

# Crops that feed the world 4. Barley: a resilient crop? Strengths and weaknesses in the context of food security

Adrian Clive Newton · Andrew J. Flavell · Timothy S. George · Philip Leat · Barry Mullholland · Luke Ramsay · Cesar Revoredo-Giha · Joanne Russell · Brian J. Steffenson · J. Stuart Swanston · William T. B. Thomas · Robbie Waugh · Philip J. White · Ian J. Bingham

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**Abstract** Barley is cultivated both in highly productive agricultural systems and also in marginal and subsistence environments. Its distribution is worldwide and is of considerable economic importance for animal feed and alcohol production. The overall importance of barley as a human food is minor but there is much potential for new uses exploiting the health benefits of whole grain and beta-glucans. The barley supply chains are complex and show added value at many stages. Germplasm resources for barley are considerable, with much potential for exploitation of its biodiversity available through the use of recently developed genomic and breeding tools. Consequently, substantial gains in crucial sustainability characteristics should be achievable in the future, together with increased understanding of the physiological basis of many agronomic traits, particularly water and nutrient use efficiency.

Barley's ability to adapt to multiple biotic and abiotic stresses will be crucial to its future exploitation and increased emphasis on these traits in elite germplasm is needed to equip the crop for environmental change. Similarly, resource use efficiency should become a higher priority to ensure the crop's sustainability in the long-term. Clearly barley is a resilient crop with much potential which can be realised in the future.

**Keywords** Barley · *Hordeum vulgare* · Quality · Yield · Supply chain · Sustainability · Resilience · Biotic stress · Abiotic stress · Food security · Physiology · Agronomy · Cultivation · Nutrient use efficiency · Water use efficiency · Germplasm · Biodiversity · Genomics

## Introduction

Barley is one of the world's oldest cultivated crops, spreading from its origins in the 'Fertile Crescent' in the Middle East (Nevo 1992). Since ancient times, the importance of barley as a basic food source has declined compared with other crops. However, it is used worldwide for animal feed and human food, with its main use for human consumption being the production of alcoholic drinks (though proportions vary greatly for cultural reasons in different countries). Increased consumer interest in nutrition and health (Newman and Newman 2006) together with barley's reputation as a stress-tolerant crop bode well for its future usefulness. However, its potential must be examined critically in the context of food security, where generally accepted views need to be assessed against a wide range of pressures, not just biotic and abiotic stress. Indeed other cereals can out-perform barley in some drought-stressed low nutrient environments (Cossani et al. 2007, 2009).

A. C. Newton (✉) · T. S. George · B. Mullholland · L. Ramsay · J. Russell · J. S. Swanston · W. T. B. Thomas · R. Waugh · P. J. White  
The James Hutton Institute,  
Invergowrie,  
Dundee DD2 5DA, UK  
e-mail: adrian.newton@hutton.ac.uk

P. Leat · C. Revoredo-Giha · I. J. Bingham  
Scottish Agricultural College,  
The Kings Buildings, West Mains Road,  
Edinburgh EH9 3JG, UK

A. J. Flavell  
University of Dundee at SCRI,  
Invergowrie,  
Dundee DD2 5DA, UK

B. J. Steffenson  
Department of Plant Pathology, University of Minnesota,  
495 Borlaug Hall, 1991 Upper Buford Circle,  
St. Paul, MN 55108–6030, USA

The food security status of a crop must be considered in its cultural, political, agronomic and economic context, and not simply a like-for-like comparison of the biology with another species. Barley has different end users from other crop species who require the crop for some specific purpose. For example malt whisky can, by definition, only be produced from barley, whereas grain whisky can be produced from any cereal for a different market. Barley is also a valuable component of crop rotation providing benefits in terms of species diversity and the control of pests and diseases. As its sowing and harvest date requirements also differ from other important crops such as wheat, its inclusion in the rotation provides opportunities for managing the workload through the season. Add to these factors a consideration of local variety, landrace or participatory breeding selection plus their interaction with local biotic and abiotic stress factors, and the position of barley in the broad food security context can be assessed.

Food security has a range of definitions, but here we use the simple definition “risk of adequate food not being available” (Chakraborty and Newton 2011). It is whether the presence of barley in the agricultural system can be maintained in sufficient amount and proportion to fulfil its diverse range of end user functions that matters. It is in this context that we review the factors affecting its supply and trade, examine the threats to its sustainability and the potential for more consistent and resilient production, as well as the development of possible new end uses and markets.

### Production, distribution and trade in barley

In terms of the world’s most important crops by production quantity, barley is ranked fourth amongst the cereals after maize, rice and wheat, although eleventh overall, and is widely grown across the world. Barley grain is used mostly as feed for animals, malt, and food for human consumption, malt being the second largest use. Farmers also use barley straw as animal feed in west Asia, north Africa, Ethiopia, Eritrea, Yemen, the Andes region and east Asia (Akar et al. 1999).

#### Barley production

Barley is grown on approximately 56 million hectares in the world (average 2006 to 2008; FAO 2010). The FAO records production in 106 countries worldwide, with an average production per year for the same period of 143.4 million tonnes. Figure 1 shows the distribution of average production across the world using averages for the period 2006 to 2008, indicating both the widespread cultivation and the particularly high levels of production in North America, Europe, Russia, China and Australia.

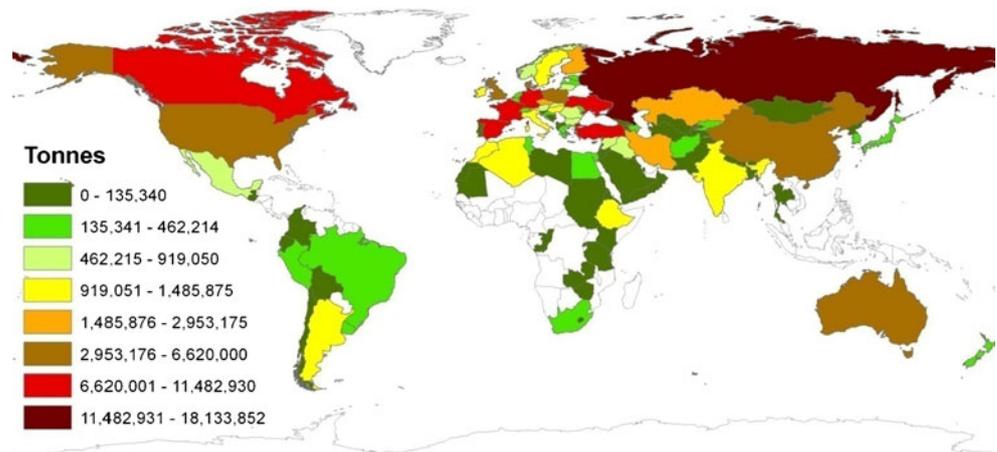
Barley has an extremely wide geographic range, wider than almost every other crop species. It is cultivated at the highest arable mountaintops down to the seacoast and from the highest north/south latitudes to the tropics (Paulitz and Steffenson 2011). Developing countries account for about 18% (26 million tonnes) of total barley production and 25% (18.5 million hectares) of the total harvested area in the world. It is a versatile crop, being tolerant of a wide variety of growing conditions from the arid conditions of the Middle East, to the cool of the Andes. In general, barley is more productive and its yield is less variable than wheat and most other small grains. Therefore, it is widely used amongst farmers with limited and poor resources in less favourable climate and soil conditions.

Amongst the top 10 producing countries (Table 1), the Russian Federation is by far the largest producer accounting for some 13% of world production. With a harvested area of over 9 million hectares, it has a production area of at least twice the size of the country with the second largest area, i.e. the Ukraine. There is then a group of countries – Germany, Canada, France, Spain and the Ukraine that each produce 7–8% of world production. The remaining producers – Turkey, Australia, the United Kingdom and the United States of America – each produce between 5% and 3% of production. In total, the top 10 producing countries account for two-thirds of world production. The major producers, i.e. the Russian Federation, Ukraine and Australia, have large areas but low average yields of close to, or under two tonnes per hectare (Fig. 1 and Table 2). This arises from less intensive production systems and occasionally difficult climatic conditions. In the more intensive production in northern Europe (France, Germany and the UK), average yields are close to 6 tonnes per hectare (Fig. 2). However, over the past 50 years there has been an overall decline in the cropped area of barley, although there has been relative stability over the past 10 years (Table 2), but there has been a continuous improvement in yield per hectare and as a result, total production has increased.

#### Supply and demand balances of barley

The commodity balance analysis for barley by continent shows that Asia and Europe are the main importers of barley; however, the continents with the lowest self-sufficiency ratios (ratio of production to aggregate demand) are Asia (60%) and Africa (67%) (Table 3). In terms of the components of aggregated demand, animal feed is the most important one (53% of the supply), with a sizable proportion of the supply being exported (20% of the supply) or processed (15% of the supply). Food represents a relatively small proportion of the supply and half of it is consumed in Africa.

**Fig. 1** Barley production across the world: average tonnages, 2006–08 (FAO 2010)



### World trade

The largest exporter for 2007 in terms of both quantity and value terms was France. Other major exporters include Germany, the Ukraine, Canada, the Russian Federation and Australia (Fig. 3). The major exporters have a particular focus on malting barley. The leading importing country in 2007 was Saudi Arabia with 7.1 million metric tonnes with other prominent importers being Belgium, The Netherlands, Japan and Germany all importing between 1.2 and 1.4 million metric tonnes (Fig. 4). Generally speaking, Asian and African countries import barley both for animal and human consumption.

Clearly, barley is grown and utilised worldwide in many different environments with a range of important uses. Its quality, quantity and reliable supply are therefore important for both local need and trade. Although grown in highly productive agriculture areas, its importance increases in more marginal and stressed regions and therefore at disproportionate threat from changes in climate. Therefore, barley as a crop has considerable socio-economic and therefore political importance leading to significant food security issues. This is particularly true for some of the

most destitute people of the world where barley is the main foodstuff. These regions include the highlands of Ethiopia, Eritrea, Yemen, Tibet, Nepal, and the Andean countries of South America. At these high elevations, barley is the major cultivated cereal crop.

### Uses of barley worldwide

Barley was one of the earliest cereals to feature in the human diet, with archaeological evidence of wild emmer and wild barley (*Hordeum vulgare* subsp. *spontaneum*) consumption dating back to 17,000BC (Kislev et al. 1992). The domestication process took several thousand years (Zohary and Hopf 1988), but cultivation of barley began at least 10 thousand years ago (Fischbeck 2002), making it one of the oldest grain crops grown (Newman and Newman 2006). During the initial domestication process, it is likely that naturally occurring mutants with a non-brittle rachis were selected for ease of harvest. Barley was domesticated as a source of human food but, over time, its primary usage has evolved to the extent that, in highly developed western

**Table 1** Barley production in ten leading countries (3 year average, 2006–2008)

Countries	Area harvested (000 ha)	Production (000 tonnes)	Yield (T/ha)	% of world production
Russian Federation	9,126	18,915	2.07	13.2
Germany	1,968	11,439	5.81	8.0
Canada	3,574	10,779	3.03	7.5
France	1,722	10,682	6.19	7.4
Spain	3,293	10,332	3.13	7.2
Ukraine	4,497	9,978	2.22	7.0
Turkey	3,230	7,594	2.33	5.3
Australia	4,357	5,666	1.29	4.0
United Kingdom	937	5,487	5.85	3.8
United States	1,378	4,571	3.31	3.2
World	56,188	143,399	2.63	66.6

**Table 2** Barley production trends in the world

Years	Area harvested (000 ha)	Proportion of first period%	Production (000 tonnes)	Proportion of first period%	Yield (T/ha)	Proportion of first period%
1961–65	68.0	100	99.7	100	1.47	100
1978–80	84.8	124	167.6	167	1.98	135
1998–00	55.8	82	132.4	133	2.37	161
2006–08	56.2	83	143.4	144	2.63	179

Based on Akar et al. (1999) and updated using FAO data (FAO 2010).

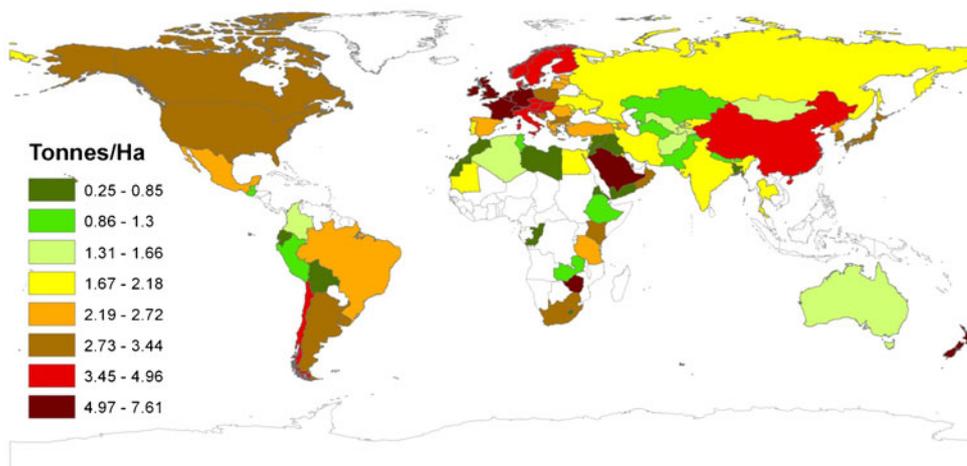
agriculture, its importance as a food crop is very limited. In the USA, for example (Fig. 5), nearly two-thirds of the barley grown is fed to livestock, with another 30% malted for the production of alcoholic beverages (Newman and Newman 2006).

There has been considerable recent interest in the nutritional properties of barley, which has stemmed largely from the discovery of the cholesterol-lowering effect of  $\beta$ -glucan, a cell-wall polysaccharide found in both oats and barley (Wood et al. 1989; Newman et al. 1989). As a consequence, efforts have been made to incorporate barley flour into items such as bread (Izydorczyk et al. 2001) and pasta (Cavallero et al. 2000), although with limited commercial development, to date. A promising new commercial product containing barley  $\beta$ -glucan is the betafiber Barliv™. This product is a natural source of soluble fiber and can be added to almost any food, including beverages (Palmer 2006). Barliv is expected to increase the utilization of barley as a foodstuff given its health benefits. In clinical trials, foods containing Barliv™ were shown to lower cholesterol and are therefore authorized to carry the United States Food and Drug Administration health claim for reducing the risk of heart disease. The action of  $\beta$ -glucan, in inhibiting absorption from the gut, probably through increased viscosity, provides further benefit in reducing post-prandial blood sugar levels (Tappy et al. 1996). However, viscosity is affected by molecular size and this can be reduced by enzymic action,

during the proving stage, when barley is included in bread flour mixes (Andersson et al. 2004). In addition to  $\beta$ -glucan, barley contains a range of other nutritionally useful components and current work (Andersson et al. 2008) is aimed at quantifying these over a wide range of genotypes, to assess the potential for enhancement within future breeding programmes.

On a global scale, however, it is the adaptability of barley to a very wide range of environments compared to other cereal crops, rather than its nutritional properties, that has been the main driver for food use. Barley can be cultivated at latitudes up to 70°N (Grando and Gomez Macpherson 2005), where six-row varieties, selected for extreme earliness and high harvest index, out-compete all other cereal species (Fischbeck 2002). Barley thus persisted as a major cereal for food in many parts of northern Europe into the 20th century, with flatbreads, made from barley meal, common in Sweden (Newman and Newman 2006). However, as improvement in living standards and ease of import has eroded dependence on locally-grown crops, consumption of barley-based foods has largely declined to a few traditional uses. An example comes from Orkney, off the north coast of Scotland, where a traditional bannock is still baked using meal from a six-rowed, landrace barley called Scots Bere (Martin and Chang 2007). This type of barley was thought to have been introduced by Viking invaders (Jarman 1996).

