EFFECTIVENESS OF THE HONEYCOMB DESIGN IN EARLY GENERATION YIELD EVALUATION IN SPRING WHEAT

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Davies Maleka Lungu

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ABSTRACT

Lungu, Maleka, Davies. Ph.D. The University of Manitoba. May, 1984. EFFECTIVENESS OF THE HONEYCOMB DESIGN IN EARLY GENERATION YIELD EVALUATION IN SPRING WHEAT. Major Professor: E.N. Larter.

The effectiveness of the honeycomb selection method for yield was evaluated in a selection experiment using spring wheat. F2 seed of two spring wheat crosses Glenlea X NB131 and Glenlea X Era were planted at the University of Manitoba research plots in the summer of 1980 in a honeycomb design. Using single plant grain yields as the primary selection criterion, plants were selected according to the honeycomb method. Two selection strategies were followed; one group of selections was based on their high yield, in another group, the selection criterion was based on low yield. Depending upon the success of selection at these two yield levels, an indication was obtained as to the effectiveness of single plant selection for yield in the honeycomb design.

Progenies of the F2 plant selections were also planted in a honeycomb design at the University of Manitoba research plots in the summer of 1981. Also planted in 1980 (solid seeded in row plots) were the unselected composite seeds for the two crosses. A second cycle of honeycomb selection on

the F3 plants for both high and low yield was done just as previously in the F2 generation. Seed of each F3 selected plant was entered in an F4 yield test at the University of Manitoba research plots in the summer of 1982.

The results of this experiment showed that the honeycomb selection for high and low grain yields in the F2 and F3 generations was effective in identifying high and low yielding progenies in the F3 and F4 generations respectively.

The overall grain yields of F3 progenies of the F2 single plant selections showed that F3 progenies of F2 plants which were selected for high yield outyielded F3 progenies of F2 plants selected for low yield. Progenies of high yielding selections from the Glenlea X NB131 cross outyielded progenies of low yielding selections from the same cross by 12.07%, while the progenies of high yielding selections from the Glenlea X Era cross outyielded low yielding selections from the same cross by 13.79%. Progenies of high yielding selections from Glenlea X NB131 and Glenlea X Era crosses outyielded the mean yield of plants of the check variety Glenlea by 4.24% and 6.73%, respectively. An inter-generation correlation of grain yields of F3 families from F2 single plant selections on their F2 parental plant grain yields, was highly significant ($r = 0.315$) and positive. This demonstrated that F3 progenies of F2 plants selected for high yield tended to give high yields, similarly those selected for low yield tended to give low yields in the F3 generation.

The F4 yield test gave similar results. The analysis of variance showed that there were significant genotypic differences for yield among the yield test entries. Single degree contrasts were calculated to make various comparisons among the average yields of high yielding selections, the low yielding selections, composite lines, and the check variety Glenlea. The analysis showed that overall, progenies of high yielding selections significantly outyielded progenies of low yielding selections for all crosses. Also high yielding selections for all crosses significantly outyielded the composite lines. Composite lines were very low yielding in that they were also outyielded by low yielding selections. However, the average grain yield of high yielding selections was not significantly different from the yield of Glenlea. Using a practical plant breeding approach of retaining lines that yield equal to or greater than the check variety for further advance in a breeding program, 57% of all high yielding selections would have been retained in comparison with only 30.8% of the low yielding selections. If we consider the two crosses separately, 71% of the high yielding selections from the Glenlea X NB131 cross would be retained as compared to 53.33% of the low yielding selections from this cross. For the Glenlea X Era cross, 34.6% and 11.8% of the high and low yielding selections, respectively, would have been retained. These results show that a higher number of the high yielding selections would have been kept than the low yielding selections.

Inter-generation correlation coefficients between F4 grain yields and grain yields measured in the F2 and F3 generations were all positive and highly significant, further illustrating the effectiveness of the honeycomb method in selecting for yield.

Using stepwise, multiple regression analyses, yield was always shown to be among the variables selected that was most valuable in determining the F4 entry mean grain yields and F3 mean family grain yields. Other variables shown to be important were the yield components; 1000-kernel weight, grain yield per spike, and number of tillers per plant.

INTRODUCTION

The science of plant breeding has had a tremendous impact on meeting human food needs since the dawn of man's civilization. Concurrent with early man's change of life style from hunter-gatherer to a more sedentary life style was the domestication of wild plants. The process of domestication involved recognition that a particular species had something to offer, such as food or fibre and the development of methods of cultivating the plant together with the method of processing the crop (Baker, 1978; Mayo, 1980). Thus, early man, in his activity of selecting which plant species to domesticate, was involved in basic plant breeding. Selection, both conscious and unconscious was a continuous part of this process changing the domesticated wild plants into the remarkable array of crops we have today. In choosing to keep for next season's planting only plump seeds from big ears or pods, borne on nondiseased plants, he was inadvertently involved in a yield improving breeding program. Unconsciously, as he harvested seeds from plants that did not lodge or shatter, he was selecting for lodging and shattering resistant types such as is the case with cultivated corn (_Zea mays_ L.) which has lost all mechanisms for self-dispersal of seeds compared to its wild proginators (Baker, 1978; Simmonds, 1976). Although early man had no knowledge of genetics, his plant breeding efforts made great contribution to agricultural development. Without these early plant breeders who fashioned our food crops from the weeds about them, we would have none of the crops that supply most of our food today.

The contribution of modern man to plant breeding has been not so much to develop new methods as to accelerate progress, a process that has gained momentum proportionately with greater understanding of the genetic systems that govern heritable variability. With the better understanding of genetics, plant breeders have achieved tremendous improvements in the yielding capacity and quality of many crops and thereby contributed to increased food production in the world (Allard, 1960; Baker, 1978; Burton, 1981). One could safely state that the over four billion people who constitute the world population today have more food than the eight million people who made up the total world population some 10,000 to 8,000 B.C. This is on the average, however. Beneath this average is a food problem of chronic hunger and malnutrition that is endemic in the economically underdeveloped Third World countries (Borlaug, 1981). Progress in food production has been achieved in the economically advanced countries while most Third World countries in Asia, Africa and Latin America have lagged behind in developing improved varieties of crops and improved production technology. Agricultural productivity is a multifaceted undertaking; it requires not only genetically improved crop varieties, but also improved scientific crop production techniques so that improved varieties can express their genetic potential in the form of increased yields and quality.

Many Third World countries have also been beset by their large and rapidly growing populations which have outstripped the rate of food production. Research at international agricultural research centers has contributed to increased food production in many Third World countries.

New high yielding varieties of wheat and rice developed at the International Wheat and Maize Improvement Center (CIMMYT) in Mexico and the International Rice Research Institute (IRRI) in the Philippines have improved food production in Third World countries. In India, for example, wheat supplies tripled between 1961 and 1980, largely as a result of the adoption of high yielding varieties rather than the expansion of the area planted to the cereal. Wheat production soared from 11.4 million tons in 1967 to 26.4 million tons in 1972 and reached 34.7 million tons in 1979 (Plucknett and Smith, 1982). India has been self-sufficient in grains in most years since the introduction of high yielding wheat and rice varieties. Bangladesh has recently come within a few thousand tons of feeding herself. The Philippines which imported rice for decades has only occasionally had to buy rice since 1970. In 1980, the Philippines exported 250,000 tons of rice. Mexico exports wheat in some years, a major turn-around considering its rapidly growing population and the fact that it had been importing substantial quantities of wheat for decades. Indonesia's food picture is much brighter now that more hectares are being planted to high yielding rice varieties (Plucknett and Smith, 1982).

Despite the gains from high yielding varieties, however, the world is still not secure from food shortages. Population projections for the year 2000 are such that, unless the Third World countries introduce vigorous birth control programs, the current world population of over four billion will swell to about seven billion people. The Third World will make the greatest contribution to the burgeoning world population. This raises an ominous possibility of widespread hunger and starvation in the Third World countries with this huge population increase (Borlaug, 1981). These predictions place a heavy responsibility on the shoulders of agricultural scientists and politicians who must devise strategies to increase food production on a sustained basis. The contributions of plant breeders will continue to be needed. More high yielding varieties of crops will have to be developed to increase food production, particularly in the food deficient developing countries. This is going to require continued, well-funded and imaginative crop improvement research.

A necessary common plant breeding procedure for the generation of variability in crops is hybridization followed by selection. Selection is usually started in the F_2 generation, since it is in this segregating generation that there is maximum genetic variability. The commonly used pedigree method employs visual selection on a single plant basis beginning in the F_2 with yield testing conducted in the F_5 or later generations. Although many good crop varieties have been developed by this method, many workers state that single plant selection early in the segregating generations for a quantitatively inherited trait such as yield is ineffective. This is largely due to the environmental influences (including interplant competition, soil heterogeneity, etc.) on the performance of a single plant which makes it difficult to distinguish between a plant that is going to give rise to superior performing progeny and one that will not (Fasoulas, 1973; Hanson et al. 1979; McGinnis and Shebeski, 1968; Shebeski, 1967; DePauw and Shebeski, 1973). The breeder thus faces problems in selecting genetically superior plants, i.e., those with a potential for giving rise to superior performing progeny and eventually high yielding varieties. This problem makes the study of selection methodology in plant breeding very important. Unless a system for identifying genotypes in a segregating generation with a potential for developing into high yielding lines is developed, success in plant breeding could remain dependent on the experience and intuition of the breeder. We therefore, need to devise reliable and efficient selection methods for detecting the yielding potential of single plants early in the segregating generation when the frequency of genotypes possessing the desired trait is greatest.

The present study involves an investigation of the honeycomb selection method proposed by Fasoulas (1973). The honeycomb selection method is based on the theory that single plant selection for yield in the F_2 can be effective if interplant competition is eliminated and if single plant yield comparison is done among plants growing under conditions of zero soil heterogeneity. Plants in the F_2 generation represent distinct genotypes, so that individual plants in an F_2 population from a specific cross represent different genotypes. If these plants are closely planted the stress created by interplant competition will affect individual plant performance, thereby preventing the plants from expressing their full genetic potential. Fasoulas (1973) believes that the masking effect of interplant competition is one of the reasons why single plant selection for yield has not been effective with current selection methods. He proposed space-planting the F_2 population to remove interplant competition. He reasoned that removing the stress due to interplant competition through adequate spacing and providing optimum growing conditions would allow the individual F_2 plants to fully express their yielding potential, thus easing the plant breeders' task of selecting truly superior plants. The second problem which the honeycomb selection method attempts to correct is the effect of soil heterogeneity. Gradients of fertility do exist in the soil. Soil heterogeneity is also one of those problems that makes single plant selection for yield ineffective with existing methods. A plant may be selected not because of its superiority but because it happened to be planted on a fertile portion of land. The honeycomb method attempts to use the nature of soil heterogeneity to the advantage of the breeder. Fisher (1931) stated that soil fertility cannot be regarded as distributed at random, since on average, nearby plots are known to be more alike than those further apart. Thus, small areas of soil approach homogeneity and basing selection on the comparative performance of individual plants grown in these small sections allows one to safely conclude that each plant is expressing its genetic potential and the differences between the yield of plants is due to genetic differences. Fasoulas (1973) proposed a spatial arrangement of plants in the field that took into account the problem of interplant competition and soil heterogeneity. He proposed a field planting pattern that permits contigous plants to share a common environment, i.e., a hexagonal arrangement--hence the term honeycomb design. Contigous plants in every hexagon are equidistantly spaced from each other and selection is based on whether a given genotype in the middle of a hexagon yields superior to its six immediate neighbouring plants of the hexagon. Since the area of soil occupied by a hexagon is small, it can be assumed to be homogeneous.

Fasoulas (1973) claims that this selection method will break yield barriers for most crops since it is an objective and scientific way of distinguishing yield superiority of genotypes in the early segregating generations. However, few studies have been done on the honeycomb selection method. It is in view of the paucity of studies on this selection method and the importance of studies on yield improving selection methods, that I set out to study the effectiveness of the honeycomb selection method. The objectives of the study were:

(i) to study the effectiveness of selecting for improved yield in bread wheat through the selection of single plants in F_2 and F_3 generations using the honeycomb method; and

(ii) to investigate the relationship of characters measured in the F_2 to the F_3 mean grain yields and, the F_2 and F_3 characters to the F_4 mean grain yields.

LITERATURE REVIEW

Cereals were among the first plants to be domesticated, having been grown long before the beginning of recorded history. Among cereals, wheat ranks as one of the most important and widely cultivated food crops. It is grown in all continents except Antarctica. Because of its extraordinarily widespread cultivation ~~at the present day~~, there are wheat plants growing and maturing at all times of the year somewhere in the world.

The three principal types of wheat used in modern food production are *Triticum aestivum* L. em Thell, *Triticum turgidum* L. var. *durum*, and *Triticum compactum* L. *Triticum aestivum* L. em Thell constitutes the bulk of the wheat production. The kernels are milled to produce flour for bread making and for cakes and cookies. It is adapted to an array of environments and can be grown under a wide range of climatic conditions and soils. However, the yield varies with climate and other factors. As a crop, it is grown most effectively in "grassland" climates with less than 30 inches (750 mm) of rainfall each year.

Triticum turgidum L. var. *durum* is mainly ground into semolina (purified middlings) instead of flour. Durum semolina is generally the best type for the production of pasta foods. <u>Triticum</u> <u>compactum</u> L. is more suitable for confectionary and cookies than for other purposes.

In this literature review, I shall endeavour to review the breeding approaches that have been followed to improve the yield and adaptability of <u>Triticum</u> <u>aestivum</u> L. em Thell, henceforth referred to simply as wheat. The review is restricted to those breeding approaches that are relevant to this study. To maintain a proper trend of thought, the review is subdivided into three subheadings as follows:

1. Selection: The Driving Force of Plant Breeding;
2. Indirect Selection for Yield in Wheat; and
3. Direct Selection for Yield in Wheat.

2.1 SELECTION: THE DRIVING FORCE OF PLANT BREEDING

2.1.1 A General Overview

Selection is the essence of plant breeding and has played an important role in the history of mankind. Evolution, via natural selection, and domestication, via artificial selection, created and improved the crop species that are so important for human survival. Ever since the potential of certain plant species as food sources was recognized, selection has been practiced for more productive plant types (Simmonds, 1976; Hallauer, 1981; and Hallauer and Miranda, 1981). In wheat, in addition to great advances achieved by domestication and early empirical breeding, significant improvements have been made as a result of development of more sophisticated breeding techniques that have occurred mainly during this century (Bushuk, 1977).

Selection is ultimately the differential reproduction of genotypes. It requires making choices, such as choice of parental genotypes for a particular cross, and the choice of maintaining specific plant selections from a cross for the purpose of their perpetuation. Effective selection, however, is also dependent on the existence of genetic variability and the heritability of the trait for which selection is being made (Falconer, 1960 and Hanson, 1963).

Selection pressure is applied on the phenotypes, that is, the observed expression of the underlying genes for a trait. The phenotypic expression, however, is also influenced by environmental effects and the effects of genotype-environment interactions (Comstock and Moll 1963 and Falconer, 1960). Thus the total phenotypic variability observed in a segregating base population on which selection pressure is to be applied results from genetic differences, environmental differences, and the effects of the interaction of genotype and environment on individual plants (Allard, 1960; Falconer, 1960 and Comstock, 1963). Since only the genetic differences are hereditary, the term "heritability" was coined to provide a quantitative measure of the relative importance of genes and environment to total variability. Falconer (1960) defined heritability as that fraction of the observed phenotypic variance which is caused by differences between genes or genotypes of individuals. In plant breeding, heritability has value primarily as a method of quantifying the concept of whether progress from selection for a plant character is relatively easy or difficult to make in a breeding program (Hanson, 1963). The magnitude of the heritability estimates gives the plant breeder an idea as to the kind of progress he or she would expect to gain in selecting for a particular trait. Traits which have low heritability estimates do not lend themselves to significant gain from selection while progress from selection would be expected for traits with high heritability estimates.

2.1.1.1 Selection for yield. Tremendous improvements in the yielding capacity of wheat has been achieved since the beginning of scientific plant breeding. Frankel (1947) in his discussion on the theoretical basis of breeding for yield came to the conclusion that improved yields can best be obtained by the elimination of yield limiting defects. He suggested that in addition to selecting for yield per se, selecting for disease resistance, lodging resistance and winter hardiness will lead to developing high yielding varieties. Frey (1971) reported that taken in total, the yielding capacities of wheat varieties in the United States have increased 35 to 60 percent in five to six decades of breeding. He attributes a sizeable portion of this increase to the introduction of semi-dwarf lodging resistant varieties.

Comparable improvements in yielding capacity of wheat varieties has been accomplished in Mexico. The yield of Mexican semi-dwarf varieties of wheat is more than double that of indigenous tall Mexican varieties. Borlaug et al., (1969) attributed much of the national improvement in wheat yields in Mexico during the 1960's to the introduction of semi-dwarf disease resistant varieties of wheat. It is important to note here, however, that these phenomenal increases in average wheat yields in Mexico and other countries such as India and Pakistan cannot be attributed entirely to plant breeding. It was a package of improvements in wheat culture (fertilization, irrigation, superior varieties, etc.) that was responsible for the large increases. Nevertheless, basic to the exploitation of better field husbandry was the availability of wheat varieties that were lodging and disease resistant and capable of responding to heavy fertilization (Frey, 1971).

2.1.1.2 Selection for protein content. Cereal grains have always provided a portion of the protein needed in man's diet. Oram and Brock (1972) estimated that approximately 50% of the world's protein needs come from cereals, 20 percent from grain legumes and 30 percent from animal products. In developing countries, cereals contribute about 70% of the protein consumed while animal products provide only 10% of the total (Axtel, 1981). Thus, in many parts of Asia, the

Near East, Africa and Latin America people are dependent directly on cereals for approximately two-thirds of their dietary protein requirement. In such instances, the low nutritive quality of the cereal proteins (Miflin and Shewry, 1979 and Osborne and Mendel, 1914) coupled with the low protein content of most cereals may result in protein malnutrition, especially in preschool children where protein needs are high in relation to caloric requirement (Nelson, 1969).

The contribution of wheat grain protein to human dietary protein needs is through the various foods produced from wheat flour. These include chapati, bread, cookies and cakes. Aside from its dietary importance, grain protein content is a major baking quality factor in wheat. Bushuk et al., (1969) in a study to evaluate the relation of grain protein content to bread baking characteristics, reported that in grains with proteins of the same quality, an improvement in bread baking characteristics occurred with an increase in protein content. Grain protein content has been shown to be positively correlated with loaf volume (Sunderman, et al., 1965). In addition, wheat proteins are known to largely govern the capacity of the flour to absorb water (Finney, 1945). Breeding for increased grain protein content in wheat therefore is imperative because protein content is an important factor in baking quality of wheat as well as in supplying human and animal dietary protein needs.

Knowledge of the heritability of wheat grain protein is important in breeding for increased protein content. Many studies have been made with wheat to determine mechanisms by which grain protein is produced. Most of these studies have led to the conclusion that production of grain protein in wheat is genetically controlled and that it is heavily influenced by environmental factors (Aamondt et al., 1935; Bushuk et al., 1969; Chapman et al., 1970; Davis et al., 1961; Haunold et al., 1962; Johnson et al., 1963; Lofgren et al., 1968; McNeal et al., 1972; Stuber et al., 1962; and Sunderman et al., 1965). Using the regression of F_3 lines on the F_2 plants, Sunderman et al. (1965) obtained estimates of heritability of grain protein synthesis ranging from 15 to 26 percent. Davis et al. (1961) obtained broad sense heritability of 54 to 69 percent. Haunold et al. (1962) obtained heritability estimates of 65 percent. These estimates suggest significant potential for progress in selecting for high grain protein content.

It is of interest to the wheat breeder to know how grain yield and protein content are related genetically in segregating populations. The aim is to improve both grain protein content and grain yield concurrently. Johnson et al. (1963) and Middleton et al. (1954) have observed winter wheat progeny with both high grain protein percent and high grain yield. However, finding this combination in recently developed high yielding spring wheats has not been easy. The apparent elusiveness of a simultaneous improvement in grain protein content and grain yield has been attributed to the negative correlation that exists between these two characters. Frey (1977) has shown that in several cereal species including wheat, grain yield and grain protein content are negatively correlated. Baker et al. (1968), McNeal et al. (1972), McNeal et al. (1982), Meizan et al. (1977) and many other workers have also reported negative correlations between grain protein content and grain yield.

Despite the negative correlation between yield and protein content, some plant breeders have obtained protein and yield increases in wheat simultaneously. Johnson et al. (1973) using 'Atlas 66' as a source of genes for high protein have isolated several 'second cycle' hard red winter wheat types which combined high grain yield with a 2.5 percent increase in protein content. Substantial increases as a result of selective breeding for grain protein content have also been reported by Davis et al. (1961). In a study designed to investigate the relationship of grain yield and protein content, Halloran (1981) reported negative but very low correlation of yield with protein content in F_4 progeny. That study suggested that no great limitation exists at the yield levels of current commercial wheats to achieve an increase in protein content through breeding.

2.2 INDIRECT SELECTION FOR YIELD IN WHEAT

Plant breeders (like researchers in other fields) are constantly searching for better and more efficient breeding methods. In the effort to develop superior yielding varieties of wheat, plant breeders have attempted application of indirect selection criteria for improvement of yield. Among these selection criteria are yield components and harvest index.

2.2.1 Yield Component

Engledow and Wadham (1923, 1924a and 1924b) were among the first to suggest the use of indirect selection criteria for yield improvement in cereals. They suggested the use of yield components which they defined as the average number of spikes per plant, the average number of kernels per spike and the average weight of a single kernel. They also investigated the usefulness of morphological and physiological parameters as indices of single plant yield. They came to a conclusion that only "migration coefficient" (similar to today's harvest index; the difference being that migration coefficient is based on fresh weight) was of any real value.

The components of yield continued to receive attention and in recent years the possibility of increasing yield through yield component selection has attracted attention of several researchers (Woodworth, 1931; Grafius, 1956, 1964; McNeal, 1960; Johnson et al., 1966; Knott and Talukdar, 1971;

Brinkman and Frey, 1977; McNeal et al., 1978). Woodworth (1931) suggested that yield must be increased in small grains by selecting for the components of yield and that parental varieties should be selected on the basis of their component attributes. Grafius (1956) represented yield in oats as the volume of a parallelepiped whose edges represented the components of yield: panicles per unit area (x), the average number of kernels per panicle (y) and the average kernel weight (z). Thus yield per unit area is the product, (x)(y)(z). He suggested that it might be easier to increase yield by increasing the smallest yield component of an otherwise good cultivar. Johnson et al. (1966) stated that increases in yield levels are progressively more difficult to obtain and that evaluation of individual yield components might provide a better basis for selection of parents and for evaluation of their progenies than yield itself. Lebsock and Amaya (1969), Knott and Talukdar (1971) and Sidwell et al. (1976) suggested that kernel weight should be a good trait to use for indirect selection for yield in wheat because it is highly heritable and favourably associated with yield.

The concept of yield components as a selection criteria embodies the assumption that a strong association exists between yield and the yield components and that these component characters are more simply inherited than yield per se. Hence yield component breeding to increase grain yield would be most effective if the components involved are highly heritable, either genetically independent or positively correlated, and either physiologically unrelated or related in a positive manner (Bhatt, 1980).

Grafius (1964) stated that in many crops including small grains, when segregating populations are space-planted the correlation between the components of yield trend toward zero indicating independent gene systems governing yield component development. Adams (1967) supported the proposal of Grafius (1964) and concluded that yield components are genetically independent and that they are developed sequentially. However, Brinkman and Frey (1977) suggested that yield components may not be inherited independently, and that the operation of a single pleiotropic gene may be responsible for the negative correlations that exist among yield components.

Heritability estimates of yield components in wheat vary in magnitude depending on the method of estimation and whether the measurements used in estimating heritability were done on space-planted or solid seeded plots. Overall yield components have shown to have higher heritability than grain yield (Stuber et al., 1962; Johnson et al., 1966; Fonseca and Patterson, 1968; Ketata et al., 1976 and Sidwell et al., 1976). Fonseca and Patterson (1968) working with wheat estimated heritability from data from hills for number of spikes, kernels per spike and kernel weight and found the first two components to have high heritability and the last one to have low heritability. However, other workers have reported the component kernel weight as being highly heritable relative to other yield components and to grain yield itself and that it is under the control of genes with predominantly additive effects (Sharma and Knott, 1964; Paroda and Joshi, 1970; Bhatt, 1972 and Edwards et al., 1976).

