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Pleiotropic effects of the semi-dwarfing gene *uzu* in barley

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Abstract The adoption of reduced height (*Rht*) genes has dramatically enhanced yield potential of cereal crops. The semi-dwarfing gene *uzu* in barley is widely used in East Asia. Its value as an *Rht* gene in the warm and dry environments in Australia was evaluated in this study. In addition to plant height, this gene showed significant effects on a wide range of characteristics. It reduced the overall plant height by an average of 33.7 % with the most significant reduction occurred on the internode below the peduncle. The gene reduces spike length by 31.6 % and grain weight by 18.8 %. It increases grain number per spike by 5.6 % and grain density by 51.8 %. Seedling assays suggested that the effects of this gene became more significant with increased temperature. It reduced coleoptile and seedling length by 19.4 % and 15.1 %, respectively at 7 °C. The reduction increased to 61 % and 46.7 %, respectively, at 25 °C. These results indicated that the *uzu* gene could have limited values in some high temperature and drought prone environments.

Keywords Reduced height · Semi-dwarfing genes · *uzu* · Barley

Introduction

Reduced height (*Rht*) genes enhance crops' resistance to lodging which could be caused by either weather factors or management practices. Together with some other factors, these genes have made tremendous contributions to a significant increase in cereal production worldwide, which has been dubbed as the 'Green Revolution' (Milach and Federizzi 2001).

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Different *Rht* genes not only affect height differently under different growth conditions, but also have different effects on many other morphological and agronomic traits. Thus selecting appropriate *Rht* genes is a major consideration in breeding for different environments (Ellis et al. 2005).

Rht genes have been reported on each of the seven chromosomes in barley (Wang et al. 2010). However, only three of them, including *denso, sdw1* and *uzu*, have been widely used in breeding programs (Hellewell et al. 2000; Zhang and Zhang 2003; Saisho et al. 2004). Surprisingly, these three widely used *Rht* genes all locate on the long arm of chromosome arm 3H, occupying two different loci. One of these loci contains at least three different alleles: *sdw1* (previously known as *sdw*), *denso* and another one reported by Barua et al. (1993). This *Rht* locus has been widely used in breeding programs in the United States, Canada and Europe (Rasmusson 1991; Mickelson and Rasmusson 1994) and contributed to many malting and feeding barley varieties (Mickelson and Rasmusson 1994). Although *sdw1* and *denso* were derived from separate mutation events, they are allelic and have similar effects on agronomic traits. They have been associated with late heading, low 1000 kernel weight, lower yield, high screenings and high β-glucan content (Powell et al. 1985; Foster and Thompson 1987; Thomas et al. 1991; Mickelson and Rasmusson 1994; Hellewell et al. 2000).

Another *Rht* locus, which locates 23 cM proximally to the *sdw1/denso* locus, contains the *uzu* gene (Li et al. 2015). It is reported that this gene reduces plant height to about 80–90 % of its normal counterpart under normal cultivation in Japan (Saisho et al. 2004). It was noted that '*uzu*' lines showed lower adaptability to deep-seeding than non-*uzu* lines (Takeda and Kakahashi 1999) and that the gene seems to have inhibitory effects on the elongation of leaf, culm, rachis internode, awn and glume (Saisho et al. 2004). Further, it was also found that the *uzu* gene suppresses elongation of coleoptiles and first internode under dark conditions (Saisho et al. 2004), possibly for the reason that light is known to reduce brassinosteroids (or BR) synthesis (Fujioka and Yokota 2003).

Previous studies demonstrated that the *uzu* phenotype is due to a single-nucleotide substitution (A>G) at position 2612 in the sequence encoding kinase domain of *HvBRI1* polypeptide. This substitution results in an amino acid change at a highly conserved

residue in the kinase domain of the BR -receptor protein (Chono et al. 2003). The marker synteny of rice and barley chromosomes suggests that the *uzu* gene is likely homologous to *D61*, a rice homolog of *Arabidopsis* BR-insensitive 1 (*BRI1*), encoding a BR-receptor protein (Chono et al. 2003). A report on a new barley semi-dwarf gene allelic with *uzu* showed that similar effects on seedling length, plant height and awn length were detected by mutating the *HvBRI1* gene at a position different from the single-nucleotide substitution characterizing the *uzu* gene (Gruszka et al. 2011).