**Fig. 2** Barley production across the world: average yields 2005–08 (FAO 2010)



**Table 3** Barley continental supply and demand balances 2005–07

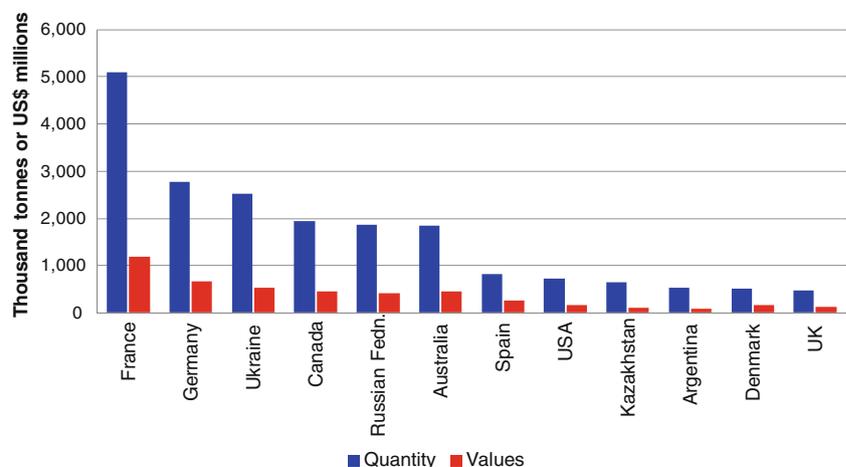
	Continent					World
	Africa	Americas	Asia	Europe	Oceania	
Aggregated supply	7,540	22,462	34,873	98,377	7,543	170,794
Production	5,070	18,035	21,107	84,936	6,865	136,013
Imports	2,373	3,531	15,048	10,380	28	31,361
Change in stocks	97	896	-1,283	3,061	650	3,421
Aggregated demand	7,540	22,462	34,873	98,377	7,543	170,794
Feed	2,270	9,186	21,293	54,759	2,671	90,179
Seed	398	611	1,491	6,699	201	9,399
Waste	385	146	2,436	1,422	82	4,471
Processing	1,267	7,020	6,438	10,855	344	25,923
Food	3,155	384	1,911	1,000	2	6,452
Exports	34	5,039	1,199	23,346	4,236	33,854
Other Utilisation	31	75	105	296	8	516

Thousand tonnes expressed in barley terms. FAO data (FAO 2010)

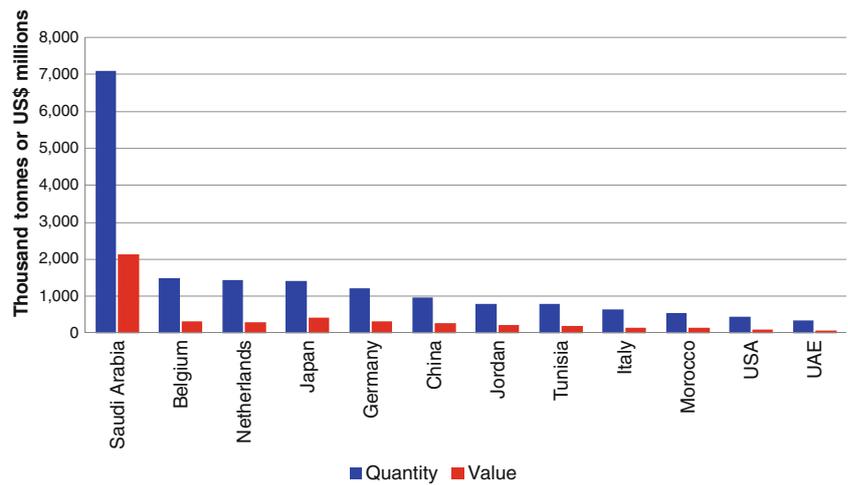
In addition to extreme latitude, Fischbeck (2002) noted that barley is also more suited than other cereals to high altitude. For that reason, barley's contemporary importance as a food crop is largely restricted to the mountainous regions of Asia, Africa and South America. Morocco has, traditionally, been the largest *per capita* consumer of food barley, although, as in other parts of north Africa, consumption declined during the second half of the 20th century (Fig. 6). This was mainly due to increased urbanisation and political support for wheat production (Amri et al. 2005), so that barley consumption is largely confined to the semi-arid and mountainous regions. Barley is used in soups, in a range of recipes as flour, semolina or whole grain or the flour is baked into bread, sometimes in a mixture with wheat flour (Amri et al. 2005). The combination of wheat and barley is taken further in Eritrea, where the two crops are grown together in a mixture, known as *hanfets*. This provides mutual protection from disease and lodging and improves the bread-making quality of the grain (Woldeamlak 2001). In addition, grain yield

and yield stability are improved (Woldeamlak et al. 2008).

Naked (hullless) barley appeared amongst the earliest cultivations of the crop, when it was still confined to the Fertile Crescent (Zohary and Hopf 1988). Hullless barley has remained a major food crop in Tibet, accounting for over 50% of total food production and being consumed by more than two million people (Tashi 2005). It is mainly used for producing a roasted barley flour, which is then cooked and consumed in a variety of ways, but barley is also used in cakes, soups, porridges and snack foods. The relatively high levels of  $\beta$ -glucan found in Tibetan hullless barleys may be the reason for lower than expected levels of the problems usually associated with diets that are largely dependent on meat and dairy products (Tashi 2005). Another part of the world where barley is grown at high altitude is in South America, where it is commonly found above 4,000 m and in soils that are more drought-prone, or with higher salt content (Capettini 2005). Again, hullless types are preferred and attract a premium price, with human

**Fig. 3** Exports of barley by major exporters, 2007. FAOstat (FAO 2010)

**Fig. 4** Imports of barley by major importers, 2007

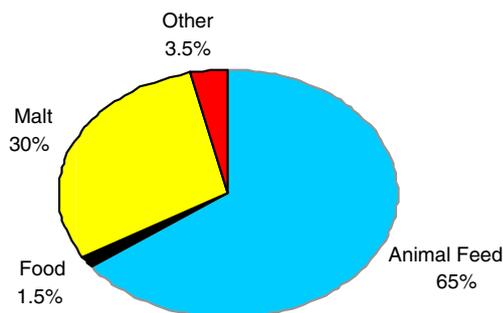


food being a major use, although there is also some grazing and hay or silage production.

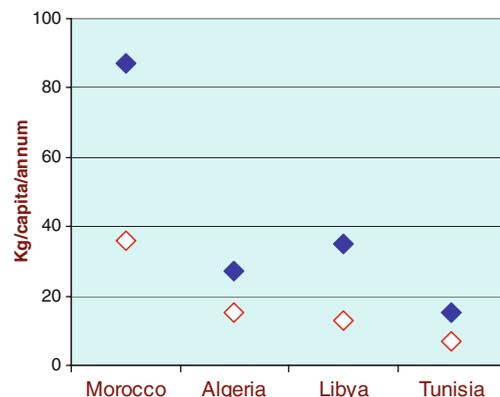
Feeding to livestock is the largest single use of barley, throughout the world. Even in countries like Morocco, with relatively high levels of human food use, around 80% of the barley grown is used to feed animals (Amri et al. 2005). Despite this, very little effort has been put into improving feed quality and the relevant industries have shown little interest in improved nutritional attributes (Ullrich 2002). Although high levels of  $\beta$ -glucan are now seen as desirable in human food, they have been associated with problems when barley has been incorporated into poultry feed. Increased viscosity in the gut has led to reduced uptake of nutrients (White et al. 1983) and ‘sticky’ faeces (Gohl et al. 1978). However, these problems have generally been addressed by the addition of enzymes, particularly  $\beta$ -glucanase, in feed preparations (Chesson 1987, 1991).

Although the quantity of barley grain protein can be increased through rate and timing of nitrogen fertiliser application, the nutritional quality remains poor due to the high hordein content (Doll 1981), with its low proportion of essential amino-acids. The identification of high lysine or low hordein mutants such as Hiproly (Munck et al. 1970) and Riso 1508 (Ingversen et al. 1973) led to attempts to

breed for improved protein quality. However pleiotropic effects of the high-lysine genes, particularly shrunken endosperms, reduced kernel weight and lower yield (Doll and Koie 1978), were never fully overcome and no varieties were ultimately released to farmers (Ullrich 2002). Cereals may therefore be used, most effectively, as a source of carbohydrate and Bowman et al. (1996) have shown the most important grain characteristics of barley for cattle feed are high starch content with low levels of protein and fibre. As this is also consistent with requirements for malting barley, there can be positive associations between malting and feed quality (Hockett and White 1981; Molina-Cano et al. 1997). Lower protein content also provides an advantage when cereals are fed to non-ruminants, as high levels of essentially low-grade protein will increase the amount of nitrogen excreted in manures (Lee and Kay 2003), a potential source of nitrogen pollution. Similarly, some environmental pollution can occur through the secretion of phosphorus in the manures of monogastric animals, resulting from their inability to degrade phytate (Taylor 1965), the main storage compound for seed phosphorus (Maga 1982). Phytate also interferes with the uptake of



**Fig. 5** Current uses of barley in the USA (Newman and Newman 2006)



**Fig. 6** Food barley consumption in N. African countries in 1961 (closed symbols) and 2002 (open symbols)

minerals such as iron and zinc, so has implications for human consumption of barley (Sandberg 1991). Barley mutants with low grain phytate content have, therefore, been developed (Rasmussen and Hatzack 1998) and breeding for low phytate barleys has been initiated in Canada and the USA (Ullrich 2002), but this has not, to date, led to significant development of improved feeding varieties.

Thus, although barley is fed, on a global basis, to a wide range of livestock, in a variety of different ways, cultivar selection is based primarily on grain yield. This preference for quantity over quality may, in part, reflect the view that feed grade is a failure to achieve malting grade (Ullrich 2002), which adversely affects the price paid to the arable farmer. Additionally, as mixed farming systems will deploy the crop on the farm of origin, having sufficient grain to meet requirements and, possibly, for sowing in the subsequent season, is likely to be the priority. In some parts of the world, contemporary varieties have limited acceptance e.g. in Syria and Iraq where there is a high level of adaptation, within the indigenous landraces (Ceccarelli et al. 1995), to environments where drought and salinity are major problems. In traditional farming systems, which are also observed in parts of northern Africa, barley can either be grazed by sheep and goats or grown to produce grain. In times of adequate rainfall, grain may still be produced following initial grazing (Fischbeck 2002).

The use of barley which brings the largest added value, however, is for the production of malt. Although a small proportion of malt and malt products are used in a variety of food applications (Bamforth and Barclay 1993), malt is used, primarily, in the production of alcoholic beverages. This probably began through fermentation, by naturally occurring yeasts, of barley-based foods (Fischbeck 2002), sometime between 3000 and 5000BC (Edney 1996). Experimentation and observation would likely have been used, both to develop early brewing skills (MacLeod 1977) and to select the type of grain best suited for the purpose. Archaeological evidence from Egypt (Palmer 1995) shows grain with a pattern of modification readily recognisable to a modern maltster, suggesting that a process of deliberate malting had been undertaken.

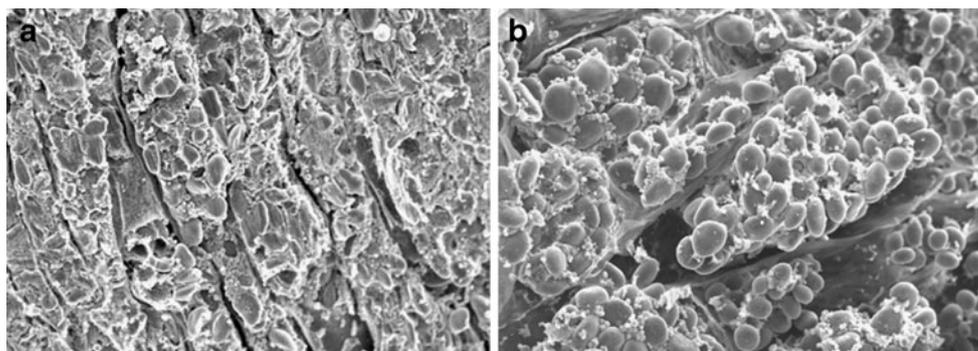
As barley expanded into other parts of the world, including Europe and Asia, malting and brewing followed. Over the subsequent millennia, this process had grown to the extent that global beer production, in the early part of the 21st Century was close to 1.3 billion litre/annum (Fischbeck 2002) requiring around 18 million tonnes of barley. Fischbeck (2002) noted, however, that other unmalted cereals, e.g. maize and rice may be added to some brewing mashes. Various types of adjunct may be deployed in brewing and as these will affect the required characteristics of the malted barley, it is difficult to give a

precise and universal definition of malting quality. One key attribute, however, is hot water extract, i.e. the amount of extractable material obtainable from a given malt, with high values generally indicative of large amounts of fermentable carbohydrate (Bamforth and Barclay 1993). This is particularly important where beverages are made primarily, or entirely, from malt and European malting barleys may, therefore, be characterised by high extract and low protein content (Friedt et al. 2000). This results from traditional selection for plump well-filled grain, with a relatively thin husk (Meredith et al. 1962), which favoured land races that originated in Central Europe (Lein 1964). These barleys were also characterised by a friable endosperm structure (Allison 1986) which may be quantified by grain hardness testing (Allison et al. 1979) or visualised by scanning electron microscopy (Fig. 7). The central endosperm of a malting barley shows the starch granules much less heavily embedded into the protein matrix compared to that of the feed barley.

By contrast, malting barley from the Upper Midwest region of the USA and adjoining provinces of Canada may be six-rowed, with very high diastatic power, i.e. starch-degrading capacity, due to the requirement to break down the starch in the unmalted grain used in large quantity, as an adjunct in brewing. Barley was introduced to North America by settlers from various parts of Europe and high diastatic power is a feature of barley from parts of Scandinavia, where rapid germination and subsequent development is necessary in a short growing season. The link between growing environment and malting characteristics was shown in a comparison between Canadian, Australian and Scottish sites, involving 12 barley varieties and three different malting regimes (Collins et al. 2004). Average values for extract and protein modification were higher under Scottish growing conditions than in the other two environments. The three laboratory malting regimes, designed to reflect commercial practice in the three countries also gave differing values for modification parameters, with the Scottish regime providing more extensive breakdown of both cell wall materials and protein. This is necessary, due to the higher initial extraction temperature used in distilling or ale brewing in the UK, which will denature enzymes required for endosperm modification.

Globally, brewing is by far the major consumer of malt, so Scotland is unique in channelling most malt (around 500,000 tonnes) into malt distilling. Unlike brewing, where malt will be expected to contribute to head retention and flavour, distilling primarily requires malt to drive alcohol production. The major requirement of a distilling barley is, therefore, high alcohol yield, resulting from a high hot water extract with a large content of fermentable material. As alcohol yields are higher in certain spring barley varieties, winter barley cultivation is restricted and typically used for feeding livestock on the farm of origin.

**Fig. 7** Central endosperm of **a** feed and **b** malting barley showing differences in starch grain size and shape



In summary, barley has three main uses globally: feeding to livestock, human food and alcohol production. In all these uses there is a wide range of diversity, reflecting the wide variation and adaptability within the crop. It is also clear that selection, over many millennia, whether by artificial selection or by deliberate breeding has reflected both the utilisation of the crop and the environment in which it is grown. Historically, it is the intrinsic diversity of the crop that has created the diversity of its utilisation. Therefore, it is not only likely to remain an important crop, but could also increase in popularity for growing under increasingly stressed or marginal environments that become unfavourable for other arable crops. Barley clearly has importance predominantly for animal feed and alcohol production but also has direct human food uses, too. Its reliable supply of appropriate quality therefore has implications for industry, agriculture and domestic spheres. Also, its proportionately greater importance in more marginal areas emphasises the welfare implications of its secure supply. Therefore, we now examine issues related to the supply chain to see where the strengths and weaknesses are.

### Supply chain issues

Here we consider key aspects of the supply chain from feed and malting barley through to beer, spirits and food consumption, giving consideration to key issues impacting on it. The main stages of the barley supply chain are shown in Fig. 8, from the supply of production inputs to the consumption of barley within food or beverages. Although the figure embraces a multitude of possibilities across the world, it does not purport to cover all eventualities and differences between developing and developed countries in particular will be noted when appropriate.

### Barley production

Barley dominates other grains in some developing countries having arid and semi-arid climates where it is the only cereal and only staple food resource, particularly in Tibet, Nepal,

Ethiopia, and the Andes on mountain slopes, and often it is the only possible rain-fed crop in north Africa, the Middle East, Afghanistan, Pakistan, Eritrea, and the Yemen. In general, barley is more productive and its yield is more stable against seasonal variation than wheat and most other small grains, so it is preferred by resource-poor farmers in order to reduce the risk of very low yield or crop failure (Akar et al. 1999). Barley flour is often added to wheat flour to make bread.

