

INHERITANCE STUDIES OF SEEDLING
VIGOR OF WHEAT

A Thesis
Submitted to the Faculty
of
Graduate Studies
The University of Manitoba
by
Christian A. Opoku

In Partial Fulfillment of the
Requirements for the Degree

of

Master of Science
Department of Plant Science

October 1979

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CHRISTIAN ADJEI OPOKU

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ACKNOWLEDGEMENTS

This study was conducted under the supervision of Dr. L.E. Evans whose guidance is very appreciated. The author also expresses his appreciation for the assistance given by the supervisory committee: Drs. Larter, LaCroix and Ridley.

Special thanks go to Mr. D. Zuzens for his assistants and comments.

Sincere thanks also go to Carolyn, Ethel and Wilson McIntyre whose concern and draft typing of the thesis is most appreciated. The author, also, acknowledges the help rendered by Emmanuel Awuku-Darkoh in the statistical analysis.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	ii
LIST OF TABLES	v
LIST OF FIGURES	vii
ABSTRACT	viii
1. INTRODUCTION	1
2. LITERATURE REVIEW	3
2.1 Measurement of Seedling Vigor	3
2.2 Effect of Seed Size Upon Seedling Vigor	5
2.3 Effect of Other Factors on Seedling Vigor	8
2.3a Protein Content	8
2.3b Energy Metabolism and Capacity of Synthesis in Relation to Rate of Growth	9
2.3c Genetic, Physiological, Cytological, Pathological, Mechanical and Storage Conditions as They Affect Seedling Vigor	11
2.4 Inheritance of Seedling Vigor	15
2.5 Seed Size and Emergence	19
2.6 Seed Size Effect on Parts of the Seedling	20
2.7 Seed Size Effect on Yield	21
3. MATERIALS AND METHODS	23
3.1 Experiment 1: Effect of Seed Size of Glenlea Wheat on Seedling Vigor	27
3.2 Experiment 2: Comparison of Seedling Vigor of Glenlea and Sinton Wheat and their F ₁ progenies	28
3.3 Experiment 3a: Comparison of Seedling Vigor of 10 Cultivars	29
3.4 Experiment 3b: Estimation of Heritability of Seedling Vigor	29

	Page
4. RESULTS AND DISCUSSION	32
4.1 Experiment 1: Effect of Seed Size on Seedling Vigor of Glenlea Wheat	32
4.2 Experiment 2a: Comparison of Seedling Vigor of Glenlea and Sinton	33
Experiment 2b: Comparison of Seedling Vigor of Glenlea, Sinton and their F_1 Progeny	35
4.3 Experiment 3a: Comparison of Seedling Vigor of Ten Cultivars	38
Experiment 3b: Estimation of Herit- ability of Seedling Vigor	39
5. GENERAL DISCUSSION	52
6. LITERATURE CITED	58
7. APPENDIX	72

LIST OF TABLES

Table	Page
1. Characteristics of Parental Cultivars Used in Crosses.	26
2. Hybrid Combinations Produced	31
3. Measurement of Seedling Vigor of Four Seed Size Classes of Glenlea Wheat	32
4. Measurement of Seedling Vigor of Five Seed Size Classes of Glenlea and Sinton Wheat	35
5. Measurement of Seedling Vigor of Five Replications of the Reciprocal F ₁ Progenies of Glenlea and Sinton Wheat	37
6. Measurement of Seedling Vigor of Glenlea, Sinton and Their Bulkcd F ₁ Progeny	37
7. Measurement of Seedling Vigor of the Ten Cultivars All From Similar Seed Size	39
8. Distribution of Seedling Vigor of Glenlea, Kite and Subsequent Generations -- High x Low	40
9. Distribution of Seedling Vigor of NB320, Kite and Subsequent Generations -- Low x Low	41
10. Distribution of Seedling Vigor of Norquay, BW42 and Subsequent Generations -- Medium x Medium	42
11. Distribution of Seedling Vigor of Norquay, Kite and Subsequent Generations -- Medium x Low	43
12. Distribution of Seedling Vigor of Glenlea x RL4137 and Subsequent Generations -- High x High	44

Table	Page
13. Distribution of Seedling Vigor of Glenlea, Norquay and Subsequent Generations -- High x Medium	45
14. Broad and Narrow Sense Heritability Estimates of the Six Crosses	50

LIST OF FIGURES

Figure	Page
1. A Box of Seedlings	24
2. A Seedling Showing the Roots Excised 2 cm Below the Seed Level	25
3. Seed Size of Glenlea Wheat Plotted Against Seedling Vigor	34
4. Seed Size of Glenlea And Sinton Wheat Plotted Against Seedling Vigor	36

ABSTRACT

Opoku, Christian Adjei. M.Sc., The University of Manitoba, October, 1979. Inheritance Studies of Seedling Vigor of Wheat. Major Professor; L. E. Evans.

Three greenhouse experiments were conducted to study the inheritance of seedling vigor of wheat, measured as seedling fresh weight 20 days after sowing. In experiment 1, the seedling vigor of different seed weights of Glenlea wheat was compared. Seed size had a positive and significant correlation with seedling vigor. In experiment 2 the seedling vigor of Glenlea, Sinton and their F_1 progenies were compared. The seedling vigor of Glenlea was significantly higher than that of Sinton at the same seed weight. There was no maternal effect on the inheritance of the trait, and the seedling vigor of the bulked F_1 progenies was equal to Glenlea and significantly higher than that of Sinton.

In the third experiment six wheat cultivars were classified as having high, medium or low seedling vigor (two cultivars within each group). Twelve crosses were made which included those between the two cultivars of each group, crosses among the three groups, and the reciprocals. The F_1 generations were advanced to F_2 and back crossed to both parents.

Estimation of the broad sense heritability ranged from 53.57 to 70.62% and the narrow sense heritability was from 30.04 to 40.55%. Seedling vigor of wheat is a heritable trait and one that should readily respond to selection.

1. INTRODUCTION

Seedling vigor was defined by Isely (1957) as the sum total of seed attributes which favor stand establishment under unfavorable field conditions. Delouche and Caldwell (1960) added a practical concept, by defining seedling vigor as the sum of all attributes which favor rapid and uniform stand establishment in the field. Derwyn et al (1973) also referred to species that consistently showed rapid germination, fast root and top growth, robust growth habit, and resistance to stress as having seedling vigor.

Failure of seeds to germinate uniformly can often result in thin unproductive stands because of competition with other crops (e.g. mixed cropping) or with weeds. Losses which result do not relate primarily to the cost of seed but rather to inefficient land use and subsequent reduction of income (Isely 1958). Even after germination seedlings which are inherently weak are more susceptible to a variety of adverse conditions, than highly vigorous ones (Delouche and Caldwell 1960). Seedling vigor is therefore important in the establishment of a crop from the seed stage.

Evans and Bhatt (1977) using wheat cultivars found a positive and significant relationship between cultivar and seedling vigor. Kneebone and Cremer (1955), working with certain grass species, and Kittock and Law (1968), with wheat

cultivars, both found similar relationships. Twamley (1973) performed three cycles of selection for seedling vigor in birdsfoot trefoil (Lotus corniculatus L.) and found an estimated improvement of 40%.

Although the above workers studied the inheritance of seedling vigor it has not been exploited as a selection criterion. Depending upon the heritability of seedling vigor, cultivars might be developed that have improved levels of early growth and improved yield.

In this study, three experiments were conducted with the following objectives: to determine the effect of seed size on seedling vigor of wheat; to compare the seedling vigor of different cultivars and to estimate its heritability.

For the purpose of this study seedling vigor is defined as the relative growth rate of early plant development (Lowe et al 1972) measured as fresh weight 20 days after sowing (Evans and Bhatt 1977).

2. LITERATURE REVIEW

2.1 Measurement of Seedling Vigor

Vigorous seedlings arise from seeds that do not age rapidly when stored (Heydecker 1969) and which germinate simultaneously without delay (Heydecker 1969; The Association of Official Seed Analysts 1976; Knittle and Burris 1976; Maguine 1962). In addition, such seeds must be free from seedborne diseases, and resistant to microbial organisms. The seedlings must be sufficiently strong to penetrate the soil (Kittock and Law 1968; Heydecker 1969; Rogler 1954), and have the ability to establish themselves under a wide range of environmental conditions. Vigorous seedlings are able to live on their own reserves until photosynthesis begins after which they exhibit a fast growth rate.

Such a description lends itself to numerous ways by which seedling vigor can be measured. For example, Trupp and Carlson (1971) used as a measure of seedling vigor the ability of the seedling to emerge from a 5 cm planting depth. To Kneebone and Cremer (1955), a vigorous seedling was one that emerged quickly and grew rapidly.

Several workers have determined seedling vigor as wet or dry weight after a certain period of time (Trupp and Carlson 1971; Knittle and Burris 1976; Burris 1977; Twamley 1967;

Venkata Rae et al 1970; Burris et al 1969). Evans and Bhatt (1977) measured seedling vigor as seedling dry weight at 20 days after planting. Boyd et al (1971) weighed it as dry weight two weeks after germination. Jones and Peterson (1976) determined the seedling vigor of rice by first soaking the seeds in distilled water for 24 hours at 30°C. They germinated the seeds in the dark on moist blotters at different temperatures and seedling weight was then used as the primary criterion for seedling vigor evaluation. Seedling vigor has also been measured simply as dry weight, hypocotyl length, radicle length and the total seedling length (Conje and Carlson 1972; Ketrang et al 1978). Perry (1977) determined the seedling vigor of barley by measuring the plumule growth in rolled paper towels after seven days at 20°C in the dark.

Ching (1973) suggested that ATP content in imbibed seeds is a useful biochemical index of seedling vigor. Because of the strength of the association between isocitratase activity and axial growth early in germination, Scholl (1974) suggested that isocitratase activity may be a good indicator of early seedling vigor.

