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GENETIC ANALYSIS OF AGRONOMIC TRAITS IN *Oryza sativa* X *O. sativa* CROSS.

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BSc. (Hons) Crop Science

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A THESIS SUBMITTED TO THE SCHOOL OF GRADUATE STUDIES, KWAME NKRUMAH UNIVERSITY OF SCIENCE AND TECHNOLOGY, IN PARTIAL FULFILLMENT OF THE REQUIREMENT FOR THE DEGREE OF MASTER OF PHILOSOPHY IN AGRONOMY

(PLANT BREEDING)

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BSc. (Hons) Crop Science

September, 2015

DECLARATION

I hereby declare that except for references to works of other researchers, which have been duly cited, this work is my original research and that neither part nor whole has been presented elsewhere for the award of a degree

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We declare that we have supervised the student in undertaking the study submitted herein and confirm that he has our permission to submit.

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ABSTRACT

The objectives of this experiment were to study the inheritance of agronomic traits, determine the inheritance of aroma, estimates the heritability of important quantitative traits in rice (*Oryza sativa* L.). Six generations *viz*., P_1, P_2, F_1, F_2, BCP_1 and BCP_2 of a cross between IET6279 and IR70445-146-3-3 were used in present study. The experiment was laid out in a randomized complete block design (RCBD) with three replications at the CSIR- Crops Research Institute, Kumasi Ghana during 2014/2015 minor cropping season. Genotypes differed significantly at ($p>0.001$) for all the traits studied, which implies that the genotypes constitute a pool of germplasm with adequate genetic variability. Generation mean analysis suggested that additive effects had a major role for the expression of plant height, number of tillers, number of panicles, panicle length, culm length, leaf length, flag leaf width, grain width, number of spikelet per panicle, number of spikelet per plant. Spikelet fertility per cent and grain yield per plant, suggested that phenotypic selection was appropriate at an early stage. Epistasis effect was significant in most of the characters. Among interactions additive x additive and additive x dominance effects were important, but additive x dominance is more important than additive x additive effect, while dominance x dominance was less important than other genetic effect in the inheritance of traits. Both additive and non-additive gene action were important for the expression of days to 50% flowering, days to maturity, leaf width, flag leaf length, grain length, 100 grain weight, number of fertile spikelet per panicle and number of fertile spikelet per plant. Therefore, selection for these characters would be fruitful, if delayed till epistasis effects are reduced to minimum. The inheritance pattern of aroma in rice was carried out in the cross among one non-aromatic and one aromatic varieties. All the F_1 and BCP_1 plants of the cross were non-aromatic indicating that the gene controlling aroma in the donor parent was recessive. The segregation ratio of aromatic to non-aromatic plants was 1:3 in F_2 and

1:1 in BCP_2 plants confirming the monogenic inheritance of aroma. High broad sense heritability estimates (63 – 83%) was observed for characters viz. plant height, culm length, grain length, grain width, days to 50% flowering, days to maturity and 100 grain weight suggesting that the traits are primary under genetic control. Low estimates of broad sense heritability (27 - 49%) for number of tillers, number of panicle, panicle length, leaf length, leaf width, flag leaf length, flag leaf width, number of spikelet per panicle, number of spikelet per plant, number of fertile spikelet per panicle, number of fertile spikelet per plant, spikelet fertility per cent per plant and grain yield per plant, indicating environmental influence on this traits.

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DEDICATION

To my family: my father Mr. Bai Kamara; my wife Mrs. Yainkain Kamara and my kid Suffian Imran Kamara. Your love and support made it easier for me to persevere to the end.

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LIST OF ABBREVIATIONS

BCP_1 = Backcross to parent 1 (Male parent) BCP_2 = Backcross to parent 2 (Female parent) cm = Centimeter

CV = Co-efficient of Variation

CSIR-CRI = Council for Scientific and Industrial Research-Crops Research Institute, Kumasi, Ghana F_1:

= First filial generation

F_2: = Second filial generation

FAO = Food and Agriculture Organization of the United Nations

FAOSTAT = Food and Agriculture Organization Statistics

H^2_b = Broad sense heritability

H^2_n = Narrow sense heritability

INGER = International Network for Genetic Evaluation of Rice

IRRI	=	International Rice Research Institute
KNUST	=	Kwame Nkrumah University of Science and Technology
KOH	=	Potassium Hydroxide
MOFA	=	Ministry of Food and Agriculture, Ghana
MAS	=	Marker Assisted Selection
P	=	Probability
P_1	=	Parent 1 (Male)
P_2	=	Parent 2 (Female)
QTL	=	Quantitative Trait Loci
SNP	=	Single Nucleotide Polymorphic
WAAPP	=	West Africa Agricultural Productivity Programme

CHAPTER ONE

1.0 INTRODUCTION

Rice belongs to the genus *Oryza,* of the family *Gramineae,* and is a widely cultivated crop (Syed and Khaliq, 2008). It is the most important staple food crop in the world, and used by more than half of the world population (Kohnaki *et al.,* 2013). On global basis, it is planted on area of 159 million hectares with production of 685 million tons. China is the leading country in production (193 million tons), followed by India (148 million tons), Indonesia (60 million tons), Bangladesh (47 million tons), Vietnam (48 million tons) and Thailand (30 million tons) (FAOSTST, 2010). On out of the total arable land of the globe, approximately 11% is cultivated on rice annually, and it is second after wheat in its ranks (Bashir *et al*., 2010). Although rice is usually associated with Asia, it has become the fastest growing food source in Africa (Nwanze *et al.*, 2006).

The world population is expected to reach 8 billion by 2030 and therefore, rice production must be increased by 50% in order to meet the growing demand (Miah *et al*., 2013). However, with an increasing world population and gradually deteriorating environment, food security has become a major challenge around the world, especially in Asia and Africa (Sasson, 2012).

In Sub-Saharan Africa (SSA), consumption is increasing at a rate of 6% per annum, the highest in the world. The rate of increase in the consumption of rice in Africa has not been matched by corresponding increases in production and the demand-supply gap is widening. For example, Africa imported 10.7 million tonnes of rice in 2011, an increase of 1.3 million tonnes over the previous year_s figure (FAO, 2012). The continent currently imports about US $5 billion worth of rice every year. However self-

sufficiency in Africa rice production is declining as demand increases, driving the urgent need to increase and improve the continent‘s production of rice to satisfy the high demand (Sanni *et al*., 2012). To attain rice self- sufficiency and meet the future demand resulting the population growth. Development of high yielding genotypes with desirable agronomic traits for diverse ecosystem is therefore a necessity (Akinwale *et al*., 2011, Mulugeta *et al*., 2012)

Moreover, it is a nutritional cereal crop, providing 20% of the calories and 15% of proteins consumed by world‘s population (Muhammad *et al*., 2015). Although it is a chief source of carbohydrates and protein in Asia, it also provides minerals and fibers. [Apart from these, the rice bran is also an important source for animal feed in many countries of the world (Muhammad *et al*., 2015)].

It is a widely cultivated crop, and a great number of rice varieties and lines have been developed through varietal improvement and genetic resource conservation, evaluation and utilization programmes at various national and international institutions (FAO, 2000).

In Ghana, rice has become a major staple in recent decades with a per capita consumption of 25 kg/annum but most of the consumption is met by imports (MOFA, 2010). In 2009, the country imported over 350,000 tons of milled rice worth 600 million US dollars (Duffuor, 2009). This represents 70% of current demand, which is about 500,000 metric tons. MoFA (2009) revealed that, the estimated national rice consumption stands at 561,400 metric tons per year, whiles rice produced locally is 107,900 metric tons leaving a gap of 453,500 metric tons, which have to be imported (Directorate of Crop Services, MoFA, 2010).

Local rice production hardly meets the annual rice demand in Ghana (Bam *et al*., 1998). Low yield is one of the main challenges of rice production in Ghana due to poor production practice, environmental stresses and plant genotype. The study of the inheritance of quantitative and qualitative traits of the Ghanaian rice germplasm for the selection of appropriate breeding procedure will facilitate the development of superior yielding varieties for farmers.

However different agronomic traits may be important to increase the rice grain production. The considered traits may include short plant height, strong culms, moderate tillering, short and erect leaves, large and compact panicles, and early maturation (Paterson *et al*., 2005). Tillering in rice is one of the most important agronomic characters for grain production (Smith and Dilday, 2003), because the productive tiller number per plant determines the panicle number, a key components of grain yield (Yan *et al*., 1998). Panicle characters represent the most important part of rice plant type in respect of yield improvement

Many studies show that rice yield related characters (tiller number, grain number and grain weight) and agronomic characters (plant height and days to flowering) are inherited quantitatively, related genetically to one another and influenced by changing environments (Kobayashi *et al*., 2003).

Hence, rice breeders are interested in developing cultivars with improved yield and other desirable agronomic characters. Genetic variability for agronomic traits is the key component of breeding programmes for broadening the gene pool of rice. Plant breeders commonly select for yield components which indirectly increase yield.

Heritability (h^2) of a trait is important in determining its response to selection. Genetic improvement of plants for quantitative traits requires reliable estimates of heritability in order to plan an efficient breeding program. Anyanwu and Obi, (2014) recorded high

broad sense heritability for panicle length (94.2%), plant height at flowering (85.8%), tillers per stand (75.7%) and days to anthesis (71.4%). Ghosh and Sharma. (2012 also reported high heritability for pollen fertility percentage (99.83 %), spikelets per panicle (99.83 %), fertile spikelets per panicle (99.79 %), spikelets fertility per cent (99.77 %), sterile spikelets per panicle (99.70 %), head rice recovery (99.46 %), pollen fertility (99.64 %), grain yield per plant (99.61 %), days to 50 % flowering (97.75 %), flag leaf length (96.27 %), productive tillers per plant (95.38 %), 1000 seed weight (91.93 %), panicle length (83.19 %), flag leaf width (76.97 %) and flag leaf area (74.57 %) and plant height (62.85%). On the other hand, Anyanwu and Obi, (2014) recorded low broad sense heritability for 1000 seed weight (13%) and percentage fertile spikelet (29.7%). Kato (1997) estimated low broad sense heritability of 16% for the number of panicles per plant and 20 % to 33% for number of spikelet per panicle. Sürek and Korkut (1998) estimated high narrow sense heritability for grain weight, moderate for the number of spikelets per panicle and low for the number of panicles per plant.

Objectives of this work were therefore to:

To study the inheritance of important agronomic traits in *Oryza sativa* x *Oryza sativa* cross.

1. To determine the inheritance of aroma in *Oryza sativa* x *Oryza sativa* cross.
2. To estimate the heritability of some important quantitative traits in *Oryza sativa* x *Oryza sativa* cross.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Rice (*Oryza sativa* L)

Rice is the main staple for more than half of the world_s population. It is the world_s most diverse cereal crop and it is cultivated in five ecosystems including irrigated, rainfed lowland, upland, deep-water and tidal wetlands. It is grown as far north as Manchuria in China (50°N) and as far south as Uruguay and New South Wales, Australia (around 35°S) (Khush and Virk, 2000).

Rice cultivation is done at elevations as high as 3000 m above sea level in Bhutan and Nepal and as low as 3m below sea level in Kerala, India (Khush and Virk, 2000). Cultivated rice (*Oryza sativa L*) belongs to the family Poaceae (Gramineae), subfamily Bamboosoideae, and tribe *Oryzeae*. This tribe has 11 genera with the genus *Oryza* being the only cultivated species. *Oryza* has 24 species, two of which are cultivated. These are the Asian rice *O. sativa*, which is cultivated worldwide and *O. glaberrima*, the African cultivated rice, which is grown on a limited scale in West Africa. The Asian rice species, *O. sativa* is spread in large parts of the world and is more diverse than *O. glaberrima* (Sarla and Swamy, 2005). *O. sativa* is broadly divided based on morphological and physiological characteristics into *indica, japonica* and *javanica* subspecies. The *indica* and the *japonica* types are by far the most important. Both *O. sativa* and *O. glaberrima* are normally grown as annuals although *O. sativa* may be maintained as a perennial if protected from frost and drought (Sohl, 2005). There are divergent views regarding the ancestry of cultivated rice. It is believed that *O. sativa* and *O. glaberrima* had a common progenitor which is unknown and may not exist following a sequence from wild perennial to wild annual to cultivated annual ancestors (Sarla and Swamy, 2005). It is well established that *O. longistaminata* and *O. barthii* are the progenitors of *O. glaberrima*, while *O. rufipogon* and *O. nivara* gave rise to *O. sativa* (Ishi *et al*., 2001). The two wild species are diploid weedy species containing

the AA genomes and are distributed widely throughout Southeastern Asia where they hybridize freely with cultivated rice (Sohl, 2005). *O. glaberrima* differs from *O. sativa* in many qualitative and quantitative traits (Sarla and Swamy, 2005). In the field, *Oryza glaberrima* differs from *Oryza sativa* by its short, roundish, tough ligules and the small number of secondary branches on its panicles (Morishima, 1984).

The two cultivated rice species originated from a common ancestor with AA genome and are thought to be an example of parallel evolution (Khush and Virk, 2000). *O. sativa* is diploid, with 12 chromosomes (2n=24) and has been classified into five major subpopulations using SSRs (Garris *et al.*, 2005). These subpopulations include the *indica, aus, aromatic/GroupV*, *tropical japonica* and *temperate japonica* groups. Segregation distortions have been detected in crosses between the various rice subpopulations (Xu *et al.*, 1997; Lanceras *et al.*, 2000). Segregation distortion may affect pollen fertility, gene segregation or favour alleles of one parent (Aluko *et al.*, 2004)

2.2 Aroma

Aromatic rice, also known as fragrant or perfumed rice, is very popular in Asia and is classified as premium quality rice in markets throughout the world, including Ghana (Fitzgerald *et al.*, 2008; Diako *et al.*, 2010). There is an increasing demand for aromatic rice being driven by improving living standards of people around the world (Chen *et al.*, 2006). Classical examples of fragrant rice are the Basmati rice cultivars of India and Pakistan, Dulha bhog of Bangladesh, Khao Dawk Mali (Jasmine) of Thailand, Azucena and Milfor of the Philippines and Rojolele of Indonesia (Khush *et al.*, 1979). A total of 114 different volatile compounds have been associated with rice fragrance (Yajima *et al.*, 1979). Of these, 2-acetyl-1-pyrroline, or 2AP has been found to be the

major compound that distinguishes fragrant rices from non-fragrant ones (Lorieux *et al.*, 1996).

Aromatic rice varieties are playing a vital role in global rice trading. Major feature of these aromatic rice varieties is aroma which is being appreciated by many people and represents a high value added trait (Dela Cruz and Khush, 2000). So, rice needs attention toward improvement in its cooking qualities as well as several biochemical and morphological characteristics (Golam *et al*., 2004). The demand for aroma rice is increasing day by day. Unfortunately, the aromatic rice often has undesirable agronomic characters, such as low yield, susceptibility to pests and diseases, and strong shattering (Berner and Hoff, 1986). The agronomic value of a variety depends on many characteristics (Huang *et al*. 1991) and the most important characteristics are high yielding ability, resistance to diseases and pests, resistance to undesirable environmental factors and high quality of the products. The final aim is to increase the grain yield of rice (Swaminathan, 1999). Methods for smelling leaf tissue, grains after heating in water, and reacting with solutions of 1.7% KOH are available (Sood and Siddiq, 1978). The identification of 2-acetyle-1-pyrroline, using gas chromatography mass spectrometry selected ion monitoring (GC-MS-SIM) is also available (Yoshihashi *et al*. 2004). Since rice aroma, a polygenic quantitative trait with complex inheritance pattern is highly influenced by environment it is difficult to identify genes that determined this trait (Pachauri *et al*. 2010). Genetic studies on the inheritance of aroma in rice revealed that a recessive nuclear gene controls aroma in rice (Dong *et al*. 2000).

Pinson (1994) reported that aroma is controlled by a single recessive gene in Jasmine 85 and p1467917 and by two genes in Amber and Dragon Eyeball. Digenic segregation for aroma were also reported by Lin (1991). A single recessive gene for aroma in

Lemont was mapped on chromosome 8 through Restriction Fragment Length Polymorphism (RFLP) analysis (Ahn *et al*., 1992).

It was revealed that rice aroma is controlled by three Quantitative Trait Loci (QTLs), *aro3.1, aro4.1* and *aro8.1* located on short arm of chromosome 3 and long arms of chromosome 4 and 8, respectively (Amarawathi *et al.* 2008). The major aroma QTL (*aro8.1*) was identified on chromosome 8 with LOD score of 11.54 between SSR markers RM223 and RM80. This QTL explained 18.9% of the phenotypic variation for aroma. This QTL was mapped in the same region as that reported earlier by Ahn *et al*. (1992) and Lorieux *et al*. (1996). Later, studies by Bradbury *et al*. (2005), Chen *et al*. (2006) and Amarawathi *et al*. (2008) identified *badh2* (recessive allele) as a candidate gene for aroma on this chromosome, which codes for enzyme betaine aldehyde dehydrogenase (BADH). This enzyme is involved in the synthesis of glycinebetaine-a powerful osmoprotectant against salt and drought stress in a large number of species. Rice does not accumulate glycinebetaine but it has two functional genes coding for the BADH enzyme. Most of the aromatic rice varieties from different isozyme groups share the same 8 bp deletion in intron 7 of *badh2* gene (Bradbury *et al*. 2005) for which Amarawathi *et al*. (2008) designed a perfect gel based marker (nksbadh2) that discriminates between aromatic and non-aromatic varieties. The *BADH1* gene located on chromosome 4 having similar biochemical function has also been anticipated to have a contributory role in aroma expression in rice (Singh *et al*. 2010).

The diversity of this gene has been studied in a large collection of varieties and results showed that an 8 bp deletion in the seventh exon of BADH2 causing a reading frame shift was present in most aromatic accessions, but other less frequent mutations

associated with aroma were also detected (Bradbury *et al*., 2005; Bourgis *et al*., 2008; Shi *et al*., 2008; Kovach *et al*., 2009; Sakthivel *et al*., 2009).

2.3 Tiller Number

Tillering in rice is one of the most important agronomic traits for grain production because tiller number per plant determines panicle number, a key component of grain yield (Liu *et al*., 2011; Zhu *et al*., 2011). Furthermore, tiller number usually serves as a suitable model trait for the study of developmental characteristics, since it changes over time. Hence, the genetic elucidation of tiller number has become a focus in rice genetic and breeding research (Liu *et al*., 2010)

Tillering or the degree of branching determines shoot architecture. The architecture of the shoot system affects a plant‘s light harvesting potential, the synchrony of flowering and seed set and, ultimately, the reproductive success of a plant (Kuraparthy *et al*. 2007). Tillers that grow from the main stem are called primary tillers and those grow from primary tillers are called secondary tillers (Kirby and Appleyard, 1981). In practice, however, only a few tiller buds grow into a tiller, and only a proportion of these tillers survive to become the ultimate number of tillers, depending on tiller appearance and tiller survival (Evers *et al*. 2006). Tillers of different genotypes show various spatial orientations at different developmental stages, giving rise to morphologically distinct plant types. Before the stem elongation, seedling growth habit (SGH) varies from prostrate to semi-prostrate to erect. After anthesis, spikes of the adult plant also differ in their compactness from spreading to compact (Li *et al*. 2002).

The number of productive tillers per plant plays an important role in the formation of grain yield in rice. The development of tillers is affected by various environmental factors including manuring, planting density, and climatic conditions such as light, temperature, water supply and so on. Tiller number per plant is a quantitative trait with

a relatively low heritability of 29.8-49.6% (Xiong, 1992). The genetics of plant tiller number at the maturity stage have been well documented by traditional statistical analysis. Murai and Kinoshita (1986) considered the additive gene effects to be more important than the non-additive effects. Ahmad *et al*., (1986) showed predominance of additive gene action without the interference of non-additive gene effects, whereas Perera *et al*., (1986) suggested that both the number of tillers at maturity and the number of panicles per plant were controlled by genes with additive, dominant, and epistatic effects. Using diallel analysis, Xu and Shen (1991) showed that an identical polygenic system appeared to be responsible for the genetic control of tiller number at different growth stages, and that the contributions of additive effects to the variation increased, while those of non-additive effects and environmental factors decreased, with the growth of rice plants

The number of fertile tiller and number of grains per panicle can be determined at vegetative and reproductive phase, respectively (Golam *et al*., 2011). Larger number of tillers can be expected at longer vegetative phase. But, the space available or optimum growth will limit the number of tillers which produce panicles (Golam *et al.,* 2011). In determining the number of panicles the maximum tiller-number stage is the most important stage (Wang *et al.,* 2007).

2.4 Plant Height

Plant height is not only a decisive factor in plant architecture, but also an important agronomic trait that is directly linked to the harvest index and yield potential (Yang and Hwa, 2008). The total number of elongated internodes and the length of each elongated internode determine plant height. A rice plant usually has 4–6 elongated

internodes and its height is mediated by qualitative genes and quantitative trait loci (QTL; Huang *et al.*, 1996), and influenced by environmental factors.

Other than yield components, plant height and heading date are two important traits related to yield potential of rice domestication and modern breeding programs. plant height plays an important role in yield improvement during breeding programs, as was shown in the most famous historical milestone with a semi-dwarf variety, IR8, invoking the ―Green Revolution‖ in the late 1960s. Varieties with reduced height can avoid wind and rain damage for resistance to lodging and for increase in yield with adequate fertilization by nitrogen (Yann *et al.,* 2011).

