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Effect of water logging in wheat

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Abstract
Globally more than one-third of the irrigated area is under waterlogging which limits our wheat production and out of which northern Indo-Gangetic plains of India alone had 2.5 million ha affected by irregular waterlogging. So, to meet out the food demand of ever-growing population we have to find some alternates to harness the potential of the waterlogged area. Waterlogging is an important factor influencing yield and yield components in wheat. The objective of this study was to evaluate the effect of waterlogging on yield, yield components, protein and proline content, and chlorophyll a and b in wheat. In the study, seven levels of waterlogging treatment, 0, 5, 10, 15, 20, 25 and 60 days of flooding were applied. Increasing waterlogging stress decreased yield, spike number per m^{-2}, seed weight and number per spike, protein content, and chlorophyll a and b; and caused increase in proline content. The waterlogging as an abiotic stress can damage to crops such as wheat during winter season. Any suitable crop management during the growth and development of this plant can reduce yield loss due to waterlogging stress. Results indicated significant linear responses for yield, spike number per m^{-2}, seed weight and number per spike, protein content, chlorophyll a and b.

Keywords: Wheat, waterlogging, protein, proline, chlorophyll content, yield, abiotic and biotic stress

Introduction

This chapter summaries the adverse conditions faced by plants when water is in excess, and acclimations and adaptations to flooding stress. We consider the situations for roots in waterlogged soils, and for shoots submerged by overland floods. Four case studies highlight important developments in plant flooding research. The chapter demonstrates that interdisciplinary research in plant sciences has improved knowledge of plant flooding tolerance, with applications in crop breeding. Tolerance of plants to soil waterlogging, and to shoot submergence, varies greatly; ranging from many very sensitive 'dryland' species (including most of our crops) to highly tolerant species such as rice and other wetland species. In addition, aquatic and marine plant species have adopted submerged lifestyles under water. Knowledge of tolerance mechanisms will underpin future breeding of more robust crops, and understanding plant responses to flooding will aid management of plant communities in flood-prone environments. Recent breakthrough in submergence tolerance research on rice resulting in new varieties will help sustain a growing world population (see Case Study 1), and has improved knowledge of plant adaptive mechanisms to flooding stress.

Waterlogging adversely affects bread wheat production in 4.7 million hectares in irrigated soils of the Indo-Gangetic Plains of Northern India (CSSRI, 1997) [17] as well as durum wheat production in irrigated heavy clay soils or Vertisols of Eastern and Central Africa, including the central highlands of Ethiopia (Tesemma *et al*., 1992; Tedla *et al*., 1994) [52, 51]. The former includes 2.5 million ha of sodic soils (Sharma and Swarup, 1988) [48] and 2.2 million ha affected by seepage from irrigation canals (CSSRI, 1997) [17]. Such problems become more acute when the soils are not levelled or irrigation is followed by excess rain (Gill *et al.,* 1992) [26]. Large areas of waterlogging occur in the irrigated rice wheat rotation systems used throughout South and SE Asia including Pakistan, India, Nepal, Bangladesh and China. Wheat is exposed to waterlogging in these sys systems since the soil preparation used for rice cultivation specifically results in subsoil compaction to optimize flooding conditions for rice (Samad *et al*., 2001) [44]. A second major cause of waterlogging in these coin countries is the use of water containing high carbonate and bicarbonate concentrations which induces sodicity in these typically fine textured soils (Quereshi and Barrett-Lennard, 1998) [41].

The introduction of new technology has completely replaced the old mode of production in Indian agriculture.

Traditional agriculture has progressively given way to modern and commercial agriculture and sooner India became the role model for the other States in the country. No doubt, the new technology has provided numerous economic gains to the State and the country as a whole in the form of increase in both production and productivity and irrigation coverage up to 95 per cent of the total cropped area in India. But India has been suffering a lot from the ecological point of view. Due to the new agricultural technology, the demand for water, chemical fertilizers, insecticides and pesticides increased very sharply in the State, which gives birth to the problem of water logging and water depletion, soil degradation and health problems.

There are many success stories of agriculture as an engine of growth early in the development process and of agriculture as a major force of poverty reduction. Agriculture growth was the precursor to the acceleration of industrial growth, very much in the way agricultural revolution predated the industrial revolution that spread across the temperate world from England in the mid-18th century to Japan in the late 19th century (World Development Report, 2008) [56]. Due to the introduction of modern methods of cultivation during 1970s which is famously known as Green Revolution the agriculture in the Country of India has made spectacular progress from the last four-five decades and there seems to be no parallel example anywhere in the world history of agricultural development (Rangi and Sidhu, 1998) [42].

