

CHAPTER 4

GENETICS OF SILICON UPTAKE IN UPLAND RICE UNDER DROUGHT CONDITION

4.1 Introduction

Despite the arguments on the essential role of Si, it has been known for almost one century that Si exerts beneficial effects on the growth of plants. Several beneficial effects of Si have been reported, including increased photosynthetic activity, increased insect and disease resistance, reduced mineral toxicity, improvement of nutrient imbalance and enhanced drought and frost tolerance (Ohyama, 1985; Ahmad *et al.*, 1992; Agarie *et al.*, 1998; Ma and Takahashi, 1991, 2001, 2002; Ando *et al.*, 2002; Ma, 2004). But the inheritance of Si uptake has been reported to be smaller than that of the other traits. Savant *et al.* (1997) reported that genetic plays an important role in Si uptake by rice plant. Genotypes differ in their Si contents and respond differently to applied Si (Garrity *et al.*, 1984; Majumder *et al.*, 1985; Winslow, 1992; Deren *et al.*, 1992). Genetic study of Si uptake in rice by using diallel cross involving seven genotypes indicated that maximum profile of this element was in leaf, followed by stem and root. Regarding its uptake, both additive and non-additive genes were involved while the former was higher in magnitude, indicating the scope of individual selection in segregating generations. Heterotic effect was also evident (Majumder *et al.*, 1985). Dai *et al.* (2005) performed quantitative trait loci (QTL) analysis to study the inheritance of Si content in rice hull (HUS), flag leaf (FLS) and stem (STS). A total of 10 QTL showing significant additive effects and 14 significant additive-by-additive (AA) interactions were detected. General contributions to the phenotype variance due to additive effects and AA effects were 29.3 and 18.6% for HUS, 14.8 and 13.6% for FLS, and 8.6 and 28.6% for STS, respectively. This indicates that gene actions at both the one- and

two-locus levels play an important role to genetically control Si content in rice. In addition, it was shown that the detection of QTLs at the one-locus level, as well as magnitude and direction of the additive effect, might be influenced greatly by digenic interactions involving loci linked to the given QTL.

Ma *et al.* (2006) described the Low Si rice 1 (*Lsi1*) gene, which controls Si accumulation in rice, a typical Si-accumulating plant. This gene belongs to the aquaporin family and is constitutively expressed in the roots. *Lsi1* is localized on the plasma membrane of the distal side of both exodermis and endodermis cells, where casparian strips are located. Suppression of *Lsi1* expression resulted in reduced Si uptake. Furthermore, expression of *Lsi1* in *Xenopus* oocytes showed transport activity for Si only. The identification of a Si transporter provides both an insight into the Si uptake system in plants, and a new strategy for producing crops with high resistance to multiple stresses by genetic modification of the root's Si uptake capacity. Vinod *et al.* (2006) reported that two candidate genes, *EXP 15* and *EXP 13*, were found to be associated with root number and Si content in the rice stem, respectively, under both well-watered and low-moisture stress conditions. However, the research of quantitative genetics on Si uptake under drought condition had not been reported at present. Therefore, the objective of this study was to determine the genetics of Si uptake for quantitative traits of upland rice grown under drought condition.

4.2 Materials and methods

Referring to Chapter 2, the experiment was designed by using high-silicon-uptake-ability genotype and low-silicon-uptake-ability genotype at tillering stage. Hao (high Si content in leaf blade), IRAT191 (low Si content in leaf blade), SMGC90002-4 (high Si content in stem), and SMG9037-2-1-1-2 (low Si content in stem) were crossed (Cross 1 = Hao x IRAT191, and Cross 2 = SMGC90002-4 x SMG9037-2-1-1-2) in order to develop F₁, F₂, BC₁ and BC₂ generations. Data were obtained on the parents (P₁ and P₂) and on their progenies (F₁, F₂, BC₁ and BC₂). Family size was deliberately varied with the kind of family. It was set at 20, 40, 200 and 100 plants for the parent, F₁, F₂ and backcross generation, respectively. All plants were individually randomized at the time of planting and seedling of each

population was planted into 25-cm-diameter pots containing sandy loam soil. The experiment was conducted at Rajamangala University of Technology Lanna – Nan on July 2006. Prior to planting, soil was amended with $(\text{NH}_4)_2\text{SO}_4$ (0.5 g kg^{-1} soil), KCl (0.2 g kg^{-1} soil), and KH_2PO_4 (0.2 g kg^{-1} soil). The rice plants were established by watering with drip irrigation. For drought condition manipulation, water was withheld to impose stress at tillering stage for 15 days, starting 31 days after the emergence of seedling. After finishing of drought stage treatment, water was applied regularly until reaching physiological grain-maturing stage.

Data collection

1) Si content in rice tissues: Si content in the young fully-expanded leaf blade of rice was analyzed at tillering stage (45 days after emergence). And Si content in leaf blade, stem, root, and hulls of rice plants were analyzed at harvesting. Rice plant samples were taken from each plant of all families and determined for the Si content by the autoclave-induced digestion method (Elliott and Snyder, 1991).

2) Rice grain yield and its components from each plant of all families were recorded.

4.3 Genetics analysis

In this study, the variation of each trait is obtained from the six basic generations, there are the parents (P_1 and P_2), F_1 hybrid, F_2 hybrid and the backcross (BC_1 and BC_2) generation while the parent generations are the true breeding lines. Mather and Jinks (1971, 1977), Kearsey and Pooni (1996) described that the six basic generations can be divided into two distinct groups with respect to their variances. The first group includes those generations that consist of genetically-identical individuals, such as the P_1 , P_2 and F_1 families. Because individuals within these generations do not show any genetic differences, they are referred to as the non-segregating generations. The second group includes the F_2 , BC_1 and BC_2 generations which contain a mixture of genotypes resulting from segregation, random assortment and recombination of alleles at those loci for which P_1 and P_2 differ and the F_1 is heterozygous. Hence, they are referred to as the segregating generations.

Because in the individuals within the P₁, P₂ and F₁ families are genetically identical, any variation between them cannot be genetical and it is conventional to refer to such variation as the environmental variation within families (E_w). This type of variation exists even between individuals which may be exposed to virtually identical environments and it is a major component of the total variation for quantitative traits.

For variation in the segregating generations, the individuals in the segregating generations will be subjected not only to non-genetical, but also to genetical variation (V_G). The expected genetic variance of an F₂ population at a single segregating locus be V_G. From statistical theory, $V_G = \sum f_i(g_i - \text{mean})^2 / (\sum f_i - 1)$ where f_i is the frequency of the i th genotype, and g_i is its genetic value. While this formula applies to small samples, it can be simplified to when $V_G = \sum f_i g_i^2 - (\sum f_i g_i)^2$ where F₂ population are dealt as a whole. The f_i now represents the proportion of individuals having the i th genotype and not the frequency, i.e. $\sum f_i = 1$ (not n). Apply this formula to gene pair A-a which P₁ and P₂ difference, the F₂ will consist of AA, Aa and aa genotypes which will be present with the proportions of 1/4 : 1/2 : 1/4 respectively. The two parameters measuring the differences between the genotype may then be defined as d , measuring the departure of each homozygote from the mid-point, and h , measuring the departure of each heterozygote from it. The contribution of A-a genotypes to the deviation of the F₂ mean from the mid-parent, will be 1/2 h_a . The contribution of AA, Aa and aa genotypes to the sum of squares of deviation from mid-parent will be:

$$\frac{1}{4} d_a^2 + \frac{1}{2} h_a^2 + \frac{1}{4} (-d_a)^2 = \frac{1}{2} d_a^2 + \frac{1}{2} h_a^2$$