In general, plant height of rice is regulated by several genes and influenced by the environment. The dwarf genes, *d-1* to *d-60*, and semi-dwarf genes, *sd-1* to *sd-7*, were found to be induced artificially by radiation or chemicals or naturally identified; some were mapped by classical genetic analysis (Kinoshita, 1995). Dozens of plant height genes were also detected in various interspecific, inter-subspecific and intrasubspecific crosses (Li *et al*., 2003; You *et al*., 2006). Quantitative trait loci (QTLs) for plant height, isolated to elucidate functions under molecular, biochemical and physiological levels, participate mostly in the metabolism and signal transduction of phytohormones. Deficiency in gibberellin acid (GA) and brassinosteroids, which can stimulate cell division and elongation, hinders plant growth and results in a dwarf stature. Examples include *D18, D35,* and *sd-1* involving a GA synthetic pathway (Itoh *et al*., 2004); *D1, SLR1, GID1* and *GID2* involving a GA signal transduction pathway (Ueguchi-Tanake *et al*., 2005); *D2* and *D11* involving a brassinosteroid synthetic pathway (Tanabe *et al*., 2005); and *D61* involving a brassinosteroid signal transduction pathway (Yamamuro *et al*., 2000). In addition, many genes involving cell division and elongation and development of apical meristem have great effect on plant height. Recently, knowledge

of the regulation mechanism of plant height has been incorporated into breeding programs to generate short but high-yield rice (Ashikari *et al*., 2005).

2.5 Days to Flowering

Transition of apical bud in-to floral bud demarcates the initiation of reproductive stage of rice in its growth cycle. Number of days taken for this transition determines the heading date or days to flowering of any rice cultivar (Yano *et al*., 2001). Maturity of rice is said to be controlled by three different types of genes namely genes controlling photoperiod sensitivity, genes determining vegetative growth and genes controlling the total number of internodes (Li *et al*. 1995). These genes determine the crop duration, crop architecture and the final grain yield of rice.

Among many agronomic characteristics, days to flowering, plant height and yield potential determine the economic production of any crop including rice (Xue *et al.* 2008). Plant height is the main determining factor of plant architecture which directly affect the final yield. Other than the plant height number of tillers/plant, number of grains per panicle and grain weight also directly affect the final yield of rice (Selvaraj *et al*. 2011). Heading date, or days to flowering, is one of the critical traits for rice adaptation in diverse environments and rice cultivation in various regions and cropping seasons (Yann *et al*., 2011). Days to flowering in rice is determined by the length of basic vegetative growth phase and photo period sensitivity of the rice cultivar (Yano *et al*, 1997). Basic vegetative growth phase and days to flowering are controlled by many already identified genes such as *Ef-1* and *Se-1-Se-7* (Poonyarit *et al*., 1989). Genetic studies in rice indicate that the flowering time gene named *Hd1* regulates days to flowering by inducing flowering in short-day conditions and inhibiting flowering in long day conditions (Lin *et al*. 2000). Different genes involved in flowering time in rice have been reported in several studies (Okumoto and Tanisaka, 1997). This genetic

differentiation has created a broad variation in days to flowering among rice cultivars. A quantitative trait loci named *DTH8* was found to regulate yield, plant height and days to flowering in rice (Wei *et al*., 2010). There are several alleles of *DTH8* and type 4, type 5, and type 6 alleles of *DTH8* were studied by Wei *et al*. (2010). The results showed that all transgene-positive plants with type 4,-5, and-6 alleles of *DTH8* were tall and late flowering with large panicles, whereas all transgene-negative plants have phenotypes with opposite features (Wei *et al*., 2010). This finding proves that tall and late flowering characters of rice inherit together if the late flowering is determined by *DTH8*.

Since panicles from those plant that start flowering earlier score higher filled grain percentages exhibiting higher sink efficiency than the panicles from plant that start flowering late in the season, the late flowering reduces dry matter accumulation in grains (Mohapatra *et al*., 1993). This emphasizes that the flowering date affects the final grain yield of rice in a given season. Effect of yield attributing traits on the final grain yield of rice has been extensively studied (Selvaraj *et al*., 2011).

In rice, heading date is a complex trait controlled by multiple genetic and epigenetic factors. Many environmental factors, such as day length, temperature, light intensity, and nutrients, control heading date in rice, and a number of genes participating in the flowering time were identified using mutants through genetic analyses in many previous studies (Yano *et al*., 2001). A total of 15 QTLs affecting heading date were detected by interval mapping of the F_2 population and several advanced backcross populations of *O. sativa* ssp. *Japonica Nipponbare* × *O. sativa* ssp. *Indica*- Kasalath, five of these-*Hd1, Hd2, Hd3, Hd5,* and *Hd6*- were regulated by day length (Yano *et al*., 2001). Numerous QTLs were also identified from several interspecific, intersubspecific and intra-subspecific crosses (You *et al*., 2006). Some rice heading

date genes, isolated via positional cloning and gene functions explored at the molecular level, were found to be involved in (1) light-controlled photoperiodic response, such as *Hd6* encoding the α subunit of casein kinase II; *Hd3a*, functioning as florigen similar to *Arabidopsis FLOWERING LOCUS T* (*FT*); and *Ehd1*, encoding a B-type response regulator acting as a floral inducer under short day; or (2) clock- controlled circadian response, such as *Hd1*, which functions as a transcription similar to *CONSTANS* (*CO*), and *Hd2*, suspected as a pseudo response regulator (Murakami *et al*., 2005). The function and structure of genes involved in flowering time in rice, a short-day plant, and in *Arabidopsis,* a long-day plant revealed a conserved floral pathway but with minor difference, of which the function of *Ehd1* is unique to rice (Izawa, 2010).

2.6 Leaf Size, Shape and Length

Much attention has been paid to leaf shape of rice in the process of ideotype breeding (Yan *et al*., 2006). The length, width, angle and area are the three traits determining the shape and size of a leaf, among which the area is attributable to the length and width with higher correlations between length and area than between width and area (Peng *et al*., 2008). Light interception by a canopy of leaves is strongly influenced by the leaves' size and shape, angle, and azimuthal orientation, vertical separation and horizontal arrangement, and by absorption by non-leaf structure (Yoshida, 1972).

Leaf area has been measured in experiments concerning some physiological phenomenon such as light, photosynthesis, respiration, plant water consumption and transpiration. In addition, leaf number and area of a plant have an important role in some cultural practices such as training, pruning, irrigation, fertilization, etc (Cirak *et al*., 2008). Leaf area estimation is an important biometrical observation for evaluating plant growth in field and pot experiments (Kumar and Sharma, 2010). Leaf area plays

an important role in photosynthesis, light interception, water and nutrient use, crop growth and development (Caliskan *et al*., 2010a; Caliskan *et al*., 2010b).

Leaves are primarily involved in photosynthesis and transpiration, influencing yield performance in crops (Wang *et al.*, 2011). The size, shape, and number of leaves determine a plant‘s photosynthetic potential and play important roles in determining plant yield, disease resistance, and stress responses (Pérez-Pérez *et al.*, 2010). In addition to these traits, the colour (or degree of leaf greenness) is also an important trait related to the leaf nitrogen status (Singh *et al.*, 2002). Many previous studies have uncovered how the leaf size and shape is controlled from the perspective of leaf development (Moon and Hakes, 2011). Leaf development starts with the recruitment of founder cells from the shoot apical meristem, which is characterized by the downregulation of *knotted1*-like homeobox genes (Byrne, 2005). The over-expression of five of these genes (*OsH1*, *OsH6*, *OsH15*, *OsH71*, and *OsH43*) in rice profoundly affects leaf formation and results in severely malformed leaves (Sentoku *et al.*, 2000). WUSCHEL-related homeobox genes also play an important role in recruiting founder cells as a meristem organizer (Kessler and Sinha, 2004). In rice, two WUSCHEL-related homeobox genes, namely *NAL2* and *NAL3* (*NAL2/3*), affect leaf lateral-axis outgrowth and leaf width (LW) (Cho *et al.*, 2013). After recruitment, several genes act to establish polarity in developing leaves, of which the class III homeodomain leucine zipper (HD-Zip III) genes specify leaf adaxial identity (Kessler and Sinha, 2004). OsHB genes are members of the rice HD-ZIP III gene family, and the ectopic expression of *OsH1*, *OsH3*, and *OsH5* results in rolled and filamentous leaves (Itoh *et al.*, 2008). In addition, some genes associated with leaf size and shape have been identified via map-based cloning in rice. For example, the mutant *nal1* exhibits reduced LW, a decreased number of longitudinal veins, and a defective vascular system. The

mutant *nal1* encodes a plant-specific protein that affects polar auxin transport and vascular patterns (Qi *et al.*, 2008). *NRL1* and *NAL7*, which are associated with leaf size and shape, were cloned and characterized using the same approach (Fujino *et al.*, 2008; Hu *et al.*, 2010).

Leaves are often the most noticeable parts of a plant; they are the predominant photosynthetic organs and are of pivotal importance for carbon fixation. Some leaf parameters, such as shape, number, size, thickness, direction and chloroplast level are very important factors influencing the biomass formation and success of a plant.

A prototypical leaf has three axes: proximodistal (tip–base), dorsiventral (adaxial–abaxial) and lateral (left–right; Champagne and Sinha, (2004); Reinhardt and Kuhlemeier, (2002). As with most grass leaves, rice leaves are clearly divided into the proximal sheath and the distal blade. Leaf blade length is controlled by proximodistal axis. In *Arabidopsis*, leaf length is specifically mediated by the number of leaf cells by the ROT4 peptide (Narita *et al.*, 2004).

2.6.1 Flag Leaf Length and Width

With increasing population, high yield has become one of targets in rice breeding. Photosynthesis is the primary source of grain yield in rice (Chen *et al*., 1995). The top three leaves of rice, particularly the flag leaf, are the main source of carbohydrates production (Abrol *et al*., 1993). At least 50% of photosynthetic products for grain are provided by flag leaf, the most important organ for photosynthesis (Li *et al*., 1998). Some traits, such as size and shape of flag leaf, affect photosynthesis to a certain extent, thereby influencing production (Yue *et al*.,

2006). Therefore, flag leaf shape is an index for ideal plant-type in rice breeding (Yang and Yang, 1998).

The leaf (source) being the organ of photosynthesis is considered to be the important determinant which is characterized for higher photosynthetic capacities (Prakash *et al*., 2011). It has been proven that the flag leaf, stem and head are the closest source to the grain (Prakash *et al*., 2011). Grain yield increase would be effectively rested with the basis of the capabilities of yield components and other closely associated traits (Xue *et al*., 2008). The morphological traits of flag leaf such as size and shape, and physiological traits of flag leaf such as chlorophyll content and photosynthesis capacity have been considered to be the important determinants of grain yield in cereals (Chen *et al*., 1995). Therefore, flag leaf is one of the greatest components in determining grain yield potential in cereal crops (Xue *et al*., 2008). Flag leaf has an important role in rice yield by increasing grain weight in amount of 41 to 43 percent (Yoshida, 1972). Flag leaf area could be chosen as a factor for increasing rice grain yield (Davood *et al*., 2009). For this reason flag leaf is an activist leaf at grain filling period. Fan *et al*. (2007) reported that flag leaf strongly contribute to grain filling after heading, while flag leaf shape is one of the main factors determining its photosynthetic ability. Rice for reaching to maximum grain yield need sufficient LAI for best photosynthesis activity while in rice 60-90% of total carbon in the panicles at harvest is derived from photosynthesis after heading, while 80% or more of nitrogen (N) in the panicles at harvest is absorbed before heading and remobilized from vegetative organs (Yoshida, 1972). Davood *et al*. (2009) reported leaf senescence during reproductive and maturity stage to be directly related to biomass production and grain yield of rice crop. Flag leaf angle had an important effect for increasing rice grain yield. Grain yield is a function of photosynthesis products and optimum distribution, and arrangement of leaves increase the efficiency of biomass production in crop cultivars. Modification of flag leaf angle have been emphasized by investigators as a means of obtaining better light utilization, with more upright leaves permitting the penetration of solar energy into

lower leaves of aerial structure of plant (Jennings *et al*., 2003). So flag leaf photosynthesis activity has an important effect on rice grain yield. Flag leaf help in maintaining photosynthesis during the grain-filling period, this could increase yield capacity because photosynthesis during ripening contributes to grain carbohydrate by 60–100% (Yoshida, 1981). Results of shading experiments by many workers have shown that carbohydrates contributed by assimilating green parts above flag leaf nodes amount to more than 85% of the total accumulation in the grain (Yap and Harvey, 1971). Flag leaf appeared to play a major role in enhancing productivity (Padmaja, 1991). Therefore efforts were made to relate the flag leaf area with yield parameters *viz*., number of panicles, panicle length, number of grains per panicle, 1000 grain weight, grain yield per plant, grain yield per m2, dry matter per m2 and yield (t/ha) in order to assess and identify the productive cultures for selection. Jennings *et al*. (1979) reported that flag leaves also help to stabilize yield because erect, moderately long flag leaves, such as those of CICA 4, help protect ripening grain against bird damage.

Besides several genes controlling leaf size and shape cloned with mutants (Hu *et al.,* 2010; Xiang *et al*., 2012), some QTLs for the traits of flag leaf size and rice yield have also been mapped with diverse populations, such as F_2, doubled haploid (DH) and recombinant inbred lines (RILs) (Wang *et al*., 2009; Jiang *et al*., 2010a). Yan and Wang (1990) studied 11 flag leaf traits in *indica-japonica* hybrids, and argued that flag leaf length (FLL), FLW and flag leaf area (FLA) were controlled by two pairs of genes with at least more than 60% heritability. In recent years, with the rapid development of molecular markers and the increase in resolution of the linkage map, numbers of QTLs for flag leaf size and shape have been reported in rice. Li *et al*. (2000) detected 13 QTLs for FLL, FLW, FLA and length-width ratio (LWR), explained 8.7% ~ 18.5% of

phenotypic variation, with DH population from a cross of Zhaiye Qing 8 and Jingxi 17. Using a DH population and a genetic map with 175

SSR markers under multi environments, Cao *et al*., (2007) detected 15 QTLs affected FLL, whose genetic intervals were 2 ~ 18 cM. Xiao *et al*., (2007) also identified 8 QTLs for the traits of FLL, FLW and FLA in the backcross recombinant inbred lines (BILs) derived from a cross between Koshihikari and Kasalath. However, most studies focused on the size and shape of the flag leaf and few involved in their relationship with yield.

2.7 Culm Length

Lodging is one of the major factors limiting the yield potential of both inbred and hybrid rice cultivars and has received particular attention. Lodging can cause severe yield loss and poor grain quality because of reduced canopy photosynthesis, increased respiration, reduced translocation of nutrients and carbon for grain filling, and increased susceptibility to pests (Hitaka, 1969). Many studies have shown that the culm characteristics contributing to lodging resistance include basal internode length and thickness, plant height, culm wall thickness, and leaf sheath wrapping and thickness (Matsuda *et al.,* 1983), but the morphological and anatomical characteristics associated with the large culm trait in rice have not been systematically identified. Nevertheless, lodging resistance is positively correlated with the culm diameter and wall thickness of the basal internodes both in wheat (Wang *et al.,* 2006) and barley (Dunn and Briggs, 1989). Moreover, aside from the thick culm, the culm vascular bundle number in rice also contributes to lodging resistance (Duan *et al.,* 2004). Zhu *et al.,* (2008) have found that a large number of quantitative trait locus alleles affecting culm length, strength, and thickness in *indica*/*japonica* crosses of rice are related to lodging resistance. Kashiwagi *et al*., (2008) obtained similar results and suggested that increasing culm

diameter in rice breeding programs can improve lodging resistance. Aside from improving lodging resistance, a thick culm may also act as a carbohydrate store for high yield in rice (Hirose *et al*., 2006). Furthermore, morphological characteristics such as culm thickness, leaf size, leaf angle, and plant height at the heading stage have been considered important traits in breeding both super rice (Chen *et al.,* 2005) and bioenergy crops (Ookawa *et al.,* 2010). Cultivars with large culms, therefore, may be ideotypes for super rice breeding because the characteristics of semi-dwarfism, lodging resistance, and heavy panicles have been considered to be important traits for super rice breeding (Duan *et al*., 2004; Ma *et al*., 2004).

2.8 Spikelet Number and Spikelet Fertility

Rice grains yield is a quantitative trait influenced by other agronomic traits and environmental factors. Spikelet number per panicle is important component of rice grain yield (Zong *et. al*., 2012). The development of sufficient sink capacity and high degree of grain filling of superior rice cultivars should consider the distribution of spikelet number per panicle and degree of grain filling. Sheehy *et al*., (2001) found that the high yielding plant type with high potential for spikelet number per panicle, was highly associated with rice grain yield. The study of inheritance of this trait is the important way for rice breeding program. Mishra and Janoria, (2003) reported that three major independent loci with complete dominance were involved with low number of spikelet without cumulative effect. Liu *et al*., (2010) and Ahamadi *et al*., (2008) detected three QTL controlling spikelet number per panicle in rice. Nevertheless, Lin and Yan, (2004) reported that spikelet number per panicle was controlled by polygenes. Kato, (2004) detected four QTL of spikelet number, which three also showed significant effects on this trait. Broad sense heritability and genetic advance are the important selection parameters for high yielding rice genotypes. Binse

et al., (2009) reported high broad sense heritability and genetic advance of spikelet per panicle. According to Padmaja *et al.,* (2008) and Liu *et al*., (2010) there is a predominance of additive gene action in this trait. However, Bharadwaj *et al*., (2007) found that moderate heritability and high genetic advance indicated that the environmental influence on this trait in considerable amounts. The number of primary and secondary branches (SBs) strongly influences the average number of SPP (Yamagishi *et al*., 2002). QTLs for the SPP have been detected using various segregating populations (Kobayashi *et al.,* 2004). Several QTLs for the SPP have also been identified in wild relatives (Onishi *et al*., 2007). These QTLs are located across the chromosomes and provide valuable information on the genes that control the SPP in different populations. In addition, SPP QTLs have been mapped as a single Mendelian factor (Zhang *et al.,* 2006, 2009) and were rarely found on chromosomes 5 and 10 (Tan *et al.,* 2008). And these studies showed that the wild rice allele leads to increased or decreased number of SPP.

Spikelet fertility was studied because F_1 hybrids had very low seed set. Hybrid sterility means a reduced fertility in the hybrid than the parents (Sano, 1997). It generally occurs upon hybridization between distantly related taxa. Spikelet sterility in F_1"s results from anther indehiscence, pollen sterility, disharmonious interactions between nuclear genes or between cytoplasm and nuclear genes as well as differences in the structure of chromosomes (Sano, 1997). A difficulty in examining the genetic basis of hybrid sterility results from the fact that the genetic basis of F_1 sterility might differ from that of F_2 sterility (hybrid breakdown). Therefore, it is difficult to examine the segregational pattern of genes controlling F_1 hybrid sterility in the F_2 generation (Sano, 1997). Sterility is an abnormality which occurs during gametogenesis to seed formation (after fertilization) often resulting in a reduced seed set. Sterility is a

complex trait because a number developmental processes cause a reduction in seed setting (Sano, 1997). INGER (1996) has ranked various levels of fertile spikelets as follows: Highly fertile (≥90%), fertile (75-89%), partly sterile (5074%), highly sterile (<50% to trace) and completely sterile (0%). Blanking or spikelet sterility caused by poor anther dehiscence and low pollen production and hence low numbers of germinating pollen grains on the stigma is induced at this stage (Jagadish *et. al*., 2007). Series of investigations have shown that spikelet sterility or blanking is induced by low temperatures during the reproductive growth phase, especially during the booting stage in areas with a cool climate (Shimono *et. al.*, 2010). Furthermore, Farrel *et al.*, (2006) reported that low temperature during reproductive growth stage disrupts proper pollen development, leading to a shortage of sound pollen at the flowering stage.

Flowering (anthesis and fertilization), and to a lesser extent booting (microsporogenesis), are the most susceptible stages of development to temperature in rice (Farrell *et al.,* 2006). Previous studies, summarized in Satake and Yoshida (1978), have shown that spikelets at anthesis that were exposed to temperatures >35ºC for about 5 d during the flowering period were sterile and set no seed. Sterility is caused by poor anther dehiscence and low pollen production, and hence low numbers of germinating pollen grains on the stigma (Prasad *et al*., 2006). There is genotypic variation in spikelet sterility at high temperature (Prasad *et al., 2006*) that can be defined by different temperature thresholds (Nakagawa *et al*., 2002). It has been suggested that Indica spp are more tolerant to higher temperatures than japonica spp (Matsui *et al*., 2000), although heat- tolerant genotypes have been found in both subspecies (Prasad *et al*., 2006). Genotypes N22 (Prasad *et al*., 2006) and Akitakomachi (Matsui *et al*., 2001) are the most tolerant genotypes found to date among *indicia* and *japonica* spp, respectively. The response to duration of exposure to

temperature >35ºC appears to be quantitative, with shorter durations at higher temperatures having the same effect as longer durations at cooler temperatures (Satake, 1995). However, interactions between temperature and duration have not been quantified. Where responses to high temperature have been modelled, spikelet sterility increases in response to daily maximum temperature (Nakagawa *et al*., 2002). If there is an interaction between temperature and duration, then the response of spikelet fertility to temperature may be better modelled by a cumulative temperature response above a threshold temperature (Vara Prasad *et al*., 1999, for peanut). Furthermore, if only a short period of high temperature causes sterility, then the timing of this episode in relation to peak flowering will be critical, both for phenotyping (i.e. to differentiate between escape and absolute tolerance) and modelling the impact of high temperature (Wheeler *et al*., 2000). It follows that effects of temperature on flowering pattern, which have not been studied, are also likely to be important with respect to escape and the total number of spikelets.

