World Academy of Science, Engineering and Technology
International Journal of Agricultural and Biosystems Engineering
Vol:11, No:11, 2017

Effects of Lateness Gene on Yield and Related Traits in *Indica* Rice

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Open Science Index, Agricultural and Biosystems Engineering Vol:11, No:11, 2017 publications.waset.org/10008213/pdf

***Abstract*—**Various genes which control or affect heading time have been found in rice. Out of them, *Se1* and *E1* loci play important roles in determining heading time by controlling photosensitivity. An isogenic-line pair of late and early lines were developed from progenies of the F_1 from Suweon 258 × 36U. A lateness gene tentatively designated as "*Ex*" was found to control the difference in heading time between the early and late lines mentioned above. The present study was conducted to examine the effect of *Ex* on yield and related traits. *Indica*-type variety Suweon 258 was crossed with 36U, which is an *Ur1* (Undulate rachis-1) isogenic line of IR36. In the F_2 population, comparatively early-heading, late-heading and intermediate-heading plants were segregated. Segregation similar to that by the three types of heading was observed in the F_3 and later generations. A late-heading plant and an early-heading plant were selected in the F_8 population from an intermediate-heading F_7 plant, for developing L and E of the isogenic-line pair, respectively. Experiments for L and E were conducted by randomized block design with three replications. Transplanting was conducted on May 3 at a planting distance of 30 cm × 15 cm with two seedlings per hill to an experimental field of the Faculty of Agriculture, Kochi University. Chemical fertilizers containing N, P_2O_5 and K_2O were applied at the nitrogen levels of 4 g/m^2, 9 g/m^2 and 18 g/m^2 in total being denoted by "N4", "N9" and "N18", respectively. Yield, yield components and other traits were measured. *Ex* delayed 80%-heading by 17 or 18 days in L as compared with E. In total brown rice yield (g/m^2), L was 635, 606 and 590, and E was 577, 548 and 501, respectively, at N18, N9 and N4, indicating that *Ex* increased this trait by 10% to 18%. *Ex* increased yield-1.5 mm sieve (g/m^2) b 9% to 15% at the three fertilizer levels. *Ex* increased the spikelet number per panicle by 16% to 22%. As a result, the spikelet number per m^2 was increased by 11% to 18% at the three fertilizer levels. *Ex* decreased 1000-grain weight (g) by 2 to 4%. L was not significantly different from E in ripened-grain percentage, fertilized-spikelet percentage and percentage of ripened grains to fertilized spikelets. Hence, it is inferred that *Ex* increased yield by increasing spikelet number per panicle. Hence, *Ex* could be utilized to develop high yielding varieties for warmer districts.

***Keywords*—**Heading time, lateness gene, photosensitivity, rice, yield, yield components.

I. Introduction

GROWTH duration is a major factor affecting regional adaptability and yield in rice. Longer growing duration allows rice plants to have sufficient vegetative growth to obtain higher biomass [7], [16]. In rice, growth duration is primarily determined by heading time. The duration from sowing to heading consists of the vegetative phase and panicle development phase. The vegetative phase is defined by the duration from sowing to the initiation of panicle development. The vegetative phase is further divided into basic vegetative phase and photoperiod sensitive phase [2]. The basic vegetative phase can be estimated by the minimum number of days from sowing to appearance of panicle primordium under the condition of short day length and optimum temperature. Since varietal difference in duration of panicle development is rather small (about 30 days); length of the vegetative phase can be approximated by number of days to heading.

In rice, more than 40 genes controlling heading time have been reported. Most of them control photoperiod sensitivity [1], [20], [13], [12]. The major photoperiod sensitive loci viz. *Se1* and *E1*, located on chromosome 6 and chromosome 7, respectively, play important roles in determining heading time [18], [19], [21], [12]. The *Se1* locus involves at least three alleles, *Se1-u*, *Se1-n* and *Sel-e*: the first two are incompletely dominant alleles controlling photosensitivity, while *Se1-e* is a recessive allele with non-photosensitivity [18]. The photoperiod insensitive allele *Se1-e* is widely distributed among the rice varieties grown in Hokkaido prefecture and Tohoku district of Japan, while the photoperiod-sensitive allele *Se1-n* is harbored in middle and late heading varieties grown in warmer regions of Japan [11], [20]. *Se1-u* allele has higher photoperiod-sensitivity than *Se1-n*, which is harbored in an *indica* variety "Morak Sepilai" [21], [19].

