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## **Estimates of variance components and heritability for seed yield in two soybean populations from an incomplete vs. complete block design**

G. Alan Lowman

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To the Graduate Council:

I am submitting herewith a thesis written by G. Alan Lowman entitled "Estimates of variance components and heritability for seed yield in two soybean populations from an incomplete vs. complete block design." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Plant, Soil and Environmental Sciences.

Fred L. Allen, Major Professor

We have read this thesis and recommend its acceptance:

Robert McLean, Vernon Reich, Dennis West

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

I am submitting herewith a thesis written by G. Alan Lowman entitled "Estimates of Variance Components and Heritability For Seed Yield in Two Soybean Populations from an Incomplete vs. Complete Block Design." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Plant and Soil Science.

*Fred L. Allen*

Fred L. Allen, Major Professor

We have read this thesis  
and recommend its acceptance:

*Robert A. McLean*

*Gerrit West*

*Vernon H. Reich*

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and Dean of The Graduate School

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Date April 18, 1990

ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITY FOR SEED  
YIELD IN TWO SOYBEAN POPULATIONS FROM  
AN INCOMPLETE VS. COMPLETE BLOCK DESIGN

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

G. Alan Lowman

May 1990

AO-VET-MED.

Thesis  
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## ACKNOWLEDGEMENTS

In the course of my quest for a Master's degree, a number of scholars have assisted me generously. In particular I am indebted to Professors Fred Allen, Robert McLean, Vernon Reich and Dennis West, who served as my major professor and committee respectively. With their consultation, criticism, and encouragement, I was able to achieve results otherwise impossible. Whatever errors remain in my work, however, are solely my responsibility.

I want to thank to Dr. John Foss and the Department of Plant and Soil Science for a Graduate Research Assistantship which enabled me to pursue a Master's degree.

Also, I hereby acknowledge with thanks Don Panter, Mark Sellmann, and Wayne Whitehead for their friendship and help. I pray that God will bless and reward them, for they are truly deserving individuals.

Finally, I want to thank my wife, Karen Lowman, for being both loving and supportive while I earned my Master's degree. I could not have chosen a better partner with whom to share my life.

## ABSTRACT

Block designs are used to control heterogeneity within an experimental area. Subsequently when conducting yield trials with several genotypes, each block of the randomized complete block design can become heterogeneous. This study was conducted to compare a RCB design with an incomplete block (ICB) design imposed ex post facto. Estimates of the variance components and heritability were compared across three statistical models for two soybean populations. Population 1 contained forty-five  $F_{4;8;9}$  soybean lines, and Population 2 contained fifty  $F_{4;8;9}$  soybean lines. Both populations were grown in replicated yield trials at six locations in 1985 and 1986. The ICB design would have been advantageous in twenty-one of forty-two (50%) tests because of the large within block heterogeneity. In 36% of the analyses, the block variance decreased with the incomplete block design, and was equal for the two designs in the remaining 14%. Additionally, the ICB design resulted, at worst, in an error variance that was not more than 2% greater than the RCB design and, in the best case, was 67% lower than the RCB estimate. Consequently, the error ratios (RCB/ICB) were greater than 100% in 64% of the analyses, less than 100% in 12% of the analyses and equal to 100% in 24% of the analyses. The ICB estimates of heritability were greater than the RCB estimates in 36% of the analyses, equal to the RCB estimates in 40% of the analyses and smaller than the RCB estimates in 24% of the analyses. The ICB design would have resulted in greater precision and accuracy in the estimation of variance components across all three statistical models. Diallel phenotypic correlation coefficients were used to place the six locations



into two sets of three locations. One set of three locations would have been adequate for selecting the superior soybean genotypes using either design.

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**PART I**

**A REVIEW OF LITERATURE CONCERNING ENVIRONMENTAL VARIATION AND METHODS OF  
REDUCING ENVIRONMENTAL VARIATION**

## INTRODUCTION

Random variation due to uncontrolled or inadequately controlled environmental sources leads to large error variation in experimental data from field research. Consequently, these random sources of variation often prevent plant breeders from determining true differences among genotypes in yield trials. The causes of such variation have been investigated as well as some possible methods for their reduction. Environmental variation has been controlled through the use of experimental designs which better aid in the control of certain types of gradients in the plot field. Several experimental designs have been available to the plant breeder for this purpose. Among these were the completely randomized design, the randomized complete block (RCB) design, the randomized incomplete block (ICB) design, and the lattice designs (2). The RCB and ICB designs were of primary interest in this review.

Anderson and Bancroft (2) gave a detailed description of the RCB and ICB designs. The following example is given to help distinguish between the two designs. If genotypes were the treatments, the RCB requires that each genotype must occur in each block once; whereas, the ICB does not require each genotype to appear in each block. The triple lattice and the single lattice which are variants of the ICB were also described. The triple lattice has three replications, and the simple lattice or lattice has only two replications. Both designs are

considered unbalanced if the number of reps (R) was less than the number of blocks (B) plus one (i.e.  $R < B + 1$ ). When comparing the ICB and RCB designs, both Zuber (19) and Weber and Horner (18) reported gains in precision with the triple lattice and simple lattice designs.

Zuber (19) compared 4 incomplete block designs (lattice square, balanced lattice, lattice and triple lattice) with the RCB using data from a corn uniformity trial. The incomplete block designs averaged a 25% gain in precision over the complete block design. The lattice square showed a 32% gain in precision, and the other designs showed the following gains in precision: balanced lattice 26%, lattice 18% and triple lattice 17%. Furthermore, Zuber observed that efficiency increased with the increased compactness of the blocks.

Weber and Horner (18) observed the effects of plot size and shape when determining seed yield, protein and oil content, and iodine number of the oil from 1088 plots. Each plot in the soybean uniformity yield trial had a basic unit size of one row 60 cm wide and 2.4 m long. They used combinations of the basic unit for the comparison of several plot configurations and experimental designs. Their optimum plot size in terms of cost and a comparable precision for estimating all traits was three times the basic unit. They found that the estimation of all traits benefitted from the use of experimental designs, and variance increased with increases in plot size. They observed that the coefficients of variation for the various plot sizes and shapes within each chemical character were not significantly different. They concluded that a single replication would be sufficient for estimating the chemical attributes as long as a measure of error variance was not

desired. Gains in precision for estimating yield averaged 31%, 16% and 18% for the lattice square, simple lattice, and triple lattice, respectively, when compared to the RCB design. These findings were similar to those reported by Zuber (19) for the lattice and triple lattice designs.

When selecting genotypes with wide general adaptation, Jensen (9) reported that the number of opportunities for environmental variation to occur increases as yield trials are conducted at different locations and in different years. He stated that an experiment station can provide a unique set of edaphic and climatic conditions. For example, certain station characteristics such as soil-type, rainfall occurrence, cultural practices, soil fertility and date of frost can affect the results obtained from experiments. Additionally, the severity of disease and insect outbreaks can vary from station to station. Furthermore, he stated that the salt concentration in the soil either from soil forming processes or irrigation water can have a greater negative effect on the performance of some genotypes than others. Consequently, genotypes can react differently to these conditions producing genotype X environment interactions (9).

Genotype X environment interactions can be grouped primarily into the following three types: genotype X year, genotype X location and genotype X year X location (4). A significant genotype X year interaction indicates an unstable ranking of genotypes across the years that the experiment was conducted (4). The cause of this change in ranking could have been the result of the effects of any one or more of the following: rainfall, temperature, insect or disease outbreak or

early frost (10). Several researchers have reported genotype X year interactions in data from their research.

Schutz and Bernard (17) observed that genotype X year interactions in regional tests of soybeans were generally smaller than the estimates of the genotype X location interactions. Consequently, they expected genotype X year interactions to have a greater effect on the error variance of a line mean, since testing over a long period of time is rarely done. Hanson et al. (7) determined genotype X year interactions were large in their work with Korean Lespedeza indicating a need to test genotypes in different years. On the other hand, Liang et al. (11) concluded genotype X year interactions were nonsignificant in yield tests of three small grains in Kansas.

A significant genotype X location interaction indicates a changeable ranking of genotypes from one location to another (4). Climate, soil-type, soil fertility, salt concentration, and cultural practices are examples of sources that can cause a genotype X location interaction (9). Researchers have tried to reduce genotype X location interactions by grouping locations based on diallel correlation coefficients and genotype X location mean squares (6,8,12).

Guitard (6) used diallel correlation coefficients to group locations based primarily on yield data. In the diallel correlations, the performance of a group of genotypes at one location was correlated with the performance of the same group of genotypes at other locations providing a direct method of determining locational relationships. He used the relative performance of nine genotypes of barley for yield, height, weight per bushel and 1000-kernel weight from ten locations to



calculate diallel correlation coefficients for all pairs of locations in the Upper Peace River region of Alberta, Canada. Three years of data were available for seven locations and only two years of data were available for the remaining three locations. Yield was the most suitable character for the grouping of locations as the other traits approximated, with a few exceptions, those location groupings established for yield. Based on yield data, he placed eight locations into three inter-related groups with each group having one location in common with the adjoining group. The average correlation coefficients among groups ranged from 0.715 to 0.828 for the three groups relative to the average correlation coefficient of 0.401 for the ungrouped association. The yield performance at the remaining two locations was not associated with any of the other locations. The relationships among locations did not appear to be based on geographical location, or soil and climatic conditions. The product of his research was a reduction in the number of yield trial locations from the original ten locations to five locations; one location from each of the 3 location groups and each one of the unassociated locations.

