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Review of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats

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Abstract

A review is presented for prospects of germplasm improvement for waterlogging tolerance in wheat, barley and oats using a mechanistic approach based on adaptive physiological traits. In 'The waterlogged environments for crop production' section, the extent of waterlogging is reviewed commencing with determination of environmental factors which may limit plant growth and development in waterlogging prone regions. This highlights that different types of waterlogging may exist, there may be large spatial and temporal variation in waterlogging, and that waterlogging may be confounded in field experiments with additional environmental factors. Environmental characterisation is therefore a key step to using mechanistic approaches for germplasm improvement for target environments, for extrapolation to other environments, and for development of screening protocols under controlled conditions that accurately reflect the field environment. In the 'Information on key components required for germplasm improvement' section, the genetic diversity in wheat, barley and oats for waterlogging tolerance is confirmed. Physiological mechanisms for waterlogging tolerance are diverse and can be grouped into adaptive traits relating to (1) phenology, (2) morphology and anatomy, (3) nutrition, (4) metabolism including anaerobic catabolism and anoxia tolerance, and (5) post anoxic damage and recovery. For wheat and barley, there is some genetic diversity for waterlogging tolerance at the germination stage, however the full potential seems yet to be exploited. Varietal differences in tolerance at the germination stage often differ from tolerance at later stages of development, and this supports the view that different mechanisms of tolerance exist at the whole plant and tissue level. Limited work from genetic studies indicates a high heritability for waterlogging tolerance. It is concluded that the best opportunities for germplasm improvement are for further exploration and utilisation of genetic diversity by improving selection criteria including the use of marker assisted selection. Additional opportunities are described for increasing genetic diversity using wide hybridisations and development of transgenic plants.

Introduction

Severe soil drainage constraints are estimated to adversely affect approximately 10% of the global land area, however values up to 20% occur for specific regions such as Eastern Europe and the Russian Federation (FAO, 2002). In the USA, 16% of soils have environmental limitations because they are too wet, and insurance indemnities for crop losses due to excess water (excluding flood) are second only to drought (Boyer, 1982). There are no published data on how these values relate to the global area sown to wheat, although earlier estimates indicate that 10–15 million ha of wheat are affected by waterlogging each year (Sayre et al., 1994). This represents 15–20% of the 70 million ha sown to wheat each year.

Waterlogging adversely affects bread wheat production in 4.7 million hectares in irrigated soils of the Indo-Gangetic Plains of Northern India (CSSRI, 1997) 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

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et al., 1992; Tedla et al., 1994). The former includes 2.5 million ha of sodic soils (Sharma and Swarup, 1988) and 2.2 million ha affected by seepage from irrigation canals (CSSRI, 1997). Such problems become more acute when the soils are not levelled or irrigation is followed by excess rain (Gill et al., 1992). 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 systems since the soil preparation used for rice cultivation specifically results in subsoil compaction to optimise flooding conditions for rice (Samad et al., 2001). A second major cause of waterlogging in these 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).

In Australia, transient waterlogging occurs primarily in sandy duplex soils, where rainfall rapidly penetrates a sandy topsoil and accumulates above a compacted clay subsoil with low hydraulic conductivity at 5–>100 cm depth (Tennant et al., 1992). These waterlogging prone duplex soils therefore often form "perched water tables" which may be many metres above the ground watertable. Duplex soils occupy about 40–60% of the agricultural area in Victoria (Fried and Smith, 1992) and Western Australia (McFarlane, 1990) respectively. Other causes of waterlogging are associated with rising groundwater and flooding in riverbasins (Grieve et al., 1986; McDonald and Gardner, 1987; Meyer and Barrs, 1988). In Western Australia (WA), waterlogging was initially estimated to affect at least 500 000 ha of wheat per year, i.e. 8% of the total cropland, with an additional 1.3 million ha/y of pastures affected (Department of Agriculture, 1991). More recent estimates of waterlogging prone areas range from 1 to 2 million ha in WA (Hamilton et al., 2000; Short and McConnell, 2001), with about 3.8 million ha of crops affected in Victoria, Australia.

The timing, duration and intensity of different types of waterlogging are discussed in the section below of this review, since environmental characterisation is critical for effective germplasm improvement for target environments. This is then followed by the 'Information on key components required for germplasm improvement' section with subsections on the genetic diversity for waterlogging tolerance in wheat, barley and oats; mechanisms for waterlogging tolerance, genetic studies and finally a General Discussion focusing on opportunities for germplasm improvement.

The waterlogged environments for crop production

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.

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.

Timing and duration of waterlogging

There are few published data that characterise the timing and duration of waterlogging in the field on heavy clay or sodic soils, although waterlogging timing would usually be concurrent with irrigation schedules, high rainfall or surface flooding events (Williamson and Kriz, 1970). 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 divesity for waterlogging tolerance' section). However, the adverse effects of waterlogging may be obscured by the initial greater beneficial effects of irrigation on water deficits.

Waterlogging measurements in heavy soils would be easy to collect and could include the time and percentage of surface area covered by ponded water, and ponding depths. When wheat was waterlogged during irrigation treatments in NSW, Australia, the grain yield declined by 69 kg ha^{-1} for each day that water

was ponded on the soil surface. Significant reductions from 5.4 to 4.9 t ha^{-1} occurred at 24 relative to 1 h of ponding, respectively, for crops at 123 kg N ha^{-1} (Melhuish et al., 1991).

Measurements with time on percentage of soil saturation or air-filled porosity in surface soil layers are also useful to characterise 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 (see Grable, 1966 for review). 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). 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 subsoils.

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.

Grable (1966) 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 0.50–0.75 m 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 continuously flooded for 8 days. Furthermore, O_2 pressures seldom dropped below 12 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).

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). 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_2in the soil water films (Gambrell et al., 1991), 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 characterisation of intermittent waterlogging in the field.

Typical changes in the timing and duration of waterlogging in duplex soils on the South Coast of Western Australia are shown in Figure 1. Measurements shown in Figure 1 were made using piezometer tubes installed in the field (Setter, 2000). Similar changes were also measured in duplex soils in other areas of Southern Australia (Condon, 1999; McFarlane et al., 1989).

The rapid fluctuations in waterlogging and in drainage on duplex soils can be explained by the soil profile. During rainfall, water rapidly penetrates through the sandy topsoil of the A horizon and accumulates within and above the compacted gravel and clay layer of the B horizon; this water accumulation occurred at about 60 cm depth in the WA soil shown in Figure 1, and resulted in a 'perched watertable' many metres above the ground watertable. When water influx ceases, the perched water table can rapidly fall as it drains to the ground watertable. This rapid drainage occurs through cracks and root channels (preferred channels) in the B horizon since (i) there is little lateral movement of water in soil profiles, (ii) the conductivity of water through B horizon soil in isolated clay layers is too low ($<$15 mm/h) to explain the rapid drainage observed in the field (as shown in Figure 1), and (iii) water movement evaluated using rhod-

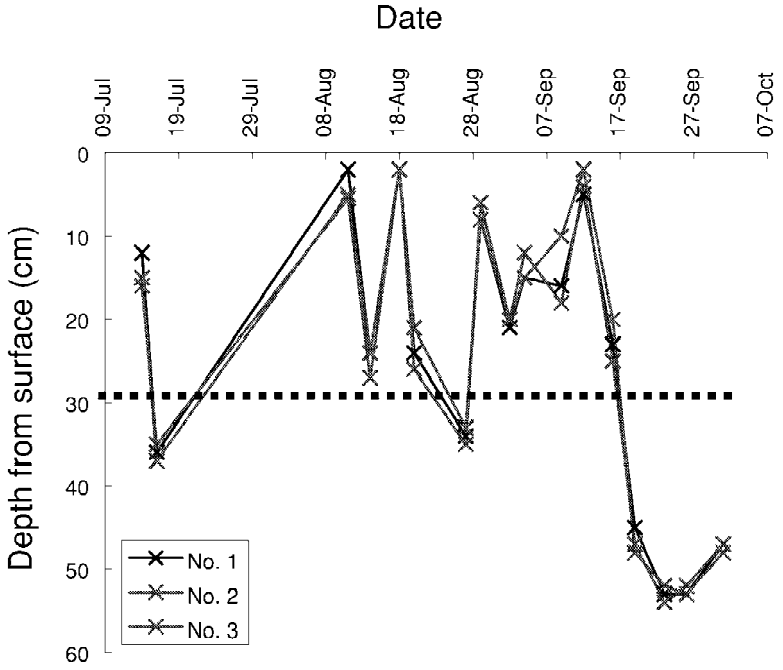

Figure 1. Changes in waterlogging with time in a duplex soil in the field at Marshall's, Esperance, Western Australia. Data show the depth to the perched water table in centimeters below the soil surface taken from 3 dipwells separated 10 m apart from each other. The dashed line indicates the depth above which waterlogging is considered to affect crop growth (SEW_{30}; see text). This location had an average SEW_{30} of 630 cm.d. Several hundred of these data may be integrated to produce SEW_{30} maps of waterlogging as in Figure 2 (Setter, 2000).

amine dye is completely confined to these 'preferred pathways' (Setter, 2000).

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), or a biological solution to waterlogging, or both.

The typical complex waterlogging regime for duplex soils exemplified in Figure 1 raises questions about how to simply quantify waterlogging intensity across large, highly variable locations used for germplasm evaluations, or in different years. At present only one approach has been used to integrate intermittent waterlogging measurements in the natural environment, SEW_{30}, and even this will be shown to have major limitations.

Waterlogging throughout the year and at different soil depths can be integrated by the **S**um of **E**xcess **W**ater that occurs each day in the primary root zone of the top 30 cm soil layer (SEW_{30}). This measure of waterlogging is referred to as SEW_{30}, and units are in centimetre days (cm d; Sieben, 1964 as cited by Cox, 1988; McFarlane et al., 1989). Hence a SEW_{30}value of 300 cm d occurs in a location where soil is waterlogged to the surface (throughout the top 30 cm of the profile) for 10 days, i.e. 30 cm(10 d)=300 cm d. Note that a SEW_{30} value of 300 cm d may also occur and is therefore considered equivalent when the soil is waterlogged 20 cm below the surface for 30 days, i.e. in a 10 cm layer within the top 30 cm of soil: (10 cm) (30 d) =300 cm d.

In the example of waterlogging presented in Figure 1, the entire waterlogging regime can be quantified as having a SEW_{30} of 630 cm d. Hence, although waterlogging was observable at the surface on only two or three times during the season, the waterlogging which occurred in the top 30 cm root zone is calculated as being equivalent to waterlogging to the soil surface for 21 days (630 cm d/30 cm = 21 d; caption, Figure 1). In order to characterise field plots used for waterlogging experiments, several hundred piezometers may be installed in a grid pattern at the site, and the perched watertable can be monitored on a daily or weekly basis for each piezometer. These data can then be integrated over the season to produce SEW_{30} maps of waterlogging intensity (Figure 2). These maps are

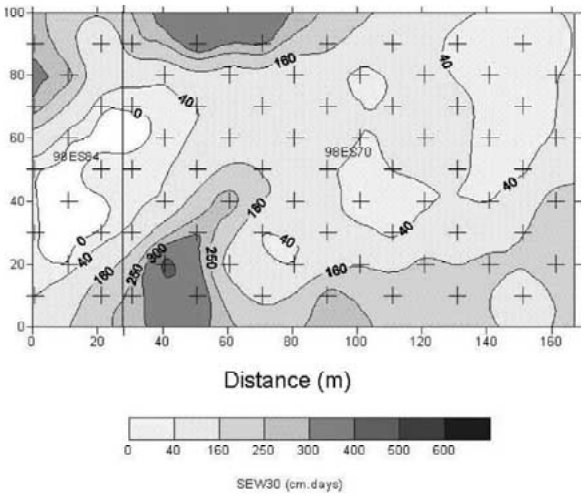

Figure 2. Variation in waterlogging with location in the field at The Oaks field site at Esperance, Western Australia. Some of the contours (available in 30 cm-d intervals) and plot indicator lines are removed to simplify the diagram (from Setter et al., 1999).