A photoperiod sensitive allele *Se1-u* at the *Se1*locus delays heading by at least 20 days as compared with its photoperiod insensitive allele *Se1-e*. Similarly, *E1-k* allele at the *E1* locus delays heading by about two weeks as compared with its non-photoperiod sensitive allele *e1* [5].

Murai developed an isogenic-line pair of late and early lines, denoted by "L" and "E", from descendants of the F_1 from Suweon 258 × 36U. L had heading time 15 days to 21 days later than E [3], [14]. The difference in heading time between the two lines is controlled by a lateness gene tentatively designated as "*Ex*". *Ex* is incompletely dominant gene controlling photosensitivity. Nevertheless, an allelism test of *Ex* with either *Se1-u* or *E1-k* has not been completed, and the locus of the *Ex* gene is still unknown.

Ghd7 allele at the *E1* locus delayed heading and has a pleiotropic effect of increasing spikelet number per panicle of main culm [4], [17]. However, any yield tests on field level regarding the effect of a lateness gene at *E1* and other loci has not been performed, as far as we know. A field experiment was

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conducted for L and E in the present study. Besides yield, yield components and other traits, viz. spikelet number per panicle, panicle number per m^2, percentage of ripened grains, 1000 grain weight and sink size etc. were measured. On the basis of the data obtained, effects of *Ex* on yielding ability was examined.

II. Materials and Methods

A. Isogenic Line Pair

The isogenic line pair of L and E was used in this study. This isogenic line pair was developed from descendents of the F_1 Suweon 258 (hereafter "S") × 36U. The maternal parent Suweon 258 is an *indica*-type low-height variety which had been developed by the cooperation between Korea and International Rice Research Institute [6]. The paternal parent 36U is the isogenic line of IR 36 carrying *Ur1* (Undulated rachis-1) gene. IR 36 is a typical improved *indica* variety developed at International Rice Research Institute [8]. IR36 is a semi-dwarf variety carrying *sd1-d* which had been broadly grown in Southeast Asia [14].The heading-time characteristic of 36U is almost same as that of IR36.

IR36 is an early-maturing variety in subtropics [8]; nevertheless, it and Suweon 258 can be regarded as middle heading in Kochi prefecture [15], [3]. Suweon 258 was crossed with 36U. Comparatively early-heading, late heading and intermediate-heading plants were segregated in the F_2 population from this cross. In F_3 and later generations, comparatively early-heading, late-heading and intermediate-heading plants appeared in a progeny population from an intermediate-heading plant of the previous generation. In the F_8 population from an intermediate-heading F_7 plant, a late-heading plant and an early-heading plant were selected for developing L and E of the isogenic-line pair, respectively. From the results of genetic analysis by using L, E, Suweon 258, 36U and descendents of mutual crosses among them, Dahal et al. [3] indicated that *Ex* is an incompletely dominant allele controlling photosensitivity over its recessive allele *ex*, and the former and latter alleles are harbored in L and E, respectively. 36U has *ex/ex* genotype. S harbors not only *Ex* but also an inhibitor gene for it.

B. Cultivation and Fertilization in the Experimental Field

Seeds were soaked with hot water of 62°C to 55°C for 15 minutes for sterilization. The seeds were sown on plastic trays filled with granulated soil containing N, P_2O_5 and K_2O and being adjusted at pH 4.5, on 21st April, 2014. Seedlings were grown at 25°C for first five days and 21°C for the later seven days in a natural-light phytotron. Seedlings were transplanted at a spacing of 30 cm × 15 cm (22.2 hills/m^2) with two seedlings per hill to an experimental field of the Faculty of Agriculture (present name: Faculty of Agriculture and Marine Science), Kochi University (Nankoku 33° 35′N) on May 3. Chemical fertilizers containing N, P_2O_5 and K_2O were applied by both basal and top dressings at the nitrogen levels of 4 g/m^2, 9 g/m^2 and 18 g/m^2 in total, which were denoted by "N4", "N9" and "N18", respectively.

