

Phenotypic effect and chromosomal localization of *Ddw3*, the dominant dwarfing gene in rye (*Secale cereale* L.)

Stefan Stojalowski · Beata Myśków ·
Monika Hanek

Received: 9 March 2014 / Accepted: 29 May 2014 / Published online: 14 June 2014
© The Author(s) 2014. This article is published with open access at Springerlink.com

Abstract Dwarfing genes play a major role in development of semi-dwarf cultivars of various cereals, but in rye this type of cultivar is still not common. Several recessive and dominant dwarfing genes in rye have been reported. Among the known dominant dwarfing genes in rye, two are well characterised: *Ddw1* from the 5RL chromosome and *Ddw2* located on 7R. This study was aimed at characterisation of the K11 source of dominantly inherited dwarfism found in plant materials grown in the Plant Breeding and Acclimatization Institute (Radzików, Poland). Mapping analyses in this study indicate that the dominant dwarf gene under investigation is located on the 1RL chromosome and is independent from previously known genes. The gene was named *Ddw3*. Phenotypic effect of the *Ddw3* was tested on two pairs of near-isogenic lines. Six morphological traits were analysed in two or three growing seasons: plant height, length of the second internode from the base, number of internodes, tillering, spike length, and number of spikelets per spike. No negative or weak influences on yield-related traits were observed. The examination of the dwarf plants' reaction to seedling treatment by gibberellic acid solution revealed sensitivity of *Ddw3* to this growth regulator. This report is the first

evidence of the dominant *Ddw3* gene in rye and its presence on the 1R chromosome.

Keywords Dwarfing gene · Genetic mapping · Near-isogenic lines · Plant height · Rye

Introduction

Dwarfing genes play a major role in the development of semi-dwarf cultivars of various cereals, including wheat, barley, and triticale. Rye (*Secale cereale* L.) is closely related to these crops but semi-dwarf cultivars of this cereal are not widely cultivated. In rye, several dwarfing genes have been reported, mainly of a recessive character (Börner et al. 1996). Among the known dominant dwarfing genes in rye, two have been thoroughly characterized: *Ddw1* and *Ddw2*. The *Ddw1* gene was discovered by Kobyljanski (1972) as the natural mutant EM-1 present in the Russian gene bank collection in St. Petersburg and was originally named as the *Humilus* (*Hl*) gene. It is located on the long arm of the 5R chromosome (Korzun et al. 1996; Tenhola-Roininen and Tanhuanpää 2010). Some attempts were made in Russia (formerly in the Soviet Union) to breed semi-dwarf rye (Kobyljanski 1975a; Kondratenko and Goncharenko 1975) but obtained cultivars never became very common. Conversely, the *Ddw1* gene was successively applied to the breeding of semi-dwarf cultivars of the currently grown triticale

S. Stojalowski (✉) · B. Myśków · M. Hanek
Department of Plant Genetics, Breeding and
Biotechnology, West-Pomeranian University of
Technology in Szczecin, Szczecin, Poland
e-mail: stef.s@wp.pl; sstojalowski@zut.edu.pl

(Wolski and Gryka 1996). The second well-characterized dominant dwarfing gene in rye (*Ddw2*) was found in Bulgarian mutant K10028 (Kobyłjanski 1975a) and localized on the 7R chromosome (Melz 1989). Additional sources of dominant dwarfing genes in rye were also reported (Węgrzyn and Grochowski 1984), but their relationships to *Ddw1* and *Ddw2* and their localisation on rye chromosomes have never been studied in detail.

Generally, the reduction of plant height in cereals is determined by two groups of dwarfing genes: those sensitive and insensitive to exogenously applied gibberellic acid (GA). The two well-known dominant dwarfing genes in rye are characterized as GA-sensitive (Börner and Melz 1988). To the best of our knowledge, no information about sensitivity to GA or chromosomal localisation of alternatives to *Ddw1* and *Ddw2* dominant dwarfing genes in rye is available.

This study aimed to characterise the K11 source of dominantly inherited dwarfism found in Polish breeding plant material by Madej and Warzecha (1977) from the Polish Institute of Plant Breeding and Acclimatization.

Materials and methods

Development, genetic analysis, and phenotyping of near-isogenic lines (NILs)

The K11 source of dwarfism in rye was provided to the West-Pomeranian University of Technology (formerly University of Agriculture in Szczecin) by L. Madej (Plant Breeding and Acclimatization Institute, Radzików, Poland). From this source, Prof. M. Łapiński (University of Agriculture in Szczecin, Poland) developed a series of dwarf inbred lines, including the 711 line used for our investigation, in the early 1980s. In 2000, the dwarf 711 line was hybridized with the L1 line (normal height). The L1 line was obtained from H.H. Geiger (University of Hohenheim, Germany) and, for more than 20 years, has been reproduced by self-pollination at the West-Pomeranian University of Technology. The subsequent F_1 hybrids were dwarf and the F_2 progeny consisting of 62 individuals who segregated into dwarf and normal plants according to the expected 3:1 ratio. Successive generations (F_3 – F_6) were obtained by forced inbreeding. For the F_6 progeny, it was stated that two inbred

lines were still segregating with respect to plant height. Dwarf and tall plants within these inbred lines were selected for development of two pairs of candidate near-isogenic lines (NILs) named 4112 and 4127. The verification of homozygosity of NILs was carried out during the next two generations (Fig. 1).

