MINIREVIEW / MINISYNTHÈSE

Genetic and molecular basis of grain size and grain number and its relevance to grain productivity in higher plants

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Abstract: Grain size and grain number constitute 2 important components of grain yield. In particular, the grain size also influences the end-use quality (e.g., flour yield and protein content) and attracts consumer preference. These 2 traits are also the components of the domestication syndrome of crop plants. A number of important studies have recently been conducted to understand the genetic and molecular basis of these 2 important yield-contributing traits. Information generated from these studies was collected and synthesized for the benefit of plant biologists, particularly plant breeders. In the present article, this information is briefly reviewed and the prospects of using this information for improvement of grain productivity in crop plants are discussed.

Key words: grain size, grain number, grain productivity, genetics, domestication.

Résumé : La taille et le nombre de grains constituent 2 composantes importantes du rendement. De plus, la taille des grains influence également la qualité (rendement en farine, contenu protéique) et représente un attrait aux yeux des consommateurs. Ces 2 caractères font aussi partie du syndrome de la domestication chez les plantes. Plusieurs études importantes ont récemment permis de mieux comprendre les assises génétiques et moléculaires de ces 2 importants caractères contribuant au rendement. L'information obtenue au cours de ces études a été colligée et synthétisée pour le bénéfice des chercheurs en biologie végétale et, particulièrement, en amélioration génétique. Dans le présent article, cette information est brièvement résumée et les perspectives d'exploitation de cette information pour des fins d'amélioration de la productivité en grains chez les plantes cultivées sont discutées.

Mots clés : taille des grains, nombre de grains, productivité en grains, génétique, domestication.

[Traduit par la Rédaction]

Introduction

Food security for an ever-increasing world population largely depends on our ability to increase grain yield in crop plants, which in turn largely depends on several yield components including grain size and (or) mass (measured as 1000 kernel mass) and grain number (counted per plant or per unit area of land). Grain size and (or) mass is the target for breeding not merely as a component of grain yield, but also because of its impact on end-use quality (e.g., flour yield and protein content, which also affect milling and baking quality) and consumer preference (e.g., long vs. short grains in rice). Grain size and grain number also constitute important components of the domestication syndrome, thus partly explaining the process of domestication of crop plants (Pozzi et al. 2004). Also, in wild seed plants, natural selection led to improvement in these traits, since propagation and dissemination of flowering plants largely depended on these 2 important traits (Moles et al. 2005*a*).

In view of the importance of grain size and grain number in plant systems, as outlined above, these 2 traits have been the subject of genetic studies for several decades. In particular, during the last decade, such studies included identification of QTLs (including epistatic interactions) for these 2 traits in several crop plants (Li and Gill 2004), and also in the model plant species *Arabidopsis thaliana* (Alonso-Blanco et al. 1999). However, it was not until the last few years that successful attempts were made to understand the molecular basis of these 2 important yield-contributing traits. Some of the most significant recent studies include identification of a number of genes and quantitative trait loci (QTLs) for seed size in *A. thaliana* (Luo et al. 2005; Ohto et al. 2005; Jofuku et al. 2005) and identification of several genes influencing these 2 traits in rice (Ashikari et al. 2005;

Received 25 March 2006. Accepted 9 May 2006. Published on the NRC Research Press Web site at http://genome.nrc.ca on 27 June 2006.

Corresponding Editor: R.S. Singh.

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doi:10.1139/G06-063

Fan et al. 2006; Sakamoto et al. 2006). These exciting recent studies attracted our attention because of our interest in the improvement of grain-quality traits (including grain size) in bread wheat (Kumar et al. 2006), and prompted us to collect information on this subject. In this article, we briefly review the current status of our knowledge of grain size and grain number in flowering plants, and discuss the prospects of using this information for improvement of grain productivity in crop plants.

Factors affecting grain size and grain number

In flowering plants, large variation exists for grain size and grain number, which ranges from the dust-like seeds of orchids (e.g., *Cycnoches ventricosum*, 0.0001 mg) to the 20 kg seeds of the double coconut (*Lodoicea maldivica*; Moles et al. 2005*b*). Similarly, number of grains produced per fruit varies from a solitary seed in *L. maldivica* to as high as 4 000 000 seeds in orchid. The above variation is also associated with a negative correlation between these 2 traits, as evident from the fact that small-seeded plants normally produce many more seeds. Several factors are known to influence these 2 traits (Moles et al. 2005*a*).

