

Influence of the Semi-dwarf Growth Type on Seed Yield and Agronomic Parameters at Low and High Nitrogen Fertilization in Winter Oilseed Rape

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ABSTRACT

In cereals like wheat (*Triticum aestivum* L.) or rice (*Oryza sativa* L.), a short-straw ideotype is characteristic for all modern cultivars, mainly due to the use of genes affecting the dwarf genotype. In oilseed rape (*Brassica napus* L.), several dwarf mutants are known but so far not widely used. An interesting approach is the production of semi-dwarf hybrids from dwarf and normal-type parents, which might have an increased harvest index (HI) and a higher grain yield, especially when nitrogen (N) availability is restricted. To this point, no systematic comparison using a large number of semi-dwarf and normal-type hybrids has been published. A double haploid (DH) population was developed that was segregating for the *bzh* dwarf locus with 54 dwarf and 54 normal-type lines. By crossing with a normal-type tester, 108 testcrosses were produced with 54 hybrids each of semi-dwarf and normal types. These were evaluated under high and zero N fertilization in five and seven environments, respectively, for yield and agronomic parameters. Quantitative trait loci (QTL) were estimated for yield-relevant traits. Semi-dwarf hybrids had a significantly higher yield compared with normal types in N-deficient conditions (2.24 and 2.05 Mg ha⁻¹). At an optimal N supply, no significant difference between growth types was found for seed yield. Oil content was slightly lower in semi-dwarfs under both N treatments, whereas this was compensated by oil yield. All major QTL for plant height, straw yield, HI, and seed yield co-segregated with the *bzh* dwarf locus on linkage group A06, indicating that the dwarf gene is not only reducing plant height but also causing increased HI and higher yield under N limitation for semi-dwarf hybrids. We conclude that semi-dwarf hybrids are of high interest for the N-balanced oilseed rape production, especially when N is scarce.

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Abbreviations: DH, double haploid; HI, harvest index; LG, linkage group; N₀, zero N fertilization; N₁, high N fertilization; QTL, quantitative trait loci.

WINTER OILSEED RAPE (*Brassica napus*) has a lower harvest index (HI) than other crops, such as wheat (*Triticum aestivum*) (Diepenbrock et al., 1999; Dreccer et al., 2000). The vegetative biomass that is not harvested costs plants assimilates, and it can lead to high N remaining in the soil after harvest. Besides other agronomic benefits, a reduction of vegetative biomass without reducing the vitality of a plant could increase seed yield and/or reduce the demand for N fertilizer. In wheat and in rice (*Oryza sativa*), a reduction of vegetative biomass combined with an increase in seed yield and HI was achieved by the introgression of dwarf mutations in genes controlling the signaling pathway or biosynthesis of gibberellic acid ('Green Revolution'; Hedden, 2003). These dwarf types developed in the mid-twentieth century are the prototypes of today's wheat and rice cultivars.

In oilseed rape, several dwarfing genes have been described. Muangprom et al. (2006) introgressed a dwarf gene from a *B. rapa* line (Zanewich et al., 1991) into *B. napus*. The dwarf gene was described as an allele of the *Brassica BrGAI* gene, which is a homolog of the *rga* gene in *Arabidopsis thaliana*, *rht* in wheat, and *d8* in maize (*Zea mays*) (Muangprom et al., 2006). Foisset et al. (1995) selected a dwarf mutant where the growth type is controlled additively by the *bzh* gene, which was mapped onto the distal end of *B.*

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napus linkage group (LG) DY6 (Foisset et al., 1996). The first semi-dwarf hybrid cultivar ('Lutin', a cross between a *bzh* dwarf line and a normal-type line) was released in 1999 to the French market (Noel, 1999). Despite better lodging resistance and advantages in harvest ability of semi-dwarf hybrids, this growth type did not gain a high market share in France and Western Europe; however, it is recommended in Eastern European countries because of improved winter hardiness (Pinochet and Renard, 2012). Wang et al. (2004) described yet another dwarf mutation, *ndf-1*, as single gene with a mainly additive effect, which is described as allelic to *bzh*. Li et al. (2011) showed that *ndf-1* was a gibberellin-insensitive dwarf type. Another gibberellin-insensitive dwarf mutation, *bnac.dwf*, was described by Zeng et al. (2011), where the recessive gene was located on *B. napus* LG N18.

It could be assumed that semi-dwarf oilseed rape cultivars would reduce N leaching and N loss after harvest, due to a higher HI and accordingly less biomass remaining in the field. Sieling and Kage (2008) tested three normal-type oilseed rape cultivars and two semi-dwarf hybrids under different N regimes and found semi-dwarfs to yield lower compared with normal types at high N fertilization (160 and 240 kg N ha⁻¹, respectively). They reported that the tested semi-dwarf cultivar was not reducing the risk of N leaching. Similar results were obtained by Koeslin-Findeklee et al. (2014), who tested 15 line and hybrid cultivars and three semi-dwarf cultivars in field trials for their suitability to reduce N surpluses after harvest. However, in both studies the normal-type and semi-dwarf cultivars had different genetic backgrounds.

Intensive winter oilseed rape cultivation depends on a high N fertilizer input, leading after harvest to a high N balance surplus, which can result in N leaching into ground and surface waters (Rathke et al., 2006; Sieling and Kage, 2008). High N fertilization and N entry into the environment are unwanted with respect to economic and environmental impacts. This was addressed in two recent European Union regulations. The nitrates directive (91/676/EEC) restricts the N balance surplus of a crop rotation (Council of the European Union, 1991), whereas a second directive (2009/28/EEC, a promotion of the use of energy from renewable sources; European Parliament and Council of the European Union, 2009) limits greenhouse gas emissions in biofuel production, including the energy-intensive production of mineral N fertilizer. The vast majority of greenhouse gas emissions from biofuels based on oilseed rape oil are caused by cultivation and processing of oilseed rape. More than 82% of greenhouse gas emissions in the cultivation of winter oilseed rape are caused by N fertilization (42%) and N₂O emissions in the field (40.8%) (Schiemenz and Gurgel, 2013). Oilseed rape cultivars with a high N efficiency and lower N fertilization rates without reductions in seed yield are therefore of high interest.

We analyzed seed yield, straw yield, HI, and agronomic parameters in 108 hybrids derived from a doubled haploid (DH) population and segregating into *bzh* semi-dwarf types and normal types. Analyzing unselected DH lines unlinks the dwarf trait from the segregating genetic background and shows the full potential of variation in contrast to selected cultivars with completely different genetic backgrounds. The 108 hybrids were evaluated at high and low N supply in five and seven environments, respectively, in the 2010–2011 to 2013–2014 seasons. A QTL mapping approach was used to analyze the effect of the growth type on QTL with effects on seed yield and other agronomic parameters.

The objectives of our study were to (i) analyze the effect of the dwarf gene *bzh* on seed yield, straw yield, and other agronomic parameters, (ii) compare the agronomic performance of semi-dwarf and normal-type hybrids at different N fertilization regimes, and (iii) investigate by QTL analysis whether the dwarf gene is the cause for differences in agronomic performance between semi-dwarf and normal-type hybrids.

