AN ABSTRACT OF THE THESIS OF

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Title: FACTORS ASSOCIATED WITH STAND ESTABLISHMENT AND

   SUBSEQUENT GRAIN YIELD OF SEVEN WHEAT CULTIVARS

   AND SELECTED PROGENY (TRITICUM AESTIVUM, L EM

   THELL) WHEN GROWN UNDER THREE DIVERSE ENVIRON-

   MENTS

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Dr. Warren E. Kronstad

Investigations were conducted at three environmentally diverse

experimental sites and in the laboratory to determine the effects of

seed source, seed size, coleoptile length, crown depth, adenosine

phosphate (ATP) and adenylate energy charge (EC) on stand establish-

ment, yield and yield components of wheat cultivars. Attempts were

also made to determine the mode of inheritance of coleoptile length,

crown depth, ATP and EC.

Six soft white winter cultivars (Hyslop, Yamhill, Moro,

Sprague, Kirac, and Luke) and one soft red facultative wheat

(Strampelli) were selected based on their morphological differences

in seedling development and adaptabilities to growing conditions

observed in the Pacific Northwest. Crosses were made in diallel

fashion including reciprocals among six cultivars (Hyslop, Yamhill,

Moro, Strampelli, Sprague and Kirac) at Hyslop Agronomy Farm

with parents, F_1 and F_2 generations being utilized in this study.

Direct and indirect effects of each trait on yield were determined

by path coefficient analysis. Heritability in narrow sense was esti-

mated through parent-progeny regressions. Broad sense heritability

estimates were determined by comparing the variance of F_2's and

parents. Field experiments were conducted at Hyslop Agronomy Farm,

Corvallis (minimum moisture stress), Sherman Experimental Station,

Moro (maximum moisture stress), and Rug Farm, Pendleton, Oregon

(intermediate moisture stress).

Effects of seed source and seed size were investigated in

solid seeding experiments conducted at the above three locations.

Highly significant locations by treatment interactions were found for

stand count, emergence percentage, number of spikes/plot, number

of spikelets/spike, number of kernels/spikelet, kernel weight, plant

height, as well as total plant yield, grain yield and harvest index.

Stand establishment had direct and indirect effects on yield even under

favorable conditions of the Hyslop site. Effects of seed source and

seed size on stand establishment and yield were found to be

cultivar and location dependent. Both traits appeared to be more

important under favorable than unfavorable climatic conditions.

Planting the seed on per weight bases alleviated the negative effects

of small seeds on stand establishment, but its effect on yield was

found to be dependent on cultivars and locations. Nonsignificant

effects of seed source and seed size on yield at the Moro site was attributed to the excessive vegetative growth early in the season.

Effects of coleoptile length and crown depth and the mode of inheritance of these traits were evaluated under space planted field experiments. Coleoptile length of the cultivars increased almost porportionally to the increase in seeding depth. Increase in crown depth due to deep seeding was cultivar-dependent and nonproportional to sowing depth. Both traits had nonsignificant direct and indirect effects on yield under high rainfall conditions at the Hyslop site but their effects increased dramatically at Pendleton and specially at Moro site. The mode of inheritance of coleoptile length and crown depth were found to be controlled mostly by additive gene actions, therefore selection for these traits in the segregating population is possible. It was also shown that seed source and seed size have negligible effects on yield in space-planted nurseries regardless of the degree of moisture stress.

Effects of temperature and imbibition period, cultivars, seed source, and seed size on ATP and EC of seedlings were determined by luciferin-luciferase method. Relationships of these biochemical traits and agronomic traits were determined by correlation coefficients and the path coefficient analysis. Seventy two hours of incubation under 20° C temperature seemed to be the most suitable

regime capable of differentiating the cultivars for ATP content. Adenosine triphosphate and EC of cultivars varied among and within cultivars depending on the seed source and the seed size. Effect of seed source was found to be cultivar-dependent. Larger seeds produced higher ATP than smaller seeds in all cultivars. When the field data were combined over locations, ATP showed fairly high total effect on yield, but the effect of this trait on the yield of cultivars grown at the Moro site was not so pronounced. This was attributed to the excessive growth of cultivars at early season and the subsequent drought at the end of growing season at this location. Adenosine triphosphate and EC appear to be inherited cytoplasmically based on the different kinds of the mitochondrial complementation. Three kinds of mitochondrial complementation were assumed to exist and were named negative, additive, and dominant complementation. Additive and dominant complementations are probably beneficial to plant breeding programs and could be selected in F_2 and later generations. However validity of assumption of different kinds of mitochondrial complementation needs further confirmation by studying F_3 and later generations. Complementation depends mostly on maternal parent of the crosses, therefore making reciprocal crosses enchances the chance of identifying the proper combinations.

Factors Associated with Stand Establishment and Subsequent
Grain Yield of Seven Wheat Cultivars and Selected
Progeny (<u>Triticum aestivum,</u> <u>L</u> <u>em</u> <u>thell</u>) When
Grown Under Three Diverse Environments

by

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Typed by Susie Kozlik for <u>Mohammad Ali Vahabian</u>

IN DEDICATION TO

My wife, Nooshin, my daughter, Yeganeh, my son

Ramin, and my mother Maryam

ACKNOWLEDGEMENTS

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FACTORS ASSOCIATED WITH STAND ESTABLISHMENT AND SUBSEQUENT GRAIN YIELD OF SEVEN WHEAT CULTIVARS AND SELECTED PROGENY (TRITICUM AESTIVUM, L EM THELL) WHEN GROWN UNDER THREE DIVERSE ENVIRONMENTS

INTRODUCTION

Wheat is an important constituent in the diet of millions of people and in many countries is the major source of food. Increasing wheat production is becoming more acute as the world population continues to increase. Wheat occupies more than 200 million hectars of the arable lands on this planet with most of the production under dryland conditions with less than 450 mm annual precipitation.

With limited land resources available it becomes extremely important that yield levels per hectar on existing land be increased. In dryland areas there are many factors hampering yield increases, the most important being stand establishment which determines the potential of a crop whose final yield will be determined by other factors.

Stand establishment is dependent on management practices to conserve as much moisture as possible and on developing cultivars which respond to management practices or capable of reasonable performance under less favorable conditions.

Differential varietal responses to stress conditions is well established, however, the details of the mechanisms involved in response is not fully understood.

Length of the coleoptile and depth of the crown are two proper-
ties which influence stand establishment. Coleptile length has been
shown to have positive association with emergence, but direct and
indirect effects of this trait on yield have not been investigated. The
mode of inheritance of coleoptile length is also a matter of debate.
Crown depth is a controversial subject. Deeper crowns generally
believed to positively affect the survival of the stand; however, in
some cases the reverse has been reported.

Seed size and source, two components of seed quality, influence
the stand establishment and yield, but their importance is not quite
clear and their interaction and compensation have not been fully
investigated.

Biochemical properties of the seed which influence emergence
have been researched mostly with regards to the protein content of
the seed, but how the higher protein exerts its effects on emergence
has not been fully investigated. Varietal differences in adenosine
triphosphate (ATP) and adenylate energy change (EC) have been
demonstrated by a few workers but their relationships to field experi-
ments is not well established. The use of such seed properties
as a plant breeding tool could offer a great deal of promises, however
much work remains to be done before such a criteria can be utilized.

The objectives of this study were to determine:

1. The effects of seed source, seed size, coleoptile length, and crown depth on stand establishment, yield and yield components.

2. The influences of seed source and seed size on ATP content and EC of the seed.

3. The mode of inheritance of coleoptile length, crown depth, ATP content and EC of the seed.

4. Possible associations of biochemical and agronomical properties of different cultivars.

LITERATURE REVIEW

Seed Source and Seed Size

The effects of seed size or seed weight on seedling growth and other agronomical traits have been studied in various crops. In crops other than cereals it has generally been demonstrated that the larger or heavier seeds give rise either to more vigorous seedlings (Rogler, 1954 in crested wheatgrass; Kneebone and Cremer, 1955 in buffalo grass, indiangrass, sand bluestem and sideoats grama; Black, 1957 in subterranean clover; Williams, 1967 in hypogeal legume ; Edwards and Hartwig, 1971 in soybean; Radvan, Shiltawi and Mahdi, 1972 in berseem clover; and Carleton, 1972 in birdsfoot trefoil, alfalfa and sainfoin) or to more vigours seedling as well as higher yield (Henson and Tayman, 1961 in birdsfoot trifoil; and Williams, Black and Donald, 1968 in annual trifoliums). In some cases no effect of seed size was observed in seedling growth and stand, but larger seeds produced more yield (Smith and Camper 1975, in soybean).

Hopper and Overholt (1975) studied the effects of seed size and temperature on the germination and emergence of soybean. Utilizing three cultivars and four seed sizes under 10, 15, 20, 25 and 30° C temperatures for germination tests and three dates of planting for emergence test, they found no difference in cultivars for germination rate, but it was shown that small seeds emerged faster than very

small, medium or large seeds.

Relationships of seed size and/or seed source and seedling growth, yield components and yield have been investigated in more detail in wheat and barley. Results obtained vary depending on cultivars, locations, origin of seed and size classes used in various experiments.

Waldron (1941) using two classes of seed size in wheat demonstrated that planting either the same weight or the same number of kernels per unit area; the heavier seed produces higher yield. He also found the effect of size is independent of source, i.e. heavy kerneled seed produced in the greenhouse outyielded the lightweight seed matured in the field.

Utilizing three cultivars of barley and three sizes with three rates of seeding over two years, Demirlicakmak, Kaufmann and Johnson (1963) found no effect of seed size on emergence but the number of culms and yield were higher for large seed over all rates, cultivars and tests. As far as the effect of seeding rate in production of seed is concerned, they found that the lowest rate (560 kernels/plot) produced the heaviest kernel and the highest rate (1680 kernels/plot) gave the lightest kernels.

Geiszler and Hoag (1967) commented that seed shrivelling has more pronounced effect on yield than seed size. They showed that in hard red spring wheat the yield of small well-formed and plump seeds

were equal to the yield produced by large plump seeds and slightly more than large shriveled seeds.

Rate of seedling growth and size of the first two leaves were shown to be positively correlated with seed size in barley cultivars grown under greenhouse conditions. It was also found that the length of the first and second leaf was positively correlated with spike weight and number of spikelets/spike (Kaufmann and Guitard, 1967).

Large and medium size seeds of wheat and barley had no difference in yield production, but the yield of small seeds was significantly lower than the other two classes (Beletskii and Kovalev, 1969). Larger seeds gave rise to seedlings with larger tops than medium seeds, however, the top/root ratio was greater in medium size seeds than large ones.

Austenson and Walton (1970) using three wheat cultivars; Thatcher, Pembina, and Manitou demonstrated that 2.5 to 4.5 percent of the observed variations in yield and number of heads/plant can be accounted for by the seed size.

Inouye, Seko and Ito (1970) investigated the effects of soil moisture content and seed size on the strength of the plumule elongation in barley as measured by mechanical vigor. Their results indicate that soil moisture content from 8-15 percent had little effect on strength. As far as seed size is concerned it was shown that on an

average the plumule strength increased from 5-10 g with every five mg

increase in seed weight, and that this increase was temperature-

independent. However, the strength was more vigorous in the plumu-

les which were grown under cool temperature conditions indicating

that optimum temperature for the strength is lower than that for

germination and elongation of plumule.

