CHAPTER 11

Waterlogging Tolerance

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More than one third of the world's irrigated areas suffer occasional or more frequent waterlogging (Donmann and Houston, 1967). Waterlogging has been shown to limit wheat yields in many regions of the world; an area estimated at 10 million ha is waterlogged each year in developing countries (Sayre et al., 1994). Waterlogging occurs when rainfall or irrigation water collects on the soil surface for prolonged periods without infiltrating the soil. Soil characteristics that contribute to waterlogging include soil physical properties that allow formation of a crust on the soil surface or of a pan in the subsoil. Waterlogging can also occur when the amount of water added through rainfall or irrigation is more than what can percolate into the soil within one or two days.

Waterlogging occurs in many wheat growing regions around the world, especially irrigated and high rainfall environments. In irrigated regions, the main culprit seems to be the lack of proper drainage systems. Irrigation facilities do not allow easy drainage of excess water, sometimes due to poorly kept irrigation canals from which water seeps out. Major examples are the Indian Subcontinent, certain river basins in China, and the Nile River Delta in Egypt. In the northern Indo-Gangetic Plains of India alone, 2.5 million ha of wheat are affected by irregular waterlogging (Sharma and Swarup, 1988).

The effects of waterlogging are most widespread in the irrigated rice-wheat regions of South and Southeast Asia (i.e., China, Vietnam, Thailand, Bangladesh, Nepal, India, and Pakistan) and in the southern United States (i.e., Georgia, Mississippi, and Louisiana). A common denominator in these countries is that rice rotations are practiced on much of the land. Soils are generally puddled to restrict water percolation and create flooded conditions for rice cultivation. Due to soil puddling, wheat that follows rice in the drier season is planted under less than optimal soil physical conditions. The soil pan that was created intentionally for rice cultivation is often left undisturbed and may create a barrier for water movement, causing waterlogging when excessive irrigation or rainfall occurs.

In South Asia, wheat is a relatively new option within rice rotation schemes. Some farmers, accustomed to applying generous amounts of water to rice, tend to over-irrigate their wheat crop. Additionally, many rice-wheat soils are silt or loam and susceptible to crusting, which creates waterlogging by restricting percolation from the surface. Declines in organic matter in the topsoil of South Asia are well documented and also contribute to poor soil physical quality (FAO, 1994; Hobbs and Morris, 1996; Nagarajan, 1998).

Waterlogging can affect other irrigated areas in Asia besides the rice-wheat growing regions. Wheat-producing areas in Egypt, Sudan, and Nigeria also suffer regularly from waterlogging. In parts of Africa and Latin America, heavy rainfall combined with heavy clay soils creates waterlogging that limits wheat production. In the traditional wheat-growing regions in the Ethiopian highlands, downpours are heavy and prolonged during the rainy season. Hence waterlogging is a common occurrence at the beginning of the wheat cycle. The situation is further exacerbated by the black vertisols in Ethiopia, consisting of heavy clays that inhibit infiltration, swell, and crack severely. Waterlogging limits wheat yields in Australia due to rising groundwater (Grieve et al., 1986; McDonald and Gardner, 1987; Meyer and Barrs, 1988).

Conditions and Symptoms Associated with Waterlogging

Except at sowing or during early germination, waterlogging will not generally destroy wheat plants nor affect plant establishment (Musgrave, 1994). The major morphological and biochemical effects will be discussed in detail later, but under mild waterlogging wheat plant growth is

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usually stunted, bottom leaves senesce, tiller survival is reduced, and florets may become sterile.

High temperatures tend to exacerbate the negative effects of waterlogging. When aerobic soil conditions re-occur, plant growth resumes slowly. Consequently, wheat yields are affected.