2.9 Grain Length and Width

Rice grain length and width are the two important quantitative traits also closely related to the exterior quality of the rice (Shi *et al.*, 2000). Genetic analyses of length and width of rice kernels have been reported by some of the researchers and most of the studies have shown that rice grain shape is quantitatively inherited (Zhang *et al*., 2005). It has been shown that rice grain shape is controlled by triploid endosperm genes, cytoplasmic genes, and maternal genes (Shi *et al*., 2005) and their genotype into environment interaction effects. The length, width and seed thickness is one of the quantitative measures of grain shape. Grain morphology i.e. color, size and shape having unique position for the breeders during the selection and evaluation process (Kasem *et al*., 2009; Bai *et al*., 2010). It is thought to relate to the largest shape

variation in small grain crops. On the other hand, length width ratio is the major genetic variation of rice grain shape and highly associated with the quantitative traits parameters and can be used in the breeding program for the improvement of the rice varieties (Iwata *et al*., 2010). The length of the hulled grain is simply a measure of the rough rice kernel in its greatest dimension while the width of the hulled grain is the measure of the rough rice kernel width in its maximum dimension. The length and width of the seed rice are variable, sometimes even within a variety, because of the variation in the length of the awn and the pedicel (IRRI, 2009). The size and shape (seed width) is a stable varietal property that can be used to identify a variety (Rickman *et al.,* 2006). Rice varieties are classified as short, medium, or long grain by rough kernel dimension ratio (Slaton *et al.,* 2000). Since kernel type and dimension are of importance to the millers and processors, these characteristics are considered in the breeding of a new variety.

2.9.1 Thousand (1,000) Grain Weight and Grain Yield

The mass of grains of individual plants directly determines the yield of a population, (Verica *et al*. 2013). As a final product of the interaction between a lot of physiological and biochemical processes in the plants, the mass of grains from plant depends on several properties, such as the number of panicles per plant, number of grains per panicle and weight of grain, (Verica *et al*. 2013). Changing any of these properties results in change of the grain yield per plant. The link of this property with other components of yield indirectly contributes to its high variability, (Verica *et al*. 2013). Therefore the study of the genetic nature can lead to faster and more reliable success in plant breeding for this purpose. Another characteristic that measures varietal purity is the thousand (1,000) hulled grain weight. This characteristic is also very important in the identification of a variety. Takeda, (1991) associated small seeds with low

seedling vigor and difficult mechanical harvesting which is a problem in crop cultivation but small seed is favored under natural selection because it is frequently linked with large number of seeds per plant, more rapid maturity and wider geographic distribution. It has been concluded that the thousand (1,000) seed weight is a useful tool in calculating the seeding rates and harvest loses Anonymous, (2007). Increase of the grain weight is a method for increasing rice yield. Genes that affect the grain size have been identified in inter-specific crosses (Li *et al*., 2004; Aluko *et al*., 2004). In most cases, wild-type alleles were associated with small grain, whereas cultivar alleles were associated with large grains. Usually, grain size is determined by grain length (GL), width, and thickness. These 3 traits are quantitatively inherited under the control of several or many genes. To date, 5 key genes controlling seed size have been isolated in rice: *GS*3, *GW*2, *qSW*5 or *GW*5, *GIF1* and *GS5*. (Weng *et al*., 2008; Li *et al*., 2011). *GS*3 has a major effect on seed length, whereas *qSW5/GW5* and *GW2* confer both the seed or grain width (GW) and weight in rice. *GIF1* encodes a cell-wall invertase that is required for carbon partitioning during early grain filling, and the over-expression of *GIF1* by using its native promoter leads to large grains (Wang *et al*., 2008). Shomura *et al*. (2008) found that a deletion in *qSW*5 was associated with grain size owing to an increase in the cell number in the outer glume of the rice spikelet.

Grain weight is one of the three yield components and is of great importance for rice yield. Generally it is indicated as one-thousand-grain weight, which is an integrated index of grain length, width and thickness. Furthermore, grain weight is important in the evolution of cereal crops because large grains tended to be selected during the early domestication process, as evidenced by the fact that most cultivated species have larger grains than their wild relatives (Li *et al*., 2004). Since the 1960‘s, breeding of large grain varieties has been developed and increasing attention has been paid to improving

rice production because large grain is considered one of the key factors for super-rice development. Grain weight is a highly heritable characteristic (40% - 60% (Ma *et al*. 2006)), and several independent studies on rice have been conducted systematically. Panwar and paroda, (1983) showed that it was determined by both additive and dominant effects. Because grain weight is a complex trait controlled by multiple genes, it is difficult to map and clone grainweight related genes. Through the use of molecular biology, a series of quantitative trait loci (QTL) for grain weight have been identified. So far, at least 89 rice grain weight related QTL have been detected and they are distributed on all of 12 chromosomes (Ma *et al*. 2006). Among them, QTL on chromosome 3 have been identified in several independent studies using different populations. Lin and Wu, (2003) identified 16 grain-weight QTL using a recombinant inbred line (RIL) population of H395/Acc8558, and five of them were located on chromosome 3. Additionally, one locus in the pericentromeric region of chromosome 3 has been frequently detected as a major QTL for both grain weight and grain length in many studies with different populations: the crosses of Lemont x Teqing (Li *et al.* 1997),

Zhenshan 97 x Minghui 63 (Xing *et al*. 2002), V20 x *Oryza rufipogon* (Xiao et al. 1998), Labelle x Black Gora (Redon˜a and Mackill, 1998), and Asominori x IR24 (Kubo *et al*. 2001). Li *et al*. (2004) recently fine-mapped a grain weight QTL, *GW3.1*, to a 93.8-kb region on chromosome 3 with a set of near-isogenic lines (NILs) from the cross between *Oryza sativa*, cv, Jefferson and *O. rufipogon* based on five generations of backcrossing and seven generations of selfing. Fan *et al*. (2006) isolated a major QTL, *GS3*, located in the same region using the BC_3F_2 of Minghui 63/Chuan 7. There seems to be a cluster of QTL/genes controlling yield-related traits in this region of chromosome 3 (Thomson *et al*., 2003). Recently, QTL *GW2* on chromosome 2 for rice

grain width and weight, a QTL *Ghd7* controlling multiple traits (including number of grains per panicle, plant height and heading date), and a newly identified QTL qSW5 for seed width have been isolated via a map-based cloning strategy (Xue *et al*., 2008, Shomura *et al.,* 2008). However, only a few QTL have been detected on chromosome 6 (Guo *et al*., 2003).

Grain yield in rice is a complex character, quantitative in nature and an integrated function of a number of component traits (Sharma and Sharma, 2007). Improvement of rice grain yield is the main target of breeding program to develop rice varieties (Ranawake *et al*., 2013). Grain yield is a complex trait, controlled by many genes and highly affected by environment (Ranawake *et al*., 2013). Different traits may be important to increase the rice grain production. The considered traits may include short plant height, strong culms, moderate tillering, short and erect leaves, large and compact panicles, and early maturation (Paterson *et al.* 2005). Rice grain yield is determined by several agronomic characters such as heading days, days to maturity, grain filling period, number of fertile tiller, number of fertile grain per panicle, panicle length, 1000 grain weight and plant height (Halil & Necmi, 2005). Study on yield contributing characters assumes greater importance of fixing up characters that influence yield (Kole and Hasib, 2008).

The grain yield of rice is determined by spikelet number per panicle, panicle number per plant, grain weight, and spikelet fertility. Although many quantitative trait loci (QTLs) for yield components have been identified (www.gramene.org), few have so far been isolated. To date, at least nine genes or loci for yield-related traits in rice have been isolated from natural variation: *Gn1a* and *APO1* for number of grains (Ikeda-Kawakatsu, 2009*,* Terao *et al*., 2010); *GS3*, *GW2*, and *qSW5* for grain size

(Shomura , 2008*)*; *DEP1* and *WFP* for panicle architecture (Huang, 2009, Miura, 2010); *SCM2* for strong culm (Ookawa, 2010); and *Ghd7* for late heading and number of grains (Xue *et al*., 2008). *APO1*, *SCM2*, and *DEP1* increased grain yield in a *japonica* genetic background in field experiments (Terao *et al.,* 2010*,* Ookawa, 2010). However, no novel cloned gene has been reported to increase grain yield in *indica* cultivars (Miura, *2011*).

In genetic improvement of rice, several genetic traits are selected to increase yield potential, yield stability and wide-scale adaptability (Khush, 2001). The grain yield of rice plants consists of three main components—number of panicles per unit area, number of spikelets per panicle and kernel weight (Peng *et al.*, 2000). These components contribute to grain yield to differing extents and their contributions vary with genotype, environmental conditions and cultivation practice. However, plant architecture may be the most important factor affecting grain yield in rice. Rice plant architecture is mainly determined by tiller pattern, plant height, leaf shape and arrangement, and panicle architecture.

2.10 Heritability

Ghosh and Sharma (2012) defined heritability estimate as a component which provide information regarding the amount of transmissible genetic variation out of the total variation and determines response to selection. The degree to which the genes of an individual influence the phenotype variation is described by the heritability of a given trait. It is important to know that heritability estimate is specific to a given population and environment (Bhadru *et al.,* 2012). The most important function of heritability in the study of quantitative characters is its role to predict and indicate the reliability of the phenotypic value as a guide to breeding value (Falconer and Mackay, 1996). Characters not greatly influenced by environment usually have a high heritability. This

may influence the choice of the breeder to decide which selection procedure to use and which selection method would be most useful to improve the character to predict the gain from selection and to determine the relative importance of genetic effects (Bhadru *et al.,* 2012). Heritability estimation in a given population depends on the partitioning of observed variation into component that reflect unobserved genetic and environmental factors

(Wray and Visscher, 2008). Heritability can be either broad sense or narrow sense. Broad sense heritability is the relative magnitude of genotypic and phenotypic variance for the traits and it is used as a predictive role in selection procedures (Allard, 1960). This gives an idea of the total variation ascribable to genotypic effects, which are exploitable portion of variation (Falconer, 1989). Narrow sense heritability is the ratio of VA/ VP and it expresses the extent to which phenotypes are determined by the genes transmitted by the parents. It is also simply known as heritability (Falconer, 1989). Fahliani *et al*. (2010) have reported both low and high heritability estimate of traits in rice. They also reported that, low heritability of a trait shows that environmental factors strongly influence character and breeding for such character is difficult. High heritability on the other hand indicates the scope of genetic improvement of these characters through selection. High heritability has been reported for flag leaf length (Ghosh and Sharma, 2012, Satyanarayana, *et al.,* 2005; Kobayashi *et al.,* 2003).

The estimate of the heritability alone is not very much useful on predicting resultant effect for selecting the best individual because it includes the effect of both additive genes as well as non-additive genes (Rita *et al*., 2009). Heritability combined with high genetic advance would be an appropriate tool in predicting the resultant effect in selecting the best genotypes for yield and its contributing traits. It helps in determining the influence of the environment on the expression of the genotypic and reliability of

characters (Singh *et al*., 2011). Moreover, knowledge of heritability is essential for selection based improvement, as it indicates the extent of transmissibility of a trait into future generations (Sabesan *et al*., 2009).

2.11 Genetic advance

The estimate of genetic advance as per cent of mean provides more reliable information regarding the effectiveness of selection in improving the traits. Genetic advance denotes the improvement in the genotypic value of the new population over the original population (Ghosh and Sharma, 2012). Rita *et al.* (2009) reported moderate to high genetic advance for yield contributing trait in rice. High heritability with high genetic advance indicates the control of additive gene and selection may be effective for such characters.

2.12 Additive and Dominance Gene Effects.

Honarnejad (1996) considerable contribution of additive effects of genes for traits such as number of tillers and plants length, but overall dominance effects of genes are related to seedling planting time until complete grain maturing, panicle length and number of wrinkled grains in each panicle, and non-additive effects which contribute much more than additive effects of genes are responsible for shaping traits, panicle length, grain number in panicle, thousand grains weight, number of wrinkled grain in panicle and weight of unhusked rice in each plant. They also observed genes dominance effects for tiller number in plant, days to 50% flowering and days to ripening. Moumeni, (1993) showed that non-additive effects of genes outweigh the additive effects for traits such as days to 50 percent flowering, panicle length, grain number in panicle, one hundred grain weight and grain yield in plant, while this was completely untrue for plant height and number of fertilized tillers. Vijayakumar *et al.,* (1996) proved non allelic interaction effects or epistasis in genetic controlling of

agronomical traits in rice and in cases where there was no epistasis, dominance effect was significant. In all cases in which additive and dominance effect was significant, additive effect level was more than dominance. Results of Verma *et al.,* (1994) indicated that epistasis plays a vital role in grain components yield except grain number in panicle. Narayana and Rangasamy, (1991) reported that additive effects of genes are important in genetic control of plant height, number of tillers in plant, panicle length, days to flowering and spike number in panicle and non-additive effects of genes are very important on shaping grain yield in plant and percent of fertile tillers. Wu *et al*., (1986) reported that heritability is high for days to flowering and grain fertilization level and is low for panicle number and grain yield. Honarnejad and Tarang (2001) reported high genetic diversity for grain yield, plant height, tillers number in plant, panicle length, number of full and wrinkled grains in evaluated families by crossing seven local and exotic rice cultivars and studying generations resulting from them. They showed that in most of the evaluated families, dominance and additive effects were involved commonly in inheritance of grain yield, plant height, tiller number and panicle length, but dominance degree in investigated families showed that dominance and overall dominance have more effects in controlling number of full and wrinkled grains. Honarnejad (2005) estimated genetic parameters using 6 Persian rice varieties in a diallel design. Results indicated importance of additive variance in the inheritance of traits. They also showed that there is dominance variance except in thousand grain weight and tiller number in plant. Grain yield and panicle length had low heritability. Rahimsorush and Mouneni (2006) by genetic structure analysis of economical agronomic rice traits using line analysis in tester reported that additive variance contribution to full grain number in panicle and days to 50% and thousand grain weight is more than that of dominance variance.

2.13 Marker Assisted Selection for quantitative and qualitative traits in rice

Molecular markers are particularly useful when they are located within a gene of interest or in linkage disequilibrium with the gene throughout a population (Dekkers, 2004). Genes for quantitative and qualitative traits have been cloned and functional markers have been developed for them (Onishi *et al*., 2007, Fan *et al.*, 2009; Chen *et al.*, 2010, Terao *et al*., 2010). Functional molecular markers derived from within or around genes may causally affect phenotypic trait variation and they can be used in breeding programmes without prior mapping if the relationships between marker polymorphisms and target traits have been established (Andersen and Lübberstedt, 2003). Functional markers for aroma are now used routinely to select for the desired grain qualities in the USA and other breeding programmes around the world (Anna McClung, DBNRRC, personal communication).

2.14 Current trends in the use of marker technologies for rice breeding Rice is a model crop for research and the sequencing of the *indica* (Yu *et al.*, 2002) and *japonica* (IRGSP, 2005) genomes have provided breeders with the necessary tools for marker-assisted selection (MAS). Simple sequence repeats **(**SSR) markers have been widely used for selection, especially in situations where they are closely linked or in linkage disequilibrium with a gene of interest (Bergman *et al.*, 2001). SNPs are rapidly replacing SSRs because they are more abundant, stable, amenable to automation, efficient, and becoming relatively cheaper (McCouch *et al.*, 2010). The ever declining cost of sequencing, increase data output and high throughput associated with modern sequencing technologies (also called next-generation and

―next-next‖ generation sequencing technologies) has enabled the plant genomics and breeding community to undertake genotyping-by-sequencing (GBS) (Thudi *et al.*, 2012). GBS provides genome-wide SNP data, enabling the breeder to impose positive

and negative selection (for desired alleles from the donor at target loci and for recovery of recurrent parent alleles in the genetic background) simultaneously. GBS is expected to become routine in a few years (Thudi *et al.*, 2012). The on-going genomic revolution is expected to immensely benefit plant genetics and breeding.

2.15 QTL mapping

2.15.1 Qualitative and Quantitative Traits

Qualitative or Mendelain traits have discrete phenotypes and are controlled by a single or few genes. They are caused by mutations that have major effects on the phenotype (macromutations). Phenotypes such as wingless flies, hairless mice and dwarf plants are conditioned by macromutations at single loci (Tanksley, 1993). Loci controlled by macromutations are easy to study because they allow the genotype of a particular locus to be predicted from the phenotype of the individual using Mendelain genetics. However, phenotypic variation is usually continuous instead of discrete and controlled by several genes with relatively small effects. Characters whose phenotypic variation is determined by several loci are called quantitative traits and their inheritance as polygenic (Tanksley, 1993). The individual loci controlling a quantitative trait are known as polygenes or quantitative trait loci (QTL) (Tanksley,
1993). Polygenes control most agronomically important traits (Jena and Mackill, 2008). These traits could not be studied by classical Mendelain techniques leading to the emergence of a subspecialty of genetics called quantitative genetics.

Quantitative genetics relies on statistics to describe the characteristics of continuous phenotypic distributions. These statistics help to estimate some genetic information including the approximate number of loci affecting a character in a particular mating, the average gene action and the degree to which the various polygenes interact with each other and the environment in determining the phenotype (Tanksley, 1993;

Falconer and Mackay, 1996). Classical quantitative genetics tools therefore consider only the aggregate effects of all the genes causing the variation and does not take account of the properties of genes individually—their gene frequencies and the magnitude of their effects on the trait of interest (Falconer and Mackay, 1996).

2.15.2 The History and Concept of QTL mapping

The first effort at tracking polygenes (QTLs) with single markers was reported by Sax in 1923 (Sax, 1923). He reported that seed size (a quantitatively inherited character) was associated with seed-coat colour (a discrete monogenic trait). In 1961, Thoday proposed the idea of using single gene markers to identify individual QTLs controlling quantitative traits (Thoday, 1961). The idea was that single markers which are scattered throughout the genome could be used to map and characterize all polygenes (QTLs) affecting a character. Putting Thoday_s ideas into practice was however, not feasible because only a few monogenic (morphological) markers had been mapped and most of these markers were not suitable for studying quantitative traits (Tanksley, 1993). Mapping of QTLs was considerably more successful with the advent and use of isozymes as molecular markers (Tanksley, 1993). The next advance in molecular markers was the introduction of 28 DNA markers (Botstein *et al*., 1980). The advent of DNA markers has made it easier to map QTLs underlying quantitative traits.

Modern QTL mapping is essentially the fulfillment of the ideas of Sax, (1923) and Thoday, (1961) with the key innovation being that defined sequences of DNA act as the linked monogenic markers (Young, 1996). The success of modern QTL mapping therefore depends on the availability of dense DNA marker maps for the organism involved. In recent years, comprehensive DNA marker maps have been developed for

many crops (Sim *et al.*, 2012; Zhang *et al.*, 2012), making the identification of QTLs throughout the genomes of most crop species very feasible.

QTL mapping involves testing DNA markers throughout a genome for the likelihood they are associated with a QTL. Individuals in a suitable mapping population (F_2, backcross, recombinant inbred) are analyzed in terms of DNA marker genotypes and the phenotype of interest. For each DNA marker, the individuals are split into classes according to marker genotype—two or three for dominant or co-dominant markers respectively. Mean and variance parameters are calculated and compared among the classes. A significant difference between the trait means of individuals that fall into each marker class suggests there is a relationship between the DNA marker and the trait of interest—in other words, the DNA marker is probably linked to a QTL (Young, 1996).

2.15.3 Methods of detecting QTLs

The methods used for detecting QTLs include single-marker analysis (SMA), interval mapping (IM), composite interval mapping (CIM) and multiple interval mapping (MIM) (Kao *et al.*, 1999).

Single-marker analysis: Single-marker analysis (also single-point analysis) is the simplest method for detecting QTLs. It does not require a complete linkage map because it is based on analysis of one marker at a time. Simple statistical methods such as t-tests, analysis of variance (ANOVA) and linear regression are therefore used for single-marker analysis. Single-marker analysis has two major disadvantages (Tanksley, 1993). First, the further a QTL is from a marker, the less likely it will be detected due to crossover events between marker and QTL that result in

misclassification. Second, the magnitude of the effect of any detected QTL will likely be underestimated, due to recombination between the marker and the QTL.

The use of a large number of segregating DNA markers covering the entire genome (usually at intervals less than 15 cM) may minimize both problems (Tanksley, 1993).

Interval mapping: interval mapping method was proposed by Lander & Botstein to overcome the problems with single-marker analysis (Lander and Botstein, 1989).

Interval mapping uses linkage maps and analyses intervals between adjacent pairs of linked markers along chromosomes simultaneously, instead of analyzing single markers (Lander & Botstein, 1989). The use of linked markers for the analysis compensates for recombination between the markers and the QTL, and is considered statistically more powerful compared to single-point analysis (Falconer and Mackay, 1996).

Composite Interval Mapping (CIM): This method combines interval mapping with linear regression and includes additional genetic markers in the statistical model as cofactors (Jansen, 1993). In theory, CIM is more precise and effective compared to single-point analysis and interval mapping, because it takes care of the effects of linked QTLs (Jansen, 1993).

Multiple Interval Mapping: Multiple interval mapping uses multiple marker intervals simultaneously to fit multiple putative QTL directly in the model for mapping QTL (Kao *et al*., 1999). The MIM model is based on Cockerham's model for interpreting genetic parameters and the method of maximum likelihood for estimating genetic parameters. MIM can be used to estimate and analyze epistasis between QTL, genotypic values of individuals, and heritabilities of quantitative traits (Kao *et al.*, 1999).

