative impact on yield. Plants in the WW plots exhibited reductions in grain yield of from 22 to 35% depending on the cultivar. The smaller grain weights of waterlogged plants was a result of both a 1–5 days shorter grain-filling period and also lower grain growth rates in the later stages of filling. Plants in the WL_{joint} and WW plots did not show reductions in leaf greenness, stomatal conductance or leaf water content during or after waterlogging at jointing. However, the plants in the WL_{joint} and WW plots, and also in the WL_{anthe} plots, suffered reductions in these parameters about 14 days after anthesis. At the same time, the plants in the WW plots showed the most marked leaf senescence and the lowest leaf water contents (0.39 $g\,g^{-1}$ in the WW plots vs 0.85 $g\,g^{-1}$ in the well-drained plots). At maturity, concentrations of water-soluble carbohydrates (WSCs) in culms were highest in the WW plots, probably indicating that remobilization of the WSCs from the culms to the grains was reduced. These results indicate that root injury by waterlogging at jointing induces rapid leaf senescence in the grain filling period. Comparisons among the WL_{joint}, WL_{anthe} and WW plots indicate that in wheat, root sensitivity to waterlogging rises markedly during the post-anthesis period.

1. Introduction

Abnormal early ripening (AER), locally known as *Kareure*, is a physiological disorder in barley (Furukawa and Koshio, 1962) and wheat (Ishikawa et al., 1993; Taniguchi et al., 1996; Hossain et al., 2009) that occurs frequently in western Japan. In wheat, the symptoms of AER appear first as a sudden senescence of the leaves in well-developed plants around 14 days after anthesis followed by a rapid withering of the spikes resulting in smaller grains and lower grain yields (Taniguchi et al., 1996; Hossain et al., 2009). Plant appearance before the sudden senescence varies with regions and cultivars (Furukawa and Koshio, 1962; Ishikawa et al., 1993). AER frequently occurs in waterlogging-prone area in fields where plant height and plant density are sometimes visibly reduced (Araki et al., 2011). However, it is an important characteristic of AER that tiller number, plant height and leaf greenness are often not at all reduced (Hossain et al., 2009), so that affected plants do not show any differences in appearance before the sudden onset of AER symptoms. Thus, it is not possible to predict which fields or parts thereof will exhibit AER. The physiological changes occurring in AER plants before symptoms appear have not yet been determined so the factors underlying AER are largely unknown.

It is suspected that AER could be induced by a physiological disorder of the roots, especially by root injury arising from waterlogging (Noda and Kimura, 1957). In field-grown wheat, Hossain et al. (2011) confirmed that waterlogging after anthesis can induce sudden leaf senescence 7–16 days after anthesis with water-soluble carbohydrates stored in culms being poorly remobilized to grains.

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Table 1
Total rainfall, air temperature and total duration of sunshine at the experimental site during wheat cropping (November–June) in 2009/10 and 2010/11.

Month	Total rainfall (mm)		Air temperature (°C)				Total duration of sunshine (h)	
	2009/10	2010/11	Maximum[a]		Minimum[a]		2009/10	2010/11
			2009/10	2010/11	2009/10	2010/11		
November	187	19	17.1	16.9	7.7	5.7	107	169
December	61	124	11.5	11.5	2.8	2.4	121	131
January	46	32	9.6	6.6	0	−1.5	131	124
February	114	112	12.1	11.8	3.4	1.4	123	126
March	237	48	13.5	12.6	4.5	1.9	115	186
April	273	92	17.9	19.4	7.8	6.8	151	208
May	194	412	23.9	24.0	12.8	14.6	199	149
June	385	297	27.7	27.5	19.3	20.1	150	98

The data was collected from the website of the Japan Meteorological Agency for Yamaguchi station, about 1 km away from the experimental site.
[a] Monthly average daily temperature.

This indicates that root injury by waterlogging 14 days after anthesis can induce AER-like symptom. However, waterlogging after anthesis does not properly account for AER in the fields as AER can often occur without waterlogging after anthesis (Araki et al., 2011).

The question of whether waterlogging before heading may induce AER-like symptoms has not been tested for field-grown wheat. On the other hand, long-term waterlogging or over-wetting of the soil before heading may induce AER-like symptoms. Kira et al. (1993) tested the effects of long-term soil over-wetting for nearly 80 days from tillering to heading, followed by mild soil dryness (about −30 kPa) after heading in greenhouse-grown wheat. They found that these soil conditions induced early and rapid withering of spikes. Other pot or greenhouse experiments also show that long-term waterlogging or over-wetting of soils induce early leaf senescence after anthesis in wheat (Nishida et al., 1993) and in barley (Ishikawa et al., 1953; Nishikawa and Takano, 1957). However, the waterlogging conditions in those experiments were too long and thus too severe to be compared to normal field soil conditions. In these studies, unlike with AER in wheat, shoot growth had already declined before the visible onset of leaf senescence.

