

Effects of the semi-dwarfing *sdw1/denso* gene in barley

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Abstract Recent advances in cereal genomics have made it possible to analyse the architecture of cereal genomes and their expressed components, leading to an increase in our knowledge of those genes that are associated with the key agronomical traits. Presently, use of a dwarfing gene in breeding process is crucial for the development of modern cultivars. In barley, more than 30 types of dwarfs or semi-dwarfs have been hitherto described. However, only a few of them have been successfully used in barley breeding programs. Both breeding and molecular mapping experiments were undertaken to enhance and evaluate the performance of semi-dwarf barley lines. The semi-dwarfing cultivars had improved lodging resistance and a higher harvest index. There have been a lot of investigations that have contributed new information to our basic understanding of the mechanisms underlying growth regulations in barley. This paper reviews semi-dwarfing genes in barley in general and special attention is paid to mapping of the *sdw1/denso* locus, changes in protein abundance and associations of the semi-dwarfness with gibberellins.

Keywords Anatomical characters · Gibberellin · *Hordeum vulgare* L · Protein abundance · *sdw1/denso* gene · Semi-dwarfing

Introduction

Semi-dwarfs in cereals have long been considered as a necessary condition for intensive agriculture. Genes responsible for the semi-dwarf growth habit in wheat and rice varieties that enabled the Green Revolution have been identified as *reduced*

height (*Rht*) genes in wheat (Peng et al. 1999) and the *semi-dwarf1* (*sd1*) gene in rice (Monna et al. 2002). The semi-dwarf rice gene (*sd1*) is one of the most important genes deployed in modern rice breeding (Spielmeyer et al. 2002). Further analysis has shown that an ortholog of the rice *sd1* gene is the barley semi-dwarf *sdw1/denso* gene (Zhang et al. 2005).

In barley, numerous mutants carrying semi-dwarfing genes are known (Kucera et al. 1975; Foster and Thompson 1987; Górný 2004). Semi-dwarf plants possess short, strong stalks and they are more resistant to lodging than tall plants. Lodging reduces not only barley yield and grain quality which indirectly affects malt quality since grain from lodged plants is often lighter in weight and lower in malt extract (Day and Dickson 1958). For this reason, breeding of barley for lodging resistance always had a great importance. Therefore, identifying semi-dwarfing genes is essential for barley breeding. This importance of semi-dwarf barley mutants has been discussed, among others, by Maluszynski and Szarejko (2005). Barley mutants with reduced height have been frequently used in breeding programs. For example, the cultivars Diamant and Triumph, originating from mutants selected in M₂ generation of the cv. Valticky after X-ray treatment were donors for about 150 cultivars bred in Europe in the twentieth century. Currently, cultivars possessing the *sdw1/denso* gene are in the pedigree of majority of modern barley cultivars bred all over the world (Gausgruber et al. 2002; Dahleen et al. 2005).

This paper reviews semi-dwarfing genes in barley in general and a special attention is paid to mapping of the *sdw1/denso* locus, changes in protein abundance and association of the semi-dwarfness with gibberellins.

Barley semi-dwarfing genes

Barley mutants with reduced growth can be divided into five groups: *brachytic*, *breviaristatum*, *erectoides*, *zeocriton* and *uzu* (Kucera et al. 1975; Foster and Thompson 1987; Górný

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Table 1 Most important semi-dwarfing genes in barley breeding