Horner and Frey (8) found that by dividing Iowa into two, three, four, and five subregions (instead of using the state as one region) a 11%, 21%, 30% and 40% reduction, respectively, in the average genotype X location mean square could be gained. A graph of the estimated mean square against the number of subregions showed a near linear decrease in the estimated mean square as the number of subregions increased up to nine subregions. From a practical standpoint, they decided that dividing Iowa into four subregions was the most efficient strategy as

dividing Iowa into five subregions would have produced two subregions with a single location each.

Using corn yield data, McCain and Schultz (12) initially used the mean square for the genotype X location interaction to group fifteen locations in Alabama into subregions. Additionally, they further grouped locations based on soil texture and geographic location. Four locations in northern Alabama and five locations in southern Alabama resulted in small mean squares indicating that these regions were relatively homogeneous. The remaining six locations had relatively high mean squares indicating a heterogeneous region which they designated as central Alabama. They indicated that it would be desirable to establish additional test locations in central Alabama to determine if it could be broken into smaller subregions.

Fehr (4) reported that a large genotype X year X location interaction indicates a variable ranking of genotypes within year-location combinations as a result of some environmental condition such as a disease and insect outbreak. Several examples of genotype X year X location interactions have been presented in the literature. For example, Rasmusson and Lambert (16) suggested that a significant genotype X year X location interaction indicated that genotypes perform differently in different environments. Miller et al. (14) found that the genotype X environment interaction in lint yield in cotton was quite large. In subsequent research, they determined that the genotype X year X location interactions were of significant magnitude while the first order interactions (genotype X year and genotype X location) were not (13). They concluded that cotton genotypes should be tested over a

number of different environments. Additionally, Ghaderi et al. (5) and Jones et al. (10) reported significant genotype X year X location interactions in wheat and flue-cured tobacco, respectively.

Heritability has been defined as the ratio of the genetic variance to the phenotypic variance. It is directly affected by the genotype X environment interactions (3). Rasmusson and Glass (15) listed the three types of heritability estimates as follows: a) broad sense where the numerator of the ratio contains the total of the genetic variance, b) narrow sense where the numerator contains only the additive genetic variance, and c) the numerator contains less than the total genetic variance but more than the additive genetic variance (most often used by geneticists and breeders).

Based on Falconer's (3) treatment of genotypic and phenotypic variance, Rasmusson and Glass's (15) major types of heritability estimates may be written as follows:

a) broad sense heritability

$$H^2 = \frac{\sigma_G^2}{\sigma_P^2} = \frac{\sigma_a^2 + \sigma_d^2 + \sigma_i^2}{\sigma_G^2 + \sigma_e^2 + \sigma_{Ge}^2}$$

b) narrow sense heritability

$$h^2 = \frac{\sigma_G^2}{\sigma_P^2} = \frac{\sigma_a^2}{\sigma_G^2 + \sigma_e^2 + \sigma_{Ge}^2}$$

c) intermediate heritability

$$h^{2'} = \frac{\sigma_G^2}{\sigma_P^2} = \frac{\sigma_a^2 + \sigma_i^2}{\sigma_G^2 + \sigma_e^2 + \sigma_{Ge}^2}$$

where:

$H^2$  = broad sense heritability

$\sigma_G^2$  = total genetic variance

$\sigma_a^2$  = additive genetic variance

$\sigma_d^2$  = dominance variance

$\sigma_i^2$  = genetic interaction variance or epistasis

$\sigma_p^2$  = phenotypic variance

$\sigma_e^2$  = environmental variance

$\sigma_{Ge}^2$  = variance associated with the genotype X environment interaction

$h^2$  = narrow sense heritability

$h^{2'}$  = heritability with more than additive genetic variance but less than total genetic variance.

The  $\sigma_{Ge}^2$  component has been thoroughly discussed by Fehr (4), and this component has been shown to contain the following interactions: genotype

X year, genotype X location and genotype X year X location.

Allard (1) discussed the over-estimation of the genotypic variance when the genotype X environment interactions were nonestimable. For example conducting an experiment at only one location in one year does not allow the quantities  $\sigma^2_{GL}$ ,  $\sigma^2_{GY}$  and  $\sigma^2_{GYL}$  to be estimated and therefore produces an inflated value of the genotypic variance. The use of several locations and two or more years allows the estimation of  $\sigma^2_{GL}$ ,  $\sigma^2_{GY}$  and  $\sigma^2_{GYL}$ . Consequently, the genotypic variance reflects more closely its true value as  $\sigma^2_{GL}$ ,  $\sigma^2_{GY}$  and  $\sigma^2_{GYL}$  are no longer confounded within the genotypic variance. Therefore, the accuracy of the estimate of heritability increases as the accuracy of the genotypic variance increases.

Rasmusson and Glass (15) expressed heritability on a line basis as follows:

$$H^2 = \frac{\sigma_G^2}{\sigma_P^2} = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{GY}^2}{y} + \frac{\sigma_{GL}^2}{l} + \frac{\sigma_{GYL}^2}{ly} + \frac{\sigma_e^2}{rly}}$$

Several points can be made about this equation. First, any of the three major types of heritability presented earlier can be estimated depending on the amount of the total genetic variance that is placed in the numerator. Second, if any one term in the denominator is reduced and the other terms in the denominator remain the same heritability will increase. For example if error variance ( $\sigma_e^2$ ) is reduced and the variances associated with the genotype X year X location, genotype X

year, genotype X location interactions and genotypes remain the same, heritability will increase. An exception is the genetic variance which is included in both the numerator and denominator. If the genetic variance decreases while the other terms in the denominator remain constant, heritability will decrease. Thirdly, the genotype X year X location variance ( $\sigma^2_{GYL}$ ) is averaged across the locations and years, and the first order interaction, genotype X year ( $\sigma^2_{GY}$ ) and genotype X location ( $\sigma^2_{GL}$ ), variances are averaged across years and locations, respectively. Finally, the heritability estimate is used to determine how much of the phenotypic difference among genotypes are actually due to genotypic differences.

The objective of this experiment was to determine what changes occurred in the estimates of the variance components and heritability when the ICB design was imposed ex post facto on data (from two different soybean populations) collected from yield trials which were conducted as RCB designs.

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PART II

VARIANCE COMPONENT AND HERITABILITY ESTIMATES FOR SEED YIELD IN TWO  
SOYBEAN POPULATIONS AS INFLUENCED BY A COMPLETE vs. AN INCOMPLETE BLOCK  
DESIGN

## CHAPTER 1

### LITERATURE REVIEW

Random variation due to uncontrolled or inadequately controlled sources leads to large error variation in data from field research. When selecting genotypes with wide adaptation, the number of opportunities for random variation to occur increases as field trials are conducted at different locations and in different years (10). Consequently, Jensen (10) reported that these random sources of variation often prevent plant breeders from determining the true differences among genotypes in yield trials.

A method of reducing random variation is through the use of experimental designs which aid in the control of certain types of gradients in the plot field. Several experimental designs are available to the plant breeder for this purpose. The randomized complete block (RCB) and randomized incomplete block designs (ICB) are of primary interest in this review. Anderson and Bancroft (2) gave a detailed statistical description of the RCB and ICB designs. In addition, the following example is given to distinguish between the two designs. If genotypes were the treatments, the RCB design requires that each genotype must occur in each block once; whereas, the ICB does not require each genotype to appear in each block. There are many variations of incomplete block designs, of which lattice designs are examples.

Upon comparing ICB and RCB designs, Weber and Horner (21) and Zuber (23) reported gains in precision with the ICB designs. Weber and Horner (21) observed the effects of plot size and shape when determining seed yield, protein and oil content, and iodine number of the oil. Each plot in the soybean uniformity yield trial had a basic unit size of 1 row 60 cm wide by 2.4 m long. In addition, they used combinations of the basic unit for the comparison of several plot configurations and experimental designs. They found that the estimation of all traits benefitted from the use of the experimental designs, and variance increased with increases in plot size. Gains in precision for estimating yield averaged 31%, 16% and 18% for the lattice square, simple lattice, and triple lattice, respectively, when compared to the RCB design. These findings were similar to those reported by Zuber (23) for the lattice and triple lattice designs. He (23) compared 4 incomplete block designs (lattice square, balanced lattice, lattice and triple lattice) with the RCB design using data from a corn uniformity trial. The incomplete block designs averaged a 25% gain in precision over the complete block design. Furthermore, the lattice square showed a 32% gain in precision while the other designs showed gains in precision as follows: balanced lattice 26%, lattice 18% and triple lattice 17%. In addition, Zuber observed that efficiency increased with decreases in block size.

A second method of obtaining more precise and accurate estimates of the sources of variation is to conduct yield trials across years and locations. Allard (1) reported that this allows the estimation of the genotype x environment interactions which receive part of the total variation that would otherwise be confounded within the genotypic

variance or the error variance. Consequently by estimating these interactions, plant breeders acquire more precise estimates of the genotypic and error variances.

Genotype x environment interactions can be grouped primarily into the following three types: genotype x year, genotype x location and genotype x year x location (3, 14, 15). A significant genotype x year interaction indicates an unstable ranking of genotypes during the years that the experiment was conducted (3). Schutz and Bernard (20) reported that genotype x year interactions were smaller than genotype X location interactions in regional tests of soybeans. However, they expected the genotype X year interaction to have the greatest effect on the error variance of a line mean since yield testing is seldomly done over a long period of time (20). Conversely, Hanson et al. (8) reported large genotype X year interactions in their work with Korean Lespedeza which they interpreted as a need to test the genotypes across years. On the other hand, Liang et al. (12) concluded genotype X year interactions were nonsignificant in yield tests of three small grains in Kansas.