MATERIALS AND METHODS

Plant Material

A DH population with 242 lines was derived from the cross Alesi-*bzh* × H30. Alesi-*bzh* is a dwarf isogenic line derived from the canola quality German winter oilseed cultivar 'Alesi' backcrossed (BC4) from the *bzh* dwarf mutant (Foisset et al., 1995). H30 is a normal-type, resynthesized rapeseed line with high erucic acid content, originating from a cross of *B. rapa* ssp. *chinensis* with *B. napus* ssp. *napus* var. *pabularia*, with moderate winter hardiness (Girke et al., 2011). The DH lines segregated into dwarf and normal types. All DH lines were crossed with a normal-type, highly homozygous and male-sterile tester line with canola seed oil quality. The hybrids segregated into semi-dwarf (*bzh/Bzh*) and normal type (*Bzh/Bzh*). Based on the availability of seed and the content of erucic acid, 54 semi-dwarf and normal-type test hybrids each were chosen for field evaluation. Within each growth type group, the hybrids segregated for erucic acid content in the seed oil with 50% high erucic acid and 50% zero erucic acid.

Field Trials and Measurements

Field experiments were performed during four seasons (2010–2011, 2011–2012, 2012–2013, and 2013–2014) at two locations in Central Germany, Einbeck and Göttingen, on brunice aerosol and alluvial meadow soils, respectively (Table 1). Each season–location combination was considered an environment, hereafter referred to by location and year.

In each trial, 108 hybrids (54 normal type, 54 semi-dwarf) were grown in blocks with two replications. Within each block, growth types were interlaced by alternately growing one strip of semi-dwarfs and one strip of normal-types. The plot sizes were 18 m² in Einbeck and 11.25 m² in Göttingen with plant densities of 50 and 90 plants m⁻², respectively.

Experiments were designed as split-split-plots with N level as a main plot factor, growth type as a sub-plot factor, and genotype within growth-type as a sub-sub-plot factor. Genotypes within growth types were sorted in a lattice design, with the exception of the 2010–2011 season, where a randomized block design was used. Weed, disease, and pest control, fertilization (with exception of N), and all agronomic treatments followed the recommendations for winter oilseed rape production in Germany. The experiments were conducted with two levels of N fertilization: zero N supply (N_0) and optimal N supply (N_1). At each location, the soil mineral N was determined in the spring at the beginning of plant growth (Table 1). Soil samples were taken from a depth of 0 to 90 cm, and soil mineral N was analyzed following the method of VDLUFA (1991). For the N_0 treatment, no N fertilizer was applied. For the N_1 treatment, 177 kg N ha⁻¹ were applied in all N_1 trials. About one half of the N was applied as ammonium sulfate fertilizer plus calcium ammonium nitrate fertilizer in the spring at the beginning of plant growth (growth stage BBCH 30; Lancashire et al., 1991), and the other half was given at the beginning of shoot development (BBCH 32, by calcium ammonium nitrate fertilizer). All plots were harvested at maturity (BBCH 89) with a plot combine harvester (Hege 160, Hans-Ulrich Hege GmbH & Co., Waldenburg-Hohebuch, Germany), and seed yield and straw yield were determined. Therefore, plots were cut at soil level, and straw was collected and weighed in a canvas tarp attached to the back of the harvester. A straw subsample including stems and pods was dried at 60°C for 48 h in a drying oven to determine straw dry matter content. Oil content, protein content, and moisture content of seeds were determined with a near infrared reflectance spectroscopy (NIRS) monochromator model 6500 (NIRSystems, Inc., Silversprings, MD) using calibrations (raps2011.eqa, raps2012.eqa, raps2013.eqa, raps2014.eqa) provided by VDLUFA Qualitätssicherung NIRS GmbH (Am Versuchsfeld 13, D-34128 Kassel, Germany). Beginning of flowering was defined as the number of days from January 1st and was recorded at BBCH 61, when 10% of the plants flowered. Plant height (in centimeters) was measured at grain maturity (BBCH 89). Not all trials could be harvested (Table 1) due to local constraints, such as a hailstorm at Einbeck in 2011–2012, where only straw yield was determined.

Statistical Analysis

Analysis of variance (ANOVA), broad sense heritability (h^2), Spearman's rank correlation coefficients, and genetic correlations were calculated using PLABSTAT software (version 3B)

(Utz, 2001). Genetic correlations were tested against the standard error following methods of Utz (2001). Genetic correlations were considered significant when they were larger than one- and two-fold their standard error, indicated with + and ++, respectively.

To include the effect of different environments (year–location combinations) into the ANOVA, the following model for a split-plot design was used:

$$Y_{ijkl} = \mu + e_i + t_k + b_{ij} + et_{ik} + \varepsilon_{ijk} + g_{kl} + eg_{ikl} + \varepsilon_{ijkl}$$

in which Y_{ijkl} was the observation of a genotype l within the growth type k in block j within environment i . Interaction effects between growth type and environment were denoted by et_{ik} , and interactions between environment and genotype were called eg_{ikl} . Whole-plot error was denoted by ε_{ijk} , and the sub-plot error was denoted by ε_{ijkl} . The factors environment, block, and genotype were considered random.

To test the effects of N levels, the following model for a split-split-plot design was used:

$$Y_{ijklo} = \mu + e_i + n_o + b_{ijo} + en_{io} + \varepsilon_{ijo} + t_k + et_{ik} + tn_{ko} + etn_{iko} + \varepsilon_{ijk} + g_{kl} + eg_{ilk} + gn_{klo} + egn_{iklo} + \varepsilon_{ijklo}$$

in which Y_{ijklo} was the observation of a genotype l within growth type k in block j within N level at environment i . The interaction effects were between environment and N level en_{io} , environment and growth type et_{ik} , environment and genotype eg_{ilk} , growth type and N level tn_{ko} , and genotype by N level gn_{klo} . Three-way interactions were environment \times genotype \times N level egn_{iklo} and environment \times growth type \times N level etn_{iko} . Whole-plot error was denoted by ε_{ijo} , sub-plot error was denoted by ε_{ijk} , and sub-sub-plot error was denoted by ε_{ijklo} . The factors environment, block, and genotype were considered random.

Linkage Map and QTL Mapping

The linkage map was constructed using MAPMAKER/EXP 3.0 (Lander et al., 1987) and marker information of 100 DH lines. A total of 426 markers (381 single nucleotide polymorphisms [SNPs], including the *bzh* locus-specific marker; 45 simple sequence repeats [SSRs]) were assigned to 22 linkage groups with a total map length of 1301 cM (Kosambi). The map was aligned with common marker loci of published genetic maps based on positions of SSR (Piquemal et al., 2005; Radoev et al., 2008) and SNP markers (KWS Saat SE; unpublished data). The linkage groups of the map were named according to the consensus nomenclature proposed by the Steering Committee of the Multinational *Brassica* Genome Project

Table 1. Overview of trials in locations Einbeck and Göttingen at low and at high nitrogen (N) supply.