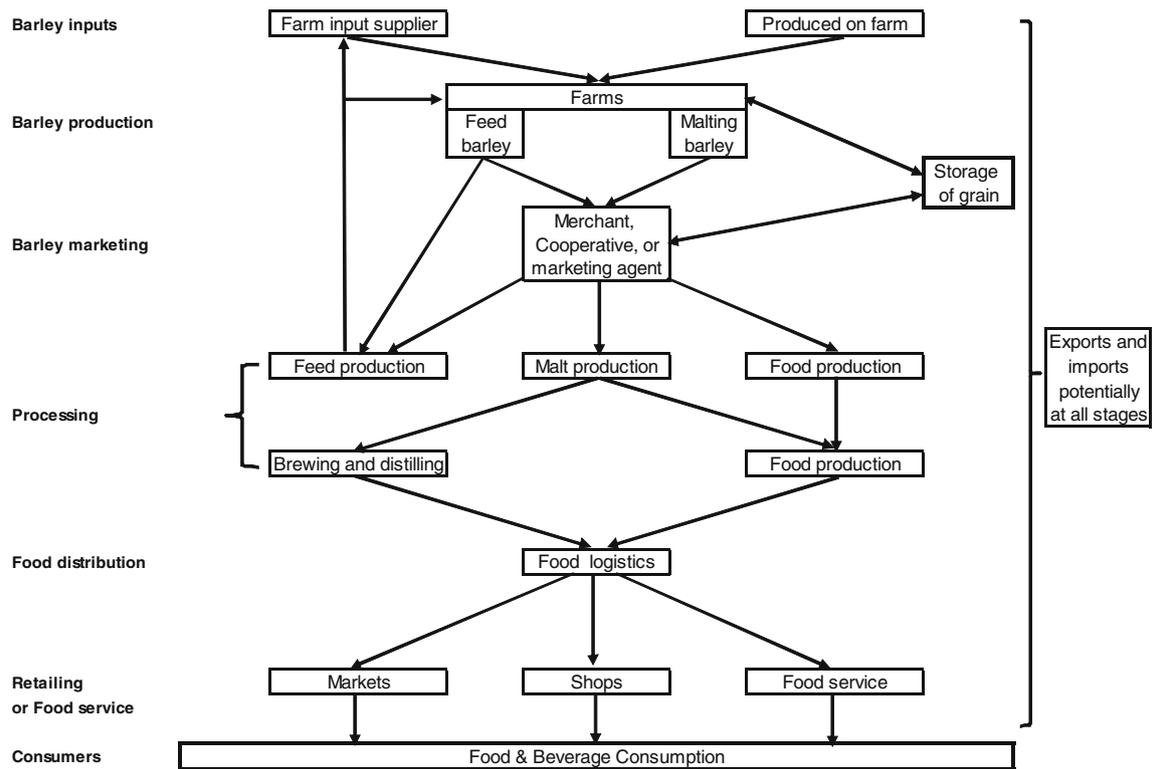
In developed countries, where the supply chain may be more complex, barley is grown predominantly for animal feed (as part of the livestock diet) and malt production, which is mostly directed to the brewing and distilling industries. Feed barley has lower protein and energy levels than wheat but it can be fed in greater quantities. It may be used directly on the producing farm, traded to other farms, or purchased by animal feedstuff producers. This trade may involve a third party of some form, such as a merchant or cooperative and the use of on-farm or off-farm storage.

### Malting barley and malt

Malting barley has special characteristics - as required by the malting, distilling or brewing industries - which lead to malting barley commanding a premium over feed barley. Malting barley is suitable for animal feed and the feed market is thus a fall-back outlet in seasons of excess malting barley supply, but feed barley is normally too high in nitrogen for malting purposes. The key requirements for malting barley are very exacting, and typically cover the following features:

UK requirements are given for illustration (HGCA 2010; MAGB 2010).

- Germination - a minimum Germinative Energy (the percentage of grains that can be expected to germinate under malting conditions). In the UK 98% is required.
- Moisture Content - maltsters usually dry to 12% for long-term storage. In the UK price deductions may apply on grain above 15%.
- Nitrogen content - is a direct indication of crude protein, and in the UK the brewing industry has a requirement for 1.6 to 1.75% Total Nitrogen (TN)



**Fig. 8** A generic representation of the barley supply chain

whilst for export (and use in lager beers) it is 1.7% to 1.85% TN. Barley for distilling malt requires a lower N level, typically about 1.5%. Higher levels to 1.65% TN may be used in difficult seasons.

- Screenings and admixture - small grains are removed using screens of 2.5 mm and 2.25 mm, whilst admixture (stones, dirt and foreign bodies) can't exceed 2%. In most countries, except England and Wales, 90% retention over a 2.5 mm sieve is required.
- Varietal purity - specific varieties are required in loads of a single variety.
- Grain that is physically damaged (e.g. splitting, skinning or insect damage), discoloured or mouldy may also be rejected.

Malting barley has a lower yield than feed barley and in the past the price premium over feed barley was to encourage production and compensate for the lower yields. Nowadays, however, the price is very much determined by global markets and international supply and demand. The supply side of the malting barley market is strongly influenced by climatic conditions, with dry summers or very wet conditions affecting yields and production. The demand side of the market is affected by the state of the beer market, as the global malt industry is very much driven by the global malt market, of which beer usage is the main component. Malt usage worldwide is approximately 22 million tonnes per year of

which 94% goes to beer production, 4% for distillation and 2% for other food uses (Euromalt 2008).

In order to ensure adequate supplies of the correct quality, at a predictable price, maltsters frequently engage in contracting malting barley, thereby securing a significant proportion of their requirements early in the season. The volatility of malting barley markets in recent years has encouraged the introduction (in May 2010) of a malting barley futures and options market by NYSE Liffe in order to assist with the management of the price risks associated with selling and purchasing malting barley. This provides for the trading of 50 tonne contracts for malting barley of EU origin with specified standards of germination, moisture, protein and variety (Euronext 2010).

#### Beer and its impact on the malting sector

Beer consumption growth over the past decade has been mainly in the emerging markets of Asia, South America, eastern Europe and Africa. Between 2002 and 2007 the world market grew by 4.4% p.a. with the Asia/Pacific market growing by 7.4% p.a. to become 32.2% of the global market and Africa increasing by 5.7% to be almost 5% of the market (Plato Logic 2008). In contrast, the mature markets for beer have been in the European Union, North America, Australia and Japan (Braks and Leijh 2005). However, since the start of the global recession in

2007, growth has slowed with the greatest difficulties occurring in Western Europe and North America (together approximately 45% of the world market).

The growth in the emerging beer markets has resulted in major developments in the international malting industry. New capacity has been established in major exporting countries such as the EU25 and Australia so as to strengthen their position in local markets, whilst traditional net importers of malt such as the USA and The Russian Federation have also been investing in new capacity to serve their own markets (Braks and Leijh 2005). In the US the recession has coincided with a shift in beer preferences with imported beer volumes declining by 5.7% in 2007/08, whilst domestic volume rose by 1.6% driven by a demand for light beers, flavoured and craft beers (Montague-Jones 2010).

### Distilling

As far as spirits distilled from barley malt are concerned, the primary product is whisky (or whiskey outside the UK) in its various forms, which has traditionally been produced in Scotland, Ireland, the US and Canada, although manufacture also occurs now in countries such as Japan and India. Whisky (e)y accounts for approximately 12% of the world spirits market by volume (2008) with the dominant product being white spirits (23%) of which vodka is a major component (Drinks International 2009). Nevertheless, because of its premium pricing, whisky is the leading product in the markets in terms of sales value. Key trends in the world market include the growth of local brands, which are seen as nurturing a market and marketing infrastructure which may be utilised by international brands. For example, in India the brand 'Bagpiper' achieves a sales volume worldwide which is close to that of 'Johnnie Walker' (Impact 2009).

As disposable incomes grow in emerging markets such as Brazil, Russia, India and China, it is expected that opportunities will exist for premium brands. Asia – Pacific is the key region for spirits consumption accounting for 49% of total spirit consumption (2008), followed by North America (20%), Western Europe (19%) and Latin America (6%) (Drinks International 2009). In Scotland the whisky sector is a major part of the economy accounting for 9,300 direct jobs (2008) with 3 to 4 times as many in indirect and induced employment, and an estimated Gross Value Added of £1.7bn (2007) (Nicol 2009). Whisky production (distilling) uses approximately 47% of malt per year in the UK (1.5 million tonnes) which derives from (1.8 million tonnes) of malting barley.

### Food use

Whilst the use of malt in food is estimated to represent only 2% of global malt usage, its widespread use in food

production is extremely important to the food industry and consumers. Malts are natural products, an important attribute for present-day health conscious consumers, and they provide flavour, colour, sweetness and moisture, as well as frequently adding specific consumer appeal (e.g. malted breads). As with beer and whisky malts, food malts are highly specific to their intended use, being available in different forms (e.g. solid, liquid, syrup) and colour and with varying nutritional, enzymatic and microbiological content. Malts are widely used in cereal products (e.g. breakfast cereals and cereal bars), bread and bakery products, confectionery, beverages, tablets, pet food, ice cream, pharmaceuticals, sauces, spreads, vinegar, etc. (Malt Products 2010). They are also a useful dietary supplement for the elderly and infants, and in the case of the latter are frequently found in baby foods. As malts are highly specific, they are normally produced by, and purchased from maltsters under contractual arrangements.

### Challenges facing the supply chain

As with supply chains of many agri-food products, a common challenge for the barley chain is how to create value, minimise unproductive costs, and ensure that the requirements of all participants are met whilst delivering the quality and traceability required by the end-user. The achievement of such objectives involves operational and logistical efficiency, as well as good communication and relationships within the chain. Full chain integration has become an important feature of some of the world's most prominent maltsters with strong involvement in seed variety selection, agronomic advice and service to farmers, malting barley selection and purchase, and malt production in-line with the specific needs of customers. Research on the UK malting barley to beer supply chain identifies five factors as characterising the most cohesive chains with strong intra-chain relationships, namely: good communication in relation to logistical issues, problem resolution, the maintenance of product quality and service and intra-chain friendships; compatibility of participants' aims; contractual relationships backed by professional regard and personal bonds; high levels of trust between chain participants and a willingness to solve problems; and commercial benefit for the businesses involved (Revoredo-Giha and Leat 2010).

### Food safety policy

One of the major policy influences affecting the chain over the past 20 years has been that of food safety policy. In Europe, and within the global market, this is seeking to ensure the free movement of safe and wholesome food and drink. In relation to crop-based products, measures have been introduced to ensure stricter standards for food quality

and product hygiene, as well as for plant production and health, and the reduction of contamination risk from external substances.

In the EU, as well as most developed countries, legislation has been introduced to cover all stages of the chain from primary production, processing, transport and distribution through to the sale of safe feed, food and drink, with legal responsibility for ensuring safety resting with the operator at each stage. The responsibility of individual businesses within the EU for food safety has led to the emergence of private-based standards and schemes, which in turn has promoted greater chain co-ordination (Young and Hobbs 2002). Traceability schemes have been put in place partly as a response to a lack of consumer trust and confidence, but also because downstream players require their adoption to meet the requirements of food safety legislation (Albisu et al. 2010).

For example, many UK brewers require their supplying maltsters to operate to the requirements of the Assured UK Malt (AUKM) scheme operated by the Maltsters Association of Great Britain (MAGB), which is a leader in guaranteeing risk prevention, traceability and quality in malt for brewers and distillers. Companies using the mark must reach prescribed standards in: compliance with MAGB's HACCP (Hazard Analysis Critical Control Point) Guide; use of assured grain from recognised and externally audited cereals assurance schemes; the traceability of grain from source to delivered malt; effective and documented quality management systems; and full compliance with all food safety legislation and due diligence in meeting these obligations.

Barley has several different major supply chains, and many more local, small-scale chains. Trade issues are many and varied and often inextricably tied-up with world grain trade matters. However, it is clear that there are many demands on this crop to not only continue to deliver both quantity and quality, but also for improvements. Furthermore, the minor uses demonstrate a wealth of potential that could diversify barley production and thereby increase its value as a reliable food source. Therefore we now examine the genetic potential for such developments.

### **Biodiversity – germplasm resources and potential**

Barley is grown across a very broad range of environments and there are contrasting end users and market demands. These needs were met by local selection and landraces originally, and by crossing and selection in targeted breeding programmes more recently. Greater understanding of the genetics, genomics, physiology and biochemistry of the crop will help identify further opportunities for improving the yield potential of the crop and its tolerance

of abiotic and biotic stresses. However, this will place greater demands on the breeding process, so the genetic resources and their potential for the global barley gene pool must be assessed.

The processes of domestication and selection have resulted in a drastic narrowing of the genetic diversity of crop species including the major cereals (Tanksley and McCouch 1997). The genetic bottlenecks arising from the transitions between wild genotypes to early domesticated germplasm, and from early domesticated germplasm to modern cultivars, has left behind many potentially useful genes. Fortunately, there exists, either within genebanks (ex situ) or in the wild (in situ), an enormous amount of natural diversity for barley. It is estimated that over 400,000 barley accessions are held in genebanks worldwide, of which 290,000 can be classified: 15% are wild relatives, 44% are landraces, 28% are breeding and genetic stocks, and 15% are cultivars (Global Strategy for the ex situ Conservation and Use of Barley Germplasm 2008). The wild progenitor of barley (*H. vulgare* subsp. *spontaneum*) can still be readily found throughout the primary habitats of the Fertile Crescent, stretching from Israel, through Jordan and Syria to south Turkey, northern Iraq and south western Iran, and in many secondary habitats, including Greece, Egypt, south western Asia and eastwards as far as Tajikistan and the Himalayas. As well as wild barley, locally adapted barleys (landraces) are an important feed crop in the Fertile Crescent, covering approximately 5 million hectares of typically marginal, low-input, drought stressed environments. This biodiversity may provide an experimental framework to identify genes with phenotypes that have been exposed to selection during crop domestication, allowing new insights into the evolutionary processes that sculptured the formation of barley as a crop, and providing the most immediate acceptable source of useful genes for conventional breeding programmes. *Hordeum bulbosum* is also a potential source of diversity from the secondary genepool of barley and has been exploited for novel resistance genes (Pickering et al. 2006).

The key to exploitation of germplasm resources is an efficient description of diversity. Until recently, diversity could only be estimated using pedigree and morphological data and agronomic performance. With the advent of DNA-based molecular markers in the 1990s, diversity has been quantified and described in more detail. Early advances in DNA-based technologies focused on the use of Restriction Fragment Length Polymorphisms (RFLPs) to determine levels of diversity. Two companion publications in Crop Science by Graner et al. (1994) and Melchinger et al. (1994) were the first to quantify diversity among a small number of barley accessions. With the advent of PCR, there was a major shift from hybridisation-based methods to PCR-based markers such as Random Amplified Polymorphic DNA (RAPD),

Amplified Fragment Length Polymorphisms (AFLP)s and Simple Sequence Repeats (SSRs) (Powell et al. 1996). These markers have been used in a wide range of diversity studies in cultivated barley (Ellis et al. 2000; Schut et al. 1997; Russell et al. 1997; 2000; Forster et al. 2000; Struss and Plieske 1998; Chalmers et al. 2001; Maestri et al. 2002; Diaz-Perales et al. 2003; Ordon et al. 2005; and many more).

As well as examining genetic diversity, these markers have been used for comparative analysis to provide information about domestication and evolution. Whether single or multiple origins are involved in crop domestication is an important issue of concern in agriculture because patterns of evolution guide strategies for future crop development and conservation. A number of molecular marker studies have compared wild and cultivated barley in order to delineate origin (Molina-Cano et al. 1999; Badr et al. 2000; Saisho and Purugganan 2007; Wei et al. 2005). Badr et al. (2000) stressed a single origin for barley in the Fertile Crescent, while others have placed emphasis on more complex domestication events occurring within the distributions of wild barley (Molina-Cano et al. 1999; Tanno et al. 2002; Allaby and Brown 2003; Morrell and Clegg 2007; Saisho and Purugganan 2007). In a recent study, we have used geo-referenced matched samples of 448 landrace and wild individuals collected from across Jordan and Syria for a more comprehensive investigation of the origins of cultivated barley in the Fertile Crescent. Based on more than 1,100 SNPs (single nucleotide polymorphism) markers with wide genome coverage and matched geographic sampling, our data supports limited origins in the sampled region, but do not preclude additional domestication events elsewhere (Russell et al. 2011).

Combining extensive eco-geographical analysis, including microclimate and soil data with genetic diversity analysis will allow us to identify adaptive variation. One natural site of wild barley located at Mount Carmel in Israel, termed 'Evolution Canyon' has over the last 20 years been extensively studied in this respect (reviewed Nevo 2006). The site is sharply subdivided ecologically into an open park forest of warm, dry tropical 'AfriAsian' savannah and a green, lush 'EuroAsian' temperate, cool slope (Nevo 1995, 1997, 2001). Using microsatellites we observed striking differences in diversity between the slopes, supporting the hypothesis of strong adaptive inter- and intra-slope divergence caused by natural selection (Nevo et al. 2005). In contrast, Hübner et al. (2009) found that SSR diversity observed in a collection of 1,020 wild barleys from 51 populations across Israel was shaped by non-selective forces such as migration, with only a suggestion that temperature and drought played a role in establishing patterns of marker variation.