An entire field will rarely be waterlogged; waterlogging is usually restricted to the lower lying areas of a field (Picture 1). Waterlogging occurs when the soil is fully saturated, and standing water replaces the air in the soil pore spaces. There is a lack of oxygen in the soil, restricting aerobic respiration by growing roots and other living organisms. Soil chemical properties change when anaerobic conditions persist for several days, increasing the availability of some major or minor elements while decreasing the availability of others. Plant transpiration is affected until wheat roots recover (when soil aerobic conditions recur) or adapt to the anaerobic conditions. However, extended waterlogging will result in root death. Waterlogging also limits the wheat plant's nutrient uptake by reducing plant transpiration and diminishing root function.

Another effect of waterlogging is to stimulate the production of certain plant hormones. In anaerobic conditions these hormones are released from the roots in greater concentrations and may affect leaf and root responses. Ethylene is produced both by the roots and by microorganisms in waterlogged soils. The hormonal effects of ethylene released under waterlogging are attracting a great deal of interest. Water acts as a barrier to the escape of ethylene produced in roots and other submerged tissue. Ethylene is known to be a trigger (not a promoter) of leaf senescence (Dong et al., 1983).

Waterlogging during sowing or germination generally kills the seed or seedling. The seedling's radicle and roots do not adapt readily to waterlogging or are more susceptible to seedling diseases that may follow (Belford et al., 1985). Generally, the wheat plant's tolerance to waterlogging increases as it ages, and the detrimental effect on yield decreases (Meyer and Barrs, 1988). Once the wheat crop is established, many genotypes can withstand waterlogging up to 10 days with no yield loss, if the wheat leaves are not submerged. Wheat crops can make an amazing recovery following early waterlogging stress, if supplied with extra nitrogen.

In waterlogged soils and in the roots of plants growing in them, exceptionally high levels of ethylene may build up, given that ethylene diffuses more slowly in water than in aerated soil. The first response of a wheat plant to anaerobic conditions involves its biochemical pathways as a response to the lack of respiration by root cells. Various hormones are stimulated and transported to the leaves, causing early senescence of older leaves within days (Dong et al., 1983; Dong and Yu, 1984). Seminal roots are generally killed or their growth greatly restricted (Huang and Johnson, 1995).

However, some wheat genotypes have nodal or adventitious roots that begin aerenchyma cell formation. Aerenchyma is tissue that can carry oxygen from the leaves to the roots under anaerobic conditions to maintain root respiration, though on a more limited basis than in aerobic conditions. The process is accelerated if temperatures are elevated. Genetic variability for this trait has been documented in the literature (Cao et al., 1995).

Winter wheat areas may also be prone to waterlogging. Winter wheats are sometimes grazed and allowed to re-grow for grain production in the spring. Trampling of saturated pasture soils by cattle can cause restricted water movement and waterlogging.

The literature documents some tolerance of winter wheats to waterlogging (Musgrave, 1994). Yet this may not be true tolerance, since the colder soil temperatures associated with waterlogging in winter-wheat-growing areas reduce the amount of oxygen required for root respiration. Thus yield reductions associated with waterlogging in colder areas are not as great as those in the more temperate and tropical areas of the world. On the other hand, some studies show soil oxygen decline under waterlogging is rapid at most temperature ranges (Trought and Drew, 1982). It should also be noted that winter wheats are longer maturing and hence less sensitive to waterlogging than the earlier maturing spring wheats (Gardner and Flood, 1993).

Picture 1. Non-uniform waterlogging in a wheat field in Bangladesh.

The literature contains many references on the possible genetic variability for tolerance of wheat to waterlogging, hypoxia, or anoxia. This chapter will review the physiological and biochemical causes of wheat yield reductions due to waterlogging. It will also explore the different options for screening wheat for waterlogging, plus the advantages of incorporating waterlogging tolerance into a breeding program. Agronomic practices developed through research or being used by farmers to alleviate the detrimental effects of waterlogging are also included in this chapter.

Effect of Waterlogging on Soil Chemistry

Decreases in yield brought about by waterlogging may be caused by numerous factors acting upon the wheat plants, such as changes in soil chemistry. As an example, denitrification of soil nitrogen as a result of waterlogging may affect the amount of nitrogen that concentrates and accumulates in the upper leaves of the plants, which will eventually have a negative effect on grain yield. Table 1 shows a list of soil chemical responses and the corresponding bibliographic references that can be consulted for further information on each.