Irrigation canals bring farmers the most important input for increased agricultural production. But irrigation has not been an unmixed blessing to the farmers. It also has the potential to turn green fields into water logging. The land in the canal areas is often flat and poorly drained. The application of irrigation water to them results in water logging over a period of time. Poor water management is leading to land degradation in irrigated areas through water logging and salinity. Due to the unplanned canal irrigation system, inadequate drainage system and over irrigation seepage, the problem of water logging becomes an important issue in the different part of India. Due to water logging, the level of groundwater rise and then it reaches to the crop root zone, it starts to have a serious impact on crop productivity, making the land totally unproductive and rendering the land into wet desert. It is not only adversely affect the cropping pattern, crop productivity and soil fertility, but it also making the bad effect on land, roads, buildings, trees etc.

Types of waterlogging tolerance and methods to mitigate their effect

The waterlogged environments for crop production

Details of the timing, duration and intensity of waterlogging in soils are important for extrapolation of results between regions, to enhance germplasm exchange relevant to specific environments, to set guidelines for controlled experiments in the glasshouse and laboratory for accurate phenotyping, and to give clues about possible adaptive traits for waterlogging tolerance.

Waterlogging occurrence extends from the sandy duplex soils of Australia characterised by intermittent waterlogging, to the heavy clay vertisols of Ethiopia which can be characterised by long durations of waterlogging. Here we examine different methods for characterising waterlogged environments. The diverse environments during waterlogging highlight that there may be different mechanisms of plant adaptation to waterlogging in these environments. This point will be raised again in the 'Genetic diversity for waterlogging tolerance' section.

Timing and duration of waterlogging

There are few published data that characterize the timing and duration of waterlogging in the field on heavy clay or sodic soils, although water logging timing would usually be concurrent with irrigation schedules, high rainfall or surface flooding events (Williamson and Kriz, 1970) [55]. Uncertainty remains whether waterlogging occurs widely during irrigation of crops on heavy soils. Evidence for adverse effects of waterlogging in heavy or sodic soils during irrigation and rainfall is supported by long term measurements of reduced oxygen flux ('Intensity of waterlogging' section), and by crop growth measurements ('Genetic diversity for waterlogging tolerance' section). However, the adverse effects of waterlogging may be obscured by the initial greater beneficial effects of irrigation on water deficits.

Measurements with time on percentage of soil saturation or air-filled porosity in surface soil layers are also useful to characterize the duration of waterlogging in such soils. There are no published data on the relationship between duration of ponded water and duration of subsoil saturation which would affect plant growth. The air-filled porosity of soils (f_A) is generally considered to be limiting when it is 10% or less (Grable, 1966 for review) [27]. During periods of high rainfall between August to October in Victoria, Australia, each 1% reduction in the mean air-filled porosity of the surface soil reduced wheat yields by 0.29 t ha−1 (McDonald and Gardner, 1987) [38]. This method is not widely used in germplasm evaluation trials presumably since it is labour intensive, results are not immediately available in the field, and it is not easy to differentiate whether the entire soil sample is at the same (mean) air-filled porosity. However, this method may be more suitable than using piezometer tubes (see below) for heavy soils, since piezometer tubes would tend to fill up from the saturated surface soil layers and therefore overestimate the extent of soil waterlogging in subsoil's.

Grable (1966) [27] has reviewed much of the early literature on a (Billings) silty clay loam where just such air trapping occurred. During irrigation of these soils, O_2 concentrations slightly increased at 0.50-0.75m depth due to the downward displacement of air. This air acted as an O_2 reservoir such that O_2 pressures in the root zone never dropped below 6 kPa for alfalfa continu continuously flooded for 8 days. Furthermore, O_2 pressures seldom dropped below12 kPa during regular irrigation cycles with 0.10-0.15 m water. Trapping of O_2 during waterlogging was also used to partly explain the maintenance of high O_2 flux densities in subsoils relative to the topsoil during waterlogging of oats ('The intensity of waterlogging' section).

A second uncertainty of waterlogged environments relates to the consequences of waterlogging in duplex soils *versus* heavy clay soils. In duplex soils, waterlogging occurs from the bottom up, purging soil gas spaces, as water accumulates above the relatively impermeable subsoils which lie close to the surface. However, in heavy clay and sodic soils, waterlogging occurs from the top down, invariably trapping soil gases in the subsoil profiles and cutting off exchange with the atmosphere. For heavy clay and sodic soils, waterlogging may therefore commence and be more intensive for surface adventitious roots; whereas for duplex soils, waterlogging may commence and be more intensive for seminal roots deep in the soil profile. There are few detailed measurements on changes upon waterlogging in the subsoil environment for heavy clay or sodic soils.

The timing and duration of waterlogging can be measured in the field using simple, inexpensive equipment consisting of 40 mm diameter slotted PVC tubes (piezometer tubes) or similar devices to measure when, and at what depths, water saturates the soil profile (Gambrell *et al*., 1991; Setter, 2000) [24, 46]. The depth to water in many cases provides a useful indication as to whether the soil is aerobic or anaerobic. Soil zones that are not water saturated are likely to contain gaseous O_2 and therefore dissolved O_2 in the soil water films (Gambrell *et al*., 1991) [24], however measurements to support this are limited.