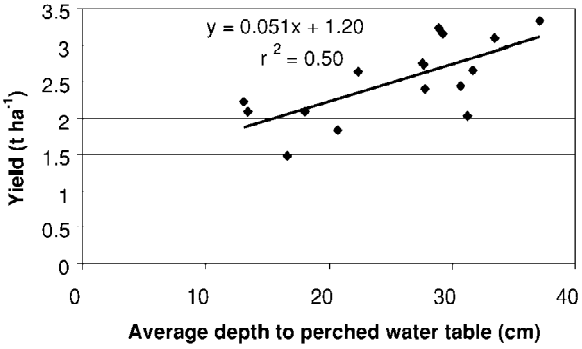

Figure 3. Grain yield of oats exposed to increasing depths of waterlogging. Waterlogging was measured at Cranbrook, WA between August and September, 1997 (with permission; Bakker et al., 2000).

used to precisely locate sampling areas in field plots which have a similar waterlogging duration during a defined time period.

Waterlogging maps as in Figure 2 demonstrate that waterlogging is highly variable in space in Australian duplex soils. Examples of SEW_{30} maps are also given by other published work (Cox, 1988; McFarlane and Wheaton, 1990; Setter, 2000). Key features of such maps for duplex soils (Setter, 2000) are that:

(i) Waterlogging timing and duration may vary by up to 400-fold over a distance of 50 m, e.g. Figure 2;

(ii) Strong waterlogging gradients can occur with intensities varying along the drains, rather than away from the drains, i.e. waterlogging is not dependant on where surface drains occur;

(iii) Differences in waterlogging occur sometimes with no differences in surface topography, e.g. the area in Figure 2 is almost level (slope <0.5%); while at other times there may be a high correlation of surface topography and waterlogging.

(iv) Waterlogging duration may differ considerably in different years.

Typically, growth reductions and adverse effects of waterlogging on crop species are considered to occur above SEW_{30} values of 100–200 cm d (Sieben, 1964), i.e. equivalent to waterlogging to the soil surface for 3–7 days. This is consistent with the time that O_2 concentrations in waterlogged soils become reduced to about 10% of air saturation ('Intensity of waterlogging' section).

SEW_{30} values to quantify intermittent waterlogging in the field were first used by Sieben (1964) who found that these most correlated with crop yields in drainage experiments in The Netherlands. These values have also been correlated (r^2 = 0.65–0.85) to wheat and oat yields for intermittent waterlogging in duplex soils of Western Australia (Cox, 1988). However, there has been no critical evaluation of whether SEW values at other depths, e.g. SEW_{10} or SEW_{20}, would give better correlations to effects on plant growth and yields.

The critical 30 cm depth for SEW_{30} is considered a reasonable assessment of waterlogging since (i) yields of oats are reduced at watertable depths of 10–35 cm in Australia (Figure 3), and (ii) wheat yields are reduced at water depths of 10 and 20 cm, but not 50 cm in the UK (Cannell and Belford, 1982). However in other studies on wheat, barley and oats in The Netherlands, there were also reductions in yield at 50–120 cm water depths, relative to a 150 cm watertable depth (Williamson and Kriz, 1970).

Some of the best data for validation of the use of SEW_{30} values for waterlogging at different soil depths come from recent pot experiments of Malik et al. (2001) who waterlogged a susceptible wheat variety (cv. Cascades) at 0, 10 and 20 cm depths using topsoil from a duplex soil. They found that plant growth was reduced proportionally as the water level was increased to the soil surface. If all the data presented by Malik et al., are analysed together, the correlation (r^2) between calculated SEW_{30} values and relative growth rates of shoots and roots during waterlogging is 0.9. However they express caution on the use of SEW_{30} values, since after a recovery period following 14 d waterlogging of wheat, there was not a significant dif-

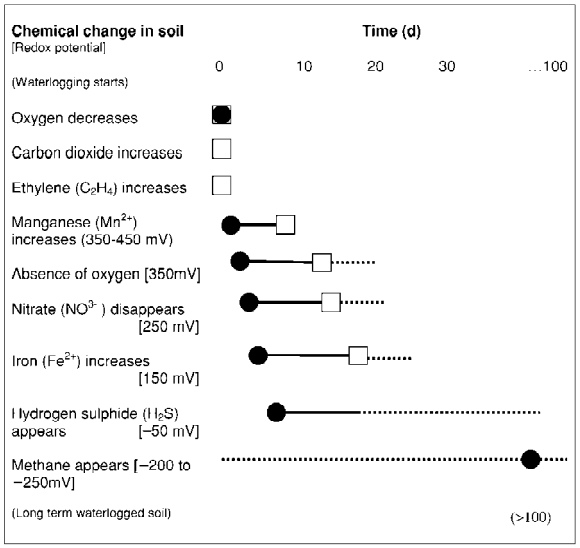

Figure 4. Schematic diagram of chemical changes in soils during waterlogging. Chemical changes were measured in a duplex soil from Muresk, Western Australia (□; 5 – 15 °C) and a heavy clay soil from the Philippines (•; 25 – 35 °C) or they were estimated from soil redox potential and known changes which occur at pH 7 (Marschner, 1986; Ponnamperuma, 1984). Modified from Setter and Belford (1990).

ference between some of the treatments waterlogged at different depths.

The limitations of SEW_{30} values are discussed by McFarlane et al. (1989), and they include no account of other major factors related to waterlogging intensity, e.g. temperature, that may influence crop production in waterlogged environments. Given that biological processes have a Q_{10} of 2–3, it would not be difficult to devise an index that takes temperature into account. Alternatively, SEW_{30}s should always be stated together with mean soil or air temperatures during the waterlogging period. The present situation is that, in environments where waterlogging is variable, SEW_{30}s enable a simple quantification of the waterlogging which has occurred at different soil depths, for different durations, throughout the season, or in different years.

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 (Figure 4). 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 (idealised in Figure 4).

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). Gases that are consumed, like O_2, will be rapidly depleted (Table 1A); while gasses that are produced, like CO_2 and ethylene, will rapidly accumulate (Table 1B). When a soil becomes waterlogged, the rate of O_2depletion is dependent on several factors, including the respiration rate of plant roots and microorganisms, the solubility of O_2in water, and the rate of O_2diffusion through the soil (Trought and Drew, 1982). Anaerobiosis usually requires hours or even days to develop once soils are waterlogged (Table 1A). It is important to note that the measurements in Table 1A 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 (Table 1A) due to a wide range of factors, e.g. low biological activity, low temperature, other plants that aerate the soil solutions due to O_2loss 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). The limited evaluation of O_2status 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; and (3) O_2flux measurements. Oxygen concentrations and redox measurements characterise 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); 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.

Blackwell (1983) reviewed the relative merits of evaluating soil oxygenation status during waterlogging using O_2concentrations based on soil solutions withdrawn from samplers in the soil, or using redox or O_2flux measurements based on bare platinum electrodes inserted into the soil (see also Armstrong, 1979; Drew, 1983; Patrick et al., 1996 for discussions of use and complexities of redox and O_2flux electrodes). His

Table 1. Effects of waterlogging on (A) O_2 depletion, (B) CO_2 and ethylene, and (C) redox potential. A (–) indicates information unknown

(A) O_2depletion

Soil type (location)	Crop	Temperature and conditions (day: night temp)	Rate of O_2 depletion (kPa O_2/d)	Time (d) to reach equilibrium with 2 kPa	Lowest O_2 conc (kPa)	Reference
Sandy loam – 28 cm	Barley	18:16 °C; Pots; environmental room	9	2	1@ 14d	Drew and Sisworo (1979)
Clay (UK) – 20 cm depth	Winter wheat	5 °C; field	2.5	9-15	2@9-15d, then maintained	Cannell et al. (1980)
Sandy loam (UK) – 20 cm depth	Winter wheat	5 °C; field	2.5	8–10	2@8-10d, then gradually increased up to 0.17	
Sandy soil – 15 cm depth	Winter wheat	14 °C; Pots (6.5dia. ×31 cm); growth cabinet	20	0.8	0 @ 3d	Trought and Drew (1980)
Clay (UK) – 20 cm depth	Winter wheat	3 °C and 10 °C; field	-	13 4	-	Cannell and Belford, (1982)
Sandy soil	Winter wheat	6 °C 18 °C; environ cabinet	17 42	1.5 0.5	1@2d, 0@0.5d	Trought and Drew (1982)
Clay (UK) – 20 cm depth	Winter wheat	4–12 °C; field lysimeter	2.6	14	0@26d	Blackwell (1983)
Sandy loam (UK)	Oats	5–10 °C; lysimeters				Cannell et al. (1985)
5 cm			2	8	0@10d	
20 cm			1	12	0@20d	
50 cm			0.3	30	0@60d	
Sandy duplex (Australia) – 20 cm depth	Spring wheat	20 °C; field	10	8	2@12–26d	Barrett-Lennard et al. (1986)

B. $CO_2$and ethylene

Gas	Soil type	Crop	Temperature; conditions	Change with time	Reference
Carbon dioxide	Sandy loam	Barley	18:16 °C environ. room	Increase from 0 to 14 kPa over 14 d	Drew and Sisworo (1979)
	Sandy soil	Winter wheat	14 °C; Pots (6.5dia. ×31 cm); growth cabinet	Increase from 2 to 14 kPa@14d; 15 cm beneath crop	Trought and Drew (1980a)
	Sandy soil	Winter wheat	6,10,14 and 18 °C; environment cabinet	Increase from 0 to 7,11,14 and 19 kPa@14d; 15 cm beneath crop	Trought and Drew (1982)
Ethylene	Clay (UK)	wheat	Unknown temp.; 30 cm beneath waterlogged wheat; field	Increase from 0 to 5–10 ppm; 30 cm beneath crop	Dowdell et al. (1972)
	Sandy loam	Barley	18:16 °C environ. room	Increase from 0 to 6 ppm over 11 d then decrease sharply; 28 cm beneath crop	Drew and Sisworo (1979)
	Sandy soil	Winter wheat	14 °C; growth cabinet; Pots (6.5dia.×31 cm)	Increase from 0 to 4 ppm@10-14d; 15 cm beneath crop	Trought and Drew (1980a)
	Sandy soil	Winter wheat	6,10,14 and 18 °C; environment cabinet	Increase from 0 to -,2,2 and 5 ppm@7d; 15 cm beneath crop	Trought and Drew (1982)

C. Redox potential. Interpolated times to 350 mV (disappearance of molecular O_2) and 150 mV (appearance of Fe^{2+}) after waterlogging; and back to aerobic conditions (≥400 mV) after drainage. Only representative data are presented in some cases

Soil type	Crop	Temperature; conditions (day: night temp)	Initial mV	Time (d) to 350 mV	Time (d) to 150 mV	Lowest mV at time	Time (d) to increase to ≥400 mV after drainage	Reference
Silt loam	Barley	19–28 °C; 7d flooding max.; 15 cm soil depth; tanks	550	4.8	-	280@ 7d	7	Leyshon and Sheard (1974)
Sandy loam	Oats	5–10 °C; depths					-	Cannell et al. (1985)
5 cm		to 80 cm;	600	10	15	−125 @ 30d		
20 cm		lysimeters	600–700	20	25	0 @ 60d		
50 cm			700	60	>90	350 @ 60d		
Sandy duplex soil	Wheat or triticale	20:15 °C; 15 cm soil depth; pots	600	7.5	13.5	−200 @ 35d	7	Thomson et al. (1992)
Sandy duplex soil	Wheat	20:15 °C; various depths to 40 cm; pots	600	8.8	15.5	40@ 28d	10	Malik et al. (2001)

conclusion was that O_2concentrations based on water withdrawn through samplers would more represent the larger pores of the bulk solution and not the soil matrix between the pores; while measurements of soil redox or O_2flux using bare platinum electrodes are more likely to represent the soil matrix. Such effects suggest that the differences between these measurements is therefore related to the soil pore size distribution, however the relationship is not so simple (Armstrong 1979; Grable, 1966).

