DETERMINATION OF CHARACTERS FOR YIELD SELECTION IN SPRING WHEAT BREEDING PROGRAMS

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Peter B. E. McVetty

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ABSTRACT

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DETERMINATION OF CHARACTERS FOR YIELD SELECTION IN SPRING WHEAT BREEDING PROGRAMS. Major Professor: L.E. Evans.

Three crosses of spring wheat (*Triticum aestivum*) currently included in the University of Manitoba wheat breeding program were used to evaluate the use of physiological and/or morphological parameters alone or in combination on F_2 plants or F_3 families as selection criteria to identify high yielding F_4 bulks.

The F_2 generation was handled as spaced plants grown in the field in two types of environments, (a) a stress-free environment and (b) a normal environment. Approximately 200 plants of each cross were measured for physiological, morphological, yield component and phenological traits as well as being visually rated for yield potential by 5 selectors. A random 50-seed sample from each of these plants was sent to Mexico in the winter of 1976-77 to generate F_4 bulks.

Groups of 49 for stress-free and 81 for normal environment grown F_2's were returned from Mexico as F_4 bulks to be yield – tested in a six – replicate partially balanced lattice design.

The same 49 and 81 groups as tested in F_4 were grown simultaneously from F_3 remnant seed in the summer of 1977.

The results indicated that the most common single F_2 parameter which identified high yield potential in F_2 was visual yield selection, however the selection intensity had to be low in order to retain a majority of the high yielding lines.

A multiple regression analysis approach on a cross - specific basis was found to be better than a single F_2 parameter approach because a majority of the high yielding lines could be retained with a much higher selection intensity. The results were similar for the F_3 generation.

A combined cross analysis using multiple regression indicated that productivity and peduncle length in F_2 were the two most important common parameters. A prediction of high yielding lines based on these two parameters retained in excess of one - third of the high yielding lines with high selection intensity. However, no acceptable common parameters were found in F_3 and it was concluded that replicated F_3 yield tests would be more suitable in such cases.

Harvest index evaluation in a productivity and height framework retained a majority of the high yielding lines while allowing a selection intensity of approximately 15%. This technique involved the use of an optimum harvest index in productivity and height extremes of statistically characterized populations. It is concluded that the harvest index - productivity - height approach to selection will enhance the effectiveness of plant breeders in their seach for high yield in spring wheat.

1. INTRODUCTION

"Cereal grains are the major food of mankind. In many of the less developed countries of the world, cereals provide two thirds or more of dietary calories. Rice in Asia, maize in South America, sorghum in Africa, and wheat in the Middle East are recognized as the staple foods on whose yields famine or feast depends. Among the developed countries there are many, such as Russia and Japan, in which cereals still provide more than half of the diet calories. Although cereals make a smaller direct contribution to the diet of developed countries such as the United States and Canada, total cereal use per person is extremely high. However, most of the grain is fed to livestock and becomes an indirect component of human diets.

World production of cereals over the last twenty years has increased more rapidly than has world population, but with more variation from year to year; for the world as a whole, increase in yield per unit area has contributed much more than increase in the area under cereal crops. This is particularly so in the developed countries, but in the less developed countries the rather smaller increases in grain production have been due about equally to increases in yield and in area.

The world average yield of cereal grains is 1.7 tonnes per hectare, more than twice as great as that of legume crops and oilseeds. Partly because of their higher yielding ability, cereals are tending to displace the pulses in many less developed countries although they complement one another both agronomically and nutritionally. Also, the rate of increase in yield, on a world scale, is much greater in the major cereals than in the legumes, with the consequences that the cereals are becoming progressively more a predominant component of the world food supply.

Greater cereal yields are the key to increased food supplies given the restrictions on further increase in the area of land under crops. Improved agronomy, such as better weed control and more timely and effective fertilizer applications, has contributed greatly to the recent increases in cereal yields, as has better control of diseases and pests, whether by genetic or chemical means. Plant breeding has played a major role in three ways, by the selection of disease and pest-resistant cultivars, developing shorter-statured forms that do not lodge at high levels of fertilizer application, and by selecting cultivars with greater yield potential which can respond to higher inputs. All three plant breeding approaches are essential and must be linked so it is difficult to partition progress among them. At low yield levels improved agronomy is most important. As fertilizer inputs increase, lodging resistance becomes more important, while in high input systems, increase in yield potential may be rate limiting.

There have been fashions in the emphasis given to particular processes as the major limitation on cereal yields, and also to the stage of the crop life cycle regarded as most critical. Watson (1952) attached greatest importance to leaf growth, canopy development and leaf area index in the early stages of the crop. In subsequent years much more emphasis has been given to the final stages of the cereal life cycle since Archbold (1945) demonstrated that grain growth is largely based on current assimilation. As a consequence, particular attention has been given to crop photosynthesis through the grain-filling period as a major determinant of yield.

More recently, however, evidence has accumulated that the capacity to store assimilates in the grain may limit yields quite as much as the capacity of the crop to provide them during the grain filling period, Evans (1975).

The storage capacity of the crop is largely determined during the middle of its life cycle, in the period between inflorescence initiation and anthesis, partly by reproductive processes leading to the formation of the inflorescence and partly by the availability of photosynthate and nutrients at that time. In "source versus sink" arguments, it is important to remember that the potential size of the sink is largely determined by the photosynthetic assimilate supply at an earlier stage in the life cycle. Currently, therefore, more attention is being given to the middle "reproductive" stages of the cereal life cycle. But the plant breeder and the crop physiologist must consider all three stages - vegetative reproductive and grain filling - because stable high yields will be obtained only when the yield - determining processes operating in all three are in balance with one another."[1]

In this study parameters were measured relating to the three developmental stages of the spring wheat plant in F_2 and F_3 of three crosses and these have been related to F_4 bulk yield in simple and multiple correlation analyses and multiple regression analyses to attempt to determine if the efficiency of selection for yield in early generations of a plant breeding program can be increased by the use of applied crop physiology.

[1] Evans, L.T. and Wardlaw, I. F. 1976. Aspects of the comparative physiology of grain yield in cereals. Adv, in Agron. 28: 301-59.

2. LITERATURE REVIEW

2.1 Yield Components: The Early Approach to Scientific Plant Breeding

Although economic yield has been the main basis of selection in most crop breeding programs, there have been numerous attempts to find selection criteria based on the morphology, physiology and biochemistry of the development of crop yield.

In cereals, Engledow and Wadham (1923, 1924a and 1924b) were among the first to suggest a scientific approach to breeding for yield. They suggested the use of yield components, namely (i) average number of ear bearing tillers per plant, (ii) average number of grains per ear and (iii) average weight of a single grain in explaining yield differences in cereal varieties. They also investigated the usefulness of morphological and physiological parameters as indices of single plant yield. It was found that only "migration coefficient" (similar to today's harvest index only on a fresh weight basis) was of any real value.

The components of yield have continued to receive much attention from breeders.

Waldron (1929) reported a significant correlation between all the yield components and yield in common and durum wheats. He concluded that particular attention must be paid to keeping the number of kernels per head high to maximize yield.

Woodworth (1931) found that yield components in wheat were inherited independently and suggested that one could obtain good values of all the yield components in one genotype.

Bridgeford and Hayes (1931) concluded on the basis of a stepwise multiple regression analysis of yield components and agronomic characters in wheat that one should select for numerous big heads per row to increase yield.

Stephens (1942) in an attempt to overcome the yield plateau in oats in Great Britain by selecting for yield components concluded that component compensation largely ruled out yield improvement with this approach.

Frankel (1947) advocated the use of yield components to increase yield but only if this was done in replicated homozygous lines because the heritable variance of yield components relative to the environmental variance is too low to enable selection for yield components on a single plant basis.

Boyce, Copp and Frankel (1947) found that selection for yield via yield components in F_2 on a plotwise basis was successful in increasing F_3 family yield while selection for yield components on F_2 plants was unsuccessful.

Grafius (1956) introduced the concept of a geometric interpretation of the yield components and indicated that maximum yield is obtained at intermediate levels of the three yield components X, Y, and Z where X = number of panicles per unit land area, Y = average number of kernels per panicle and Z = average kernel weight. When $X + Y + Z = 3$, maximum yield is obtained when X = Y = Z = 1. Since increases in the smallest component of yield will result in the largest yield gain, it seemed logical to take a good variety and attempt to improve its most limiting yield component.

Stoskopf and Reinbergs (1965) found that in oats and barley the number of grains per head was the most reliable yield component to use in estimating yield per plant. However, the authors go on to say that none of the three yield components can be used to predict yield on a plot basis and that although the three yield components effectively describe yield per plant they do not determine yield per unit area.

Quinlan and Sagar (1965) studied the effect of doubling seeding rate on the yield components of two varieties of wheat. In one variety tiller number was reduced by half while in the other both tiller number and grain number per spike were reduced; in both varieties seed weight remained constant.

Johnson et al. (1966) studied yield components in four winter wheats differing in height. It was found that yield components determined on a plot basis had no consistent relationship with yield per plot over the four varieties. They concluded that yield components are of little value to the plant breeder and that he should look at yield itself instead.

Adams (1967) dealt with a major pitfall of yield components - that of yield component compensation. He indicated that the negative correlations between yield components are due to strong interplant and intraplant competition. Correlations are low or near zero in plants under noncompetition but are significant and negative for competitive plants. If these were true genetic correlations they would be much more constant. The author suggested that inputs of photosynthate to the sink are oscillatory and that yield component compensation results from the input level being high during some phases of sink development and low during others. Therefore the negative correlations of X, Y, and Z have little to do with establishment of actual yields. It is concluded that plant breeders should breed for an XYZ optimum.

Fonseca and Petterson (1968) arrived at conclusions completely contrary to those of Adams (1967) by studying yield components in winter wheat. These authors found that the majority of the variation in plot yield could be accounted for by its association with the three yield components. However they concluded that progress by selection for yield components per se may be limited by the strong negative correlations among the yield components.

Hsu and Walton (1970a, 1970b and 1971) studied yield components and agronomic characteristics in a 5 x 5 diallel of spring wheats and found that selection for agronomic traits associated with an increase in photosynthetic area above the flag leaf node would be more successful in increasing yield than selection for yield components.

Rasmusson and Cannell (1970) tested yield components as yield selection criteria in the early generations of barley crosses and found that supposed linkage between the yield components led to yield component compensation and made selection for yield components unwise.

Adams and Grafius (1971) in commenting on Rasmusson's and Cannell's (1970) paper, disagreed with the idea of linkage in yield components and suggested that yield component compensation is due to the oscillatory response of sequential components to limited resources. Plant breeders were encouraged to select for yield advancement by selecting for optimal geometry of the yield components in their environment.

Knott and Talukdar (1971) studied the relationship between yield components on a plot basis and obtained a highly significant negative correlation between 1000 kernel weight and kernel number per plot. In spite of this negative correlation, they were able to increase yields by selecting for increased kernel weight.

Syme (1972a) conducted a study of greenhouse grown single plants of each of the forty-nine cultivars grown in the fifth ISWYN and found that 100 kernel weight was useful in yield performance prediction but not as good as harvest index or days from sowing to the emergence of the seventh leaf.

Walton (1972) found that yield components were useful in explaining yield differences in spring wheat varieties. The only trait which was better at explaining yield differences was leaf area duration.

Kaltsikes (1973) reported that in spring rye the yield components measured on a plot basis accounted for 97.3% of the variability observed in yield per plot in a stepwise multiple regression - and thus were good in explaining yield variation.

Lee and Kaltsikes (1973) in a study of durum wheat, found that the yield components had high correlations with yield, and that the most important predictors of yield were number of kernels per plant, 1000 kernel weight and days to maturity. These parameters in a multiple regression equation accounted for 78% of the variation in yield.

The latest and most ambitious paper on yield components was by Grafius *et al*. (1976). They reported that in barley, selection of parents based on wide differences in yield components on a plot basis followed by one backcross to either parent resulted in advanced generations with yields which could be predicted quite accurately on the basis of parental yield component regressions. The authors attributed their success to the backcross which tended to preserve the integrity of an already proven system while adding factors from another system.

2.2 Growth Analysis

The second wave of scientific endeavor to simplify the search for yield was initiated by Watson in 1947. Growth analysis as used by Watson and others involved the use of sequential harvests of plant material throughout the growing season combined with an estimate of photosynthetic area or leaf area (LA) at each harvest. Parameters measured or derived from the analysis included leaf area index (LAI), leaf area duration (LAD), leaf area ratio (LAR), crop growth rate (CGR), relative growth rate (RGR), net assimilation rate (NAR), and grain to leaf ratio (G).

Watson (1947) in a comprehensive comparative study of wheat, barley, potatoes, mangolds and sugar beets grown in one metre rows, investigated NAR and LA. He found a similar seasonal trend in NAR for all species but found significant differences in NAR between the species, with the rate increasing in the order wheat, barley, potatoes, mangolds and sugar beets. No significant varietal differences were observed in wheat. This was in contrast to LA, which varied significantly from variety to variety. Watson concluded that in general, variation in LA was the main factor determining differences in total dry matter (DM) production and yield, with variation in NAR being of minor importance.

Watson (1952) in a review paper of British results with growth analysis, covering NAR and LAI in wheat concluded that total DM production and yield were more dependent on LAI than on NAR. It was recommended that breeders attempt to increase yield by increasing LAI to a maximum or optimum while paying little attention to NAR.

Thorne and Watson (1955) reported that nitrogen application in any form at or near anthesis increased LAD and yield by 2% in Yeoman winter wheat. The G value remained nearly constant over all treatments and indicated that under British conditions yield is closely associated with LAD.

Lupton (1961) studying NAR in six wheat cultivars including tall and short varieties found significant differences and suggested that these varietal differences should be of considerable interest to plant breeders.

Watson *et al*. (1963) carried out a complete growth analysis of new and old spring and winter wheats with the following results: (i) LAI of old winter wheats was higher than LAI of new ones, with this trend reversed for spring wheats, (ii) LAD of winter wheats was slightly greater than that for spring wheats but there were no significant differences in LAD between old and new wheats, (iii) NAR of spring wheats was greater than that of winter wheats, (iv) G values of new varieties were much higher than for old varieties and finally (v) yields of the two wheat types were equal.

Lupton *et al*. (1963) studied varietal differences in growth patterns of wheat and their importance in determining yield. Only shoot dry weight and LAD were significant in explaining yield variation in hybrid populations. When considering the prediction of yield from characters measured in a different season, the authors found the best correlation was that between the two estimates of yield itself.

Davidson (1965) controlled the LAI of Olympic wheat at 1 and 3, removed all leaves or half of all leaves at anthesis and compared these treatments with a control which had LAI 12. It was found that leaf removal at anthesis had no effect on yield while maintaining LAI at 1 and 3 reduced yield by 80% and 60% respectively. These treatments reduced yield by reducing both grain number per spike and mean grain weight by about 50%. The author recommended for Australian conditions that LAD before ear emergence be given much greater attention than LAD after ear emergence. This is because Australian varieties senesce very rapidly in the increasing heat and drought before harvest.

Welbank et al. (1966) investigated the dependence of yield of wheat varieties on LAD in four British wheats. Grain yields were found to be nearly proportional to LAD of either the whole plant or just the flag leaf node and above after anthesis. The authors studied G values as well and found that they were nearly constant over all varieties and treatments and concluded that yield was more dependent on LAD than on NAR.

Fisher and Kohn (1966) looked at the relationship of grain yield to vegetative growth and post-flowering LA in the wheat crop (cv Heron) under conditions of limited soil moisture. Higher sowing rates, higher N applications or delayed sowing all decreased yield by increasing water stress in the plant before and after flowering and thus advancing maturity. Grain yield was found to be closely related to LAD after flowering (.969***[1]). Grain yield was also correlated with total DM at flowering (.875***). These results showed that LAD was important in determining yield and that there is an optimum level of vegetative growth for maximum yields in Australia.

Bingham (1967) experimented with three British wheats by artificially varying grain number per ear. The overall conclusion was that sink and source are equally important

[1]*** = significant at .001

in limiting yield and that one should increase sink size by increasing grain number and increase source size by increasing LAD to obtain higher yields.

In 1968 Thorne et al. reported a study on the effect of daylength and temperature at three periods on development in wheat, (i) to ear emergence, (ii) to anthesis and (iii) to maturity. It was found that effects of environmental differences on grain dry weight could not be explained by differences in LAD except when a cool long daylength treatment followed anthesis. It appeared therefore, that environmental differences in periods (i) and (ii) controlled grain dry weight by altering the capacity of the ear to accumulate carbohydrates as determined by the number of grains per ear.

Watson (1968) reviewed British growth analysis endeavors to 1968 and found that increases in yield in Britain were closely related to increases in LAI or LAD. The review also indicated that sink strength is related to number of grains per tiller, and since semi-dwarfs have more grains per tiller, they have a higher harvest index. The reviewer concluded that yield in wheat is a product of both sink and source.

A study on tall and semi-dwarf wheat varieties for yield, harvest index, LAD, G and total DM production was reported by Thorne et al. (1969). Yields were found to be equivalent since DM of semi-dwarfs was less but harvest index was higher. In a similar vein, the LAD of semi-dwarfs was less but the G value was higher. The authors speculated that the increased G values of semi-dwarfs may be due to an increased photosynthetic rate or increased translocation to the grain. It is suggested that if semi-dwarfs produced as much DM as tall varieties, their yield would be outstanding.

An excellent review covering both wheat and rice was published by Yoshida (1972). He indicated that for both cereals LAD has a great effect on yield and that increased LAI results in increased productivity up to a plateau. As well, increased total DM production results in increased yield, up to an optimum level of total DM after which yield begins to decline. High yield in both wheat and rice is related to small upright leaves, short plants and high harvest index. The author's final conclusion is that grain yield in the cereals is limited by both sink and source capacity.

Khalifa (1973) studied the effect of nitrogen on LAI, LAD, NAR and yield in wheat and found that nitrogen application early in the growing season increased LAI, LAD and yield while late application had no effect on LAI, LAD or yield. Total DM at harvest was highly correlated with LAD (r = .96**) and with LAI at anthesis (r = .75*). Yield was also highly correlated with LAD (r = .79*) and LAI at anthesis (r = .85*) leading the author to conclude that increased yield in wheat will follow increased LAI at anthesis.

Tarlowski _et al_. (1976) found in a comparative study of tall and semi-dwarf varieties using growth analysis techniques that the tall varieties had a higher tiller number than the semi-dwarfs (as single plants) and had a time lag in ear development past the point of maximum culm and sheath dry weight which was not observed in the semi-dwarfs. The tall varieties had a greater LAI (9-10) than the semi-dwarfs (5-8), but the semi-dwarf LAI maximum and NAR maximum coincided while NAR maximum occurred when LAI was declining in the tall varieties. The semi-dwarfs were more efficient at resource utilization and this could be attributed to (i) reaching maximum LAI 10-20 days before tall varieties, (ii) simultaneous maximizing of NAR and LAI, (iii) a longer grain filling period and (iv) a greater sink capacity. The authors conclude that semi-dwarfs have the potential to outyield tall varieties, especially if they are planted at higher densities to achieve higher LAI.

2.3 Morphology and Agronomy in Relation to Photosynthesis

Studies centered on the morphology and agronomy of wheat in relation to photosynthesis commenced in 1950 with a paper by Asana and Mani (1950). This publication reported on a study of varietal differences in photosynthesis by the leaves, stem and ear in wheat by shading and defoliation experiments. Varietal differences in the photosynthetic contribution made by the various plant parts were found and this led the authors to suggest that plant breeders might be able to exploit these differences in a plant breeding program. Asani and Mani later (1955) reported that differences in ear photosynthesis were due to the presence or absence of awns and differences in spikelet number. The variation in photosynthetic contribution by leaves could be accounted for by differences in LAD. They suggested that varietal differences in yield may be accounted for by such attributes as leaf and stem size, spikelet number and presence or absence of awns and their functional period.

Watson et al. (1958) studied physiological differences in grain yield among three varieties of barley and found that the high yielding varieties Proctor and Herta had larger ears with greater photosynthetic efficiency than Plumage-Archer while photosynthetic contributions from other plant parts was equal. Therefore it was concluded that the differences in yield observed were due to differences in ear photosynthesis.

Lupton (1961) experimented with six varieties of wheat and found significant varietal differences in ear photosynthesis and net assimilation rates. He concluded that plant breeders could choose parents for crosses using physiological criteria.

Thorne (1965) studying photosynthesis of ears and flag leaves of wheat and barley reported that the ears of wheat photosynthesize very little and that the flag leaf contributes most of the photosynthates supplied to the ear while in barley the photosynthetic contributions from the ear and flag leaf were approximately equal because the photosynthetic rate of the barley ear was high due to the presence of awns. Therefore, in wheat the plant breeder should select for flag leaves with enhanced photosynthetic capacity while in barley the ears deserve more consideration.

Carr and Wardlaw (1965) completed investigations on the supply of photosynthetic assimilates to the grain from the flag leaf and ear of wheat and found awned wheat varieties had an ear photosynthetic contribution greater than for the flag leaf while this was reversed for awnless varieties.

Buttrose and May (1965) used Gabo wheat grown in either the summer or winter in a greenhouse to study ear photosynthesis contribution to yield. It was found that ear photosynthesis contributed 51% to yield in summer but only 28% to yield in winter. In both cases final yield was the same so other compensating factors came into play. It was concluded that the amount of photosynthate the ear contributes to yield is light intensity dependent.

Kriedemann (1966) studied the photosynthetic activity of the wheat ear in Sabre wheat using various shading techniques. The estimates of ear photosynthetic contribution to yield were variable from 9.7 to 44% and were dependent on the shading technique employed and by the environment. This is because ear photosynthesis comprises two processes, the assimilation of atmospheric CO_2 and the photosynthetic refixation of the ear's respiratory CO_2. The latter component can make a substantial contribution to grain yield, comprising more than half of the ear's total CO_2 assimilation according to the author.

Voldeng and Simpson (1967) studied the relationship between photosynthetic area and grain yield per plant in wheat using seven lines of wheat in shading experiments.

In all cases the ear and flag leaf photosynthates made up a very high proportion of the total contribution to grain dry weight. On a single plant basis, the correlation between flag leaf area and yield per tiller was (.74*). When the authors included ear area with flag leaf area versus yield per tiller the correlation rose to (.87*). It is concluded that selection of plants with a large flag leaf and ear area should identify the higher yielding plants among a mixture of genotypes.