And its contribution to the sum of squares from the F₂ mean then becomes:

$$F_2 \text{ Variance} = \frac{1}{2} d_a^2 + \frac{1}{2} h_a^2 - (\frac{1}{2} h_a)^2 = \frac{1}{2} d_a^2 + \frac{1}{4} h_a^2$$

Assuming that non-allelic genes make independent contribution to it, the genetical variance produced by all genes segregating in F₂ will be the sum of their individual

contribution. It thus becomes $\frac{1}{2} S(d^2) + \frac{1}{4} S(h^2) = \frac{1}{2} D + \frac{1}{4} H$ where we define $D = S(d^2)$ and $H = S(h^2)$. Thus, the genetical variance comprises two parts, the D component, depending on the d's which measure the departure of homozygotes from the mid-parent and H component which depends on the h's measuring the departures of heterozygotes from the mid-parent. The D variation can in principle be fixed by the selection of homozygous lines and so may be referred to as fixable variation. The H variation depends on the properties of heterozygotes and is therefore unfixable. The total phenotypic variation of an F₂ also includes the environmental variation, therefore,

$$V_{F_2} = \frac{1}{2} D + \frac{1}{4} H + E_w$$

In respect of A-a are back-crossed to the larger parent, P₁, will comprise $\frac{1}{2}$ AA and $\frac{1}{2}$ Aa individuals and that to the smaller parent, P₂, $\frac{1}{2}$ Aa and $\frac{1}{2}$ aa individuals. Then as, $\bar{BC}_1 = \frac{1}{2} d_a + \frac{1}{2} h_a$ and $\bar{BC}_2 = \frac{1}{2} d_a - \frac{1}{2} h_a$. The contributions of A-a to the variances of the two backcrosses will thus be,

$$\frac{1}{2} d_a^2 + \frac{1}{2} h_a^2 - \left[\frac{1}{2} (d_a + h_a) \right]^2 = \frac{1}{4} (d_a - h_a)^2 \text{ to } V_{BC_1}$$

and similarly, $\frac{1}{4} (d_a + h_a)^2$ to V_{BC_2} . Then assuming independence of the contributions of the different genes, the genetical portions of the backcross variance become $\frac{1}{4} S(d + h)^2$ and $\frac{1}{4} S(d - h)^2$ respectively. Clearly d and h do not make independent contributions and $F = S(dh)$ might introduce a further components of variation, to give the expressions

$$V_{BC_1} = \frac{1}{4} D - \frac{1}{2} F + \frac{1}{4} H + E_w \text{ and } V_{BC_2} = \frac{1}{4} D + \frac{1}{2} F + \frac{1}{4} H + E_w$$

E_w representing the environmental variation as mentioned earlier.

Mather and Jinks procedures (1971, 1977), the data in this study were analyzed by using statistical procedures to elucidate the genetic component of the six basic generations; variances in terms of D, H, F and E_w as follows.

$$\begin{aligned}
 E_w &= \frac{1}{4} (V_{P_1} + V_{P_2} + 2V_{F_1}) \\
 D &= 4 V_{F_2} - 2 (V_{BC_1} + V_{BC_2}) \\
 H &= 4 (V_{BC_1} + V_{BC_2} - V_{F_2} - E_w) \\
 F &= V_{BC_2} - V_{BC_1}
 \end{aligned}$$

From these estimates, the heritability (h^2) was calculated to the broad and narrow-sense heritability of Si uptake for yield and yield component traits in upland rice under drought condition as follows (Kearsey, 1993):

- a. Broad-sense heritability (h^2_b) may be estimated from the formula:

$$h^2_b = (\frac{1}{2} D + \frac{1}{4} H) / (\frac{1}{2} D + \frac{1}{4} H + E_w)$$

- b. Narrow-sense heritability (h^2_n) may be estimated from the formula:

$$h^2_n = (\frac{1}{2} D) / (\frac{1}{2} D + \frac{1}{4} H + E_w)$$

Calculated mean of parents and variance of F_1 , F_2 families are used for estimating the number of genes. A formula proposed for estimating the number of genes involved in the inheritance of Si uptake for yield and their components in upland rice under drought conditions:

$$N = (\bar{X}_{P_1} - \bar{X}_{P_2})^2 / 8 (V_{F_2} - V_{F_1})$$

In the formula, \bar{X}_{P_1} and \bar{X}_{P_2} are the means of pure-line parent, and V_{F_2} and V_{F_1} are the variance of F_2 and F_1 generations, respectively (Poehlman and Sleper, 1995). However, this method of estimating number of genes is based on the assumptions that the genes have equal effects, no dominance or epistasis is present, and that no two loci are in the same chromosome (hence no linkage). The estimating number of genes are ceased if the data do not follow the assumptions.

However, Kearsey and Pooni (1996) described the step for data analysis as follow. Providing that the experiment is adequately randomized, the individuals of P_1 , P_2 and F_1 are deemed to be exposed to the same range of environmental conditions.

Their variances should thus provide independent estimates of E_W which are not expected to differ from each other. Therefore, the estimate of E_W will be meaningful only when the variances of generations are homogeneous. The homogeneity among P_1 , P_2 and F_1 variances could be checked by using an F-test, which were applied using the ratio of the largest to the smallest of the three variances (P_1 , P_2 and F_1 variances). If the F-test is not shown to differ significantly among the parental and F_1 variances and so the pooled estimate of E_W will be accepted for using to estimating genetic components. Alternatively, when the variances of P_1 , P_2 and F_1 are shown to be heterogeneous, V_{E1} , V_{E2} and V_{E3} are replaced with three separate parameters to account for differences between them. Now, there are six parameters in the model and their contributions to the variances will be:

$$\begin{aligned} s^2_{P1} &= E_{W1} \\ s^2_{P2} &= E_{W2} \\ s^2_{F1} &= E_{W3} \\ s^2_{F2} &= \frac{1}{2} D + \frac{1}{4} H + \frac{1}{4} E_{W1} + \frac{1}{2} E_{W2} + \frac{1}{4} E_{W3} \\ s^2_{BC1} &= \frac{1}{4} D - \frac{1}{2} F + \frac{1}{4} H + \frac{1}{2} E_{W1} + \frac{1}{2} E_{W3} \\ s^2_{BC2} &= \frac{1}{4} D + \frac{1}{2} F + \frac{1}{4} H + \frac{1}{2} E_{W2} + \frac{1}{2} E_{W3} \end{aligned}$$

Table 4.1 Expectations of the within-family variances in terms of the additive dominance genetic and the additive environmental components of variation (Kearsey, 1993).

Generation	Parameters			
	E_W	D	H	F
P_1	1.0			
P_2	1.0			
F_1	1.0			
F_2	1.0	$\frac{1}{2}$	$\frac{1}{4}$	
BC_1	1.0	$\frac{1}{4}$	$\frac{1}{4}$	$-\frac{1}{2}$
BC_2	1.0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$

For estimating of genetic components, there are thus six observed statistics from the population of six families which must estimate four parameters, D, H, F and E_w (Table 4.1). The expectations of the within-family variances in terms of the additive dominance genetic and the additive environmental components of variation are shown in Table 4.1. The weighted least squares procedure (WLS) is applied to determine the parameters. With variances, no such replicate variances are available, and hence, we do not have empirical weights. The theoretical variance of an observed variance (s^2) is equal to $2(\epsilon s^2)^2/df$, but the expected variance, ϵs^2 , is not known. Hayman (1960) solved this problem by using iteration the parameter estimates to calculate expected variances which will approximate to the true values. These are then used to calculate new weights for a second iteration. This process is repeated through successive iterations until the test statistic, χ^2 , reaches a minimum.