Fehr (3) reported that a significant genotype x location interaction indicates a changeable ranking of genotypes from one location to another. Several researchers have used genotype x location interactions to help reduce the number of locations at which yield trials were conducted. Guitard (6) used data from barley yield trials conducted at ten locations to calculate diallel correlation coefficients which established relationships between each pair of locations. He found that eight of the locations could be placed into three groups with each group having an individual location in common with another group.

The remaining two locations did not associate with any of the other locations. Based on the locational relationships, he reduced the number of locations at which barley yield trials were conducted from ten to five. Horner and Frey (9) found that by dividing Iowa into two, three, four, and five subregions (instead of using the state as one region) a 11%, 21%, 30% and 40% reduction, respectively, in the average genotype x location mean square could be gained. McCain and Schultz (13) used the mean square for the genotype x location interaction in addition to soil texture and geographic location to group fifteen locations in Alabama into three subregions for conducting corn yield trials.

Research on different crops has measured significant genotype x year x location interactions (4,11,14,18). Evidence of this nature has led to the practice of testing genotypes over a number of different environments in order to identify those genotypes with the best adaptation to the target region.

Allard (1) discussed the over estimation of the genotypic variance when an evaluation of genotypes is conducted only within a single year at an individual location. Conducting an experiment at only one location in one year does not allow for the estimation of the quantities  $\sigma^2_{GL}$ ,  $\sigma^2_{GY}$  and  $\sigma^2_{GYL}$  and produces an inflated value of the genotypic variance. By using several locations and at least two years, the values for  $\sigma^2_{GL}$ ,  $\sigma^2_{GY}$  and  $\sigma^2_{GYL}$  can be estimated. Consequently, the genotypic variance reflects more closely its true value as  $\sigma^2_{GL}$ ,  $\sigma^2_{GY}$  and  $\sigma^2_{GYL}$  are no longer confounded within it. As a result, the precision and accuracy of estimating the heritability and genotypic variances increases.

The objective of this experiment was to determine the changes in the estimates of the variance components and heritability when an ICB design was imposed ex post facto on data collected from yield trials of two different soybean populations which were conducted as RCB designs.

## CHAPTER 2

### MATERIALS AND METHODS

#### Plant Populations

Data on soybean lines from previous experiments by Panter and Allen (16) (hence referred to as Population 1) and Whitehead and Allen (22) (hence referred to as Population 2) were used to make comparisons between the RCB and ICB designs. Population 1 consisted of fifty  $F_4$ -derived breeding lines which were advanced via modified single seed descent in the  $F_2$  and  $F_3$  generations. These breeding lines represented eighteen different pedigrees from maturity groups IV, V and VI. Single plants were selected in the  $F_4$  generation. Seed from each single plant were planted as a single family in the  $F_5$  generation.

Population 2 consisted of forty-eight  $F_4$ -derived breeding lines which were advanced via modified single seed descent in the  $F_2$  and  $F_3$  generations. These breeding lines represented six different pedigrees from maturity groups IV, V and VI. The same procedure was followed for both populations in the  $F_4$  and  $F_5$  generations.

In 1985 and 1986, Population 1 was evaluated in yield trials at six locations (Knoxville, Ames, Springfield, Crossville, Greeneville, and Milan) representing different edaphic and climatic regions of Tennessee. Two cultivars, 'Essex' and 'Forrest' were included as checks. Three

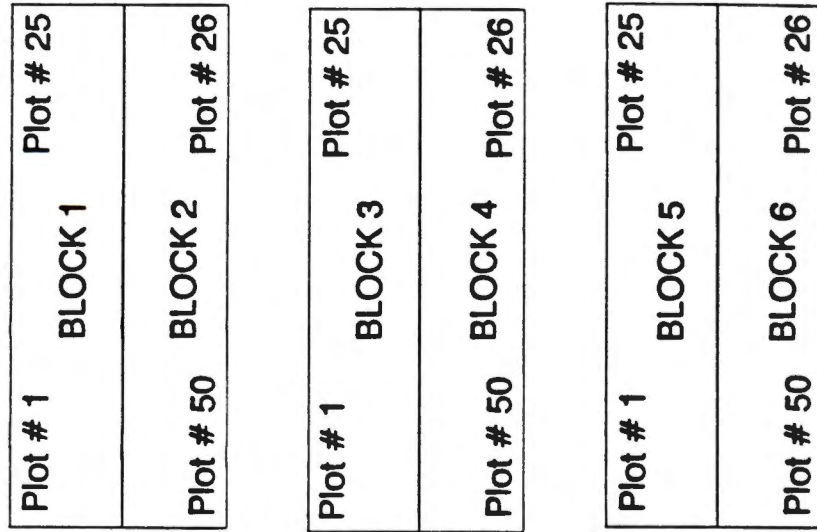
replications were used at each location, and the plots consisted of three rows, 6 m long with a 90 cm row spacing. All three rows were trimmed to 4.9 m and harvested with a plot combine. Yields were adjusted to 130 g kg<sup>-1</sup> of moisture. Due to a large number of missing observations across all six locations, seven entries were dropped from Population 1 bringing the total number of genotypes to forty-five. The same procedure as outlined above was followed for Population 2 except that no genotypes were dropped from the data set.

#### Complete vs. Incomplete Block Designs

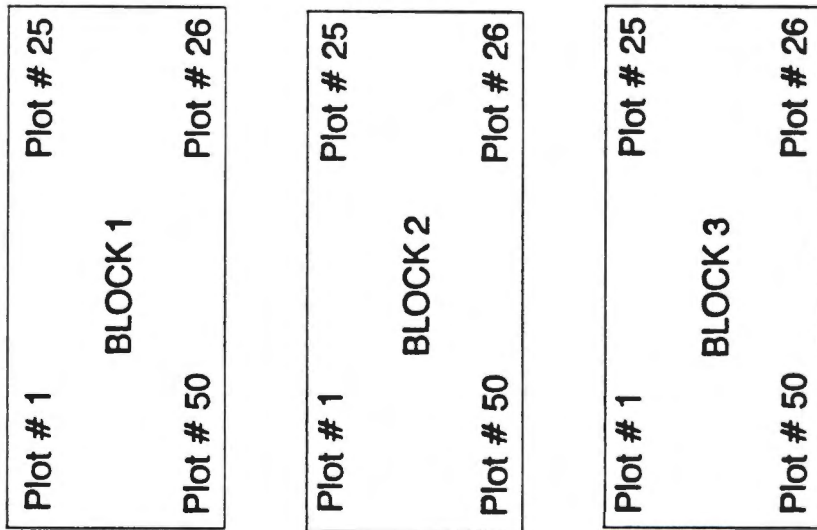
Both populations were planted in the field as randomized complete block designs. The ICB design was imposed ex post facto on the data from each location. Each large, complete block from the RCB design was divided into two smaller, incomplete blocks of equal area for the ICB design (Fig. 1). The smaller, incomplete blocks of the ICB design were expected to reduce the heterogeneity within the larger, complete blocks of the RCB design. Consequently, an assumption was made that strong inter-block ties were maintained by only reducing the large blocks by one-half (more than twenty genotypes remained in each small block); therefore, little efficiency was lost in estimating the error variance.



ICBD



RCBD



REP 1

REP 2

REP 3

Figure 1. Graphic depicting the ex post facto use of the Incomplete Block Design (ICBD) on an experiment conducted in the field as a Randomized Complete Block Design (RCBD).

## Analysis of Variance

Analyses of variance (ANOVA) were performed on each population as a RCB and an ICB design. The ANOVA procedures were conducted via the Statistical Analysis System (SAS) computer software (19). Separate ANOVAs were performed on each population according to each of the following statistical models:

a) by location

$$Y_{ij} - \mu + B_j + G_i + e_{ij}$$

b) across locations within years

$$Y_{ijk} - \mu + L_k + B_j(L_k) + G_i + G_i L_k + e_{ijk}$$

c) across locations and years

$$Y_{hijk} - \mu + Z_h + L_k + Z_h L_k + B_j(Z_h \times L_k) + G_i + G_i Z_h + G_i L_k + G_i Z_h L_k + e_{hijk}$$

where:

- $Y_{hijk}$  = the yield of the  $i^{\text{th}}$  genotype in the  $j^{\text{th}}$  replication at the  $k^{\text{th}}$  location in the  $h^{\text{th}}$  year
- $\mu$  = mean yield
- $Z_h$  = the effect of the  $h^{\text{th}}$  year
- $L_k$  = the effect of the  $k^{\text{th}}$  location
- $Z_h L_k$  = the effect of the interaction of the  $h^{\text{th}}$  year with the

- $k^{\text{th}}$  location
- $B_j$  = the effect of the  $j^{\text{th}}$  block (RCB block=rep)
- $B_j(Z_{h \times L} \ k)$  = the effect of the interaction of the  $j^{\text{th}}$  block within the  $h^{\text{th}}$  year at the  $k^{\text{th}}$  location
- $G_i$  = the effect of the  $i^{\text{th}}$  genotype
- $G_i Z_h$  = the effect of the interaction of the  $i^{\text{th}}$  genotype with the  $h^{\text{th}}$  year
- $G_i L_k$  = the effect of the interaction of the  $i^{\text{th}}$  genotype with the  $k^{\text{th}}$  location
- $G_i Z_h L_k$  = the effect of the interaction of the  $i^{\text{th}}$  genotype,  $h^{\text{th}}$  year, and  $k^{\text{th}}$  location
- $\epsilon_{hijk}$  = the effect of the random error associated with the  $h^{\text{th}}$  year,  $i^{\text{th}}$  genotype,  $j^{\text{th}}$  replication, and  $k^{\text{th}}$  location