Many workers have found associations between components of yield and grain yield. McNeal (1960) correlated six plant characters with grain yield in F_2 and F_3 of a cross between two spring wheat varieties, Lemhi and Thatcher. He observed that only kernel number per plant was highly associated with grain yield in both generations. Obviously, number of kernels per plant should have a high positive association with plant yield since it includes all yield components except kernel weight. In a study to investigate the relationship between mature plant characters and the weight of seed from which the plants were grown, Austenson and Walton (1969) concluded that spike number per plant was the most important component of yield. A finding consistent with this was reported by Hsu and Walton (1971) who in their study of the relationships between yield components of wheat grown under field and greenhouse conditions found that the number of spikes per plant was the most important component in determining grain yield per plant. A different result to that of McNeal (1960) and Hsu and Walton (1971) was observed by Knott and Talukdar (1971). Knott and Talukdar (1971) transferred the high seed weight character from Selkirk to Thatcher spring wheat by backcrossing. Correlations involving yield and yield components using Thatcher and Thatcher backcross lines showed only the kernel weight component to be positively correlated with grain yield. In a study involving selection for yield and yield components for seven generations (F_2 to F_8) in a wheat cross, McNeal et al. (1978) observed that kernel weight and kernel number per spike were dependable indicators of yield potential. They also suggested that although single character selection can improve yield, long-range improvements probably result from concomitant improvement in all yield components. Hence, characters that affect yield component expression should be considered simultaneously. In a similar study Sinha and Sharma (1979) found all three yield components, i.e., kernel weight, number of grains per spike, and number of spikes per plant, to be positively and strongly correlated with grain yield in three Indian semi-dwarf wheat varieties. In durum wheat, Lebsock and Amaya (1969) and Gebeyehou et al. (1982) found the components, kernels per spike and kernel weight, to have significant positive correlation to grain yield.

Studies with other small grain crops have shown the presence of positive relationships between grain yield and yield components. In barley, positive correlations between grain yield and yield components have been observed (Rasmusson and Cannell, 1970; Dashora et al., 1977; Chaudhary, 1977 and Puri et al., 1982). Stoskopf and

Reinberg (1966) working with barley and oats in Ontario during the period 1956 to 1961, found that the number of grains per head was the most reliable component for predicting yield. Similar conclusions were arrived at by Lawes (1977) working with oats.

Despite the preponderance of evidence on the usefulness of the component approach to yield, yield components have not been used extensively as selection criteria by plant breeders for the improvement of yield. Explanations for the failure of plant breeders to more fully utilize components have been advanced by Frankel (1935) and Adams (1967). These reports indicate that components of yield are greatly influenced by the environment and that negative correlations among them are common. Since the morphological development of yield components follow a sequential pattern of development in the plants (Adams, 1967), they are differentially affected by variation in environment. A consequence of differing times of development of components and their variable responses to environmental change is their compensatory effect on yield (Adams, 1967; Grafius et al., 1976 and Bhatt, 1980). Because of compensatory effects and negative intercomponent correlations, selection for one of the components may fail to result in yield increases. Another explanation for the lack of interest in the component approach is that given by Frey (1971). Frey (1971) assigns three reasons for this lack of interest: (1) the relationship between yield and yield components is often not linear, (2) the environment affects the relationship between yield and yield components, and (3) collection of yield component data may be more expensive than collecting yield data.

In the cases where yield components have been used as selection criteria for grain yield they have been valuable to some extent. For example, Taylor (1928) selected for seed size in wheat for six years producing successive yield increases which were as high as 18.7 percent by the end of the period. Knott and Talukdar (1971) backcrossed high seed weight from Selkirk into Thatcher spring wheat and recovered Thatcher backcross lines with high seed weight that outyielded Thatcher. The highest yielding backcross line outyielded Thatcher by 13.3 percent over a two year period. Several other lines yielded 10 percent more than Thatcher over the same period. McNeal et al. (1978) selected for grain yield and individual yield components for seven generations (F_2 to F_8) in a spring wheat cross. Selected lines were all evaluated simultaneously in a performance trial to establish the value of yield component selection. Their results indicated that selection for yield components increased overall yield. Selection for kernel weight and kernels per spike at the F_8 generation gave 11 and 16 percent increases respectively, in grain yield over the midparent value whereas direct selection for yield at the F_8 generation resulted in yields that were significantly lower (-13 percent) than the midparent. They concluded, however, that although single character selection can improve yield, long range yield improvement requires consideration of all yield components. Derera and Bhatt (1972) mass selected for kernel size in three heterogeneous wheat populations and improved yield by an average of 33 percent per cycle over a two year period. In oats, Frey (1967) conducted mass selection for seed width in oat populations and after five cycles the resulting F_7 populations had heavier seed weight and approximately 9 percent greater yield. In another selection experiment, Frey and Huang (1969) increased the mean yield of heterogeneous oat populations by 9 percent by selection for intermediate seed weight.

2.2.2 Harvest Index

Harvest index was defined by Donald (1962) as the ratio of grain dry weight to the total above ground weight at maturity of the crop. As a ratio of the economic yield to the biological yield, harvest index is a measure of the plant's efficiency to mobilize photosynthate and transport it to organs having economic value. This has led many workers to suggest that selection for high harvest index may have value for improving grain yield of cereal crops (Donald, 1962, 1968; Sims, 1963; Syme, 1970, 1972; Singh and Stoskopf, 1971; Nass, 1973; Bhatt, 1976; Fischer and Kertez, 1976; Takeda et al., 1979 and Bhatt, 1980). Indeed, in many instances increasing harvest index has accounted for grain yield improvement. That is, improvement in grain yield of cereals frequently has been due to an increase in harvest index with little or no change in biological yield. Van Dobben (1962) compared old wheat cultivars evolved since the turn of the century with the leading wheats of the 1960's and found a progressive increase in harvest index from 34 to 40 percent. High yielding semi-dwarf wheat cultivars developed at Washington State University had an improved grain-to-straw ratio (harvest index) over taller cultivars of from 32 to 38 percent (Vogel et al., 1963). In a study similar to that of Van Dobben (1962), Mackey (1966) compared old land varieties and present-day varieties of wheat in Europe. He observed that the old land varieties were high tillering, but developed small spikes while the modern varieties bred in Northern France, Belgium, The Netherlands and Sweden had low tillering capacity but produced large kernels. This change was closely associated with a shift in harvest index from a low value in low yielding old land varieties to the high harvest index of superior yielding modern varieties. In a study of the relationship of harvest index with different factors influencing this criterion, Singh and Stoskopf (1971) reported correlations of 0.62, 0.66 and 0.50 between harvest index and grain yield for winter wheat, spring barley and oats, respectively. Nass (1973), in a study to determine characters for yield selection in spring wheat, observed a significant positive relationship between harvest index and grain yield. He concluded from this study that ears per plant, yield per ear and harvest index considered together in a selection program should be an effective means of selecting for increased yield. In oats, Simms (1963) claimed that the improvement in grain yields in Australian oat cultivars has been due almost entirely to an increased harvest index without an accompanying increase in straw yield or total dry matter production when compared to the old cultivars. All these studies, however, were conducted with named cultivars or advanced lines. Different associations might be obtained with segregating material.

The presence of considerable variation in harvest index and its positive correlation with grain yield is important in improving harvest index genetically and thereby indirectly increasing yield. Selection in early segregating generations is usually on an individual plant basis whereby the plants in the population are space-planted. The question is whether harvest index can be a reliable selection criterion, i.e., whether selection pressure applied on space-planted genotypes in the early segregatng generations for high harvest index can be reflected as improved yields of derived lines which are seeded at commercial densities. In other words, is the heritability of the harvest index trait high enough to enable its improvement in a breeding program and if so, what would be the optimum plant density to use in the segregating population? There are varying opinions as to the best plant density for early segregating generations. For example, Syme (1972), Fischer and Kertez (1976) and Donald and Hamblin (1976) are of the opinion that measurements on spaced plants could reliably predict a genotypic yielding ability when seeded at commercial densities. Syme (1972) measured 16 characters of greenhouse-grown plants of the 49 entries of the 5th International Spring Wheat Yield Nursery. He found a remarkably high correlation (r = 0.85) between single plant harvest index and mean grain yield across 63 sites widely distributed in the world, whereas grain weight per single plant showed no relationship to mean yield (r = 0.10). The study indicates that harvest index of spaced plants may be a useful predictor of crop yields in the field. Results obtained by Fischer and Kertez (1976) in Mexico showed the superiority of harvest index of spaced plants over their grain yield for prediction of crop performance with correlations of 0.56 and 0.33, respectively. In a study of the response of two wheat crosses to a two-way selection for harvest index, Bhatt (1977) discovered that the F_3 progenies of plants selected for low harvest index in the space-planted F_2 generation gave a low harvest index in the F_3, while F_3 progenies of plants selected for high harvest index in the F_2 generation segregated for a high and medium harvest index. Simple and partial correlations of plant weight and grain yield with harvest index gave a moderate to high positive correlation of grain yield with harvest index in the

F_3 generation. A different result was obtained by Okolo (1977). In his study of progeny of four wheat crosses, he found no significant correlation between the harvest index of selected F_2 spaced plants and their F_3 and F_4 bulk yields.

Few studies have been made in cereals on the inheritance of harvest index (Bhatt, 1976; Rosielle and Frey, 1977 and Bhatt, 1977). All of these studies have reported high heritability estimates of harvest index and also that harvest index seemed to be controlled primarily by additive gene action. This provides scope therefore for the improvement of harvest index via plant breeding and thereby the improvement of yield.

2.3 DIRECT SELECTION FOR YIELD IN WHEAT

2.3.1 Early Generation Selection for Yield

The primary objective in most breeding programs is to develop high yielding cultivars. Since the segregating F_2 generation contains individually distinct genotypes, it is the logical generation in which to begin looking for potentially high yielding progeny. Mckenzie and Lambert (1961), Shebeski (1967) and Sneep (1977) suggested that the identification of the high yielding genotypes should be started in the earliest possible segregating generation, preferably in the F_2 generation. Shebeski (1967) and Sneep (1977) supported their contention by demonstrating mathematically that without positive selection for yield during the early generations, the expected frequency of high yielding genotypes decreases at a rapid rate. They concluded that delayed selection for yield would result in an irretrievable loss of high yielding genotypes and would thereby seriously limit genetic advance. Several other workers have concluded that plants carrying favourable yield genes should be indentified in the earliest possible generation (Bhatt, 1980; Chebib et al., 1973; Fasoulas and Tsaftaris, 1975; McVetty and Evans, 1980; Ogilvie and Kaltsikes, 1977; Shebeski and Evans, 1973 and Valentine, 1979).

The added advantage of early generation selection for yield is that the breeder advances only a manageable number of promising lines for extensive yield testing and other evaluations when the lines have reached homozygosity. Yield testing and evaluation of new breeding lines is expensive and time consuming. It is thus economical to spend resources on promising lines instead of advancing a lot of poor lines which are later discarded if early generation selection is delayed. The disadvantage of early generation selection is that it is possible to misclassify and discard some good genotypes as a result of the difficulty of accurately assessing the yielding potential of an F_2 plant (Seitzer and Evans, 1978).

It appears imperative that selection for yield be started as early as possible. A requirement for a successful early generation selection for yield is that there should be a high correlation between the yield performance of genotypes selected in early generations and yield performance of their progenies in later generations. The most commonly followed method of handling the F_2 generation in wheat breeding has been space-planting the F_2 population and conducting visual selection on individual plants. Thus the plant breeder visually evaluates the F_2 plants and selects to advance only those plants that he believes have potential to give rise to high yielding progenies (Allard, 1960). However, although outstanding varieties have been produced by this method, visual selection of single plants for yield is commonly reported to be unreliable because visually assessed differences for yield among individual wheat plants have not usually been realized in subsequent generations (McGinnis and Shebeski, 1968; Shebeski, 1967; Knott, 1972; Depauw and Shebeski, 1973). Briggs and Shebeski (1970) found that visual selection for yield in wheat was superior to random sampling although the ability to visually identify the highest yielding lines was limited. They went on to suggest that when visual selection is used as a means of screening lines in a plant breeding program, the intensity of selection should be relatively low in order to reduce the possibility of inadvertently discarding otherwise valuable lines. In a selection experiment using triticale (X Triticosecale Wittmack), Salmon and Larter (1978) concluded that visual evaluation may be a useful method for identifying high yielding lines of triticale. Most plant breeders, however, are of the view that selection on a single plant basis in the F_2 generation is best restricted to selection for characters of high heritability such as plant height and disease resistance and not for a low heritability complex character such as yield (Hanson et al., 1979).

The alternative to visual selection is to measure the yield of individual plants and select accordingly. Unfortunately, this method has been shown to be also unreliable. Measured differences in yield between individual plants are rarely realized in subsequent generations (Bhatt, 1980; McGinnis and Shebeski, 1968; Knott, 1972). This lack of repeatability of F_2 performance in later generations can be attributed to the plant breeder's inability to accurately assess the true yielding potential of a single F_2 plant since the yield of a single plant in early generation is greatly influenced by both environmental variability and the non-fixable dominance and epistatic gene effects. Hence, environmental variation and heterozygosity greatly impair the breeder's ability to select superior genotypes (Grafius et al., 1961; Thakare and Qualset, 1978). Brim and Cockerham (1961) showed from a study with soybeans (Glycine max L. Merr.) that progress expected from selecting among progenies increased as inbreeding increased and the progenies approached homozygosity. Lupton and Whitehouse (1957) concluded that selection for characters such as yield and grain quality in autogamous crops should be delayed until a relatively high degree of homozygosity has been reached. Jinks and Pooni (1981) did a study to compare the results of selection in the early and late stages of an inbreeding program with tobacco (Nicotiana rustica). Their results showed that selection is more successful if it is delayed until later generations.

Space-planting is also said to be another contributing factor to ineffective early generation selection for yield. The argument is that space-plant conditions do not represent the planting density used in agricultural production and that selection at low plant density might not favour the desired genotypes that will eventually have to perform at commercial seeding rate (Wiebe et al., 1963; Khalifa and Qualset , 1975; Nass, 1978, 1980). Chebib et al. (1973) found that closer plant spacing reduced non-genetic variation caused by wide planting but magnified variability due to genotypic competition. However, they were able to double the efficiency of single plant selection by sowing uniformly sized seed at a competitive density. Nass (1978) compared the efficiency of early generation selection for grain yield in four spring wheat crosses grown at high and low population densities. He found that mean yields of F_4 lines selected at a high F_2 population density were greater for all crosses compared to lines selected in the F_2 at a low plant density. He recommended that F_2 selection should be done under a high population density.

Use of F_3 yield testing as an effective selection criterion, with its advantage of progeny row rather than individual plant performance, has attracted the attention of many workers (Shebeski, 1967; DePauw and Shebeski, 1973; Knott and Kumar, 1975). Although some of these workers have reported effective selection for yield in F_3 generation, F_3 yield testing has some limitations. These include the limited amount of seed produced from individual F_2 plants which in turn restricts the size of plots and the number of replications that can be sown. In order to increase the number of replications, Shebeski and Evans (1973) suggested a replicated hill-plot evaluation of F_3 progeny at several locations thereby enabling a more representative environment in which to conduct selection. However, increased population also requires more resources in the form of labour and land.

The effectiveness of F_3 yield test has been tested by a number of breeders with conflicting results. Using two barley crosses, Mackenzie and Lambert (1961) reported highly significant correlations of 0.1313 and 0.543 between yields of related F_3 and F_6 lines. In spring wheat Briggs and Shebeski (1971) reported extensive results of yield tests on F_3 progenies and of F_5 lines derived from them. They observed a high rank correlation of 0.83 in one year but no significant correlation in two additional years. DePauw and Shebeski (1973) obtained a highly significant correlation of 0.59 between the yields of F_3 wheat lines and the related

F_5 yields. Yields were expressed as a percent of the adjacent control. Knott and Kumar (1975) conducted F_3 yield tests with single row plots in three replications and concluded that F_3 yield testing was of doubtful value. O'Brien et al. (1978) studied response to selection for yield in the F_3 generation of four wheat crosses. The F_3 yield tests involved three replicates of three-row plots in which all three rows were harvested. They reported good correlations between yields of F_3 and yields of later generations in only two of four crosses and therefore, could not draw firm conclusions about the effectiveness of early generation selection for yield.

Many studies have been done to try and improve the efficiency of early generation selection for yield. Several methods have been proposed. These include: (i) selecting under stress-free environment; (ii) using control plots; (iii) using moving means; (iv) stratifying environments; and (v) using the honeycomb design as a selection method.

2.3.1.1 Selecting under stress-free environment. This involves growing the segregating population under optimum growing conditions so that the greatest differential genetic manifestation can be obtained and thereby aid the breeder in accurately selecting genetically superior plants. This method has been reported to improve the efficiency of early generation selection by improving the heritability of yield compared to that obtained when selection is conducted under stress (Gotoh and Osanai, 1959; Frey, 1964; Johnson and Frey, 1967). Krull et al. (1966, 1967) found with spring wheat that not only does selection in stress-free environment evolve high yielding lines but that lines produced under these conditions have a better adaptation.

2.3.1.2 Using control plots. Since soil fertility differences have an influence on crop yields, systematically arranged control plots (check varieties) are sometimes used to correct for soil heterogeneity in yield tests. Shebeski (1967) studied the possibility of correcting for effects of soil heterogeneity in early generation selection for yield by expressing the yield of each line as a percentage of an adjacent control plot. He found that this method effectively eliminated the influence of soil heterogeneity on selection resulting in a highly significant correlation ($r = 0.84$, $p < 0.001$) between the yield of F_2-derived F_3 lines and their respective F_5 means. Other workers have found control plots to be useful in this way (Briggs and Shebeski, 1971; McGinnis and Shebeski, 1968; Skorda, 1973). Baker and Mackenzie (1967), however, question the use of control plots as proposed by Shebeski (1967).

3.2.1.3 Using moving means. Where lines in a yield test are not replicated, a rolling plot mean, also called moving mean as proposed by Townley-Smith and Hurd (1973), can be used to minimize the effect of soil heterogeneity. Knott (1972) attempted to reduce environmental variability in the F_3 generation by expressing yield as a percent of adjacent checks, also as a percent of replicate means, and as a percent of moving mean. He concluded that expressing the yield of F_3 lines as a percent of moving mean increased the efficiency of early generation yield tests.

2.3.1.4 Stratifying environments. Field stratification has been used as another means of reducing soil variability found within large plots. One such method is the grid selection proposed by Gardner (1961). This method involves subdividing a large plot into small subplots which are used as selection units. Individual plant selection is done within subplots where it is assumed that soil heterogeneity is minimal compared to that of the whole nursery plot. Using this method, Gardner (1961) achieved an average yield improvement of 3.5 percent per year over a four-year period. Longuist et al. (1966) reported continued progress from mass selection using this technique.

3.2.1.5 Using honeycomb design. The honeycomb design proposed by Fasoulas (1973) is another form of field stratification. In this method, plants are space planted but are arranged in hexagonal patterns that resemble a honeycomb.

Each plant is surrounded by six equidistantly spaced plants. A given plant is selected if it outyields its six immediate neighbours. Thus spacing reduces interplant competition which otherwise might affect individual plant yield. By comparing the yield of a single plant with those of its neighbours in a small, therefore more homogeneous area of land, provides a better comparison of genetic differences between plants. Mitchell et al. (1982), however, concluded that the honeycomb method is not sufficiently superior to mass selection to warrant the extra effort required in its application.

3. MATERIALS AND METHODS

3.1 DESCRIPTION OF CONDUCT OF THE EXPERIMENT

3.1.1 The F_2 generation

The F_2 seed from two crosses, Glenlea x NB131 and Glenlea x Era was planted at the University of Manitoba Field Laboratory in June of 1980 to provide the F_2 plant population on which to conduct the initial cycle of selection in this experiment. The pedigrees of the parental cultivars involved in the crosses are given in Table 1.

TABLE 1. Country of origin and pedigree of cultivars used in the crosses.

Cultivar	Country of Origin	Pedigree
Glenlea	Canada	Pembina 2*/Bage//CB100(2)
NB131	Canada	Tobari 66/Gaines
Era	U.S.A.	11-55-10/4/Pembina/11-52-329/3/ 11-53-38/111-58-4/11-53-546(3)

These crosses were chosen because of the high yielding potential of the parents their good adaptability to western Canada, and also because seed from these crosses was readily available.

The F_2 population was space-planted by hand using corn hand planters in a honeycomb design as shown in Fig. 1. The interplant spacing used was 50 cm. Two seeds were planted in each hole and later thinned to one plant at the four to five leaf stage. Glenlea was used as a common check and was planted in such a way that every F_2 plant was contiguous to a Glenlea plant as shown in Fig. 1.

The F_2 plant population size, included a total of 3553 plants, with 1155 plants belonging to the cross Glenlea x NB131 and 2398 to the cross Glenlea x Era.

Every plant was tagged for identification while in the field, each was observed individually and notes taken where necessary. At harvest all plants were pulled by hand and placed intact into large jute sacks in preparation for drying. After drying, each plant was measured for plant height, the above-ground portion of the plant was weighed, and the number of tillers per plant was counted. Each plant was then threshed individually and the grain yield per plant recorded. Grain yield and other characters measured on each selected F_2 plant are given in Table 2.

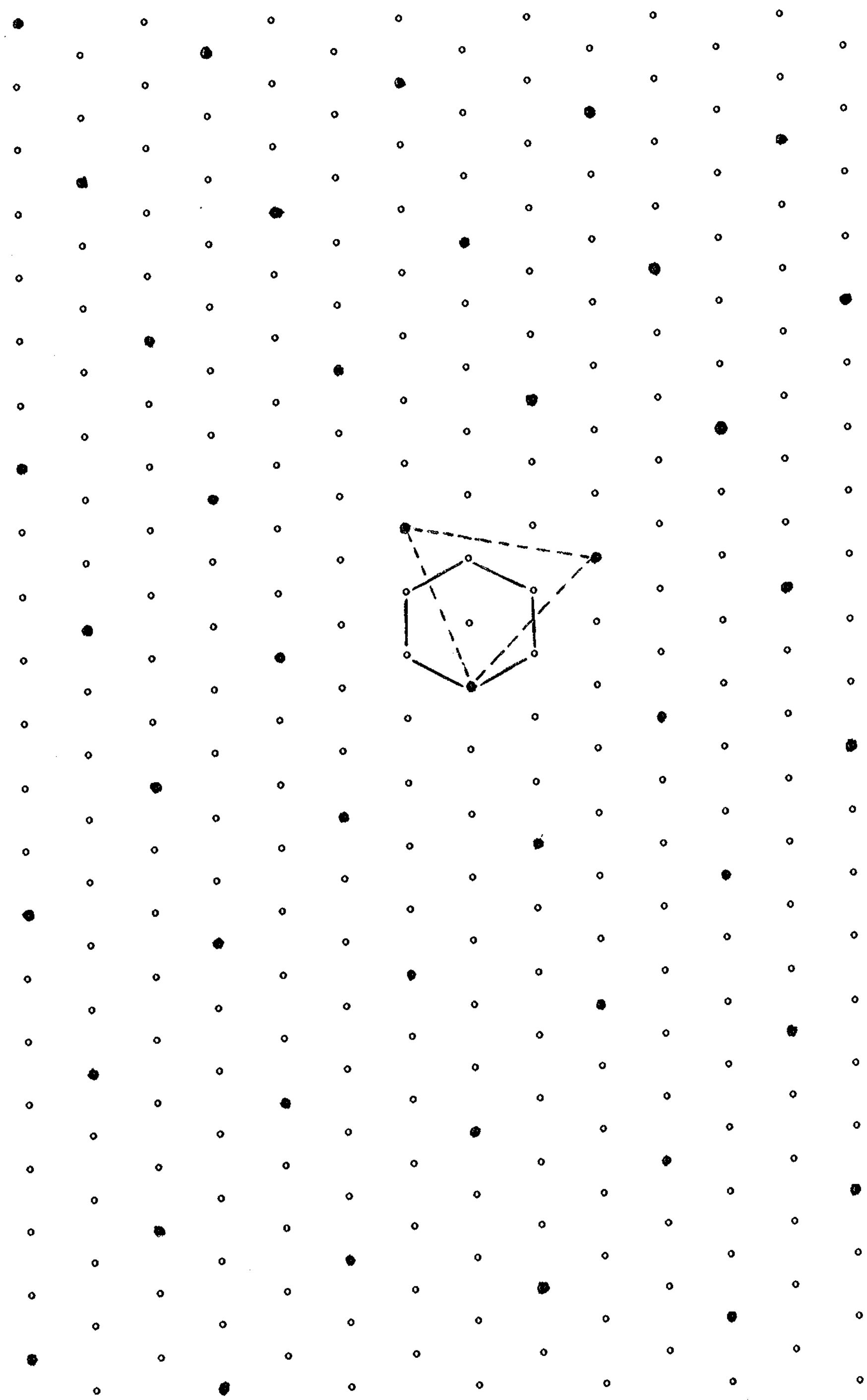

Fig 1. the field layout of the honeycomb design in the F2 generation.

Note: The solid circles are Glenlea plants while open circles are F2 plants.

TABLE 2. Characters measured on F_2 plants in the honeycomb design.

Characters	Unit of Measurement	Abbreviation
Plant height	cm	F2HT
Biological yield	g	F2BYLD
Grain yield	g	F2YLD
Grain yield of each plant as a percent of yield of a check plant	-	F2YPC
Grain yield of each selected plant adjusted by subtracting the mean grain yield of the surrounding six plants	g	F2YADJ
Grain yield of each selected plant expressed as a percent of the mean grain yield of three nearest check plants (see triangle in dotted lines on fig. 1)	-	F2YPTR
Harvest index	-	F2HI
Thousand kernel weight	g	F2TKW
Number of tillers	-	F2TILL
Grain yield per spike	g	F2YLD/S
Grain protein content at 14% moisture	-	F2PRO

Harvest index is the ratio of plant grain yield to total above-ground plant dry weight, or the biological yield. Thousand kernel weight is the weight of one thousand dry whole kernels of wheat. Weight of grain per spike was found by dividing the grain yield by the number of tillers.