Season	Location	Low N	High N	Seed yield	Straw yield	Sowing date	N_{min}^{\dagger}	Preceding crop
2010–2011	Einbeck	x‡	–	x	–	4 Sept. 2010	35	Winter wheat
2010–2011	Göttingen	x	–	x	x	25 Aug. 2010	27	Winter barley
2011–2012	Einbeck	x	x	–	x	1 Sept. 2011	27	Winter wheat
2011–2012	Göttingen	x	x	x	x	22 Aug. 2011	27	Winter barley
2012–2013	Einbeck	x	x	x	x	22 Aug. 2012	na§	Winter wheat
2012–2013	Göttingen	x	x	x	x	30 Aug. 2012	24	Winter barley
2013–2014	Göttingen	x	x	x	–	26 Aug. 2013	63	Winter barley

[†] Soil mineral N (kg N ha⁻¹) measured in the spring.

‡ 'x' = trial present; '–' = no trial.

§ na = not analyzed.

(<http://www.brassica.info/resource/maps/lg-assignments.php>) as A01 to A10 and C01 to C09.

The complete map is described in Miersch (2014). For the QTL mapping, a subset of 339 highly informative markers was selected from the full map, with distances between adjacent markers of ~5 to 10 cM. QTL detection was performed with WinQTL Cartographer software, version 2.5 (Wang et al., 2006). QTL were detected by composite interval mapping (CIM), as described by Zeng (1994), with the following parameters: Window size of 10 cM, five markers selected in forward and backward regression, and CIM by 1-cM intervals. The experiment-wise significance thresholds for QTL detection were calculated by permutation analysis (500 times) for each trait separately. Such QTL were designated as significant if the LOD score exceeded a significance threshold representing a 5% probability of detecting a false positive QTL (type I error). Since the N stress level varied between environments and since the ANOVA across environments revealed strong genotype × environment interactions for most traits (Table 2), QTL analyses were calculated for each environment.

RESULTS

Seed and Straw Yield across Growth Types and N Levels

Significant variation for seed yield was revealed for environment, N level, genotype, and interactions of environment with N level, growth type, and genotype (Table 2). Environment and N level were by far the largest sources of variation. The effect of the growth type was very small and not significant.

At low N supply, seed yield of semi-dwarf hybrids was about 0.19 Mg ha⁻¹ higher than that of normal types (Table 3). The difference in seed yield between growth types varied between single environments, resulting in a significant growth type × environment interaction

(Table 4). Genotypes within growth types differed significantly for seed yield (Table 4; Fig. 1).

At high N supply, seed yield of semi-dwarfs was non-significant and 0.1 Mg ha⁻¹ higher than that of normal types (Tables 3 and 4). Among single environments, the performance of growth types was inconsistent with respect to seed yield (Table 3), with environment being the biggest source of variation at the high N level (Table 4). Genotypes within growth types showed a significant variation for seed yield (Table 4; Fig. 1), as was already observed at low N supply.

For straw yield, the largest sources of variation were environment and N level. The effect of the growth type was higher than for seed yield, with about 33% of the size of the effect of the N level (Table 2). Straw yield of semi-dwarf hybrids was significantly reduced by about 0.5 Mg ha⁻¹ compared with normal types at low N supply. The combination of higher seed yield and less straw resulted in a significantly higher HI of semi-dwarf hybrids (0.41) compared with normal types (0.34) (Table 3). At high N fertilization, semi-dwarf hybrids formed significantly less straw (0.78 Mg ha⁻¹) than normal-type hybrids and revealed a higher HI (Tables 3 and 4).

In general, it was observed that N fertilization increased seed and straw yield significantly but with varying effects in single environments (Table 3). With respect to straw yield, growth types responded differently to the level of N fertilization. Normal types produced relatively more straw in response to higher N supply (14.5%) than did semi-dwarf types (11.2%), but the interaction significance of growth type and N level for straw yield was not high ($P = 0.10$; Table 2).

Table 2. Components of variance (Var. comp.) and respective *F*-tests from the analysis of variance combined for low and high levels of nitrogen supply. A total of 108 hybrids (54 semi-dwarf and 54 normal type) were tested at different environments (Einbeck in 2011–2012 and 2013–2013; Göttingen in 2011–2012, 2012–2013, and 2013–2014). Negative estimates for variance components are reported as '0'.

Source	Beginning of flowering		Plant height		Seed yield		Straw yield		Harvest index		Oil yield		Oil content	
	df	Var. comp.	df	Var. comp.	df	Var. comp.	df	Var. comp.	df	Var. comp.	df	Var. comp.	df	Var. comp.
Environment (E)	4	154.07**	3	428.52**	3	0.52**	3	78.78**	2	0.005**	3	0.12**	4	0.25**
Nitrogen level (N)	1	0.23*	1	7.26	1	0.30†	1	46.93*	1	0.0003	1	0.04	1	2.22*
Growth type (T)	1	0.17	1	522.90**	1	0.003	1	15.33*	1	0.002*	1	0	1	0.26**
Genotype (G)	106	6.00**	106	3.70**	106	0.01**	106	3.90**	106	0.0003**	106	0.003**	106	0.69**
N × E	4	28.06**	3	18.00**	3	0.15**	3	6.46	2	0.001**	3	0.04**	4	1.09**
T × E	4	27.05**	3	39.13**	3	0.01**	3	5.37**	2	0.0001**	3	0.003**	4	0.02*
T × N	1	10.19	1	7.49	1	0	1	0.88†	1	0	1	0.12	1	0.05
G × N	106	0.38	106	0.25	106	0.0004	106	0.57†	106	0	106	0.02	106	0
G × E	424	1.31**	318	5.60**	318	0.02**	318	2.48**	212	0.0002	318	0.03**	424	0.11**
<i>h</i> ²		0.48		0.62		0.52		0.73		0.74		0.60		0.90

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† Significant at the 0.10 probability level.

Agronomic Traits Affected by Growth Type and N Level

The greatest source of variation for the flowering time was the environment. Furthermore, the beginning of flowering showed significant variation for genotype and

N supply (Table 2). Within the same N level, growth types showed no significant difference in beginning of flowering (Tables 3 and 4). Growth types and genotypes within growth types differed significantly in plant height

Table 3. Agronomic performance of 54 semi-dwarf and 54 normal-type hybrids tested with low and high nitrogen (N) supply at seven environments: years 2010–2011, 2011–2012, 2012–2013, and 2013–2014 at the two locations Einbeck and Göttingen.