When any soil is saturated with water, the soil solution may vary from aerobic to anaerobic. The oxidation status of the soil relates to the intensity of waterlogging described in the next section. The remainder of this section is focused on characterization of intermittent waterlogging in the field.

In many duplex soils, when drainage does occur, it tends to move vertically down through the profile rather than laterally. The key impact of this soil characteristic is that wide surface drains are often ineffective and uneconomical on these soils because water can not readily move laterally to the drains. This supports the use of smaller more frequent surface drains as in raised beds (Hamilton *et al*., 2000) [30] or a biological solution to waterlogging or both.

Intensity of waterlogging

Measurements of the intensity of waterlogging relate to the chemical changes which are associated with the oxidation and reduction status of the soil environment. However, with time of waterlogging the soil gradually loses much or all of its O_2, concentrations of other gases increase, certain microelements are reduced and increase in concentration in the soil solution, and phytotoxins accumulate.

Gas concentrations of soil solutions are the first chemical changes that occur during waterlogging because gases diffuse 10 000 times more slowly in water than in air (Armstrong, 1979) [2]. Gases that are consumed, like O_2, will be rapidly depleted; while gasses that are produced, like CO_2 and ethylene, will rapidly accumulate. When a soil becomes waterlogged, the rate of O_2 depletion is dependent on several factors, including the respiration rate of plant roots and microorganisms, the solubility of O_2 in water, and the rate of O_2 diffusion through the soil (Trought and Drew, 1982) [53]. Anaerobiosis usually requires hours or even days to develop once soils are waterlogged. It is important to note that the measurements are from bulk soil solutions, and do not represent extremes that may occur adjacent to rapidly respiring root tissues or other biologically active regions in the soil. In some waterlogged soils, anaerobiosis may never occur due to a wide range of factors, e.g. low biological activity, low temperature, other plants that aerate the soil solutions due to O_2 loss from roots, movement of water due to percolation or seepage through soil profiles, or a combination of the above (see Grable, 1966 for further discussion) [27]. The limited evaluation of O_2 status in waterlogged soils in a wide range of field environments makes the importance of these latter factors unclear.

Three methods are routinely used to evaluate the oxygenation status of soils:

1) O_2 concentration measurements of soil solutions.
2) Redox potential measurements.
3) O_2flux measurements.

Oxygen concentrations and redox measurements characterize the current state of oxidation-reduction in a soil, whereas O_2 flux measurements characterise the *potential* of the soil to supply O_2. Oxygen flux is partly dependent on the concentration gradient of O_2 (Armstrong, 1979) [2]; therefore as O_2 concentration decreases, the O_2 flux decreases proportionally. Both O_2 flux and redox potential are measured using bare platinum electrodes.

Sodic soils are slow to drain due to their low hydraulic conductivity. In an irrigated sodic soil in India, measurements of soil O_2 flux at 15 cm depth decreased more than 90% following 12 h irrigation to a wheat crop (Sharma and Swarup, 1988) [48]. After surface water was removed, the O_2 flux only increased gradually and always remained at less than 25% of initial values during the subsequent 12 days. Extrapolation of the O_2 flux rate indicated that a recovery to initial values would occur only after about 40 days following removal of surface water. Longer duration of irrigation at 2, 4 and 6 days, not only delayed the commencement of the increase in O_2 flux after drainage, but it also reduced the rate of return of O_2 flux to the fully drained condition (Sharma and Swarup, 1988) [48]. The above data on O_2 flux would be useful to relate to data on redox potential or even soil saturation to facilitate future measurements and interpretation of results at a wide range of locations in similar soils. An effect of these treatments on plant growth and grain yield were substantial and is discussed further in the 'Genetic diversity for waterlogging tolerance' section.

The recovery periods following waterlogging are often assumed as a time when soils rapidly become fully aerobic; this is clearly not true for sodic soils and to some extent in other soils. In all other studies where redox potentials were measured after waterlogged soils were drained, it took 7–10 days before redox potentials reached aerobic conditions (>400 mV; Table 1C). Furthermore, when soil O_2 concentrations were measured in soils growing wheat that were drained after three durations of waterlogging, it took between 9 and 16 days for soil profiles to return to the oxygenated states prior to waterlogging (at 14-15 ◦C; Meyer and Barrs, 1988) [39]. Such results indicate that anoxic shocks and aerobic shocks that often occur in solution culture in glasshouse experiments may result in inaccurate extrapolations to what happens in the field.

Information on key components required for germplasm improvement

The following sections relate to three criteria required for germplasm improvement (Hallauer, 1981; Lagudah and Appels, 1994; Reynolds *et al*., 2001; Simmonds, 1979) [29, 34, 43, 49]:

i) Genetic diversity for tolerance.
ii) Accurate phenotyping including elucidation of mechanisms of tolerance and reselection in a breeding program.
iii) Heritability of traits. This is then followed by a General Discussion on various prospects for germplasm improvement.