Genetic Improvement of Waterlogging Tolerance

Some studies have suggested that the waterlogging tolerance trait is highly heritable (Cao et al., 1995; Boru, 1996); others demonstrated there is little variability for waterlogging tolerance among durum wheat lines (Tesemma et al., 1991). Some authors have found that the trait is controlled by a single gene (Cao et al., 1992; Cao et al., 1995), while others maintain it is polygenic (Hamachi et al., 1989; Boru, 1996). Closely related species of wheat may be sources of waterlogging tolerance (Cao and Cai, 1991; Taeb et al., 1993; Cai et al., 1994); however, there may be other sources of tolerance within wheat. Boru (1996) concluded that there were four genes involved in waterlogging tolerance: one major gene, two intermediate ones, and one minor gene. Triticale has proved to be superior to bread wheat in tolerance to waterlogging (Johnson et al., 1991a). The Chinese have reported considerably more work on breeding waterlogging tolerant lines in the literature than any other country.

Screening techniques in the laboratory or the field are well documented in the literature. While waterlogging tolerance is directly related to the ability to quickly form roots with aerenchyma cells under anaerobic conditions, there may be concurrent tolerance to Mn toxicity (Wagatsuma et al., 1990). Tolerance to Mn toxicity seems to be secondary to the formation of aerenchyma cell in roots for extending tolerance. Wagatsuma et al. (1990) also determined that when any tolerance was expressed, it was not due to the ability of plant roots to tolerate low O_2 levels.

One study showed differences in nodal roots and aerenchyma cell formation among wheat and triticale varieties (Thomson et al., 1992). Those lines with increased nodal and aerenchyma forming abilities endured waterlogging with fewer detrimental effects. Data suggest that waterlogging tolerance may be related to the ability to produce more crown roots and more aerenchyma in those roots, to maintain stomatal opening, and to more quickly resume seminal root growth and stomatal opening when aerobic conditions recur (Huang et al., 1994). Boru (1996) showed that aerenchyma cell formation and yield were highly correlated in lines that survived severe waterlogging. Their cortical tissue had dissolved to form the aerenchyma; in contrast, sensitive genotypes expressed little or no aerenchyma formation after waterlogging.

Techniques for screening for waterlogging tolerance

The authors feel that screening for waterlogging is best done in the field, using simple designs, rather than in less realistic laboratory conditions.

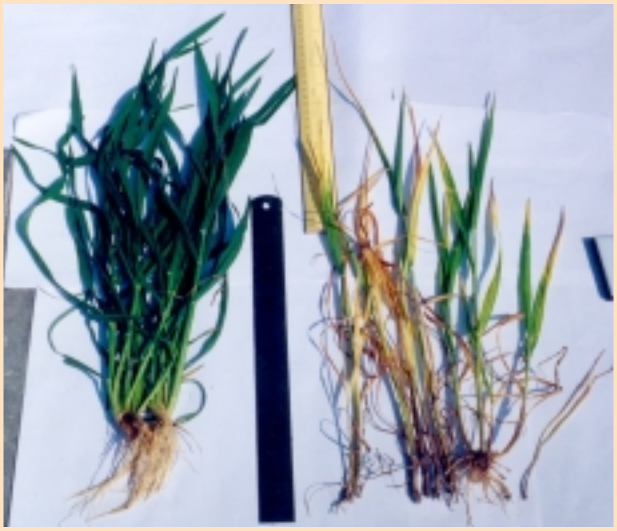
Table 1. Soil chemical responses to waterlogging as reported in the literature.

