Theor Appl Genet (1992) 84:952–957

THEORETICAL AND APPLIED GENETICS

Genetic analysis of a grass dwarf mutation induced by wheat callus culture *

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Received June 10, 1991; Accepted February 5, 1992
Communicated by K. Tsunewaki

Summary. Genetic variation induced by passage through tissue culture (somaclonal variation) has been characterized for many agronomic traits of wheat. The study presented here was conducted to genetically and phenotypically characterize a mutation influencing plant height that was induced by wheat callus culture. Dwarf plants were identified in the progeny of a tall plant regenerated from immature embryo-derived callus tissue of the hard red winter wheat 'TAM 105'. The dwarfs are significantly shorter, later in heading, and have a greater number of tillers, fewer seeds per spike, lower grain yield per plant, and lower floret fertility than 'TAM 105'. The dwarfs also exhibit branching at the aerial nodes when grown under cool temperatures (< 20 °C) and short daylengths (< 12 h). We hypothesize that a single, partially dominant gene which acts in a complementary manner with the grass-dwarf gene *D1* is responsible for this phenotype. Based on phenotype and the dominance relationship between mutant and wild-type alleles, we hypothesize that the mutation is a new allele at either the *D2* or *D4* grass-dwarfism locus. The utilization of genotypes lacking any of the grass-dwarfism alleles would greatly reduce the chance of recovering these undesirable genotypes by mutations arising during tissue culture. It is also important to recognize the grass-dwarf phenotype. If transgenic plants, somatic hybrids, or regenerants from in vitro selection strategies have a grass-dwarf phenotype, they can be induced to enter reproductive development by long daylengths (> 14 h) and high temperatures (> 26 °C).

Key words: Somaclonal variation – Dwarf mutation – Pleiotrophic effects – *Triticum aestivum* L. em Thell.

Introduction

Several classes of dwarfing genes in wheat (*Triticum aestivum* L. em Thell.) have been characterized and recently reviewed by Gale and Youssefian (1985). The reduced height genes (*Rht1* through *Rht10*) are commonly used in cultivar development programs worldwide. Grass-clump dwarfs (McMillan 1937), hybrid dwarfs (Hermsen 1967; Worland and Law 1980) and grass-dwarfs (Moore 1966) are synonymous names for dwarfs that are observed in the F_1 or F_2 segregates from crosses of normal-height wheats. Grass-dwarf genes have only recently been utilized in developing cultivars adapted to environments with high temperatures and long daylengths (Moore 1983).

Grass-dwarfs have a tufted habit and very short, dark green leaves when compared to their normal parents (Hermsen 1967; Moore 1966). Apical dominance is often impaired, which results in branching at the aerial nodes. Grass-dwarfs have increased tiller number, shorter stature, and later heading date. They also have greatly reduced spike length, spikelet number, seed number, and grain yield. Moore (1983) found that an increase in tillering of grass-dwarf lines does not result in increased yield because of low seed number per spikelet and small seed size as a result of the spike not fully emerging when temperatures are low.

Grass-dwarfs are further distinguishable from the semi-dwarf phenotype as semi-dwarfs flower normally while grass-dwarfs generally require inductive treatments such as high temperatures and long daylengths to pro-

* Submitted as Manuscript No. J.-6016. Research supported in part by the Oklahoma Wheat Research Foundation and the Oklahoma Agricultural Experiment Station, Project H-1996
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mote flowering (Moore 1966). Hermsen (1967) and Moore (1969, 1983) described three types of grass-dwarfs based on their phenotype and temperature and daylength requirements for reproductive development.