Subsequently, the variance components were estimated by the restricted maximum-likelihood method (for the analyses at each location) and by the MIVQUE0 method (for both the analyses across locations within years and across locations and years). Next, the variance component estimates were used to calculate estimates of the phenotypic variance and heritability for seed yield. Subsequently, heritability on a line basis (17) was calculated for each population according to the following equations:

a) by location

$$H^2 = \frac{\sigma_G^2}{\sigma_P^2} = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_e^2}{r}}$$

b) across locations within each year

$$H^2 = \frac{\sigma_G^2}{\sigma_P^2} = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{GL}^2}{l} + \frac{\sigma_e^2}{rl}}$$

c) across locations and years

$$H^2 = \frac{\sigma_G^2}{\sigma_P^2} = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{GY}^2}{y} + \frac{\sigma_{GL}^2}{l} + \frac{\sigma_{GYL}^2}{ly} + \frac{\sigma_e^2}{rly}}$$

where:

- $\sigma_G^2$  = the estimate of genetic variance
- $\sigma_P^2$  = the phenotypic variance
- $\sigma_{GY}^2$  = the estimate of variance of the interaction of the genotype and year
- $\sigma_{GL}^2$  = the estimate of variance of the interaction of the genotype and the location
- $\sigma_{GYL}^2$  = the estimate of variance of the interaction of the genotype, year, and location
- $\sigma_e^2$  = the estimate of error variance
- r = the number of reps
- l = the number of locations
- y = the number of years

Following the estimation of heritability for yield, the standard errors

for the genotypic variance ( $SE\sigma_G^2$ ) and heritability ( $SEh^2$ ) were calculated according to Hallauer and Miranda (7) as follows:

a) the equation for the standard error of the genotypic variance at a single location,

$$SE\sigma_G^2 = \sqrt{\frac{(MS \text{ Genotype})^2}{(G+1)} \times \frac{2}{R^2}}$$

b) the equation for the standard error of the genotypic variance across locations within year,

$$SE\sigma_G^2 = \sqrt{\left( \frac{(MS \text{ Genotype})^2}{(G+1)} + \frac{(MS \text{ GxL})^2}{(G-1) \times ((L-1)+2)} \right) \times \frac{2}{(R \times L)^2}}$$

c) the equation for the standard error of the genotypic variance across locations and years,

$$SE\sigma_G^2 = \sqrt{\left( \frac{(MS \text{ Genotype})^2}{G+1} + \frac{(MS \text{ GxYxL})^2}{(G-1)(Y-1)(L-1)+2} + \frac{(MS \text{ GxL})^2}{(G-1)(L-1)+2} + \frac{(MS \text{ GxY})^2}{(G-1)(Y-1)+2} \right) \left( \frac{2}{(R \times L \times Y)^2} \right)}$$

and d) the equation for the standard error of the heritability estimate,

$$SEH^2 = \frac{SE\sigma_G^2}{\sigma_P^2}$$

where:

R = number of replications

G = number of genotypes

Y = number of years

L = number of locations

MS Genotype = mean square for genotypes

MS GxL = mean square for the genotype X location interaction

MS GxY = mean square for the genotype X year interaction

MS GxYxL = mean square for the genotype X year X location interaction

$\sigma_P^2$  = phenotypic variance

The error ratio was calculated as follows:

$$\text{Error ratio} = \left( \frac{\text{RCB } \sigma_e^2}{\text{ICB } \sigma_e^2} \right) \times 100$$

where:

RCB  $\sigma_e^2$  = the error mean square for the RCB design

ICB  $\sigma_e^2$  = the error mean square for the ICB design

## Location Associations

In addition to determining the effects of the ex post facto use of the ICB design on the estimates of the variance components and heritability, a comparison could be made between the estimates from six locations versus the estimates from either of two subsets of locations. Based on research by F.L. Allen (1989, Unpublished data) the six locations were grouped into the following groups of locations: Knoxville - Ames - Springfield and Crossville - Greeneville - Milan (Table 1). The grouping was accomplished by first calculating diallel phenotypic correlation coefficients between each location and each of the other five locations based on soybean yield data from Graves (5), Panter and Allen (16), and Whitehead and Allen (22). The diallel phenotypic correlation coefficients were calculated from data on at least fifty genotypes in 1985. Subsequently, the phenotypic correlation coefficients for each location were summed. The three locations with the greatest sums of the correlation coefficients (i.e., Knoxville, Ames and Springfield) were grouped together; whereas the three locations with the smallest sums of the correlation coefficients (i.e., Crossville, Greeneville and Milan) were grouped together. A comparison between the two groups was made based on the estimates of the variance components and heritability from the analyses across locations within each year and across locations and years.



Table 1. Diallel phenotypic correlation coefficients† for seed yield between locations in Tennessee.

	Locations					Sum r	
	A‡	K	S	G	C		M
A‡		.739	.551	.561	.659	.651	3.161
K			.496	.489	.853	.470	3.047
S				.627	.557	.309	2.540
G					.350	.366	2.393
C						-.141	2.278
M							1.655

† Diallel correlation coefficients were calculated from data on 50 to 134 genotypes in 1985 (Allen, 1989. Unpublished data).

‡ A=Ames, K=Knoxville, S=Springfield, G=Greeneville, C=Crossville, and M=Milan.

## CHAPTER 3

### RESULTS AND DISCUSSION

The rationale for changing from a larger, balanced, complete block design (i.e. RCB) to a smaller, unbalanced, incomplete block design (ICB) is that significant heterogeneity exists within the larger block. In this study, the ICB design was imposed, ex post facto, on experiments which were conducted in a RCB design. Imposing the ICB design required little additional time or resources and data analyses for either design were conducted with similar effort and time. In addition, the total amount of variation in the data from the experiments did not change, but the relative amounts partitioned into the different components (sources) did change. As a result, the goal was to determine which design resulted in the best partitioning of variation into the different sources in order to obtain the least biased mean value of each line's performance.

The comparisons of ICB vs. RCB designs were based on the estimates of the variance components (block, error, genotypic and phenotypic) and heritability in Population 1 and in Population 2 obtained by analyzing the data based on the following hierarchy: (a) individual locations within each year, (b) combining data over locations within each year, and (c) combining data over locations and years.

## Analyses of Tests at Each Location Each Year

Three general responses are expected in the magnitude of the estimate of the block variance component when changing from the RCB to the ICB design. The expected responses are that the estimate will be: (a) larger (due to heterogeneity within the block of the RCB), (b) very similar (due to a similar amount of heterogeneity within the blocks of the RCB and ICB designs), or (c) smaller (due to an overestimation of the among block heterogeneity in the RCB).

The ICB design estimate of the block variance was greater than the RCB estimate in some cases in both populations and both years. For example, in Population 1 the block variance increased in 1985 at Knoxville (0 to 3.6), Ames (7.1 to 17.2) and Milan (35.6 to 39.0) and in 1986 at Greeneville (19.5 to 26.3) when the design was changed from RCB to ICB (Table 2). The same type of response was observed in Population 2 at Knoxville in 1985, at Ames, Milan and Crossville in 1985 and 1986, and at Springfield and Greeneville in 1986 (Table 3).

All of the tests that were conducted at the different locations (except Milan and Greeneville) in Population 1 in 1986 are examples of the second type of response; since, the estimates of the block variance for the RCB and ICB designs were the same or very similar (Table 2). The same type of response was also observed in Population 2 at Greeneville in 1985 (Table 3).

The third type of response, lower block variance values from the ICB design, was obtained from tests of Population 1 in 1985 at Springfield and Crossville and in 1986 at Milan (Table 2). The same was

Table 2. Estimates of variance components, heritability and error ratios for seed yield from a Randomized Complete (RCBD) versus an Incomplete Block Design (ICBD) for soybean Population 1 evaluated at six locations in 1985 and 1986.

Loc	Yr	Design	$\sigma^2_b$ †	$\sigma^2_e$ †	$\sigma^2_g \pm SE$ †	$\sigma^2_p$ †	$H^2 \pm SE$ †	Error Ratio
			----- (Kg/Ha) <sup>2</sup> x 10 <sup>3</sup> -----					
K ‡	85	RCBD	0	98.4	128.4±33.6	161.2	80±21	
		ICBD	3.6	94.5	130.8±34.1	162.3	81±21	104
	86	RCBD	0	330.1	163.6±57.0	273.6	60±21	
		ICBD	0	330.1	163.6±58.4	273.6	60±21	100
A ‡	85	RCBD	7.1	94.4	111.2±29.8	142.7	78±21	
		ICBD	17.2	85.7	111.0±28.8	139.5	80±21	110
	86	RCBD	0	127.9	14.3±11.9	56.9	25±21	
		ICBD	0	127.9	14.3±11.6	56.9	25±20	100
S ‡	85	RCBD	101.4	55.0	77.4±20.0	95.7	81±21	
		ICBD	84.0	53.3	78.2±19.8	96.0	81±21	103
	86	RCBD	0	68.6	44.1±14.0	67.0	66±21	
		ICBD	0	68.6	44.1±13.3	67.0	66±20	100
M ‡	85	RCBD	35.6	80.6	47.4±15.5	74.3	64±21	
		ICBD	39.0	69.5	53.7±15.9	76.9	70±21	116
	86	RCBD	1.5	49.4	18.1± 7.2	34.6	52±21	
		ICBD	0.3	50.4	17.8± 7.2	34.7	51±21	98
C ‡	85	RCBD	10.8	73.4	57.3±17.0	81.7	70±21	
		ICBD	7.5	75.0	57.6±17.8	82.6	70±21	98
	86	RCBD	22.5	81.7	115.4±29.7	142.6	81±21	
		ICBD	22.5	76.8	121.6±30.1	147.3	83±20	106
G ‡	85	RCBD	0	119.6	148.2±39.2	188.1	79±21	
		ICBD	0	119.6	148.2±38.5	188.1	79±20	100
	86	RCBD	19.5	201.8	35.0±21.3	102.2	34±21	
		ICBD	26.3	202.4	24.5±18.6	92.0	27±20	100

†  $\sigma^2_b$ ,  $\sigma^2_e$ ,  $\sigma^2_g$ ,  $\sigma^2_p$ , and  $H^2$  = block, error, genotypic, phenotypic variances and heritability, respectively; SE = standard error.