Chemical response	Reference
Increased Mn concentration that could be toxic to plant growth	Sparrow and Uren, 1987; Wagatsuma et al., 1990
Decreased soil oxygen; generally greater at warmer temperatures	Belford et al., 1985
Decreased Mo availability; Mo application in waterlogged, acid soils retained plastid pigments, cyclic phosphorylation, and CO_2 fixation within wheat plants	Salcheva et al., 1984
Denitrification of both organic and inorganic soil N	Feigenbaum et al., 1984; Singh et al., 1988; Mascagni and Sabbe, 1991; Humphrey et al., 1991
Mineral (Fe) coating of epidermal surface of roots under waterlogging	Ding and Musgrave, 1995
Volatile fatty acids and phenolic compounds accumulated in soils high in organic matter affect root metabolism and growth	Lynch, 1978; Jackson and St. John, 1980

Specific Physiological Responses of Wheat to Waterlogging as Reported in the Literature

1. Chlorosis of lower leaves (Sparrow and Uren, 1987; van Ginkel et al., 1992) (Picture 2).
2. Early senescence of lower leaves (Dong et al., 1983; Dong and Yu, 1984).
3. Decreased plant height (Sharma and Swarup, 1989; Wu et al., 1992).
4. Delayed ear emergence (Sharma and Swarup, 1989).
5. Reduced root and shoot growth (Huang and Johnson, 1995).
6. Lower number of spike-bearing tillers (Belford et al., 1985; Sharma and Swarup, 1989; Wu et al., 1992) (Picture 3).
7. Fewer grains per spikelet and reduced kernel weight (Belford et al., 1985; Musgrave, 1994; van Ginkel et al., 1992).
8. Reduced diameter of metaxylem and protoxylem vessels of the nodal roots (Huang et al., 1994).
9. Enhanced formation of aerenchyma cells in the cortical tissue of both seminal and nodal roots (Huang et al., 1994; Boru, 1996).
10. Leakage of cell electrolytes (Wang et al., 1996a).
11. Reduced uptake of N, P, K, Ca, Mg, and Zn while increasing Na, Fe, and Mn absorption under alkaline soil conditions (Sharma and Swarup, 1989; Stieger and Feller, 1994a).
12. Reduced root respiration (Wu et al., 1992; Wang et al., 1996b).
13. In wheat oxygen concentrations between 33 and 66 $\mu g\ m^2\ s^{-1}$ were categorized as deficient and < 33 $\mu g\ m^2\ s^{-1}$ as critical. Roots were significantly reduced by the small amount of oxygen available, especially at lower depths. Temperature also influenced root reduction, with 15^{o} C appearing to be the best soil temperature for root growth (Box et al., 1991).
14. Decreases in wheat yields of 37-45% due to waterlogging have been observed (Musgrave, 1994; Wu et al., 1992; Cai et al., 1994; van Ginkel et al., 1992; Boru, 1996). Wheat yield depression was due to reduced kernel number and weight rather than to an effect on stand establishment.
15. Waterlogging was shown in one study to cause only slight suppression of flag-leaf photosynthesis and leaf conductance in waterlogging intolerant wheat lines (Musgrave, 1994). Other studies showed overall lowered rates of plant photosynthesis, stomatal conductance, and transpiration (Dong and Yu, 1984).
16. Root carbohydrate supply was shown in some studies not to be a limiting factor for root growth and respiration (Huang and Johnson, 1995).
17. Anoxia (waterlogging) inhibited the transport of sugars from the shoots to the roots by more than 79% in seedlings. However, there are interactions between temperature and other environmental factors that could affect interpretation of data on tolerance of wheat to anoxia, which explains the lack of consistent results in the literature (Waters et al., 1991).
18. Data collected on wheat under waterlogged conditions (i.e., deficient in oxygen) in the field and glasshouse showed that the biosynthesis of new tissue was more inhibited than the supply of substrates for growth (Attwell et al., 1985).
19. Flower sterility associated with waterlogging is linked to lower transpiration and, hence, to less uptake of boron (and other nutrients) (Somrith, 1988; Saifuzzaman and Meisner, 1996; Rawson et al., 1996; Misra et al., 1992; Kalidas, 1992; and Subedi, 1992).
20. Ethylene production increases and acts as a trigger (not promoter) of accelerated wheat plant senescence (Dong et al., 1983). Exogenous cytokinins applied to wheat seedlings at the onset of waterlogging delayed degradation of chlorophyll and other biochemical processes (Dong and Yu, 1984). Enhancement of ACC (1-aminocyclopropane-1-carboxylic acid), its precursor, and ethylene was more pronounced in older leaves than in younger ones during waterlogging (Dong et al., 1986).
21. Less nitrogen concentrates and accumulates in the upper leaves of waterlogged wheat, probably due to the denitrification of soil nitrogen (McDonald and Gardner, 1987).
22. Nitrogen remobilization from lower leaves is accelerated on flooded soils and explains their chlorosis (Stieger and Feller, 1994b).
23. Reduced rooting depth and increased root porosity (Yu et al., 1969).