CHAPTER THREE

3.0 MATERIALS AND METHODS

3.1. Site of Experiment

The study was conducted at the Crops Research Institute (CRI) Fumesua. The experiment was in two phases, the first phase which involved the making of crosses was done in pots, whilst the second phase which involved planting of populations for the genetic analyses was done in the field.

3.2. Source of plant materials

The experimental material consisted of two lowland varieties with diverse traits: IET 6279 (P1) is non- aromatic, short to medium grains, high tillering, high yielding, long duration and IR70445-146-3-3 (IR66295-71-2/IR67015-1-4) (P2) which is aromatic, has long slender grains, low tillering ability, low yielding, and short duration. Seeds of the two rice varieties were obtained from the Cereals Division, CSIR-Crops Research Institute, Kumasi- Ghana.

3.2.1 Crosses

Crosses were made between the two parents to obtain F_1 individuals. The F_1 were grown, and backcrossed to both parent. The two parents, F_1, F_2, BCP_1 and BCP_2 generations where grown in the field at the same time.

3.3 Pot culture of F_1 plants

The F_1 seeds were pre-germinated in a white tissue paper for three days nursed for 21 days and transplanted one seedlings per bucket. The buckets were filled with sterilized top soil to avoid soil contamination. Sowing of the varieties were staggered over a three –week‘s period in order to synchronize flowering in the varieties. The hybrid

plants were provided with 10 g of N P K (15:15:15) at tillering and 10g of urea at panicle initiation. Standard agronomic operations like irrigation, application of insecticides and hand weeding were employed whenever necessary.

Some F_1 were allowed to self to produce F_2. Some panicles from the same F_1 plants were backcrossed to either parent to generate the backcross populations. New crosses between parents were also made to generate fresh F_1 seeds.

3.4 Evaluation of parents and other generations

3.4.1 Field experiment

F1 seeds were pre germinated on white tissue paper for three days and nursed for 21 days together with Parental seeds, F_2 and Backcrosses. All seedlings were transplanted to an irrigated lowland field in a randomized complete block design in three replications at CSIR-CRI Fumesua during the minor season of 2014. Each replicate had 60 plants of parents, 25 F_1s, 300 F_2, 60 BCP_1 and BCP_2 plants. Spacing of 40 and 20 cm between-row and within- row respectively at a density of a single plant per hill and data were taken on individual plants for all the populations. The recommended fertilizer rate of 90-60-60- Kg/ha- N-P_2O_5-K_2O was applied: 6060-60 kg/ha applied two weeks after transplanting top-dressed with 30kg/ha N at panicle initiation. Weeds were controlled by spraying with a post emergence selective weedicide Pronil-plus and Propanil. This was followed with hand picking.

Field was irrigated whenever necessary.

3.5 Data collection

Some morphological traits were measured at the physiological maturity stage taking on individual plants from each genotype. Plant height was measured in centimeter (cm) from the plant base to the tip of the highest panicle. Culm length was measured in

centimeter (cm) from the base to the neck of the highest panicle. Tillers of each plant were counted to determine the total number of tillers per plant. Productive tillers of each plant were counted to determine the total number of panicles in each plant. The panicle length of the central tiller of each plant was measured in centimeter (cm). The leaf length, leaf width, flag leaf length and flag leaf width were measured in centimeter (cm) of main tiller of each plant with respect to the each genotype. The number spikelet‘s per panicle, number of spikelet per plant, number of fertile spikelet per panicle, number of fertile spikelet per plant and number of unfilled grains per plant were counted separately after harvesting. Per cent spikelet fertility per plant was determined after harvesting. Grain yield per plant was measured in grams after harvesting. The 100 grain weight of each genotype was measured in grams after harvesting. The grain length and grain width were measured in millimeter (mm) after harvesting for each genotype. Days to 50% flowering of each genotype was determined when 50% of each plants has flowered starting from the date of sowing and days to maturity of each genotypes was determined at the maturity stage when 85% of each plants has matured starting from the date of sowing.

3.5.1 Data on aroma

After 60 days of seeding, determination of presence or absence of aroma was made according to the method described by Sood and Siddiq (1978) and Dong *et al.* (2001 b). Two grams of green leaves were harvested from individual plants cut into small pieces and kept in the test tubes. About 10 ml of 1.7% potassium hydroxide (KOH) solution was added to each test tube. The test tubes were covered immediately after the addition of alkali and left under room temperature for about ten minutes. The test tubes were opened one by one and the content in each was immediately evaluated by smelling. The samples were classified According to the degree of aroma, a rating scale

from zero to three was used; with zero indicating no aroma, one indicating faint aroma, two indicating aroma and three indicating strong aroma. The evaluation of aroma for individual plants was conducted in three replications by 5 panelists. To prevent overwhelming panel members‟ senses, no more than 20 samples were evaluated at a time. For each set of data the aromatic and non-aromatic parents were included as controls; where a panel member failed to evaluate the controls, the data was rejected. Samples were divided into three groups based on the average of rating scale values: (i) aromatic (1.5 - 3.0) (ii) questionable (1.2 - 1.4) (iii) non-aromatic (less than 1.2). Any questionable sample was re-evaluated until it was classified as either aromatic or non-aromatic

3.6 Data Analysis

Analysis of variance (ANOVA) for each of the six populations was conducted using Genstat version 12.1. The means and variances obtained were used to estimate genetic parameters such as broad sense and narrow sense heritability.

3.6.1 Gene action controlling twenty one quantitative traits in IET6279 X IR70445-146-3-3 cross

Generation mean analysis was used to estimates genetic control of the twenty one quantitative traits according to the methodology proposed by Mather and Jinks (1971):

The Generation mean analysis model is stated below:

$\mathbf{Y = m + \alpha a + \beta d + \alpha 2 aa + 2\alpha\beta ad + \beta 2 dd}$ α and β are the coefficients for a and d, respectively. Y = the observed mean m = mean = mean of the F2

a = pooled additive effects d = pooled dominance effects aa = additive x additive gene interaction

effects ad = additive x dominance gene interaction

effects dd = dominance x dominance gene interaction

effects

The mode of inheritance of the twenty one quantitative traits was estimated by generation mean analysis with six generations (P_1, P_2, F_1, F_2, BCP_1 and BCP_2) of IET6279 and IR70445-146-3-3. Following significant differences in the twenty one quantitative traits of the various generations, their means and variances were used to perform generation mean analysis.

3.6.2 Heritability of twenty quantitative traits in the broad sense

Broad sense heritability (H^2_b), of twenty quantitative traits of rice was estimated by the formula of Allard (1960). $H^2_b = (VF_2 – VE) / VF_2$: Where;

H^2_b = Broad sense heritability

V E = Error variance = $(VP_1 + VP_2 + VF_1) / 3$

VF_2 = Variance of F_2 family

VP_1 = Variance of parent 1

VP_2 = Variance of parent 2

VF_1 = Variance of F_1 family

3.6.3 Narrow sense heritability

Narrow sense heritability (h^2_n) was calculated according to the method of Halloran *et al.* (1979) as follows:

$h^2_n = [2VF_2 - VBCP_1 - VBCP_2] / VF_2$, where: VF_2, $VBCP_1$, and $VBCP_2$ are the variances of the F_2, IET6279 x F_1 and IR70445-146-3-3 x F_1 respectively.

3.6.4 Aroma

Chi-square values of the aroma data obtained from segregating population of the cross were computed following the procedure described by Gomez and Gomez (1984).

CHAPTER FOUR

4.0 RESULTS

4.1 Genetic analysis of aroma

The F_1 and the backcross to IET6279 (BCP_1) from these cross were non-aromatic. The F_2 and the backcross to IR70445-146-3-3 (BCP_2) from these cross were aromatic (Table 1).

Table 1. Number of plants expressing aromatic and non-aromatic grain type according to KOH test

Generations	No. of plants tested	No. of plants	
		Aromatic plants	Non-aromatic plants
IET6279 (P_1)	60	0	60
IR70445-146-3-3 (P_2)	60	60	0
F_1	45	0	45
F_2	792	203	589
BCP_1	60	0	60
BCP_2	171	79	92

Table 2. Inheritance pattern of aroma in F_2 and BCP_2 populations of IET6279 X IR70445-146-3-3 cross **No. of plants**

Cross	No. of plants tested	Aromatic plants		Non-aromatic plants		Ratio	Chi-square	P value
		Observed	Expected	Observed	Expected			
F_2	792	203	198	589	594	1:3	0.14	3.84
BCP_2	171	79	85.5	92	85.5	1:1	0.84	3.84

The data obtained on the presence and absence of aroma of the F_2 and BCP_2 plants in the cross is presented in Table 2.

The F_2 generation segregated into 203 aromatic and 589 non-aromatic plants fitting into 1:3 ratio ($\chi^2 = 0.14$). The backcross to IR70445-146-3-3 (BCP_2) cross segregated into a ratio of 79 aromatic to 92 non-aromatic plants fitting into a 1:1 ratio ($\chi^2 = 0.84$).

These indicate that aroma in IR70445-146-3-3 is under the control of a single recessive gene.

Table 3. Mean, ranges, variance and coefficient of variation (c v) of days to 50% flowering, days to maturity and plant height of six generations in IET6279 X IR70445-146-3-3 cross

Trait	Generation	Mean	Range	Variance	C.V
Days to 50% flowering	IET6279	115.03	109-123	12.72	3.06
	IR70445-146-3-3	92.78	90-96	2.02	1.60
	F_1	88.11	82-96	11.44	3.84
	F_2	95.78	82-120	50.47	7.42
	BCP_1	95.11	83-111	29.59	6.62
	BCP_2	91.95	83-120	43.70	7.19
	L S D (0.05)	1.77			
	C V %	6.8			
Days to maturity	IET6279	139.78	122-152	16.48	2.90
	IR70445-146-3-3	122.78	114-132	12.21	2.85
	F_1	117.27	111-126	16.75	3.49
	F_2	121.75	106-151	41.33	5.28
	BCP_1	122.58	111-138	31.60	4.58
	BCP_2	120.36	111-148	32.40	4.73
	L S D (0.05)	1.62			
	C V %	4.9			
Plant height (cm)	IET6279	134.27	120-150	40.01	4.77
	IR70445-146-3-3	113.15	88-137	88.71	8.32
	F_1	123.66	97-147	83.28	7.38
	F_2	123.70	77-187	247.80	12.73
	BCP_1	123.61	96-162	184.70	10.06
	BCP_2	119.88	90-149	191.70	9.19
	L S D (0.05)	3.80			
	C V %	11.4			

Days to 50% flowering ranged from 82 to 123. The mean performance of IET6279 (115.03) was higher than IR70445-146-3-3 (92.78). Mean for F_2, BCP_1 and BCP_2 were all within parental limits except for F_1 (88.11) which had mean lower than both parents. The range of variation and variance in F_2 was higher than IR70445-146-3-3, F_1 and BCP_1. The CV in F_2 was the highest (7.42%) followed by BCP_2 (7.19%) and IR70445-146-3-3 recorded the lowest (1.60%). Days to maturity varied from 106 to 152 days. IET6279 (139.78) had the longest maturity duration while F_1 (117.27) had

the shortest days to maturity. The range of variation and variance in F_2 was higher than parents, F_1, BCP_1 and BCP_2. F_2 recorded the highest CV (12.73%) followed by BCP_1 (10.06%) and IET6279 recorded the lowest (4.77%). Plant height varied from 77 to 187 cm. The maximum and minimum mean performance for plant height were recorded in IET6279 (134.27 cm) and IR70445-146-3-3 (113.15 cm) respectively. The Mean of F1, F_2, BCP_1 and BCP_2 were all within parental limits. The range of variation and variance in F_2 was higher than parents, F_1, BCP_1 and BCP_2. The CV in F_2 was highest (12.73%) followed by BCP_1 (10.06%) and IET6279 recorded the lowest (4.77%).

Table 4. Mean, ranges, variance and coefficient of variation (c v) of number of tillers per plant, number of panicles per plant and panicle length of six generations in IET6279 X IR70445-146-3-3 cross

Trait	Generation	Mean	Range	Variance	C.V
No. of tillers per plant	IET6279	23.40	16-35	15.26	16.69
	IR70445-146-3-3	20.48	9-36	30.93	27.85
	F_1	19.48	6-33	42.00	33.26
	F_2	18.57	5-44	42.70	34.88
	BCP_1	20.24	7-40	40.84	31.57
	BCP_2	19.12	5-39	41.84	34.62
	L S D (0.05)	1.72			
	C V %	33.6			
No. of Panicles per plant	IET6279	22.17	14-35	16.31	18.22
	IR70445-146-3-3	19.70	9-30	36.50	31.09
	F_1	18.36	5-30	35.87	32.63
	F_2	17.12	5-43	37.87	36.46
	BCP_1	18.19	4-39	35.68	33.19
	BCP_2	17.36	5-38	34.62	34.34
	L S D (0.05)	1.63			
	C V %	34.0			
Panicle length (Cm)	IET6279	26.10	23-29	2.13	5.59
	IR70445-146-3-3	29.97	18-36	10.30	10.71
	F_1	30.68	27-36	5.40	7.74
	F_2	30.08	16-41	10.18	10.61
	BCP_1	29.51	19-39	10.07	10.58
	BCP_2	30.43	20-40	9.29	10.04
	L S D (0.05)	0.86			
	C V %	10.6			

The number of tillers per plant ranged from 5 to 44. The maximum and minimum mean obtained were 23.40 and 18.57 in IET 6279 and F2 respectively. The range of variation and variance in F_2 was higher than parents, F_1, BCP_1 and BCP_2. . F_2recorded the highest CV (34.78%) followed by BCP_2 (34.62%) and IET6279 recorded the lowest (16.35%). Number of panicle per plant varied between 4 and 43. .IET6279 recorded the highest mean for number of panicles per plant (22.17) followed by IR70445-146-3-3 (19.70) and F2 recorded the lowest (17.12). The mean for both parents were slightly greater than F_1, BCP_1 and BCP_2. The range of variation and variance of IR70445-146-3-3, BCP_1 and BCP_2 were slightly higher than their corresponding F_2. This deviates from how the various generations normally behave. The CV in F_2 is highest (35.46%) followed by BCP_2 (35.34%) and IET6279 recorded the lowest (18.22%). The range of Panicle length varied from 16 cm to 41 cm. F_1 registered the maximum panicle length (30.68) followed by BCP_2 (30.43) while the minimum value for panicle length was observed in IET6279 (26.10).The range of variation and Variance in IR70445-146-3-3, BCP_1 and BCP_2 were slightly higher than their corresponding F_2. This deviates from how the various generations normally behave. The CV in IR70445-146-3-3, BCP_1 and BCP_2 were also slightly higher than their corresponding F_1, F_2 and IET6279 respectively.

Table 5. Mean, ranges, variance and coefficient of variation (c v) of leaf length, leaf width and culm length of six generations in IET6279 X IR70445-146-3-3 cross

Trait	Generation	Mean	Range	Variance	C.V
Leaf length (cm)	IET6279	44.35	31-60	33.89	13.13
	IR70445-146-3-3	55.18	37-70	45.17	12.18
	F_1	52.69	37-71	66.32	15.45
	F_2	57.51	33-90	95.24	16.97
	BCP_1	52.59	23-77	95.33	18.57
	BCP_2	53.82	33-76	65.26	15.01
	L S D (0.05)	0.04			
	C V %	16.6			
Leaf width (cm)	IET6279	2.02	1.60-2.20	0.02	7.67
	IR70445-146-3-3	1.42	1.00-1.90	0.04	14.13
	F_1	1.47	1.00-2.00	0.04	14.70
	F_2	1.43	1.00-2.10	0.05	15.05
	BCP_1	1.56	1.00-2.20	0.05	14.46
	BCP_2	1.47	1.00-2.20	0.04	15.01
	L S D (0.05)	0.06			
	C V %	14.5			
Culm length (cm)	IET6279	108.17	93-122	40.28	5.87
	IR70445-146-3-3	83.18	62-108	72.49	10.24
	F_1	92.98	70-144	65.51	8.71
	F_2	93.58	55-153	202.40	15.20
	BCP_1	94.10	70-130	128.80	12.06
	BCP_2	89.46	64-120	205.10	11.46
	L S D (0.05)	3.45			
	C V %	13.6			

Leaf length varied between 23 cm and 90 cm. The minimum and maximum recorded mean for leaf length were 44.35 and 57.51 cm in IET6279 and F_2. The range of variation and variance in F_2 was higher than parents, F1 and BCP_2. BCP1 reported the highest CV (18.57%) followed by F_2 (16.97%) and IR70445-146-3-3 recorded the lowest (12.18%). Leaf width varied between 1cm and 2.2 cm with a maximum means of (2.02) in IET6279 and a minimum mean of (1.42) in IR70445-146-3-3. The range of variation and variance in F_2 was higher than IR70445-146-3-3. F_2 recorded the highest CV (15.09%) followed by BCP_2 (15.01%) and IET6279 recorded the lowest

(7.67%). Culm length varied from 55 to 153 cm with a maximum and minimum mean of 108.20 and 83.18 cm for IET6279 and IR70445-146-3-3 respectively. Mean for F_1, F_2, BCP_1 and BCP_2 were all within parental limits. . The range of variation and variance in F_2 was higher than parents, F_1, BCP_1 and BCP_2. F_2 recorded the highest CV (15.20%) followed by BCP_1 (12.06%) and IET6279 recorded the lowest (5.87%).

Table 6. Mean, ranges, variance and coefficient of variation (c v) of flag leaf length, flag leaf width and number of unfilled grains per plant of six generations in IET6279 X IR70445-146-3-3 cross

Trait	Generation	Mean	Range	Variance	C.V
Flag leaf length (cm)	IET6279	30.75	20-44	20.29	14.65
	IR70445-146-3-3	40.43	26-61	45.76	16.73
	F_1	41.35	28-57	54.49	17.85
	F_2	43.89	20-83	66.88	18.63
	BCP_1	39.59	17-59	58.65	19.24
	BCP_2	42.17	26-67	69.30	19.74
	L S D (0.05)	2.15			
	C V %	18.7			
Flag leaf width (cm)	IET6279	2.24	2-2.8	0.03	8.31
	IR70445-146-3-3	1.73	1.4-2.2	0.05	10.97
	F_1	1.86	1.6-2.2	0.03	8.92
	F_2	1.83	1.2-2.8	0.06	12.87
	BCP_1	1.96	1.4-2.4	0.06	12.03
	BCP_2	1.88	1.4-2.8	0.05	12.50
	L S D (0.05)	0.06			
	C V %	12.3			
No. of unfilled grains per plant	IET6279	576.10	193-1102	33909	31.96
	IR70445-146-3-3	830.70	220-2355	226800	57.33
	F_1	311.60	28-1224	52564	73.59
	F_2	428.20	43-2108	84363	67.83
	BCP_1	397.60	43-2042	78911	70.66
	BCP_2	408.90	81-2804	78001	68.31
	L S D (0.05)	79.43			
	C V %	66.2			

Flag leaf length varied between 17 cm and 83 cm. The maximum Flag leaf length mean was observed in F_2 (43.89 cm) followed by BCP_2 (42.17 cm) while the minimum Flag leaf length was observed in IET6279 (30.75 cm). The range of variation and variance

in F_2 was higher than parents, F_1 and BCP_1. BCP_2 recorded the highest CV (19.74%) followed by BCP_1 (19.34%) and IET6279 recorded the lowest (14.64%). Flag leaf width varied between 1.2 cm and 2.8 cm. The minimum and maximum recorded mean for Flag leaf width were 1.73 and 2.24 cm in IR70445146-3-3 and IET6279 respectively. The range of variation and variance in F_2 was higher than parents, F_1 and BCP_2. F_1 recorded the highest CV (12.87%) followed by BCP_2 (12.50%) and IET6279 recorded the lowest (8.13%). Number of unfilled Grain per plant showed highest amount of variability and ranged between 28 and 2355 with F_1 recording the highest CV (73.59%) followed by BCP_1 (70.66%) and IET6279 recorded the lowest (31.96%). IR70445-146-3-3 registered the maximum number of unfilled grain per plant (831) followed by IET6279 (576) and F_1 (312) recorded the minimum number of unfilled grain per plant. The range of variation and variance in IR70445-146-3-3 was higher than their corresponding F_2, this deviates from how the various generations normally behave

Table 7. Mean, ranges, variance and coefficient of variation (c v) of number of spikelet per panicle, number of spikelet per plant and 100 grain weight of six generations in IET6279 X IR70445-146-3-3 cross

Trait	Generation	Mean	Range	Variance	C.V
No of Spikelet per panicle	IET6279	191.40	138.60-245.40	600.40	12.80
	IR70445-146-3-3	150.30	88.20-153.6	1222	23.26
	F_1	161.80	64.65-268.2	1897	26.91
	F_2	150.50	61.31-298.2	1813	28.28
	BCP_1	156.20	72.55-295.2	1740	25.95
	BCP_2	148.60	69.57-223.1	1336	22.67
	L S D (0.05)	10.93			
	C V %	26.3			
No of Spikelet per plant	IET6279	4232	2634-7671	849954	21.78
	IR70445-146-3-3	2975	977-7191	158309	42.30
	F_1	3011	664-5788	1836159	45.01
	F_2	2586	502-8915	1572501	48.40
	BCP_1	2836	536-9412	1568563	44.17