4.4 Results

4.4.1 The variances of the six basic generations

Results of study of the variances of the six basic generations are presented in Tables 4.2 to 4.11, the six basic generations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2) of all traits showed that there were phenotypic variations among the individual plants within families in both crosses. The variances of F_2 , BC_1 and BC_2 generations of all traits in both crosses were higher than P_1 , P_2 and F_1 generations, since parents and F_1 are consisted the genetically-identical individuals. In addition, the variances of P_1 , P_2 and F_1 generations of all traits in each cross also were homogeneous when checked with $s^2P_1 = s^2P_2 = s^2F_1$ by using the ratio of the largest to smallest of the three variances or F-test.

Furthermore, the variances of F_1 in both crosses for all traits were significantly smaller than the variances of F_2 and backcross generations, as well, the average variances between BC_1 and BC_2 were smaller than the variance of F_2 generation. When comparing variances between BC_1 and BC_2 , it was found that variances of BC_2 for all traits in both crosses were higher than BC_1 ' variance; except the Si content in hull trait of cross 1 (Table 4.6).

Table 4.2 Within-family variances for the six basic generations for Si content in leaf blade at tillering stage.

Generation	Within-family variance	
	Cross 1 (Hao x IRAT191)	Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)
P ₁	58.770	59.149
P ₂	65.055	54.481
F ₁	50.240	69.174
F ₂	146.821**	118.461**
BC ₁	106.506**	93.424*
BC ₂	146.785**	97.931**
F-test [†] for checked $s^2P_1 = s^2P_2 = s^2F_1$ (P)	>0.05	>0.05
The pooled estimate of E _w	54.699	61.743
Remark:	[†] the ratio of the largest to smallest of three variances (s^2P_1 , s^2P_2 and s^2F_1); P = the value of probability which showed that the parental and F ₁ variances did or did not differ significantly from each other. ** and * = significant at the 0.01 and 0.05 probability levels by F-test to determine whether or not the F ₂ and the backcross variances are significantly larger than E _w .	

Table 4.3 Within-family variances for the six basic generations for Si content in leaf blade at harvesting stage.

Generation	Within-family variance	
	Cross 1 (Hao x IRAT191)	Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)
P ₁	19.335	58.387
P ₂	14.694	66.550
F ₁	29.575	50.070
F ₂	44.902**	146.845**
BC ₁	33.060*	88.830*
BC ₂	37.394**	157.273**
F-test [†] for checked $s^2P_1 = s^2P_2 = s^2F_1$ (P)	>0.05	>0.05
The pooled estimate of E _w	19.598	54.675
Remark:	[†] the ratio of the largest to smallest of three variances (s^2P_1 , s^2P_2 and s^2F_1); P = the value of probability which showed that the parental and F ₁ variances did or did not differ significantly from each other. ** and * = significant at the 0.01 and 0.05 probability levels by F-test to determine whether or not the F ₂ and the backcross variances are significantly larger than E _w .	

Table 4.4 Within-family variances for the six basic generations for Si content in stem at harvesting stage.

Generation	Within-family variance	
	Cross 1 (Hao x IRAT191)	Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)
P ₁	56.668	22.511
P ₂	54.255	28.156
F ₁	57.634	24.612
F ₂	138.522**	103.161**
BC ₁	94.855*	64.774**
BC ₂	131.824**	93.994**
F-test [†] for checked $s^2P_1 = s^2P_2 = s^2F_1$ (P)	>0.05	>0.05
The pooled estimate of E _w	56.492	24.661
Remark:	[†] the ratio of the largest to smallest of three variances (s^2P_1 , s^2P_2 and s^2F_1); P = the value of probability which showed that the parental and F ₁ variances did or did not differ significantly from each other. ** and * = significant at the 0.01 and 0.05 probability levels by F-test to determine whether or not the F ₂ and the backcross variances are significantly larger than E _w .	

Table 4.5 Within-family variances for the six basic generations for Si content in root at harvesting stage.

Generation	Within-family variance	
	Cross 1 (Hao x IRAT191)	Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)
P ₁	64.204	83.204
P ₂	82.007	72.781
F ₁	62.625	68.538
F ₂	154.446**	156.493**
BC ₁	102.790*	106.022*
BC ₂	180.187**	150.651**
F-test [†] for checked $s^2P_1 = s^2P_2 = s^2F_1$ (P)	>0.05	>0.05
The pooled estimate of E _w	66.195	72.329
Remark:	[†] the ratio of the largest to smallest of three variances (s^2P_1 , s^2P_2 and s^2F_1); P = the value of probability which showed that the parental and F ₁ variances did or did not differ significantly from each other. ** and * = significant at the 0.01 and 0.05 probability levels by F-test to determine whether or not the F ₂ and the backcross variances are significantly larger than E _w .	

Table 4.6 Within-family variances for the six basic generations for Si content in hull at harvesting stage.

Generation	Within-family variance	
	Cross 1 (Hao x IRAT191)	Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)
P ₁	53.011	43.409
P ₂	62.232	23.253
F ₁	72.625	48.324
F ₂	160.687**	112.045**
BC ₁	143.469**	79.145**
BC ₂	130.272**	106.580**
F-test [†] for checked $s^2P_1 = s^2P_2 = s^2F_1$ (P)	>0.05	>0.05
The pooled estimate of E _w	62.993	33.297

Remark: [†] the ratio of the largest to smallest of three variances (s^2P_1 , s^2P_2 and s^2F_1); P = the value of probability which showed that the parental and F₁ variances did or did not differ significantly from each other.
** = significant at the 0.01 probability levels by F-test to determine whether or not the F₂ and the backcross variances are significantly larger than E_w.

Table 4.7 Within-family variances for the six basic generations for grain yield.

Generation	Within-family variance	
	Cross 1 (Hao x IRAT191)	Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)
P ₁	2.582	1.990
P ₂	4.046	1.339
F ₁	2.326	1.955
F ₂	7.385**	6.440**
BC ₁	5.420**	3.501**
BC ₂	6.380**	5.704**
F-test [†] for checked $s^2P_1 = s^2P_2 = s^2F_1$ (P)	>0.05	>0.05
The pooled estimate of E _w	2.569	1.707

Remark: [†] the ratio of the largest to smallest of three variances (s^2P_1 , s^2P_2 and s^2F_1); P = the value of probability which showed that the parental and F₁ variances did or did not differ significantly from each other.
** = significant at the 0.01 probability level by F-test to determine whether or not the F₂ and the backcross variances are significantly larger than E_w.

Table 4.8 Within-family variances for the six basic generations for number of panicles per plant.

Generation	Within-family variance	
	Cross 1 (Hao x IRAT191)	Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)
P ₁	0.621	0.471
P ₂	1.157	0.379
F ₁	0.681	0.438
F ₂	1.694**	1.254**
BC ₁	1.088**	0.879**
BC ₂	1.854**	1.071**
F-test [†] for checked $s^2P_1 = s^2P_2 = s^2F_1$ (P)	>0.05	>0.05
The pooled estimate of E _w	0.707	0.426
Remark:	[†] the ratio of the largest to smallest of three variances (s^2P_1 , s^2P_2 and s^2F_1); P = the value of probability which showed that the parental and F ₁ variances did or did not differ significantly from each other. ** = significant at the 0.01 probability level by F-test to determine whether or not the F ₂ and the backcross variances are significantly larger than E _w , respectively.	

Table 4.9 Within-family variances for the six basic generations for number of spikelets per panicles.

