# Inheritance of elongated uppermost internode and identification of RAPD marker linked to *eui* gene in rice

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**In hybrid rice seed production, one of the major impediments for high seed yield is incomplete panicle exsertion in the wild abortive cytoplasmic male sterility (CMS) lines. Gibberellic acid ($GA_3$) spray to improve panicle exsertion increases seed production cost by at least 10%. Elongated uppermost internode (EUI) trait has been widely used in China as an alternative to $GA_3$. The present study employed segregating populations from crosses between non-EUI (IR58025A, IR58025B) and EUI (IR91-1591-3) parents to elucidate the inheritance of EUI trait and to tag the trait with DNA markers. In $F_{2-3}$ and test crosses, EUI exhibited a monogenic recessive inheritance. Bulk segregant analysis using RAPD markers identified an association of $OPAG01_{1000}$ with EUI, which was further confirmed by co-segregation and linkage analyses. The marker was linked with EUI at an average map distance of 3.6 cM, promising to be useful in MAS for developing CMS lines with EUI trait.**

AFTER the successful demonstration of the use of hybrids developed by making use of the wild abortive (WA) type of cytoplasmic male sterility (CMS) in China, more than 20 countries worldwide have started hybrid rice programmes. As a result of intensive efforts, 56 rice hybrids have been released worldwide. In India, 17 hybrids have been released for commercial production during the last decade[1]. In China, the annual area under hybrid rice is about 15.50 million hectares (m ha), 50% of the total rice area accounting for nearly 60% of the total rice production[2]. Currently, India is reported to have around 2,80,000 ha under hybrid rice annually, and it could be 3–4 m ha during the next decade[1].

Rice, being a self-pollinated crop, must involve use of an efficient and effective male sterility system to develop and produce $F_1$ hybrids. These may be CMS, thermosensitive genic male sterility (TGMS) or photosensitive genic male sterility (PGMS). Most of the indica/indica hybrids developed in India and elsewhere are utilizing CMS system having the WA cytoplasm. But incomplete panicle exsertion in almost all the WA-based CMS lines is one of the major impediments in obtaining higher seed yield, as 30–40% of the panicles are enclosed in the flag leaf and the enclosed spikelets are not available for cross-pollination, thus resulting in lower seed yield. Seed set can be increased by practices such as clipping the flag-leaves of the CMS lines, applying gibberellic acid ($GA_3$) to promote panicle exsertion, pulling a rope across the field to increase the outcrossing and selecting pollinator parents that are 10–20 cm taller than the sterile parent to increase pollen shedding on female panicles[3]. Among these practices, $GA_3$, an efficient and effective plant growth regulator, which stimulates cell elongation, has been routinely used to effect panicle exsertion. About 50–75 g $ha^{-1}$ of $GA_3$ spraying is recommended in the package developed for hybrid rice production in India[4]. However, it is too costly to use in India[5], where of the total cost of hybrid seed production, about 8–10% is being spent towards the use of $GA_3$. In addition to the increased cost, another problem that arises from application of $GA_3$ is reduced seed quality[6]. Therefore, plant breeders have long been looking for a genetic means to solve the panicle exsertion problem.

Rutger and Carnahan[7] found a recessive gene (*eui*) that can cause elongation of the uppermost internode, in japonica rice 76 : 4512. The finding has drawn worldwide attention and is recognized as the fourth genetic element in hybrid rice seed production. Genetic analysis of a spontaneous mutant for elongated uppermost internode (EUI) in the variety Ishikari showed that EUI was controlled by single recessive gene and it is allelic to the original EUI mutant[8,9]. In China, this gene has been introduced into CMS lines, which would cause better panicle exsertion. CMS plants with *eui* gene do not need $GA_3$ for promotion of panicle exsertion[10–12]. It was also transferred to indica restorer cultivar IR50 by backcrossing to improve pollination efficiency[13]. EUI is a recurring mutation in California cultivars and the three EUI mutants isolated independently from California cultivars were allelic with the original *eui* mutant[14].