Other methods of measurement include the respiration test (i.e. oxygen uptake and respiratory quotient); temperature stress test (survival and germination over a wide range of temperature); penetration test (ability of seedlings to emerge through a mechanical obstruction); cold test (ability to survive in cold soil of high pathogenic potential and then to later germinate under warm conditions); and the self-

protection test which includes a comparison of establishment with and without fungicidal dressing (Heydecker 1969).

2.2 Effect of Seed Size Upon Seedling Vigor

A positive relationship between seed weight and seedling vigor has been established. Evans and Bhatt (1977) working with spring wheat and Ries et al (1976) with winter wheat found a positive and significant correlation between seed weight and seedling vigor for a large number of cultivars. Similar results were reported by Khayrallah and Lawson (1976) with birdsfoot trefoil (Lotus corniculatus) and Carleton and Cooper (1972) with other forage legumes. Generally, plants from large seeds are superior to those from small seeds in early growth rate and therefore in early seedling weight (McFadden et al 1960; Trupp and Carlson 1971).

In measuring seedling vigor as the ability of seedlings to emerge from various depths of planting Rogler (1954) found a highly significant positive correlation between seed weight and emergence.

Harper and Obeid (1967), working with commercial samples of oil-seed and fiber flax (Linum usitatissimum L.) confirmed that in the early seedling development both leaf area and dry weight were closely related to seed size. Significantly taller plants were obtained from the large seeds. Tropical legume seeds were germinated and grown in the dark and light under controlled conditions to determine an estimate of seedling vigor. Heavier seed weight conferred an advantage in

early shoot and root growth. Ultimate length of dark grown seedlings and shoot length of light grown seedlings at day 45 were positively related to seed weights (Crowder and Chow 1974). Working with corn (Zea mays) Hunter and Kannenberg (1972) found that plants from small seeds were shorter than those from large seeds 40 days after planting.

Kneebone and Cremer (1955) separated buffalograss, indiangrass, sand bluestem, sideoats grama, and switchgrass caryopses into various seed size classes. On evaluation of seedling vigor it was observed that the larger the seed within a lot, the more vigorous were the seedlings. Seedlings from large seeds grew faster relative to small seeds. In another experiment, Kneebone (1956) reports that large seeded sand bluestem (Andropogon hallii Hack) selections tended to set more seed, to have less seed damaged in processing, and to have more vigorous progenies than did small seeded selections.

Rothman and Bowman (1967) reported that if favorable environmental conditions prevailed, low-test-weight seeds of spring oats produced seedlings which reached the same weight as those from high-test-weight. On the other hand, unfavorable weather could play a limiting role, leading to smaller seedlings from the low-test-weight samples. In experiments in which four oats cultivars were used, each with five test weights ranging from 17-38 pounds/bushel, it was reported that seedlings from the seed lots ranging from 17 to 28 pounds/bushel initially weighed from 50 to 75% as much as

those from seed lots which weighed more than 30 pounds/bushel. It required from 7 to 10 weeks after planting, for the plants from light-test-weight seed to reach the same weight as those from high-test-weight samples (Frey and Wiggans 1956).

Thomas (1966) used a number of measurements of seedling vigor within six populations of Lolium perenne, and found a high positive and significant correlation between seed size and seedling vigor but showed that the correlations decreased as the plants became older. Studying the effects of seed size on seedling vigor of six varieties and strains of birdsfoot trefoil, Henson and Tayman (1961) showed that seedlings from large seeds produced more top growth than those from smaller seeds, and that basal shoots appeared earlier on seedlings derived from large seeds. Twamley (1972) in studying the seed size/seedling vigor relationship of 20 birdsfoot trefoil (Lotus corniculatus) families concluded that wide variations existed within and among families for both seed size and seedling vigor. In an experiment with birdsfoot trefoil, Twamley (1967, 1969) found that even large seeds sometimes produced poorer materials but on the whole, seedlings from larger seeds outperformed seedlings from smaller ones. In addition plants arising from large seeds had a pronounced tendency to tiller early.

In seedlings of two lines of Phalaris tuberosa selected for high and low herbage nitrogen content, the seedling weights were correlated with the weights of seeds from which they originated and with nitrogen absorbed (Clements 1973).

Black (1957b) assessed the significance of seed weight in the growth of subterranean clover (Trifolium subterraneum L.) under both spaced plants and sward conditions and found that the dry weights of plants were proportional to seed weight over almost the entire growing period.

2.3 Effect of Other Factors on Seedling Vigor

2.3a Protein Content. Several investigators have found that the level of protein content has a positive and significant correlation with seedling vigor (Evans and Bhatt 1977; Ries and Everson 1973; McDaniel 1969; Welch 1977; Ries et al 1976; Abdul-Baki 1969; Schweizer and Ries 1969). Using seeds of a Mexican semidwarf wheat obtained from a nitrogen fertilizer field trial, Lowe and Ries (1973) observed that a large positive correlation existed between protein content of the aleurone layer and endosperm and the seedling dry weight. There was no relationship between the seedling dry weight and the embryo protein content. When embryos were transferred from one endosperm type to another it was found that high protein endosperm produced more vigorous seedlings regardless of the embryo, indicating that the factor(s) responsible for the greater growth of high protein seed is in the endosperm. In another experiment Lowe and Ries (1972) showed that seedlings grown from high protein seeds were more advanced in morphological development than those grown from low protein seeds. Lowe et al (1972) also reported that percent glutamic acid was positively related to seedling growth. However,

several other amino acids were found to be negatively correlated. In an attempt to study the relationship between seed size, protein content and seedling vigor Ayers et al (1976) used foliar applications of urea on winter wheat (Triticum aestivum L. cv. Logan). Seedling vigor was found to be closely related to the total protein content of the whole seed and endosperm and to the salt-insoluble and salt-soluble endosperm fractions. In a fertilizer study conducted by Schweizer and Ries (1969) it was observed that wheat seed that contained more protein as a result of field application of nitrogen, produced larger seedlings.

2.3b Energy Metabolism and Capacity of Synthesis in Relation to Rate of Growth. McDaniel (1969) reported that seedling fresh weight, seedling mitochondrial protein and mitochondrial biochemical activity were positively correlated with seed weight. He explained that the increased quantity of mitochondrial protein of seedlings produced from heavy seeds was indicative of a higher respiratory rate and greater energy (ATP) production. Thus, these seedlings had a greater growth potential than seedlings produced from lighter seeds of the same pure line. This explanation is further supported by Ching and Kronstad's (1972) finding that faster growing seedlings (i.e. higher seedling vigor) metabolize and synthesize energy (ATP) faster than slow growing seedlings. Burris et al (1971) also indicated that large seeds exhibited a higher respiratory rate both in the cotyledons and in the

root-shoot axis. Ching (1973) confirmed that the ATP content in imbibed seeds correlated significantly with seedling size (i.e. seedling vigor) and that it indicated viability in seed lots. He also cited Bashirelahi and Dallam (1970) who observed that there may be other differences in efficiency such as nuclear phosphorylation capacity related to seed size.

Studying the rates of respiration in Zea mays L. at different stages of germination and seedling development, Cantrell (1972) observed a high positive correlation between 24 hour kernel respiration rates and seedling vigor, a low correlation between root tip respiration rate and seedling vigor, and a negative relationship between seedling shoot respiration rate and seedling vigor. Abernethy et al (1977) studied the association of seedling respiration metabolism and adenylate energy charge with seed weight of Panicum antidotah. The results indicated that the rates of respiration through the first 72 hours, content of free sugar (mg./seed), and the adenylate phosphate content, were all higher for the heavier seed-weight selections. Although energy charge values were not significantly different during germination, the value for unimbibed seed was greater for heavy seed-weight selections. Heavy seed also contained more free sugar for respiratory substrate and more adenylate phosphates for further phosphorylation. It is explained that the larger seedlings resulted from increased rates of ATP formation which in turn resulted from the enhanced respiratory metabolism.

Working with wheat seeds Kittock and Law (1968) reported significant positive correlation between rate of emergence and vigor (ability to emerge from deep seeding), emergence and rate of respiration, and between vigor and both tetrazolium reduction and rate of respiration. Similar results by Burris et al (1969) with soybean (Glycine max (L.) Merr) indicated a correlation between glucose levels, respiration of the imbibed seed and tetrazolium tests with seed quality and subsequent seedling vigor. A highly significant correlation between adenosine triphosphate (ATP) content in imbibed lettuce seeds and seedling height and weight was reported by Ching and Danielson (1972).

The literature indicates that the higher the protein content of the seed the higher the seedling vigor. Heavy seeds are considered to have more mitochondria, which leads to higher respiration rate. This, in turn results in greater energy (ATP) production, and thus a greater growth potential. The greater growth potential could lead to a faster rate of emergence for heavier seeds and the production of larger seedlings.

2.3c Genetic, Physiological, Cytological, Pathological, Mechanical and Storage Conditions as They Affect Seedling Vigor. Genetic. In a diallel crossing experiment with hybrid maize (Zea mays) Burris (1977) observed that both the location of the experiment and the female parentage had a highly significant effect on germination and shoot and root

dry weight. Male parentage had only a moderate effect on these characters. Tull (1733) as cited by Ries and Everson (1973), believed that seed source is an important factor in subsequent crop growth and yield.

Physiological and Cytological. Such factors include defects due to premature harvest of the seeds; deterioration of cell membranes; lack of vital cell constituents or inability to utilize these; and detrimental changes in the chromosomes (Heydecker 1969). Wijandi and Copeland (1974) conducted studies to compare the laboratory and field performances of hand-threshed Michigan and Idaho-grown bean-seed after impaction at comparable moisture levels. The level of injury increased significantly as the seed moisture content decreased. There was also a significant reduction in germination and seedling vigor in seed harvested prior to complete maturity.