The ecogeographical factors that influence grain size and grain number include photoperiod, edaphic conditions, precipitation, microflora (in case of orchids and legumes), concentration of atmospheric CO_2, temperature, altitude, latitude, etc. However, effects of these factors are rather indirect through various other traits that are more directly influenced. For example, resource restrictions and an abiotic stress may influence leaf area, carpel mass, number of fertile florets, etc., leading to a reduction in grain size and grain number. Consequently, even large-seeded plants, which withstand abiotic stress more effectively, exhibit a relative reduction in seed size under abiotic stress conditions (Leishman et al. 2000). Similarly, photoperiod may influence grain size and grain number through its effect on the dry mass of an inflorescence (e.g., spike), stem elongation (during late reproductive phase), duration of the late reproductive phase, and number of florets at anthesis.

Several physiological factors also influence grain size by their effect on rate and (or) duration of grain filling (reviewed in Yang and Zhang 2005); these factors include rates of photosynthesis, mobilization of reserves, and “sink capacity” (number and size of cells in a developing grain). Other physiological factors that indirectly influence grain size include senescence, lodging, kernel water content, and leaf area index.

Seed size and seed number also depend on a number of seed developmental processes during pre-anthesis and post-anthesis periods. The processes that act in the pre-anthesis period mediate their effects through their indirect influence on source (assimilate) availability and sink (number of florets per square metre) capacity; these processes include development of vegetative and reproductive organs. Similarly, the processes that act in maturation and (or) the grain-filling phase of the post-anthesis period and influence grain size and (or) number include nutrient partitioning and accumulation of storage material (particularly carbohydrates, proteins, and fatty acids), which account for a major fraction of the final grain mass (for a review, see Coventry et al. 2003).

Table 1. List of genetic, ecological, and physiological traits known to be correlated with grain size and grain number (compiled from Coventry et al. 2003 and other published literature).

Trait	Grain mass	Grain no.
Grain yield	+	+*
Grain mass	NA	–
Grain protein content	–	NA
Grain number	–	NA
Rate of grain filling	+	NA
Carpel mass at anthesis	+	NA
Number of endosperm cells	+	NA
Increase in temperature (°C)	–	NA
Desiccation tolerance	+	NA
Volume of endosperm cells	+	NA
Plant biomass	+	–
Growth rate	+	NA
Adventitious nodal root mass	+	NA
Use of nitrogen (N) fertilizer	–	NA
Plant height	NA	–
Lodging resistant	–	NA
Seeding rate	+	NA
Floweret size (floral meristem)	+	NA
Oil content	–	NA

Note: NA, not available.
*An inverse relationship was also reported.

As a consequence of the indirect effects of a variety of factors on both grain size and grain number, significant correlations between each of these 2 traits and a number of other traits have been witnessed. For example, grain size is often positively correlated with seed viability, seed germinability, seedling vigor, seedling survival, carpel mass at anthesis, and rate of grain filling, whereas it is negatively correlated with increase in temperature, lodging resistance, and grains per square metre (Coventry et al. 2003). Similarly, grain number shows positive correlations with dry mass of inflorescence and number of florets at anthesis, and negative correlations with plant biomass and number of tillers. These correlations of seed size and seed number with other traits are summarized in Table 1.

Genetic and molecular basis of grain size and grain number

Genes identified through cytogenetic/QTL analysis and linkage disequilibrium (LD) / association analysis

A number of cytogenetic and QTL studies conducted in the last few decades successfully resolved, at least in part, the genetic architecture of grain size and grain number in seed plants. Although cytogenetic studies previously allowed identification of chromosomes carrying genes and QTLs, QTL mapping studies later allowed identification of the specific regions of these chromosomes that carry these genes and QTLs. For example, using monosomics and intervarietal chromosome substitution lines in bread wheat, all 21 chromosomes were shown to influence yield and yield-contributing

Table 2. Chromosomes identified in major cereals, which carry intervals carrying gene(s) or QTL(s) for grain size and (or) grain number.