Grass-dwarfs result from the complementary gene action of four loci (*D1/d1, D2/d2, D3/d3*, and *D4/d4*). The uppercase designation is for alleles that contribute to the dwarf phenotype, but does not imply dominance. McMillan (1937) developed the first hypothesis on the genetics of grass-dwarfs. He proposed a four-gene theory with two genes closely linked in repulsion. Since two were linked and could not be separated by test crosses, Hermsen (1967) developed a simpler three-gene theory and proposed *D1* to be the strongest and completely dominant, *D2* to be partially dominant, and *D3* to be the weakest and also partially dominant. Using four tester varieties he described six classes of normal height genotypes carrying the grass-dwarfing genes and two pure breeding dwarfs. Moore (1969) using monosomic analysis, supported the three-gene theory and found that *D1* and *D2* interacted by complementation. *D2* is only effective in the homozygous or hemizygous condition, and *D3* has an additive interaction with *D1* and *D2*. He suggested multiple allelism at these three loci. Moore also supported the work of Hurd and McGiniss (1958) by locating *D2* on chromosome 2B and that of Hermsen (1963) by locating *D1* on chromosome 2D and *D3* on chromosome 4B. Silbaugh and Metzger (1970) located a fourth gene, *D4*, on chromosome 2D that is linked to *D1* with a recombination frequency of 12%. They proposed a four-gene hypothesis in which *D4* was partially dominant and similar in potency to *D2*. Worland and Law (1980) confirmed the four-gene hypothesis with the utilization of monosomic and intervarietal chromosome substitution lines. They found the potency of these genes to be $D1 > D3 > D4 \geq D2$. They also found multiple alleles at the *D1* and *D2* loci. Under this hypothesis six homozygous genotypes give pure breeding grass-dwarfs: *D1D1D2D2D3D3D4D4; D1D1D2D2D3D3d4d4; D1D1D2D2d3d3D4D4; D1D1d2d2D3D3D4D4; D1D1D2D2d3d3d4d4* and *D1D1d2d2d3d3D4D4*.

Genetic variation induced by passage through tissue culture (somaclonal variation; Larkin and Scowcroft 1981) has been reported in wheat for many traits, including the presence or absence of awns, plant height, α- and β-amylases, storage proteins, biomass, spike density, freezing tolerance, and tolerance to aluminum (Larkin et al. 1984; Ahloowalia and Sherington 1985; Cooper et al. 1986; Maddock and Semple 1986; Chen et al. 1987; Ryan et al. 1987; Lazar et al. 1988; Carver and Johnson 1989; Galiba and Sutka 1989). The research presented here describes the isolation and characterization of euploid and homozygous grass-dwarf lines from a tissue culture of a hard red winter wheat cultivar. We hypothesize that a mutation involving one of the grass-dwarfism loci occurred during tissue culture and is the probable cause of this phenotype.

Materials and methods

Tissue culture and plant regeneration

Immature embryos of the hard red winter wheat 'TAM105' were aseptically excised from tagged plants approximately 7–14 days after anthesis and cultured individually in tubes (25 × 150 mm) containing callus induction medium. Embryos which showed precocious germination were discarded. The callus induction medium contained the major and minor minerals of Murashige and Skoog (1962), Gamborg B-5 vitamins (Gamborg et al. 1976), 1 mg/l 2,4-dichlorophenoxy-acetic acid (2,4-D), 30 g/l sucrose, and 7 g/l agar at pH 5.8. After 4–6 weeks, calli were transferred to the same medium lacking 2,4-D to regenerate plantlets. After a further 2–3 weeks, plantlets were transferred to one-half strength basal medium for additional root development. Well-rooted plants were transferred to soil in pots for seed production under greenhouse conditions. Regenerated plants were designated as the R_0 generation (Chaleff 1981). R_1 selfed seed were harvested from individual R_0 plants.

Isolation and characterization of dwarfs

R_1 seeds were planted in the greenhouse for further increase. Progeny from one phenotypically normal R_0 plant were observed to segregate for plant height and tiller number in the R_1 generation. R_2 seeds were sown in the field where segregation was again noted for plant height and tiller number in some families derived from tall R_1 plants. All of the progeny from R_1 dwarf plants were dwarfs in the R_2 generation.

Five R_3 dwarf (D) lines (D294, D295, D296, D297, and D298) were obtained from selfed seed of five R_2 plants selected for their short stature and excessive tillering capacity. All five dwarfs were from the same R_0 plant. Ten plants of each R_3 dwarf line and ten 'TAM 105' plants were vernalized (10 °C day/5 °C night with an 8-h photoperiod for 8 weeks) and transplanted to the greenhouse on February 7, 1989 for characterization and crossing. Heating and cooling systems attempted to maintain temperatures at 20° and 15 °C during the day and night, respectively. No supplemental lighting was used. Daylengths did not exceed 12 h until after heading for all genotypes. Chromosome number, plant height, days to heading, tiller number, number of seeds per spike, percent fertility, 100-kernel weight, grain yield per plant, and percent of tillers with aerial branching were determined. Concurrently, five dwarf lines were crossed as females with 'TAM 105'. Aneuploid plants were discarded, and the analysis of plant traits and crosses was performed only on plants with 42 chromosomes.