Grain yields of F_2 plants, including the common check plants were entered into a computer and using a honeycomb selection program plants were selected to advance to F_3 generation. This program was developed in the University of Manitoba's Plant Science Department by Dr. J.L. Sernyk. It is designed to select both the highest and lowest yielding plants from the surrounding six plants in each hexagon. Single plant yield data are entered into the computer in the form of an array which corresponds to actual field layout in terms of location of each plant. Selection is done sequentially, i.e. it begins with plant yields in the first row, then second row, third row, etc., as central plants in a series of hexagons. Hence the yield of the first plant in the first row is considered first as the central plant in a hexagon and compared to the yields of its immediate surrounding neighbours. If it yields greater than the surrounding plants, it is selected. Then the second plant in the first row is considered as the central plant whose yield is then compared to the yield of the surrounding plants and it is selected only if it outyields the surrounding plants in a hexagon. The yields of the rest of the plants in the first row are similarly compared and either selected or not, depending on how they yield relative to the yields of their immediate surrounding neighbours. Once selection has been done for the first row, plants in the second row are then individually considered as central plants and their yields compared to those of their surrounding plants. Once each plant yield in the second row has been compared to those of six surrounding plants, then plants in the third row are selected, then those in the fourth row, etc., until yields of plants in all rows have been sequentially compared to those of their six surrounding immediate neighbours in a series of hexagons.

Selection of low yielding plants is done in the same way, the only difference being that the selection criterion is low yield. For a central plant to be selected it must yield lower than its surrounding plants.

A central plant has to be surrounded by at least four plants for it to be a candidate for selection. Thus, any plant that is surrounded by less than four plants is not processed and selection proceeds to the next plant in a row. Also, if the central plant is a check plant, it is simply ignored since we are not interested in selecting check plants. In addition to selecting high and low yielding plants, the program also calculates a percent ratio of the yield of the selected plant to the yield of a contigous check plant. A large number of lines was selected using this computer program. The actual number of F_2 plants progenies used for further studies, however, was reduced to 126 after eliminating many lines on the basis of other criteria such as disease reaction, maturity, lodging, and the relative yield of selected plants to the common check. Also, a number of plants were attacked by mice while in storage awaiting threshing and this was also taken into account when eliminating some computer selected lines. The selection intensity was 3.5%.

Of the 126 lines saved, 75 were selected for high yield and 51 for low yield potential. The aim for the bidirectional selection strategy was to determine if F_2 yield performances could be repeated in F_3 and F_4 generations. If this holds true, it would indicate that it is possible to select for yield on a single plant basis in the F_2 generation and expect the F_2 performance to be expressed in subsequent generations. In addition, an unselected composite was made for each cross by blending five grams of grain from each plant of a particular cross. The F_2 selections were assigned alpha-numeric codes as shown in Table 3.

3.1.2 The F_3 generation

The progenies of F_2 selections were planted at Winnipeg in the summer of 1981 in a honeycomb design at an

Table 3. Plant number, cross and the code assigned to selected F2 plants.

Plant[a] No.	Cross[b]	Code[c]	Plant[a] No.	Cross[b]	Code[c]	Plant[a] No.	Cross[b]	Code[c]	Plant[a] No.	Cross[b]	Code[c]	Plant[a] No.	Cross[b]	Code[c]	Plant[a] No.	Cross[b]	Code[c]	Plant[a] No.	Cross[b]	Code[c]
2-11	Glenlea x NB131	1A	15-15	Glenlea x NB131	1B	30-12	Glenlea x NB131	1C	57-14	Glenlea x Era	1D	90-29	Glenlea x Era	1E	22-46	Glenlea x NB131	1F	55-39	Glenlea x Era	1G
2-24	"	2A	15-23	"	2B	33-4	"	2C	59-18	"	2D	94-28	"	2E	25-38	"	2F	59-11	"	2G
2-38	"	3A	16-6	"	3B	33-30	"	3C	60-10	"	3D	95-12	"	3E	28-6	"	3F	95-21	"	3G
4-14	"	4A	16-24	"	4B	33-43	"	4C	64-28	"	4D	4-39	Glenlea x NB131	4E	30-10	"	4F	69-21	"	4G
5-12	"	5A	16-30	"	5B	33-46	"	5C	64-31	"	5D	5-18	"	5E	33-9	"	5F	73-10	"	5G
7-20	"	6A	16-33	"	6B	34-5	"	6C	70-14	"	6D	6-20	"	6E	33-29	"	6F	73-30	"	6G
-	-	7A	-	-	7B	-	-	7C	-	-	7D		-	7E	-	-	7F	-	-	7G
7-39	Glenlea x NB131	8A	18-22	Glenlea x NB131	8B	34-26	Glenlea x NB131	8C	71-7	Glenlea x Era	8D	6-15	Glenlea x NB131	8E	34-44	Glenlea x NB131	8F	76-10	Glenlea x Era	8G
8-5	"	9A	19-24	"	9B	34-31		9C	71-19	"	9D	7-7	"	9E	41-32	Glenlea x Era	9F	76-35	"	9G
8-8	"	10A	22-22	"	10B	34-47		10C	71-41	"	10D	8-25	"	10E	42-14	"	10F	77-40	"	10G
8-11	"	11A	22-35	"	11B	35-29		11C	71-48	"	11D	11-15	"	11E	95-30	"	11F	77-45	"	11G
11-28	"	12A	22-37	"	12B	36-1		12C	74-27	"	12D	12-26	"	12E	46-4	"	12F	79-45	"	12G
12-18	"	13A	23-13	"	13B	45-35	Glenlea x Era	13C	77-5	"	13D	12-47	"	13E	50-24	"	13F	81-12	"	13G
-	-	14A	-	-	14B	-	-	14C	-	-	13D	-	-	14E	-	-	14F	-	-	14G
12-30	Glenlea x NB131	15A	25-8	Glenlea x NB131	15B	48-6	Glenlea x Era	15C	77-19	Glenlea x Era	15D	13-21	Glenlea x NB131	15E	52-39	Glenlea x Era	15F	82-27	Glenlea x Era	15G
12-33	"	16A	27-9	"	16B	48-48	"	16C	78-24	"	16D	14-34	"	16E	53-36	"	16F	83-46	"	16G
12-44	"	17A	28-34	"	17B	49-26	"	17C	79-2	"	17D	18-39	"	17E	55-3	"	17F	86-48	"	17G
14-8	"	18A	29-19	"	18B	52-4	"	18C	80-31	"	18D	18-43	"	18E	55-12	"	18F	88-34	"	18G
14-24	"	19A	29-27	"	19B	53-28	"	19C	83-6	"	19D	21-45	"	19E	55-17	"	19F	89-23	"	19G
14-36	"	20A	29-42	"	20B	54-30	"	20C	86-13	"	20D	22-19	"	20E	55-37	"	20F	89-26	"	20G
-	-	21A	-	-	21B	-	-	21C	-	-	21D	-	-	21E	-	-	21F	-	-	21G

[a] The plant number is the number of the plant as labled in the field, the first digit is a row number and the second digit is a number of the plant in the row.

[b] The cross is the cross to which the F_2 plant belongs.

[c] The assigned code is important for setting up the field layout for the next cycle of selection involving the progeny of the F_2 plant selections. Note that the code 7 or multiples of seven 14, and 21 are the Glenlea check. Codes 1A to 3E are high yielding selections and 4E to 20G are low yield selections.

interplant spacing of 50 cm. Forty-seven F_3 plants from each selected plant were planted in a pattern that allowed the progenies of each F_2 plant to be distributed throughout the entire field as identified by their family code numbers. Glenlea was used as a common check. The field layout is shown in Fig. 2.

The two composites were also planted. Each of the two composites was sown in 12 row plots. The rows in each plot were 30 cm apart and 40 m long. Planting was done using a small tractor-drawn seed drill so that each row was solid seeded. At maturity a Hege combine harvester was used to harvest only a diagonal strip of each plot so as to sample all 12 rows of each composite.

When the honeycomb experiment reached maturity, measurements of plant height and tiller counts were done for each plant. Each plant was then harvested separately by clipping the spikes from each plant and placing them separately into paper bags. These were in turn stored in cloth bags. The spikes from each plant were threshed separately and then weighed.

Average of progeny data gave a measure of line performance.

The grain yield data were entered into a computer and a second bidirectional cycle of selection was done using the computer program as described previously. After computer selection, the author reduced the number of lines which were

21A		9A		18F		6F		15C		3C		12A	
	5A		14E		2F		11C		20C		8C		17A
1A		10A		19E		7E		16C		4C		13A	
	6A		15E		3E		12C		21C		9C		18A
2A		11E		20E		8E		17C		5C		14G	
	7A		16E		4E		13C		1C		10C		19G
3G		12E		21E		9E		18C		6C		15G	
	8G		17E		5E		14B		2C		11G		20G
4G		13E		1E		10E		19B		7C		16G	
	9G		18E		6E		15B		3B		12G		21G
5G		14D		2E		11B		20B		8B		17G	
	10G		19D		7E		16B		4B		13G		1G
6G		15D		3D		12B		21B		9B		18G	
	11D		20D		8D		17B		5B		14F		2G
7G		16D		4D		13B		1B		10B		19F	
	12D		21D		9D		18B		6B		15F		3F
8F		17D		5D		14A		2B		11F		20F	
	13D		1D		10D		19A		7B		16F		4F
9F		18D		6D		15A		3A		12F		21F	
	14C		2D		11A		20A		8A		17F		5F
10F		19C		7D		16A		4A		13F		1F	
	15C		3C		12A		21A		9A		18F		6F
11C		20C		8C		17A		5A		14E		2F	
	16C		4C		13A		1A		10A		19E		7F
12C		21C		9C		18A		6A		15E		3E	
	17C		5C		14G		2A		11E		20E		8E
13C		1C		10C		19G		7A		16E		4E	
	18C		6C		15G		3G		12E		21E		9E
14B		2C		11G		20G		8		17E		5E	
	19B		7C		16G		4G		13E		1E		10E
15B		3B		12G		21G		9G		18E		6E	
	20B		8B		17G		5G		14D		2E		11B
16B		4B		13G		1G		10G		19D		7E	
	21B		9B		18G		6G		15D		3D		12B
17		5B		14F		2G		11D		20D		8D	
	1B		10B		19F		7G		16D		4D		13B
18B		6B		15F		3F		12D		21D		9D	
	2B		11B		20F		8F		17D		5D		14A
19A		7B		16F		4F		13D		1D		10D	
	3A		12F		21F		9F		18D		6D		15A
20A		8A		17F		5F		14C		2D		11A	
	4A		13F		1F		10F		19C		7D		16A

Fig. 2 Field layout of the honeycomb design in the F3 generation.

Note: Letters with 7 or multiples of 7 represent Glenlea plants.

to be advanced to the F_4 yield test. The most critical criterion was grain yield. A plant had to yield more than 19 grams in order to provide enough seed for the F_4 yield test and for protein analysis. Grain yields were very depressed in 1981 compared to the yields of F_2 plants in the previous year. This meant that there were no selections from some lines, while others contributed more than one progeny to the F_4 yield test (see Appendix Table 4). With such depressed yields it was not possible to select for extremes in high and low yields as was the case in the F_2 generation. The small selection differential (i.e. F3YLD of high and low selections) in this generation could have affected response to selection in the F_3 generation. High yielding plants were obtained from F_3 lines that were originally selected for high yield in the F_2 generation and conversely, low yielding plants were selected from lines that were originally selected for low yield in the F_2. A total of 135 plants was selected.

The characters measured in the F_3 generation are given in Table 4.

3.1.3 F_4 generation

The F_4 yield test sown in the summer of 1982 included 135 lines from F_3 single plant selections, 8 entries from the two composites and the cultivar Glenlea. Because there was an abundance of seed available from each composite, it

TABLE 4. Characters measured in F_3 generation in the honeycomb design.

Character+	Unit of Measurement	Abbreviation
F_3 family grain yield obtained as the average of F_3 progeny of each F_2 line.	g	F3FYLD
F_3 family tiller number calculated as the average number of tillers for all F_3 progeny of each F_2 line.	-	F3FTILL
F_3 family height calculated as the average plant height of all F_3 progeny of each F_2 line.	cm	F3FHT
F_3 family grain yield per spike obtained from the average yield per spike of all F_3 progeny of each F_2 line.	g	F3FYLD/S
F_3 plant grain yield	g	F3YLD
Grain yield of each plant expressed as a percent of yield of a check plant	-	F3YPC
Grain yield of each selected plant adjusted by subtracting the mean grain yield of the surrounding six plants	g	F3YADJ
Grain yield of each selected plant expressed as a percent of the mean grain yield of three nearest check plants	-	F3YPTR
F_3 number of tillers	-	F3TILL
F_3 plant height	cm	F3HT
F_3 plant grain yield per spike	g	F3YLD/S
F_3 thousand kernel weight++	g	F3TKW
F_3 grain protein content at 14% moisture	-	F3PRO

+The characters F3YLD, F3TILL, F3HT, F3YLD/S, F3TKW, and F3PROT were measured on individual F_3 plant selections that were to constitute the entries in the F_4 yield test.

++Because of limitation on the amount of seed, only 100 kernels were counted and weighed. This weight was then multiplied by 10 to obtain the thousand kernel weight.

was decided to enter each composite in the yield test in quadruplicate in order to better sample the yielding ability of the two composites. Therefore, each composite was sampled four times and each of the samples was considered as an entry in the yield test. In all, 144 entries were included in a yield trial.

The experiment was replicated four times with 12 incomplete blocks and 12 entries per incomplete block, i.e. a 12 x 12 quadruple lattice design. Because of the limitation on the amount of seed from single plants, single row plots were used per entry per replication. The single row plots were 2.4 m (8 ft.) long and the seeding rate used was 150 seeds per row. Each row was bordered on both sides by a row of M1, a semi-dwarf Glenlea variety. The purpose of bordering each entry row with a common dwarf variety was to provide uniform competition for all entries.

Preharvest data collected included height and number of days from seedling emergence to heading for each entry.

At maturity each entry row was harvested, placed in cloth bags and was dried. When dry, each plot was then threshed separately and further characters measured which are shown in Table 5.

The climatic condition during the growing season in 1982 were excellent for wheat development. There was an early frost in September which fortunately did not affect the experiment.

TABLE 5. Characters measured in the F_4 yield trial.

Characters	Unit of Measurement	Abbreviation
Grain yield	g	F4YLD
Plant height	cm	F4HT
Days to heading |	days	F4DH
Grain protein content	-	F4PROT
Protein yield ||	g	F4PYLD
Test weight	kg/hl	F4TEW
Thousand kernel weight	g	F4TKW

| Days to heading were calculated from the day when more than 50% of the seedlings had emerged after planting to when more than 50% of the plants in each row had headed or produced spikes.

|| Protein yield was calculated by multiplying each grain yield by the grain protein content for each plot.

3.2 STATISTICAL ANALYSIS

3.2.1 Intra-generation correlations and regressions

Simple correlations and multiple regressions were done to investigate the relationships among F_2, F_3, and F_4 variables. Further information on the interrelationships among the characters studied was obtained by path coefficient analyses of the phenotypic correlation coefficients (Puri et al., 1982, Dewey and Lu, 1959, Li, 1956).

3.2.2 Inter-generation correlations and regressions

In order to investigate relationships among the characters across different generations, simple correlations were calulated between F_2 and F_3 characters, F_2 and F_4 characters and between F_3 and F_4 characters. Correlation coefficients between similar characters from different generations gave estimates of heritability in standard units for the characters concerned (Frey and Horner, 1957).

To investigate the functional relationships between F_4 mean grain yields and F_2 and F_3 characters, also the functional relationship between F_3 family grain yields and F_2 single plant characters, a stepwise multiple regression analysis was used. Stepwise multiple regression analyses were important in identifying which F_2 and F_3 characters were important in determining yields of F_4 entries. Grain yields of F_4 progenies were used as the dependent variable, while the F_2 and F_3 characters were considered as independent variables in each model. Stepwise multiple regression was also used to determine which F_2 characters were important in determining F_3 family grain yields.

The selection criterion used in the stepwise multiple regression was the maximum R^2 improvement variable selection technique (MAXR) developed by Goodnight (1982). This selection technique begins by finding the one variable model producing the highest R^2. After the one variable model has been found, then another variable, the one that would yield the greatest increase in R^2, is added. To get a three variable model, each of the variables in the model is compared to each variable not in the model. The MAXR program determines various variable switches and additions that would yield the largest increase in the R^2. This process of comparisons, switching and additions of variables is continued until all the variables in the model are included. This way variables that are important in explaining the variation observed in the dependent variable (F3FYLD and F4YLD) can be identified.

3.2.3 Analysis of variance

The F_4 yield test data was analysed as a 12 x 12 quadruple lattice design with four replications (Cochran and Cox, 1960), using a LATANAL computer program. Various comparisons of performance among entries (Steel and Torrie, 1980) were done to determine the response to selection.

4. RESULTS AND DISCUSSION

4.1 F2 GENERATION

Data collected on the F2 selections are presented in Appendix Table 1. Table 6 below presents means and ranges of the F2 measurements. The two selection groups (i.e. high and low yielding) were selected for extreme differences in grain yield. High yielding F_2 single plant selections on average produced more than four times the yield of low yieldings F_2 selections (see Table 6). Despite the great differences in the grain yields between high yielding and low yielding F_2 selections, there was very little difference between the two groups in kernel weight, grain yield per spike, harvest index, grain protein, and plant height. Overall, however, high yielding selections exhibited superiority in the characters measured over low yielding selections. An exception was in the case of grain protein whereby low yielding selections had a higher overall grain protein content than did their high yielding counterparts (Table 6). The expression of grain protein content by the two groups is in agreement with the commonly observed relationship between yield and protein content, i.e. that grain yield is inversely related to protein content (see Grant and McCalla, 1949; Malloch and Newton, 1934; Schlehuber and Tucker, 1959; Sunderman et al., 1965; Hsu and Sosulski, 1969; Baker et al., 1968).

TABLE 6. Means of characters measured on F2 single plant selections.

Variable	High Yielding Selections Mean	High Yielding Selections Range	Low Yielding Selections Mean	Low Yielding Selections Range
F2YLD	113.11±1.199	89.60-138.20	24.86±0.553	17.1-32.00
F2TKW	44.81±0.627	31.70-57.50	37.13±0.968	23.3-51.20
F2YPC	218.01±16.129	128.90-837.0	34.73±1.598	18.93-69.20
F2YADJ	45.66±1.482	20.50-79.16	-47.05±1.68	-21.90-73.80
F2YPTR	171.34±3.920	120.67-329.80	35.03±1.08	22.27-54.72
F2TILL	52.48±0.954	37-80	22.10±1.092	1 0-48
F2YLD/S	2.1932±0.037	1.16-2.83	1.26±0.063	0.43-2.46
F2BYLD	236.75±2.854	162.90-291.40	71.79±3.558	39.7-156.50
F2HI	47.91±0.448	39.70-64.20	37.18±1.274	17.7-50.20
F2PRO	13.61±0.086	12.08-15.61	14.91±0.222	12.47-19.06
F2HT	97.22±0.873	81.00-116.00	86.19±1.453	62.00-104.00

4.1.1 Simple Correlations and Path Analysis

An intra-generation simple correlation analysis was conducted among F2 characters in order to study correlations between these characters. Tables 7 and 8 present correlation coefficients between different characters. The correlation coefficients in Table 7 reveal that single plant grain yield was highly correlated with total plant productivity, or biological yield.

Table 7: Simple correlations between F2 single plant yields and other characters measured on the entire F_2 population.

Character	r
F2TKW	0.551**
F2TILL	0.882**
F2YLD/S	0.795**
F2BYLD	0.969**
F2HI	0.641**
F2PRO	-0.488**
F2HT	0.491**

**Indicates significance at the 0.01 level of probability.

These results indicate that the larger, more vigorous F_2 plants tended to produce the most grain yield as reflected in

TABLE 8. Inter-character correlations among characters measured in the F2 generation.

	F2TKW	F2YLD	F2TILL	F2YLD/S	F2BYLD	F2HI	F2PRO	F2HT
F2TKW		0.551**	0.273**	0.721**	0.489**	0.481**	-0.264**	0.307**
F2YLD			0.882**	0.795**	0.969**	0.641**	-0.488**	0.491**
F2TILL				0.440**	0.916**	0.368**	-0.329**	0.523**
F2YLD/S					0.703**	0.777**	-0.519**	0.298**
F2BYLD						0.454**	-0.435**	0.575**
F2HI							-0.437**	-0.002
F2PRO								-0.113
F2HT								

**Indicates significance at the 0.01 level of probability.

the positive significant correlation of grain yield and plant height. Grain yield was also positively highly correlated with the three yield components, 1000-grain weight, number of spikes per plant (as represented by the number of tillers), and grain yield per spike. Grain yield also exhibited a strong positive correlation with harvest index (0.64). The positive correlation between harvest index and grain yield in a given generation of plant material confirms the results of Chaudhary et al. (1977) in his studies with wheat. As expected, grain protein content was negatively correlated with grain yield (-0.49). All other inter-character correlations (see Table 8) were significant except for the correlations between protein content and plant height, and between harvest index and plant height which were nonsignificant. Protein content was negatively correlated with all other characters.

Correlations between grain yield and its components and between yield and other characters, measure mutual relationships without presumption of causation. Though this information is important, a breeder needs more information on how early generation yield expression is directly or indirectly correlated with other plant characters measured in any particular generation. This information is important in explaining the performance of the advanced lines (in this case the F4 lines). It is interesting to the breeder to determine how the yields of advanced lines seeded at commercial seeding rates are influenced by early generation characters. Knowledge of the way in which these early generation characters are related in a cause and effect manner, and how they influence advanced generation yield would aid the breeder in deciding which character(s) to use as his selection criteria.

Path coefficient analysis provides an effective means of untangling direct and indirect causes of associations between characters. It permits an initial examination of the specific forces acting to produce a given correlation and measures the relative importance of each character (Dewey and Lu, 1959 and Li, 1968, 1975). In the present study, a path coefficient analysis was conducted as described by Dewey and Lu (1959) and Li (1968, 1975) using F2 data to obtain further information on the inter-relationships among the various characters. Grain yield was considered the resultant variable and 1000-kernel weight, number of tillers, grain yield per spike, biological yield, harvest index, grain protein content and plant height the causal variables.

The diagram shown in Fig. 3 facilitates the understanding of the nature of the cause and effect system. The double arrows indicate mutual association as measured by correlation coefficients and single arrows represent direct influence as measured by path coefficients. Table 9 presents a summary of the direct and indirect path coefficients of various factors on grain yield.

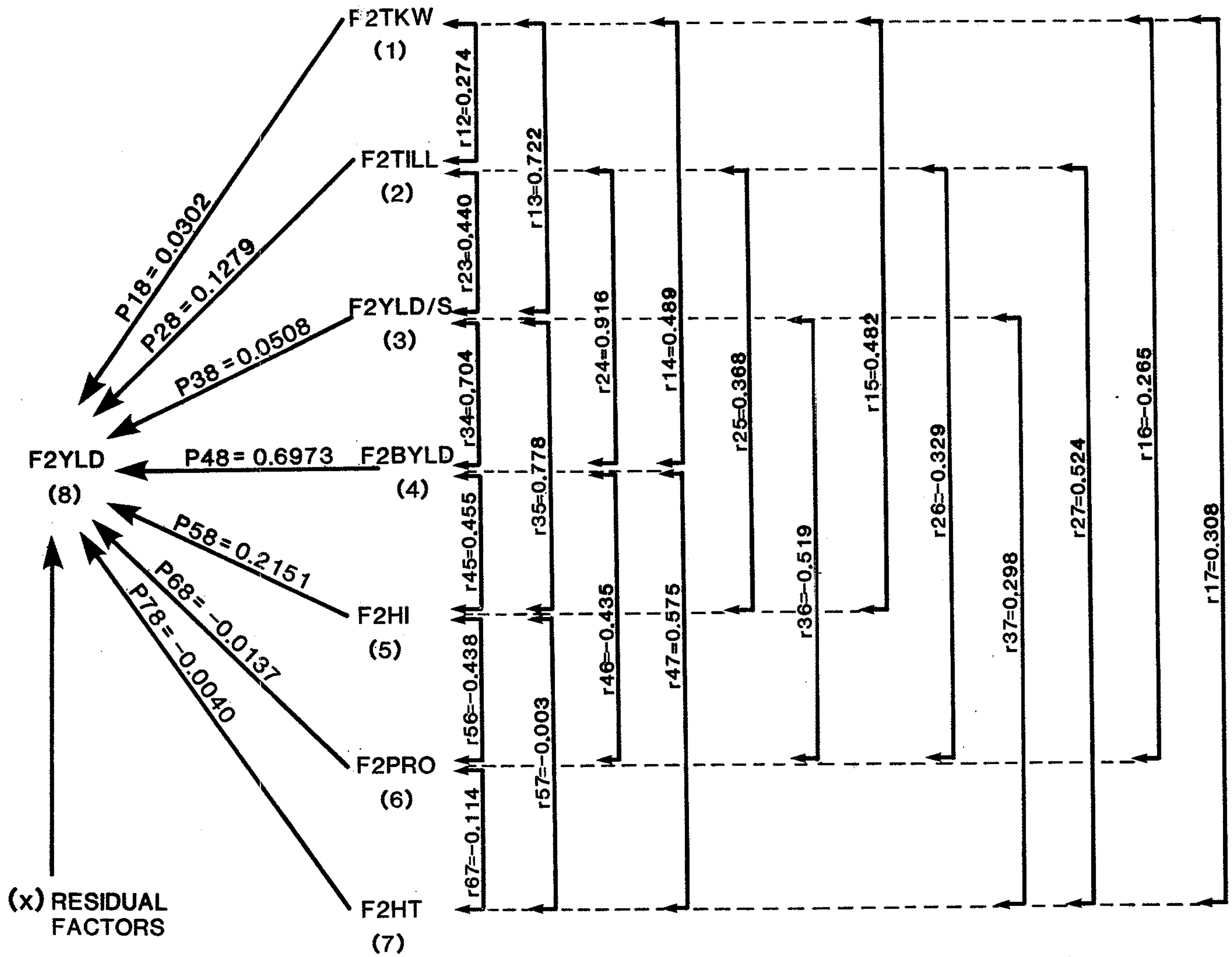

Fig. 3 PATH DIAGRAM AND COEFFICIENTS OF FACTORS INFLUENCING PLANT GRAIN YIELD IN THE F2 GENERATION.