An experiment was conducted in an attempt to correlate several kernel maturity indices with seedling vigor in a maturing seed corn crop (Knittle and Burris 1976). The belief was that production of high quality seed corn would be facilitated by the harvesting of the seed at a kernel maturity which is highly correlated with maximum seedling vigor. The results indicated that although germination percentages were high over all harvest dates, both shoot and root dry weights were highly dependent on the date of harvest. The dates of maximum vigor and kernel maturation patterns were specific for each hybrid. Maximum kernel dry weight was correlated with maximum shoot and root dry weights. An

investigation by Mukherjee et al (1973) was carried out on rice seeds in the early imbibitional phase to determine the effect of temperature treatments on changes in germination percentage, seedling growth, and other characters. It was found that treatment for 30 minutes at 50°C caused a variable increase in all the characters studied, and a positive correlation existed between seedling vigor and hydrolase activities. However, treatment for 30 minutes at 60°C had a retarding influence on these characters.

In an experiment on the effect of air temperature on seed production and seedling vigor of two alfalfa cultivars under controlled environmental conditions, Walter and Jenson (1970) reported that seeds produced under cool temperature were heavier and had a higher percentage of hard seed than those produced under hot temperatures. Seeds produced under cool temperatures also produced larger seedlings in one of the cultivars. But for certain cultivars of upland cotton, Peacock and Hawkins (1970) observed that higher temperatures and lower rainfall were associated with lower yield and poorer seedling vigor. Gubbels (1976) has reported that the seedling vigor of corn was enhanced by high initial seed moisture, pregermination, imbibition of gibbelleric acid, and phosphorous applied with the seed. In another observation involving Phalaris tuberosa L. Clements (1973) concluded that seedlings from a high nitrogen line were smaller than those of the low nitrogen line, but had similar whole-plant relative growth rates.

Singh and Tomar (1972) have demonstrated that the soaking of paddy rice seeds for 48 hours in one percent sodium hypochlorite, enhanced the germination percentage as well as the rate of elongation of plumule and radicle. The next best treatment was sodium hydroxide presoaking. The pretreatment of sorghum seed with the fungicide "TMTP" for storage (Venkata Roa et al 1970), gave a higher viability and germination than the untreated seeds.

Pathological. McFadden et al (1960) have confirmed that small and medium sized seeds carry more loose smut (Ustilago nuda) (Jens) Rostr. inoculum than large seeds in composite samples of barley. They suggest the use of large seeds only for seeding purposes because this would be a practical means of reducing losses from loose smut. There is evidence that seedlings inherently weak in vigor are more susceptible to a variety of adverse conditions including microbial attack than are highly vigorous ones (Delouche and Caldwell 1960).

Mechanical injuries. Schweitzer (1972) mechanically abused seeds of several bean (Phaseolus vulgaris L.) cultivars by dropping them 9.2 m onto a steel plate. The impaction treatment physically damaged up to 37% of the seeds, depending on their moisture content and cultivar. Of the remaining undamaged seeds, he found that their germination and vigor was influenced by the germination environment as well as by cultivar and moisture content during impaction. The emergence was reduced up to 50%, and of those that emerged, 62% had morphological defects. On investigation of the growth

potential of morphologically normal seedlings, he observed a significant decline in vigor of seedlings grown from damaged seeds. The decline in vigor due to hidden injury, which had resulted from the mechanical abuse, was about one third as great as the loss in vigor caused by excision of one cotyledon.

Accelerated aging has a negative effect on seedling vigor (Perl et al 1978; Gelmond et al 1978). Komolafe (1975) observed that the percentage germination and seedling vigor of cashewnuts decreased with increase in age. However, storage of cashewnuts in baskets or coarse bags helps to retain the viability to some extent. Ching and Danielson (1972) have indicated that aging reduces ATP content as well as germination percentage and seedling size of lettuce. The response to seed treatments (e.g. fungicidal treatment) aimed at increasing the vigor of the subsequent seedling is higher in low vigor seedlings than in high ones (Das Gupta and Austenson 1973). When seeds are allowed to mature before harvesting, there is little relationship between seed weight and viability (Whalley et al 1966c).

2.4 Inheritance of Seedling Vigor

Cultivar effect is an important aspect of the inheritances of seedling vigor. Evans and Bhatt (1977) working with wheat; Jones and Peterson (1976) with rice; Whalley and McKell (1967), with Phalaris; Stickler and Wassom (1963), with birds-foot trefoil; Kneebone and Cremer (1955) and Maquine (1962),

with certain grass species; Henson and Tayman (1961), with birdsfoot trefoil; and Kittock and Law (1968), with wheat, all found a positive and significant effect of cultivar on seedling vigor.

In a report on the analysis of a diallel cross in intermediate wheatgrass (Agropyron intermedium) Hunt and Miller (1965) suggest that there is a strong maternal influence on coleoptile length. In inheritance studies of upland cotton, Scholl (1974) found that the results from reciprocal hybrids indicated that the level of isocitratase activity and axial growth rate were maternally inherited. He believes that isocitratase activity is a good indicator of early seedling vigor. However, Twamley (1970) observed no effect of maternal inheritance on seedling vigor of birdsfoot trefoil.

In another experiment, Twamley (1974) studied recurrent selection for seedling vigor of "Leo" birdsfoot trefoil (Lotus corniculatus L.). He selected only large seeds for the experiment. In each of the three cycles the most vigorous lines were selected to be the parents of the next cycle. In 1972, nursery material representing cycle 0, 1, 2, and 3 was established and harvested for seeds. He performed three types of test to evaluate the progress: 1) the bulk test 2) pedigree test and 3) a series of routine tests to identify superior lines. The results were as follows: for the bulk test the percentage improvement in seedling vigor for cycles 1, 2 and 3 over cycle 0 the initial Leo population was 10, 34 and 40% respectively. For the pedigree test improvement of vigor was

20, 36 and 36% respectively, while for the four routine tests the average improvement was 30, 47 and 57% respectively. The average improvement based on seed size was 36% for seed size. In earlier work, Twamley (1972) had indicated that the best method of selecting good germplasm for seedling vigor was the selection of the most vigorous seedlings from the most vigorous progeny lines.

There was a 5% increase in seedling vigor over the parent material when two cultivars of birdsfoot trefoil (Lotus corniculatus) were crossed (Conje and Carlson 1972). Townsend (1974, 1972) reported that there is enough variation among progenies for seedling vigor of cicer milkvetch (Astragalus cicer L.) to indicate that improvement can be made for this character, and that the improvement of seedling vigor through selection for large seeds is more promising in cicer milkvetch than in falcatus milkvetch (A. falcatus Lam.).

From his own work and additional estimates derived from published information Kneebone (1956) observed that variations in seed size were at least partly heritable and that progress could be made in breeding for large caryopses. He found, also, that one cycle of selection in sideoats grama for more vigorous seedlings gave increases in seedling vigor. On evaluation of three cycles of phenotypic recurrent selection for seedling vigor in Boutelovia curtispindula (Michx.) Torr., Voigt and Brown (1969) found that the third cycle had more (35%) and taller (24%) seedlings, (over the five trials), relative to the base materials. In a study aimed at developing

a technique which could select against seeds of inherent low vigor, using birdsfoot trefoil (Lotus corniculatus) it was shown that the heritability was very low and not significant. The explanation given was that a high proportion of the variability was environmentally controlled (Khayrallah and Lawson 1976). Three cycles of selection for seedling vigor in birdsfoot trefoil resulted in an estimated improvement of 40% (Twamley 1973). In the same experiment it was observed that selection for seed size alone could likely result in substantial improvement for seedling vigor.

Clements and Latter (1974) performed an experiment to investigate the response to selection for seed weight and seedling vigor in Phalaris. The results demonstrated significant responses to three cycles of directional selection for seed weight, seedling weight, leaf size and rate of leaf appearance. When they selected for high seed weight the result was an increase in leaf size, but the selection for heavy seedlings or large leaves did not significantly increase seed weight. On the other hand, the selection for light seedlings or small leaves gave a decrease in seed weight. On crossing the parents of the high leaf size line with those of the high rate of leaf appearance line, the resulting hybrid population had seedlings nearly as heavy as those of the high seedling weight line and significantly heavier than the mean of the two parent lines. It was suggested that this effect in addition to other evidence of the effect of inbreeding on all characters, indicated some degree of directional

dominance, particularly for leaf size.

From his work on selection methods for seedling vigor in birdsfoot trefoil, Twamley (1971) observed that the genotype method was effective, straight forward and quite reliable. The geno-phenotype method was more variable in results, but could be potentially more rewarding. The phenotype method was the least desirable.

2.5 Seed Size and Emergence

Seed size has been reported to have a positive correlation with emergence (Hunt and Miller 1965; Kaufman and McFadden 1963; Kittock and Patterson 1962; Townsend 1972; Boyd et al 1971), particularly in cases of deeper planting (Harper and Obeid 1967; Rogler 1954; Stickler and Wassom 1963). More vigorous seedlings have also been shown to germinate (Whalley et al 1966a; Gelmond et al 1978) or emerge (Kittock and Law 1968) more rapidly than less vigorous ones. Kneebone and Cremer (1955) in an attempt to evaluate the vigor of seedlings in terms of emergence observed that the seedlings from larger seeds emerged faster and grew at a faster rate. Frey and Wiggans (1956) have reported similar results.

In an experiment with beardless wheat-grass seedlings to investigate the effect of planting depth and seed size on emergence (Vogel 1963) it was found that planting depth influenced both the rate of emergence and the total amount of emergence. At each depth, significantly fewer seedlings emerged from small seed as compared to large seeds. Coleop-

tile length, seedling height and culm length; i.e. seedling vigor, have all been reported to correlate positively with emergence (Gul and Allan 1976).