Examining diversity in landraces provides further insight into the evolution of barley as a crop. Genetically heterogeneous landraces are still the backbone of agriculture in developing countries in marginal environments

(Newton et al. 2010a). During millennia of cultivation under adverse conditions, natural and artificial selection have resulted not in an architecture of a set of different traits, but rather an architecture of genotypes representing different sets of traits. In marginal conditions a population with such a structure is probably the best solution to long-term stability. A large collection of barley landraces from farmers' fields which was made in 1980 and is maintained at the International Center for Agricultural Research in the Dry Areas (ICARDA) (Weltzien 1988), has become a key resource for studying environmental adaptation in the cultivated genepool (Ceccarelli et al. 1987). These stands have been the subject of several diversity studies that have demonstrated geographically-based genetic differentiation (Russell et al. 2003; 2010). This maintenance of population genetic structure in the face of human seed exchange, which could potentially have swamped pre-existing landraces, suggests local adaptation and human selection for plant performance, under varying rainfalls and soil types, has occurred across Jordan and Syria. Other landrace studies have also shown a close association between diversity and adaptive traits in the regions where landraces are still grown, including West Asia and North Africa, China and Tibet (reviewed and references in Newton et al. 2010a; Gong et al. 2009; Hadado et al. 2010).

The potential of these resources has as not yet been fully realised, but with the considerable genomics efforts in barley that are currently underway, we will soon be able to mine this treasure store of potentially useful alleles for crop improvement. Given the stress-tolerance and adaptability to both climate and a wide range of industrial and food uses, such resources will be invaluable for accessing traits for enhancing this crop's utility for a changing climate.

Whilst we clearly show the genetic potential of barley, this underlines the imperative to preserve the genetic resources and make them available. This requires considerable investment and international co-ordination as well as targeted use of technologies to access and assess this potential (Newton et al. 2010a). Furthermore, our understanding of the genetic basis of the agronomic and physiological potential needs to increase. The modern genomic tools are beginning to facilitate such progress whereby we make better use of the genetic potential. In the next section, we evaluate the physiological and agronomic potential.

### **Agronomy and crop physiology: the potential for sustainable yield production**

#### **Crop production system**

There is wide diversity in the systems used for barley production throughout the world. Systems are tailored to

the climatic and soil conditions that prevail in a particular region and the end user requirements of the crop. In this section, we describe just one system to illustrate how agronomic factors can be varied to meet the yield and grain quality targets of the grower. The example given is for barley production in the cool temperate climate of the UK with its associated high yield potential.

Barley can either be sown in the autumn season or the spring season. If sown in the autumn, then vernalisation genes are generally used to prevent crops from flowering too early and suffering frost damage at flowering (anthesis) and consequent yield loss. Alternatively, so-called facultative types, which do not require long-term cold-chilling to satisfy a vernalisation requirement but do have some cold hardiness genes, may be deployed and have the advantage of also being suitable for spring sowing. Autumn sowing is typically done in September or early October, whilst spring varieties can be sown from January to April depending on the latitude, cold hardiness of the variety and whether the soil conditions are suitable for cultivation and the passage of machinery. In addition to a division according to sowing season, barley can also be divided into two different morphological types based upon different ear types (two and six-rowed). Different alleles at two major vernalisation loci, *Vrn1* and *Vrn2*, generally differentiate between winter and spring habit although variation at *Vrn3* may also play a part (Distelfeld et al. 2009). Different alleles at two morphological loci, *vrs1* and *Int-c*, generally differentiate between two- and six-rowed spike types (Lundqvist et al. 1997). Whilst *Vrn2* and *Int-c* are located on the same chromosome, they are on different arms and so will segregate independently and the other two *Vrn* loci are located on different chromosomes (Lundqvist et al. 1997). There are, therefore, no genetic barriers preventing breeders from generating any of the four genotypic classes.

Under high input situations, barley is generally sown by a seed drill at a rate calculated to produce around 250 established plants per m<sup>2</sup> for the winter crop and 300–350 for the spring crop. The target is sowing at a depth of 2–3 cm into a fine seed bed with sufficient moisture for germination and establishment. Emergence is still heavily dependent upon temperature and benchmarking studies have shown that it takes approximately 150° days (thermal time) from sowing to 50% crop emergence of autumn-sown varieties (HGCA 2006). Once emerged, the high input management strategy is designed to produce a fertile shoot number of around 800 per m<sup>2</sup> in the UK and rapid and prolonged canopy formation during the active phase of plant growth. These aspects are usually achieved by the use of application of N-fertiliser prior to stem extension to encourage tillering, if necessary, and then further applications at the start of stem extension to promote tiller survival and maintain canopy formation. Phosphorous and potassi-

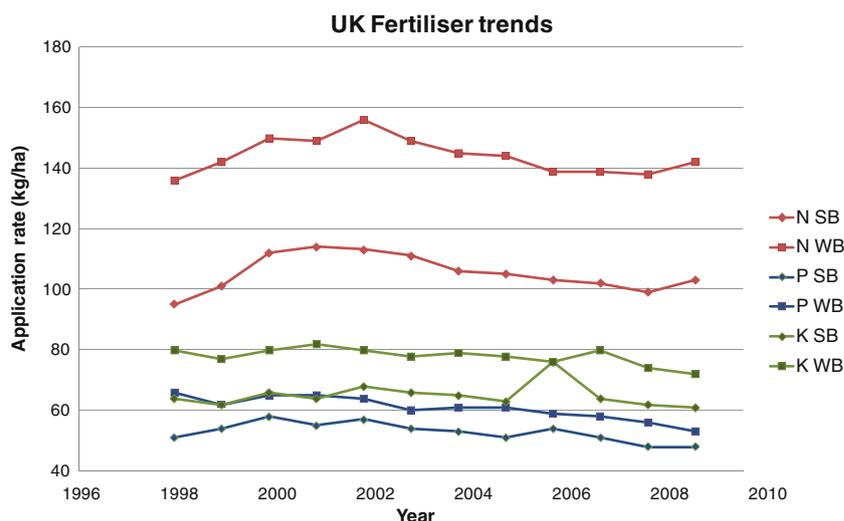
um are generally applied early in the form of a compound fertiliser, which can often also include sulphur. The trends in average total application rates to UK barley crops show little change over a 12 year window (Fig. 9). There was a small increase in rate of application of N to both winter and spring crops between 1998 and 2002, but increasing costs of fertilizer and a greater awareness of the pollution problems associated with inefficient capture of N by crops has forced rates back down. There has also been a slight decline in the rate of phosphorus applied to winter crops.

The average application of nitrogen to winter barley is some 50 kg ha<sup>-1</sup> greater than that to spring barley, reflecting its greater yield potential. The potassium and phosphorous application rates are also slightly higher in the winter than the spring crop, but not by as much. In the winter crop, the application rate of N is 30–50 kg ha<sup>-1</sup> lower when farmers target the malting market, which reflects the maltsters' desire to purchase barley with a grain nitrogen content of less than 1.85%. The application of nitrogen to the spring malting crop is 20 kg ha<sup>-1</sup> less than to the feed crop.

The application of fertiliser will also increase the height and weight of the crop, rendering it more prone to lodging. Where there is a lodging risk, farmers will apply plant growth regulators to reduce crop height and produce stiffer straw. These are typically applied between the start of stem extension and ear emergence. Many spring varieties possess semi-dwarf genes that reduce overall plant height without penalising the yield potential and the use of plant growth regulators on them is much less than on the winter crop, where major dwarfing genes have generally not been deployed.

During the growing season, current high input regimes utilise fungicides to prevent the build up of foliar diseases in the crop. This is to ensure that the crop maintains the large canopy area created by the appropriate seed rate and fertiliser inputs. Excessive build up of foliar diseases not only reduces the yield of a crop but may also reduce the grain quality by increasing grain nitrogen content and the amount of grain that passes through (screenings) the standard sieve for grain trading, which is generally 2.5 mm in Europe. After anthesis, there is a period of grain filling when the grain accumulates dry matter. The length of this period depends upon the climate but can take around 40 days under the cool moist conditions of the UK. This is then followed by a ripening period, during which the canopy senesces further and the grain moisture content declines until the grain is ready to harvest. Whilst grain is generally traded on the basis of 15% moisture content, farmers will cut crops at moisture contents up to 25% and then dry them on farm, especially if the harvest weather is unfavourable. The longer harvest is delayed, the more the crop suffers from spoilage under adverse weather and so

**Fig. 9** The trends in average total nutrient application rates to UK barley crops. *N* nitrogen, *P* phosphorus, *K* potassium, *SB* spring barley, *WB* winter barley



may be rejected for malting. The premium for malting barley can be sufficiently high and, provided it can be secured, will more than compensate for the drying cost.

After harvest, drying and treatment, if necessary, the grain may be stored on farm before being moved off farm by the purchaser or used as part of a feed ration in a mixed farming exercise. When storing on farm for periods exceeding several weeks, care must be taken to ensure that the moisture content of the grain is sufficiently low to prevent localised heating and spoilage as well as infestation by pests such as weevils. Depending upon the type of farm, the residual straw is either chopped and spread on the stubble during combining or is baled-up. In the case of the former, it is then incorporated into the soil along with the stubble during preparations for the next crop. If it is baled, it is transported off the field and used or sold as livestock bedding and/or a low grade feedstuff.

#### Barley physiology – yield potential

Farm yields of barley vary enormously by location. Average national yields of barley producing countries for the years 2000–2009 ranged from 0.25 to 7.32  $\text{tha}^{-1}$  (FAO statistics 2010). In part, the range reflects regional differences in the climatic potential yield of the crop and in part the extent to which biotic and abiotic factors reduce the growth of the crop so that its yield potential is not realised. Yield potential is usually defined as the yield of adapted varieties in a given location where water and nutrients are non-limiting and weeds, pests and disease are absent. To increase food security, progress is required to both increase the yield potential and to close the gap between attained and potential yield through better control of weed, pests and diseases and the alleviation of abiotic stress (Slafer et al. 2005).

The yield potential (YP) of a crop can be expressed quantitatively as a function of the amount of photosynthet-

ically active radiation intercepted by the canopy (RI), the efficiency with which energy from the radiation is converted into dry matter (radiation use efficiency, RUE) and the fraction of the dry matter partitioned into harvested parts (harvest index, HI) (Reynolds et al. 2005).

$$YP = RI \times RUE \times HI \quad (1)$$

High yields of barley are possible when each of these components is maximised. Typically, high yielding environments are those with high radiation receipts and where temperatures permit a long growing season. Thus grain yields as high as 9.4  $\text{tha}^{-1}$  (@ 100% dry matter) have been reported for two-row winter barley crops grown in the temperate maritime climate of the UK (Bingham et al. 2007). The relative simplicity of equation 1 masks the dynamic nature of RI, RUE and assimilate partitioning; it is how these processes vary and interact through the season that determines the yield potential (Reynolds et al. 2005). Similarly, biotic and abiotic stresses, including water and nutrient deficiencies may reduce yield via effects on one or more of RI, RUE and HI depending on the nature of the stress and its timing in relation to crop development (Bingham et al. 2009).

In common with other cereal species, the growth and yield formation of barley can be considered in two main phases. The first, from crop emergence to anthesis, establishes the machinery for resource capture and assimilation (i.e. the canopy and the root system) plus the yield bearing structures (potential grain sites). The second, from anthesis to maturity, involves the development and filling of the grain. Dry matter for grain filling is derived from post-anthesis photosynthetic activity and remobilisation of storage reserves deposited before anthesis. Within the constraints set by the environment, crop management is usually designed to try and maximise the capacity for both

dry matter production (source) and its storage in the grain (sink) and to keep the capacities of source and sink in reasonably close balance (Slafer et al. 2005; Bingham et al. 2007).

The proportion of the incident radiation that can be intercepted by the crop is governed by the size and structure of the canopy. Canopy size (green area) is determined by the number of main shoots and tillers produced and the number and expansion of their individual leaves. Maximum canopy area is reached at around anthesis after which the canopy begins to senesce. The relationship between canopy size (GAI; green area index; green area per unit ground area) and radiation interception is non-linear and a barley canopy with a GAI of 5 intercepts around 95% of incident radiation depending on the canopy architecture and its light extinction coefficient (Bingham and Topp 2009). Canopies with prostrate leaves tend to intercept more radiation with a given canopy area than those with erect leaves, but the effect is greatest when the canopy area is small (Angus et al. 1972; Bingham and Newton 2009). Although barley varieties can differ widely in their height, leaf and tiller growth habit, the effect on radiation interception is often limited in canopies of adequate GAI. Thus the greatest scope for increasing the amount of radiation intercepted is to improve the rate of canopy establishment early in the season and to prolong its green area during grain filling.

A range of agronomic factors can be used to manage the growth rate, peak area and duration of the canopy, including sowing date, seed rate and N fertilizer regime. However, the climatic conditions and the cultivar's response to them will determine the limits within which these management practices can be manipulated. For example, depending on the region, sowing date may be dictated by the risk of frost, the winter-hardiness of the variety, its vernalisation requirement for flowering, ground conditions for tillage and sowing, and the availability of soil moisture for germination and seedling establishment. Similarly, avoidance of adverse conditions at sensitive times during later development, for example, high temperatures or water deficits at flowering, may necessitate the selection of rapidly developing varieties of lower yield potential. Climate change may offer new opportunities for increasing the yield potential of barley in some regions such as Finland, where warmer temperatures will extend the thermal growing season and may enable winter varieties to be grown (Peltonen-Sainio et al. 2009). In other warmer, drier regions the available growing season may be reduced unless genetic improvement to reduce sensitivity to high temperature and water stress can be made. Alternatively, facultative or winter barleys may be grown in such areas to escape the warmer, drier environment. In addition to genetic improvements to extend the growing season, several seedling traits, with high heritability, have been

identified that might improve the rate of crop establishment and early canopy growth in wheat (Richards 2000); similar traits are likely to be effective in barley. Large genetic variability can be found in barley for the rate of leaf appearance and tillering characteristics (Abeledo et al. 2004; Borràs et al. 2009).

Radiation use efficiency is the quotient of dry matter gain per unit of intercepted (or absorbed) radiation. It is usually measured and expressed in terms of above ground dry matter and is, therefore, the net outcome of dry matter assimilated in photosynthesis minus the costs of shoot growth and maintenance respiration plus the dry matter translocated to the roots. Theoretical estimates of the RUE for cereals such as wheat and barley are 2.7–4.7 gMJ<sup>-1</sup> of PAR (photosynthetically active radiation) (Reynolds et al. 2000). In well-managed barley crops grown in favourable conditions, measured values have been reported in the range 2.0–3.7 (Bingham et al. 2007; Bingham and Topp 2009), and thus there may be scope for some improvement in RUE to increase yield potential. However, there is little evidence of significant improvement in RUE from breeding to date, and the prospects for an increase via a greater specificity of Rubisco for CO<sub>2</sub> and reduction in photorespiration are distant (Reynolds et al. 2000). Modification of canopy architecture by selection for an erect leaf habit could, theoretically, increase RUE by reducing the extent to which the upper leaves are saturated with light and by allowing more light to penetrate to the lower leaf layers (Angus et al. 1972; Reynolds et al. 2005). However, in high radiation environments the benefits may only be observed in large canopies (Reynolds et al. 2000). In smaller canopies, benefits from the altered distribution of light within the canopy associated with an erect leaf habit may be offset by a reduction in the total amount of radiation intercepted (Bingham and Newton 2009).

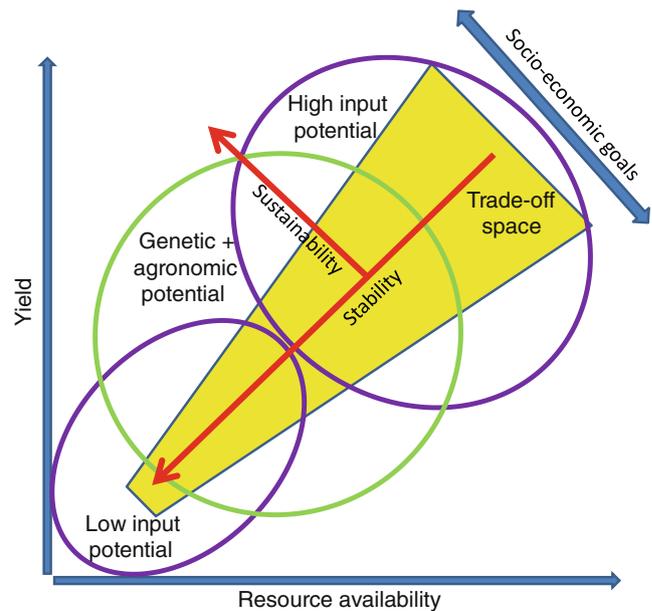
The greatest potential for improvements in RUE appears to lie with alterations in the source-sink balance of the crop. The yield of barley in a wide range of environments is considered to be limited by the number and capacity of grains to store dry matter (sink-limitation) rather than the availability of assimilate for grain filling (source-limitation) (Arisnabarreta and Miralles 2008; Bingham et al. 2007). A limited sink capacity can lead to a feed-back inhibition of photosynthesis thereby reducing RUE below its potential. It has been suggested that increasing the number of grains set could lead to an increase in harvest index and yield potential, with the additional assimilate requirement for grain filling being met by a relief of feedback inhibition of RUE. Evidence for feedback inhibition of RUE during the latter stages of grain filling has been presented for winter barley crops grown at several sites in the UK (Bingham et al. 2007). Moreover, increasing the number of grains per ear in spring wheat was found to increase rates of flag leaf

photosynthesis under irrigated conditions in the high radiation environment of Mexico (Reynolds et al. 2005). It has been proposed that the genetic improvement of grain number in barley, as in wheat, might be achieved by increasing dry matter partitioning to the ear during the period of stem extension. This is a period when significant spikelet mortality occurs, a process that is sensitive to incident radiation and potential assimilate supply (Arisnabarreta and Miralles 2008, 2010; Borràs et al. 2009). An increase in assimilate supply to the ear might be achieved by extending the duration of the stem elongation phase without altering the total time to anthesis through selection for higher sensitivity to photoperiod (Slafer et al. 2005; Borràs et al. 2009).

