

BURLEIGH DODDS SERIES IN AGRICULTURAL SCIENCE

Achieving sustainable cultivation of barley

Edited by Professor Glen Fox
University of California-Davis, USA and The University
of Queensland, Australia

Professor Chengdao Li
Murdoch University, Australia



Contents

Series list	xii
Introduction	xviii

Part 1 Plant physiology and genetics

1	Advances in understanding of barley plant physiology: plant development and architecture	3
	<i>Andrea Visioni, International Center for Agricultural Research in the Dry Areas (ICARDA), Morocco</i>	
	1 Introduction	3
	2 Barley plant structure/morphology and growth habit	4
	3 Molecular control of vegetative development	7
	4 Molecular control of reproductive development	11
	5 Implications for breeding	14
	6 References	16
2	Advances in understanding barley plant physiology: responses to abiotic stress	23
	<i>Alessandro Tondelli, Cristina Crosatti, Stefano Delbono and Luigi Cattivelli, CREA Research Centre for Genomics and Bioinformatics, Italy</i>	
	1 Introduction	23
	2 Cold acclimation: a coordinated metabolic rearrangement leading to frost tolerance	25
	3 New methodologies for dissecting an old phenotype: resilience to drought	28
	4 Adaptation to soil salinity	33
	5 Low nitrogen: a stress condition matching crop sustainability	36
	6 Adaptation to environment: a key target for future breeding improvement	38
	7 Acknowledgements	40
	8 Where to look for further information	40
	9 References	41

3	Advances in the understanding of barley plant physiology: factors determining grain development, composition, and chemistry <i>Ljudmilla Borisjuk, Hardy Rolletschek and Volodymyr Radchuk, Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Germany</i>	53
	1 Introduction	53
	2 Spike growth and how it influences traits of the grain	54
	3 Role of cell death in barley grain development	57
	4 Sucrose allocation during the grain-filling stage	62
	5 The use of starch in the developing caryopsis	67
	6 Proteins and barley grain quality	71
	7 Particularities of energy metabolism in barley grain	73
	8 Functional orchestration of the barley grain	80
	9 Conclusion	83
	10 Acknowledgements	83
	11 Where to look for further information	84
	12 References	84
4	Exploring barley germplasm for yield improvement under sulphur-limiting environments <i>Tefera Tolera Angessa, Murdoch University, Australia; Kefei Chen, Curtin University, Australia; David Farleigh, Jenifer Bussanich and Lee-Anne McFawn, Department of Primary Industries and Regional Development-Western Australia, Australia; Kevin Whitfield, CSBP Limited, Australia; Brendon Weir, Mullewa, Australia; Steve Cosh, Department of Primary Industries and Regional Development-Western Australia, Australia; Achalu Chimdi, Gudeta Nepir Gurm and Tadesse Kenea Amentae, Ambo University, Ethiopia; and Chengdao Li, Murdoch University, Australia</i>	97
	1 Introduction	97
	2 The origins of barley	98
	3 Genetic diversity in barley	99
	4 Using genetic diversity in breeding	101
	5 The role of sulphur in barley growth	102
	6 Assessing the effects of sulphur nutrition on barley and wheat grain yield	104
	7 The effects of sulphur on yield, quality and response to stress	109
	8 Farming systems and sulphur nutrition	113
	9 Genotypic differences in sulphur use	114
	10 Conclusion	117
	11 Acknowledgement	117
	12 References	118

5	Mapping and exploiting the barley genome: techniques for mapping genes and relating them to desirable traits <i>Hélène Pidon and Nils Stein, Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Germany</i>	123
	1 Introduction	123
	2 New possibilities for genetic mapping in the genomics era	124
	3 Classical mapping strategies and their improvement in the genomics era	129
	4 The association mapping boom	130
	5 Multiparental populations: the perfect balance?	131
	6 From an interval to the causal gene: from high-resolution mapping to gene cloning	132
	7 Emerging mapping strategies: fast NGS-enabled technologies	133
	8 Conservation of barley germplasm	138
	9 Genetic and genomic resources of barley	139
	10 Case study: from <i>rym4</i> to <i>rym11</i> , illustration of paradigm shift in disease resistance mapping and cloning	140
	11 Conclusion and future trends	142
	12 Acknowledgement	144
	13 Where to look for further information	144
	14 References	145

Part 2 Advances in breeding

6	Advanced designs for barley breeding experiments <i>Alison Kelly, Queensland Department of Agriculture and Fisheries and Queensland Alliance for Agriculture and Food Innovation (QAAFI), The University of Queensland, Australia; and Clayton Forknall, Queensland Department of Agriculture and Fisheries, Australia</i>	159
	1 Introduction	159
	2 Background to experimental design of field trials	161
	3 Designs for late-generation field trials	164
	4 Designs for early-generation field trials	169
	5 Incorporating a genetic relationship matrix	172
	6 Multi-phase design for laboratory experiments	176
	7 Conclusions	178
	8 References	179
7	Advances in molecular breeding techniques for barley: genome-wide association studies (GWAS) <i>W. T. B. Thomas, James Hutton Institute, UK</i>	183
	1 Introduction	183
	2 Progress in barley breeding	184

3	Mapping of malting quality and yield traits	187
4	Genome-wide association studies (GWAS) mapping in barley	188
5	Application of results from genome-wide association studies (GWAS) in barley improvement	192
6	Conclusion and future trends	195
7	Acknowledgements	197
8	References	197
8	Advances in molecular breeding techniques for barley: targeted induced local lesions in genomes (TILLING) <i>Serena Rosignoli and Silvio Salvi, University of Bologna, Italy</i>	203
1	Introduction	203
2	Technical details on artificial mutagenesis and mutation discovery in TILLING	204
3	TILLING resources in barley	209
4	Current and future trends of barley TILLING	209
5	TILLING versus other reverse genetics tools in barley	212
6	Conclusion	214
7	Where to look for further information	214
8	References	215
Part 3 Cultivation techniques, pest and disease management		
9	Advances in postharvest storage and handling of barley: methods to prevent or reduce mycotoxin contamination <i>Zhao Jin and Paul Schwarz, North Dakota State University, USA</i>	227
1	Introduction	227
2	Postharvest handling and storage operations for barley	228
3	Mycoflora and mycotoxins in barley	237
4	Prevention or decontamination of mycotoxins in barley storage	248
5	Post-storage treatment of barley	252
6	Conclusion and future trends	255
7	Where to look for further information	256
8	References	257
10	Fungal diseases affecting barley <i>Robert S. Brueggeman, Shyam Solanki, Gazala Ameen and Karl Effertz, Washington State University, USA; Roshan Sharma Poudel, North Dakota State University, USA; and Aziz Karakaya, Ankara University, Turkey</i>	265
1	Introduction	265
2	Understanding plant genetic resistance to fungal pathogens	267
3	Biotrophic foliar diseases: stem rust	270

4	Leaf rust	274
5	Stripe rust	276
6	Powdery mildew	278
7	Necrotrophic diseases: spot blotch	282
8	Net blotch	286
9	Ramularia leaf spot	291
10	Septoria speckled leaf blotch	294
11	Scald	297
12	Fusarium head blight	300
13	A seed-borne disease: barley stripe	304
14	Conclusion	304
15	References	305
11	Integrated disease management of barley <i>Adrian C. Newton, James Hutton Institute and SRUC, UK; and Henry E. Creissen, Neil D. Havis, and Fiona J. Burnett, SRUC, UK</i>	323
1	Introduction	323
2	Barley production context: requirements and constraints	324
3	Diseases overview	326
4	Inoculum management: sources and epidemiological conditions	330
5	Varietal resistance	331
6	Crop protectants	334
7	Agronomy	339
8	IPM knowledge sources and tools	339
9	Uptake and communication of IPM	340
10	Farming systems, soil and research platforms	342
11	Conclusion and future trends	344
12	Acknowledgements	345
13	Where to look for further information	345
14	References	345
12	Integrated weed management in barley cultivation <i>Michael Widderick, Queensland Department of Agriculture and Fisheries, Australia</i>	353
1	Introduction	353
2	Integrated Weed Management	354
3	Weed control tactics	356
4	IWM in practice	366
5	Examples of IWM in barley	367
6	Conclusion	368
7	Where to look for further information	368
8	References	369

Part 4 Quality

13	Developing barley crops for improved malt quality <i>Glen Fox, University of California-Davis, USA and The University of Queensland, Australia; and Reg Lance, Queensland Department of Agriculture and Fisheries, Australia</i>	377
	1 Introduction	377
	2 Malting quality	379
	3 Case study: modern varieties for twenty-first century brewing	388
	4 A brief history of barley improvement in Australia	393
	5 Requirements for successful programmes in malting quality improvement	394
	6 Conclusion	396
	7 Future trends	396
	8 Where to look for further information	397
	9 References	397
14	Developing barley crops for improved brewing quality <i>Søren Knudsen, Finn Lok and Ilka Braumann, Carlsberg Research Laboratory, Denmark</i>	405
	1 Introduction	405
	2 Converting barley into beer	407
	3 Breeding barley for the brewing process	408
	4 Brewing traits related to the quality of the final product	413
	5 Conclusion and future trends	416
	6 Acknowledgements	418
	7 Where to look for further information	418
	8 References	419
15	Optimising the use of barley as an animal feed <i>David M. E. Poulsen, Queensland University of Technology, Australia</i>	427
	1 Introduction	427
	2 What is 'feed barley'?	429
	3 What do we want from 'feed barley'?	430
	4 Optimising feed barley use	433
	5 Understanding and optimising feed barley quality for different livestock species	442
	6 Future trends and research opportunities	450
	7 Conclusion	456
	8 Where to look for further information	456
	9 References	456

16	Nutritional and bioactive compounds in barley <i>Nancy Ames, Joanne Storsley, Lovemore Malunga and Sijo Joseph Thandapilly, Agriculture and Agri-Food Canada, Canada</i>	467
	1 Introduction	467
	2 Key issues and challenges	468
	3 Barley bioactives	470
	4 Health benefits of barley foods	477
	5 Enhancing barley bioactivity	482
	6 Summary	484
	7 Future trends	485
	8 Where to look for further information	486
	9 References	486
	Index	497

Introduction

This collection reviews advances in research on improving barley cultivation across the value chain. Part 1 reviews advances in understanding barley physiology in such areas as plant growth, grain development and plant response to abiotic stress. Chapters also review current developments in exploiting genetic diversity and mapping the barley genome. Building on this foundation, the second part of the book summarizes advances in breeding with chapters on breeding trial design as well as advances in molecular breeding techniques such as genome wide association studies (GWAS) and targeted induced lesions in genomes (TILLING). Part 3 looks further along the value chain at ways of optimizing cultivation practices. There are chapters on post-harvest storage as well as fungal diseases, weeds and integrated methods for their management. The final part of the book assesses current developments in optimising barley for particular end uses such as malting, brewing and animal feed as well as current research on the nutraceutical properties of barley.