During waterlogging in a clay soil there was a close relationship between soil O_2concentrations and O_2flux ($r^2>0.8$; calculated from Figure 5 of Blackwell, 1983; see also Cannell et al., 1985 for a sandy loam soil), making either of these methods valuable. However, during drainage after 42 days of waterlogging, the values of soil O_2 concentrations (bulk soil) rose rapidly over the first 3–4 days, while there was little or no change in the O_2flux. Redox potential values recovered intermediate between these two methods. Results support that these different techniques measure different components of the waterlogged soil. After about 6 days of drainage, both O_2 concentrations and O_2flux measurements were similar to initial values in drained soil (Blackwell, 1983).

Other experiments can be used to demonstrate that O_2concentration measurements using samples of soil solutions measure the bulk soil solution. When a soil solution sample was collected within 2 min of re-waterlogging a soil with aerated solution, the bulk soil solution decreased from an equilibrium concentration of 21 kPa in the added water, to 5 kPa in the new bulk solution (Setter and Waters, unpublished). In these experiments, 3 kg pots of sandy loam soil were waterlogged for 5 days and then drained for 2 days before re-waterlogging. This rapid large decrease in soil O_2concentrations could only be explained by a large volume of anoxic solution or deoxygenated gas space in the drained soil matrix diluting and re-equilibrating the added aerated water.

Comprehensive data have been collected in relation to waterlogging intensity at the Letcombe Laboratory in UK for different depths of soil. Following waterlogging of oats in lysimeters, the changes in O_2concentrations and O_2flux were similar with time after waterlogging, with delays in the decline of soil redox potential (Cannell et al., 1985). In summary, at depths of 5, 20 and 50 cm, it took 10, 20 and 60 days to reduce soil O_2concentrations and O_2flux to zero, and soil redox potential (Eh) to 350 mV (Table 1C; this Eh value is associated with the absence of molecular O_2as in Figure 4). These data for a sandy loam soil demonstrate the reduced waterlogging intensity with soil depth under this type of waterlogging, and they highlight opportunities for adaptations of different plant tissues for continued growth and survival. In the case where oats were grown under these conditions, at 18–38 days after waterlogging, root biomass at 38–65 cm soil depths *increased* two-fold for plants grown in waterlogged relative to free draining soils. There were reductions in root biomass during waterlogging at almost all soil profiles above this depth.

Sodic soils are slow to drain due to their low hydraulic conductivity. In an irrigated sodic soil in India, measurements of soil O_2flux at 15 cm depth decreased more than 90% following a 12 h irrigation to a wheat crop (Sharma and Swarup, 1988). After surface water was removed, the O_2flux only increased gradually and always remained at less than 25% of initial values during the subsequent 12 days. Extrapolation of the O_2flux 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_2flux after drainage, but it also reduced the rate of return of O_2flux to the fully drained condition (Sharma and Swarup, 1988). The above data on O_2flux 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. Effects of these treatments on plant growth and grain yield was 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). 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.

The previous waterlogging history of the soil and the consequent microbial flora may also affect the rate of lowering the soil redox potential following waterlogging. This was indicated by Waldren et al. (1987), who showed that when previously waterlogged compost was dried and then re-waterlogged, the soil reduction occurred much more rapidly than during the initial period of waterlogging. They interpreted this result as a large population of anaerobic microorganisms that had built up during the initial flooding. Data were not presented to evaluate the possible contribution of other factors such as anaerobic solution or gases from soil matrices present during re-waterlogging.

Measurements of O_2, soil redox, and O_2 flux from the above research highlight that soil O_2 concentrations are one of the most widely used measurements to monitor soil oxygenation status during the short term or within days after waterlogging. However, what soil O_2 concentrations mean in terms of potential O_2supply to roots is less clear. Once O_2 is depleted, then soil redox measurements are necessary to characterise further reductions in the soil oxygenation status. Redox measurements relate to the soil matrix which is a key environment of plant roots, and they are particularly important in indicating potential adverse effects from microelement toxicities (Figure 4). The robust nature of the equipment, reliability, and ease in making measurements make this a valuable tool where long term or intermittent waterlogging occur. Surprisingly there are few or no published data of soil redox potentials for naturally waterlogged crops in the field (cf. Table 1C). This needs to be achieved to assure accurate simulation of conditions in glasshouse experiments aimed at germplasm improvement for waterlogging prone environments.

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): (i) genetic diversity for tolerance; (ii) accurate phenotyping including elucidation of mechanisms of tolerance and reselection in a breeding program; and (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) and in other reviews relating more specifically to nutrition (Drew, 1983, 1991; Marschner, 1986), aeration (Armstrong, 1978, 1979), phytotoxins and microorganisms (Drew and Lynch, 1980), mechanisms of tolerance to flooding (Armstrong et al., 1994) and anoxia (Greenway and Gibbs, 2003; Gibbs and Greenway, 2003). 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.

The adverse effects of waterlogging are summarised by the schematic diagram in Figure 5. Note that this diagram tends to imply that the environmental factors associated with waterlogging act independently, when it is most likely that several of these factors act simultaneously (Jackson and Drew, 1984). For example, there are likely interactions of effects of low O_2, high CO_2 and high ethylene on many cereals exposed to either waterlogging or flooding. For wheat, there are few effects of inclusion of 10 kPa CO_2 in N_2 gas used to deoxygenate roots, relative to plants exposed to anaerobic conditions by flushing with N_2 gas alone (Trought and Drew, 1980c). However, flushing roots with low partial pressures of ethylene either under aerobic or anaereobic conditions has substantial effects on root and shoot development (reviewed by Jackson and Drew, 1984).

In 1980, Levitt divided tolerance to 'flooding stress' into either the 'avoidance of toxin accumulation' or the 'tolerance of toxin accumulation'. The term 'waterlogging' is defined here as a condition of the soil where excess water inhibits gas exchange of roots with the atmosphere. Waterlogging is distinguished from 'flooding' because the latter results in additional factors of partial or complete submergence of the shoot. In Figure 5, we have added two additional factors that may be involved during waterlogging, being energy deficiency and changes in root permeability to water. These factors are in addition to toxin accumulations, and they have been highlighted in earlier reviews by Drew (1983), Jackson and Drew (1984), Marschner (1986), Armstrong et al. (1994), and recently in relation to the 'energy crisis' associated with exposure to anoxia (Greenway and Gibbs, 2003; Gibbs and Greenway, 2003).

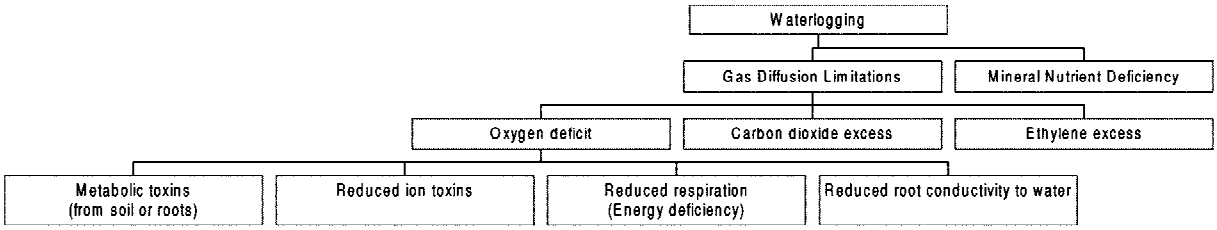

Figure 5. Schematic diagram of adverse effects of waterlogging on plant growth and survival. Diagram revised from Levitt (1980) and including components from Drew (1983), Jackson and Drew (1984), Marschner (1986), Armstrong et al. (1994), and Gibbs and Greenway (2003). Oxygen deficit includes low soil redox potential.

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). 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.

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 can not 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 result 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) to characterise high grain yield of wheat during waterlogging.

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.

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 SEW_{30} 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 waterlogging. 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). 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). Similar results were found in winter wheat grown in lysimeters (Cannell et al., 1980), where immediately after germination, (i) waterlogging for 16 d at 12 °C killed all seedlings, and (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).

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, and (ii) the yield reductions are a consequence of reductions in grains per ear (Gardner and Flood, 1993). 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) 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).

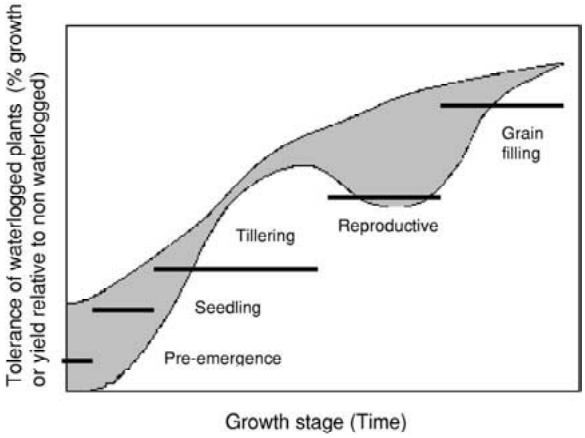

Figure 6. Schematic diagram of tolerance of wheat and barley to waterlogging at different stages of development. Shaded area indicates the level of tolerance and the genetic diversity in tolerance measured by growth, survival, or grain yield, for both wheat and barley waterlogged at different stages of development relative to non waterlogged plants (based on references cited in the 'Genetic divesity for waterlogging tolerance' section).

When 14 of the worlds 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 (Sayer et al., 1994; Table 3). 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 Sayer et al. (1994) as likely reflecting the adaptation to late season waterlogging that occurs in many spring wheat areas of Southern China.

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; Sayer et al., 1994; see also Watson et al., 1976) and shoot biomass production for barley (Leyshon and Sheard, 1974, 1978). There are no published studies where a range of varieties are waterlogged for constant durations at different stages of development. Trends from Figure

6 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). 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; and (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. × 15 cm) 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). 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.

After their preliminary screening, Takeda and Fukuyama (1987) selected 435 of the barley varieties that had more than 90% germination after 4 d 'waterlogging' at 25 °C, and they used these for evaluation of 'super-tolerant' varieties able to tolerate 8 d 'waterlogging.' From this second screening, only about 33 varieties (1% of the original total) had 80% germination or more and were defined as 'super-tolerant'. These super-tolerant varieties were all 6-row varieties consisting of 24 varieties from Japan, 3 from Korea, 3 from China, 2 from Nepal and one from North Africa. These varieties were not named in the original publication but were: Kara Marumi 1, Ou 2, Bizen Wase 53, Kaikei 39, Benkei 3, Sazanshu, Koshu Rokkaku, Yatomi Mochi, Zenkoji, Hachikoku, Raiden, Tankiaze 105, Yukiwarimugi, Koike Rokkaku 2, Konosu 60, Rokujo, Omungi 5, Genpachi, Shirogoro, Wasejiro, Takayama, Tokushima Mochimugi 1, Konosu 50, Mochi Hadaka, Boseong Baitori 1, Suweon Shin 1, Haman Waedong 2, Tayeh 9, Hsinantiea 3, Chengchou 5, Trisuli Bazar 8, Keronja 3 and 10247 (K. Takeda, Pers. Comm.).