Demirlicakmak et al (1963) suggest no effect of seed size on emergence. Delouche and Caldwell (1960), however, sound a word of caution; they warn that the view that vigor is manifested by rapidity and "strength" of germination and growth rate of seedlings is somewhat inadequate. Their reason is that this view does not sufficiently cover mechanical damage which is an important area of seed quality. That could be particularly true when the concept is applied to seeds with recently sustained mechanical injuries. They also warn that the application of this concept to seeds with short-termed post-harvest dormancy could lead to very erroneous conclusions.

2.6 Seed Size Effect on Parts of The Seedling

In an experiment in which Burris et al (1971) compared the growth and respiratory rates of four cultivars and four seed sizes of soybeans, they found that the larger seeds produced larger embryos, although the relative rate of dry matter accumulation did not vary appreciably. An increase in seed size increased the weight of the cotyledons at emergence (Black 1956, 1957). Dry matter in the early vegetative stage was also found to be proportional to seed size, and total leaf area, and leaf numbers showed similar trends. Working with seeds of three peanut (Arachis hypogaea L.) cultivars,

Ketring (1978) reported that the seeds with a high degree of vigor produced the greatest amount of ethylene over a given time.

The partial removal of the endosperm of seedlings of sorghum resulted in decreased root and shoot growth and in decreased leaf area per seedling (Perl 1978). Black (1957) in an experiment in which he determined the relationship between the early vegetative growth of three strains of subterranean clover and seed size, showed that dry weight at any one time and leaf area per plant were linearly related to embryo weight. Rooting depth of seedlings at emergence was determined (Tadmor and Cohen 1968) by radioisotope tracing (P^{32}) for six range plants. The results indicated that generally root length was correlated with mean seed weight.

2.7 Seed Size Effect on Yield

Some experimental evidence indicates that seed size of the sown grain has a positive and significant correlation with yield (Ching and Foote, 1961; Kiesselbach, 1924; Beveridge and Wilsie, 1959; Derera and Bhatt, 1972). Kaufmann and McFadden (1963) conducted two series of tests to determine the influence of seed size on barley yield. Their results indicated that large seed produced more tillers and greater yields on the average than small, medium or bulk seed. Austenson and Walton (1970) observed that the size of the individual seeds of spring wheat accounted for 2.5 to 4.5% of the variation

in yield and other mature plant characters. Ries and Everson (1973) also suggest that within a genotype, seed with a higher protein content and/or seed that is larger sometimes produces higher yields.

McNeal and Berg (1960) found little effect of wheat seed weight on yield and Ries et al (1970) observed that yield of wheat was only correlated with seed protein but not with seed size. In their determination of the responses to seed weight and seedling vigor in Phalaris, Clements and Latter (1974) found that the plants in the high seed weight line matured earlier and had fewer heads. But because they had heavier seeds and more seeds per head, no apparent decrease in seed yield per plant in this line was noted.

Results obtained from the determination of the competitive interaction between barley plants grown from large and small seeds revealed that plants from large seeds yielded more than those from smaller seeds both in the greenhouse and in the field with inter-plant competition. Moreover, increased competition favoured plants from large seeds, and superior production resulted mainly from a greater number of heads on plants grown from large seeds (Kaufmann and McFadden 1960). Burris (1975) has demonstrated that in many genotypes reduction in seedling vigor results in reduced yield.

3. MATERIALS AND METHODS

Ten wheat cultivars (Triticum aestivum L.) (Table 1) were multiplied under comparable conditions on the experimental fields of the University of Manitoba in the summer of 1978. They were harvested when mature, dried at room temperature and hand-threshed. This seed source was utilized for the following experiments.

Throughout the study seedling vigor was regarded as the relative growth rate during early plant development (Lowe et al 1972). The procedure outlined by Evans and Bhatt (1977) wherein seedling vigor was measured as fresh weight accumulated at 20 days after sowing was applied. Seeds were first stratified into different seed sizes by passing them through screening sieves and were then weighed individually. Only sound and disease-free seeds were used. The weight of the seeds determined the seed size class into which each was placed. Seeds were soaked and held at 4°C for four days to break dormancy, then returned to room temperature to germinate (Belderok 1968; Ching and Foote 1961).

Germinated seeds of each class were sown, embryo side up, to a depth of 3.5 cm in boxes (Fig. 1) and spaced 4 cm between rows and 2 cm within rows. A 1:2 soil and sand mixture was used rather than sand alone which in a preliminary



Fig. 1 A box of seedlings



Fig. 2 Seedlings showing roots excised 2 cm below seed level

TABLE 1. Characteristics of parental cultivars used in crosses

Cultivar	Seed character	Mean seed* length (mm)	Weight/1000 kernels (gm)
Glenlea	very long	7.2	66.67
Kite	long	6.0	41.67
Era	long	6.2	53.48
Tordo	long	6.0	45.04
NB320	intermediate	5.9	44.12
Sinton	round	5.4	47.03
BW42	long	6.2	51.72
Norquay	intermediate	5.8	52.35
RL4137	very long	6.8	63.39

*Seed length was obtained from a 15 seed sample.

study resulted in very poor growth of the seedlings. The mixture provided a minimum nutritional level to seedlings. Watering was provided from below till the soil was saturated and then excess water was drained off. Seedlings were grown at a temperature of 18 - 22°C with 16 hour photoperiod. No fertilizer or nutrient solution was applied. At 20 days after planting, individual plants were carefully extracted from the soil mixture and the root excised 2 cm below (Fig. 2) the seed level. Each plant within a replicate was weighed and the replicate treatment means used in the analysis. All experiments were conducted in the greenhouse.

Fresh weight of a seedling has been shown (Evans and Bhatt 1977) to be a reliable estimate of the whole seedling dry weight regardless of whether the shoot is cut off at the seed level or at the soil surface. Measurements were taken 20 days after sowing based on the acceptance of the assumption by Evans and Bhatt (1977) that negligible interplant competition would occur prior to this stage and also on the fact that seedlings were easily handled at this stage.

The above procedure of measurement of seedling vigor was quick and readily applicable to large populations of single plants. It was also non-destructive. These requirements were necessary because in some cases the measured seedlings were grown to maturity and then crossed to produce F_1 and subsequent generations.

Experiment 1

Effect of Seed Size of Glenlea Wheat on Seedling Vigor

Glenlea, a utility wheat, was used for this experiment conducted in October, 1978. The seed size classes obtained after stratification and weighing of seeds were: 30-35; 40-45; 50-55; and 60-65 mg per seed which were considered as treatments (designated as 1 to 4 respectively). Germinated seeds of each class were sown, as described above, in plastic boxes measuring 44 x 27 x 7 cm. There were ten rows of ten seeds each, with the two outer ones serving as guard rows. Each box, serving as a replication, contained 100 seeds (20 per treatment) arranged in a randomized complete

block design. There were five replications.

Experiment 2

Comparison of Seedling Vigor of Glenlea and Sinton Wheat and their F_1 progenies

This experiment was conducted in two separate parts. Four populations (Glenlea, Sinton, and their reciprocal F_1 progenies) were produced under similar environmental conditions.

2a) Comparison between the seedling vigor of the parents.

Seeds of Glenlea and Sinton were stratified and weighed into five seed size classes, viz: 30-35; 40-44; 45-49; 50-54 and 55-60 mg per seed. Germinated seeds were sown in wooden boxes measuring 57 x 27 x 7 cm. There were 12 rows, of ten seeds each, to a box. The outer rows served as guard rows. Each box, forming a replicate, contained 120 seeds. A randomized complete block design with five replications was used with seed size classes as treatments and cultivars as blocks.

2b) Comparisons between the seedling vigor of the reciprocal F_1 progenies and the parents. Only one seed size class (30-35 mg per seed) was used for all four populations (Glenlea, Sinton, Glenlea x Sinton F_1 , Sinton x Glenlea F_1). A randomized complete block design with four replications was used, with cultivars or hybrids serving as treatments and replications as blocks. Each plastic box served as one replication.

Experiment 3a

Comparison of Seedling Vigor of 10 Cultivars

The experiment was conducted to estimate cultivar effect on seedling vigor. Ten cultivars (Table 1) were examined to determine if they could be grouped as "high", "medium" or "low" with respect to seedling vigor. The vigor of all ten cultivars was based on seedlings grown from seeds of one size class viz: 40-45 mg per seed. A randomized complete block design was used, with four replications. Cultivars served as treatments, and each wooden box contained one replicate.

Experiment 3b

Estimation of heritability of Seedling Vigor

Based on the results of Experiment 3a, two cultivars from each of three seedling vigor classes, i.e. high, medium and low seedling vigor, were selected for the estimation of seedling vigor heritability. The six selected cultivars were Glenlea and RL4137 for high; Norquay and BW42 for medium; and Kite and NB320 for low seedling vigor.

After the seedling vigor measurements in Experiment 3a, the seedlings were transplanted directly into a 2:1:½ soil-sand-peat mixture in 15 cm-clay pots. Three seedlings were planted per pot. Each pot consisted of plants of the same cultivar. All pots were watered to saturation and placed in the greenhouse at a temperature of 18 - 22°C, with 16 hour photoperiod. The plants were watered to saturation every

third day. A 20:20:20 liquid fertilizer, mixed according to the manufacturer's recommendation,¹ was applied every third week at constant rate. The fertilizer was applied one day after the plants had been watered.

The hybrids produced are listed in Table 2. The F_1 generations were selfed to produce F_2 and were back crossed to both parents.

Heads of all plants were allowed to mature before they were harvested, dried at room temperature for one week and hand threshed.

Separate seedling vigor measurements were conducted on all the parents, all the F_1 's, the F_2 's, BC_1 's and BC_2 's. In each case one seed size class (40-45 mg per seed) was used. Germinated seeds were grown in plastic boxes. There were ten rows per box, the six inner rows consisted of each of the six cultivars or hybrids, and the four outer rows served as guard rows. There were ten seeds per row. A randomized complete block design with four replications was used. Cultivars or hybrids served as treatments, and boxes as replicates.