Locus symbol (synonym)	Chromosomal locations	Locus name or phenotype	References
<i>ari-a</i> (<i>ari-6</i> , <i>lk7</i>)	3HS	<i>breviaristatum-a</i>	Tsuchiya 1974; Kucera et al. 1975
<i>ari-e</i> (<i>ari-1</i> , <i>lk9</i> , <i>GPert</i>)	5HS	<i>breviaristatum-e</i>	Thomas et al. 1984; Milach and Federizzi 2001; Forster 2001
<i>ari-m</i> (<i>ari-28</i>)	7HS	<i>breviaristatum-m</i>	Kucera et al. 1975; Franckowiak 1995
<i>ari-o</i> (<i>ari-40</i>)	7HL	<i>breviaristatum-o</i>	Kucera et al. 1975; Franckowiak 1995
<i>ari-r</i> (<i>ari-14</i>)	5H	<i>breviaristatum-r</i>	Kucera et al. 1975; Franckowiak 1995
<i>Ari-s</i> (<i>ari-265</i>)	5H or 7H	<i>breviaristatum-s</i>	Franckowiak and Lundqvist 2011
<i>brh1</i> (<i>br</i> , <i>ari-i</i> , <i>dx1</i>)	7HS	<i>brachytic 1</i>	Powers 1936; Franckowiak 1995; Dahleen et al. 2005
<i>ert-a</i> (<i>ert-6</i>)	7HS	<i>erectoides-a</i>	Persson and Hagberg 1969; Lundqvist et al. 1997
<i>ert-c</i> (<i>ert-1</i>)	3HL	<i>erectoides-c</i>	Persson and Hagberg 1969; Lundqvist et al. 1997
<i>ert-v</i> (<i>ert-57</i>)	6H	<i>erectoides-v</i>	Hagberg et al. 1958; Persson and Hagberg 1969; Lundqvist et al. 1997
<i>ert-zd</i> (<i>ert-159</i> , <i>br7</i>)	7HL	<i>erectoides-zd</i>	Tsuchiya 1976; Franckowiak 1995
<i>hcm1</i>	2HL	<i>short culm 1</i>	Swenson and Wells 1944; Lundqvist et al. 1997; Franckowiak et al. 2005
<i>uzu1</i>	3HL	<i>uzu 1</i> or <i>semi brachytic 1</i>	Tsuchiya 1976; Chono et al. 2003
<i>sdw1</i> (<i>denso</i>)	3HL	<i>semidwarf 1</i>	Haahr and von Wettstein 1976; Barua et al. 1993; Laurie et al. 1993; Mickelson and Rasmusson 1994; Hellewell et al. 2000; Jia et al. 2009; Kuczyńska et al. 2012
<i>sdw2</i>	3HL	<i>semidwarf 2</i>	Lundqvist et al. 1997; Franckowiak et al. 2005
<i>sdw3</i>	2HS	<i>semidwarf 3</i>	Börner et al. 1999; Gottwald et al. 2004
<i>sdw4</i>	7HL	<i>semidwarf 4</i>	Yu et al. 2010; Franckowiak and Yu 2011

2004). The major semi-dwarfing genes used in barley improvement are the *short culm 1* (*hcm1*) (Swenson and Wells 1944), *semi-brachytic 1* (*uzu1*) (Tsuchiya 1976), *semi-dwarf 1* (*sdw1*, syn. *denso*) (Haahr and von Wettstein 1976) and *breviaristatum-e* (*ari-e*) (Thomas et al. 1984). The best-known barley semi-dwarfing genes are presented in Table 1. Plants carrying the listed genes differ in their response to the exogenous application of gibberellic acid (GA₃) (gibberellic acid). There are both, sensitive to GA₃ treatment – plants possessing *sdw1/denso* gene for instance (Franckowiak and Pecio 1992), and GA₃ insensitive – plants possessing *sdw3* and *uzu1* genes (Gottwald et al. 2004; Chono et al. 2003). Most of *brachytic* mutants were classified as insensitive to GA₃ treatment (Franckowiak and Pecio 1992; Górný 2004), although Börner reported that *ari-i.38* (*brh1*) seedlings are sensitive to gibberellic acid. Pakniyat et al. (1997) demonstrated that mutants at the *ari-e* (*breviaristatum-e*) locus are characterized by a reduced sensitivity to GA₃ treatment. Also Forster (2001) indicates that all the *ari-e* mutants (including the cv. Golden Promise) showed very little response to exogenously applied GA₃.

Certain *ari* mutants can be placed in the *brachytic* class of semidwarfs (*ari-m*, *ari-o*, *ari-r*) with the 1/2 - 1/3 height reduction (Franckowiak 1995). Based on the chromosomal position of retained SNP markers and morphological characteristics of Bowman backcross-derived line BW051, for instance, the *ari-m.28* might be an allele at the *brh1* locus (Druka et al. 2011). A common phenotypic effect of *ari* loci

is an instable expression of awn length in plants with a specific gene which ranges from 1/2 and less than 1/3 of normal length in *ari-m* and *ari-r* plants, respectively, to 3/4 of normal length in *ari-e* and *ari-o* ones (Kucera et al. 1975). Mutant alleles at the *ari-e* locus were extensively used in the breeding programs. The cv. Golden Promise is the *ari-e.GP* mutant and is described as an elongation (*elo*) type of the semi-dwarf mutant with a cell size reduction in leaf blades (Ellis et al. 2002). Pleiotropic effects of this gene on yield and grain size were observed by Forster (2001). The cv. Golden Promise is noted to have desirable agronomic traits such as earliness, short stiff straw and reduced awn length and better adaptability to salt stressed environments than other semi-dwarf mutants (Pakniyat et al. 1997). An example of the dominant allele for the *breviaristatum* class is the *Ari-s* gene. Homozygous plants for the *Ari-s* allele are characterized by slightly shortened rachis internodes and wide, short and globe-shaped grains. Sterile lateral spikelets and glumes are about half of normal length, plants are 3/4 to 5/6 of normal height, and plant vigour is reduced (Franckowiak and Lundqvist 2011).