Five R_4 seeds from one R_3 plant (D298) selected for its short stature and excessive tillering were increased in the growth chamber in the summer of 1989 along with five F_1 seeds from the cross D298/'TAM 105'. Forty F_2 seeds from each F_1 plant were transplanted to the greenhouse after vernalization on February 9, 1990 in a completely randomized design including ten F_1 plants and ten plants of each parent (D298 and 'TAM 105'). Supplemental lighting provided a 14-h photoperiod. Heating and cooling systems attempted to maintain temperatures at 20° and 15 °C during the day and night, respectively. Days to heading, plant height, tiller number, number of seeds per spike, 100-kernel weight, percent fertility, percent of tillers with aerial branching, and grain yield per plant were measured.

Genetic and statistical analysis

Analysis of variance was performed individually for each year for all traits. A combined analysis across years was conducted for a reduced set of genotypes common to both years for testing of genotype × year interactions for all traits. Year effects were assumed to be fixed. Three-dimensional rotational plots were utilized to separate clusters of F_2 plants based on traits that differed significantly between the parents. Once clusters were established, individuals in each cluster were identified and histograms for each trait were constructed. Genetic hypotheses were tested by chi-square analysis. All data manipulation, analyses, and plotting were performed with the Data Desk Professional statistical software (Velleman 1990).

Results

Characterization of dwarf phenotype

Characterization of the five dwarf lines tested in the greenhouse in 1989 demonstrated that these lines had traits most often associated with grass-dwarfs (Table 1). The dwarfs were late in heading with profuse tillering and short stature. Leaves were small and dark green, and tillering occurred at the aerial nodes. They had low spikelet and seed number, and many heads failed to fully emerge from the leaf sheath, resulting in poor fertility. Seed yields were greatly reduced in the dwarfs. All dwarf lines appeared to be homozygous and homogenous. There were no significant differences among the dwarf lines in 1989 for days to heading, plant height, tiller number, seeds per spike, percent fertility, 100-kernel weight, and grain yield per plant (Table 1). However, D294 had a significantly greater percent of tillers with aerial branching than D295 or D297. All dwarf lines exhibited branching at the aerial nodes, while 'TAM 105' did not. 'TAM 105' had significantly greater plant height, number of seeds per spike, 100-kernel weight, grain yield per plant, and percent fertility than D298 in both 1989 and 1990. 'TAM 105' also had significantly earlier heading and significantly fewer tillers for both years than D298. During 1990 no tillers with aerial branching were observed in the D298, 'TAM 105', F_1 D298/'TAM 105', or F_2 D298/'TAM 105' populations.

Analysis of variance across years showed that D298 and 'TAM 105' differed significantly for all eight traits (Table 2). Genotype × year interactions were significant

Table 1. Means for eight plant traits of five dwarf lines, 'TAM 105', and the F_1 and F_2 populations from the cross D298/'TAM 105'

Genotype	Year	Plant trait[a]							
		Hd (days)	Ht (cm)	Till	Sd/Spk	Fert (%)	Kwt (g)	Yld (g)	Brch (%)
D294	1989	46	42.3	58	15	82	3.27	19.84	48
D295	1989	46	47.4	64	18	88	3.17	24.40	22
D296	1989	48	47.7	59	17	78	3.32	21.14	35
D297	1989	47	44.9	60	19	88	3.34	22.01	29
D298	1989	46	41.8	65	15	89	3.48	22.88	40
	1990	44	50.4	16	19	68	3.28	6.37	0
TAM 105	1989	37	60.6	29	47	95	4.61	30.43	0
	1990	30	74.7	10	49	86	3.85	15.44	0
F_1 D298/TAM 105	1990	32	70.7	13	36	73	3.66	12.70	0
F_2 D298/TAM 105	1990	34	66.4	13	37	78	3.48	11.78	0
Mid-parent	1990	37	62.6	13	34	77	3.52	10.91	–
LSD (0.05)	1989	3	6.1	10	6	20	0.43	4.63	15
	1990	5	7.7	3	9	8	0.30	2.57	–