Pearce et al. (1967) observed photosynthesis in plant communities as influenced by leaf angle by tilting flats at 0, 30 and 60 degrees from the horizontal to obtain different leaf angles. LAI was also altered by planting 25, 50 and 100 g of seed per flat. The authors found that differences in net photosyntheses due to leaf angle increased as LAI increased above 2 and that the upright leaves had a higher net photosynthesis than the more horizontal leaves. It was concluded that more upright leaves allow a greater LAI to be developed which leads to greater net photosynthesis which in turn may lead to greater yields.

Simpson (1968) conducted an investigation into the association between grain yield and photosynthetic area above the flag leaf node in wheat grown in a greenhouse. On a per tiller basis significant correlations were found between yield per tiller and (i) area of head (r = .75*), (ii) area of flag leaf sheath (r = .73*), (iii) total photosynthetic area (r = .76*), and (iv) LAD (r = .75*). On a per plant basis significant correlations were found between grain weight per plant and (i) flag leaf lamina area (r = .84*), (ii) flag leaf sheath area (r = .91*), (iii) head area (r = .91*), and (iv) total photosynthetic area above the flag leaf node (r = .93*). Therefore photosynthetic area above the flag leaf node has a good relationship to yield either on a per tiller or per plant basis.

Puckridge (1968) studied the interaction of photosynthetic organs in wheat under field conditions using shading, defoliation or tiller removal at 5 days post anthesis and found that only kernel weight varied in these experiments. It was concluded that the flag leaf photosynthesizes at a maximum rate but that this is not necessarily true for the rest of the plant. A further conclusion was that good compensation by ears, stems and sheaths occurs which indicates that sink size is important in the control of photosynthesis and translocation in wheat.

Lupton (1968) analyzed grain yield of wheat in terms of photosynthetic activity and efficiency of translocation and found that when photosynthetic activity and translocation percentage of carbohydrate from the ear, flag leaf and second leaf were integrated, a very reasonable estimate of final grain weight was obtained. In contradiction to Puckridge (1968), this author found that the rate of photosynthesis of leaves was not limited by the size of sink to which photosynthates are translocated.

Lupton (1969) continued the above work and reported that 60% of the carbohydrate in the grain was derived from current photosynthesis from flag leaves and sheaths, about 10% from the ear and 18% from the second leaf. Photosynthesis before anthesis contributed 12% of the grain carbohydrate. Yield predictions based on an integral of photosynthetic rate and translocation proportion were found to be quite accurate. The author suggested that plant breeders could measure photosynthetic rate and translocation proportion to select parents for a hybridization program.

The effect of defoliation on the CO_2 uptake of a community of wheat plants in the field was reported on by Puckridge (1969). The results indicated that only the top 3 leaves in wheat photosynthesize in the 20 day period centered around anthesis. Removal of all leaves and ears was found to decrease photosynthesis by 66% but it should be noted that the stem and sheaths still photosynthesize at 44% of the control value. Since the leaf sheaths and stems form 50% or more of the total green area after ear emergence, the author suggested that this area could be quite important in maintenance of yield in areas where water stress causes leaf senescence.

Evans and Rawson (1970) used Gabo, Sonora 64 and Pitic 62 wheat in an investigation of photosynthesis and respiration by the flag leaf and components of the ear during grain development. It was discovered that developing grains photosynthesize with a light maximum of 700-900 foot candles and that grain photosynthesis almost balanced the grain respiration until the late stages of grain development. Ear photosynthesis contributed 20 to 30% to grain growth in the varieties studied. Further findings were that the photosynthetic rate of the flag leaf blade varied in response to sink demand and that photosynthesis by the ear and flag leaf blade alone could account for the needs of the ear at all times, therefore grain growth was not limited by the supply of assimilates.

Evans and Dunstone (1970) published a very interesting paper on some physiological aspects of evolution in wheat. They reported that there has been a parallel increase in leaf and grain size in wheat over evolutionary time but that this has been coupled with a progressive reduction in the rate of photosynthesis per unit leaf area. Therefore, maximum wheat yields are probably not being achieved by the presently available wheat varieties.

Loomis *et al.* (1971) indicated that photosynthesis is an important factor to be considered in agricultural productivity and suggested that differences in C_3 and C_4 photosynthesis should be exploited to maximize agricultural productivity.

Moss and Musgrave (1971) believe that the limiting factor on photosynthesis and yield is light and that plant form modifications or increased biochemical capacity to enhance photosynthesis per unit ground area will increase yield.

With regard to canopy modification Duncan (1971) used computer simulation techniques to deduce the effects of leaf angles and areas on canopy photosynthesis. The results show that for LAI under 3, differences in leaf angle have little effect on canopy photosynthesis but at higher LAI (7-10) leaf angle becomes very important with vertical leaves in the top of the canopy grading to horizontal leaves lower in the canopy being the most desirable. The author cautioned that leaf angle is of greatest importance in the tropics and of least importance in the far north with respect to photosynthesis and LAI.

Gifford et al. (1973) used the barley variety Resibee to assess photosynthetic limitation to grain yield in a field crop and found that both sink and source act as partial limitations to yield. The authors concluded that increasing photosynthesis in the variety would be ineffective unless the sink was simultaneously increased.

Moss (1974) indicated that physiologists are playing a large role in designing plants for higher yield by (i) choosing plant characters to be investigated, (ii) evaluating importance of the characters to yield and (iii) identifying new characters to include in an ideotype development program. Moss cites the work done in photosynthesis which led to the incorporation of delayed leaf senescence, upright leaves, awns and efficient stem carbohydrate storage into an ideotype for high yield in barley as evidence of physiologist's contribution to breeding.

2.4 Early Generation Selection for Yield

Early generation selection has been developed and advocated by many individuals based on the information documented by Shebeski (1967) and Sneep (1977) that for a character controlled by many genes such as yield, a genotype possessing all of the desirable genes in homozygous or heterozygous condition occurs most often in the F_2 with its frequency declining in subsequent generations. Thus selection which occurs in the early generations, preferably F_2, is considered to be the most efficient way to select for yield.

Since the F_2 generation is the first generation in which selection for yield can occur once the parents for a cross have been chosen and the cross made, it must be asked if selection in F_2 on single plants can be successful. Several authors have investigated this question including Shebeski (1967) who found that all F_2 selections retained by the breeder irrespective of the basis of selection were random for yield. It is suggested that early generation testing starting with F_3 plots would be best because the breeder has no ability to select for yield potential in F_2 plants.

McGinnis and Shebeski (1968) investigated the same problem, coming to a different conclusion - that selection of well tillered (but not excessively tillered) F_2 plants which are vigorous would increase the general yielding capacity of the F_3 lines and would consequently be advantageous to a breeding program.

Knott (1972) also looked at the effect of selection for

F_2 plant yield on subsequent generations in wheat and found significant regressions between F_2 yield and F_3 progeny yield but indicated these were so small as to be of little value in a plant breeding program.

Skorda (1973) attempted to overcome the lack of replication in F_2 by planting the seeds of two F_2 families and their parents in a six replicate randomized complete block with a commercial seeding rate. From each replication the 20 highest yielding F_2 plants (first selection) and the next 20 highest yielding F_2 plants (second selection) were selected and grown in F_3 replicated yield tests. When the two groups of selections were combined within each cross, highly significant correlations ($r = .848^{**}$ and $r = .871^{**}$) were obtained. From these, Skorda concluded that selection in F_2 was effective because the F_3 lines with high mean yields were derived from the higher yielding F_2 plants.

Fasoulas (1976) reported on the use of a honeycomb design method of F_2 plant evaluation whereby F_2 plants were selected on the basis of yield in the absence of interplant competition. Fasoulas has shown that selected high yielding F_2 plants produced high yielding progeny when the yield of both generations was measured as single plant yield in the honeycomb design.

In spite of the few successes in F_2 single plant selection for yield potential most breeders agree with Allard (1960) that selection for heritable high yield in the F_2 is futile because environmental effects are too great. Most breeders concede that if selection for yield potential is to be via yield, then the F_3 generation is the earliest possible generation in which this can occur.

Briggs and Shebeski (1970) studied the usefulness of visual selection in F_3 for yield in single replicate plots with control plots every third plot. The selectors were 2.5 times better than random at a 10% selection intensity level but they missed many high yielding lines so the authors concluded that visual selection for high yield in F_3 plots was largely ineffective.

Briggs and Shebeski (1971) improved upon their previous study by measuring grain yield on whole single replicate F_3 plots and expressing these yields as percent of an adjacent control. The authors reported a significant rank correlation (r = .71*) between F_3 and F_5 yields, but only when the whole F_3 yield range was sampled to develop F_5 lines. It is concluded that F_3 selection based on these results could not be recommended, particularly at a high selection intensity.

Townley-Smith <u>et al</u>. (1973) conducted an investigation into selection techniques for yield in wheat and concluded that breeders must test large populations in early generations in order to breed for increased yield. It is further concluded that all plots must be harvested and that adjustment of plot yields using moving means should be used to increase heritability. Relatively large numbers of genotypes should be selected for the next generation of testing.

Shebeski and Evans (1973) reported on the logical extension of early generation testing - the use of replicated F_3

yield measurements to increase the precision of the yield measurement and to provide preliminary estimates of wide range adaptability. Although final results were not presented, preliminary results indicated that replicated F_3 hill plots would allow selection of high yielding and wide range adapted material.

Depauw and Shebeski (1973) used the same nursery design as Briggs and Shebeski (1971) to evaluate an early generation yield testing procedure in F_3, F_4 and F_5 in wheat. Significant rank correlations between F_3 and F_5 bulks (r = .59*) were obtained as were significant rank correlations between F_3 and F_5 family means (r = .56*). The authors concluded that yield testing in unreplicated F_3 plots was effective because the highest yielding F_4 bulks and F_5 families came from high yielding F_3 lines. As previous (1971), a wide range of F_3 material had to be chosen to ensure inclusion of all high yielding lines in F_4 or F_5.

O'Brien (1977) completed an evaluation of F_3 selection for yield incorporating replicated F_3 testing in 3 row plots and hill plots. The outcome was sufficiently successful to be given consideration by plant breeders.

2.5 Attempts to Find Yield Selection Criteria

Many breeders and physiologists in the last few years have proposed the use of mophological and/or physiological traits as yield selection criteria rather than yield itself. Many traits have been suggested and it is to these and their advocates that this review now turns.

Tanner *et al.* (1966) reported some observations on upright leaf type small grains. The wheat, oat and barley nurseries at the Ontario Agricultural College were ranked for yield using only leaf angle (upright) and leaf width (narrow) as selection criteria. Three hundred varieties were evaluated as high, medium or low yielders. Out of 50 high yielding lines predicted, 48 were correct and 2 which were very unusual varieties were incorrect.

MacKey (1966) described ideotypes of wheat for dry and wet-land adapted varieties based on physiological concepts. His dry-land adapted ideotype has moderate sized leaves which wilt early, with emphasis on photosynthesis by ears, culms, and leaf sheaths (therefore awned ears), high tillering capacity and good translocation ability. All of these components are related to water use efficiency.

The wetland adapted ideotype has large leaves with the lower leaves wilting early, a large ear with multifloral spikelets with large seeds with the plant being moderately tillered. The plant should be short since the primary sink is the ear. All of the components emphasized are related to the ear's capacity to accept the copious amounts of photosynthates produced by the flag leaf. The author makes a general statement that efficiency in crop production will ultimately depend on photosynthetic activity, loss by respiration, size of effective assimilating surface and its duration to function in relation to the environment where the crop is grown.

Langer (1967) reviews physiological approaches to yield determination in wheat and barley to the mid 1960's. The review covers the changes from the population census methods of the 1920's, through the source of carbohydrate studies, translocation, sink and source relationships and ending with tiller production studies of the 1960's. It is concluded that further research should be directed towards DM distribution in the plant and response to the environment by plants. The author concluded with the quote

> "When physiologists have a clear definition of yield determination and genotypic differences, plant breeders will quit ignoring the physiologist."

Hurd (1968) reported that varieties which have the greatest yield potential do not necessarily yield the most under limiting conditions. This is thought to be due to the possession of yield limiting genes by the maximum yield potential genotypes when they are grown under limiting conditions. The author's approach was to select genotypes where yield expression was not limited (moderately tillered F_2 plants in dry land areas) and to yield test in F_3 as many lines as possible.

Donald (1968) expanded on the ideotype concept stating that the successful crop ideotype would (i) be a weak competitor, (ii) make a minimum demand on resources per unit DM produced, (iii) have each unit of DM with sufficient capacity to accept all photosynthates. An ideotype is described for wheat which has a short strong stem, a few small erect leaves, a large erect awned ear and a single culm per plant. The author also suggested F_2 spaced plant selection criteria. It is recommended that plant breeders retain the poorest yielding plants in F_2 populations so as to retain the highest yielding monoculture plants.

Baker et al. (1968) studying the cross CT 423 X Prelude found that the genotypic correlation between percent N in the grain and yield of (-.92*). This correlation was taken to indicate that one can not increase yield without reducing protein or vice versa. From this it can be concluded that selection for yield via percent protein might be successful.

Kaufmann et al. (1969) extended the above work and found that selecting late tall lines would increase yield by reducing percent N in the grain. They concluded that the large negative relationship between nitrogen content and yield (r = -.70*) observed in the study was undesirable from the standpoint of a breeding program.

Walton (1969) conducted an inheritance study of morphological characters associated with yield in spring wheat. It was found that flag leaf lamina area, extrusion of the head from the flag leaf sheath, head length and yield were all controlled by minor genes with additive gene action. Partial dominance was present for yield, flag leaf area and head length. In summary, he concluded that breeding for increased yield via increased extrusion length or increased flag leaf area is feasible because of the genetic systems involved.

Austenson and Walton (1970) studied the relationship between initial seed weight and mature plant characters in spring wheat and found that large kernels gave rise to plants with more tillers and ultimately more yield. The correlations obtained were significant although low (r = .20*). The authors conclude that it is possible to breed for increased yield simply by selecting larger kernels. This is one of the simplest selection criteria available to plant breeders and has led to the development of large seeded utility varieties.

Syme (1970) studied a high yielding Mexican semi-dwarf, WW 15 and the relationship of yield to harvest index (HI) along with eight other varieties. For the nine varieties over 15 locations, the correlation between HI and yield was (.96**). The possibility of breeding for yield via HI became immediately obvious.

Singh and Stoskopf (1971) found a high degree of variability in the HI of winter wheat, winter barley, winter rye, spring barley and oats over a 4 year period. The authors conclude that considerable improvement in cereal grain yield could be made by selecting for higher HI values by choosing short plants with high yield from segregating populations.

Walton (1971) used factor analysis to determine characters for yield selection in wheat in an 8x8 diallel, finding that head volume per plant, kernels per plant, heads per plant, 1000 kernel weight, days to anthesis and flag leaf breadth accounted for 93.7% of the variation in yield on a plot basis in a multiple regression analysis. Factor analysis yielded complimentary information, allowing the author to conclude that plant breeders should select for increased heads per plant, increased kernels per plant and increased 1000 kernel weight to increase yield.

In 1972 Walton reported on a similar study in which it was found that LAD and yield components were the most important components determining yield on a plot basis.

Syme (1972) in a study where cultivars grown as single potted plants in a greenhouse were used to predict field mean yield performance found that HI, days from sowing to emergence of leaf seven and 100 grain weight accounted for 78.5% of the variation in cultivar mean yield. He suggested the use of multiple regression of these variables on other cultivars grown under the same single plant conditions to predict their relative yields.

Nass (1973) studied twenty-two cultivars of spring wheat by sampling in yield plots and found that ears per plant, yield per ear and HI considered together should be an effective means of selecting for increased yield.

Fisher (1975) outlined the future role of physiology in wheat breeding. He pointed out that physiology has worked in rice where decreases in height, increases in HI and development of upright leaves has led to substantially increased yields. Fisher believes that grain yield in cereals grown under optimum conditions is simultaneously limited by both sink and source. For Mexican cultivars the best relationships with yield were for HI, height, grains per square metre and total DM for semi-dwarfs. He concluded that the future for physiologists is to identify physiological selection criteria for yield potential and to combine these into a single selection index. Physiologists must also exploit the physiological complementation concept, crossing parents with excess sink capacity to those with excess source capacity.

Donald and Hamblin (1976) in an excellent review of biological yield and HI of cereals as agronomic and plant breeding criteria stated

> "The lack of interest by plant breeders and many agronomists in biological yields has seriously limited the understanding of cereal performance and biotype behaviour."

High HI in a crop will be achieved with many ears, each with a high yield of grain relative to short light stems and few short narrow leaves per stem. Grain yield, however, depends not only on the HI but equally on the biological yield per unit area. HI is negatively correlated with all vegetative plant parts especially stems and leaves but also with height while it is positively correlated with grain yield. HI is also negatively correlated with biological yield, however attempts must be made to combine high HI with high biological yield varieties to increase yield.

Evans and Wardlaw (1976) reported on the comparative aspects of grain yield in cereals. They feel that there is simultaneous source and sink capacity limitation in cereals and that further advancement in yield will depend on more control over the agricultural environment so that more reserves of potential yield can be mobilized into actual grain yield. In other words, it is the correlative and feedback mechanisms operating within the cereals that require modification to permit advances in yield as much as the photosynthetic and storage systems.

Bhatt (1976) studied HI in several wheat cultivars finding large variability and high heritability with predominately additive gene action. It is concluded that yield improvement by selection for high HI in early generations is a good possibility.

Rosielle and Frey (1976) studied the contribution of vegetative growth rate and HI to grain yield in oats, concluding that the magnitude of vegetative growth is the major limiting factor in grain yielding capacity of oat cultivars in Iowa.

Fisher and Kertez (1976) found that HI on spaced plants of 40 homozygous spring wheat lines was sufficiently correlated with large plot yield (.56*) that it could be recommended as an early generation selection criteria for large plot yield over other parameters.

Okolo (1977) took the final step in the evolution of the HI criteria concept and tested HI of F_2 plants as a yield potential estimator in common wheat. For four crosses of spring wheat no significant correlations between HI of the selected F_2 plants and either F_3 or F_4 bulk yields occurred.

In summarizing the literature review it can be seen that there has been an evolution of ideas from yield components to growth analysis to photosynthetic considerations to early generation selection for yield to attempts to find yield selection criteria which has culminated in the evaluation of HI in a breeding program as a yield potential estimator for F_2 spaced plants.

The logical extension of this trend is to evaluate as many F_2 spaced plant parameters as it is practical to measure and determine whether any of these parameters alone or in combination will serve as useful yield potential selection criteria, and to perform a similar analyses on F_3 families.

3. MATERIALS AND METHODS

3.1 Description of Cultivars

Four common wheat (Triticum aestivum L.) cultivars, Glenlea, Neepawa, Era and NB 320 were used in this study. The origin and pedigree of these cultivars is given in Table 1.

TABLE 1. Origin and pedigree of cultivars

Cultivar	Origin	Pedigree (1)
Glenlea	U. Manitoba	Pembina 2*/Bage//CB 100 (2)
Neepawa	Agr. Canada Winnipeg Canada	(Thatcher 7*/Frontana)/ (Thatcher 6*/Kenya Farmer)// (Thatcher 2*/Frontana-Thatcher)
Era	U.S.D.A. Minnesota U.S.A.	II-55-10/4/Pembina/ II-52-329/3/II-53-38/ III-58-4//II-53-546 (3)
NB 320	Agr. Canada Swift Current Canada	Tobari 66/Romany

(1) Pedigree written according to Purdy et al. (1968).
(2) CB 100 is a Mexican strain having the cultivars Sonora 64, Tezanos Pintos Precoz and Nainari 60 in its pedigree.
(3) Includes in its pedigree Frontana, Thatcher, Mida, Kenya 117A, Kenya 58, Lee, Newthatch and a Polk sib.

Glenlea is a tall hard red spring utility wheat with a high yield relative to other Canadian grown varieties, (Evans et al. 1972).

Neepawa is a tall hard red spring wheat of the low yield, high quality Thatcher type, (Campbell 1970).

Era is a two gene semi-dwarf hard red spring wheat with yield and quality intermediate between Neepawa and Glenlea, (Heiner et al. 1971).

NB 320 is a two gene semi-dwarf hard red spring utility wheat with yields approaching Glenlea, (Hurd, 1975).

An agronomic description of spaced plants of the four cultivars for yield, productivity, harvest index, leaf area duration and grain to leaf ratio is given in Table 2.

TABLE 2. Agronomic description of space planted plants of the cultivars.

Cultivar	Yield g	Productivity g	Harvest Index %	Leaf Area Duration cm^2 days	Grain to Leaf Ratio mg/dm^2 days
Glenlea	74±14	227±35	33±3	7344±1108	10±3
Neepawa	56±10	166±19	33±3	5111±608	11±2
Era	58±11	147±22	38±6	4717±745	12±2
NB 320	75±16	211±24	36±6	6887±645	11±2

Three crosses were made that involved Glenlea as a common female parent with Neepawa, Era and NB 320 as male parents. They were representative of the types of crosses currently being used in the U. of M. spring wheat breeding program to develop high yielding bread wheat and utility wheat advanced lines. Thus the use of physiological estimators of yield was tested in an actual breeding program situation.

3.2 Field and Laboratory Methods

An outline of the generation and year sequence used for each cross is shown in Figure 1.

Figure 1. Outline of the generation and year sequence for each cross

Year	
1976	200 F_2 spaced plants per cross plus 65 spaced plants of each parental cultivar were grown at Winnipeg
1976-77	200 F_3 bulks (50 random seeds per bulk) per cross plus adequate parental materials were grown at Cuidad Obregon, Mexico
1977	120 F_4 bulks per cross plus 6 Glenlea checks plus 4 male parent checks were grown at Winnipeg

Two hundred F_2 single plants per cross and sixty-five single plants of each parent were grown on U. of M. experimental land at Winnipeg in the summer of 1976 in rows 100 cm apart with 60 cm inter-plant spacing within the rows. During the growing season and at harvest, several single plant characters were measured or estimated. These are outlined in Figure 2.

The F_2 populations were divided into 2 groups, the first group receiving preferential treatment to ensure growth in a near stress-free field environment (including pre-germination and hardening indoors followed by biweekly watering and fastidious weed control in the field) and the second group being handled in the standard fashion (direct seeded in the field, minimal weed control, no watering). The purpose being to see if F_2 populations should be grown under stress-free or normal conditions to improve the probability of identifying high yielding lines from F_2 plants.