Yang *et al.*[15] obtained two types of EUI mutants (XQZeB-1 and XQZeB-2) from $M_2$ population of Xieqing-

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zaoB (XQZB) treated with γ-rays. One mutant referred as *eui1* (t) was allelic to the original EUI mutant, whereas the other mutant *eui2* was nonallelic to the original *eui* and *eui1*, and was referred as *eui2* (t)[6,16]. Several B and R lines and hybrids were developed involving *eui1* and *eui2*, and both these genes significantly affected several height-related traits in addition to panicle exsertion. Further, many T(P)GMS lines and restorer lines possessing *eui* gene were obtained directly after irradiation, but their allelic relationships have not been reported. These new lines have solved the problem of unstable fertility of TGMS lines and overuse of $GA_3$ during seed production[16–18].

There are two loci with genes for EUI. One locus is mapped onto chromosome 5 through trisomic analysis by Librojo and Khush[19] and linked to a RFLP marker RG435 at a genetic distance[20] of 33.6 cM. It has three alleles [*Eui, eui* and *eui1* (t)]. The other locus has two alleles [*Eui2* and *eui2* (t)] and is located[16,21] in the middle of the long arm of chromosome 10 linked to RM258, RM269, RM271 and RM304 with genetic distances of 12.0, 12.9, 35.1 and 1.4 cM respectively. Thus, identification of molecular markers closely linked to *eui1* and *eui2* makes it possible to develop hybrid rice parental lines possessing EUI leading to higher outcrossing potential, which would reduce the need for application of $GA_3$. The study reported here is aimed at elucidating the inheritance of *eui* gene in IR91-1591-3 donor and identification of more closely linked markers to *eui* employing segregation analysis and bulked segregant analysis.

## Materials and methods

### *Plant material and populations*

The CMS line IR58025A and its maintainer IR58025B representing the non-EUI trait and IRRI line IR91-1591-3 as a source of EUI trait were obtained from the International Rice Research Institute (IRRI), Manila, Philippines (Figure 1). The $F_1$ of the crosses IR58025A/IR91-1591-3 and IR58025B/IR91-1591-3 grown during the dry season of 2000–01 were selfed to obtain $F_2$ segregating for the EUI trait. A test cross of IR58025A/IR91-1591-3//IR91-1591-3 was also attempted during the same season.

Two $F_2$ populations from $F_1$ plants of each of the above crosses and a test cross population, consisting of 473, 310 and 22 progenies respectively, were grown along with the parents and $F_1$ in the wet season of 2001 at the Maharajpet experimental farm of MAHYCO Research Foundation, Hyderabad, India. Three-week-old seedlings were transplanted one per hill at a row spacing of 30 cm and hill spacing of 25 cm. Fertilizer was applied at a rate of 100–80–80 kg (N-$P_2O_5$-$K_2O$) $ha^{-1}$. Water level was maintained at 5 cm throughout the crop growth. The $F_2$ plants phenotyped as EUI and non-EUI[16], were advanced to $F_3$ to determine the genotype of the $F_2$ individuals as homozygote (*Eui/Eui*; *eui/eui*) or heterozygote (*Eui/eui*) for EUI trait.

Exserted panicle length above the flag-leaf sheath after anthesis was measured in centimetres and panicle exsertion ratio (PER) was calculated as PER (%) = (Length of exserted panicle/Total length of panicle) × 100. Total length of panicle was measured in centimetres from base of the panicle to the tip of the panicle. Other phenotypic traits such as days to flowering, panicle length, plant height, number of productive tillers per plant and total number of tillers per plant were noted on $F_{2-3}$ families.

### *DNA extraction*

The genomic DNA was extracted from freshly harvested young leaves of individual $F_2$ plants of both the populations using the Dellaporta method[22] with minor modifications. The concentration of each sample was estimated by visual comparison on agarose gels.


**Figure 1.** Parental rice lines used and their panicle phenotype: IR58025A (non-EUI) (***a***), IR58025B (non-EUI) (***b***) and IR91-1591-3 (EUI) (***c***).

*Bulk segregant analysis*

DNA from 10 each of EUI and non-EUI $F_2$ plants in equal quantity formed the EUI and non-EUI bulks respectively. The EUI and non-EUI parents formed the references. A total of 202 random decamer DNA primers (Operon Technologies, USA) were used to screen the parental polymorphism in IR58025A, IR58025B and IR91-1591-3 for the markers.