Many of the existing *Rht* genes in barley have negative effects on grain yield and other traits of agronomic importance (Hellewell et al. 2000) thus additional genes are highly desirable. Although the *uzu* gene has been widely used as a semi-dwarfing gene in East Asia (Chono et al. 2003; Rikiishi et al. 2008), its usefulness in other regions including Australia has not been reported. In the course of fine-mapping a locus controlling several characteristics of spike morphology (Chen et al. 2012), it was found that it co-located with the well-known semi-dwarf gene *uzu*. When investigating possible effects of plant height on Fusarium crown rot resistance, it was also noticed in experiments conducted in growth cabinet that the *uzu* gene has more drastic effect on plant height in environments of higher temperatures (Chen et al. 2014). These findings led to the systematic study described here which showed that the so-called semi-dwarfing gene *uzu* affects many characteristics and that the magnitudes of its effects are temperature-dependent.

Materials and methods

Near isogenic lines (NILs) for the *uzu* gene

The 15 pairs of NILs used in this study were developed in a study investigating possible effects of plant height on Fusarium crown rot resistance (Chen et al. 2014). They were developed from two F_2 populations (TX9425/Franklin and TX9425/Gairdner) based on the heterogeneous inbred family method (Tuinstra et al. 1997). The co-dominant simple sequence repeat (SSR) marker HVM33, which was most closely linked to the peak of the QTL controlling plant height, was used to select F_2 individuals that were heterozygous at the marker locus (Chen et al. 2014). Briefly, 15

individual heterozygous F_2 plants were identified and self-pollinated. Six F_3 plants were grown from each heterozygous F_2 plant, and a single heterozygote was again selected and self-pollinated. This process of heterozygous individual selection followed by self-pollination was repeated until the F_8 generation. From each of the 15 original F_2 plants, two homozygous F_8 lines, one with and the other without the 'TX9425' allele, were selected and were treated as a pair of NILs. A 'fast generation' procedure described by Zheng et al. (2013) was used in developing these NIL pairs.

Field trials in assessing the effects of the *uzu* gene on plant height and other traits of agronomic importance

The NILs were assessed in two field trials conducted at the CSIRO Research Station at Gatton, Queensland, Australia (27°34′S, 152°20′E) in 2012 and 2013, respectively. Two replicates of the test lines were planted in two separate blocks and a randomized complete block design were applied in each of the trials. Twenty seeds of each NIL were grown in a single 1.5 m row in each replicate, and the space between rows was 25 cm. Measurements of plant height, spike length (excluding awns), seed number per spike, grain weight (100 kernel weight), grain density (number of grains per cm spike) and internode (counted from the spike downward) length were taken on the six tallest tillers in each row, and the average values were used in subsequent statistical analyses.

The NILs and the genotype TX9425 (the donor of the *uzu* gene to the NILs used in this study) were also assessed in two field trials conducted at University of Tasmania, Launceston, Australia (41°26′S, 147°8′E) in 2013 and 2014. Two replicates of the 15 pairs of NILs were planted in two separate blocks and a randomized complete block design were applied in each of the trials. Twenty seeds of each NIL were grown in a single 1.5 m row in each replicate, the space between rows was 25 cm. Internode lengths were taken on the six tallest tillers in each row, and the average values were used in subsequent statistical analyses.

Effects of the *uzu* gene on coleoptile and seedling lengths at different temperatures

These experiments were conducted in growth cabinet using four pairs of the NILs. Seeds were surface

sterilised in 0.5 % hypochlorite solution for 30 s and then rinsed in sterile de-ionised water. The sterilised seeds were then germinated in Petri dishes on three layers of filter paper saturated with water and newly germinated seedlings were then planted into 56-well seedling trays (Rite Grow Kwik Pots, Garden City Plastics, Australia) containing sterilised University of California mix C (50 % sand and 50 % peat v/v). Seven seedlings per line were used in each replicate and two replicates were used in each trial. Seedling trays were then placed into the growth cabinets pre-set at 7 °C, 15 °C, 20 °C, or 25 °C with a fixed lighting period of 14 h. Measurements of coleoptiles (from soil surface to tip of coleoptile) and seedling lengths (from soil surface to tip of longest leaf) were taken when seedlings of the tall isolines reached 15–20 cm.