Part 1 Plant physiology and genetics

Chapter 1 summarizes recent advances in understanding the genetics of barley development and architecture. In particular it discusses developments in understanding barley plant structure and morphology; molecular control of vegetative development; and molecular control of reproductive development. Finally, the chapter looks at the implications of these developments for breeding more resilient and productive varieties.

The next chapter addresses the importance of cold acclimation as a coordinated metabolic rearrangement leading to frost tolerance, before going on to consider new methodologies for understanding barley's resilience to drought. The chapter considers barley's adaptation to soil salinity, its resistance to low nitrogen, and the importance of environmental adaptation as a key target for future breeding improvement. The chapter concludes by looking ahead to future research trends in this area and gives detailed suggestions on further reading.

Chapter 3 highlights the progress in our understanding of barley grain, its functional architecture, and energy metabolism shaped by the constraints of internal hypoxia. The chapter provides a current view on the relevance of programmed cell death for grain development, and mechanisms regulating sugar intake. Finally, the chapter discusses the outcome of multiscale metabolic modelling studies and how they have advanced our understanding of grain

physiology. This provides an insider's view on the life of the developing barley grain and raises new questions, which remain to be answered by applying the most advanced approaches, including nuclear magnetic resonance imaging.

Following that, Chapter 4 reviews genetic diversity in barley and its role in improving varieties, including adaptation to abiotic stresses. Sulphur is an essential macronutrient required in plants for normal growth and development. Its deficiency in agricultural soils reduces grain yield and grain quality traits. Studies conducted with barley and wheat varieties demonstrate substantial variations among crops and varieties in their response to application of different levels of sulphur. The chapter looks at factors affecting sulphur nutrition in barley and the potential role of genetic differences in breeding more resilient varieties.

Finally, Chapter 5 discusses recent changes in the field of genetic mapping that allow for new possibilities of mapping barley genomes. The chapter evaluates ways in which these strategies can be used to efficiently breed for traits that will improve the resistance of barley to various stresses as well as to meet the requirements of its several uses. This section includes a case study of the shift from rym4 to rym11. The chapter concludes by looking ahead to future research trends in this area and suggests further reading on the topic.

Part 2 Advances in breeding

Part 2 begins with a review of key developments in experimental design in barley breeding. After a brief history to set the scene, Chapter 6 covers the background of experimental design for field trials, highlighting the key principles that are still fundamental for modern comparative experiments, including model-based design. The following section explores the quantification of genetic relationships through either pedigree or molecular marker information. Finally, the chapter presents the principles of multi-phase experiments for testing material both in the field and in the laboratory. Three case studies are included to highlight non-standard experimental designs that should be in the toolkit of every agricultural scientist and which are essential for modern plant breeding programs.

Chapter 7 begins by summarizing progress in barley breeding and how the advent of molecular markers has seen development in genome mapping with relation to malting quality and yield traits. This chapter shows how genome wide association studies (GWAS) have highlighted contrasts between different breeding germplasm groups, revealing where crossing between groups can produce greater advances than continuing to cross within. GWAS can also be used as training populations for genomic selection but will remain a key R&D technology as it provides a route to candidate gene identification and hence to suitable sources of genetic diversity to maintain breeding progress. Integration

of multi-environment GWAS with climatic variables is essential to breed for adaptation to climate change.

Chapter 8 introduces artificial mutagenesis and mutation discovery in TILLING, following a review of advances in TILLING resources in barley. The chapter evaluates the efficiency and TILLING versus other reverse genetics tools in barley. It also assesses the range of TILLING applications in barley. It gives special emphasis to developments in molecular screening approaches, and on opportunities for using TILLING in barley breeding.

Part 3 Cultivation techniques, pest and disease management

Part 3 opens with Chapter 9 which focuses on post-harvest storage and handling practices of barley grain and how these methods can be used to mitigate mycotoxin contamination. It also discusses management of insect pests in stored barley. The chapter goes on to review the various mycotoxins and fungi that are associated with barley, followed by the various post-storage treatments of feed and malting barley. It concludes by summarising how post-harvest storage is an important component in the sustainable production of barley and highlights potential areas for future research.

Chapter 10 reviews current research on the main fungal diseases affecting barley. It first reviews what we know about the mechanisms of barley genetic resistance to fungal pathogens. The chapter then focuses on the description of major fungal pathogens effecting barley production, new insights into their mechanisms of virulence and implications for achieving sustainable resistance to these important pathogens. The chapter reviews current knowledge about biotrophic foliar diseases: stem rust, leaf rust, stripe rust and powdery mildew. It then discusses necrotrophic diseases: spot blotch, net blotch, ramularia leaf spot, septoria speckled leaf blotch, scald and fusarium head blight. The chapter finally discusses barley stripe.

The following chapter, Chapter 11, looks at how integrated pest management (IPM) can be applied to barley production, considering the different disease threats, the tools available to counteract them and possible approaches to deploying them. The chapter evaluates varietal disease resistance, the range of crop protectants available and how agronomy can be used to optimise protection. The chapter also discusses barriers to IPM use in practice. Finally, the chapter looks ahead to future research trends in this area. Chapter 12 examines the problem of weeds in barley and explains the application of integrated weed management (IWM) in barley cultivation. The chapter outlines weed control tactics and the practical implementation of IWM, focussing on specific examples of IWM in barley. Finally, the chapter provides detailed further reading on this issue.

Part 4 Quality

Chapter 13 introduces current challenges for improving malting barley. It goes on to review typical traits of malting quality, such as grain size, protein and germination. It also highlights the importance of malt extract obtained after the malting process, and reviews other important traits such as starch degrading enzymes, malt colour, grain hardness and other traits that are not routinely measured. A case study on modern varieties for twenty-first century brewing is also included. The chapter concludes by discussing requirements for successful programs in malting quality improvement and potential future trends in research.

Chapter 14 follows the application of barley throughout the brewing process. The chapter describes the different traits relevant during mashing, such as starch quality and heat stability of starch degrading enzymes; as well as traits during wort boiling, filtration, maturation as well as in the final product, putting special emphasis on barley-derived off-flavours. The chapter discusses breeding strategies to improve brewing quality. Finally, the chapter looks ahead to future research trends in this area.

Chapter 15 discusses the use of barley as feed for a range of livestock. The chapter reviews ways of optimising the use of barley for animal feed, from production and breeding through to the application of new technologies such as near infrared spectroscopy and molecular markers. The chapter then examines the specific grain quality and nutritional requirements of the major animal species routinely fed barley-based diets. The chapter concludes by assessing future research trends in optimising the use of feed barley.

The final chapter, Chapter 16, reviews the known and potential bioactive compounds in barley. Whole grain barley has been widely recognized as a valuable source of a number of biologically active compounds with unique health benefits. The great number of bioactive nutrients make barley an ideal raw material for the development of functional foods. This chapter discusses key issues and challenges currently faced by barley growers and manufacturers in producing high-quality products with health-promoting properties. It also reviews the known and potential bioactive compounds in barley, as well as research that has been carried out on barley and its health benefits. It concludes by discussing research that examines potential influences of barley bioactivity as well as future trends in research.

Part 1

Plant physiology and genetics

Chapter 1

Advances in understanding of barley plant physiology: plant development and architecture

Andrea Visioni, International Center for Agricultural Research in the Dry Areas (ICARDA), Morocco

- 1 Introduction
- 2 Barley plant structure/morphology and growth habit
- 3 Molecular control of vegetative development
- 4 Molecular control of reproductive development
- 5 Implications for breeding
- 6 References

1 Introduction

Crop plant improvement for food security in the face of population growth and climate change remains a key challenge for breeders. The intensive crop production achieved in recent years, which relies heavily on fertilizers, insecticides and fungicides, is not sustainable and is not a viable strategy for the future. Future crops need to be more resource-efficient and also able to adapt to their environment in a better way. Plant adaptation to environmental conditions can be enhanced by manipulating the architecture of agronomic traits with a consequent increase in grain yield.

The barley genome is large and complex but, at the same time, it offers a large reservoir of genes that can be exploited by breeders to develop new varieties with increased grain yield. The availability of barley mutants and the advances in genomics have led to an increased knowledge of the genetic factors controlling plant architecture that can be exploited by breeders. Epigenetics can also play an important role in generating further information that can be related to phenotypic response in adaptation to climate change. Ideotype breeding, proposed by Donald in 1968, is an alternative breeding strategy that aims at designing crops with optimal adaptation to target environments by combining a set of predefined traits. The recent advances in genetics and genomics could facilitate the obtainment of such ideotypes.

The on-going revolution in genomics also needs to be complemented by high-throughput phenotypic approaches to increase the rate of identification of trait-gene associations. Combining genetic knowledge of plant architecture with information about developmental processes is crucial for breeding varieties with increased adaptation and resilience to climate change, which are able to deliver competitive yields with lower inputs.