Trait	2010–2011		2011–2012		2012–2013		2013–2014	Total mean
	Einbeck	Göttingen	Einbeck	Göttingen	Einbeck	Göttingen	Göttingen	
Low nitrogen supply								
Beginning of flowering, d								
Semi-dwarf	110	110	104*‡	115	121	125†	95	111
Normal type	110	110	104	114	121	124	95	111
Plant height, cm								
Semi-dwarf	100**	92**	72**	70**	110**	93*	–	89**
Normal type	126	119	108	90	143	122	–	117
Seed yield, Mg ha ⁻¹								
Semi-dwarf	1.80	1.70*	–	1.28**	2.24	3.39**	3.09	2.24*
Normal type	1.70	1.29	–	1.05	2.25	3.07	3.14	2.05
Straw yield, Mg ha ⁻¹								
Semi-dwarf	–	3.49**	1.77	1.98**	3.61**	3.20†	–	2.81*
Normal type	–	4.01	1.89	2.29	4.64	3.64	–	3.29
Harvest index								
Semi-dwarf	–	0.33**	–	0.39**	0.38**	0.52†	–	0.41**
Normal type	–	0.25	–	0.32	0.33	0.46	–	0.34
Oil yield, Mg ha ⁻¹								
Semi-dwarf	0.88†	0.84**	–	0.63**	1.10	1.71**	1.50	1.11**
Normal type	0.76	0.64	–	0.51	1.12	1.55	1.56	1.03
Oil content, %								
Semi-dwarf	51.63	49.15	47.85	49.43	49.22	50.35	48.64	49.47†
Normal type	52.26	49.49	48.21	49.24	49.55	50.66	49.81	49.95
High nitrogen supply								
Beginning of flowering, d								
Semi-dwarf	–	–	104	115	122	125**	96	113
Normal type	–	–	104	115	122	126	96	112
Plant height, cm								
Semi-dwarf	–	–	78**	67*	115**	92**	–	88**
Normal type	–	–	129	91	147	128	–	124
Seed yield, Mg ha ⁻¹								
Semi-dwarf	–	–	–	2.97**	2.75**	3.76	3.75	3.31
Normal type	–	–	–	2.64	2.88	3.78	3.56	3.21
Straw yield, Mg ha ⁻¹								
Semi-dwarf	–	–	3.01**	3.21**	4.46**	3.46**	–	3.54*
Normal type	–	–	3.34	3.94	5.40	4.12	–	4.22
Harvest index								
Semi-dwarf	–	–	–	0.48**	0.38**	0.52	–	0.46
Normal type	–	–	–	0.40	0.34	0.48	–	0.41
Oil yield, Mg ha ⁻¹								
Semi-dwarf	–	–	–	1.38**	1.29†	1.76**	1.69	1.53
Normal type	–	–	–	1.26	1.37	1.80	1.64	1.52
Oil content, %								
Semi-dwarf	–	–	47.55**	46.67**	46.81**	46.92	45.15	46.62**
Normal type	–	–	48.98	47.91	47.62	47.56	46.06	47.63

* Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

† Significant at the 0.10 probability level.

‡ Significance is reported between growth types.

(Tables 3 and 4), but plant height was not significantly affected by the N supply (Table 2).

Oil content and oil yield were significantly affected by genotype and environment and their interaction (Table 2), whereas N level and growth type affected only oil content significantly. For oil content, N level was the greatest source of variation, being about 10-fold larger

than the effect of the environment. The effect of the growth type on oil content was much higher than that on oil yield (Table 2). Oil content was for both growth types significantly higher at low compared with high N supply (Table 2; Table 3). Among growth types, normal-type hybrids had significantly higher oil content than semi-dwarf hybrids at both N levels (Table 3).

Table 4. Components of variance (Var. comp.) and respective *F*-tests from the analysis of variance for agronomic traits of 108 hybrids (54 semi-dwarf and 54 normal type) tested at low and at high nitrogen supply at different environments (Einbeck in 2010–2011, 2011–2012, 2012–2013, and 2013–2014). Negative estimates for variance components are reported as '0'.

Source	Beginning of flowering		Plant height		Seed yield		Straw yield		Harvest index		Oil yield		Oil content	
	df	Var. comp.	df	Var. comp.	df	Var. comp.	df	Var. comp.	df	Var. comp.	df	Var. comp.	df	Var. comp.
Low nitrogen supply														
Environment (E)	6	103.14**	5	274.85**	5	0.754**	4	0.923*	3	0.0070**	5	0.188**	6	1.43**
Growth type (T)	1	0	1	402.74**	1	0.016*	1	0.106*	1	0.0020**	1	0.003†	1	0.09†
Genotype (G)	106	0.25**	106	4.20**	106	0.009**	106	0.007	106	0.0002**	106	0.003**	106	0.87**
T × E	6	0.09**	5	16.07**	5	0.016**	4	0.054**	3	0.0001	5	0.005**	6	0.07*
G × E	636	0.26**	528	7.41**	528	0.009**	424	0.059**	317	0.0003**	528	0.002**	636	0.18**
<i>h</i> ²		0.82		0.54		0.60		0.17		0.46		0.64		0.90
High nitrogen supply														
Environment (E)	4	154.75**	3	456.81**	3	0.274**	3	0.574**	2	0.0680**	3	0.054**	4	0.88**
Growth type (T)	1	0	1	622.62**	1	0	1	0.222*	1	0	1	0	1	0.49**
Genotype (G)	106	0.22**	106	3.74**	106	0.012**	106	0.060**	106	0.0031**	106	0.004**	106	0.51**
T × E	4	0.12**	3	59.63**	3	0.015*	3	0.039**	2	0.0041†	3	0.003†	4	0.04*
G × E	424	0.38**	318	5.29**	318	0.032**	318	0.055**	212	0.0052**	318	0.007**	424	0.23**
<i>h</i> ²		0.69		0.54		0.39		0.66		0.40		0.47		0.80

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† Significant at the 0.10 probability level.