‡ K=Knoxville, A=Ames, S=Springfield, M=Milan, C=Crossville, G=Greeneville.

Table 3. Estimates of variance components, heritability and error ratios for seed yield from a Randomized Complete (RCBD) versus an Incomplete Block Design (ICBD) for soybean Population 2 evaluated at six locations in 1985 and 1986.

Loc	Yr	Design	$\sigma^2_{\epsilon}$ †	$\sigma^2_{\delta}$ †	$\sigma^2_{\epsilon} \pm SE$ †	$\sigma^2_{\delta}$ †	$H^2 \pm SE$ †	Error Ratio
			----- (Kg/Ha) <sup>2</sup> x 10 <sup>3</sup> -----				----- % -----	
K ‡	85	RCBD	19.0	56.6	17.9 ± 7.3	36.8	49 ± 20	
		ICBD	21.0	52.2	16.9 ± 6.7	34.3	49 ± 20	108
	86	RCBD	33.3	187.3	13.8 ± 15.1	76.2	18 ± 20	
		ICBD	24.3	189.7	13.7 ± 15.3	77.0	18 ± 20	99
A ‡	85	RCBD	0	241.1	10.3 ± 17.9	90.6	11 ± 20	
		ICBD	88.9	144.0	56.1 ± 21.1	104.1	54 ± 20	167
	86	RCBD	5.8	72.7	26.6 ± 10.0	50.8	52 ± 20	
		ICBD	7.8	71.3	24.7 ± 9.4	48.4	51 ± 19	102
S ‡	85	RCBD	64.0	69.9	99.4 ± 24.3	122.7	81 ± 20	
		ICBD	60.3	62.4	101.0 ± 22.4	121.7	83 ± 18	112
	86	RCBD	15.9	188.7	67.0 ± 25.7	129.8	52 ± 20	
		ICBD	19.5	188.9	57.9 ± 23.1	120.9	48 ± 19	100
M ‡	85	RCBD	114.1	152.9	44.9 ± 19.0	95.8	47 ± 20	
		ICBD	119.6	130.7	44.7 ± 17.3	88.2	51 ± 20	117
	86	RCBD	16.2	263.0	77.7 ± 32.7	165.4	47 ± 20	
		ICBD	31.4	254.9	66.8 ± 29.1	151.7	44 ± 19	103
C ‡	85	RCBD	10.2	29.8	133.1 ± 28.3	143.1	93 ± 20	
		ICBD	12.2	26.5	135.2 ± 26.2	144.0	94 ± 18	113
	86	RCBD	0	79.9	115.5 ± 28.1	142.2	81 ± 20	
		ICBD	13.2	66.2	127.3 ± 29.4	149.4	85 ± 20	121
G ‡	85	RCBD	5.9	148.7	172.7 ± 44.0	222.3	78 ± 20	
		ICBD	5.1	149.1	172.1 ± 43.5	221.8	78 ± 20	100
	86	RCBD	0	141.7	74.7 ± 24.1	122.0	61 ± 20	
		ICBD	4.0	137.6	75.6 ± 23.8	121.5	62 ± 20	103

†  $\sigma^2_{\epsilon}$ ,  $\sigma^2_{\delta}$ ,  $\sigma^2_{\epsilon}$ ,  $\sigma^2_{\delta}$ , and  $H^2$  = block, error, genotypic, phenotypic variances and heritability, respectively; SE = standard error.

‡ K=Knoxville, A=Ames, S=Springfield, M=Milan, C=Crossville, G=Greeneville.

true for tests of Population 2 at Springfield (60.3 vs. 64.0) in 1985 and Knoxville (24.3 vs. 33.3) in 1986 (Table 3).

Since the block variance is only one of the components making up the total variance, a change in its magnitude will result in changes in the magnitude of the other variance components. Because this study simulates typical kinds of yield tests that plant breeders might conduct, changes in the estimates of the error, genotypic, and phenotypic variances and heritability when using an ex post facto ICB design were also of interest.

The estimates of error variance were expected to show three types response when changing from the RCB to ICB design. The responses were that the error variance estimates from the ICB design would be smaller, similar to, or greater than the estimates of error variance from the RCB design. The ratio of error variances reflected the amount and direction of change in the estimate of error variance. The same three types of responses as described above were expected for the error ratio. For example in three analyses, the ICB design estimates of the error variance were not more than 2% larger than the RCB estimates. In the other twenty-one analyses, the ICB design estimates of the error variance were either less than or similar to the RCB estimates.

Changing from a RCB to an ICB design in some cases resulted in smaller error variances in both populations. The ICB design produced smaller error variances based on the error ratios in Population 1 in 1985 at Knoxville, Ames, Springfield and Milan and in 1986 at Crossville (Table 2). Similar results occurred in Population 2 in 1985 at Knoxville, Ames, Springfield, Milan and Crossville and in 1986 at

Ames, Milan, Crossville and Greeneville (Table 3).

On the other hand, changing to an ICB design resulted in some cases in both populations where the error variances were similar or equal to the RCB design estimates. This type of response occurred in Population 1 at Greeneville (in 1985 and 1986) and in 1986 at Knoxville, Ames, and Springfield (Table 2). As a result, the error ratios were equal to 100% at these locations (Table 2). In Population 2 this type of response occurred in 1985 at Greeneville and in 1986 at Springfield (Table 3).

In three other cases, changing from a RCB to an ICB design produced estimates of the error variance that were greater than the RCB design estimates. Out of the twenty-four tests conducted on Populations 1 and 2, two responses of this type occurred in Population 1 (Crossville, 1985; Milan, 1986)(Table 2) and once in Population 2 (Knoxville, 1986)(Table 3). However, these increases in the error variance were small since the ratio of errors were 98% in Population 1 (Table 2) and 99% in Population 2 (Table 3).

The ICB design estimates of the genotypic variance exhibited the same three types of response when compared to the RCB design estimates as reported previously for the block and error variances. Although the estimates of the genotypic variance from both designs were of similar magnitude at several locations each year in both populations, there were several cases in which genotypic variance was either over-estimated or under-estimated in the RCB design. The most extreme case was in Population 2 at Ames in 1985. In this case, the ICB design estimate of the genotypic variance was  $56.1 \pm 21.1$  while the RCB design estimate was  $10.3 \pm 17.9$  (Table 3). The ICB design resulted in smaller estimates of

the genotypic variance in Population 1 in 1985 at Ames and in 1986 at Milan and Greeneville (Table 2). Analogous results occurred in Population 2 at Greeneville in 1985, Ames and Springfield in 1986, and Knoxville and Milan in 1985 and 1986 (Table 3).

Some of the ICB design estimates of the genotypic variance were identical to the RCB design estimates. This was true in Population 1 in 1985 at Greeneville and in 1986 at Knoxville, Ames and Springfield (Table 2). No analogous results were observed in Population 2 (Table 3).

On several occasions, the ICB design resulted in greater estimates of the genotypic variance than the RCB design. In Population 1, this type of response occurred in 1985 at Knoxville, Springfield and Milan, and at Crossville in 1985 and 1986 (Table 2). Similar outcomes occurred in Population 2 at Springfield in 1985, at Greeneville in 1986, and at Crossville in 1985 and 1986 (Table 3).

The block, error and genotypic variances exhibited comparable types of responses when the ICB design was placed ex post facto on the experiments conducted as a RCB design. For example in Population 1 at Ames in 1986, the ICB and RCB designs resulted in equal estimates of the block, error and genotypic variances (Table 2). On the other hand in Population 1 at Greeneville in 1986, the RCB and ICB design estimates of the error variance were similar (201.8 vs 202.4), but the estimate of the block variance increased (19.5 vs. 26.3) and the genotypic variance decreased ( $35.0 \pm 21.3$  vs.  $24.5 \pm 18.6$ ) as a result of changing from the RCB to the ICB design (Table 2). Similarly in Population 2 at Ames in 1985, the block variance increased (0 vs. 88.9), the error variance decreased



(241.1 vs. 144.0) and genotypic variance increased ( $10.3 \pm 17.9$  vs.  $.56.1 \pm 21.1$ ) when the ICB design was imposed (Table 3). Very often in both populations, the ICB and RCB designs produced nearly the same outcomes.