Increasing the yield potential of barley will increase the demand for water and nutrients unless there are corresponding increases in water and nutrient use efficiency. Management strategies designed to maximise yield potential can lead to the profligate and inefficient use of soil resources and can result in a reduction in yield stability in environments where the supply is variable and unpredictable. Clearly this is counter-productive in terms of efforts to improve food security. Approaches are therefore required to increase resource use efficiency so that yield potential can be increased with lower inputs of water and fertilizer. Trade-offs between resource supply, yield potential, yield stability and grain quality exist that are shaped by socio-economic considerations. For example, in order to achieve the low N grain concentrations required for distilling malt, N fertilizer applications are restricted with the loss of some yield (yield less than potential). Similarly in environments where the supply of water is unpredictable, practices that help conserve water and maintain stability of yield across years, but at lower potential levels, may be preferred to those that maximise yield potential in favourable years when water is non-limiting (Fig. 10).

### Nutrient use efficiency

At its simplest, the concept of nutrient use efficiency (NUE) provides a measure of the output per unit of input. In practice, though, like many measures of biological efficiency, there are a number of components that contribute to the overall efficiency and several definitions that are used (Ladha et al. 2005). There is ample evidence of intraspecific variation in NUE in barley and thus potential for improving resource use efficiency through breeding. However, progress requires the development of an understanding of the phenotypic traits that govern NUE, their genetic control and their expression in a range of environments. Large genotype-by environment interactions are often found in measurements of NUE and an understanding of



**Fig. 10** Trade-off concepts in yield and resource availability defining drivers for stability and inputs relationships. Genetic and agronomic potential (interactive) will influence both the position and slope of the relationship between the two axes which define the trade-off space. Red arrows indicate the direction of increasing stability and sustainability. The drivers of agronomic and genetic potential improvements are socio-economic

the basis of these interactions would allow variety characteristics to be matched more effectively to environmental conditions (soil and climate) and agronomic practice.

Most studies on nutrient use efficiency consider only one or two nutrients (typically N and/or P) so that it is unusual to have estimates of use efficiency for a suite of nutrients. The focus on P and N arises because of global concerns over diminishing supplies of P and the energy costs associated with the production of N fertilizers. In addition, inefficient use of P and N fertilizers can cause problems with pollution.

Overall P and N use efficiency results from the combined efficiencies of nutrient capture and utilization in growth. Nutrient uptake is dependent on the growth and distribution of the root system and its response to the local availability of nutrients. Genotypic variation exists in root characteristics which offers scope for the genetic improvement of nutrient capture, but growth is also influenced strongly by soil properties (including strength, temperature and nutrient availability) and soil management techniques (including tillage, drainage and fertilizer applications) which may contribute to the large genotype-by environment interaction observed in NUE. Moreover, because the relative mobilities and distribution of phosphate and nitrate in the soil differ (phosphate is far less mobile and concentrated in the upper soil layers compared with nitrate), the root traits sought for efficient uptake of P may differ

from those for N. Thus a compromise may need to be found when selecting root systems for efficient nutrient capture.

Proliferation of roots around fertiliser granules and in nutrient-rich zones is commonly observed. The response depends on the nutrient ion, the form of fertiliser and its reactions in the soil, and also the plant species so that root proliferation in the enriched zone with suppression elsewhere is not a universal response (Robinson 1996). Robinson (1996) demonstrated that the production of additional lateral (branch) roots was highly beneficial in the exploitation of locally available P principally because of its low diffusion coefficient (low mobility).

Production of root hairs is another means by which root systems can access P. Gahoonia and Nielsen (1997) and L. K. Brown et al. (SCRI unpublished data) have demonstrated that differences in the length and density (number per mm of root) of root hairs could affect P uptake by barley cultivars. Subsequent studies with a hairless root mutant of barley and wild type barley have confirmed the importance of root hairs in a low-P soil, and the fact that both phenotypes grew and reproduced normally with a high nutrient supply may allow identification of candidate genes for root-hair formation in cereals (Gahoonia and Nielsen 2003). In field experiments barley genotypes with long root hairs (about 1 mm) produced similar grain yields (~6 t/ha) irrespective of the amount of P fertiliser applied (0, 10 and 20 kg/ha) while genotypes with short root hairs (about 0.5 mm) had lower yields when no fertiliser P was applied but responded to applications of P fertiliser (Gahoonia and Nielsen 2004).

The importance of different root system architecture, in response to soil conditions or as a consequence of genotypic differences in root growth, for nutrient uptake is not well understood except in the most general terms. The relative distribution of roots in different soil layers can influence the acquisition of resources, such as P, that are largely confined to shallow soil layers. Liao et al. (2004a) crossed a deep-rooted and a shallow-rooted genotype of bean to obtain recombinant inbred lines and found that lines with shallow root systems demonstrated the highest P acquisition efficiencies. There appears to be robust genetic variation for root architectural traits in barley that could influence the distribution of the root system in the field (Wahbi and Gregory 1989; Forster et al. 2005; Hargreaves et al. 2009; White et al. 2009). Barley, like other plants, employs various strategies to mobilize and acquire Pi from the soil including (1) acidifying the rhizosphere, (2) secreting low-molecular-weight organic anions and phosphatase enzymes into the soil to mobilize Pi from inorganic and organic P sources, (3) increasing the abundance of Pi transporters and (4) fostering symbiotic relationships with mycorrhizal fungi, that might be amenable to modification to improve P uptake efficiency (White et al. 2005; White

and Hammond 2008). In addition to the variation in P uptake efficiency described above, variation has also been found in the efficiency with which P is utilized in growth (physiological P use efficiency). Quantitative trait loci (QTL) for physiological P use efficiency have been identified in barley, but they appear to be sensitive to agricultural practice and to differ between spring and winter varieties (George et al. 2010).

Genotypic differences in N uptake have been demonstrated in many species but the reasons for such differences are not fully understood. Both plant growth rate and soil N availability play a role in addition to any inherent differences in internal N use efficiency (Devienne-Barret et al. 2000). In NW Europe, barley breeding for greater yield has increased both the nitrogen uptake and nitrogen utilization efficiency (Bingham et al. 2010). The latter was associated with a greater partitioning of dry matter and N to the grain; the mechanisms underlying the increase in N uptake efficiency are not currently known. Liao et al. (2004b) compared growth and N uptake of a vigorously-growing breeding line of wheat with four commercial cultivars in field and column experiments and found that uptake efficiency at tillering was 16–22% greater in the breeding line than three of the four cultivars. They concluded that, on the sandy soils on which they worked, the inclusion of traits leading to vigorous early shoot and root growth into breeding programmes for wheat could result in improved N uptake efficiency and reduced N leaching. Modelling studies have suggested that in contrast to P, a deeper root system is beneficial for N uptake in leaching environments (Dunbabin et al. 2003; King et al. 2003). Also in contrast to P uptake, the value of proliferation of lateral roots for efficient uptake of N has been questioned (Robinson 1996). Hodge et al. (1999) and Robinson et al. (1999) suggested that root proliferation was only important for N capture when plants were in competition with other species for organic patches containing a finite supply of mixed N sources. In an agricultural context, then, root proliferation may benefit N capture by plants when the plant is in a mixed cropping system and when N is released slowly (Hodge 2004). Such systems would include the increasingly popular barley-legume intercrops.

The requirement for the continued development of sustainable cropping systems will place even greater emphasis on the timely application of the spatially appropriate level of nutrients. The integration of fertilisers and organic manures and waste products to aid sustainability will be a challenging area of future research and require a greater understanding of the biological processes in soils that influence nutrient availability. Genetic manipulation via standard breeding or transgenic approaches offer novel means of studying and understanding nutrient acquisition from soils and complementary means of improving agro-

onomic and recovery efficiencies in addition to soil management technologies.

### Water use efficiency (WUE) and barley

Barley is cultivated in many climatic regions of the world and the most common stress limitation to yield is a lack of water during the growing period (Ceccarelli et al. 2010; Tester and Bacic 2005). The nature of water stress can, however, vary in rain fed growing areas, from periodic transient stress to crops having to complete their entire growth cycle on stored water (Salekdeh et al. 2009). At the same time, soils can be deficient in nutrients, saline or the crops more susceptible to pest and disease attack (Richards 2006). Drought conditions are therefore unpredictable, complex and make the exact functional impact on crop yield difficult to simulate and interpret (Richards 2006). It also makes the traits that confer drought tolerance difficult to unravel as they appear to be both genotype and site specific.

One strategy that has been widely studied, with a view to helping breeders and growers to combat drought conditions, is to evaluate physiological efficiency mechanisms that confer low water use and high yields (Reynolds and Tuberosa 2008). The aim is to increase crop water use efficiency (Richards et al. 2002) or 'more crop per drop' (Kijne et al. 2003). To screen cultivars based on functional traits that cause the plant to lose less water involves measurements of gas exchange, assimilatory area and the timing of critical crop growth stages. The  $\Delta^{13}\text{C}$  discrimination proxy measure of WUE in  $\text{C}_3$  plants has been used successfully to select for high yielding wheat (Condon et al. 2002) and barley (Anyia et al. 2007) cultivars growing on stored water. It is, however, a relatively expensive analytical measurement to use in breeding programmes and cheaper surrogates that are related to  $\Delta^{13}\text{C}$  have been studied which include ash content (Monneveux et al. 2004) and chlorophyll concentration (Bort et al. 1998) of shoot material in cereals to screen for WUE genotypes. Slow early canopy expansion and reduced rates of internal water conduction are other areas of physiology that have been identified that allow optimised seasonal distribution of stored soil moisture (Richards 2006) and which can translate into high WUE for cereal grain yield. Selecting for high WUE does not, however, work for all drought situations and cultivars that exhibit high WUE on stored water or irrigated sites may not perform well in rain fed regions where drought could occur at any time during the crop growth cycle (Condon et al. 2002). Critically, lack of water availability during the reproductive phase of growth, in particular grain filling, can severely depress barley yield (Samarah et al. 2009). Favourable leaf water relations and canopy temperatures that are maintained under drought

conditions can be associated with low WUE (Pinheiro et al. 2005; Zong et al. 2008; Blum 2009). However, the ability of plants to maintain transpiration under drought conditions in the field has been associated with deep root systems and continuous water extraction (Blum 2009). Other avoidance strategies include a shortened growth cycle thus negating excessive soil water deficits during grain filling, particularly on stored soil water (Araus et al. 2002). WUE is, therefore, not the only trait considered for the maintenance of yield under drought conditions. The effective use of water (EUW) by enhanced rooting has also been identified as significant for high yields in water scarce environments (Blum 2009).

Whilst phenotype selection for drought tolerance has achieved some success, other approaches are being developed that will give more rapid development of high stable-yielding cultivars under water scarce conditions. The identification of quantitative trait loci (QTLs) and candidate genes can provide new insights into the underlying biochemical and biophysical mechanisms that constitute drought tolerance (Tuberosa and Salvi 2006; Fleury et al. 2010). These approaches aim to combine physiological measurement with molecular genetics to identify high yield traits under water-scarce soil conditions. These studies need to be carried out under realistic field conditions with diverse barley plant material, i.e. using adapted and non-adapted landraces, old and modern varieties, in the presence of multiple biotic and abiotic stresses including drought (von Korff et al. 2008; Fleury et al. 2010). It is envisaged that these techniques will provide more rapid development of appropriate drought tolerant crops compared with conventional breeding and phenotype selection.

### Threats: abiotic stresses

A number of abiotic factors can limit both the climatic yield potential and the attained yield of barley. These limitations represent a threat to the security of barley production and a major research effort is focussed on minimising their impact on crop growth. Climatic factors that affect the duration of the growing season for barley include extreme temperatures and rainfall patterns. At high latitudes, barley production is restricted by low temperatures. The winter hardiness of barley is often associated with frost tolerance, which has been defined as the ability of plants to survive freezing temperatures, prevent damage to vegetative tissues, and minimize negative effects on future yield potential (Prášil et al. 2007; Galiba et al. 2009). Frost tolerance is a complex trait involving many physiological mechanisms and biochemical processes (Prášil et al. 2007; Galiba et al. 2009). Two linked QTL for frost tolerance (Fr-H1 and Fr-H2) have been identified on chromosome 5H (Francia et al.

2004; 2007). The Fr-H1 QTL co-locates with the Vrn-H1 QTL, which contains the transcription factor HvBMA5, one of three genes controlling vernalization in barley (Francia et al. 2004; von Zitzewitz et al. 2005). The Fr-H2 QTL co-locates with QTL for the expression of several cold-regulated (*HvCor*) genes and contains at least eleven C-repeat Binding Factor (*HvCBF*) genes (Francia et al. 2004; 2007; Stockinger et al. 2007; Galiba et al. 2009). The CBF genes are transcription factors that control the expression of *HvCor* genes, and are also known as Dehydration Responsive Element Binding (DREB) factor genes. The current hypothesis for the molecular basis of frost tolerance is that both a regulatory and a structural component act together to improve tolerance (Stockinger et al. 2007; Galiba et al. 2009). It has been proposed that the first component is the winter allele of HvBM5A at the Fr-H1 locus and that the second component is the allelic constitution and expression of the HvCBF genes at the Fr-H2 locus (Stockinger et al. 2007; Akar et al. 2009; Fricano et al. 2009; Galiba et al. 2009). These major QTL can be used to develop molecular markers suitable for marker-assisted selection (MAS) of frost-tolerant barley genotypes, which could ultimately extend the climatic range of barley production.

In drier regions, barley production can be restricted by the occurrence of drought. Drought tolerance is also a complex trait, whose expression is conditioned by the precise environment and water availability (Nevo and Chen 2010). Many physiological processes are implicated in drought tolerance, including seedling vigour, root development, tillering, flowering time, water use efficiency, leaf waxiness, the presence of awns, leaf water potential, relative water content (RWC), osmotic adjustment, accumulation of osmolytes and ABA production (Cattivelli et al. 2002). Many QTL affecting these traits have been identified (e.g. Cattivelli et al. 2002; Diab et al. 2004; Forster et al. 2004; von Korff et al. 2006). Trials of diverse barley germplasm and populations derived from biparental crosses grown across a range of drought environments have also identified numerous QTL affecting yield under these conditions (Forster et al. 2004; von Korff et al. 2006; Comadran et al. 2007). In addition, there is considerable genetic diversity for drought tolerance in wild barley (*H. vulgare* subsp. *spontaneum*) that can be used directly to improve the drought tolerance of cultivated barley (Nevo and Chen 2010). Traits associated with drought tolerance in wild barley include deeper seed dormancy, the production of fewer, longer seminal roots with greater gravitropism, a higher capacity for osmotic adjustment, desiccation tolerance of seedlings, lower stomatal conductance, and yield stability (Nevo and Chen 2010). Several chromosomal loci in wild barley have been suggested to confer drought tolerance. These include dehydrin genes (*Dhn1*, *Dhn6*), whose expression is associated with drought tolerance

(Suprunova et al. 2004), *Hsdr4* (*H. vulgare* subsp. *spontaneum* dehydration responsive 4), which is mapped to the long arm of chromosome 3H within a region harbouring a QTL for RWA and a QTL for osmotic adjustment in cultivated barley (Diab et al. 2004; Suprunova et al. 2007), *EIB11*, a gene located on barley chromosome 3H that affects cuticle formation, water loss and drought tolerance (Chen et al. 2009) and various QTL from *H. vulgare* subsp. *spontaneum* wild barley that improve barley yield under drought conditions in the field (Forster et al. 2004; Talamè et al. 2004; Inostroza et al. 2009). Dehydrins are involved in these and several other stress responses in barley (Kosová et al. 2010).