¹Plant Growth Fertilizer. Recommendation: 1 tablespoon per 4.5 liters.

TABLE 2. Hybrid combinations produced

1. High x High

Glenlea x RL4137; RL4137 x Glenlea

2. High x Medium

Glenlea x Norquay; Norquay x Glenlea

3. High x Low

Glenlea x Kite; Kite x Glenlea

4. Medium x Medium

Norquay x BW42; BW42 x Norquay

5. Medium x Low

Norquay x Kite; Kite x Norquay

6. Low x Low

Kite x NB320; NB320 x Kite

4. RESULTS AND DISCUSSION

Experiment 1

Effect of Seed Size on Seedling Vigor of Glenlea Wheat

Seedling vigor measurement of four seed size classes (30-35; 40-45; 50-55; and 60-65 mg/seed) of Glenlea indicated that seedling vigor was highly correlated with seed size, ($r = 0.79$). The f test for differences in seedling vigor due to seed size was significant at the 0.01% probability level (Appendix Table 1) and each of the treatments were significantly different. (Table 3; Appendix Table 2)

TABLE 3. Measurement of seedling vigor of four seed size classes of Glenlea Wheat

Treatment: Seedling vigor (mg/seedling)

Seed Size (mg/seed)	Replications					Means
	1	2	3	4	5	
1: 30-35mg	322.10	272.10	234.9	290.7	320.05	287.97 a
2: 40-45mg	414.46	351.54	331.52	417.97	409.60	385.01 b
3: 50-55mg	474.22	496.65	553.26	553.47	551.12	522.69 c
4: 60-65mg	741.49	657.72	628.28	620.86	599.08	653.36 d

a - d means followed by the same letter are not significantly different ($P \geq 0.01$)

Analysis of regression showed that a linear regression line was the best fit. The linear regression equation showing

the relationship of seedling vigor with the seed size was:
 $\gamma = -96.01 + 13.100X$ where γ is the seedling weight (seedling vigor) in mg, and X is the seed size in mg. The linear regression line is shown in Figure 3. From these data it is obvious that an increase in seed size increases the seedling vigor.

Since only one genotype (Glenlea) was used and since the environmental conditions were the same throughout the experiment, difference in seedling vigor can only be attributed to difference in seed size, the only variable. While this fact has no direct breeding implication, it is nonetheless of interest in terms of production: because weight per seed is a yield component does it necessarily mean that large seeds will result in increased yield? If planting of large seeds should result in increased yield, then improvement in yield could be achieved simply by planting only large heavy seeds. But large seeds may not necessarily result in higher yields -- increased seedling vigor due to seed size might stimulate vegetative growth, at the expense of reproductive phase resulting in decreased yields. It would therefore be of interest to continue this experiment to investigate the effect of increased seed size on yield.

Experiment 2

2a) Comparison of Seedling Vigor of Glenlea and Sinton

The seedling vigor of Glenlea and Sinton at seed size classes 30-35; 40-44; 45-49; 50-54 and 55-60 mg per seed are shown in Table 4. There was no seed size-cultivar interaction,

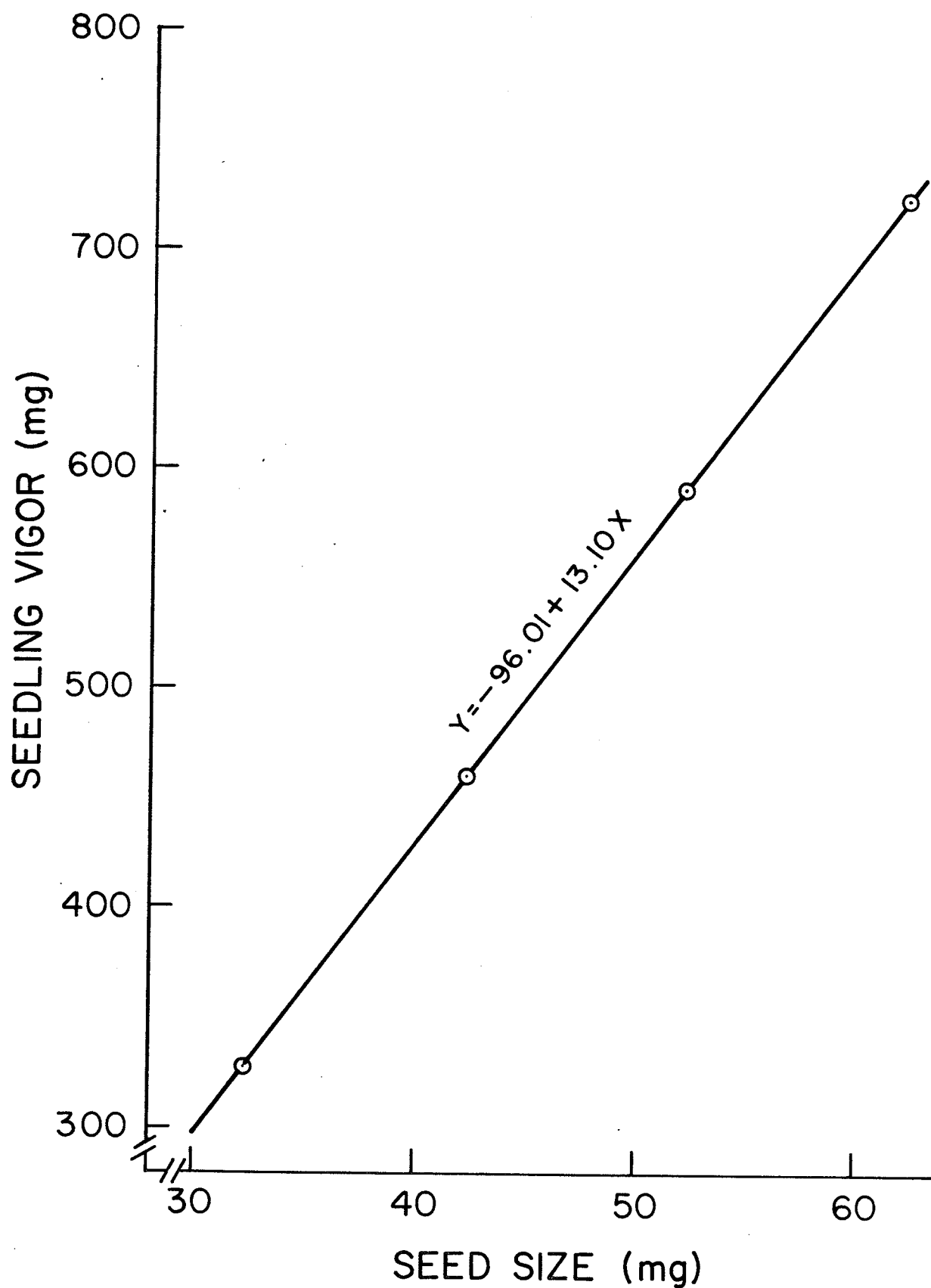


Fig. 3. Seed size of Glenlea wheat plotted against seedling vigor (seed size in mg/seed and seedling vigor in mg/seedling)

as the seedling vigor of Glenlea was always greater than that of Sinton within the range used in the experiment. From the analysis of variance it was evident that the seedling vigor of the two cultivars was significantly different and cultivar had an influence on the seedling vigor.

The linear regression equations for Glenlea and Sinton were calculated to be $-95.462 + 12.439X$ and $-71.18 + 10.719X$, respectively, where X is the seed size class. The graph (Figure 4) shows Glenlea always exceeds Sinton in seedling vigor at each seed weight class. The comparison between the cultivars was at the same seed weights and therefore the variation in the seedling vigor must be due to the cultivars. However, within each cultivar the increase in seedling vigor was primarily due to the increase in seed size or seed weight as was observed in Experiment 1.

TABLE 4. Measurement of seedling vigor of five seed size classes of Glenlea and Sinton Wheat

Cultivar	<u>seed size classes (mg)</u>					Mean
	30-35	40-44	45-49	50-54	55-60	
Glenlea	280.05	377.50	493.5	530.10	578.12	451.85
Sinton	274.40	314.20	416.50	464.20	532.98	400.46

Cultivar differences at $\alpha = 0.01$

2b) Comparison of Seedling Vigor of Glenlea, Sinton and their F_1 Progeny

The analysis of variance, of the first part of this experiment which compared seedling vigor of the reciprocal F_1