The genetic relationships between these NILs and their ancestral parents (711 and L1 inbred lines) were analysed using Diversity Arrays Technology (DArT) markers. The calculation of genetic similarity was done in two ways: with consideration of all molecular markers and by taking into account only polymorphic markers for ancestral parent lines. The last method of calculation better reflects the progress obtained during development of near-isogenic lines because the results are of relative character—similarity between lines 711 and L1 is assumed to be zero. The marker scores were used to calculate a relative genetic similarity matrix (SM—simple matching function was applied) and then a cluster analysis was performed to construct an UPGMA (Unweighted Pair-Group Method with Arithmetic Averages) dendrogram using the NTSYS-pc v.2.20j software (Rohlf 2005).

Starting from the F_0 generation, during the next three growing seasons these two pairs of NILs were assessed with respect to their morphological trait performance: plant height, number of internodes in the main tiller, length of the second internode from the bottom, number of productive tillers per plant, spike length, and number of spikelets per spike. Sixteen to 48 plants (depending on the year of study) representing each NIL were grown in 8-dm³ buckets arranged in a random design in the greenhouse of West-Pomeranian University of Technology in Szczecin. For statistical analysis, plants were considered as replications. We assessed mean values, standard deviation, correlation coefficients, and significant differences between NILs by the non-parametric Kruskal–Wallis test calculated using Statistica 9.0 software (Statsoft).

Assessment of the response of inbred lines to exogenous gibberellic acid (GA₃)

The GA₃-seedling test was performed as described by Börner (1991) in three replications. Dry kernels of dwarf parental line 711, as well as near-isogenic lines 4112Dw, 4112N, 4127Dw, 4127N, were placed on filter paper moistened by distilled water for the

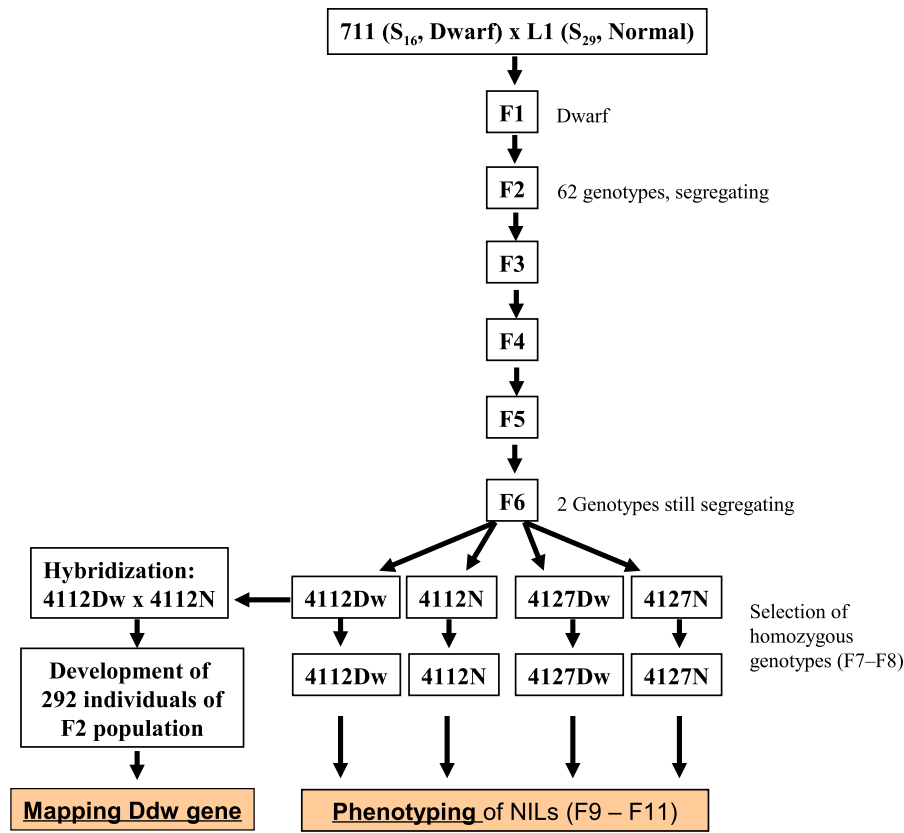


Fig. 1 Scheme illustrating the development of near-isogenic lines and mapping population

synchronisation of germination at 4 °C for 48 h. Next, they were moved into 20 °C and transferred into special plastic boxes containing single-grain trays (20 plants per tray). Each tray contained seeds of a given inbred line and constituted one replication. Three trays, each with a studied line, were placed into standardised nutrition solution (control); three other trays were placed into nutrition solution supplemented with 5-ppm GA₃. At the 2–3-leaf stage, seedlings were measured. Statistical analyses for morphological traits were performed with the use of a non-parametric Kruskal–Wallis test (as mentioned above).