Crop	Trait	Chromosomes with interval(s) carrying QTLs (chromosomes arranged in homoeologous groups)						
Barley	Grain mass	1H (*Sgh1*)	**2H** (*Ppd-H1, Vrs1*)	**3H** (*Sdw1*)	4H (*Sgh2*)	5H (*Sgh3*)	6H	7H
	Grains/spike	1H	—	3H	4H	5H	6H	—
Wheat	Grain mass	1A, 1B*, 1D	**2A*** (*Br*), 2B, 2D	**3A**, 3B, 3D	**4A**, 4B, 4D	5A (*Q*, *Vrn-A1*), **5B**	6A, 6B, 6D	7A, 7B, 7D
	Grains/spike	1A, 1B, 1D	2A, 2B, 2D	3A, 3B, 3D	4A, 4B (*Rht-B1*)	5A, 5B, 5D	6A	7A, 7B, 7D
Rice	Grain mass	5	4, 7	**1**	**3**	9, 11, 12	2	6, 8
	Grains/panicle	5, 10	4	1	3	12	2	6, 8
Pearl millet	Grain mass	2, 5	—	6	2, 5	1	—	2, 5
	Grains/panicle	5	—	—	5	1	—	5
Maize	Grain mass	1	2, 7	3	**5**	—	4	—
	Grains/spike	—	—	—	—	—	—	—
Sorghum	Grain mass	E, C	B, F	G	C	I	D, F	A
	Grains/panicle	—	—	—	—	—	—	—

Note: Chromosomes carrying major QTLs are shown in bold; those carrying DSFs are marked with an asterisk. Genes, wherever known, are given in italics. For references, see Table S1[2].

traits (Kuspira and Unrau 1957; for references, also see Kumar et al. 2006); later QTL mapping studies further resolved the genetic architecture of grain size and grain number through identification of marker intervals on almost all the chromosomes of bread wheat (see Table S1)[2]. To identify chromosomes influencing these 2 traits, trisomics were also used in maize (chromosomes 2 and 7; Fox and Weber 1977), faba bean (chromosome 6; Vaz Patto et al. 1999), and rice (chromosome 6; Satoh et al. 2003); in these crops also, QTL mapping identified segments (marker bins and (or) intervals) of those chromosomes that were earlier known to carry genes and QTLs for these traits, although QTL analysis in each of these cases detected QTLs on some other chromosomes as well (Table S1)[2].

The QTL mapping studies in some crops suggested that QTLs are often scattered throughout the genome of a crop, with their relative abundance in gene-rich regions (GRRs). For example, in chromosome 3A of bread wheat, 9 of the 17 QTLs for 7 agronomic traits (including grain size and grain number) overlapped with GRRs earlier identified in this chromosome (Dilbirligi et al. 2006). Later, results of QTL mapping were also used for the detection of corresponding genetic loci in other crops (where molecular maps were available), simply by looking for their syntenic positions on the molecular maps; e.g., loci that corresponded to each of the major QTLs for grain size on chromosome 4 and grain number on chromosome 3 of Triticeae were identified on the syntenous chromosomes of other cereals, i.e., chromosomes 3 and 1 in rice and chromosomes 5 and 3 in maize (Paterson et al. 1995; Dilbirligi et al. 2006). A similar situation was also observed for a number of other QTLs for grain size and number (see Table 2).

Some QTLs also overlapped the domestication syndrome factors, which often coincided with GRRs (Peng et al. 2003) or else resided in close proximity to the genes influencing one or more of the domestication traits (see Table 2; for details on domestication traits, see section dealing with domestication). Other than the major QTLs with main effects as described previously, a number of minor QTLs were also detected, which may be responsible for a large proportion of variation for grain size and grain number (Wan et al. 2006). Most of these minor QTLs mediate their effects via epistatic interactions.

LD-based association mapping has also been used to identify additional QTLs for grain size and grain number. For example, in a study conducted in bread wheat, 14 loci (6 on 2D and 4 each on 5A and 5D) showing significant association with different grain morphology traits (including grain mass, area, length, and width) were identified (Breseghello and Sorrells 2006). Similarly, a solitary locus in maize (chromosome 5) and 4 loci in rice showing association with 1000-kernel mass were identified (Buntjer et al. 2005; Zhang et al. 2005). Near-isogenic lines (NILs) were also developed in rice for these 2 traits, which facilitated positional cloning of the underlying genes, *OsCKX2* encoding cytokinin oxidase/dehydrogenase and *GS3* encoding a transmembrane protein (Ashikari et al. 2005; Fan et al. 2006).