[a] Hd, Days to heading; Ht, height; Till, tillers; Sd/Spk, seeds/spike; Fert, fertility; Kwt, 100-kernel weight; Yld, grain yield; Brch, aerial branching

Table 2. Significance levels from the analysis of variance years (1989 and 1990) for D298 and 'TAM 105'

Source of variation	*df*	Plant traits[b]							
		Hd	Ht	Sd/Spk	Fert	Till	Kwt	Yld	Brch
Genotype[a]	1	**	**	**	*	**	*	**	**
Year × genotype[a]	1	**	ns	ns	ns	**	ns	ns	**
Error	33	–	–	–	–	–	–	–	–

[a] *F*-test significant at $*P = 0.05$ and $** P = 0.01$. ns = non-significant ($P > 0.05$)

[b] Hd, Days to heading; Ht, height; Till, tillers; Sd/Spk, seeds/spike; Fert, fertility; Kwt, 100-kernel weight; Yld, grain yield; Brch, aerial branching

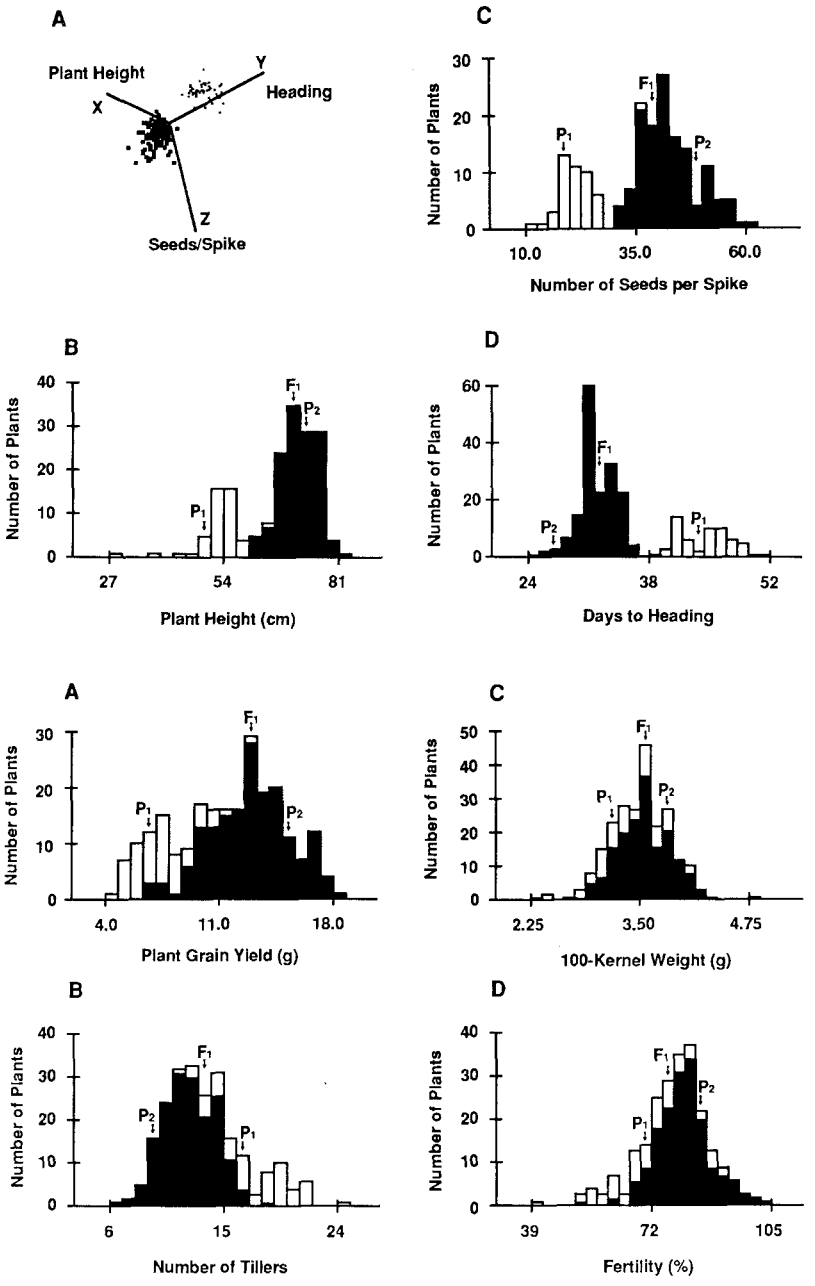

Fig. 1A–D. Three-dimensional rotational graph (**A**) and individual histograms of pooled F_2 D298/'TAM 105' populations for plant height (**B**), seeds per spike (**C**), and days to heading (**D**). Individuals highlighted (*large squares*) in three-dimensional graph are also highlighted (*black*) in individual histograms. P_1, P_2, and F_1 indicate the population means for D298, 'TAM 105', and F_1 D298/'TAM 105', respectively