This chapter summarizes recent advances in understanding the genetics of barley development and architecture. In particular it discusses developments in understanding: (i) barley plant structure and morphology, (ii) molecular control of vegetative development and (iii) molecular control of reproductive development. Finally, the chapter looks at the implications of these developments for breeding more resilient varieties.

2 Barley plant structure/morphology and growth habit

The barley embryo is located dorsally near the basal mark of the seed. It is composed of four parts: scutellum, radicle, epicotyl and a nodal region between the epicotyl and radicle (MacLeod and Palmer 1966; Rossini et al. 2018). Vegetative development starts a few days after germination with the formation of the radicle from the apical-basal axis. The roots are then originated from the radicle. The epicotyl also starts to grow from the axis and initiates the shoot (Shaaf et al. 2019). The barley embryo contains shoot and root apical meristems (SAM and RAM, respectively). The SAM and the leaf primordia enclosed by the coleoptile are part of the epicotyl, while the RAM together with the radicle is part of the coleorhiza.

Both SAM and RAM are responsible for the architecture of the aerial and basal parts of the barley plant. SAM controls the development of the above-ground structures including the nodes, internodes, leaves, axillary meristems and the inflorescence (Sussex 1989; Babb and Muehlbauer 2003). The SAM structure has been described by Doring et al. (1999) as a system composed of two main and clonally distinct layers: L1 (*tunica*) and L2 (*corpus*). Its activity starts with the development of three or four-leaf primordia during embryogenesis. As reviewed by Rossini et al. (2014), lateral buds are located in the axil of the coleoptile and in the axil of the first leaf. Shoot architecture consists of units or modules called phytomers. The basic module of plant architecture, the phytomer, is made of an internode, a leaf and axillary bud (Sharman 1942). The basal region of the plant (also known as the crown) is composed of the first set of phytomers developed from the SAM. Their internodes do not elongate. In fact, internode elongation in barley occurs only after the transition from the vegetative to reproductive phase. The number of leaves produced, and consequently the number of basal internodes at the barley culm, depends on genetic and environmental factors. A part of those internodes will elongate after

the transition from the vegetative to reproductive phase (Kirby and Appleyard 1987).

Tiller development in barley occurs as a result of the proliferation of axillary meristems (AXMs) located between the stem and the leaf/coleoptile. As reported by Hussien et al. (2014), the AXM produce an axillary bud that may produce a lateral shoot with a structure similar to the main culm. The AXM produces a stem cell accumulation in the leaf axil. Afterward, cells differentiate into primordial leaves that finally result in axillary buds. Tillers will finally originate only from subsets of the axillary buds while the rest will remain at the bud stage. Tillers are usually classified as primary tillers if they are originated from the main stem and as secondary tillers when they are derived from the primary tillers (Hussien et al. 2014). Tillers production is reiterative and further tillers (tertiary tillers) can originate from secondary tillers. Tiller outgrowth is controlled by a tangled network of hormonal and regulatory signals that leads to a high morphological diversity between genotypes and within the same genotypes (Kebrom et al. 2012; Shaaf et al. 2019). In barley and wheat the number of stems produced depends on genetic and environmental factors and, in general, winter genotypes produce more tillers (Kirby and Appleyard 1987). The transition phase between the vegetative stage and the reproductive stage is also under the control of genetic, environmental and hormonal factors.

Stem elongation begins when aerial internodes start to grow at the beginning of the reproductive phase. Elongation starts from basal internodes located at the bottom of the plant and continues toward the top with the elongation of internodes located in a more apical position (Briggs 1978). The process is complete when the last internode (called a peduncle) completes its elongation. Usually the internodes of a mature barley plant are longer than those immediately below. The only exception in some cases is the peduncle (Briggs 1978). A meristematic zone located in the base of the internode ensures the restoration of a vertical stem orientation in the case of lodging. The meristem is capable of asymmetric growth and delayed lignification (Briggs 1978). The inner layer of the internode is composed of a cavity pith surrounded by the parenchyma that contains additional vascular bundles and by a ring of sclerenchyma. The outer part is composed of alternate vertical files and sclerenchyma fibers supporting vascular bundles surrounded by a silicified epidermis (Briggs 1978).

Leaves originate from a ring of founder cells recruited on the SAM flank (Bossinger et al. 1992; Shaaf et al. 2019). The leaf primordium is located in the insertion disk at the node (Sharman 1942). A barley leaf has a strap-like appearance and is divided into a distal blade and proximal sheath that wraps around the culm and supports the blade (Rossini et al. 2018). The blade is the major photosynthetic organ of the plant. The ligular region, composed of a ligule and two auricles, separates the blade from the sheath (Rossini et al.

2018). Cell division ensures the differentiation and the growth of the leaf. The expansion pattern occurs in a basipetal wave, from the tip to the base, with the sheath cells still dividing when the blade cells are fully differentiated (Sylvester et al. 1990; Kołodziejek et al. 2006). Cell division undergoes both longitudinal and transverse divisions to support leaf growth in width and length (Sylvester and Smith 2009). The final leaf size (an important factor for photosynthesis efficiency) and leaf shape depends on the spatial and temporal coordination of these processes (Shaaf et al. 2019). Leaf orientation and angle also plays an important role in photosynthesis efficiency and is determined by the lamina joint that connects the blade to the sheath (Shaaf et al. 2019).

Inflorescence development starts with the transition of the SAM to an inflorescence meristem through the so-called double ridge phase. During this phase the apex is elongated about 1 mm. Each inflorescence primordium is composed of a leaf primordium and a lateral meristem (Kirby and Appleyard 1987). The lateral meristem then becomes the main growing point from where three spikelet triplet meristem (one central and two laterals) will originate, while the leaf primordium will not develop further (Bossinger et al. 1992; Rossini et al. 2014). The three-spikelet meristem stage is also called the triple-mound stage where each spikelet meristem will evolve into a floral meristem. Afterward, two outer glumes primordia originate from the floral meristems to give rise to the floral organ primordia. The final step of floral development is the sequential differentiation of glume, lemma and stamen primordium in the mature spikelet (Rossini et al. 2014). A spikelet located in the central region of inflorescence axis will develop earlier than basal and apical spikelets. The final number of spikelets is defined by the apex that continues to initiate new spikelet meristems until the awn primordium stage. At this stage the spike layout and spikelet structure are completed (Kirby and Appleyard 1987). The fully developed barley spike is composed of floral units (spikelets) located on the floral stem. Each spikelet consists of a floret and two subtending bracts called the outer glume. The spikelets are usually organized in triplets at each rachis node.

The spikelet axis also bears the so-called lemma, an abaxial floral bract that encloses single florets and carries the awn. Several authors have reported that this complex can be considered to be a reduced vegetative leaf where the lemma corresponds to the leaf blade while the awn is considered as the sheath (Dahlgren et al. 1985; Clifford 1988; Pozzi et al. 2000; Rossini et al. 2014). Spikelet fertility is different between two- and six-rowed barley varieties. In the first, each triplet contains only one fertile spikelet while, in the second, all three are fertile. Lateral spikelets develop slower than the central spikelet and this may result in the development of very rudimentary and sterile structures that represent the typical two-rowed barley structure. The six-rowed barley spike structure is the result of a recessive mutation at the *Vrs1* gene locus. *Vrs1* locus promote the development of the lateral spikelets that become morphologically

indistinguishable from the central spikelet, resulting in the typical six-rowed barley spike (Kirby and Appleyard 1987; Komatsuda et al. 2007).

3 Molecular control of vegetative development

The pre-anthesis developmental phase in barley consists of the vegetative and early and late reproductive stages. All of these three phases impact grain yield. During the vegetative and early reproductive phases in particular, the number of tillers, plant height, biomass accumulation and leaf angle and area can have a direct impact on grain yield.

Tillering is one of the most important and critical traits for improving grain yield in temperate cereals (Sreenivasulu and Schnurbusch 2012; Jia et al. 2011). Cereals such as barley are able to increase grain yield through an increased number of tillers (Evers and Vos 2013). On the other hand, as reviewed by Shaaf et al. (2019), tillering potential needs to be carefully balanced to avoid a number of problems (Peng et al. 1994; Kennedy et al. 2017; Tripathi et al. 2003; Kuczynska et al. 2013; Mew 1991):

- 1 an excessive number of tillers will result in unfertile spikes;
- 2 unfertile tillers divert resources from developing spikes;
- 3 tillers can have negative effects on other traits related to biomass accumulation; and
- 4 a crowded canopy can foster the spread of disease.

Numerous mutants have been identified and characterized recently. Many of them have been used to develop near-isogenic (NI) lines in the cv. Bowman collection (Druka et al. 2011). These have been classified into:

- 1 mutants which fail to develop auxiliary buds (single culms mutants);
- 2 mutants with weak auxiliary bud development;
- 3 mutants with low tillering reduction; and
- 4 mutants producing high tiller number.

A comprehensive and more detailed review of available barley tillering mutants can be found in a recent publication from Shaaf et al. (2019). Tillering is considered as a complex trait that is strongly influenced by environmental and growing conditions such as light intensity and water availability and in which phytohormones also play a crucial role (Kebrom et al. 2013; Alqudah et al. 2016). As reviewed by several authors, phytohormones regulate bud growth through a very complex pathway in which different phytohormones interact (Evers and Vos 2013; Kebrom et al. 2013). Recent evidence suggests that

sugars might also be involved in the branching process through the regulation of phytohormonal gene expression (Barbier et al. 2015).