Seed size in wheat cultivars Inia 66 and Romano 50 did not

significantly affect plant height, number of tillers, number of

spikes, grain yield or water use efficiency, but the kernels produced

by plants established with larger seeds were significantly larger than

kernels obtained from planting small seeds (Dennis and Farahi, 1971).

Ten-day old seedlings of wheat obtained from large seeds were

shown to have 1.7 times more dry matter than those from small

seeds (Gubanov and Bertii, 1971). The amount of phosphorus and

ascorbic acid content and redox-enzyme activity were also markedly

higher in larger seeds.

Morrison, Reisenauer, Entenmann and Suderland (1973) studied

the effect of seed size on yield of Nugaines wheat utilizing three seed

sizes and five locations over three years. They observed that under

low rainfall conditions large seed outyielded the medium seed by 3.6

bu/A and the small seed by 10.9 bu/A. Under slightly higher

rainfall conditions the superiority of large seed decreased to

1 bu/A over medium sized seed and 6 bu/A over small size seed.

Garay (1975) found that smaller seeds of the wheat cultivars Yamhill, Paha, and Hyslop germinated faster than larger seeds and produced longer roots and shoots during the early stages of growth, but they had slower growth rate at later stages.

Grabe and Garay (1975) reported that wheat cultivars Hyslop and Yamhill obtained from 18 locations varied in yield by as much as 22 and 18 bu/A, respectively. They found that in the cultivar Hyslop the lowest yielding lot usually had the smallest seeds, but not necessarily so in the cultivar Yamhill. They concluded that there is no consistent yield differences due to the seed source, percent protein, seedling growth rate or energy charge of seed.

The effect of seed size in wheat is mainly due to endosperm size of the kernel and that the embryo size had negligible effect on growth (Bremmer, Eckersall and Scott, 1963). They concluded that the relationship between seed size and plant growth is governed mainly by the amount of reserve material in the seed.

Lowe and Ries (1973) working with the cultivar Inia 66 of wheat showed that small (35 mg) high protein seed (4.7 mg protein/seed) produced larger seedlings than large (45 mg) low protein seed (4.3 mg protein/seed). Similar results were found in snap beans through the work of Ries (1971) and in wheat (Ries and Everson, 1973). In a further attempt to delineate the effect of seed protein content on early growth, Lowe, Ayers and Ries (1972) found that mole percent

glutamic acid was positively related to seedling growth (r = 0.84).
Several other amino acids showed negative correlation with seedling
growth. They commented that although amino acid analysis eluci-
dated the possible source of the protein causing the increase in
seedling vigor, it did not prove to give a better estimate of seedling
vigor or yield than protein per se.

Tandom and Gulati (1966) conducted genetic studies on seed
size of barley. Utilizing the seeds from the lateral and central rows
of ears of barley, they demonstrated that progenies from larger seeds
produced higher yield as well as better seed weight, more tillers,
greater height and were earlier in maturity than progenies from
smaller seed with a similar genotype background. They found that
number of tillers and grain/plant were the traits most affected by
seed size, therefore, they concluded that variability in seed size
can be a source of serious bias in studies of quantitative traits.

Coleoptile Length

Depth of sowing in a rainfed area is mainly dependent on the
depth of the soil moisture reserved which in some years necessitates
deep planting. Under this condition one of the important factors
which influences stand establishment is the length of the coleoptile.
Coleoptile length became of great concern in breeding with the
introduction of semi-dwarf wheat cultivars. The main concern was

the possible linkage or pleiotropism between the culm length and cole-
optile length because the semi-dwarf selections had a much shorter
coleoptile than standard height cultivars (Allan, Vogel, Burleigh
and Peterson, 1961).

Both culm and coleoptile length were shown to have high
heritability values and at least in some crosses close associations
were noticed (Allen, et al., 1961). Although there were some indi-
cations of differences between the mode of inheritance of culm and
coleoptile length, the pattern was not the same for all crosses. It
was concluded that pleiotropism between coleoptile length and plant
height can not be ruled out.

In further studies, Allen, Vogel and Peterson (1962) obtained
a significant difference between the emergence rate index of a group
of standard height and semi-dwarf cultivars. They observed that
indices were positively correlated with mature plant height and
coleoptile length of seedlings grown in a dark growth chamber at 50°
and 90° F. They mentioned that genetic mechanisms that affect the
plant height may also partially influence the coleoptile length.
Similar results were obtained by Sunderman (1964) utilizing labora-
tory data for coleoptile length and field studies for emergence
measurements in nine winter wheats. Allan, Pritchett and Patterson
(1968) found similar results, too; however in their experiments no
association was found between culm length and coleoptile length in

crosses between cultivars with standard height.

Chowdhery and Allan (1963) using two semi-dwarf and two standard height cultivars and their F_1's and F_2's studied the mode of inheritance of coleoptile length and seedling height and their association to plant height. Although they found significant positive correlations between the coleoptile length and seedling height, degree of association of coleoptile length and seedling height with mature plant height was low for three out of four crosses. Consequently, they concluded that breeding semi-dwarf cultivars with long coleoptile seems conceivable. Comparable data were presented by Parodi, Patterson and Nyquist (1970) in diallel crosses among the soft red winter wheat genotypes, which shows a low and nonsignificant correlation coefficient between coleoptile length and mature plant height. Similar findings were reported by Scarascia and Porceddu (1973) in durum wheats.

Relationships of coleoptile length, seeding depth and temperature were studied by Burleigh, Allan and Vogel (1965) using four standard height and four semi-dwarf wheat cultivars. Cultivars were planted at two, three and four inches depths in growth chamber under 50° and 90° F constant temperature. They found significant cultivar by depth of planting interaction at 50° F but not at 90° F. The percentage of emergence was affected by depth of planting in both temperatures. Reduction in emergence rate due to deep seeding

was much greater for semi-dwarf than for standard-height cultivars.

A significant difference was obtained between the coleoptile length

of semi-dwarf and standard-height cultivars under 50° F temperature

regime, but not under 90° F. Similar results for the emergence rate

and coleoptile length were obtained in a greenhouse study of tall and

semi-dwarf wheat cultivars (Feather and Qualset, 1968). They also

found highly significant correlations between the coleoptile length

and mature plant height under field conditions.

Different results have been presented by various workers on

the mode of inheritance of coleoptile length. Most of the experiments

were conducted under greenhouse or growth chamber conditions and

the data varied based on cultivars, temperature and depth of planting.

Results can be summarized as follows:

1. Normal curve distribution of F_2 in some crosses indicated

   polygenic inheritance (Allan, et al., 1961).

2. Higher broad sense heritability (H_{bs}) than narrow sense

   heritability (H_{ns}) plus manifestation of dominance in F_1,

   implied that in addition to additive genetic variance, domi-

   nance deviations and non-allelic interactions were present.

   Numbers of genes estimated to govern coleoptile length

   varied from 1 to 5 in different crosses (Chowdhery and

   Allan, 1963).

3. Regression coefficients of F_1 on midparent and F_2 on F_1

were 0.957 and 0.783, respectively (Parodi et al., 1970),
which suggested that a large portion of the genetic variance
was additive.

4. Evidence that the coleoptile length is quantitatively inherited
   with both additive and non-additive gene actions being in-
   volved was reported by Hoff, Kolp and Bohenblust (1973).

5. Polygenic type of inheritance was also reported by Scarascia
   and Porceddu (1973); however, they found that most of the
   genetic variability was due to additive and a smaller amount
   due to dominance gene effects.

Crown Depth

Unlike the coleoptile length, the effect of crown depth or the
subcrown internode length on stand establishment and winter survival
of cultivars is a controversial subject among the plant breeders.

Taylor and McCall (1936) presented data obtained under con-
trolled conditions showing the positive association between the sub-
crown internode length and temperature. They also showed that the
depth of the crown is dependent upon sowing depth.

Webbe and Stephens (1936) reported on crown and root
development in winter cultivars. They mentioned that in some
parts of the Columbia River Basin, spring wheat often does not
form crown roots and grow to maturity from seminal roots alone.

Even fall-planted wheat under certain conditions may mature with few or no crown roots causing the breaking of plants below the soil surface and reduction in yield. The results of their studies based on measurements on approximately 125,000 plants showed that the crown depth of wheat is affected by environment especially temperature, and depth of the planting, and it is also a varietal character. They also noticed that the crown is formed deeper in the soil in winter wheat than in spring wheat. Among winter wheats, the hardy culti-vars have deeper crown than the nonhardy ones. The effect of tem-perature is in accordance with the results of Taylor and McCall (1936), i.e. when the temperature between planting and emergence is lower, it causes the plants to crown deeper. Deep seeding in-creases the crown depth, but this increase is not proportional to the difference in planting depth. They also noticed the varietal differ-ences in the time required for crown development.

The effect of temperature on crown depth development was re-searched by Dail, Kolp and Bohenenblust (1972) in winter barley. They found that the response to temperature is cultivar dependent. Some cultivars crowned significantly deeper than others at a given temperature but they did not respond the same way in all tempera-tures studied. Some cultivars did not respond to temperature and they crowned at about the same depth at all temperatures. They found that depth of the crown of plants grown at 10° C under controlled conditions was significantly correlated with winter survival under field conditions (r = 0.65).

Pauli (1960) artificially froze Pawnee winter wheat plants from one to five times to study the relation of crown tissue to winter survival. He found decrease in percent survival and recovery rates following successive freezes which seemed to be directly related to the decrease in amount of living vascular connections between tops and root.

Wheat isolines of three plant height in nine genetic backgrounds were examined after exposure to the temperature of -18° C. In six backgrounds the short sibs had 5-31% deeper crown than their tall sibs. In two backgrounds the crown of medium height sibs were deeper than their tall sibs (Allan, Gul, and George, 1975).

Utilizing six wheat cultivars planted at five depths in dark growth chamber, Ashraf and Taylor (1974), measured the morpho-development characteristics including the length of subcrown inter-node. Planting depth was shown to affect the length of subcrown internode. They correlated the length of subcrown of cultivars measured in growth chamber and the field winter survival. A positive association was noticed indicating that cultivars with shallow crown depths are superior to those with deep crown in the ability of surviving winter.

4. Adenosine Phosphates and Energy Charge

Many investigators have shown that growth and vigor are positively correlated with the efficiency of mitochondrial oxidative phosphorylation; (Dobrenz, McDaniel, Schneiters, and Schonhorst, 1975 in Alfalfa; Doney, Wyse and Theurer, 1975 in sugar beet; Hanson, Moreland and Shriner, 1975 in maize and soybean; McDaniel and Sarkisian 1968 in maize; Sarkisian and Srivastava, 1969 in wheat; and Zobl, Fischbeck, Keydel and Latzko, 1972 in wheat).