Mapping of the *Ddw* gene

Homozygous dwarf and tall F₇ lines representative of the 4112 genotype (lines 4112Dw and 4112N) were crossed to develop a mapping population (Fig. 1). Five dwarf F₁ hybrid plants were self-pollinated, producing 292 F₂ individuals that were phenotyped (by visual

assessment and measuring of plant height) in field conditions at Szczecin. The phenotypic distribution of plant height to the monogenic model of inheritance was verified by a standard Chi square test. Individuals from the F₂ generation were self-pollinated, and F₃ progenies were visually assessed for plant height in order to confirm the normal height of recessive homozygotes and to distinguish dwarf heterozygotes from dominant homozygotes. Due to low heterogeneity and low viability of mapping population amounts of collected F₃ seeds were limited. A set of genotypes with an extremely low number of collected seeds were excluded from studies of the F₃ generation. It was assumed that confirmation of the homozygous character of recessive tall plants was proved when more than five individuals in F₃ were of normal height. Dwarf genotypes of F₂ were considered as homozygous when at least 11 F₃ progenies revealed dwarfism. Segregating F₃ generations indicated that the studied F₂ genotype was heterozygous. Leaves of the F₂

population collected in the early spring were used for DNA isolation. A set of 94 genotypes was randomly chosen from the group of individuals clearly classified during the phenotyping of F_2 and F_3 generations and used for genotyping by Diversity Arrays Technology. Resultant segregation data as well as DArT results were used for mapping purposes.

The identification and localisation of markers tightly linked with the *Ddw* gene were performed with the use of the JoinMap 3.0 software (Van Ooijen and Voorrips 2001). Linkage groups containing the dwarf locus and DArT markers were constructed at $LOD = 20$ and compared to the RIL-S consensus genetic map of the rye genome (Milczarski et al. 2011).

Results

Two pairs of NILs (named 4112 and 4127) in the F_8 generation were homogeneous with respect to height and other morphological traits (Fig. 2). The time of heading and flowering of both 4127 lines (dwarf and normal) was 1–2 days later than the 4112 genotypes. No differences with respect to the earliness of dwarf and normal variants of both NILs were observed. Diversity Arrays Technology applied to genetic analysis of six inbred lines (711, L1, 4112Dw, 4112N, 4127Dw, and 4127N) revealed data for 3615 markers. The majority of them were monomorphic—genetic differences between parental lines 711 and L1 were indicated by 957 DArTs (estimated genetic similarity—0.74). Among those, 603 did not show differences when 4127Dw and 4127N lines were compared (relative genetic similarity between these NILs was assessed as 0.63 and 0.90 when all molecular markers were taken under account). For lines 4112Dw and 4112N, only 115 DArT polymorphic markers were found (the relative genetic similarity considering only markers polymorphic for parental lines was 0.88 and the application of all markers revealed 0.97 similarity of these near-isogenic lines). The NIL 4112 are classified as more similar to the L1 parental line, while the 4127 genotypes are closer to the 711 line, shown in the dendrogram constructed by the UPGMA method (Fig. 3). The high genetic similarity of the 4112 near-isogenic lines resulted in the selection of these two genotypes as parental forms in the development of the mapping population used for the localisation of the dwarfing gene.

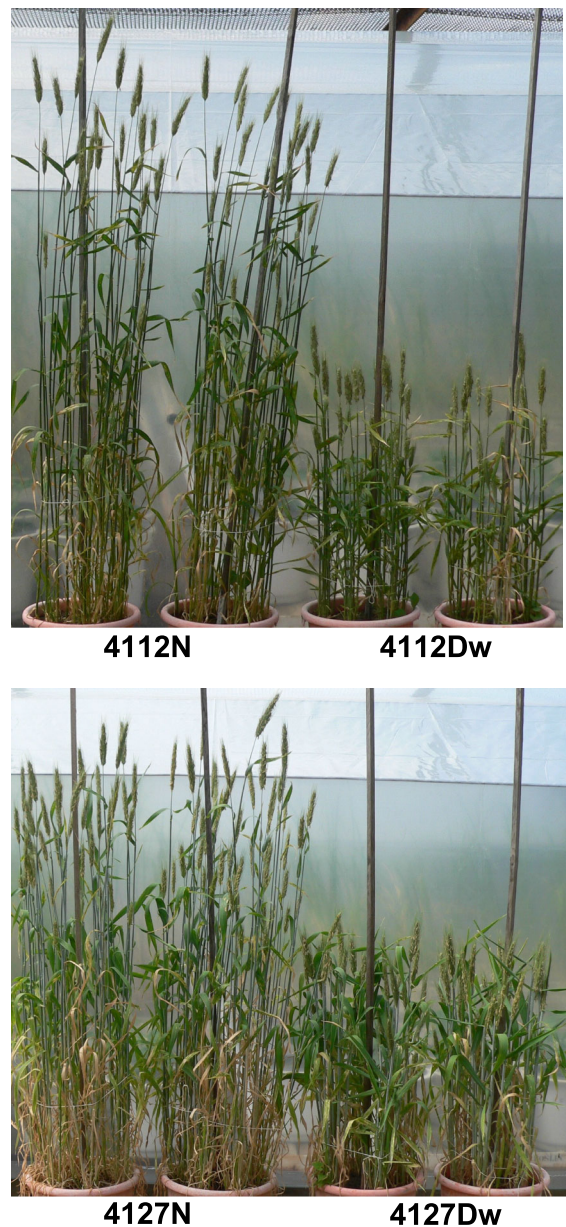
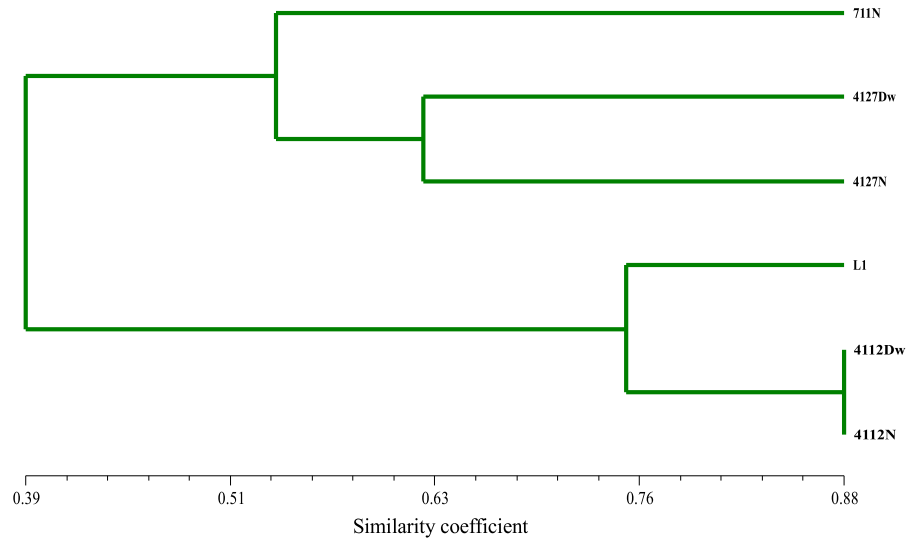