Two parameters which reflect the cumulative effects of the variance components are the phenotypic variance and the heritability. Each of these two showed the same type of responses reported for the variance components. For example, in Population 1 at Knoxville in 1985, the phenotypic variance and heritability estimates increased when the ICB design was used (Table 2). The next year at Knoxville, both designs produced equal estimates of the phenotypic variance and heritability (Table 2). Additionally in population 1 in 1985 at Ames, the ICB design estimate of the phenotypic variance decreased and the heritability estimate increased. An example of the third type of response in Population 1 was at Greeneville in 1986, in which the ICB design estimates for both the phenotypic variance and heritability were smaller than the coinciding RCB design estimates (Table 2). These types of responses were also observed in Population 2 (Table 3).

On an individual location basis within each year, the ICB and RCB design estimates of the heritability were often equal or very similar. In Population 1 for example, the ICB estimates of the heritability were equal to the RCB estimates in one-half of the analyses (Table 2). In one-fourth of the analyses, the ICB estimates of heritability increased by as much as six percentage points; however, in most cases, the increases were only about two percentage points (Table 2). The remaining one-fourth of the analyses showed that the ICB estimates

decreased by as much as seven percentage points with the majority of the decreases being about two percentage points (Table 2). The standard errors of the heritability estimates were equal between the designs in seven analyses in Population 1 (Table 2). In the remaining five cases, the standard errors decreased by one percentage point (Table 2). Six examples in Population 1 illustrate the types of responses seen in the estimates of the heritability and its standard error. In the first example, the estimates of the heritability and its standard error were equal between the two designs at Knoxville in 1986 ( $60 \pm 21$ , Table 2). In the second type of response, the heritability values were equal between the two designs, and the estimate of the standard error from the ICB design decreased by a percentage point at Ames in 1986 ( $25 \pm 21$  vs.  $25 \pm 20$ , Table 2). In the third type of response, the ICB design estimate of the heritability increased and its standard error decreased at Crossville in 1986 ( $81 \pm 21$  vs.  $83 \pm 20$ , Table 2). The fourth example occurred at Milan in 1985 where the heritability from the ICB design increased and the estimate of the standard error was equal to the RCB estimate ( $64 \pm 21$  vs.  $70 \pm 21$ , Table 2). The next type of response occurred at Milan in 1986 where the ICB design estimate of the heritability decreased and its standard error was unchanged from the RCB design estimate ( $52 \pm 21$  vs.  $51 \pm 21$ , Table 2). In the final example which occurred at Greeneville in 1986, the ICB design estimates of the heritability and its standard error decreased ( $34 \pm 21$  vs.  $27 \pm 20$ , Table 2). In Population 2, the heritability estimates between the two designs were equal only one-fourth of the time (Table 3). In one-half of the analyses the ICB design heritability estimates were greater than the estimates from the

RCB design (Table 3). Typically, the ICB estimates were no more than four percentage points greater than the heritability estimates from the RCB design except at Ames (Table 3). At Ames, the ICB design estimate for the heritability estimate was forty-three percentage points greater than the RCB estimate (Table 3). In the remaining one-fourth of the analyses, the ICB estimates of the heritability were no more than four percentage points smaller than the RCB design estimates. The standard errors included with the heritability estimates in Population 2 were equal between the two designs in seven of the analyses (Table 3). In the remaining five analyses, the ICB estimate of the standard error decreased by one or two percentage points (Table 3).

The advantages of the ICB design were generally not as well defined as at Ames in Population 2 in 1985. In the instances where the ICB design produced greater estimates of the random error, the error variance was never more than 2% greater than the comparable RCB design estimate. Consequently, there was no advantage gained from the use of the ICB design at these locations. At those locations where there was a reduction of the random error, the ICB design was desirable. In most cases, the data showed that little would be lost by using the ICB design ex post facto to reduce the larger blocks of the RCB design by one-half. In those cases where the error variance decreased with the ICB design, more precise and accurate estimates of the variance components were gained. Consequently, a tangible benefit was gained when calculating the least square means for genotypes as more of the block effects were adjusted out of the mean yield for each of the genotypes.

## Analyses of Tests Across Locations in a Single Year

The next step in the hierarchy of simulating analyses that might be conducted in a breeding program was to combine the tests across all the locations (ALL) in a single year. This was beneficial because it added two additional variance components, locations and the genotype by location interaction to the statistical model. As a result, the genotypic variance estimates were less biased than the estimates from a single location (1). Additionally, the six locations were grouped into two sets of three locations based on the sum of each location's diallel correlation coefficients (Allen, 1989. Unpublished data). The three locations (KAS) that correlated the best with six locations were grouped together as one set and the three that had the lowest correlations (MCG) were grouped together in another set. Because of a smaller number of observations, the variance component estimates in either set of three locations contained more bias than the comparable estimates from the set of six locations. However, these biases may be outweighed by the reduction in costs of conducting yield trials at three instead of six locations.

When the ICB design was used ex post facto and the six locations were combined together (ALL) for a particular year, the same three types of response observed at each individual location (increase, decrease, and remain the same) occurred for the variance components (location, block, error, genotype by location, genotypic and phenotypic variances) and heritability. For example, in Population 1 in 1985 the location and genotype by location variances increased; whereas the block, error,

genotypic and phenotypic variances decreased and the heritability estimate remained the same (Table 4). On the other hand, the combined analyses for Population 1 in 1986 revealed that the location, genotypic and phenotypic variances, and the heritability estimates increased; whereas the block, error and genotype by location variances decreased (Table 4).

Similar results occurred in Population 1 in the KAS location set in 1985 and in the MCG location set in 1985 and 1986 (Table 4). In the KAS set in 1986, the ICB and RCB design estimates of the variance components and heritability were equal in Population 1 (Table 4).

In Population 2, there were no instances where the ICB and RCB designs produced estimates of the variance components that were equal (Table 5). In Population 2 in the ALL location set in 1985, the location, block, genotypic, genotype by location interaction and phenotypic variances increased; whereas the error variance decreased and the heritability estimate was unchanged with the ICB design (Table 5). In the ALL location set in 1986, the ICB estimates of the location and block variances increased; whereas the estimates of the error, genotypic, genotype X location and phenotypic variances and heritability decreased (Table 5). These same types of response were present in the KAS and MCG location sets in 1985 and 1986 (Table 5).

Table 4. Estimates of variance components, heritability and error ratios for seed yield from a Randomized Complete (RCBD) versus an Incomplete Block Design (ICBD) for soybean Population 1 for combined analyses of six versus two sets of three location groups each year (1985 and 1986).

Loc	Yr	Design	$\sigma^2_{\epsilon}$	$\sigma^2_{\beta}$	$\sigma^2_{\alpha}$	$\sigma^2_{\delta}$	$\sigma^2_{\sigma}$	$\sigma^2_{\sigma} \pm SE$	$\sigma^2_{\sigma_{axl}}$	$\sigma^2_{p}$	$H^2 \pm SE$	Error Ratio RCBD/ICBD*100
------(Kg/Ha) <sup>2</sup> x 10 <sup>3</sup> -----%												
KAS †	85	RCBD	125.0	36.0	82.7	48.5±16.6	57.1	76.7	63±22			
		ICBD	129.8	35.4	77.5	47.0±16.0	60.4	75.7	62±21			107
	86	RCBD	985.6	0	175.5	20.0±13.2	54.0	57.5	35±23			
		ICBD	985.6	0	175.5	20.0±13.4	54.0	57.5	35±23			100
MCG †	85	RCBD	94.8	14.9	91.8	45.0±14.6	39.1	68.2	66±21			
		ICBD	96.9	14.3	89.7	44.7±14.5	40.6	68.2	66±21			102
	86	RCBD	351.0	14.5	111.0	5.7±8.5	50.5	34.8	16±24			
		ICBD	353.7	14.2	110.4	5.9±8.1	48.6	34.4	17±23			101
ALL †	85	RCBD	129.0	25.4	87.3	51.6±13.3	43.1	63.7	81±21			
		ICBD	132.2	24.4	83.8	50.8±12.9	45.4	63.0	81±20			104
	86	RCBD	670.4	6.8	143.7	14.1±6.6	50.9	30.5	46±21			
		ICBD	671.4	6.5	143.4	14.8±6.6	50.1	31.1	48±21			100

†  $\sigma^2_{\epsilon}$ ,  $\sigma^2_{\beta}$ ,  $\sigma^2_{\alpha}$ ,  $\sigma^2_{\delta}$ ,  $\sigma^2_{\sigma}$ ,  $\sigma^2_{\sigma_{axl}}$ ,  $\sigma^2_{p}$  and  $H^2$  = location, block, error, genotypic, genotype x location and phenotypic variances and heritability, respectively; SE = standard error.

† KAS, MCG and ALL = Knoxville, Ames and Springfield; Milan, Crossville and Greeneville; and all 6 locations grouped together, respectively.

Table 5. Estimates of variance components, heritability and error ratios for seed yield from a Randomized Complete (RCBD) versus an Incomplete Block Design (ICBD) for soybean Population 2 for combined analyses of six versus two sets of three location groups each year (1985 and 1986).