The characteristics measured on F_2 plants cover the five major areas of research into scientific plant breeding, these

Figure 2. Characteristics measured on F_2 spaced plants

Parameter	Abbreviation
1) Yield per plant	F_2Y
2) Productivity per plant	F_2P
3) Leaf area duration per plant	F_2LAD
4) Harvest Index	F_2HI
5) Grain to leaf ratio	F_2G
6) Height	F_2HT
7) Kernel number per plant	F_2KN
8) Peduncle length	F_2PD LN
9) Days to anthesis	F_2D→A
10) Days anthesis to maturity	F_2DA→M
11) Days in growing season	F_2DGS
12) Visual yield estimate, selector one	F_2VYE 1
13) Visual yield estimate, selector two	F_2VYE 2
14) Visual yield estimate, selector three	F_2VYE 3
15) Visual yield estimate, selector four	F_2VYE 4
16) Visual yield estimate, selector five	F_2VYE 5
17) 1000 kernel weight	F_2MK WT
18) Tiller number per plant	F_2TN
19) Spikelet number per tiller	F_2SN/T
20) Kernel number per tiller	F_2KN/T
21) Yield per tiller	F_2Y/T
22) Productivity per tiller	F_2P/T
23) Leaf area duration per tiller	F_2LAD/T
24) Flag leaf area per tiller	F_2FLA/T
25) Maximum leaf area per tiller	F_2MAX LA/T

being (i) yield components (17, (18), and (20), (ii) growth analysis (3), (5), and (23), (iii) morphology and agronomy in relation to photosynthesis (6), (7), (8), (19), (24), and (25), (iv) early generation selection for yield (1) and (21), and (v) yield selection criteria (2), (4), (9), (10), (11), and (22).

As a control, five selectors were asked to visually rate the F_2 populations for yield potential (12), (13), (14), (15) and (16).

A definition of each of the F_2 parameters studied is as follows:

Yield per plant: total grain dry weight measured on material dried to constant weight at 30°C.

Productivity per plant: total above ground dry weight measured on material dried to constant weight at 30°C.

Leaf area duration per plant: determined from nondestructive biweekly measurements of leaf area using a leaf area scale devised by Owen (1968) plus stem, sheath and ear areas calculated as cylinder surfaces for the main tiller multiplied by tiller number and time integrated from anthesis to maturity. Amount of photosynthetically active material was visually determined by green coloration at each measurement.

Harvest index: Obtained by dividing yield per plant by productivity per plant and multiplying by 100.

Grain to leaf ratio: obtained by dividing yield per plant by leaf area duration per plant.

Height: measured three weeks after anthesis, the measurement being made from ground level to the tip of the main tiller excluding awns.

Kernel number per plant: a count of all kernels produced by a plant measured with an electronic seed counter.

Peduncle length: measured three weeks after anthesis, taken as the distance from the flag leaf node to the base of the ear on the main culm.

Days to anthesis: taken as the time in days from sowing to anthesis.

Days anthesis to maturity: taken as the time in days from anthesis to visually assessed maturity.

Days in growing season: taken as the time in days from sowing to visually assessed maturity.

Visual yield estimates: a visual assessment of a single plant's yield potential expressed on a scale of 1 to 5 with 1 low yielding and 5 high yielding with 3 equal to the check variety yield.

1000 kernel weight: determined by dividing yield per plant by kernel number per plant and multiplying by 1000.

Tiller number per plant: taken as the number of fertile tillers on the plant measured one week before maturity.

Spikelet number per tiller: taken on the main tiller ear three weeks after anthesis.

Kernel number per tiller: determined by dividing kernel number per plant by tiller number per plant.

Yield per tiller: determined by dividing yield per plant by tiller number per plant.

Productivity per tiller: determined by dividing productivity per plant by tiller number per plant.

Leaf area duration per tiller: determined from nondestructive biweekly measurements of leaf area plus stem, sheath and ear areas and time integrated from anthesis to maturity on the main tiller.

Flag leaf area per tiller: taken as the area of the flag leaf of the main tiller measured with a nondestructive leaf area scale at anthesis.

Maximum leaf area per tiller: determined from nondestructive measurement of leaf area, stem, sheath and ear area on the main tiller at anthesis.

3.2.1 F_3 Nursery

The F_3 generation was handled in two ways. In the first, a random sample of 50 seeds from every F_2 plant was sent to Cuidad Obregon, Mexico in the winter of 1976-77 and planted in 1 m short rows to generate F_4 bulk seed for testing in Winnipeg in the summer of 1977. In the second, one 3 row by 3 m plot of each F_3 line represented in the F_4 yield trials was grown in the summer of 1977 with replicated random inside row samples taken for the determination of the parameters listed in Figure 3.

Figure 3. Characteristics measured on F_3 inside row samples

Parameter	Abbreviation
26) F_3 Yield	F_3Y
27) F_3 Productivity	F_3P
28) F_3 Harvest Index	F_3HI
29) F_3 Leaf Area Duration	F_3LAD
30) F_3 Grain to Leaf Ratio	F_3G
31) F_3 Height	F_3HT
32) F_3 Tiller number per ½m sample	$F_3TN/\frac{1}{2}m$
33) F_3 Flag Leaf Area per tiller	F_3FLA/T
34) F_3 Maximum Leaf Area per tiller	$F_3MAX\ LA/T$

A definition of each of the F_3 parameters studied is as follows:

Yield: mean of two random ten tiller samples, total grain dry weight measured on material dried to constant weight at 30°C.

Productivity: mean of two random ten tiller samples, total dry weight measured on material dried to constant weight at 30°C.

Harvest index: obtained by dividing yield by productivity and multiplying by 100.

Leaf area duration: determined as a mean of four random tillers from nondestructive biweekly measurements of leaf area using a leaf area scale, plus stem, sheath and ear areas time integrated from anthesis to maturity.

Grain to leaf ratio: obtained by dividing mean yield by mean leaf area duration.

Height: measured three weeks after anthesis, the measurement being made on a typical tiller in the plot from ground level to the tip of the chosen tiller.

Tiller number per ½ m sample: a count of the number of tillers in a ½ m inside row random sample.

Flag leaf area per tiller: determined as a mean of four random flag leaves (same as for LAD) measured using a leaf area scale.

Maximum leaf area per tiller: determined as a mean of four random tillers (same as for LAD) measured at anthesis for leaf area plus stem, sheath and ear areas.

3.2.2 F_4 Nursery

The F_4 generation (from F_3 bulks grown in Mexico) was used as a yield trial generation. 120 F_4 bulks from each cross (45 from stress-free grown F_2's and 75 from normally grown F_2's) were grown in a 6 replicate, partially balanced lattice design at Winnipeg with plots 3 row X 3 metres with 15 cm row spacing in plots and 60 cm spacing between plots. The entire plot was harvested using a Hege 125 mobile plot combine. The seed was dried to constant weight and then weighed, yield being expressed in g per plot. The F_4 yield is hereafter abbreviated as F_4Y.

3.3 Statistical Methods

Simple and multiple correlation analyses were used to investigate the relationship of F_2 parameters with themselves and with F_4 bulk yield and to investigate the relationship of F_3 parameters with themselves and with F_4 bulk yield, Steel and Torrie (1960).

As well, a stepwise multiple regression analysis was used to investigate the relationship of F_2 parameters to F_4 bulk mean yield and F_3 parameters to F_4 bulk mean yield. This technique allows the regressing in an exploratory manner the independent variable on the dependent variable (F_4 bulk mean yield). Taking various independent variables into a single regression equation, the statistical technique minimizes the amount of unexplained residual variance in the dependent variable, thus generating predictions of F_4 bulk mean yields which can be compared with actual F_4 bulk mean yields to determine how efficient the parameters selected are in predicting yield potential, Draper and Smith (1960).

The F_4 yield data were analyzed as a 6 replicate partially balanced lattice design analysis of variance. Coefficients of variation were determined for each cross. Appropriate adjusted mean bulk yields were calculated for each F_4 bulk tested and these adjusted means were used in the preceeding statistical analyses, Cochran and Cox (1957).

4. RESULTS AND DISCUSSION

4.1 Handling of F_2's

Since the F_2 populations from each cross were grown under two different regimes (stress-free and normal field conditions) to see if the handling of the F_2 has any effect on the ability to select promising F_2 genotypes, it is necessary to show that growth was significantly different in the two regimes (growth measured in terms of yield and productivity) Table 3.

TABLE 3. Differences in F_2 populations from stress-free field environment and normal field environment.

	Stress-free	Normal	$P(\bar{x}_{s.f.} = \bar{x}_n)$
	Glenlea X Neepawa		
Yield	68.0 ± 16.5	46.3 ± 18.7	<.01
Productivity	167.7 ± 34.5	137.7 ± 41.6	<.01
	Glenlea X Era		
Yield	79.9 ± 24.1	56.8 ± 19.4	<.01
Productivity	178.2 ± 43.4	146.2 ± 43.0	<.01
	Glenlea X NB 320		
Yield	73.9 ± 34.3	59.8 ± 23.9	<.01
Productivity	164.4 ± 69.8	151.2 ± 52.3	>.1

Yield and Productivity expressed in g per plant

As can be seen from Table 3, the plants grown in a stress-free field environment were significantly larger and gave significantly higher yields than plants grown in normal field conditions. Therefore the F_2 populations are significantly different and any difference in the ability to predict high yielding F_4 bulks from the F_2's will be real and valid.

4.2 Characterization of F_2, F_3, and F_4 Populations

Because of the copious amounts of data collected in the F_2 and F_3 for each cross, it is possible to present here only the means and standard deviations for the parameters measured in these generations. As well, the F_4 bulk mean yields are presented in Tables 4 through 9 for intercross comparative purposes.

It is noted that the Glenlea X Neepawa cross was the lowest yielding in F_2 in both stress-free and normal field environments while it was the highest yielding cross in F_4 (as a mean of all bulks tested). Even though the Glenlea X Neepawa populations had the highest mean yields in F_4, they had the smallest standard deviations of the mean and the fewest high yielding bulks in F_4 with only a small number of F_4 bulks significantly outyielding the check. The other two crosses, in contrast, had lower mean yields in F_4 but much larger standard deviations from the mean with many F_4 bulks exceeding the check in yield.

Since all of the following analyses rely on comparisons with F_4 yield trial results, the results of the F_4 yield trials are presented at this time.

The complete analysis of variance for each F_4 population of the three crosses are presented in appendix Tables 1 and 2 and the appropriate adjusted mean yields for each F_4 bulk of the six F_4 populations are presented in appendix Tables 3 through 8.

The coefficients of variation for the F_4 yield trials ranged from 10.2% to 12.6% with L.S.D.'s ranging from 105.2 g to 128.5 g. In all cases variety effects (differences among F_4 bulks) were significant at the 0.1% level, therefore indicating that there were highly significant differences in yield among the F_4 bulks tested in each population. Using the information presented in Tables 1 through 8 of the appendix, it is possible to determine the number of bulks significantly higher yielding than the mean in each F_4 population. This determination indicates that Glenlea X Neepawa stress-free had two, Glenlea X Era stress-free had eight, Glenlea X NB 320 stress-free had eight, Glenlea X Neepawa normal had six, Glenlea X Era normal had sixteen and Glenlea X NB 320 normal had seventeen F_4 bulks significantly higher yielding than their respective population means.

A statistician would no doubt use the foregoing significant high yielding bulks to provide values upon which F_2 and F_3 comparisons would be drawn, however a plant breeder would use a different approach. The plant breeder would first ascertain the mean yield of his high yielding check variety (in this case Glenlea with a mean yield of 1000 g), and then consider all F_4 bulks which equalled or exceeded this figure as being high yielding and draw comparisons on these. This latter approach was used in this project to simulate a breeding program as closely as possible, however in this particular case it makes little difference which of the two methods is

TABLE 4. Characterization of F_2, F_3 and F_4 generations of Glenlea X Neepawa Stress-Free

Variable Number		Variable Name	Mean	Standard Deviation
F_2	1)	F_2Y	68.0 g	16.5
	2)	F_2P	167.7 g	34.5
	3)	F_2 LAD	178036.5 cm^2 days	43100.1
	4)	F_2 HI	40.7 %	6.5
	5)	F_2 G	39.8 mg/dm^2 days	10.9
	6)	F_2 HT	87.6 cm	5.2
	7)	F_2 KN	1712.2 kernels	397.7
	8)	F_2 PD LN	24.1 cm	2.6
	9)	F_2 D→A	44.3 days	2.6
	10)	F_2 DA→M	60.7 days	3.3
	11)	F_2 DGS	105.0 days	2.7
	12)	F_2 VYE 1	2.6	0.6
	13)	F_2 VYE 2	2.3	0.7
	14)	F_2 VYE 3	2.1	0.6
	15)	F_2 VYE 4	2.5	0.7
	16)	F_2 VYE 5	1.4	0.6
	17)	F_2 MK WT	39.8 g	3.8
	18)	F_2 TN	34.5 tillers	7.2
	19)	F_2 SN/T	14.5 spikelets	1.6
	20)	F_2 KN/T	50.7 kernels	11.1
	21)	F_2 Y/T	2.0 g	0.5
	22)	F_2 P/T	4.9 g	0.9
	23)	F_2 LAD/T	5145.5 cm^2 days	532.9
	24)	F_2 FLA/T	27.4 cm^2	3.7
	25)	F_2 MAX LA/T	172.7 cm^2	17.8
F_3	26)	F_3 Y	11.9 g	2.2
	27)	F_3 P	28.3 g	4.4
	28)	F_3 HI	42.0 %	5.6
	29)	F_3 LAD/T	4999.4 cm^2 days	493.3
	30)	F_3 G	23.9 mg/dm^2 days	4.5
	31)	F_3 HT	101.9 cm	4.9
	32)	F_3 TN/½m	40.6 tillers	10.9
	33)	F_3 FLA/T	30.6 cm^2	4.0
	34)	F_3 MAX LA/T	207.8 cm^2	14.7
F_4	35)	F_4 Y	904.6 g	72.1

TABLE 5. Characterization of F_2, F_3 and F_4 generations of Glenlea X Era Stress-Free

Variable Number	Variable Name	Mean	Standard Deviation
F_2 1)	F_2Y	79.9 g	24.2
2)	F_2P	178.2 g	43.4
3)	F_2 LAD	157884.1 cm^2 days	43841.8
4)	F_2 HI	44.6 %	6.3
5)	F_2 G	51.5 mg/dm^2 days	12.4
6)	F_2 HT	83.2 cm	7.4
7)	F_2 KN	2131.0 kernels	619.6
8)	F_2 PD LN	21.0 cm	619.6
9)	F_2 D→ A	45.2 days	2.5
10)	F_2 DA→ M	60.4 days	4.0
11)	F_2 D GS	105.8 days	3.3
12)	F_2 VYE 1	3.0	0.5
13)	F_2 VYE 2	1.9	0.6
14)	F_2 VYE 3	2.3	0.6
15)	F_2 VYE 4	2.4	0.9
16)	F_2 VYE 5	1.8	0.7
17)	F_2 MK WT	37.8 g	4.6
18)	F_2 TN	32.7 tillers	6.7
19)	F_2 SN/T	15.6 spikelets	1.5
20)	F_2 KN/T	65.1 kernels	15.3
21)	F_2 Y/T	2.4 g	0.6
22)	F_2 P/T	5.5 g	1.2
23)	F_2 LAD/T	4795.9 cm^2 days	701.8
24)	F_2 FLA/T	26.2 cm^2	4.8
25)	F_2 MAX LA/T	160.9 cm^2	21.1
F_3 26)	F_3 Y	14.9 g	3.8
27)	F_3 P	32.8 g	5.3
28)	F_3 HI	45.8 %	8.9
29)	F_3 LAD/T	5101.2 cm^2 days	908.9
30)	F_3 G	30.2 mg/dm^2 days	9.3
31)	F_3 HT	98.6 cm	7.5
32)	F_3 TN/½m	40.2 tillers	11.2
33)	F_3 FLA/T	31.8 cm^2	4.7
34)	F_3 MAK LA/T	202.5 cm^2	22.1
F_4 35)	F_4 Y	900.3 g	140.4

TABLE 6. Characterization of F_2, F_3 and F_4 generations of Glenlea X NB 320 Stress-Free

Variable Number	Variable Name	Mean	Standard Deviation
F_2 1)	F_2Y	73.9 g	34.3
2)	F_2P	164.4 g	69.8
3)	F_2 LAD	147980.5 cm^2 days	65163.2
4)	F_2 HI	44.7 %	6.2
5)	F_2G	49.5 mg/dm^2 days	14.0
6)	F_2 HT	79.9 cm	8.9
7)	F_2 KN	1830.7 kernels	806.2
8)	F_2 PD LN	19.0 cm	4.2
9)	F_2 D→A	47.8 days	5.8
10)	F_2 DA→M	57.6 days	6.5
11)	F_2 DGS	105.3 days	3.9
12)	F_2 VYE 1	3.0	0.6
13)	F_2 VYE 2	2.1	0.8
14)	F_2 VYE 3	2.3	0.9
15)	F_2 VYE 4	2.4	1.0
16)	F_2 VYE 5	1.9	0.7
17)	F_2 MK WT	40.2 g	5.5
18)	F_2 TN	27.9 tillers	9.6
19)	F_2 SN/T	15.8 spikelets	1.8
20)	F_2 KN/T	63.9 kernels	15.0
21)	F_2 Y/T	2.6 g	0.6
22)	F_2 P/T	5.8 g	1.2
23)	F_2 LAD/T	5159.1 cm^2 days	833.9
24)	F_2 FLA/T	24.1 cm^2	3.8
25)	F_2 MAX LA/T	172.0 cm^2	22.2
F_3 26)	F_3 Y	17.6 g	3.0
27)	F_3 P	39.9 g	5.2
28)	F_3 HI	44.2%	6.9
29)	F_3 LAD/T	5381.9 cm^2 days	775.8
30)	F_3 G	33.4 mg/dm^2 days	7.8
31)	F_3 HT	102.9 cm	10.5
32)	F_3 TN/½m	35.0 tillers	6.8
33)	F_3 FLA/T	31.8 cm^2	5.2
34)	F_3 MAX LA/T	225.7 cm^2	26.7
F_4 35	F_4 Y	874.2 g	115.8

TABLE 7. Characterization of F_2, F_3 and F_4 generations of Glenlea X Neepawa Normal

Variable Number	Variable Name	Mean	Standard Deviation
F_2 1)	F_2Y	46.3 g	18.7
2)	F_2P	137.8 g	41.6
3)	F_2 LAD	155921.9 cm^2 days	63526.2
4)	F_2 HI	33.4 %	7.8
5)	F_2 G	30.9 mg/dm^2 days	9.4
6)	F_2 HT	88.8 cm	11.8
7)	F_2 KN	1253.2 kernels	489.9
8)	F_2 PD LN	22.7 cm	3.9
9)	F_2 D→ A	58.9 days	7.2
10)	F_2 DA→ M	43.6 days	6.3
11)	F_2 DGS	102.6 days	12.2
12)	F_2 VYE 1	2.9	0.6
13)	F_2 VYE 2	1.9	0.7
14)	F_2 VYE 3	2.1	0.7
15)	F_2 VYE 4	2.3	0.9
16)	F_2 VYE 5	1.4	0.7
17)	F_2 MK WT	35.6 g	7.3
18)	F_2 TN	23.1 tillers	7.3
19)	F_2 SN/T	16.2 spikelets	2.3
20)	F_2 KN/T	54.2 kernels	15.9
21)	F_2 Y/T	1.9 g	0.6
22)	F_2 P/T	5.9 g	1.1
23)	F_2 LAD/T	6496.8 cm^2 days	1239.5
24)	F_2 FLA/T	33.3 cm^2	5.5
25)	F_2 MAX LA/T	202.7 cm^2	29.3
F_3 26)	F_3 Y	12.6 g	2.31
27)	F_3 P	30.9 g	4.8
28)	F_3 HI	40.9 %	4.8
29)	F_3 LAD/T	4778.0 cm^2 days	760.6
30)	F_3 G	27.4 mg/dm^2 days	6.9
31)	F_3 HT	105.1 cm	5.4
32)	F_3 TN/½m	40.3 tillers	11.7
33)	F_3 FLA/T	32.1 cm^2	4.6
34)	F_3 MAX LA/T	208.9 cm^2	19.2
F_4 35)	F_4 Y	909.9 g	81.5

TABLE 8. Characterization of F_2, F_3 and F_4 generations of Glenlea X Era Normal

Variable Number	Variable Name	Mean		Standard Deviation
F_2 1)	F_2Y	56.9	g	19.4
2)	F_2P	146.3	g	43.0
3)	F_2 LAD	151285.1	cm^2 days	56080.5
4)	F_2 HI	38.6	%	5.3
5)	F_2 G	39.5	mg/dm^2 days	9.6
6)	F_2 HT	84.7	cm	7.9
7)	F_2 KN	1708.4	kernels	533.9
8)	F_2 PD LN	19.8	cm	4.1
9)	F_2 D→A	62.5	days	3.4
10)	F_2 DA→M	44.8	days	3.8
11)	F_2 DGS	107.3	days	3.0
12)	F_2 VYE 1	2.8		0.5
13)	F_2 VYE 2	1.9		0.6
14)	F_2 VYE 3	2.1		0.6
15)	F_2 VYE 4	2.9		0.9
16)	F_2 VYE 5	2.2		0.8
17)	F_2 MK WT	33.7	g	5.3
18)	F_2 TN	22.5	tillers	6.9
19)	F_2 SN/T	17.8	spikelets	1.4
20)	F_2 KN/T	77.5	kernels	18.5
21)	F_2 Y/T	2.6	g	0.6
22)	F_2 PIT	6.7	g	1.6
23)	F_2 LAD/T	6661.3	cm^2 days	1084.2
24)	F_2 FLA/T	35.3	cm^2	5.5
25)	F_2 MAX LA/T	209.1	cm^2	26.3
F_3 26)	F_3 Y	15.3	g	2.3
27)	F_3 P	33.9	g	5.4
28)	F_3 HI	45.7	%	5.7
29)	F_3 LAD/T	4987.9	cm^2 days	813.4
30)	F_3 G	31.5	mg/dm^2 days	6.9
31)	F_3 HT	101.8	cm	9.2
32)	F_3 TN/½m	28.3	tillers	6.2
33)	F_3 FLA/T	33.7	cm^2	4.1
34)	F_3 MAX LA/T	205.1	cm^2	22.7
F_4 35)	F_4 Y	872.2	g	131.0

TABLE 9. Characterization of F_2, F_3 and F_4 generations of Glenlea X NB 320 Normal

Variable Number	Variable Name	Mean	Standard Deviation
F_2 1)	F_2Y	59.8 g	23.9
2)	F_2P	151.2 g	52.2
3)	F_2 LAD	186892.0 cm^2 days	80331.1
4)	F_2 HI	38.9 %	7.1
5)	F_2 G	33.7 mg/dm^2 days	9.2
6)	F_2 HT	83.9 cm	8.2
7)	F_2 KN	1687.7 kernels	665.4
8)	F_2 PD LN	20.1 cm	3.9
9)	F_2 D→A	60.9 days	2.6
10)	F_2 DA→M	45.1 days	4.9
11)	F_2 DGS	106.1 days	4.4
12)	F_2 VYE 1	3.1	0.6
13)	F_2 VYE 2	1.9	0.7
14)	F_2 VYE 3	2.2	0.6
15)	F_2 VYE 4	2.8	0.9
16)	F_2 VYE 5	2.2	0.6
17)	F_2 MK WT	35.7 g	6.4
18)	F_2 TN	26.1 tillers	9.4
19)	F_2 SN/T	18.4 spikelets	1.5
20)	F_2 KN/T	65.3 kernels	13.8
21)	F_2 Y/T	2.3 g	0.6
22)	F_2 P/T	5.9 g	1.2
23)	F_2 LAD/T	7012.7 cm^2 days	1143.3
24)	F_2 FLA/T	34.5 cm^2	4.9
25)	F_2 MAX LA/T	212.7 cm^2	28.1
F_3 26)	F_3 Y	16.9 g	2.8
27)	F_3 P	38.6 g	5.3
28)	F_3 HI	43.9 %	5.7
29)	F_3 LAD/T	5257.7 cm^2 days	893.7
30)	F_3 G	33.0 mg/dm^2 days	7.3
31)	F_3 HT	99.9 cm	10.5
32)	F_3 TN/½m	24.9 tillers	6.5
33)	F_3 FLA/T	31.5 cm^2	4.9
34)	F_3 MAX LA/T	215.9 cm^2	25.2
F_4 35)	F_4 Y	856.3 g	146.7

used since the high yielding bulks chosen are identical in 47 out of 52 cases.

