

Phenotypic characterization and genetic analysis of dwarf and early flowering mutants of rice variety Nagina22

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ABSTRACT

Plant height and flowering time are two of the important traits that affect plant architecture. Efforts were made in this study to characterize morphologically the-EMS-induced dwarf and early flowering mutants of rice variety Nagina22 and to study their mode of inheritance. Nine true breeding mutants generated earlier by EMS treatment were analysed for differences in their phenotypic characteristics recorded according to the national guidelines for Distinctness, Uniformity and Stability (DUS). The mutants exhibited variation from Nagina22 for maximum of 11 DUS characteristics to a minimum of 4 DUS descriptors, while retaining majority of the wild type features. Plant height of the dwarf mutants ranged from 69 to 101cm, while tiller number was in the range of 9 to 60. The early flowering mutants were weak in their plant stature, but flowered approximately 20-25 days earlier than Nagina22. Significant correlation among various traits of the selected mutants was observed. The mutant traits exhibited monogenic inheritance giving 3:1 phenotypic segregation ratio in F2 generation. These mutants have potential usage in functional analysis of the traits and in rice improvement programs.

Key words: rice variety Nagina22, DUS, dwarf mutant, early flowering, inheritance

Genetic variation is essential for understanding traits and development of new crop genotypes. Mutagenesis is one of the approaches that create new genetic variation (Ahloowalia and Maluszynski, 2001). Since the 1960s, number of mutants from different crop species have been isolated and effectively used in different areas of crop breeding (Fu *et al.*, 2008). Of the more than 2250 mutant varieties that have been released worldwide, 64% were created through exposure to gamma-rays, 22% through exposure to x-rays and the rest by other mutagenic treatments (Ahloowalia *et al.*, 2004; Shu and Lagoda, 2007).

In rice, mutants have been useful for genetic and physiological assessments of yield-limiting factors

(Babaei *et al.*, 2011). They have played an important role in the development of dwarf rice varieties and in broadening the genetic base of the present dwarf varieties (Singh *et al.*, 1979). Many mutant genes controlling important traits like plant height, tiller number and panicle length have been cloned and characterized at molecular level (Ashikari *et al.*, 1999; Hong *et al.*, 2003; Itoh *et al.*, 2004; Sasaki *et al.*, 2002). Genetic analysis of mutants can help understand the molecular basis of a particular trait under consideration, thereby unearthing novel genes/alleles that may have potential in breeding. Further it helps in exploring the nature of interaction among genes/alleles and the mechanisms by which they control the trait variation.

A number of mutants in different *indica* and *japonica* backgrounds have been generated using different mutagens. For instance, Wu *et al.* (2005) have advanced 38,000 independent lines to M4 generation and their database has over 3000 mutants for 90 distinct phenotypes. These were generated using four different mutagenic agents, including EMS, in order to have different sizes of genetic lesions in the population. EMS in particular produces different alleles for a gene, thus helps analyze a series of alleles for their utilization in crop improvement. Such materials need to be analyzed for trait variance and to study the expression of desired traits. Dwarfism is one of the important agronomic traits that play part in increasing rice yield. As many as 80 dwarf mutants of rice have been reported including 6 high tillering dwarfs. They have been extensively analyzed for their modes of inheritance and their responses to plant hormones, such as gibberellins (GAs) (Ashikari *et al.*, 1999; Ueguchi-Tanaka *et al.*, 2000) and brassinosteroids (BRs) (Clouse and Sasse, 1998). However, a very few of the dwarf mutants had potential to be utilized in breeding because of their pleiotropic effect on major yield contributing traits.