	BCP_2	2569	653-7686	1190538	42.46
	L S D (0.05)	332.3			
	C V %	44.9			
100 Grain weight (g)	IET6279	2.69	2.46-2.92	0.01	3.71
	IR70445-146-3-3	3.04	2.77-3.33	0.02	4.43
	F_1	2.76	2.49-3.12	0.02	5.03
	F_2	2.77	2.27-3.91	0.10	8.12
	BCP_1	2.74	2.24-3.21	0.04	7.06
	BCP_2	2.80	2.28-3.57	0.05	7.72
	L S D (0.05)	0.06			
	C V %	7.5			

Number of spikelets per panicle was greatly varied from 61 to 298. The mean maximum and the minimum number of spikelet per panicle was recorded in IET6279 (191.40) and IR70445-146-3-3 (150.30) respectively. However, the range of variation and variance in F_1 was higher than the corresponding parents, F2. BCP_1 and BCP_2 respectively. F_2 recorded the highest CV (28.28%) followed by F_1 (26.91%) and IET6279 recorded the lowest (12.80%). Number of spikelet per plant varied from 502 to 9412. The maximum and minimum number of spikelet per plant were recorded for IET6279 (4232) and BCP_2 (2569). The range of variation and variance in F_1 were higher than parents, F_2, BCP_1 and BCP_2. F_2 recorded the highest CV (48.50%) followed by F_1 (45.10%) and IET6279 recorded the lowest (21.78%). 100 grain weight per plant varied between 2.24 g and 3.19 g. The maximum mean performance of 100 seed weight was recorded for IR70445-146-3-3 (3.04) and the minimum 100 grain weight (2.69) was recorded for IET6279. Mean for F_1, F_2, BCP_1 and BCP_2 were all within parental limits. The range of variation and variance in F_2 was higher than the corresponding parents, F_1. BCP_1 and BCP_2 respectively. F_2 recorded the highest CV (8.12%) followed by BCP_2 (7.72%) and IET6279 recorded the lowest (3.71%)

Table 8. Mean, ranges, variance and coefficient of variation (c v) of fertile spikelet per panicle, fertile spikelet per plant and % Spikelet fertility per plant of six generations in IET6279 X IR70445-146-3-3 cross

Trait	Generation	Mean	Range	Variance	C.V
Fertile spikelet per panicle	IET6279	165.30	112.80-213.40	473.90	13.17
	IR70445-146-3-3	107.90	47.65-190.50	814.70	26.45
	F_1	145.00	59.65-222.00	1534	27.02
	F_2	125.40	54.38-273.40	1471	30.58
	BCP_1	134.60	53.68-262.00	1366	37.46
	BCP_2	124.80	49.70-207.90	1182	24.43
	L S D (0.05)	9.83			
	C V %	28.2			
Fertile spikelet per plant	IET6279	3656	2329-6569	660790	22.23
	IR70445-146-3-3	2144	645-5475	848726	42.97
	F_1	2699	509-5348	1048976	44.60
	F_2	2158	435-7595	1171937	50.18
	BCP_1	2438	480-7370	1192843	43.48
	BCP_2	2153	559-5775	849821	42.80
	L S D (0.05)	284.1			
	C V %	45.9			
% Spikelet fertility per plant	IET6279	86.39	97.26-94.89	10.75	3.80
	IR70445-146-3-3	72.39	52.36.88.99	45.63	8.78
	F_1	89.76	67.76-98.15	36.49	6.25
	F_2	83.16	57.31-98.33	60.70	9.45
	BCP_1	85.95	53.79-95.29	46.70	7.74
	BCP_2	83.85	62.20-95.59	46.25	8.11
	L S D (0.05)	2.02			
	C V %	8.9			

Total number of fertile spikelets per panicle was greatly varied from 61 to 298. The maximum and the minimum number of spikelet per panicle were recorded in IET6279 (165.30) and IR70445-146-3-3 (107.90) respectively. However, the range of variation and variance in F_1 was higher than the corresponding parents, F_2. BCP_1 and BCP_2 respectively. F_2 recorded the highest CV (30.58%) followed by BCP_1 (27.46%) and IET6279 recorded the lowest (13.17%). The number of fertile spikelets per plant was greatly varied from 47 to 273. The lowest number of fertile spikelet per plant was recorded in IR70445-146-3-3 (2144) while the highest was recorded in IET6279 (3656). The mean of F_1, F_2, BCP_1 and BCP_2 were all within parental limits. The range

of variation and variance in F_1 was higher than the corresponding F_2. F_2 recorded the highest CV (50.18%) followed by F_1 (44.60%) and IET6279 recorded the lowest (22.23%). Percentage spikelet fertility per plant ranged from 52.36 to 98.33%, with a maximum mean of 89.76% for (F1) while the minimum value for fertility (%) was observed in IR70445-146-3-3 (72.39 %). Mean for F_2, BCP_1 and BCP_2 were all within parental limits. The range of variation and variance in F_2 was higher than IR70445-146-3-3, F_1, BCP_1 and BCP_2. F_2 recorded the highest CV (7.86%) followed by IR70445-146-3-3 (7.25%) and IET6279 recorded the lowest (3.80%).

Table 9. Mean, ranges, variance and coefficient of variation (c v) of grain yield per plant, grain length and grain width of six generations in IET6279 X IR70445-146-3-3 cross

Trait	Generation	Mean	Range	Variance	C.V
Grain yield per plant (g)	IET6279	97.78	61,75-170.60	441.70	21.49
	IR70445-146-3-3	65.64	17.18-151.10	766.50	42.18
	F_1	74.05	13.98-150.70	1096.00	44.71
	F_2	59.13	10.79-188.90	837.80	48.95
	BCP_1	66.41	11.90-193.50	838.40	43.60
	BCP_2	59.74	15.48-156.50	680.80	43.67
	L S D (0.05)	7.71			
	C V%	45.2			
Grain length (mm)	IET6279	8.15	7.66-8.63	0.05	2.68
	IR70445-146-3-3	10.89	9.51-12.09	0.21	4.60
	F_1	9.32	8.08-10.02	0.17	4.88
	F_2	9.67	7.53-11.83	0.39	6.49
	BCP_1	9.21	7.72-11.81	0.35	6.17
	BCP_2	9.73	7.48-11.90	0.34	6.09

	L S D (0.05)	0.18			
	C V%	6.8			
Grain width (mm)	IET6279	3.00	2.78-3.19	0.01	3.48
	IR70445-146-3-3	2.49	2.28-2.70	0.01	3.51
	F_1	2.63	2.43-3.05	0.01	4.65
	F_2	2.56	2.13-3.13	0.03	6.23
	BCP_1	2.68	2.25-3.13	0.03	6.99
	BCP_2	2.57	2.24-3.13	0.02	5.01
	L S D (0.05)	0.04			
	C V%	6.1			

Grain yield per plant varied between 10.79 g and 193.50 g. IET6279 registered the maximum average grain yield per plant (97.78) followed by F_1 (74.05) while F_2 recorded the minimum average (59.13) grain yield per plant. The range of variation and variance in F_1 and BCP_1 were higher than their corresponding F_2. This deviates from how the various generations normally behave. F_2 recorded highest CV (48.95%) followed by F_1 (44.71%) and IET6279 recorded the lowest (21.49%). Grain length range between 7.66 mm and 12.09 mm. The minimum and maximum mean obtained were 8.15 and 10.89 for IET6279 and IR70445-146-3-3 respectively. The range of variation and variance in F_2 was higher than IET6279, F_1, BCP_1 and BCP_2. F_2 recorded the highest CV (6.47%) followed by BCP_1 (6.17%) and IET6279 recorded the lowest (2.28%). Grain width varied between 2.13 mm and 3.19 mm. The maximum and minimum mean reported for Grain width were 3.00 and 2.49 mm in IET6279 and IR70445-146-3-3 respectively. The range of variation and variance in F_2 was higher than IR70445-146-3-3 and F_1. BCP_1 had the highest CV (6.99%) followed by F_2 (6.23%) and IR70445-146-3-3 recorded the lowest (3.48%)

4.2 Heritability estimates

Heritability was estimated for twenty quantitative traits, the results are presented in

(Table 10). The magnitude of heritability is classified as low (< 50%), medium (5060%) and high (> 60%) Babu *et al*., (2012) and Ashok *et al*., (2013). Broad sense heritability estimates was high for plant height, culm length, days to flowering, days to maturity, 100 grain weight, grain length and grain width but low for number of tillers, number of panicle, panicle length, leaf length, leaf width, flag leaf length, flag leaf width, number of spikelet per panicle, number of spikelet per plant, number of fertile spikelet per panicle, number of fertile spikelet per plant, spikelet fertility per cent per plant and grain yield per plant. Days to 50% flowering recorded highest heritability for broad sense (83%) with a narrow sense of (55%) followed by plant height which recorded (71%) and narrow sense of (48%). This was followed by culm length (71%) and (35%), 100 grain weight (67%) and (50%), grain width (67%) and (33%), grain length (64%) and (23%) and days to maturity (63%) and (45%) for both broad sense and narrow sense heritabilities respectively. This indicate that the phenotype is highly correlated with the genotype and that contribution of environmental conditions was relatively low for these traits. While heritability estimates of other characters like, number of tillers, number of panicle, panicle length, leaf length, leaf width, flag leaf length, flag leaf width, number of spikelet per panicle, number of spikelet per plant, number of fertile spikelet per panicle, number of fertile spikelet per plant, % spikelet fertility per plant and grain yield per plant were observed to possess low broad sense heritability. The number of spikelet per plant had the lowest (27%) heritability. Low heritability of this traits shows that the phenotype is not highly correlated with the genotype and that contribution of environmental conditions was relatively high and strongly influencing this

characters.

Table 10. Heritability estimates for twenty quantitative traits calculated from estimated variance component in IET 6279 X IR70445-146-3-3 cross

	Heritability	
Character	Broad Sense (%)	Narrow Sense (%)
Days to 50% flowering	83	55
Plant height	71	48
No of tillers plant^{-1}	31	06
Culm length	71	35
No of panicles plant^{-1}	30	14
Panicle length	42	10
Leaf length	49	31
Leaf width	40	20
Flag leaf length	40	09
Flag leaf width	33	17
Days to maturity	63	45
No of spikelet panicle^{-1}	32	29
No of spikelet plant^{-1}	40	25
No of fertile spikelet panicle^{-1}	36	27
No of fertile spikelet plant^{-1}	27	26
Spikelet fertility (%) plant^{-1}	49	47
Grain yield plant^{-1}	32	19
100 Grain weight	67	50
Grain length	64	23
Grain width	67	33

4.3 Gene action controlling twenty one quantitative traits in IET6279 X IR70445-146-3-3 cross

Following significant differences in twenty quantitative traits of the various generations of IET6279 and IR70445-146-3-3, their means and variances were used to perform generation means analysis. Vital results from regression analysis from SAS are presented in (Table 11, 12, 13,14,15,16 and 17).

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Table 11 nalysis of variance and parameter estimates for genetic control of plant height, leaf length and leaf width obtained through generation mean analysis with IET6279 X IR70445-146-3-3 cross.

		Plant height				Leaf length				Leaf width			
Variable	DF	Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value
intercept	1	131.83	22.27	5.29	0.00	62.55	10.39	6.02	0.00	1.45	0.33	4.45	0.00
rep	1	0.20	1.73	0.11	0.91	1.81	0.81	2.22	0.04	-0.01	0.03	-0.49	0.63
a	1	-9.97	1.71	-5.84	0.00	5.50	0.91	6.07	0.00	-0.30	0.03	-9.13	0.00
d	1	-26.83	49.78	-0.54	0.60	-21.93	24.00	-0.91	0.38	-0.01	0.76	-0.02	0.99
aa	1	-7.25	21.76	-0.33	0.75	-16.26	10.22	-1.59	0.14	0.32	0.31	1.01	0.33
ad	1	12.19	10.98	1.11	0.29	-9.36	5.75	-1.63	0.13	0.41	0.19	2.11	0.05
dd	1	18.35	29.04	0.63	0.54	9.22	14.36	0.64	0.53	0.05	0.47	0.10	0.92

Note: (a) additive; (d) dominance; (aa) additive x additive; (ad) additive x dominance; (dd) dominance x dominance gene effects

The results obtained from regression analysis revealed that additive gene effect (a) was highly significant for plant height, leaf length and leaf width, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were not significant for plant height, leaf length and leaf width in the exception of additive x dominant which is significant for leaf width. It is evident that the magnitude of non-allelic interactions and absolute total of non-fixable gene effects (additive x dominance gene effect) was greater than the corresponding fixable effects (additive gene effects) for leaf width. The negative significant additive gene action (a) for plant height and leaf width and the negative (ad) for leaf length though not significant were in the direction of the reducer parent for all the three characters (Table 11)

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Table 12. nalysis of variance and parameter estimates for genetic control of flag leaf length, flag leaf width and culm length obtained through generation mean analysis with IET6279 X IR70445-146-3-3 cross.

Variable	DF	Flag leaf length				Flag leaf width				Culm length			
		Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value
intercept	1	45.75	4.36	10.50	0.00	1.57	0.25	6.24	0.00	101.69	19.11	5.32	0.00
rep	1	0.82	0.36	2.28	0.04	0.01	0.02	0.43	0.68	0.71	1.37	0.52	0.62
a	1	4.82	0.44	11.02	0.00	-0.24	0.03	-8.82	0.00	-11.76	1.38	-8.50	0.00
d	1	-7.42	10.21	-0.73	0.48	0.66	0.58	1.13	0.28	-29.50	42.98	-0.69	0.51
aa	1	-11.80	4.26	-2.77	0.02	0.40	0.24	1.65	0.13	-6.56	18.76	-o.35	0.74
ad	1	-4.80	2.57	-1.87	0.09	0.29	0.15	1.99	0.07	13.95	9.52	1.47	0.17
dd	1	1.08	6.22	0.17	0.87	-0.36	0.35	-1.04	0.32	19.21	25.14	0.76	0.46

Note: (a) additive; (d) dominance; (aa) additive x additive; (ad) additive x dominance; (dd) dominance x dominance gene effects

Additive gene effect (a) was highly significant for flag leaf length, flag leaf width and culm length, while dominance gene effect (d) and nonadditive gene effects with their interactions (aa), (ad) as well (dd) were non-significant for flag leaf length, flag leaf width and culm length in the exception of additive x additive gene effect which is significant for flag leaf length.. However, it is evident that the significant fixable additive component was greater in magnitude than its corresponding significant fixable additive x additive component. The negative significant (aa) for flag leaf length and the negative significant (a) for flag leaf width and culm length were in the direction of the reducer parent for all the characters (Table 12).

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Table 13 nalysis of variance and parameter estimates for genetic control of panicle length, grain length and grain width obtained through generation mean analysis with IET6279 X IR70445-146-3-3 cross.

Variable	DF	Panicle length				Grain length				Grain width			
		Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value
intercept	1	28.57	3.24	8.82	0.00	11.04	0.81	13.63	0.00	2.43	0.23	11.19	0.00
rep	1	-0.02	0.25	-0.09	0.93	-0.08	0.04	-1.78	0.10	-0.03	0.02	-1.48	0.17
a	1	1.93	0.34	5.68	0.00	1.38	0.07	21.09	0.00	-0.24	0.02	-14.87	0.00
d	1	4.03	7.74	0.52	0.61	-3.23	1.95	-1.66	0.13	0.35	0.51	0.68	0.51
aa	1	-0.42	3.18	-0.13	0.90	-1.36	0.79	-1.71	0.11	0.36	0.21	1.96	0.12
ad	1	-1.83	2.03	-0.90	0.39	-1.17	0.51	-2.30	0.04	0.23	0.13	1.74	0.11
dd	1	-.1.99	4.72	-0.42	0.68	1.63	1.19	1.36	0.20	-0.10	0.31	-0.34	0.74

Note: (a) additive; (d) dominance; (aa) additive x additive; (ad) additive x dominance; (dd) dominance x dominance gene effects

The regression analysis revealed additive gene effect (a) was highly significant for panicle length, grain length and grain width, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non-significant for panicle length, grain length and grain width in the exception of additive x dominance (ad) which is significant for grain length. However, the magnitude of the significant fixable gene action (a) in grain length has greater magnitude compared with the non-fixable (ad). The negative (ad) for panicle length though not significant and the negative significant (ad) for grain length as well as the negative significant (a) for grain width were in the direction of reducer parent for all the characters (Table 13).

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Table 14. nalysis of variance and parameter estimates for genetic control of number of tillers per plant, number of panicle per plant and number of unfilled grains per plant obtained through generation mean analysis with IET6279 X IR70445-146-3-3 cross.

Variable	DF	Number of Tillers/Plant				Number of Panicle/Plant				Number of unfilled grains/Plant			
		Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value
intercept	1	14.24	6.81	2.09	0.06	15.71	6.03	2.61	0.02	787.07	374.91	2.10	0.06
rep	1	1.27	0.65	1.95	0.08	1.03	0.53	1.95	0.08	4.57	32.45	0.14	0.89
a	1	-1.38	0.72	-1.92	0.04	-1.30	0.64	-2.03	0.05	106.76	59.26	1.80	0.10
d	1	3.41	15.78	0.22	0.83	-3.99	14.10	-0.28	0.78	-986.75	863.74	-1.14	0.28
aa	1	4.61	6.57	0.70	0.50	2.72	5.88	0.46	0.65	-146.47	367.27	-0.40	0.70
ad	1	-0.59	4.03	-0.15	0.89	0.56	3.60	0.15	0.88	-142.10	224.39	-0.63	0.54
dd	1	-0.24	9.65	-0.03	0.98	5.02	8.64	0.58	0.57	463.33	512.61	0.90	0.39

Note: (a) additive; (d) dominance; (aa) additive x additive; (ad) additive x dominance; (dd) dominance x dominance gene effects

The generation mean analysis indicated that additive gene effect (a) was significant for both number of tillers per plant and number of panicle per plant, but not significant for number of unfilled gains per plant. Dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non-significant for all the three character. However, negative additive (a) gene effect for number of tiller per plant and number of panicle per plant as well as negative (ad) for number of unfilled grains per plant though not significant were in the direction of the reducer parent for all the character (Table 14).

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Table 15 nalysis of variance and parameter estimates for genetic control of number of spikelet per panicle, number of spikelet per plant and 100 grain weight obtained through generation mean analysis with IET6279 X IR70445-146-3-3 cross.

		Number of spikelet/panicle				Number of Spikelet / Plant				100 Grain weight			
Variable	DF	Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value
intercept	1	157.89	35.60	4.43	0.00	3169.20	1625.90	1.95	0.08	2.84	0.19	14.71	0.00
rep	1	3.33	2.97	1.12	0.29	283.23	136.52	2.07	0.06	0.00	0.01	0.10	0.92
a	1	-20.61	3.60	-5.72	0.00	-707.33	169.52	-4.17	0.00	0.17	0.01	12.04	0.00
d	1	-55.85	82.17	-0.68	0.51	-4364.36	3722.14	-1.17	0.27	-0.20	0.45	-0.45	0.66
aa	1	5.70	35.23	0.16	0.87	-358.29	1591.40	-0.23	0.83	0.01	0.19	0.05	0.96
ad	1	26.25	19.44	1.35	0.20	155.95	904.82	0.17	0.87	-0.24	0.01	-2.27	0.04
dd	1	55.99	49.75	1.13	0.29	4053.40	2221.50	1.82	0.10	0.10	0.26	0.36	0.72

Note: (a) additive; (d) dominance; (aa) additive x additive; (ad) additive x dominance; (dd) dominance x dominance gene effects

The regression analysis revealed additive gene effect (a) was highly significant for number of spikelet per panicle, number of spikelet per plant and 100 grain weight, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were nonsignificant for number of panicle per panicle, number of spikelet per plant and 100 grain weight in the exception of additive x dominance (ad) gene effect which is significant for 100 grain weight. The highly significant of additive (a) gene effect on this traits indicating the important of additive gene effect in control of number of panicle per panicle, number of spikelet per plant and 100 grain weight in this study. However, the magnitude of the significant fixable gene action (a) for 100 grain weight has greater magnitude compared with the non-fixable (ad). The negative

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significant additive (a) gene action for number of spikelet per plant and number of spikelet per plant and the negative significant (ad) for 100 grain weight were in the direction of the reducer parent for the three characters (Table 15).

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Table 16 nalysis of variance and parameter estimates for genetic control of number of fertile spikelet per panicle, number of fertile spikelet per plant and grain yield per plant obtained through generation mean analysis with IET6279 X IR70445-146-3-3 cross.

		Number of fertile spikelet / Panicle				Number of fertile spikelet / plant				Grain yield /plant			
Variable	DF	Para. Est.	Std. error	T Value	P value	Para. Est.	Std. error	T Value	P value	Para. Est.	Std. error	T Value	P value
intercept	1	112.25	27.62	4.06	0.00	1261.84	1129.97	1.12	0.29	46.62	30.46	1.56	0.15
rep	1	3.62	2.22	1.63	0.13	270.21	94.63	2.86	0.02	6.20	2.65	2.33	0.04
a	1	-28.89	2.65	-10.92	0.00	-798.39	113.13	-7.06	0.00	-17.32	3.22	-5.38	0.00
d	1	-4.26	63.88	-0.07	0.95	289.94	2592.11	0.11	0.91	-22.57	70.00	-0.32	0.75
aa	1	16.26	27.29	0.60	0.56	934.67	1103.46	0.85	0.42	17.48	29.56	0.59	0.57
ad	1	38.46	15.16	2.54	0.03	1347.26	629.48	2.14	0.05	21.63	17.30	1.25	0.24
dd	1	32.38	38.76	0.84	0.42	783.47	1577.10	0.50	0.63	41.20	42.87	0.96	0.36

Note: (a) additive; (d) dominance; (aa) additive x additive; (ad) additive x dominance; (dd) dominance x dominance gene effects

The regression analysis revealed additive gene effect (a) was highly significant for number of fertile spikelet per panicle, number of fertile spikelet per plant and grain yield per plant, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non-significant for number of fertile spikelet per panicle, number of fertile spikelet per plant and grain yield per plant in the exception of additive x dominance (ad) gene effect which is significant for number of spikelet per panicle and number of fertile spikelet per plant. The highly significant of additive (a) gene effect on this traits indicate the important of additive gene effect in control of the three trait. However, the magnitude of the significant fixable gene action (a) in number of fertile spikelet per panicle and number of fertile spikelet per plant has smaller magnitude

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compared with the non-fixable (ad). The significant negative additive (a) gene action was in the direction of depress parent for all the three trait (Table 16).