4.3 Simple Correlation Analysis

A simple correlation analysis for F_2, F_3 and F_4 parameters in all possible combinations was performed for each population of each cross and the results appear in appendix Tables 9 through 14.

For Glenlea X Neepawa stress-free, the significant simple correlations with F_4 bulk yield were:

a) F_2 MAX LA/T (25), r = .50**
b) F_2 SN/T (19), r = .35*
c) F_3 HT (31), r = .35*
d) F_2 LAD/T (23), r = .34*
e) F_2 MKWT (17), r = .31*
f) F_2 D→ A (9), r = .28*

It is noted that all correlations are positive with F_2 MAX LA/T, F_2 LAD/T and F_2D→ A indicating source limitation on yield and F_2 SN/T plus F_2 MK WT indicating sink limitation on yield in this cross. Thus, for this particular cross both source and sink capacity would have to be increased to increase yield, with the major emphasis being placed on increased source capacity.

If one were to attempt to use a single F_2 parameter to select F_2 genotypes which give rise to high yielding F_4 bulks, it would in this case be MAX LA/T. Retention of all plants with MAX LA/T of 175.0 cm^2 or greater results in the retention of 21 out of 49 (or 43%) plants and 5 out of 5 of the high yielding F_4 bulks. This success is achieved only at the expense of a low selection intensity however.

For F_3, the single most efficient parameter would be F_3 height. In this cross, retaining all plots with a height of 103 cm or greater results in retention of 22 out of 49 (or 45%) of the F_3 lines and 5 out of 5 of the high yielding F_4 bulks. As per usual, the ability to retain high yielding lines is tied to the low selection intensity used.

For Glenlea X Era stress-free, the significant correlations with F_4 bulk mean yield were:

a) F_2 VYE 3 (14), r = .44**
b) F_2 PD LN (8), r = -.41**
c) F_2 VYE 4 (15), r = .40**
d) F_2 KN/T (20), r = .39**
e) F_3 HT (31), r = -.39**
f) F_2 KN (7), r = .38**
g) F_2 VYE 1 (12), r = .36**
h) F_3 G (30), r = .35*
i) F_3 Y (26), r = .35*
j) F_2 FLA/T (24), r = .34*
k) F_2 VYE 2 (13), r = .31*
l) F_2 Y (1), r = .30*
m) F_2 P (2), r = .30*
n) F_2 Y/T (21), r = .29*
o) F_2 VYE 5 (16), r = .29*
p) F_2 G (5), 4 = .29*

You will note that all five selectors' visual yield estimates on F_2 spaced plants were significantly correlated with F_4 bulk mean yield. Clearly if there are differences in kernel number, tiller number, head type and plant type as there were in this cross, then visual selection can be successful in picking high yielding F_2 genotypes from the F_2 population. Selectors were consistent in picking large plants with high yield per plant regardless of height.

With regards to the correlations of F_2 and F_3 parameters versus F_4 yield, two are negative, F_2 PD LN, r = -.41** and F_3 HT, r = -.39**. This indicates that in this cross one should select plants with reduced height to get maximum yield.

However, the most important parameters relating to F_4 bulk yield were those describing sink capacity with F_2 KN/T., F_2 KN, F_3 Y, F_2 Y and F_2 Y/T substantiating this point. Therefore sink capacity must be increased to increase yield.

The best single F_2 parameter to select F_2 genotypes which give rise to high yielding F_4 bulks was VYE 3. In this cross retaining all plants with a visual yield potential assessment of 3 or greater results in the retention of 16 out of 49 (or 33%) plants and 6 out of 11 (or 55%) of the high yielding F_4 bulks. Again the success is achieved at the expense of a low selection intensity.

For F_3, the best single parameter would be F_3 height. In this cross, retaining all plots with a height of 90 cm or less results in the retention of 10 out of 49 (or 20%) of the F_3 lines and 5 out of 11 (or 46%) of the high yielding F_4 bulks.

For Glenlea X NB 320 stress-free, the significant correlations with F_4 bulk mean yield were:

a) F_2 VYE 1 (12), r = .48**
b) F_2 Y/T (21), r = .43**

c) F_2 Y (1), r = .43**
d) F_2 KN (7), r = .43**
e) F_2 D→A (9), r = .40**
f) F_2 P (6) r = .40**
g) F_2 KN/T (20), r = .37**
h) F_2 P/T (22), r = .37**
i) F_3 P (27), r = .35*
j) F_2 SN/T (19), r = .32*
k) F_2 HI (3), r = .30*
l) F_2 DA→M (10), r = .30*
m) F_2 VYE 2 (13), r = .29*
n) F_3 FLA/T (33), r = .29*
o) F_2 TN (18), r = .28*
p) F_2 VYE 3 (14), r = .28*

Again it is noted that three selectors' visual yield estimates on F_2 spaced plants were significantly correlated with F_4 bulk mean yield. As in the Glenlea X Era cross, differences in kernel number, tiller number, head type and plant type were used by selectors to successfully pick high yielding F_2 genotypes from the F_2 population.

However, the most important parameters relating to F_4 bulk yield were those describing sink capacity with F_2 Y/T, F_2 Y, F_2 KN, F_2 KN/T and F_2 SN/T all indicating this. Again sink capacity must be increased to increase yield.

The best single F_2 parameter to select F_2 genotypes which give rise to high yielding F_4 bulks was VYE 1. In this cross retaining all plants with a visual yield potential rating of 3 or greater results in the retention of 40 out of 49 (or 82%) plants and 6 out of 7 (or 86%) of the high yielding F_4 bulks. It is particularly obvious in this cross that success at retaining high yielding F_4 bulks is achieved only at the expense of a low selection intensity when single F_2 parameter like visual selection estimates are used.

For F_3 the best single parameter to select F_3 lines which give rise to high yielding F_4 bulks would be F_3 productivity. In this cross, retaining all plots with a 10 tiller productivity of 42 g or greater results in the retention of 17 out of 49 (or 35%) of the F_3 plots and 6 out of 7 (or 86%) of the high yielding F_4 bulks. Thus success at retaining high yielding F_4 bulks is again at the expense of a low selection pressure.

For Glenlea X Neepawa normal, the significant correlations with F_4 mean bulk yield were:

a) F_3 MAX LA/T (34), r = .42**
b) F_3 P (27), r = .42**
c) F_3 FLA/T (33), r = .41**
d) F_3 Y (26), r = .36**
e) F_2 MAX LA/T (25), r = .29**
f) F_2 LAD/T (23), r = .28**
g) F_3 HT (31), r = .25*
h) F_3 LAD/T (29), r = .24*

Note that as in Glenlea X Neepawa stress-free, the correlations are all positive and nearly all indicate source limitation on yield in the cross progeny, (F_3 MAX LA/T, F_3 P, F_3 FLA/T, F_2 MAX LA/T, F_2 LAD/T and F_3 LAD/T). Many of the same parameters are significantly correlated with F_4 bulk mean yield in both Glenlea X Neepawa stress-free and Glenlea X Neepawa normal crosses (for example F_2 MAX LA/T and F_2 LAD/T) with the levels of significance being nearly identical in both cases. One could conclude from this that it does not matter how the F_2's are handled in relation to the strength of single parameter simple correlations with F_4 bulk yield.

The best single F_2 parameter to select F_2 genotypes was MAX LA/T, the same as it was for the Glenlea X Neepawa stress-free population. In this case retaining all plants with a MAX LA/T of 210 cm^2 or greater results in the retention of 28 out of 81 (or 35%) plants and 7 out of 7 of the high yielding F_4 bulks. The selection intensity is again quite low but did result in the retention of all the high yielding F_4 bulks.

For F_3 the best single parameter would be F_3 MAX LA/T, the same as in F_2 which serves to emphasize the source limitation present in this cross. In this case retaining all plots with a MAX LA/T of 215 cm^2 or greater results in the retention of 30 out of 81 (or 37%) of the F_3 plots and 6 out of 7 (or 86%) of the high yielding F_4 bulks. This success is achieved at a low selection intensity of 37%.

For Glenlea X Era normal, the significant correlations with F_4 mean bulk yield were:

a) F_2 HT (6), $r = -.39$**
b) F_3 HT (31), $r = -.32$**
c) F_2 PD LN, $r = -.29$**
d) F_2 G (5), $r = -.28$**
e) F_2 LAD (3), $r = -.26$*
f) F_2 LAD/T (23) $r = -.25$*
g) F_3 LAD/T (29) $r = -.24$*
h) F_2 VYE 5 (16) $r = .24$*
i) F_2 MKWT (17) $r = -.23$*

In this case all correlations are negative except for VYE 5. The results in this case are consistent with Glenlea X Era stress-free where it was concluded that sink size must be increased to increase yield. In this case source parameters are important in determining yield (F_2 G, F_2 LAD, F_2 LAD/T, and F_3 LAD/T) but the correlations with F_4 bulk yield are negative indicating that the source capacity is too large relative to the sink capacity, or stated in another way, the sink capacity is too small.

The most highly correlated parameter with F_4 bulk yield was height where plants with reduced height gave greater yield than taller plants, probably due to a more favourable balance of sink and source capacity in the shorter plants.

Since the correlation of F_4 yield with height is negative, one has to select the short plants (those less than 80 cm tall) in the F_2 population. Retaining all plants with a height of 80 cm or less results in the retention of 23 out of 81 (or 28%) plants and 5 out of 10 of the high yielding F_4 bulks. The selection intensity is moderately low here but only half of the high yielding lines are retained.

The best F_3 parameter to use would be F_3 HT. Retaining all plots with a height of 95 cm or less results in the retention of 20 out of 81 (or 25%) of the F_3 plots and 5 out of 10 of the high yielding F_4 bulks.

For Glenlea X NB 320 normal, the significant correlations with F_4 bulk mean yield were:

a) F_2 VYE 1 (12), r = .29**
b) F_2 KN (7), r = .29**
c) F_2 P (2), r = .24*
d) F_2 VYE 4 (15), r = .24*
e) F_2 TN (18), r = .23*
f) F_2 HI (4), r = .23*
g) F_3 LAD/T (29), r = .22*

Two selectors' visual yield estimates were significantly correlated with F_4 bulk yield. Again, differences in kernel number, plant type and head type were used by selectors to successfully pick high yielding F_2 genotypes from the F_2 population.

However, the most important parameters are again those relating to sink capacity (F_2 KN, F_2 TN and F_2 HI) with an increase in sink size required to obtain increased yields.

The best single F_2 parameter to use to select F_2 genotypes which gave rise to high yielding F_4 bulks was VYE 1. Retaining all plants with a visual yield potential rating of 3 or greater results in the retention of 56 out of 81 plants (or 69%) plants and 13 out of 13 high yielding F_4 bulks. The selection intensity is very low but all high yielding lines were retained by this selection method.

The F_3 parameter to be used to identify high yielding F_4 bulks would be F_3 LAD/T in this case. Retaining all plots with an LAD per tiller of 5500 cm^2 days or greater results in the retention of 34 out of 81 (or 42%) of the F_3 plots and 6 out of 13 (or 46%) of the high yielding F_4 bulks. This is not significantly different from random even though a low selection intensity was used.

This then covers all the significant simple correlations between F_2 and F_3 parameters versus F_4 bulk yield. However, it is important to also look at the simple correlations among F_2 and F_3 parameters to see if attempts to increase sink or source capacity in the cross progeny are likely to be hindered by strong negative correlations. Only strong negative correlations will be discussed since strong positive correlations are beneficial and zero correlations imply independence and so would not be detrimental to the plant breeding program.

For Glenlea X Neepawa stress-free, the significant negative correlations among F_2 and F_3 parameters were:

a) F_2 LAD versus F_2 HI r = -.35*
b) F_2 LAD versus F_2 G r = -.60**
c) F_2 LAD versus F_2 KN/T r = -.41**
d) F_2 LAD versus F_2 Y/T r = -.43**
e) F_2 LAD versus F_2 P/T r = -.35*
f) F_2 G versus F_2 HT r = -.38**
g) F_2 D→A versus F_2 DA→M r = -.61**
h) F_2 HI versus F_2 TN r = -.36*
i) F_2 G versus F_2 TN r = -.51**
j) F_2 TN versus F_2 KN/T r = -.48**
k) F_2 TN versus F_2 Y/T r = -.40**
l) F_2 TN versus F_2 P/T r = -.44**
m) F_3 LAD/T versus F_3 G r = -.35*
n) F_3 TN/½m versus F_2 KN/T r = -.29*
o) F_3 TN/½m versus F_2 Y/T r = -.28*
p) F_3 TN/½m versus F_2 P/T r = -.21*

It appears from the above that F_2 LAD is the parameter which will cause the most trouble to the plant breeder since it has already been ascertained that yield increases in this cross depend on increases of source capacity. To increase source capacity, LAD would have to be increased but at the same time KN/T, Y/T and P/T would inevitably decline. The only answer would seem to be to increase tiller number to increase LAD but again the breeder would run into strong negative correlations with KN/T and Y/T declining as tiller number goes up. The same trend is true in F_3 where increases in TN/½m results from decreased KN/T and Y/T selections in F_2. It is obvious that if these negative correlations were perfect then it would be impossible to breed for increased yield in the Glenlea X Neepawa stress-free cross. However, the correlations are not perfect and there are exceptions to the general rules determined from the population. By choosing these exceptions, yield advancement can be made in this cross. However any yield advancement obtained will be minimal and have involved the expenditure of a great deal of time and effort because of the size and number of negative correlations present in the progeny of this cross make the breeder's job difficult.

For Glenlea X Era stress-free, the significant negative correlations among F_2 and F_3 parameters were:

a) F_2 G versus F_2 LAD/T r = -.29*
b) F_2 HT versus F_2 HI r = -.37**
c) F_2 HT versus F_3 G r = -.28*
d) F_2 PD LN versus F_2 D→A r = -.29*
e) F_2 PD LN versus F_3 G r = -.31*
f) F_2 D→A versus F_2 DA→M r = -.57**

g) F_2 D→A versus F_2 MK WT r = -.32*
h) F_2 MK WT versus F_2 KN/T r = -.32*
i) F_2 MK WT versus F_3 TN/½m r = -.35*
j) F_3 HI versus F_3 LAD/T r = -.34*
k) F_3 HI versus F_3 MAX LA/T r = -.39**
l) F_3 LAD/T versus F_3 G r = -.52**
m) F_3 MAX LA/T versus F_3 G r = -.38**

The strong negative correlations in this cross are consistent and very easy to interpret and are such that no major problem for the plant breeder is likely to arise. The most noticeable correlations are those between the yield components where it appears that increases in MK WT results in a decrease in KN/T or decreases in TN/½m. Since these negative correlations are not very strong, it is likely that the problem of yield component compensation can be largely circumvented in this cross. The other correlations of note are between HI or G and LAD. Here it is obvious that the source potential in this cross is too large relative to the sink potential, or as previously stated, the sink capacity is too small to accept all the available photosynthate in this cross.

For Glenlea X NB 320 stress-free, the significant negative correlations among F_2 and F_3 parameters were:

a) F_2 HI versus F_2 HT r = -.35*
b) F_2 HI versus F_2 FLA/T r = -.35**
c) F_2 HI versus F_2 MAX LA/T r = -.31*
d) F_2 HI versus F_3 HI r = -.28*
e) F_2 HI versus F_3 FLA/T r = -.52**
f) F_2 HI versus F_3 MAX LA/T r = -.31*
g) F_2 HI versus F_3 HI r = -.33*
h) F_2 D→A versus F_2 DA→M r = -.80**

i) F_2 DA→M versus F_2 SN/T r = -.35*
j) F_2 DA→M versus F_2 MAX LA/T r = -.35*
l) F_2 G versus F_2 LAD/T r = -.35*
m) F_2 FLA/T versus F_3 HI r = -.31*
n) F_2 FLA/T versus F_3 G r = -.29*
o) F_2 MAX LA/T versus F_3 HI r = -.35*
p) F_3 LAD/T versus F_3 HI r = -.35*
q) F_3 LAD/T versus F_3 G r = -.68**
r) F_3 HT versus F_3 HI r = -.30*

Again, like the Glenlea X Era stress-free cross, these correlations are consistent with the known sink limitations in the Glenlea X NB 320 stress-free cross. In fact nearly all of the strong negative correlations observed except for those between HT and HI and D→A versus DA→M are consistent with a sink limited cross. When the breeder is able to increase the sink capacity of this cross relative to the source capacity most of these negative correlations will disappear or be reduced.

For Glenlea X Neepawa normal, the significant negative correlations among F_2 and F_3 parameters were:

a) F_2 Y versus F_3 G r = -.23*
b) F_2 LAD versus F_2 G r = -.33**
c) F_2 HI versus F_3 Y r = -.23*
d) F_2 HI versus F_3 P r = -.34**
e) F_2 HI versus F_3 G R = -.44**
f) F_2 HI versus F_3 FLA/T r = -.24*
g) F_2 G versus F_2 TN r = -.32**
h) F_2 G versus F_2 MAX LA/T r = -.36**
i) F_2 G versus F_3 P r = -.23*
j) F_2 G versus F_3 G r = -.27*
k) F_2 Y/T versus F_3 G r = -.24*

l) F_3 HI versus F_3 HT r = -.28*
m) F_2 D→A versus F_3 LAD/T r = -.22*
n) F_3 LAD/T versus F_3 G r = -.45**

The two parameters of greatest concern to the plant breeder in this cross have to be HI and G. The results are anomalous and suspect since they indicate that reductions in HI and G will result in greater productivity and indirectly, to greater yield. This will be accomplished by increasing LAD and height and by increasing the length of the grain filling period, i.e. increasing source capacity. When this cross is grown under normal field conditions no sink limitations are evident which is different from what is observed when this cross is grown under a stress-free regime.

For Glenlea X Era normal, the significant negative correlations among F_2 and F_3 parameters were:

a) F_2 Y versus F_2 D→A r = -.48**
b) F_2 P versus F_2 D→A r = -.31**
c) F_2 LAD versus F_2 G r = -.51**
d) F_2 LAD versus F_2 D→A r = -.52**
e) F_2 LAD versus F_2 P/T r = -.27*
f) F_2 HI versus F_2 D→A r = -.53**
g) F_2 HI versus F_2 P/T r = -.25*
h) F_2 G versus F_2 HT r = -.26*
i) F_2 G versus F_2 DA→M r = -.22*
j) F_2 G versus F_2 TN r = -.42**
k) F_2 G versus F_2 LAD/T r = -.43**
l) F_2 G versus F_3 MAX LA/T r = -.34**
m) F_2 HT versus F_2 D→A r = -.34**
n) F_2 HT versus F_3 G r = -.36**
o) F_2 KN versus F_2 D→A r = -.32**
p) F_2 PD LN versus F_3 G r = -.37**

q) F_2 D→A versus F_2 DA→M   r = -.66**
r) F_2 D→A versus MK WT   r = -.41**
s) F_2 D→A versus F_2 TN   r = -.50**
t) F_2 D→A versus F_2 LAD/T   r = -.33**
u) F_2 MK WT versus F_2 KN/T   r = -.34**
v) F_2 TN versus F_2 KN/T   r = -.38**
w) F_2 TN versus F_2 Y/T   r = -.27*
x) F_2 TN versus F_2 P/T   r = -.45**
y) F_3 P versus F_3 HI   r = -.44**
z) F_3 HI versus F_3 LAD/T   r = -.26*
ai) F_3 HI versus F_3 HT   r = -.35**
bi) F_3 HI versus F_3 FLA/T   r = -.34**
ci) F_3 HI versus F_3 MAX LA/T   r = -.24*
di) F_3 LA D/T versus F_3 G   r = -.69**
ei) F_3 G versus F_3 HT   r = -.41*
fi) F_3 G versus F_3 MAX LA/T   r = -.29**

The correlations in this cross are consistent with sink limitations on yield. Harvest index is negatively correlated with both productivity and leaf area duration as well as with leaf area. Reductions in source capacity or increases in sink capacity to more evenly balance the two is required to attain maximum yield in this cross. The negative correlation between TN and KN/T will make increasing sink capacity difficult but not impossible since MK WT can be increased by lengthening the DA→M period which will automatically reduce the length of the D→A period.

As with all crosses involving a tall and a semi-dwarf parent, reductions in height increase yield by increasing HI.