During early stages of germination of the wheat embryo, there is prolific polyribosome formation concomitant with a rapid increase in the capacity to incorporate amino acids. In vitro polyribosome formation can be achieved with extracts of dry unimbibed wheat embryo if adenosine triphosphate (ATP) is supplemented; therefore, it seems that the level of ATP may be a limiting factor in the regulation of embryo germination (Ching, 1972). ATP is formed during the light reaction of photosynthesis and during glycolysis, but the most important pathway during the early stages of growth is through oxidative phosphorylation (Ching, 1972). A genotype with a fast growth rate requires more energy than a slow growing genotype, this extra energy required by the fast growing genotype is obtained probably from more efficient mitochondria (Ching, 1972). During seed germination in both fast and slow growing seedlings, ATP content increases very rapidly thereby providing the

energy required for the early events of germination (Ching, 1972).

The concept of Energy Charge (EC) as a regulatory parameter was first introduced by Atkinson (1968). He suggested that EC of the adenylate system could serve as a single parameter by which the effects exerted on enzymes could be related to the energy level of cells. He defines the EC as half the number of anhydride-bound phosphate groups per adenine moiety, therefore; $EC = ATP + 1/2$ $ADP/ATP + ADP + AMP$. With Escherechia coli, Chapman, Fall, and Atkinson (1971), demonstrated that growth occurred only at EC values greater than 0.8 and that at values between 0.8 and 0.5 viability was maintained; however, if the EC was less than 0.5 senescence and death of the organism occurred. In higher organisms the synthesis of nucleotides especially adenosine mono phosphate (AMP), and adenosine di phosphate (ADP) in the new cells are high during early stages of growth. This results in low value of the overall cellular EC in the tissue. It is only after stabilization of the cell number in the tissue that EC values increases to a steady state characteristics of the tissue (Ching, 1976, personal communication).

The relationship between ATP level during germination and the early stages of growth, and the rate of growth have been demonstrated in wheat (Ching and Kronstad, 1972; Garay, 1975; Obendorf and Marcus, 1974), clover, ryegrass and rape (Ching 1973; and Ching, Crane and Stamp, 1974), and lettuce (Ching and Danielson,

1972). In addition, positive correlations between EC and early growth rate were shown by Ching and Kronstad (1972) in wheat and by Ching, Crane and Stamp (1974) in pod walls and seeds of maturing rapes.

Mitochondrial efficiency and complementation have been used by some researchers as a biochemical index of growth in crosses between various cultivars in different crops. This is done by measuring the rate of oxidation and phosphorylation (adenosine diphosphate (ADP):O) in a mixture of the mitochondria from two cultivars or species as compared to the average activities of parental mitochondria. The usefulness of the method has been emphasized by many workers with a variety of crops including wheat, barley, maize, sugar beet and alfalfa (Dobrenz, McDaniel, Schneiter and Schonhorst, 1975; Doney, Wyse and Theurer, 1975; McDaniel, 1969a; McDaniel, 1973; McDaniel and Sarkisian, 1968; Sage and Hobson, 1973; Sarkisian and Srivastava, 1969; and Schneiter, McDaniel, Dobrenz and Schonhorst, 1974). However, the suitability of the method has been questioned by Hanson, Moreland and Schriner (1975) in maize and soybean; by Ellis, Brunton and Palmer (1973) and Ellis and Hanson (1974) in barley; and by Zobl, Fischbeck, Keydel and Latzko (1972) in wheat.

The relationship between seed size or seed weight and seedling vigor in barley and wheat was demonstrated by Boyd, Gordon and

La Cruix (1971) and Kittock and Law (1968). The effect of seed size

in wheat was attributed to the endosperm size rather than to embryo

size (Bremmer, Eckersall and Scott, 1963). Positive correlations

were reported between seed size or seed weight and ATP content

of the seed by Ching (1973) on clover, ryegrass and rape and by

Abernethy, Wright, Matsuda (1973) in blue panicgrass. Similar

results have been obtained by Garay (1975) in wheat cultivars, although

he also observed that smaller seeds germinated faster than larger

seeds and produced longer roots and shoots during the very early

stages of growth but not at later stages. In barley cultivars heavy

seeds contain more mitochondria and result in more oxidative

phosphoylation (McDaniel, 1969b).

The effects of temperature on respiration of mitochondria of

wheat, rye, tomato, cucumber and sweet potato were studied in

relation to chilling injuries and hardiness (Lyons and Raiaon, 1970;

Miller, De La Roche, and Pomeroy, 1974; and Pomeroy and

Andrews, 1975). These effects were also investigated in relation

to changes in ATP level in spinach (Heber and Santarius, 1964), and

cotton (Stewart and Guinn, 1969). Ching (1975) reported

on changes in ATP, ADP, and AMP level of crimson clover seeds

during germination under 10, 20, and 30° C temperature regimes.

The rate of initial increase in adenosine phosphates was correlated

with temperature and water uptake. At 10° C a sigmoid increase of

ATP pool was observed for 24 hr indicating a relative slow ATP utilization at this temperature. At 30° C, ATP increased rapidly for six hr and then declined quickly. This rapid decline was attributed to the excessive utilization of energy for various biosynthesis. Under 20° C the peak of ATP content occurred at 12 hr after imbibition. ATP content declined after 12 hr but this decline was much slower than decline at 30° C.

MATERIALS AND METHODS

Six soft white winter wheat cultivars (<u>Triticum</u> <u>aestivum</u>, <u>L.</u> <u>em</u> <u>thell.</u>), Hyslop, Yamhill, Sprague, Luke, Moro and Kirac, and a soft red wheat, Strampelli, were used in three studies conducted over three locations in Oregon in 1974-75. A description of cultivars is provided in Appendix I. The cultivars selected for use in these studies represent wide genetic diversity for coleoptile length, crown depth, and the ability to produce and utilize ATP. The first five cultivars have been in commercial production and are adapted to Pacific Northwest. Kirac is a cultivar from Turkey known for its fast emergence ability under deep seeding and/or late seeding conditions. Strampelli was included because of its shallow crown.

Crosses were made in a diallel fashion including reciprocals among six of the above cultivars (cultivar Luke was excluded because of the progressive necrosis in the F_1 crosses of this cultivar with Hyslop and Yamhill). Not all the cultivars or crosses were used in every experiment.

Three experimental sites were utilized for the field studies: Hyslop Agronomy Farm, near Corvallis, Oregon; Sherman Experiment Station at Moro, Oregon, and Rug farm located northeast of Pendleton, Oregon. The experimental sites were chosen to represent a wide range of

environmental conditions. Climatic conditions during the experimental period and the soil types of the stations are described in Appendix II.

Experimental field was under peas-wheat rotation at Rug farm. Wheat-fallow rotation was practiced at both Sherman Experiment Station and Hyslop Agronomy Farm. One hundred and twenty three kg/ha amonium nitrate (34% N) were applied prior to planting at the Hyslop site. In addition, plots at this site were top-dressed with 100 kg/ha urea (46% N) at the mid tillering stage. Sixty kg of N in the form of urea were applied at Sherman station before planting. No fertilizer was used at Rug farm because of residual nitrogen remaining following the previous pea crop.

Measurements on agronomic traits were taken as follows:

Stand count. Number of plants emerged between 25 to 45 days after planting was counted in $2m^2$ of the two middle rows of each plot.

Spikes per plot. Number of spikes was counted prior to harvesting in the same area where stands was counted.

Spikelets per spike. Two random samples of five spikes each were chosen in each plot. Number of spikelets was counted (in both sides of spikes) and then were divided by the number of spikes.

Height. In each plot two areas were randomly selected. The height of the plants were measured in cm from the soil surface to

the tip of spike excluding awns and then were averaged.

Total plant yield. Plots were harvested by sickle, cutting the culms as close to the soil surface as possible. Harvesting in solid seeding plots was done in $2m^2$ of two middle rows of each plot after descarding the borders. In space planted plots the whole plot was cut. Harvested plots were weighed in grams before threshing. This weight was taken as total plant yield in contrast to the grain yield.

Grain Yield. Harvested plots were threshed using either a Vogel Thresher or Hege 125. Seeds were cleaned lightly and weighed in grams.

Harvest Index. The ratio of grain yield to total plant yield was calculated and designated as H. I.

Kernel Weight. Samples of 500 kernels of each plot were counted and weighed in hundredths of a gram, then were converted to the weight of kernel in milligrams.

Number of Kernels per Spikelet. This component was calculated as:

$$\text{Kernel per Spikelet} = \frac{\text{Grain yield/plot X 1000}}{\text{No. of spikes/plot X no. of spikelets/spike X Kernel weight}}$$

Statistical analyses. Analysis of variance was used to detect the significant differences between treatments (Snedecor and Cochran, 1967). Differences within treatments were obtained using Duncan's new multiple range test (Steel and Torri, 1960). Combined analysis

of variance over locations was performed based on the methods described by Kempthorne (1952, Chapter 28) and Cochran and Cox (1957, Chapter 14) assuming the homogeneity of error variance and taking locations as random and treatments as fixed variables. Degrees of freedom of treatments were then broken among the components of treatments (cultivar (C), Sources (S), Sizes (Z), and their interactions). Significance of each variable was tested against the proper error term (or interactions) by the F test.

Regression analysis (Draper and Smith, 1966) provided information about the association between various traits.

Path coefficient analysis, first introduced by Wright (1921) was used to find the direct and indirect effects of agronomic traits on yield.

Narrow sense heritability (H_{ns}) was computed by regression of F_1's on midparents (Kronstad and Foote, 1964), or regression of F_{n+k} on F_n, $n > 1$, $k > 0$ (Hanson and Robinson, 1963).

Broad sense heritability (H_{bs}) was estimated following the method described by Mahmud and Kramer (1951); the F_2 genotypic variance was calculated by subtracting the mean of parental variances (estimating environmental variance) from the F_2 variance. Details of material and methods for each study are as follows:

Study 1. Effects of seed size and seed source on stand establishment and yield.

Experiments were conducted at three sites; Hyslop, Moro, and Rug farm in 1974-75 using a randomized block design with three replications.

Seven cultivars, Hyslop, Yamhill, Moro, Strampelli, Sprague, Kirac and Luke were utilized. Seeds were obtained from two sources, Hyslop and Pendleton Experiment stations, and were further screened to make three grades; large seeds (seeds remaining on the top of oblong screen with 7/64 inch width), small seeds (those seeds passing through the screen of 6/64 inch wide), and unsized seeds. Also two more grades of seed based on seed weight were included in the experiment to simulate the farmers practice which use equal seed weight (or volume) regardless of the seed size; therefore fewer seeds per unit land area when the seeds are large will be planted and vice versa. The commercial seed rates used in the Willamette Valley (100 kg/ha), and in Pendleton and Moro (67.3 kg/ha) were followed and equal seed weights were used for large and small seeds. Each treatment was hand planted in four-row plots, 4 m long, 30 cm apart at Hyslop station and 36.5 cm apart at Moro and Pendleton. Number of seeds per row was 276 at Hyslop and 215 at Moro and Pendleton which for the average of unsized seeds corresponds to 100 and 67.3 kg/ha, respectively.

Study 2. Effects of coleoptile length and crown depth on yield

and yield components, and inheritance of coleoptile length and crown depth.