TABLE 9. Path coefficient analysis for F2 single plant characters upon F2 single plant grain yields.

Type of effect	Coefficient
Thousand kernel weight (F2TKW)	
Direct, P18	0.030
Indirect via number of tillers (F2TILL), r12 P28	0.035
Indirect via grain yield per spike (F2YLD/S), r13 P38	0.036
Indirect via biological yield (F2BYLD), r14 P48	0.341
Indirect via harvest index (F2HI), r15 P58	0.103
Indirect via protein content (F2PRO), r16 P68	- 0.003
Indirect via plant height (F2HT), r17 P78	- 0.001
Number of tillers per plant (F2TILL)	
Direct, P28	0.127
Indirect via thousand kernel weight (F2TKW), r12 P18	0.008
Indirect via grain yield per spike (F2YLD/s), r23 P38	0.022
Indirect via biological yield (F2BYLD), r24 P48	0.639
Indirect via harvest index (F2HI), r25 P58	0.079
Indirect via protein content (F2PRO), r26 P68	- 0.004
Indirect via plant height (F2HT), r27 P78	- 0.002
Grain yield per spike (F2YLD/S)	
Direct, P38	0.050
Indirect via thousand kernel weight (F2TKW), r13 P18	0.021
Indirect via tiller number per plant (F2TILL), r23 P28	0.056
Indirect via biological yield (F2BYLD), r34 P48	0.490
Indirect via harvest index (F2HI), r35 P58	0.167
Indirect via grain protein content (F2PRO), r36 P68	0.007
Indirect via plant height (F2HT), r37 P78	- 0.001
Biological yield (F2BYLD)	
Direct, P48	0.697
Indirect via thousand kernel weight (F2TKW), r14 P18	0.014
Indirect via tiller number per plant (F2TILL), r24 P28	0.117
Indirect via grain yield per spike (F2YLD/S), r34 P38	0.035
Indirect via harvest index (F2HI), r45 P58	0.097
Indirect via grain protein content (F2PRO), r46 P68	0.006
Indirect via plant height (F2HT), r47 P78	- 0.002
Harvest index (F2HI)	
Direct, P58	0.215
Indirect via thousand kernel weight (F2TKW), r15 P18	0.014
Indirect via tiller number per plant (F2TILL), r25 P28	0.047
Indirect via grain yield per spike (F2YLD/S), r35 P38	0.039
Indirect via biological yield (F2BYLD), r45 P48	0.317
Indirect via grain protein content (F2PRO), r56 P68	0.006
Indirect via plant height (F2HT), r57 P78	0.0001
Grain protein content (F2PRO)	
Direct, P68	- 0.031
Indirect via thousand kernel weight (F2TKW), r16 P18	- 0.008
Indirect via tiller number per plant (F2TILL), r26 P28	- 0.042
Indirect via grain yield per spike (F2YLD/S), r36 P38	- 0.026
Indirect via biological yield (F2BYLD), r46 P48	- 0.303
Indirect via harvest index (F2HI), r56 P58	- 0.094
Indirect via plant height (F2HT), r67 P78	0.001
Plant height (F2HT)	
Direct, P78	- 0.004
Indirect via thousand kernel weight (F2TKW), r17 P18	0.009
Indirect via number of tillers (F2TILL), r27 P28	0.067
Indirect via grain yield per spike (F2YLD/S), r37 P38	0.015
Indirect via biological yield (F2BYLD), r47 P48	0.401
Indirect via harvest index (F2HI), r57 P58	- 0.001
Indirect via grain protein content (F2PRO), r67 P68	0.002
Residual (X)[a]	0.014

a The residual is calculated using the following formula:

$$Px8 = 1-[P18^2 + P28^2 + P38^2 + P48^2 + P58^2 + P68^2 + P78^2 + 2P18r12P28 + 2P18r13P38 + 2P18r14P48 + 2P18r15P58 + 2P18r16P68 + 2P18r17P78 + 2P28r23P38 + 2P28r24P48 + 2P28r25P58 + 2P28r26P68 + 2P28r27P78 + 2P38r34P48 + 2P38r35P58 + 2P38r36P68 + 2P38r37P78 + 2P48r45P58 + 2P48r46P68 + 2P48r47P78 + 2P58r56P68 + 2P58R57P78 + 2P68r67P78]$$

Path coefficient analysis showed that biological yield had the largest direct effect on seed yield (0.697). Harvest index and number of tillers per plant were second (0.215) and third (0.128), respectively, in magnitude of direct effect on grain yield compared to biological yield, followed by grain yield per spike with a direct path coefficient of 0.051.

All characters except protein content had large positive indirect effects on yield via biological yield. Grain protein on the other hand had a large negative indirect effect via biological yield. Other large indirect effects on yield were those of 1000-kernel weight and grain yield per spike via harvest index. The indirect effect of protein on yield via harvest index was also large but negative (-0.094).

One thousand kernel weight had a small direct positive effect on yield. Its indirect effect via number of tillers, grain yield per spike, plant height and protein were equally small. Numbers of tillers per plant had small indirect effect via all characters except biological yield. Similarly, grain yield per spike had small positive direct and positive and negative indirect effects on grain yield. Grain protein had a small negative direct effect on yield and small negative and positive indirect effects. Plant height on the other hand had the smallest overall direct and indirect effects on yield except for the large positive effect via biological yield.

It is important to note that in general, negative indirect effects on yield were mostly small in magnitude. These negative forces can, in combination, offset much of the influence on yield by direct forces.

On the basis of the path coefficient analysis, the variable relationship investigations in the F2 generation therefore, suggests that the biological yield, harvest index, number of tillers per plant, and yield per spike are the most important yield determinants for considerations in the selection process. Selection for these variables along with grain yield rather than yield per se could constitute the criteria for the improvement of grain yield in spring wheat. It is interesting to note that biological yield, harvest index, and tiller number are important factors that affect grain yield. What makes this combination important is that concomitant with the need for a high harvest index is the requirement that a plant develop adequate vegetative matter to support maximum grain yields. Also the negative influence of grain protein content indicates the impracticability of selecting for improved yield and high protein content simultaneously.

4.2 F3 GENERATION

F3 family data are presented in Appendix Table 2. The F3 yields were very much lower compared to F2 plant grain yields (Table 10). The reduced grain yields of F3 could be attributed to environmental effects as was evidenced from the equally depressed yields of single plants of Glenlea grown along with the F3 population. A possible further cause for depressed F3 grain yields could have been a reduction in heterosis in F3 compared to the F2 generation arising from selfing.

Although the high yielding selections yielded more than four times greater than the low yielding selections in the F2, this extreme yield difference was not repeated in the progeny of the F2 selections in the F3 generation. All high yielding selections, however, produced slightly higher yields than both the low yielding selections and the check cultivar Glenlea. High yielding selections from the crosses Glenlea X NB131 and Glenlea X Era yielded 12.1 and 13.8%, respectively, more than the low yielding selection from these crosses. High yielding selections from both crosses yielded only slightly higher than Glenlea (4.2% for Glenlea X NB131 and 6.7% for Glenlea X Era), while in both crosses, low yielding selections yielded below the check variety Glenlea by -7.0 and -6.2% for Glenlea X NB131 and Glenlea X Era, respectively.

In summary, the two selection groups yielded about the same in the F3 generation. However, it is important to note that these yields were from space-planted plants and were averaged to obtain the yields on a per plant basis. On this

TABLE 10. Mean grain yields of F3 plants from F2 single plant selections.

Cross	Yield Classification	Grain Yield++ (gm)		SE	Number of Plants Involved
Glenlea X NB131	High	13.63	±	0.265	1655
Glenlea X NB131	Low	12.16	±	0.563	764
Glenlea X Era	High	13.96	±	0.401	991
Glenlea X Era	Low	12.27	±	0.441	1028
Glenlea+	Check	13.08	±	0.240	791

+Glenlea is a spring wheat variety.
++Overall average grain yields per plant obtained from pooling single plant grain yields for all progeny of F2 single plant selections for each cross and yield classification.

basis, a 12.1% and 13.8% yield advantage of high yielding selections might appear to be of little statistical significance. However, if such a performance can be repeated in subsequent generations, these yield advantages could be quite substantial when translated into tons per hectare under commercial field conditions.

4.2.1 Simple Correlations

Simple correlations among F3 variables (Table 11) show average grain yield in F3 to be highly correlated to grain yield per spike and tiller number per plant. Grain yield was also significantly correlated to plant height. These correlations between F3FYLD and F3FTILL, F3FHT and F3YLD/S are consistent with those observed in the F2 generation. The number of tillers per plant was negatively correlated to grain yield per spike, indicating that those plants that tillered relatively well tended to have lower kernel weight per spike due to a compensating effect between the two yield components.

Table 11: Simple correlations among F3 family characters.

	F3FYLD	F3FTILL	F3FHT	F3FYLD/S
F3FYLD		0.431**	0.250**	0.712**
F3FTILL			-0,109	-0.273**
F3FHT				0.348**
F3FYLD/s				

**Indicates significance at the 0.01 level of probability.

An inter-generation simple correlation analysis was conducted to study the relationship between F3 family yields and F2 characters. The analysis revealed that F3 family grain yields were significantly correlated with all F2 characters (Table 12). The correlation between F3 family grain yield and the grain yield of their F2 parental plants was positive and significant. The magnitude of the correlation coefficient of F3FYLD-F2YLD revealed that there were some high yielding F2 selections that performed relatively poorly in the F3 generation, and conversely, some low yielding F2 selections yielded relatively well in the F3 generation. It is important to note also that the F3FYLD-F2YLD correlation coefficient is also a heritability estimate in standard units (Frey and Horner 1957). The correlation coefficients between F3FYLD and F2YPC, F2YADJ and F2YPTR were positive and larger than that between F3FYLD and F2YLD. These correlations indicate that the honeycomb field stratification technique in the F_2 generation was effective.

Table 12: Inter-generation simple correlation coefficients between F3 family yields and F2 plant characters.

Character	r
F2TKW	0.217*
F2YLD	0.315**
F2TILL	0.243**
F2YLD/S	0.275**
F2BYLD	0.283**
F2HI	0.260**
F2PRO	-0.181*
F2HT	0.244**
F2YPC	0.339**
F2YADJ	0.329**
F2YPTR	0.405**

*, **Indicates significance at the 0.05 and 0.01 levels of probability respectively.

F3 family grain yield was negatively correlated with protein content (-0.181), just as was the case in the intra-generation correlation in the F2. The complete array of calculated F2-F3 inter-generation correlation coefficients is presented in Table 13 in which heritability estimates as measured by such coefficients are underlined. The results show that plant height had the highest heritability (0.678) and hence would be the easiest of the four family characters measured to improve through selection. Grain yield per spike was second highest heritable character (0.478), plant grain yield third (0.315) and lastly number of tillers per plant (0.270). From these results, it appears that number of tillers per plant is greatly influenced by environmental variation and hence would be very difficult to improve through breeding.

TABLE 13. Inter-generation correlations between F3 family characters and F2 plant characters.

	F3FYLD	F3FTILL	F3FHT	F3FYLD/S
F2TKW	0.217*	-0.386**	0.307**	0.567**
F2YLD	0.315**	0.118	0.215*	0.354**
F2YPC	0.339**	0.318*	0.004	0.133
F2YADJ	0.329**	-0.029	-0.023	0.466**
F2YPTR	0.405**	0.181	0.236	0.386**
F2TILL	0.243**	0.270**	0.176*	0.131
F2YLD/S	0.275**	-0.098	0.191*	0.478**
F2BYLD	0.283**	0.140	0.265**	0.293**
F2HI	0.260**	0.059	-0.029	0.332**
F2PRO	-0.181*	-0.106	0.175*	-0.212*
F2HT	0.244**	0.008	0.678**	0.259**

*, **Indicates significance at the 0.05 and 0.01 levels of probability respectively.

Note underlined correlation coefficients are equivalent to heritabilities in standard units.

4.2.2 Stepwise Multiple Regression

A stepwise multiple regression analysis was conducted using F3 family yield as the dependent variable and F2 variables as independent variables. The multiple regression model employed was the following:

$$F3FYLD = b_0 + b_1F2TKW + b_2F2YLD + b_3F2TILL + b_4F2YLD/S + b_5F2BYLD + b_6F2HI + b_7F2PRO + b_8F2HT + b_9F2YPC + b_{10}F2YADJ + b_{11}F2YPTR$$

where b_0 is intercept and b_1 to b_{11} are partial regression coefficients.

The stepwise multiple regression showed that the coefficient of multiple determiniation (R^2) did not increase greatly with additions of all variables to the model (Table 14). R^2 ranged from 16.83% to 24.37%. With the addition of variables beyond F2YLD, the F2YLD partial regression coefficient became non-significantly different from zero. The results show that in this model, F2YLD is the most important variable since it accounted for 16.83% of the total variability observed in the F3 family grain yields, while the inclusion of the other ten variables increased the R^2 by only 7.54%. A combination of the variables F2YLD, F2BYLD and F2HI generated an R^2 of 21.11, thereby indicating the importance of the three variables in accounting for a portion of the total F3 family yield variability.

TABLE 14. Stepwise multiple regression of F3 family grain yields on F2 plant characters.

Intercept (b0)	b1	b2	b3	b4	b5	b6	b7	b8	b9	b10	b11	R^2%
11.45	0.020** F2YLD	-	-	-	-	-	-	-	-	-	-	16.83 **
11.92	0.047* F2YLD	-	-	-	-0.015 F2BYLD	-	-	-	-	-	-	19.16 **
17.07	0.129 F2YLD	-	-	-	-0.051 F2BYLD	-0.125 F2HI	-	-	-	-	-	21.11 **
15.65	0.123 F2YLD	0.035 F2TKW	-	-	-0.048 F2BYLD	-0.123 F2HI	-	-	-	-	-	22.05 **
13.07	0.111 F2YLD	0.031 F2TKW	-	-	-0.045 F2BYLD	0.099 F2HI	-	0.021 F2HT	-	-	-	22.60 *
14.51	0.104 F2YLD	0.030 F2TKW	-	-	-0.042 F2BYLD	-0.095 F2HI	-0.136 F2PRO	0.027 F2HT	-	-	-	23.21 *
14.68	0.100 F2YLD	0.034 F2TKW	-	-	-0.041 F2BYLD	-0.099 F2HI	-0.130 F2PRO	0.023 F2HT	0.001 F2YPC	-	-	23.52 *
13.91	0.096 F2YLD	0.030 F2TKW	-	-	-0.040 F2BYLD	-0.098 F2HI	-0.111 F2PRO	0.025 F2HT	0.001 F2YPC	0.014 F2YADJ	-	23.63
13.48	0.091 F2YLD	0.038 F2TKW	-	-0.269 F2YLD/S	-0.037 F2BYLD	-0.083 F2HI	-0.126 F2PRO	0.025 F2HT	0.001 F2YPC	0.015 F2YADJ	-	23.71
14.80	0.105 F2YLD	0.041 F2TKW	-0.072 F2TILL	-1.841 F2YLD/S	-0.025 F2BYLD	0.043 F2HI	-0.132 F2PRO	0.026 F2HT	0.001 F2YPC	-	-	24.32
14.24	0.103 F2YLD	0.039 F2TKW	-0.070 F2TILL	-1.793 F2YLD/S	-0.025 F2BYLD	-0.044 F2HI	-0.120 F2PRO	0.026 F2HT	0.001 F2YPC	0.009 F2YADJ	-	24.37
14.16	0.103 F2YLD	0.039 F2TKW	-0.070 F2TILL	-1.791 F2YLD/S	-0.024 F2BYLD	-0.043 F2HI	-0.120 F2PRO	0.027 F2HT	0.001 F2YPC	0.009 F2YDJ	-0.001 F2YPTR	24.37

*, **Indicates significance at the 0.05 and 0.01 levels of probability, respectively.

4.2.3 F3 Single Plant Selections

Single plant selection was done in the F3 generation to obtain F4 lines for a yield trial. Data collected from the F3 individual plant selections are presented in Appendix Table 3.

Results of simple correlation analyses among variables measured on F3 individual plant selections indicate positive correlations between individual plant yields (F3YLD) and all other characters measured on the F3 single plants (Table 15). F3YLD was positively and significantly correlated to the yield components F3TILL, F3YLD/S and F3TKW. As observed in the F2 generation, F3 grain yield was positively correlated with plant height, although the size of the correlation coefficient value was small (0.275). The correlation between F3YLD and F3PRO was positive but non-significantly different from zero, a departure from the significant negative correlation coefficient for these same two variables as observed in the F2 generation. Number of spikes per plant as represented by F3TILL was positively correlated with F3HT indicating that taller plants tended to have more tillers than shorter plants. Positive but non-significant correlations were obtained between spike number (F3TILL) and protein, between plant height and yield per spike and 1000-kernel weight. Similarly, yield per spike was positively associated with 1000-kernel weight. Tiller number however, exhibited a negative association with both yield per spike and 1000-kernel

TABLE 15. Simple correlations among characters measured on individual F3 plant selections.

	F3YLD	F3TILL	F3HT	F3YLD/S	F3TKW	F3PRO
F3YLD		0.425**	0.275**	0.469**	0.456**	0.024
F3TILL			0.230**	-0.564**	-0.247**	0.130
F3HT				0.008	0.035	0.204*
F3YLD/S					0.629**	-0.128
F3TKW						-0.188*
F3PRO						

*, **Indicates significance at the 0.05 and 0.01 levels of probability respectively.

weight. The negative correlations among the yield components (F3TILL, F3YLD/S and F3TKW) showed compensatory effects which would make indirect selection for yield using these yield components difficult to achieve (Adams, 1967; Grafius et al; 1976 and Bhatt, 1980).

A path coefficient analysis was carried out to investigate the direct and indirect effects of various factors on F3 individual plant grain yields.

The maximum direct effect toward grain yield was shown by number of tillers per plant (Fig 4; Table 16). Number of tillers per plant also contributed positively through plant height and grain protein content. Through grain yield per tiller and 1000-kernel weight, the character number of tillers per plant contributed negatively. Grain yield per spike had the second largest direct effect on grain yield. Indirectly, grain yield per spike had a strong positive effect toward grain yield via 1000-kernel weight and a small positive influence via plant height. However, its indirect influence on yield via number of tillers per plant was negative. Plant height, 1000-kernel weight and grain protein content had minor positive influences on grain yield. The magnitude of their indirect effects were also small. The results of this analysis indicated that the yield components, number of tillers per plant and grain yield per spike, are important factors influencing single plant grain yield, furthermore, that an early generation program for the

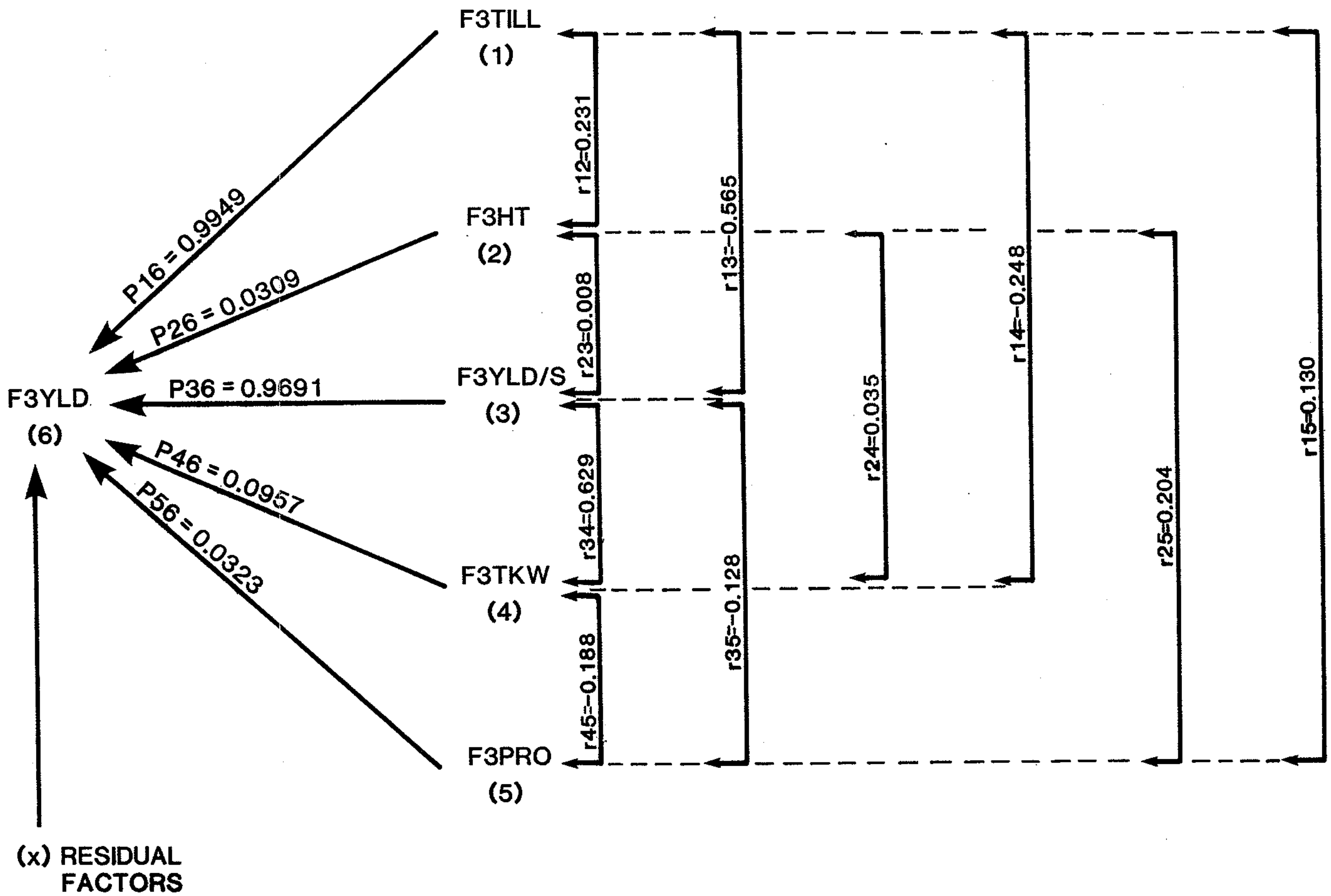

Fig. 4 PATH DIAGRAM AND COEFFICIENTS OF FACTORS INFLUENCING PLANT GRAIN YIELD IN THE F3 GENERATION.

TABLE 16. Path coefficient analysis for F3 individual plant variables upon F3 individual plant yields.

Type of effect	Coefficient
Number of tillers per plant (F3TILL)	
Direct, P16	0.994
Indirect via plant height (F3HT), r12 P26	0.007
Indirect via grain yield per spike (F3YLD/S), r13 P36	-0.547
Indirect via 1000 - kernel weight (F3TKW), r14 P46	-0.023
Indirect via grain protein content (F3PRO), r15 P56	0.004
Plant height (F3HT)	
Direct, P26	0.030
Indirect via number of tillers per plant (F3TILL), r12 P16	0.229
Indirect via grain yield per spike (F3YLD/S), r23 P36	0.008
Indirect via 1000 - kernel weight (F3TKW), r23 P46	0.003
Indirect via grain protein content (F3PRO), r25 P56	0.006
Grain yield per spike (F3YLD/S)	
Direct, P36	0.969
Indirect via number of tillers per plant (F3TILL), r13 P16	-0.561
Indirect via plant height (F3HT), r23 P26	0.000
Indirect via 1000 - kernel weight (F3TKW), r34 P46	0.060
Indirect via grain protein content (F3PRO), r35 P56	0.004
Thousand kernel weight (F3TKW)	
Direct, P46	0.095
Indirect via number of tillers per plant (F3TILL), r14 P16	-0.246
Indirect via plant height (F3HT), r24 P26	0.001
Indirect via grain yield per spike (F3YLD/S), r34 P36	0.610
Indirect via grain protein content (F3PRO), r45 P56	-0.006
Grain protein content (F3PRO)	
Direct, P56	0.032
Indirect via number of tillers per plant (F3TILL), r15 P16	0.129
Indirect via plant height (F3HT), r25 P26	0.006
Indirect via grain yield per spike (F3YLD/S), r35 P36	-0.124
Indirect via 1000 - kernel weight (F3TKW), r45 P46	-0.018
Residual (X)[b]	0.064

b The residual is calculated using the following formula:

$$Px6 = 1 - [P16^2 + P26^2 + P36^2 + P46^2 + P56^2 + 2P16r12P26 + 2P16r13P36 + 2P16r14P46 + 2P16r15P56 + 2P26r23P36 + 2P26r24P46 + 2P26r25P56 + 2P36r34P46 + 2P36r35P56 + 2P46r45P56]$$

improvement of yield should include the selection for yield components as well as for yield per se. However, the F2 and F3 path coefficient analyses indicated that differences in environmental effects also affect the association of various traits with grain yield. Only tiller number per plant consistently had a strong positive direct effect on yield in both the F2 and F3 generations. In contrast, grain yield per spike had a strong direct effect on grain yield only in the F3 generation.