The first *brachytic* mutant was found in the cultivar Himalaya (Powers 1936). *Brachytic* mutants are insensitive to gibberellic acid treatment (Boulger et al. 1981). Dahleen et al. (2005) widely characterized 18 loci located on barley chromosomes and identified those as having the *brachytic* phenotype. *Brachytic* plants are characterized by short leaves, culms, spikes and awns (Holm and Aastveit 1966), small seeds and – as a consequence - a low yield (Franckowiak 1995).

A large number of *erectoides* (*ert*) mutants were induced by Swedish researchers from Svalof AB during the 1950–1970s (Lundqvist 2009). The dense spike (so-called *erectoides*) mutants were the first of the viable mutants induced by irradiation. The *erectoides* mutants have a reduced rachis internode length, which makes their spikes dense and broad. In all of this kind of mutants the rachis internodes are shorter than in parental forms. In some extreme mutants, the internodes are shortened by 50 % (Persson and Hagberg 1969). Strong reduction of rachis internodes in *ert-a* mutants has resulted in the development of compact spikes (Persson and Hagberg 1969). Twenty-nine gene loci were identified and most of them have different phenotypic characteristics (Górný 2004; Lundqvist 2009). Plants with the *ert-a* allele are 10 to 15 cm shorter than parental cultivars (Hagberg et al. 1952). The effects of the *ert-a* on spike density can be partially reversed by GA₃ treatments (Stoy and Hagberg 1967). Gustafsson (1963) found that several *ert*-mutants are interesting from a practical point of view. They have retained the same yield as the initial cultivars and have better straw stiffness. GA₃ treatment of plants at the flag leaf stage caused a decrease in spike density (Stoy and Hagberg 1967). The *ert-v* mutants form spikes that appear abnormal with irregular placement of kernels and reduced rachis internode length. Plants are weak and semi-sterile, anthers are often whitish, and culm length is about ¾ of normal height (Persson and Hagberg 1969). Mutants at the *ert-zd* locus have a *brachytic*-like pattern of growth and are about ¾ of normal height (Tsuchiya 1976). Thomas et al. (1984) determined the chromosomal location of the *erectoides* semi-dwarfing gene (*arie.GP*) on the short arm of chromosome 7 (5H).

The *short culm 1* (*hcm1*) gene is present mainly in USA's six-rowed barley cultivars (Franckowiak 2000). It is located on chromosome 2HL in the hot-spot region. The *hcm1* locus is linked to QTLs for Fusarium head blight (FHB) resistance, earliness and the *vrs1* (*six-rowed spike 1*) locus. It is reported that homozygous plants for the *hcm1* allele have ca. 10 cm reduced height (Swenson and Wells 1944; Franckowiak 2000; Yu et al. 2010).

The *uzu1* gene is located on the long arm of chromosome 3HL close to the centromere (Tsuchiya 1976) and it has been widely used in barley breeding in East Asia. The *sdw1/denso* gene is also located on chromosome 3HL, but more distally from the centromere than *uzu1* (Barua et al. 1993).

In barley, four *sdw* genes have been identified: *sdw1*, *sdw2*, *sdw3* and *sdw4*. Plants with the semi-dwarfing *sdw2* gene are about ¾ of normal height, rachis are thin with narrow, short, erect leaves and the flag leaf is narrow and short. It has been localized on 3HL chromosome (Szarejko and Maluszynski 1984). The *sdw3* gene of barley is located close to the centromere on the short arm of chromosome 2H and reveals a synteny with a region of the rice chromosome 7 L

(Gottwald et al. 2004). It is responsible for a GA-insensitivity but further studies are needed to explain that the underlying defect may represent either a loss-of-function mutation of a positive regulator in GA signalling or a loss-of-control mutation of a negative regulator (Gottwald et al. 2004; Vu et al. 2010). The *sdw4* barley gene is positioned on the long arm of the chromosome 7H and reduces plant height by about 20 to 30 % affecting the length of the 3rd and 4th culm internodes proportionally more than the upper internodes (Sameri et al. 2006; Sameri et al. 2009; Yu et al. 2010). The *sdw4* gene is not associated with a delayed maturity like the *sdw1/denso* gene (Zhang and Zhang 2003).