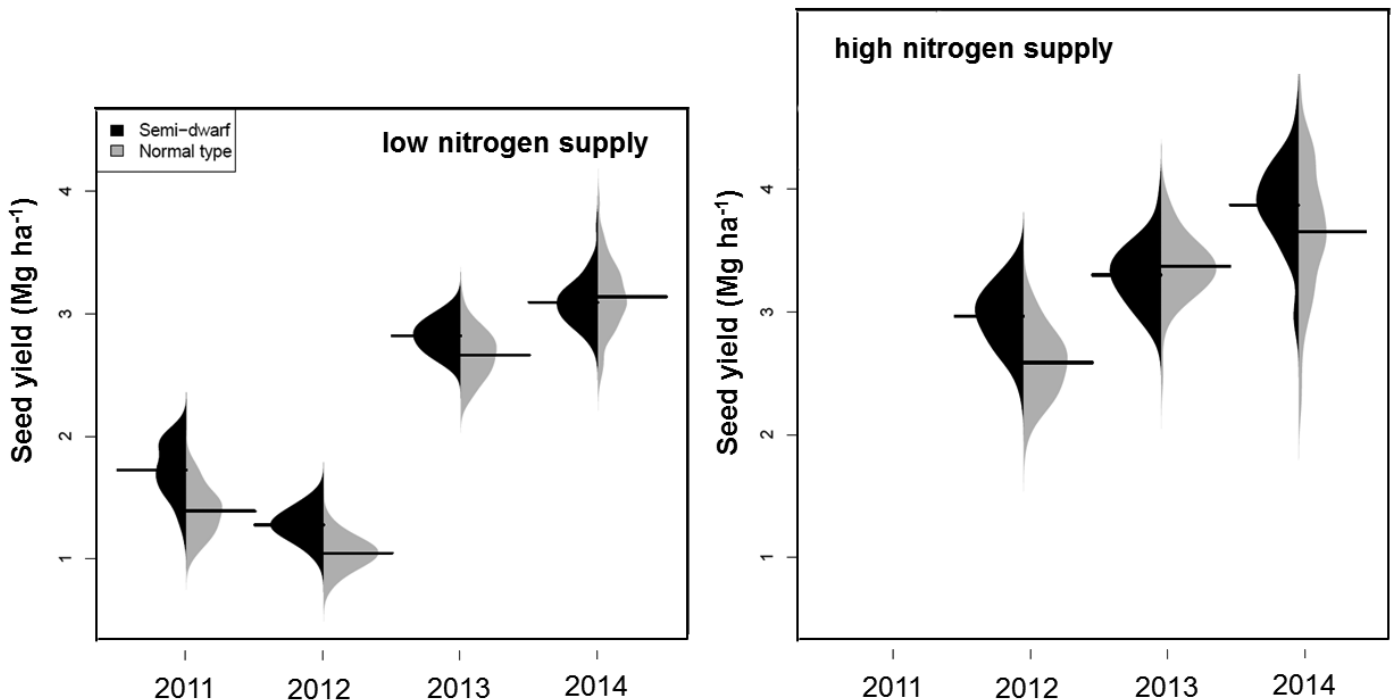


Fig. 1. Variation in seed yield of 54 semi-hybrids and 54 normal-type hybrids evaluated at low nitrogen (N) supply (2010–2011, Einbeck and Göttingen; 2011–2012, Göttingen; 2012–2013, Einbeck and Göttingen; 2013–2014, Göttingen) and high N supply (2011–2012, Göttingen; 2012–2013, Einbeck and Göttingen; 2013–2014, Göttingen).

For oil yield, however, the reduction in oil content of semi-dwarfs under low N supply was compensated for by higher seed yield. Because of this, the oil yield of semi-dwarf hybrids was significantly higher compared with normal types at low N and about equal at high N fertilization (Table 3).

Genetic and Phenotypic Correlations between Traits for Growth Type and N Levels

Genetic correlations were partially higher than phenotypic correlations because phenotypic correlations are biased by the experimental error (Table 5). This is of importance for traits with high experimental errors, such as straw yield. The correlation between straw yield and plant height can be assumed to be high. However, the phenotypic correlation was small, with $r = 0.54$ and 0.34 at low and high N fertilizations, respectively, in comparison to the genetic correlations, which were higher with $r = 0.95$ and 0.64 , respectively. The difference between phenotypic and genetic correlations could be explained by a high experimental error at straw harvest, which is removed in the calculation of the genetic correlation, but not in the estimation of the phenotypic correlation. The genetic correlation of oil content and seed yield was high, with $r = 0.63$ at low N supply in comparison to high N supply ($r = 0.11$). At high N supply, seed yield and straw yield showed a strong and negative genetic correlation

($r = -0.36$), whereas at zero N fertilization, this correlation was positive, with $r = 0.34$.

QTL Analysis

The effect of the dwarf *bzh* locus is reflected in the co-localization of the plant height-related QTL in the distal region of LG A06 (Table 6). The major QTL for plant height was estimated to be constitutive at low and high N supply within the region of the *bzh* locus. The QTL on LG A06 explained 79 to 93% of the phenotypic variation. The allele with a high and positive effect on plant height was originating from parent H30, which corroborates the fact that the dwarf locus was derived from parent Alesi-*bzh*. Another QTL on LG C03 was detected in two environments (Table 6). Here, the effect was much smaller (1–2% of the phenotypic variation) compared with the QTL on LG A06, and the allele reducing plant height was inherited from parent H30.

The QTL for straw yield co-localized with the *bzh* locus, and it was detected in all environments, with exception of location Einbeck in 2011–2012, where no significant QTL was estimated for straw yield. The allele increasing the straw yield was inherited from parent H30, aside from location Göttingen in 2010–2011, where a small but negative effect was found.

For HI as a ratio of seed yield to total aboveground biomass, the QTL on LG A06 was detected in all

Table 5. Spearman's Rank phenotypic and genetic correlations of yield and agronomic traits at high and low nitrogen supply. A total of 108 hybrids (54 semi-dwarf and 54 normal type) were tested at locations Einbeck (2012–2013) and Göttingen (2011–2012, 2012–2013).

Trait	Beginning of flowering							Phenotypic correlations	
	Plant height	Seed yield	Straw yield	Harvest index	Oil yield	Oil content			
Low nitrogen supply									
Genetic correlations	Beginning of flowering	–	0.14	0.08	0.08	–0.05	0.07	–0.02	Phenotypic correlations
	Plant height	0.27	–	0.14	0.54**	–0.41**	0.11	–0.06	
	Seed yield	0.36†	0.34	–	0.04	0.41**	0.96**	0.22*	
	Straw yield	–0.02	0.95‡	0.03	–	–0.88**	0.02	–0.06	
	Harvest index	0.09	–0.82‡	0.34†	–0.96‡	–	0.42**	0.16	
	Oil yield	0.27†	0.20	0.97‡	–0.05	0.35‡	–	0.49**	
	Oil content	0.01	0.03	0.63‡	–0.07	0.27†	0.81‡	–	
High nitrogen supply									
Genetic correlations	Beginning of flowering	–	0.20*	–0.03	0.31**	–0.26**	–0.10	–0.17	Phenotypic correlations
	Plant height	0.43†	–	0	0.34**	–0.27**	–0.04	–0.10	
	Seed yield	–0.08	–0.14	–	0.03	0.58**	0.92**	0.04	
	Straw yield	0.68‡	0.64‡	–0.36†	–	–0.73**	–0.03	–0.14	
	Harvest index	–0.46‡	–0.54‡	0.85‡	–0.81‡	–	0.58**	0.14	
	Oil yield	–0.18	–0.21	0.89‡	–0.38†	0.80‡	–	0.41**	
	Oil content	–0.20†	–0.18†	0.11	–0.18†	0.19†	0.58‡	–	

* Significant at the 0.05 probability level (phenotypic correlation).

** Significant at the 0.01 probability level (phenotypic correlation).

† $r >$ standard error (genetic correlation).

‡ $r > 2 \times$ standard error (genetic correlation).

Table 6. *bzh*-locus and QTL for seed yield and agronomic traits estimated for 100 hybrids derived from DH population Alesi x H30 crosses with a male-sterile tester. Hybrids were grown at low and high nitrogen (N) supply at locations Einbeck (Ei) and Göttingen (Go) in the seasons 2010–2011 through 2013–2014.