Seven cultivars and F_1 diallel crosses among six of them were utilized in this study. Experiments were conducted at three sites; Hyslop, Moro and Rug farm. Parental lines were obtained from two sources, i. e. Hyslop and Pendleton, and were graded to three sizes namely; small, unsized and large in the same way that was described in Study 1. Seeds were sown in space-planted nurseries with 20 cm distance between and within rows. Each plot consisted of four rows, each row 1 M long. Two depths, 5 cm and 12 cm were exercised. A wooden board with holes at every 20 cm within and between rows and a metal rod with the marks on 5 and 12 cm were used for planting. Holes were made in the soil with the rod and one seed was placed in each hole, then holes were covered by racking the soil gently and frequently to avoid any change in depth. Experimental design was randomized blocks split plot design with depth as the sub plot and three replications.

After emergence 10 plants in each plot were marked at the soil surface with a colored paint. Plants so marked were dug up by a shovel and were transferred to the laboratory. Coleoptile length was measured in mm from the seeding depth to the tip of coleoptile. Crown depth was recorded in mm from the soil surface down to the place where crown was initiated. Length and the width of leaf was

recorded on the longest seeding leaf. Data on each trait were aver-
aged for each treatment and noted as the average crown depth,
average coleoptile length, or the average length or width of the first
leaf.

Data were analyzed in two sets. One set consists of data taken
on cultivars where seed source and size were included; this set was
used to study the effects of coleoptile length and crown depth on
yield and yield components. The effects of seed source and seed
size on crown depth and coleoptile length as well as their effects on
yield and its components were also studied in this set of data. The
other set of data were comprised of measurements of F_1's as well as
measurements on unsized seeds of varieties from Hyslop source
and was utilized to study the heritability of crown depth and coleop-
tile length.

Study 3. Relationships between adenosine triphosphate and
energy charge, and stand establishment and yield.

Adenosine triphosphate (ATP), adenosine diphosphate (ADP),
adenosine monophosphate (AMP) and energy charge (EC) of the afore
mentioned seven cultivars, the F_1 diallel crosses including recipro-
cals, and the F_2's of main crosses (not reciprocals) were measured in
the laboratory using luciferine-luciferase method (Ching and Ching,
1972). This study consisted of three distinct parts as described
below:

Part A. Effects of temperature during imbibition on the level of adenosine phosphates and energy charge. Seeds of seven cultivars harvested from Hyslop Agronomy Farm in 1974 were used for this study. Two temperatures and three periods of imbibition were used as follows: 1) 10° C for 72 hr, 2) 10° C for 96 hr, 3) 10° C for 92 hr, 4) 20° C for 72 hr, and 5) 20° C for 96 hr. Four seeds of each cultivar were used in each temperature regime, seeds were chosen so that having the average weight equal to the average kernel weight of the respective cultivars as were harvested from the field. Seeds were germinated in sandwich boxes between four layers of Whatman No. 1 filter paper with 8 ml of glass distilled water. Boxes were incubated in a growth chamber in the dark for the designated periods and temperatures. After the incubation period the embryos or seedlings were dissected and were quickly extracted in 10 ml of boiling glass distilled water for 5 minutes. The extract from each seed was cooled in an ice bath and then diluted with the buffer containing 0.025 M N-2 hydroscyethylpiperazine-N-2-ethanesufonic acid (HEPES) and 0.025 M magnesium acetate at PH 7.5. ATP, ADP and AMP were measured using an Aminco chem-Glow Photometer. Energy charge was calculated as described by Atkinson (1969). Details of the procedure of measuring ATP, ADP, AMP, and EC are provided in Appendix III.

Part B. Effects of seed source and seed size on the level of ATP and EC, and correlations between agronomic and biochemical traits. Seeds of the seven cultivars were obtained from three sources, Hyslop Agronomy Farm, Sherman and Pendleton Experiment Stations. Seeds from Hyslop and Pendleton were from the same lots which were used to plant study 1 and 2. Ten kernels from each source were chosen so that to have two following properties: 1) the seed size ranged from the smallest possible to the largest available in the lots . 2) nine out of ten seeds can be further classified in three grades each grade consisting of three seeds with their average weight being equal or very close to average kernel weight of the three seed sizes which were planted in the field. Each seed was weighed to the closest tenth of a milligram. Method of germination and assaying AP's and EC were the same as were described in Part A, but only one temperature regime namely 20° C, 72 hr was utilized.

Data were analyzed in two sets: 1) data on ten seeds per cultivar per source were analyzed to find the effect of seed source and size on AP's and EC. 2) Data on 9 seeds per cultivar from Hyslop or Pendleton source were averaged in three classes corresponding to three seed sizes of the respective cultivars grown in study 1. Correlation coefficients were calculated between values of AP's and EC and values of agronomic traits obtained from study 1 in 1974-75

to determine the importance of biochemical measurements in stand establishment studies.

Part C. Inheritance of ATP and EC. Diallel crosses were made among six cultivars; Hyslop, Yamhill, Sprague, Strampelli, Kirac and Moro in 1973 and 1974 at Hyslop station and in the greenhouse. F_1 seeds were grown in the same location in 1973-74 season in a space planted nursery and F_2 seeds were harvested in 1974.

Adenosine triphosphate and EC of parents, F_1's, reciprocal F_1's and F_2's were determined in 1974. Ten seeds of each cultivar or F_1 and 40 seeds of each F_2 were chosen and weighed individually. These seeds ranged in size from small to large in each parent or F_1, but in the F_2 each treatment had four sets of ten seeds, each set ranging in size similar to those of cultivars and F_1's. Method of germination, incubation and assaying ATP and EC were the same as in Part B. Values on each four seeds (corresponding to one size) of each F_2 were then averaged to make ten values for these generations similar to the parents and F_1's.

Data were analyzed in two sets. One set having measurements on ten seeds per treatment, the other set containing values on four seeds. These four values were on those seeds (set of four seeds each for F_2) which their average weights were equal or very close to the kernel weight of the treatments harvested from the field.

RESULTS AND DISCUSSIONS

Study 1. Effects of Seed Source and Seed Size on Stand Establishment and Yield

Analysis of variance for ten agronomic traits were calculated for each experimental site. Data were further combined over locations and combined analysis of variance was performed.

At Hyslop Experiment Station varietal differences were significant for all traits except for percentage of emergence (Table 1). Duncan's new multiple range test (DMRT) also demonstrated these differences except for the stand count and percentage of emergence (Table 2). Highest varietal responses to different traits were observed as follows: Hyslop for grain yield, number of kernels per spikelet, and harvest index; Yamhill for kernel weight; Moro for number of spikelets per spike; Strampelli for percentage of emergence; Sprague for stand count; and Luke for total plant yield and number of spikes per plot.

Seed source had a significant effect on grain yield, number of spikes/plot, number of spikelets/spike, and stand count. However, the highly significant seed source x seed size (S x Z) and cultivar x seed source x seed size (C x S x Z) interactions makes it difficult to draw conclusions about the main effect of cultivar, seed source or seed size on stand count.

Table 1. Mean squares from the analysis of variance for ten traits measured on the seven wheat cultivars grown at Hyslop Agronomy Farm, Corvallis, Oregon, in 1974-75.

Source of Variation	d. f.	Stand Count	% Emergence	Total plant yield per plot	Grain yield per plot	Harvest Index	No. spikes per plot	No. spikelets per spike	No. kernels per spikelet	Kernel Weight	Height
Cultivar (C)	6	5996**	48.13	6921250**	1998610**	0.0372**	529131**	59.57**	2.167**	608.14**	8287.6**
Seed source (S)	1	4154**	49.52	516931	95872*	0.0004	76610*	3.89*	0.004	0.18	7.2
C x S	6	411	77.46**	253258	25335	0.0005	5546	0.59	0.031	2.82	48.9*
Seed size (Z)	4	300679**	99.51**	125160	7941	0.0004	31984*	1.02	0.189*	4.09	25.1
C x Z	24	5340**	46.71**	153825	19170	0.0003	18923	0.89	0.072	2.75	12.1
S x Z	4	8849**	75.67*	56668	3331	0.0005	3113	2.75*	0.031	1.19	24.9
C x S x Z	24	3658**	56.62**	173604	25774	0.0003	11204	1.04	0.063	1.79	17.7
Error	138	1138	25.84	145665	21927	0.0004	12129	0.97	0.073	1.91	18.9
Total	209										
Coefficient of Variability		8.07	7.83	11.8	12.44	5.50	13.87	5.54	13.05	3.36	3.74

* Significant at the 5% level
** Significant at the 1% level

Table 2. Means of nine traits of seven wheat cultivars and five seed sizes from the experiment grown at Hyslop Agronomy Farm in Corvallis, Oregon in 1974-75.

Cultivars	Stand Count	% Emergence	Total plant yield per plot (g)	Grain yield per plot (g)	Harvest index	No. spikes per plot	No. spikelets per spike	No. kernels per spikelet	Kernel weight (mg)
Hyslop	419.5a[1]	69.2a	3693a	1487a	0.403a	768 bc	17.8 bc	2.49a	43.8 b
Yamhill	392.3a	67.7a	3704a	1464a	0.396ab	665 c	19.2ab	2.36ab	49.0a
Moro	419.7a	67.5a	3191ab	1032 b	0.322 bc	757 bc	20.2a	1.90 bc	36.1 e
Strampelli	413.0a	71.1a	2603 b	956 b	0.366 b	742 bc	17.1 c	1.95 bc	39.0 cd
Sprague	440.2a	69.4a	2821 b	1063 b	0.376ab	920ab	16.8 c	1.88 bc	36.9 de
Kirac	417.7a	67.9a	2883 b	900 b	0.312 c	674 c	17.6 bc	1.78 c	43.3 b
Luke	424.4a	68.7a	3742a	1428a	0.382abc	1020a	16.1 c	2.15ab	40.1 c
Size [2]									
1	388.8 b	70.45a	3170a	1173a	0.369a	785a	18.1a	2.03a	41.2a
2	382.7 b	69.38a	3219a	1179a	0.362a	753a	17.7a	2.17a	41.2a
3	381.3 b	69.04a	3316a	1205a	0.361a	807a	17.9a	2.03a	41.4a
4	568.5a	66.28a	3211a	1191a	0.368a	824a	17.7a	2.02a	40.7a
5	367.7 b	68.97a	3254a	1201a	0.365a	793a	17.7a	2.11a	41.4a
Mean	417.86	68.82	3234	1190	0.365	793.8	17.86	2.07	41.22
c.v.	8.07	7.38	11.8	12.44	5.50	13.87	5.54	13.05	3.36

1/ Duncan's new multiple range test; means followed by the same letter are not significantly different at the 5% level.

2/ Numbers under size column stand for: 1, small; 2, unsized; 3, large; 4 and 5, equal weight (4=small seeds and 5=large seeds)

Seed from Hyslop source was superior to that from Pendleton source

in percentage of emergence and number of spikelet per spike and

inferior in stand count, total plant yield, grain yield and number of

spikes/plot.