Several QTL and GWAS studies in the past decade have suggested a correlation between tillering and other important regulatory traits such as vernalization and photoperiod sensitivity, flowering time and plant height (Abeledo et al. 2004; Borràs et al. 2009; Alqudah and Schnurbusch 2013; Alqudah et al. 2016). Several authors reported that *Vrn-H1*, *Vrn-H2* and *Ppd-H1* have a significant effect on tiller production. In particular, it was reported that tiller number increased in genotypes with a strong vernalization requirement and reduced photoperiod sensitivity (Karsai et al. 1999; von Korff et al. 2006; Wang et al. 2010). On the basis of these studies, it was suggested that those three genes may regulate tillering indirectly by controlling flowering time (Corbesier et al. 2007; Tamaki et al. 2007).

The *Vrs1* and *Int-C* genes are responsible for spike morphology and are also related to tillering. *Vrs1* is a major gene controlling the row type of barley spike. *Vrs1* encodes for the two-row spike while mutations in the gene result in the six-row spike. Alqudah and Schnurbusch (2014) found significant differences in tiller number associated with row number under different growing conditions. Furthermore pleiotropic effects on tiller number are associated with allelic status at the *Vrs1* locus. *Int-C* is the barley homolog of maize *TB1* (*TEOSINTE BRANCHED 1*). It inhibits bud outgrowth by regulating the *GT1* gene (*GRASSY TILLERS 1*; Alqudah et al. 2016). *Int-C* has been identified as a major gene-controlling lateral spikelet development that also represses the number of tillers in barley early in development (Ramsay et al. 2011).

A more recent study revealed that there are five major row-type loci (*Vrs1*, *Vrs2*, *Vrs3*, *Vrs4* and *Vrs5*) that can convert spikes from the two-rowed to six-rowed type (Zwirek et al. 2019). The recessive alleles at *vrs4* and *vrs5* also affect tillering. Genotypes carrying *Vrs1* and paired *vrs3*, *vrs4* or *vrs5* recessive alleles showed increased spikelet fertility and variation in tillers numbers. In the case of *vrs3* in *vrs4* background, Zwirek et al. (2019) reported loss of spikelet identity and determinacy, improved grain homogeneity and increased tillering, while *vrs5* in the same background was reported to be associated to decreased tiller number and increased grain weight.

A further study by Alqudah et al. (2016) investigated QTL underlying natural variation in number of tillers per plant at different pre-anthesis stages, and differences in plant height at harvest based on differences in row type and photoperiod response in a spring barley collection. This work clearly demonstrated a link between tillering, heading date and plant height. The study from Alqudah et al. (2016) revealed that the major loci controlling tillering were *Vrs1* and *Ppd-H1*. Accessions carrying the *Ppd-H1* allele showed several QTL associated with an increased number of productive tillers. Two-rowed accessions showed a more complex genetic make-up of tillering than six-rowed

accessions. The *Vrs1* gene was seen to have a pleiotropic effect in increasing the number of tillers, probably as compensation for the reduced number of seed produced. Experimental evidence suggests that the *Vrs1* gene also controls plant height. Accessions carrying this allele were taller than accession carrying the *Vrs1* allele. The QTL detected for plant height seems to collocate with genes involved with flowering time regulators and sugar-related genes. Interestingly, QTL for tillering and plant height are co-localized in genomic regions harboring plant stature-related phytohormones and sugar-related genes.

Brassinosteroids, gibberellins and stringolactones are the three phytohormones that play a key role in determining plant height. Dwarf and semi-dwarf phenotypes can be the results of lower production or insensitivity to those phytohormones, which usually arise from disorders in their biosynthesis or signaling pathways (Marzec and Alqudah 2018). Semi-dwarf varieties were one of the key factors in the success of the Green Revolution. Shorter plants usually have increased stem sturdiness, lodging resistance, improved response to fertilizers and enhanced grain yield. These semi-dwarf varieties were achieved using mutations in gibberellin pathway genes and metabolism (Hedden 2003). Semi-dwarf wheat and rice varieties introduced during the Green Revolution have dramatically increased yield due to the repartitioning of assimilate from stems to grain production (Khush 2001).

Since the beginning of Green Revolution, reduced plant height has always been a priority for breeders, especially to increase lodging resistance. For this reason numerous loci involved in plant height have been identified through QTL mapping and GWAS (Salvi et al. 2013; Rossini et al. 2018). A huge number of mutants have been identified and classified into different categories on the basis of their phenotypic changes, pleiotropic characteristics that often accompany short culm phenotypic changes, parental background such as brachytic (*brh*), brevistaristatum (*ari*), dense spike (*dsp*), erectoides (*ert*), semibrachytic (*uzu*), semi-dwarf (*sdw*) or slender dwarf (*sld*) (Franckowiak and Lundqvist 2013; Dockter et al. 2014). More information about barley mutants can be found in recent reviews (Rossini et al. 2014; Dockter and Hansson 2015). These mentioned pleiotropic effects have limited the use of semi-dwarfing genes in breeding programs due to the negative effects on phenotypes such as low vigor and reduced yield (Rossini et al. 2018).

Uzu is a semi-dwarf gene that seems to be the ortholog of Arabidopsis and rice BRASSINOSTEROID-INSENSITIVE1 (*BRI1*), encoding a brassinosteroid receptor (Li and Chory 1997; Chono et al. 2003). It is one of the few genes shaping plant height that have been successfully used in breeding. Accessions carrying the *uzu1.a* allele show sturdy culm, lodging resistance and tolerance to dense planting due to leaf erectness. *Uzu1.a* expression is sensitive to temperature, exhibiting a mild phenotype at 14°C and a stronger phenotype at 26°C as reported by Dockter et al. (2014). This sensitivity to heat is a

limitation to the diffusion of this allele that is mainly restricted to East Asia. However recently new uzu alleles, less sensible to high temperature, have been identified and they could represent an alternative to uzu1.a (Dockter and Hansson 2015).

Two mutations that are more extensively used by breeders in Europe and North America and Australia include *sdw1* and *denso* (Hellewell et al. 2000), both located on chromosome 3H and thought to be allelic (Hellewell et al. 2000; Jia et al. 2009). Beside mutants, many QTL and GWAS studies have identified loci and candidate genes controlling plant height, like the brassinosteroid biosynthesis gene *DWARF4* (*HvD4*), that has not been described in other species, and *HvCPD* that encodes a protein involved in brassinosteroid biosynthesis (Alqudah et al. 2018; Dockter et al. 2014; Marzec and Alqudah 2018).

Leaf angle is regulated by phytohormones, among which brassinosteroids play a major role (Sakamoto et al. 2006a; Hartwig et al. 2011). Brassinosteroids have been reported to control many physiological processes like cell expansion, stomata development, photo-morphogenesis, plant height, grain size and stress response (as reviewed by Shaaf et al. 2019). The leaf angle is controlled at the lamina joint level by brassinosteroids. The phytohormone seems to promote cell proliferation on the adaxial side while it suppresses cell division on the abaxial side (Sun et al. 2015). Enlarged leaf angle is associated with increased brassinosteroid content or increased brassinosteroid signaling, while brassinosteroid-deficient mutants have erect leaves (Shaaf et al. 2019).

As mentioned before, the *uzu1.a* allele is associated with erect leaves, making genotypes carrying this allele suitable for high-density planting. *Uzu1.a* was the first gene cloned among the brassinosteroid mutants in barley. Gruszka et al. (2016) identified two semi-dwarf barley mutants for *HvDWARF*, the barley ortholog of rice *OsDWARF*. A mutation on the rice gene causes reduced plant height and erect leaves (Hong et al. 2002). Resequencing of the barley mutants showed that missense mutation in the coding sequence can potentially affect the conserved sequence of the protein. The mutants also showed a reduced transcription of *HvBAK1*, another component of the brassinosteroid signal pathway. In rice and *Arabidopsis* this is associated with changes in plant height, leaf erectness, grain morphological features and disease resistance (Li et al. 2009). *HvDWARF4* has been identified as one of the genes from the brassinosteroid pathway controlling plant height in barley that could also play a role in controlling leaf angle as its rice ortholog *OsDWARF4*. Further work on its functional characterization may confirm the role of *HvDWARF4* in determining leaf angle (Sakamoto et al. 2006b; Dockter et al. 2014).

Leaf area is also an important trait for breeding. The size and the shape of leaves and their position are closely related to photosynthesis, photosynthetic efficiency and with the amount of assimilates produced by plants (Jiang et al. 2015; Driever et al. 2014). The amount of assimilates produced by plants

generally means more fertile tillers, more spikes and increased spikelets survival with direct consequences on grain yield (Marzec and Alqudah 2018).

A recent GWAS analysis identified nine genes involved in the genetic control of leaf area in barley, all involved in different phytohormone pathways (gibberellins, brassinosteroids and stringolactones), suggesting that these phytohormones might regulate the leaf area independently from other traits such as branching (Marzec and Alqudah 2018; Alqudah et al. 2016). Results showed the effect of the Ppd-H1 gene, while the less photoperiod-sensitive allele (ppd-H1) was also associated with increased leaf areas when associated with the Ppd-H1 allele. Other associations with leaf area were found for other genes related to heading time and sugar-related genes (Alqudah et al. 2018). Molecular regulation of leaf area development needs to be further investigated in order to identify genes and use these genes in breeding programs.

4 Molecular control of reproductive development

Because of its relationship with grain yield and grain number, understanding the genetic control of barley inflorescence development is of primary importance in plant breeding. Dozens of barley mutants with altered spike and spikelet morphology have been described and mapped, providing an ideal starting point for the genetic analysis of inflorescence development (Druka et al. 2011; Franckowiak and Lundqvist 2010; Sreenivasulu and Schnurbusch 2012; Rossini et al. 2014). Most of the differences in spike morphology in grasses are reflected by the extent of inflorescence branching (Koppulu and Schnurbusch 2019). Several studies suggest that branched inflorescence is the basis of the evolution of most evolved/derived inflorescences (Vegetti and Anton 1995; Endress 2010; Kellogg et al. 2013).