Generation	Within-family variance	
	Cross 1 (Hao x IRAT191)	Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)
P ₁	349.747	342.285
P ₂	573.293	275.883
F ₁	404.594	292.452
F ₂	1102.466**	896.927**
BC ₁	602.567*	660.108**
BC ₂	966.572**	808.155**
F-test [†] for checked $s^2P_1 = s^2P_2 = s^2F_1$ (P)	>0.05	>0.05
The pooled estimate of E _w	407.300	297.000
Remark:	[†] the ratio of the largest to smallest of three variances (s^2P_1 , s^2P_2 and s^2F_1); P = the value of probability which showed that the parental and F ₁ variances did or did not differ significantly from each other. ** and * = significant at the 0.01 and 0.05 probability levels by F-test to determine whether or not the F ₂ and the backcross variances are significantly larger than E _w .	

Table 4.10 Within-family variances for the six basic generations for spikelet fertility.

Generation	Within-family variance	
	Cross 1 (Hao x IRAT191)	Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)
P ₁	239.390	84.816
P ₂	219.550	87.083
F ₁	349.760	85.161
F ₂	759.748**	201.000**
BC ₁	417.790*	150.870**
BC ₂	687.400**	193.100**
F-test [†] for checked $s^2P_1 = s^2P_2 = s^2F_1$ (P)	>0.05	>0.05
The pooled estimate of E _w	265.589	85.532

Remark: [†] the ratio of the largest to smallest of three variances (s^2P_1 , s^2P_2 and s^2F_1); P = the value of probability which showed that the parental and F₁ variances did or did not differ significantly from each other.

** and * = significant at the 0.01 and 0.05 probability levels by F-test to determine whether or not the F₂ and the backcross variances are significantly larger than E_w.

Table 4.11 Within-family variances for the six basic generations for 100-grain weight.

Generation	Within-family variance	
	Cross 1 (Hao x IRAT191)	Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)
P ₁	0.233	0.232
P ₂	0.256	0.292
F ₁	0.245	0.319
F ₂	0.650**	0.999**
BC ₁	0.491**	0.540**
BC ₂	0.531**	0.885**
F-test [†] for checked $s^2P_1 = s^2P_2 = s^2F_1$ (P)	>0.05	>0.05
The pooled estimate of E _w	0.244	0.281

Remark: [†] the ratio of the largest to smallest of three variances (s^2P_1 , s^2P_2 and s^2F_1); P = the value of probability which showed that the parental and F₁ variances did or did not differ significantly from each other.

** = significant at the 0.01 probability level by F-test to determine whether or not the F₂ and the backcross variances are significantly larger than E_w.

4.4.2 Estimation of genetical components

From the results in Tables 4.2 to 4.11, variances of P_1 , P_2 , and F_1 generations in both crosses for all traits were homogeneous, therefore, the pooled estimate of environmental variances (E_w) were accepted for using in the estimation of variance components. When the variances of F_2 and the backcross generations were compared with E_w by F-test, it showed that the variances of F_2 and the backcross generations were significantly larger than E_w (Tables 4.2 to 4.11), indicating that genetic variation existed in these segregating generations which were derived from crossing between the parents.

The variances of the six basic generations were used to estimate variance components by the weighted least squares procedure for fitting the perfect model which consisted of four parameters, D, H, F and E_w . The chi-square test for fitting the perfect model did not show significant difference for each trait in both crosses. Results of the estimation of variance components are presented in Tables 4.12 to 4.21. However, some parameters such as H and F in the model did not show significant difference from zero by the T-test. The data were then proceeded to the fitting model in order to obtain the best statistical model by using different combinations of parameters. The most appropriate model for each trait in crosses required at least two parameters, D and E_w , which both of them were fitting to the chi-square test (Tables 4.22 to 4.31). F was particularly found in some traits in both crosses. In cross 1 (Hao x IRAT191), F was found for Si content in root (Table 4.25), number of panicles per plant (Table 4.28), number of spikelets per panicle (Table 4.29), and spikelet fertility (Table 4.30), and in cross 2 (SMGC90002-4 x SMG9037-2-1-1-2), F was found for Si content leaf blade (Table 4.23), grain yield (Table 4.27) and 100-grain weight (Table 4.31).

4.4.3 Heritability

By using the data obtained from the perfect fit values of D, H, F and E_w in Tables 4.12 to 4.21, the heritability was estimated in both types of heritability, broad-sense heritability (h^2_b) (Table 4.32) and narrow-sense heritability (h^2_n) (Table

4.33). The estimations of h^2_b and h^2_n in crosses 1 were different from cross 2 for all traits. The average h^2_b of Si content in rice tissues in both crosses were 0.56, 0.60, 0.68, 0.56 and 0.66 for the young leaf blade, mature leaf blade, stem, root and hull, respectively (Table 4.32) while the average h^2_n of Si content in rice tissues in both crosses were 0.33, 0.38, 0.41, 0.27 and 0.32 for the young leaf blade, mature leaf blade, stem, root and hull, respectively (Table 4.33).

For yield and yield components, the average h^2_b in both crosses were 0.70, 0.62, 0.65, 0.61 and 0.67 for grain yield, number of panicles per plant, number of spikelets per panicle, spikelet fertility and 100-grain weight, respectively (Table 4.32) while the average h^2_n in both crosses were 0.49, 0.35, 0.47, 0.47 and 0.38 for grain yield, number of panicles per plant, number of spikelets per panicle, spikelet fertility and 100-grain weight, respectively (Table 4.33).

However, when h^2_b and h^2_n estimated from the most appropriate fit values, the estimated of h^2_b and h^2_n in crosses 1 showed difference from cross 2 for all traits. But the h^2_n of each trait in both crosses were similar to h^2_b . The average h^2_b and h^2_n of Si content in rice tissues in both crosses were 0.56, 0.60, 0.68, 0.56 and 0.66 for the young leaf blade, mature leaf blade, stem, root and hull, respectively (Tables 4.34 and 4.35) while the average h^2_b and h^2_n for yield and yield components in both crosses were 0.67, 0.62, 0.65, 0.61 and 0.67 for grain yield, number of panicles per plant, number of spikelets per panicle, spikelet fertility and 100-grain weight, respectively.

4.4.4 The number of genes

In this study, the formula $N = (\bar{X}_{P1} - \bar{X}_{P2})^2 / 8 (V_{F2} - V_{F1})$ cannot estimate the number of genes for controlling the expression of Si content in rice tissues, yield and yield components because this method did not meet the requirement of the assumptions that the genes control have equal effects, either dominance or epistasis is not present, and no linkage among loci in the same chromosome. In all traits, it was found that the different variances between F_2 and F_1 were very high (Tables 4.36 and 4.37), when compared with the means of parent and reduced the number of genes as it should be correct number ($N < 0.5$ for all traits; Tables 4.36 to

4.38). In addition, the data in Tables 4.12 to 4.21 supported the variation of Si content in rice tissues, yield and yield components which were influenced by D, H, F and E_w variances in the initial weight in an iterative process. So that, the number of genes control for studied traits did not follow the assumption of this method.

Table 4.12 Results of estimated variance components by the variances of six basic generations to fit the perfect model for Si content in leaf blade at tillering stage.

Parameter	Estimated variance components			
	Cross 1 (Hao x IRAT191)		Cross 2 (SMGC90002-4 x SMG9037-2-1-1-2)	
	Observed	Expected	Observed	Expected
D	80.702		91.134	
H	207.086		44.605	
F	40.279		4.507	
E_w	54.699**		61.743**	
$\sqrt{(H/D)}$	1.602		0.699	
S_D	78.256		63.130	
S_H	123.915		98.890	
S_F	25.768		19.238	
S_{E_w}	8.888		10.005	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P_1	58.770	54.699	59.149	61.743
P_2	65.055	54.699	54.481	61.743
F_1	50.240	54.699	69.174	61.743
F_2	146.821	146.821	118.461	118.461
BC_1	106.506	106.506	93.424	93.424
BC_2	146.785	146.785	97.931	97.931
$\chi^2_{[2]}$	0.440		0.412	
P	0.75-0.90		0.75-0.90	

Remark: ** = significant at the 0.01 probability level by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero.