4.3 F4 GENERATION

F4 lines selected from F2-derived F3 families were tested for their yielding ability. Not all F2-selected lines were advanced to the F4 yield test. Some lines were dropped at the F3 generation stage on account of their poor performance in that generation. Thus some F2-selected lines were represented more than once in the F4 yield test (see Appendix Table 4). For those F2-derived lines that were retained and included in an F4 yield test, only seed from single F3 plants selected from F2-derived F3 families was used. This procedure reduced plant heterogeneity within each line which would otherwise be high if bulk seed of each selected family was planted. Furthermore, using progeny of single F3 plants was in keeping with the practice followed in actual breeding (pedigree) program. As a result, most of the F4 lines in the yield test appeared uniform in the field with segregation being most noticeable within composite lines as expected.

The major objective of this study was to ascertain whether early generation single plant selection using the honeycomb method was a reliable index of the breeding potential of the selected plants. An F4 yield test was important to answer this question, the data from which are presented in Appendix Table 5.

4.3.1 Analysis of Variance

The F4 yield test was analysed as a 12 x 12 quadruple lattice design with four replications. The analyses of variance detected significant differences among genotypes in each of the six traits studied, namely, grain yield per plot, grain protein, protein yield per plot, test weight, 1000-kernel weight and plant height (Table 17).

In order to identify possible significant differences among the yield selection groups (i.e., high yielding selections, low yielding selections, composites, and the check variety Glenlea) various single degree contrasts were calculated (Table 18). These contrasts were non-orthogonal. Although it is recommended that in the planning of experiments orthogonality should be strived for, under certain

TABLE 17. Analysis of variance of F4 entry grain yields, grain protein content, protein yield, test weight, 1000-kernel weight and plant height.

Source of Variation	df	F4YLD(g/plot) MS	F4YLD(g/plot) F[a]	F4PRO(%) MS	F4PRO(%) F	F4PROYLD(g) MS	F4PROYLD(g) F	F4TEWT(kg/hl) MS	F4TEWT(kg/hl) F	F4TKWT(g) MS	F4TKWT(g) F	F4HT(cm) MS	F4HT(cm) F
Replications	3												
Entries	143	13155.752	5.662**	1.355	9.183**	222.207	5.618**	19.105	5.364**	67.962	10.681**	296.894	19.426**
Blocks (adjusted)	44	5084.882		0.726		102.157		8.384		14.893		28.039	
Intra-block error	385	2095.043		0.133		34.197		3.394		5.931		14.754	
Total	575	μ=0.0163329 C.V.=14.15% R.E.=108.12%		μ=0.0226651 C.V.=2.82% R.E.=134.23%		μ=0.0184790 C.V.=13.48% R.E.=112.69%		μ=0.0165331 C.V.=2.49% R.E.=108.46%		μ=0.0167155 C.V.=6.10% R.E.=108.78%		μ=0.0131613 C.V.=3.79% R.E.=104.17%	

[a]All F-ratios are adjusted F-ratios obtained by dividing the adjusted entry mean squares by the intra-block mean square.

**, Indicates significance at the 0.01 level of probability.

conditions an experiment is more effective with non-orthogonal contrasts (Johnson, 1963).

The average mean pooled grain yields of all high yielding selections were significantly different from those of all low yielding selections (Table 18). Similar comparisons of all high yielding selections against all composite lines, and of all low yielding selections against all the composite lines, gave statistically significant grain yield differences. However, there was no significant difference between either the high or low yielding selections and the check variety Glenlea.

Comparing the two crosses separately, it was shown that the high yielding selections clearly outyielded low yielding selections as well as the composites in each cross.

Table 19 gives overall mean grain yields for all the yield selection groups for both crosses combined. The overall mean grain yields show that the high yielding selections generally gave high yields. However, there was some overlapping among the high and low yielding selections (see Appendix Table 5) in terms of their F4 yields. Some low yielding F3 selections gave very high yields in the F4 (e.g. entry 76, which outyielded Glenlea by 33%). Conversely, some high yielding F3 selections yielded poorly in the F4.

The composite lines produced low yields and were outyielded by both the high and low yielding selection groups.

TABLE 18. Analysis of variance for F4 grain yields with various comparisons among high yielding selections, low yielding selections, composites, the check cultivar, Glenlea.

Source of Variation	df	ms	F
Replications	3		
Entries[c]	143	13155.752	
Contrasts			
All highs vs all lows	1	176487.89	18.240 **
All highs vs all composites	1	74768.638	35.688 **
All lows vs all composites	1	19984.063	9.538 **
All highs vs Glenlea	1	351.818	0.167
All lows vs Glenlea	1	2822.200	1.347
Glenlea X NB131 highs vs Glenlea X NB131 lows	1	61450.597	29.331 **
Glenlea X Nb131 highs vs Glenlea X NB131 composites	1	74394.324	35.509 **
Glenlea X NB131 lows vs Glenlea X NB131 composites	1	74825.520	11.849 **
Glenlea X NB131 highs vs Glenlea	1	3234.275	1.543
Glenlea X NB131 lows vs Glenlea	1	0.867	0.000
Glenlea X Era highs vs Glenlea X Era lows	1	39865.695	19.028 **
Glenlea X Era highs vs Glenlea X Era composites	1	22387.653	10.686 **
Glenlea X Era lows vs Glenlea X Era composites	1	2877.077	1.373
Glenlea X Era highs vs Glenlea	1	5204.235	2.484
Glenlea X Era lows vs Glenlea	1	9691.556	4.625 *
Glenlea X NB131 highs vs Glenlea X Era highs	1	183153.279	87.422 **
Glenlea X NB131 lows vs GLenlea X Era lows	1	156185.519	74.550 **
Blocks (adjusted)	44	5084.882	
Intra-block Error	385	2095.043	
Total	575		

[c]Adjusted treatment means were used in calculating these non-orthogonal contrasts.

*,** indicates significance at the 0.05 and 0.01 levels of probability respectively.

TABLE 19. Overall mean grain yields for high and low yielding F4 selections, composites and the check variety Glenlea.

Selection Group		No. of Entries	Mean SE	Range
High yield selections (H)		71	352.65±6.24	255.29-451.59
Low Yield Selections (L)		64	316.43±6.92	218.28-455.62
Composites (Co)		8	289.96±10.22	255.39-344.93
Glenlea (check var.)		1	343.21	
Response to selection I	(H - L)	36.22**		
Response to selection II	(H - Co)	62.69**		
	(L - Co)	26.47**		
Response to selection III	(H - Glenlea)	9.44		
	(L - Glenlea)	-26.78		

**, indicates significance at the 0.01 level of probability.

Note: The yield values involved in calculating the overall selection group means were adjusted means of the entries in the yield test. Each adjusted entry mean was the average yield over four replications adjusted for block effects.

The response to selection was measured using three methods. The first measure of response was calculated as the difference between the overall means of the high and low yielding selections (Response I). The second response (II) was calculated as the difference between both high and low yielding selections and the yields of the respective composite lines. The third response to selection (III) was the difference between high and low yielding selections and the check cultivar, Glenlea.

Responses I and II were both statistically significant (Table 18). High yielding selections outyielded low yielding selections and composites by 11.45% and 21.6%, respectively. Low yielding selections outyielded the composites by 9.1%. The overall yield performance of both the high and low yielding groups was not significantly different from that of Glenlea.

Examination of the results of the two crosses separately (Tables 20 and 21), shows that the high yielding selections from each significantly outyielded both the low yielding groups and composites. However, there were observable differences between crosses in terms of the yield potential. The cross, Glenlea X NB131, produced comparatively more high yielding lines than did the cross, Glenlea X Era. High yielding selections from Glenlea X NB131 yielded 8.4% more than Glenlea while those from the Glenlea X Era cross were on

TABLE 20. Overall mean grain yields of F4 entries from the Glenlea X NB131 cross.

Selection Group		No. of Entries	Mean SE (g)	Range
High yield selections (H)		45	371.96±7.33	249.10-451.59
Low Yield Selections (L)		30	342.74±10.37	222.71-455.62
Composites (Co)		4	300.80±18.79	255.39-344.93
Glenlea (check var.)		1	343.21	
Response to selection I	(H - L)	29.22**		
Response to selection II	(H - Co)	71.16**		
	(L - Co)	41.94**		
Response to selection III	(H - Glenlea)	28.75		
	(L - Glenlea)	-0.47		

**, indicates significance at the 0.01 level of probability.

Note: The yield values involved in calculating the overall selection group means were adjusted means of the entries in the yield test. Each adjusted entry mean was the average yield over four replications adjusted for block effects.

TABLE 21. Overall mean grain yields of F4 entries from the Glenlea X Era cross.

Selection Class		No. of Entries	Mean SE (g)	Range
High yield selections (H)		26	319.26±7.96	255.29-408.47
Low Yield Selections (L)		34	293.23±7.31	218.28-401.77
Composites (Co)		4	279.12±7.48	261.55-297.10
Glenlea (check var.)		1	343.21	
Response to selection I	(H - L)	26.03**		
Response to selection II	(H - Co)	40.14**		
	(L - Co)	14.11		
Response to selection III	(H - Glenlea)	-23.95		
	(L - Glenlea)	-49.98*		

*,**, indicates significance at the 0.01 level of probability.

Note: The yield values involved in calculating selection group means were adjusted means of the entries in the yield test. Each adjusted entry mean was the average yield over four replications adjusted for block effects.

the average 7.0% lower yielding than the check cultivar (response III).

Since, with only few exceptions, high and low yielding selection groups were non-significantly different from Glenlea in their overall F4 grain yield performance, one can view this response in light of practical plant breeding. Glenlea is a very high yielding spring wheat variety. Hence in practical plant breeding all those lines which yield equal to or greater than Glenlea would be retained for further advance in a breeding program, while low yielders would be suspended from further yield testing. Therefore, the total number of entries that yield equal to or greater than Glenlea compared to those that yield less than Glenlea provided another measure of selection response, designated as IV (Table 22).

Thus if response to selection IV were used as the basis for retaining lines in a breeding program, the honeycomb selection method would have resulted in 57.8% of the high yielding selections being retained. Among the low yielding selections, however, only 30.8% of the lines would have been retained. A similar trend is observed for each cross. This measure of selection response also revealed what had previously been observed on the basis of other selective response measures, i.e., that the cross Glenlea X NB131 contained a greater proportion of high yielding lines compared to the Glenlea X Era cross. Within the top yielding 20% of the F4

TABLE 22. Response to selection IV measured as the total number of F4 entries yielding less than Glenlea and those yielding equal to or greater than Glenlea.

Selection Group	Entries yielding < Glenlea: No. of Lines	Entries yielding < Glenlea: % of Group Total	Entries yielding ≥ Glenlea: No. of Lines	Entries yielding ≥ Glenlea: % of Group Total
All high yielding selections	30	42.25%	41	57.75%
All low yielding selections	45	69.23%	20	30.77%
Glenlea X NB131 high yielding selections	13	28.89%	32	71.11%
Glenlea X NB131 low yielding selections	14	46.67%	16	53.33%
Glenlea X Era high yielding selections	17	65.38%	9	34.62%
Glenlea X Era low yielding selections	30	88.24%	4	11.76%

lines from both crosses combined (ranging in yield from 114.02% to 132.75% of Glenlea), 19 of the total of 27 were selected from the Glenlea X NB131 cross.

In summary, using the honeycomb technique, divergent selection for both high and low grain yields in the F2 and F3 generations was effective as measured by the F3 mean yields (Table 10) and yield trials of the selected plants in the F4. As might be expected, there was some overlapping in the F4 yield performance of high and low F2 and F3 selections. Composite lines from both crosses produced the lowest yields contrary to expectations that they might yield intermediate between the high and low yielding selections. Probably four entries from each composite was not a large enough sampling of the yield potential of the two crosses.

These results are in agreement with the findings of Niehaus (1980) and Mitchell et al. (1982) who both applied the honeycomb selection method with durum wheat (*Triticum Turgidum* L. Var. *durum*).

4.3.2 Simple Correlations

A simple correlation analysis was conducted on F4 variables to determine the association between certain agronomic characters. The results indicated F4 yield to be negatively and significantly correlated with protein content (Table 23; Fig. 5). This negative correlation only re-enforces the difficulty of attempting to simultaneously improve grain

TABLE 23. Simple correlations among characters measured on F4 yield test entries.

	F4YLD	F4PRO	F4PROYLD	F4TEW	F4TKW	F4HT	F4DH
F4YLD		-0.308**	0.966**	0.483**	0.697**	0.296**	0.016
F4PRO			-0.064	0.214*	-0.020	0.385**	0.226**
F4PROYLD				0.559**	0.715**	0.413**	0.091
F4TEW					0.408**	0.409**	0.090
F4TKW						0.456**	-0.094
F4HT							0.295**
F4DH							

*, **, indicates significance at the 0.05 and 0.01 levels of probability respectively.

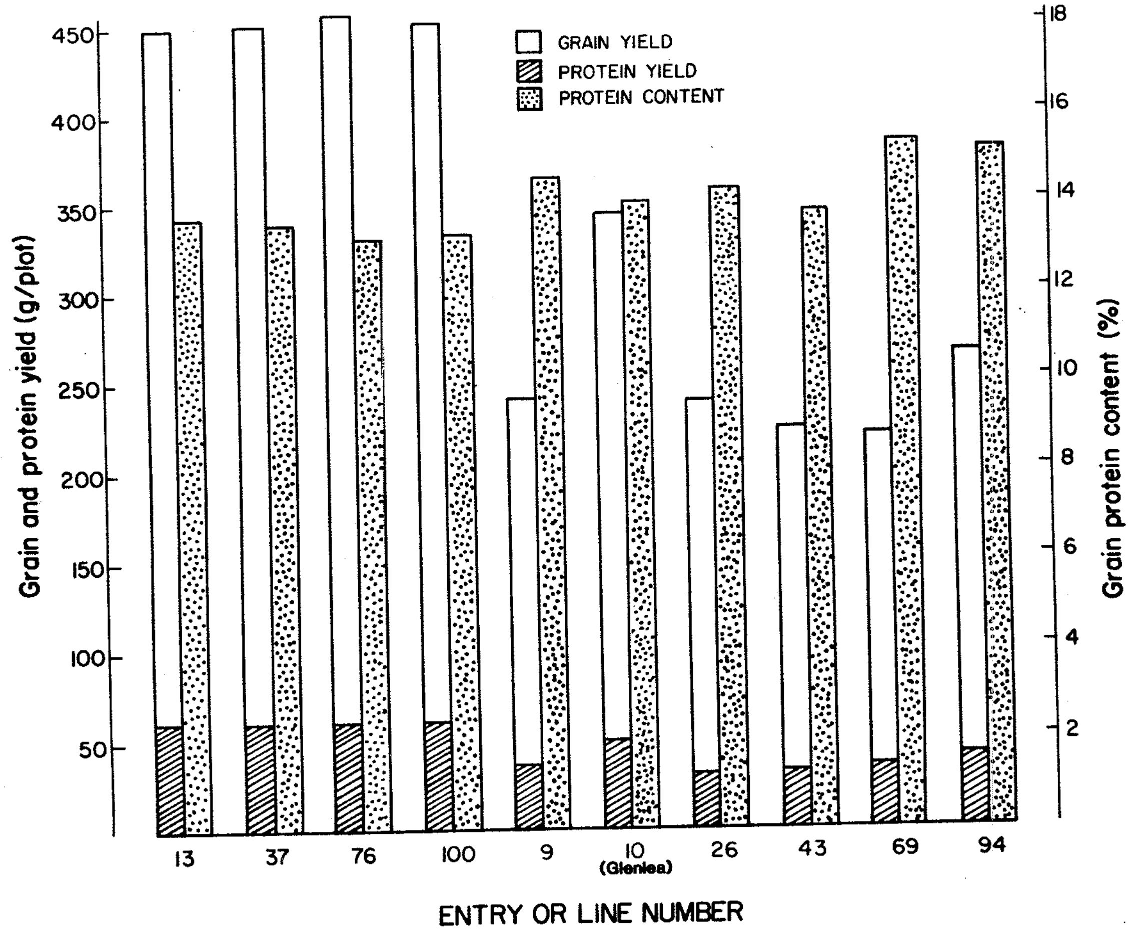

Fig. 5. Grain yield, protein yield, and protein content means of the highest yielding and lowest yielding F_4 lines plus Glenlea.

yield and protein content. The very strong correlation between grain yield and grain protein yield (r=0.97) is due to the fact that protein yield as a variable is calculated from grain yield, also because the range in grain protein content among entries was relatively narrow, i.e. from approximately 13% to slightly over 15% (see Appendix Table 5). F4 grain yield was also significantly correlated with test weight, 1000-kernel weight, and plant height. The significant correlation of grain yield with plant height is interesting in light of the popularity of commercial semi-dwarf varieties. This correlation indicates that tall, vigorous lines are high yielding, provided they also have lodging resistance. The number of days to harvest (F4DH), as a measure of earliness of maturity, was not significantly correlated with grain yield. This result is not surprising since entries did not differ greatly in their heading dates (Appendix Table 5). All entries in the yield test were early maturing which was reflected by the fact that none of the lines was damaged by the early fall frost which occurred on August 27, 1982.

Inter-generation correlations were calculated between characters measured on F4 lines and those of their parental F3 individual plant selections (Tables 24 and 25). The F4 mean grain yield was positively correlated with F3 individual plant grain yield, adjusted individual plant grain yield, F3 plant grain yield per spike, and F3 1000-kernel weight. The

TABLE 24. Inter-generation simple correlation coefficients between F4 line mean grain yields and characters measured on their parental F3 individual plant selections.

Characters	r
F3YLD	0.234**
F3YPC	0.154
F3YADJ	0.267**
F3YPTR	0.154
F3TILL	-0.240*
F3HT	0.110
F3YLD/S	0.456**
F3TKW	0.465**
F3PRO	-0.069

*, **, Indicates significance at the 0.05 and 0.01 levels of probability, respectively.

NOTE: underlined correlation coefficients are equivalent to heritabilities in standard units.

TABLE 25. Inter-generation correlations among characters measured on F4 entries and their parental F3 individual plant selections

	F3YLD	F3TILL	F3HT	F3YLD/S	F3TKW	F3PRO	F3YPC	F3YADJ	F3YPTR
F4YLD	0.234**	-0.240**	0.110	0.456**	0.465**	-0.069	0.154	0.267**	0.155
F4PRO	-0.040	0.104	0.368**	-0.174*	-0.108	0.230**	-0.047	-0.113	0.021
F4PROYLD	0.234**	-0.215*	0.213*	0.423**	0.450**	-0.002	0.151	0.252	0.172
F4TEW	0.230**	-0.014	0.370**	0.192*	0.224**	-0.024	0.060	0.179	0.034
F4TKW	0.202*	-0.316**	0.241**	0.457**	0.577**	0.070	0.766	0.053	0.206
F4HT	0.244**	0.024	0.705**	0.140	0.217*	0.157	0.191	0.232	0.412
F4DH	0.157*	0.264**	0.375**	-0.080	-0.152	0.202*	0.185	0.245*	-0.027

*, **, indicates significance at the 0.05 and 0.01 levels of probability, respectively.

NOTE: underlined correlation coefficients are equivalent to heritabilities in standard units.

correlation coefficient between F4 grain yield and F3 tiller number per plant was negative.

The following stepwise multiple regression model of F4 mean grain yields on F3 individual plant characters was used:

$$F4YLD = b_0 + b_1F3YLD + b_2F3TILL + b_3F3HT + b_4F3YLD/S + b_5F3TKW + b_6F3PRO + b_7F3YPC + b_8F3YADJ + b_9F3YPTR$$

The analysis revealed F3 yield per spike (F3YLD/S) to be the most important variable influencing F4 grain yield (Table 26). F3YLD/S alone reduced the residual error by 14.46%. Adding the remaining variables increased the R^2 by only 6.64%. A surprising observation was that the partial regression coefficient for F3 grain yield (F3YLD) was non-significantly different from zero.

Simple correlations were calculated between variables measured on F4 lines and those from their parental F3 families. Grain yield was positively correlated with F3 family mean grain yield (r=0.279), plant height (r=0.184), grain yield per spike (r=0.530) (Tables 27 and 28). F3 tiller number was negatively correlated with F4 yields (r=-0.229). All of the correlations between F4 yield and F3 family characters were significant. However, the correlation coefficient of F4 grain yield and F3FYLD/S was the largest in magnitude, indi-

TABLE 26. Stepwise multiple regression of F4 entry mean grain yields on characters measured on F3 individual plant selections.

Intercept (b0)	b1	b2	b3	b4	b5	b6	b7	b8	b9	R^2%
238.63	-	-	-	93.970** F3YLD/S	-	-	-	-	-	14.46 **
244.62	-	-	-	82.150** F3YLD/S	-	-	-	0.950 F3YADJ	-	17.36 **
214.64	-	-	-	80.330** F3YLD/S	-	-	-	0.902 F3YADJ	1.080 F3YPTR	18.47 **
180.16	-	-	-	65.720 F3YLD/S	1.58 F3TKW	-	-	0.838 F3YADJ	1.027 F3YPTR	19.29 **
122.91	-	-	0.671 F3HT	64.530 F3YLD/S	1.803 F3TKW	-	-	0.706 F3YADJ	0.968 F3YPTR	20.13 **
125.20	-1.147 F3YLD	-	0.798 F3HT	73.344* F3YLD/S	2.072 F3TKW	-	-	0.974 F3YADJ	1.004 F3YPTR	21.003**
150.89	-1.119 F3YLD	-	0.847 F3HT	72.514 F3YLD/S	2.02 F3TKW	-1.688 F3PRO	-	0.953 F3YADJ	0.949 F3YPTR	21.09 *
157.91	-0.957 F3YLD	-0.179 F3TILL	0.849 F3HT	67.711 F3YLD/S	2.007 F3TKW	-1.727 F3PRO	-	0.955 F3YADJ	0.938 F3YPTR	21.095
157.48	-0.967 F3YLD	-0.176 F3TILL	0.848 F3HT	67.707 F3YLD/S	2.005 F3TKW	-1.674 F3PRO	-0.002 F3YPC	0.981 F3YADJ	0.956 F3YPTR	21.097

*, **, indicates significance at the 0.05 and 0.01 levels of probability, respectively.

TABLE 27. Inter-generation simple correlation coefficients between F4 line mean grain yields and characters measured on their parental F3 families.

Characters	r
F3FYLD	0.279**
F3FTILL	-0.229**
F3FHT	0.184*
F3FYLD/S	0.530**

*, **, Indicates significance at the 0.05 and 0.01 levels of probability respectively.

NOTE: underlined correlation coefficients are equivalent to heritabilities in standard units.

TABLE 28. Inter-generation simple correlations among characters measured on F4 entries and characters from their parental F3 families.

	F3FYLD	F3FTILL	F3FHT	F3FYLD/S
F4YLD	0.279**	-0.229**	0.184*	0.530**
F4PRO	0.138	0.222**	0.251**	-0.100
F4PROYLD	0.322**	-0.187*	0.258**	0.527**
F4TKW	0.226**	-0.407**	0.314**	0.581**
F4HT	0.274**	-0.033	0.667**	0.226**

*, **, indicates significance at the 0.05 and 0.01 levels of probability, respectively.

NOTE: underlined correlation coefficients are equivalent to heritabilities in standard units.

cating the importance of this yield component in influencing the F4 grain yield.

A stepwise multiple regression analysis of F4 grain yield on F3 family variables was conducted using the following model:

$$F4YLD = b_0 + b_1F3FYLD + b_2F3FTILL + b_3F3FHT + b_4F3FYLD/S$$

The yield component F3FYLD/S was found to be the most important variable in this model (Table 29). It alone explains 28.12% of the variability observed in F4 mean grain yields. F3FLYD and F3FTILL were also important variables. Partial regression coefficients of F3FTILL were negative suggesting that this yield component variable had a depressing effect on F4 grain yields. Plant height (F3FHT) had the least influence on grain yield. Inclusion of this variable in the model increased the R^2 by only 0.251%

Another source of information on inter-generation relationship was a correlation and regression analysis between characters measured on F4 entries and characters of their parental F2 single plant selections. F4 grain yield was found to be significantly correlated with all the F2 variables except grain protein content (Table 30 and 31). The significant correlation between grain yields of F4 lines and their respective parental F2 single plant yields shows that single plant selections in the honeycomb design was effective in selecting divergently for both high and low yields. The

TABLE 29. Stepwise multiple regression of F4 entry mean grain yields on F3 family characters.