Mutants with non-canonical spike branching have been identified in barley. Recessive mutations at the branched1 (*brc1*) and compositum (*com1* and *com2*) loci cause the development of branches from rachis nodes in the basal portion of the spike (Franckowiak and Lundqvist 2010; Druka et al. 2011). Wild-type *COM1* and *COM2* genes determine spikelet meristem characteristics and branching (Franckowiak and Lundqvist 2013; Koppulu and Schnurbusch 2019). Paired or supernumerary spikelet formation in barley seems to be under the control of the *flo* locus. The underlying genetic mechanism is not known but was recently elucidated in wheat (Boden et al. 2015; Dixon et al. 2018). The loss of function of the photoperiod-insensitive *Ppd-D1* allele attenuates *FT1* expression, thus promoting paired spikelet formation (Boden et al. 2015). Interestingly, *TB1* (that also regulate the expression of *FT1*) promotes paired spikelet formation by interacting directly with *FT1*. *TB1* competitively binds *FT1*, making it less available and delaying meristem maturation (Dixon et al. 2018).

A characteristic feature of the barley spike is the triplet spikelet meristem. In wild and two-rowed barley the lateral spikelets are sterile. Each spike node develops one central fertile grain-bearing spikelet and two lateral sterile spikelets. The characteristic two-row shape comes from the position of the two fertile central spikelets that are located at the rachis. Six-rowed barley shows three fertile spikelets that form six rows of grains (Zohary and Hopf 2000). Lundqvist and Lundqvist (1988) identified 11 loci that can modify lateral spikelet fertility and that can independently convert two-rowed barley into a six-rowed barley. The genes are *vrs1*, *vrs2*, *vrs3*, *vrs4* and *Int-C*. In natural six-rowed barley the predominant genotype is *vrs1.a* that promotes lateral spikelet fertility. *Vrs1* also affects leaf primordium size and leaf area (Thirulogachandar et al. 2017). Different combinations of *vrs1* and *Int-c* alleles are found in barley germplasm, leading to various levels of lateral spikelet development and fertility (Ramsay et al. 2011). For example, *Int-c.a* is the less functional allele of *HvTB1*, the barley orthologous of the maize teosinte branched gene. It facilitates the growth of lateral spikelets together with the *vrs1.a* allele and contributes to increased grain size (Ramsay et al. 2011). On the other hand, the recessive *int-c.b* allele is commonly found in two-rowed (*Vrs1*) cultivars where it inhibits anther development in lateral florets, while in six-rowed (*vrs1*) cultivars it results in reduced lateral spikelet development (Rossini et al. 2014). It has been found that in several six-rowed barley accessions the mutation in *Vrs1* is absent and this accession also does not show alterations in *Vrs1* expression (Komatsuda et al. 2007; Youssef et al. 2017b), suggesting that the suppression of lateral spikelet fertility might also be controlled by other genes.

It has also been reported that intermediate spike morphology is under the control of *Vrs3*. Genotypes carrying the *Vrs3* mutant allele show a two-rowed condition in the lower third of their spike. The weaker six-rowed genotype may indicate a specific developmental regulation for *Vrs3* across the spike (Koppulu and Schnurbusch 2019).

Rachis length and the number of spikelets per spike units (spike density) are generally correlated traits. In fact, longer rachis correlates positively with longer internodes and also negatively with spike density. The allelic variation that controls rachis development results in a range of phenotypes, often associated with alterations in other traits (Rossini et al. 2014). As reviewed by Terzi et al. (2017) several loci are involved in the modulation of spike density, such as *dense spike*, *zeocriton*, *lax spike* and *laxatum*.

The *laxatum* mutant phenotype is characterized by long rachis internode, a large base of lemma awns and five anthers instead of the regular three (Civáň and Brown 2017; Jost et al. 2016). The spike density seems to be under the control of several major genes, for example, *dense spike* genes (*dsp*) which control rachis internode length, resulting in dense or compact spikes. The *Dsp.ar* and *Dsp1* gene seems to be located on the same position on chromosome

7H close to the *lks2* gene that produces short awns (Shahinnia et al. 2012; Taketa et al. 2011). As reviewed by Terzi et al. (2017), the transcription factor HvAP2 (ortholog of APETALA2), which is driven by microRNA 172, regulates the length of the critical developmental window required for the elongation of the inflorescence internodes which has a critical effect on spike density.

The awn, the extension of the lemma, is a photosynthetic organ that plays an important role in grain size and yield and also shows a wide natural variation in length and shape (Terzi et al. 2017). Mutants can show this variation. A study conducted by Yuo et al. (2012) on the short awn 2 (*lks2*) gene demonstrated that this mutation affects the awn's cell proliferation, resulting awns 50% shorter than the wild type. Natural recessive variants of the *lks2* gene are widespread in Eastern Asia, possibly offering adaptation to high-precipitation conditions (Rossini et al. 2014). The so-called hooded phenotypes are another example of awns morphology variation, where a mutation causes the appearance of an extra flower of inverse polarity on the lemma. The mutant phenotype is caused by a 305-base pair duplication in intron 4 at the single dominant genetic locus *Knox3* (Müller et al. 1995). Hooded barley cultivars represent an interesting option for feed use as the presence of awns is unsafe for animals (Blake et al. 2011).

In covered barleys, the typical barley is used for both animal feed and malting. A lipid layer is present and favors the adhesion of the hull to the caryopsis surface. Hullless or naked barley results from a mutation on the *nud* gene that regulates the deposition of lipids on the epidermis of the pericarp. The *nud* gene is a transcription factor of the ethylene response factor (ERF) family regulating the lipid biosynthesis pathway (Terzi et al. 2017; Taketa et al. 2008). Naked barley is becoming popular in several countries as a health food due to its nutritional properties (i.e. β -glucans). Naked barley does not need to be pearled, thus reducing production costs while also preserving its nutraceutical content.

Barley is an autogamous plant and its stigmas become receptive before anther extrusion. When the anthers become ready for pollination, the stigmas are able to capture sufficient pollen. Another feature of barley florets is cleistogamy that ensures self-pollination through floret morphology. Florets show smaller lodicules in comparison with the non-cleistogamous types. In typical barley florets, palea and lemma remain tightly closed throughout the period of pollen release. Lodicule development is under the control of the *Cly1* gene, an APETALA2 transcription factor (Nair et al. 2010). A mutation on the recessive allele of *Cly1* gene leads to an increased expression that produces lodicule reduction. In genotypes carrying the *Cly1* dominant allele, the downregulation of the *Cly1* gene expression promotes the growth and the swelling of the lodicules, making the plant chasmogamous (Rossini et al. 2014).

5 Implications for breeding

Barley is generally known as an adaptable crop with the ability to cope with both abiotic and biotic stresses. However, even though it could be considered as a more resilient 'climate change' crop, it is still susceptible to major abiotic and biotic stresses. To ensure food security, breeders need to continue to develop new varieties that are capable of adapting to climate change and lower inputs. Current knowledge of plant architectural traits can be exploited to achieve improved genotypes.

In the case of rice, grain yield increase through the manipulation of tiller numbers was achieved by the International Rice Research Institute (IRRI; www.irri.org) by reducing the number of unproductive tillers (Peng et al. 2008). The Chinese 'super rice' initiative also achieved a significant grain yield increase by exploiting natural variation available in rice germplasm, combining optimal plant architecture and number of tillers (Qian et al. 2016; Wenfu et al. 2007). In barley the genetic factors controlling tillering plasticity are still only partially understood. However, it has been shown that vernalization and flowering time can be manipulated to increase grain yield by optimizing the number of fertile tillers (Shaaf et al. 2019). New insights on genes controlling tillering at the pre-anthesis developmental phase can be found in a GWAS study by Alqudah et al. (2016). This identified a QTL on chromosome 2H shown to be associated with the production of productive tillers in six-row genotypes. The QTL overlaps with the HvDRM1 gene in wheat. The expression of the DRM1-like gene is associated with tiller bud dormancy in a tiller inhibition mutant (Kebrom et al. 2012). Alqudah et al. (2016) identified three further QTL on chromosomes 1H, 2H and 5H associated with productive tiller production. The QTL on 2H is located near the HvBRD locus, an important regulator of plant height in barley. Once validated, these QTLs might be useful for breeders to genetically manipulate the number of tillers in barley to increase grain yield. The same study also identified novel QTL for plant height and suggested the role of Vrs1 in controlling plant height in addition to lateral spikelet development and tillering.

Alqudah et al. (2016) also reported a QTL for plant height located in a putatively sugar-related chromosomal region on chromosome 3H, suggesting that sugars may also be involved in plant height regulation. A few genes controlling plant height have been used in breeding such as *uzu1.a*, *sdw* and *denso*. New *uzu* alleles which are less sensitive to temperature have been identified which might help to overcome the limitations of *uzu1* (Docker and Hansson 2015). Recent GWAS studies have demonstrated the effect of loci-involved brassinosteroid biosynthesis (i.e. HvD4 and HvCPD) in regulating plant height. The link between tillering and plant height needs to be further investigated for a better understanding of the genetic relationship between the two traits that may then lead to the identification of useful genes for breeders.