Fig. 2A–D. Histograms of pooled F_2 D298/'TAM 105' population for grain yield per plant (**A**), tiller number (**B**), 100-kernel weight (**C**), and fertility (**D**). Individuals highlighted in *black* were identified as being in the same phenotypic class based on plant height, days to heading, and seeds per spike (Fig. 1A). P_1, P_2, and F_1 indicate the population means for D298, 'TAM 105', and F_1 D298/'TAM 105', respectively

only for days to heading, tiller number, and percent of tillers with aerial branching.

Genetic analysis

Comparisons of the F_1 with mid-parent values indicated that the dominance relationship between the mutant and the wild-type allele varied depending on the trait (Table 1). The F_1 value was significantly greater than the midparent value for days to heading and plant height; for other traits, the F_1 value was not significantly different than the mid-parent value. The mean of the F_1 was not significantly different than the mean of the F_2 for all traits.

Three-dimensional rotational graphs, derived from a single F_1 plant, were constructed for each F_2 family on the basis of days to heading, plant height, and number of seeds per spike. These traits allowed for the separation of the F_2 population into two distinct classes. Individuals in each class were identified, and chi-square analysis of individual families did not differ significantly from a 3:1 (normal:dwarf) genetic model (Table 3). Since heterogeneity between families was also non-significant, families were pooled and a pooled analysis was performed. A three-dimensional rotational graph of the 200 pooled F_2 plants was constructed (Fig. 1A), and individual histograms for plant height, number of seeds per spike, and

Table 3. Chi-square analysis of F_2 populations derived from individual F_1 plants from the cross D298/'TAM 105'

F_2 family	Normal	Dwarf	χ^2 (3:1)	*df*	Probability
1	31	9	0.133	1	0.70
2	28	12	0.530	1	0.47
3	33	7	1.200	1	0.35
4	32	8	0.530	1	0.47
5	28	12	0.530	1	0.47
Total	–	–	2.923	5	0.72
Pooled	152	48	0.107	1	0.75
Heterogeneity	–	–	2.816	4	0.61

days to heading supported the classification of F_2 plants by three-dimensional analysis (Fig. 1 B–D). Individuals in the cluster with the greatest number of plants resembled 'TAM 105' and the F_1 by being earlier maturing and taller, and by having a greater number of seeds per spike. A separation of the F_2 individuals into separate classes based on grain yield per plant, tiller number, 100-kernel weight, and percent fertility was not clear (Fig. 2 A–D). The F_2 distributions were skewed toward 'TAM 105' and the F_1 for tiller number and grain yield. However, the F_2 distributions were not skewed toward 'TAM 105' and the F_1 for percent fertility or 100-kernel weight and appeared to be near normal.

Discussion

Characterization of dwarf phenotype

Dwarfs isolated from wheat callus culture are phenotypically similar to the Type II grass-dwarfs described by Moore (1966). The dwarfs entered reproductive development in both short (1989 greenhouse) and long (1990 greenhouse) daylength environments where daytime temperatures exceeded 26 °C for brief periods. Even though the greenhouse has cooling capabilities, an unseasonably warm 2-week period shortly after transplanting occurred in 1990 resulted in daytime temperatures exceeding 30 °C for brief periods. This is the probable cause of the significant reductions in days to heading, height, tiller number, percent fertility, 100-kernel weight, and grain yield per plant in 1990 compared to 1989. The longer daylength and warmer temperatures in 1990 completely eliminated the expression of branching at the aerial nodes.