It is not the purpose of this review to extensively discuss the adverse effects of waterlogging on plants since this has been done elegantly beforehand by Jackson and Drew (1984) [33] and in other reviews relating more specifically to nutrition (Drew, 1983, 1991; Marschner, 1986) [19], aeration (Armstrong, 1978, 1979) [1], phytotoxins and microorganisms

(Drew and Lynch, 1980) [23], mechanisms of tolerance to flooding (Armstrong *et al*., 1994) [3] and anoxia (Greenway and Gibbs, 2003) [28]. Nevertheless it is valuable to present a summary of main factors affecting growth and survival of some cereal crops exposed to waterlogging, since these relate to mechanisms of tolerance and hence phenotypes for germplasm improvement.

Genetic diversity for waterlogging tolerance

Waterlogging tolerance is defined in physiological studies as survival or the maintenance of high growth rates under waterlogging relative to non-waterlogged (usually drained soil) conditions. This contrasts to the agronomic definition of waterlogging tolerance, which is the maintenance of relatively high *grain yields* under waterlogged relative to non- or less-waterlogged conditions. Such different definitions are justified, since there is usually a strong correlation between the total above ground biomass and grain yield in waterlogging treatments, e.g. Sayre *et al*. (1994) [45]. A discussion on the impact of these different definitions on the discovery of germplasm suitable for particular waterlogged environments is given in the 'Phenology' section. Examples in support of genetic diversity for waterlogging tolerance using both these definitions are described here.

Screening without non waterlogged 'controls' obviously has advantages since twice the number of genotypes can be evaluated. The positive impact of basing varietal selections on such screening strategies is that yields may be high in this germplasm when grown in waterlogged environments; however this may have nothing to do with waterlogging tolerance. Furthermore, highly tolerant lines may have been discarded simply because they are low yielding genotypes. In breeding programs for abiotic stress tolerance, it is important to first accurately select for the key trait, and once found, add in additional traits required for the target environment, i.e. combine waterlogging tolerance genes with high grain yield genes.

Several studies have been published claiming to describe waterlogging tolerance for cereal germplasm. However data are often not presented on the grain yields, biomass or survival of varieties under waterlogged and under non waterlogged conditions. Without the latter controls, or expression of results relative to such controls, true waterlogging tolerance cannot be confirmed. In studies where only data for waterlogging treatments are presented, it is impossible to know whether the high yields, biomass or survival are simply the results of high yield potential or high seed vigour. However, it may be useful for plant breeders and growers simply to know that some genotypes yield well under waterlogging even if they are not truly tolerant; this approach has been used by Collaku and Harrison (2002) [15] to characterise high grain yield of wheat during waterlogging.

In subsections below, the response of cereals to intermittent *versus* continuous waterlogging is discussed, followed by the effects of waterlogging at different stages of plant development. These set the background to subsequent subsections on genetic diversity for waterlogging tolerance of seeds and whole plants.

Intermittent versus continuous waterlogging

A major concern of using SEW30 values described in the 'Timing and duration of waterlogging' section to define intermittent waterlogging is that they mathematically remove the very factor of repeated aerobic-anaerobic and anaerobic-aerobic transitions of the roots which might make these environments worse relative to those with continuous water logging. For example, if the frequency of anoxic and aerobic shocks is an *added* stress in intermittent waterlogging, we would hypothesise that several intermittent waterlogging events would be worse than one continuous waterlogging event for the same duration. Environmental measurements indicate that intermittent waterlogging treatments could be worse for other reasons, since during multiple drainage periods soils often might not completely return to aerated conditions ('Intensity of waterlogging' section), i.e. during intermittent waterlogging, anaerobic conditions will tend to be longer than just the time that the soil is saturated with water. There are several published experiments on intermittent waterlogging, e.g. Watson *et al*. (1976) [54]. However in all these experiments, the intermittent waterlogging treatments had shorter durations of waterlogging relative to the continuous waterlogging treatments. There are no published data comparing intermittent and continuously waterlogged cereals exposed to the same total time of waterlogging.

Waterlogging tolerance at different stages of development

In rainfed and irrigated environments, waterlogging may occur at any stage of development due to excess rainfall. Evaluation of genetic diversity for waterlogging tolerance during different stages of development is therefore essential.

Larger reductions in grain yield for wheat, barley and oats were caused by 6 weeks of continuous waterlogging starting at 2 weeks after sowing, in comparison to starting at 6 weeks or 10-14 weeks (ear emergence) after sowing (Watson *et al*., 1976) [54]. Similar results were found in winter wheat grown in lysimeters (Cannell *et al*., 1980) [9], where immediately after germination,

i) Waterlogging for 16 d at 12 ◦C killed all seedlings
ii) Waterlogging for 6 d reduced populations to 12-38% of the non-waterlogged plants

For the latter treatment, there was vigorous recovery growth, and grain yields were reduced by only about 15% relative to non-waterlogged controls. When plants were waterlogged after emergence, the plant populations were not affected, and there were little or no effects on grain yields (Cannell *et al*., 1980) [9].