Fig. 2 Phenotypes of homozygous (F_8 generation) dwarf and tall near-isogenic lines

During each year of the study, phenotyping of the two pairs of NILs revealed significant differences between the dwarf and normal variants regarding plant height and the length of the second internode from the bottom (Table 1). The dwarfing gene present in lines 4112Dw and 4127Dw led to approximately a 40 % reduction of plant height (in comparison to the “normal” variants of both inbred lines). An analysis

Fig. 3 Genetic relationships between two pairs of near-isogenic lines and their ancestral parents



of the remaining morphological traits in general showed the slightly lower performance of dwarf genotypes with respect to their tall versions. This tendency seemed to occur routinely in every year of the study, but supposed differences between dwarf and tall NILs were small and in most cases not statistically significant (Table 1). Only two traits (spike length and number of spikelets per spike) in some years revealed significant differences within 4112 tall and dwarf genotypes.

We observed a strong correlation between plant height and the length of the second internode in both pairs of NILs (Table 2). The number of internodes was only slightly correlated with plant height of NILs 4127 and was completely independent in 4112 genotypes, so the reduction of plant height in dwarf plants was due to the shorter length of internodes not to a reduction in their number. A statistically significant association was found between plant height and length of spikes as well as numbers of spikelets per spike (Table 2).

The dwarfing gene we studied revealed to be sensitive to GA. Seedlings treated by GA₃ solution showed an increased length of about 10–40 % and all observed differences were statistically significant (Table 3). On the other hand, the same level of sensitivity to GA₃ was stated for normal versions of both NILs.

The mapping population used to localise the *Ddw* gene consisted of 292 individuals. Among them, 227 were dwarf and 65 were tall (normal height). The observed segregation stayed in accordance with the

expected 3:1 ratio (Table 4). The plant height within the class of dwarf plants ranged from 39 to 75 cm and the variation within the class of tall individuals was 95–121 cm (Fig. 4). Therefore, dwarf and normal genotypes of the mapping population were easy to distinguish by visual assessment. The identification done of dominant (dwarf) homozygotes from heterozygotes as well as the verification of normal height of recessive homozygotes in the F₃ generation was based only on visual assessment. The number of F₃ plants sufficient for the classification of F₂ genotypes was obtained for 210 individuals of the mapping population: 43 were defined as dominant homozygotes, 117 as heterozygotes, and 50 were confirmed to be recessive homozygotes (Table 4).

DARt analyses revealed 171 markers segregating within the mapping population. The majority of them were assigned to chromosomes 1R, 3R, and 4R, wherein the most numerous were markers from the 1R chromosome (96 DARts). Linkage grouping procedures resulted in the construction of one numerous group consisting of 64 DARts localised on the 1R chromosome and several smaller groups containing no more than 12 markers, which were distributed on 1R, 3R, and 4R. The *Ddw* locus was included in the set of markers from 1R. The length of the linkage group localised on the 1R was <9 cM and the *Ddw3* gene was located between two completely linked DARts (XrPt399789 and XrPt505185) and the XrPt506649 (Fig. 5). The distance of the *Ddw3* to the nearest flanking loci was about 0.25 cM (in both directions). A

Table 1 Performance of morphological traits within two pairs of near-isogenic lines