TABLE I
Chemical Fertilizers Applied on Experimental Field

Fertilizer level	Chemical fertilizers applied	Basal or top-dressing	N (g/m^2)	P_2O_5 (g/m^2)	K_2O (g/m^2)
N18	Ordinary chemical fertilizer	Basal	1.3	1.3	1.3
	ECOLONG® 424-100 type	Additional basal	4.7	4.7	4.7
	ECOLONG® 413-180 type	Top-dressing	12.0	9.4	11.1
	Total		**18.0**	**15.4**	**17.1**
N9	Ordinary chemical fertilizer	Basal	1.3	1.3	1.3
	ECOLONG® 424-100 type	Additional basal	1.7	1.7	1.7
	ECOLONG® 413-180 type	Top-dressing	6.0	4.7	5.6
	Total		**9.0**	**7.7**	**8.6**
N4	Ordinary chemical fertilizer	Basal	1.3	1.3	1.3
	ECOLONG® 424-100 type	Additional basal	0.0	0.0	0.0
	ECOLONG® 413-180 type	Top-dressing	2.7	2.1	2.5
	Total		**4.0**	**3.4**	**3.8**

ECOLONG® 424-100 type and ECOLONG® 413-180 type: see text.

Just before ploughing, an ordinary chemical fertilizer containing N, P_2O_5 and K_2O was applied as basal dressing at the rate of 1.3 g/m^2 for each of the three nutrient elements on April 10 (Table I). Additional basal application was performed at the rate of 4.7g/m^2 and 1.7 g/m^2 of each of N, P_2O_5 and K_2O for N18 and N9, respectively, with a slow release and coated fertilizer ECOLONG® 424-100 type (7% of each nutrient element is readily available) manufactured by Chisso-Asahi Fertilizer Co., Ltd. four days after transplanting. Hence, total basal application was 6 g/m^2, 3 g/m^2 and 1.3 g/m^2 for each of N, P_2O_5 and K_2O in N18, N9 and N4, respectively (Table I). Moreover, top-dressing was performed 63 days or 64 days before 80%-heading for L and E with another slow release and coated fertilizer ECOLONG® 413-180 type (3% of each nutrient element is readily available) containing N, P_2O_5 and K_2O at the rate of 14%, 11% and 13%, respectively, manufactured by the company mentioned above. Accordingly, 12.0 g/m^2, 6.0 g/m^2 and 2.7 g/m^2 of nitrogen were top-dressed for N18, N9 and N4, respectively. The total amounts of N, P_2O_5 and K_2O (basal application + top-dressing) for the three fertilizer levels were summarized in Table I. Each plot comprised 29 hills × 5 rows (145 hills). Experiment for L and E in the three fertilizer levels was conducted by randomized block design with three replications.

C. Measurements of Yield, Yield Components and Related Traits

All panicles of 25 hills were sampled from the 3rd to 27th hill of the central row of each plot at maturity, and dried in drying ovens with a temperature ranging from 30°C to 45°C for 20 hours to 30 hours until average rough rice moisture lowered to 11% or less. The panicle weight of each hill was checked after cutting at 1.5 mm below panicle bases.