For Glenlea X NB 320 normal, the significant negative correlations among F_2 and F_3 parameters were:

a) F_2 Y versus F_2 D→A r = -.23*
b) F_2 LAD versus F_2 G r = -.43**
c) F_2 LAD versus F_2 D→A r = -.25*
d) F_2 HI versus F_2 D→A r = -.23*
e) F_2 HI versus F_3 FLA/T r = -.26*
f) F_2 HI versus F_3 MAX LA/T r = -.22*
g) F_2 G versus F_2 HT r = -.31**
h) F_2 G versus F_2 TN r = -.43**
i) F_2 G versus F_2 LAD/T r = -.24*
j) F_2 G versus F_2 MAX LA/T r = -.25*
k) F_2 HT versus F_2 D→A r = -.26*
l) F_2 PD LA versus F_2 D→A r = -.27*
m) F_2 D→A versus F_2 DA→M r = -.44*
n) F_2 D→A versus F_2 MK WT r = -.23*
o) F_2 D→A versus F_2 TN r = -.26*
p) F_2 D→A versus F_2 Y r = -.23*
q) F_2 D→A versus F_3 G r = -.30**
r) F_2 DA→M versus F_3 TN/½m r = -.30**
s) F_2 TN versus F_3 P r = -.27*
t) F_2 TN versus F_2 P/T r = -.43**
u) F_2 P/T versus F_3 G r = -.23*
v) F_3 LAD/T versus F_3 G r = -.66**
w) F_3 G versus F_3 HT r = -.50**
x) F_3 G versus F_3 FLA/T r = -.23*
y) F_3 G versus F_3 MAX LA/T r = -.47**

The strong negative correlations are consistent with sink limitations in this cross. HI is negatively correlated with FLA/T and MAX LA/T while G is negatively correlated with LAD/T, thus indicating that the source is too large to be in harmony with the sink capacity.

To increase yield, increases in sink capacity are required and these can be obtained by increasing MK WT and KN/T simultaneously since no strong negative correlations exist between these two. HI will be increased by the above modifications. HI increases could also be achieved by reducing height. Therefore although there are a great number of negative correlations present, few are of a magnitude that would prevent yield improvement by the plant breeder.

4.4 Multiple Regression and Correlation Analysis

Multiple regression and correlation involves linear relations among more than two variables. It is used primarily in estimation or prediction of values of one character from the knowledge of several others (in this study, F_4 bulk yield from F_2 and F_3 parameters). The F_2 and F_3 parameters considered are exclusive of the F_2 visual yield estimates by the selectors since these are not quantifiable data. The F_2 parameters are considered separately from the F_3 parameters and the F_2 is considered separately over the two environmental regimes.

The partial regression coefficients from the stepwise multiple regression analysis on F_4 bulk yield for F_2 parameters of the three crosses are given in Tables 10 through 15. Characters which explained less than 0.02 of the variance for F_4 bulk yield were not included in the tables even though they were significant in some cases. This is an arbitrary decision based on the assumption that plant breeders would not take the time to measure variables which account for less than 0.02 of the variance.

TABLE 10. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_2 parameters of the Glenlea X Neepawa stress-free cross

MAX LA/T	MK WT	DA→M	Y	R^2
2.01**	-	-	-	.246**
1.83**	4.19	-	-	.292**
1.81**	4.56	-4.95	-	.344**
2.10**	5.86*	-5.73*	-1.11	.397**

The first thing most readers will notice is that the amount of F_4 yield variance accounted for by the selected variables is low when compared with studies like Kaltsikes (1973) where in excess of 97% of the yield variance was accounted for by a regression on selected variables. However it must be remembered that in this study the F_2 parameters were measured on spaced plants in 1976 and the F_4 yield trials were conducted in plots in 1977. Thus the regressed parameters are separated by time and space and yet still nearly 40% of F_4 yield variance is accounted for by the selected F_2 parameters.

It should be noted that parameters defining both source capacity (MAX LA/T) and sink capacity (MK WT Y) enter into the regression with F_4 bulk yield. It is also noted that the time from anthesis to maturity must be shortened to increase yield and yet MK WT must be increased. Obviously LAI at anthesis must be increased substantially in order to increase yield.

The best multiple linear regression equation derived from the analysis was:

$$F_4\ Y = 731.00 + 2.10\ (\text{MAX LA/T}) + 5.86\ (\text{MK WT}) - 5.73\ (\text{DA}\rightarrow\text{M}) - 1.11\ (\text{Y})$$

In order to assess the usefulness of the multiple regression approach in plant breeding, a comparison with a random selection approach was drawn, using the hypergeometric distribution. In this cross there were 5 high yielding lines in the F_4 bulk population of 49 lines. A prediction based on the above regression equation resulted in 7 predicted high yielding lines with 3 of 7 of these predicted high yielding lines being correct. Using random selection, in only 1 out of 63 attempts would the outcome be as good or better than that obtained using multiple regression. Thus the multiple regression method is significantly better than random.

TABLE 11. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_2 parameters of the Glenlea X Era stress-free cross

PD LN	KN/T	FLA/T	R^2
-13.70**	-	-	.171**
-12.18**	3.13**	-	.284**
-12.34**	2.50*	7.70	.349**

The amount of F_4 yield variance accounted for by these 3 significant parameters is only about one third of the total variance, however again it must be remembered that the regression is based on different genotypes, phenotypes, spacings and years — a reflection of an actual breeding program.

Parameters defining both source and sink capacity enter the regression (FLA/T and KN/T respectively) but the most significant parameter is PD LN where a decrease in length of the peduncle results in substantial increases in yield, presumably by locating the ear closer to the flag leaf and thus increasing the sink demand on the source.

The best multiple regression equation derived from the analysis was:

$$F_4Y = 794.69 - 12.34\ (PD\ LN) + 2.50\ (KN/T) + 7.70\ (FLA/T)$$

Again, in order to assess the usefulness of the multiple regression approach in plant breeding, a comparison with a random selection approach was drawn using the hypergeometric distribution. In this cross there were 11 high yielding lines in the F_4 bulk population of 49 lines. A prediction based on the above regression equation resulted in 15 predicted high yielding lines with 6 out of 15 being correct. This is 21** times better than random.

TABLE 12. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_2 parameters of the Glenlea X NB 320 stress-free cross

Y/T	D→A	PD LN	G	R^2
82.09**	-	-	-	.187**
66.56**	6.12*	-	-	.275**
73.80**	6.56*	-6.70	-	.333**
116.36**	6.82*	-7.34*	-2.84*	.401**

As in the first two crosses, the amount of F_4 yield variance accounted for is less than 50%, however the amount of F_4 yield variance accounted for by F_2 parameters is greatest in this cross.

As in the Glenlea X Era stress free cross, a reduction in the length of the peduncle is required to make yield gains.

The necessity of reducing the G value to increase yield runs contrary to the sink-source relationship created by placing the ear closer to the flag leaf since a reduction in the G value would involve a lessening of photosynthate demand by the ear. These opposing trends would have to be balanced to get maximum yield.

The other two parameters which enter the regression equation are an estimate of sink capacity (Y/T) and an estimate of source capacity ($D \rightarrow A$) with Y/T being by far the most significant parameter to modify to increase yield. The increase in Y/T will be accomplished by a simultaneous increase in both harvest index and productivity.

The best multiple regression equation derived from the analysis was:

$$F_4Y = 527.79 + 116.36\ (Y/T) + 6.82\ (D \rightarrow A) - 7.34\ (PD\ LN) - 2.84\ (G)$$

In this particular cross there were 7 high yielding lines in the F_4 bulk population of 49 lines. A prediction based on the above regression equation resulted in 8 predicated high yielding lines with 4 out of 8 correct. In only one case out of 115 would random selection result in an outcome as good or better than that observed and therefore the multiple regression approach is significantly better than random.

Summarizing the multiple regression analysis results for the 3 stress-free crosses, it was observed that the amount of F_4 yield variance accounted for by selected F_2 parameters varied from 35 to 40%. It was also observed that in all crosses the regression equation developed included a sink component and a source component, the relative magnitudes of which depended on the nature of the cross combination relative to sink and source capacity. Finally it was observed that predictions based on multiple regression techniques were significantly better than random in all cases, i.e. selection of 15%, 30% and 15% of the lines in the stress-free crosses resulted in retention of 42%, 40% and 50% respectively of the high yielding lines.

Would the results be as good as this if one grew the F_2 plants under normal field conditions?

TABLE 13. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_2 parameters of the Glenlea X Neepawa normal cross

MAX LA/T	MK WT	KN	D→A	DA→M	SN/T	R^2
.81**	-	-	-	-	-	.085**
.74**	1.72	-	-	-	-	.108**
.88**	2.14	-.03	-	-	-	.135**
.84**	2.78*	-.03	-1.60	-	-	.151**
1.02**	.52	-.04	-3.22	4.94	-	.195**
.80*	-.13	-.05	-5.06**	4.64	10.49	.226**

It will be noted first of all that the amount of F_4 yield variance accounted for by F_2 parameters is down to 23% in this cross while it was nearly 40% in Glenlea X Neepawa stress-free. Clearly the greater environmental variance present in the normally treated F_2 population is detrimental to the precision of the regression equation.

Parameters defining both source capacity (MAX LA/T, D→A and DA→M) and sink capacity (MK WT, KN and SN/T) are included in the regression equation on F_4 bulk yield with SN/T and DA→ M being the most important.

It is evident from the analysis that increased leaf area at anthesis is required to get greater seed set on the spikelets of each tiller and that SN/T must be increased as well to get increased yield in this cross.

The results of the Glenlea X Neepawa stress-free and normal crosses are in good agreement even though the precision of the normal grown cross is only half that of the stress-free cross.

The best multiple linear regression equation derived from the analysis was:

$$F_4Y = 737.57 + 0.80\ (\text{MAX LA/T}) - 0.13\ (\text{MK WT}) - 0.05\ (\text{KN}) - 5.06\ (\text{D}\rightarrow \text{A}) + 4.64\ (\text{DA}\rightarrow \text{M}) + 10.49\ (\text{SN/T})$$

In this cross there were 7 high yielding lines in the F_4 bulk population of 81 lines. A predication based on the above regression equation resulted in 10 predicted high yielding lines with 4 correct. This is 286*** times better than random, and compares favourably with the Glenlea X Neepawa stress-free cross where the multiple regression analysis method was 63** times better than random.

TABLE 14. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_2 parameters of the Glenlea X Era normal cross

HT	SN/T	G	P	HI	$\bar{R}^2$
-6.49**	-	-	-	-	.156**
-7.30**	25.03*	-	-	-	.222**
-6.45**	26.29**	2.87*	-	-	.263**
-8.62**	24.64*	2.45	0.61	-	.287**
-9.04**	23.42*	2.95	0.76	-4.67	.319**

The amount of F_4 yield variance accounted for by F_2 parameters in this cross is 32%, while in the Glenlea X Era stress-free cross it was 35% so that the change of environment had minimal effect in this cross even though growth was enhanced in the stress-free environment.

The results indicate that increased yields will be associated with increased SN/T mainly, especially when combined with height reductions and a reduction in HI. Obviously MK WT will have to decline to satisfy the above requirements.

As well, increases in G, which will be effected simultaneously with HT reductions and increases in P are required to obtain maximum yields.

There will be some difficulty in obtaining all these modifications simultaneously since reductions in height usually result in increased harvest index and decreased productivity. The plant types taken forward for progeny testing will be compromises of what is desired versus what is obtainable and the rate of progress in yield advancement will be slowed accordingly.

The best multiple regression equation derived from the analysis was:

$$F_4Y = 1173.83 - 9.04\ (HT) + 23.42\ (SN/T) + 2.95\ (G) + .76\ (P) - 4.67\ (HI)$$

In this cross there were 10 high yielding lines in the bulk F_4 population of 81 lines. A prediction based on the above regression equation resulted in 14 predicted high yielding lines with 5 correct. In only 1 case out of 97 would random selection be expected to produce results as good or better than that obtained using a multiple regression analysis approach. This is significantly better than random and compares favourably with the Glenlea X Era stress-free cross where the multiple regression approach was 21** times better than random.

TABLE 15. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_2 parameters of the Glenlea X NB 320 normal cross

KN	FLA/T	MAX LA/T	R^2
.06**	-	-	.084**
.07**	-4.55	-	.106**
.07**	-5.95	.82	.129**

The first thing of note in this cross is that the amount of F_4 yield variance accounted for by F_2 parameters is down to 13% while it was 40% in the Glenlea X NB 320 stress-free cross. It was noted that the flowering and maturity dates of the normal material were quite variable (spread over nearly 4 weeks) while the flowering and maturity dates were nearly synchronous for the Glenlea X NB 320 stress-free material. Since the stress-free material was grown for a week in a cool greenhouse prior to transplanting to the field while the normal material was direct seeded into the field during what turned out to be a hot spring, it is assumed that residual winter genes in NB 320 and its progeny were the cause of the difference in the two populations. The asynchrony in the normal population results in reduced precision of the regression equation.

The regression analysis indicates that the progeny of the

Glenlea X NB 320 normal cross are sink limited with moderate increases in KN resulting in increased yield. It appears as well that there is a slight source limitation at or just before anthesis (perhaps due to the flag leaf shading the rest of the plant) which may be the cause of the inadequate KN in this cross.

The best multiple regression equation derived from the analysis was:

$$F_4Y = 775.49 + .07\ (KN) - 5.95\ (FLA/T) + .82\ (MAX\ LA/T)$$

In this cross there were 13 high yielding lines in the bulk F_4 population of 81 lines. A prediction based on the above regression equation resulted in 5 predicted high yielding lines with 4 correct. In only one case out of 526 would random selection be expected to produce a result as good as or better than that obtained even though the regression equation accounts for only 13% of the F_4 yield variance. This outcome compares favourably with the Glenlea X NB 320 stress-free cross and is significantly better than random.

Summarizing the multiple regression analysis results for the 3 normal crosses, it was observed that the amount of F_4 yield variance accounted for by selected F_2 variables varied from 13 to 32%. It was also observed that in all crosses the regression equation developed included a sink component and a source component, the relative magnitude of which depended on the nature of the cross combination relative to sink and source capacity. Finally it was observed that predictions based on multiple regression techniques were significantly better than random in all cases, i.e. selection of 12%, 17% and 6% of the lines in the latter 3 crosses resulted in retention of 57%, 50% and 31% respectively of the high yielding lines.

The ability to predict which F_2 genotypes will give rise to high yielding progeny is as good from normal grown F_2 plants as it was from stress-free grown F_2's so that any increased genetic potential expressed by the genotypes grown under stress-free conditions in the F_2 is lost due to the dissimilarity of that environment to the one under which the plants are yield tested in F_4. Therefore F_2 plants should be grown under the prevailing field conditions when selection is to be practised on them - not a surprising conclusion considering that this is what plant breeders have normally done.

Having dealt successfully with the F_2 to F_4 relationships relative to yield, it is now time to turn to the F_3 to F_4 relationships. The partial regression coefficients from the stepwise multiple regression analysis on F_4 bulk yield for F_3 parameters for the six populations of the three crosses are given in Tables 16 through 21. Parameters which explained less than .02 of F_4 yields variance are not included in the tables.

Before commencing the F_3-F_4 analysis it should be recalled that duplicated inside row samples from 3 row X 3 m plots grown in the same year as the F_4 plots were used to obtain F_3 parameters.

TABLE 16. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_3 parameters of the Glenlea X Neepawa stress-free cross

HT	TN/½m	G	R^2
5.04*	-	-	.121**
5.32**	-1.73	-	.188**
5.17*	-1.58	2.54	.213*

It is of interest that the amount of F_4 yield variance accounted for by F_3 parameters is only half of what was explained by the F_2 parameters even though the F_3's were grown in the same planting pattern and year as the F_4's. It should also be noted that the parameters which enter the regression equation are completely different from those which entered the F_2-F_4 regression. This is due to the difference in planting pattern. The most important parameter in the F_3-F_4 regression analysis (and the only statistically significant one) is height. Height of tillers in the plot must be increased to obtain maximum yields – and this is in a cross where minimal height differences between the parents occurred. At the same time that height is increased, TN/½m must be reduced and G must be increased. All of these changes are clearly related to the source capacity of the cross progeny since increases in height would spread the leaves better in the canopy, a reduction in tiller number would allow more light penetration into the lower levels of the canopy and increased G values would imply obtaining more yield from the same leaf area duration.

Note that although the same parameters are not present in the F_2 and F_3 regression equations, the information they contain is similar. The F_2 analysis called for increased source capacity per tiller combined with increased MK WT to obtain maximum yields. This is also what is called for in F_3 since reduced TN/½m increases the source capacity per tiller but also requires that the sink be able to accept more photosynthates - possibly through increased MK WT. Therefore it does not seem to matter which field environment or planting pattern is used to deduce the relationships between physiological or morphological parameters and plot yield.

The best multiple regression equation derived from the analysis was:

$$F_4 \text{ yield} = 381.00 + 5.17\,(HT) - 1.58\,(TN/\tfrac{1}{2}m) + 2.54\,(G)$$

In this cross there were 5 high yielding lines in the bulk F_4 population. A prediction based on the above regression equation resulted in 3 predicted high yielding with 2 correct. This is 43** times better than random, comparing favourably with the F_2 result which was 63** times better than random.

TABLE 17. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_3 parameters of the Glenlea X Era stress-free cross

HT	Y	MAX LA/T	R_2
-7.26**	-	-	.151**
-7.64**	13.69**	-	.288**
-11.39**	14.27**	1.72	.321**

In this particular cross the amount of F_4 yield variance accounted for by F_3 parameters is nearly identical with the amount explained by F_2 parameters (32%) versus 35%). As well, in this particular cross there is particularly good agreement between the parameters which enter the F_3 regression and those which enter the F_2 regression equation, i.e., HT compared with PD LN, Y compared with KN/T, and MAX LA/T compared with FLA/T. Not only do the parameters between F_3 and F_2 correspond well, but the amount of yield variance each accounts for is very similar, e.g. F_3 HT, 15% compared to F_2 PD LN, 17% and so on. It would appear for this particular cross at least that the planting pattern or field environment have little effect on the regression analysis results.

The two most important (and highly significant) parameters entering the F_3 regression equation were HT and Y. Substantial reductions in HT and simultaneous increases in Y (per tiller and therefore substantial increases in HI) are required to maximize yield. As well a slight increase in MAX LA/T which has to be derived from larger LAI at anthesis may be required to maximize yields.

The best multiple regression equation derived from the analysis was:

$$F_4Y = 1460.46 - 11.39\ (HT) + 14.27\ (Y) + 1.72\ (MAX\ LA/T)$$

In this cross there were 11 high yielding lines in the bulk F_4 population. A prediction based on the above regression equation resulted in 14 predicted high yielding lines with 7 correct. In only one case out of 162 would random selection be expected to produce a result as good as or better than that obtained, thus the outcome is significantly better than random. The ability to predict high yielding bulks was marginally better from the F_3 than from the F_2 in this cross since the F_2 regression analysis was only 21** times better than random.

TABLE 18. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_3 parameters of the Glenlea X NB 320 stress-free cross

P	FLA/T	R^2
7.94*	-	.126**
10.33**	-9.11**	.283**

In this cross the F_3 parameters account for nearly 3/4 as much of the F_4 yield variance as the F_2 parameters did even though there are only 2 F_3 parameters while there were 4 F_2 parameters. As well, the parameters which enter the F_3 regression equation are completely different from those entering the F_2 regression equation. Clearly in this cross the planting pattern and field environment had considerable effect on the regression analysis.

In this case, increases in productivity (which would be on a tiller basis) and a simultaneous decrease in the FLA/T are required to achieve maximum yields. Depending on the height of the plants chosen, this increase in productivity can be interpreted as representing increased source capacity (tall plants) or increased sink capacity (short plants). Combined with a decrease in source capacity as represented by FLA/T however, productivity must be interpreted as indicating sink limitations in this cross.

The best multiple regression equation derived from the analysis was:

F_4 Y = 751.57 + 10.34 (P) - 9.11 (FLA/T)

In this cross there were 7 high yielding lines in the bulk F_4 population. A prediction based on the above regression equation resulted in 6 predicted high yielding lines with 3 correct. This is 35** times better than random but not as good as the F_2 regression analysis result which was 116*** times better than random.

TABLE 19. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_3 parameters of the Glenlea X Neepawa normal cross

MAX LA/T	P	TN/½m	R^2
1.81**	-	-	.180**
1.22*	4.53*	-	.234**
1.20*	4.63*	-1.23	.265**

In this cross the F_3 parameters explain slightly more of the F_4 yield variance than did the F_2 parameters (27% as compared to 23%). This outcome is similar to the F_3 of Glenlea X Neepawa stress-free cross where 21% of F_4 yield variance was explained by 3 selected variables. TN/½m is common to the F_3's of the cross while MAX LA/T was common to the normal grown cross.

The 3 parameters chosen for this regression equation are consistent with source capacity limitations on yield since increasing MAX LA/T, P and decreasing TN/½m simultaneously would serve to increase source size (bigger leaves) and source activity (by reducing tiller number per unit row, more light is able to penetrate lower into the canopy). Increasing productivity serves to increase the size of the potential source on which the developing grain can draw during the grain filling period.

It is noteworthy that two parameters in each of the 2 F_3 populations for the Glenlea X Neepawa cross are in disagreement. HT and G surface as important parameters in the stress-free F_3 population while MAX LA/T and P surface are important parameters in the normal F_3 population — and this is material of the same generation, grown in the same type of plots in the same part of a field in the same year. There is no adequate answer to the above paradox but part of the answer must be soil heterogeneity and perhaps moisture gradients since the field was a sloping one.

The best multiple regression equation derived from the analysis was:

$$F_4\ Y = 1.20\ (\text{MAX LA/T}) + 4.63\ (P) - 1.23\ (TN/\tfrac{1}{2}m) + 565.9$$

In this cross there were 7 high yielding lines in the bulk F_4 population of 81 lines. A prediction based on the above regression equation resulted in 8 predicted high yielding lines with 5 correct. This is an incredible 25,000*** times better than random. This compares with 63*** times better than random for the F_3 stress-free cross and 286*** times better than random for the F_2 normal cross.