*PCR analysis*

PCR amplification mix of 20 µl total volume contained 10X reaction buffer with 1.5 mM $MgCl_2$ (2.00 µl); 10.00 mM dNTPs (1.00 µl); 1 Unit Taq polymerase (DyNAzyme$^{TM}$ II, Finnzymes, Finland; 0.25 µl); 15 pmol of the random decamer primer (1.00 µl); 20 ng of template genomic DNA (1.00 µl) and sterile distilled water (14.75 µl). The amplification was carried out in PE9700 Thermocycler (Perkin Elmer, USA) for 45 cycles. The thermal profile was as follows: hot start at 95°C for 4 min + 45 cycles of denaturation at 95°C for 5 s, annealing at 36°C for 1 min and extension at 72°C for 2 min + final extension at 72°C for 7 min. Ten µl of completed amplification product was run on 1.2% agarose gel and stained with ethidium bromide (100 mg $l^{-1}$).

*Scoring*

Presence or absence of EUI-specific OPAG01-1000 bp band ($OPAG01_{1000}$) was scored as '+' or '–' respectively, in parents, bulk and $F_2$ individuals.

*Data analysis*

The *eui* allelic segregation pattern was studied by the fixed ratio chi-square test as outlined by Gomez and Gomez[23]. Simple correlation ($r$) of exserted length with six other traits was also calculated. At the phenotypic level, the inheritance of the RAPD marker was studied by segregation analysis employing chi-square test for goodness-of-fit. Linkage and per cent recombination were studied by testing independence of co-segregation[24] of EUI trait and RAPD marker.

## Results and discussion

*Inheritance of EUI trait*

The mean values of exserted panicle length, total panicle length and PER of parents, $F_1$, $F_2$ and $F_3$ generations are presented in Table 1. In both the crosses, viz. IR58025A/IR91-1591-3 and IR58025B/IR91-1591-3, the $F_1$ plants had non-EUI phenotype. However, the average panicle length in both the $F_1$s increased slightly because of per se heterosis or the heterozygous nature (*Eui*/*eui*) of $F_1$ plants for EUI trait (Table 1). Analysis of both $F_2$ populations showed 3 non-EUI : 1 EUI segregation (Table 2). Further confirmation of this inheritance pattern was obtained from the $F_3$ and the test cross data. All the $F_{2-3}$ families analysed for EUI and non-EUI phenotypes gave 113 non-EUI, 251 segregating and 109 EUI families in IR58025A/IR91-15913 and 72 non-EUI, 169 segregating and 69 EUI families in IR58025B/IR91-1591-3 cross. These data fit well with the expected 1 : 2 : 1 ratio of non-EUI homozygotes (*Eui*/*Eui*): heterozygotes (*Eui*/*eui*): EUI homozygotes (*eui*/*eui*). The test cross population fits well into the expected 1 non-EUI : 1 EUI ratio (Table 2). Thus, the results indicate that the EUI phenotype is recessive to non-EUI phenotype and the chi-square values suggest that EUI trait is regulated by single Mendelian locus, supporting earlier observations that the mutant EUI phenotypes were controlled by single recessive gene[7,9,16]. Mean values of the exserted length of panicles in both the $F_2$ populations were not significantly different by $t$ test, which indicates

**Table 1.** Mean values of panicle-trait phenotypes in parents, $F_1$, $BC_1$, $F_2$, and $F_3$ generations of crosses between EUI and non-EUI parents in rice

| Generation | No. of plants observed (phenotype) | Average panicle exsertion (cm) | Total panicle length (cm) | PER (%) |
|---|---|---|---|---|
| (P1) IR58025A | 5 (non-EUI) | –11.00 ± 0.69 | 23.90 ± 0.64 | –46.03 |
| (P2) IR58025B | 5 (non-EUI) | 0.80 ± 0.37 | 24.10 ± 0.73 | 3.32 |
| (P3) IR91-1591-3 | 5 (EUI) | 11.50 ± 0.55 | 29.08 ± 0.94 | 39.55 |
| $F_1$ (P1/P3) | 5 (non-EUI) | –6.78 ± 0.23 | 29.14 ± 0.42 | –23.27 |
| $F_1$ (P2/P3) | 5 (non-EUI) | 1.12 ± 0.29 | 24.52 ± 0.71 | 4.57 |
| $BC_1$ (P1/P3//P3) | 12 (EUI) | 10.46 ± 0.58 | – | – |
| | 10 (non-EUI) | – | – | – |
| $F_2$ (P1/P3) | 109 (EUI) | 8.09 ± 0.24 | – | – |
| | 364 (non-EUI) | – | – | – |
| $F_2$ (P2/P3) | 69 (EUI) | 8.65 ± 0.29 | – | – |
| | 241(non-EUI) | – | – | – |
| $F_{2-3}$ (P1/P3) | 464 (segregating) | –0.68 ± 0.21 | 24.07 ± 0.11 | –2.83 |
| $F_{2-3}$ (P2/P3) | 307 (segregating) | 1.63 ± 0.25 | 24.14 ± 0.11 | 6.75 |