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Fig. 1 Classification of brown rice by thickness in L

TABLE II. A
CLASSIFICATION OF GRAINS BY THICKNESS IN EACH FERTILIZER LEVEL IN EACH OFL AND E. PERCENTAGES ON THE BASIS OF GRAIN NUMBER

Grain thickness	Fertilizer level	Allele				LSD (0.05)
		Ex		*ex*		
		L		E		
>1.7mm	N18	66.6	b	70.6	ab	4.9
	N9	70.6	ab	73.3	a	
	N4	69.6	ab	72.0	a	
1.5-1.7mm	N18	11.6	a	9.4	a	3.4
	N9	11.0	a	9.0	a	
	N4	10.3	a	10.0	a	
<1.5mm	N18	21.7	a	20.0	a	4.4
	N9	18.4	a	17.7	a	
	N4	20.1	a	18.0	a	

TABLE II. B
CLASSIFICATION OF GRAINS BY THICKNESS IN EACH FERTILIZER LEVEL IN EACH OFL AND E. PERCENTAGES ON THE BASIS OF GRAIN WEIGHT

Grain thickness	Fertilizer level	Allele				LSD (0.05)
		Ex		*ex*		
		L		E		
>1.7mm	N18	83.0	a	86.5	a	4.9
	N9	84.6	a	87.7	a	
	N4	83.0	a	85.8	a	
1.5-1.7mm	N18	11.1	a	8.6	a	3.5
	N9	10.2	a	8.0	a	
	N4	9.5	a	9.1	a	
<1.5mm	N18	6.0	a	4.9	a	3.3
	N9	5.2	a	4.2	a	
	N4	7.5	a	5.1	a	

Values followed by the same letter within each rank by grain thickness are not significantly different at the 0.05 level, determined by LSDs in the table. Analysis of variance was conducted for percentage data of all combinations of the fertilizer levels and lines in each rank by grain thickness (%).

Out of nine hills randomly selected from 25 hills of each plot, five hills having intermediate panicle weight were selected. The panicles of the five hills were threshed, and all spikelets in each hill were counted. Each spikelet was dehulled and examined for endosperm development as described by Murai [9]: a spikelet containing any developed endosperm containing starch was regarded as fertilized in the present study. The number of fertilized spikelets was counted in each hill. Grains after hulling (hereafter "grains") were sieved by both 1.7 mm and 1.5 mm sieves to separate grains into three ranks by thickness: above 1.7 mm, from 1.5 mm to 1.7 mm, and below 1.5 mm. Grains in each rank were separately counted and weighed in each of the five hills. The number of grains below 1.5 mm was estimated by subtracting the number of grains above 1.5 mm from the fertilized spikelets in each hill. The percentage of grain weight of each of the three ranks to panicle weight was calculated in the five selected hills of each plot; then, the grain weight of each rank of 25 hills of each plot was estimated from these three percentages. The moisture content (%) of grains above 1.7 mm in each plot was measured, and the grain weight at 15% moisture was estimated. For *japonica* rice in Japan, brown rice just after hulling is separated with 1.7 mm-sieve or a wider one to select brown-rice grains with sufficiently high quality for milling from grains with lower quality. However, both in L and E, grains with thickness from 1.5 mm to 1.7 mm can be regarded as possessing quality sufficient for milling (Fig. 1). Accordingly, we included the grains from 1.5 mm to 1.7 mm thickness into ripened grains. The number of grains from 1.5 mm to 1.7 mm thickness accounted for 10.3% to 11.6% and 9.0% to 10.0% of all fertilized grains in the three fertilizer levels in L and E, respectively (Table II (a)). Grain weight from 1.5 mm to 1.7 mm thickness accounted for 9.5% to 11.1% and 8.0% to 9.1% of all fertilized-grain weight in the three fertilizers levels in L and E, respectively (Table II (b)). The total grain weight above 1.5 mm thickness was denoted by "yield-1.5mm sieve". Furthermore, "total brown rice yield" was the brown rice weight of all fertilized spikelets.