Statistical analysis

All statistical analyses were performed using GenStat for Windows in the 11th edition (copy right Lawes Agricultural Trust, Rothamsted Experimental Station, UK). Descriptive statistics and an analysis of variance (ANOVA) were conducted to detect if there were significant genetic effects for *uzu* in the 15 pairs of tall and dwarf NILs. Within each trial, the following mixed effects model was used: $Y_{ij} = l + r_i + g_j + w_{ij}$, where Y_{ij} observation on the j_{th} genotype in the i_{th} replication; l general mean; r_i effect due to i_{th} replication; g_j effect due to the j_{th} genotype; w_{ij} error or genotype by replication interaction, where genotype was treated as a random effect and that of replicates as fixed effect.

Results

Effects of the *uzu* on plant height and internode lengths

Highly significant reductions in plant height caused by the *uzu* gene were detected from each of the 15 NIL pairs assessed in both field trials, although the effects of this gene varied between genetic backgrounds and environments. Plant heights of the dwarf isolines ranged from 41.3 to 63.3 cm in 2012 and 43.5 cm to 68.5 cm in 2013, while the heights of the tall isolines ranged from 75.8 cm to 92.6 cm in 2012 and 67.5 cm to 104.0 cm in 2013. Plant heights between the *uzu*

lines and their tall counterparts among the 15 NIL pairs differed between 18.6 and 46.9 % in 2012 and between 10.2 and 50.9 % in 2013, with an average reduction of 37 % and 30.4 %, respectively, in the two seasons (Table 1).

Based on the experiments conducted at Launceston in Australia, the reduction in plant height conferred by the *uzu* gene was not evenly distributed across the various internodes. The gene had the largest effect on the 2nd internode (the one below the peduncle) with an average reduction of 64.4 % (Table 2). An extreme example is shown in Fig. 1.This internode hardly elongated in some of the *uzu* lines in the spring sowing trial under Australian environments. The reductions of the gene on the 1st (peduncle) and the 3rd internode were similar, with an average of 49.7 % and 40.8 %, respectively. The gene showed a much small reduction on the 4th internode, with an average of 24.6 % between the two seasons. Unexpectedly, the *uzu* gene increased the 5th internode by an average of 45.9 % between the two experiments conducted (Table 2). However, this internode was very short in the non-*uzu* isolines and the low baseline could have contributed to the observed differences between the *uzu* isolines and their counterparts.

Effects of the *uzu* gene on spike characteristics

Barley yield is the product of the number of spikes, the number of grains per spike and the average kernel weight. Thus a gene affecting any characteristic of spikes could have significant implication in yield potential. Based on the trials conducted at the CSIRO Gatton Research Station, the *uzu* gene reduced spike length across the 15 pairs of NILs by an average of 32.3 % and 30.9 %, respectively, over the two seasons. The dramatic decrease in spike length was accompanied by a slight increase in grain number per spike. The combined effects resulted in dramatic changes in grain density, which was increased by an average of 48.7 % and 54.8 %, respectively, over the two seasons across the 15 pairs of NILs. Kernel weight of the *uzu* isolines was also significantly lower than that of their counterparts, with an average difference across the 15 pairs of NILs of 18.1 % and 19.5 %, respectively, over the two seasons (Table 3).

Table 1 Effects of the *uzu* gene on plant height across the 15 pairs of near isogenic lines assessed

NIL lines	2012			2013		
	Tall	Dwarf	Difference (%)	Tall	Dwarf	Difference (%)
NIL01	83.3	63.3	24.00	84.0	66.5	20.80
NIL02	83.3	58.5	29.80	79.0	62.5	20.90
NIL03	92.6	58.3	37.00	97.5	56.3	42.30
NIL04	91.2	62.0	32.00	71.0	59.0	16.90
NIL05	75.9	58.6	22.80	85.5	60.0	29.80
NIL06	79.3	64.5	18.60	88.0	61.0	30.70
NIL07	83.8	44.9	46.50	81.0	44.5	45.10
NIL08	83.0	44.1	46.90	104.0	64.0	38.50
NIL09	90.7	51.7	43.00	86.5	62.5	27.70
NIL10	88.7	54.3	38.80	73.5	66.0	10.20
NIL11	85.3	53.2	37.60	78.8	68.5	13.10
NIL12	77.5	41.3	46.80	81.0	39.8	50.90
NIL13	81.7	46.0	43.70	67.5	43.5	35.60
NIL14	85.9	48.8	43.20	86.5	58.5	32.40
NIL15	75.8	42.6	43.80	86.5	50.5	41.60
Mean	83.9 ± 5.2	52.8 ± 7.6	37.00	83.4 ± 9.1	57.5 ± 8.6	30.40