Genes identified and cloned through analysis of mutants and (or) positional cloning

Genome-wide transcriptional studies, mutant analysis (in particular, the artificially induced mutants) and functional characterization of genes and QTLs in a variety of crop plants suggested that genes involved in or associated with a number of pathways may contribute to final grain size and grain number. These pathways include those involved in nutrient partitioning (synthesis and transport of carbohydrates, proteins, and fatty acids), biosynthesis of various phytohormones (e.g., BR, CK, ABA, GA, etc.), and signal transduction (for details of specific genes involved in these pathways and proteins encoded by them, see Table 3). It was apparent that attainment of final grain size and grain number also requires coordinated and temporal expression of a variety of genes (e.g., *HOR2* for B-hordein, *At2S* for 2S albumin)

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[2] Supplementary data for this article are available on the journal Web site (http://genome.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5045. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Table 3. List of genes involved in regulation of grain size and number.

Gene	Homologs	Proteins encoded and their function
Genes involved in grain size		
Maize, *miniature1* (*mn1*)	—	Cell wall invertase required for normal development of endosperm
Maize, *crinkly4* (*cr4*)	—	Ser (thr) kinase
Rice, *grain size3* (*GS3*)	Tomato, *OVATE*	Putative transmembrane protein
Rice, *OsDWARF4*	*Arabidopsis*, *DWARF4*	Cytochrome P450 (CYP90B2)
Rice, *dwarf11* (*d11*)	*Arabidopsis*, *CYP724A1*	Cytochrome P450 (CYP724B1)
Wheat, *photoperiod* (*ppd*)	Barley, *ppd-H1*	Pseudo-response regulator (PRR)
Barley, *endosperm1* (*end1*)	—	Gives rise to the cells that differentiate into transfer cells
Barley, *hordein2* (*hor2*)	—	Encoding B-hordein
Barley, *photoperiod-H1* (*ppd-H1*)	Wheat, *ppd*	Pseudo-response regulator (PRR)
Arabidopsis, fertilization independent seeds (*fis, fis2*)*, *medea* (*mea*)*, *fertilization independent endosperm* (*fie*)*, *ira1 multicopy suppressor* (*msi1*)*	—	Polycomb complex (regulates endosperm development before double fertilization)
Arabidopsis, haiku1 (*iku1*)[†]	—	Regulation of expression of both *MINI3* & *IKU2*
Arabidopsis, haiku2 (*IKU2*)[†]	—	LRR receptor kinase
Arabidopsis, miniseed3 (*mini3*)[†]	—	Transcription factor of WRKY family
Arabidopsis, apetala2 (*ap2*)[†]	—	Transcription factor of AP2/EREBP family
Arabidopsis, transparent testa glabra2 (*ttg2*)*	—	WRKY transcription factor
Arabidopsis, cyclin-dependent kinase inhibitor2 (*ick2*)	—	Cyclin-dependent kinase inhibitor
Arabidopsis, cyclin-dependent kinase2a (*cdc2a*)	—	Signal from fertilized egg cell initiates endosperm proliferation
Arabidopsis, demeter (*dme*)	—	Activation of *MEA* and *FWA* in the central cell
Arabidopsis, leafy cotyledon2 (*lec2*)	—	B3 domain transcription factor
Arabidopsis, short integument1 (*sin1*)	—	Processing of critical RNA involved in embryonic pattern formation
Vicia, Rb	—	ADP-glucose pyrophosphorylase large subunit
Pea, *E2748*	—	Blocked transfer cell formation
Genes involved in grain number		
Maize, *ramosa1* (*ra1*)	—	EPF zinc-finger domain transcription factor
Maize, *ramosa2* (*ra2*)	Rice, *LOB*	LOB domain transcription factor
Maize, *ramosa3* (*ra3*)	—	—
Maize, *barren stalk1* (*ba1*)	Rice, *LAX*	Basic helix–loop–helix (bHLH) protein
Maize, *thick tassel dwarf1* (*td1*)	*Arabidopsis*, *clv1*	LRR receptor-like protein
Maize, *fasciated ear2* (*fea2*)	*Arabidopsis*, *clv2*	ERF transcription factor
Maize, *branched silkless1* (*bd1*)	Rice, *fzp*	ERF transcription factor
Maize, *barren inflorescence2* (*bif2*)	—	Maintenance of axillary meristem in inflorescence
Maize, *indeterminate spikelet1* (*ids1*)	Wheat, *WAP2*; *Arabidopsis*, *AP2*	AP2 family transcription factor
Maize, *teosinte branched1* (*tb1*)	Rice, *OsTB1*	bHLH transcription factor
Rice, *OsCKX2*	—	Cytokinin oxidase/dehydrogenase
Rice, *frizzy panicle* (*fzp*)	Maize, *bd1*	ERF transcription factor
Rice, *floral organ number1* (*fon1*)	*Arabidopsis, clv1*	LRR-type receptor kinase
Rice, *lax panicle* (*lax*)	Maize, *ba1*	bHLH protein
Rice, *qGY2–1*	—	Leucine-rich repeat receptor kinase
Wheat, *wheat apetala2* (*wap2*)	Maize, *ids1*, *Arabidopsis, AP2*	AP2 family transcription factor
Barley, *Vrs1*	—	Homeodomain-leucine zipper protein (Hvhox1)
Arabidopsis, erecta (*erl*)	—	Receptor protein kinase with extracellular LRRs
Arabidopsis, brevipedicellus (*bp*)	—	KNOX family homeodomain protein KNAT1
Arabidopsis, revoluta (*rev*)	—	HD-ZIP transcription factor
Tomato, *blind* (*bl*)	Maize, *Arabidopsis, R2R3 Myb*	Myb transcription factor