Table 4.13 Results of estimated variance components by the variances of six basic generations to fit the perfect model for Si content in leaf blade at harvesting stage.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	38.700		95.174	
H	23.817		178.332	
F	4.334		68.443*	
E _w	19.598**		54.675**	
$\sqrt{(H/D)}$	0.784		1.369	
S _D	22.924		78.128	
S _H	36.110		123.580	
S _F	7.092		25.671	
S _{E_w}	3.302		8.888	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	19.335	19.598	58.387	54.675
P ₂	14.694	19.598	66.550	54.675
F ₁	29.575	19.598	50.070	54.675
F ₂	44.902	44.902	146.845	146.845
BC ₁	33.060	33.060	88.830	88.830
BC ₂	37.394	37.394	157.273	157.273
$\chi^2_{[2]}$		3.279		0.506
P		0.10-0.25		0.75-0.90

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero, respectively.

Table 4.14 Results of estimated variance components by the variances of six basic generations to fit the perfect model for Si content in stem at harvesting stage.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	100.730		95.108	
H	126.658		123.784	
F	36.969		29.220	
E _w	56.492**		24.661**	
$\sqrt{(H/D)}$	1.121		1.141	
S _D	72.229		52.577	
S _H	113.745		78.597	
S _F	23.087		16.223	
S _{E_w}	9.110		3.987	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	56.668	56.492	22.511	24.661
P ₂	54.255	56.492	28.156	24.661
F ₁	57.634	56.492	24.612	24.661
F ₂	138.522	138.522	103.161	103.161
BC ₁	94.855	94.855	64.774	64.774
BC ₂	131.824	131.824	93.994	93.994
$\chi^2_{[2]}$		0.024		0.233
P		0.95-0.99		0.75-0.90

Remark: ** = significant at the 0.01 probability level by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero.

Table 4.15 Results of estimated variance components by the variances of six basic generations to fit the perfect model for Si content in root at harvesting stage.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	51.831		112.626	
H	249.344		111.405	
F	77.397**		44.629	
E _w	66.195**		72.329**	
$\sqrt{(H/D)}$	2.193		0.995	
S _D	85.516		81.731	
S _H	139.954		130.744	
S _F	29.479		26.192	
S _{E_w}	10.724		11.705	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	64.204	66.195	83.204	72.329
P ₂	82.007	66.195	72.781	72.329
F ₁	62.625	66.195	68.538	72.329
F ₂	154.446	154.446	156.493	156.493
BC ₁	102.790	102.790	106.022	106.022
BC ₂	180.187	180.187	150.651	150.651
$\chi^2_{[2]}$		0.426		0.222
P		0.75-0.90		0.75-0.90

Remark: ** = significant at the 0.01 probability level by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero.

Table 4.16 Results of estimated variance components by the variances of six basic generations to fit the perfect model for Si content in hull at harvesting stage.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	95.266		76.730	
H	200.245		161.533	
F	-13.197		27.435	
E _w	62.993**		33.297**	
$\sqrt{(H/D)}$	1.450		1.451	
S _D	84.776		58.676	
S _H	134.048		90.730	
S _F	27.550		18.868	
S _{E_w}	10.247		5.683	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	53.011	62.993	43.409	33.297
P ₂	62.232	62.993	23.253	33.297
F ₁	72.625	62.993	48.324	33.297
F ₂	160.687	160.687	112.045	112.045
BC ₁	143.469	143.469	79.145	79.145
BC ₂	130.272	130.272	106.580	106.580
$\chi^2_{[2]}$		0.681		4.174
P		0.50-0.75		0.10-0.25

Remark: ** = significant at the 0.01 probability level by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero.

Table 4.17 Results of estimated variance components by the variances of six basic generations to fit the perfect model for grain yield.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	5.940		7.350*	
H	7.384		4.234	
F	0.960		2.203*	
E _w	2.569**		1.707**	
$\sqrt{(H/D)}$	1.115		0.759	
S _D	3.799		3.208	
S _H	5.854		4.733	
S _F	1.190		0.951	
S _{E_w}	0.422		0.279	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	2.582	2.569	1.990	1.707
P ₂	4.046	2.569	1.339	1.707
F ₁	2.326	2.569	1.955	1.707
F ₂	7.385	7.385	6.440	6.440
BC ₁	5.420	5.420	3.501	3.501
BC ₂	6.380	6.380	5.704	5.704
$\chi^2_{[2]}$	1.479		1.223	
P	0.25-0.50		0.50-0.75	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero, respectively.

Table 4.18 Results of estimated variance components by the variances of six basic generations to fit the perfect model for number of panicles per plant.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	0.892		1.116	
H	2.165		1.079	
F	0.766		0.192	
E _w	0.707**		0.426**	
$\sqrt{(H/D)}$	1.558		0.983	
S _D	0.914		0.639	
S _H	1.474		0.974	
S _F	0.306		0.197	
S _{E_w}	0.117		0.069	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	0.621	0.707	0.471	0.426
P ₂	1.157	0.707	0.379	0.426
F ₁	0.681	0.707	0.438	0.426
F ₂	1.694	1.694	1.254	1.254
BC ₁	1.088	1.088	0.879	0.879
BC ₂	1.854	1.854	1.071	1.071
$\chi^2_{[2]}$	1.648		0.247	
P	0.25-0.50		0.75-0.90	

Remark: ** = significant at the 0.01 probability level by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero.

Table 4.19 Results of estimated variance components by the variances of six basic generations to fit the perfect model for number of spikelets per panicle.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	1271.600*		651.200	
H	237.400		1097.400	
F	364.000*		148.000	
E _w	407.300**		297.000**	
$\sqrt{(H/D)}$	0.432		1.298	
S _D	547.978		466.219	
S _H	828.064		719.861	
S _F	161.895		148.324	
S _{E_w}	66.558		47.958	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	349.747	407.300	342.285	297.000
P ₂	573.293	407.300	275.883	297.000
F ₁	404.594	407.300	292.452	297.000
F ₂	1102.466	1102.450	896.927	896.950
BC ₁	602.567	602.550	660.108	660.150
BC ₂	966.572	966.550	808.155	808.150
$\chi^2_{[2]}$	1.055		0.227	
P	0.50-0.75		0.075-0.90	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero, respectively.

Table 4.20 Results of estimated variance components by the variances of six basic generations to fit the perfect model for spikelet fertility.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	828.588*		116.058	
H	319.449		229.755	
F	269.613*		42.230	
E _w	265.589**		85.532**	
$\sqrt{(H/D)}$	0.621		1.407	
S _D	380.933		106.532	
S _H	576.724		170.141	
S _F	114.324		34.828	
S _{E_w}	43.704		13.784	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	239.390	265.589	84.816	85.532
P ₂	219.550	265.589	87.083	85.532
F ₁	349.760	265.589	85.161	85.532
F ₂	759.748	759.745	201.000	201.000
BC ₁	417.790	417.792	150.870	150.870
BC ₂	687.400	687.405	193.100	193.100
$\chi^2_{[2]}$	1.661		0.004	
P	0.25-0.50		0.95-0.99	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero, respectively.