Intercept (b0)	b1	b2	b3	b4	R^2%
114.17	-	-	-	298.427** F3FYLD/S	28.138**
161.53	-	-1.954 F3FTILL	-	285.025** F3FYLD/S	28.744**
362.15	17.484** F3FYLD	-14.353** F3FTILL	-	-	31.277**
275.58	11.944 F3FYLD	-10.132** F3FTILL	-	113.730 F3FYLD/S	32.404**
237.05	11.428* F3FYLD	-9.858** F3FTILL	0.529 F3FHT	114.524 F3FYLD/S	32.655**

*, **, indicates significance at the 0.05 and 0.01 levels of probability, respectively.

TABLE 30. Inter-generation simple correlation coefficients between F4 entry mean grain yields and characters measured on their parental F2 plants.

Characters	r
F2YLD	0.334**
F2TKW	0.489**
F2YPC	0.187*
F2YADJ	0.537**
F2YPTR	0.280**
F2TILL	0.205*
F2YLD/S	0.346**
F2BYLD	0.295**
F2HI	0.242**
F2PRO	-0.163
F2HT	0.255**

*,** Indicates significance at the 0.05 and 0.01 levels of probability, respectively.

Note: underlined correlation coefficients are equivalent to heritabilities in standard units.

TABLE 31. Inter-generation simple correlations among characters measured on F4 entries and characters on their F2 parental plant selections.

	F2YLD	F2TKW	F2YPC	F2TILL	F2YLD/S	F2BYLD	F2HI	F2PRO	F2HT	F2YADJ	F2YPTR
F4YLD	0.334**	0.489**	0.187*	0.205*	0.346**	0.295**	0.242**	-0.163	0.255**	0.537**	0.280**
F4PRO	-0.108	-0.188*	-0.029	-0.040	-0.140	-0.026	-0.278**	0.117	0.069	-0.353**	-0.162
F4PROYLD	0.336**	0.471**	0.208*	0.234**	0.318**	0.302**	0.222**	-0.106	0.323**	0.487**	0.288**
F4TKW	0.172*	0.570**	0.044	0.020	0.265**	0.133	0.154	0.008	0.207*	0.371**	0.152
F4HT	0.220*	0.199*	0.185*	0.188*	0.184*	0.207*	0.144	0.110	0.517**	-0.002	0.224*

*,** Indicates significance at the 0.05 and 0.01 levels of probability, respectively.

Note: underlined correlation coefficients are equivalent to heritabilities in standard units.

correlations between F4YLD and F2 yield components F2TKW, F2TILL and F2YLD/S were significant with a high correlation coefficient being found between F4YD and F2TKW (r=0.49). Although both F2 and F3 honeycomb selection cycles were based primarily on single plant grain yields, the strong correlations as found to exist between F4YLD and both F2TKW and F3TKW (r=0.49 and 0.47 respectively), suggests that 1000-kernel weight would be an important indirect selection criterion for improving yield. Adujsted F2 grain yields, i.e., F2 grain yields expressed as a percent of the yields of contiguous check plants (F2YPC), F2 yields expressed as differences between F2 plant yields and mean yields of surrounding six plants (F2YADJ) and F2 plant yields expressed as a percent of the mean yield of the three nearest check plants (F2YPTR), were significantly correlated with F4 grain yields. The high correlation coefficient value between F4YLD and F2YADJ (r=0.537) suggested a possible value in the use of adjusted yields in predicting the yield performance of F4 lines. F2 biological yield, F2 harvest index and F2 height were also positive and significantly correlated with F4 grain yield. The significant correlation between F2HI and F4YLD is consistent with the findings of Niehaus (1980). In a honeycomb selection experiment using durum wheat (Triticum Turgidum L. var durum), Niehaus (1980) found a positive correlation between F2HI and F4YLD, thus indicating the potential use of HI as an indirect selection criterion for yield.

In addition to inter-generation correlation a stepwise multiple regression was conducted on grain yield of F4 lines to find the relative influence of different characters measured in F2. The following model was used:

$$\begin{aligned} F4YLD = {} & b_0 + b_1 F2YLD + b_2 F2TKW + b_3 F2YPC \\ & + b_4 F2TILL + b_5 F2YLD/S + b_6 F2BYLD \\ & + b_7 F2HI + b_8 F2PRO + b_9 F2HT \\ & + b_{10} F2YADJ + b_{11} F2YPTR \end{aligned}$$

The results of this analysis indicated that the variables F2YLD, F2TKW, F2TILL F2YLD/S and F2YADJ in most instances, had a significant influence in determining F4YLD (Table 32). However, F2TILL and F2YLD/S had negative influence on grain yields as observed from their partial regression coefficients in the model. This could have been caused by compensating influences among the yield components or simply the effect of multicollinearity on the regression coefficients as a result of the presence of correlations among the independent (F2) variables (Table 8).

The foregoing analyses have shown that in all of the intergeneration correlations involving grain yield, i.e. F3FYLD-F2YLD, F4YLD-F3YLD, F4YLD-F3FYLD and F4YLD-F2YLD, correlation coefficients were positive and highly significant. Although the correlation coefficients were not large (r=0.24 to 0.34) the statistical significance of these correlation coefficients, which are also estimates of heritability provides a good indication of the value of the honeycomb selection method in using the yields of single F2 and F3 plants as an index of the yielding potential of their progenies.

TABLE 32. Stepwise multiple regression of mean F4 entry grain yields on F2 characters.

Intercept (b0)	b1	b2	b3	b4	b5	b6	b7	b8	b9	b10	b11	R^2%
138.64	-	-	-	-	-	-	-	-	-	4.679 ** F2YADJ	-	28.83 **
136.97	-	-	-	-0.517 F2TILL	-	-	-	-	-	5.175 ** F2YADJ	-	30.57 **
2.52	-	-	-	-0.973 * F2TILL	-	-	-	-	1.591 * F2HT	5.316 ** F2YADJ	-	34.76 **
-0.70	-	0.924 F2TKW	-	-0.959 * F2TILL	-	-	-	-	1.500 F2HT	4.667 ** F2YADJ	-	35.42 **
-17.29	-	1.566 F2TKW	-	-0.746 F2TILL	- 15.320 F2YLD/S	-	-	-	1.490 F2HT	4.909 ** F2YADJ	-	36.28 **
169.57	2.727 * F2YLD	-	-	-5.676 * F2TILL	- 99.314 * F2YLD/S	-	-	-	1.601 * F2HT	5.001 ** F2YADJ	-	39.89 **
150.53	2.62 * F2YLD	1.320 F2TKW	-	-5.363 * F2TILL	-104.177 * F2YLD/S	-	-	-	1.501 F2HT	4.477 ** F2YADJ	-	40.87 **
174.30	2.385 F2YLD	1.264 F2TKW	-	-5.440 * F2TILL	-109.835 * F2YLD/S	-	-	-	1.333 F2HT	4.405 ** F2YADJ	0.379 F2YPTR	41.68 **
136.42	2.448 F2YLD	1.342 F2TKW	-	-5.543 * F2TILL	-110.619 * F2YLD/S	-	-	2.521 F2PRO	1.322 F2HT	4.393 ** F2YADJ	0.392 F2YPTR	41.96 **
160.04	2.509 F2YLD	1.326 F2TKW	-	-5.635 * F2TILL	-106.042 * F2YLD/S	-	-0.601 F2HI	2.978 F2PRO	1.165 F2HT	4.406 ** F2YADJ	0.411 F2YPTR	42.18 **
163.45	2.542 F2YLD	1.428 F2TKW	0.043 F2YPC	-5.693 * F2TILL	-105.057 * F2YLD/S	-	-0.922 F2HI	3.541 F2PRO	1.079 F2HT	4.491 ** F2YADJ	0.341 F2YPTR	42.47 **
188.19	2.940 F2YLD	1.349 F2TKW	0.039 F2YPC	-5.44 * F2TILL	- 96.373 F2YLD/S	-0.253 F2BYLD	-1.672 F2HI	3.701 F2PRO	1.042 F2HT	4.456 ** F2YADJ	0.346 F2YPTR	42.56 **

*,** Indicates significance at the 0.05 and 0.01 levels of probability, respectively.

In the stepwise multiple regression analyses, grain yield as a variable was always one of the most valuable in determining both the F3 mean family grain yields and F4 line mean yields. Other variables that were identified from stepwise multiple regession analyses as having an important influence were the yield components, 1000-kernel weight, grain yield per spike and number of tillers per plant. However, the variables number of tillers per plant and yield per spike were inconsistent in their effects on yield as demonstrated by changes in sign and magnitude of their partial regression coefficient values.

5. GENERAL DISCUSSION AND CONCLUSION

The study was conducted to assess the value of the honeycomb design as a selection method for improving the yield of wheat. The honeycomb method was proposed as a solution to the commonly observed ineffectiveness of yield predictions on the basis of single plant selections by reducing the problem of soil heterogeneity and inter-plant competition (Fasoulas, 1973). To attempt to evaluate the method, a dual selection strategy was followed. Single plant selections were made within the F2 and F3 progenies from two crosses of wheat. High yielding and low yielding plants were selected according to the honeycomb selection method (Fasoulas, 1973). In addition, the yields of selected plants were compared to the yields of plants of the commercial wheat cultivar Glenlea grown contigously within the honeycomb design. The objective was to carry out divergent selection for yield, i.e. for plants that yielded greater than Glenlea, also for those that yielded lower than the commercial check variety. All selections were evaluated in an F4 progeny yield trial in which comparisons were made between yields of progeny from F2 high and low-yielding selections, also between these progenies and those from unselected composited F2 plants. The cultivar Glenlea was used as a commercial standard in the test.

The results of this experiment demonstrated that it is possible to select for high yield on the basis of single F2 plant grain yields using the honeycomb selection method.

Although, no statistical test was done to determine differences in yields between high and low yielding selections in the F3, the overall mean grain yields of F3 families (Table 10) indicated that plants from high yielding F2 selections generally exceeded the progenies of low yielding F2 selections in yield. The magnitude of these differences for the two crosses, Glenlea X NB131 and Glenlea X Era, was 12.1 and 13.8%, respectively. Furthermore, a yield differential of 4.2 and 6.7% respectively, was found to exist between these same high yielding selections and the check cultivar, Glenlea.

Analysis of variance for yield and other characters measured in the F4 yield trial revealed the presence of significant genotypic differences among the entries for the characters analysed. With the results of the analysis of variance indicating genotypic differences among the entries, various single degree contrasts were analysed in order to determine whether there were significant differences among lines in different yield categories. Results (Table 18, 19, 20 and 21) showed that in both crosses, high yielding selections significantly outyielded low yielding ones, also the unselected composites. Considering each group of selections within progenies of both crosses, collectively, high yielding selections outyielded low yielding selections by 11.5% and composites by 21.6%. Low yielding selections exceeded composites by 9.1%. The yields of each selection class were not significantly different from the yields of Glenlea.

Analysing progenies from the two crosses separately, the same results were observed. Comparisons of the high yielding selections with low yielding selections, composites and the check cultivar revealed that significant differences existed. F4 families from the Glenlea X NB131 high yielding selections outyielded low yielding selections by 8.5% and composites by 23.7%. Low yielding selections had a 13.9% yield advantage over composites. Again there was no significant difference between the yields of the high and low yielding selections and the Glenlea check. High yielding selections from the cross Glenlea X Era significantly outyielded the low yielding selections by 8.9% and the composites by 14.4%. On the other hand, low yielding selections exceeded the yields of composites by 5.1%. There was no significant difference between the average yield of high yielding selections and Glenlea in this cross. However, low yielding selections yielded significantly lower than Glenlea by 14.5%.

Comparing the number of F4 families that yielded equal to or greater than Glenlea with the number that yielded less, it was revealed that a pattern emerged similar to that obtained when the high yielding and low yielding selection classes from each cross were compared (Table 22). Thus if only entries yielding equal to or greater than Glenlea were retained for further evaluation in a breeding program, 57% of all high yielding selections would be retained compared to only 30.8% of the low yielding selections. Considering the two crosses separately, 71% of the high yielding selections from the Glenlea X NB131 cross would be retained as compared to 53% of the low yielding selections. For the Glenlea X Era cross, 34.6% of the high yielding selections would be retained compared to 11.8% of their low yielding counterparts. These results also show that there was some overlapping in the yield performance of progenies from both the high and low yielding groups of selections.

Another objective of the experiment was to investigate the relationships between yield and other yield related attributes themselves both within and across generations. In order to determine the various phenotypic relationships, intra-generation simple correlations, path coefficient analyses, inter-generation simple correlations and stepwise multiple regression analyses were conducted.

In the F2 generation the important feature of intra-generation correlations between yield and other plant characters was that the majority of yield components had a strong positive association with yield. The F2YLD was positively correlated with F2TKW, F2TILL, F2YLD/S, F2BYLD, F2HI and F2HT. It was however, negatively correlated with grain protein (Table 7). A path coefficient analysis of F2 grain yield upon other F2 characters revealed that F2TILL, F2BYLD, F2HI and to a lesser extent F2YLD/S were important characters affecting grain yield (F2YLD) and hence worthy of further consideration as indirect yield selection criteria.

F3 grain yield was significantly correlated with all other characters measured in the F3 except with protein content (Tables 11 and 15). On the basis of a path coefficient analysis conducted in the F3, F3TILL and F3TYLD/S and F3TKW were shown to have the greatest direct influence on F3 single plant grain yields. The two path coefficient analyses (F2 and F3) revealed that the character, grain yield per spike, did not have as much direct influence on single plant grain yields in the F2 as in the F3 generation. This could be a reflection of environmental influences on character associations. Number of tillers per plant however, maintained its strong positive direct influence on yield in both generations. A stepwise multiple regression analysis of F3FYLD on F2 characters conducted to find the relative importance of F2 characters towards F3 yields, indicated F2YLD, F2BYLD and F2HI as the most important characters influencing plant yields in the F3.

From the combined results of F3 family yields, from inter-generation correlations and from the stepwise multiple regression analysis, it was possible to conclude that the first cycle of the honeycomb selection had in general been effective in selecting high and low yielding genotypes.

In the F4 yield trial results, grain yield was correlated with F4PROYLD, F4TEW, F4TKW and F4HT. It was however negatively correlated with grain protein (Table 23). All inter-generation correlation coefficients between F4 mean bulk grain yields and single plant yields measured in the F3 and F2 generations were positive and highly significant (Tables 24, 27 and 30). Stepwise multiple regression analyses of F4 yields on F3 and F2 plant characters showed that single plant yield was among the most valuable characters influencing F4YLD. Other F3 and F2 characters which were important in explaining the variation in F4 yields were F3YLD/S, F3TKW, F3FYLD/S, F3TILL, F2TKW, F2YLD/S, F2TILL, F2YADJ, F3YADJ and F2HT. Thus, these results show that in addition to single plant yields, the yield components yield per spike, 1000-kernel weight and number of tillers per plant were the most important characters determining F4 bulk yields. Although the character number of tillers per plant was shown to consistently have a strong positive direct influence on plant yields in the two path analyses, it appeared to have erratic influences on F4 yield as observed from changes in sign of its partial regression coefficients in stepwise regressions. The importance of F2YADJ and F3YADJ indicates that this way of expressing single plant yield in a segregating generation planted in a honeycomb pattern could be of value in selection. The F3FYLD-F2YADJ, F4YLD-F3YADJ and F4YLD-F2YADJ intergeneration correlations were all positive and highly significant. These correlation coefficients were also consistently larger than the F3FYLD-F2YLD, F4YLD-F3YLD and F4YLD-F2YLD correlation coefficients. These results indicate that the honeycomb field stratification technique was effective.

The results of multiple regression analyses and path coefficient analyses partially agreed. These results indicated that path coefficient analyses in segregating generations could be useful in identifying phenotypic characters that strongly influence advanced generation yields. However, the observed changes in relative importance of some characters to yield suggests that utilizing both the path coefficient analyses and stepwise multiple regression analyses is the better approach. Thus on the basis of the two methods (i.e. path coefficient and stepwise multiple regression analyses), characters that consistently influence yield can be identified and included with yield per se as a selection criterion.

These results were similar to the findings of Mitchell et al. (1982) who applied the honeycomb selection program with durum wheat. Niehaus (1980) also obtained a significant response to selection for yield with durum wheat in a honecomb selection design. He, however, selected only for high yield in the F2 and in addition maintained an unselected composite line. He obtained a 4.3% yield advantage of selected lines over the composite line in the one cross he used. Compared to the findings of Niehaus (1980), more positive results were obtained in the present study. The reason for this could be due to the fact that his F4 yield trials suffered heavy bacterial leaf damage shortly after heading.

On the basis of this study, it is clear that early generation selection for single plant yield can result in significant response. However, more studies comparing the honeycomb method with other established selection methods need to be carried out. Only if the honeycomb design proves to be sufficiently superior to other methods is it going to be considered as a viable selection method. The reason for this is the fact that the method requires more work in sowing segregating populations, more effort and care in harvesting and analysing data, and also it requires more note taking since each plant has to be observed individually.

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APPENDIX

Appendix Table 1. Data obtained from the honeycomb selected F2 single plants.

F2 selection Code	F2 plant No.	Cross	F2YLD	F2TKW	F2YPC(%)	F2TILL	F2YLD/S	F2BYLD	F2HI(%)	F2PRO(%)	F2HT	F2YADJ	F2YPTR
1A	2-11	GlenleaxNB131	113.6	46.2	237.2	45	2.52	226.6	50.0	13.17	88.0	32.84	207.68
2A	2-24	"	113.5	52.0	151.3	46	2.46	267.0	42.0	13.96	111.0	38.60	189.80
3A	2-38	"	118.9	47.9	152.2	50	2.38	240.1	49.0	12.47	95.0	52.94	164.23
4A	4-14	"	102.6	43.0	213.8	49	2.14	223.8	46.0	12.54	103.0	35.70	136.07
5A	5-12	"	106.9	50.0	174.4	42	2.54	237.3	45.0	14.51	101.0	39.70	204.00
6A	7-20	"	121.1	44.8	128.9	52	2.33	235.6	51.0	13.02	81.0	44.23	173.99
8A	7-39	"	110.5	51.6	228.3	47	2.35	228.0	48.0	13.49	96.0	75.4	166.77
9A	8-5	"	105.0	41.5	153.3	54	1.94	256.2	41.0	13.33	100.0	45.85	153.44
10A	8-8	"	103.6	44.1	234.4	47	2.20	220.8	47.0	12.39	90.0	30.42	159.07
11A	8-11	"	111.7	50.9	157.8	46	2.43	230.9	48.0	14.12	97.0	42.46	168.30
12A	11-28	"	113.1	47.4	215.8	44	2.57	229.9	49.0	13.10	104.0	41.17	213.68
13A	12-18	"	118.2	48.3	144.1	42	2.81	214.3	55.0	12.63	96.0	26.27	233.74
15A	12-30	"	123.1	53.5	214.3	55	2.24	291.4	42.0	14.90	109.2	47.77	190.85
16A	12-33	"	134.0	44.5	163.4	57	2.35	291.1	46.0	13.25	94.0	53.48	172.84
17A	2-44	"	116.1	47.0	671.1	45	2.58	228.0	50.9	13.10	92.0	67.85	202.37
18A	14-8	"	112.2	48.7	207.4	57	2.38	237.7	47.2	12.16	104.0	67.48	154.48
19A	14-29	"	100.5	45.3	182.7	37	2.71	201.8	49.8	13.25	105.0	36.25	174.69
20A	14-36	"	131.4	42.0	179.0	54	2.43	249.2	52.7	13.10	86.0	79.16	191.18
1B	15-15	"	111.8	57.5	159.0	44	2.54	228.2	48.9	13.80	104.0	36.12	149.52
2B	15-23	"	130.0	47.7	218.0	53	2.45	262.3	49.5	13.49	100.0	63.50	180.05
3B	16-6	"	132.5	49.7	175.0	51	2.59	254.6	52.0	13.25	99.0	40.24	224.84
4B	16-24	"	110.3	47.2	185.0	47	2.35	229.6	48.0	13.10	100.0	28.78	165.78
5B	16-30	"	101.8	50.1	203.0	43	2.37	220.0	46.2	13.65	104.0	34.32	156.69
6B	16-32	"	138.2	49.4	275.0	56	2.46	289.7	47.7	12.86	91.0	64.92	214.03
8B	18-22	"	123.1	49.1	311.0	51	2.41	212.8	57.8	13.33	100.0	53.30	177.12
9B	19-24	"	117.6	49.4	297.0	46	2.55	228.8	51.3	12.08	94.0	40.46	207.66
10B	22-22	"	107.3	48.0	236.8	46	2.33	201.2	53.3	13.88	94.0	49.75	152.78
11B	22-35	"	102.1	48.0	190.0	44	2.32	209.6	48.7	12.16	90.0	31.36	147.97

Appendix Table 1. Continued

F2 selection Code	F2 plant No.	Cross	F2YLD	F2TKW	F2YPC(%)	F2TILL	F2YLD/S	F2BYLD	F2HI(%)	F2PRO(%)	F2HT	F2YADJ	F2YPTR
12B	22-37	GlenleaxNB131	108.7	43.7	175.0	51	2.13	215.2	50.5	12.39	90.0	28.02	139.66
13B	23-13	"	127.3	52.2	183.0	53	2.40	242.5	52.4	13.65	94.0	52.22	218.24
15B	25-8	"	114.1	53.0	171.6	50	2.28	242.6	47.0	14.12	104.0	50.50	160.70
16B	27.9	"	119.2	51.2	119.2	44	2.70	243.3	48.9	13.96	97.0	53.18	158.15
17B	28-34	"	108.6	43.4	159.0	51	2.13	221.5	49.0	12.47	85.0	37.00	121.16
18B	29-19	"	103.4	43.0	323.0	50	2.07	218.8	47.2	13.17	100.0	53.36	174.66
19B	29-27	"	121.3	47.4	174.0	47	2.58	238.8	50.7	13.41	90.0	37.17	134.92
20B	29-42	"	124.3	50.9	203.0	44	2.83	228.8	54.3	13.10	90.0	61.38	189.28
1C	30-12	"	120.4	52.5	177.0	54	2.23	260.5	46.2	15.06	99.0	28.78	179.25
2C	33-4	"	130.0	43.5	234.0	54	2.41	269.6	48.2	13.57	97.0	68.12	257.78
3C	33-30	"	123.8	46.9	132.0	50	2.48	256.0	48.3	12.86	90.0	43.80	152.14
4C	33-43	"	109.6	52.4	154.8	45	2.43	220.1	49.7	13.72	98.0	30.95	140.69
5C	33-46	"	106.0	57.1	163.6	51	2.08	209.2	50.6	14.35	89.0	35.72	166.40
6C	34-5	"	103.5	43.2	186.5	55	1.88	216.8	47.7	13.33	90.0	20.50	126.99
8C	34-26	"	125.8	41.4	144.0	60	2.09	263.0	47.8	13.33	100.0	26.37	151.80
9C	34-31	"	130.7	51.4	837.0	56	2.33	272.2	48.0	13.72	100.0	56.28	329.80
10C	34-47	"	106.6	47.7	164.0	41	2.60	221.4	48.1	13.33	85.0	32.75	145.23
11C	35-29	"	108.4	41.7	203.0	58	1.87	235.0	46.1	13.33	83.0	37.36	151.54
12C	36-1	"	112.3	46.0	188.7	46	2.44	226.4	49.6	14.12	100.0	29.64	163.23
13C	43-35	GlenleaxEra	114.7	42.1	214.0	62	1.85	246.9	46.4	13.96	96.0	55.86	176.19
15C	48-6	"	103.0	49.4	154.8	48	2.14	218.4	47.1	15.14	102.0	41.55	139.37
16C	48-48	"	89.6	37.8	178.5	52	1.72	194.0	46.1	14.82	92.0	38.98	135.69
17C	49-26	"	106.2	38.1	244.0	65	1.63	267.4	39.7	14.35	103.0	45.03	147.77
18C	52-4	"	92.5	35.3	186.0	56	1.65	217.8	42.4	13.33	100.0	30.37	164.68
19C	53-28	"	127.4	38.5	159.0	80	1.59	277.9	45.8	14.27	107.0	63.60	147.97
20C	54-30	"	106.0	49.3	154.0	50	2.12	228.0	46.4	15.14	100.0	47.46	128.84
1D	57-14	"	114.4	40.0	309.0	71	1.61	247.0	46.3	13.33	98.0	53.76	159.11
2D	59-18	"	113.1	32.5	132.0	74	1.52	264.8	42.7	13.41	91.0	56.10	145.06