Flowering time is another important agronomic trait, controlled by different endogenous genetic factors as well as environmental signals (Yano *et al.*, 2001). Several workers have genetically characterized rice mutants like *ehd1* and *rh1* for heading date. Heading date1 (Hd1) is one of the first flowering-related genes to have been cloned from a natural variant of rice (Yano *et al.*, 2000). Recent accumulation of information about the genetic control of flowering in rice has been largely based on the analysis of natural variations (Doi *et al.*, 2004; Kojima *et al.*, 2002; Xue *et al.*, 2008; Yano *et al.*, 2001). However, a major part of the control pathway remains to be analyzed compared with *Arabidopsis*, in which analysis of this pathway has progressed mainly by using various flowering mutants (Kobayashi and Weigel, 2007; Koornneef *et al.*, 1998; Turck *et al.*, 2008). These studies show that it is necessary to create further allelic variation for a particular trait and to comprehensively analyze them to understand the genetic control of dwarfism and flowering in rice.

In rice, numerous studies have reported inheritance patterns for dwarf plant height and early flowering. Ram Rao and Reddy (1997) studied mode of inheritance of five semi-dwarf mutants and observed

monogenic inheritance patterns in all of the crosses. Jiang *et al.* (2006) analyzed a novel excessive tillering mutant for its inheritance which was found to show monogenic and recessive mode of inheritance. The inheritance is the first step as a prerequisite for further structural and functional characterization of a gene for a given trait. In view of this, the present study was undertaken to morphologically characterize dwarf and early flowering EMS-induced mutants of rice variety Nagina22 and to understand their inheritance pattern.

MATERIALS AND METHODS

Rice (*O.sativa ssp.indica* cv.Nagina22) mutants generated earlier were used for their further characterization. A total of nine mutants (semi-dwarf and early flowering) were selected and maintained through selfing. No segregation was obtained within a line in these selected mutants which were beyond M6 generation. Three lines of each mutant were grown (17 plants line⁻¹) in transplanted conditions in the field of Indian Agricultural Research Institute, New Delhi with row to row spacing of 20cm and plant to plant spacing of 15cm. The data was recorded from five plants of middle line of a particular mutant at different stages of crop growth.

The morphological characterization of selected mutants was done according to the national guidelines for Distinctness, Uniformity and Stability (DUS). The phenotype data was recorded through visual assessment of the characters at three different stages, *viz.* seedling, vegetative and reproductive stages. The characteristics that required measurements were done according to the usual procedure. The plant height was measured from the base of the plant to the tip of main panicle. The grain data such as grain size, shape, color, etc were recorded after the harvesting and drying of the material. The characters like presence of apicular pigment, absence of awns, grain and panicle morphology, leaf and stem characters and sheath colour were visually scored. Data for quantitative characters like plant height, panicle length, tiller number and 100 grain weight was also taken from the same plants. The correlation studies among these and other characters were performed using the software SPSS Version 16.

To study the mode of inheritance, all the mutants (female parent) were crossed with Nagina22 (male parent) by conventional hand emasculation and

pollination. The hybrid (F1) seeds were collected from all cross combinations, the F1 plants were raised in pots during off season (2010-2011) at Central Rice Research Institute, Cuttack and seeds were collected. The F2 plants were raised during wet season 2011-2012 at Indian Agricultural Research Institute, New Delhi, under transplanted field conditions. Data on all the characters that are specific to the respective mutants were recorded before maturity in F2 population. Chi-square analysis was used to test the goodness of fit of F2 segregation data with expected ratios.

RESULTS AND DISCUSSION

Comparative morphological analysis revealed that the mutants differed from Nagina22 for a maximum of 11 DUS characteristics to a minimum of 4 DUS descriptors (Table 1). While differing for many of the traits, most of the mutants retained the original characteristics of Nagina22 like pale yellow colour of the leaves and anthocyanin coloration of the tip of keel. The isolated mutants also differed from the original parent for a number of yield related traits (Table 2) revealing thereby, that a number of traits were altered in the phenotypically distinct mutants. Several semi-dwarfs carrying mutation in the *sd1* or other genes and high-tillering dwarfs like *d27* and *d88* have been identified and characterized in rice. The plants of IR8 and Calrose 76 carrying mutation in *sd1* showed short stature and conferred a yield advantage of 14% over their parent lines (Rutger 2009). They were shown to be 25% shorter than their parents and produced more than 14% yields. Because of such advantages these mutants were employed in numerous cross-breeding programs and served as ancestral source of semi-dwarfism to many currently used cultivars. So far more than 60 dwarf mutants have been isolated and characterized in rice. Similarly, early flowering loci have been molecularly identified in rice (Yano *et al.*, 2001, Rutger *et al.*, 2007, Zhao *et al.*, 2012). The mutants used in this study show similar phenotypes resembling with those of mutants characterized earlier by several workers. The test of allelism which is being studied will show whether these mutations are in the same genes reported earlier or in new genes. In the absence of allelic relationships mutants used in this study have been designated with tentative nomenclature namely, *sd1* for semi-dwarf indica, *dit* for dwarf and increased tillering and *efl* for early flowering (Table 1 and 2).