TABLE III
DATES OF HEADING AND MATURITY IN L AND E

Traits	Fertilizer level	Allele		Difference
		Ex	*ex*	
		L	E	
80%-heading	N18	24-Aug	6-Aug	
	N9	24-Aug	5-Aug	
	N4	24-Aug	6-Aug	
Number of days to 80%-heading	N18	125	107	18
	N9	125	106	19
	N4	125	107	18
Maturity	N18	4-Oct	11-Sep	
	N9	4-Oct	10-Sep	
	N4	1-Oct	9-Sep	

Among the four yield components, ripened-grain percentage was the ratio (%) of the number of ripened grains to the total number of spikelets. Moreover, the percentage of ripened grains to the fertilized spikelets, without unfertilized spikelets, was calculated. This trait and fertilized-spikelet percentage (fertilized spikelets ÷ all spikelets, %) enable to examine whether the failure of spikelet fertilization or insufficient grain-filling lowered the ripened-grain percentage. The mean spikelet number per hill of the 25 hills in each plot was estimated from that of the five hills and the ratio of the mean panicle weight of the 25 hills to that of the five hills. Both, "sink size-1" (single grain weight × spikelet number per m^2) and "sink size- 2" (single grain weight × fertilized-spikelet number per m^2) were estimated. Sink size- 2 provides the more exact estimate of the sink capacity of a line than the sink size-1 [9].

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III. Results

A. Number of Days to Heading

As shown in Table III, 80%-heading was on 24th August at all fertilizers levels in L, while that of E was on 5th August at N9 and on 6th August at N18 and N4. The number of days to 80%-heading was 125 days in L and 106 days or 107 days in E. Hence, the 80%-heading of L was 18 or 19 days later than E. Number of days to 80%-heading from top-dressing date was 63 days , and 63 days or 64 days at all fertilizer levels in L and E, respectively. Number of days from 80%-heading to maturity was from 38 days to 41 days in L and 34 days to 36 days in E.

TABLE IV
ANALYSIS OF VARIANCE FOR YIELD AND ITS COMPONENTS IN THREE FERTILIZER LEVELS IN L AND E

Traits	Source of variation				
	Lateness gene (A)		Fertilizer level (B)		Interaction (A×B)
Total brown rice yield (g/m^2)	26.23	**	6.72	*	<1
Yield-1.5mm sieve (g/m^2)	20.00	**	8.50	**	<1
Spikelets/panicle	176.12	**	<1		1.17
Panicles/m^2	4.91		18.47	**	<1
1000 kernel weight (g)	13.67	**	1.11		<1

Degrees of freedom for lateness gene, fertilizer level and the interaction are 1, 2 and 2, respectively. Degrees of freedom for replication and error are 2 and 10, although these items are abridged in the table.

**, **Significant at 0.05 and 0.01 levels, respectively.*

B. Yield and Yield Components

Table IV shows the results of analysis of variance for yield and yield components except percentage of ripened grains in the three fertilizer levels in L and E. Effects of the lateness gene and fertilizer level were statistically significant in total brown rice yield and yield-1.5 mm sieve, but the interactive effect between them was not significant. Regarding spikelet number per panicle and 1000-kernel weight, the effect of *Ex* was significant, but the effects of fertilizer level and the interaction were not significant. In panicle number per m^2, the effect of fertilizer level was significant but effects of lateness gene and the interaction were not significant.

Total brown rice yield (g/m^2) including all grains with thickness above and below 1.5mm, L was 635, 606 and 590, and E was 577, 548 and 501, respectively, at N18, N9 and N4. Hence, *E x* increased this trait by 10% to 18%. Regarding yield-1.5mm sieve (g/m^2), L was 597, 575 and 545 at N18, N9 and N4, respectively, which correspond 109%, 110% and 115% to those of E. Regarding fertilizer response from N4 to N18, total brown rice yield was increased by 45 g/m^2 and 76 g/m^2, respectively, in L and E, and yield-1.5 mm sieve was increased by 52 g/m^2 and 72 g/m^2 in the former and later, even though the effect of lateness gene × fertilizer interaction was not significant. Spikelet number per panicle was 129.0 to 129.9 in L and 106.2 to 111.2 in E, showing that *Ex* increased this trait by 16% to 22% in the three fertilizer levels. *Ex* decreased 1000-kernel weight by 2% to 4% in the three fertilizer levels. Panicle number per m^2 was not significantly different between L and E at every fertilizer level. From N4 to N18, this trait was increased by 43 and 38, respectively, in L and E.