QTL name†	Linkage group	Confidence interval	Position	Maximum LOD	Effect‡	R ² §
		cM				
<i>bzh</i> -locus	A06		3.0			
Low nitrogen supply						
BFL-N0-A01-Ei2013	A01	19.4–36.1	32.5	4.3	0.35	0.14
BFL-N0-A03-Ei2013	A03	62.3–74.4	68.8	3.2	0.28	0.09
<i>BFL-N0-A06-Go2013</i>	A06	1.4–5.2	3.0	39.2	0.53	0.78
BFL-N0-A07-Go2011	A07	65.0–69.3	68.3	4.1	–0.25	0.10
BFL-N0-C06-Ei2013	C06	54.0–72.7	64.9	3.2	–0.29	0.10
BFL-N0-C07-Ei2012	C07	0.0–7.0	1.0	5.4	–0.56	0.18
PH-N0-A03-Ei2012	A03	93.2–114.6	102.5	3.4	1.99	0.01
<i>PH-N0-A06-Ei2011</i>	A06	0.0–2.6	1.0	54.0	10.30	0.79
<i>PH-N0-A06-Ei2012</i>	A06	1.4–5.2	3.0	65.4	18.75	0.90
<i>PH-N0-A06-Go2012</i>	A06	1.9–5.2	3.0	72.0	9.93	0.93
<i>PH-N0-A06-Ei2013</i>	A06	3.5–9.0	5.0	48.2	16.66	0.87
<i>PH-N0-A06-Go2013</i>	A06	1.4–5.2	3.0	87.0	14.90	0.93
PH-N0-C03-Ei2012	C03	41.0–62.4	51.3	3.6	–1.91	0.01
PH-N0-C03-Ei2013	C03	59.4–78.1	71.1	3.0	–2.63	0.02
<i>SeedY-N0-A06-Ei2011</i>	A06	2.6–36.3	20.0	3.4	–0.57	0.09
<i>SeedY-N0-A06-Go2011</i>	A06	0.0–2.1	1.0	26.1	–2.39	0.54
<i>SeedY-N0-A06-Go2012</i>	A06	1.3–10.1	3.0	19.8	–1.20	0.48
<i>SeedY-N0-A06-Go2013</i>	A06	1.0–12.2	3.0	11.2	–1.57	0.33
SeedY-N0-C07-Ei2011	C07	40.2–51.0	47.1	2.9	0.51	0.08
<i>StrY-N0-A06-Go2011</i>	A06	0.0–2.3	0.0	4.2	–0.02	0.12
<i>StrY-N0-A06-Go2012</i>	A06	0.0–12.2	0.0	9.4	1.57	0.26
<i>StrY-N0-A06-Ei2013</i>	A06	2.8–14.6	7.0	18.5	0.51	0.53
<i>StrY-N0-A06-Go2013</i>	A06	0.0–2.9	0.0	11.3	2.76	0.36
<i>HI-N0-A06-Go2012</i>	A06	3.0–8.1	4.0	25.5	–0.04	0.53
<i>HI-N0-A06-Ei2013</i>	A06	3.0–16.0	8.0	15.7	–0.03	0.46
<i>HI-N0-A06-Go2013</i>	A06	0.7–3.8	2.0	21.4	–0.03	0.52
HI-N0-A07-Ei2013	A07	46.2–56.3	50.7	4.5	–0.02	0.09
HI-N0-A07-Go2013	A07	55.7–65.3	55.8	3.5	–0.01	0.06
Oil-N0-A05-Ei2012	A05	0.0–7.0	3.7	3.6	0.44	0.13
<i>Oil-N0-A06-Ei2011</i>	A06	0.0–2.5	1.0	5.8	0.32	0.06
<i>Oil-N0-A06-Go2011</i>	A06	0.0–36.3	3.0	3.5	0.26	0.05
Oil-N0-A08-Ei2011	A08	0.0–4.2	0.0	29.8	0.97	0.52
Oil-N0-A08-Go2011	A08	0.0–4.2	2.0	20.6	0.74	0.43
Oil-N0-A08-Go2012	A08	1.8–6.6	4.0	22.4	0.85	0.55
Oil-N0-A08-Ei2013	A08	2.9–7.8	4.8	15.5	0.99	0.44
Oil-N0-A08-Go2013	A08	3.1–8.3	4.8	26.1	0.96	0.57
OilY-N0-C01-Ei2013	C01	21.4–30.0	25.9	3.9	0.04	0.14
OilY-N0-A03-Go2013	A03	33.9–48.1	43.6	3.2	–0.05	0.11
High nitrogen supply						
BFL-N1-A01-Ei2013	A01	44.8–56.0	50.4	3.2	0.28	0.11
BFL-N1-A06-Go2013	A06	11.2–19.9	15.0	39.0	0.51	0.81
BFL-N1-C01-Ei2012	C01	37.2–50.8	42.8	3.5	0.48	0.11
BFL-N1-C06-Ei2012	C06	58.1–67.0	61.3	3.9	–0.49	0.12
BFL-N1-C07-Ei2012	C07	0.0–11.6	4.0	3.1	–0.48	0.11
BLF-N1-C07-Go2012	C07	38.3–43.7	40.7	3.2	–0.18	0.10
<i>PH-N1-A06-Ei2012</i>	A06	1.4–5.2	3.0	73.6	25.37	0.94
<i>PH-N1-A06-Go2012</i>	A06	1.0–5.3	3.0	87.2	12.06	0.94
<i>PH-N1-A06-Ei2013</i>	A06	1.4–5.2	3.0	55.5	16.06	0.89
<i>PH-N1-A06-Go2013</i>	A06	1.4–5.2	3.0	102.6	18.39	0.95
PH-N1-C03-Ei2012	C03	52.5–78.1	71.1	3.5	–2.15	0.01

Table continued.

Table 6. Continued.

QTL name†	Linkage group	Confidence interval	Position	Maximum LOD	Effect‡	R ² §
		cM				
<i>SeedY-N1-A06-Go2012</i>	A06	0.2–3.0	3.0	15.1	–1.82	0.42
<i>SeedY-N1-A06-Ei2013</i>	A06	0.0–30.2	12.0	3.0	0.08	0.14
<i>StrY-N1-A06-Ei2012</i>	A06	1.3–13.3	4.0	11.1	1.71	0.34
<i>StrY-N1-A06-Go2012</i>	A06	0.2–3.0	2.0	17.5	3.91	0.50
<i>StrY-N1-A06-Ei2013</i>	A06	0.9–12.4	6.0	21.0	0.61	0.65
<i>StrY-N1-A06-Go2013</i>	A06	0.0–2.5	2.0	11.8	0.36	0.32
<i>HI-N1-A06-Go2012</i>	A06	0.8–6.0	2.0	24.2	–0.04	0.60
<i>HI-N1-A06-Ei2013</i>	A06	0.0–10.2	3.0	9.8	–0.02	0.30
<i>HI-N1-A06-Go2013</i>	A06	0.0–2.5	2.0	11.6	–0.02	0.33
<i>Oil-N1-A06-Ei2012</i>	A06	0.0–3.0	2.0	20.0	0.71	0.37
<i>Oil-N1-A06-Go2012</i>	A06	0.9–10.1	4.0	16.5	0.70	0.31
<i>Oil-N1-A06-Ei2013</i>	A06	0.0–13.8	1.0	4.4	0.40	0.16
<i>Oil-N1-A06-Go2013</i>	A06	0.0–14.9	1.0	4.2	0.33	0.07
Oil-N1-A08-Ei2012	A08	1.4–17.0	4.0	17.4	0.65	0.30
Oil-N1-A08-Go2012	A08	7.4–10.8	7.8	21.7	0.82	0.43
Oil-N1-A08-Go2013	A08	3.0–7.2	4.8	21.2	0.88	0.51
OilY-N1-A01-Go2014	A01	0.0–7.7	0.0	3.3	–0.07	0.12

† Abbreviations in QTL names: BFL, beginning of flowering; PH, plant height; SeedY, seed yield; StrY, straw yield; HI, harvest index; Oil, oil content; OilY, oil yield; N₀, zero N fertilization; N₁, high N fertilization. Years address the harvest year. QTL within the genomic region of the *bzh* locus are underlined and in italics.