Four *sdw1* alleles are known. One of them was found in a spontaneous mutant selected from the cv. Abed Denso at the Abed Plant Breeding Station in Denmark (Haahr and von Wettstein 1976) and this mutated gene (named *denso*) has been introduced to numerous cultivars. Three other *sdw1* alleles have been obtained with the use of physical mutagens. From a breeding point of view, the most important is the allele that originates from a mutant selected from the M₂ generation of the cv. Valticky after X-ray treatment. This mutant was characterized by a shortened stem and a semi-prostrate growth habit. It was officially released in Czechoslovakia in 1965 as the cv. Diamant and its allele has been used for the breeding of about 150 new European cultivars (Bouma 1967; Grausgruber et al. 2002). The other *sdw1* allele was induced by X-rays in the Norwegian six-rowed barley cv. Jotun and this source became known as line no. 66/86 (Mickelson and Rasmusson 1994). An additional *sdw1* allele was found in the M₂ generation of the cv. Bomi after treatment with partly moderated fission neutrons in the reactor. The accession was named Riso no. 9265 and was considered very promising for breeding semi-dwarf cultivars (Haahr and von Wettstein 1976).

Initially, *sdw1* and *denso* were considered as different genes because they were derived from different sources: the *sdw1* gene from the cv. Jotun, while *denso* from the cv. Diamant. However they proved to be allelic (Haahr and von Wettstein 1976; Mickelson and Rasmusson 1994) and map to the same region of the long arm of chromosome 3H (Hellewell et al. 2000).

The main phenotypic effect of the *sdw1/denso* gene is a 10–20 cm decrease of plant height, depending on environmental conditions (e.g. Hellewell et al. 2000). The morphological marker of the *sdw1/denso* gene is that of a juvenile growth habit type; namely, plants possessing the *sdw1* gene are characterized by a prostrate growth, whereas plants with its dominant allele are characterized by erect growth (Fig. 1). Modern, high-yielding barley cultivars are mainly related to the sources of semi-dwarfness associated with the *sdw1/denso* locus, for example the cv. Maresi possessing this gene is described as stable yielding on the dominating sandy soils characteristic for the Middle Europe (Górný 2001).



Fig. 1 Different juvenile barley growth habits: erect plants with the dominant *Sdw1* allele (left) and prostrate plants with the recessive *sdw1* allele (right) (fot. A.Kuczyńska)

Effects of the *sdw1/denso* gene on agronomical traits

The influence of the *sdw1/denso* locus on plant height and various agronomic and physiological characteristics has been observed in numerous studies. Some QTLs for heading date, yield and yield-related traits were localized in the *sdw1/denso* region. In addition to the reduced plant height, semi-dwarf plants were observed to have an increased time to heading, late maturity, decreased thousand-grain weight, grain weight per ear and per plant (Table 2). Grain yield per plot appeared to be also associated with *sdw1/denso* gene, but results of different studies were not the same, for example Thomas et al. (1991) and Hellewell et al. (2000) reported on decreased yield, whereas Thomas et al. (1995), Yin et al. (1999) and Jia et al. (2011) found that *denso*-carrying plants were characterized by an increased yield.

Studies conducted by Yin et al. (1999) indicated that at the same position as the *sdw1/denso* locus or very close to this

gene QTLs for some physiological characters determining yield were located. Positive effects of this gene were observed on increased leaf thickness, increased fraction of shoot biomass partitioned to leaves during vegetative phase, which may stimulate the formation of photosynthetic area, and to ears during early kernel filling, which may promote an increased harvest index. As a consequence, the *sdw1/denso* gene appeared to be associated with increased yield.

Grain yield is a complex trait and several different regions of the genome are responsible for this trait (Kandemir et al. 2000; von Eeuwijk et al. 2010). Inconsistency in evaluation of yielding of *sdw1/denso*-carrying genotypes is not unexpected; yield in cereals is the results of action of many genes with major and minor effects, which control traits directly associated with the yield potential, such as grain and tiller number, grain weight per ear and per plant, and indirectly such as those that affect root development, ear morphology, photosynthesis and metabolic processes. Thus, yielding of genotypes possessing *sdw1/denso* gene may vary depending on the genetic background.