TABLE 20. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_3 parameters of the Glenlea X Era normal cross

HT	$TN/\frac{1}{2}m$	R^2
-4.48**	-	.099**
-4.61**	2.59	.119**

This cross is the first large departure from the trend set in the F_3 regression analysis. The amount of F_4 yield variance accounted for by F_3 parameters is very low. The one significant parameter which entered the regression equation (HT) is consistent throughout the F_3 stress-free population and the F_2 normal cross. Not only is height consistent but it is the most important parameter in all cases, appearing first in the regression equations (i.e. HT has the highest simple correlation with F_4 yield). It is very clear that height must be reduced in the Glenlea X Era cross to achieve maximum yields. The F_3 population from stress-free F_2's indicated that increased yield per tiller was required to obtain maximum yields per plot while this regression analysis indicates that increased tiller number per unit row length is also a technique which can be used to achieve maximum yields.

The best multiple regression equation derived from the analysis was:

$$F_4\ Y = 1268.84 - 4.61\ (HT) + 2.59\ (TN/\tfrac{1}{2}m)$$

In this cross there were 10 high yielding lines in the bulk F_4 population of 81 lines. A prediction based on the above regression equation resulted in 10 predicted high yielding lines with 3 correct. This is 12* times better than random but is poor in comparison to the F_3 stress-free cross result which was 162*** times better than random and the F_2 normal cross where the regression analysis based prediction was 97*** times better than random. The relative inadequacy of this result is directly related to the small amount of F_4 yield variance accounted for by the selected F_3 parameters in the regression equation. However the reason for this is not obvious — it is probably related to environmental heterogeneity.

TABLE 21. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for F_3 parameters of the Glenlea X NB 320 normal cross.

LAD/T	HT	Y	R^2
.03*	-	-	.049*
.07*	-3.58	-	.075*
.06*	-3.60	7.75	.096*

This cross is the second departure from the trend set in the F_3 regression analysis. The amount of F_4 yield variance accounted for by F_3 parameters is only 10%. This is caused by several factors, primarily poor stand which was caused by herbicide damage when the plots were sprayed for wild oats. This damage was confined to this cross because it was on the end of a block of land where spraying started and finished.

The regression analysis indicates that moderate increases in LAD/T, substantial reductions in height and large increases in yield are required to achieve maximum yields in this cross. These results are in poor agreement with the F_3 stress-free derived population and the F_2 normal population of this cross, which is probably to be expected since this particular cross was grown under exceptional circumstances.

The decreases in height required and the increases in yield per sample are most probably valid because these parameters should be affected only minimally by a thin stand. LAD/T however would be affected considerably by thin stand and the reduction in FLA/T called for in the F_3 stress-free population is not an important change needed in the normal F_2 population. Therefore it is necessary to take into account the growth of the F_3 population before placing too much emphasis on the regression analysis.

The best multiple regression equation derived from the analysis was:

$$F_4\ Y = 756.27 + .06\ (LAD/T) - 3.60\ (HT) + 7.75\ (Y)$$

In this cross there were 13 high yielding lines in the bulk F_4 population of 81 lines. A prediction based on the above regression equation resulted in 12 predicted high yielding lines with 4 correct which is 13* times better than random. This compares poorly with 116*** times better than random for the F_3 stress-free population and 526 *** times better than random for the F_2 normal population. Again the relative inadequacy of this result is directly related to the small amount of F_4 yield variance accounted for by the selected F_3 parameters in the regression equation due to the environmental heterogeneity previously outlined.

Summarizing the multiple regression analysis for the 6 F_3 populations of the 3 crosses, it was observed that the amount of F_4 yield variance accounted for by selected F_3 parameters varied from 10 to 32%. It was also observed that in most crosses the regression equation developed included a sink component and a source component. As well, it was concluded that the predictions of high yielding F_4 bulks based on multiple regression techniques involving F_3 parameters were significantly better than random in all cases, i.e. selection of 6%, 29%, 12%, 10%, 12% and 15% of the lines in these six crosses resulted in the retention of 40%, 64%, 43%, 71%, 30% and 30% respectively of the high yielding lines.

The crosses have been dealt with successfully in the foregoing discussions as single units versus F_4 bulk yield. It is interesting and informative however to combine the crosses in F_2 and F_3 to determine if a general multiple regression technique can be used to predict high yielding F_4 bulks from F_2 or F_3 parameters.

To retain consistency with the previous analyses, any parameter which explained less than 0.02 of the F_4 yield variance was omitted from consideration.

TABLE 22. Partial regression coefficients from the stepwise multiple regression on F_4 bulk yield for all F_2 populations from the three crosses

P	PD LN	R^2
0.43**	-	0.033**
0.50**	-4.25**	0.054**

It is clear that the crosses and environments in which they were grown were sufficiently different to make it difficult to find a set of parameters common to all the crosses which will explain large amounts of the F_4 yield variance. In fact the two parameters which enter the regression equation are of major importance in only 2 out of the 3 crosses.

Productivity is important in the Glenlea X Neepawa and Glenlea X NB 320 crosses while PD LN is important in the Glenlea X Era and Glenlea X NB 320 crosses. Therefore it is not surprising that these two parameters explain only 5% of the F_4 yield variance. The best regression equation derived from the analysis was:

F_4 yield = 896.45 = .50 (P) - 4.25 (PD LN)

In the combined 3 crosses there were 52 high yielding bulks in the F_4 out of a total of 390 lines. A prediction based on the above regression resulted in 64 lines being predicted with 18 correct. This is a surprising 3,319*** times better than random, i.e. selection of only 16% of the combined F_2 population retained 35% of the high yielding lines in F_4. This is much better than would have been expected based on the amount of F_4 yield variation accounted for by the selected F_2 parameters in this regression equation. A possible explanation for this is that productivity enters the regression equation and due to the pleiotropic nature of productivity (and the fact that it encompasses such attributes as seedling vigor, drought tolerance, disease resistance and growth rate – which is supremely important in a short season environment), the prediction of high yielding lines is significantly better than expected.

The outcome for the combined F_3 analysis is however, not as satisfactory as for the combined F_2 analysis. There are no F_3 parameters in the combined population which account for more than .02 of F_4 yield variance and therefore no multiple regression equation was generated. If the .02 of F_4 yield variance requirement is dropped, then a regression equation is generated. However the regression is non-significant and all F_3 parameters entering the regression equation are also non-significant. Thus F_3 populations could not be successfully combined although the F_2 populations could be successfully combined. Clearly F_2 spaced plants of several crosses act more similarly than do F_3 plots of several crosses. This must be due in part to the wide range of competition that would occur in F_3 plots where plants were segregating for height as compared to F_3 plots where all the plants were of the same height. There was as well, in F_3, as previously stated, an environmental heterogeneity not present in F_2. It is concluded that replicated F_3 yield tests would be better than a physiological/morphological yield prediction approach. The physiological/morphological approach proved to be very satisfactory for F_2 populations both within and between populations. The results show however that the regressions are most satisfactory when developed on a cross and environment specific basis.

There are drawbacks to the use of a multiple linear regression approach in a practical plant breeding program. These drawbacks include the necessity to choose a specific set of parameters and to determine the magnitude and sign of the regression coefficients entering the regression equation since it would be unwise to use the parameters and coefficients determined in this project from a limited sampling of crosses. Such information could be empirically determined on a wide range of representative crosses if the time and resources were available. However a more straightforward and more readily utilizable approach is required which can be applied to spaced F_2 plants.

In an excellent review paper by Donald and Hamblin (1976) it is suggested that the two most important parameters plant breeders must consider in their breeding programs to increase yield are productivity and harvest index.

They say:

> "Though biological yield and harvest index may seem blunt instruments for the better analysis of the growth of cereals in the field, their wider use in agronomic research and plant breeding would make a notable contribution to the understanding and advancement of crop performance."

These comments, coupled with the fact that the multiple regression analysis indicated that F_2 productivity was the single most important parameter to be considered when predicting F_4 bulk yields from F_2 parameters, leads one to the conclusion that productivity and harvest index must be included in any selection criteria developed for F_2 single plants.

As well, the frequency with which height entered the regression equations of all crosses and because of the fact that height has a strong relationship to productivity necessitates its inclusion in the selection criteria set. What is obtained therefore, is a type of F_2 single plant analysis which can be appropriately called a harvest index evaluation within a productivity and height framework.

4.5 Harvest Index - Height-Productivity Analyses

The results of the harvest index-height-productivity analyses are given in Tables 23 through 28.

TABLE 23. Harvest index evaluation in a productivity and height framework for F_2 of the Glenlea X Neepawa stress-free cross

Productivity	Harvest Index	Height	Selection Criteria
168 ± 34	.41 ± .06	88 ± 5	P > 202 .35 < HI < .47 HT any

The selection criteria developed for the F_2 of the Glenlea X Neepawa stress-free cross are based on the fact that high yield in plots is obtained from high productivity for tall plants (especially when a moderate harvest index is superimposed on this high productivity). Height is an unimportant parameter in this cross because the parents differ little in height.

A selection of the F_2 population based on the above criteria retained 9 out of 49 (or 18%) F_2 plants and 2 out of 5 high yielding F_4 bulks. This is 5* times better than random.

TABLE 24. Harvest index evaluation in a productivity and height framework for the F_2 of the Glenlea X Era stress-free cross

Productivity	Harvest Index	Height	Selection Criteria
178 ± 43	.45 ± .06	83 ± 7	135 > P > 221 .39 < HI < .51 76 > HT > 90

The selection criteria developed for the F_2 of the Glenlea X Era stress-free cross are based on the facts that for tall plants (HT>90 cm) high yield is achieved by high productivity ($P > \bar{x} + 1\sigma$) and moderate harvest index (HI .39 - 51), while for short plants (HT<76 cm) high yield is achieved by low productivity ($P < \bar{x} - 1\sigma$) on spaced plants coupled with moderate to high harvest index (HI .39 - 51).

A selection of the F_2 population based on the above criteria retained 10 out of 49 (or 20%) F_2 plants and 4 out of 11 (or 36%) high yielding F_4 bulks. This is 9* times better than random.

TABLE 25. Harvest index evaluation in a productivity and height framework for the F_2 of the Glenlea X NB 320 stress-free cross

Productivity	Harvest Index	Height	Selection Criteria
164 ± 70	.45 ± .06	80 ± 9	94>P>234 .39<HI<.51 71>HT>89

The selection criteria developed for the F_2 of the Glenlea X NB 320 stress-free cross are predicated on the same principles as the Glenlea X Era stress-free cross.

A selection of the F_2 population based on the above criteria retained 9 out of 49 (or 18%) F_2 plants and 5 out of 7 (or 71%) high yielding F_4 bulks. This is 874*** times better than random.

TABLE 26. Harvest index evaluation in a productivity and height framework for the F_2 of the Glenlea X Neepawa normal cross

Productivity	Harvest Index	Height	Selection Criteria
138 ± 42	.33 ± .08	89 ± 12	P>180 .25<HI<.41 HT any

The selection criteria developed for the F_2 of the Glenlea X Neepawa normal cross are based on the same rationalizations as for the Glenlea X Neepawa stress-free cross. Because the plants did not grow as well under normal field conditions as they did under stress-free conditions, the absolute values for productivity and harvest index are lower but the same fraction of the F_2 population is sampled nevertheless.

A selection of the F_2 population based on the above criteria retained 12 out of 81 (or 15%) and 3 out of 7 (or 43%) high yielding F_4 bulks. This is 18** times better than random.

TABLE 27. Harvest index evaluation in a productivity and height framework for the F_2 of the Glenlea X Era normal cross

Productivity	Harvest Index	Height	Selection Criteria
146 ± 43	.39 ± .05	85 ± 8	103>P>189 .34<HI<.44 77>HT> 93

The selection criteria developed for the Glenlea X Era normal cross are predicated on the same principles as the Glenlea X Era stress-free cross.

A selection of the F_2 population based on the above criteria retained 10 out of 81 (or 12%) of the F_2 population and 2 out of 11 (18%) high yielding lines. This is 4* times better than random.

TABLE 28. Harvest index evaluation in a productivity and height framework for the F_2 of the Glenlea X NB 320 normal cross

Productivity	Harvest Index	Height	Selection Criteria
151 ± 52	.39 ± .07	84 ± 8	$99 > P > 203$ $.32 < HI < .46$ $76 > HT > 92$

The selection criteria developed for the Glenlea X NB 320 normal cross are predicated on the same principles as the Glenlea X NB 320 stress-free cross.

A selection of the F_2 population based on the above criteria retained 10 out of 81 (or 12%) and 4 out of 13 (or 31%) high yielding F_4 bulks. This is 24** times better than random.

In summarizing the results of the harvest index evaluation in a productivity and height framework, it is noted that the predictions based on productivity, harvest index, and where appropriate, height are all significantly better than random. It must also be pointed out that in no case are all of the high yielding lines retained by the selection procedure. The benefits of obtaining productivity, harvest index and height data are derived through an increased probability of selecting high yielding F_2 genotypes, with a high intensity of selection rather than through the retention of all high yielding F_2 genotypes with a low intensity of selection.

There are specific selection recipes which can be developed for any type of cross, depending on the parents which are involved in the cross.

For instance in tall X tall crosses, one selects positively for productivity on F_2 spaced plants, taking the largest plants because there is a strong positive correlation between spaced plant productivity and plot productivity for tall plants and a strong positive correlation between plot productivity and yield.

However in short X short crosses, one selects negatively for productivity on F_2 spaced plants, taking the smallest plants because there is a strong negative correlation between spaced plant productivity and plot productivity for short plants and a strong positive correlation between plot productivity and yield.

Thus one selects the best plants from tall X tall F_2 populations and the poorest plants from short X short F_2 populations. In the case of tall X short crosses, one would select both the best and the poorest plants from the F_2 populations to retain the highest yielding genotypes.

5. GENERAL DISCUSSION AND CONCLUSIONS

Many studies have looked at the relationship of physiological and morphological parameters to yield in pure genotypes on single greenhouse or field grown plants, on microplots grown in the field or on large field grown plots. However, even though some investigators have looked at spaced plants in the field for yield components, no investigators had until now done a thorough investigation into the use of physiological and/or morphological parameters on F_2 spaced plants or F_3 plot samples to determine if it would be possible to improve the efficiency of selection for yield in a practical plant breeding program in F_2 or F_3 by using these characters either individually or in combination.

The results of this project show that one can use single parameters in F_2 or F_3 in simple correlation analysis with F_4 bulk yield to determine whether the progeny of a particular cross are primarily source limited or sink limited (always remembering that sink limitations may be caused by insufficient source capacity during the sink development phase). It is also possible to use a single F_2 or F_3 parameter to select for yield potential in F_2 or F_3. However the most common parameter entering the analyses in F_2 is a visual yield selection estimate which is highly dependent on the cross and the environment where it is grown. In any case, although there is a degree of success at picking high yielding genotypes from the F_2 using a single parameter, this success is achieved only when a low selection intensity is employed. What this really means is that plant breeders have a good ability to discard poor yielding plants in the F_2 but have little ability to select high yielding plants.

The most common single F_3 parameter entering the analyses is height. This is a relatively stable characteristic over environments and within lines however the ability to select high yielding F_4 bulks by using F_3 height is successful only at low selection intensities. It was concluded that replicated yield testing in F_3 would be the more desirable alternative.

When one combines two or more parameters measured on F_2 plants or F_3 plot samples into a multiple regression equation to explain F_4 bulk yield variance, it is found that 10 to 40% of the variance is accounted for by the regression equations which are in all cases statistically significant. More importantly, the predictions of high yielding F_4 bulks from F_2 or F_3 generated regressions are significantly better than random, and in most cases, retention of only 10-20% of the F_2 or F_3 population results in retention of greater than 50% of the high yielding lines. This represents a dramatic improvement over either visual selection or single plot yield as selection criteria.

The regression technique as it stands is of little value to the plant breeder however because the parameters chosen to estimate yield potential are cross specific in many cases or have different magnitudes and signs from cross to cross.

A combined cross analysis indicated that productivity and peduncle length were important common parameters in these crosses — but each of the parameters was of primary importance in only two out of three of the crosses studied. When one also takes into account that there are four types of high yielding plant forms available to breeders (i) tall productivity dependent, (ii) tall harvest index dependent, (iii) semi-dwarf productivity dependent and (iv) semi-dwarf harvest index dependent and that there are six logical ways of combining these plant types to achieve high yield through physiological complimentation, then it becomes obvious that many more crosses must be investigated and many more multiple regression equations generated before the multiple regression approach to early generation selection becomes feasible. The outcome of the multiple regression analysis however does suggest that a multiple parameter approach should be successful. Because of this, a harvest index-productivity-height approach was evaluated in the final section of the thesis. It was shown quite clearly that simultaneous consideration of productivity, harvest index and in cases where parents differ in stature, height, results in the retention of 18 to 71% of the high yielding F_4 bulks with a selection intensity of approximately 10-15% which is an acceptable level to most breeders.

An ongoing test of the ability of the harvest index evaluation within a height and productivity framework procedure to select high yielding F_2 genotypes on a wide range of crosses is currently in progress and will determine the usefulness and universality of this approach in plant breeding programs.

Provided the harvest index-productivity-height selection procedure turns out to be useful in selecting high yielding F_2 genotypes, then it would be logical to do the following:

1) Characterize potential parents in a breeding program for their harvest index, height and productivity so that they can be slotted into one of four categories listed above (e.g. tall productivity dependent).

2) Make appropriate crosses using physiological complimentation as a guideline (e.g. cross tall productivity dependent parents with tall harvest index dependent parents).

3) Generate appropriate selection recipes for the F_2 populations based on positive combinations of the physiological components present in the parents (e.g. for the example cross type, one would select the largest plants with the highest harvest index).

4) Use replicated F_3 bulk testing of selected F_2 progenies to determine the best bulks.

5) Extract lines and develop new high yielding varieties from the best bulks.

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APPENDIX TABLE 1. Analysis of variance of F_4 bulk yields at Winnipeg*

Cross	Source of Variation	df	MS	F
Glenlea X Neepawa stress-free	Replications	5	259,924	31.57***
	Blocks	36	37,733	4.58***
	Varieties	48	32,955	4.00***
	Error	204		
	TOTAL	293		
	C.V. = 12.4%, L.S.D. $_{.05}$ = 127.3			
Glenlea X Era stress-free	Replications	5	38,081	2.95*
	Blocks	36	37,811	2.93*
	Varieties	48	126,319	9.80***
	Error	204	12,887	
	TOTAL	293		
	C.V. = 12.6%, L.S.D. $_{.05}$ = 128.5			
Glenlea X NB 320 stress-free	Replications	5	219,072	20.37***
	Blocks	36	32,927	3.06*
	Varieties	48	82,008	7.63***
	Error	204	10,755	
	TOTAL	293		
	C.V. = 11.9%, L.S.D. $_{.05}$ = 117.4			

*replicated triple lattice design

APPENDIX TABLE 2. Analysis of variance of F_4 bulk yields at Winnipeg*

Cross	Source of Variation	df	MS	F
Glenlea X Neepawa Normal	Replications	5	20,263	2.34*
	Blocks	48	29,172	3.37***
	Varieties	80	40,523	4.68***
	Error	352	8,646	
	TOTAL	485		
	C.V. = 10.2%, L.S.D. .05 = 105.2			
Glenlea X Era Normal	Replications	5	43,601	4.81***
	Blocks	48	41,757	4.61***
	Varieties	80	107,809	11.90***
	Error	352	9,060	
	TOTAL	485		
	C.V. = 10.9%, L.S.D. .05 = 107.7			
Glenlea X NB 320 Normal	Replications	5	222,550	19.14***
	Blocks	48	28,527	2.45*
	Varieties	80	132,345	11.38***
	Error	352	11,625	
	TOTAL	485		
	C.V. = 12.6%, L.S.D. .05 = 122.0			

*replicated triple lattice design

APPENDIX TABLE 3. Glenlea X Neepawa Stress-Free Adjusted F_4 bulk yields

1. 974	17. 934	33. 889
2. 802	18. 925	34. 887
3. 975	19. 912	35. 912
4. 879	20. 838 N	36. 860
5. 859	21. 938	37. 859
6. 820	22. 884	38. 925
7. 940	23. 900	39. 837
8. 904	24. 920	40. 1136* G
9. 807	25. 1079*	41. 835
10. 1019 G	26. 819	42. 926
11. 884	27. 932	43. 887
12. 847	28. 934	44. 893
13. 794	29. 1024	45. 912
14. 964	30. 775 N	46. 1009
15. 904	31. 952	47. 874
16. 789	32. 940	48. 903
		49. 918

$\bar{x}$ = 904.6, L.S.D. $_{.05}$ = 127.3

G = Glenlea, N = Neepawa

APPENDIX TABLE 4. Glenlea X Era Stress-Free Adjusted F_4 bulk yields

1.	954	17.	708	33.	1131*
2.	775	18.	917	34.	867
3.	890	19.	961	35.	836
4.	345	20.	922 E	36.	799
5.	945	21.	905	37.	946
6.	970	22.	1010	38.	905
7.	1066*	23.	818	39.	837
8.	926	24.	669	40.	964 G
9.	824	25.	1013	41.	954
10.	797 G	26.	858	42.	873
11.	680	27.	888	43.	1053*
12.	827	28.	929	44.	867
13.	918	29.	784	45.	1036*
14.	830	30.	1067* E	46.	1012
15.	922	31.	1181*	47.	1165*
16.	766	32.	811	48.	949
				49.	1050*

$\bar{x}$ = 900.3, L.S.D. $_{.05}$ = 128.5

G = Glenlea, E = Era

APPENDIX TABLE 5. Glenlea X NB 320 Stress-Free Adjusted F_4 bulk yields

1. 924	17. 894	33. 830
2. 662	18. 779	34. 798
3. 831	19. 761	35. 637
4. 885	20. 885 NB 320	36. 993*
5. 1044*	21. 803	37 692
6. 910	22. 856	38. 970
7. 918	23. 856	39. 836
8. 1117*	24. 914	40. 861 G
9. 852	25. 877	41. 1064*
10. 877 G	26. 745	42. 778
11. 921	27. 828	43. 1141*
12. 975	28. 962	44. 842
13. 864	29. 863	45. 603
14. 922	30. 1002*NB 320	46. 924
15. 828	31. 718	47. 1004*
16. 975	32. 828	48. 1040*
		49. 746