Year	Plant height (cm)			Length of 2-nd internode (cm)			Number of internodes					
	4112Dw	4112N	4127Dw	4127N	4112Dw	4112N	4127Dw	4127N	4112Dw	4112N	4127Dw	4127N
2011	Mean	54.13	112.36	51.59	89.25	4.59	9.03	4.36	8.37	5.72	5.95	5.60
	SD	3.13	9.27	2.48	4.71	0.52	1.01	0.54	0.78	0.33	0.23	0.25
2012	Mean	57.82	100.00	51.32	87.15	5.00	8.28	5.44	12.57	5.91	6.50	5.73
	SD	5.78	9.65	4.79	8.96	0.51	0.94	1.14	3.97	0.30	0.52	0.46
2013	Mean	58.67	100.88	64.40	106.91							
	SD	3.11	7.37	5.07	8.41							
Total	Mean	57.66	103.68	59.64	96.54	4.76	8.73	5.08	11.24	5.80	6.17	5.69
	SD	3.96	9.66	7.87	12.52	0.55	1.04	1.10	3.84	0.33	0.46	0.40
Year	Number of tillers per plant			Spike length [cm]			Number of spikelets per spike					
	4112Dw	4112N	4127Dw	4127N	4112Dw	4112N	4127Dw	4127N	4112Dw	4112N	4127Dw	4127N
2011	Mean	4.67	5.78	6.00	7.83	5.94	6.52	7.10	7.33	26.29	29.10	31.75
	SD	1.59	1.52	1.34	1.99	0.66	0.60	0.41	0.51	2.78	1.64	1.51
2012	Mean	2.73	3.08	4.91	5.38	4.60	5.60	7.10	8.54	22.50	27.80	28.00
	SD	0.90	1.16	2.20	2.38	0.14	0.60	0.92	1.29	2.12	2.86	4.64
2013	Mean					5.92	7.13	7.71	7.60	23.41	27.23	27.57
	SD					0.57	0.58	0.87	1.13	2.39	2.30	3.93
Total	Mean	3.85	4.70	5.27	6.16	5.90	7.01	7.65	7.62	23.68	27.46	27.88
	SD	1.64	1.91	2.00	2.52	0.59	0.66	0.86	1.12	2.56	2.32	3.96

Significant differences between lines within pair of NILs (based on the Kruskal–Wallis test) are exhibited by bold values

Table 2 Correlation coefficients between studied traits

	Plant height	Length of 2-nd internode	Number of internodes	Number of tillers per plant	Spike length	Number of spikelets per spike
Plant height	X	0.91**	0.39*	0.25	0.47**	0.62**
Length of 2-nd internode	0.82**	X	−0.11	0.23	0.40*	0.55**
Number of internodes	0.08	0.26	X	−0.01	0.30	0.43*
Number of tillers per plant	0.27	0.08	−0.02	X	0.53**	0.41*
Spike length	0.36*	0.30	−0.56**	0.02	X	0.90**
Number of spikelets per spike	0.55**	0.16	−0.27	0.41*	0.66**	X

Results from NILs 4112 are shown above the diagonal, from NILs 4127—below the diagonal

Significant at: * $P < 0.01$; ** $P < 0.001$

Table 3 Reaction of studied inbred lines to treatment by gibberellic acid (in italic—lines of normal height)

Genotype	Mean length of seedlings (mm)		GA ₃ treated seedlings length relative to the control (%)	Level of significance in the Kruskal–Wallis test
	Control (H ₂ O)	GA ₃ treated		
711	145	160	110.3	$P < 0.05$
4112Dw	119	153	128.6	$P < 0.01$
4127Dw	185	219	118.4	$P < 0.01$
<i>4112N</i>	<i>152</i>	<i>210</i>	<i>138.2</i>	$P < 0.01$
<i>4127N</i>	<i>185</i>	<i>235</i>	<i>127.0</i>	$P < 0.01$

comparison of the created linkage map to the consensus genetic map of the rye genome revealed 22 common DArTs located on the long arm of 1R (Fig. 5). Distances between DArT loci located on the consensus map were approximately two times longer—segregating markers were mapped on a distance of about 16 cM (<10 % of the total length of 1R chromosome). Since none of the rye dominant dwarfing genes was mapped in this genomic region before, the gene of interest was named *Ddw3*.