The only study we are aware of where genetic diversity was evaluated for waterlogging tolerance of temperate cereal seeds *in soil* is presented in Table 2 (Setter, 2000). This involved a comparison of wheat, barley, oat and triticale varieties grown in Western Australia, in addition to a collection of international wheat germplasm that had previously been identified as having waterlogging tolerance at the whole plant stage (Sayre et al., 1994; van Ginkel et al., 1992; see next section). Seeds were sown beneath 30 mm of soil in beakers at 15 °C, and exposed to waterlogging for 4 days; there were 4 replicates of 50 seeds. After treatments, seeds were removed from the soil and sown on filter paper . Survival was assessed by germination tests relative to non waterlogged seeds according to the International Seed Testing Association (ISTA, 1984) guidelines.

The mean survival of all varieties waterlogged in soil was 86, 75, 68 and 41% for oats, triticale, Australian wheats and Australian barleys, respectively (Table 2). 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 (84 *versus* 68%, respectively; Table 2). 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%.

The data in Table 2 for barley at 15 °C contrast with results of Takeda and Fukuyama (1987) where they found that 13% of varieties had more than 90% germination after 4 d waterlogging at the high temperature of 25 °C. No Australian barleys achieved this level of tolerance. Therefore, either there are worse effects

Table 2. Genetic diversity for waterlogging tolerance at the seed stage (survival ± sem) in wheat, barley, oats and triticale. All varieties were waterlogged for 4 days at constant 15 °C in a gravelly sand from a waterlogging prone duplex soil at Esperance, Western Australia. National and international wheats are selected from reports / publications of their waterlogging tolerance at the vegetative stage ('Genetic diversity for waterlogging tolerance' section). Survival is expressed as a% of non waterlogged treatments which all exceeded 95% germination; 4 replicates of 50 seeds used for each analysis (from Setter, 2000). WADA, Department of Agriculture, Western Australia; VIDA, Victorian Institute of Dryland Agriculture; TAS, Tasmania; UA, University of Adelaide, SA; USyd, University of Sydney, NSW; France, FR

Cereal (Crop mean±sem; *n*)	Variety (Source)	Survival
Australian Wheats	Cadoux (WADA)	91±2
(68±17; *n*=18)	Cunderdin (WADA)	88±15
	Eradu (WADA)	85±10
	Brookton (WADA)	84±5
	Cascades (WADA)	80±19
	Spear (UA)	78±3
	Gamenya (USyd/WADA)*	62±14
	Westonia (WADA)	57±5
	Champtal (P. Benoist, FR)	47±3
	Stiletto (UA)	36±9
	Camm (WADA)	32±5
International Wheats	Pr/Sa (CIMMYT)	98±3
	Chara (VIDA)	94±6
	Yanac (VIDA)	93±2
	Norin 46 (CIMMYT)	92±5
(84±9; *n*=13)	Mira (VIDA)	89±6
	Vee/Myna (CIMMYT)	83±4
	VG187 (VIDA)	83±2
	Ducula-2 (CIMMYT)	82±1
	Goldmark (VIDA)	81±2
	Yang 85-85 (CIMMYT)	79±9
	Ducula-3 (CIMMYT)	73±2
	Ducula-1 (CIMMYT)	71±2
	Ducula-4 (CIMMYT)	68±2
Australian Barleys	Skiff (UA)	72±12
(41±17; *n*=7)	Fitzgerald (WADA)	47±8
	Onslow (WADA)	45±3
	Franklin (TAS)	42±6
	Molloy (WADA)	33±8
	Harrington (Canada)	31±13
	Gairdner (WADA)	19±7
Australian Triticale	Abacus (UA)	91±2
(75±17; *n*=3)	Tahara (USyd)	75±5
	Muir (WADA)	47±8
Australian Oats	Dalyup (WADA)	96±3
(86±11; *n*=6)	Coomallo (WADA)	95±4
	Carrolup (WADA)	95±1
	Pallinup (WADA)	81±11
	Toodyay (WADA)	81±8
	Mortlock (WADA)	70±8

*Originally developed in NSW, this is an in-line selection made at WADA.

in waterlogged soils relative to seeds in stagnant water, or in Australia there is a selection of barley germplasm that is relatively intolerant to waterlogging. Similar results of low tolerance of germplasm from specific regions were observed for the germplasm screened by Takeda and Fukuyama (1987) from Western India.

The above data clearly indicate a large genetic diversity for waterlogging tolerance at the seed stage for most temperate cereals. However, whether effects of different seed sources are important in these studies is unclear. 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

Genetic diversity for waterlogging tolerance in temperate cereals is clearly demonstrated from a review of published information (Table 3). This should be considered carefully, however since some of these experiments were only conducted once in one location, and there were often few or no environmental measurements taken. Furthermore, there are no published data on the effects of different plant densities on waterlogging tolerance of cereals. The data in Table 3 are based on tolerance of plants grown under waterlogging conditions in the field or glasshouse, relative to control plants grown in free drained or 'less' waterlogged conditions. Hence the results presented here are a measure of the genetic diversity for waterlogging tolerance, and not just the result of selection for plants with high yield potential.

Wheat. 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) 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

Table 3. Genetic diversity for waterlogging tolerance at the vegetative stage in temperate cereals based on grain yields. Waterlogging duration is the time in days of saturated soil to the soil surface or equivalent for intermittent waterlogging based on SEW_{30} values (see text). DAS, days after sowing; LS, long season wheat type; WL, waterlogging; (+) naked barley; (-) data not presented. (*) indicates same varieties were also evaluated by van Ginkel et al. (1992) where these varieties had grain yields of >2 t/ha and >1000 other varieties and crossbreds had little or no grain yield

Cereal and variety (Tolerant or Susceptible)	Germplasm Origin	Waterlogging duration and timing	% Grain yield of WL relative to non WL plants (WL grain yield)	Conditions	Reference
WHEAT					
KRL1-4	India	6d ponded water versus 12 h irrigation	99 (-)	Field exp.; 8 varieties; sodic (pH9.1) soil; India	Sharma et al. (1991)
KRL1-6			99 (-)		
KRL 9			75 (-; most intol.)		
CSW540-2	India	12 d ponded water versus 12 h irrigation	94 (59 g/m row)	Field exp.; 10–25 varieties evaluated; sodic (pH 8.0–9.6) soil; India	Gill et al. (1992)
Kharchia Mutant 5C-E2			86 (49 g/m row)		
Kharchia 65			79 (54 g/m row)		
HD2329			79 (46 g/m row)		
HD2009			62 (48 g/m row)		
Peck	Australia	Intermittent WL for 4 weeks or more during mid- to late-tillering	103 (3.8 t/ha)	Field exp. on duplex soils (loam over clay). Genotypes with different maturity (see text); Victoria, Australia	Gardner and Flood (1993)
UJO77296			94 (4.7 t/ha)		
Hill 81			87 (4.1 t/ha)		
Gallahad			81 (4.1 t/ha)		
Birch 75			79 (3.4 t/ha)		
Lawson			78 (3.9 t/ha)		
Birch 41			77 (4.0 t/ha)		
Braemar Velvet			75 (4.0 t/ha)		
M4195			71 (3.2 t/ha)		
Quarrion			51 (2.5 t/ha)		
Kellalac			44 (2.3 t/ha)		
Matong			32 (1.5 t/ha)		
Meering			26 (1.0 t/ha)		
Ducula-1*	CIMMYT Mexico	42 days, equal to SEW_{30} of 1260; WL commencing 10 d after emergence to mid boot	34 (2.2 t/ha)	Field exp.; 16 genotypes evaluated; 150 kg N/ha; coarse sandy clay; CIMMYT, Mexico*	Sayre et al. (1994)
Ducula-2* (T)			43 (2.7 t/ha)		
Ducula-3* (T)			44 (2.9 t/ha)		
Ducula-4* (T)			41 (2.5 t/ha)		
Vee/Myna* (T)			43 (2.3 t/ha)		
PRL/SARA* (T)			37 (2.0 t/ha)		
46 WR Norin (T)	Unknown	mid boot	34 (1.8 t/ha)		
Mikn Yang #11 (T)	China		32 (1.8 t/ha)		
Zhen 7853 (T)	China		20 (1.5 t/ha)		
PF8442 (T)	Brazil		14 (0.7 t/ha)		
Seri 82 (S)	Mexico		21 (1.5 t/ha)		
BR34 (S)	Brazil		26 (1.4 t/ha)		
Zhemai 2	China	15 d WL at boot stage (most sensitive stage)	77 (-)	Field exp.; harvest of 3 reps of 10 plants each.	Bao (1997)
Caizihuang	China		68 (-)		
Ningmai 3	China		61 (-)		
Shuilizhan	China		61 (-)		
Nonglin 46	Japan		48 (-)		
Emai 6	China		41 (-)		
Ning 8319	China		40 (-)		

Table 3. contd.

Pato	Mexico		37 (-)		
Alondras	-		36 (-)		
Su 8060	China		24 (-)		
Champtel (LS)	France	Intermittent WL	81 (1.3 t/ha)	Field exp.; 24	Setter et al. (1999)
Currawong (LS)	Australia	in the field;	59 (0.7 t/ha)	genotypes	
Carnamah		$SEW_{30} \geq 160$	53 (1.5 t/ha)	evaluated;	
Cunderdin		(equiv. to ≥6 d	37 (1.2 t/ha)	Esperance,	
Spear		WL to soil	33 (1.0 t/ha)	Western Australia	
Brookton		surface)	29 (1.0 t/ha)		
Gamenya			27 (0.6 t/ha)		
Cascades			23 (0.7 t/ha)		
Cadoux			18 (0.5 t/ha)		
AR-584A-3-	USA	WL at 3–4 leaf	85 (2.4 t/ha)	Silt-loam soil;	Collaku and
Pioneer 2643		stage for 5	73 (2.5 t/ha)	240 kg/ha N-P-K;	Harrison (2002)
Roberts		weeks	73 (2.3 t/ha)	plus 90 kg N/ha at	
Pioneer 2684		continuously	67 (3.1 t/ha)	end of WL; data	
Pioneer 2691			66 (3.0t/ha)	are means of 3	
Shelby			64 (3.3 t/ha)	years	
Terral LA			62 (3.4 t/ha)		
Florida 304			55 (2.7 t/ha)		
Jaypee			55 (2.7 t/ha)		
Pioneer			53 (2.8 t/ha)		
LA 87167			53 (2.5 t/ha)		
Mason			49 (2.6 t/ha)		
Savannah			47 (2.4 t/ha)		
Coker 9663			43 (2.3 t/ha)		
FFR 502W			40 (2.0 t/ha)		
BARLEY					
Sanyuehuang shandong	China	WL at Leaf 3,	≥99 (2.5 g/pl)	Field Exp. with	Calculated from
Qingpuhong barley		Stem Elongation	≥99 (2.0 g/pl)	4572 varieties; 16	Qui and Ke
Purple four-rowed barley		and Heading	≥99 (1.8 g/pl)	varieties had <1%	(1991)
Xifen barley		stages for 10–15	≥99 (2.6 g/pl)	yield reduction	
Winter barley (Shanxi)		d each.	≥99 (2.4 g/pl)	relative to non	
Awned barley (Shanxi)			≥99 (2.9 g/pl)	WL plants; 60%	
Barley (Shanxi)			≥99 (2.3 g/pl)	of varieties had	
Zhenjiang 21			≥99 (2.1 g/pl)	≥20–40% yield	
Suichang Yang damai^{+}			≥99 (2.2 g/pl)	reductions; China	
Long-spike Qing langtou^{+}			≥99 (1.6 g/pl)		
Hainan white six-rowed barely^{+}			≥99 (2.3 g/pl)		
1234 other barley varieties			60–79.9 (-)		
1298 other barley varieties			0–60(-)		
Stirling	Australia	Intermittent WL	49 (1.3 t/ha)	Field exp.; 24	Setter et al. (1999)
Fitzgerald		in the field;	47 (1.8 t/ha)	genotypes	
Molloy		$SEW_{30} \geq 160$	44 (1.8 t/ha)	evaluated; WL	
Skiff		(equiv. to ≥6 d	35 (1.3 t/ha)	yields are relative	
Onslow		WL to soil	30 (1.0 t/ha)	to plants at	
Harrington		surface)	29 (0.8 t/ha)	SEW_{30}=40 cm d	
Franklin			16 (0.6 t/ha)	(equiv to ~1d WL	
				to soil surface);	
				Western Australia	

Table 3. contd.