Over 40% of the world's arable land suffers from soil acidity (FAO 2010). Crop production on acidic soils is primarily restricted by Al and Mn toxicities (Mengel et al. 2001; Fageria 2009). Excessive Al<sup>3+</sup> at the root tip inhibits root elongation and alters root architecture (Mengel et al. 2001). Plants reduce Al<sup>3+</sup> in the rhizosphere by secreting organic acids or mucilage, raising rhizosphere pH, and binding Al to cell wall components (Ma et al. 2001; Delhaize et al. 2007). Aluminium entering plant cells is rendered non-toxic by its sequestration in the vacuole complexed with organic acids (Ma et al. 2001). Differences between barley genotypes in their Al-tolerance have been attributed to differences in the amounts of citrate released at the root apex, which is associated with allelic variation at the Alp locus on chromosome 4H (Ma et al. 2004). A transport protein from the multi-drug and toxin extrusion (MATE) family is thought to underpin this trait (Delhaize et al. 2007). In addition, transgenic barley plants expressing *TaALMT1*, a malate-efflux transporter from wheat, have improved Al-tolerance (Delhaize et al. 2004). Manganese toxicity is thought to be a consequence of increased oxidative damage to plant tissues (Mengel et al. 2001). Barley is relatively sensitive to Mn-toxicity, although large differences in Mn-tolerance exist between barley genotypes (Fageria et al. 2011). Chromosomal loci associated with these differences have not been identified to our knowledge.

It is estimated that up to one third of the world's agricultural soils are calcareous and susceptible to soil alkalisation (FAO 2010). The phytoavailability of several essential mineral elements limits crop production on such soils. These elements include P, whose concentration as phytoavailable orthophosphate rarely exceeds 10 µM (White and Hammond 2008), Fe, Zn, Cu and Mn (Mengel et al. 2001; He et al. 2005; Broadley et al. 2007; Fageria 2009; White and Greenwood 2011). Factors influencing the uptake efficiency of P have been discussed above. Barley genotypes also vary in their ability to acquire and utilise essential cations (e.g. Graham et al. 1983; Jokinen and Tahtinen 1988; Zhu et al. 2002; Lombnæs and Singh 2003; Hebborn et al. 2005; Karaman et al. 2007; Lonergan et al.

2009; White and Broadley 2009; Karaman et al. 2010). Several QTL for the acquisition and physiological utilisation of Zn have been identified (Loneragan et al. 2009). The release of phytosiderophores and organic acids coupled to a more extensive root system or interactions with mycorrhizal fungi, and more efficient physiological utilization of essential elements, are thought to form the physiological basis for plant tolerance of low Fe, Zn, Cu and Mn phytoavailability. Deficiencies in these elements can also be remedied by the application of mineral fertilisers (White and Broadley 2009; White and Greenwood 2011).

Crop production is restricted on saline or sodic soils by Na, Cl or B toxicities (White and Broadley 2009; Munns and Tester 2008; Reid 2010). These soils occur throughout the world, but mostly in the arid subtropics where rainfall is low. Sodium toxicity is thought to limit crop production on up to 15% of all potential agricultural land (Munns and Tester 2008). Crop yields on saline soils can be improved by management practices that reduce  $\text{Na}^+$  concentrations, or the ratio of  $\text{Na}^+$  to other cations, in the soil solution, and by the cultivation of Na-tolerant crops. Crop yields on soils with high B phytoavailability can be improved by management practices that reduce B concentrations in the soil solution and by the cultivation of B tolerant crops. Several QTL affecting Na and B accumulation have been identified in barley (Cattivelli et al. 2002; Sutton et al. 2007; Loneragan et al. 2009; McDonald et al. 2010). Barley is a relatively salt tolerant crop. In both wild and cultivated barley, salt tolerance is largely conferred by restricting  $\text{Na}^+$  uptake by roots and  $\text{Na}^+$  movement to actively growing shoot tissues (Munns and Tester 2008; Nevo and Chen 2010). This strategy is also apparent in halophytic relatives of barley (Garthwaite et al. 2005). Excessive Na accumulation in shoots is prevented by plasma membrane  $\text{Na}^+/\text{H}^+$  antiporters, which transport  $\text{Na}^+$  from the root symplasm to the external solution, by tonoplast  $\text{Na}^+/\text{H}^+$  antiporters such as those encoded by NHX genes, which transport  $\text{Na}^+$  from the root symplasm to vacuoles, and by HKT transporters, which retrieve  $\text{Na}^+$  from the xylem (Huang et al. 2008; Munns and Tester 2008; Hauser and Horie 2010). Similarly, restricting B transport from the root to the shoot prevents the excessive accumulation of B in leaves, and greater expression of genes encoding B exporters (*BOR*), which remove B from plant cells, has been associated with increased tolerance of barley to high B concentrations in the environment (Sutton et al. 2007; Reid 2010). However, barley cultivars with greater expression of *BOR* genes do not always yield better than other varieties in field trials conducted in rain-fed semi-arid environments (McDonald et al. 2010; Reid 2010).

Barley production can, occasionally, be restricted by the accumulation of toxic heavy metals. The term “heavy metal” is rather inexact, but is generally taken to include the

elements Cr, Mn, Fe, Co, Ni, Cu, Zn, Pb and Cd (Duffus 2002). These elements can be present at high concentrations in soils as a result of weathering of the underlying rock (e.g. Ni, Co, Pb and Cd), soil acidity (e.g. Mn and Zn), or human activities (e.g. Cr, Co, Ni, Cu, Zn, Mo, Pb, and Cd; White and Greenwood 2011). Several of these elements (Mn, Fe, Ni, Cu, Zn) are essential to plant nutrition, but all are toxic to plants at high tissue concentrations (White and Brown 2010; White and Greenwood 2011). Barley, like many cereals, cannot survive high concentrations of these elements in its leaves, but genotypes have been found to vary in their ability to prevent their uptake and to tolerate them in tissues (e.g. Petterson 1977; Broadley et al. 2001; Persson et al. 2006; Tiryakioglu et al. 2006; Wu et al. 2007; Chen et al. 2008; Juknys et al. 2009). This has consequences not only for crop yields on contaminated soils but also for the transfer of these elements through the food chain (Chen et al. 2007; White and Broadley 2009; White and Brown 2010). Tolerance of high soil concentrations of these elements is generally achieved by their exclusion from the plant, but their chelation in non-toxic forms or sequestration in non-metabolic compartments can also make an important contribution in some genotypes.

#### Threats: biotic stresses (pests and diseases)

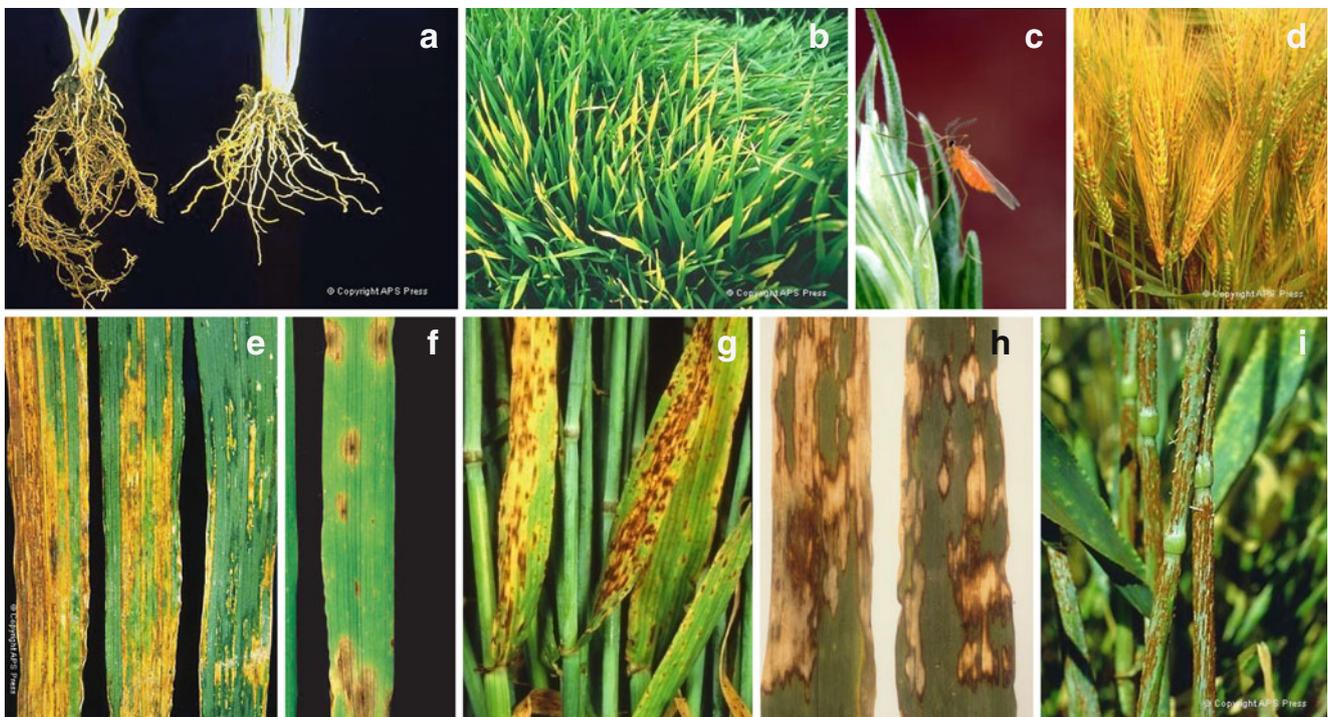
The most common cause of total crop failure is drought, and water availability is frequently a major constraint to yield. However, pest and pathogen attack also cause considerable yield losses whatever other factors are limiting, although these factors, in particular moisture, may also limit pest and pathogen activity. Characteristically, pests and pathogens are highly adaptable due to specific mechanisms generating variability (Gregory et al. 2009) and their population size and will try to exploit any unoccupied trophic niche. Where crops are introduced to new areas, or where the climate of a growing area changes, crops may be particularly vulnerable to pest and pathogen attack as they have not been selected to express effective and durable resistance for that environment.

Predicting whether particular pests and pathogens might increase or decrease and thereby affect yield and food security in future requires not only knowledge of their response to climate trends, but also of spatial and temporal changes in epidemiological conditions for the regions where the crop will be grown in the future, together with their rotational and agronomic context. Therefore, deployment of robust/durable resistance, together with complementary crop protection and agronomy treatments, is the most desirable and sustainable strategy for ensuring reliable productivity (Newton et al. 2011a). Here we will consider several representative current and emerging pest and

disease problems that could threaten food security to illustrate the types of risks that may be faced (Fig. 11). For barley, the main ones are: (1) some of the rusts, due to predictable climate trends and new virulence in adapted pathotypes; (2) aphid-borne viruses, also predictable from climate trends; (3) rice blast (*Magnaporthe grisea*) extending its climatic range and exploiting pleiotropic susceptibility of a mildew resistance gene in barley; (4) Fusarium Head Blight (FHB), again predictable from climate trends but also from enhanced inoculum from changes in maize cropping patterns; (5) nematodes such as cereal cyst nematode, as soil condition changes extend their ranges; (6) Ramularia, not directly related to climate change but correlated with other changes in agronomic or crop production practices; (7) Rhynchosporium on cool temperate climate winter crops where milder wetter winters are predicted; (8) Orange Wheat Blossom Midge, already becoming a problem in new areas for wheat and likely to affect barley; and (9) cereal bacterial leaf streak. The list is increasingly speculative, and we could add many other diseases such as spot blotch, crown root rot, the smuts and bunts, net blotch, glume blotch or ‘*Septoria nodorum*’,

powdery mildew, eyespot and sharp eyespot, take-all, tan spot, soil/fungal-borne viruses, fusarium foot rot and seedling blights, leaf spot, black point and leaf stripe. These are all pests and pathogens of barley that are important in different locations and times and require either effective resistance or crop protection programmes tailored to their risk status.

1) Brown rust (*Puccinia hordei*) is predicted to increase substantially in response to mean spring and summer temperature rise alone (Davis et al. 2007). Yellow rust (*Puccinia striiformis* f. sp. *hordei*), in contrast, is generally intolerant of higher summer temperatures and may decline in some areas. However, this may not always be the case because new isolates of wheat stripe rust (*Puccinia striiformis* f. sp. *tritici*) were found in the eastern USA that were more aggressive than established isolates at higher temperatures. These new isolates have supplanted populations of the older isolates and are causing significant yield loss in areas previously considered non-congenial to stripe rust epidemics (Milus et al. 2009). Currently, one of the



**Fig. 11** Representative current and emerging pest and disease problems that could threaten barley food security. **a** cereal cyst nematode, **b** Barley Yellow Dwarf Virus, **c** orange blossom midge, **d** Fusarium head blight, **e** cereal bacterial leaf streak, **f** rice blast (on barley), **g** Ramularia Leaf Spot, **h** rhynchosporium or scald, **i** stem rust (on barley). Image a courtesy R Cook, b courtesy B Cunfer, d and i courtesy B Steffenson, e courtesy V Peterson, all reproduced by permission from Compendium of Barley Diseases, 2nd Ed., 1997,

American Phytopathological Society, St. Paul, MN, USA; image c courtesy and copyright of Rothamsted Research Ltd, Harpenden, UK. Image f courtesy of B. Steffenson; image g courtesy of Dr Neil Havis at SAC, Edinburgh, UK; image h by permission, from Paulitz, T. C., and Steffenson, B. J. 2011. Biotic Stress in Barley: Disease Problems and Solutions. Pages 307–354 in: Barley: Production, Improvement, and Uses. S.E. Ullrich, Ed. John Wiley & Sons, Inc., Ames, IA

most important food security issues of small grain cereals worldwide is the emergence of the black stem rust (*Puccinia graminis* f. sp. *tritici*) race TTKSK (isolate synonym Ug99) from Uganda in 1999. Race TTKSK is virulent for more than 70% and 90% of wheat and barley varieties worldwide, respectively (Chakraborty et al. 2011; Singh et al. 2008, B. Steffenson, unpublished). It, and other variants with virulence for wheat and barley stem rust resistance genes *Sr31* and *Rpg1*, respectively, have spread throughout countries in eastern Africa and into South Africa, Yemen, and also Iran. Germination and infection by *P. graminis* urediniospores can occur over a wide range of temperatures, but 15–20°C is optimum (Roelfs et al. 1992). Race TTKSK was shown to have 87% and 98% larger mean pustule areas than the common North American race QFCSC after infection at lower temperatures (16°C and 12°C, respectively) (Rouse and Jin 2009). These data indicate that race TTKSK may be more aggressive than other races under cooler climatic conditions with respect to mean sporulating area. In Kenya, race TTKSK has caused significant damage on barley at high elevation sites like Mau Narok (2,829 m) where the average temperature throughout the year is very cool - from 11 to 13.5°C. These examples demonstrate the real potential of different rust pathogens for adapting to different temperature conditions, warmer for stripe rust and cooler for stem rust.

- 2) Aphids tend to arrive earlier in warmer climates and their fecundity increases (Harrington et al. 1995, 2007). This may be balanced by the fecundity of parasitic wasps and other predatory insects that feed on them; however, the population dynamics of these species may not respond to climate in the same way. On barley, damage is caused more from the viruses they carry, but like the wasps, these may multiply at different rates. However, in general, the trend will be for earlier and more severe aphid-borne virus losses as the climate changes (Newton et al. 2011a). In addition to the increased fecundity of the aphid vectors and viruses, elevated temperatures also will likely shorten virus acquisition, latent period, and transmission times, regardless of whether barley is cultivated as an autumn or spring sown crop. Diseases such as barley yellow dwarf (caused by *Barley Yellow Dwarf Virus*) are becoming much more severe and extensive in unusually warm summers, but aphid predators tend to lag in their increased numbers.
- 3) Rice blast, caused by *Magnaporthe grisea*, is widely known as one of the most important diseases of rice worldwide, but can also infect barley, wheat and triticale (Anjos and Charchar 2000; Lima et al. 2007;

Urashima et al. 2004). Both the foliage and more devastating head/neck phase of the disease have been reported on barley in South America and southeast Asia (Kongprakhon et al. 2009; Lima and Minella 2003; Lima et al. 2007). Rice blast of barley and wheat is increasing in South America (Agropages.com. 2010-5-24) and could spread elsewhere on the continent and beyond. Should the disease reach barley production areas where cultivars with the *mlo* resistance gene are widely deployed, the consequences could be very serious because the presence of this gene is correlated with enhanced susceptibility to rice blast (Jarosch et al. 1999).