Picture 2. Lower leaf chlorosis.



Picture 3. Waterlogging reduces the number of spike-bearing tillers.

Retaining water on the surface is easier to achieve on heavy soils than on lighter soils. To administer waterlogging stress on heavy soils, wheat lines can be irrigated such that water is retained at or slightly above the soil surface from emergence to the boot stage (van Ginkel et al., 1992; Sayre et al., 1994). In the former study, carried out using extreme waterlogging stress, only three genotypes were shown to be tolerant out of a total of 1,344 lines. In lighter soils, waterlogging may be more difficult to induce.

Our experience shows that even "over-watering" (i.e., keeping the soil slightly at or above field capacity at various growth periods) can induce waterlogging that is adequate for screening wheat lines.

Evaluating differences among varieties in leaf chlorosis or withering after 15 days of waterlogging has been shown to be a quick method for assessing tolerance. Using this method the number of green leaves remaining on the main stem was correlated with the number of fertile grains in the main ear and grain weight per plant (Cai and Cao, 1990; van Ginkel et al., 1992). Field studies in Mexico and Bangladesh on hundreds of CIMMYT wheat lines over years have shown clear evidence of variability to waterlogging tolerance. Fields were kept flooded from emergence to boot stage. Percentage foliar chlorosis at heading and simple agronomic scores during grainfilling appeared to be highly correlated with yield in large plots. Many lines can be screened rapidly using this simple methodology (van Ginkel et al., 1992).

Studies in Japan showed that assessing leaf senescence in early generations was useful for screening for waterlogging tolerance (Hamachi et al., 1989). Wiengweera et al. (1997) used a "stagnant" nutrient solution in agar closely resembling waterlogged soil for rapid screening of wheat seedlings in the lab. Studies in China indicated that an index based on the number of grains per ear and one thousand grain weight was effective for evaluating waterlogging tolerance (Lin et al., 1994). Musgrave (1994) found that flag leaf photosynthesis in winter wheat correlated well with grain weight under waterlogging.

Although waterlogging during early seed germination and seedling growth is very detrimental to the wheat crop, studies have shown there are genetic differences in the ability of wheat genotypes to withstand early waterlogging stress (Johnson et al., 1991b). Mineral (Fe) coating of rice roots (showing oxygen release from the roots) is highly correlated to rice yields, but the trait was negatively correlated to wheat yields in 12 cultivars grown under waterlogged conditions (Ding and Musgrave, 1995).

Since tiller production decreases during waterlogging, tiller production, shoot dry matter, and root penetration were used for screening Triticeae species for tolerance. When these criteria were used, many wild species expressed a level of tolerance to waterlogging that was better than that of wheat (Taeb et al., 1993).

Agronomic Practices Known to Reduce Waterlogging

Setting planting dates to coincide with reduced rainfall patterns is one way to avoid waterlogging (Aggarwal et al., 1987). However, this may not always be possible due to rotation restrictions, and may be associated with lower yields due to sub-optimal climatic conditions.

Application of nitrogen fertilizer after waterlogging has been shown to reduce the detrimental effects of this stress (Trought and Drew, 1980a; Swarup and Sharma, 1993; de Oliveira, 1991). Waterlogging under optimum soil nutrient (N) supply conditions resulted in less growth restriction than under a sub-optimal nutrient supply (Guyot and Prioul, 1985). Further studies provided evidence that doubling the concentration of nutrients supplied to the plants under waterlogging reduced the rate of decline in photosynthetic rate, chlorophyll content, and number of nodal roots, while improving shoot N status and growth (Huang et al., 1994).