Plant height was measured from bottom of crown to tip of awn

Table 2 Effects of the *uzu* gene on the top five internodes of barley plants based on 15 pairs of near isogenic lines

Internodes	Tall	Dwarf	Difference (%)
Internode 1 (peduncle)	26.3 ± 3.3	13.2 ± 3.7	49.7
Internode 2	12.9 ± 2.0	4.6 ± 2.7	64.4
Internode 3	11.2 ± 1.3	6.6 ± 1.1	40.8
Internode 4	9.6 ± 1.1	7.2 ± 1.6	24.6
Internode 5	4.9 ± 1.7	7.1 ± 2.7	−45.9

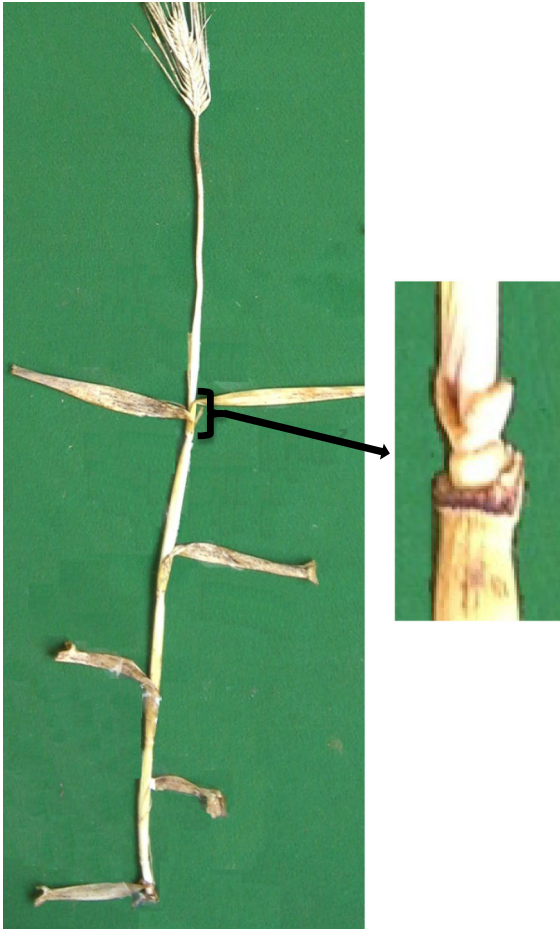Internodes were counted from spike downward

Fig. 1 Showing that the reduction in plant height conferred by the *uzu* gene was not evenly distributed across the various internodes (*left panel*). The gene had the largest effect on the 2nd internode which was hardly elongated in some of the *uzu* lines sown in spring under Australian environments (*right panel*)

Effects of the *uzu* gene on coleoptile and seedling lengths at different temperatures

As coleoptile length is strongly associated with stand establishment and grain yield of deep-sown crops (Rebetzke et al. 2007), possible effects of the *uzu* gene on these characteristics was assessed using four pairs of the NILs at four different temperatures. Data from these experiments showed that the *uzu* gene had highly significant effects on both of these characteristics and its effects are temperature dependent. The gene reduced coleoptile length by an average of 17.4 % at 7 °C, 23.4 % at 15 °C, 40.1 % at 20 °C, and 61.8 % at 25 °C across the four NIL pairs. The gene reduced total seedling length by an average of 15.1 %, 20.0 %, 33.6 % and 46.5 % at 7 °C, 15 °C, 20 °C, and 25 °C, respectively (Table 4). Clearly, the effects of the *uzu* gene on coleoptile and seedling lengths increased with increased temperature.