In L and E, the positive fertilizer response in total brown rice yield as well as in yield-1.5 mm sieve is considered to be caused by that in panicle number per m^2, because significant fertilizer response was not noticed in spikelet number per panicle.

TABLE V
YIELD AND ITS COMPONENTSAT THREE FERTILIZER LEVELS IN L AND E

Traits	Fertilizer Level	Allele						LSD (0.05)
		Ex				*ex*		
		L				E		
Total brown rice yield (g/m^2)	N18	635	a	(110)	1)	577	bc	52
	N9	606	ab	(111)		548	cd	
	N4	590	abc	(118)		501	d	
Yield -1.5mm sieve (g/m^2)	N18	597	a	(109)		548	bc	48
	N9	575	ab	(110)		525	c	
	N4	545	bc	(115)		476	d	
Spikelets/panicle	N18	129.2	a	(116)		111.2	b	6
	N9	129.0	a	(118)		109.2	b	
	N4	129.9	a	(122)		106.2	b	
1000 kernel weight (g)	N18	20.6	bc	(96)		21.5	a	0.7
	N9	20.6	bc	(97)		21.3	ab	
	N4	20.5	c	(98)		21.0	abc	
Panicles/m^2	N18	338	a	(98)		344	a	21
	N9	308	bc	(94)		327	ab	
	N4	295	c	(97)		306	bc	

1) Percentage of L to E.

Values followed by the same letter within each trait are not significantly different at the 0.05 level, determined by LSDs in the table.

TABLE VI
ANALYSIS OF VARIANCE FOR RIPENED-GRAIN PERCENTAGE AND OTHER TRAITS IN THREE FERTILIZER LEVELS IN L AND E

Traits	Source of variation				
	Lateness gene (A)		Fertilizer level (B)		Interaction (A×B)
Ripened-grain percentage	<1		3.76		<1
Fertilized-spikelet percentage	5.90	*	2.72		<1
Percentage of ripened grains to fertilized spikelets	1.73		2.02		<1
Spikelets/m^2	37.19	**	14.81	**	<1
Sink size-1[1] (g/m^2)	15.92	**	13.85	**	<1
Sink size-2[2] (g/m^2)	32.75	**	14.75	**	<1
Culm length（cm）	128.76	**	9.93	**	<1
Panicle length (cm)	20.57	**	9.19	**	1.36

Degrees of freedom for lateness gene, fertilizer level and interaction are 1, 2 and 2, respectively. Degrees of freedom for replication and error are 2 and 10, although these items are abridged in the table.

*, **Significant at 0.05 and 0.01 levels, respectively.

1) Single grain weight at 1.5mm sieve ×spikelets/m2.

2) Single grain weight at 1.5mm sieve × fertilized spikelets/m2.

C. Ripened Grain Percentage and Other Traits

As shown in Table VII, statistically significant difference between L and E was not noticed for ripened-grain percentage, fertilized-spikelet percentage and percentage of ripened grains to fertilized spikelets at each of the fertilizer level; even though the effect of the lateness gene was significant at the 0.05 level in the second trait (Table VI). Effects of fertilizer and the interaction were not significant in the three traits mentioned above (Table VI).

Regarding spikelet number per m^2, sink size-1, sink size-2, culm length and panicle length; both lateness gene and fertilizer level were significantly effective but the interaction between them was not significant. Spikelet number per m^2 in L was 38379, 39683 and 43688 at N4, N9 and N18 which corresponds to 111%, 114% and 118% of those in E. Regarding fertilizer response from N4 to N18, this trait was increased by 5309 and 5752, respectively, in L and E. *Ex* significantly increased sink size-1 (g/m^2) and sink size- 2 (g/m^2) by 7% to 15% and 10% to 17%, respectively, in L and E, in the three fertilizer levels. From N4 to N18, sink size-1 and sink size-2 was increased by 114 g/m^2in L and 141 g/m^2in E, and 82 g/m^2 in L and 106 g/m^2 in E, respectively. *Ex* increased culm length and panicle length by 6% or 7% and 4% or 8%, respectively, in the three fertilizer levels. Increases from N4 to N18 in culm length and panicle length were 2.2 cm and 1.9 cm, and 1.8 cm and 0.9 cm, respectively, in L and E (Table VII).