Table 17 nalysis of variance and parameter estimates for genetic control of spikelet fertility per cent /plant, days to 50% flowering and days to maturity obtained through generation mean analysis with IET 6279 X IR70445-146-3-3 cross.

		% spikelet fertility /plant				days to 50% flowering				days to maturity			
Variable	DF	Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value	Para. Est.	Std. error	T value	P value
intercept	1	72.02	9.62	7.49	0.00	113.01	12.71	8.89	0.00	134.39	7.23	18.59	0.00
rep	1	0.54	0.69	0.78	0.45	0.09	0.47	0.20	0.85	0.02	0.48	0.03	0.98
a	1	-6.63	1.19	-5.59	0.00	-11.24	0.58	-19.30	0.00	-7.97	0.50	-16.05	0.00
d	1	22.72	22.11	1.03	0.33	-43.75	29.50	-1.48	0.17	-32.96	16.41	-2.01	0.07
aa	1	6.59	9.47	0.70	0.50	-9.29	12.64	-0.74	0.48	-2.75	7.16	-0.38	0.71
ad	1	10.12	5.39	1.88	0.09	15.72	6.84	2.30	0.04	12.94	3.64	3.55	0.00
dd	1	-4.79	13.00	-0.37	0.72	17.84	17.33	1.03	0.33	15.46	9.57	1.62	0.13

Note: (a) additive; (d) dominance; (aa) additive x additive; (ad) additive x dominance; (dd) dominance x dominance gene effects

The generation mean analysis indicated that additive (a) gene effects was highly significant for % spikelet fertility per plant, days to50% flowering and days to maturity, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non-significant for all the three characters in the exception of additive x additive gene effect which is significant for days to flowering and days to

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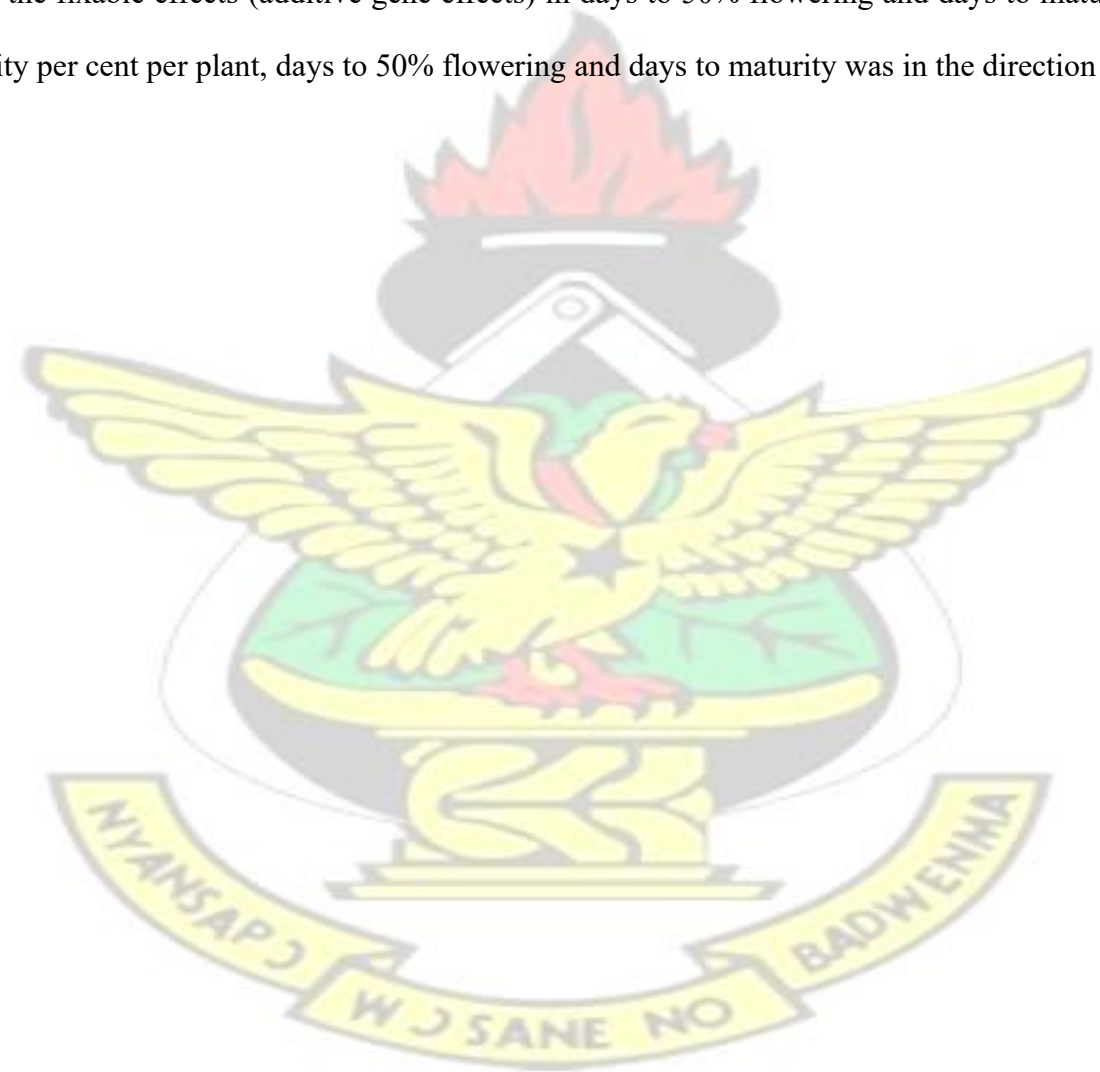
maturity. However, it is evident that the magnitude of non-allelic interactions and absolute total of non-fixable gene effects (additive x additive gene effect) was greater than the fixable effects (additive gene effects) in days to 50% flowering and days to maturity. The negative additive (a) gene action for spikelet fertility per cent per plant, days to 50% flowering and days to maturity was in the direction of reducer parent (Table 17).



CHAPTER FIVE

5.0 DISCUSSION

This experiment is very relevant in the area of genetics and plant breeding. Very little progress can be achieve in planting breeding without information on the mode of inheritance of traits of economic importance. The inheritance of aroma as well as days to flowering, days to maturity, plant height, number of tillers per plant, culm length, number of panicles per plant, panicle length, leaf length, leaf width, flag leaf length, flag leaf width, number of spikelet per panicle, number of spikelet plant, number of fertile spikelet per panicle, number of fertile spikelet per plant, spikelet fertility per cent per plant, grain yield per plant, 100 grain weight, grain length, grain width and number of unfilled grain per plant were chosen for the study. The results are discussed below.

5.1 Inheritance of aroma

IR70445-146-3-3 was used as donor in an attempt to incorporate aroma into IET6279. F_1 of IET6279 / IR70445-146-3-3 was non-aromatic. A recessive gene(s), therefore, controls aroma in IR70445-146-3-3. The F_2 for IET 6279/ IR70445-146-3-3 segregated into 203 aromatic: 589 non-aromatic plants, indicating a 1: 3 ratio ($\chi 2$ = 0.14). A backcross (test cross), BCP_2 (IET6279/ IR70445-146-3-3 // IR70445-146-33) segregated into 79 aromatic: 92 non-aromatic plants were obtained, indicating a 1:1 ratio (χ^2 = 0.84). BCP_1 (IET6279/ IR70445-146-3-3// IET6279) plants were all non-aromatic. The segregation ratios (F_2 and BCP_2) indicate that a single recessive gene, controls aroma in IR70445-146-3-3. These shows that there would be a high probability of success in selecting for aroma using Pedigree breeding in early

generations of F_2 (Table 2). Single gene control of aroma has been widely reported (Sood & Siddiq, 1978; Berner & Hoff, 1986; Pinson, 1994; Dong *et al*., 1992, 2000, 2001a & b). However, multiple gene control of aroma has also been reported (Geetha, 1994; Pinson, 1994; Dong *et al*., 2000 & 2001b). Dong *et al*., (2000) also reported that Della, Hokkaido 270 and Shiroikichi each contain a single gene and HB-1 has two recessive genes for aroma. Berner & Hoff (1986) had reported the monogenic recessive inheritance of Della using the same method (the KOH solution method) by Sood & Siddiq, (1978). This report has also validated Pinson (1994) "s report that J85 was under the control of a single recessive gene. It must be noted that some researchers have used the same method (Sood & Siddiq, 1978) on different cultivars and have reported both monogenic and digenic inheritance depending on cultivar used (Pinson, 1994; Dong *et al*., 2000 & 2001b). Tsuzuki & Shimokwa, (1990) has reported that the lack of agreement among researchers as to whether a single recessive gene or, two or three recessive or dominant genes control 54 aroma in rice appears to be related to the differences in the aromatic varieties used and also the differences in the methods used in evaluating aroma. It is suggested that some aromatic cultivars contain a single gene whilst others contain two or more aroma genes; and that the difference in opinion on the inheritance of aroma is mainly due to cultivar differences.

5.2 Genetic analysis of plant height

Plant height is not only a decisive factor in plant architecture, but also an important agronomic trait that is directly linked to the harvest index and yield potential (Yang and Hwa, 2008). Therefore, morphological characteristics such as plant height have been considered important traits in breeding both super rice and bio-energy crops. Plant height varied from 77 cm to 187 cm. The maximum and minimum mean performance for plant height were recorded in IET6279 (134.27) and IR70445-1463-3 (113.15)

respectively. The Mean of F_1, F_2, BCP_1 and BCP_2 were all within parental limits. The range of variation and variance in F_2 was higher than parents, F_1, BCP_1 and BCP_2. The CV in F_2 was highest (12.73%) followed by BCP_1 (10.06%) and IET6279 recorded the lowest (4.77%) (Table 3). High broad sense heritability was recorded for plant height (Table 10). This agrees with the findings of Fahliani *et al*., (2010), Venkata *et al.,* (2011), Ashok, *et al*., (2013), Lingaiah, *et al*., (2014), Ketan and Sarkar, (2014) and Tuhina, *et al*., (2015) who reported high broad sense heritability estimates for plant height. The present results indicate that the phenotype is highly correlated with the genotype and that contribution of environmental conditions was relatively low for this trait. However, the findings of Sabu *et al*., (2009) and Sandhya *et al*., (2014) do not support the results obtained from present study, who reported low broad sense heritability for plant height.

The results obtained from regression analysis revealed that the additive gene effect (a) was highly significant for plant height while dominance gene effect (d) and nonadditive gene effects with their interactions (aa), (ad) as well (dd) were non-significant. The non-significant of dominance and epistatic effects for plant height indicate the predominance of additive gene effect in control of the trait. (Table 11). Similar results earlier reported by Honarnejad (1996), Narayana and Rangasamy (1991), Singh *et al*. (1996), Gnanasekaran *et al*., (2006), Praveen *et al*., (2009), Upadhyay and Jaiswal, (2015). The non-significance of dominance and epistatic effects in this trait indicated that there would be a high probability of success in selecting for plant height in early generations. The significant and negative additive gene action (a) for plant height shows that gene action was in the direction of the reducer parent.

5.3 Genetic analysis of days to 50% flowering

Transition of apical bud in-to floral bud demarcates the initiation of reproductive stage of rice in its growth cycle. Number of days taken for this transition determines the heading date or days to flowering of any rice cultivar (Yano *et al*., 2001). Days to flowering ranged from 82 days to 123 days. The mean performance of IET6279 (115.03) was higher than IR70445-146-3-3 (92.78). Mean for F_2, BCP_1 and BCP_2 were all within parental limits except for F_1 (88.11) which had mean lower than both parents. The range of variation and variance in F_2 was higher than IR70445-146-3-3, F_1 and BCP_1. The CV in F_2 was the highest (7.42%) followed by BCP_2 (7.19%) and IR70445-146-3-3 recorded the lowest (1.60%) (Table 3). High broad sense heritability was recorded for days to 50% flowering (Table 10). Similar results were earlier reported by Bihari et *al., (*2004), Sankar *et al*., (2006), Karthikeyan *et al.,* (2009), Venkata, *et al.,* (2011), Ashok *et al.,* (2013), Lingaiah *et al.,* (2014), Ketan and Sarkar, (2014) and Tuhina *et al.,* (2015). The present results indicate that the phenotype is highly correlated with the genotype and that contribution of environmental conditions was relatively low in influencing this character. These results do not agreed with the findings by Sathya and Jebaraj, (2013) and Sellammal, *et al*., (2014) who reported low broad sense heritability for this trait.

The generation mean analysis indicated that both additive gene effects and additiveby-dominance genet effect were significance for days to 50% flowering, while (d), (aa) and (dd) were non-significant. The non-significance of (d), (aa) and (dd) indicating the importance of additive gene effect and non-additive interaction in control of days to 50% flowering (Table 17). Similar results were earlier reported by Patel *et al*., (2014). However, it is evident that the magnitude of non-allelic interaction and absolute total of non-fixable gene effects (additive x dominance) was larger than the magnitude of

the fixable effect (additive gene effects) for days to flowering (Hakizimana, *et al.*, 2004). Since additive effects were equally important as non-additive effects for grain length, breeding progress might be slow. Therefore, improvement of these traits appears to be beset with difficulties as simple selection techniques will not be able to fix superior lines in the early segregating generations. Postponement of selection of superior lines to later generations in pedigree breeding will be effective. One or two cycles of recurrent selection followed by pedigree breeding will be effective and useful to utilize both additive and non-additive gene effects. The negative significant additive (a) gene action for days to 50% flowering was in the direction of parent with reduced value.

5.4 Genetic analysis of days to maturity

Days to maturity varied from 106 days to 152 days. IET6279 (139.78) had the longest maturity duration while F_1 (117.27) had the shortest days to maturity. The range of variation and variance in F_2 was higher than parents, F_1, BCP_1 and BCP_2. F_2 recorded the highest CV (12.73%) followed by BCP_1 (10.06%) and IET6279 recorded the lowest (4.77%) (Table 3). High broad sense heritability was recorded for days to maturity (Table 10). This is in conformity with the findings of Chanbeni *et al*., (2012), Awaneet and Senapati, (2013), Akinwale *et al*., (2011), Venkata *et al.,* (2011), Ashok et al., (2013) and Tuhina, *et al.,* (2015) who had reported high broad sense heritability for this trait. The present results indicates that the phenotype is highly correlated with the genotype and that contribution of environmental conditions was relatively low in influencing this character. However, the finding on these study was contrary to the observation of Bekele et al., (2013) and Osekita *et al*.,

(2014) who reported low broad sense heritability for days to maturity.

The generation mean analysis indicated that both additive gene effects and additive x dominance gene effect were highly significance for days to maturity, while (d), (aa) and (dd) were non- significant. The absent of significance of (d), (aa) and (dd) indicated the importance of additive gene effect and non- additive gene interaction in the inheritance of days to maturity (Table 17). Similar results were earlier reported by Patel *et al*., (2014). However, it is evident that the magnitude of non-allelic interaction and absolute total of non-fixable gene effects (additive x dominance) was larger than the magnitude of the fixable effect (additive gene effects) for days to maturity (Hakizimana, *et al*., 2004). Since additive effects were equally important as non-additive effects for days to maturity, breeding progress might be slow. Therefore, improvement of these traits appears to be beset with difficulties as simple selection techniques will not be able to fix superior lines in the early segregating generations. Postponement of selection of superior lines to later generations in pedigree breeding will be effective. One or two cycles of recurrent selection followed by pedigree breeding will be effective and useful to utilize both additive and nonadditive gene effects. The negative significant additive (a) gene action for days to maturity was in the direction of reducer parent.

5.5 Genetic analysis of number of tillers per plant

Tillering in rice is one of the most important agronomic traits for grain production because tiller number per plant determines panicle number, a key component of grain yield (Liu *et al*., 2011; Zhu *et al*., 2011). Furthermore, tiller number usually serves as a suitable model trait for the study of developmental characteristics, since it changes over time. Hence, the genetic elucidation of tiller number has become a focus in rice genetic and breeding research (Liu *et al*., 2010). The number of tillers per plant ranged from 5 to 44. The maximum and minimum mean obtained were 23.40 and

18.57 in IET6279 and F_2 respectively. The range of variation and variance in F_2 was higher than parents, F_1, BCP_1 and BCP_2. F_2 recorded the highest CV (34.78%) followed by BCP_2 (34.62%) and IET6279 recorded the lowest (16.35%) (Table 4). Low broad sense heritability was reported for number of tillers per plant (Table 10). These results were in conformity to the findings of Akinwale *et al*., (2011), Mulugeta *et al*., (2012), Sabu *et al*., (2009) who also reported low broad sense heritability for number of tillers per plant. The present results indicate that the phenotype is not highly correlated with the genotype and that contribution of environmental conditions was relatively high and strongly influencing this character (Saleem *et al*.,
2010). However, the finding in this study was contrary to the observation of Anyanwu and Obi, (2014), Ammar *et al*., (2014) and Tuhina, *et al.,* (2015) who reported high degree of broad sense heritability for this trait.

The results obtained from regression analysis revealed that the additive gene effect (a) was highly significant for number of tiller per plant while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non- significant. The non-significance of dominance and epistatic effects for number of tillers per plant indicated the predominance of additive gene effect in control of number of tiller per plant. (Table 14). Similar results was earlier reported by Honarnejad (1996), Narayana and Rangasamy, (1991), Praveen *et al*., (2009) and Jarwar *et al*., (2014). The non-significance of dominance and epistatic effects in this trait indicated that there would be a high probability of success in selecting for number of tiller per plant in early generations. The significant and negative additive gene action (a) for number of tiller per plant was in the direction of the reducer parent.

5.6 Genetic analysis of culm length.

Lodging is one of the major factors limiting the yield potential of both inbred and hybrid rice cultivars and has received particular attention. Lodging can cause severe yield loss and poor grain quality because of reduced canopy photosynthesis, increased respiration, reduced translocation of nutrients and carbon for grain filling, and increased susceptibility to pests (Hitaka, 1969). Culm length varied from 55 cm to 153 cm with a maximum and minimum mean of (108.17) and (83.18) for IET6279 and IR70445-146-3-3 respectively. Mean for F_1, F_2, BCP_1 and BCP_2 were all within parental limits. . The range of variation and variance in F_2 was higher than parents, F_1, BCP_1 and BCP_2. F_2 recorded the highest CV (15.20%) followed by BCP_1 (12.06%) and IET 6279 recorded the lowest (5.87%) (Table 5). High broad sense heritability were reported for culm length (Table 10). These results were in conformity to the findings of Sabu *et al*., (2009) and Arpita *et al.*, (2014) who also reported earlier on high broad sense heritability for this trait. The present results indicate that the phenotype is highly correlated with the genotype and that contribution of environmental conditions was relatively low for this trait.

The generation mean analysis indicated that additive gene effects is highly significant for culm length, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non-significant for culm length. The lack of significant of (d), (aa), (ad) and (dd) gene effect indicating the predominance of additive gene effect in control of this character (Table 12). Similar findings were observed by Arpita *et al*., (2014). The non-significance of dominance and epistatic effects in this trait indicated that there would be a high probability of success in selecting for culm length in early generations of F_2. The significant and negative additive gene effect (a) was in the direction of the reducer parent

5.7 Genetic analysis of number of panicles per plant

The number of panicles is the result of number of tillers produced and the proportion of effective tillers, which survived to produce panicle (Hossain *et al*., 2008). Number of panicle per plant varied between 4 and 43. IET6279 recorded the highest mean for number of panicles per plant (22.17) followed by IR70445-146-3-3 (19.70) and F_2 recorded the lowest (17.12). The mean for both parents were slightly greater than F_1, BCP_1 and BCP_2. The range of variation and variance of IR70445-146-3-3, BCP_1 and BCP_2 were slightly higher than their corresponding F_2. This deviates from how the various generations normally behave. The CV in F_2 is highest (35.46%) followed by BCP_2 (35.34%) and IET6279 recorded the lowest (18.22%) (Table 4). Low broad sense heritability was observed for number of panicle per plant (Table 10). These is in conformity with the findings of (Rafii *et al*., 2014) who reported low degree of broad-sense heritability for number of panicle per plant. The present results indicated that number of panicle per plant is influenced more by environmental factors such as geographical effects and climate (Saleem *et al*., 2010). These findings did not agrees with the results from previous study by Sathya and Jebaraj, (2013), who recorded high degree of broad sense heritability for this character.

The regression analysis revealed additive gene effect (a) was highly significant for number of panicle per plant, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non-significant for number of panicle per plant. The non-significance of dominance and epistatic effects indicated the predominance of additive gene effect in the inheritance of the trait (table 14). Similar findings was observed by Hasib *et al*., (2002), Praveen *et al*., (2009), Mulugeta *et al*., (2012) and Jarwar *et al*., (2014). The non-significant of dominance and epistatic effects in this trait indicated that there would be a high probability of

success in selecting for number of panicles per plant in early generations. The significant and negative additive gene effect (a) was in the direction of the reducer parent for number of panicle per plant.