Table 4.21 Results of estimated variance components by the variances of six basic generations to fit the perfect model for 100-grain weight.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	0.556		1.146*	
H	0.511		0.581	
F	0.040		0.345	
E _w	0.244**		0.281**	
$\sqrt{(H/D)}$	0.959		0.712	
S _D	0.332		0.497	
S _H	0.512		0.736	
S _F	0.103		0.147	
S _{E_w}	0.040		0.046	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	0.233	0.244	0.232	0.281
P ₂	0.256	0.244	0.292	0.281
F ₁	0.245	0.244	0.319	0.281
F ₂	0.650	0.650	0.999	0.999
BC ₁	0.491	0.491	0.540	0.540
BC ₂	0.531	0.531	0.885	0.885
$\chi^2_{[2]}$	0.042		0.714	
P	0.95-0.99		0.50-0.75	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero, respectively.

Table 4.22 Results of estimated variance components by the variances of six basic generations to fit the most appropriate model for Si content in leaf blade at tillering stage.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	196.350**		114.904**	
H	-		-	
F	-		-	
E _w	58.146**		63.536**	
S _D	33.104		30.879	
S _H	-		-	
S _F	-		-	
S _{E_w}	8.468		9.147	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	58.770	58.146	59.149	63.536
P ₂	65.055	58.146	54.481	63.536
F ₁	50.240	58.146	69.174	63.536
F ₂	146.821	156.321	118.461	120.989
BC ₁	106.506	107.233	93.424	92.263
BC ₂	146.785	107.233	97.931	92.263
	$\chi^2_{[4]} = 4.604$		$\chi^2_{[4]} = 0.663$	
	P = 0.25-0.50		P = 0.95-0.99	

Remark: ** = significant at the 0.01 probability level by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero.

Table 4.23 Results of estimated variance components by the variances of six basic generations to fit the most appropriate model for Si content in leaf blade at harvesting stage.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	51.866**		197.236**	
H	-		-	
F	-		52.549*	
E _w	20.330**		58.350**	
S _D	10.970		33.192	
S _H	-		-	
S _F	-		23.191	
S _{E_w}	3.071		8.497	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	19.335	20.330	58.387	58.350
P ₂	14.694	20.330	66.550	58.350
F ₁	29.575	20.330	50.070	58.350
F ₂	44.902	46.263	146.845	156.968
BC ₁	33.060	33.297	88.830	81.384
BC ₂	37.394	33.297	157.273	133.933
	$\chi^2_{[4]} = 4.017$		$\chi^2_{[3]} = 2.588$	
	P = 0.25-0.50		P = 0.25-0.50	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero, respectively.

Table 4.24 Results of estimated variance components by the variances of six basic generations to fit the most appropriate model for Si content in stem at harvesting stage.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	169.859**		167.607**	
H	-		-	
F	-		-	
E _w	58.681**		25.587**	
S _D	32.237		19.934	
S _H	-		-	
S _F	-		-	
S _{E_w}	8.591		3.896	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	56.668	58.681	22.511	25.587
P ₂	54.255	58.681	28.156	25.587
F ₁	57.634	58.681	24.612	25.587
F ₂	138.522	143.611	103.161	109.390
BC ₁	94.855	101.146	64.774	67.488
BC ₂	131.824	101.146	93.994	67.488
	$\chi^2_{[4]} = 3.115$		$\chi^2_{[4]} = 4.673$	
	P = 0.50-0.75		P = 0.25-0.50	

Remark: ** = significant at the 0.01 probability level by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero.

Table 4.25 Results of estimated variance components by the variances of six basic generations to fit the most appropriate model for Si content in root at harvesting stage.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	189.197**		171.156**	
H	-		-	
F	54.867*		-	
E _w	72.055**		74.093**	
S _D	36.993		38.507	
S _H	-		-	
S _F	26.635		-	
S _{E_w}	10.213		10.854	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	64.204	72.055	83.204	74.093
P ₂	82.007	72.055	72.781	74.093
F ₁	62.625	72.055	68.538	74.093
F ₂	154.446	166.654	156.493	159.671
BC ₁	102.790	91.921	106.022	116.882
BC ₂	180.187	146.788	150.651	116.882
	$\chi^2_{[3]} = 3.600$		$\chi^2_{[4]} = 3.293$	
	P = 0.25-0.50		P = 0.50-0.75	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero, respectively.

Table 4.26 Results of estimated variance components by the variances of six basic generations to fit the most appropriate model for Si content in hull at harvesting stage.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	208.903**		170.066**	
H	-		-	
F	-		-	
E _w	67.580**		35.459**	
S _D	37.042		23.689	
S _H	-		-	
S _F	-		-	
S _{E_w}	9.752		5.491	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	53.011	67.580	43.409	35.459
P ₂	62.232	67.580	23.253	35.459
F ₁	72.625	67.580	48.324	35.459
F ₂	160.687	172.032	112.045	120.492
BC ₁	143.469	119.806	79.145	77.975
BC ₂	130.272	119.806	106.580	77.975
	$\chi^2_{[4]} = 3.044$		$\chi^2_{[4]} = 8.460$	
	P = 0.50-0.75		P = 0.05-0.10	

Remark: ** = significant at the 0.01 probability level by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero.

Table 4.27 Results of estimated variance components by the variances of six basic generations to fit the most appropriate model for grain yield.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	10.226**		9.979**	
H	-		-	
F	-		1.893*	
E _W	2.712**		1.766**	
S _D	1.627		1.285	
S _H	-		-	
S _F	-		0.886	
S _{E_W}	0.404		0.272	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	2.582	2.712	1.990	1.766
P ₂	4.046	2.712	1.339	1.766
F ₁	2.326	2.712	1.955	1.766
F ₂	7.385	7.825	6.440	6.755
BC ₁	5.420	5.269	3.501	3.314
BC ₂	6.380	5.269	5.704	5.207
	$\chi^2_{[4]} = 3.488$		$\chi^2_{[3]} = 2.024$	
	P = 0.25-0.50		P = 0.50-0.75	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_W are significantly different from zero, respectively.

Table 4.28 Results of estimated variance components by the variances of six basic generations to fit the most appropriate model for number of panicles per plant.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	2.096**		1.744**	
H	-		-	
F	0.585*		-	
E _w	0.761**		0.445**	
S _D	0.403		0.272	
S _H	-		-	
S _F	0.279		-	
S _{E_w}	0.110		0.066	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	0.621	0.761	0.471	0.445
P ₂	1.157	0.761	0.379	0.445
F ₁	0.681	0.761	0.438	0.445
F ₂	1.694	1.809	1.254	1.318
BC ₁	1.088	0.993	0.879	0.881
BC ₂	1.854	1.577	1.071	0.881
	$\chi^2_{[3]} = 3.806$		$\chi^2_{[4]} = 2.131$	
	P = 0.25-0.50		P = 0.50-0.75	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero, respectively.

Table 4.29 Results of estimated variance components by the variances of six basic generations to fit the most appropriate model for number of spikelets per panicle.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	1411.800**		1289.700**	
H	-		-	
F	348.000*		-	
E _w	413.500**		314.900**	
S _D	246.838		193.179	
S _H	-		-	
S _F	151.993		-	
S _{E_w}	63.032		46.217	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	349.747	413.500	342.285	314.900
P ₂	573.293	413.500	275.883	314.900
F ₁	404.594	413.500	292.452	314.900
F ₂	1102.466	1119.400	896.927	959.750
BC ₁	602.567	592.450	660.108	637.325
BC ₂	966.572	940.450	808.155	637.325
	$\chi^2_{[3]} = 1.137$		$\chi^2_{[4]} = 3.125$	
	P = 0.75-0.90		P = 0.50-0.75	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_w are significantly different from zero, respectively.