The semi-dwarf mutants used in the study were having plant height in the range of 95-101 cm (Table 2, Figure 1). The leaves were darker than the wild type and stems were thicker than those of Nagina22. One of the mutants, *sd1* had short white awns and the grains were sparsely spaced. The grain length and grain width

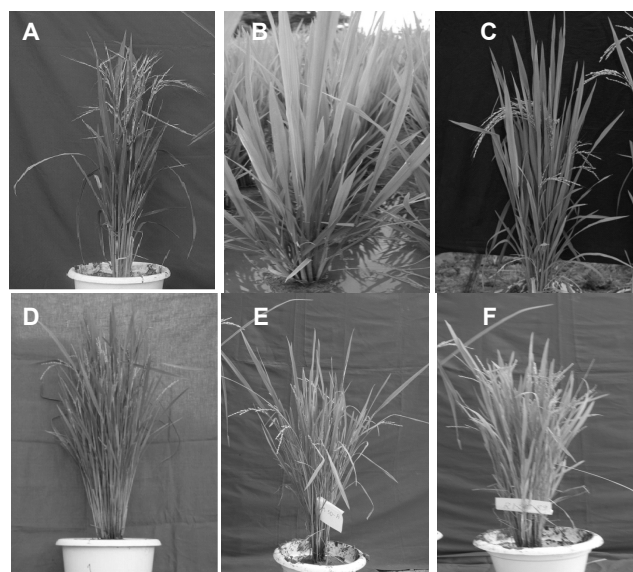


Fig. 1. Plant types of EMS-induced dwarf mutants of Nagina22 (A: *sd1*, B: *sd3* C: *sd4* D: *dit1*, E: *dit2*, F: *dit3*,

were more than the Nagina22 that resulted in increased grain weight (Table 2). Other semi-dwarf mutants differed from Nagina22 in characters like orientation and width of leaf blade, flowering duration, and curvature of main axis of panicle and leaf senescence. Variation in plant height has been reported earlier by several workers and superior alleles of the *sd1* locus have been identified for developing high yielding varieties (Ashikari and Sakamoto, 2008). Based on the morphological analysis, it is possible that the semi-dwarf mutants analyzed in this study might carry new mutation in *sd1* giving newer alleles.

The high-tillering dwarfs used in this study had a plant height in the range of 69-76cm, much shorter than the wild type, which was 120 cm tall (Table 2, Figure 1). Earlier studies have shown that dwarf phenotypes result from either shorter internodes or fewer internodes or both. The length of each of the internodes was also measured, considering upper internode as first. The comparison of each of the

Table 1. Recorded DUS characteristics of dwarf and early flowering mutants used in this study