OATS					
Carrolup	Australia	Intermittent WL	61 (1.3 t/ha)	Field exp.; 5	Setter (2000)
Coomallo		in the field;	60 (0.9 t/ha)	genotypes	
Pallinup		$SEW_{30} \geq 160$	58 (1.0 t/ha)	evaluated; WL	
Mortlock		(equiv. to ≥6 d	46 (0.9 t/ha)	yields relative to	
Dalyup		WL to soil	37 (0.8 t/ha)	SEW_{30}=40 cm d	
		surface)		(equiv to ∼1d WL	
				to soil surface)	

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); these included: Ning 8675 (China), Nonglin 46 (Japan), Yang 85-85 (China), Pato (Argentina) and *Triticum macha* (Soviet Union).

Ning 8675 was bred in China, with a yield potential of 5–6 t ha^{-1}. This variety had only 14% leaf damage after continuous waterlogging for 11 d imposed at seven days after flowering, making it slightly more tolerant than other waterlogging tolerant varieties like Nonglin 46 from Japan (Cao and Cai, 1991). Nonglin 46 is a red seeded wheat which also showed good waterlogging tolerance at tillering and reproductive stages of development based on leaf damage and 1000-grain weights in multi-locational trials. Tolerance of this variety was also indicated later by plant survival relative to other varieties during waterlogging commencing at stem elongation and at 30 °C for 20 d (Cao et al., 1992).

Yang 85-85 is also a red seeded wheat developed in Jiangsu Province reported to have good waterlogging tolerance with only 18% leaf damage after waterlogging treatments at the booting stage (Cao and Cai, 1991). *Triticum macha* is a native variety from Western Georgia, USSR, originating from the damp forest zones. During waterlogging trials this variety has less leaf damage than Nonglin 46. Since *T. macha* can be crossed with hexaploid wheats, this variety was subsequently used to enhance waterlogging tolerance of other varieties ('Genetic studies on waterlogging tolerance in wheat and barley' section).

Unfortunately no data were presented on grain yields or biomass of plants under waterlogged relative to non waterlogged plants in the above studies, hence it is unclear how the observations on leaf damage or 1000-grain weights relate to definitions of tolerance used here. For example, Sayre et al. (1994) found that 1000-grain weights from plants grown under waterlogged conditions were not correlated with non waterlogged wheat yields, and there were variable correlations with waterlogged wheat depending on the duration of waterlogging.

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 (i) number of green leaves per main stem, (ii) grains per ear (GPE), (iii) 1000-grain weight (GW) and (iv) 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.

Some of the largest field screenings for waterlogging tolerance have been carried out at the International Maize and Wheat Breeding Centre (CIMMYT), Mexico. For example, out of 1344 genotypes evaluated by van Ginkel et al. (1992) for waterlogging tolerance from emergence to boot stage, only 29 entries (about 2%) produced seed; and of these only 6 had grain yields that were 22–63% higher than the waterlogging tolerant check variety Pato (* varieties in Table 3). Sayre et al. (1994) extended this work to evaluate growth of these and additional tolerant varieties during waterlogging at different stages of development.

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) 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.

Barley. Extensive screening of barley germplasm for waterlogging or 'wet tolerance' has occurred in China and Japan (Table 3). Work by Qui and Ke (1991) involved screening 4572 varieties in Shanghai Province, China. Waterlogging was imposed at three times (leaf 3 stage, stem elongation and heading) for 10–15 days each. Calculation of a 'damage index' was based on yield of plants in waterlogging treatments expressed as a percentage of yield under non waterlogged conditions. Varieties were classified into one of five grades of damage: 0.4% of varieties had $\leq$ 1% damage; 5% had 1–10% damage; 30% had 10–20% damage; 32% had 20–40% damage; the remaining 33% had >40% damage. The majority of the 16 varieties identified with the highest waterlogging tolerance (Table 3) also had either very early, early or medium maturity, indicating that recovery was not the mechanism of tolerance (see next section). These varieties also showed other attractive qualities such as large grain size and stiff stems (Qui and Ke, 1991).

Prof. K. Takeda and colleagues at Okayama University, Japan, evaluated 4096 barley varieties for tolerance to waterlogging commencing at Leaf 3 stage. The most tolerant varieties survived waterlogging for more than one month at 25 °C, and 21 of these were tolerant to waterlogging for the entire growth duration except for the germination stage: Omugi Shin 1, Aichi Yokozuna, Wasemugi, Kinai 8, Shirochinko, Rokuji, Kikai Hadaka, Shirochunko, Harumaki Rokkakumugi, Tayeh 9, Thonje 13, Thangja 3, Meladongri, Gangori 2, 2525, Wien, 3626, Deder 2, Dabat 5, Jimma 6 and Byng (K. Takeda, Pers. Comm.).

In Australia, grain yield of barley varieties exposed to intermittent waterlogging in the field (SEW_{30} $\geq$160 cm d; equivalent to $\geq$6 d waterlogging to the soil surface) was 16–49% of non waterlogged plants (Table 3). Stirling had the highest percentage grain yield (49%), however it also had the lowest yield of the barley cultivars when not waterlogged. Fitzgerald and Molloy gave the highest yields during waterlogging, even above Stirling, however this was a consequence of exceptionally high yields for non waterlogged plants (Table 3).

Oats. Among temperate cereals, oats appears to have one of the greatest abilities for recovery from waterlogging; this is supported by observations from several groups (Cannell et al., 1985; Watson et al., 1976; see also next section). During waterlogging of oats for 90 days in a sandy loam soil in UK, the shoot dry weights were only 60%, and total root weight was reduced more than 50%, relative to plants in a freely drained treatment. However by maturity, shoot weights and grain yields were both about 93% of freely drained plants (Cannell et al., 1985). An obviously important factor in this result is that recovery, from the end of waterlogging to maturity, occurred over a long duration of 118 days in this environment.

There are few or no published data available on waterlogging tolerance of oat varieties. This is unfortunate since in some regions there is a perception that cereals like oats and triticale are more waterlogging tolerant than wheat and barley. Perhaps this is because they tend to maintain green leaves during waterlogging, while other crops like wheat and barley often become chlorotic. Data from two field experiments (Setter et al., 1999; Setter, 2000) indicate some diversity for tolerance among five Australian oat varieties (Table 3), while the overall mean percentage grain yield for these varieties (52%) was greater than that measured for Australian wheats (31%) and barley (31%) grown in the same environments and under identical waterlogging treatments (calculated from data in Table 3).

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.

Native wetland plants provide opportunities for investigating mechanisms of waterlogging tolerance (Brändle, 1991), as well as their potential use in development of transgenic plants with increased waterlogging tolerance (see 'General discussion'). The main strategies of waterlogging and flooding tolerance in wetland plants involve: (1) maintenance of high internal aeration through constitutive aerenchyma and creation of an oxidised zone around root tips through radial O_2 loss (Armstrong et al., 1994); (2) metabolic adaptation that maintains energy production under hypoxia (Brändle and Crawford, 1987); and (3) substantial storage of carbohydrates for fermentation under conditions of low O_2 (Brändle, 1991). These strategies are similar to those present in cereals which are not as well adapted to waterlogging.

Mechanisms of tolerance to waterlogging in cereals can be divided into traits that relate to adaptations before, during or after waterlogging. Alternatively they may be divided into mechanisms including (1) phenology, (2) morphology and anatomy, (3) nutrition, (4) metabolism, including anaerobic carbohydrate catabolism and anoxia tolerance, and (5) recovery and prevention of post-anoxic damage (Table 4).

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 listed in Table 4 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). 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 in data in Table 3. 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.

Genetic diversity for tolerance during waterlogging, compared to recovery ability after waterlogging, is shown in few publications where several varieties are compared. Huang et al. (1994a) showed that there is good genetic diversity for tolerance of wheat to hypoxic solution cultures (see also Table 5). Varieties Savannah and Gore were the most tolerant wheats to solutions at 5 kPa O_2, based on shoot growth. This was also reflected in data on roots. The length of the longest seminal root and the total length of seminal roots after 14 d hypoxia decreased by an average of 42–50%, respectively, for Bayles, BR34, Coker-9766 and FL302; but roots were not significantly affected for Gore and Savannah. Root dry weight decreased significantly for all varieties except for Savannah (Huang et al., 1994a). There was less genetic diversity in the recovery of shoots for these same varieties during 7 d of aeration following hypoxia (data calculated from Huang et al., 1994a) relative to shoot growth of aerated plants over same period (Table 5).

In a glasshouse experiment with 14 wheat varieties and several doubled haploid wheat lines, there was good genetic diversity for waterlogging tolerance based on shoot growth both during continuous waterlogging for 28 days, and after waterlogging during 21 days of recovery period following drainage (Table 5).