Singh et al. (1992) found that the use of green manures, straw, and animal manures increased the availability of Fe and Mn several fold under flooded conditions. Organic manures can also improve soil physical factors and reduce soil surface crusting, enhance plant rooting, and alleviate the effects of pan formation on yields. Therefore the use of manures is considered beneficial in waterlogging-prone environments.

Seed treatments such as calcium peroxide (Thomson et al., 1983) were tried with mixed results for alleviating the detrimental effects of waterlogging during germination or early seedling growth.

Several cultivation and sowing techniques have been shown to give yield increases under waterlogged conditions. For example, Rasmussen (1988) found that direct drilled wheat was more sensitive to waterlogging between germination and emergence than conventionally plowed wheat. The furrow or bed planting system has significant yield advantages, even when there is no waterlogging. Furrows also make it possible to drain fields or keep a large portion of the root system out of waterlogged soils (Abebe et al., 1991; Tedia et al., 1994).

Shifting from basin flooding to furrow or sprinkler irrigation on waterlogging-prone soils has been shown to reduce the problem significantly (Melhuish et al., 1991). Surface seeded wheat (sown on top of uncultivated, saturated soil) showed the least sensitivity to waterlogging compared to wheat sown in conventionally plowed and chiseled soil (Table 2).

Screening for Waterlogging Tolerance under Bangladesh Conditions

Identification of waterlogging tolerant wheat genotypes began during the 1993 wheat season in Bangladesh. In the northwestern part of the country, screening of wheat genotypes for waterlogging tolerance spanned four seasons. The soil type at the Dinajpur Wheat Research Centre experiment station is deep, sandy loam. Over three seasons (1993-95), 162 wheat genotypes were subjected to waterlogging by irrigating at 10-day intervals from 10 to 100 days after sowing (DAS). The field was flooded and the land submerged for 24-36 hours in each of the 10 irrigations.

However, under those soil conditions (sandy loam), our treatments were closer to "over-irrigation" than true waterlogging, since the water percolated quickly within 36 hours of waterlogging. Five replications were used during the first two seasons, and three replications were practiced in the other two seasons to collect data on 2.5-m plots consisting of three rows, 20 cm wide. The experiments were sown at normal sowing time (third week of November). Seeding rate was 120 kg/ha, and fertilizer rates were as recommended (100: 60: 40: 20: kg/ha of NPKS). Additional N fertilizer was top-dressed just after the second irrigation, as recommended in Bangladesh (33:0:0).

In contrast to previous years, in which waterlogging resembled "over-watering," in the 1996 season 64 wheat genotypes were subjected to true waterlogging as in a rice field; the field was irrigated consecutively for three days at three growth stages: crown root initiation, booting, and grainfilling. Crop growth was severely affected during this season, and most genotypes did not produce sufficient spikes for sampling to record spikelet/spike, grains/spike and one thousand grain weight (TGW). Some genotypes produced only a few small spikes with hardly any grain.

Twenty-one waterlogging tolerant and twenty waterlogging sensitive wheat genotypes were identified from lines subjected to various modes of waterlogging over the years. As an example, the scores of lines tolerant and sensitive to waterlogging in 1994 are presented in Table 3.

Another experiment with eight waterlogging treatments (including a control) was conducted in central Bangladesh during the 1996 growing season. Soils were heavy 2:1 montmorillanitic. Waterlogging treatments were imposed at 10 (T2), 20 (T3), 30 (T4), 40 (T5), 50 (T6), 60 (T7), and 70 (T8) DAS, which correspond to Zadoks' growth stages 12, 21, 31, 42, 52, 63, and 73. Control was normal irrigation (T1). Water left standing for four days in the treatment plots was considered waterlogging in these soils. The control plot received three normal irrigations. The objective of this experiment was to observe the effect of waterlogging on seed set and yield, as well as to determine which crop growth stages are critically related to poor seed set and yield in wheat under simulated waterlogging conditions compared with the other years and locations.