Descriptor	Nagina22	<i>sd1</i>	<i>sd12</i>	<i>sd13</i>	<i>sd14</i>	<i>dit1</i>	<i>dit2</i>	<i>dit3</i>	<i>eff1</i>	<i>eff2</i>
Basal Leaf: sheath colour	light purple	green	light purple	light purple	light purple	light purple	light purple	light purple	light purple	light purple
Leaf: intensity of green colour	medium	medium	medium	medium	medium	medium	medium	medium	medium	medium
Leaf: anthocyanin coloration	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent
Leaf: auricles	present	present	present	present	present	present	present	present	present	present
Leaf: anthocyanin coloration of auricles	colourless	colourless	colourless	colourless	colourless	colourless	colourless	colourless	colourless	colourless
Leaf: collar	present	present	present	present	present	present	present	present	present	present
Leaf: anthocyanin coloration of collar	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent
Leaf: ligule	present	present	present	present	present	present	present	present	present	present
Leaf: shape of ligule	split	split	split	split	split	split	split	split	split	split
Leaf: colour of ligule	light purple	light purple	light purple	light purple	light purple	light purple	light purple	light purple	light purple	light purple
Leaf: length of blade	medium	long	long	long	long	medium	medium	medium	medium	medium
Leaf: width of blade	medium	broad	medium	medium	medium	medium	medium	medium	medium	medium
Culm: attitude	semi-erect	semi-erect	semi-erect	semi-erect	semi-erect	semi-erect	semi-erect	semi-erect	semi-erect	semi-erect
Time of heading (50% of plants with panicles)	medium	medium	early	medium	medium	medium	medium	medium	very early	very early
Flag leaf: attitude of blade (early observation)	semi-erect	semi-erect	semi-erect	erect	erect	erect	erect	erect	erect	erect
Male sterility	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent
Lemma: anthocyanin colouration of keel	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent
Lemma: anthocyanin colouration of area below apex	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent
Lemma: anthocyanin colouration of apex	strong	absent	absent	absent	absent	strong	strong	strong	medium	medium
Spikelet: colour of stigma	white	white	white	white	white	white	white	white	white	white
Stem: thickness	medium	medium	medium	medium	medium	thin	thin	thin	thin	thin
Stem: length (excluding panicle)	medium	medium	medium	medium	medium	very short	very short	very short	very short	very short
Stem: anthocyanin colouration of nodes	absent	absent	absent	absent	absent	absent	absent	absent	absent	absent
Panicle: length of main axis (late observation)	medium	medium	long	long	long	short	short	very short	very short	very short
Flag leaf: attitude of blade (late observation)	semi-erect	semi-erect	semi-erect	erect	semi-erect	erect	semi-erect	erect	erect	semi-erect
Panicle: curvature of main axis	straight	drooping	straight	semi-straight	semi-straight	straight	straight	straight	straight	semi-straight
Panicle: number plant ¹	medium	medium	medium	medium	medium	many	many	many	few	few
Spikelet : colour of tip of lemma	purple	yellowish	yellowish	yellowish	yellowish	purple	purple	purple	purple	purple
Lemma and Palea: colour	straw	straw	straw	straw	straw	straw	straw	straw	straw	straw
Panicle : awns	absent	present	absent	absent	present	absent	absent	absent	absent	absent
Panicle: colour of awns (late observation)	-	yellowish	-	-	yellowish	-	-	-	-	-
Panicle: length of longest awn	-	short	-	-	long	-	-	-	-	-
Panicle: distribution of awns	-	tips only	-	-	whole length	-	-	-	-	-
Panicle: presence of secondary branching	present	present	present	present	present	absent	present	absent	absent	absent
Panicle: secondary branching	weak	weak	clustered	strong	clustered	-	weak	-	-	clustered
Panicle: attitude of branches	semi-erect	spreading	semi-erect	erect to semi-erect	semi-erect	semi-erect	semi-erect	semi-erect	semi-erect	semi-erect
Panicle: exertion	exerted	exerted	exerted	exerted	exerted	exerted	well-exerted	exerted	well-exerted	partially exerted
Time of maturity	medium	medium	medium	late	medium	medium	medium	medium	early	early
Leaf: senescence	medium	medium	medium	medium	medium	medium	medium	medium	medium	medium