Discussion

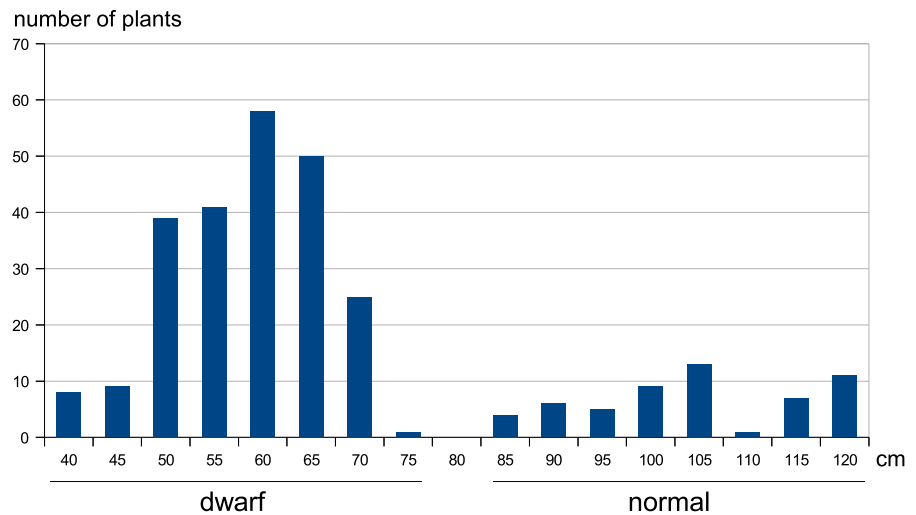
Lodging susceptibility is still a serious problem in the breeding of rye cultivars. In wheat and barley, currently grown cultivars are well suited to modern farming practice. This was achieved by selecting dwarfing genes such as *Rht* in wheat. These *Rht* dominant genes, which are insensitive to GA treatment, exhibit a reduction in internode length but this does not affect the length of the spikes (Börner et al. 1996). In contrast to wheat and to barley as well, the dwarfing genes do not play a significant role in determining plant height in elite rye breeding resources. When studying the genetic architecture of plant height within currently bred plant germplasm, numerous QTLs with a low phenotypic effect were found (Miedaner et al. 2011, 2012; Myśków et al. 2014). Some attempts of introducing the *Ddw1* gene into East European and Finnish rye breeding programs were undertaken (Kobyłjanski 1975a; Kondratenko and Goncharenko 1975; Tenhola-Roininen and Tanhuanpää 2010) but frequently observed negative effects in yielding or yield stability were the disadvantage of these activities (Miedaner et al. 2011).

Table 4 Genetic classification of individuals within F₂ mapping population and results of verification analyzes in F₃ generation

Generation	Number of plants				Chi ²	Probability*
	Dominant homozygotes	Heterozygote	Recessive homozygotes	Total		
F ₂	227		65	292	1.17	0.5–0.25
F ₃	43	117	50	210	3.21	0.25–0.1

* Rejection of null hypothesis if $P < 0.05$

Fig. 4 Distribution of plant height within the studied F₂ population



In rye, both well-studied dominant dwarfing genes (*Ddw1* and *Ddw2*) are sensitive to exogenous GA (Börner and Melz 1988). Among several known recessive dwarfing genes in rye, sensitive and insensitive cases were reported (Börner and Melz 1988; Börner 1991; Börner et al. 1996). The *Ddw3* gene from our study reveals a significant reaction to treatment by GA, but NILs representing the normal height expressed comparable reaction for GA (significant elongation of seedlings).

Common dwarfing genes in cereals are divided into two categories (Börner et al. 1996):

- GA sensitive, where a deficiency of endogenous gibberellins leads to the reduction of plant height and normal growth can be restored by application of exogenous GA.
- GA insensitive, which have an unsuitable response for this group of growth regulators.

In rye plants carrying the *Ddw3* mutation, the mechanism of response to GA is efficient, so this gene is classified as sensitive to exogenous gibberelic acid. On the other hand, the application of gibberellins to the NILs of normal height resulted in a comparable increase of the length of seedlings. Thus we suppose that treatment by GA might not be sufficient for the elimination of dwarfism. Perhaps the synthesis of other growth regulators or a response to them is engaged in the mechanism of plant height reduction. The final phenotypic effect must be connected with the repression of internode elongation.

The possible usage of the *Ddw3* gene in breeding rye cultivars strongly depends on its pleiotropic effect on yield-related traits. Regarding the *Ddw1* gene, the most commonly utilized in rye breeding, significant positive effects for some traits were reported. Increased spike length and higher number of spikelets per spike were reported by Kobyljanski (1975b) and Kondratenko and Goncharenko (1975). In addition, Kobyljanski (1975b) suggested the increased tillering of plants with short stems but unfavorable relationship between the *Ddw1* gene and flowering time has also been described (Börner et al. 2000). In our study, the effectiveness of tillering was not affected by the *Ddw3* and the phenological traits were also not related to this gene. Unfortunately, correlation between plant height and the length of spikes as well as number of spikelets within spikes was observed, which could be unfavorable for practical applications. However, this correlation is rather weak and it is not recognized if it results from the pleiotropic activity of the *Ddw3* or it is a consequence of the “linkage drag”. Regardless of the genetic background, the reported correlation can hamper the utilization of *Ddw3* in future breeding and we can not be truly sure that it will result in significant changes of the currently observed genetic architecture of rye plant height (Miedaner et al. 2011, 2012).