‡ Effect of substituting the allele of parent Alesi-*bzh* by the allele of parent H30.

§ Proportion of phenotypic variance explained by the QTL.

environments and was constitutive at low and high N supply, with the exception of location Göttingen in 2010–2011. The allele increasing the HI was derived from parent Alesi-*bzh*. On LG A07, an additional QTL with a small effect was detected at low N supply at locations Einbeck and Göttingen in 2012–2013.

A seed yield-related QTL in the genomic region of the *bzh* locus was detected at low N supply in four out of six environments, explaining 9 to 54% of the phenotypic variation, and at high N supply in two out of four environments, with 14% and 42%, respectively. The allele increasing seed yield was inherited from parent Alesi-*bzh*, with the exception of location Einbeck in 2012–2013, where a very small positive effect of parent H30 was detected. Another QTL for seed yield was found only at location Einbeck, in 2010–2011. It was localized on LG C07, and here the allele from parent H30 increasing seed yield explained 8% of the phenotypic variation.

A QTL related to oil content within the genomic region of the *bzh* locus was found in two out of seven environments at low N supply, where they explained 5 and 6% of the phenotypic variation, and in four out of five environments with N fertilization, where the phenotypic variation explained was higher (7–37%). A second QTL for oil content was localized on the distal end of LG A08; it explained 30 to 57% of the phenotypic variation. The allele that was increasing the oil content for both QTL was derived from parent H30.

For flowering time, the QTL analysis did not provide consistent results, since QTL were detected in one or two environments only. With respect to the dwarf locus, only

in location Göttingen, 2012–2013, was a QTL detected within the genomic region of the *bzh* locus. This QTL explained a high proportion (78%) of the phenotypic variation of the beginning of flowering.

DISCUSSION

Effect of Growth Type on Seed Yield

Semi-dwarf hybrids yielded as high as normal types under optimal fertilization in the present study, which is contrary to findings of Koeslin-Findeklee et al. (2014) and Sieling and Kage (2008). The latter observed a lower seed yield and HI of semi-dwarf cultivar ‘Belcanto’ compared with three winter oilseed rape cultivars. Koeslin-Findeklee et al. (2014) found that dwarf types yielded significantly higher than lines and significantly lower than normal-type hybrids. The present study differs by two major points: by the high number of genotypes tested and by their genetic relationship. In contrast to the cultivars tested by Koeslin-Findeklee et al. (2014) and Sieling and Kage (2008), we tested a higher number of hybrids, all descending from the DH population Alesi-*bzh* × H30. This experimental design allowed for dissecting the effect of the dwarf gene from the segregating genetic background.

With respect to the analysis of genetic effects, it can be assumed that the power of detection in a non-preselected DH population with 108 individuals or their respective testing hybrids segregating for the monogenic trait of interest is higher than that in a test set of four or 18 cultivars, respectively (Sieling and Kage, 2008; Koeslin-Findeklee et al., 2014). In this study, the *bzh* locus was

analyzed in a single DH population. Further analyses in genetically different populations would be needed to estimate the importance of the genetic background.

However, if semi-dwarf hybrids yield equally to normal-type hybrids, the question remains why semi-dwarf cultivars do not have a higher market share? One disadvantage for the semi-dwarf growth type could be that the breeding effort for semi-dwarf hybrids is probably much lower than that in breeding programs for normal-type hybrids, therefore not yet leading to comparable results in commercial hybrids.

Effect of N Supply on Seed Yield and Agronomic Parameters

Normal-type hybrids responded to high N availability with a much stronger formation of straw than did semi-dwarf hybrids (Table 3). Due to higher or similar seed yields and less straw yield, the HI of semi-dwarf hybrids was significantly improved at both N levels compared with normal hybrids, whereas the improved HI of semi-dwarfs was mostly based on a reduction in straw yield. The reduction of vegetative biomass (straw) did not reduce seed yield at high N supply, and it brought benefits like a swifter harvest and improved lodging resistance. Shorter genotypes are discussed to be more resistant to lodging. Wang et al. (2004) argued that the differing branching structure of semi-dwarfs, with branches starting at lower stem sections, led to a more even weight distribution throughout the plant. In this study, lodging was not scored in all environments, but, as an example, semi-dwarfs at location Einbeck in 2012–2013 revealed a higher resistance to lodging compared with normal types at high N fertilization (data not shown).

Earlier studies suggested that a shorter plant ideotype was higher-N efficient, but equal in seed yield (Nyikako et al., 2014). In the present study, semi-dwarf hybrids outperformed normal types under N constraints, which is contrary to the observations of Sieling and Kage (2008). Koeslin-Findeklee et al. (2014) found the mean seed yield of three dwarf genotypes at zero N was equal to line cultivars but significantly lower than that of normal-type hybrids.

In our study, normal-type hybrids responded to N deficiency by a stronger reduction in seed yield than did semi-dwarf types (Table 3). However, there was no significant interaction effect between growth type and N level (Table 2), which could be explained by the ANOVA design, where the growth type \times N level interaction has only one degree of freedom, which would demand for strong effects to exceed the significance threshold. The genotype \times N level interaction was also small and nonsignificant (Table 2). The correlation for seed yield between low and high N supply was, however, not high ($r = 0.60$; Fig. 2), and the highest yielding hybrids within the two growth types ranked differently for seed yield under low

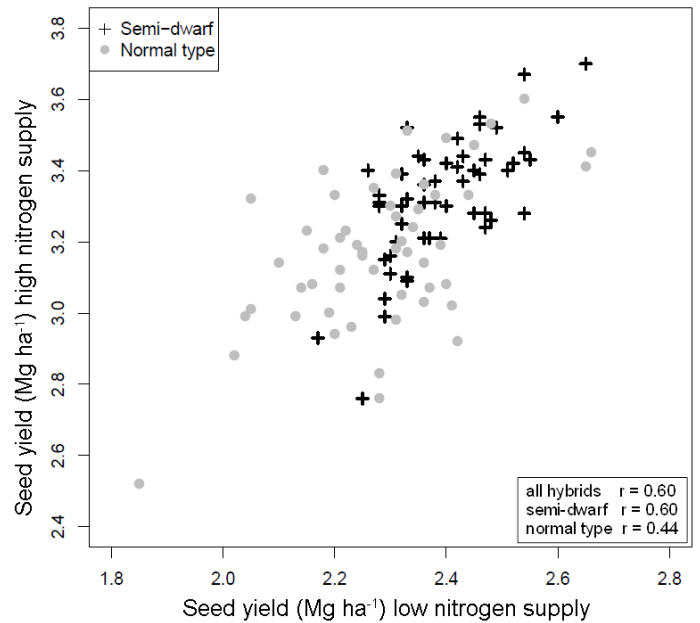


Fig. 2. Mean seed yield of 54 semi-hybrids and 54 normal-type hybrids evaluated at low and high nitrogen fertilization levels in five environments (Einbeck in 2011–2012 and 2012–2013; Göttingen in 2011–2012, 2012–2013, and 2013–2014).