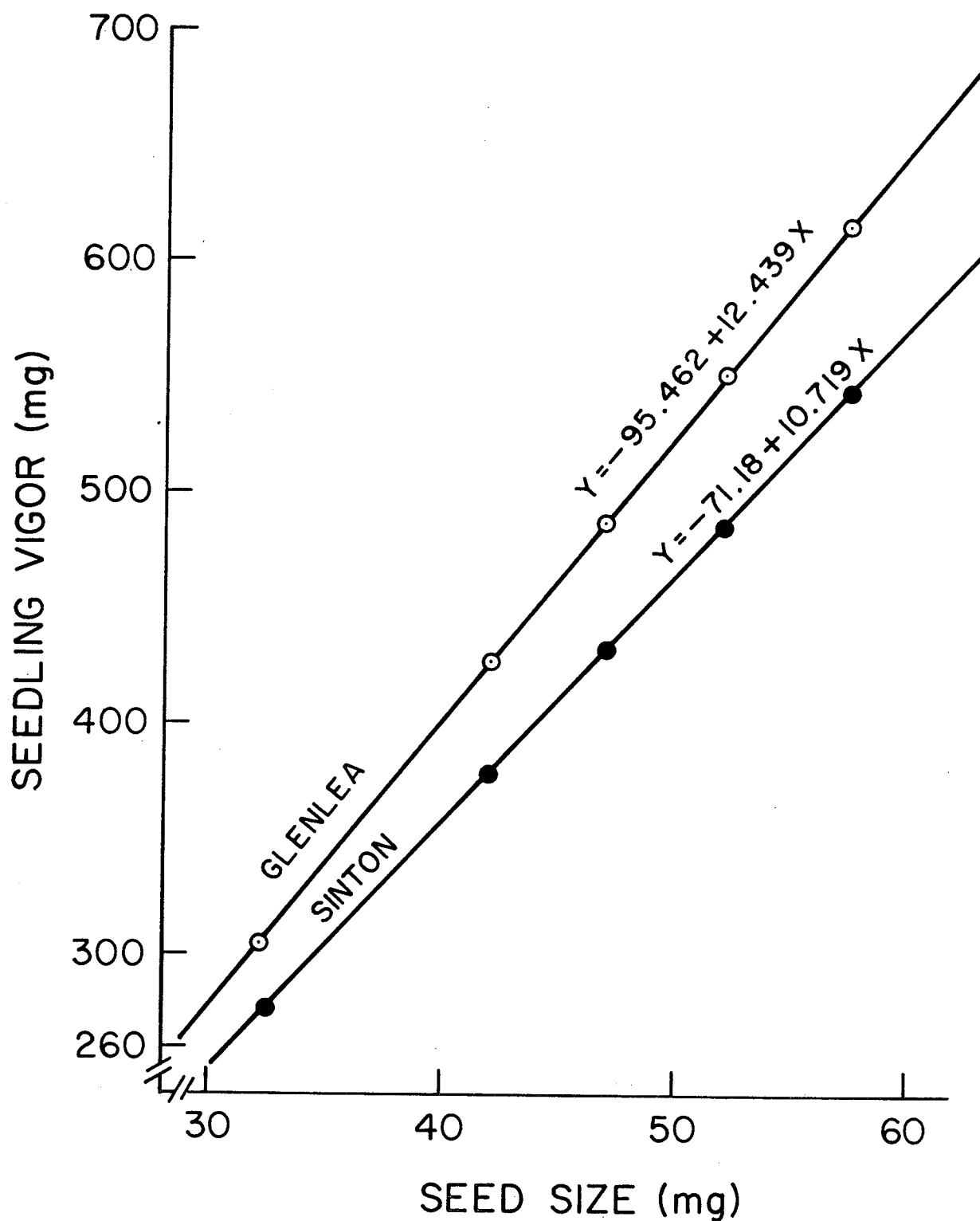


Fig. 4. Seed size of Glenlea and Sinton wheat plotted against seedling vigor (seed size in mg/seed and seedling vigor in mg/seedling)

progenies of Glenlea and Sinton, indicated that there was no significant differences. This result suggests that there was no maternal influence on seedling vigor (Table 5). For the rest of the experiment, therefore, seeds of reciprocal crosses were bulked.

TABLE 5. Measurement of seedling vigor of five replications of the reciprocal F_1 progenies of Glenlea and Sinton wheat

Treatment	Seedling vigor (mg)					Means
	Replications					
	1	2	3	4	5	
(SxG) F ₁	398	474	432	378	480	432.40 NS
(GxS) F ₁	433	430	493	448	412	443.20 NS

No differences between treatments at $\alpha = 0.05$.

NS means not significant.

The analysis of variance of seedling vigor of Glenlea, Sinton and their bulked F_1 progeny (Table 6) showed significant treatments effects.

TABLE 6. Measurement of seedling vigor of Glenlea, Sinton and their bulked F_1 progeny

Treatment	Mean seedling vigor (mg)
Glenlea	407.19 a
Sinton	349.00 b
F_1 (bulkcd)	416.89 a

a,b Means followed by the same letter are not significantly different ($P \geq 0.01$).

Glenlea and the F_1 were significantly higher than Sinton, but no significant differences existed between Glenlea and the F_1 . Although it is probably a gross oversimplification, the genotypes of Glenlea and Sinton could be represented as AA and aa respectively, with the genotype of the F_1 being Aa. On this basis AA = 407.19; aa = 349.00 and Aa = 416.89 mg per seedling. Because AA = Aa (no significant differences), therefore there is positive heterosis which is due to Dominance gene action (Allard 1966).

Experiment 3

3a) Comparison of Seedling Vigor of Ten Cultivars

Seedling vigor measurements, at the same seed size (55-60 mg per seed), of ten cultivars indicated significant differences attributable to cultivars (Table 7). When the cultivars were arbitrarily grouped into high, medium and low with respect to seedling vigor, the multiple range test showed significant differences among the means of all three groups (Table 7).

TABLE 7. Measurement of seedling vigor of the ten cultivars all from similar seed size

Cultivar	Mean seedling vigor (mg)
Glenlea)) High	594.0 a (Mean H x H)
RL4137)	587.9 a 590.9 m
K321	565.0 b
Era	535.5 c
Norquay)) Medium	528.5 c,d (Mean M x M)
BW42)	520.5 d 524.5 n
Sinton	493.0 e
Tordo	480.0 e,f
NB320)) Low	472.0 f (Mean L x L)
Kite)	452.0 g 462.0 p

K321, Era, Sinton and Tordo were omitted from further study.

a - g; m, n, p Mean followed by the same letter are not significantly different ($P \geq 0.01$).

3b) Estimation of Heritability of Seedling Vigor

The data for the six crosses (the reciprocal crosses were bulked) are presented as frequency distributions in Tables 8 through 13 (level of significance is 0.01%).

For the high x low or Glenlea x Kite cross there were 10 F_2 and four BC_1 seedlings that had higher seedling vigor than the high parent. The F_1 mean was not significantly below the mean of the better parent (Glenlea). The F_1 mean was however significantly above the mean of the lower parent.

TABLE 8. Distribution of Seedling Vigor of Glenlea, Kite and Subsequent Generations
High x Low

Family	Class centre (seedling weight in mg)																N	$\bar{X}$	VARIANCE		
	225	250	275	300	325	350	375	400	425	450	475	500	525	550	575	600				625	650
Glenlea					1	3	6	7	16	9	10	2	1						55	438.1a	0.169
Kite		2	4	8	11	15	8	3	3										54	351.7d	0.179
F ₁					1	3	7	10	13	9	5	2	1						51	432.3a	0.170
F ₂		2	5	8	10	10	16	14	17	11	8	6	4	6	3	1			121	426.4a	0.577
BC ₁ (P ₁)				1	1	1	3	5	4	3	2	2	0	2	1	1			26	411.54b	.440
BC ₂ (P ₂)		2	1	3	3	2	5	4	2	1	1								24	375.10c	.480

a - d means followed by the same letter are not significantly different ($P \geq 0.01$)

TABLE 9. Distribution of Seedling Vigor of NB320, Kite and Subsequent Generations
Low x Low

Family	Class center (seedling weight in mg)															N	$\bar{X}$	VARIANCE
	225	250	275	300	325	350	375	400	425	450	475	500	525	550	575			
NB 320		3	3	5	12	11	7	2	3							46	346.2ab	0.198
Kite		3	5	8	16	11	6	3	2							54	334.1bc	0.231
F ₁		1	1	3	2	4	3	3	2							19	351.7a	.290
F ₂	2	3	3	4	6	5	4	2	2							31	330.3c	.817
BC ₁ (P ₁)	1	1	0	1	1	0	0	1	1							6	339.5abc	.638
BC ₂ (P ₂)		1	0	1	1	0	1	1	1							6	350.9a	.744

a - c means followed by the same letter are not significantly different ($P \geq 0.01$)

TABLE 10. Distribution of Seedling Vigor of Norquay, BW42 and Subsequent Generations
Medium x Medium

Family	Class centre (seedling weight in mg)														N	$\bar{X}$	VARIANCE
	225	250	275	300	325	350	375	400	425	450	475	500	525	550			
Norquay		1	2	1	5	8	13	15	7	2	1	1			56	391.9b	0.219
BW42		1	2	4	5	8	12	14	9	1	1				57	383.8bc	0.211
F ₁				1	1	3	7	11	8	4	1	1	1		38	417.4a	0.194
F ₂	2	2	1	4	8	10	13	19	7	5	2	3	2	2	80	394.3b	0.448
BC ₁ (P ₁)			1	1	1	2	3	4	1	2	2	1			18	386.8bc	0.370
BC ₂ (P ₂)			1	2	1	2	4	3	3	2	1	0	1		20	377.8c	0.414

a - c means followed by the same letter are not significantly different ($P \geq 0.01$)

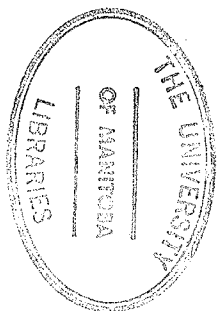


TABLE 11. Distribution of Seedling Vigor of Norquay, Kite and Subsequent Generations
Medium x Low

Family	Class centre (seedling weight in mg)																N	$\bar{X}$	VARIANCE
	225	250	275	300	325	350	375	400	425	450	475	500	525	550	575	600	625		
Norquay		1	0	1	5	11	10	12	6	3	1	0						50	385.0a 0.188
Kite		2	3	4	9	5	7	2	2	1								35	340.8d 0.221
F ₁		2	1	3	3	5	6	4	2	1								27	371.8bc .285
F ₂	2	3	6	9	11	13	8	3	1	2								58	363.0bc .548
BC ₁ (P ₁)		1	1	1	2	1	2	2	0	1	1	1						13	375.4b .433
BC ₂ (P ₂)	1	1	0	1	2	2	1	1	1	1								11	359.9c .480

a - d means followed by the same letter are not significantly different ($P \geq 0.01$)

TABLE 12. Distribution of Seedling Vigor of Glenlea, RL4137 and Subsequent Generations
High x High