Table 2. Quantitative trait data of the mutants used in this study

Plant type	Plant height (cm)	Panicle length (cm)	Tiller number	Grain length (mm)	Grain width (mm)	Decorticated grain length (mm)	Decorticated grain width (mm)	100 grain weight (g)
Nagina22	120	20	10	8.07	2.85	5.68	2.458	1.944
<i>sdi1</i>	95.4*	22	10	8.24	3.23	4.83	2.60	2.294
<i>sdi2</i>	102.4*	24	11	8.17	2.52*	5.87	2.232*	2.177
<i>sdi3</i>	98*	22	12	8.42	2.60	5.91	2.22*	2.165
<i>sdi4</i>	101*	23	9	8.48	2.408*	6.058*	2.114*	2.306
<i>dit1</i>	69.2*	13.8*	64.4*	7.3*	2.59	5.214*	2.24*	1.910
<i>dit2</i>	73.8*	13.8*	51.4*	7.206*	2.93	5.158*	2.212*	1.904
<i>dit3</i>	76.4*	14*	46.4*	7.78	2.5*	5.296*	2.244*	1.276
<i>efl1</i>	92.4*	16.4*	11	7.67	2.67	5.358*	2.31	1.657
<i>efl2</i>	95.6*	15.6*	10	7.198*	2.502*	4.996*	2.214*	1.959

The * represents significant difference between the wild-type (Nagina22) and the mutants determined by the Student's t-test at $P < 0.05$.

internodes with wild type showed that each internode is shortened evenly. The tiller number of these mutants was in the range 46-60 at maturity which was 4-5 times more than that of Nagina22. The mutants had very weak and thin stem. These mutants showed tiller growth even after culm elongation and therefore, had high tiller number. The leaves were pale yellow like the wild type and there was no difference in the flowering dates.

apicular pigmentation, yellowish leaf color, auricle and ligule colour, seedling basal leaf sheath colour, awning and other characters were present in all the high tillering dwarf mutants. A set of high-tillering dwarf mutants such as *d14*, *d27*, *d61*, *htd1* and *d88* have been identified in rice and the genes mapped onto the chromosomes (Ishikawa *et al.*, 2005; Jiang *et al.*, 2009; Zhang *et al.*, 2011; Zou *et al.*, 2005). It would be

Table 3. Correlation analysis of the mutants for measured quantitative traits

Trait	Plant height (cm)	Panicle length (cm)	Tiller number	Grain length (mm)	Grain width (mm)	Decorticated grain length (mm)	Decorticated grain width (mm)
Panicle length (cm)	0.981**						
Tiller number	-0.910**	-0.964**					
Grain length (mm)	0.890**	0.899**	-0.940**				
Grain width (mm)	0.111	0.204	-0.280	0.148			
Decorticated grain length (mm)	0.631	0.572	-0.512	0.593	-0.663		
Decorticated grain width (mm)	0.019	0.080	-0.120	0.033	0.957**	-0.748	
100 grain weight	0.870*	0.839*	-0.744	0.693	0.342	0.323	0.246

* and ** significant at 0.05 and 0.01 level respectively.

The panicle size was reduced but the grain characteristics remained unchanged. Other characteristics like culm attitude, attitude of flag leaf blade, lemma and palea colour, secondary branching and leaf senescence didn't have any differences among mutants and between mutant and the wild type. The peculiar characteristics of Nagina22 like presence of

interesting to see whether the mutations induced in the present study are allelic to any of these genes.

The dwarf mutants used in this study differed from each other significantly for one or more traits, indicating the presence of substantial variability for the traits of agronomic importance. Correlation analysis

revealed that plant height was positively correlated with panicle length (0.981), grain length (0.890) and grain weight (0.870), whereas negatively correlated with tiller number (-0.910). All these correlations were significant at p-value of 0.01 (Table 4). Earlier, 100 grain weight has been shown to be positively correlated with plant height, grains panicle⁻¹ and grain breadth (Sabesan *et al.*, 2009). The negative correlation between tiller number and plant height has also been observed in several dwarf mutants and cultivated rice varieties (Yan *et al.*, 1998). Besides plant height, tiller number also had strong negative correlation with grain length (-0.940), grain width (-0.280) and 100 grain weight (-0.744). This suggested that tiller number was associated with all of these traits that strongly affect the final grain yield. These observations are in accordance with many previously reported studies.