and high N supply (within semi-dwarf and normal types, with $r = 0.60$ and $r = 0.44$, respectively; Fig. 2). Similar results were observed by Nyikako et al. (2014) when testing a segregating DH population at two N levels ($r = 0.6$), except they detected a significant genotype \times N level interaction. Higher correlations for seed yield under low and high N fertilization were presented in studies evaluating broader genetic variation, such as by testing resynthesized lines and hybrid cultivars ($r = 0.96$; Kessel et al., 2012), hybrids, line cultivars and breeding lines ($r = 0.88$; Koeslin-Findeklee et al., 2014), or high-yielding cultivars ($r = 0.92$; Berry et al., 2010). However, segregating DH populations, as tested in the present study, gave a better idea of the broad genetic variation in a breeding program. When aiming to select genotypes adapted to low N supply, cultivar development should be based on yield experiments under low N supply. The definition of ‘low N’ is still under discussion, also because the plants’ reaction to zero N (equaling soil mineral N) and to a minimum level of N fertilization (more relevant in low-input agriculture) might be different.

The oil content of normal-type hybrids was significantly higher at both N levels compared with semi-dwarf hybrids (Table 3). At high N supply, the difference was $\sim 1\%$ in oil content. The reason for variation in oil content between growth types at low and high N supply is unknown. Oil yield as a product of seed yield and oil content were about equal for both growth types at high N supply and significantly higher for semi-dwarf hybrids at low N supply.

QTL Mapping

The mapping population Alesi-*bzh* × H30 was small (100 DH lines) with respect to mapping accuracy. An indicator of the QTL detection quality in the mapping population was the significance of minor QTL that were not related to the dwarf gene but still detected in different environments, such as for seed oil content on LG A08 and for plant height on LG C03 (Table 6).

All marker analyses were performed with DH lines of DH population Alesi-*bzh* × H30, whereas all phenotypic data were obtained from hybrids derived from crosses of these DH lines with a male-sterile tester. These hybrids carry one allele of the DH line and one unknown of the male-sterile tester. Consequently, genetic effects of QTL detected in the hybrids are always confounded by interactions with tester alleles. If the tester would carry an allele that is completely dominant over the allele of the DH lines, no QTL would be detected (Schön et al., 1994). Test cross hybrid mapping is better known for crops like maize, but it was also successfully applied in oilseed rape (Radoev et al., 2008).

Effect of the *bzh* Dwarf Locus on Plant Height, Seed Yield, and Agronomic Parameters

By using an allele-specific SNP marker, the *bzh* dwarf locus was mapped to the distal part of LG A06 (Table 6), which was in accordance with Foisset et al. (1996), who had mapped the *bzh* locus onto LG DY06, which corresponds to LG A06. Plant height was mainly affected by the dwarf locus; however, a second QTL for plant height on LG C03 was localized within a genomic region (Table 6), where Quijada et al. (2006) had also described a QTL for plant height. This finding is in accordance with the observation of significant variation for plant size within the growth types at both N levels (Table 4).

Most of the QTL detected in this study that explained a high proportion of phenotypic variation were mapped to the genomic region of the *bzh* dwarf gene (Table 6). The co-localization of the *bzh* dwarf allele with QTL for plant height, straw yield, and HI at both N levels was not unexpected. With respect to seed yield, the positive effect of the Alesi-*bzh* allele is in accordance with the results of the ANOVA (Table 4) and the mean seed yield results of the field experiments (Table 3), where the effect of the dwarf gene is positive and higher at low N supply than at high N supply. This positive effect of the dwarf locus on seed yield is not in accordance with earlier findings of Sieling and Kage (2008) and Koeslin-Findeklee et al. (2014). It could be assumed that the major change in plant architecture, which is resulting in a reduction in straw yield, would consequently lead to a shift of sources, such as nutrients and assimilates, from the straw as a sink to the direction of the seeds as a sink, leading to better nutrient

and assimilate use efficiencies. Furthermore, it could be speculated whether there is a linkage drag of the Alesi-*bzh* cultivar allele in contrast to the 'non-domesticated' allele of H30, since the resynthesized line was not preselected for seed yield. Finally, the positive effect of the Alesi-*bzh* allele on seed yield could also be explained by pleiotropic effects in our genetic backgrounds. The dwarf gene *bzh* is part of the signaling pathway of the plant hormone gibberellic acid (Li et al., 2011), which is known to affect stem and root extension, leaf expansion, and floral induction, among others (Sun and Gubler, 2004). It could also be discussed if there is a more basic explanation for the positive effect of the Alesi-*bzh* dwarf gene on seed yield. Since this effect is higher when N is limited, N uptake and N utilization could differ in semi-dwarf and normal-type hybrids, resulting in variation in seed yield. This aspect will be discussed in a following publication.

In contrast to the QTL for seed yield, the QTL allele of parent Alesi-*bzh* on LG A06 affected the oil content negatively (Table 6), which was also shown by the significant reduction in oil content in semi-dwarf hybrids compared with normal-type hybrids (Table 3). The Alesi-*bzh* allele reduced the oil content at both N levels but with a larger effect at high N supply (Table 6). The second major QTL affecting oil was detected on LG A08 within the genomic region of fatty acid elongase (*FAE1*), which was described by Ecke et al. (1996) to co-localize with a QTL for oil content. The *FAE1* enzyme is found in high erucic acid oilseed rape, but not in modern rapeseed (canola) cultivars with low glucosinolate and zero erucic acid content. Since H30 is a resynthesized line with high erucic acid and Alesi-*bzh* has a low erucic acid content, the resulting DH population segregates for erucic acid content. The coincidence of the *FAE1* locus and QTL for oil content had been found earlier (Ecke et al., 1996; Qiu et al., 2006), whereas the physiological background for the resulting increase in oil content is still open to discussion.

CONCLUSIONS

The *bzh* semi-dwarf hybrids yielded significantly higher than normal type hybrids in N-deficient conditions. At optimal N supply, the difference between both growth types in seed yield was not statistically significant despite the fact the semi-dwarfs were outperforming normal types in four out of five environments. Oil content was slightly lower in semi-dwarfs under both N treatments, whereas oil yield was significantly higher in semi-dwarfs compared with normal types at zero N fertilization and equal at optimal N supply. We conclude therefore that *bzh* semi-dwarf hybrids should be of high interest, especially when N is limited.

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