Many different QTLs mapped at the same position as the *sdw1/denso* locus may indicate on pleiotropic effects of this gene on traits other than plant height or on a tight linkage between genes conditioning those traits linked with this semidwarfism and located in the same *sdw1/denso* region. As it was found by Snape and Simpson (1981a) and Kaczmarek et al. (2004), pleiotropy and complete linkage (i.e. no recombination) between genes controlling two quantitative traits have the same phenotypic effects, i.e. means, variances and the level of association between traits are similar in homozygous populations derived from different generations. Barua et al. (1993) revealed genetic factors influencing heading date to be linked to the *sdw1/denso* locus. Results of their study showed that the QTL for heading date could not be genetically separated from the *sdw1/denso* locus, which could indicate either on a pleiotropic effect of the *sdw1/denso* gene

Table 2 Characteristic of traits associated with *sdw1/denso* locus

Traits	Reference
Plant height (decreased)	Ali et al. 1978; Snape and Simpson 1981b; Powell et al. 1985; Thomas et al. 1991, 1995; Barua et al. 1993; Laurie et al. 1993; Bezant et al. 1996
Heading date /or pre-flowering duration (increased)	Ali et al. 1978; Snape and Simpson 1981b; Powell et al. 1985; Thomas et al. 1991; Barua et al. 1993; Laurie et al. 1993; Bezant et al. 1996; Yin et al. 1999
Number of productive tillers (increased)	Jia et al. 2011
1000-grain weigh (decreased)	Ali et al. 1978; Snape and Simpson 1981b; Powell et al. 1985; Thomas et al. 1991; Laurie et al. 1993
Grain weight per main spike (decreased)	Thomas et al. 1991; Laurie et al. 1993
Grain weight per plant (decreased)	Ali et al. 1978; Snape and Simpson 1981b; Powell et al. 1985; Thomas et al. 1991; Laurie et al. 1993
Grain yield per plot (increased)	Thomas et al. 1995; Yin et al. 1999; Jia et al. 2011
Grain yield per plot (decreased)	Thomas et al. 1991; Hellewell et al. 2000

on heading date or on a very tight linkage between *sdw1/denso* and gene(s) responsible for heading date. Thomas et al. (1991) reported that the magnitude of additive genetic variance in heading date decreased in single seed descent (SSD) inbred lines (32.7 %) in comparison with doubled haploid lines (71.8 %) derived from hybrids between the cv. Keg and the breeding line TS57/72/6 carrying *sdw1/denso* gene, which may indirectly prove that *sdw1/denso* locus is tightly linked to genetic factor(s) controlling heading date. Moreover, based on DH lines derived from the cross [Blenheim × E224/3], Thomas et al. (1995) suggested that the localization of QTLs for some traits associated with *sdw1/denso* (e.g. plot yield, percentage of grain fraction >25 mm sieve) in their cross was in a similar region of 3HL chromosome as in the crosses studied by Hayes et al. (1993) and Han and Ullrich (1994), in which neither parent possessed *sdw1/denso*, could also indicate that association of this gene with these traits was due to linkage. On the other hand, Yin et al. (1999) and Hellewell et al. (2000) suggested that the major QTL for so many different traits mapped at the same position as the *sdw1/denso* gene has proved of the pleiotropy of this gene.

The question “pleiotropy whether linkage” of the *sdw1/denso* gene is still under consideration. Till now, results of studies have not univocally proven one out of these two phenomena. Probably, either effects of pleiotropy or tight linkages between genes directly and indirectly affect associated traits can not be excluded. Relative contributions of the both phenomena may vary in different crosses.

Effects of the *sdw1/denso* gene on morphological and anatomical characteristics

Phenotypic semi-dwarfing effects on the plant size may be accomplished through a variety of mechanisms influencing cell division frequency, size of meristematic tissues, cell growth rate and duration, leading to reduced cell numbers or dimensions in the different organs. The mode of action certainly depends on the identity of the semi-dwarfing gene. For the *sdw1/denso* locus, research has focused on modifications of major crop related traits (Hellewell et al. 2000; Grausgruber et al. 2002; Sameri et al. 2006), while its anatomical effects have not often been analysed.