$\bar{x}$ = 874.2, L.S.D. $_{.05}$ = 117.4

G = Glenlea, NB 320 = NB 320

APPENDIX TABLE 6. Glenlea X Neepawa Normal Adjusted F_4 bulk yields

1.	814	21.	1080*	41.	931	61.	862
2.	703	22.	920	42.	931	62.	957
3.	925	23.	993	43.	946	63.	970
4.	818	24.	901	44.	964	64.	920
5.	946	25.	850	45.	970	65.	974
6.	843	26.	924	46.	669	66.	912
7.	816	27.	909	47.	861	67.	786
8.	891	28.	848	48.	995	68.	965
9.	945	29.	998	49.	883	69.	905
10.	823	30.	779 N	50.	894 N	70.	897 N
11.	930	31.	905	51.	860	71.	849
12.	916	32.	939	52.	938	72.	946
13.	886	33.	886	53.	788	73.	927
14.	899	34.	829	54.	952	74.	851
15.	852	35.	864	55.	741	75.	976
16.	890	36.	882	56.	923	76.	783
17.	973	37.	918	57.	1025*	77.	997
18.	901	38.	950	58.	856	78.	1017*
19.	892	39.	986	59.	1003	79.	890
20.	1083* G	40.	1178* G	60.	984 G	80.	900
						81.	1028*

$\bar{x}$ = 909.9, L.S.D. $_{.05}$ = 105.2

G = Glenlea, N = Neepawa

APPENDIX TABLE 7. Glenlea X Era Normal Adjusted F_4 bulk yields

1.	1063*		21.	884		41.	942		61.	1024*	
2.	716		22.	1044*		42.	992*		62.	856	
3.	560		23.	940		43.	873		63.	940	
4.	681		24.	1061*		44.	1002*		64.	990*	
5.	831		25.	850		45.	772		65.	620	
6.	788		26.	503		46.	812		66.	843	
7.	764		27.	815		47.	770		67.	961	
8.	893		28.	890		48.	703		68.	953	
9.	810		29.	820		49.	834		69.	984*	
10.	870		30.	959	E	50.	965	E	70.	991*	E
11.	983*		31.	955		51.	881		71.	916	
12.	1088*		32.	773		52.	974		72.	933	
13.	997*		33.	730		53.	1008*		73.	867	
14.	492		34.	931		54.	1006*		74.	954	
15.	714		35.	940		55.	802		75.	1072*	
16.	978		36.	895		56.	749		76.	765	
17.	932		37.	921		57.	929		77.	845	
18.	943		38.	975		58.	1095*		78.	916	
19.	579		39.	762		59.	874		79.	793	
20.	814	G	40.	926	G	60.	762	G	80.	965	
									81.	655	

$\bar{x} = 872.2$, L.S.D. $_{.05} = 107.7$

G = Glenlea, E = Era

APPENDIX TABLE 8. Glenlea X NB 320 Normal Adjusted F_4 bulk yields

1.	566		21.	880		41.	949		61.	513	
2.	983*		22.	775		42.	943		62.	865	
3.	491		23.	912		43.	695		63.	998*	
4.	872		24.	1042*		44.	963		64.	986*	
5.	608		25.	783		45.	1112*		65.	989*	
6.	1124*		26.	928		46.	796		66.	789	
7.	946		27.	617		47.	767		67.	838	
8.	824		28.	846		48.	937		68.	749	
9.	1003*		29.	880		49.	820		69.	889	
10.	803		30.	876	NB 320	50.	952	NB 320	70.	910	NB 320
11.	951		31.	870		51.	731		71.	764	
12.	852		32.	1058*		52.	742		72.	877	
13.	756		33.	1036*		53.	825		73.	886	
14.	1059*		34.	844		54.	772		74.	1011*	
15.	867		35.	873		55.	749		75.	903	
16.	868		36.	671		56.	583		76.	958	
17.	947		37.	1013*		57.	910		77.	1060*	
18.	1020*		38.	920		58.	804		78.	822	
19.	649		39.	377		59.	1075*		79.	769	
20.	786	G	40.	725	G	60.	744	G	80.	1073*	
									81.	949	

$\bar{x}$ = 856.3, L.S.D. $_{.05}$ = 122.0

G = Glenlea, NB 320 = NB 320

APPENDIX TABLE 9. Simple correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Neepawa stress-free

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
1	76 37	30 61	52 65	55 46	48 13	91 32	31 33	31 40	-12 46	-16 03	58 27	54 22	52 22	69 -15	56 05	31 33	32 04
2	-- 53	62 14	-14 20	11 37	68 22	71 47	23 51	46 41	-12 56	30 -10	33 31	58 20	75 39	67 -08	59 17	21 48	66 20
3	62 15	-- -41	-35 -43	-60 -35	53 54	38 24	30 40	06 12	04 17	11 -04	09 04	46 08	58 35	40 07	14 06	-16 24	91 14
4	-14 -14	-35 71	-- 70	69 17	-17 -09	46 -14	16 -17	-14 05	-04 -06	-19 16	38 00	07 04	-18 -13	17 -14	07 -17	23 -11	-36 -15
5	11 15	-61 84	69 90	-- 69	-10 -38	40 07	-00 -09	18 20	-10 25	05 -00	32 22	05 06	-02 -11	22 -14	34 00	43 10	-51 -09
6	68 45	53 08	-17 04	-09 20	-- 33	52 45	36 45	21 33	03 33	23 08	32 30	46 16	55 43	56 -16	26 10	-04 39	47 07
7	71 28	38 59	46 47	40 27	52 13	-- 31	33 25	28 33	-17 34	06 06	60 19	54 20	51 16	62 -12	54 -00	-10 19	41 -08
8	23 01	30 10	16 06	-00 -05	36 23	33 15	-- 17	-27 09	28 08	08 02	18 07	29 05	12 35	34 03	00 -18	-03 09	22 -06
9	46 44	06 18	-15 22	19 44	21 00	28 32	-27 35	-- 16	61 29	22 -12	16 02	42 13	46 13	28 -19	68 30	12 14	12 28
10	-12 -12	04 -17	-04 -11	-10 -13	03 05	-17 08	28 -00	-61 14	-- 13	64 03	-09 07	-17 11	-17 -09	-05 09	-26 -08	08 01	01 -21
11	30 27	11 -03	-19 08	05 27	23 06	06 41	08 34	22 33	64 44	-- -08	05 10	19 26	24 01	33 -08	34 19	22 15	12 01
12	33 14	09 48	38 42	32 29	32 07	60 14	18 08	16 22	-09 15	05 15	-- -04	22 20	16 02	42 -12	26 -18	-00 -15	-09 09

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APPENDIX TABLE 9 continued. Simple correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Neepawa stress-free

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
13	58	46	07	05	46	54	29	42	-17	19	22	--	70	62	58	07	40
	34	17	18	17	31	22	28	11	16	-03	07	08	24	-15	17	27	09
14	75	58	-18	-03	55	51	12	46	-16	24	16	70	--	52	61	09	61
	31	-00	03	16	17	36	37	33	30	15	16	25	39	-10	16	43	21
15	67	40	17	22	56	62	34	28	05	33	42	62	52	--	47	28	34
	41	30	36	37	29	38	35	27	36	-04	20	16	36	-02	08	33	03
16	59	14	07	34	26	54	00	68	-26	34	26	58	61	47	--	13	25
	38	29	33	40	-09	33	32	31	33	04	09	25	09	-12	16	16	04
17	21	-16	23	42	-04	-10	-03	12	08	22	-01	07	09	28	13	--	-20
	24	11	48	47	01	05	19	18	27	-07	17	07	16	-09	10	33	31
18	66	91	-36	-51	47	41	22	18	00	12	09	40	61	34	25	-20	--
	10	-48	-50	-44	15	12	20	16	17	02	01	13	29	18	03	18	01
19	53	16	-14	15	45	28	01	44	-12	27	14	34	31	41	38	24	10
	--	18	26	49	23	58	62	51	63	-07	30	31	44	-09	34	50	35
20	14	-41	71	84	08	59	09	18	-17	-03	48	17	-00	30	30	11	-48
	18	--	92	71	03	23	09	18	22	00	23	04	-09	-29	01	07	-05
21	20	-43	70	90	04	47	06	22	-11	08	42	18	03	36	33	48	-50
	26	92	--	81	04	22	17	23	31	-03	27	07	-03	-28	07	19	08
22	37	-35	17	69	20	27	-06	44	-13	27	29	17	16	37	40	47	-44
	49	71	81	--	13	43	39	29	47	-15	36	07	08	-31	22	35	26
23	22	54	-09	38	33	13	23	-00	05	06	07	31	17	29	-09	01	15
	23	03	04	13	--	39	62	05	13	-09	11	-00	24	-27	12	24	34
24	47	24	-14	07	45	31	15	32	08	41	14	22	36	37	32	04	11
	58	23	22	43	39	--	69	34	39	-03	21	20	23	-05	18	36	24

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APPENDIX TABLE 9 Continued. Simple correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Neepawa stress-free

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
25	51 62	40 09	-17 17	-09 39	45 62	25 69	17 --	35 53	-00 52	34 09	08 27	28 36	37 42	35 -22	32 40	19 45	20 50
26	40 51	12 18	05 23	20 29	33 05	33 34	09 53	16 --	14 72	33 52	22 19	11 84	33 26	27 -17	31 29	18 35	16 27
27	56 63	17 22	-06 31	25 47	33 13	34 40	08 52	29 72	13 --	44 -20	15 40	16 46	30 34	36 -18	33 40	27 50	17 19
28	-10 -07	-04 00	16 -03	-00 -15	08 -09	06 -02	02 09	-12 52	03 -20	-08 --	15 -19	-03 62	15 -03	-04 01	04 -07	-07 -09	02 11
29	31 30	05 23	01 27	22 36	30 11	19 21	07 27	02 20	07 40	10 -19	-04 --	07 -35	16 38	20 -07	09 43	17 74	01 04
30	20 31	09 04	04 07	06 07	16 -00	20 20	05 36	13 84	11 46	26 62	20 -35	08 --	25 05	16 -13	25 05	07 -05	13 21
31	39 44	35 -09	-14 -03	-12 08	43 24	16 23	35 42	13 26	-09 34	01 -03	02 38	24 05	39 --	36 07	09 10	16 58	29 35
32	-08 -09	07 -29	-14 -28	-14 -31	-16 -27	-12 -05	03 -22	-19 -17	09 -19	-08 01	-12 -07	-15 -13	-10 07	-03 --	-13 -09	-09 -04	18 -23
33	17 34	06 01	-17 07	00 22	09 12	-00 18	-18 40	30 29	-08 40	19 -07	-18 43	17 05	16 10	08 -09	16 --	10 51	03 19
34	48 50	24 07	-11 19	10 35	39 24	19 36	09 45	14 35	01 50	15 -09	-15 74	27 -05	43 58	33 -04	16 51	33 --	18 15

$r_{.05}$ (df = 47) = 28 $r_{.01}$ (df = 47) = 36

APPENDIX TABLE 10. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Era Stress-free

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
1	90 42	70 60	61 71	47 42	26 40	92 35	-05 32	09 39	36 34	48 21	65 -07	58 33	58 -05	67 -24	63 24	18 -00	67 30
2	-- 42	72 47	21 58	28 57	43 48	82 42	04 43	17 38	30 46	45 11	69 06	57 24	64 04	68 -20	62 38	16 09	65 30
3	72 22	-- -01	22 13	-27 00	37 66	60 34	04 45	03 14	29 23	34 -02	54 01	54 08	41 06	40 -27	44 19	28 08	86 09
4	21 19	22 54	-- 56	59 -04	-18 01	59 04	-16 -04	-05 19	21 -03	26 26	18 -24	21 28	12 -16	27 -19	28 -09	06 -14	29 12
5	28 29	-27 85	59 79	-- 53	-19 -29	50 02	15 -16	05 31	13 07	18 34	23 -22	14 37	19 -20	39 03	30 03	-15 -21	-16 29
6	43 31	37 -01	-18 18	-19 34	-- 56	11 33	60 51	-03 -02	21 41	24 -37	07 47	19 -28	11 64	24 -06	22 37	32 59	15 -20
7	82 35	60 70	59 62	50 34	11 21	-- 31	-17 19	21 34	22 22	40 26	66 -16	52 36	55 -19	64 -12	58 16	-20 -12	66 38
8	04 -07	04 -13	-16 03	-15 14	60 27	-18 -02	-- 16	-29 -09	15 09	04 -21	-19 36	-06 -31	-11 57	-12 -15	07 05	35 36	-12 -41
9	17 09	03 23	-05 10	05 18	-03 05	21 16	-29 27	-- -06	-57 -03	05 -02	11 -03	04 -04	31 -21	22 -01	18 23	-32 01	03 24
10	30 01	29 -02	21 19	13 04	21 11	22 -11	15 -12	-57 05	-- 02	72 01	30 -02	17 02	08 20	19 -19	04 -08	45 00	33 -10
11	45 02	34 14	26 29	18 15	24 16	40 -03	04 04	05 -01	72 00	-- -05	45 -01	24 -05	30 06	37 -25	20 05	29 01	40 13
12	69 39	54 38	18 37	23 32	07 26	66 22	-18 18	11 32	30 18	45 26	-- -16	60 34	59 -15	61 -15	50 11	-07 -26	52 36

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APPENDIX TABLE 10 Continued. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Era stress-free

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
13	57 37	54 25	21 29	14 19	19 27	52 38	-06 24	04 37	17 31	24 23	60 -09	-- 34	54 -10	60 -08	69 07	06 -10	48 31
14	64 29	41 33	12 35	19 34	11 23	55 32	-11 26	31 09	08 14	30 01	59 -09	54 13	-- -24	55 -05	62 20	05 -05	40 44
15	68 31	40 43	27 46	39 37	24 11	64 28	-12 14	22 25	19 19	37 17	61 -12	60 27	55 -09	-- -05	53 31	-01 -13	45 40
16	62 43	44 44	28 48	30 37	22 30	58 50	07 37	18 49	04 37	20 31	50 -09	69 46	62 -00	53 -07	-- 12	07 -00	35 29
17	16 06	28 -32	06 15	-15 09	32 47	-20 01	35 23	-32 -00	45 12	29 12	-07 12	06 -13	05 26	-01 -35	07 10	-- 22	08 -23
18	65 04	86 -06	29 -04	-16 -24	15 22	66 17	-12 05	03 13	33 07	40 07	52 -15	48 15	40 -15	45 -22	35 14	08 -07	-- 13
19	42 --	22 42	19 48	29 44	31 33	35 40	-07 44	09 32	01 38	02 14	39 10	37 25	29 27	31 -01	43 33	06 25	04 13
20	47 42	-01 --	54 88	85 68	-01 08	70 26	-13 20	23 35	-02 20	14 30	38 -10	25 36	33 -13	43 07	44 07	-32 -14	-06 39
21	58 48	13 88	57 --	79 79	18 35	62 29	03 37	10 38	19 32	29 24	37 -00	29 31	35 02	46 -08	48 16	15 -01	-04 29
22	57 44	00 68	-04 78	53 --	34 39	34 34	14 50	18 32	04 44	15 07	32 19	19 15	34 15	37 02	37 30	09 11	-24 27
23	48 33	66 08	01 35	-29 39	56 --	21 40	27 81	05 10	11 34	16 -14	26 29	27 -08	23 33	11 -16	30 18	47 28	22 01
24	42 40	34 26	04 29	02 34	33 40	31 --	-02 66	16 29	-10 45	-03 01	22 09	38 22	32 03	28 -05	50 21	01 12	17 34

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APPENDIX TABLE 10 Continued. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Era stress-free

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
25	43	45	-04	16	51	19	16	27	-12	04	18	24	26	14	37	23	05
	44	20	37	50	81	66	--	16	51	-19	37	-06	35	-26	30	43	16
26	38	14	19	31	-03	34	-10	-06	05	-01	32	37	09	26	48	-00	13
	32	35	38	32	10	29	16	--	61	77	04	81	06	-15	23	-02	35
27	46	23	-03	08	41	22	09	-03	02	00	18	31	14	19	37	12	07
	38	20	32	44	34	45	51	61	--	-02	53	22	34	-22	54	49	21
28	11	-02	26	34	-37	26	-21	-02	01	05	26	23	01	17	31	-12	07
	14	30	24	07	-14	01	-19	77	-02	--	-34	83	-20	03	-13	-39	28
29	06	01	-24	-22	47	-16	36	-03	-02	-01	-16	-09	-09	-12	-10	12	-15
	10	-10	-00	19	29	09	37	04	53	-34	--	-52	58	-02	39	61	-08
30	24	08	28	37	-28	36	-31	-04	02	-05	34	34	13	27	46	-13	15
	25	36	31	15	-08	22	-06	81	22	83	-52	--	-27	-04	-03	-38	35
31	04	06	-16	-19	64	-19	57	-21	20	06	-15	-10	-24	-09	-00	26	-15
	27	-13	02	15	33	03	35	06	34	-20	58	-27	--	-20	20	74	-39
32	-20	-27	-19	03	-06	-12	-15	-01	-19	-26	-15	-08	-05	-05	-07	-35	-22
	-02	07	-07	01	-16	-05	-26	-15	-22	03	-02	-04	-20	--	-22	-25	06
33	38	19	-09	03	37	16	05	23	-08	05	11	07	20	31	12	10	14
	33	07	16	30	18	21	30	23	54	-13	39	-03	20	-22	--	49	16
34	08	08	-14	-21	59	-12	36	01	00	01	-26	-10	-05	-13	-00	22	-07
	25	-14	-01	11	28	12	43	-02	49	-39	71	-38	74	-25	49	--	-19

$r_{.05}$ (df = 47) = 28 $f_{.01}$ (df = 47) = 36

APPENDIX TABLE 11. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X 320 stress-free

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
1	96 22	87 56	35 69	25 50	48 50	96 10	31 34	48 16	-12 45	52 -17	80 14	81 03	86 37	85 -01	69 -20	24 37	88 43
2	-- 22	89 50	09 61	17 59	63 54	93 22	40 43	55 21	-17 55	54 -21	81 23	76 02	85 52	86 02	68 -04	21 48	89 40
3	89 16	-- 19	15 33	-17 25	55 71	81 17	35 47	42 23	-03 47	57 -12	76 36	77 -07	82 45	79 -10	63 -02	30 45	95 30
4	09 -03	15 33	-- 42	30 -20	-35 -02	33 -36	-09 -31	-21 -14	30 -28	18 08	13 -24	35 03	17 42	14 -04	22 -52	19 -31	21 13
5	17 -01	-17 65	30 65	-- 52	00 -35	27 -11	05 -18	20 -13	-12 03	10 -18	14 -22	09 09	15 01	20 22	18 -23	-02 06	-08 11
6	63 -06	55 09	-35 24	00 49	-- 42	42 52	71 62	34 08	-09 52	35 -33	38 47	31 -20	53 82	56 10	40 38	23 60	49 00
7	93 24	81 66	33 64	27 47	42 36	-- 05	28 26	55 17	-22 36	44 -10	77 03	78 12	82 30	80 06	60 -29	-01 30	87 43
8	40 -25	35 09	-09 18	05 28	71 21	28 34	-- 27	13 18	15 27	43 -02	22 33	26 -06	32 54	43 13	36 28	14 38	36 -13
9	55 35	42 34	-21 27	20 43	34 15	55 04	13 49	-- 28	-80 54	16 -12	47 17	42 10	41 50	44 04	33 -22	-22 56	44 40
10	-17 -38	-03 -22	30 -04	-12 -24	-09 14	-22 -02	15 -35	-80 -11	-- -25	47 06	-12 -06	-08 -06	-05 -25	-09 01	07 24	46 -35	-06 -30
11	54 -11	57 14	18 32	10 24	35 45	44 03	43 15	16 23	47 38	-- -08	49 15	49 05	52 32	50 08	59 08	43 25	54 10
12	81 17	76 46	14 54	14 50	38 47	77 09	22 26	47 20	-12 33	49 -05	-- 17	64 06	65 31	78 -02	52 -10	19 34	76 48

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APPENDIX TABLE 11 Continued. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X 320 stress-free

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
13	76	77	35	09	31	78	26	42	-08	49	64	--	74	74	78	20	81
	24	37	43	25	39	15	24	15	41	-14	27	-06	22	-11	-12	30	29
14	85	82	17	15	53	82	32	41	-05	52	65	74	--	76	67	22	82
	06	37	46	37	44	17	31	28	52	-11	14	13	39	07	-11	38	28
15	86	79	15	20	56	80	43	44	-09	50	78	74	76	--	73	25	79
	15	42	56	51	47	22	30	29	45	-03	23	08	45	02	07	42	26
16	68	63	22	18	40	60	36	33	07	59	52	78	67	73	--	38	65
	20	28	46	36	40	17	30	27	53	-13	26	03	34	13	05	41	22
17	21	30	19	-02	23	-01	14	-22	46	43	19	20	22	25	38	--	15
	-01	-25	27	17	53	19	25	01	34	-27	37	-23	22	-19	35	35	03
18	89	95	21	-08	49	87	36	44	-06	54	76	81	82	79	65	15	--
	12	25	30	18	48	13	30	21	39	-08	23	00	38	-00	-12	37	28
19	22	16	-03	-01	-06	24	-25	35	-38	-11	17	24	06	15	20	-01	12
	--	28	26	26	27	-04	25	04	28	-20	02	02	03	-01	-05	17	32
20	50	19	33	65	09	66	09	34	-22	14	46	37	37	42	28	-25	25
	28	--	82	66	01	-06	00	02	01	-01	-20	17	-04	19	-36	01	38
21	61	33	42	65	24	64	18	27	-04	32	54	43	46	56	46	27	30
	26	82	--	79	31	04	21	05	29	-20	-06	09	16	03	-16	21	43
22	59	25	-20	52	49	47	28	43	-24	24	50	25	37	51	36	17	18
	26	66	79	--	32	29	41	17	50	-24	12	08	42	01	16	41	37
23	54	71	-02	-35	42	36	21	15	14	45	47	39	44	47	40	53	48
	27	01	31	32	--	25	66	23	45	-13	47	-16	40	-26	27	43	26
24	22	17	-36	-11	52	05	34	04	-02	03	09	15	17	22	17	19	13
	-04	-06	04	29	25	--	42	-05	31	-31	43	-29	43	-01	51	42	-03

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APPENDIX TABLE 11 Continued. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X 320 stress-free