When 14 of the world's most waterlogging tolerant wheats were screened for different periods of waterlogging at 5 different growth stages, there were some varieties like the Ducula sister lines (Ducula-1 to Ducula-4) which had relatively stable performance under all conditions. There were other varieties like Mikn Yang #11 and Zhen 7853 from China which had a relatively low waterlogging tolerance over 42 d waterlogging from 10 d after emergence to mid boot (Sayre *et al*., 1994; Table 3) [45]. However, when this same set of varieties was waterlogged from anthesis to grain filling, the two varieties from China had the highest waterlogging tolerance of any of the lines evaluated (93 and 83% of non-waterlogged grain yields). Such results were interpreted by Sayre *et al*. (1994) [45] as likely reflecting the adaptation to late season waterlogging that occurs in many spring wheat areas of Southern China.

Other work on wheat suggests that early reproductive states are more adversely affected by waterlogging than tillering stages because

i) Earlier maturing genotypes yield much less than late maturing genotypes on undrained relative to drained field plots.

ii) The yield reductions are a consequence of reductions in grains per ear (Gardner and Flood, 1993) [25].

An additional explanation could be a longer recovery period for late maturing varieties which might enable a reduction in spikelet sterility. This work is supported from studies in China, where Bao (1997) [4] found that for 20 wheat varieties the order of intolerance to waterlogging at different stages was booting stage > jointing stage > tillering stage > grain filling stage. In studies on waterlogged sodic soils in India, there were no significant differences in waterlogging tolerance of wheat waterlogged for 4-12 d at tillering *versus* flowering (from 10 varieties; Table 1 of Gill *et al*., 1992) [26].

A schematic diagram of waterlogging tolerance of wheat and barley at different stages is presented in Figure 6. This is based on observations for grain yields of wheat described above (Belford and Cannell, 1979; Cannell *et al*., 1980; Gardner and Flood, 1993; McDonald and Gardner, 1987; Sayre *et al*., 1994; see also Watson *et al*., 1976) [6, 9, 25, 38, 45, 54] and shoot biomass production for barley (Leyshon and Sheard, 1974, 1978) [35]. There are no published studies where a range of varieties are waterlogged for constant durations at different stages of development. Trends from Figure6 reflect that plants are least tolerant to waterlogging at pre-emergence, seedling growth and reproductive stages. These results demonstrate the importance of evaluating waterlogging tolerance at different stages of development, particularly at stages which reflect the incidence of waterlogging in the target environment.

Waterlogging tolerance at the germination stage

There is a lack of published information on waterlogging tolerance of temperate cereals at germination and emergence stages, particularly for wheat. This is surprising in view of the ease in obtaining this information.

The major evidence for genetic diversity for 'waterlogging' tolerance at the germination stage comes from the comprehensive work on barley of Takeda and Fukuyama (1987) [50]. In their studies, they screened the world collection of cultivated barley varieties preserved at the Barley Germplasm Centre at Okayama University, Japan. They made three important observations:

1) Seed samples with low viability (40-90%) have an even lower tolerance to 'waterlogging' than could be explained by viability alone.
2) There are negligible effects of 'waterlogging' for up to 8 days when seeds are treated at 0-5 ◦C, however there can be up to 100% death after only 4 d 'waterlogging' at 25 ◦C.
3) There is a large genetic diversity among barley varieties for 'waterlogging' tolerance at the germination stage.

In their experiments, duplicate samples of 50 seeds were 'waterlogged' by placing them into a test tube (1.8 cm dia. × 15cm) containing stagnant deionised water, and then germination was tested after these treatments by transferring seeds to Petri dishes.

A total of 3457 barley varieties with viability >97% were screened for tolerance to 'waterlogging' for 4 days at 25 ◦C using the above methods (Takeda and Fukuyama, 1987) [50]. Interestingly, varieties from China, Japan, Korea and Nepal, as well as some varieties from North Africa, Ethiopia, and SW Asia tended to show the highest 'waterlogging' tolerance. However, a large number of varieties from Western India tended to show some of the lowest tolerance. It was interpreted that there may be some natural or artificial selection for this trait relative to the differences in climatic conditions in these countries.

The mean survival of all varieties waterlogged in soil was 86, 75, 68 and 41% for oats, triticale, Australian wheats and Australian barleys, respectively. Furthermore, there was a significantly greater mean germination of International wheats which were selected for waterlogging tolerance at the whole plant stage, relative to Australian wheats. In the Australian wheats that were not specifically selected for waterlogging tolerance, the range in survival of varieties after 4 d waterlogging was from 32% to 91%.