Discussion

Rht genes have played a key role worldwide in increasing yield potential of cereal crops. The barley semi-dwarfing gene *uzu* has been widely used in East Asia and we assessed its potential for Australian breeding programs. Our results showed that this gene has drastic effects on not only plant height but a wide array of other characteristics. Importantly, the effects of this gene are temperature-dependent, and its effects on these characteristics become more drastic in environments of higher temperatures. The drastic effects of this gene on some of these characteristics could make it difficult to exploit in breeding varieties for high temperature environments. For example, deep-sowing is often necessary to get better seed-zone moisture in high temperature and drought prone environments and it is known that genotypes with long coleoptiles improve stand establishment, vigour and grain yield of deep-sown crops (Rebetzke et al. 2007). Thus the significant reduction in coleoptile length conferred

Table 3 Effects of the *uzu* gene on spike characteristics based on 15 pairs of near isogenic lines

Trials	2012			2013		
Traits	Tall	Dwarf	Difference (%)	Tall	Dwarf	Difference (%)
Spike length (in cm)	9.3 ± 1.7	6.3 ± 0.7	32.3	7.7 ± 1.0	5.3 ± 0.9	30.9
Kernel number per spike	33.2 ± 2.7	34.5 ± 3.6	−3.9	23.9 ± 3.7	25.6 ± 4.9	−7.2
Kernel weight (gram/100)	4.7 ± 0.6	3.81 ± 0.6	18.1	4.1 ± 0.7	3.3 ± 0.7	19.5
Kernel density	3.7 ± 0.8	5.5 ± 0.6	−48.7	3.12 ± 0.4	4.8 ± 0.6	−54.8

Awn was excluded when measuring spike length, and kernel density was measured as number of kernel per cm spike

Table 4 Effects of the *uzu* gene on coleoptile and seedling length at different temperatures based on four pairs of near isogenic lines

Temperature	Coleoptile length (in cm)			Seedling length (in cm)		
	Tall	Dwarf	Difference (%)	Tall	Dwarf	Difference (%)
At 7 °C	2.8 ± 0.2	2.3 ± 0.1	17.40	16.4 ± 1.0	13.9 ± 0.8	15.10
At 15 °C	2.4 ± 0.3	1.9 ± 0.2	23.40	19.9 ± 1.8	16.5 ± 2.4	20.00
At 20 °C	4.2 ± 0.5	2.5 ± 0.2	40.10	18.2 ± 2.73	12.1 ± 2.3	33.60
At 25 °C	2.8 ± 0.2	1.1 ± 0.2	61.80	15.4 ± 1.39	8.2 ± 1.5	46.50

Coleoptile length was measured from soil surface to tip of the coleoptile and seedling length was measured from soil surface to tip of the longest leaf

by the *uzu* gene would restrict the exploitation of this gene in breeding for such environments. Further, the significant reduction on grain weight by this semi-dwarfing gene in high temperature environments is also of concern as it would lead to reduced grain quality due to increased screenings.

Considering that the *uzu* gene is due to a single nucleotide substitution which results in an amino acid change (Chono et al. 2003), it could be difficult to apprehend the substantial effects of this gene on so many characteristics. In fact, the effects of this gene are not limited to the characteristics described in this paper. We noticed that it also affects many other characteristic including leaf size and flowering time although no measurements were taken on these traits in the study reported here. It has been reported that this gene plays an inhibitory role in the elongation of various tissues including reducing coleoptile length in the dark (Saisho et al. 2004), possibly for the reason that light is known to reduce BR synthesis (Fujioka and Yokota 2003). However, the effect of darkness on the functions of the *uzu* gene is debatable based on the results from this study. We observed significant inhibitory effect of the gene on coleoptile elongation in the condition of 14 h lighting as well, and this is the

case at each of the four temperatures assessed. It has also been reported that genotypes with the *uzu* gene show dark green leaves and suppressed plant regeneration from calli derived from immature embryos (Rikiishi et al. 2008).

Pleiotropic effects of this gene have also been noted in several other species. For example, it has been reported that BR-deficient mutants show greatly reduced longitudinal cell expansion (Takahashi et al. 1995; Kauschmann et al. 1996; Szekeres et al. 1996; Azpiroz et al. 1998) and exhibit delayed flowering (Chory et al. 1991; Li and Chory 1997; Azpiroz et al. 1998). In *Prunus avium*, the gene reduces fertility and extends life span and delays senescence (Hewitt et al. 1985). Clearly, although the *uzu* gene has routinely been referred to as a semi-dwarfing gene in barley (Chono et al. 2003; Saisho et al. 2004; Rikiishi et al. 2008), it significantly affects a wide range of characteristics related to plant development in not only barley but other plant species as well. Results from this study show that the pleiotropic effects of this gene on plant development and kernel quality need to be considered when exploiting it to modulate plant height and this is especially the case in high temperature and drought prone environments.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

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