Kuczyńska and Wyka (2011) compared morphological and anatomical traits of aboveground vegetative organs of the *sdw1/denso* and wild type plants to further document the mode of action of the gene and to test whether organ size changes may be explained at the level of cellular dimensions. To study the morpho-anatomical effects of the *sdw1/denso* locus, they analysed 20 barley lines (ten of which carried the *denso* gene) developed *via* the SSD-technique from the [Maresi × Pomo] hybrid. The analyses were performed at two growth stages, i.e. at the tillering and spike emergence.

They measured several macro- and microscopic traits and detected reductions in the leaf size, which at the tillering stage was also reflected in smaller sizes of some categories of epidermal cells. Lower cell division frequencies were deduced for cell files with unchanged cell length. Leaf blades of *denso* lines were thinner and had smaller vascular bundles and narrower tracheal elements compared to the wild type. Kuczyńska and Wyka (2011) explained that these differences could not have been caused by differences in developmental timing, as had been suggested by Yin et al. (1999), but rather were due to gene effect on either cell production rate or cellular growth, or both. In addition, a lack of effect was noted for sizes of stomata and spike size. Studies on the narrower vessels showed that their formation might be an indirect result of reduction in lamina size but could alternatively represent a direct effect of *sdw1/denso* gene activity. In turn, the smaller vessels could have provided a feedback mechanism to blade expansion by restricting water supply and thus contributing to the leaf size reduction and could also have consequences for a lower potential in stomatal opening and gas exchange capacity (Fricke 2002). Experiments carried out by Kuczyńska and Wyka (2011) confirmed that the *sdw1/denso* gene has a multilevel effect on cells, tissues and organs, although not all organs and cells were affected to the same extent, and cell size or division frequency were modified depending on the cell type.

Mapping of the *sdw1/denso* locus

Although breeders may exploit semi-dwarfing genes with little knowledge of their detailed genetic control, it was, however, obvious that a precise genetic analysis can greatly improve activities. For example, knowledge of the chromosomal location of a gene may be used to exploit or avoid known linkage relationships. Some of the dwarfing genes have rarely or never been used in barley breeding programs, although they have been genetically characterized. Barua et al. (1993) used a combination of isozymes, RFLPs, RAPDs, and a disease resistance locus in conjunction with a doubled haploid population to genetically map the *sdw1/denso* locus to a specific chromosome arm. They examined a population derived from a cross between the cv. Blenheim and the SCRI breeding line E224/3. Blenheim is a semi-prostrate cultivar which, in its pedigree, has the cv. Triumph carrying the *sdw1/denso* gene that originated from the cv. Diamant. Linkage analysis has identified associations between seven markers and the *sdw1/denso* locus. These markers had previously been mapped to the chromosome 3HL (Heun et al. 1991) thus Barua et al. (1993) concluded that the *sdw1/denso* locus is located on this chromosome arm. Obviously, such chromosomal location of the *sdw1/denso* locus has a number of important implications: the *sdw1/denso* gene influences

several agronomic and quality traits (Powell et al. 1985; Thomas et al. 1991). In addition, these analyses concentrated further markers in this genome region and such an approach has been used, among others, by Chalmers et al. (1993) to locate quantitative trait loci responsible for the milling energy requirement in barley.

In the AFLP marker map constructed for the [Prisma Apex] RIL population, the *denso* gene was mapped at the position of 126.4 cM in the chromosome 3H (Yin et al. 1999). The QTL having an important effect on pre-flowering duration was associated with the presence of the *sdw1* gene from the cv. Prisma and was likely to be a pleiotropic effect of the *sdw1* gene. Chloupek et al. (2006) measured root system size in 157 doubled-haploid lines and their parents, the cv. Derkado and B83-12/21/5, with the semi-dwarfing genes *sdw1* and *ari-e.GP*, respectively. They mapped the *sdw1/denso* gene on the long arm of the chromosome 3H between two SNP markers abc08541 and abc08208. The SNP marker abc08208 was used by Malosetti et al. (2011) to generate a BOPA2 marker and to map the *sdw1* onto the chromosome 3H at 127.1 cM, i.e. at the same position identified by Chloupek et al. (2006).