Different seed sizes produced meaningful differences on

kernel/spikelet, spikes/plot, percentage of emergence and stand

count, but the last two traits also showed significant C x Z and C x S x Z

interactions. Duncan multiple range test showed significant differ-

ences in stand count due to the seed size but not in other traits.

despite the significant F ratio for these traits. Small seeds produced

the best emergence, harvest index (H. I.) and number of spikelets

per spike, but seed size 4 (small, planted on per weight basis) gave

the highest stand which is due to a greater number of seeds planted.

The highest yield (total and grain) was produced by large seeds if C x Z in-

teraction is ignored. This interaction though not significant might have a

great effect on varietal responses as it is delineated in Figure 1 for

grain yield. For instance the cultivar Hyslop responded to seed

size; yield decreased using small seeds even on per weight basis,

while for cultivar Moro the number of seeds were more important

than the seed size. Cultivars Yamhill and Luke produce about the

same yield regardless of seed size or seed number.

Significance of varietal differences for various traits in analysis

of variance and DMRT at Pendleton site were very similar to
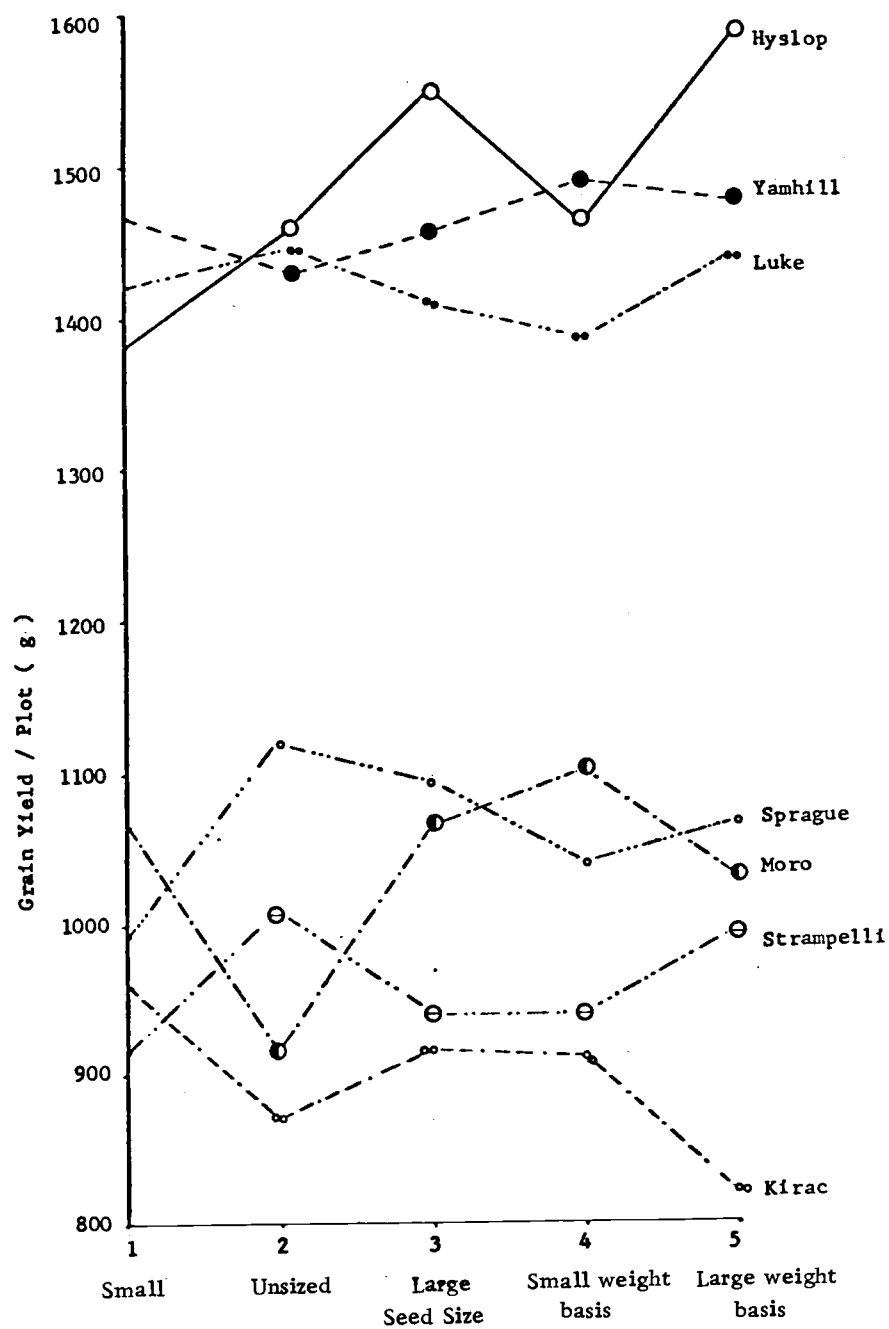
Figure 1. Grain yield of seven wheat cultivars grown at Hyslop
Agronomy Farm, Corvallis, Oregon in 1974-75 in relation
to seed size.

those in Hyslop station (Tables 3 and 4). Cultivar Hyslop outyielded the other cultivars for grain yield; Yamhill was superior in kernel weight; and cultivars Moro, Strampelli, Kirac and Luke exceeded the others for stand count, percent emergence, and number of spikelets/ spike; harvest index; number of spikes/plot and total plant yield respectively.

Seed source had a significant effect at the 5% level on grain yield, spikes/plot, and kernel weight. Seeds from Pendleton were superior in all these cases. Hyslop source seed produced higher percent emergence and number of kernels/spikelet than Pendleton source seed but the differences were not significant.

Effects of seed size in different traits were more drastic than those of seed source. Differences due to seed size were significant in total yield per plant and number of kernels per spikelet, and highly significant in stand count, emergence percentage, and number of spikes per plot. However in three traits namely stand count, total plant yield and spikes per plot there were also highly significant cultivar by seed size interaction. Seed size number 4 (small seed planted on per weight basis) produced the best stand and was significantly different than others in DMRT. However large seeds had better emergence percentage, total plant yield, grain yield and kernel weight. Cultivar by seed size interaction was not significant for grain yield, however there was great varietal fluctuations because

Table 3. Mean squares from the analysis of variance for ten traits measured on the seven wheat cultivars grown at Pendleton, Oregon, in 1974-75.

Source of Variation	d.f.	Stand Count	% Emergence	Total plant yield per plot	Grain yield per plot	Harvest index	No. spikes per plot	No. spikelets per spike	No. kernels per spikelet	Kernel weight	Height
Cultivar (C)	6	3947**	70.7	2234430**	294384**	0.0688**	665287**	30.56**	2.57**	323.88**	6744.2**
Seed source (S)	1	2986	6.8	495429	92610*	0.0000	26253	9.47*	0.21	23.00*	214.0
C x S	6	834	85.1	80525	9205	0.0004	28505	2.91	0.10	1.56	21.7
Seed size (Z)	4	31659**	897.5**	475821*	38663	0.0019	104214**	1.29	0.40*	5.02	72.8
C x Z	24	1609*	70.2*	136104	19786	0.0007	18358	2.21	0.16	4.75	17.6
S x Z	4	6536**	43.5	586560**	51388	0.0005	75907**	0.21	0.04	0.76	26.7
C x S x Z	24	1048	55.2	205329	25640	0.0009	29231*	2.13	0.12	5.77	26.6
Error	138	956	46.2	163236	21879	0.0009	18292	1.79	0.14	5.01	34.6
Total	209										
Coefficient of Variability		13.75	7.69	14.49	13.41	7.56	15.23	6.72	17.28	6.27	5.72

* Significant at the 5% level
** Significant at the 1% level

Table 4. Means of nine traits measured on the seven wheat cultivars and the five seed sizes from the experiment conducted at Pendleton, Oregon in 1974-75.

Cultivars	Stand Count	% Emergence	Total plant yield per plot (g)	Grain yield per plot (g)	Harvest index	No. spikes per plot	No. spikelets per spike	No. kernels per spikelet	Kernel weight (mg)
Hyslop	228a[1]	49.1a	3011a	1231a	0.410 bc	858abcd	17.0ab	2.26ab	37.9a
Yamhill	203a	45.8a	2797a	1128 b	0.406 bcd	669 d	17.9ab	2.46a	39.7a
Moro	235a	49.7a	2701a	991 b	0.367 cdef	796 bcd	18.5a	2.21ab	31.4 c
Strampelli	219a	49.1a	2479a	1155 b	0.467a	799 bcd	16.7ab	2.26ab	38.8a
Sprague	224a	46.6a	2404a	1051 b	0.440ab	984abc	15.7 b	2.08ab	33.1 bc
Kirac	233a	49.3a	3058a	973 b	0.321 f	1092a	16.3ab	1.54 b	36.2ab
Luke	230a	49.1a	3059a	1186 b	0.390 bcde	1017ab	16.0 b	2.27ab	32.7 bc
Size [2]									
1	202 b	47.1a	2629a	1065a	0.410a	807a	16.9a	2.31a	35.4a
2	220ab	51.4a	2742a	1096a	0.404a	874a	17.0a	2.16a	35.4a
3	214 b	49.8a	2881a	1134a	0.398a	910a	17.0a	2.11a	35.7a
4	272a	41.0a	2800a	1084a	0.393a	933a	16.6a	2.04a	35.5a
5	214 b	52.7a	2883a	1133a	0.396a	915a	16.8a	2.15a	36.2a
Mean	224.9	48.4	2787	1102	0.400	888	16.89	2.16	35.6
c.v.	17.76	7.69	14.49	13.41	7.56	15.23	6.72	17.28	6.27

1/ Duncan's new multiple range test; means followed by the same letter are not significantly different at the 5% level

2/ Numbers under size column stand for: 1, small; 2, unsized; 3, large; 4 and 5, equal weight (4=small seeds and 5=large seeds)

of this interaction (Figure 2). Response of Hyslop and Yamhill cultivars was similar to those at Hyslop site but cultivar Moro did not respond to seed classes. Yield of Luke was about the same for all sizes except size 4 (probably due to excess tillering and luxurious vegetative growth in this size).

At the Moro site climatic conditions during the spring of 1975 were not favorable for growth. Drought influence was reflected in the shrieveled seeds of cultivars. Under these circumstances, differential varietal responses extended over all traits (Table 5). However due to higher coefficient of variability at this location compared to the other two sites DMRT did not detect the differences for stand count, percentage of emergence and total plant yield (Table 6). Sprague produced the highest stand, but Yamhill gave the highest total plant yield, grain yield, harvest index, kernels/spikelet and kernel weight. Cultivar Moro was the best in only one trait (spikelet/spike).