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
25	43 25	47 03	-31 21	-18 41	62 66	26 42	27 --	49 11	-35 56	15 -35	26 46	24 -23	31 65	30 -11	30 35	25 58	30 19
26	21 04	23 02	-14 05	-13 17	08 23	17 -06	18 11	28 --	-12 48	23 70	20 -09	15 77	28 19	29 -00	27 -01	01 27	21 20
27	55 28	47 01	-28 29	03 50	52 45	36 31	27 56	54 48	-25 --	38 -27	33 30	41 17	52 62	45 -19	53 26	34 61	39 35
28	-21 -20	-12 -01	08 -20	-18 -24	-33 -13	-10 -31	-02 -35	-12 70	06 -27	-08 --	-05 -35	-14 71	-11 -30	-03 12	-13 -25	-27 -23	-08 -06
29	23 02	36 -20	-24 -06	-22 12	47 47	03 43	33 46	17 -09	-06 30	15 -35	17 --	27 -68	14 54	23 -12	26 40	37 58	23 02
30	02 02	-07 17	03 09	09 08	-20 -16	12 -29	-06 -23	10 77	-06 17	05 71	06 -68	-06 --	13 -17	08 10	03 -24	-23 -15	00 13
31	52 03	45 -04	-42 16	01 42	82 40	30 43	54 65	50 19	-25 62	32 -30	31 54	22 -17	39 --	45 09	34 38	22 80	38 03
32	02 -01	-10 19	-04 03	22 01	10 -26	06 -01	13 -11	04 -00	01 -19	08 12	-02 -12	-11 10	07 09	02 --	13 -14	-19 10	-00 -12
33	-04 -05	-02 -36	-52 -16	-23 16	38 27	-29 51	28 35	-22 -01	24 26	08 -25	-10 40	-12 -24	-11 38	07 -14	05 --	35 26	-12 -29
34	48 17	45 01	-31 21	06 41	60 43	30 42	38 58	56 27	-35 61	25 -23	34 58	30 -15	38 80	42 10	41 26	25 --	37 19

$r_{.05}$ (df = 47) = 28 $r_{.01}$ (df = 47) = 36

APPENDIX TABLE 12. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Neepawa normal

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
1	83 18	78 47	64 64	29 28	31 62	89 13	21 35	-11 -01	33 02	11 -05	53 26	60 -23	59 29	69 -03	51 06	36 27	66 05
2	-- 32	85 20	14 29	04 32	39 57	80 29	08 50	-03 12	21 25	09 -15	59 14	58 -01	69 47	65 -05	52 24	26 37	79 13
3	85 24	-- -01	25 13	-33 -06	33 74	70 25	06 56	-06 03	22 16	07 -18	48 11	49 -11	66 40	63 -08	46 22	32 26	87 13
4	14 -09	25 57	-- 78	59 07	01 38	48 -14	24 -07	-15 -23	38 -34	11 09	17 31	25 -44	13 -10	30 02	18 -24	34 -02	12 -06
5	-04 -10	-33 74	59 79	-- 53	-04 -19	24 -21	20 -36	-03 -06	21 -23	09 25	08 23	13 -17	-13 -21	01 13	03 -27	10 -02	-32 -10
6	39 80	33 38	02 14	-04 20	-- 29	53 23	71 34	72 07	63 17	75 -12	71 -03	50 08	52 30	51 -00	40 22	42 09	58 12
7	80 34	70 60	48 51	24 25	53 48	-- 17	37 32	17 -00	39 07	30 -10	71 14	64 -13	66 33	76 -04	57 03	26 19	73 -02
8	08 43	06 42	24 25	20 06	71 05	37 07	-- -03	53 -00	50 -07	57 08	41 11	29 -15	21 06	38 13	20 -04	30 -00	30 -06
9	-03 69	-06 29	-15 -05	-03 11	72 -02	17 14	53 01	-- 08	63 12	92 -04	49 -22	20 20	27 06	18 -00	16 09	41 -12	26 -06
10	21 60	22 45	38 40	21 24	63 39	39 04	50 01	63 05	-- 03	89 04	50 05	34 -05	37 -02	32 04	29 05	71 -01	36 14
11	09 72	07 40	11 18	09 19	75 19	30 10	57 01	92 07	89 09	-- 00	55 -10	30 09	35 03	27 02	25 08	61 -08	34 03
12	59 55	48 45	17 27	08 26	71 34	71 18	41 29	49 -12	50 08	55 -29	-- -16	49 -00	59 29	61 -16	47 13	38 05	65 08

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APPENDIX TABLE 12 Continued. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Neepawa normal

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
13	58 40	49 37	25 33	13 23	50 37	64 08	29 25	20 06	34 10	30 -02	49 -00	-- 02	66 28	54 -03	64 08	30 12	54 15
14	69 48	66 20	13 17	-13 14	52 51	66 23	21 40	27 06	37 19	35 -17	59 05	66 06	-- 32	55 -11	58 19	36 23	71 16
15	65 33	63 32	30 28	01 07	51 41	76 17	38 35	18 -03	32 -02	27 -06	61 09	54 -13	55 38	-- -19	60 10	23 13	68 06
16	52 33	46 35	18 30	03 28	40 45	57 08	20 34	16 11	29 17	25 -09	47 -01	64 09	58 21	60 -06	-- 25	27 15	41 17
17	26 55	32 22	34 36	10 23	42 48	26 04	30 18	41 09	71 15	61 -08	38 02	30 -00	36 03	23 02	27 10	-- 06	34 20
18	79 47	87 -00	12 -05	-32 -18	58 44	73 19	30 37	26 -00	36 12	34 -18	65 01	54 -04	71 38	68 -06	41 18	34 14	-- 04
19	32 --	24 26	-09 07	-10 25	80 26	34 29	43 34	69 15	60 27	72 -16	55 -10	40 15	48 21	33 04	34 21	55 08	47 19
20	20 26	-01 --	57 83	74 64	38 23	60 05	42 05	29 01	45 -05	40 09	45 17	37 -13	20 05	32 07	35 -16	22 07	-00 04
21	29 07	13 83	78 --	79 67	14 44	51 01	25 10	-05 -01	40 -11	18 14	27 30	33 -24	17 00	28 07	30 -13	36 15	-05 06
22	32 25	-06 64	07 67	53 --	20 28	25 19	06 24	11 23	24 23	19 06	26 11	23 12	14 16	07 10	28 11	23 30	-18 16
23	57 26	74 23	38 44	-19 28	29 --	48 29	05 67	-02 09	39 19	19 -14	34 15	37 12	51 30	41 -06	45 20	48 27	44 28
24	29 29	25 05	-14 01	-22 19	23 29	17 --	07 57	14 14	04 21	10 -12	18 01	08 -12	23 17	17 -07	08 24	04 25	19 07

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APPENDIX TABLE 12 Continued. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Neepawa normal

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
25	50 34	57 05	-07 10	-36 24	34 67	32 57	-03 --	01 28	01 44	01 -22	29 06	25 04	40 40	35 -09	34 38	18 32	37 29
26	12 15	03 01	-23 -01	-06 23	07 10	-00 14	-00 28	08 --	05 75	07 48	-12 26	06 56	06 13	-03 08	11 46	09 37	-00 36
27	25 27	16 -05	-34 -11	-23 23	17 19	07 21	-07 44	12 75	03 --	09 -20	08 12	10 49	19 35	-02 -02	17 54	15 51	12 42
28	-15 -16	-18 09	09 14	25 06	-12 -14	-10 -12	08 -22	-04 48	04 -20	00 --	-29 21	-02 19	-17 -28	-06 08	-09 -05	-08 -12	-18 -03
29	14 -10	11 17	31 30	23 11	-03 15	14 01	11 06	-22 26	05 12	-10 21	-16 --	-00 -45	05 26	09 18	-01 25	02 71	02 24
30	-01 15	-11 -13	-44 -24	-18 12	08 -12	-13 -12	-15 04	20 56	-05 49	09 19	-00 -45	02 --	06 01	-13 -08	09 27	-00 -14	-04 11
31	47 21	40 05	-10 00	-21 16	30 30	33 17	06 40	06 13	-02 35	03 -28	29 26	28 01	32 --	38 -13	21 49	03 61	38 25
32	-05 04	-08 07	02 07	13 10	-00 -06	-04 -07	13 -09	-00 08	04 02	02 08	-15 18	-03 -08	-11 -13	-19 --	-06 -15	01 -01	-06 -18
33	24 21	22 -16	-24 -13	-27 11	22 20	03 24	-04 38	09 46	05 54	08 -05	13 25	08 27	19 49	10 -15	25 --	10 60	18 41
34	37 08	26 07	-02 15	-02 30	09 27	19 25	-00 32	-12 37	-01 51	-08 -12	05 71	12 -14	23 61	13 -01	15 60	06 --	14 42

$r_{.05}$ (df = 79) = 22 $r_{.01}$ (df = 79) = 28

APPENDIX TABLE 13. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Era normal

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
1	92	80	52	05	54	84	32	-48	65	28	73	66	73	74	57	36	76
	14	15	39	09	41	21	31	08	-04	14	18	-06	17	04	08	10	-12
2	--	77	15	-03	63	83	38	-31	58	38	78	63	76	78	62	22	73
	19	19	32	24	43	29	40	09	03	05	20	-08	29	02	17	20	-09
3	77	--	30	-51	59	62	31	-52	61	18	52	56	62	64	42	37	90
	18	-30	-09	-27	60	26	48	09	01	07	19	-07	18	-05	09	13	-26
4	15	30	--	23	-04	33	-03	-53	41	-09	16	26	17	21	10	42	29
	-07	01	32	-25	11	-11	-12	03	-16	26	01	01	-19	07	-18	-19	-10
5	-03	-51	23	--	-26	08	-15	25	-22	02	07	01	-02	-07	08	02	-42
	-11	64	69	57	-43	-13	-34	01	-09	15	-04	00	00	09	-06	-02	28
6	63	59	-04	-26	--	41	72	-34	40	12	43	44	42	49	31	34	41
	19	-02	18	18	56	19	54	-05	06	-15	44	-36	51	-01	16	33	-39
7	83	62	33	08	41	--	23	-32	58	36	70	51	67	68	51	-12	66
	10	39	31	14	24	19	18	01	-13	16	09	-03	08	13	10	06	-04
8	38	31	-03	-15	72	23	--	-19	38	26	26	29	28	34	25	20	23
	-05	08	20	21	39	20	27	-14	-07	-07	35	-37	33	13	06	12	-29
9	-31	-52	-53	25	-34	-32	-19	--	-66	31	-18	-32	-22	-24	-12	-41	-50
	-16	29	02	33	-33	-08	-14	-04	-01	-04	-17	11	04	01	14	-02	15
10	58	61	41	-22	40	58	38	-66	--	51	49	45	48	48	36	22	52
	-01	05	18	-04	47	15	19	00	-07	10	25	-21	02	-02	-02	02	-12
11	38	18	-09	02	12	36	26	31	51	--	41	20	36	33	32	-20	09
	-19	39	24	33	22	09	07	-04	-10	08	12	-14	07	-01	14	00	02
12	78	52	16	07	43	70	26	-18	49	41	--	45	53	58	49	05	54
	21	27	29	21	21	05	14	-03	-09	04	09	-08	16	07	07	06	04

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APPENDIX TABLE 13 Continued. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Era normal

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
13	63 11	56 -02	26 18	01 03	44 24	51 21	29 22	-32 07	45 -09	20 21	45 12	-- -04	72 07	49 08	58 -04	31 08	55 -01
14	76 07	62 06	17 15	-02 05	42 21	67 26	28 21	-22 05	48 -04	36 12	53 07	72 -00	-- 18	57 09	56 09	15 08	65 00
15	78 18	64 12	21 21	-07 11	49 35	68 33	34 33	-24 -02	48 -01	33 -00	58 21	49 -16	57 20	-- 01	60 12	14 09	61 -14
16	62 28	42 22	10 33	08 28	31 31	51 20	25 25	-12 17	36 08	32 09	49 08	58 09	56 10	60 10	-- 21	13 12	36 24
17	22 06	37 -34	42 30	02 04	34 42	-12 05	20 32	-41 22	22 24	-20 -01	05 28	31 -10	15 29	14 -13	13 01	-- 26	18 -23
18	73 10	90 -38	29 -27	-42 -45	46 22	66 22	23 17	-50 -06	52 -17	09 11	54 02	55 -03	65 07	61 04	36 -07	18 -03	-- -20
19	19 --	18 00	-07 05	-11 08	19 24	10 18	-05 25	-16 17	-01 28	-19 -15	21 01	11 11	07 04	18 02	28 21	06 11	10 18
20	19 00	-30 --	01 78	64 81	-02 07	39 -03	08 07	29 07	05 -01	39 12	27 11	-02 -04	06 04	12 05	22 21	-34 10	-38 20
21	32 05	-09 78	32 --	69 83	18 32	31 02	20 25	02 21	18 15	24 10	29 27	18 -09	15 18	21 -00	33 24	30 24	-27 00
22	24 08	-27 81	-25 83	57 --	18 26	14 06	21 31	33 20	-04 25	33 -04	21 26	03 -08	05 29	11 -05	28 34	04 34	-45 13
23	43 24	60 07	11 32	-43 26	56 --	24 23	39 82	-33 30	47 33	22 -05	21 40	24 -10	21 25	35 -15	31 37	42 33	22 -25
24	29 18	26 -03	-11 02	-13 06	19 23	19 --	20 42	-08 17	15 21	09 -02	05 01	21 17	26 05	33 -03	20 22	05 15	22 -06

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APPENDIX TABLE 13 Continued. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X Era normal

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
25	40	48	-12	-34	54	18	27	-14	19	07	14	22	21	33	25	32	17
	25	07	26	31	82	42	--	30	39	-12	34	-05	29	-19	42	38	-21
26	09	09	03	01	-05	01	-14	-04	00	-04	-03	07	05	-02	17	22	-06
	17	07	21	20	30	17	30	--	67	34	20	54	14	12	35	41	07
27	03	01	-16	-09	06	-13	-07	-01	-07	-10	-09	-09	-04	-01	08	24	-17
	28	-01	15	25	33	21	39	67	--	-44	38	19	41	02	57	58	-03
28	05	07	26	15	-15	16	-07	-04	10	08	04	21	12	-00	09	-01	11
	-15	12	10	-04	-05	-02	-12	34	-44	--	-26	42	-35	08	-34	-24	10
29	20	19	01	-04	44	09	35	-17	25	12	09	12	07	21	08	28	02
	02	11	27	26	40	01	34	20	38	-26	--	-69	66	-02	46	73	-24
30	-08	-07	01	00	-36	-03	-37	11	-21	-14	-08	-04	-00	-16	09	-10	-03
	11	-04	-09	-08	-10	17	-05	54	19	42	-69	--	-41	08	-09	-29	19
31	29	18	-19	00	51	08	33	04	02	07	16	07	18	20	10	29	07
	04	04	18	29	25	05	29	14	41	-35	66	-41	--	08	40	69	-32
32	01	-05	07	09	-01	13	13	01	-02	-01	07	08	09	01	10	-13	04
	02	05	00	-05	-15	-03	-19	12	02	08	-02	08	08	--	07	-04	10
33	17	09	-18	-06	16	10	06	14	-02	14	07	-04	09	12	21	01	-07
	21	21	24	34	37	22	42	35	57	-34	46	-09	40	07	--	59	-12
34	20	13	-19	-02	33	06	12	-02	02	00	06	08	08	09	12	26	-03
	11	10	24	34	33	15	38	41	58	-24	73	-29	69	-04	59	--	-17

$r_{.05}$ (df = 79) = 22 $r_{.01}$ (df = 79) = 28

APPENDIX TABLE 14. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X 320 normal

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
1	92 31	82 18	56 43	10 10	42 55	83 23	14 30	-23 16	44 22	35 -04	63 21	62 -04	74 08	81 -20	52 -10	50 20	76 21
2	-- 39	89 04	22 23	-13 10	53 59	83 29	08 44	-15 15	32 27	26 -10	72 29	58 -10	75 15	81 -16	51 -02	34 31	83 24
3	89 33	-- -20	21 -05	-43 -24	51 64	79 17	08 43	-25 13	29 21	17 -06	62 13	56 03	64 02	72 -18	34 -12	21 19	94 23
4	23 -08	21 45	-- 67	56 04	-07 23	37 01	16 -12	-23 01	47 -10	38 12	09 -11	37 11	30 -19	33 -12	22 -26	56 -22	18 -01
5	-13 -09	-43 74	56 81	-- 59	-31 -24	-08 -00	-01 -25	09 -04	19 -12	26 08	-11 05	-07 -11	00 02	-02 01	10 -00	38 -10	-43 -05
6	53 16	51 -19	-07 10	-31 16	-- 65	28 44	52 67	-26 29	10 41	-05 -02	32 43	31 -13	31 45	48 -15	24 19	37 31	36 03
7	83 31	79 23	37 15	-08 -12	28 37	-- 18	-05 19	-14 02	28 17	22 -15	59 14	45 -05	60 -02	67 -15	44 -20	04 19	82 29
8	08 -18	08 -20	16 11	-01 -00	52 19	-05 27	-- 12	-27 21	21 32	07 -05	01 34	15 -17	04 26	26 -04	07 11	41 10	04 -08
9	-15 19	-25 21	-23 -00	09 20	-36 -14	-14 02	-27 11	-- -23	-44 -12	11 -17	09 17	-33 -30	01 25	-12 28	13 27	-23 28	-26 04
10	32 -07	29 12	47 36	19 14	10 34	28 -05	21 -16	-44 -02	-- -11	84 09	23 -12	38 08	34 -20	24 -30	19 -02	46 -20	22 -03
11	26 03	17 26	38 39	26 28	-05 27	22 -04	07 -11	11 -16	84 -20	-- -00	31 -04	22 -08	38 -07	19 -17	29 14	37 -05	09 -01
12	72 28	62 -01	09 07	-11 -01	32 28	59 21	01 29	09 06	23 11	31 -04	-- 14	29 -07	65 13	66 -06	36 04	11 23	64 29

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APPENDIX TABLE 14 Continued. Simple Correlations X 10^2 between all F_2, F_3 and F_4 variables, Glenlea X 320 normal

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
13	58 18	56 -07	37 21	-07 -01	31 47	45 25	15 26	-33 14	38 15	22 01	29 03	-- 10	63 -08	55 -17	42 -02	45 09	52 02
14	75 32	64 09	30 26	00 11	31 47	60 24	04 33	01 08	34 20	38 -12	65 14	63 -04	-- 06	72 -19	60 -06	34 27	58 18
15	81 31	72 03	33 26	-02 05	48 48	67 24	26 32	-12 23	24 26	19 02	66 27	55 -05	72 14	-- -12	50 00	38 23	68 24
16	51 36	34 23	22 36	10 31	24 40	44 18	07 25	13 22	19 24	29 03	36 25	42 -02	60 20	50 -08	-- 01	29 35	26 04
17	34 03	21 04	56 68	38 45	37 51	04 21	41 23	-23 22	46 15	37 13	11 26	45 -09	34 20	38 -10	29 16	-- 07	05 -08
18	83 27	94 -27	18 -20	-43 -43	36 37	82 13	04 21	-26 06	22 16	09 -12	64 04	52 05	58 -08	68 -13	26 -20	05 18	-- 23
19	39 --	33 07	-08 08	-09 17	16 26	31 07	-18 28	19 19	-07 13	03 11	28 21	18 -01	32 16	31 02	36 -02	03 33	27 19
20	04 07	-20 --	45 75	74 61	-19 06	23 07	-20 03	21 -03	12 -08	26 06	-01 09	-07 -09	09 03	03 -00	23 04	04 -04	-27 08
21	23 08	-05 75	67 --	81 76	10 35	15 19	11 17	-00 13	36 03	39 14	07 21	21 -11	26 16	26 -06	36 12	68 02	-20 -02
22	10 17	-24 61	04 76	59 --	16 29	-12 20	-00 31	20 18	14 13	28 11	-01 39	-01 -23	11 37	05 00	31 40	45 20	-43 -01
23	59 26	64 06	23 35	-24 29	65 --	37 28	19 70	-16 24	34 20	27 14	28 25	47 -01	47 19	48 -17	40 16	51 14	37 08
24	29 07	17 07	01 19	-00 20	44 28	18 --	27 32	02 04	-05 04	-04 03	21 18	25 -08	24 10	24 05	18 22	21 17	13 -10

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APPENDIX TABLE 14 Continued. Simple Correlations X10^2 between all F_2, F_3 and F_4 variables, Glenlea X 320 normal

	2 19	3 20	4 21	5 22	6 23	7 24	8 25	9 26	10 27	11 28	12 29	13 30	14 31	15 32	16 33	17 34	18 35
25	44 28	43 03	-12 17	-25 31	67 70	19 32	12 --	11 25	-16 31	-11 03	29 37	26 -11	33 47	32 07	25 24	23 36	21 15
26	15 19	13 -03	01 13	-04 18	29 24	02 04	21 25	-24 --	-02 66	-16 58	06 27	14 51	08 22	23 -11	22 11	22 19	06 20
27	27 13	21 -08	-10 03	-12 13	41 20	17 04	32 31	-12 66	-11 --	-20 -20	11 47	15 08	20 38	26 -10	24 12	15 40	16 21
28	-10 11	-06 06	12 14	08 11	-02 14	-15 03	-05 03	-17 58	09 -20	-00 --	-04 -12	01 57	-12 -10	02 -04	03 -00	13 -19	-12 02
29	29 21	13 09	-11 21	05 39	43 25	14 18	34 37	17 27	-12 47	-04 -12	14 --	03 -66	14 77	27 07	26 35	26 73	04 22
30	-10 -01	03 -09	11 -11	-11 -23	-13 -01	-05 -08	-17 -11	-30 51	08 08	-08 57	-07 -66	10 --	-04 -50	-05 -11	-02 -23	-09 -47	05 -06
31	15 16	02 03	-19 16	02 37	45 19	-02 10	26 47	25 22	-20 38	-07 -10	13 77	-08 -50	06 --	14 10	20 32	20 75	-08 07
32	-16 02	-18 -00	-12 -06	01 00	-15 -17	-15 05	-04 -07	28 -11	-30 -10	-17 -04	-06 07	-17 -11	-19 10	-12 --	-07 16	-10 10	-13 -09
33	-01 -02	-12 04	-26 12	-00 40	19 16	-20 22	11 24	27 11	-02 12	14 -00	04 35	-02 -23	-06 32	00 16	01 --	16 24	-20 -01
34	32 33	19 -04	-22 02	-10 20	31 14	19 17	10 36	28 19	-20 40	-05 -19	23 73	09 -47	27 75	23 09	35 24	07 --	18 15

$r_{.05}$ (df = 79) = 22 $r_{.01}$ (df = 79) = 28