Appendix Table 1. Continued

F2 selection Code	F2 plant No.	Cross	F2YLD	F2TKW	F2YPC(%)	F2TILL	F2YLD/S	F2BYLD	F2HI(%)	F2PRO(%)	F2HT	F2YADJ	F2YPTR
3D	60-10	GlenleaxEra	111.4	42.9	153.0	53	2.10	228.2	48.8	14.19	95.0	53.90	175.07
4D	64-28	"	109.3	38.5	197.0	66	1.66	269.5	40.5	14.19	118.0	38.32	140.25
5D	64-31	"	101.4	38.2	173.6	58	1.75	212.5	47.7	13.88	93.0	29.7	120.67
6D	70-14	"	118.0	38.8	157.9	62	1.90	253.4	46.5	13.41	104.0	52.23	164.50
8D	71-7	"	101.2	41.7	331.0	50	2.02	206.5	49.0	13.96	97.0	52.76	180.39
9D	71-19	"	104.8	39.6	161.0	47	2.23	196.9	53.2	12.86	92.0	33.32	167.06
10D	71-41	"	101.6	38.7	222.0	54	1.88	238.7	42.5	14.90	110.0	42.55	180.37
11D	71-48	"	111.7	44.0	193.0	51	2.19	246.5	45.3	14.12	100.0	55.23	195.96
12D	74-27	"	119.1	31.7	192.7	73	1.63	263.4	45.2	14.12	90.0	58.54	161.47
13D	77-5	"	101.2	41.2	162.9	58	1.74	218.4	46.3	14.35	100.0	36.13	146.24
15D	77-19	"	104.7	39.0	830	46	2.27	162.9	64.2	13.02	94.0	46.35	176.17
16D	78-24	"	124.5	38.2	134.0	60	2.07	274.3	45.3	13.72	100.0	61.62	177.67
17D	79-2	"	103.2	43.4	163.0	57	1.81	243.2	42.4	15.61	104.0	45.52	162.69
18D	80-31	"	100.7	40.3	229.9	48	2.09	234.8	42.8	14.04	112.0	47.42	154.14
19D	83-6	"	103.5	40.1	164.5	50	2.07	207.1	49.9	14.27	86.0	45.03	150.15
20D	86-13	"	109.7	41.8	173.0	53	2.06	235.8	46.5	13.72	105.0	57.37	148.04
1E	90-29	"	126.6	34.1	185.0	70	1.81	274.2	46.1	13.33	90.0	62.82	235.45
2E	94-28	"	102.7	45.1	191.0	59	1.74	224.6	45.7	13.88	116.0	32.15	149.86
3E	95-12	"	126.0	36.7	196.9	64	1.95	255.4	49.3	14.35	87.0	57.50	224.59
4E	4-39	GlenleaxNB131	29.4	44.9	37.9	21	1.40	90.6	32.4	14.04	103.0	-45.70	47.04
5E	5-18	"	32.0	43.0	40.2	14	2.28	66.9	47.8	14.51	89.0	-42.45	42.94
6E	5-20	"	29.9	31.5	53.5	27	1.10	88.2	33.9	16.47	91.0	-28.76	43.65
8E	6-15	"	20.9	45.1	22.9	22	0.95	76.2	27.4	13.72	93.0	-48.20	29.42
9E	7-7	"	17.6	33.8	25.6	18	0.98	46.4	37.9	14.98	89.0	-63.46	26.67
10E	8-25	"	19.8	40.0	26.5	30	0.66	107.6	18.4	19.06	102.0	-63.82	27.65
11E	11-15	"	17.1	24.4	22.7	21	0.81	55.7	30.7	16.55	84.0	-55.60	27.45
12E	12-26	"	31.4	46.5	59.9	23	1.36	86.7	36.2	12.78	89.0	-37.94	42.07
13E	12-47	"	28.1	37.1	69.2	19	1.47	65.9	42.6.	14.19	81.0	-45.70	46.78

Appendix Table 1. Continued

F2 selection Code	F2 plant No.	Cross	F2YLD	F2TKW	F2YPC(%)	F2TILL	F2YLD/S	F2BYLD	F2HI(%)	F2PRO(%)	F2HT	F2YADJ	F2YPTR
15E	13-21	GlenleaxNB131	28.4	44.4	33.0	23	1.23	76.3	37.2	14.35	77.0	-31.88	54.72
16E	14.34	"	28.8	46.3	45.3	23	1.25	77.6	37.1	16.39	78.0	-51.05	39.83
17E	18-39	"	23.7	38.5	26.3	14	1.69	53.3	44.4	14.35	78.0	-71.60	32.72
18E	18-43	"	19.7	46.3	28.6	13	1.51	39.7	49.6	14.04	77.0	-50.88	32.24
19E	21-45	"	29.0	46.2	37.5	15	1.93	63.5	45.6	13.80	81.0	-32.68	37.37
20E	22-19	"	29.7	47.0	39.9	19	1.56	65.6	45.2	15.76	89.0	-53.28	37.89
1F	22-46	"	32.7	32.3	36/0	22	1.48	66.3	49.3	14.66	68.0	-51.93	42.96
2F	25-38	"	29.5	32.4	31.7	21	1.40	61.1	48.3	13.02	67.0	-63.80	33.48
3F	28-6	"	25.6	34.4	32.0	23	1.11	67.5	37.9	13.02	80.0	-59.60	30.62
4F	30-10	"	23.5	51.2	32.0	11	2.13	51.2	45.8	16.00	84.0	-59.00	32.56
5F	33-9	"	20.3	39.7	26.9	14	1.45	49.1	41.3	12.78	85.0	-65.20	24.81
6F	33-29	"	24.6	44.2	25.0	10	2.46	50.6	48.6	12.70	86.0	-73.80	30.24
8F	34-44	"	26.4	44.8	24.0	14	1.88	61.3	43.0	16.86	83.0	-55.84	34.78
9F	41-32	GlenleaxEra	28.0	45.5	31.4	21	1/33	72.1	38.8	15.37	88.0	-27.13	32.74
10F	42-14	"	27.7	35.6	63.7	21	1.32	74.2	37.3	14.66	94.0	-24.88	46.69
11F	95-30	"	25.9	33.0	48.0	17	1.52	51.6	50.2	17.80	62.0	-48.58	50.68
12F	46-41	"	20.0	31.9	32.7	20	1.00	50.7	39.4	13.57	84.0	-51.35	40.22
13F	50-24	"	20.3	33.6	30.1	18	1.12	43.1	47.1	14.82	92.0	-50.12	32.79
15F	52-39	"	25.9	23.3	28.4	26	0.99	76.2	33.9	13.64	88.0	-46.78	30.23
16F	53-36	"	24.3	29.6	27.1	15	1.62	54.3	44.7	13.96	94.0	-49.23	25.44
17F	55-3	"	27.7	41.0	58.9	36	0.77	105.0	26.4	15.37	104.0	-42.82	41.82
18F	55-12	"	18.5	35.0	18.93	30	0.61	59.3	31.2	15.14	93.0	-59.03	22.27
19F	55-17	"	23.1	28.1	32.12	34	0.68	86.9	26.6	18.82	101.0	-38.13	29.27
20F	55-37	"	27.1	30.8	28.0	25	1.08	61.2	44.3	14.98	74.0	-41.9	31.50
1G	55-39	"	25.7	35.4	34.0	22	1.17	59.0	43.5	16.47	82.0	-36.68	40.26
2G	59-11	"	18.4	29.6	25.3	26	0.17	60.5	30.4	14.04	92.0	-55.0	24.54
3G	95-21	"	21.7	40.0	22.6	20	1.08	48.8	44.4	17.10	80.0	-61.88	25.10
4G	69-21	"	20.4	39.0	29.7	36	0.56	84.6	24.1	14.19	85.0	-43.78	33.63

Appendix Table 1. Continued

F2 selection Code	F2 plant No.	Cross	F2YLD	F2TKW	F2YPC(%)	F2TILL	F2YLD/S	F2BYLD	F2HI(%)	F2PRO(%)	F2HT	F2YADJ	F2YPTR
5G	73-10	GlenleaxEra	23.0	35.2	27.0	17	1.35	60.5	38.0	16.86	98.0	-62.48	28.54
6G	73-30	"	21.3	36.5	30.0	12	1.77	48.8	43.6	14.43	82.0	-48.47	25.95
8G	76-10	"	24.0	39.1	25.0	32	0.75	75.5	31.7	12.63	95.0	-44.27	29.01
9G	76-35	"	27.5	40.7	37.4	20	1.375	63.2	43.5	14.51	83.0	-30.48	43.46
10G	77-40	"	28.6	27.6	57.3	34	0.84	105.0	27.2	16.31	104.0	-21.92	37.96
11G	77-45	"	24.2	33.4	28.0	24	1.01	59.2	40.9	13.96	63.0	-42.80	28.00
12G	79-45	"	20.2	42.2	26.7	12	1.68	50.5	40.0	14.51	103.0	-40.24	25.49
13G	81-12	"	24.8	27.5	38.0	32	0.77	84.3	29.4	14.59	95.0	-42.72	42.54
15G	82-27	"	26.7	39.8	30.2	17	1.57	59.0	45.2	16.55	68.0	-30.05	35.27
16G	83-46	"	22.7	33.6	31.3	24	0.94	72.2	31.4	12.47	84.0	-41.92	29.42
17G	86-48	"	23.1	46.5	45.0	48	0.48	130.0	17.7	17.57	86.0	-34.38	32.31
18G	88-34	"	25.5	24.1	30.1	36	0.71	81.3	31.3	14.74	83.0	-47.92	40.24
19G	89-23	"	27.0	32.5	41.0	16	1.68	161.0	16.7	13.02	83.0	-39.53	44.31
20G	89-26	"	26.5	30.5	36.6	19	1.39	156.5	16.9	14.27	102.0	-43.11	38.95

Appendix Table 2. F3 family data obtained as means of vari ables measured in F3 progeny phase of F2 single plant selections.

F2 section code	F3FYLD	F3FTILL	F3FHT	F3FYLD/s
1A	12.49	15.94	67.00	0.8049
2A	11.74	16.28	86.70	0.7474
3A	13.43	19.06	82.70	0.7450
4A	10.41	14.93	76.18	0.7218
5A	14.92	18.60	77.50	0.8595
6A	15.29	20.37	71.60	0.7700
8A	11.61	17.11	75.57	0.7405
9A	15.05	17.88	78.69	0.8435
10A	15.88	18.68	71.37	0.8504
11A	14.57	17.91	75.26	0.8046
12A	15.35	17.25	76.16	0.8981
13A	12.98	16.11	77.84	0.8385
15A	11.76	17.14	83.87	0.7380
16A	13.33	18.42	66.76	0.7843
17A	13.36	18.95	71.08	0.7432
18A	12.43	17.14	83.41	0.7525
19A	11.03	16.91	83.33	0.7464
20A	12.13	18.90	73.94	0.7353
1B	12.92	19.10	85.14	0.6879
2B	12.86	16.97	80.21	0.7608
3B	17.37	18.41	76.42	0.9425
4B	14.41	17.82	80.53	0.7966
5B	14.33	17.97	81.33	0.7687
6B	11.51	16.61	70.42	0.6729
8B	15.05	18.67	79.16	0.8075
9B	16.43	19.66	78.84	0.09078
10B	12.7	16.03	74.68	0.7741
11B	11.06	15.79	70.16	0.6781
12B	15.24	19.03	73.20	0.8348
13B	17.42	19.23	73.16	0.9142
15B	14.68	18.09	77.80	0.7873
16B	14.73	19.06	79.26	0.7951
17B	12.49	15.21	67.45	0.8130
18B	16.04	20.18	82.00	0.8130
19B	14.69	18.62	70.80	0.7800
20B	15.55	18.03	72.36	0.8623
1C	13.68	14.88	81.80	0.9300
2C	10.74	16.21	77.60	0.6847
3C	11.58	17.02	82.63	0.7158
4C	16.26	16.60	79.27	0.9556
5C	14.37	19.21	74.58	0.7827
6C	10.78	18.56	71.39	0.5978
8C	14.66	18.24	76.63	0.8280
9C	14.14	17.57	77.10	0.8130
10C	12.63	16.88	66.42	0.7529
11C	13.09	18.41	73.91	0.7359
12C	11.73	17.57	77.90	0.7109

Appendix Table 2. Continued

F2 section code	F3FYLD	F3FTILL	F3FHT	F3FYLD/s
13C	16.66	22.73	76.59	0.7478
15C	15.11	19.25	81.12	0.7922
16C	13.06	19.69	74.66	0.6566
17C	15.99	23.35	82.33	0.7005
18C	11.64	20.10	75.71	0.5889
19C	10.11	19.22	74.83	0.5391
20C	15.55	19.65	83.70	0.8159
1D	15.51	21.00	67.38	0.7458
2D	12.00	24.67	65.42	0.5036
3D	19.99	24.76	77.40	0.7978
4D	12.53	21.86	78.95	0.6019
5D	11.65	20.88	75.60	0.5752
6D	12.34	20.37	75.60	0.6350
8D	14.81	21.94	73.58	0.6728
9D	11.70	18.55	69.11	0.6719
10D	14.56	17.76	80.94	0.6898
11D	16.77	21.17	77.05	0.8118
12D	12.98	26.83	66.00	0.4941
13D	13.24	18.42	77.00	0.7244
15D	15.03	22.58	71.36	0.6390
16D	15.66	22.90	80.23	0.6781
17D	12.91	19.85	85.37	0.6515
18D	15.34	21.72	79.52	0.7168
19D	12.84	17.67	67.95	0.7570
20D	14.95	20.86	81.74	0.7454
1E	11.30	21.57	66.38	0.5522
2E	12.86	17.05	88.90	0.7663
3E	13.86	22.00	67.66	0.6208
4E	8.4	14.34	85.41	0.5809
5E	10.14	16.97	72.05	0.6104
6E	15.29	18.03	78.33	0.8073
8E	15.34	21.0	73.06	0.7183
9E	15.44	18.89	80.83	0.7917
10E	10.18	14.48	84.12	0.6870
11E	12.84	17.43	74.26	0.7374
12E	11.69	17.78	74.50	0.6701
13E	13.59	19.50	74.65	0.7067
15E	13.28	17.02	64.71	0.7670
16E	7.09	13.70	67.88	0.5610
17E	15.05	19.58	70.61	0.8140
18E	14.38	18.33	65.52	0.7487
19E	12.90	17.45	67.58	0.7451
20E	13.99	18.55	83.89	0.7546
1F	7.01	21.37	67.30	0.3731
2F	11.40	16.57	65.96	0.7210
3F	11.00	16.48	71.64	0.7038
4F	11.24	17.45	76.58	0.6412

Appendix Table 2. Continued

F2 section code	F3FYLD	F3FTILL	F3FHT	F3FYLD/s
5F	11.42	16.37	68.35	0.7116
6F	10.76	16.57	71.88	0.6508
8F	14.02	16.55	75.29	0.7938
9F	12.86	17.78	70.38	0.6792
10F	12.88	18.03	74.20	0.6806
11F	12.64	20.23	74.71	0.6229
12F	12.47	21.03	72.4	0.6022
13F	15.50	21.17	76.20	0.7554
15F	10.98	18.42	71.90	0.6004
16F	14.17	18.26	80.80	0.7956
17F	11.72	17.61	77.41	0.6544
18F	14.53	19.68	73.6	0.7107
19F	13.92	19.55	88.95	0.6827
20F	12.23	24.62	63.38	0.4813
1G	11.58	19.33	62.93	0.6086
2G	11.19	17.20	68.81	0.6325
3G	10.93	15.00	72.89	0.7092
4G	14.42	19.72	68.42	0.7246
5G	8.62	15.29	70.88	0.5317
6G	14.58	20.11	67.08	0.7399
8G	14.06	16.85	74.05	0.8053
9G	9.86	15.73	73.47	0.6294
10G	11.32	19.16	78.28	0.5802
11G	5.33	18.66	60.80	0.2829
12G	13.27	17.72	80.66	0.7537
13G	10.55	17.51	71.45	0.6051
15G	14.16	17.03	79.95	0.8126
16G	17.59	23.89	73.81	0.7224
17G	8.94	12.50	75.75	0.6516
18G	12.32	24.79	69.91	0.4985
19G	10.86	18.13	61.95	0.5804
20G	12.27	22.94	83.44	0.5433

Appendix Table 3. F3 individual plant data measured on the honeycomb selected F3 single plants that were to be put in an F4 yield test.

F4 yield No.	Test entry	F2 selection Code	F3 plant No.	Cross	Selection Category	F3YLD	F3TILL	F3HT	F3YLD/S	F3TKW	F3PRO(%)	F3YPC	F3YADJ	F3YPTR
1		18B	85-19	GlenleaxNB131	H	27.8	27	84.0	1.0296	37.0	14.35	212.21	12.37	197.16
2		8B	11-6	"	H	37.3	35	104.0	1.0657	34.0	17.33	219.41	20.25	227.44
3		12C	43-13	"	H	25.9	27	88.0	0.9593	29.0	17.33	784.84	14.95	291.01
4		11D	72-7	GlenleaxEra	H	31.4	29	78.0	1.0828	37.0	15.37	202.58	15.58	186.35
5		11E	73-3	GlenleaxNB131	L	24.5	27	78.0	0.9074	34.0	14.59	92.11	-1.75	96.46
6		17C	58-34	GlenleaxEra	H	29.4	33	84.0	0.8909	35.0	15.68	115.29	13.60	227.38
7		16B	15-17	GlenleaxNB131	H	27.0	29	92.0	0.9310	32.0	16.55	164.63	11.73	155.79
8		4C	53-2	"	H	35.0	26	80.0	1.3462	36.0	15.29	330.18	23.88	330.19
9		19F	20-18	GlenleaxEra	L	36.6	35	92.0	1.0457	27.0	16.23	78.54	-4.05	103.09
10		Glenlea check								39.0	11.76	-	-	-
11		19B	16-36	GlenleaxNB131	H	30.9	33	74.0	1.1182	34.0	16.31	161.84	21.50	182.67
12		15D	24-59	GlenleaxEra	H	38.2	44	86.0	0.8682	31.0	15.53	329.31	24.93	314.92
13		4C	18-33	GlenleaxNB131	H	32.7	32	88.0	1.0219	37.0	16.94	115.54	14.27	192.01
14		19F	34-39	GlenleaxEra	L	20.3	28	90.0	0.7250	22.5	14.27	72.50	-4.94	86.49
15		5B	17-18	GlenleaxNB131	H	36.6	28	88.0	1.3071	37.0	15.84	223.17	18.25	166.89
16		4F	49-20	"	L	25.0	31	80.0	0.8065	25.0	17.33	86.50	-2.12	150.33
17		3D	40-59	GlenleaxEra	H	30.8	34	80.0	0.9059	33.0	15.53	263.25	16.40	228.65
18		GlenleaxEra Composite								32.0	13.88	-	-	-
19		19E	54-54	GlenleaxNB131	L	25.2	32	70.0	0.7875	30.0	15.53	83.44	-3.22	96.92
20		6B	45-19	"	H	26.6	30	78.0	0.8867	31.0	16.94	166.25	14.62	228.72
21		3D	82-17	GlenleaxEra	H	28.1	31	80.0	0.9065	31.0	14.19	221.26	13.47	177.85
22		3D	26-59	"	H	29.6	37	86.0	0.8000	31.0	16.08	116.08	18.70	176.51
23		4B	59.17	GlenleaxNB131	H	29.0	29	80.0	1.000	32.0	15.14	221.37	13.97	268.52
24		13E	31-47	"	L	27.2	32	86.0	0.8500	32.0	17.00	81.93	-2.62	104.21
25		18F	40-32	GlenleaxEra	L	27.4	38	84.0	0.7211	31.0	15.14	97.51	-3.23	122.70
26		16G	48-57	"	L	31.4	34	92.0	0.9235	32.0	14.74	89.46	-2.94	128.37
27		20A	85-42	GlenleaxNB131	H	31.1	27	76.0	1.1519	37.0	14.04	252.84	18.23	252.84
28		16G	90-57	GlenleaxEra	L	39.9	39	76.0	1.0231	36.0	13.88	95.00	-2.76	160.69

Appendix Table 3. Continued

F4 yield No.	Test entry	F2 selection Code	F3 plant No.	Cross	Selection Category	F3YLD	F3TILL	F3HT	F3YLD/S	F3TKW	F3PRO(%)	F3YPC	F3YADJ	F3YPTR
29		8B	88-58	GlenleaxNB131	H	32.6	26	80.0	1.2538	38.0	13.82	142.98	13.19	224.83
30		8E	91-3	"	L	43.2	30	76.0	1.4400	39.0	14.43	92.11	-1.55	141.64
31		18G	27-49	GlenleaxEra	L	22.6	43	70.0	0.5256	25.0	15.61	83.08	-3.64	90.21
32		3E	13-55	"	H	32.4	45	76.0	0.7200	29.0	14.51	184.09	15.52	382.52
33		1D	32-30	"	H	31.2	34	70.0	0.9176	32.0	15.68	187.95	18.30	152.42
34		10G	2-48	"	L	29.5	35	90.0	0.8429	29.0	15.45	82.40	-3.60	103.69
35		9F	43-52	"	L	17.4	22	76.0	0.7909	30.0	15.75	79.09	-3.74	118.61
36		GlenleaxNB131	Composite							37.0	14.35	-	-	-
37		4C	67-2	GlenleaxNB131	H	31.6	19	84.0	1.6632	40.0	15.14	145.62	15.07	240.30
38		8A	45-21	"	H	19.0	27	86.0	0.7037	34.0	13.72	118.76	7.18	141.47
39		5B	31-39	"	H	37.6	38	90.0	0.9895	36.0	16.55	152.23	23.67	338.74
40		15G	13-4	GlenleaxEra	L	36.9	34	80.0	1.0853	34.0	16.78	90.44	-1.95	132.92
41		17E	11-36	GlenleaxNB131	L	23.8	18	70.0	1.322	33.0	15.76	96.35	-1.77	122.68
42		9F	1-52	GlenleaxEra	L	37.7	31	90.0	1.2161	37.0	15.76	84.72	-2.45	114.94
43		3F	21-61	GlenleaxNB131	L	25.9	29	66.0	0.8931	30.0	15.21	88.69	-1.73	103.72
44		11C	15-54	"	H	26.9	41	78.0	0.6561	29.0	16.78	152.84	10.87	102.79
45		3C	88-11	"	H	28.1	21	84.0	1.3381	36.0	15.14	262.62	17.33	272.81
46		GlenleaxNB131	Composite							40.0	14.35	-	-	-
47		17F	68-52	GlenleaxEra	L	19.4	15	80.0	1.2933	35.0	14.35	69.78	-4.54	94.17
48		3A	9-52	GlenleaxNB131	H	20.5	19	70.0	1.0789	40.0	13.05	200.98	6.48	120.09
49		10E	56-57	"	L	24.2	27	85.0	0.8963	28.0	16.47	90.30	-1.30	163.95
50		17E	46-4	"	L	31.4	23	70.0	1.3652	40.0	15.76	80.10	-3.33	92.43
51		15G	13-25	GlenleaxEra	L	20.8	25	85.0	0.8320	30.0	17.10	77.32	-3.90	79.69
52		GlenleaxEra	Composite							34.0	13.96	-	-	-
53		11	4-19	GlenleaxEra	L	24.7	28	80.0	0.8821	26.0	14.98	85.47	-2.06	109.43
54		13B	70-18	GlenleaxNB131	H	26.9	17	74.0	1.5824	34.0	13.70	116.45	9.00	126.47
55		1C	87-56	"	H	29.1	22	74.0	1.3227	38.0	15.29	150.00	12.42	188.10
56		12G	5-37	GlenleaxEra	L	21.5	20	84.0	1.0750	29.0	16.47	78.72	-5.33	84.64

Appendix Table 3. Continued

F4 yield No.	Test entry	F2 selection Code	F3 plant No.	Cross	Selection Category	F3YLD	F3TILL	F3HT	F3YLD/S	F3TKW	F3PRO(%)	F3YPC	F3YADJ	F3YPTR
57		8F	15-30	GlenleaxNB131	L	24.9	29	92.0	0.8586	35.0	13.03	95.04	-1.02	109.07
58		4B	73-17	"	H	30.8	27	80.0	1.1407	32.0	16.23	170.16	16.77	192.13
59		5F	42-10	"	L	23.8	29	74.0	0.8207	27.0	16.78	88.47	-2.95	101.27
60		6E	34-47	"	L	21.0	26	84.0	0.8077	33.0	17.10	74.47	-4.54	81.17
61		3B	52-5	"	H	30.7	23	76.0	1.3348	38.0	14.27	124.29	15.92	146.89
62		8D	62-49	GlenleaxEra	H	35.5	38	76.0	0.9342	29.0	16.23	295.83	24.58	314.99
63		16C	2-12	"	H	27.6	29	76.0	0.9621	32.0	16.00	317.24	13.30	186.48
64	GlenleaxNB131 Composite									40.0	14.43	-	-	-
65		12G	33-58	GlenleaxEra	L	32.3	32	90.0	1.0094	33.0	16.00	96.42	-3.54	108.75
66		8G	2-4	"	L	38.8	35	96.0	1.1086	38.0	16.94	98.73	-3.06	114.45
67		3D	12-38	"	H	43.6	41	84.0	1.0634	32.0	14.82	300.68	29.28	243.98
68		16F	19-41	"	L	27.4	33	100.0	0.8303	32.0	16.23	87.82	-2.77	128.21
69		1G	56-6	"	L	18.5	23	65.0	0.8043	38.0	15.21	71.43	-5.62	86.33
70		3D	19-49	"	H	33.2	34	90.0	0.9765	34.0	15.66	167.67	12.85	241.80
71		3B	17-16	GlenleaxNB131	H	30.7	33	90.0	0.9303	35.0	15.21	208.84	13.70	159.89
72	GlenleaxEra Composite									32.0	13.80	-	-	-
73		8E	7-45	GlenleaxNB131	L	23.8	23	72.0	1.0348	27.0	17.00	88.8	-2.98	118.88
74		17B	8-49	"	H	22.9	21	66.0	1.0905	31.0	16.00	224.51	6.98	132.37
75		9B	32-59	"	H	34.6	29	92.0	1.1931	37.0	14.98	288.33	20.88	205.09
76		8F	80-40	"	L	36.0	33	76.0	1.0909	37.0	15.76	90.68	-3.28	104.13
77		9A	73-43	"	H	32.0	37	78.0	0.8649	36.0	16.16	240.60	21.74	346.69
78		18D	3-31	GlenleaxEra	H	31.2	28	92.0	1.1143	31.0	17.72	216.67	20.52	208.00
79		9A	87-43	GlenleaxNB131	H	33.1	23	79.0	1.4391	36.0	15.68	348.42	15.40	320.42
80		13B	7-8	"	H	28.3	28	76.0	1.0107	33.0	17.80	479.66	19.75	277.45
81		20B	30-58	"	H	34.6	34	82.0	1.0176	35.0	13.02	191.16	15.80	218.02
82		5A	2-32	"	H	23.6	38	82.0	0.6211	30.0	15.21	536.36	11.72	382.49
83		9E	7-4	"	L	35.6	30	88.0	1.1700	38.0	17.02	99.44	-2.02	214.45
84		20F	27-9	GlenleaxEra	L	19.0	24	63.0	0.7917	25.0	16.71	68.34	-5.15	124.43