**Table 2.** Segregation of EUI genotypes based on $F_2$, $F_{2-3}$ and test cross data of crosses between EUI and non-EUI parents in rice

| Generation | No. of plants/ family observed | EUI genotype | | | Expected ratio | $\chi^2$ | $P$ |
|---|---|---|---|---|---|---|---|
| | | *Eui/Eui* | *Eui/eui* | *eui/eui* | | | |
| $F_2$ (P1/P2)† | 473 | 364 | – | 109 | 3 : 1 | 0.96 | 0.50 ~ 0.25 |
| $F_2$ (P2/P3) | 310 | 241 | – | 69 | 3 : 1 | 1.24 | 0.50 ~ 0.25 |
| $F_{2-3}$ (P1/P2) | 473 | 113 | 251 | 109 | 1 : 2 : 1 | 1.85 | 0.50 ~ 0.25 |
| $F_{2-3}$ (P2/P3) | 310 | 72 | 169 | 69 | 1 : 2 : 1 | 1.96 | 0.50 ~ 0.25 |
| $BC_1$ (P1/P3//P3) | 22 | – | 10 | 12 | 1 : 1 | 1.80 | 0.75 ~ 0.50 |

†Notations as in Table 1.

**Table 3.** Correlation ($r$) of exserted panicle length with other phenotypic traits in crosses between EUI and non-EUI parents in rice

| Trait | Cross (P1/P3)† | | | Cross (P2/P3)† | | |
|---|---|---|---|---|---|---|
| | *N* | Mean ± SE | *r* | *N* | Mean ± SE | *r* |
| Days to first flowering | 427 | 118.16 ± 0.30 | –0.02 | 301 | 120.46 ± 0.37 | –0.09 |
| Days to 50% flowering | 427 | 122.37 ± 0.28 | –0.03 | 301 | 124.08 ± 0.35 | –0.10 |
| Panicle length (cm) | 427 | 24.15 ± 0.12 | 0.40* | 301 | 24.17 ± 0.11 | 0.50* |
| Plant height (cm) | 427 | 91.60 ± 0.61 | 0.65* | 301 | 91.74 ± 0.65 | 0.71* |
| Productive tillers | 427 | 25.22 ± 0.31 | 0.08 | 301 | 20.91 ± 0.29 | 0.08 |
| Total tillers | 427 | 29.52 ± 0.33 | 0.10* | 301 | 22.69 ± 0.31 | 0.13* |

*Significant at 0.05 level of probability.
†Notations as in Table 1.

that EUI expression is not affected by the sterile cytoplasm (Table 1). Thus, this gene can be utilized for development of CMS and maintainer lines with EUI trait for better panicle exsertion and higher outcrossing.

### *Influence of eui on other traits*

Significant positive correlation was observed between exserted length of panicle and the total panicle length, plant height and total tillers per plant, in both the populations (Table 3). Further, when the means of all the six traits of non-EUI homozygotes (*Eui/Eui*), heterozygotes (*Eui/eui*) and EUI homozygotes (*eui/eui*) were compared using *t* test, the mean values of the EUI homozygotes (*eui/eui*) for the exserted panicle length, total panicle length and plant height in both the populations and days to 50% flowering in IR58025B/IR91-1591-3 were significantly greater than the segregating (*Eui/eui*) and non-EUI homozygotes (*Eui/Eui*). However, days to flowering in homozygous EUI lines was later compared with non-EUI homozygotes and segregating lines in both the populations. This also indicated the dosage effect of the *eui* allele on the traits. It can be recalled that these traits showed significantly positive correlation with the exserted panicle length (Table 3).