Table 4. Adaptive traits for waterlogging tolerance of wheat, barley and oats identified from experiments in waterlogged soils and anaerobic solution cultures

Type		Trait		References
Phenology	1.	Seed/seedling vigour	1.	Gardner and Flood (1993)
	2	Long season	2.	McDonald and Gardner (1987); Gardner and Flood (1993)
	3	Dormancy (seeds or whole plant tissues)	3.	Setter (2000)
	4.	Slow growth	4	McDonald et al. (2001a).
Morphology and anatomy	1.	Nodal/adventitious root development	1.	Belford (1981); Trought and Drew (1982); Barrett-Lennard et al. (1988); Thomson et al.(1992); Huang et al. (1994a, 1997); Malik et al. (2002)
	2.	Survival of seminal roots		
	3.	Aerenchyma	2.	Armstrong (1979); Trought and Drew (1982); Barrett-Lennard et al. (1988); Thomson et al. (1990); Watkin et al. (1998).
	4.	Increased root porosity/intercellular spaces		
	5.	Increased suberin / lignin; barriers to radial O_2 loss	3.	Armstrong (1979); Benjamin and Greenway (1979); Belford (1981); Erdmann and Wiedenroth (1986, 1988); Barrett-Lennard et al. (1988); Thomson et al. (1990, 1992); Huang et al. (1994a,b); Varade et al. (1970); Trought and Drew (1980c); Drew and Sisworo (1979); Watkin et al. (1998); McDonald et al. (2001a,b).
	6.	Root membrane integrity	4.	Yu et al. (1969); Erdmann et al. (1986); Thomson et al. (1992); Huang et al. (1997); Malik et al. (2001); McDonald et al. (2001a,b).
			5.	Arikado (1959); Jackson and Drew (1984); see also Watkin et al. (1998); McDonald et al. (2001b).
			6.	Hiatt and Lowe (1967); Greenway et al. (1992); Sangen et al. (1996)
Nutrition and nutrient toxicities	1.	Root length and depth	1.	Erdmann and Wiedenroth (1986); Huang et al. (1997); McDonald et al. (2001a,b).
	2.	Cell function for nutrient uptake, incl. K^+/Na^+ selectivity	2.	Leyshon and Sheard (1974); Drew and Sisworo (1977, 1979); Trought and Drew (1980b,c); Buwalda et al. (1988); Thomson et al. (1989); Greenway et al. (1992); Akhtar et al. (1994); Huang et al. (1995)
	3.	Leaf chlorosis		
	4.	Microelement tolerance – Fe^{2+}	3.	Drew and Sisworo (1977; 1979);
	5.	Microelement tolerance – Mn^{2+}	4.	Stieger and Feller (1994); Ding and Musgrave (1994); Huang et al. (1995); Yuanmin et al. (1997);
			5.	Sparrow and Uren (1987); Stieger and Feller (1994); Huang et al. (1995); Ding and Musgrave (1994); Yuanmin et al. (1997);
Root Metabolism: Respiration,	1.	Reduced respiration	1.	Huang and Johnson (1995)
Anaerobic catabolism and	2.	Anaerobic catabolism	2.	Harberd and Edwards (1982); Thomson et al. (1989); Waters et al. (1991b)
anoxia tolerance	3.	High carbohydrate concentrations	3.	Limpinuntana and Greenway (1979); Benjamin and Greenway (1979); Barrett-Lennard et al. (1988); Albrecht et al. (1993); Huang and Johnson (1995)
	4.	Anoxia tolerance		
	5.	Phytotoxin tolerance	4.	Waters et al (1991a,b); Greenway et al. (1992)
			5.	Drew and Lynch (1980)
Recovery and prevention of	1.	Recovery ability	1.	Barrett-Lennard et al. (1988); Buwalda et al. (1988); Albrecht et al. (1993); Malik et al. (2002)
Post anoxic damage	2.	Antioxidants and antioxidative enzymes, e.g. SOD, catalyse, glutathione reductase. . .	2.	Albrecht and Wiedenroth (1994); Wang et al. (1996); Biemelt et al. (1998)

Table 5. Genetic diversity for waterlogging tolerance at the vegetative stage in temperate cereals based on shoot dry matter increases during and after (A) exposure to hypoxia in solution culture, or (B) waterlogging in soil. Growth is calculated from changes in shoot dry weight during continuous waterlogging or hypoxia as compared to drained or aerated controls. In (B) Lines 96W639-D1-17, 96W639-D6-5 and 96W639-D6-32 and are doubled haploid lines from a Ducula-4/2* Brookton population (Setter et al., 1999)

Variety / line	Shoot growth during waterlogging (% of drained or aerated plants)	Shoot growth after waterlogging (% of drained or aerated plants)	Reference and conditions
A. Hypoxic relative to aerated solutions			
WHEAT			Calculated from Huang et al.
Savannah	102	74	(1994a). Plants 14 d old
Gore	93	86	exposed for 14d to aerated or
FL302	91	64	hypoxic (5kPa O_2) flushed
C9766	88	79	solution culture. Recovery is
Bayles	61	67	for 7 days aeration after 14 d
BR34	53	79	hypoxia.
B. Waterlogging in soil			
WHEAT			Setter and Waters (unpub).
SARC1	78	12	Plants 21 d old then either
Ducula – 4	60	45	waterlogged or freely drained
Chara	60	7	for 28 d. Recovery for 21 d
96W639-D6-32	60	27	after waterlogging.
Savannah	57	22	
96W639-D6-5	49	44	
Carnamah	49	42	
HD2329	48	24	
Camm	48	8	
Spear	47	25	
Westonia	44	41	
Brookton	44	35	
96W639-D1-17	36	26	
Cascades	36	15	
OATS			
Dalyup	47	41	
Toodyay	36	49	

The most tolerant varieties during the waterlogging treatment included several of those varieties identified earlier as having tolerance to waterlogging or other stresses, such as SARC1 (Pakistan), Ducula-4 (Mexico), Chara (Australia), 96W639-D6-32 (a doubled haploid wheat from Ducula-4/2*Brookton; Australia) and Savannah (USA). These varieties had up to twice the shoot growth of the waterlogging intolerant variety Cascades which is widely grown in waterlogging prone areas in the South Coast region of Western Australia. However, these varieties which did well during waterlogging, did not all have a good recovery after waterlogging. There was nearly a 7-fold difference in ability of shoot growth to recover following waterlogging. Chara for example had only 7% of shoot growth relative to non waterlogged plants. The best varieties for recovery included Ducula-4, with 45% shoot growth after waterlogging relative to plants grown in free draining soil (Table 5).

There appears to be no published information on genetic diversity for recovery of barley varieties to waterlogging. In the yield data presented in Table 3, it is not possible to separate out the effects of waterlogging from the recovery. In the experiment described in Table 5, it is interesting that two oat varieties which were also evaluated, have moderate to

poor shoot growth during waterlogging, but they have high shoot growth after waterlogging that was equal to the most tolerant wheat varieties evaluated (Table 5). High recovery of oats following waterlogging is consistent with published information on waterlogging tolerance of oats discussed in the 'Genetic diversity for waterlogging tolerance' section.

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) 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) 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) 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, and (ii) this will allow anthesis to occur late enough to avoid waterlogging damage in spring (cf. sensitive stages of crop development in Fig 6). 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

There are two main types of aerenchyma which are usually associated with different plant types. Schizogenous aerenchyma arises by the separation of cells and is involved in the increases in root porosity in several wetland plants (Justin and Armstrong, 1987). Lysigenous aerenchyma arises by the partial breakdown of the root cortex and this is the type formed in roots of the Gramineae (Armstrong et al., 1994) including cereals like wheat (Barrett-Lennard et al., 1988; Benjamin and Greenway, 1979; Belford, 1981; Drew and Sisworo, 1979; Erdmann and Wiedenroth, 1986, 1988; Huang et al., 1994a,b; McDonald et al., 2001a,b; Thomson et al., 1990, 1992; Trought and Drew 1980c; Varade et al., 1970; Watkin et al., 1998), barley (Arikado, 1959), oats (Setter and Waters, unpublished), and triticale (Thomson et al., 1992; Watkin et al., 1998). Reviews on the occurrence and mechanisms of aerenchyma formation are given by Armstrong (1979), Jackson and Drew (1984), Armstrong et al. (1994) and Jackson and Armstrong (1999).

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.

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 development and shoot growth or grain yield under hypoxic or waterlogged conditions (Figure 8A and B, respectively).

Huang et al. (1994a) grew 6 wheat varieties for 14 d in aerated nutrient solution culture, and then imposed treatments of continued aeration (21 kPa O_2) or hypoxia (5 kPa O_2). After 21 d hypoxia, aerenchyma was measured based on the percentage of the cortical area of adventitious roots determined microscopically. When the aerenchyma is compared with shoot growth for plants in hypoxia there is a correlation of r^2=0.88 (Figure 8A).

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 (Figure 8B, r^2=0.59). These results are consistent with Huang et al. (1994a) discussed above, except that the aerenchyma in field grown plants accounted for substan-

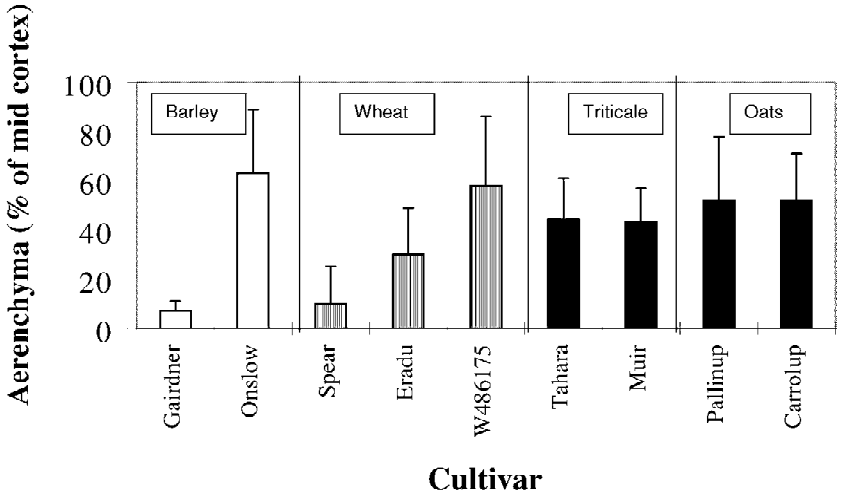

Figure 7. Aerenchyma (% of mid cortex of adventitious roots) of barley, wheat, triticale and oat varieties grown under waterlogged conditions at Esperance, Western Australia. Plants were grown for the equivalent of at least 6 days continuous waterlogging to the soil surface ($SEW_{30} \geq 160$; 1998–99); vertical bars are sem. Data from Waters, Kuo, Burgess, Millar and Setter, unpublished.

tially less of the variation in plant growth or grain yield.

The relationship between aerenchyma development and relative grain yield under waterlogged conditions did not hold for long season wheats or for barley (Setter et al., 1999; Setter, 2000). 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 (Table 4) 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), 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). 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 a top priority in future genetic studies; to our knowledge, this basis of tolerance has only been used in genetic studies described by Bao (1997). 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.

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). 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

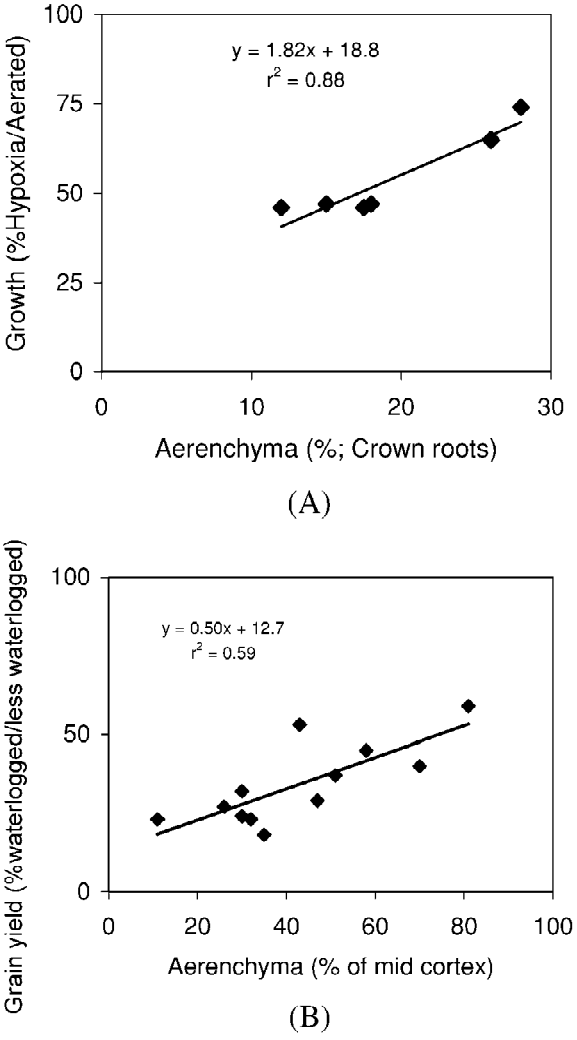

Figure 8. Relationship between aerenchyma formation and (A) hypoxia tolerance and (B) waterlogging tolerance in wheat. Data are based on the % of mid cortex of crown/adventitious roots of waterlogged plants. Plants in (A) were grown as described in Table 5 and sampled for aerenchyma and shoot growth after 21 d hypoxia (calculated from data of Huang et al., 1994a). Plants in (B) were grown in the field at Esperance, Western Australia, under intermittent waterlogging; grain yield was estimated as the percentage of waterlogged plants ($SEW_{30} \geq 160$ cm.d) relative to less waterlogged plants (SEW_{30} = 40 cm.d; from Setter et al., 1999).

tolerance of F2 plants. Chi squared tests showed that segregation ratios were consistent with a 3:1 ratio indicating that the waterlogging tolerance of Nonglin 46 is genetically controlled by a single dominant gene. Backcrossing experiments confirmed that waterlogging tolerance of Nonglin 46 is controlled by one dominant gene: (1) backcrosses from both the F1s with the waterlogging tolerant Nonglin 46 produced only 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).