Waterlogging tolerance at the seed stage may possibly correlate with one or more of the mechanisms of waterlogging tolerance of tissues at the whole plant stage. Such possibilities and the rapid time to conduct and repeat experiments, make further studies on seed physiology during waterlogging particularly valuable. For example, there is no information on what effects other environmental variables, e.g. acid or alkaline soils, salinity, etc., have on the survival of seeds during waterlogging. It would seem reasonable that the outcomes of such work could be valuable in developing rapid screening protocols for germplasm improvement based on metabolic traits in early stage generations for breeding programs. To our knowledge, such information is not being utilised for germplasm improvement, nor have the mechanisms of tolerance been explored for wheat, barley or oats at the seed germination and emergence stage (see also 'Genetic diversity for waterlogging tolerance' section).

Waterlogging tolerance at the whole plant stage

Some of the largest early screenings of wheat for waterlogging tolerance have come from work in Central and Eastern China in the area of the Yangtze and Huan Rivers. Cao and Cai (1991) [10] screened over 1000 varieties and breeding lines for what they defined as waterlogging tolerance, i.e. low percentage of leaf damage, maintenance of 1000-grain weight or grain weight per mainstem. Out of more than 10 years of field trials, only 20 varieties were identified as tolerant and also having good agronomic traits (Cao and Cai, 1991) [10]; these included: Ning 8675 (China), Nonglin 46 (Japan), Yang 85-85 (China), Pato (Argentina) and *Triticum macha* (Soviet Union).

Additional screenings include work of Lin *et al*. (1994) in Shanghai Province, China, who evaluated waterlogging tolerance in 50 mainly Chinese wheat varieties. They used a 'waterlogging tolerance index', i.e. response of waterlogged plants relative to non-waterlogged plants and they calculated an indices sum based on the four key traits of

Number of green leaves per main stem.

i) Grains per ear (GPE).
ii) 1000-grain weight (GW).
iii) Seed setting rate per ear.

These experiments identified three varieties which had GPE and GW waterlogging tolerance indices greater than 0.9 and 0.5, respectively: Zhemani No. 2 and Zhengzhou 761 from China and Nonglin No. 46 from Japan. The lowest scores were for three varieties which had GPE and GW indices both <0.5; the remaining varieties had intermediate ratios.

Other examples of genetic diversity for waterlogging tolerance of wheat are based on biomass production of plants in soil or hypoxic solution culture (see 'Mechanisms of tolerance to waterlogging' section). However, not all studies have been able to demonstrate such genetic diversity. Musgrave (1994) [40] found no significant difference in relative grain yields of 8 winter wheat varieties from Louisiana, USA, when plants were waterlogged in river silt for what appeared to be the entire growth duration from 10 d after sowing. The large temporal and spatial variation for waterlogging tolerance found in some field sites ('Timing and duration of waterlogging' section) indicates that until tolerant germplasm is found, the best option is to select for the highest yielding variety.

Mechanisms of tolerance to waterlogging

Mechanisms of survival or maintenance of high biomass production and grain yields during waterlogging may be important at the germination and emergence stages, during vegetative and reproductive stages, or both. Much research has supported the benefits of adaptive traits for waterlogging including increases in: aerenchyma and root porosity, root suberisation, ethanolic fermentation, carbohydrate reserves, tolerance to post anoxic shock, and recovery mechanisms. However, not all of these are clearly shown to contribute to waterlogging tolerance of wheat, barley and oats; and sometimes conflicting reports have occurred where different varieties or conditions have been used.

Two of the most promising criteria for waterlogging tolerance are discussed in further detail below. Firstly, it is important to determine if the best strategy for plants in waterlogged environments is to grow or merely to survive and not grow during waterlogging periods. In environments where waterlogging is for a short time, and there are long growth durations, changes in plant phenology, or dormancy during waterlogging combined with a rapid recovery ability, offers a ready escape from waterlogging problems. Where waterlogging is for a long time and the growth duration is long, there is an increasing amount of data in support of aerenchyma development for wheat and perhaps other temperate cereals for both continuous and intermittent waterlogged environments.

In the 'Waterlogged environments for crop production' section it was concluded that there is often more than one factor which limits growth in the waterlogged environment. Hence it is reasonable that there may be combinations of adaptive traits which will give the best level of tolerance to a particular environment. Furthermore, combinations of these traits may have either synergistic or antagonistic effects (see 'Concluding remarks'). Several of these traits, particularly maintenance of adequate nutrition, will relate to approaches of crop management for waterlogging tolerance. The latter will not be considered here, since these topics are discussed in detail in other reviews, e.g. Drew (1983, 1991) [19]. Here we focus on the adaptive traits that relate to germplasm improvement for waterlogging tolerance.

Phenology-optimising growth phases and whether to grow or not to grow

The agronomic definition of waterlogging tolerance based on grain yields ('Genetic diversity for waterlogging tolerance' section) alludes to the possibility that the ideal cereal plant type for waterlogging prone environments may be one that has little or no growth *during* waterlogging events, but has rapid growth *after* waterlogging. These varieties could exist through mechanism(s) of tolerance associated with dormancy or slow growth during stress periods, and a rapid recovery following stress; such mechanisms are confounded. The possibility that waterlogging tolerance is partly or completely based on recovery also applies to other data where waterlogging tolerance is defined on maintenance of high grain yields, except where the waterlogging events are during and to the end of the grain filling period when recovery would not be possible.