The localisation of *Ddw3* on the long arm of the 1R chromosome is reported here for the first time and the identification of numerous molecular markers strongly linked to this gene may be helpful in the introduction of this new dominant dwarfing gene to the breeding

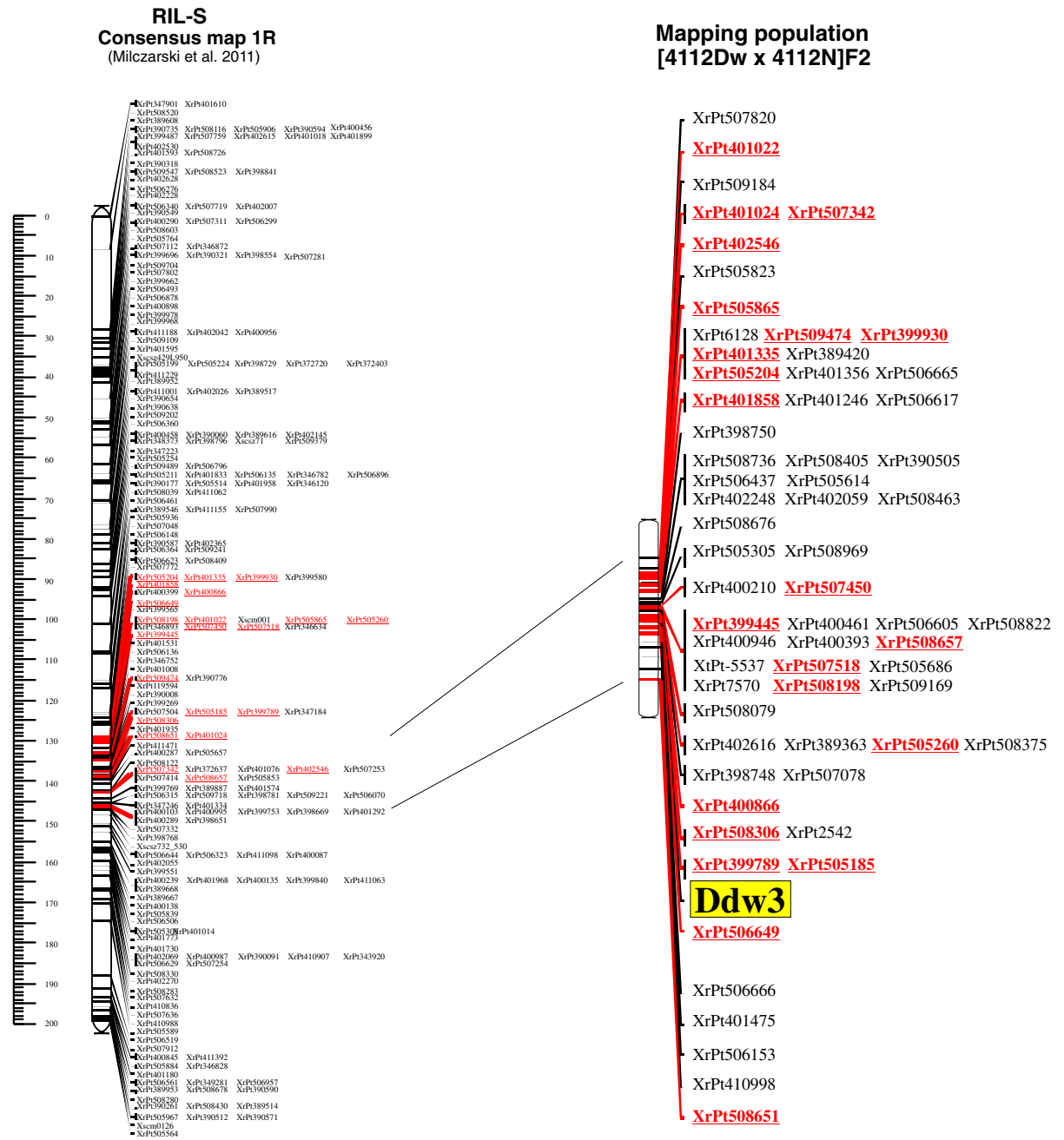


Fig. 5 Comparative mapping of the linkage group containing the studied dwarfing gene (*Ddw3*) with the consensus genetic map of rye genome by Milczarski et al. (2011). Markers common for both linkage maps are *underlined*

practice. Dwarfism is a morphological trait easy to assess before flowering through visual observations. However, the purification of lines and/or populations from heterozygous plants may be facilitated by a simple and cost-effective marker system. It can be

developed by comparative mapping and the adaptation of PCR-based markers located on other genetic maps of the 1R chromosome (Hackauf and Wehling 2003; Khlestkina et al. 2004; Hackauf et al. 2009; Myśków et al. 2010; Milczarski et al. 2011) or by utilizing

sequences of DArT clones. However sequences of DArTs for rye genome are not published yet, but there are available sequences for clones of barley, wheat, and brassica, (<http://www.diversityarrays.com/dart-map-sequences>) as well as for oat (Tinker et al. 2009). It can be expected that rye sequences will follow soon.

Acknowledgments Przemysław Tomczak, Hanna Stojalowska and Sandra Świącka are greatly thanked by authors for their excellent technical assistance.

Open Access This article is distributed under the terms of the Creative Commons Attribution License which permits any use, distribution, and reproduction in any medium, provided the original author(s) and the source are credited.