Table 2. Wheat plant population under waterlogged conditions at sowing and early germination in different tillage systems.

Tillage and sowing system	Wheat plant population (plants m^{-2})
Conventional tillage: broadcast sowing	136a[†]
Chisel tillage: broadcast sowing	142a
Zero tillage: surface seeding	225b

[†] LSD among the rows are designated by letters.

Source: Unpublished field data from Bangladesh (Badaruddin, 1997).

Table 3. Characteristics of selected waterlogging tolerant and sensitive wheat genotypes grown under varying waterlogging conditions, WRC, Nashipur, Dinajpur, Bangladesh, 1994.

Genotypes	Avg. grain yield (kg ha^{-1})	Avg. TGW (g)	Avg. grains spikelet^{-1}	Visual sterility (%)	Leaf yellowing[†] (1-5)	Plant vigor[‡] (1-5)
Waterlogging tolerant						
MOZ-2 (Bangladesh)	4,333	49.8	1.80	0	1	5
BAW-451 (Bangladesh)	4,233	30.1	2.67	0	1	5
BR-16 (Brazil)	3,767	42.1	1.90	17	1	5
IAS58/4/KAL/BB/CJ/3/ALD/5/VEE CM88971-9Y-0M-0Y-3M-0Y	3,700	49.9	1.86	34	3	5
MOZ-1 (Bangladesh)	3,533	49.1	1.64	0	1	5
Waterlogging sensitive						
HD 22629 (India)	1,167	42.6	1.92	68	3	2
BAW-905 = K 9162 (Bangladesh)	1,233	42.8	1.93	12	4	1
K 8962	1,233	38.4	2.20	16	4	1
Aestivum Roelz W9047	1,300	35.3	2.24	0	3	3
FLN/ACC//ANA/3/DOVE CM65720-3Y-1M-1Y-1M	1,367	38.6	1.85	74	3	2

[†] Recorded in the field at 65 DAS using 1 to 5 scale, where 1 = yellowing of lower leaves and 5 = of flag leaves.

[‡] Judged using a 1 to 5 scale at 65 DAS, where 1 = very poor growth and 5 = excellent plant vigor.

There was no significant influence of waterlogging on spikes per unit area (Figure 1), which is consistent with the literature. Grains m^{-2} was used as an indicator of wheat seed set (Meisner et al., 1992). Waterlogging affected seed set. Misra et al. (1992) also reported that waterlogging affected seed set in wheat in Nepal. Seed set was most affected when waterlogging was imposed at 30 DAS (T4), followed by 10 DAS (T2). The highest number of grains m^{-2} was obtained in the control treatment (T1), followed by waterlogging treatments T6, T5, and T8 (Figure 2). Waterlogging stress during Zadoks' 31 was identified as being most critical for seed set in wheat, followed by Zadoks' 12. This is consistent with the data of van Ginkel et al. (1992). The wheat crop was found to be sensitive to waterlogging stress, though to a lesser degree, during Zadoks' 21 and 63.

One thousand grain weight was not affected by imposing waterlogging treatments at different growth stages (Figure 3) in our experiment. Differences in grain weight did not occur because waterlogging treatments were applied at and before anthesis but not from grainfilling onward. Other studies show contrasting results (van Ginkel et al., 1992).

Wheat grain yields differed with waterlogging treatments (Figure 4). Luxmoore et al. (1973) also observed negative effects on wheat grain yields when waterlogging was imposed for 30 days during grainfilling at 15 and 25^{0}C soil temperatures, which reduced grain yield by 20 and 70%, respectively. Waterlogging reduced wheat yields due to poor seed set and fewer spikes per unit area.