5.8 Genetic analysis of panicle length

The range of Panicle length varied from 16 cm to 41cm. F_1 registered the maximum panicle length (30.68) followed by BCP_1 (30.43) while the minimum value for panicle length was observed in IET6279 (26.10).The range of variation and Variance in IR70445-146-3-3, BCP_1 and BCP_2 were slightly higher than their corresponding F_2. This deviates from how the various generations normally behave. The CV in IR70445-146-3-3, BCP_1 and BCP_2 were also slightly higher than their corresponding F_1, F_2 and IET6279 respectively (Table 4). Low broad sense heritability was reported for panicle length (Table 10). These results were in conformity to the findings of Sabu *et al*., (2009), Fahliani *et al*. (2010) and Sathya and Jebaraj, (2013) who reported low heritability for panicle length. The present results indicate that the phenotype is not highly correlated with the genotype and that contribution of environmental conditions was relatively high and strongly influence this character (Saleem *et al*., 2010). These findings do not support the results from previous study by Hasan *et al*., (2010), Yadav *et al*., (2011), Mulugeta *et al*., (2012), Vanisree *et al.*, (2013), Ammar *et al*., (2014) and Sandhya *et al*., (2014) who reported high broad sense heritability for this character.

The regression analysis revealed additive gene effect (a) was highly significant for panicle length while dominance (d), additive x additive (aa), additive x dominance (ad) and dominance x dominance (dd) gene effect were non-significant for panicle length. The non-significant of dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) for panicle length, indicating the predominance of additive gene effect in control of this trait (Table 13). Similar results was earlier

reported by Narayana and Rangasamy, (1991) and Jarwar *et al*., (2014). However, the presence of significant (a) gene effect and the non-significance of dominance and epistatic effects would make selection from early generation effective for panicle length. Although, (aa) gene effect was not significant, the associated negative sign indicates that gene effect was in the direction of the reducer parent for panicle length.

5.9 Genetic analysis of leaf length

Leaves are often the most noticeable parts of a plant; they are the predominant photosynthetic organs and are of pivotal importance for carbon fixation. Some leaf parameters, such as shape, number, size, thickness, direction and chloroplast level are very important factors influencing the biomass formation and success of a plant.

Much attention has been paid to leaf shape of rice in the process of ideotype breeding (Yan *et al*., 2006). The length, width, angle and area are the three traits determining the shape and size of a leaf, among which the area is attributable to the length and width with higher correlations between length and area than between width and area (Yan and Wang 1990; Peng *et al*., 2008). Light interception by a canopy of leaves is strongly influenced by the leaves' size and shape, angle, and azimuthal orientation, vertical separation and horizontal arrangement, and by absorption by non-leaf structure (Yoshida, 1972). Leaf length varied between 23 cm and 90 cm. The minimum and maximum recorded mean for leaf length were 44.35 and 57.51 cm for IET6279 and F_2. Leaf length varied between 31 and 90 cm. The range of variation and variance in F_2 was higher than parents, F_1 and BCP_2. BCP_1 reported the highest

CV (18.57%) followed by F_2 (16.97%) and IR70445-146-3-3 recorded the lowest (12.18%) (Table 5). Low broad sense was recorded for this character (Table 10). The present results indicate that the phenotype is not highly correlated with the genotype and that contribution of environmental conditions was relatively high and strongly

influence this character **(**Saleem *et al*., 2010). These results do not agree with the findings of Abhishek *et al.,* (2014) who reported high degree of broad sense heritability for this trait.

The results obtained from regression analysis revealed that additive gene effect (a) was highly significant for leaf length, while dominance gene effect (d) and nonadditive gene effects with their interactions (aa), (ad) as well (dd) were not significant for leaf length. However, the significance of additive (a) gene effect shows its predominance in the inheritance of this character (Table 11). Similar findings were observed by Abhishek *et al.,* (2014). The non-significance of dominance and epistatic effects in this trait indicated that there would be a high probability of success in selecting for leaf length in early generations The negative (ad) for leaf length, though not significant, was in the direction of the depress parent for this characters

5.9.1 Genetic analysis of leaf width.

Leaves are often the most noticeable parts of a plant; they are the predominant photosynthetic organs and are of pivotal importance for carbon fixation. Some leaf parameters, such as shape, number, size, thickness, direction and chloroplast level are very important factors influencing the biomass formation and success of a plant.

Leaf width varied between 1 cm and 2.2 cm with a maximum means of (2.02) for IET6279 and a minimum mean of (1.42) for IR70445-146-3-3. The range of variation and variance in F_2 was higher than IR70445-146-3-3. F_2 recorded the highest CV (15.09%) followed by BCP_2 (15.01%) and IET6279 recorded the lowest (7.67%) (Table 5). Low broad sense was recorded for this character (Table 10). The present results indicate that the phenotype is not highly correlated to the genotype and that contribution of environmental conditions was relatively high and strongly influence

this character (Saleem *et al*., 2010). These results do not agree with the findings of Abhishek *et al.,* (2014) who reported high degree of broad sense heritability for this trait. The generation mean analysis indicated that both additive gene effects and additive x dominance gene effect were significant for leaf length. The dominance (d), additive-by additive (aa) and dominance x dominance (dd) gene effect were non-significant for this character. However, the non-significance of (d), (aa) and (dd) shows the predominance of additive and additive x dominance gene effect in the inheritance of this character (Table 11). The present results were in partial agreement with the findings of Abhishek *et al.,* (2014) who reported the predominance role of additive gene effect in the inheritance of the character. It is evident that the magnitude of non-allelic interactions and absolute total of nonfixable gene effects (additive x dominance gene effect) was greater than the corresponding fixable effects (additive gene effects) for leaf width (Hakizimana *et al*., 2004). Since additive effects were equally important as non-additive effects for leaf width, breeding progress might be slow. Therefore, improvement of these traits appears to be beset with difficulties as simple selection techniques will not be able to fix superior lines in the early segregating generations. Postponement of selection of superior lines to later generations in pedigree breeding will be effective. One or two cycles of recurrent selection followed by pedigree breeding will be effective and useful to utilize both additive and non-additive gene effects. The negative significant

(a) for leaf width was in the direction of the reducer parent.

5.9.2 Genetic analysis of flag leaf length.

With increasing population, high yield has become one of targets in rice breeding. Photosynthesis is the primary source of grain yield in rice (Chen *et al*., 1995). The top three leaves of rice, particularly the flag leaf, are the main source of carbohydrates production (Abrol *et al*., 1993). At least 50% of photosynthetic products for grain are

provided by flag leaf, the most important organ for photosynthesis (Li *et al*., 1998). Some traits, such as size and shape of flag leaf, affect photosynthesis to a certain extent, thereby influencing production (Yue *et al*., 2006). It has been proven that the flag leaf, stem and head are the closest source to the grain (Prakash *et al*., 2011). Grain yield increase would be effectively rested with the basis of the capabilities of yield components and other closely associated traits (Xue *et al*., 2008). The morphological traits of flag leaf such as size and shape, and physiological traits of flag leaf such as chlorophyll content and photosynthesis capacity have been considered to be the important determinants of grain yield in cereals (Chen *et al*., 1995). Flag leaf length varied between 17 cm and 83 cm. The maximum Flag leaf length mean was observed for F_2 (43.89 cm) followed by BCP_2 (42.17 cm) while the minimum Flag leaf length was observed for IET6279 (30.75 cm). The range of variation and variance in F_2 was higher than parents, F_1 and BCP_1. BCP_2 recorded the highest CV (19.74%) followed by BCP_1 (19.34%) and IET6279 recorded the lowest (14.64%) (Table 6). Low broad sense heritability was recorded for this character (Table 10). These results agreed with the findings of Muhammad *et al*., (2002) who reported low broad sense heritability for this trait. The present results indicate that the phenotype is not highly correlated with the genotype and that contribution of environmental conditions was relatively high and strongly influence this character **(**Saleem *et al*., 2010). This result do not agree with the findings of Hasan *et al*., (2010), Priyanka *et al*., (2010), Yadav *et al*., (2011) and Chanbeni *et al*., (2012) who reported high broad sense heritability for this character. The regression analysis indicated that both additive gene effect (a) and additive x additive gene effect were significant for flag leaf length, while dominance gene effect (d) (aa) and (dd) were non-significant for this trait. The significance of additive (a) and additive x additive (aa) gene effect of this trait indicate the predominance of additive

gene effect and additive x additive gene effect in the control of the trait (Table 12). The present results were in partial agreement with the findings of Chakraborty *et al.,* (2009), Yadav *et al*., (2011) and Arpita *et al*., (2014) who reported predominant role of additive gene effects in controlling the inheritance of flag leaf length in rice. However, it is evident that the significant fixable additive component was greater in magnitude than its corresponding significant fixable additive x additive component. Since additive effects were equally important as non-additive effects for flag leaf length, breeding progress might be slow. Therefore, improvement of these trait appears to be beset with difficulties as simple selection techniques will not be able to fix superior lines in the early segregating generations. Postponement of selection of superior lines to later generations in pedigree breeding will be effective. One or two cycles of recurrent selection followed by pedigree breeding will be effective and useful to utilize both additive and non-additive gene effects. The negative significant additive x additive (aa) gene effect for flag leaf length was in the direction of the reducer parent.

5.9.3 Genetic analysis of flag leaf width

With increasing population, high yield has become one of the targets in rice breeding. Photosynthesis is the primary source of grain yield in rice (Chen *et al*.,
1995). The top three leaves of rice, particularly the flag leaf, are the main source of carbohydrates production (Abrol *et al*., 1993). At least 50% of photosynthetic products for grain are provided by flag leaf, the most important organ for photosynthesis (Li *et al*., 1998). Some traits, such as size and shape of flag leaf, affect photosynthesis to a certain extent, thereby influencing production (Yue *et al*.,
2006). Therefore, flag leaf shape is an index for ideal plant-type in rice breeding (Yang and Yang, 1998). Flag leaf width varied between 1.2 and 2.8 cm. The minimum and maximum recorded mean for Flag leaf width were 1.73 cm and 2.24 cm in IR70445-

146-3-3 and IET6279 respectively. The range of variation and variance in F_2 was higher than parents, F_1 and BCP_2. F_1 recorded the highest CV

(12.87%) followed by BCP_2 (12.50%) and IET6279 recorded the lowest (8.13%) (Table 6). Low broad sense heritability was reported for flag leaf width (Table 10). These results were in conformity to the findings of Yadav *et al*., (2011) and Sandhya *et al*., (2014) who earlier reported low broad sense heritability for Flag leaf width. The present results indicate that the phenotype is not highly correlated with the genotype and that contribution of environmental conditions was relatively high and strongly influence this character (Saleem *et al*., 2010). On the contrary, these results do not agree with the findings of Priyanka *et al*., (2010) and Chanbeni *et al*., (2012) who reported high degree of broad sense heritability for this trait. The generation mean analysis shows high degree of significance of additive gene effect (a) for flag leaf width while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non-significance for these trait. The lack of significant of (d), (aa) (ad) and (dd) indicate the predominant role of additive gene effect in the inheritance of flag leaf width (Table 12). These results are in agreement with results obtained by Sardana and Borthakur (1987) and Kiani *et al*., (2013). The non-significance of dominance and epistatic effects on this trait indicated that there would be a high probability of success in selecting for flag leaf width in early generations. Negative significant sign for (a) demonstrated that predominance was towards the reducer parent.

5.10 Genetic analysis of number of Spikelet per panicle

Rice grains yield is a quantitative trait influence by other agronomic traits and environmental factors. Spikelet number per panicle is important component of rice grain yield (Zong *et. al*., 2012). The development of sufficient sink capacity and high

degree of grain filling of superior rice cultivars should consider the distribution of spikelet number per panicle and degree of grain filling. Sheehy *et al*., (2001) found that the high yielding plant type with high potential for spikelet number per panicle, was highly associated with rice grain yield. The study of inheritance of this trait is the important way for rice breeding program. Total number of spikelets per panicle was greatly varied from 61 to 298. The mean maximum and the minimum number of spikelet per panicle was recorded in IET6279 (191.40) and IR70445-146-3-3 (150.30) respectively. However, the range of variation and variance in F_1 was higher than the corresponding parents, F_2. BCP_1 and BCP_2 respectively. F_2 recorded the highest CV (28.28%) followed by F_1 (26.91%) and IET6279 recorded the lowest (12.80%) (Table 7). Low broad sense heritability was reported for number of spikelet per panicle (Table 10). These results were in conformity to the findings of Anyanwu and Obi, (2014) and Osekita, *et al*., (2014) who also reported earlier on low heritability for this trait. The present results indicate that the phenotype is not highly correlated with the genotype and that contribution of environmental conditions was relatively high and strongly influence this character (Saleem *et al*., 2010). These findings do not support the results from previous study by Yadav *et al*., (2011),

Mulugeta *et al*., (2012), Ammar *et al*., (2014) and Sandhya *et al*., (2014), who reported high degree of broad-sense heritability for this trait. The regression analysis revealed additive gene effect (a) was highly significant for number of spikelet per panicle, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non-significant for number of spikelet per panicle. The highly significant additive (a) gene effect on this trait indicated the importance of additive gene effect in the inheritance of the character (Table 15). Similar results were earlier reported by Narayana and Rangasamy, (1991), Padmaja *et al*., (2008), Praveen *et al*.,

(2009), Liu *et al*. (2010) and Mulugeta *et al*., (2012) who suggested preponderance of additive gene action in the expression of the character. The lack of dominance and epistatic effects on this trait indicated that there would be a high probability of success in selecting for number of spikelet per panicle in early generations. The significant negative additive (a) gene action for number of spikelet per panicle was in the direction of the reducer parent.

5.10.1 Genetic analysis of number of spikelet per plant

Rice grains yield is a quantitative trait influence by other agronomic traits and environmental factors, of which spikelet number per panicle is important component of rice grain yield (Zong *et. al*., 2012). The development of sufficient sink capacity and high degree of grain filling of superior rice cultivars should consider the distribution of spikelet number per plant and degree of grain filling. Sheehy *et al*., (2001) found that the high yielding plant type had high potential for spikelet number per plant, which highly associated with rice grain yield**.** Total number of spikelets per plant greatly varied from 502 to 9412. The maximum and minimum number of spikelet per plant were recorded for IET6279 (4232) and BCP_2 (2569). The range of variation and variance in F1 were higher than parents, F_2, BCP_1 and BCP_2. F_2 recorded the highest CV (48.50%) followed by F_1 (45.10%) and IET6279 recorded the lowest (21.78%) (Table 7). Very low broad sense heritability (27%) was recorded for this character (Table 10). The present results indicate that the phenotype is not highly correlated with the genotype and that contribution of environmental conditions was relatively high and strongly influence this character **(**Saleem *et al*., 2010). These results do not agree with the findings of Pallabi *et al*., (2013).who reported high degree of broad sense heritability for this trait, possibly because the author might have used different genotypes and the environmental conditions under which their study was conducted.

The regression analysis revealed additive gene effect (a) was highly significant for number of spikelet per plant, while dominance gene effect (d) additive x additive (aa) additive x dominance (ad) and dominance x dominance (dd) gene effect were not significant for this character. The significant additive (a) gene effect on this traits indicate the importance of additive gene effect in the control of number of spikelet per plant (table 15). Similar findings were observed by Pallabi *et al*., (2013). The non-significance of dominance and epistatic effects in this trait indicated that there would be a high probability of success in selecting for number of spikelet per plant in early generations. The significant negative additive (a) gene action was in the direction of the reducer parent.

5.10.2 Genetic analysis of number of fertile spikelet per panicle.

Total number of spikelets per panicle was greatly varied from 61 to 298. The mean maximum and the minimum number of spikelet per panicle were recorded in IET6279 (165.30) and IR70445-146-3-3 (107.90) respectively. However, the range of variation and variance in F_1 was higher than the corresponding parents, F_2. BCP_1 and BCP_2 respectively. F_2 recorded the highest CV (30.58%) followed by BCP_1 (27.46%) and IET6279 recorded the lowest (13.17%) (Table 8). Low broad sense heritability was recorded for this character (Table 10). These results agreed with the findings of Osekita *et al*., (2014) who reported low broad sense heritability for this trait. The present results indicate that the phenotype is not highly correlated with the genotype and that contribution of environmental conditions was relatively high and strongly influence this character (Saleem *et al*., 2010). However, the results do not agree with the findings by Sathya and Jebaraj, (2013) and Tuhina *et al* (2015) who reported high broad sense heritability for the character. Both additive gene effect (a) and additive x dominance gene effect (ad) were significant for number of fertile spikelet per panicle, while

dominance gene effect (d), (aa) and (dd) were nonsignificant for number of fertile spikelet per panicle. The significant additive (a) and additive x dominance (ad) gene effect of this trait indicate the predominance of additive gene effect and additive x dominance gene effect in control of the trait

(Table 16). The present results was in partial agreement with Deepa *et al.,* (2006), Bagheri *et al*., (2008), Kundu *et al*., (2008), Venkata *et al.,* (2011) who reported predominance role of additive gene effects in controlling the inheritance of number of fertile spikelet per panicle in rice and Li *et al*., (1997) found that epistasis has important effect on complex traits such as grain number per each panicle. The significant fixable gene action (a) has smaller magnitude compared to corresponding additive x dominance non-fixable (ad) component (Hakizimana *et al.,* 2004). Since additive effects were equally important as non-additive effects for number of fertile spikelet per panicle, breeding progress might be slow. Therefore, improvement of these traits appears to be beset with difficulties as simple selection techniques will not be able to fix superior lines in the early segregating generations. Postponement of selection of superior lines to later generations in pedigree breeding will be effective. One or two cycles of recurrent selection followed by pedigree breeding will be effective and useful to utilize both additive and non-additive gene effects. The negative significant additive (a) gene action for number of spikelet was in the direction of the reducer parent

5.10.3 Genetic analysis of number of fertile spikelet per plant.

Spikelet fertility was studied because F1 hybrids had very low seed set. Hybrid sterility means a reduced fertility in the hybrid than the parents (Sano, 1997). It generally occurs upon hybridization between distantly related taxa. Spikelet sterility in F1‟s results from anther indehiscence, pollen sterility, disharmonious interactions between nuclear genes or between cytoplasm and nuclear genes as well as differences in the

structure of chromosomes (Sano, 1997). A difficulty in examining the genetic basis of hybrid sterility results from the fact that the genetic basis of F_1 sterility might differ from that of F_2 sterility (hybrid breakdown). Therefore, it is difficult to examine the segregational pattern of genes controlling F_1 hybrid sterility in the F_2 generation (Sano, 1997). The number of fertile spikelets per plant was greatly varied from 47 to 273. The lowest number of fertile spikelet per plant was recorded in IR70445-146-3-3 (2144) while the highest was recorded in IET6279 (3656). The mean of F_1, F_2, BCP_1 and BCP_2 were all within parental limits. The range of variation and variance in F_1 was higher than the corresponding F_2. F_2 recorded the highest CV (50.18%) followed by F_1 (44.60%) and IET6279 recorded the lowest (22.23%) (Table 8). Low degree of broad sense heritability is reported for this trait (Table 10). The present results indicate that the phenotype is not highly correlated with the genotype and that contribution of environmental conditions was relatively high and strongly influence this character (Saleem *et al*., 2010). These results were contrary to the finding of Pallabi *et al*., (2013) who reported very high degree of broad sense heritability for this trait, probably due to differences in genotypes used and the environmental conditions under which their study was conducted. The regression analysis revealed additive gene effect (a) and additive x dominance were significant for number of fertile spikelet per plant. However, neither dominance gene effect (d) nor additive x additive (aa) and dominance x dominance (dd) gene effects were significant for number of fertile spikelet per plant. The significant of additive (a) and dominance x dominance (dd) gene effect in this traits indicate the importance of additive and non-additive gene effect in control of the trait (Table 16). The significant fixable gene action (a) for number of fertile spikelet per plant has smaller magnitude compared with the non-fixable (ad). Since additive effects were equally important as non-additive effects for number of fertile spikelet per

panicle, breeding progress might be slow. Therefore, improvement of these traits appears to be beset with difficulties as simple selection techniques will not be able to fix superior lines in the early segregating generations. Postponement of selection of superior lines to later generations in pedigree breeding will be effective. One or two cycles of recurrent selection followed by pedigree breeding will be effective and useful to utilize both additive and non-additive gene effects. The significant and negative additive (a) gene action was in the direction of depress parent for the trait.