Table 4.30 Results of estimated variance components by the variances of six basic generations to fit the most appropriate model for spikelet fertility.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	1018.200**		242.673**	
H	-		-	
F	246.500*		-	
E _W	272.900**		90.695**	
S _D	52.874		47.718	
S _H	-		-	
S _F	33.659		-	
S _{E_W}	41.689		13.012	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	239.390	272.900	84.816	90.695
P ₂	219.550	272.900	87.083	90.695
F ₁	349.760	272.900	85.161	90.695
F ₂	759.748	782.000	201.000	212.031
BC ₁	417.790	404.200	150.870	151.363
BC ₂	687.400	650.700	193.100	151.363
	$\chi^2_{[3]} = 1.968$		$\chi^2_{[4]} = 2.757$	
	P = 0.50-0.90		P = 0.50-0.75	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_W are significantly different from zero, respectively.

Table 4.31 Results of estimated variance components by the variances of six basic generations to fit the most appropriate model for 100-grain weight.

Parameter	Estimated variance components			
	Cross 1		Cross 2	
	(Hao x IRAT191)		(SMGC90002-4 x SMG9037-2-1-1-2)	
D	0.853**		1.505**	
H	-		-	
F	-		0.302*	
E _W	0.256**		0.290**	
S _D	0.146		0.202	
S _H	-		-	
S _F	-		0.137	
S _{E_W}	0.037		0.045	
Generation	Within-family variance		Within-family variance	
	Observed	Expected	Observed	Expected
P ₁	0.233	0.256	0.232	0.290
P ₂	0.256	0.256	0.292	0.290
F ₁	0.245	0.256	0.319	0.290
F ₂	0.650	0.683	0.999	1.042
BC ₁	0.491	0.469	0.540	0.515
BC ₂	0.531	0.469	0.885	0.817
	$\chi^2_{[4]} = 1.147$		$\chi^2_{[3]} = 1.338$	
	P = 0.75-0.90		P = 0.50-0.75	

Remark: ** and * = significant at the 0.01 and 0.05 probability levels by t-test to determine whether or not the value of D, H, F or E_W are significantly different from zero, respectively.

Table 4.32 The h^2_b of Si content in rice tissues, yield and yield component traits calculated from the expected value of parameter in the perfect model.

Traits	h^2_b		
	Cross 1	Cross 2	Average
Si content in leaf blade at tillering stage	0.63	0.48	0.56
Si content in leaf blade at harvesting stage	0.56	0.63	0.60
Si content in stem at harvesting stage	0.59	0.76	0.68
Si content in root at harvesting stage	0.57	0.54	0.56
Si content in hull at harvesting stage	0.61	0.70	0.66
Grain yield	0.65	0.74	0.70
Number of panicles per plant	0.58	0.66	0.62
Number of spikelets per panicle	0.63	0.67	0.65
Spikelet fertility	0.65	0.57	0.61
100-grain weight	0.62	0.72	0.67

Table 4.33 The h^2_n of Si content in rice tissues, yield and yield component traits calculated from the expected value of parameter in the perfect model.

Traits	h^2_n		
	Cross 1	Cross 2	Average
Si content in leaf blade at tillering stage	0.27	0.38	0.33
Si content in leaf blade at harvesting stage	0.43	0.32	0.38
Si content in stem at harvesting stage	0.36	0.46	0.41
Si content in root at harvesting stage	0.17	0.36	0.27
Si content in hull at harvesting stage	0.30	0.34	0.32
Grain yield	0.40	0.57	0.49
Number of panicles per plant	0.26	0.44	0.35
Number of spikelets per panicle	0.58	0.36	0.47
Spikelet fertility	0.55	0.38	0.47
100-grain weight	0.43	0.32	0.38

Table 4.34 The h^2_b of Si content in rice tissues, yield and yield component traits calculated from the expected value of parameter in the most appropriate model.

Traits	h^2_b		
	Cross 1	Cross 2	Average
Si content in leaf blade at tillering stage	0.63	0.47	0.55
Si content in leaf blade at harvesting stage	0.56	0.63	0.60
Si content in stem at harvesting stage	0.59	0.77	0.68
Si content in root at harvesting stage	0.57	0.54	0.56
Si content in hull at harvesting stage	0.61	0.71	0.66
Grain yield	0.65	0.68	0.67
Number of panicles per plant	0.58	0.66	0.62
Number of spikelets per panicle	0.63	0.67	0.65
Spikelet fertility	0.65	0.57	0.61
100-grain weight	0.62	0.72	0.67

Table 4.35 The h^2_n of Si content in rice tissues, yield and yield component traits calculated from the expected value of parameter in the most appropriate model.

Traits	h^2_n		
	Cross 1	Cross 2	Average
Si content in leaf blade at tillering stage	0.63	0.47	0.55
Si content in leaf blade at harvesting stage	0.56	0.63	0.60
Si content in stem at harvesting stage	0.59	0.77	0.68
Si content in root at harvesting stage	0.57	0.54	0.56
Si content in hull at harvesting stage	0.61	0.71	0.66
Grain yield	0.65	0.68	0.67
Number of panicles per plant	0.58	0.66	0.62
Number of spikelets per panicle	0.63	0.67	0.65
Spikelet fertility	0.65	0.57	0.61
100-grain weight	0.62	0.72	0.67

Table 4.36 The number of genes (N) in crosses 1 (Hao x IRAT191) for controlling the expression of Si content in rice tissues, yield and yield components.

Traits	\bar{X}_{P1}	\bar{X}_{P2}	V_{F2}	V_{F1}	N (genes)
Si content in leaf blade at tillering stage (mg g ⁻¹)	52.9	36.6	146.82	50.24	0.34
Si content in leaf blade at harvesting stage (mg g ⁻¹)	52.0	46.1	44.90	29.58	0.28
Si content in stem at harvesting stage (mg g ⁻¹)	41.2	39.2	138.52	57.63	0.01
Si content in root at harvesting stage (mg g ⁻¹)	51.5	40.8	154.45	62.63	0.16
Si content in hull at harvesting stage (mg g ⁻¹)	19.7	26.9	160.69	72.63	0.07
Grain yield (g plant ⁻¹)	4.1	4.0	7.39	2.33	0.01
Number of panicles per plant (panicles plant ⁻¹)	3.1	3.0	1.69	0.68	0.01
Number of spikelets per panicle (spikelets panicle ⁻¹)	73.0	72.0	1,102.47	404.59	0.01
Spikelet fertility (%)	90.9	88.9	759.75	349.76	0.01
100-grain weight (g)	2.9	2.5	0.65	0.25	0.06

Table 4.37 The number of genes (N) in crosses 2 (SMGC90002-4 x SMG9037-2-1-1-2) for controlling the expression of Si content in rice tissues, yield and yield components.

Traits	\bar{X}_{P1}	\bar{X}_{P2}	V_{F2}	V_{F1}	N (genes)
Si content in leaf blade at tillering stage (mg g ⁻¹)	54.3	51.5	118.46	69.17	0.02
Si content in leaf blade at harvesting stage (mg g ⁻¹)	25.8	40.1	146.85	50.07	0.26
Si content in stem at harvesting stage (mg g ⁻¹)	45.8	56.2	103.161	24.61	0.17
Si content in root at harvesting stage (mg g ⁻¹)	39.1	39.5	156.49	68.54	0.01
Si content in hull at harvesting stage (mg g ⁻¹)	31.6	22.8	112.05	48.32	0.15
Grain yield (g plant ⁻¹)	5.3	3.4	6.44	1.96	0.10
Number of panicles per plant (panicles plant ⁻¹)	3.0	2.5	1.25	0.44	0.04
Number of spikelets per panicle (spikelets panicle ⁻¹)	81.0	76.0	896.93	292.45	0.01
Spikelet fertility (%)	71.7	84.6	201.00	85.16	0.18
100-grain weight (g)	2.5	2.4	1.00	0.32	0.01

Table 4.38 The average number of genes in both crosses for controlling the expression of Si content in rice tissues, yield and yield components.