- 4) Fusarium Head Blight (FHB) is a devastating and insidious disease of barley due to its ability to cause high yield loss, reduce end use quality, and contaminate grain with various mycotoxins that are harmful to humans and animals (Steffenson 2003). The disease is caused by different species of, or a complex of *Fusarium* species and *Microdochium nivale*. Since the last decade of the 20th century, FHB has become an increasingly serious problem in many production areas. This will likely continue into the future if current cropping systems and climate pattern trends remain the same. *Fusarium* inoculum is ubiquitous, but has increased substantially in cereal fields due to the widespread adoption of minimum or conservation tillage that leaves more crop debris and therefore inoculum on the soil surface available for re-infection. Maize stalks, being large and more resistant to decay, provide the largest substrate and hence source of FHB inoculum (Paulitz and Steffenson 2011). With respect to the most common FHB pathogen *F. graminearum* and its ability to attack many cereal hosts, the encroachment of or rotation with maize crops will certainly result in higher disease severities and mycotoxin contamination of barley. It also will result in population changes with respect to the causal FHB pathogens as *F. graminearum* often supplants other *Fusarium* species once maize enters a cropping system (Chakraborty and Newton 2011). This also will result in changes to the mycotoxins found in grain as each species (and sometimes even isolates within a species) has a signature profile for mycotoxin production. Rainfall and temperature are the most critical weather factors in the development of FHB. In more arid production areas where FHB is seldom observed, timely rainfall may be the only factor limiting the development of epidemics as sufficient inoculum is often present (Steffenson 2003). Inoculum production and infection by *Fusarium* can occur over a wide range of temperatures—from 16 to 31°C and 20 to 30°C, respectively (Sutton 1982). Warmer and wetter con-

ditions generally favour increased FHB development; however, epidemics may still develop at cooler temperatures if a sufficiently longer wetness period is provided. Several investigators have documented differences in populations of causal FHB pathogens under cooler and warmer climates; therefore, regardless of which direction climate change alters temperature in a given region, it is likely that FHB and mycotoxin contamination will increase given sufficient inoculum and timely rainfall. The main concerns regarding FHB from a food security perspective are yield and food safety. Infections that occur early in the flowering and kernel development stages will result in severe yield losses, whereas those coming in late will have little impact on yield. Although these late infections may not greatly impact yield, they nonetheless may render the crop useless due to high mycotoxin levels (Steffenson 2003).

- 5) Nematodes can be an important pathogen limiting barley production in many areas. They are highly responsive to soil temperature and type, pH and water conditions in the presence of a susceptible crop (Lewis 2001). Moreover, the damage they cause can be particularly severe when the host plant is drought-stressed (Nicol et al. 2007). Among the nematodes attacking barley, the cereal cyst nematodes (CCNs) may become particularly problematic due to the complex of species involved, presence of pathotypes within the species, and their spread throughout the world. Chemical control of CCNs is not a sustainable or economically feasible control strategy for barley. Management can, however, be achieved through crop rotation and use of resistant cultivars. However, these strategies are predicated on a thorough knowledge of the pathogen species present in an area, their population dynamics, and relationship between population density and economic damage in the host (Holgado et al. 2006). Thus, the key to managing this disease is to keep CCN populations below the economic threshold. Additionally, it is also critical to implement effective strategies for limiting the spread of the nematodes so as to not increase their epidemiological range.
- 6) *Ramularia collo-cygni* (Rcc) is the causal agent of ‘Ramularia’ or Ramularia Leaf Spot (RLS). It has increased markedly in the last ~15 years (Walters et al. 2008), although this is probably not directly related to climate change. Rather it is likely a response to changes in agronomic or crop production practices, particularly fungicide treatments of the seed and growing crop. However, it is stress-responsive in its symptom expression, probably particularly to water, light and developmental stage (Makepeace et al. 2008; Walters et al. 2008). Symptoms result from light-activation of its Rubellin toxins (Heiser et al. 2003) causing yield reduction from loss of green leaf area. It is likely that RLS is now present in many other production areas, but has not been recognized due to difficulties in distinguishing it from other abiotic/biotic stress symptoms and isolating the pathogen from infected plants (Walters et al. 2008).
- 7) ‘Rhynchosporium’, ‘scald’ or ‘barley leaf blotch’ are caused by *Rhynchosporium secalis* and continues to be a problematic disease to control through fungicides, various agronomic practices or host resistance (Zhan et al. 2008). In the maritime climates where winter barley grows particularly well, the predicted milder wetter winters are likely to make this disease worse. This disease may also increase in nascent winter barley regions in temperate continental climates. In the US state of Minnesota, scald is very rarely observed. However, in the first winter barley trials established in St. Paul, severe infection was observed in some plots (BJ Steffenson, unpublished). It is not known whether pathogen inoculum was surviving at low levels on some alternative host or was introduced in the seed of the winter barley cultivars. Regardless, this result highlights the potential of scald to cause severe disease under a different cropping system.
- 8) Insect pests can extend their ranges rapidly as climate changes (Davis et al. 2007). One such pest, the orange wheat blossom midge (OWBM), has become a more frequent problem in the Northern Hemisphere during warmer seasons, especially in the UK. In addition to wheat, the OWBM also can damage barley (Kurppa 1989) and may exacerbate infection by FHB pathogens (Oakley et al. 2005). Forecasting systems have been developed for the OWBM and should be used assess the potential for outbreaks of the pest and to avoid unnecessary and costly insecticide sprays (Oakley et al. 1998). In addition to chemical control, a concerted effort should be made to identify and incorporate resistance to this insect pest in barley cultivars.
- 9) Bacterial leaf streak (sometimes referred to as bacterial blight) caused by *Xanthomonas translucens sensu lato* (Bragard et al. 1997) can be found on barley in many regions of the world with quite diverse climatic patterns. It is most severe, however, on crops grown in areas with frequent precipitation or under sprinkler irrigation. Recent epidemics have occurred in the north-central region of the USA with some fields exhibiting up to 80% severity (B. Steffenson, unpublished). Aside from changes in climate, there are several factors that may contribute to increased levels of bacterial leaf streak in barley: (1) ability of the pathogen to readily survive in seed and be widely

distributed in the grain trade; (2) ability of the pathogen to infect and survive on many grass hosts; (3) ability of the pathogen to survive on host residue, now dramatically increasing on-farm due to the increased use of minimum or no-till practices; and (4) effective control of fungal leaf spots (by fungicides or host resistance) that provide an open niche for bacterial leaf streak infection (Paulitz and Steffenson 2011). To minimize the impact of this disease, measures must be taken to produce clean seed, eliminate alternative hosts, and reduce infected residue in production fields. As variation for reaction to bacterial leaf streak has been reported in barley, greater efforts should be made to breed for resistance. Key issues that determine whether potential problems are realised are the following: (a) the status of inoculum; (b) occurrence of conditions suitable for (i) infection and (ii) epidemic development; and (c) susceptibility or resistance expression status of the host.

- a. For diseases such as FHB and scald/Rhynchosporium, the severity of disease is correlated with amount of local inoculum surviving on crop debris, so phytosanitation is important. Rusts and powdery mildews can establish following long distance aerial spore transmission. However, for some diseases, inoculum is both transmitted in or on seed and propagated asymptotically on the crop (Newton et al. 2010b). This symptomless infection occurs in both susceptible and resistant cultivars, for example for scald/Rhynchosporium and RLS. Potentially susceptible cultivars require triggers for infections to become symptomatic, whereas resistant cultivars do not respond to these triggers in the same way. The nature of the triggers is generally not well understood but can include inoculum pressure (/quorum sensing), developmental stage (such as anthesis), light or other abiotic stresses. Some of these will be modified by climate change making prediction of future disease threats more difficult, but emphasising the need to understand both the symptomless inoculum state of barley and the pathogenicity triggers (Newton et al. 2010b).
- b. Even if inoculum is present, many pathogens have specific requirements for successful infection. Sporulation of *Rcc* is highly correlated with periods of leaf wetness 1–2 days before spore dispersal (Oxley et al. 2010). The rusts require surface moisture for infection, which can be mediated by dew or light rain, whereas powdery mildews are inhibited by surface water. Most pathogens have clear temperature optima and maxima for infection, and these are likely to result in a shift in their

geographic distribution as the climate changes in the future.

- c. Many environmental variables can affect the efficacy of resistance expression. A classic example is the temperature sensitive expression of resistance to rusts. In barley line Q21861, the stem rust resistance gene *rpg4*, together with the closely linked gene *Rpg5* and possibly others (Steffenson et al. 2009) confer resistance to several races of wheat stem rust including races QCCJ and TTKSK. This resistance is highly effective against the former at 18°C, but is rendered completely ineffective at temperatures above 27°C (Jin et al. 1994). There is little information about barley rusts but for wheat brown rust (leaf rust) (caused by *Puccinia triticina*) about half of the wheat cultivars on the UK Recommended List ([www.hgca.com](http://www.hgca.com)) showed differential resistance expression when tested against isolates at 10°C and 25°C, changing from resistance to susceptibility or vice versa with the temperature change (Gregory et al. 2009). Such effects are not necessarily attributable simply to resistance gene expression response to temperature as isolates too showed differential temperature responses independent of resistance responses (Dyck and Johnson 1983; Browder and Eversmeyer 1986). In wheat stem rust, the classical temperature sensitivity of the *Sr6* gene was extensively reported by Samborski and co-workers (e.g. Harder et al. 1979).

Other environmental variables are gaseous atmospheric changes and drought. Again there is little published data for barley, but for wheat, for example, stem rust was found to be strongly inhibited by ozone but unaffected by CO<sub>2</sub> (Tiedemann and Firsching 2000). High CO<sub>2</sub> also compensated for the negative effects of ozone on plant growth, but not the negative effects of the rust on yield. Drought stress can reduce the impact or symptoms from pest or pathogen attack because the crop has reduced trophic value (Huber and Gillespie 1992). However, resistance expression can also be changed and in particular reduced due to drought (Christiansen and Lewis 1982). Loss of resistance expression can be temporary due to stress or stress relief. For example, in barley a sudden relief of drought stress compromised the effectiveness of the *mlo* resistance gene against powdery mildew (caused by *Blumeria graminis* f. sp. *hordei*) (Newton and Young 1996). The significance of this is that speed of pathogen recognition and response is often crucial to effective defence and this effect is probably common to other resistance sources, but notably in *mlo* as it is particularly critical for its efficacy of expression. Stress-related and defence-related gene expression were shown to

be compromised in stress-relieved barley plants compared to non-stressed plants (Barker 1998; Stewart 2002). The same breakdown problem occurred in response to sudden relief of cold stress but not salt stress (Stewart 2002). We cannot therefore assume that resistance genes currently in use will continue to be equally effective under environments with changed abiotic stress.

Actions need to be taken to improve drought stress tolerance of crops generally, and the effects on resistance mechanism expression in particular, to make barley more resilient to climate change. Novel resistance sources are needed, many of which may be available in landraces (Newton et al. 2010a) and these may best be deployed for resilience and enhanced crop function in blends or mixtures (Newton et al. 2009). Integrated crop protection approaches are needed where valuable resistance and pesticides are used in ways sympathetic to the ecology of the crop, where the emphasis is as much on promoting beneficial barley-microbe interactions as it is on minimising the impact of pests and pathogens (Newton et al. 2011b).

Amongst the beneficial interactions are endophytes that can confer both biotic and abiotic stress tolerance. The best example of this is *Piriformospora indica*, a root endophyte of barley and a wide spectrum of other monocots and dicots. It was able to enhance the growth of barley, increase grain yield (mainly through increased ears per plant), tolerate moderate (100 mM) salt stress, induce local resistance against the root pathogens *Fusarium culmorum* and *Cochliobolus sativus*, and induce systemic resistance against the biotrophic foliar pathogen *B. graminis* f.sp. *hordei* (Waller et al. 2005). In fact, the effect is probably attributable to an intimately associated bacterium, *Rhizobium radiobacter* (Sharma et al. 2008). Other endophytes of grasses can confer drought tolerance. For example, *Elymus virginicus* was only half as much affected by drought if infected with an endophyte *Epichloe elymi* (Rudgers and Swafford 2009).

Barley breeding programmes as well as common agronomic practices, particularly high soil disturbance and high agrochemical inputs in general, are likely to inhibit endophyte infections in particular and will decrease the likelihood of detecting beneficial microbial interactions in general. By contrast, some grasses are bred with endophyte infections, and enhancing these interactions is becoming a breeding objective in some programmes, indeed endophyte-infected grasses are being patented (e.g. US patent 6815591, 6111170, 6072107 etc.). There is therefore the potential to incorporate optimum matching of both host and endophyte genotypes, although multi-strain endophytes and endophyte hybrids may be used (Cheplick and Faeth 2009).

There is a wide range of effective pesticides available for use on barley, though these will have reduced availability in the EU following the recent directive EC/41/414. The major

issues for pesticides are selection for resistance in pathogens and lack of efficacy against some seed-borne pathogens such as *Rcc*. In addition to conventional pesticides, there are also resistance elicitors that may have important roles in integrated crop management strategies (Walters et al. 2007) together with biological control agents, encouraging beneficial microbes, use of disease tolerant cultivars and many other agronomic treatments (Newton et al. 2011b).

Barley breeding companies tend to be increasingly international, increasing the exchange of germplasm across geographically-separated programmes and therefore increasing the exposure of elite germplasm to likely new pest and disease threats. Developing country and national or local regional breeding groups need to guard against their germplasm pools becoming too narrow. Lack of diversity is a danger both at the genotypic level and in deployment, and this includes diversity in strategy in both areas (Chakraborty and Newton 2011). Thus resistance to a disease should rely on major and minor genes, sometimes together where appropriate, and crop canopy/morphology traits such as height, leaf angle and development speed. These should be deployed with different scales of diversification, from region through field to mixed stands, with particular emphasis on preventing dominance of single varieties with susceptibility to any disease.

Whilst generally grown in monocultures in high-input farming, barley is frequently grown as landraces in subsistence agriculture (Newton et al. 2010a). The advantages of heterogeneous landraces, particularly stability, can be exploited in high-input farming in multilines, composite crosses, or most practically, in cultivar mixtures or blends (Newton et al. 2009). Furthermore, by mixing elite lines with contrasting traits, particularly disease resistance, yields exceeding the mean of the components and as good as the best component can frequently be achieved. Crude or patchy mixtures are as or more effective than homogeneous mixtures, eliminating the cost of special mixing (Newton and Guy 2009). Disease can be reduced considerably by a combination of three effects: the barrier of resistant plants, reduced density of susceptible plants, and induced resistance (Chin and Wolfe 1984), achieving reductions of up to 75% in the case of scald/Rhynchosporium (Newton et al. 2008). This is achieved largely by reducing the risk of epidemics, giving a wider window for disease control practices. In general, introducing heterogeneity into the crop through mixtures increases its resilience to stress, be it from biotic or abiotic sources.

Maltsters tend not to accept cultivar mixtures due to perceived difficulties of processing a heterogeneous crop, preferring to control the market through individual cultivars. In practice, single cultivar monocultures offer an acceptable range of heterogeneity of the characteristics that

maltsters require but mixtures from the same number of sites or environments offers a narrower and more consistent range of characteristics (Swanston et al. 2006), so enhancing barley further as a resilient crop. In the feed market, mixtures are acceptable as it is generally not traded by cultivar name except for re-sowing. Furthermore, winter cultivars available in the UK have more complementary traits than within the spring barley cultivars, offering greater synergies when grown together. Winter barley is also grown over a longer, more stress-exposed period, offering more opportunities for expressing the enhanced resilience.

Pests and pathogens will always be a threat to food security for any crop. Short-term and high input options have dominated strategies, particularly for the commercially-driven breeding and crop protection. However, where recognition of market failure and public-good have driven research funding, longer-term strategies for durable resistance and integrated pest management approaches are enhancing the security of the crop. As with all the crop traits needed, enhancing resilience rather than attempting to eliminate the pest or pathogen will prove to be the best approach to achieving sustainable crop protection (Chakraborty and Newton 2011).

## Breeding

### Breeding objectives

The prime aim in any breeding programme is to produce a variety that will be adopted by growers and thus needs to fulfil different, often conflicting, needs. Whilst yield for the grower may be the most obvious requirement of any breeding programme, it is essential that the variety producing that yield is accepted by the market, if the grower wishes to sell the seed. In the developed world, the feed market accepts most varieties provided that the grain meets basic trading standards but the demand is limited. The malting market is more discerning as it only accepts approved varieties and then applies more stringent grain quality standards to select the best grain lots from amongst those available for their preferred varieties. As it takes approximately 10 years from making a cross to potentially occupying at least 10% of marketed seed, breeders must anticipate future market needs in setting their objectives, i.e. breeders making crosses in 2010 are breeding for the growing and market conditions of the 2020s. Barley is, however, a global commodity and has such a diverse range of growing conditions that useful genetic variation exists for most breeding targets and the breeder has to design the most efficient strategy to incorporate such targets into germplasm adapted for a specific range of growing

conditions. For example, *Fusarium* head blight, whilst not currently a major problem in the UK, can cause severe yield loss in other regions such as North America and also render the crop unsuitable for malting. Resistance does exist in Asian germplasm and there is currently a major effort to introgress resistance from resistant Asian lines into North American germplasm and the same could be done in the UK, should the disease become a problem.