Appendix Table 3. Continued

F4 yield No.	Test entry	F2 selection Code	F3 plant No.	Cross	Selection Category	F3YLD	F3TILL	F3HT	F3YLD/S	F3TKW	F3PRO(%)	F3YPC	F3YADJ	F3YPTR
85		GlenleaxNB131	Composite									-	-	-
86		13C	15-14	GlenleaxEra	H	28.0	37	84.0	0.7568	29.0	16.39	105.60	7.8	132.70
87		20B	23-6	GlenleaxNB131	H	40.1	29	70.0	1.3828	42.0	15.68	145.28	16.62	184.79
88		6A	51-34	"	H	28.3	31	72.0	0.9129	32.0	15.53	283.00	16.50	300.10
89		1A	36-54	"	H	25.3	18	74.0	1.4056	33.0	15.21	176.92	9.82	182.93
90		12D	2-8	GlenleaxEra	H	33.3	47	70.0	0.7085	25.0	15.21	223.49	24.20	180.29
91		20E	89-3	GlenleaxNB131	L	35.8	31	84.0	1.1548	37.0	16.39	81.18	-5.03	124.74
92		12A	69-22	"	H	25.8	32	76.0	0.8063	32.0	16.78	263.26	10.50	228.32
93		18D	24-62	GlenleaxEra	H	28.0	33	86.0	0.8485	32.0	16.00	243.48	17.00	178.00
94		16G	41-5	"	L	22.4	28	80.0	0.8000	26.0	15.92	63.63	-4.68	106.31
95		11A	76-31	GlenleaxNB131	H	30.1	27	75.0	1.1148	38.0	15.53	436.23	15.05	356.21
96		20D	11-60	GlenleaxEra	H	31.2	30	72.0	1.0400	33.0	15.53	288.88	15.77	208.97
97		11A	6-31	GlenleaxNB131	H	31.3	26	82.0	1.2038	35.0	15.92	143.58	16.68	197.73
98		13F	18-42	GlenleaxEra	L	30.1	36	88.0	0.8361	29.0	14.82	92.90	-3.02	135.58
99		9E	21-25	GlenleaxNB131	L	20.7	29	86.0	0.7138	28.0	17.80	81.49	-3.48	88.35
100		2C	52-46	"	H	28.9	31	78.0	0.9323	31.0	16.39	401.38	16.80	230.65
101		16D	73-29	GlenleaxEra	H	26.9	27	84.0	0.9963	34.0	16.62	256.19	14.67	247.47
102		10A	80-12	GlenleaxNB131	H	23.5	22	71.0	1.0682	34.0	11.76	133.52	5.70	189.06
103		18F	26-32	GlenleaxEra	L	24.4	27	80.0	0.9037	31.0	16.55	85.31	-2.32	106.55
104		13A	41-44	GlenleaxNB131	H	26.5	19	70.0	1.3947	34.0	15.53	311.76	15.23	314.35
105		8F	43-30	"	L	21.6	18	75.0	1.2000	30.0	13.41	89.63	-2.87	114.70
106		12E	10-56	"	L	29.1	30	78.0	0.9700	34.0	14.35	97.98	-3.53	165.00
107		13G	19-17	GlenleaxEra	L	32.5	32	82.0	1.0156	25.0	14.35	69.74	-4.93	115.38
108		16D	17-8	"	H	30.9	30	98.0	1.0300	29.0	16.39	114.02	14.92	179.13
109		8E	21-45	GlenleaxNB131	L	31.5	31	74.0	1.0161	34.0	16.55	91.83	-3.34	125.85
110		15E	32-2	"	L	26.6	31	66.0	0.8581	33.0	18.51	96.37	-2.27	118.22
111		15E	32-44	"	L	22.8	34	66.0	0.6706	38.0	14.19	80.56	-2.75	93.17
112		16F	29-62	GlenleaxEra	L	25.8	30	84.0	0.8600	32.0	16.23	78.89	-3.32	96.27

Appendix Table 3. Continued

F4 yield No.	Test entry	F2 selection Code	F3 plant No.	Cross	Selection Category	F3YLD	F3TILL	F3HT	F3YLD/S	F3TKW	F3PRO(%)	F3YPC	F3YADJ	F3YPTR
113		9B	4-38	GlenleaxNB131	H	44.6	29	90.0	1.5379	41.0	15.21	384.48	38.56	963.28
114		5C	25-3	"	H	32.4	32	87.0	0.9818	32.0	16.31	314.56	17.35	200.00
115		19G	70-3	GlenleaxEra	L	23.5	32	65.0	0.7344	30.0	15.53	95.53	-1.62	128.62
116		20C	31-54	"	H	27.4	32	90.0	0.8563	32.0	16.55	222.76	14.68	207.10
117		11D	30-49	"	H	34.8	32	84.0	1.0875	31.0	14.90	322.22	22.1	245.59
118		16A	21-11	GlenleaxNB131	H	21.8	27	73.0	0.8074	38.0	14.12	156.83	9.68	186.32
119		19G	7-35	GlenleaxEra	L	28.7	28	66.0	1.0250	31.0	14.66	97.62	-1.90	123.17
120		4F	7-62	GlenleaxNB131	L	30.4	31	82.0	0.9806	33.0	15.76	97.43	-3.38	142.25
121		18E	53-16	"	L	31.0	31	65.0	1.000	32.0	15.92	87.08	-3.46	164.28
122		GlenleaxEra	Composite							33.0	13.64	-	-	-
123		16D	24-39	GlenleaxEra	H	31.5	35	85.0	0.9000	31.0	16.08	83.11	3.88	130.87
124		11B	21-48	GlenleaxNB131	H	31.4	32	88.0	0.9813	36.0	17.10	158.58	11.93	186.13
125		13C	15-35	GlenleaxEra	H	30.9	29	80.0	1.0655	33.0	16.23	135.52	14.63	127.68
126		16F	12-30	"	L	26.7	20	72.0	1.3350	32.0	15.92	68.81	-3.60	119.19
127		6G	22-17	"	L	22.4	24	66.0	0.9333	30.0	14.66	80.86	-6.02	130.23
128		11D	30-28	"	H	35.0	34	90.0	1.0294	33.0	15.45	204.67	19.52	239.73
129		18E	32-5	GlenleaxNB131	L	26.7	23	68.0	1.1609	31.0	16.31	85.30	-4.87	134.38
130		13E	17-26	"	L	23.8	30	76.0	0.7033	30.0	16.55	99.58	-2.01	138.69
131		12F	39-31	GlenleaxEra	L	19.4	26	78.0	0.7462	29.0	12.94	71.06	-4.73	118.58
132		20E	12-34	GlenleaxNB131	L	24.5	17	88.0	1.4412	37.0	16.79	95.33	-2.55	106.84
133		4G	1-26	GlenleaxEra	L	26.1	30	72.0	0.8700	31.0	17.72	93.88	-3.47	93.88
134		5D	26-61	"	H	31.2	37	84.0	0.8432	29.0	14.66	236.36	20.88	203.92
135		15C	30-11	"	H	29.2	32	84.0	0.9125	35.0	17.72	147.47	17.23	185.16
136		6E	6-26	GlenleaxNB131	L	37.9	30	84.0	1.2633	38.0	15.53	98.95	-1.78	147.29
137		15B	8-47	"	H	47.6	35	82.0	1.3600	41.0	15.45	357.89	34.30	290.77
138		11F	32-19	GlenleaxEra	L	22.7	43	94.0	0.5279	27.0	16.39	90.44	-1.30	120.94
139		3G	43-4	"	L	18.7	25	80.0	0.7480	31.0	13.41	73.33	-2.18	101.24
140		20G	42-46	"	L	25.7	35	79.0	0.7343	31.0	16.71	91.13	-2.10	112.08

Appendix Table 3. Continued

F4 yield No.	Test entry	F2 selection Code	F3 plant No.	Cross	Selection Category	F3YLD	F3TILL	F3HT	F3YLD/S	F3TKW	F3PRO(%)	F3YPC	F3YADJ	F3YPTR
141		5E	13-57	GlenleaxNB131	L	22.6	36	78.0	0.6278	27.0	16.00	85.93	-3.33	118.32
142		9G	30-5	GlenleaxEra	L	28.0	28	68.0	1.0000	36.0	14.82	91.8	-3.20	103.43
143		19A	22-51	GlenleaxNB131	H	21.6	23	90.0	0.9391	30.0	19.37	111.34	4.85	200.00
144		18D	24-41	GlenleaxEra	H	29.7	38	88.0	0.7816	32.0	16.86	277.57	18.63	344.15

Appendix Table 4. Representation of the F2-selected lines in the F4 yield test.

Line	Yield Test Entries	Line	Yield Test Entries	Line	Yield Test Entries	Line	Yield Test Entries	Line	Yield Test Entries	Line	Yield Test Entries	Line	Yield Test Entries
1A	1	1B		1C	1	1D	1	1E		1F		1G	1
2A		2B		2C	1	2D		2E		2F		2G	
3A	1	3B	2	3C	1	3D	4	3E	1	3F	1	3G	1
4A		4B	2	4C	2	4D		4D		4F	2	4G	1
5A	1	5B	2	5C	1	5D	1	5E	1	5F	1	5G	
6A	1	6B	1	6C		6D		6E	2	6F		6G	1
8A	1	8B	2	8C		8D	1	8E	3	8F	3	8G	1
9A	2	9B	2	9C		9D		9E	2	9F	2	9G	1
10A	1	10B		10C		10D		10E	1	10F		10G	1
11A	2	11B	1	11C	1	11D	2	11E	1	11F	2	11G	
12A	1	12B		12C	1	12D	1	12E	1	12F	1	12G	2
13A	1	13B	2	13C	2	13D		13E	2	13F	1	13G	1
15A		15B	1	15C	1	15D	2	15E	2	15F		15G	2
16A	1	16B		16C	1	16D	2	16E		16F	3	16G	3
17A		17B	1	17C	1	17D		17E	2	17F	1	17G	
18A		18B	2	18C		18D	3	18E	2	18F	2	18G	1
19A	1	19B	2	19C		19D	1	19E	1	19F	3	19G	3
20A	1	20B	2	20C	1	20D	1	20E	2	20F		20G	1

Appendix Table 5. Adjusted means of yield and other variables measured in the F4 yield test.

F4 yield entry	Test No.	Cross	Selection Category	F4YLD	F4PRO	F4PYLD	F4TEW	F4TKW	F4HT	F4DH[b]
	1	GlenleaxNB131	H	432.22	13.46	58.20	78.22	45.68	114.02	41
	2	"	H	388.40	14.02	54.44	78.92	44.28	120.52	45.5
	3	"	H	287.35	13.71	39.44	74.21	39.88	109.69	42.5
	4	GlenleaxEra	H	303.72	14.14	43.01	78.35	40.26	118.47	42.5
	5	GlenleaxNB131	L	388.64	12.77	49.62	76.20	41.89	92.48	40.5
	6	GlenleaxEra	H	349.01	13.72	47.77	75.56	38.48	105.87	45
	7	GlenleaxNB131	H	400.62	13.99	55.97	78.05	43.64	111.65	43
	8	"	H	401.51	13.67	54.85	75.39	44.91	111.37	42.5
	9	GlenleaxEra	L	239.03	14.54	35.00	76.27	38.10	108.11	43
	10	Glenlea check variety		343.21	13.91	47.68	76.61	43.78	110.79	43
	11	GlenleaxNB131	H	353.72	12.90	45.40	74.10	44.44	96.11	41.5
	12	GlenleaxEra	H	295.12	13.24	38.81	74.97	33.30	91.74	45.5
	13	GlenleaxNB131	H	448.04	13.74	61.82	78.57	47.45	114.35	41
	14	GlenleaxEra	L	298.26	14.27	42.42	77.57	41.82	108.81	43
	15	GlenleaxNB131	H	418.16	13.40	55.79	76.40	42.74	117.80	44.5
	16	"	L	378.19	13.15	49.84	76.53	43.01	107.31	43
	17	GlenleaxEra	H	313.00	13.41	41.56	76.64	38.56	106.37	41.25
	18	GlenleaxEra Composite		297.10	13.60	40.30	77.30	37.31	106.51	40.5
	19	GlenleaxNB131	L	344.08	12.93	44.14	73.57	40.36	99.04	40
	20	"	H	400.51	12.74	51.24	74.84	42.17	98.57	44.5
	21	GlenleaxEra	H	369.26	12.74	47.09	78.46	37.85	105.14	40.5
	22	"	H	343.81	13.85	47.61	79.21	40.50	104.90	40.5
	23	GlenleaxNB131	H	378.67	13.09	49.71	77.99	43.52	110.47	42
	24	"	L	358.58	13.64	48.93	77.03	44.13	105.08	40
	25	GlenleaxEra	L	344.76	14.70	50.64	79.47	40.95	106.09	43.5
	26	"	L	243.81	14.20	34.60	78.04	42.00	102.12	39.25
	27	GlenleaxNB131	H	291.00	12.76	36.65	70.75	37.62	102.78	43
	28	GlenleaxEra	L	266.82	13.74	36.55	76.44	39.64	106.64	40.25
	29	GlenleaxNB131	H	389.29	14.44	56.43	79.64	45.68	109.63	43
	30	"	L	408.59	12.61	51.54	76.04	45.45	96.43	41
	31	GlenleaxEra	L	253.62	13.24	33.62	70.41	30.55	85.47	40
	32	"	H	307.38	13.16	40.14	75.31	34.15	88.56	44
	33	"	H	257.85	12.91	33.13	74.92	36.97	89.42	43.5
	34	"	L	262.08	13.99	36.52	74.14	37.35	111.96	45.5
	35	"	L	262.88	15.11	39.74	74.58	38.56	94.11	41
	36	GlenleaxNB131 Composite		312.18	13.51	41.71	75.26	42.80	109.42	42.5
	37	GlenleaxNB131	H	449.97	13.45	59.95	78.82	47.85	105.95	44.5
	38	"	H	290.33	13.79	39.85	73.97	43.64	106.08	42.5
	39	"	H	424.88	13.06	59.65	78.62	46.19	112.11	44.5
	40	GlenleaxEra	L	259.	15.01	38.98	75.79	43.53	104.42	42.5
	41	GlenleaxNB131	L	395.81	12.27	48.56	76.23	43.97	85.22	41.25
	42	GlenleaxEra	L	381.37	13.42	51.41	77.81	45.25	106.87	42
	43	GlenleaxNB131	L	222.71	13.64	30.03	66.04	34.18	96.76	42.5
	44	"	H	277.85	13.23	36.57	71.77	37.58	95.66	43.5
	45	"	H	312.42	13.21	41.00	73.42	42.02	106.00	43
	46	GlenleaxNB131 Composite		290.71	13.30	38.76	75.25	43.05	110.93	42
	47	GlenleaxEra	L	337.50	14.21	48.14	78.75	41.40	102.63	44
	48	GlenleaxNB131	H	423.96	12.33	52.21	75.46	44.01	98.28	41.5
	49	"	L	350.90	13.44	47.27	77.12	43.79	104.86	41
	50	"	L	375.70	12.45	46.46	74.96	42.95	91.35	40.5
	51	GlenleaxEra	L	263.97	14.86	39.18	76.59	45.41	106.19	40.25
	52	GlenleaxEra Composite		274.48	13.75	37.79	75.90	37.61	108.17	41

Appendix Table 5. Continued

F4 yield entry	Test No.	Cross	Selection Category	F4YLD	F4PRO	F4PYLD	F4TEW	F4TKW	F4HT	F4DH[b]
	53	GlenleaxEra	L	244.49	13.68	36.57	74.59	36.39	101.44	41
	54	GlenleaNB131	H	427.31	13.56	41.00	78.06	45.59	97.38	45
	55	"	H	334.40	13.98	38.75	76.95	47.63	115.51	41.25
	56	GlenleaxEra	L	318.53	13.64	48.14	76.30	42.65	107.39	43
	57	GlenleaxNB131	L	411.39	13.09	52.21	78.37	47.45	109.54	42
	58	"	H	369.01	13.32	47.27	75.49	43.45	115.69	43
	59	"	L	293.48	12.69	46.46	70.77	36.65	99.49	42.5
	60	"	L	391.35	13.92	39.18	77.77	47.07	112.25	43
	61	"	H	413.63	13.39	37.79	78.03	44.22	108.55	42
	62	GlenleaxEra	H	335.88	13.63	33.46	78.17	38.91	97.16	43.5
	63	"	H	290.78	14.15	58.00	77.73	36.03	98.97	41
	64	GlenleaxNB131	Composite	255.39	13.33	46.61	75.42	42.40	111.96	41.5
	65	GlenleaxEra	L	295.51	13.71	43.45	74.17	42.81	107.91	43
	66	"	L	334.54	13.75	46.24	77.49	44.27	104.88	42
	67	"	H	339.30	13.65	46.12	78.20	40.29	107.07	40.25
	68	"	L	279.22	13.78	38.49	76.89	37.33	110.65	41
	69	"	L	218.28	15.28	33.39	74.77	37.27	97.68	39
	70	"	H	355.88	13.53	48.13	79.31	38.48	111.45	44
	71	GlenleaNB131	H	366.45	13.11	48.14	78.21	44.83	117.06	42
	72	GlenleaxEra	Composite	261.55	14.06	36.98	75.37	37.50	104.13	41.25
	73	GlenleaxNB131	L	304.59	12.95	39.27	74.33	40.70	93.30	41.5
	74	"	H	329.92	12.91	42.38	71.08	39.23	92.90	40.75
	75	"	H	414	13.62	56.79	78.27	44.60	109.50	41.5
	76	"	L	455.62	13.09	59.67	78.08	46.65	108.40	42
	77	"	H	371.33	13.27	49.11	77.16	47.18	114.66	40.5
	78	GlenleaxEra	H	302.16	15.03	45.44	76.98	42.23	114.43	45.5
	79	GlenleaxNB131	H	406.58	13.41	54.14	75.53	46.50	116.88	40.5
	80	"	H	374.52	13.82	51.42	76.56	46.15	99.54	42.5
	81	"	H	326.74	12.73	41.44	74.75	41.36	101.06	41.5
	82	"	H	394.01	13.70	53.89	78.34	47.17	112.56	45
	83	"	L	417.36	13.47	56.47	77.52	43.58	110.86	44
	84	GlenleaxEra	L	256.02	13.06	33.16	76.79	31.98	77.31	43.5
	85	GlenleaxNB131	Composite	344.93	13.61	46.88	76.50	44.49	111.92	41
	86	GlenleaxEra	H	322.55	13.57	44.12	78.89	36.75	103.45	44.5
	87	GlenleaxNB131	H	392.83	12.71	50.36	76.15	44.59	101.80	40.5
	88	"	H	325.36	13.57	44.25	73.20	39.03	92.59	41.5
	89	"	H	405.53	13.15	53.23	75.34	44.84	96.10	40.75
	90	GlenleaxEra	H	255.29	13.75	34.87	73.53	30.96	80.68	45
	91	GlenleaxNB131	L	281.30	13.87	39.13	76.48	44.56	111.74	42.5
	92	"	H	374.27	13.19	49.49	78.01	45.26	111.92	44
	93	GlenleaxEra	H	266.16	13.98	37.37	75.69	40.51	118.47	44.5
	94	"	L	261.74	14.30	37.49	73.74	36.28	110.06	42
	95	GlenleaxNB131	H	350.87	12.95	45.80	76.54	43.86	99.27	40.5
	96	GlenleaxEra	H	298.66	12.96	38.73	75.25	37.30	97.16	40.5
	97	GlenleaxNB131	H	363.76	13.15	47.77	76.78	44.85	99.42	42.5
	98	GlenleaxEra	L	301.20	12.83	38.70	76.46	38.27	100.87	43
	99	GlenleaxNB131	L	291.13	13.29	52.10	77.17	46.37	106.98	41.75
	100	"	H	451.59	13.33	60.35	75.85	45.71	110.87	44
	101	GlenleaxEra	H	365.28	13.58	49.87	79.30	37.15	112.99	43
	102	GlenleaxNB131	H	397.30	12.62	50.20	77.00	43.16	94.52	41.5
	103	GlenleaxEra	L	361.27	14.47	52.17	79.60	41.26	106.94	43.5
	104	GlenleaxNB131	H	383.21	12.56	47.77	76.88	44.33	100.26	41
	105	"	L	387.81	12.56	49.03	76.09	44.46	103.67	40.5

Appendix Table 5. Continued

F4 yield entry	Test No.	Cross	Selection Category	F4YLD	F4PRO	F4PYLD	F4TEW	F4TKW	F4HT	F4DH[b]
	106	GlenleaxNB131	L	364.08	13.14	47.86	76.45	42.44	94.03	42.5
	107	GlenleaxEra	L	331.00	13.09	43.50	77.40	34.33	102.76	43
	108	"	H	300.86	13.92	42.07	78.40	35.21	113.67	43
	109	GlenleaxNB131	L	326.28	13.28	43.05	75.88	40.55	93.92	41
	110	"	L	341.02	13.39	44.57	77.03	52.16	92.06	39.75
	111	"	L	273.79	13.33	36.20	73.69	42.09	90.21	40.25
	112	GlenleaxEra	L	260.11	13.82	35.94	76.34	37.44	105.38	40.75
	113	GlenleaxNB131	H	399.38	13.49	53.72	78.03	44.88	104.14	40.75
	114	"	H	249.10	14.52	35.91	75.82	40.10	107.92	45
	115	GlenleaxEra	L	247.94	12.98	31.95	77.32	34.59	81.63	42-25
	116	"	H	360.52	13.41	48.20	76.41	44.72	104.95	43
	117	"	H	334.17	13.90	46.32	78.41	37.13	117.27	45
	118	GlenleaxNB131	H	316.98	13.57	42.81	73.87	40.14	92.21	43
	119	GlenleaxEra	L	244.36	13.12	32.09	75.18	32.13	84.20	42
	120	GlenleaxNB131	L	324.35	13.29	43.05	76.66	41.63	107.85	42.5
	121	"	L	353.52	12.82	46.62	75.19	39.12	92.39	40.5
	122	GlenleaxEra Composite		283.36	13.72	38.84	77.51	37.40	108.23	40.75
	123	GlenleaxEra	H	401.77	13.04	52.62	78.75	40.80	112.18	44
	124	GlenleaxNB131	H	366.63	12.51	45.89	74.82	41.42	94.95	42.5
	125	GlenleaxEra	H	352.39	13.78	48.43	79.02	40.12	100.85	41.5
	126	"	L	298.07	13.19	39.28	73.35	34.27	89.93	40
	127	"	L	324.23	14.27	46.40	77.84	40.50	92.86	40.75
	128	"	H	408.47	13.22	53.85	80.40	42.48	109.66	45.5
	129	GlenleaxNB131	L	294.99	13.04	38.26	73.05	38.22	91.56	40.5
	130	"	L	302.66	13.46	40.79	72.90	41.94	103.51	40
	131	GlenleaxEra	L	320.61	13.24	42.49	76.55	34.93	101.48	40
	132	GlenleaxNB131	L	290.15	13.64	39.42	75.92	44.10	109.92	43
	133	GlenleaxEra	L	299.30	14.33	42.79	75.36	37.56	98.66	40.25
	134	"	H	245.47	14.06	34.65	74.25	34.55	108.33	43
	135	"	H	351.65	13.58	47.89	76.70	43.10	110.40	42.25
	136	GlenleaxNB131	L	342.55	13.36	46.11	79.01	46.31	110.20	41.25
	137	"	H	336.15	13.53	45.22	75.06	45.73	107.83	44
	138	GlenleaxEra	L	295.51	13.51	39.83	76.48	36.64	99.33	43
	139	"	L	301.93	13.32	40.07	77.85	38.02	105.08	40.5
	140	"	L	296.67	14.23	42.12	76.54	36.00	102.64	45.5
	141	GlenleaxNB131	L	256.48	13.20	33.86	69.24	31.89	93.09	40.75
	142	GlenleaxEra	L	308.40	13.24	40.65	74.71	43.52	97.13	40.25
	143	GlenleaxNB131	H	327.49	13.37	44.13	74.72	41.02	113.42	45.5
	144	GlenleaxEra	H	274.65	14.16	38.95	74.79	38.51	111.42	45.5

a) For the yield selection category, H and L stand for high and low yield selections respectively.

b) The means of days to harvest (F4DH) were not adjusted means.