Traits	Average number of genes (genes)
Si content in leaf blade at tillering stage	0.183
Si content in leaf blade at harvesting stage	0.271
Si content in stem at harvesting stage	0.090
Si content in root at harvesting stage	0.085
Si content in hull at harvesting stage	0.112
Grain yield	0.055
Number of panicles per plant	0.025
Number of spikelets per panicle	0.010
Spikelet fertility	0.095
100-grain weight	0.035

4.5 Discussion

The six basic generations can be divided into two distinct groups with respect to their variances. The first group includes those generations that consist of genetically-identical individuals, such as the P_1 , P_2 and F_1 families because individuals within these generations do not show any genotypic difference and are referred to as non-segregating generations. So, any variation between them cannot be genetical and it is conventional to refer to such variation as the environmental variation within families. The second group includes the F_2 and back-cross generations (BC_1 and BC_2) which contain a mixture of genotypes resulting from segregation, random assortment and recombination of alleles at those loci for which P_1 , P_2 differ and the F_1 is heterozygous. Hence, they are referred to as the segregating generations (Kearsey and Pooni, 1996).

In this study, the individuals of P₁, P₂ and F₁ families of all traits were exposed to the same range of environmental conditions in both crosses. There were no interactions between the micro-environmental and genotypic variations because the variances of the P₁, P₂ and F₁ generations were homogeneous. These results showed that the parental and F₁ variances of all traits in both crosses did not differ significantly from each other, so the estimates of environmental variances were pooled together to obtain E_w of each trait in both crosses. When the variances of the F₂ and backcross generations of each trait were compared with the non-segregating generations, they were significantly larger than the E_w. These results indicated that genetic variance of all traits existed in generations derived from crossing between parents. Thus, the expected variation among F₂ individuals for all traits which consisted of $\frac{1}{2} D + \frac{1}{4} H + E_w$ was significantly larger than E_w. Consequently, the F₂ variance was segregating at a large number of genes with small effect or a few genes with large effect. When investigating the variance of F₂ generation of each trait, the value of F₂ generation variance was larger than the variance of P₁, P₂ and F₁. Based on this reason, Si content in rice tissues, yield and yield components traits might be also controlled by a large number of genes with small effect (Kearsey and Pooni, 1996).

The variance components of the six basic generations of each trait in both crosses which were estimated by the weighted least squares procedure for fitting the perfect model were four parameters, D, H, F and E_w. The chi-square test showed that these component variances fitted the perfect model and was not significantly different for each trait in both crosses. So that, the variation of each trait in both crosses seemed to be adequate to fit the D, H, F and E_w model. However, some parameters in the D, H, F and E_w model showed non-significant difference from zero when checked with the T-test. These conditions indicated that the effects of individual genes are very small (Kearsey and Pooni, 1996). The data were then proceeded to the fitting model in order to obtain the best statistical *cum* biological model by using model which is fitted with different combinations of parameters. The most appropriate model required at least two parameters, D and E_w, both of which were significant and the chi-square test of goodness of fit was non-significant for most traits. But some traits of both crosses required three parameters, D, F and E_w for the most appropriate model. Cross 1 was found in Si content in root at harvesting, number of panicles per

plant, number of spikelets per panicle, and spikelet fertility traits, and cross 2 was found in Si content in mature leaf blade, grain yield and 100-grain weight traits. These results were different from the results reported by Majumder *et al.* (1985), who reported that the variations of Si content in all the organs of rice were controlled by both additive and non-additive gene effects. However, their research was studied in rice under phosphorus-stress condition.

Since D variance could be fixed principally by selecting of homozygous lines and might be referred to as fixable gene effects (Mather and Jinks, 1971, 1977), so it was possible to improve the upland rice for drought stress condition by selecting genotypes which is able to accumulate high Si content in rice tissues together with high yield performance under drought stress condition. However, the whole traits under study were non-significant for H variance, indicating that every trait of parents in both crosses may be governed mostly by the dominant alleles and dominance gene effect was complete, therefore, H variances of all traits were zero (Kearsey and Pooni, 1996). Moreover, Kearsey and Pooni (1996) reported that detection of H was difficult because the basic generations were inefficient for determining dominance variance. The reasons were that firstly, because there may not be enough generations to fit a full trigenic interaction model and secondly, the number of parameters in a linkage model varies considerably with the particular set of generations in the experiment.

The data of six generation variances were used to estimate heritability of each trait which the genetic components were fitted to both the perfect fit values of D, H, F and E_w model and the most appropriate model. The results showed that the estimated h^2_n from the most appropriate model for each trait was similar to the estimated h^2_b and also similar to the estimated h^2_b from the perfect fit values of D, H, F and E_w model. However, the most reliable heritability should be estimated from the most appropriate model because it involves only those components that are shown to be significant statistically (Kearsey and Pooni, 1996). The results of estimated heritability from the most appropriate model showed that the average h^2_n of Si content in rice tissues in both crosses were 0.56, 0.60, 0.68, 0.56 and 0.66 for the young leaf blade, mature leaf blade, stem, root and hull, respectively. Average estimated h^2_n of Si content in rice tissues in both crosses was 61.2% or was accounted for about 61.2% of the total phenotypic variance.

While the average h^2_n for yield and yield components in both crosses were 0.67, 0.62, 0.65, 0.61 and 0.67 for grain yield, number of panicles per plant, number of spikelets per panicle, spikelet fertility and 100-grain weight, respectively, average estimated h^2_n among yield and yield components in both crosses was about 64.4% or was accounted for about 64.4% of the total phenotypic variance.

However, estimated h^2 values from the perfect model in these studies indicated that the non-additive genetic variance may affect Si content in rice tissues, yield and yield components because the dominance variance of all traits were not significant from zero and the dominant ratio [$\sqrt{(H/D)}$] was actually large (Table 4.12 to 4.21).

These results indicated that the selection and breeding of upland rice for drought resistance might be successful if selection is made from high Si content in rice tissues, together with high yield and yield components. However, selection of Si content in rice plant tissues should be made at tillering stage. In addition, selection for drought resistance in upland rice should be carried out in various locations in order to decrease the environmental effects or formulate more gene frequency of traits by delaying selection until late generation, in order to allow every gene to become fully homozygous as suggested by Srinivese (1988), Chahal and Gosal (2002).

Results of this study could be concluded that under drought stress condition at tillering stage, Si content in both crosses of upland rice showed significance of genetic variation in all traits. The Si content in rice tissues was controlled largely by a number of genes with small effects. Most phenotypic variation of Si content in rice tissues was contributed by D and E_w . Average h^2_n of Si content in rice tissues was 61.2% and average h^2_n among yield and yield components was 64.4%. Since, high accumulation of Si in rice tissues are attributed to the ability of the roots to take up Si (Takahashi et al., 1990; Richmond and Sussman, 2003), therefore, the h^2_n of Si uptake were rather high in this study. These results suggested that the ability of Si uptake in rice tissues can be employed and helpful as a selection criterion for breeding and improvement of drought tolerance in upland rice crops if crossing is made between biparental high Si uptake ability and followed by using more efficient selection methods.