Loc	Yr	Design	$\sigma^2_{\tau}$	$\sigma^2_{\beta}$	$\sigma^2_{\alpha}$	$\sigma^2_{\epsilon} \pm SE \dagger$	$\sigma^2_{\text{env}}$	$\sigma^2_{\rho}$	$H^2 \pm SE \dagger$	Error Ratio RCBD/ICBD*100
------(Kg/Ha) <sup>2</sup> x 10 <sup>3</sup> -----										
KAS †	85	RCBD	141.7	27.3	122.8	11.1 ± 7.7	31.3	35.2	32 ± 22	144
		ICBD	140.9	61.3	85.4	20.5 ± 8.5	38.4	42.9	48 ± 20	
	86	RCBD	726.3	18.5	149.5	30.4 ± 10.0	5.5	48.8	62 ± 21	100
		ICBD	729.6	17.0	149.9	28.3 ± 9.2	4.1	46.3	61 ± 20	
MCG †	85	RCBD	58.8	43.4	110.4	20.4 ± 14.3	96.5	64.8	31 ± 22	108
		ICBD	65.4	45.7	102.6	14.1 ± 13.0	101.2	59.3	24 ± 22	
	86	RCBD	21.8	6.2	160.8	4.0 ± 11.9	85.5	50.4	8 ± 24	105
		ICBD	21.6	13.5	153.8	3.0 ± 11.3	86.3	48.9	6 ± 23	
ALL †	85	RCBD	101.0	35.4	116.6	25.8 ± 8.3	53.8	41.3	63 ± 20	124
		ICBD	104.0	53.0	93.9	26.0 ± 7.8	61.6	41.5	63 ± 19	
	86	RCBD	417.5	12.4	155.1	22.6 ± 7.6	40.1	37.9	60 ± 20	102
		ICBD	419.2	14.9	151.9	21.4 ± 7.0	39.6	36.4	59 ± 19	

†  $\sigma^2_{\tau}$ ,  $\sigma^2_{\beta}$ ,  $\sigma^2_{\epsilon}$ ,  $\sigma^2_{\alpha}$ ,  $\sigma^2_{\text{env}}$ ,  $\sigma^2_{\rho}$  and  $H^2$  = location, block, error, genotypic, genotype x location and phenotypic variances and heritability, respectively; SE = standard error.

† KAS, MCG and ALL = Knoxville, Ames and Springfield; Milan, Crossville and Greeneville; and all 6 locations grouped together, respectively.

Additional trends were observed in the location variance estimates, and the estimates of the genotypic variance and heritability among the location sets. In five of the six comparisons across both populations, the location variance estimates were greater in 1986 than in 1985. In Population 1, the location variance was greatest in 1986 in all three location sets (Table 4). The same was true in Population 2 except for the MCG set where the location variance was greater in 1985 (Table 5).

Estimates of the genotypic variance and heritability from the ICB and RCB designs were not different based on the standard errors associated with each estimate. In Population 1, the genotypic variance and heritability estimates, when considered with the standard errors, were not different for the ICB and RCB designs (Table 4). However, the ICB and RCB design numerical values for these estimates did vary slightly in Population 1 (Table 4). For example, the ICB design estimates of the genotypic variance decreased in three of the analyses (Table 4). Conversely in two of the remaining analyses, the ICB design estimates of the genotypic variance were greater than the RCB design estimates (Table 4). In the remaining analysis, the ICB and RCB design estimates of the genotypic variance were equal (Table 4). Population 2 showed the same type of responses in the ICB design estimates of the genotypic variance. For example, the ICB design estimates of the genotypic variance decreased in four of the six analyses; whereas in the two remaining analyses, the ICB estimates of the genotypic variance increased (Table 5).

The ICB estimates of the heritability and its standard error showed responses similar to the genotypic variance in both populations. For



example in Population 1, the ICB and RCB design estimates of heritability were the same in one-half of the analyses (Table 4). In two of the remaining three analyses, the ICB design estimates of heritability were greater than the RCB design estimates by either one or two percentage points. In the remaining analysis, the ICB design estimate of the heritability was one percentage point smaller than the RCB design estimate (Table 4). The ICB and RCB design estimates of the standard errors of the heritability were equal in one-half of the analyses; whereas, the ICB design estimates of the standard error of the heritability were one percentage point smaller than the RCB estimates in the remaining analyses (Table 4). An example from Population 1 where the ICB design estimates of the heritability and its standard error were equal to the RCB estimate occurred in the KAS location set in 1986 (Table 4). In the KAS location set in 1985, the ICB estimates of the heritability and its standard error were smaller than the RCB estimates (Table 4). In the final example in the ALL location set in 1986, the ICB estimate of the heritability increased relative to the RCB estimate and its standard error was equal to the RCB estimate (Table 4).

The ICB design estimates of the heritability and its standard error responded in a similar fashion in Population 2. In four of the six analyses, the ICB design estimates of the heritability were generally one or two percentage points smaller than the RCB estimates except at MCG in 1985 where there was a difference of seven percentage points. In the other two analyses, the ICB estimates were either sixteen percentage points greater or equal to the RCB estimates (Table 5). The ICB design estimates of the standard errors of the heritability were one percentage

point smaller in five of the six analyses, and the ICB and RCB estimates were equal in the sixth analysis (Table 5). An example of contrasting results from the ICB design in the same population at the same locations in different years is Population 2 for the KAS set in 1985 and 1986. In 1985 the estimate of heritability increased and the standard error decreased; whereas in 1986, both the heritability and its standard error decreased (Table 5). The previous trend (in 1986 in the KAS set) was also observed in 1986 for the MCG set in Population 2 (Table 5). In the MCG set in 1985, the ICB design estimate of the heritability was smaller than the RCB estimate, and the standard error was equal for both designs (Table 5).

In most of the analyses of combined locations within each year, the estimates of the genotypic variance and heritability from the ICB and RCB designs were equal for all practical purposes. For example in Population 1 in 1986 at KAS, both designs produced equal estimates for all of the variance components and heritability indicating that the distribution of the total variation was the same (Table 4). Had the ICB design not been at least equal to the RCB design in distributing the total variation, this result at KAS would not have occurred. However, the ICB design would have been beneficial in some cases. Three examples from Population 2 are worth noting. In 1985 in KAS, the ICB design estimates of the genotypic variance and heritability were greater than the RCB design estimates while the ICB estimate of the error variance was smaller (Table 5). This demonstrated that the ICB design resulted in a more precise and favorable partitioning of the variance components. The result was that heritability increased 16% (32 to 48%) while the

standard error decreased by 2% (22 to 20%) (Table 5). On the other hand, the ICB design estimates of the genotypic variance and heritability from the MCG set in 1985 and 1986 were less than the RCB design estimates (Table 5). The RCB design estimates of the genotypic variance and heritability were overestimated while the estimates of the location (in 1985), block (in 1985 and 1986) and genotype X location interaction (in 1985 and 1986) variances were underestimated (Table 5). Again, the ICB design provided a more precise partitioning of the total variation. In the final example from Population 2, the ICB design estimates of the genotypic variance and the heritability from KAS in 1986 were smaller while the estimate of the error variance was slightly larger (the error ratio was 100%) (Table 5). The ICB estimates were better because the RCB estimates of the certain variance components (location, block, genotypic and genotype X location) appeared to be improperly estimated due to the larger block sizes (Table 5). The heritability value decreased by 1% as did its standard error. Consequently, the ex post facto use of the ICB design was advantageous.

Based on the magnitudes of the estimates for genotypic variance and heritability in both populations and regardless of the design, in general, 1985 was a better year for selection than 1986. The exception to that trend was in Population 2 for the KAS set in which 1986 was the best year for selection (Table 5). This latter case is a clear example where the ICB design would have been beneficial since the heritability value would have increased from  $32 \pm 22\%$  using a RCB design to  $48 \pm 20\%$  using a ICB design (Table 5).

The next step was to compare the location sets to determine how the

sets with three locations (KAS and MCG) compared to the set with six locations (ALL). The KAS location set contributed the most to the ALL set based on the ICB design estimates of the genotypic variance and the heritability. The estimates of the genotypic variance and heritability at KAS were most like the estimates at ALL in Population 1 in both 1985 and 1986 with the exception of the heritability estimates in 1985 where the MCG set was most like the ALL set (Table 4). In Population 2, the estimates at KAS were most like the estimates from all six of the locations (Table 5). The results from these two populations indicate that an effective selection program could have been based on testing at the KAS locations and which would have reduced the cost of genotypic evaluations by one-half without a significant loss of information.

#### Analyses of Tests Across Locations and Years

The final step in the hierarchy of simulating yield testing in a breeding program was to analyze the data across locations and years. According to Allard (1), variance component and heritability estimates from these types of analyses should be even less biased than those of combined locations within each year because of the addition of years, year X location, genotype X year, and genotype X year X location variance components to the statistical model. The reduction of bias occurs in the estimation of the genotypic variance since more of the genotype X environment interactions can be estimated and removed (e.g. genotype X year variation can be estimated and averaged across years,

genotype X location variance can be estimated and averaged across locations, genotype X year X location variance can be estimated and averaged across years and locations, and the error variance can be averaged across the reps, locations and years). The locations were combined over years and analyzed according to the same three sets described previously (ALL, KAS and MCG).

The ICB design produced the same types of response (increase, decrease, or remained similar) in the estimates of the variance components as were observed in the analyses at individual locations and in the analyses across locations within each year. Two examples of these responses from Population 1 are presented. In the ALL set, the ICB design estimates of the year and location variances remained the same; whereas the block, error, genotype X year, and genotype X location variances decreased, and the year X location, genotypic, genotype X year X location, and phenotypic variances and heritability increased (Table 6). In the KAS set, the year, location, genotypic, genotype X year and genotype X location variances and heritability remained equal; the location X year and error variances increased; and the block, genotype X year X location and phenotypic variances decreased (Table 6). Similar responses similar occurred in Population 2 (Table 7). The lowest error ratios in either population occurred at KAS (98%) and MCG (99%) in Population 1 (Table 6).