Unexpectedly the effects of seed source and seed size at the Moro site were not as prominent as in the other two sites where less moisture stress was observed. Seed source had a significant effect only on total plant yield with seeds from Pendleton being superior to seed from Hyslop, but there was also C x S interaction thereby masking the main effects of cultivar and source for this trait. The differences in other traits due to the seed source were negligible.
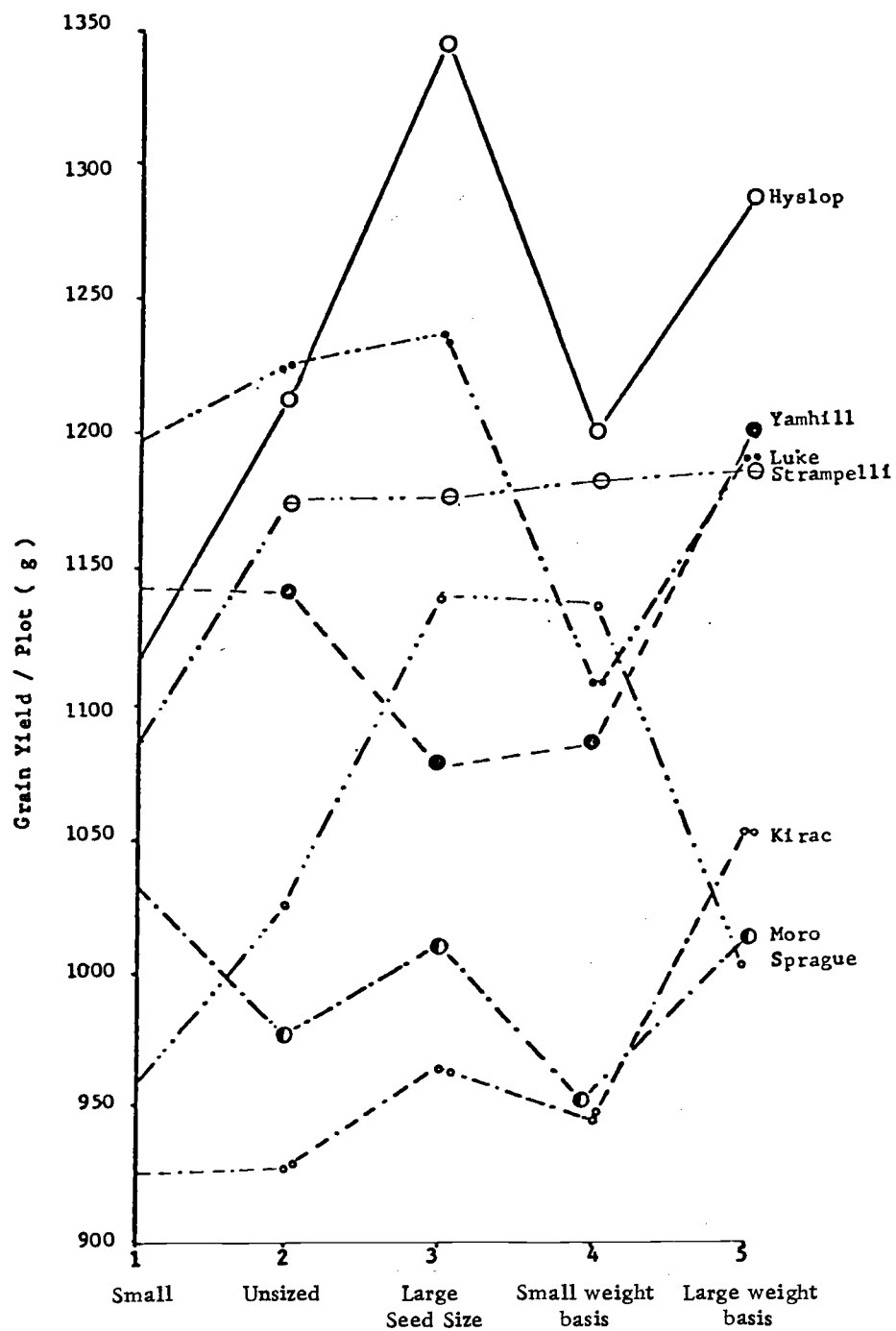
Figure 2.   Grain yield of seven cultivars grown at Pendleton, Oregon
in 1974-75 in relation to seed size.

Table 5. Mean squares from the analysis of variance for ten traits measured on the seven wheat cultivars grown at Moro, Oregon, in 1974-75.

Source of Variation	d.f.	Stand Count	% Emergence	Total plant yield per plot	Grain yield per plot	Harvest index	No. spikes per plot	No. spikelet per spike	No. kernels per spikelet	Kernel weight	Height
Cultivar (C)	6	5286**	186.6**	221918**	107317**	0.0264**	569163**	41.38**	1.2776**	423.29**	575.5**
Seed source (S)	1	254	54.5	211217*	1652	0.0017	7227	2.56	0.0002	3.70	19.5
C x S	6	231	85.5	128515*	21669**	0.0025*	24421	0.68	0.1297	7.70	48.9
Seed size (Z)	4	127203**	150.6	29016	1709	0.0016	129127**	3.17*	0.1944*	0.77	23.3
C x Z	24	1854	63.6	47932	5033	0.0004	19669	1.15	0.0394	3.08	12.4
S x Z	4	2136	62.6	23430	3178	0.0003	7598	1.48	0.0243	3.15	14.2
C x S x Z	24	2681**	55.6	44189	5499	0.0005	11617	1.13	0.0259	4.01	25.9
Error	138	1403	51.5	50291	6521	0.0009	15572	1.06	0.0642	3.73	21.5
Total	209										
Coefficient of Variability		15.69	14.21	15.6	23.42	12.77	14.97	6.83	19.28	8.92	6.91

* Significant at the 5% level
** Significant at the 1% level

Table 6. Means of nine traits measured on the seven wheat cultivars and the five seed sizes from the experiment conducted at Moro, Oregon in 1974-75.

Cultivars	Stand Count	% Emergence	Total plant yield per plot (g)	Grain yield per plot (g)	Harvest index	No. spikes per plot	No. spikelets per spike	No. kernels per spikelet	Kernel weight (mg)
Hyslop	238a [1]	50.7a	1478a	375ab	0.252a	824abcd	15.13 b	1.30ab	23.15 b
Yamhill	219a	49.0a	1590a	431a	0.270a	651 d	15.71ab	1.46a	29.02a
Moro	242a	50.4a	1316a	283ab	0.215abc	699 cd	17.24a	1.39a	17.14 d
Strampelli	253a	55.2a	1465a	391ab	0.264a	776 bcd	15.41ab	1.51a	21.63 bc
Sprague	256a	51.8a	1391a	329ab	0.235ab	988ab	14.06 b	1.25ab	19.21 cd
Kirac	229a	47.5a	1402a	261 b	0.185 b	1017a	14.02 b	0.89 b	20.56 bc
Luke	232a	48.8a	1417a	343ab	0.241a	876abc	14.11 b	1.37a	20.86 bc
Size 2/									
1	202 b	47.3a	1403a	353a	0.247a	776a	15.16a	1.42a	21.71a
2	222 b	51.7a	1436a	344a	0.239a	822a	15.22a	1.32a	21.75a
3	224 b	52.2a	1428a	335a	0.232a	823a	15.07a	1.30a	21.48a
4	335a	50.5a	1476a	347a	0.233a	926a	14.65a	1.23a	21.54a
5	208 b	50.7a	1441a	344a	0.236a	819a	15.38a	1.29a	21.78a
Mean	238.7	50.5	1437	344.8	0.237	833	15.09	1.31	21.65
c.v.	15.69	14.21	15.6	23.42	12.77	14.97	6.83	19.28	8.92

1/ Duncan's new multiple range test; means followed by the same letter are not significantly different at the 5% level

2/ Number under size column stand for; 1, small; 2, unsized; 3, large; 4 and 5, equal weight (4 =small seeds and 5=large seeds)

Significant seed size effects were observed on stand count,
spikes/plot, spikelet/spike, and kernels/spikelet, but not in total
plant yield or grain yield. Similar to Pendleton and Hyslop locations,
the highest stand was counted in seed size 4 (small, per weight basis),
but higher percentage of large seeds had· emerged. Unlike the other
locations, the small seeds yielded more at this site but the differ-
ences were very small. Nonsignificance of seed size in highly
stressed conditions at Moro could be interpreted if one assumes that
the optimum number of seeds had emerged in plots planted with
small seeds. Therefore extra plants in larger seeded plots were
luxurious plants causing unnecessary vegetative growth. This can be
further illustrated by comparing the stand count at Moro and Pendleton.
At Pendleton the grain yield was about 3 times as large as that at
Moro with nearly the same number of plants per unit area.

Changes in the grain yield of cultivars due to the seed size are
depicted in Figure 3. Yamhill showed slight increase in yield when
large seed was used. This is the cultivar which had the lowest
stand count and therefore did not suffer as much as other cultivars
from the late drought and consequently responded to the large seed
size. Yield of Hyslop cultivar was very consistent over the different
seed sizes. The yield of Moro, Strampelli, and Luke decreased by
increasing seed size or seed number.
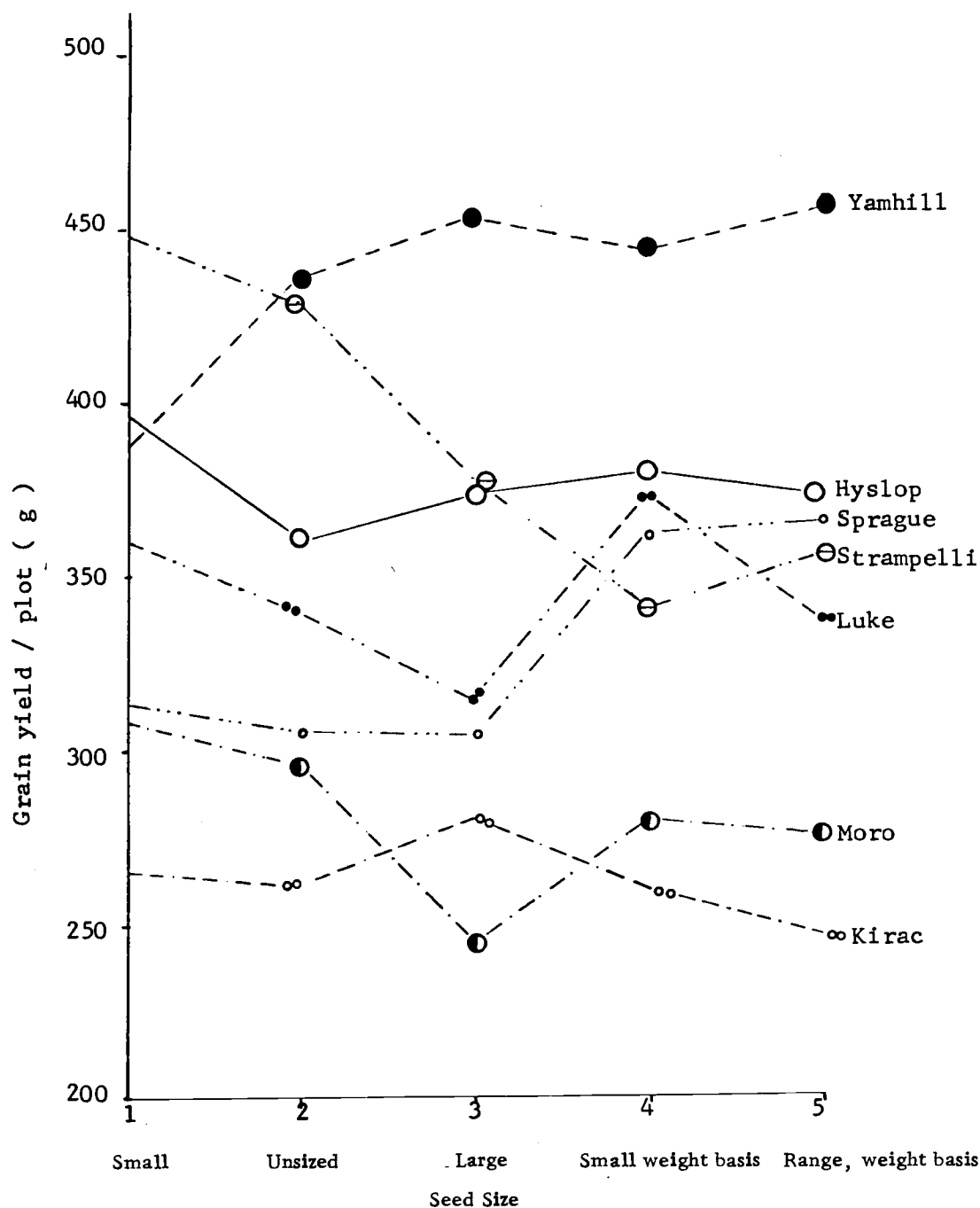
Figure 3. Grain yield of seven wheat cultivars grown at Sherman Experiment Station, Moro in 1974-75 in relation to seed size.