### *Identification of RAPD marker tag*

Among the 202 random decamer primers used, 81 showed polymorphism among the parents. When the two bulked DNA samples along with parents were screened with these 81 primers, two primers shared consistent polymorphism between the bulk. Further, one primer OPAG01 (5′CTACGCCTTC3′) produced a distinct polymorphic band (1000 bp) between the EUI, non-EUI parents and their respective bulk in both the populations (Figure 2). When $F_2$ individuals of both the populations, $F_2$ (IR58025A/IR91-1591-3), $n = 153$ and $F_2$ (IR58025B/IR91-1591-3), $n = 152$ were scored for the marker $OPAG01_{1000}$, the marker showed 3 present : 1 absent ratio, with the nonsignificant chi-square values of 0.11 and 0.00 respectively, indicating monogenic Mendelian inheritance of the marker (Figure 3).

### *Co-segregation and linkage of RAPD marker with EUI*

The chi-square values of data on joint segregation of the RAPD marker $OPAG01_{1000}$ with EUI phenotype showed significance in both the crosses, indicating co-segregation of the EUI trait with the marker. The linkage of the

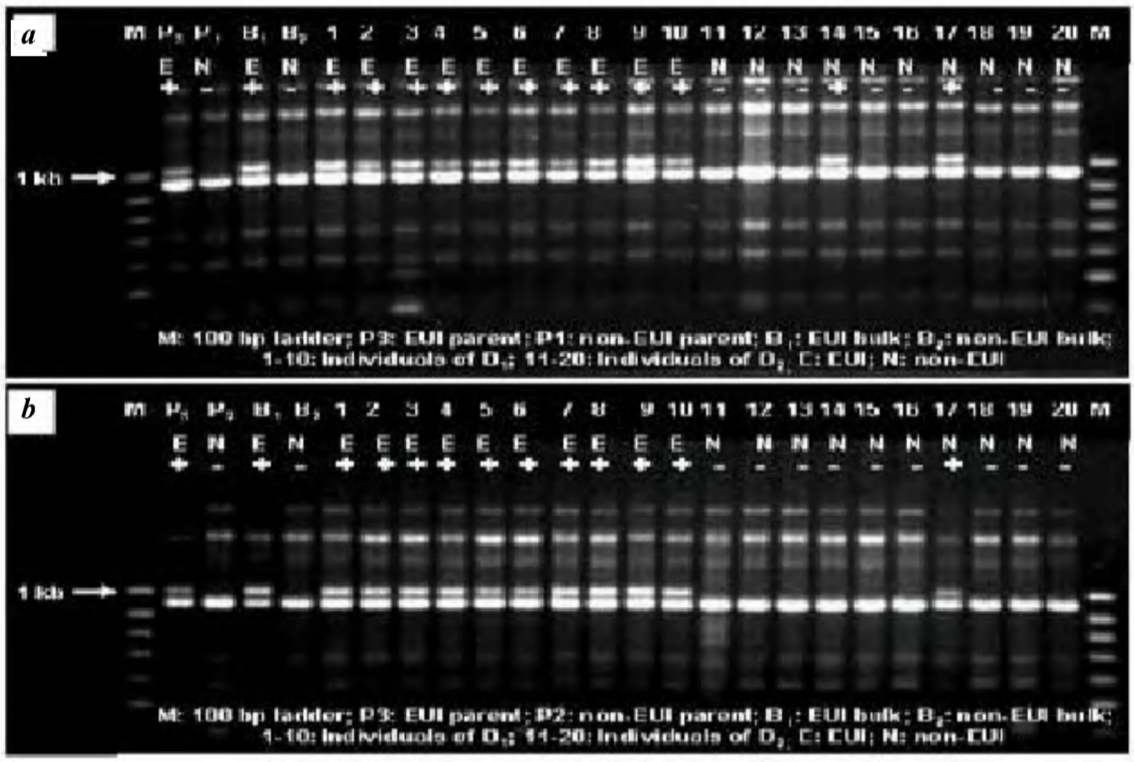


**Figure 2.** Polymorphism of $OPAG01_{1000}$ in parents (EUI and non-EUI); bulk (EUI and non-EUI) and individuals of the bulk in rice. ***a***, $F_2$ of IR58025A/IR91-1591-3; ***b***, $F_2$ of IR58025B/IR91-1591-3.