5.10.4 Genetic analysis of % Spikelet fertility per plant

Spikelet fertility was studied because F1 hybrids had very low seed set. Hybrid sterility means a reduced fertility in the hybrid than the parents (Sano, 1997). It generally occurs upon hybridization between distantly related taxa. Spikelet sterility in F_1"s results from anther indehiscence, pollen sterility, disharmonious interactions between nuclear genes or between cytoplasm and nuclear genes as well as differences in the structure of chromosomes (Sano, 1997). A difficulty in examining the genetic basis of hybrid sterility results from the fact that the genetic basis of F_1 sterility might differ from that of F_2 sterility (hybrid breakdown). Therefore, it is difficult to examine the segregation pattern of genes controlling F_1 hybrid sterility in the F_2 generation (Sano, 1997). The number of % spikelet fertility per plant ranged from 52.36 to 98.33%, with a maximum mean of 89.76% for (F_1) followed by

IET6279 (86.39) and minimum value was observed in IR70445-146-3-3 (72.39 %). Mean for F_2, BCP_1 and BCP_2 were all within parental limits. The range of variation and variance in F_2 was higher than IR70445-146-3-3, F_1, BCP_1 and BCP_2. F_2 recorded the highest CV (7.86%) followed by IR70445-146-3-3 (7.25%) and IET6279 recorded the lowest (3.80%) (Table 8). Low broad sense heritability was reported for % spikelet fertility per plant (Table 10). These result were in agreement with the earlier findings

of Hasan *et al*., (2010), Pallabi *et al*., (2013), Vanisree *et al*., (2013) and Anyanwu and Obi, (2014). The present results indicate that the phenotype is not highly correlated to the genotype and that contribution of environmental conditions was relatively high and strongly influenced this character (Saleem *et al*.,

2010). These findings do not support the results from previous study by Sathya and Jebaraj, (2013) and Ammar *et al*., (2014), who reported high degree of broad-sense for this character. The generation mean analysis indicated that additive gene effects was highly significant for % spikelet fertility per plant, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non-significant for % spikelet fertility per plant. The non-significance of (d), (aa), (ad) as well (dd) indicate the predominance of additive gene effect in control of this character (Table 17). Similar results were earlier reported by Hasib *et al*., (2002), Saleem *et al*., (2005). The absence of dominance and epistatic effects in this trait indicated that there would be a high probability of success in selecting for % spikelet fertility per plant in early generations. However, the significant negative additive (a) gene action for % spikelet fertility per plant was in the direction of the reducer parent.

5.11 Genetic analysis of grain length.

Grain length range between 7.66 mm and 12.09 mm. The minimum and maximum mean obtained were 8.15 and 10.89 in IET6279 and IR70445-146-3-3 respectively. The range of variation and variance in F_2 was higher than IET6279, F_1, BCP_1 and BCP_2. F_2 recorded the highest CV (6.47%) followed by BCP_1 (6.17%) and IET6279 recorded the lowest (2.28%) (Table 9). High broad sense heritability was recorded for grain length (Table 10). This agrees with the findings of Rabiei *et al*., (2004), Vanaja and Babu, (2006), Awaneet and Senapati, (2013), Kiani *et al*., (2013) and Tuhina *et al.,* (2015) who reported high broad sense heritability estimate for grain length. The

present results indicates that the phenotype is highly correlated with the genotype and that contribution of environmental conditions was relatively low for the trait. These result did not agree with previous findings by Ketan and Sarkar, (2014) and Rafii *et al*., (2014) who reported low heritability for grain length, possibly because the authors might have used different genotypes in their study. The regression analysis revealed additive gene effect (a) and additive x dominance were significant for grain length, while (d), (aa) and (dd) were not significant. The significant of (a) and (ad) indicate the predominance of additive (a) gene action and non- additive (ad) gene action in the inheritance of the trait (Table 13). Similar results were earlier reported by Patel *et al*., (2014). It is evident that the magnitude of non-allelic interaction and absolute total non-fixable gene effects (additive x dominance) was smaller than the fixable effect (additive gene effects) in grain length (Hakizimana *et al*., 2004). Since additive effects were equally important as nonadditive effects for grain length, breeding progress might be slow for grain length.

The presence of significant (a) gene effect would make selection from early generation effective while selection at advanced generations would also be effective because of significant (ad). The implication is that selection for grain length should commence from the segregation population through advanced level where varieties are at evaluation stage. The significant and negative additive x dominance gene action (ad) was in the direction of the reducer parent.

5.11.1 Genetic analysis of grain width.

Grain width varied between 2.13 mm and 3.19 mm. The maximum and minimum mean reported for Grain width were 3.00 and 2.49 mm in IET6279 and IR70445146-3-3 respectively. The range of variation and variance in F_2 was higher than IR70445-146-3-3 and F_1. BCP_1 had the highest CV (6.99%) followed by F_2 (6.23%) and IR70445-

146-3-3 recorded the lowest (3.48%) (Table 9). High broad sense heritability was recorded for grain length (Table 10). This agrees with the findings of Rabiei *et al.,* (2004), Vanaja and Babu, (2006), Awaneet and Senapati, (2013), Kiani *et al*. (2013), Ketan and Sarkar. (2014) and Tuhina *et al*., (2015) who reported high broad sense heritability estimate for grain width. The present results indicate that the phenotype is highly correlated with the genotype and that contribution of environmental conditions was relatively low for these trait. These result do not support the previous study by Rafii *et al*., (2014) and Osekita *et al*., (2014) who reported low heritability for grain width. The regression analysis revealed additive gene effect (a) was highly significant for grain width, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were non-significant for grain width. The lack of significant (d), (aa), (ad) and (dd) indicate the importance of additive gene effect in control of this traits (Table 13).

Similar findings was observed by Jarwar *et al*., (2014) and Arpita *et al*., (2014). The non-significance of dominance and epistatic effects in this trait indicated that there would be a high probability of success in selecting for grain width in early generations. The significant negative additive (a) gene action was in the direction of the reducer parent.

5.12 Genetic analysis of grain yield per plant

Rice grains yield is a quantitative trait influenced by other agronomic traits and environmental factors, of which spikelet number per panicle is important component of rice grain yield (Zong *et. al*., 2012). The development of sufficient sink capacity and high degree of grain filling of superior rice cultivars should consider the distribution of spikelet number per panicle and degree of grain filling. Sheehy *et al*. (2001) found that the high yielding plant type had high potential for high spikelet number per

panicle, which was highly associated with rice grain yield. The study of inheritance of this trait is important for rice breeding program. Grain yield per plant varied between 10.79 g and 193.50 g. IET6279 registered the maximum average grain yield per plant (97.78g) followed by F_1 (74.05g) while F_2 recorded the minimum average (59.13g) grain yield per plant. The range of variation and variance in $F_1$and BCP_1 were higher than their corresponding F_2. This deviates from how the various generations normally behave. F_2 recorded highest CV (48.95%) followed by F_1 (44.71%) and IET6279 recorded the lowest (21.49%) (Table 9). Low broad sense heritability was reported for grain yield per plant (Table 10). Similar results were earlier reported by Mulugeta *et al*., (2012) and Rafii *et al*., (2014). The present results indicate that the phenotype is not highly correlated to the genotype and that contribution of environmental conditions was relatively high and strongly influence this character (Saleem *et al*., 2010). On the contrary, these results do not agreed with the findings of Hasan *et al*., (2010), Yadav *et al*., (2011), Sathya and Jebaraj, (2013), Vanisree *et al.*, (2013) and Ammar *et al*., (2014) who reported high degree of broad sense heritability for this trait, possibly because the authors might have used different genotypes in their study. The regression analysis revealed additive gene effect (a) was highly significant for grain yield per plant, while dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were notsignificant. The significant additive (a) gene effect on this trait indicate the predominance of additive gene effect in control of the trait (Table 16). Similar findings was observed by Deepa, *et al.* (2006) and Singh *et al*., (2014). The nonsignificance of dominance and epistatic effects in this trait indicated that there would be a high probability of success in selecting for grain yield per plant in early generations. The significant and negative additive (a) gene action was in the direction of reducer parent.

5.13 Genetic analysis of 100 grain weight.

The mass of grains of individual plants directly determines the yield of a population, (Verica *et al*., 2013). As a final product of the interaction between a lot of physiological and biochemical processes in the plants, the mass of grains from plant depends on several properties, such as the number of panicles per plant, number of grains per panicle and weight of grain, (Verica *et al*., 2013). Changing any of these properties result in change of the grain yield per plant. The link of this property with other components of yield indirectly contributes to its high variability, (Verica *et al*., 2013). 100 grain weight per plant varied between 2.24 g and 3.19 g. The maximum mean performance of 100 seed weight was recorded for IR70445-146-3-3 (3.04) and the minimum 100 grain weight (2.69) was recorded for IET6279. Mean for F_1, F_2, BCP_1 and BCP_2 were all within parental limits. The range of variation and variance in F_2 was higher than the corresponding parents, F1. BCP_1 and BCP_2 respectively. F_2 recorded the highest CV (8.12%) followed by BCP_2 (7.72%) and IET6279 recorded the lowest (3.71%) (Table 7). High broad sense heritability was recorded for this character (Table 10). Similar findings were previously reported by Rita *et al*., (2009) and Tuhina *et al*., (2015). The present results indicate that the phenotype is highly correlated with the genotype and that contribution of environmental conditions was relatively low for the trait. These results do not agree with the findings by Sathya and Jebaraj, (2013) who reported low heritability for 100 grain weight. The regression analysis revealed both additive and additive x dominance effects were significant for 100 grain weight, while dominance gene effect (d), (aa) and (dd) were nonsignificant for 100 grain weight. The lack of significant (d), (aa) and (dd) shows the relevance of additive gene effect and additive x dominance gene effect in the control of 100 grain weight (Table 15). The present results were in partial agreement with Vanaja *et al*. (2003), Deepa *et al.* (2006),

Praveen et al., (2009) and Pallabi *et al*., (2013) who reported major role of additive gene effects in controlling the inheritance of seed weight in rice and Bagheri *et al*., (2008) who reported the relevance of epistasis in the inheritance of the character. The significant fixable gene action (a) has greater magnitude compared to corresponding additive x dominance non-fixable (ad) component (Hakizimana *et al*., 2004) (Table 9). Since additive effects were equally important as non-additive effects for 100 grain weight, breeding progress might be slow. Therefore, improvement of these traits appears to be beset with difficulties as simple selection techniques will not be able to fix superior lines in the early segregating generations. Postponement of selection of superior lines to later generations in pedigree breeding will be effective. One or two cycles of recurrent selection followed by pedigree breeding will be effective and useful to utilize both additive and non-additive gene effects. The negative significant additive (ad) gene action for 100 grain weight was in the direction of the reducer parent.

5.14 Genetic analysis of number of unfilled grains per plant.

Blanking or spikelet sterility caused by poor anther dehiscence and low pollen production and hence low numbers of germinating pollen grains on the stigma is induced at this stage (Jagadish *et. al*., 2007). Flowering (anthesis and fertilization), and to a lesser extent booting (microsporogenesis), are the most susceptible stages of development to temperature in rice (Farrell *et al.,* 2006). Previous studies, summarized in Satake and Yoshida (1978), have shown that spikelets at anthesis that were exposed to temperatures >35^{o}C for about 5 d during the flowering period were sterile and set no seed. Sterility is caused by poor anther dehiscence and low pollen production, and hence low numbers of germinating pollen grains on the stigma (Prasad *et al*., 2006). Unfilled Grain per plant showed highest amount of variability and ranged between 28 and 2355 with F_1 recording the highest CV (73.59%) followed by BCP1 (70.66%) and

IET6279 recorded the lowest (31.96%). IR70445146-3-3 registered the maximum number of unfilled grain per plant (831) followed by IET6279 (576) and F_1 (312) recorded the minimum number of unfilled grain per plant. The range of variation and variance in IR70445-146-3-3 was higher than their corresponding F_2. This deviates from how the various generations normally behave (Table 6). The generation mean analysis indicated that neither additive gene effect

(a), dominance gene effect (d) and non-additive gene effects with their interactions (aa), (ad) as well (dd) were significant for number of unfilled gains per plant, which suggested that selection of this trait could not be done in specific generations and that this might be due to the dependence of this trait upon number of spikelet per plant and number of fertile spikelet per plant. In this case, the selection for this trait could be concurrently carried out with number of spikelet per plant and number of fertile spikelet per plant. Thus, the heritability of number of unfilled gains per plant would be important to consider. The negative additive x additive (aa) gene for number of unfilled grains per plant though not significant were in the direction of the reducer parent (Table 14).

CHAPTER SIX

6.0 CONCLUSION AND RECOMMENDATIONS

6.1 CONCLUSION

Result from this study favored a single recessive gene control of aroma as opposed to multiple gene control. However, a careful review of literature compared to this work suggests that, there are differences in the number of genes controlling aroma in different varieties. An F_2 ratio of 1:3 (aromatic: non-aromatic) plants and a backcross (IET6279/ IR70445-146-3-3 // IR70445-146-3-3) ratio of 1:1 indicate that a single recessive gene controls aroma in IR70445-146-3-3. These shows that there would be a high probability of success in selecting for aroma using Pedigree breeding in early generations of F_2.

Broad sense heritability estimates were high for plant height, culm length, days to flowering, days to maturity, 100 grain weight, grain length and grain width. This indicates that the phenotype is highly correlated with the genotype and that contribution of environmental conditions was relatively low for these traits. Low broad sense heritability estimate was observed for number of tillers, number of panicle, panicle length, leaf length, leaf width, flag leaf length, flag leaf width, number of spikelet/panicle, number of spikelet per plant, number of fertile spikelet per panicle, number of fertile spikelet per plant, % spikelet fertility per plant and grain yield per plant. This shows that the phenotype is not correlated with the genotype and environmental factors strongly influence this characters.

The findings indicated that additive gene actions governs the expression of traits *viz.,* plant height, number of tillers, number of panicle, panicle length, culm length, leaf length, flag leaf width, grain width, number of spikelet per panicle, number of spikelet

per plant, % Spikelet fertility per plant and grain yield per plant, which further suggested that phenotypic selection was appropriate at an early stage. Further, days to 50% flowering, days to maturity, leaf width, flag leaf length, grain length, number of fertile spikelet per panicle, number of fertile spikelet per plant and 100 grain weight are controlled by additive and epistatic genetic components. In such circumstances simple pedigree method of selection alone is ineffective to fix superior lines in the early segregating generations. Probably, this could be one of the reasons for the inability of rice breeders to effectively combine desired yield attributing traits. To overcome this problem, postponement of selection of superior lines to later generations in pedigree breeding will be effective. One or two cycles of recurrent selection followed by pedigree breeding will be effective and useful to utilize both additive and non-additive gene effects

6.2 RECOMMENDATION

It is recommended that further breeding work be carried out in the genotypes used to develop superior yielding varieties for farmers using molecular procedures.

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APPENDICES

Analysis of variance

Variate: pht

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	15522.1	3104.4	15.82	<.001
Residual	1286	252403.5	196.3		
Total	1291	267925.6			

Tables of means

Variate: pht

Grand mean 123.18

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	123.61	119.88	123.66	123.70	134.27	113.15
rep.	153	171	56	792	60	60

Analysis of variance

Variate: cuL

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	22092.2	4418.4	27.34	<.001
Residual	1286	207844.3	161.6		

Total	1291	229936.5

Tables of means

Variate: cuL

Grand mean 93.26

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	94.10	89.46	92.98	93.58	108.17	83.18
rep.	153	171	56	792	60	60

Analysis of variance

		s.s.	m.s.	v.r.	F pr.
					<.001

Variate: PanL

Source of variation	d.f.				
Gen	5	996.865	199.373	20.04	
Residual	1286	12791.608	9.947		
Total	1291	13788.473			

Tables of means

Variate: PanL

Grand mean 29.894

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	29.510	30.427	30.679	30.080	26.100	29.967
rep.	153	171	56	792	60	60

Analysis of variance

Variate: TillNo

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	1647.35	329.47	8.16	<.001
Residual	1286	51914.42	40.37		
Total	1291	53561.78			

Tables of means

Variate: TillNo

Grand mean 19.19

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	20.24	19.12	19.48	18.57	23.40	20.48

Analysis of variance

			s.s.	m.s.	v.r.	F pr.
						<.001
rep.	153	171	56	792	60	60

Analysis of variance

Variate: PanNo

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	1782.02	356.40	9.84	<.001
Residual	1286	46587.65	36.23		
Total	1291	48369.67			

Tables of means

Variate: PanNo

Grand mean 17.69

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	18.19	17.36	18.36	17.12	22.17	19.70
rep.	153	171	56	792	60	60

Analysis of variance

Variate: UnfillG

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	11738442.	2347688.	27.38	<.001
Residual	1286	110258950.	85738.		

Total	1291	121997393.

Tables of means

Variate: UnfillG

Grand mean 442.5

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	397.6	408.9	311.6	428.2	576.1	830.7
rep.	153	171	56	792	60	60

Variate: TGW

Source of variation	d.f.			
Gen	5	95243.7	19048.7	23.61
Residual	1286	1037451.6	806.7	
Total	1291	1132695.3		

Tables of means

Variate: TGW

Grand mean 62.82

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	66.41	59.74	74.05	59.13	97.78	65.64
rep.	153	171	56	792	60	60

Analysis of variance

Variate: GW_100

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	4.77350	0.95470	21.77	<.001
Residual	1286	56.40584	0.04386		

Analysis of variance

		s.s.	m.s.	v.r.	F pr.
					<.001
Total	1291	61.17935			

Tables of means

Variate: GW_100

Grand mean 2.7802

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	2.7410	2.7971	2.7643	2.7728	2.6883	3.0360
rep.	153	171	56	792	60	60

Analysis of variance

Variate: Number of spikelet/ panicle

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	102598.	20520.	12.64	<.001
Residual	1286	2088091.	1624.		
Total	1291	2190689.			

Tables of means

Variate: Number of spikelet/ panicle

Grand mean 153.3

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	156.2	148.6	161.8	150.5	191.4	150.3
rep.	153	171	56	792	60	60

Analysis of variance

Variate: Number of spikelet/ plant

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	1.660E+08	3.320E+07	22.13	<.001

Residual	1286	1.929E+09	1.500E+06
Total	1291	2.095E+09	

Tables of means

Variate: Number of spikelet/ plant Grand mean 2726.

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	2836.	2569.	3011.	2586.	4232.	2975.
rep.	153	171	56	792	60	60

Analysis of variance

Variate: Number of fertile spikelet/panicle

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	137534.	27507.	20.94	<.001
Residual	1286	1689173.	1314.		
Total	1291	1826707.			

Tables of means

Variate: Number of fertile spikelet/panicle

Grand mean 128.3

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	134.6	124.8	145.0	125.4	165.3	107.9
rep.	153	171	56	792	60	60

Variate: Number of fertile spikelet/plant

Source of variation	d.f.			
Gen	5	1.430E+08	2.860E+07	26.07
Residual	1286	1.411E+09	1.097E+06	
Total	1291	1.554E+09		

Tables of means

Variate: Number of fertile spikelet/plant Grand mean 2283.

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	2438.	2153.	2699.	2158.	3656.	2144.

Analysis of variance

			s.s.		m.s.	v.r.	F pr.
							<.001
rep.	153	171	56	792	60		60

Analysis of variance

Variate: Spikelet fertility (%)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	11130.34	2226.07	40.23	<.001
Residual	1286	71158.36	55.33		
Total	1291	82288.69			

Tables of means

Variate: Spikelet fertility (%)

Grand mean 83.52

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	85.95	83.85	89.76	83.16	86.39	72.39
rep.	153	171	56	792	60	60

Analysis of variance

Variate: GR_LEN

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	260.8711	52.1742	122.50	<.001
Residual	1286	547.7281	0.4259		
Total	1291	808.5991			

Tables of means

Variate: GR_LEN

Grand mean 9.597

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	9.213	9.727	9.315	9.674	8.151	10.893
rep.	153	171	56	792	60	60

Analysis of variance

Variate: GR_WID

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	12.51912	2.50382	98.44	<.001
Residual	1286	32.70989	0.02544		
Total	1291	45.22901			

Tables of means

Variate: GR_WID

Grand mean 2.5977

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	2.6817	2.5744	2.6295	2.5617	2.9982	2.4947
rep.	153	171	56	792	60	60

Analysis of variance

Variate: Leaf_L

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	12894.06	2578.81	30.36	<.001
Residual	1286	109234.20	84.94		
Total	1291	122128.26			

Tables of means

Variate: Leaf_L

Grand mean 55.51

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	52.59	53.82	52.69	57.51	44.35	55.18
rep.	153	171	56	792	60	60

Variate: Leaf_W

Source of variation	d.f.			
Gen	5	20.66665	4.13333	89.90
Residual	1286	59.12654	0.04598	

Analysis of variance

		s.s.	m.s.	v.r.	F pr.
					<.001
Total	1291	79.79319			

Tables of means
Variate: Leaf_W
Grand mean 1.4783

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	1.5562	1.4702	1.4679	1.4290	2.0200	1.4217
rep.	153	171	56	792	60	60

Analysis of variance
Variate: Flag_LL

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	11387.83	2277.57	36.39	<.001
Residual	1286	80491.29	62.59		
Total	1291	91879.12			

Tables of means
Variate: Flag_LL
Grand mean 42.27

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	39.59	42.17	41.35	43.89	30.75	40.43
rep.	153	171	56	792	60	60

Analysis of variance
Variate: Flag_LW

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.

Gen	5	12.07657	2.41531	46.17	<.001
Residual	1286	67.28178	0.05232		
Total	1291	79.35835			

Tables of means

Variate: Flag_LW

Grand mean 1.8660

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	1.9647	1.8801	1.8607	1.8263	2.2367	1.7333
rep.	153	171	56	792	60	60

Analysis of variance

Variate: FD_50

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	28622.05	5724.41	134.20	<.001
Residual	1286	54854.00	42.65		
Total	1291	83476.05			

Tables of means

Variate: FD_50

Grand mean 95.61

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	95.11	91.95	88.11	95.78	115.03	92.78
rep.	153	171	56	792	60	60

Analysis of variance

Variate: M_DATE

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Gen	5	20662.75	4132.55	116.51	<.001
Residual	1286	45615.47	35.47		
Total	1291	66278.22			

Tables of means

Variate: M_DATE

Grand mean 122.36

Analysis of variance

	s.s.	m.s.	v.r.	F pr.
				<.001

Gen	BC1P1	BC1P2	F1	F2	P1	P2
	122.58	120.36	117.27	121.75	139.78	122.78
rep.	153	171	56	792	60	60