Quantitative investigations of the effects of short-term waterlogging during the reproductive stages of wheat are not common (Hossain et al., 2011). Tokimasa (1950) imposed a single waterlogging treatment for 20 days on pot-grown wheat at different growth stages and concluded that the negative impacts of waterlogging varied with growth stage; the greatest and second greatest reductions of grain yield were found at tillering and after heading, respectively. In that study, changes in leaf greenness and grain filling after anthesis were not recorded. Thus, many uncertainties remain including: if sensitivity to the short-term waterlogging treatments varies with growth stage during the reproductive phase; if early leaf senescence occurs during waterlogging, immediately after waterlogging or at some other specific growth stage; if the physiological processes involved in poor grain filling in waterlogged wheat are similar to those in AER wheat; and, lastly, if multiple waterlogging events during the reproductive phase have cumulative, negative effects on grain filling compared with a single waterlogging event.

In this study, we test whether waterlogging of field grown wheat at jointing induces sudden leaf senescence in the same way as occurs in AER. We assume that waterlogging at this stage does not affect leaf greenness and water status immediately after the waterlogging but may then induce sudden leaf senescence and withering of spikes during grain filling. The processes of grain filling of waterlogged wheat are compared with those of AER wheat. Japanese wheat cultivars having different levels of tolerance to AER (Taniguchi et al., 1996) were used, hypothesizing that their tolerance to AER may be related to their tolerance of waterlogging during the reproductive stages. The processes and severity of early leaf senescence and poor grain filling were compared in plants subjected to a single waterlogging event imposed either at jointing or after anthesis, and to two waterlogging events, one at each stage. The comparisons should show whether root injury by waterlogging at jointing and/or after anthesis induces similar symptoms to AER.

2. Materials and methods

2.1. Experimental site and growth environment

The field experiments were conducted at the Experimental Farm, Faculty of Agriculture, Yamaguchi University, Yamaguchi, Japan (34°09.6′N, 131°27.2′E; 18 m asl) in two successive growing seasons, 2009/10 and 2010/11. The region is characterized by a humid temperate climate with annual rainfall of about 1900 mm. Data on the meteorological parameters during the two wheat cropping seasons (November–June) is shown in Table 1. The topsoil (0–15 cm) of the experimental field is a clay loam of pH 6.7 (in water extract) and contained 1.62 g kg^{-1} N, 133 mg kg^{-1} P, 285 mg kg^{-1} K, 1.36 g kg^{-1} Ca and 110 mg kg^{-1} Mg. More soil properties are described in Hossain et al. (2011).

2.2. Plant materials and experimental design

The field experiments were carried out using a split-plot design with three replicates (blocks). Each block consisted of three or four main plots where waterlogging treatments were allocated randomly. Each of the main plots was divided into two or three subplots where the cultivars were assigned randomly (Fig. 1). In 2009/10, three waterlogging treatments were imposed: control (drained), waterlogged at jointing (WL_{joint}) and waterlogged at jointing and after anthesis (WW). In 2010/11, a fourth waterlogging treatment was added; waterlogging after anthesis (WL_{anthe}). The two wheat cultivars Chikugoizumi and Norin 61 were used in 2009/10 and a third cultivar Kinuiroha was included in 2010/11. Chikugoizumi, Norin 61 and Kinuiroha are reported to be AER tolerant, AER medium and AER susceptible, respectively (Taniguchi et al., 1996). Although tolerance to waterlogging for these cultivars has not been evaluated quantitatively, wheat-breeder colleagues suggested that Chikugoizumi is probably more tolerant than Norin 61 and Kinuiroha.

In 2009/10, plants of each cultivar were grown in subplots, 0.6 m wide × 4.0 m long in three rows 0.2 m apart (Fig. 1). The long edges of the subplots abutted one another with drainage channels (0.2 m wide × 0.3 m deep) being dug in alternate gaps between subplots so that each plot had a single adjacent drainage channel. In the remaining gaps, shallow (0.2 m deep) irrigation channels were dug, so that each plot could be exposed to an adjacent pool of still water for waterlogging treatment. In 2010/11, the subplots were 1.2 m