Results of the combined analysis of variance for nine traits over three sites are given in Table 7. Locations were found to have significant effects over all traits except number of spikes per plot. Differential varietal responses were significant for all the characteristics measured except percentage of emergence and total plant yield. Differences due to seed source were not significant in any trait. A highly significant difference in stand count was observed due to seed size but differences in other traits were not significant.

Effects of seed source on nine agronomic traits over three locations are summarized in Table 8. When the effects of seed size are averaged over locations, seeds from Hyslop source were superior to those of Pendleton source for five out of eight characteristics measured namely, stand count, total plant yield, grain yield, spikes/ plot and spikelet/spike. Seeds from Pendleton source had higher harvest index, kernels/spikelet and kernel weight than Hyslop source seed however none of the differences were significant. This implies that either seed source in the range used in these experiments did not affect the agronomic traits or their effects were confounded or masked by the interactions.

Significant varietal differences were noted for all traits except stand count and total plant yield (Table 9). The best stand was obtained from Sprague followed by Hyslop and Strampelli (nonsignificant differences). Cultivars Luke and Hyslop produced the

Table 7. Mean squares from the combined analysis of variance for ten traits measured on the seven wheat cultivars grown at Hyslop Experiment Station, Corvallis, Rug Farm, Pendleton, and Sherman Experiment Station, Moro, Oregon in 1974-75.

Source of Variation	d. f.	Stand Count	% Emergence	Total plant yield per plot	Grain yield per plot	Harvest index	No. spikes per plot	No. spikelets per spike	No. kernels per spikelet	Kernel weight	Height
Location (L)	2	2431920**	26477**	183801000**	45368600**	1.5420**	472164	414.84**	45.608**	21357.7**	135757**
Error (a)	4	3123	141	526835	37872	0.0036	106841	3.48	0.758	14.1	159
Treatment (T): 69											
Cultivar (C)	6	1038250**	163	5201290	1461750*	0.1070**	1284840**	121.65**	4.651**	1187.9**	11267**
Source (S)	1	6079	97	1181180	142832	0.0003	91465	2.44	0.087	3.6	55
C x S	6	774	217	230319	19489	0.0013	27095	1.96	0.071	3.2	33
Size (Z)	4	385342**	560	393034	19959	0.0028	195859	3.05	0.459	5.4	45
C x Z	24	4953	67	118500	15601	0.0004	14190	1.54	0.094	4.1	16
S x Z	4	15317	114	180105	17702	0.0000	38335	0.52	0.049	1.3	40
C x S x Z	24	3230	55	137106	16937	0.0005	20977	1.58	0.077	3.8	33
L x T	138	45411**	534**	2839785**	579748**	0.0171**	359664**	18.69**	1.191**	111.0**	2389**
Errors (b)	414	1166	41	119731	16776	0.0007	15329	1.28	0.092	3.5	25
Total	629										
Coefficient of Variability		11.62	11.45	13.92	14.73	8.18	14.76	6.96	16.4	5.69	5.24

* Significant at the 5% level
** Significant at the 1% level

Table 8. Means of nine agronomic traits in relation to the seed source, measured in experiments conducted over three sites in Oregon in 1974-75.

Location	Seed Source	Stand Count	% Emergence	Total plant yield per plot (g)	Grain yield per plot (g)	Harvest index	No. spikes per plot	No. spikelets per spike	No. kernels per spikelet	Kernel weight (mg)
Hyslop	Hyslop	413	69.3	3184	1168	0.364	774	18.0	2.08	41.1
	Pendleton	422	68.3	3283	1211	0.367	813	17.7	2.07	41.2
Pendleton	Hyslop	221	48.6	2738	1081	0.401	877	16.6	2.19	35.3
	Pendleton	228	48.2	2835	1123	0.400	899	17.1	2.12	36.0
Moro	Hyslop	237	51.0	1405	342	0.240	827	15.0	1.31	21.8
	Pendleton	239	50.0	1469	347	0.235	839	15.2	1.31	21.5
Average of 3 locations	Hyslop	291	56.3	2443	864	0.335	826	16.5	1.86	32.7
	Pendleton	297	55.5	2529	894	0.334	850	16.6	1.84	32.9

Table 9. Means of eight agronomic traits measured on the seven wheat cultivars grown over three locations in Oregon in 1974-75.

Cultivar	Stand Count	Total plant yield per plot (g)	Grain yield per plot (g)	Harvest index	No. spikes per plot	No. spikelets per spike	No. kernels per spikelet	Kernel weight (mg)
Hyslop	295a*	2728a	1031a	0.355a	817 c	16.6abc	2.01a	34.9 b
Yamhill	271a	2697a	1007a	0.357a	662 f	17.6ab	2.09a	39.2a
Moro	299a	2403a	768 bc	0.301 bc	751 e	18.6a	1.83ab	28.2 d
Strampelli	295a	2182a	834abc	0.366a	772 d	16.4 bc	1.91ab	33.1 bc
Sprague	307a	2205a	814abc	0.350a	964a	15.5 bc	1.73ab	29.7 d
Kirac	293a	2447a	711 c	0.272 c	928 b	16.0 bc	1.40 b	33.3 bc
Luke	294a	2739a	985ab	0.337ab	973a	15.4 c	1.93ab	31.2 cd
Mean	293	2486	879	0.334	838	16.6	1.85	32.8
c.v.	11.7	14.1	15.0	8.3	15.1	6.8	16.8	5.8

* Duncan's new multiple range test; means followed by the same letter are not significantly different at the 5% level.

highest and second highest total plant yield respectively. The most

grain yield per plot was noticed for Hyslop followed by Yamhill and

Luke. Strampelli had the highest harvest index but it was signifi-

cantly better than only Kirac and Moro. Cultivars differed the most

in number of spikes/plot (seven cultivars were classified in six

groups), and kernel weight (cultivars were categorized into four

groups).