In earlier work cited in the 'Genetic diversity for waterlogging tolerance' section, late season wheats appeared to have a clear yield advantage over early season wheats. Gardner and Flood (1993) [25] suggested this was due to much of the yield reduction being associated with decreased grain numbers per ear. However an additional explanation could have been a longer recovery period for late maturing varieties. Suggestions for later maturity as a means to escape waterlogging are not always supported by other researchers. Sayre *et al*. (1994) [45] found that grain yields during waterlogging were not correlated with days to maturity for any of 5 waterlogging treatments they used. However, this may have been because all of the treatments used by Sayre *et al*., included at least part of the reproductive phase, i.e. there was inadequate time for recovery.

McDonald and Gardner (1987) [38] have supported the use of long season wheats for two reasons

i) They will enable early sowing so as to avoid waterlogging damage at the intolerant stage of germination and emergence
ii) This will allow anthesis to occur late enough to avoid waterlogging damage in spring (cf. sensitive stages of crop development

They clearly state that one disadvantage of this strategy in the Australian environment is that flowering and grain set would occur in conditions of higher evaporative demands and higher temperatures. Similar concerns make such late maturity plant types unsuitable for waterlogging prone wheat production areas in Northern India. These areas require waterlogging tolerance during the waterlogging events such as the adaptations offered by increases in aerenchyma or root porosity.

Morphology-aerenchyma, root porosity and barriers to radial O_2 loss

In physiological studies, a difference in aerenchyma development is sometimes described between two different varieties or crops exposed to waterlogging or anaerobic treatments. However, the random probability that this will be consistent with the relative growth rates, yield or survival is 50:50. There are only two published studies (Huang *et al*., 1994a; Setter *et al*., 1999) with large numbers of cereal germplasm where positive correlations are shown between aerenchyma developments and shoot growth or grain yield under hypoxic or waterlogged conditions.

When cereal crops are grown in the field in Australia under intermittent waterlogging conditions, there is a variation in the % aerenchyma in the mid cortex of adventitious roots of wheat, barley, oats and triticale varieties (Figure 7) that is consistent with the general observation of tolerance of oats and triticale > wheat > barley ('Genetic diversity for waterlogging tolerance' section). For wheat and barley, the range in values for aerenchyma in the mid cortex across all varieties was 10-81% (n = 24) and 7-63% (n = 8) respectively. There is a positive correlation between the% aerenchyma in adventitious roots and the yield of 17. Spring wheat cultivars grown under intermittent waterlogging conditions in the field in Australia. These results are consistent with Huang *et al*. (1994a) discussed above, except that the aerenchyma in field grown plants accounted for substantially less of the variation in plant growth or grain yield.

The relationship between aerenchyma development and relative grain yield underwater logged conditions did not hold for long season wheats or for barley (Setter *et al*., 1999; Setter, 2000) [46, 47]. A lack of, or poor relationship between quantity of aerenchyma and waterlogging tolerance raises the question about not just the quantity of aerenchyma, but the quality, i.e. the capacity to provide a continuous, low resistance pathway, with low radial O_2 loss, for O_2 diffusion to root tips. The proliferation of aerenchyma during waterlogging is of little value if radial O_2 losses from roots exceed the capacity of aerenchyma to diffuse O_2 for the growth and survival of tissues. This issue will be discussed further in the 'Concluding remarks'.

In other studies by Ding and Musgrave (1995) [18], aerenchyma formation in waterlogged roots was associated with Fe, Mn and P coatings on roots, and these mineral coatings were negatively correlated with grain yield under waterlogged conditions (Ding and Musgrave, 1995; Musgrave and Ding, 1998) [18]. In studies by Ding and Musgrave, aerenchyma was determined on plants grown under different conditions from those used for studies of root coatings, so these results need to be confirmed in the same experiment. Such results certainly raise the question whether development of aerenchyma is ideal under some environmental conditions of waterlogging.

Genetic studies on waterlogging tolerance in wheat and barley

The early published research in genetic studies on waterlogging tolerance of wheat and barley was done in China and Japan, respectively. All of this work defined waterlogging tolerance based on leaf chlorosis or leaf/plant death or on other traits as described below. It is often less certain or unknown how such measurements correlate specifically to waterlogging tolerance based on grain yield of the tolerant and intolerant parents used in these studies. Clearly grain yield per plant is one of the simplest criteria to measure and should be made top priority in future genetic studies; to our knowledge, this basis of tolerance has only been used in genetic studies described by Bao (1997) [4]. For the sake of this discussion, we will assume that there is a high negative correlation between leaf chlorosis (or death) and grain yield as found by van Ginkel *et al*. (1992) for 16 varieties (r = -0.98 to -1.00); this condition is essential for the genetic studies by Boru (1996) discussed below.