Table 1 Table of genes involved in barley plant development and architecture

Gene abbreviation	Chromosome	Gene product annotation	References
Vrs-3	1H	Putative jumonji C-type (JMJC) H3K9me2/3 histone demethylase	Bull et al. (2017), van Esse et al. (2017)
Ppd-H1	2H	PPR pseudo response regulator	Turner et al. (2005)
Vrs-1 (HvHox1)	2H	Homeodomain-leucine zipper class I protein (HD-ZIP I)	Komatsuda et al. (2007)
HvAP2	2H	APETALA2 transcription factor	Houston et al. (2013)
Cly1	2H	Cleistogamy 1 gene	Wang et al. (2015)
HvDRM1	2H	DORMANCY-ASSOCIATED1	Alqudah et al. (2016)
HvBRD	2h	BRASSINOSTEROID-DEFICIENT DWARF2	Dockter et al. (2014), Alqudah et al. (2016)
Vrs-4 (HvRA2)	3H	RAMOSA2	Koppolu et al. (2013)
uzu (HvBR1)	3H	Brassinosteroid insensitive	Chono et al. (2003), Dockter et al. (2014)
uzu1.a (HvBR1)	3H	Brassinosteroid insensitive	Chono et al. (2003), Dockter et al. (2014)
sdw1/denso	3H	Gibberellin 20-oxidase gene (HvGA20ox2)	Kuczynska et al. (2013), Xu et al. (2017)
Vrn-H2 (HvZCCT-Hb)	4H	ZCCT gene family member	von Zitzewitz et al. (2005)
Vrs-5 or Int-C (HvTB1)	4H	TEOSINTE BRANCHED1	Ramsay et al. (2011)
HvD4	4H	Brassinosteroid biosynthesis gene DWARF4	Dockter et al. (2014), Alqudah et al. (2018)
Vrn-H1 (HvBM5A)	5H	HvBM5A; MADS-box	von Zitzewitz et al. (2005)
Vrs-2	5H	Homolog of the Arabidopsis SHORT INTERNODES gene	Youssef et al. (2017a)
HvCPD	5H	BRASSINOSTEROID C-23 HYDROXYLASE	Dockter et al. (2014)
FT1	7H	FLOWERING LOCUS T	Faure et al. (2007)
lks2	7H	NA	Shahinnia et al. (2012), Taketa et al. (2011)
Dsp1	7H	NA	Shahinnia et al. (2012), Taketa et al. (2011)
Dsp.ar	7H	NA	Shahinnia et al. (2012), Taketa et al. (2011)
Nud	7H	Ethylene response factor (ERF) family	Taketa et al. (2008)

Index

- AA. *see* Amino acid (AA)
- AAL. *see* Apparent attenuation limit (AAL)
- Abiotic stress. *see* Physiology
- Adopt-a-Crop online platform 340
- AED. *see* Apparent energy digestibility (AED)
- Afghanistan 100
- Aflatoxins (AFs) 238, 243
- AGG. *see* Australian Grains Genebank (AGG)
- AGOUEB. *see* Association Genetics of UK Elite Barley project (AGOUEB)
- Agricultural and Horticultural Development Board (AHDB) 184
 - Barley Disease Management Guide for the United Kingdom 340
- AGT. *see* Appressorial germ tube (AGT)
- AHDB. *see* Agricultural and Horticultural Development Board (AHDB)
- Alberta Agriculture breeding programme 438
- Algeria 100
- Alkylresorcinols 473–474
- Alternative oxidases (AOX) 74
- American Society of Brewing Chemists method 382
- Amino acid (AA) 72–73
- Amplified Fragment Length Polymorphisms and Simple Sequence Repeats 184
- α -Amylases 449
- Amylose-to-amylopectin ratio 69
- Animal feed 427
 - feed barley and 429–433
 - breeding varieties 434–436
 - cattle 443–445
 - modern selection tools for improving feed quality 438–441
 - pigs 445–448
 - poultry 448–450
 - Premium Grains for Livestock Program 436–438
 - processing 441–442
 - production, optimising 433–434
 - sheep 445
 - future trends 450–455
- Anthocyanins 475
- A-optimality criterion 165
- AOX. *see* Alternative oxidases (AOX)
- Apparent attenuation limit (AAL) 385
- Apparent energy digestibility (AED) 447, 448
- Appressorial germ tube (AGT) 279
- Arabinoxylan 383, 384
- Argentina 100, 233
- Association Genetics of UK Elite Barley project (AGOUEB) 192, 193
- Australia 101, 233, 274, 282, 355, 364, 365
- Australian Barley Board 388
- Australian Grains Genebank (AGG) 100, 395
- Australian Grain Technologies 393
- Australian Journal of Agricultural Research* 436
- Australian Winter Cereals Molecular Marker Program (AWCMMP) 439
- Autoregressive process 165
- Avena fatua* 358, 367, 368
- AWCMMP. *see* Australian Winter Cereals Molecular Marker Program (AWCMMP)
- Awn 13
- Axillary meristems (AXMs) 5
- Barley Breeding Australia (BBA) 392, 393
- Barley Oligo Pooled Arrays 185
 - mapping, and yield traits 187–188
- Barley stripe 304
- Bass variety 392
- BBA. *see* Barley Breeding Australia (BBA)
- Beauvericin (BEA) 246

- Beta-amylase 387, 411–412
 Bile acids 478
 Bin dryer 232
 Biocontrol 254
 approaches 252
 Biostimulant 334–335
 Biotrophic foliar diseases 270–274
 Biotrophs 268
 Bi-parental mapping 188
Bipolaris sorokiniana 282–285
 Black point. *see* Kernel blight
 Blocking 162–163
Blumeria graminis f. sp. *hordei* 278, 281
 Brassinosteroids 10, 16
 Breeding experiments advanced
 designs 159–161
 early generation field trials
 designs 169–172
 field trials experimental design 161–164
 genetic relationship matrix 172–173
 partially replicated design
 incorporating genetic
 relatedness 173–175
 late-generation field trials designs
 164–165
 case study 166–168
 multi-phase designs for laboratory
 experiments 176–178
 multi-phase design in laboratory 178
 Brewer's spent grain (BSG) 485
 Brewers Clarex® 415
 Brewing quality improvement 405–406
 barley conversion to beer and 407–408
 beta-glucans and impact on mashing and
 filterability and 412–413
 breeding barley for brewing process
 and 408–412
 final product quality traits 413
 colloidal haze formation 415–416
 off-flavours elimination through
 targeted breeding 413–415
 future trends 416–418
 Brown rust 275
 BSA. *see* Bulk segregant analysis (BSA)
 BSG. *see* Brewer's spent grain (BSG)
 Bulk segregant analysis (BSA) 134, 135, 191
 Buloke variety 392

 Canada 365, 429, 467
 Canadian Grain Commission 235
 Canola 114
 Canopy senescence 30

 CAP. *see* Co-ordinated Agricultural Project
 (CAP)
 Carbon dioxide 237
 Caryopsis 56, 63, 76
CBF genes 27
 CDC PolarStar 414
 Chasmothecia 280
 Chloroplast 26
 CIM. *see* Composite interval mapping (CIM)
 Clustered Regularly Interspaced Short
 Palindromic Repeats (CRISPR) 212,
 213
 Cly1 gene 13
 Commander variety 392
 Compass variety 392
 Composite interval mapping (CIM)
 129–130
 Conidia 287–288, 298, 299
 Conservation Agriculture systems 355
 Co-ordinated Agricultural Project
 (CAP) 190
 COR genes 26
 cp TILLING 209
 CRISPR. *see* Clustered Regularly Interspaced
 Short Palindromic Repeats (CRISPR)
 Crop Monitor online platform 340
 Cutlass variety 108

 DArT. *see* Diversity Arrays Technology (DArT)
 DE. *see* Digestible energy (DE)
 Demethylation inhibitors (DMIs) 299
 Denmark 337, 364
 Deoxynivalenol (DON) 240, 241, 249, 254,
 301, 303–304
 DH. *see* Doubled haploid (DH) lines
 Diastatic power (DP) 378, 388, 409
 relationship with % Malt Extract 389
 Diatomaceous earth-based grain
 protectants 237
 Digestible energy (DE) 432, 445–446
 Dimethyl sulphide (DMS) 414, 415
 Disease escape 333
 Disease tolerance 332–333
 Distinctness, Uniformity and Stability (DUS)
 tests 184, 193, 333
 Diversity Arrays Technology (DArT) 174
 DMIs. *see* Demethylation inhibitors (DMIs)
 DMS. *see* Dimethyl sulphide (DMS)
 DON. *see* Deoxynivalenol (DON)
 Doubled haploid (DH) lines 129
 Double knock approach 357
 Dovetail Chicago™ 138

- DP. *see* Diastatic power (DP)
- Drought 24
resilience to 28–33
- Dry rolling 441
- DUS. *see* Distinctness, Uniformity and Stability (DUS) tests
- Economic Commission for Europe 103
- Edstar Genetics 393
- EFSA. *see* European Food Safety Authority (EFSA)
- EMC *see* Equilibrium moisture content (EMC)
- EMS. *see* Ethyl methanesulfonate (EMS)
- Endosperm transfer cells (ETC) 58, 59, 62, 63, 64
- Enniatins (ENNs) 246
- Ensembl Plants database 140
- eQTL. *see* Expression QTL (eQTL)
- Equilibrium moisture content (EMC) 233
- Ergot 238, 243
- ETC. *see* Endosperm transfer cells (ETC)
- Ethiopia 100, 101
- Ethiopian Biodiversity Institute 100
- Ethyl methanesulfonate (EMS) 205
mutation 135
- European Brewery Convention method 382
- European Food Safety Authority (EFSA) 241
- Exome capture 127
- Expression QTL (eQTL) 143
- FDA. *see* US Food and Drug Administration (FDA)
- Fermentable sugars 383
- FHB. *see* Fusarium Head Blight (FHB)
- Field fungi 247
- Flagship variety 174, 392
- Flavonoids 474–475
- Flinders variety 392
- Florets 13
- Foliar fungicides 278, 299
- Fragment Analyzer™ 135
- FRAG-UK. *see* Fungicide Resistance Action Group UK (FRAG-UK)
- Friability 386
- Frost tolerance 25–28, 38
- FT1 11
- FTIR microspectroscopy 64
- Fumigation 237
- Fumonisin 240, 243
- Fungal diseases 265–267
fusarium head blight 300–304
leaf rust 274–276
necrotrophic diseases 282–286
net blotch 286–291
plant genetic resistance to fungal pathogens and 267–269
powdery mildew 278–281
Ramularia leaf spot 291–294
scald 297–300
seed-borne disease 304
Septoria speckled leaf blotch 294–297
stem rust 270–274
stripe rust 276–278
- Fungicide Resistance Action Group UK (FRAG-UK) 340
- Fungicides 278, 280–281, 334–335
application methods 336
modes of action 337
stewardship 337–339
- Fusarium graminearum* 301–302
- Fusarium Head Blight (FHB) 249, 433
- G × E × M effects 433
- γ-aminobutyric acid (GABA) 79
- GBSS. *see* Granule-bound starch synthase (GBSS)
- Genebank genomics 196
- Gene editing 333
- Gene-for-gene hypothesis 268
- GENEVESTIGATOR database 139
- Genome mapping and exploitation 123–124
association mapping boom 130–131
case study 140–142
classical strategies and improvement in genomics era 129–130
fast NGS-enabled technologies 133–138
future trends 142–144
genetic and genomic resources 139–140
germplasm conservation 138–139
high-resolution mapping and gene cloning 132–133
multiparental populations 131–132
new possibilities in genomics era 124–128
- Genome-wide association studies (GWAS) 8, 10, 11, 14, 130, 183–184
barley breeding progress 184–187
in barley improvements, application of results from 192–195