TABLE VII
RIPENED-GRAIN PERCENTAGE AND OTHER TRAITS AT THREE FERTILLIZER LEVELS IN L AND E

Traits	Fertilizer Level	Allele						LSD (0.05)
		Ex				*ex*		
		L				E		
Ripened-grain percentage	N18	66.3	a	(99)	1)	66.7	a	4.1
	N9	70.2	a	(101)		69.1	a	
	N4	69.2	a	(99)		69.9	a	
Fertilized-spikelet percentage	N18	84.7	abc	(102)		83.3	c	2.5
	N9	86.0	ab	(102)		84.0	bc	
	N4	86.5	a	(102)		85.2	abc	
Percentage of ripened grains to fertilized spikelets	N18	78.3	a	(98)		80.0	a	4.4
	N9	81.6	a	(99)		82.3	a	
	N4	79.9	a	(97)		82.0	a	
Spikelets/m^2	N18	43688	a	(114)		38272	bc	3221
	N9	39682	b	(111)		35685	cd	
	N4	38379	bc	(118)		32520	d	
Sink size-1 (g/m^2) 2	N18	902	a	(109)		825	ab	76.7
	N9	819	b	(107)		762	b	
	N4	788	b	(115)		684	c	
Sink size-2 (g/m^2) 3	N18	764	a	(111)		687	bc	55
	N9	705	b	(110)		638	c	
	N4	682	bc	(117)		581	d	
Culm length (cm)	N18	71.9	a	(107)		67.2	c	1.5
	N9	70.2	b	(106)		66.4	cd	
	N4	69.7	b	(107)		65.3	d	
Panicle length (cm)	N18	24.3	a	(108)		22.6	bc	1.0
	N9	23.2	b	(104)		22.3	bc	
	N4	22.5	bc	(104)		21.7	c	

Values followed by the same letter within each trait are not significantly different atthe0.05 level, determined by LSDs in the table.
1) Percentage of L to E.
2) Single grain weight at 1.5mm sieve ×spikelets/m^2.
3) Single grain weight at 1.5mm sieve × fertilized spikelets/m^2.

IV. DISCUSSION

Lateness allele *Ex* in L delayed heading by18 days or 19 days compared with its photoperiod insensitive allele *ex* in E. Statistically significant difference was not noticed between L and E for ripened-grain percentage, fertilized-spikelet percentage, percentage of ripened grains to fertilized spikelets and panicle number per m^2in each fertilizer level. *Ex* decreased 1000-grain weight by 2% to 4%. On the other hand, *Ex* significantly increased total brown rice yield by 10% to 18%, spikelet number per m^2 by 11% to 18% and sink size-2 by 10% to 17%, by increasing spikelet number per panicle by 16% to 22%. Hence, it is inferred that the effect of *Ex* on increased yield was mainly due to increasing spikelets per panicle.N18 is extremely high fertilizer level in Japan. It is noteworthy that L ($635 g/m^2$) was 9% higher than E in yield-1.5mm sieve. IR36, a typical improved *indica* variety, occupied the widest cultivated area in Southeast Asia during 1980s [14]. Suweon 258 achieved brown rice yield of about 1000 g/m^2 by heavy fertilizer application in a field test in Kagawa Prefecture, a neighboring prefecture of Kochi [22]. L and E have typical plant type of improved *indica* variety with short culms and erect leaves, which are inherited from IR36 and Suweon 258. It is inferred that L and E are donated positive responsiveness to higher fertilizer application from Suweon 258. Late varieties with higher photosensitivity attain heading stages in late August or early September in Kyusyu district of Japan [10]. Maturity of L corresponds to those of them. Consequently, *Ex* could be utilized to develop high yielding varieties for sufficiently warm districts in which late varieties can be cultivated.

Open Science Index, Agricultural and Biosystems Engineering Vol:11, No:11, 2017 publications.waset.org/10008213/pdf

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