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). In these studies, three intolerant and four waterlogging tolerant wheats were used including Shuilzhan (syn. Shur-Bian-Zhan; '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)

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). 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). 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).

Boru (1996) extended the research of van Ginkel et al. (1992) at CIMMYT in screening for waterlogging tolerance (see 'Genetic diversity for waterlogging tolerance' section) by genetic studies with several of the tolerant wheat varieties. Boru (1996) proposed that in three waterlogging tolerant wheat genotypes, tolerance was conditioned by four major genes. The

three tolerant wheat genotypes used in his study (Parula/Sara, Ducula-4 and Vee/Myna) carried different genes, although they all posses one tolerant gene (*Wt1*) in common. Boru (1996) proposed that these different genes could relate to different mechanisms of tolerance to waterlogging, therefore waterlogging tolerance could be substantially improved by combining all tolerance genes into one genotype. Of course this may not be so where genes relate to different strategies of growth *versus* non growth during waterlogging (see 'Mechanisms of tolerance to waterlogging' section: Phenology). Some of the work in China (Cao et al., 1994; see above) also indicated that additive gene action is the major determinant of the inheritance of waterlogging tolerance.

The only work to evaluate the heritability of waterlogging tolerance based on plant grain yield using 20 wheat varieties is Bao (1997) for experiments conducted in Zhenhai, south of Shanghai, China. He found that heritability for tolerance to 15 days waterlogging in the field at the tillering stage and the booting stage was 74.7 and 80.2%, respectively.

In barley, 8 parental lines and their F1 and F2 hybrids were grown under waterlogged conditions at the internode elongation stage, selecting for a reduction in numbers of dead leaves as the waterlogging tolerance indicator (Hamachi et al., 1989). Heterosis for tolerance expressed as reduction in damage was observed in the F1s, and frequency distributions of damage in F2s showed continuous variation. These results indicated that screening for waterlogging tolerance by the amount of dead leaves was a useful criterion and that endurance was under polygenic control.

Wheat can tolerate the addition of entire genomes, thus amphiploids can be made by hybridisations with related species. These amphiploids can also be used to produce aneuploid stocks for each chromosome including chromosome addition lines, substitution lines, translocation lines and recombinant lines (Forster et al., 1992). In preliminary screening of nine amphiploids, Taeb et al. (1993) identified two (CS/*Thinopyrum elongatum* and CS/*Secale montanum*) as producing significantly longer roots in soil waterlogged for at least three weeks relative to the wheat (*T. aestivum*) parent, Chinese Spring (CS). These results demonstrate that genes for waterlogging tolerance in some, but not all, wild species can be expressed in a wheat genetic background (Forster et al., 1992). Subsequent research involved evaluation of the disomic addition line 2E and 4E of the CS/*T. elongatum* amphiploid, where root penetration into waterlogged soil of the 2E and 4E addition lines was significantly greater than the CS parent and up to 88% of the amphiploid. Results that tolerance (root penetration) was in the order of amphiploid > 2E addition > 4E addition > CS suggests that root growth in waterlogged soils is controlled by more than one gene on more than one chromosome (Forster et al., 1992). A major caveat to this conclusion is that this may only relate to root penetration ability derived from *Thinopyrum elongatum.* Contrasting results to this work, and the potential for increasing waterlogging tolerance from other wild relatives of wheat is discussed further below.

General discussion

There are good prospects for cereal germplasm improvement for waterlogging tolerance based on a mechanistic approach to selection of adaptive traits. Key ingredients are available for this to occur including: (i) increasing familiarity with the target environment and elucidation of the problem(s) ('The Waterlogged environments for crop production' section), (ii) evaluation of local and international germplasm under conditions in target environments and demonstration of good genetic diversity for maintenance of high growth rates, high grain yields, or survival of both seeds and plants ('Genetic diversity for waterlogging tolerance' section), (iii) supporting physiological research on a wide range of adaptive traits ('Mechanisms of tolerance to waterlogging' section), and (iv) demonstration of high levels of heritability for at least some correlated adaptive traits for waterlogging tolerance based on yield ('Genetic studies on waterlogging tolerance in wheat and barley' section).

Information presented in the 'Genetic diversity for waterlogging tolerance' section, and the large number of root traits associated with mechanisms of waterlogging tolerance ('Mechanisms of tolerance to waterlogging' section), suggest that the greatest prospects for the new waterlogging tolerant cereal varieties will come from more efficient selection of parental lines from existing germplasm, using approaches like marker assisted selection (Miflin, 2000; Ribaut et al., 2001) or non destructive or non invasive physiological traits as a basis for rapid screening protocols (Armstrong et al., 1994). Other prospects exist through wide hybridisations. The latter approach may enable researchers to obtain greater levels of expression of existing traits or include new, more diverse traits

Plate 1. Germplasm improvement for waterlogging tolerance in wheat. A new Ducula-4/2*Brookton doubled haploid breeding line (96W639-D4-13; Left) and the commercial wheat variety cv. Cascades (Right). Screening trial October, 2002; Katanning, Wa. Plants were waterlogged for 6 weeks at 3 weeks after sowing.

(Lagudah and Appels, 1994; Skovmand et al., 2001). There is ongoing work in both improved selection and wide hybridisations for increasing waterlogging tolerance which is discussed further below, followed by a review of recent work using transgenic approaches.

The only published progress on commercial germplasm improvement for waterlogging tolerance in wheat comes from two sources in China and Australia. Cao et al. (1996) in China refer to the breeding of 41 varieties or lines using a range of waterlogging tolerant parents. This includes 8 varieties from Norin 46 (syn. Nonglin 46) and 19 lines from Compton. More recent work of Cao et al. (1998) refers to two new waterlogging tolerant lines, Ningmaizi66 and Ningmaizi67, produced from crosses between *Triticum macha* and common wheat (see earlier discussion in the 'Genetic studies on waterlogging tolerance in wheat and barley' section). However no data are presented on differences in grain yield or the criteria used to assess waterlogging tolerance.

In Australia, one of the waterlogging tolerant wheats selected by CIMMYT (Ducula-4) was crossed with an intolerant commercial Western Australian variety (Brookton) to produce over 200 doubled haploid lines. Twenty of these lines have a level of waterlogging tolerance in the field, based on shoot biomass and grain yield relative to non waterlogged plants, that is up to three times higher than either of the parents or existing commercial varieties (Plate 1). Three of these promising lines are now in the final stages of breeding evaluations (R. Wilson, Pers. Comm.; see also top two doubled haploid lines in Table 5). Such programs highlight that one reason for the lack of numerous releases of waterlogging tolerant cereals is the need for extensive field testing and the inclusion of other essential agronomic traits required for new germplasm in local environments. If waterlogging tolerance is incorporated into the new germplasm, but there is a substantial yield penalty, or if other desirable traits have been lost on the way, then this germplasm may never be released.

Prospects for germplasm improvement through improved selection

The development of molecular markers for waterlogging tolerance would be particularly welcome in relation to the numerous complex root traits which can be so variable in space and time during waterlogging in the natural environment. This would seem readily achievable in relation to data in support of a single dominant gene for waterlogging tolerance in wheat ('Genetic studies on waterlogging tolerance in wheat and barley' section).

One of the crucial aspects of developing molecular markers is accurate, reproducible phenotyping (Miflin, 2000; Ribaut et al., 2001). In the published studies on genetic diversity for waterlogging tolerance few

presented information on repeatability with the same germplasm either in the same or different locations. Once this is achieved, and molecular markers are developed, the process of validation in another population is essential before markers can be considered for more widespread application.

There are numerous molecular markers available for various abiotic stresses in wheat (Ribaut et al., 2001), however to our knowledge there are currently no molecular markers available for waterlogging tolerance in cereals. This might be achievable based on sequences from genes of known function, i.e. 'candidate genes.' For example, Waters et al. (1991b) demonstrated that low rates of alcoholic fermentation, and hence low ATP, led to injury of root cells in a waterlogging intolerant wheat (Gamenya; Table 3) exposed to anoxia. The activities of pyruvate decarboxylases (PDC) and rates of alcoholic fermentation indicate that the alcoholic fermentation is usually limited in root tips, and this may be one factor contributing to wheat being more intolerant to anoxia than rice (Waters et al., 1991b). Similar limitations in PDC and over-expression of the *Pdc* gene in rice exposed to submergence resulted in increases in both rates of alcoholic fermentation and survival (see below). This highlights the opportunity that evaluation of polymorphisms for known sequences of *Pdc* or other candidate genes in wheat or other cereals may therefore lead to the identification of waterlogging tolerant genotypes based on this mechanism of anoxia tolerance.

Researchers in a joint project with the Department of Agriculture, Western Australia, The University of Western Australia and Murdoch University are currently involved in development of molecular markers for various adaptive traits for waterlogging using specific doubled haploid populations based on crosses of international germplasm like the Ducula lines from CIMMYT with locally adapted varieties ('Genetic diversity for waterlogging tolerance' section). This work is linked to development of waterlogging tolerant doubled haploid wheat populations for Australia and India, and it is supported by the Grains Research and Development Corporation (GRDC) and the Australian Centre for International Agricultural Research (ACIAR). Research will involve mapping the Ducula-4/2*Brookton doubled haploid population described above, as well as evaluation of up to five additional DH populations based on crosses of tolerant × intolerant and tolerant × tolerant parents.

Several alternative methods offer a simple, rapid approach to screening for waterlogging tolerance, such as leaf chlorosis, as long as they are validated in the target environment. Leaf chlorosis has been used successfully at CIMMYT and in China for many years, results are strongly correlated to grain yield in these specific locations, and this is a highly heritable trait ('Genetic diversity for waterlogging tolerance' and 'Genetic studies on waterlogging tolerance in wheat and barley' sections; Samad et al., 2001). However, leaf chlorosis is not a good selection criteria in all waterlogged environments. In Western Australia, where wheat, barley and oats were exposed to intermittent waterlogging, there was no correlation between leaf chlorosis and grain yields under waterlogged conditions. Other evidence supporting a lack of relationship includes: (i) barley generally develops 2–3 fold greater chlorosis than wheat, yet varieties have similar grain yields to wheat; and (ii) some of the most waterlogging tolerant wheats and barleys (like Champtal and Stirling; Table 3) have up to 2-fold greater chlorosis than other varieties, yet grain yields of these chlorotic varieties are up to twice that of other varieties (Setter et al., 1999; Setter 2000).