Table 4. Segregation of the mutant traits in F2 population

Mutant ID	Number of F2 plants			Chi sq value	p value
	Nagina22	Mutant-type	Total		
<i>sdi1</i>	126	52	178	1.69	0.19
<i>sdi2</i>	129	41	170	0.07	0.79
<i>sdi3</i>	127	43	170	0.01	0.93
<i>sdi4</i>	131	47	178	0.19	0.67
<i>dit1</i>	129	41	170	0.07	0.79
<i>dit2</i>	91	34	125	0.32	0.57
<i>dit3</i>	167	58	225	0.07	0.79
<i>efl1</i>	129	41	170	0.07	0.79
<i>efl2</i>	133	37	170	0.95	0.33

Besides dwarf mutants, two early flowering mutants were also analyzed for their phenotype and inheritance patterns. Both the mutants flowered in approximately 55 days (50% flowering) of seeding, whereas wild type took approximately 75-80 days. The mutants were very weak (Figure 2) and had less tillers. There was reduction in the plant height and panicle size; however, no or little differences in grain characteristics were observed (Table 2). The flag leaf attitude and curvature of main axis of panicle were erect and straight, respectively while those were semi-erect in Nagina22. The length of main axis of panicle was short and had less number of grains than that of Nagina22. The other distinguishable characters of Nagina22 were all present in these two mutants.

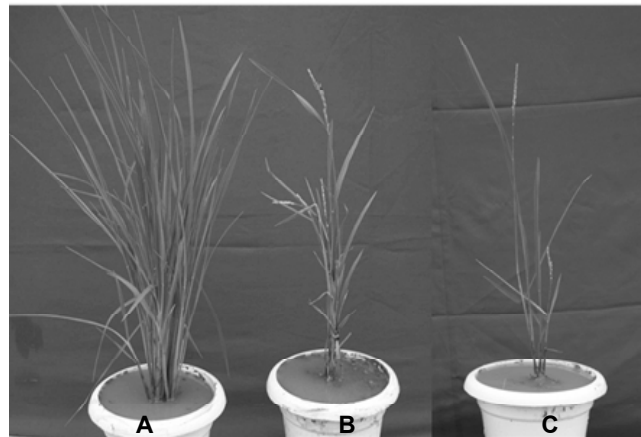


Fig. 2. EMS-induced early flowering mutants of Nagina22. A: Nagina22; B: *efl2* and C: *efl3*

Although there is rapid accumulation of early flowering mutants (Rutger *et al.*, 2006; Wu *et al.*, 2005), there have been very few reports of their use in comprehensive analysis of genetic control of flowering (Matsubara *et al.*, 2008).

To analyze the inheritance of selected dwarf and early flowering mutants, crosses were made and F1 seeds were raised. All the F1s of mutants had wild type phenotype indicating dominance of parental phenotype over mutant phenotype in each case. Among the individuals of the F2 population, the number of mutant-type individuals was around 25% of the total number of F2 plants, showing their recessive nature. The ratio of wild type to mutant plants conformed to the expected 3:1 at 5% probability and 1 degree of freedom (Table 5). Inheritance in many rice mutants for different traits has been studied in the recent past. Although plant height and flowering time are known to be quantitative in nature, in the mutants they behaved as qualitative traits. The traits in such mutants are controlled by a single gene each (Kinoshita, 1995). Monogenic recessive inheritance has been observed in mutants like *dwl1*, *d88* and *htd3* (Gao *et al.*, 2009; Jiang *et al.*, 2008; Zhang *et al.*, 2011). Similarly, the mutants analyzed in this study were also recessive in nature, which indicates that loss of function seems to be more prevalent over gain of function. Besides, it has been observed that the flowering time is often associated with plant size; however, in rice little is known about how flowering time genes affect plant

architecture. The monogenic control of flowering as observed in the present study is expected to help us in understanding the nature of the gene(s) controlling flowering time in rice. Combinations of mutants with different time of flowering and photoperiod treatments can further help to reveal effects of flowering genes on plant architecture traits (Endo-Higashi and Izawa, 2011). Thus the flowering mutants characterized in this study can be utilized in understanding the genetic and molecular basis of the transition from the vegetative phase to the reproductive phase under distinct photoperiod conditions.

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