Other genetic work in China indicated that there may be multiple genes for waterlogging tolerance because tolerance to waterlogging at 20 d after booting was mainly governed by additive factors and it was also affected by non-additive ones (Cao *et al*., 1994) [12]. In these studies, three intolerant and four waterlogging tolerant wheats were used including Shuilzhan (syn. Shur-Bian-Zhang; 'Genetic diversity for waterlogging tolerance' section), Nonglin 46, Xifeng and Pato; together with three intolerant parents. A high potential for developing improved germplasm was indicated by a high heritability demonstrated by a General Combining Ability of 77-100% for traits such as green leaves per stem, plant height, grains per ear and 1000-grain weight (Cao *et al*., 1994) [12].

A highly waterlogging tolerant wheat variety from Japan, Nonglin 46 (syn. Norin 46; see 'Genetic diversity for waterlogging tolerance' section), was crossed with two intolerant varieties Ningmai 3 and Zhen 7853 (Cao *et al*., 1992) [11]. Results showed that all F1 progeny from both crosses survived waterlogging with a level of tolerance similar to Nonglin 46; this indicated that waterlogging tolerance in Nonglin 46 is dominant. Segregation occurred in the waterlogging live plants with a segregation ratio of 1:0 following waterlogging treatments; while (2) backcrosses of the F1s with the intolerant parents resulted in segregation ratios of 1:1. The heritability of grain weight per plant was calculated as 75%. It was therefore concluded that waterlogging tolerance is genetically controlled, and the waterlogging tolerance of Nonglin 46 is heritable (Cao *et al*., 1992, 1995) [11].

In later work by the same group, six populations using three tolerant parents (Nishikaz-Komugi, Yang 87-142 and Norin 46 (syn, Nonglin 46)) and two intolerant parents (Ningmai 3 and Zhen 7853) were evaluated for tolerance to waterlogging conditions based on the number of green leaves after waterlogging at the booting stage. All the F1 plants were the same as the tolerant parents, and the F2 hybrids of the tolerant/intolerant parent again segregated at a 3:1 ratio, indicating that waterlogging tolerance was controlled by a single dominant gene (Cao *et al*., 1995) [13]. A diallel cross was subsequently used to evaluate waterlogging tolerance in 10 varieties (including Nonglin 46, Yang 87-142, Ningmai 3 and Zhen 7853) and their F1s based on the number of green leaves per stem after 25 days of waterlogging at the booting stage (Cai *et al*., 1996) [8]. The broad sense heritability was estimated to be 71.5%, hence it was concluded that it is possible to improve waterlogging tolerance in wheat by appropriate selection of parents and phenotyping progeny in early generations (Cai *et al*., 1996) [8].

Conclusion

The highly variable nature of waterlogging in the field, in both space and time, emphasises the complexity of the problems of screening germplasm in the field. Equally it highlights the diverse opportunities for germplasm improvement. In countries like China and Japan, a focus on breeding and genetic studies has resulted in substantial achievements in these areas, with little or no information on the physiological mechanisms involved in tolerance. Hence the breeding programs in these countries have not realized opportunities for mechanistic plant breeding which include increased efficiencies in germplasm improvement by phenotyping physiological traits. This concern is encapsulated in the view of Miflin (2000) that the genotypic view and emphasis on genomics needs to be balanced by a phenotypic approach; a phenotypic approach places the emphasis on discovering the important genes and hence phenotypes that are important for germplasm improvement.

Tolerance to long term waterlogging requires plants not only to 'survive' but also to grow during the waterlogging event(s). The key strategy used for long term waterlogging is the development of aerenchyma in roots to facilitate gas diffusion (Armstrong, 1979; Blom, 1999; Jackson and Armstrong, 1999). Other important traits in long term adaptation include suberisation of adventitious roots to provide a barrier to radial O_2 loss which contributes to 'effective' functioning of the aerenchyma (Armstrong, 1979; Colmer, 2002).

If molecular markers can be developed for traits such as aerenchyma development, this could be used to assess a large number of lines quickly without the constraints of field variations. It would be unlikely to find a single gene that relates to such a complex physiological trait such as aerenchyma development. However a transduction signal could initiate a gene cascade involved with this trait, which would make such traits possible to monitor collectively in a breeding program.

The correlation of aerenchyma and grain yield from field studies on wheat ('Mechanisms of tolerance to waterlogging' section) suggests that intermittent waterlogging may have similar effects to continuous waterlogging or exposure to O_2 deficits; this is supported by slow return of drained soils to fully aerated conditions ('Intensity of waterlogging' section). With all this work on aerenchyma, and even more work on root porosity, it would be valuable to manipulate the levels of aerenchyma in one genotype by different physiological pre-treatments, and then use one measure of waterlogging tolerance to evaluate the impacts of different levels of aerenchyma. This has not been done.

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