There appears to be good potential for development of rapid screening criteria for waterlogging tolerance in large populations based on root traits including aerenchyma production plus reduced radial O_2 loss, Fe^{2+} toxicity, and Mn^{2+}toxicity during waterlogging. Breeding programs across the world routinely screen for tolerance to mineral nutrient toxicities by measurements of root growth (length) in nutrient solution cultures, e.g. Al (Baier et al., 1995; Hede et al., 2001) and B tolerance (Campbell et al., 1998). Similar procedures could be developed and optimised to screen for waterlogging tolerance or the combined effects of mineral nutrient toxicities and waterlogging.

Development of wide scale screening protocols for root traits in a large number of breeding lines using deoxygenated nutrient solutions to simulate waterlogging can be difficult and expensive. Wiengweera et al. (1997) used stagnant nutrient solutions containing agar (0.1% - which still maintains a liquid media) on wheat to simulate the changes in gas composition associated with waterlogging. They found that wheat grown in stagnant agar solutions developed up to 10-fold greater aerenchyma in adventitious roots than roots in N_2 flushed solutions or in non flushed solution without agar, and these values in plants from stagnant agar were closer to values found for plants grown in soils.

Measurement of root lengths of seedlings grown in stagnant agar solutions might therefore be used as a rapid screening protocol to select for the combined effects of [root aerenchyma plus low radial O_2 loss] for donor parents (Watkin et al., 1998). Such approaches could also be used to non-destructively screen for tolerant progeny through a breeding program. Once screened and selected, these breeding lines can be transferred to soil media and subsequently used to develop the next generation.

This method could also be combined with other measurements. For example, Sangen et al. (1996) observed that solute leakage from barley roots exposed to waterlogging was twice that of wheat, and this was interpreted as the explanation for differences in waterlogging tolerance of these two crops. Whether this was the cause or the result of waterlogging tolerance/intolerance remains unclear. However, this approach could easily be used to rapidly screen for differences in membrane integrity associated with waterlogging.

Green and Etherington (1977) used a similar method as described above with stagnant agar to investigate the effects of ferrous iron on mechanisms of waterlogging tolerance in rice. A nutrient solution culture containing 0.5% agar was deoxygenated and ferrous sulphate was added at 10–320 mg L^{-1} Fe^{2+}. When the agar had set, O_2diffusion across the agar interface was reduced to a negligible amount, and below about 1 cm the iron remained in the ferrous form for a considerable time. Germinated seeds were stabbed into the agar and allowed to grow for up to 30 days to screen germplasm. A similar approach could be used to screen for waterlogging tolerance of wheat at high Fe^{2+}. The lower agar concentration of 0.1% could still be used to keep the medium liquid rather than solid, and the deoxygenation which would develop naturally would keep the iron in the ferrous state. Once deoxygenated, these solutions would enable efficient screening for tolerance of wheat to high Fe^{2+} under anaerobic conditions. Similar approaches might be used for screening for tolerance to Mn^{2+} under anaerobic conditions.

Prospects for germplasm improvement through wide hybridisations

Several publications discussed earlier have indicated that there is not always a clear relationship between the amount of aerenchyma and waterlogging tolerance; this has sometimes been shown for wheat, triticale, and barley (Setter et al., 1999; Setter, 2000). An explanation for this is given by the extensive modelling work of Armstrong (1979) because the diffusion of $O_2$to root tips will be related to several tissue and root media characteristics such as the amount of aerenchyma, the radial O_2loss, and tissue respiration.

In wheat and barley, a major constraint to O_2diffusion through roots during waterlogging is the general lack of an effective barrier to radial O_2loss (McDonald et al., 2001a). This group has now begun a search for potential donors of this trait in wild relatives of wheat. The presence of a combination of traits such as high root porosities and low radial O_2 loss (ROL) for waterlogging tolerance in species within the tribe Triticeae such as *Critesion marinum* (syn. *Hordeum marinum*; McDonald et al., 2001a) offer good prospects for enhancing these traits in cereal crops because wide-hybridisations are possible between *Hordeum* and *Triticum* (Jiang and Dajun, 1987).

Some concerns with wide hybridisations remain, and these include the application of adaptive traits in species with low relative growth rates to those with high relative growth rates. This point may explain the lack of substantial improvements in an amphiploid of *Triticum aestivum* (cv. Chinese Spring) and *Lophopyrum elongatum* (syn. *Thinopyrum elongatum*; 'Genetic studies on waterlogging tolerance in wheat and barley' section) a species from a salt marsh habitat. In experiments in stagnant solutions or waterlogged soil, there were often no significant differences in growth between Chinese Spring and the amphiploid CS/*L. elongatum* or 7 disomic addition lines (McDonald et al., 2001b), even though *L. elongatum* was more tolerant of deoxygenated stagnant nutrient solution or waterlogged soils. These results contrast with earlier studies of Taeb et al. (1993) described in 'Genetic studies on waterlogging tolerance in wheat and barley' section. This difference could partly be due to the growth stages of plants used by McDonald et al. some of which were delayed in germination by up to 17 d to produce plants at the same developmental stages at the time of treatments (this was not done for root penetration measurements of Taeb et al.; 'Genetic studies on waterlogging tolerance in wheat and barley' section). Other explanations for the differences may relate to the shorter duration of waterlogging treatments (21d vs 5 months, McDonald et al., 2001b and Taeb et al., 1993, respectively) or the lack of measurements on recovery growth after waterlogging by Taeb et al. (1993).

Prospects for germplasm improvement through development of transgenic plants

Genetic engineering provides opportunities for germplasm improvement as well as evaluating the impact of different mechanisms of tolerance to waterlogging without the confounding effects of complete changes in the genetic background which occurs using crossbreds. Two approaches have been used to try and identify limiting factors in the response to waterlogging: (1) Over- or under-expression of single candidate genes, eg. for ethanol synthesis, using sense and anti-sense constructs; and (2) Over-expression of transcription factors like the *Arabidopsis* Myb transcription factor (AtMYB2) to control a gene cascade (Dennis et al., 2000; Dolferus et al., 2002).

Over-expression of candidate genes for anaerobic tolerance has had mixed success across a wide range of plants. This is understandable, since many of the anaerobically induced genes for numerous mechanisms of tolerance (Table 4) do not limit growth or survival under anaerobiosis. Even where limiting steps are relieved due to over-expression of genes, another step in the pathway may subsequently become limiting. Such effects are partly a consequence of the sensitivity coefficients of different steps in a metabolic pathway (Kacser and Burns, 1979, as reviewed by Gibbs and Greenway, 2003). Two types of studies using over-expression of candidate genes appear to have been successful in resulting in moderate increases in tolerance to anaerobiosis: (1) non-symbiotic hemoglobins in *Arabidopsis* (Hunt et al., 2001) and (2) over-expression of the first enzyme in the metabolic pathway for ethanolic fermentation, pyruvate decarboxylase (*PDC*) in *Arabidopsis* (Ismond et al., in preparation; as cited by Dolferus et al., 2002) and in rice.

There are intriguing results in shoots of rice transformed to over-express *pdc1* to increase rates of ethanolic fermentation during submergence. Quimio et al. (2000) found that Taipei 309 transformed with *pdc1* linked to a constitutive 35S promoter had up to 3-fold higher PDC activities and ethanol synthesis rates when exposed to anoxia compared to non-transformed controls. Increasing ethanol production up to 6-fold in a range of transgenic lines exposed to anoxia was correlated with an 8-fold increase in percentage survival of lines during submergence under hypoxic conditions (r^2=0.69; Quimio et al., 2000).

These results with rice need to be repeated, since there are concerns in relation to physiological results and potential extrapolation to other varieties. Firstly, the observation is made by Quimio et al. (2000) that a trebling in the activity of PDC in transgenic lines resulted in a trebling in the rates of ethanol production. This is unusual for two reasons: (i) work by Gibbs et al. (2000) demonstrates that rates of ethanol synthesis in coleoptiles of two other rice varieties exposed to anoxia (IR22 and Calrose) are more limited by PFK, than PDC by an order of magnitude; and (ii) when the limiting step in a metabolic pathway is relieved, the effects on end products are the consequence of the sum of all other limitations in the pathway. The impact is that usually a doubling in the activity of a limiting enzyme will result in a less than doubling in the production of end products, since other limitations in the pathway will occur (see review by Gibbs and Greenway, 2003).

In later studies with Taipei 309 transformed with *Pdc1*, two transgenic rice lines had over 2-fold greater PDC activity, and they had up to 43% greater rates of ethanol synthesis, however the survival of seedlings exposed to anoxia was even less than that of non-transformed plants (Rahman et al., 2001). The contrasting results in these studies relative to Quimio et al. (2000) could be due to several factors including (1) differential expression of PDC in shoot and root tissue, (2) the use of different constitutive (35S; Quimio et al., 2000) and inducible (6XARE; Rahman et al., 2001) promoters; or (3) less severe but longer term treatment conditions used by Quimio et al. (2000) (14 d submergence under hypoxic conditions and 21 d recovery) relative to Rahman et al. (2001) (1d hypoxia and 2.75 d anoxia, followed by 10 d recovery).

With the large number of at least 20 anaerobically induced genes observed in crops like maize after exposures to only 1–55 h of anaerobiosis (Sachs et al., 1996), it is reasonable that transcription factors are a key target of current work on anaerobic metabolism. This is particularly supported from genetic studies indicating a 'single gene' for waterlogging ('Genetic studies on waterlogging tolerance in wheat and barley' section) or submergence tolerance (Setter et al., 1997). Such an approach of over-expression of a transcription factor has the potential for a balanced increase in expression of all genes related to a particular phase of adaptation, rather than the one gene thought to limit metabolism. So far, only one transcription factor has been identified from *Arabidopsis*, AtMYB2 (Hoeren et al., 1998). This transcription factor is induced by several abiotic stresses such as low O_2 concentrations, cold, drought, and wounding. Initial work indicates that constitutive, over-expression of this gene is lethal,

since no transformants could be produced; this work is therefore continuing using anaerobically inducible promoters linked to AtMYB2 (Dennis et al., 2000; Dolferus et al., 2002).

In summary, there are currently no crops where transgenic plants have been produced and field tested to confirm increased waterlogging or submergence tolerance. Genetic engineering remains a powerful tool to unravel complexities of plant response to these stresses. However, it is the very complexity of these stresses which will, at least for now, assure that traditional approaches are maintained for germplasm improvement for waterlogging prone areas.

Concluding remarks

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 realised 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.

It is possible that the intermittent nature of waterlogging in specific environments like Western Australia may influence different strategies for waterlogging tolerance of plants. Short term or intermittent waterlogging primarily requires plants to maintain processes associated with survival, while growth is a secondary priority. Strategies that could be used include diverse traits such as high rates of alcoholic fermentation to overcome energy deficiency during anoxia, high carbohydrate concentrations to sustain alcoholic fermentation, maintenance of membrane integrity and reduced metabolite leakage, increased efficiency of nutrient uptake, and decreased damage due to O_2 free radicals associated with return to aerobic conditions following waterlogging events.

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).

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 (Table 4), 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.

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 shown in Figure 1. 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.

It is recommended that to achieve waterlogging tolerance, an incremental process be followed by firstly incorporating adaptive traits from local, national or international germplasm with known tolerance, and then combining other adaptive traits relevant to the target environment. Finally, this review has not considered important interactions of waterlogging with other stresses in the natural environment. There is some information on this for wheat or barley in relation to acid (Waters et al., 1991b) and alkaline conditions (Gill et al., 1993), and salinity (Barrett-Lennard et al., 1999; John et al., 1987; McFarlane, 1990). Implications for breeding for salt-waterlogging interactions are discussed further by Barrett-Lennard et al. (1999).

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