Genetic analysis

Our genetic analysis clearly indicates segregation for a single gene in the F_2 population that significantly influences plant height, days to heading, and number of seeds per spike. The same gene also influences grain yield and number of tillers, although some overlap between phenotypic classes was observed. The warm period and longer daylength during the 1990 growing season which accelerated development probably contributed to the narrowing of the magnitude of the differences observed between parental genotypes. The near normal distribution of the F_2 for 100-kernel weight and fertility is probably a result of near-ideal growing conditions in the greenhouse during anthesis and seed development. Under field conditions dwarf genotypes would be under both high temperature and drought stress during anthesis and seed development due to their significantly later heading date. These conditions would result in higher floret and tiller mortality and lower 100-kernel weights and grain yields.

Based on the D298 phenotype and dominance relationships between the mutant and wild-type alleles, we hypothesize that a mutation occurred during tissue culture at either the *D2* or *D4* locus and that 'TAM 105' is homozygous for the *D1* allele. Using Hermsen's (1967) classification, this would make 'TAM 105' a Class III carrier of grass-dwarfing genes. Grass-dwarfing genes are widely dispersed in wheat cultivars (Canvin and Evans 1963; Moore 1966; Morriosn 1957; Worland and Law 1980, 1986; Zeven 1970). Many of these cultivars are found in the pedigrees of winter wheat cultivars adapted to the United States (Cox et al. 1984). Because these genes are so widespread, it has been speculated that they are linked to genes selected for in breeding programs (Worland and Law 1980). Chromosomes containing grass-dwarfism loci also contain genes conferring resistance to *Puccinia recondita, Puccinia graminus, Puccinia striiformis, Erysyphe graminus*, reduced height (*Rht 8*), vernalization (*Vrn 2*), and photoperiod sensitivity (*Ppd 2*) (McIntosh and Cusick 1987; Worland and Law 1986). Another possibility is that the grass-dwarf genes, in combinations that do not confer the extreme grass-dwarf phenotype, are important in adaptation and yield component determination in some environments. Although it has not been established, it is possible that 'TAM 105' is homozygous for the *D1* allele. This would explain the tall phenotype of the R_0 plant if a single mutation occurred at either the *D2* or *D4* locus. Dwarf phenotypes would be observed in the R_1, and they would be true breeding since the *D1* allele is fixed in the population. D298's genotype would be *D1D1D2D2d3d3d4d4* or *D1D1d2d2d3d3D4D4*. This would make it a Type II dwarf, and previously described dwarfing alleles at these loci are partially dominant. The *D3* locus was eliminated from our hypothesis because the R_0 plant would have to have been a grass-dwarf in order to identify true breeding dwarfs in the R_1. A mutation at the *D1* locus would have resulted in the R_0 being dwarfed, with segregation observed in the R_1 for normal and dwarf types. Neither the *D1* or *D3* hypotheses are supported by our observations. Another possibility would be that simultaneous mutations occurred at *D1* and either *D2* or *D4*. In this scenario the R_0 would be tall, and segregation would be observed in the R_1. How-

ever, dwarf R_1 plants would not always be true breeding because the genotypes *D1d1D2D2d3d3d4d4* or *D1d1d2d2d3d3D4D4* would be dwarfs; normal plants would therefore be present in their progeny (*d1d1D2D2d3d3d4d4* or *d1d1d2d2d3d3D4D4*). In addition, our data would not have fitted a 3:1 segregation ratio in the F_2 D298/'TAM 105'. The final test of our hypothesis will be to cross D298 with 'Chinese Spring' (*d1d1d2d2d3d3d4d4*) (Worland and Law 1980). If the mutation is at the *D2* locus the F_2 should segregate 13:3 (normal:dwarf); if the mutation is at the *D4* locus, the F_2 segregation ratio should be distorted due to coupling linkage (12 map units) of *D1* and *D4*.

A final conclusion with practical implications concerns the selection of wheat genotypes to minimize somaclonal variation. Bingham (1986) suggested that if transformation or somatic cell fusion are the research goals, then somaclonal variation should be reduced or eliminated if possible. Ryan et al. (1987) and Carver and Johnson (1989) both concluded that selecting donor genotypes of wheat can minimize somaclonal variation. Our research also supports this idea. The utilization of genotypes lacking any of the grass-dwarfism alleles would greatly reduce the chance of recovering these undesirable genotypes by mutations arising during tissue culture. It is also important to recognize the grass-dwarf phenotype. If transgenic plants, somatic hybrids, or regenerants from in vitro selection strategies have a grass-dwarf phenotype, they can be induced to enter reproductive development under long daylengths (>14 h) and high temperatures (>26 °C).

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