Breeding objectives are therefore specific to the target environment and subject to change but in the UK, the objectives largely reflect the characters used to establish Value for Cultivation and Use in the official trialling protocol (<http://www.fera.defra.gov.uk/plants/plantVarieties/nationalListing/index.cfm>) (Table 4). In addition, the Maltsters Association of Great Britain issues a list of required characteristics for varieties used in their industry (Table 5) so breeders also include these in their objectives when targeting the malting market.

### Research methods

The adoption of molecular technology within breeding programmes has been accelerating over the last 20 years in particular as the tools to deploy marker assisted selection (MAS) have been developed and refined (Moose and Mumm 2008; Collard and MacKill 2008). In barley, this has resulted in some notable successful applications of MAS in the crop, for example *Yd2*-based virus resistance (Jefferies et al. 2003), pyramiding BaYMV resistance genes (Werner et al. 2005) and boron tolerance (Emebiri et al. 2009). These have enabled the development of cultivars resistant to specific biotic and abiotic stresses that can drastically limit production in particular agricultural regions. These MAS successes have targeted well characterised major genes, but for traits that are controlled by multiple genes of small genetic effect and that frequently show significant environmental dependency (i.e. quantitative trait loci (QTL)) such as yield and quality, MAS has had limited impact on barley breeding (Schmierer et al. 2004; Rae et al. 2007). A number of reasons have been cited for this: a lack of appropriate types and numbers of molecular markers, a lack of experimentally-derived associations between markers and traits that breeders both want to enhance and are present in the germplasm within which they are practising selection, and the need for new approaches that improve the effectiveness of how markers could or should be used in breeding programmes.

Recent advances in the development of highly multiplex gene-based genotyping technologies (Close et al. 2009) and their use in both bi-parental mapping and more recently genome-wide association studies (Rostoks et al. 2006; Cockram et al. 2010) are addressing the former constraints as the discovery of single nucleotide polymorphisms (SNP)

**Table 4** Value for cultivation and use criteria in the official UK trialling protocol

Assessment	Character	Description
1. Yield	Grain yield (treated and untreated)	Plot produce weighed and corrected to 15% moisture to give variety yield
2. Quality	Specific weight	Specific weight of grain
	Weight of 1000 seeds	
	Sieving fraction	Grain passing through specified aperture sieve
	Hot water extract	Soluble carbohydrate extract
	Nitrogen content	% nitrogen in the grain
3. Resistance to Disease	Resistance to infection by:	Presence and severity of disease infection recorded in the field, which may include inoculated trials
	Mildew	
	Brown rust	
	Rynchosporium/Scald	
	Net Blotch (WB)	
	Barley Mild Mosaic Virus/Barley Yellow Mosaic Virus (WB)	
	Barley Yellow Dwarf Virus (SB)	
Yellow rust		
4. Reaction to environment	Straw strength (treated and untreated)	A measure based on lodging (% of plants leaning >45°) also taking leaning at <45° into account
	Brackling	% of plants with stems buckling.
	Straw length	Stem length
	Ripening	Number of days from sowing to ripening
	Shedding	Grains lost per m <sup>2</sup> from the ear prior to harvest
	Sprouting	% of grains showing sprouting in harvested grain
	Winter hardiness	1–9 where a high score indicates high resistance to frost damage

within elite breeding material and their deployment in high multiplex genotyping platforms has enabled the interrogation of lines of direct relevance to current barley breeding (Close et al. 2009). The ability to track genomic regions through a breeding programme also opens up the possibility of using more un-adapted material or mutated lines as a

source of novel alleles within breeding programmes as marker-assisted backcrossing allows the introduction of potentially new desirable alleles at target loci with the minimum of linkage drag (Collard and MacKILL 2008).

The emerging approach of genomic selection (GS), borrowed from the world of animal breeding (Meuwissen et al. 2001), looks promising for addressing the issue of simultaneous selection of multiple genes of small genetic effect in barley (Heffner et al. 2009). In GS, dense genome-wide marker information is merged with phenotypic data to develop a selection index that is subsequently used to predict 'better performing' progeny based on genotype alone. GS is thought to be especially valuable for traits where the accuracy of conventional selection is difficult or low such as resource efficiency traits, traits with low heritabilities, traits with few recordings of data because of cost, and traits where phenotypic scoring is not possible until after the reproductive phase. Moreover, in these circumstances traditional trait mapping approaches often lead to very biased estimates of QTL effects which greatly reduce the efficiency of MAS. GS is effectively a two-step, cyclical process (Heffner et al. 2009; Zhong et al. 2009). The first involves a training cycle where phenotypic and

**Table 5** Maltsters association of Great Britain required characteristics for malting in the UK

Character	Brewing	Distilling
Absence of splitting	Y	Y
Soft endosperm	Y	Y
Water uptake (rapid and even)	Y	Y
Low nitrogen	Y	Y
Germinative energy	Y	Y
Starch content		Y
Hot water extract	Y	Y
Fermentability/PSY	Y	Y
Low beta glucan	Y	Y
High diastatic power	Extract	Grain
Low glycosidic nitriles		Y

molecular data are assembled and analysed. This allows development of a Genome Estimated Breeding Value (GEBV) to predict trait values of lines from their genome-wide marker genotypes without prior selection of statistically significant marker-trait associations. The second involves one or more generations of recombination and selection using GEBVs to predict which individuals in the population will most likely be the highest performers. Phenotypic and genotypic data obtained from the 'predicted best performing lines' are then used cyclically to update the training dataset, recalibrate the allelic values associated with each marker and estimate GEBVs in the following selection cycle.

While the efficient multiplex genotyping platform has very clear applications in barley breeding, it also has powerful applications in understanding the structure and dynamics of the barley genome. It provides an 'access key' that allows, based on conservation of synteny among grass genomes (Salse et al. 2009), prediction of regional gene content and order in barley that in turn allows targeted genetic marker development and the identification of positional and functional candidate genes in positional cloning projects. However, it also highlights genetic constraints in the barley genome, identifying blocks of gene-rich but rarely-recombining regions that, in the main, span each of the genetic centromeres (Comadran et al. 2010). Analysis of germplasm collections shows that these regions often exhibit complete linkage disequilibrium (LD) and may span over half the physical length of individual barley chromosomes. In these regions, using recombination either to narrow-down the location of a target gene, or to release genetic diversity in plant breeding programmes, is difficult at best. Indeed the latter has prompted investigations into interventions (genetic and environmental) that increase the frequency, or change the distribution, of recombination events and alter patterns of LD across the barley genome.

Currently, outside of the genetic centromeres, the identification of genes controlling target phenotypes (e.g. Komatsuda et al. 2007; Brueggeman et al. 2002; Burton et al. 2009) is a reality that is largely due to the availability of a considerable array of genomics tools and genetic resources. This will likely accelerate with the promise of a draft barley genome sequence (Schulte et al. 2009). In addition, the new sequencing capabilities driven by rapid technological advances will find applications within barley breeding (including MAS) as it has already in genomic research (Metzker 2009; Varshney et al. 2009). The prospect of having whole genome information of multiple individuals within a breeding programme would provide information on an unparalleled scale that has profound implications for breeding methodology not least in the informatics needed to handle and analyse such data sets in a timely fashion.

Once target genes have been identified, *Agrobacterium*-mediated transformation, generally of the barley cultivar Golden Promise, is now routine to validate gene function (Bartlett et al. 2008). This raises the possibility of developing genetically modified (GM) barley for general cultivation and use. While the industry (particularly in Europe) remains recalcitrant to the use of GM technology, it seems likely that the technology would be adopted if a relevant target trait was proving intractable by other routes given the probable pressures of future food security.

Commercial breeding in barley has been predominantly for relatively high inputs, whilst participatory breeding has been mainly for subsistence agriculture (Newton et al. 2010a). However, this dual approach has served the sustainability requirements of the crop well for these contrasting types of agriculture and associated end-users. For the likely future of barley, a different model may be required whereby resource-use efficiency is the main driver ensuring better utilisation of inputs for both economic and environmental reasons. For these objectives to be achieved, breeders must utilise the developments in both physiology and genetics in parallel, looking for synergies hitherto exploited only serendipitously.

## Conclusions

Barley is clearly a robust and adaptable crop species with many end uses. These uses differ widely in scale from the production and international trade of barley in the drinks industry, through to its consumption in the human diet in some subsistence agricultural systems. Many of the threats to the continued security of barley production are shared in common with other crop species. As barley is traded internationally, climatic and political events occurring in different parts of the world impact on its supply and demand and influence price volatility. There is a need to increase the yield potential of barley and reduce the gap between potential and realised yield by improving the tolerance of abiotic and biotic stress factors in order to secure sufficient supply in the future. Barley has the advantage of being robust and locally adapted land races can often be grown in regions where other crop species fail. There is a large, relatively untapped reserve of genetic variation within landraces and wild relatives that might be utilized to improve the tolerance of abiotic and biotic stress and to improve the nutritional quality of barley as a human food source. Great advances have been made in recent years in understanding the genetics of barley and mapping potentially useful genes and traits for use in breeding programmes, which bodes well for the future. However, threats to production from specific pests and diseases, drought or other adverse soil conditions tend to be local in

nature and thus require local solutions used in conjunction with generic approaches to increase resilience. The major question, therefore, is not whether improvements can be made in the tolerance of varieties to these threats, but whether the technology will be made available and affordable to the poorer, less developed, countries where the need is arguably greatest.

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**Adrian Clive Newton** has 30 years experience of plant pathology research focussing mainly on cereal diseases, particularly on barley. Other interests include climate change and diversity research in crops. Main research themes are: (1) the genetics of resistance to disease in barley, (2) the pathogen response to resistance, particularly resistance diversity, and (3) induced resistance in crop protection. His PhD was in Genetics at the University of

Birmingham, UK and the former Plant Breeding Institute in Cambridge, UK. After a post-doc he then moved to the Scottish Crop Research Institute near Dundee in Scotland, UK. His research and some recent publications are described at: [www.hutton.ac.uk/staff/Adrian-Newton](http://www.hutton.ac.uk/staff/Adrian-Newton).



**Philip Leat** is senior food marketing economist in the Food Marketing Research Team of the Land Economy and Environment Research Group, Scottish Agricultural College (SAC), and is based in Aberdeen. He has over 30 years of experience in domestic and international research, focussing on the analysis and development of agri-food supply systems, along with related policy development. His research has involved projects for the Scottish Government, the

Department for Environment, Food and Rural Affairs (Defra), the European Commission, the Home Grown Cereals Authority (HGCA) and a variety of other Government Departments and NGOs.



**Andrew J. Flavell** is Professor of Plant Genomics at the University of Dundee at SCRI. His research is centred upon the study of crop plant genomes, using genomics-based tools, particularly high throughput molecular markers and direct DNA sequencing to address issues of the diversity and evolution of crop species. He has coordinated three European consortia, with substantial EU funding, addressing the issues of genomic diversity and the role of transposable

genetic elements in crop genome evolution and has published 95 research articles in the field.



**Barry Mullholland** is a Research Leader in crop water use at the James Hutton Institute and has over 20 years research experience in whole plant stress physiology and the environmental manipulation of crop product quality. He heads a group that is currently exploring the physiological mechanisms of whole plant water use and the water footprint of crops in the context of food security. Dr Mullholland has an extensive record of delivering research with industry

and disseminating the findings to academic, industry and public audiences. He has a recognised expertise in protected cropping and has acted as consultant to a number of commercial and educational Horticulture projects within the UK.



**Timothy S. George** is employed as a Rhizosphere Scientist at SCRI and is specifically interested in understanding the physiology of and genetic controls on plant responses to nutrient and water deficiency. He has specific expertise in understanding how the external environment mitigates plant physiological and genetic responses to a lack of phosphorus. He was recently awarded a Royal Society of Edinburgh Fellowship to study plant response to the combined stress of water and

nutrient deficiency. Earlier in his career he was awarded a Marie Curie International Fellowship to study the impact of phosphatase enzymes on P availability. This fellowship was held at CSIRO Plant Industry in Australia and followed on from a post-doctoral position in the same lab in Australia, working on the transgenic expression of phytases in pasture plants. His PhD studies were focused on P acquisition by plant species used in agroforestry systems in Africa.



**Cesar Revoredo-Giha** is senior economist and head of the Food Marketing Research Team in the Land Economy and Environment Research Group, Scottish Agricultural College (SAC), based at the King's Buildings Campus in Edinburgh. He received a PhD from the University of California, Davis in 2001 and subsequently worked at the University of Georgia (Georgia Experiment Station, Griffin Campus), The University of Cambridge (Department of Land

Economy), before moving to SAC in 2005. His areas of specialisation are industrial organisation of food markets, international trade and econometrics. His main areas of interest are food policy and the operation and performance of agri-food supply chains (domestic and international). He has worked as a consultant for United Nations, The World Bank, The International Food Policy Research Institute (IFPRI), the UK Department of Environment Food and Rural Affairs (Defra), the UK Home Grown Cereal Authority (HGCA), the Food Standard Agency - Scotland and the Scottish Government.



**Brian J. Steffenson** is a Professor and Lieberman-Okinow Endowed Chair in the Department of Plant Pathology at the University of Minnesota. He has worked on diseases of barley for over 30 years. His primary research responsibilities include exploiting wild species for cultivated cereal improvement, including traits such as disease resistance, abiotic stress resistance, yield, and quality. His research specialties include genetic diversity and evolution of

wild cereal progenitors, host-parasite genetics, and virulence/molecular diversity in plant pathogenic fungi. He has a strong international scope to his research program and has projects with collaborators in the United Kingdom, South Africa, Czech Republic, China, and Kenya.



**J. Stuart Swanston** is a Senior Research Scientist in the Genetics Programme at SCRI, specialising in grain and processing quality in cereals. He began his career at the former Scottish Plant Breeding Station, spending 10 years in the barley breeding team, then managing the cereal quality laboratory at SCRI. He received his PhD from Heriot-Watt University in 1994. He has collaborated extensively with a Spanish group, comparing the effects of UK and Mediterranean growing conditions

on grain filling and malting quality in barley. He has also been part of a major UK project to improve the breeding and cultivation of soft wheat for grain distilling and ethanol production.



**Robbie Waugh** is the head of the Genetics department at the Scottish Crop Research Institute in Dundee where he has worked for the last 25 years. His main interests are in developing and applying state of the art genomics technologies with the aim of identifying the genes controlling key traits, largely in barley and potatoes, two major Scottish crops. He plays a significant role in national and international organisations that promote and co-ordinate global

Triticeae research including 'Monogram' and the 'International Triticeae Mapping Initiative', respectively. He has published approaching 200 primary research articles in international peer reviewed journals. His research and some recent publications are described at: [www.hutton.sari.ac.uk/staff/Robbie-Waugh](http://www.hutton.sari.ac.uk/staff/Robbie-Waugh).



**Philip J. White** leads the Environment Plant Interactions Programme at the Scottish Crop Research Institute. He is Special Professor in Plant Ion Transport at the University of Nottingham and Visiting Associate Professor at the Comenius University, Bratislava. He convenes the Plant Transport Group of the Society of Experimental Biology (UK) and is a member of the International Council on Plant Nutrition. He has published >200 scientific

articles and edited books on Plant Nutritional Genomics (2005) and The Ecophysiology of Plant-Phosphorus Interactions (2008). He is currently engaged on projects addressing plant mineral nutrition, from the genes to the harvest. His research has three broad objectives: (1) to optimise the use of mineral fertilisers in crop production, (2) to reduce the entry of toxic elements into the food chain, and (3) to improve the nutritional quality of crops through their biofortification with essential minerals, such as calcium, selenium, zinc and iron.



**Ian J. Bingham** is a senior researcher in crop physiology at SAC, UK. His research interests are in developing and applying an understanding of the physiological determinants of resource use efficiency (especially N use efficiency) and the response of crops to foliar disease to guide variety improvement and crop management practice. Physiological questions are addressed at the tissue, whole plant and crop scales. Increasingly modelling is being used to integrate

understanding across these scales and to investigate the complex interactions between soil, root and crop canopy processes. In addition to the publication of results in scientific journals, his research has contributed to the production of several crop and disease management guides used by growers. He was adviser to the HGCA, the UK's cereal and oilseeds levy board, on root-soil interactions from 2000 to 2003 and currently manages projects funded by both government and industry.