- future trends 195-197
 mapping, in barley 188-192
 Germplasm for yield improvement 97-98
 barley origins 98-99
 genetic diversity in barley 99-101
 in breeding 101-102
 see also Sulphur
 β -Glucanases 449
 Gluten 417
 GrainGenes database 139
 Grains Research and Development Corporation (GRDC) 393
 Gramene 140
 Granule-bound starch synthase (GBSS) 68
 GRDC. see Grains Research and Development Corporation (GRDC)
- Halophytes plants 34
 Haustoria 271
 Heated drying 233
 Heat Shock Factors 32
 Heirloom varieties 379
 Hemoglobins 77
 Herbicide resistance 355, 359-362
 HGCA. see Home-Grown Cereals Authority (HGCA)
 Hindmarsh variety 392
 Home-Grown Cereals Authority (HGCA) 229
 Hooded phenotypes 13
 Hop creep 383
 Hordeins 111
 HR. see Hypersensitive response (HR)
 Hulled barley 56, 435, 443, 475
 Hulless barley 285, 432, 435, 440, 443, 446-450
 HvDWARF4 10
 Hypersensitive response (HR) 268
- IB. see Incomplete block (IB)
 ICARDA 100
 ICP. see Integrated crop protection (ICP)
 IDF. see Insoluble dietary fibre (IDF)
 IMPROMALT project 193
 Incomplete block (IB) 163
 In-crop herbicides 358
 India 100, 277
 Inflorescence development 6
 In-situ dry-matter digestibility (ISDMD) 440
 Insoluble dietary fibre (IDF) 471-472
 Institute of Brewing method 382
- INTEGRA project 193
 Integrated crop protection (ICP) 299
 Integrated pest management (IPM) 323-324
 agronomy 339
 barley production context 324, 326
 crop protectants 334-339
 diseases overview 326-329
 farming systems, soil and research platforms 342-344
 future trends 344
 inoculum management 330-331
 knowledge sources and tools 339-340
 uptake and communication of 340-342
 varietal resistance 331-333
 Integrated weed management 353-356
 examples, in barley 367-368
 in practice 366-367
 weed control tactics
 crop competition 364-365
 crop rotation 363-364
 harvest weed seed control 362-363
 herbicides 356-362
 on-farm hygiene 366
 Intercropping farming system 113, 339, 344
 InterGrain Pty. Ltd. 389, 393
 Intermediate microflora 247
 International Barley Core Collection 138
 International Rice Research Institute (IRRI) 14
 International Survey of Herbicide Resistant Weeds 359
 Intracellular wash fluids (IWFs) 289
 IPK Gatersleben (Germany) 100
 IPM. see Integrated pest management (IPM)
 Irradiation 251
 IRRI. see International Rice Research Institute (IRRI)
 ISDMD. see In-situ dry-matter digestibility (ISDMD)
 IWFs. see Intracellular wash fluids (IWFs)
- JEKYL gene 61, 63
- KASP™ 191, 193
 Kernel blight 282
 Kinship matrix 174
- Landrace Collection LRC1485 139
 Latinised row-column designs 165

- La Trobe variety 392-393
 Lattices 164
 Lauter tuns 408
 LD. *see* Linkage disequilibrium (LD)
 Leaf angle 10
 Leaf area 10-11
 Leaf spot disease severity scale 282-283
 Leaves 5-6
 Lemma 6
 Linear mixed models (LMM) 106
 Linkage disequilibrium (LD) 130
 Lipoxygenase (LOX) 385, 414
 LMM. *see* Linear mixed models (LMM)
 LOX. *see* Lipoxygenase (LOX)
- MA. *see* Modified atmospheres (MA)
 Mace variety 108
 MAGB. *see* Maltsters Association of Great Britain (MAGB)
 MAGIC. *see* Multi-parent advanced generation inter-cross (MAGIC)
 Malteurop 393
 Malting and Brewing Industry Barley Technical Committee (MBIBTC) 394
 Malting Barley Accreditation 394
 Malting Barley Committee 186
 Malting quality 186
 Malt quality improvement 377-378
 barley improvement history in
 Australia 393
 Barley Australia 394
 craft brewing 378-379
 future trends 396-397
 malting quality
 after malting 381-384
 germination 381
 grain hardness (endosperm texture) 386-387
 grain size 379-380
 linked traits but not routinely measured 385-386
 malt colour (wort colour) 385
 protein 380-381
 starch-degrading enzymes 384-385
 successful programmes
 requirements 394-396
 twenty-first century brewing modern varieties 388-393
 Maltsters Association of Great Britain (MAGB) 186
- MAMPs. *see* Microbe-associated molecular patterns (MAMPs)
 Mapping-by-sequencing 136
 Marker-Assisted Selection (MAS) 188
 Mashing 407, 412-413
 efficient breakdown of starch
 during 409-412
 MBCs *see* Methyl benzimidazole carbamates (MBCs)
 MBIBTC. *see* Malting and Brewing Industry Barley Technical Committee (MBIBTC)
 Mendel's law 132
 Methanol extracts 481
 Methyl benzimidazole carbamates (MBCs) 299
 N-Methyl-N-nitroso-urea (MNU) 205
 METs. *see* Multi-environment trials (METs)
 Met-S-methyltransferase (MMT) 414-415
 Mexico 277
 Microbe-associated molecular patterns (MAMPs) 267
 Micro-malting 186
 Mildew-resistance locus O (MLO) 211
 Mississippi Crop Situation online platform 340
Mla gene 281
 MLO. *see* Mildew-resistance locus O (MLO)
mlo gene 281, 294
 MMT. *see* Met-S-methyltransferase (MMT)
 MNU *see* N-Methyl-N-nitroso-urea (MNU)
 Mode of action (MOA) 334, 337, 359, 360
 Modified atmospheres (MA) 237
 Monocropping system 113
 Morex BAC library 141
 morexGenes database 139
 Multi-environment trials (METs) 159
 Multi-parent advanced generation inter-cross (MAGIC) 131, 132
 MutChromSeq 137, 138
 MutMap 135
 MutMap-Gap 136
 MutRenSeq 136, 137
 Mycotoxins 228, 237-241
 and fungi 241, 243-246
 prevention and decontamination, in
 barley storage 248
 mycotoxin-contaminated barley removal 249-250
 stored barley treatment 250-252
 toxigenic fungi stability and development during barley storage and 246-248

- NABGMP. *see* North American Barley Genome Mapping Project (NABGMP)
- Naked barley 13, 56
- NAM. *see* Nested association mapping (NAM)
- NaN₃ *see* Sodium azide (NaN₃)
- National Institute of Agricultural Botany (United Kingdom) 340
- National Variety Trials 358
- ND24260 174
- Near infra-red (NIR) 435, 437
and molecular markers 438-441
- Near isogenic lines (NILs) 132
- Necrotrophic effectors (NEs) 268, 288-289
- Necrotrophic-effector-triggered susceptibility (NETS) 268
- NEs. *see* Necrotrophic effectors (NEs)
- Nested association mapping (NAM) 131, 132
- Net form net blotch (NFNB) 286, 289
- NETS. *see* Necrotrophic-effector-triggered susceptibility (NETS)
- Next-generation sequencing (NGS) 124, 127, 207
- NFNB. *see* Net form net blotch (NFNB)
- NGS. *see* Next-generation sequencing (NGS)
- NILs. *see* Near isogenic lines (NILs)
- Nitrogen-use efficiency (NUE) 36, 37
- NLR. *see* Nucleotide-binding-leucine-rich repeat (NLR)
- Non-fermentable sugars 383
- North American Barley Genome Mapping Project (NABGMP) 439
- NSGC Barley Core 138, 139
- Nuclear projection 59
- Nucleotide-binding-leucine-rich repeat (NLR) 268
genes 136, 137
- Nud gene 13
- NUE. *see* Nitrogen-use efficiency (NUE)
- N-uptake efficiency (NUpE) 36
- N-utilization efficiency (NUE) 36
- Nutritional and bioactive compounds 467-468
arabinoxylans 471-472
barley activity enhancement
food matrix 483-484
genotypic and environmental influences 484
processing 482-483
beta-glucan 470-471
future trends 485
- health benefits
antioxidant activity 481-482
blood pressure lowering 482
cholesterol 477-478
glycaemic response 478-480
gut health 480-481
key issues and challenges 468-470
phenolics 473-475
plant sterols 475-476
protein/peptides 476
resistant starch 472
tocols 476
- Ochratoxins 240
- od package 175
- Okayama University Barley Germplasm Resources (Japan) collection 100
- Open reading frames (ORFs) 141, 142
- OsDWARF4 10
- Osmotic adjustment 29, 38
- Ozone 250-251
- PAs. *see* Proanthocyanidins (PAs)
- Pattern-triggered immunity (PTI) 267-268
- PCD. *see* Programed cell death (PCD)
- Pearling process 250
- Pesticides 237
- PGSB PlantsDB database 140
- PGT. *see* Primary germ tube (PGT)
- Pgt* race QCCJB 272-273
- Pgt* race TTKSK 273
- Ph*. *see* *Puccinia hordei* (*Ph*)
- Phenotyping malting quality 190
- Photoperiod 25, 27
- PHS. *see* Preharvest sprouting (PHS)
- Physiology 23-25
adaptation to environment 38-40
cold acclimation 25-28
low nitrogen 36-37
new methodologies 28-33
soil salinity adaptation 33-36
- Phytohormones 7, 9, 10
- Phytosterols 475-476
- Pinoxaden 358
- Plant development and architecture 3-4
breeding implications 14-16
reproductive development molecular control 11-13
structure/morphology and growth habit 4-7
vegetative development molecular control 7-11