**Table 4.** Co-segregation of EUI phenotype and $OPAG01_{1000}$ marker in $F_{2-3}$ of crosses between EUI and non-EUI parents in rice

| Cross | Total | Marker $OPAG01_{1000}$ | EUI phenotype | | | $\chi^2$ | Recombination frequency (%) |
|---|---|---|---|---|---|---|---|
| | | | Non-EUI | Segregating | EUI | | |
| $F_3$ (P1/P3)† | 153 | Present | 04 | 74 | 35 | 14.35* | (6/153) × 100 = 3.92 |
| | | Absent | 38 | 02 | 0 | | |
| | | Total | 42 | 76 | 35 | | |
| $F_3$ (P2/P3) | 152 | Present | 03 | 73 | 38 | 15.15* | (5/152) × 100 = 3.29 |
| | | Absent | 36 | 02 | 0 | | |
| | | Total | 39 | 75 | 38 | | |

*Significant at 0.01 level of probability.
†Notations as in Table 1.

marker with the recessive *eui* allele is in repulsion phase, with a map distance of 3.92 and 3.29 cM in the $F_2$ (IR58025A/IR91-1591-3) and $F_2$ (IR58025B/IR91-1591-3) populations respectively (Table 4). This marker was validated on 34 CMS lines having more than –6 cm exserted panicle length. The 1000 bp band was detected in three of the CMS lines and their respective maintainer counterparts. However, in 31 CMS lines and their respective maintainer lines the band was absent (data not shown), as all of them were having WA cytoplasm.

Attempts are under way to convert this RAPD marker into a sequence tagged amplified region-marker, which would be useful in marker-assisted selection targetted at improving seed recovery in hybrid rice seed production programmes.

To identify the chromosomal location of the *eui* gene in the present study, chromosome 10 and chromosome 5-specific SSR primers were used. No markers on the chromosome 10 co-segregated with the trait. However, the markers specific to chromosome 5 co-segregated with the trait (data not shown), indicating that the *eui* gene in the present study is located on chromosome 5. Librojo and Khush[19] also reported the *eui* locus to be on chromosome 5 through trisomic analysis and a study[20] employing