Family	Class center (seedling weight in mg)															N	$\bar{X}$	VARIANCE
	225	250	275	300	325	350	375	400	425	450	475	500	525	550	575			
Glenlea					2	4	4	6	14	12	12	4				58	443.3b	0.186
RL4137						3	9	6	12	9	6	3	3			51	439.7b	0.214
F ₁							4	4	12	16	8	4	4			52	466.1a	0.156
F ₂			4	2	3	5	9	12	7	8	4	2	3	1	1	61	410.3c	0.493
BC ₁ (P ₁)				1	2	2	0	2	7	5	4	3	1	1		28	433.9b	.4145
BC ₂ (P ₂)			1	1	1	2	3	2	4	6	3	1	2	1		27	412.8c	.3745

a - c means followed by the same letter are not significantly different ($P \geq 0.01$)

TABLE 13. Distribution of Seedling Vigor of Glenlea, Norquay and Subsequent Generations
High x Medium

Family	Class center (seedling weight in mg)																	N	$\bar{X}$	VARIANCE
	225	250	275	300	325	350	375	400	425	450	475	500	525	550	575	600	625			
Glenlea					3	6	7	6	10	13	8	5	4					62	451.2a	0.210
Norquay			1	2	6	10	9	7	6	2								43	372.4c	0.159
F ₁					2	3	5	8	9	6	3							36	420.8b	.227
F ₂				4	3	7	16	13	20	15	6	2	2					88	416.5b	.501
BC ₁ (P ₁)			2	1	1	3	0	3	5	6	6	4	3	2				36	439.2a	.454
BC ₂ (P ₂)		1	0	3	3	5	7	4	3	2	2							30	408.1b	.395

a - c means followed by the same letter are not significantly different ($P \geq 0.01$)

In a breeding program aimed at improving the seedling vigor of Kite, therefore, success should be readily achieved. The mean of the F_2 population is below that of the F_1 population. Percentage heterosis determined by the formula:

$$\frac{F_1 - \text{midparent}}{\text{midparent}} \times 100$$

was 9.5% for the high x low cross.

There were no F_2 or BC seedlings in the low x low or NB320 x Kite cross, higher than the seedling vigor of the parents. There were two F_2 and one BC_1 seedlings lower than the smaller parent. It is interesting however that the F_1 mean was higher than that of either parent. This is because there was smaller F_1 spread, compared to those of the parents. Percentage heterosis for the low x low cross was 3.5%.

In the medium x medium or Norquay x BW42 cross there were four F_2 , one F_1 and one BC_2 seedlings that had higher vigor than the two parents. Two F_2 seedlings were lower in vigor than either parent. Heterosis was 7.6%.

For the medium x low or Norquay x Kite cross there were three F_2 or BC_2 seedlings of lower vigor than the parent. There was one BC_1 seedling of higher vigor. The F_1 mean was lower than that of the better parent but the two means were not significantly different. Percentage heterosis was 2.5%.

In the cross Glenlea x RL4137 or high x high, there were seedlings both lower and higher in vigor than the parents among the F_2 , BC_1 and BC_2 . Heterosis was 5.6%. The mean of the F_1 parent was higher than that of both parents.

There was one BC_2 seedling of lower and two BC_1 seedlings of higher vigor than the parents in the high x medium or Glenlea x Norquay cross. The F_1 mean was lower than that of the better parent. Heterosis was 2.3%.

In all six crosses parental seedling vigor was recovered. There was transgressive segregation either above or below the range of the parents involved in the cross. The best example of transgressive segregation, both above and below the parental range, is shown in the F_2 's, BC_1 's and BC_2 's of the Glenlea x RL4137 or high x high cross. The presence of Transgressive segregation indicates that at least more than one gene determines seedling vigor. It also shows that breeding for higher or lower seedling vigor is possible.

The variance of the parental seedling vigor ranged from 0.159 to 0.231. The F_1 variance range was from 0.156 to 0.290; for F_2 it was from 0.448 to 0.817; BC_1 variance ranged from 0.370 to 0.638 and for BC_2 the range was 0.374 to 0.744. For all crosses the variance of the F_2 individuals was larger than those of either parental or F_1 generation. This was expected since the difference between individuals within each parental line and that of the F_1 distribution are both assumed to be solely environmental (parents are pure lines), but on the other hand variance of the F_2 individuals is assumed to consist of two components; one genetical, the other environmental. Thus the variance of the F_2 distribution was inflated by segregation. This is illustrated by the spread of the F_2 distribution being greater than that of the

parents and F_1 (Lawrence and Jinks 1973; Strickberger 1976; Dudley and Moll 1969). For example, theoretically if the parents are AA and aa all the individuals are expected to be AA in one case and aa in the other, hence there is uniformity with respect to genotype. The F_1 should all be Aa -- also uniform. The F_2 however, will be $\frac{1}{4}$ AA, $\frac{1}{2}$ Aa and $\frac{1}{4}$ aa -- hence the genotype is not uniform. Therefore, while environmental differences exist in all three generations, F_2 population has genotypic differences as well. And this inflates the variance.

In general the further apart the parents are with respect to seedling vigor, the higher the percentage heterosis. It will therefore be advantageous to cross parents which have large differences in seedling vigor, unless both parents have high seedling vigor as found in the Glenlea x RL4137 cross.

Genetic Analysis. For simplicity, the following discussion will be limited to the Glenlea x Kite or high x low, cross and subsequent generations. Because the variance of the F_2 population is inflated by segregation, it allows for the estimation of the proportion of the total phenotypic variance that is due to genetic differences.

A joint estimate of the environmental variance component can be obtained as the weighted average of the parental and the F_1 family variances. Thus, we have:

Family	Expected Variance	Observed
P ₁ (G)	$r^2_{P_1} = E$	0.169)
P ₂ (K)	$r^2_{P_2} = E$	0.179) 0.173
F ₁	$r^2_{F_1} = E$	0.170)
F ₂	$r^2_{F_2} = E + GF_2 = E + \frac{1}{2}D + \frac{1}{4}H$	0.577
BX ₁ + BX ₂	$r^2_{B_1} + r^2_{B_2} = 2E + \frac{1}{2}D + \frac{1}{2}H$	0.920

where r^2 = the variance of the distribution; E = the variance component due to the environment; GF_2 = the variance component of the F₂ generation due to genetic differences between individuals; D = additive genetic effects and H = dominance effects.

$$\begin{aligned}\text{Therefore } r^2_{F_2} &= E + GF_2 = 0.173 + GF_2 \\ &= 0.577\end{aligned}$$

$$GF_2 = 0.577 - 0.173 = 0.404$$

$$\text{Therefore } \hat{h}^2_{F_2} = \frac{0.404}{0.577} \times 100 = 69.99\%$$

This percentage suggests a broad sense heritability which includes all genetic factors.

Estimation of the Narrow Sense Heritability. Defined as broad sense heritability, the estimate includes dominance, epistasis and additive gene action. Of the three, it is additive gene action that determines how much of the trait is genetically fixable. An estimate of additive gene action is possible by a measurement of narrow sense heritability.

From the broad sense heritability calculation we can subtract E and 2E from $r^2_{F_2}$ and $r^2_{B_1} + r^2_{B_2}$ respectively and we have:

$$\frac{1}{2}D + \frac{1}{4}H = 0.577 - 0.173 = 0.404 \text{ ----- (1)}$$

$$\frac{1}{2}D + \frac{1}{2}H = 0.920 - (2 \times 0.173) = 0.574 \text{ -- (2)}$$

$$\text{Therefore (2) - (1) = 0.170}$$

$$\frac{1}{2}D = 0.404 - 0.170 = 0.234$$

$$\begin{aligned} \hat{h}^2_{F_2} &= \frac{\frac{1}{2}D}{\frac{1}{2}D + \frac{1}{4}H + E} \\ &= \frac{0.234}{0.234 + 0.170 + 0.173} \times 100 \\ &= 40.55\% \end{aligned}$$

Similarly the heritability of NB320 x Kite; Norquay x BW42; Norquay x Kite; Glenlea x RL4137 and Glenlea x Norquay are estimated. The results are shown in Table 14.

TABLE 14. Broad and narrow sense heritability estimates of the six crosses

	Heritability	
	Broad	Narrow
Glenlea x Kite	69.99	40.55
NB320 x Kite	70.62	30.97
Norquay x BW42	53.57	33.04
Norquay x Kite	57.85	33.33
Glenlea x RL4137	62.407	39.63
Glenlea x Norquay	60.08	30.48

Additive gene action was meaningful in all the crosses,

the lowest being 30.48% and the highest 40.55. This shows that seedling vigor is a heritable trait that should respond to selection.

5. GENERAL DISCUSSION

Measurement of seedling vigor of four seed size classes in Glenlea indicated that seedling vigor was highly correlated with seed size ($r = 0.79$). The observed correlation of seed size and seedling vigor compliments previous findings (Cummings 1914; Evans and Bhatt 1977; Kaufmann and Guitard 1967; Kiesselbach and Helm 1917; Khayrallah and Lawson 1976; Miller and Pammel 1901; Murphy and Arny 1939; Sivasubramanian and Ramakrishnan 1974; Whalley et al 1966; and Whalley and McKell 1976).