Conclusions

Realistic but cautiously optimistic conclusions can be drawn based on the above review of the literature and on data from the case study in Bangladesh. Waterlogging is a widespread problem in the irrigated and high rainfall wheat-growing regions of the world. Despite the breadth of the problem, understanding of the basic soil and plant processes involved in waterlogging tolerance is improving. The good news is that there is genetic variability for waterlogging tolerance within wheat, and that the genetics of waterlogging tolerance appears to be relatively simple, with medium to high heritabilities. Therefore, the prospects are good that varieties suitable for areas suffering from waterlogging stress can be bred and/or identified.

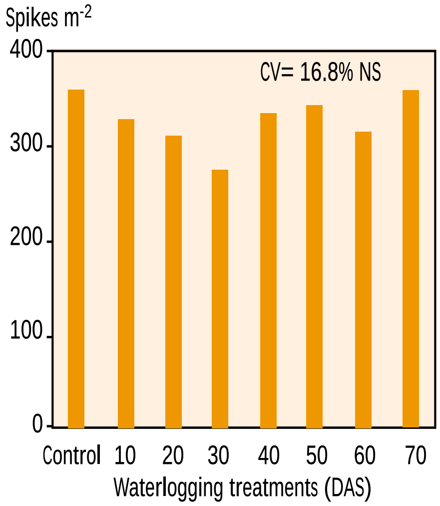


Figure 1. Waterlogging at different growth stages (days after sowing-DAS) affected spikes per unit area in 1995-96 at Joydebpur, Bangladesh.

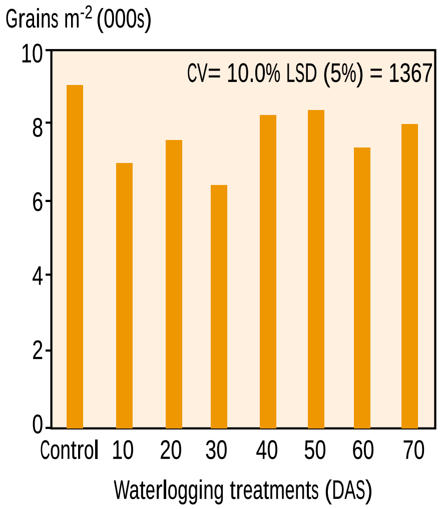


Figure 2. Waterlogging at different growth stages (days after sowing-DAS) affected grains per unit area in 1995-96 at Joydebpur, Bangladesh.

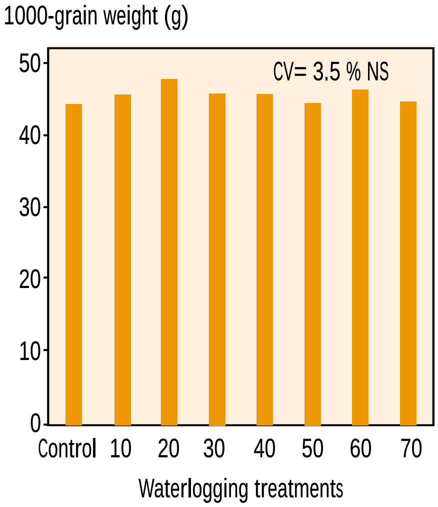


Figure 3. Waterlogging at different growth stages (days after sowing-DAS) affected 1000-grain weight in 1995-96 at Joydebpur, Bangladesh.

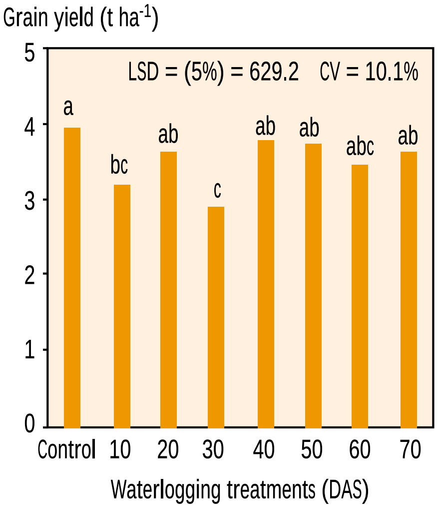


Figure 4. Waterlogging at different growth stages (days after sowing-DAS) affected grain yield in 1995-96 at Joydebpur, Bangladesh.

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