References

- Börner A (1991) Genetical studies of gibberelic acid insensitivity in rye (*Secale cereale* L.). *Plant Breed* 106:53–57
- Börner A, Melz G (1988) Response of rye genotypes differing in plant height to exogenous gibberellic acid application. *Arch Züchtungsforsch Berl* 18(2):71–74
- Börner A, Plaschke J, Korzun V, Worland AJ (1996) The relationships between the dwarfing genes of wheat and rye. *Euphytica* 89:69–75
- Börner A, Korzun V, Voylokov AV, Worland AJ, Weber WE (2000) Genetic mapping of quantitative trait loci in rye (*Secale cereale* L.). *Euphytica* 116:203–209
- Hackauf B, Wehling P (2003) Development of microsatellite markers in rye: map construction. *Plant Breed Seed Sci* 48:143–151
- Hackauf B, Rudd S, van der Voort JR, Miedaner T, Wehling P (2009) Comparative mapping of DNA sequences in rye (*Secale cereale* L.) in relation to the rice genome. *Theor Appl Genet* 118:371–384
- Khlestkina EK, Than MHM, Pestsova EG, Röder MS, Malyshev SV, Korzun V, Börner A (2004) Mapping of 99 new microsatellite-derived loci in rye (*Secale cereale* L.) including 39 expressed sequence tags. *Theor Appl Genet* 109:725–732
- Kobylyanski VD (1972) On the genetics of the dominant factor of short-strawed rye. *Genetika* 8:12–17
- Kobylyanski VD (1975a) Genetic resources of world's rye collection for solving of more important breeding problems. *Hod Rośl Aklim Nas* 19(5/6):439–446
- Kobylyanski VD (1975b) Effect of the dominant character of short straw. *Hod Rośl Aklim Nas* 19(5/6):495–501
- Kondratenko FT, Goncharenko AA (1975) The breeding of dwarf winter rye varieties. *Hod Rośl Aklim Nas* 19(5/6):527–530
- Korzun V, Melz G, Börner A (1996) RFLP mapping of the dwarfing (*Ddw1*) and hairy peduncle (*Hp*) genes on chromosome 5 of rye (*Secale cereale* L.). *Theor Appl Genet* 92:1073–1077
- Madej L, Warzecha R (1977) Informacja o nowym źródle karłowatości u żyta. *Prace Zesp. Bad. Hod. Żyta w 1976 roku. IHAR Radzików*: 23–26 (in Polish)
- Melz G (1989) Beiträge zur Genetik des Roggens (*Secale cereale* L.). DSc thesis, Berlin
- Miedaner T, Müller BU, Piepho HP, Falke KC (2011) Genetic architecture of plant height in winter rye introgression libraries. *Plant Breed* 130(2):209–216
- Miedaner T, Hübner M, Korzun V, Schmiedchen B, Bauer E, Haseneyer G, Wilde P, Reif JC (2012) Genetic architecture of complex agronomic traits examined in two testcross populations of rye (*Secale cereale* L.). *BMC Genom* 13:706
- Milczarski P, Bolibok-Bragoszewska H, Myśków B, Stojalowski S, Heller-Uszyńska K, Góralska M, Brągoszewski P, Uszyński G, Kilian A, Rakoczy-Trojanowska M (2011) A high density consensus map of rye (*Secale cereale* L.) based on DArT markers. *PLoS One* 6(12):1–14. doi:10.1371/journal.pone.0028495.t005
- Myśków B, Stojalowski S, Milczarski P, Masojć P (2010) Mapping of sequence-specific markers and loci controlling preharvest sprouting and alpha-amylase activity in rye (*Secale cereale* L.) on the genetic map of an F2 (S120×S76) population. *J Appl Genet* 51:283–287
- Myśków B, Hanek M, Banek-Tabar A, Maciorowski R, Stojalowski S (2014) The application of high-density genetic maps of rye for detection of QTLs controlling morphological traits. *J Appl Genet* 55:15–26
- Rohlf FJ (2005) NTSYSpc: numerical taxonomysystem ver. 2.20. Exeter Publishing Ltd, Setauket
- Tenhola-Roininen T, Tanhuanpää P (2010) Tagging the dwarfing gene *DDw1* in a rye population derived from doubled haploid parents. *Euphytica* 172:303–312
- Tinker NA, Kilian A, Wight CP, Heller-Uszyńska K, Wenzl P, Rines HW, Bjørnstad A, Howarth CJ, Jannink J-L, Anderson JM, Rossnagel BG, Stuthman DD, Sorrells ME, Jackson EW, Tuvešson S, Kolb RL, Olsson O, Federizzi LC, Carson ML, Ohm HW, Molnar SJ, Scoles GJ, Eckstein PE, Bonman JM, Ceplitis A, Langdon T (2009) New DArT markers for oat provide enhanced map coverage and global germplasm characterization. *BMC Genom* 10:39
- Van Ooijen JW, Voorrips RE (2001) JoinMap[®] 3.0, software for the calculation of genetic linkage maps. *Plant Res Intern, Wageningen, The Netherlands*
- Węgrzyn S, Grochowski L (1984) Influence of dominant dwarf on inheritance of chosen traits of the rye hybrids. *Hod Rośl Aklim Nas* 28(1):45–55
- Wolski T, Gryka J (1996) Semi-dwarf winter triticale. In: Guedes-Pinto H et al (eds) *Triticale—today and tomorrow. Developments in plant breeding*, vol 5. Kluwer, Dordrecht, pp 581–587; ISBN: 978-94-010-6634-1