*Gametophytic expression.

[†] Sporophytic expression.

involved in these pathways. More than a dozen *cis* regulatory elements (e.g., AACA box, prolamin box, RY element) available in the promoter regions of these genes (these elements facilitate coregulation of these genes), and a number of other genes encoding various transcription factors (particularly those belonging to bZiP, DOF, MYB, B3, and RITA families) were also identified (see Table 3; Zhu et al. 2003; Vicente-Carbajosa and Carbonero 2005).

Among the genes listed in Table 3, the most important gene is perhaps the gene *OsCKX2* in rice (isolated through positional cloning), which encodes the cytokinin oxidase/dehydrogenase that degrades cytokinin, thus influencing grain number adversely; its loss of function (*lf*) mutation, therefore, would be desirable to achieve higher seed number (Ashikari et al. 2005). An equally important gene identified in *Arabidopsis* is *APETALA2* (*AP2*), which encodes a transcription factor from the AP2/EREBP family, and mediates its effect on grain size by influencing sugar metabolism (Ohto et al. 2005; Jofuku et al. 2005). Similarly, the gene *LEAFY COTYLEDON2* (*LEC2*), encoding a B3-domain transcription factor, influences grain size by regulating the expression of more than a dozen genes involved in the maturation phase of seed development (e.g., *LOB40*, *AGL15*, *EEL*, etc.); to exercise this regulation, LEC2 protein binds a conserved RY motif available in the 5′ flanking regions of these genes (Braybrook et al. 2006). However, there are also other genes that influence grain size and number through their involvement in several biosynthetic pathways (e.g., brassinosteroid biosynthesis (*CYP90B2/OsDWARF4* and *CYP724B1/D11* in rice) and starch biosynthesis (Suc synthase, ADP Glc pyrophosphorylase, starch synthase, and starch branching enzyme)), thus suggesting a complex genetic architecture for these 2 traits.

Domestication involving grain size and grain number

As mentioned earlier, grain size and grain number are also important components of domestication syndrome in crop plants. It has been shown that often only a few major genes influence a large proportion of domestication-related genetic variability, even though a large number of genes might have been affected by artificial selection exercised during the domestication process (Wright et al. 2005). Some of this variability may also be due to epistatic interactions or pleiotropy (see Hancock 2005 for review). Several clusters of QTLs associated with domestication syndrome (it involves about a dozen traits including grain size and grain number) have actually been assigned to specific chromosome segments (domestication syndrome factors) in durum wheat (Peng et al. 2003), rice (Li et al. 2006), and common bean (Koinange et al. 1996). Such clustering of genes or QTLs would perhaps reduce the level of recombination and segregation between these adaptively important genes and QTLs (see Hancock 2005).