The growth of a grass seedling can be divided into three distinct phases; heterotrophic, transitional and autotrophic (Whalley et al 1966a). The sources of energy for the stages are first the endosperm, then the endosperm and the new leaf material, and thirdly the new leaf material, respectively. The endosperm, therefore, becomes a very important source of energy for the developing seedling; the extent of the energy available to the developing seedling determines the size of the plant and the extent of its leaf surface at the time of exhaustion of the reserve material when the plant then becomes wholly dependent on photosynthesis (Bremner et al 1963). The positive correlation between seed size and seedling vigor can therefore be partly explained by the fact that the larger seeds had larger endosperms and therefore more

energy. This explanation is supported by Cooper and MacDonald's (1970) evidence that there was a decrease in the growth of the roots and shoots and a decrease in leaf area per seedling (hence a decrease in seedling vigor) as a result of the partial removal of the endosperm at the seedling stage. Is is further supported by Whalley et al (1966a) who attribute the seedling vigor/seed weight relationship in part to the proportion of the endosperm reserves remaining intact when the shoot emerges above the surface of the soil; and Bremner et al (1963) who arrived at the conclusion, from their study on the relative importance of embryo size and endosperm size, that differential seedling size in wheat was produced by differences in reserve material in the seed rather than in the embryo. The above evidence demonstrates the endosperm to be one of the factors that determine the vigor of the seedling; the larger the seed, that is, the larger the endosperm, the higher the seedling vigor.

Another important factor of the seed size/seedling vigor relationship is the biochemical and physiological activity of the seedling; generally the higher the physiological activity the higher the seedling vigor (Derwyn et al 1973). As observed by McDaniel (1969), the quantity and the biochemical competence of mitochondria are responsible for the seedling vigor in the seed weight/seedling vigor relationship. Because heavy seeds have a greater quantity of mitochondrial protein and thus a higher respiratory rate and a greater amount of energy (ATP) production, it follows therefore that seedlings

from larger seeds have a greater growth potential than seedlings produced from lighter seeds of the same pure line (McDaniel 1969).

In other supporting evidence it was shown that heavy seeds contained more free sugar for respiratory substrate and more adenylate phosphate for further phosphorylation. The increased respiratory metabolism resulted in increased rates of ATP formation and thus larger seedlings (Abernethy et al 1977).

A third factor of the seed that affects the seedling vigor is the protein content. There is evidence in the literature that the protein content of the seed is probably one of the major contributors of seedling vigor (Evans and Bhatt 1977; Ries et al 1976; Lowe and Ries 1972; Ries and Everson 1973; Welch 1977). The greater the protein content the higher the seedling vigor.

In the present study seedling vigor was found to be cultivar dependent. This supports other findings (Evans and Bhatt 1977; Jones and Peterson 1976; Kneebone and Cremer 1955; Stickler and Wassom 1963). The differences in seedling vigor between different cultivars could be due to differences in the rate and efficiency of various catabolic and anabolic reactions in the seeds. The cultivar with a higher seedling vigor could have higher rates and efficiency of metabolic reactions than those of a cultivar with a lower seedling vigor. Ching and Kronstad (1972) reported that during the germination of a vigorous wheat cultivar there is a more dynamic syntheses and utilization of "energy rich" adenylate phosphate nucleotides

and a higher energy charge as well.

The estimation of heritability in the present study gave a range of 53.57 to 70.62 for the broad heritability and 30.48 to 40.55 for the narrow heritability. Since the additive genetic effect or the narrow heritability ranged from 30.48 to 40.55 it means that seedling vigor is heritable.

The frequency tables show that there was transgressive segregation either below or above the range of the parents involved in the cross: which is possible only in the presence of more than one gene influencing this trait. That, there is more than one gene influencing seedling vigor is further evidenced by the fact that the F_2 population distributions are generally found to be continuous. If a single gene determined seedling vigor, three distributions corresponding to the three genotypes AA, Aa and aa would be observed in the F_2 family. On this basis even if the environment component causes some overlapping, three distributions for each of the 3 genotypes, AA, Aa and aa, should still be evident. However, the F_2 distribution, as shown in Table 8 is continuous. It is therefore clear that this simple hypothesis does not satisfactorily account for these observations and it must be assumed that more than one gene is involved in the determination of seedling vigor. The fact that there is more than one gene influencing seedling vigor and also that there is transgressive segregation shows that breeding for higher (or lower) seedling vigor is possible.

From the experiments it has been shown that first, it is

possible to calculate the heritability of seedling vigor and secondly, that the value of the heritability makes it possible to improve the seedling vigor of cultivars. The importance of this finding cannot be underemphasized. Generally the higher the seedling vigor the faster the rate of germination, and the less prone the seedlings are to attack by microorganisms (Delouche and Caldwell 1970). Vigorous seedlings are more resistant to unfavourable conditions (e.g. water stress) which result in better standing establishment and consequently better grain yield (Kaufmann and McFadden 1963). Seedling vigor in general plays an important role in establishment and therefore final yield of the crop.

The present experiment has demonstrated that seed size and cultivar have effect on seedling vigor. It has further been demonstrated that seedling vigor is a heritable trait. It would now be of interest to investigate whether the higher seedling vigor which resulted from large seed will result in higher yields. To do this, seeds of Glenlea could be stratified into various seed sizes. Then using randomized complete block design, the seeds could be sowed at a constant rate to test for the yield of each seed size class.

Another investigation of interest would be to perform yield trials on the F_4 of the six crosses from the present experiment. A common seed size class together with a constant rate of planting in a randomized complete block design could be used. The yield results could be compared with the seedling vigor of each line to establish the effect of the seedling

vigor of each line on yield.

These two experiments will show whether it is worthwhile planting large seeds and also whether breeding for higher yields should consider seedling vigor as a criterion.

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APPENDIX

APPENDIX TABLE 1. Analysis of variance of the effect of seed size of Glenlea wheat on seedling vigor

Source	df	SS	Ms	F
Treatment	3	33,050.981	11,016.994	20.162**
Error	16	8,742.672	546.417	
Total	19	41,793.653		

** indicates significance at the 1% level.

APPENDIX TABLE 2. Use of Duncan's multiple range test to test for significance among treatment means of Experiment 1

The critical value, $R_p = r \alpha (p, f) S_{\bar{y}i}$ where

$$S_{\bar{y}i} = \sqrt{\frac{MSE}{n}} = \sqrt{\frac{546.417}{50}} = 3.306$$

		R_p
$T_4 - T_1$	= 113.28**	14.71
$T_4 - T_2$	= 84.50**	14.35
$T_4 - T_3$	= 28.29**	13.65
$T_3 - T_1$	= 84.99*	14.35
$T_3 - T_2$	= 56.21**	13.65
$T_2 - T_1$	= 28.78**	13.65

where T_1 (159.7); T_2 (188.48); T_3 (244.69) and T_4 (272.98) are the treatment means in mg per seed.

** indicates significance at the 1% level.

f = degrees of freedom.

p = range of pairs of means.

APPENDIX TABLE 3. Analysis of variance of comparison of seedling vigor of Glenlea and Sinton wheat

Source	df	SS	Ms	F
Block	1	6,604.386	6,604.386	16.829*
Treatment	4	102,488.860	25,622.215	
Error	4	1,569.731	392.433	
Total	9			

* indicates significance at the 5% level

APPENDIX TABLE 4. Analysis of variance of comparison of seedling vigor of F_1 progenies of Glenlea x Sinton and Sinton x Glenlea

Source	df	SS	Ms	F
Treatment	1	29.16	29.16	0.09144 NS
Error	8	2,551.00	318.875	
Total	9	2,580.16		

NS - not significant

APPENDIX TABLE 5. Analysis of variance of comparison of seedling vigor of Glenlea, Sinton and their F_1 progeny

Source	df	SS	Ms	F
Treatment	2	4,952.0096	2,476.005	4.37387*
Error	54	30,568.8900	566.090	
Total	56	35,525.090		

* indicates significance of the 5% level

APPENDIX TABLE 6. Use of Duncan's multiple range test to test for significance among seedling vigor of Glenlea, Sinton and their bulked F_1

The critical value, $R_p = r_{\alpha}(p, f) \bar{S}_{yi}$ where

$$\bar{S}_{yi} = \sqrt{\frac{MSE}{n}} = \sqrt{\frac{566.090}{30}} = 4.34$$

$F_1 - G$	=	9.70 NS	R_p 16.33
$F_1 - S$	=	67.89**	17.03
$G - S$	=	58.19**	16.32

where F_1 (416.89), G (407.19) and S (349.00) are the treatment means of the seedling vigor of F_1 (bulk), Glenlea and Sinton (respectively) in mg.

** indicates significance at the 1% level.

NS indicates not significant.

f = degrees of freedom.

p = range of pairs of means.

APPENDIX TABLE 7. Analysis of variance of comparison of seedling vigor of 10 cultivars

Source	df	SS	Ms	F
Block	3	2,081.3158	693.772	1.7613
Treatment	9	34,746.858	3,860.762	9.8013**
Error	38	14,968.345	393.90	
Total	49			

** indicates significance at the 1% level

APPENDIX TABLE 8. Use of Duncan's multiple range test to test for significance among seedling vigor of ten cultivars

Critical value = $r_{\alpha}(p,f) \bar{S}_{yi}$ where

$$\bar{S}_{yi} = \sqrt{\frac{MSE}{n}} = \sqrt{\frac{393.9}{50}} = 2.8067.$$

<u>differences of means</u>			<u>R_p</u>
Glenlea - RL4137	= 6.1 NS		10.72
Glenlea - Norquay	= 65.5**		11.20
Glenlea - BW42	= 73.5**		11.90
Glenlea - NB320	= 122.0**		12.27
Glenlea - Kite	= 142.0**		12.38
Norquay - BW42	= 8.0 NS		10.72
Norquay - NB320	= 56.5**		11.704

APPENDIX TABLE 8. (Continued)

<u>differences of means</u>		<u>R_p</u>
Norquay - Kite	= 76.5**	11.90
NB320 - Kite	= 20.0**	10.72

High - Medium seedling vigor	= 66.45**	10.72
High - Low seedling vigor	= 128.95**	11.20
Medium - Low seedling vigor	= 62.5**	10.72

** indicates significance at the 1% level.

NS indicates not significant.

f = degrees of freedom.

p = range of pairs of means.