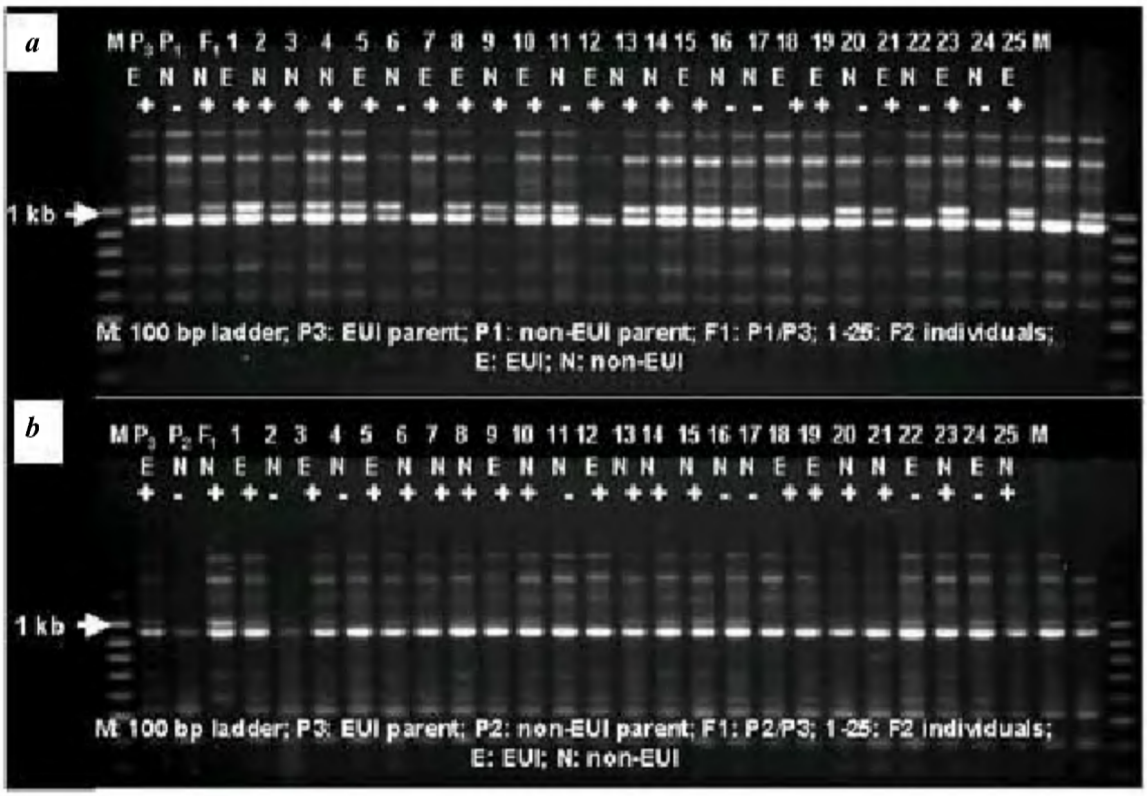


**Figure 3.** Co-segregation of $OPAG01_{1000}$ with EUI phenotype in $F_2$ of crosses between EUI and non-EUI parents in rice. ***a***, $F_2$ of IR58025A/IR91-1591-3; ***b***, $F_2$ of IR58025B/IR91-1591-3.

RFLP marker RG435 indicated the same. Hence, the RAPD marker $OPAG01_{1000}$ is the first PCR based marker for *eui* gene on chromosome 5 which can be useful in marker-aided selection.

## Summary

Incomplete panicle exsertion in the WA-based rice CMS lines is a major impediment in obtaining higher hybrid seed yields. Introduction of EUI trait controlled by recessive gene *eui* results in better panicle exsertion in the CMS lines. In this study, we report inheritance of EUI trait and RAPD marker linked to the *eui* gene. Chi-square data of $F_2$, $F_{2-3}$ and test crosses suggest that the EUI phenotype is recessive to non-EUI and is regulated by single Mendelian locus. Bulk segregant analysis and $F_2$-individual analysis show that the RAPD marker $OPAG01_{1000}$ is linked to *eui* at map distances of 3.92 and 3.29 cM in two different populations and is located on chromosome 5. The RAPD marker is being converted to STS-marker that would be handy for transfer of *eui* into several promising rice CMS lines.

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ACKNOWLEDGEMENTS. We thank Dr Gurdev S. Khush, IRRI, Manila, Philippines for providing seeds of IR91-1591-3; Dr Usha B. Zehr, Director and Dr George Thottappilly, Executive Director, MAHYCO Research Foundation, Hyderabad, for support and encouragement.

Received 27 January 2004; revised accepted 3 April 2004

# A study of rainfall along the west coast of India in relation to low level jet and air–sea interactions over the Arabian Sea

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**Indian summer monsoon has a large inter-annual as well as intra-seasonal variability over temporal and spatial scales. Onset dates, monsoon activity within a monsoon season and quantity of monsoon rainfall are also found to vary from year to year. One important synoptic feature associated with the onset of monsoon is the existence of a strong cross equatorial low level jet (LLJ), with its core around 850 hPa over the Indian Ocean and South Asia. This LLJ generally supports the large-scale moisture and momentum transport from ocean to atmosphere and the consequent rainfall over the Indian mainland. In the present study, buoy data at a stationary position in the Arabian Sea (15.5°N, 61.5°E) have been used to understand the air–sea interface processes before, during and after the onset of monsoon 1995.**

A remarkable feature of the summer monsoon over the Indian Ocean (IO) is the gradual formation of a low-level jet (LLJ)[1] over the western IO. Bunker[2] first reported the presence of LLJ off Somalia during the International Indian Ocean Expedition (IIOE, during 1962–66) in a preliminary analysis. Joseph and Raman[3] have further found the existence of similar LLJs with a core speed of 20–30 m/s near 1.5 km asl over peninsular India, on several days during July. Later studies by Findlater[1,4] have explained the importance of LLJ in the monsoonal activity over the Indian subcontinent. Findlater[4] and Krishnamurti[5] have studied the mean monthly air flow at low-levels (1.0–1.5 km) over western IO and found that the Kenyan highlands appear to be a western boundary for this major low-level air current, which is known to have a maximum mean wind speed (19 m/s) near 1.5 km level. In February, a clockwise gyre of air can be seen 10° south of the equator. Its month-by-month northward progress[5] appears to continue until June. Thereafter, its position is relatively steady in the belt of 10–20°N until September. After September, with the cessation of the SW monsoon, the LLJ proceeds back southwestwards to the southern IO. The major axis of the jet passes through the points

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