Future prospects for the improvement of grain productivity

We know that improvement in grain productivity can be achieved by increasing both grain size and grain number despite a negative correlation between these 2 traits. The knowledge generated about the genetics and molecular basis of these 2 traits will help in this direction. An important example of the use of information generated about the genetics of grain number for improvement of grain productivity is provided by the recent successful introgression of one QTL for grain number (*Gn1a* identified as *OsCKX2* gene) and another for plant height (*Ph1* identified as *sd1* gene) in rice employing a QTL-pyramiding breeding strategy. In this study, a significant increase in grain productivity involving increased number of grains per panicle and resistance to lodging was achieved by crossing NILs carrying desirable alleles of the 2 genes or QTLs; this resulted in a novel genotype carrying desirable alleles of the 2 genes or QTLs (Ashikari et al. 2005). Similarly, in tomato, Gur and Zamir (2004) combined 3 independent yield-promoting genomic regions derived from drought-tolerant *S. pennellii* into a new genotype through the use of segmental introgression lines (ILs) derived from a cross between *S. pennellii* (a wild tomato species) and *S. lycopersicum* ‘M82’ (an elite inbred); the derived genotypes outperformed the available commercial tomato varieties both in yield and drought resistance. More recently, to improve both yield and organoleptic properties of tomato fruits, an IL library derived from a cross between *S. pennellii* (donor) and *S. lycopersicum* ‘Roma’ was screened for variation in the level of different fruit metabolites, and the data was used to study the genetics of these variations (Schauer et al. 2006). This not only facilitated mapping of ~1200 new metabolite QTLs (including 326 loci that influence yield-associated traits), it also revealed a sizable number of correlations between fruit quality and yield-contributing traits. This knowledge can facilitate development of ideal genotypes using the notion of breeding by design. It may also allow development of desirable combinations of QTLs in a single plant by crossing ILs among themselves and also with an elite variety (‘Roma’) following marker-assisted selection (MAS). Similarly, in rice, one could also think of combining the QTL for grain length and mass (*GS3*, identified as a transmembrane protein) with genes encoding cytochrome P450 (*CYP90B2/OsDWARF4* and *CYP724B1/D11*) involved in brassinosteroid biosynthesis by crossing NILs for these genes or QTLs. Genetic engineering may also be used to combine beneficial genes from different cereals.

The benefits of whole-genome sequence information generated in rice and *Arabidopsis* (the 2 model plant species) could also be extended to other crop plants using the synteny and (or) collinearity relationships among these model plant systems and major crop plants. For example, rice chromosome 1 shows regions of sequence similarity with chromosomes 3, 6, and 8 in maize (Salse et al. 2004) and group 3 chromosomes in bread wheat (Dilbirligi et al. 2006), where some QTLs for grain yield and other agronomic traits have been mapped. *Gn1a* (*OsCKX2* gene) in rice might correspond to these maize and wheat QTLs, and orthologous *CKX* genes might regulate yield in other cereal crops, such as rice (Ashikari et al. 2005). Once identified through synteny, these genes for grain size and (or) number can be manipulated to improve grain yield. The study of the epigenome and its effect on grain size and (or) number will also prove useful for improvement of these traits.

Conclusion

Significant progress has been made in our understanding of the physiology, genetics, and molecular biology of the processes influencing grain size and grain number in flowering plants. A number of genes and (or) QTLs have been identified that are involved in specific biosynthetic and (or) signal-transduction pathways influencing these 2 traits. In some cases, details of these pathways are also known. In future, this information will certainly be used to help improve grain yield in crops through approaches like MAS, metabolic engineering, and transgenics.

Acknowledgements

The work was done during the P.K.G.'s tenure as Senior Scientist of the Indian National Science Academy, New Delhi, and that of S.R. as Senior Research Fellow of the Council of Scientific and Industrial Research, New Delhi. N.K. was employed in research and development project (BT/AB/03/AR/2002) with the Department of Biotechnology, Government of India. Thanks are also owed to Head, Department of Genetics and Plant Breeding, CCS University, Meerut, for providing facilities. Suggestions from Rama Singh and 2 anonymous referees also proved useful for improvement of the manuscript.

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