Comparative analyses performed by Smilde et al. (2001) revealed that the barley chromosome 3H is syntenic to the rice chromosome 1, to which the rice semi-dwarf gene *sd1* was mapped. Further analysis revealed that the *sdw1/denso* gene is in the same syntenic region with the rice *sd1* gene closely linked with the common RFLP marker R1545. This syntenic relationship was further confirmed through wheat and rice comparative analyses (Zhang et al. 2005). Both the barley *sdw1/denso* and rice *sd1* appear to be GA-sensitive semi-dwarf genes. Thus, the *sdw1/denso* in barley is most likely an orthologue of the *sd1* in rice (Zhang et al. 2005). The rice *sd1* orthologous gene was partially isolated from barley based on the conserved sequences between rice, wheat and maize. The barley gene has the same structure as its orthologous gene in rice with three exons and two introns. The barley and rice genes shared an 88.3 % sequence similarity and an 89 % amino acid identity. Moreover, the gene expression level of the *Hv20ox₂* gene encoding GA20 oxidase can be used as a marker to distinguish different alleles of *sdw1/denso* (Jia et al. 2011). This result is similar to the gene expression pattern of the different alleles of the *sd1* mutants in rice (Ashikari et al. 2002; Spielmeier et al. 2002). Thus, Jia et al. (2011) concluded that *Hv20ox₂* is a functional gene controlling the barley *sdw1/denso* semi-dwarfing mutants. They showed that the expression level of *Hv20ox₂* gene was closely associated with plant height. Jia et al. (2011) observed that the semi-dwarfing gene increased grain yield through increasing the number of productive tillers. The QTL for grain yield co-located with the eQTL of *Hv20ox₂*, but was negatively correlated, indicating that high yield is associated with a lower expression of *Hv20ox₂*. They postulated that a reduced expression of *Hv20ox₂* in the semi-dwarfing mutants results in a lower

GA level in the apical meristem, which inhibits apical growth and reduced internode length, plant height and promotes the development of more tillers.

Changes in protein abundance as an effect of the *sdw1/denso* locus

In barley proteome studies, several authors have mainly focused either on a more descriptive overview of occurring proteins (Kristoffersen and Flengsrud 2000; Finnie and Svensson 2003; Finnie et al. 2009) or they have investigated changes in protein synthesis during seed development (Østergaard et al. 2004). Kuczyńska et al. (2012) identified proteins involved in barley semi-dwarfness and this experiment was the first proteome analysis of effects of the *sdw1/denso* gene on tillering node proteins in different juvenile growth habits. Two-dimensional electrophoresis and mass spectrometry were applied to investigate changes in protein abundance associated with the prostrate or erect juvenile growth habit in barley recombinant inbred lines derived from the [Maresi × Pomo] cross combination. Half of these lines carried the semi-dwarfing *sdw1/denso* gene from the parental cv. Maresi, which possesses the semi-dwarfing gene from the cv. Diamant being in its pedigree. Most of the identified proteins were involved in metabolism and disease defence-related processes. In the lines with a prostrate growth habit at the tillering stage they observed a significantly higher abundance of such proteins as heat-shock proteins (HSPs), a RuBisCO large subunit-binding or protein chloroplast translational elongation factor. An interesting result was obtained for the ES2A protein (a gibberellic acid inducible protein). The expression of the gene coding for ES2A is GA₃-responsive and GA-related genes are known to be responsible for the semi-dwarfing habit (Speulman and Salamini 1995). It was found by Kuczyńska et al. 2012 that ES2A protein displayed increased synthesis in barley lines with the prostrate growth habit at the juvenile stage. For the same barley lines, a decrease in the expression of ES2A protein was noticed during tillering and their growth habit that could be partially due to reduced amount of this protein. Moreover, the authors have identified an increased synthesis of the Germin-like protein 1 (GLP) in barley plants with the prostrate and erect growth habit at the three leaf stage, and this accumulation level decreased during tillering. GLPs are encoded in plants by a gene family with proposed functions in plant development and defence (Zimmermann et al. 2006). Germins are accumulated in expanding shoots of developing seedlings and young barley leaves. The expression of GLPs is associated with remodelling of the plant cell walls during pathogen attack or abiotic stress (Manosalva et al. 2009). This is a possible explanation of the lower accumulation level of that protein in the analysed barley lines during tillering. Kuczyńska et al.

(2012) also suggested that a deeper analysis of the many identified proteins would be necessary in order to better understand their role in relation to the growth habit of barleys.