The ICB design estimates of the variance components in Population 1 revealed that some estimates from the RCB estimates appeared to be either overestimated or underestimated (Table 6). For example in the ALL set, the RCB estimates of the block and error variance appeared to

Table 6. Estimates of variance components, heritability and error ratios for seed yield from a Randomized Complete (RCBD) versus an Incomplete Block Design (ICBD) for soybean Population 1 for combined analyses of six versus two sets of three location groups across two years (1985 and 1986).

Variance Components	KAS †		MCG †		ALL †	
	RCBD	ICBD	RCBD	ICBD	RCBD	ICBD
	----- (Kg/Ha) <sup>2</sup> x 10 <sup>3</sup> -----					
$\sigma^2_Y$ ‡	0	0	0	0	0	0
$\sigma^2_L$ ‡	0	0	266.7	266.7	106.0	106.0
$\sigma^2_{LY}$ ‡	855.9	859.4	70.2	72.9	374.3	377.3
$\sigma^2_B$ ‡	17.6	14.6	14.7	13.3	16.1	13.7
$\sigma^2_e$ ‡	129.5	132.6	101.4	102.7	115.5	113.5
Error Ratio (%) ‡	98		99		102	
$\sigma^2_{\pm SE}$ ‡	14.4±10.8	14.4±10.8	5.2±8.1	5.2±7.9	11.6±7.3	12.8±7.2
$\sigma^2_{GXY}$ ‡	19.9	19.9	20.2	20.2	21.3	20.7
$\sigma^2_{GXL}$ ‡	12.6	12.6	3.3	3.3	6.2	6.1
$\sigma^2_{GXYXL}$ ‡	42.8	39.3	41.5	38.7	40.8	41.7
$\sigma^2_P$ ‡	42.9	42.4	28.9	28.5	29.9	30.7
H <sup>2</sup> ± SE (%) ‡	34±25	34±25	18±28	18±28	39±24	41±24

† KAS, MCG and ALL = Knoxville, Ames and Springfield; Milan, Crossville and Greeneville; and all 6 locations grouped together, respectively.

‡  $\sigma^2_Y$ ,  $\sigma^2_L$ ,  $\sigma^2_{LY}$ ,  $\sigma^2_B$ ,  $\sigma^2_e$ ,  $\sigma^2_G$ ,  $\sigma^2_{GXY}$ ,  $\sigma^2_{GXL}$ ,  $\sigma^2_{GXYXL}$ ,  $\sigma^2_P$ , H<sup>2</sup> and Error ratio = year, location, year x location, block, error, genotypic, genotype x year, genotype x location, genotype x year x location and phenotypic variances, heritability, Error ratio=(RCBD error variance÷ICBD error variance) x 100, respectively; SE = standard error.

Table 7. Estimates of variance components, heritability and error ratios for seed yield from a Randomized Complete (RCBD) versus an Incomplete Block Design (ICBD) for soybean Population 2 for combined analyses of six versus two sets of three location groups across two years (1985 and 1986).

Variance Components	KAS †		MCG †		ALL †	
	RCBD	ICBD	RCBD	ICBD	RCBD	ICBD
----- (Kg/Ha) <sup>2</sup> x 10 <sup>3</sup> -----						
$\sigma^2_Y \ddagger$	0	0	301.4	301.4	74.2	74.2
$\sigma^2_L \ddagger$	0	0	58.3	58.3	0	0
$\sigma^2_{LY} \ddagger$	1092.4	1094.3	7.3	10.6	469.4	471.9
$\sigma^2_B \ddagger$	22.8	34.8	24.8	30.2	23.8	32.5
$\sigma^2_e \ddagger$	135.3	123.3	135.6	130.3	135.9	122.4
Error Ratio (%) †	110		104		111	
$\sigma^2_{\pm SE} \ddagger$	2.3±6.3	2.3±6.3	0±9.6	0±9.0	4.4±5.7	5.5±5.7
$\sigma^2_{GY} \ddagger$	17.9	17.9	16.4	16.4	19.7	16.8
$\sigma^2_{GL} \ddagger$	0	0	52.2	52.2	18.0	17.7
$\sigma^2_{GYL} \ddagger$	26.0	24.1	38.7	35.4	28.9	33.4
$\sigma^2_P \ddagger$	23.1	22.1	39.6	38.7	23.5	23.0
H <sup>2</sup> ± SE (%) †	10±27	10±28	0±24	0±23	19±24	24±25

† KAS, MCG and ALL = Knoxville, Ames and Springfield; Milan, Crossville and Greeneville; and all 6 locations grouped together, respectively.

‡  $\sigma^2_Y$ ,  $\sigma^2_L$ ,  $\sigma^2_{LY}$ ,  $\sigma^2_B$ ,  $\sigma^2_e$ ,  $\sigma^2_G$ ,  $\sigma^2_{GY}$ ,  $\sigma^2_{GL}$ ,  $\sigma^2_{GYL}$ ,  $\sigma^2_P$ , H<sup>2</sup> and Error ratio = year, location, year x location, block, error, genotypic, genotype x year, genotype x location, genotype x year x location and phenotypic variances, heritability, Error ratio=(RCBD error variance÷ICBD error variance) x 100, respectively; SE = standard error.

be overestimated while the estimate of location X year variance was underestimated (Table 6). Additionally, in the KAS and MCG location sets, the RCB design estimates of block and the three-way interaction variances appear to be overestimated while the error and year X location interaction variances appeared to be underestimated when compared to the ICB design estimates (Table 6). Furthermore, estimates of the other sources of variation and heritability and its standard error from both designs were very similar within the KAS and MCG location sets; whereas, in the ALL location set, the ICB estimate of the heritability increased with the ICB design, but the standard error estimate remained the same (Table 6). This difference in the ICB design estimate of the heritability in the ALL set can be attributed to the larger genotypic variance (Table 6).

The ICB design estimates of the variance components exhibited the same three types of response (decreased, increased, or similar to) in Population 2. For example, the ICB design resulted in smaller estimates of the error variance and a greater partitioning of the total variation to the smaller, incomplete blocks while essentially no change occurred in the estimates of the genotypic variance or heritability (Table 7). The standard errors of the heritability estimates increased by one percent in the KAS and ALL location sets and decreased by the same amount in the MCG set (Table 7). In both populations, the ICB design would have permitted a more precise ranking of the genotypes based on their least-square means because the means would have been adjusted for the more precise block effects.

In both populations, the KAS location set contributed more to the



estimates in the ALL location set than the MCG location set based on the genotypic variance and heritability estimates. In Population 1, the ICB design estimates of the genotypic variance and heritability were likely not statistically different among the location sets based on the standard errors associated with each estimate. However, based on the numerical values, the selection of superior genotypes would have been easier in the KAS than the MCG location set (Table 6). The advantage of the higher heritability estimate at ALL was diminished by the extra cost of conducting the yield trials at three additional locations. The effects were more dramatic in Population 2 (Table 7). The data suggests that yield trials could have been more effectively conducted at the three locations, Knoxville, Ames and Springfield (KAS), than in the Milan, Crossville, and Greeneville (MCG) set. On the other hand, the heritability values were approximately doubled when all six locations were used even when using the RCB design (10 vs. 19%)(Table 7). Using an ICB design instead of the RCB design would have resulted in further benefits from a heritability basis (19 vs. 24%, respectively)(Table 7).

## CHAPTER 4

### CONCLUSION

Comparisons of a randomized complete block design with the ex post facto use of an incomplete block design were made using two soybean populations at six locations for two years. The ex post facto use of the ICB design was advantageous over the RCB design in several tests because the smaller, incomplete blocks accounted for more of the heterogeneity within the larger complete blocks. Consequently, in the use of three hierarchies to analyze the data (i.e. individual locations within each year, combined locations within each year, and combined locations over years), the ICB design resulted, at worst, in an error variance that was 2% greater than the RCB design estimate and in the best case was 67% lower than the RCB estimate. Additionally, the estimates of the variance components and heritability consistently showed three types of responses (i.e. increases, decreases, or remained equal to the RCB estimates) when the ICB design was imposed. The standard errors of the heritability estimates from the ICB were either equal to or lower (i.e. maximum of two percentage points) than the RCB design estimates. Using the ICB design ex post facto in several of the tests would have resulted in greater precision and accuracy of the estimates of the variance components across all three hierarchies in both populations. Consequently, with the ICB design, least square mean yields for the genotypes would be more accurate estimates of their

genetic yield potential because of a better allocation of the variance components such as block and error. Therefore, more confidence could be placed in the ranking of the genotypes based on the least square means for yield.

The use of six locations across two years allowed for a comparison of three location sets: (a) six locations combined together (ALL) and (b) two sets of three locations each, KAS and MCG, using two hierarchies (across locations within a single year and across locations and years). The location sets containing three locations were determined based on the relative sum of the diallel correlation coefficients. The estimates from the sets of three locations contained more bias than those from the set of six locations due to a fewer number of locations involved in calculating the estimates. However, this disadvantage of the two sets containing three locations would have been diminished by the reduced cost of conducting yield trials at only three locations instead of six. There were two distinct differences between the two sets of three locations. The KAS set of locations appeared to contribute more information to the ALL set. The MCG set consistently produced lower numerical values for the genotypic variance and the heritability than the KAS location set. These results indicate that yield trials conducted at the three locations: Knoxville, Ames and Springfield (KAS) would have been adequate for selecting the superior yielding soybean genotypes in both populations tested.

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**LIST OF REFERENCES**

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## VITA

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