- Plants evolved cell-surface pattern
 recognition receptors (PRRs) 267
- Plasma 251
- PLEXdb database 139
- Polyvinylpyrrolidone (PVPP) 415
- Postharvest storage and handling 227-228
 future trends 255-256
 operations 228-229
 general considerations 229-233
 insects management in stored
 barley 236-237
 storage considerations for dormant
 and preharvest sprouted
 barley 235-236
 stored barely management 233-235
 post-storage treatment 252
 feed barley 253
 malting barley 253-255
 see also Mycotoxins
- Pre-emergent herbicides 357-358
- Preharvest sprouting (PHS) 235
- Primary germ tube (PGT) 279
- Proanthocyanidins (PAs) 415, 416
- Programed cell death (PCD) 58, 59-60,
 61, 268
- Proteases 386-387
- Proteomics 383, 453-454
- PRRs. see Plants evolved cell-surface pattern
 recognition receptors (PRRs)
- PTI. see Pattern-triggered immunity (PTI)
- Puccinia graminis* 270, 271, 273
- Puccinia hordei* (*Ph*) 274-275
- Puccinia striiformis* f. sp. *hordei* 276-277
- PVPP. see Polyvinylpyrrolidone (PVPP)
- Pyrenophora teres* f. *maculata* 286, 287, 291
- Pyrenophora teres* f. *teres* 286, 287, 291
- Quantitative trait loci (QTL) 8, 9, 10, 14, 30,
 36, 131, 132, 188-192, 300, 440-441
- Queensland barley programme 438
- Rachis 12
- RAM. see Root apical meristems (RAM)
- Ramularia collo-cygni* (*Rcc*) 291-294, 340
- Randomised complete block (RCB) 162
- Rapid Visco-Analyzer (RVA) 235
- RCB. see Randomised complete block (RCB)
- Rcc*. see *Ramularia collo-cygni* (*Rcc*)
- rcc5* gene 285
- Recombinant inbred lines (RILs) 129, 132
- Recommended List Trials (RLT) 184
- Reduced height-1 (*Rht1*) genes 213
- Residual maximum likelihood (REML) 106
- Resistance elicitors 334, 339
- Resorcinolic lipids. see Alkylresorcinols
- Restriction fragment length polymorphisms
 (RFLPs) 125, 184
- R-genes 281, 296
- RGT Planet variety 392
- Rht1*. see Reduced height-1 (*Rht1*) genes
- Rhynchosporium commune* 297, 298,
 299, 300
- RLT. see Recommended List Trials (RLT)
- RMRL. see *rpg4/Rpg5*-mediated resistance
 locus (RMRL)
- Root apical meristems (RAM) 4
- Row-column alpha designs 165
- Rpg1* gene 272
- rpg4/Rpg5*-mediated resistance locus
 (RMRL) 273
- Rph* genes 275
- rrBLUP* package 174
- Rumen 444
- RVA. see Rapid Visco-Analyzer (RVA)
- Rym1* gene 140
- rym4/rym5* gene 140, 141
- rym11* gene 140, 141, 142
- Salt tolerance, in shoot tissues 35
- SAM. see Shoot apical meristems (SAM)
- Scepter variety 108
- SCFA. see Short-chain fatty acids (SCFA)
- SDF. see Soluble dietary fibre (SDF)
- SECOBRA Recherches 393
- Seed storage proteins (SSP) 71, 73
- Semi-dwarf phenotypes 9
- Septoria passerini* 295, 296
- SFNB. see Spot form net blotch (SFNB)
- sgRNA. see Single guide RNA (sgRNA)
- Shoot apical meristems (SAM) 4
- SHOREmap 135
- Short-chain fatty acids (SCFA) 472, 477, 479
- Single guide RNA (sgRNA) 212, 213
- Single nucleotide polymorphism
 (SNP) 127, 191
- S-methyl-l-methionine (SMM) 414
- SNP. see Single nucleotide polymorphism
 (SNP)
- SNP iSelect platform 100
- Sodium azide (NaN₃) 205
- Soluble dietary fibre (SDF) 470-471
- South Australian Barley Improvement
 programme 393
- Speed-breeding 143

- Spike growth, influence on grain traits 54
 barley grain in botanical terms 55-56
 cell death role in grain development 57
 cellular mechanisms and main actors
 in cell death 60-61
 death events arrangement in
 grain 57-60
 implications 61
 energy metabolism particularities 73-74
 barley grain photosynthesis and
 respiration 74-76
 hypoxia management at structural and
 metabolic levels 78-80
 main energy metabolism components
 and pathways 74
 O₂ gradients and indications of
 hypoxia 76-77
 O₂ sensing mechanisms and balancing
 in seeds 77
 functional orchestration of barley
 grain 80-83
 grain growth temporal sequence 56-57
 proteins and barley grain quality 71
 properties and deposition 71-72
 protein storage regulation and
 manipulation 72-73
 starch in caryopsis development 67
 starch storage variability and quality in
 mature grain 69-70
 transient starch physiological
 role 68-69
 sucrose allocation during grain-filling
 stage 62
 cellular sucrose allocation pathways
 within grain 62-64
 membrane transport events and active
 transporters 64, 66-67
 sucrose concentration gradients in
 grain 64, 65
- Spot blotch 282-286
- Spot form net blotch (SFNB) 286,
 290-291
- Spring barleys 28
- SSP. *see* Seed storage proteins (SSP)
- Stagonospora avenae* f. sp. *triticea* 295, 296
- Starch gelatinization temperature 410
- Starch quality, in brewing 409-411
- Stay-green phenotype 30
- Steam flaking 441-442
- Stem elongation 5
- Storage fungi 247
- SUE. *see* Sulphur-use efficiency (SUE)
- Sugars Will Eventually be Exported
 Transporters (SWEET) 66-67
- Sulphur
 effects on yield, quality, and response to
 stress 109-110
 adaptation to abiotic and biotic stress
 factors 112-113
 quality 111-112
 yield 110-111
 nutrition, and farming systems 113-114
 nutrition effects assessment, on barley
 and wheat grain yield
 data analysis 106-107
 materials and methods 104-106
 results 107-109
 role, in barley growth 102-103
 use, genotypic differences in
 associated genes 116-117
 varietal differences 114-116
- Sulphur-use efficiency (SUE) 114, 115, 116
- Svalbard Global Seed Vault (Norway) 100
- SWEET. *see* Sugars Will Eventually be
 Exported Transporters (SWEET)
- Syngenta 393
- T2N. *see* Trans-2-nonenal (T2N)
- TACCA. *see* Targeted chromosome-based
 cloning via long-range assembly
 (TACCA)
- TALENS 133
- Targeted chromosome-based cloning
 via long-range assembly
 (TACCA) 137, 138
- Targeted induced local lesions in
 genomes (TILLING) 135, 141,
 142, 203-204
 artificial mutagenesis and mutant
 discovery
 mutagen choice 204-206
 mutation density 206-207
 searching for mutations 207-208
- TILLING *in silico* 208
 tissue and organ for
 mutagenizing 204
 current and future trends 209-212
 resources, in barley 209
 and reverse genetics tools
 compared 212-213
 by Sequencing (TbyS) 207
 and wheat Tilling compared 212-214
- TB1 11
- TCA. *see* Tricarboxylic acid (TCA) cycle

- TCAP *see* Triticeae Co-Ordinated Project (TCAP)
- Teliospores 271
- THOD. *see* Trihydroxyoctadecenoic acid (THOD)
- Tillering 7
- Tillers 5
- TILLING. *see* Targeted induced local lesions in genomes (TILLING)
- Tissue tolerance 35
- Total protein digestibility (TPD) 447
- ToxA NE 284
- TPD. *see* Total protein digestibility (TPD)
- Trans-2-nonenal (T2N) 386, 414
- Tricarboxylic acid (TCA) cycle 78, 79
- Trichothecenes 240, 241
- Trihydroxyoctadecenoic acid (THOD) 386
- Triplet spikelet meristem 12
- Triticale 427
- Triticeae Co-Ordinated Project (TCAP) 189
- UK Cereal Pathogen Virulence Survey 330
- United Kingdom 338, 340
- United States 467
- Urediniospores 271
- US Food and Drug Administration (FDA) 241, 477
- Uzu gene 9-10
- Value for Cultivation and Use (VCU) 333
- Vernalization 27
- Voluntary initiatives (VI) 338
- Vomitoxin. *see* DON
- VPE genes 61
- Vrn-H1 gene 27
- Vrs 1 gene 9
- Vrs3 12
- Weed seeds 366
- Western Australian Department of Agriculture 389
- Whole-genome sequencing (WGS) 135, 136
- Wild Barley Diversity Collection 139
- Wort, meaning of 407
- Wort beta-glucan 383, 384
- Yield stability 40
- Zearalenone (ZEA) 241, 243