Association of the semi-dwarfness with gibberellins

Gibberellins (GA) are one of the most important hormones involved in plant growth and development, e.g. in seed germination, stem elongation, leaf expansion, flowering, stamen, anther and fruit formation (Hooley 1994; Davies 1995; Gocal et al. 2001; Murray et al. 2003; Yamaguchi 2008; Plackett et al. 2011). There are both GA-sensitive and GA-insensitive barley mutants identified (Hanson et al. 1980; Boulger et al. 1981; Franckowiak 1995). Similarly to rice mutants (Monna et al. 2002; Sasaki et al. 2003; Sakamoto et al. 2004), the short-statured barley plants, in which semi-dwarfness is caused by a deficiency in the gibberellin biosynthesis pathway, are known to be GA-sensitive and respond to exogenous GA (Franckowiak and Pecio 1992). GA₃ application to leaf blades in the barley mutant *dbg576* possessing a *denso* allele results in a leaf sheath and blade elongation followed by an internode extending. Such first symptoms are noticed after 8 h of the gibberellin treatment (Speulman and Salamini 1995).

More than 100 GAs have been identified but only a few are biologically active, including GA₁, GA₃, GA₄, GA₇ (Hedden and Phillips 2000; Olszewski et al. 2002). The GA biosynthesis pathway depends on a series of enzymatic steps. GA 20-oxidases (GA20ox), GA 3-oxidases (GA3ox) and GA 2-oxidases (GA2ox) are the fundamental enzymes responsible for gibberellin homeostasis (Hedden and Proebsting 1999; Olszewski et al. 2002; Yamaguchi 2008; Salas Fernandez et al. 2009). GA20ox and GA3ox catalyse oxidations on C-20 and C-3 in GA molecules, respectively, activating GAs as a consequence (Hedden and Phillips 2000; Yamaguchi 2008). GA20ox converts GA₅₃ to GA₄₄ and GA₁₉ to GA₂₀, while GA3ox alters GA₂₀ to GA₁ (Crozier et al. 2000; Hedden and Phillips 2000; Spielmeier et al. 2004; Yamaguchi 2008). In contrast, GA2ox is a crucial enzyme in the deactivation of GAs. It catalyses GA₂₀ and GA₁ to GA₂₉ and GA₈, respectively, via 2β-hydroxylation (Hedden and Phillips 2000; Spielmeier et al. 2004; Yamaguchi 2008). Regulation of the expression of the oxidase genes is associated with the amount of GA. A lower GA concentration induces gene expression that promotes GA synthesis. In turn, increased GA expressions repress GA2ox and GA3ox, decreasing GA quantity. Inversely, GA2ox expression is induced in the response to a high level of GA, thereby gibberellin inactive forms are produced (Salas Fernandez et al. 2009).

Any functional disorders in essential enzymes of the GA biosynthesis appear to affect plant stature. Loss of GA20ox or GA3ox functions decreases the GA level and leads to reductions in plant height, whereas their overexpression stimulates an extensive growth. In turn, an enhanced expression of GA2ox

causes a dwarf phenotype, while a loss of its function intensifies an elongation of the internodes (Sasaki et al. 2003; Lo et al. 2008; Salas Fernandez et al. 2009; Jia et al. 2009, 2011).

Concluding remarks

The exploitation of semi-dwarfing genes in barley breeding still plays an important role in improving its productivity. Effects of the *sdw1/denso* gene on plant height and several morphological, anatomical, physiological and agronomical traits appear to be dependent on genetic background and/or specific growth conditions. Many different QTLs mapped at the same position as the *sdw1/denso* locus may indicate a pleiotropy of this gene or a tight linkage between genes conditioning observed/associated traits. Till now, it is difficult to distinguish between pleiotropy and a tight linkage on the basis of phenotypic observations and QTL analyses. Undoubtedly, results of barley genome sequencing will allow us to know relative contribution of pleiotropy and/or linkage in the genetic control of semi-dwarfism and other traits associated with the reduced height. Therefore, a more consistent harmonized approach between molecular and agronomic research is needed. In addition, to providing new information necessary to effectively use this gene in a breeding program, such experiments will offer opportunities to pursue an analysis on the *sdw1/denso* associated physiological characters determining yield. It is also crucial to know the *sdw1/denso* gene sequence to distinguish the *sdw1/denso* alleles, which may exist in modern barley cultivars and breeding lines. For that purpose association studies should be performed on broad plant materials of different genetic background.

With more detailed QTL localization studies, it should be possible to detect parallelism between QTLs commonly found in many crosses and even in related species. On the basis of corresponding QTL composition in parental genotypes, it should be possible to create specific transgressions in breeding programmes by choosing appropriate parents before a cross is made and by selecting among progenies for the desired QTL arrangements.

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