One interesting aspect of analysis of variance in Table 7 is the

existence of highly significant location x treatment interaction for

all the traits measured. This implies that the differences in these

traits were not independent from locations and therefore all of them

should be studied for each location separately. Under these circum-

stances graphical presentations of the grain yield responses of various

cultivars to seed size at each location provides some insight to the nature

of interactions (Figure 4 through 10). These figures depict the grain yield

responses of various cultivars to seed size at each location. No

cultivar responded the same way over all locations. Hyslop,

Strampelli and Luke had similar pattern at Pendleton and Hyslop

sites but not at Moro station. Cultivar Yamhill had the most con-

sistent pattern among all the cultivars but differential responses to

small seeds (sizes 3 and 4) at Pendleton and Hyslop sites were ob-

served. Highest yield of the cultivar Moro in all locations were

obtained from small seeds; however, responses to other seed sizes
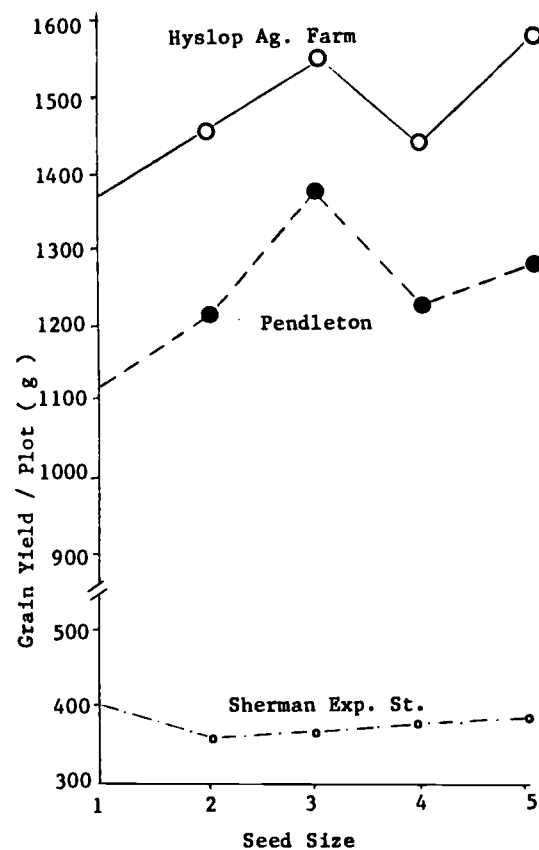
Figure 4. Yield of Hyslop cultivar grown at 3 locations in Oregon in relation to seed size.
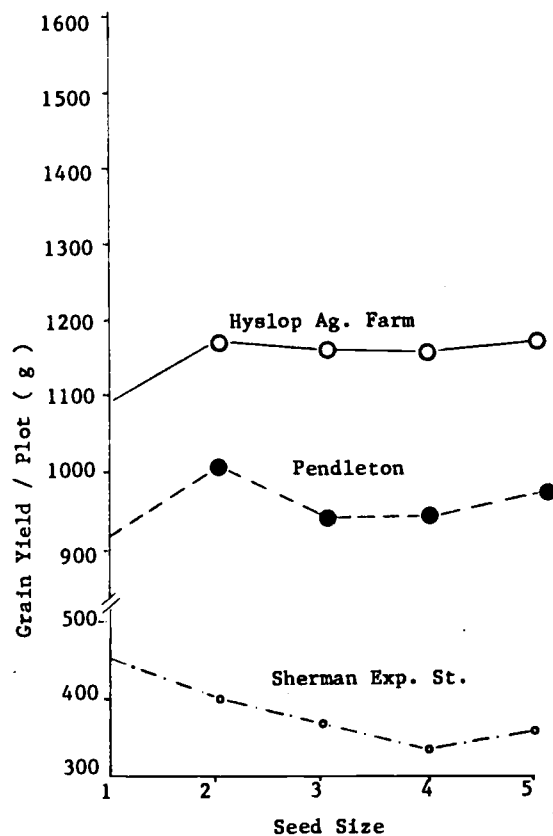
Figure 5. Yield of Strampelli cultivar grown at 3 locations in Oregon in relation to seed size.
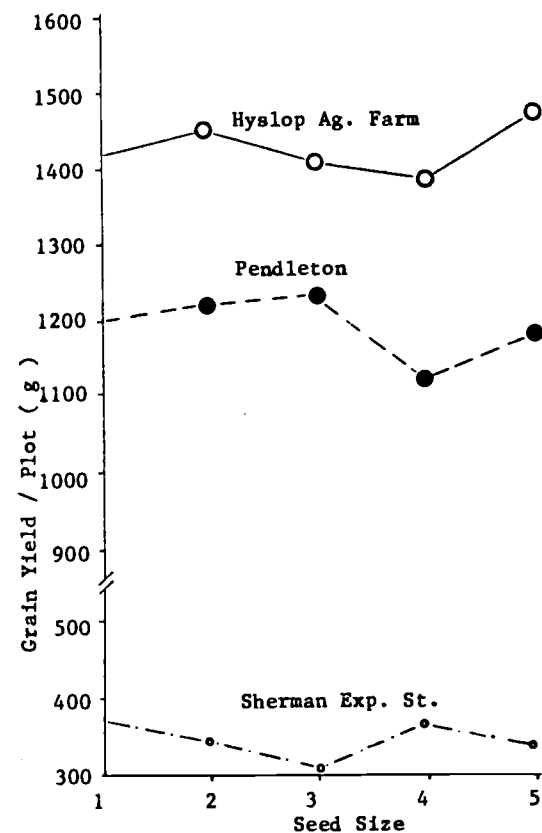
Figure 6. Yield of Luke cultivar grown at 3 locations in Oregon in relation to seed size.
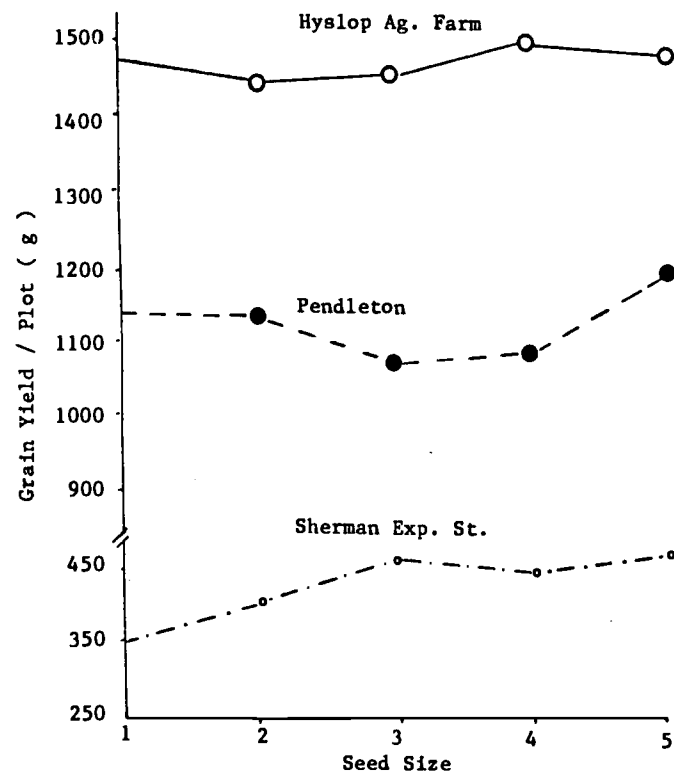
Figure 7. Grain yield of Yamhill cultivar grown at 3 locations in Oregon in relation to seed size.
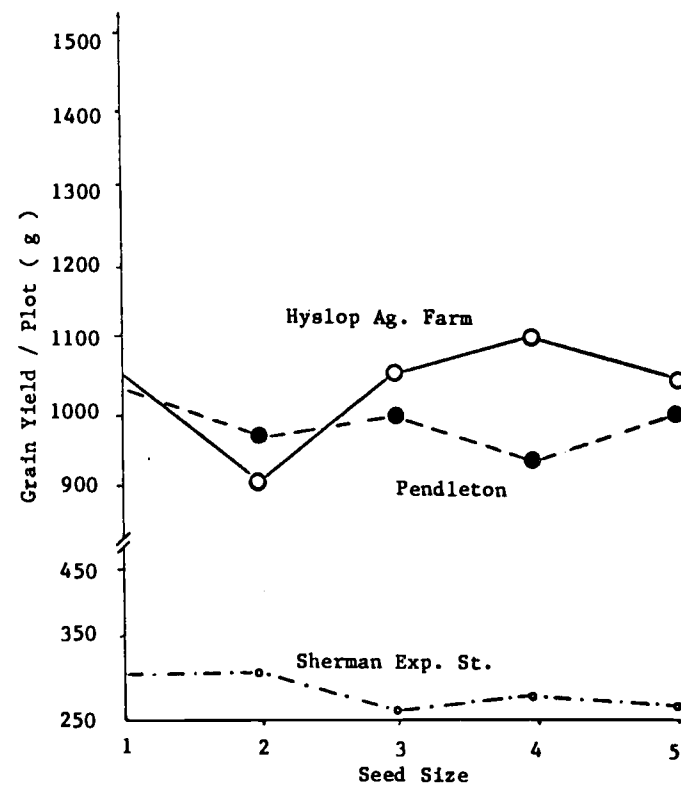
Figure 8. Grain yield of Moro cultivar grown at 3 locations in Oregon in relation to seed size.
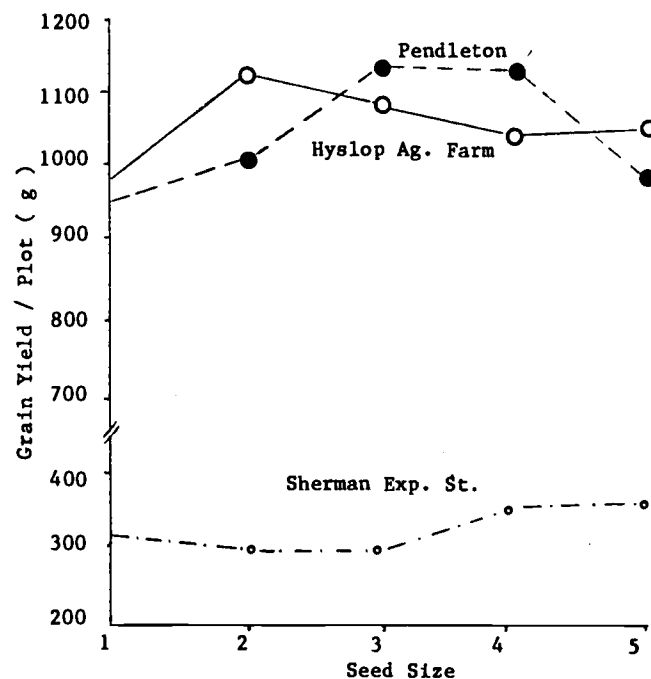
Figure 9.   Grain yield of Sprague cultivar
grown at 3 locations in Oregon
in relation to seed size.
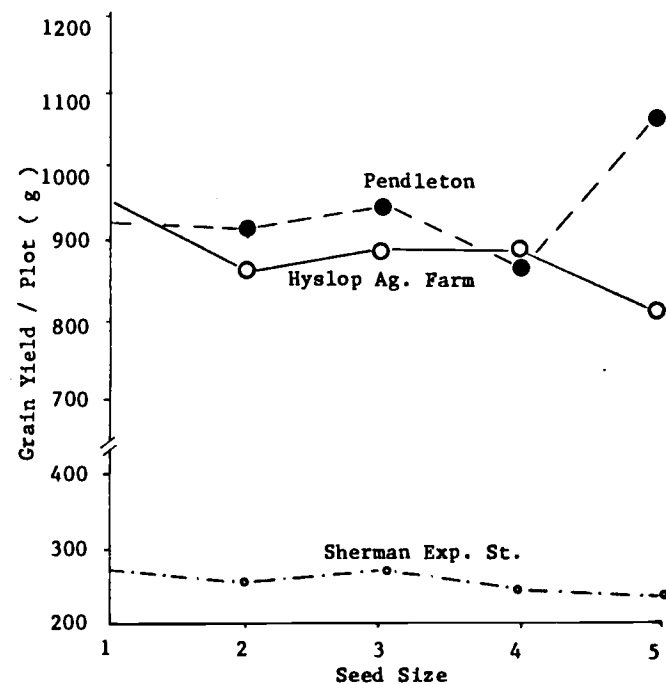
Figure 10.   Grain yield of Kirac cultivar
at 3 locations in Oregon in
relation to seed size.

were not similar over locations. Finally the curves of Sprague and Kirac cultivars are different in all three sites.

Utilizing the combined data simple correlation coefficient among all traits were computed and are presented in Table 10. These coefficients were used to calculate the direct and indirect effects of nine characteristics on grain yield through the path-coefficient analysis (Table 11). Kernel weight had the largest positive direct effect on yield, it also unexpectedly had a large positive indirect effect through number of kernels/spikelet; this could indicate that the environmental conditions did not satisfy the production capability of the cultivars, i.e. cultivars did not develop the maximum number of kernels/spikelet. This was probably due to the unfavorable climatic conditions during the anthesis, expecially at Moro site.

Number of kernels/spikelet was the second most important trait showing large direct and indirect effect (mainly via kernel weight) on yield.

Direct association of number of spikelets/spike and yield was positive but not high; however, this trait had high total "r" value because of its positive indirect effects on number of kernels/spikelet and kernel weight. This implies that the limiting factor in yield production was actually the number of spikelets/spike rather than number of kernels/spikelet. A large number of spikes/plot (resulted

Table 10. Simple correlation matrix for 10 variable measured over 3 locations in Oregon in 1974-75 in studying the effects of seed source and seed size.

Variables	Seed source	Seed size	Stand count	No. spikes per plot	No. spikelets per spike	No. Kernels per spikelet	Kernel weight	Grain yield per plot	% Emergence	Height
Location	-0.000	-0.000	-0.659**	0.084	-0.572**	-0.573**	-0.870**	-0.805**	-0.634**	-0.818**
Seed source		0.000	0.028	0.063	0.031	-0.022	0.008	0.035	-0.038	-0.012
Seed size			0.147**	0.137**	-0.036	-0.066	0.008	0.019	0.001	0.014
Stand count				0.037	0.271**	0.138**	0.441**	0.371**	0.738**	0.454**
No. spikes per plot					-0.349**	-0.298**	-0.171**	0.104*	-0.0218	-0.036
No. spikelets per spike						0.327**	0.529**	0.481**	0.296**	0.610**
No. kernels per spikelet							0.660**	0.779**	0.161**	0.436**
Kernel weight								0.864**	0.443**	0.470**
Grain yield per plot									0.366**	0.653**
% Emergence										0.434

 * Significant at the 5% level
** Significant at the 1% level

Table 11. Path coefficient analyses of the direct and indirect influences of nine traits on grain yield per plot of seven wheat cultivars planted over three locations in Oregon in 1974-75.

Relationships of yield and:	Direct effect	Indirect effects via									Total (r)
		Source	Size	Stand	% Emergence	Spikes per plot	Spikelet per spike	Kernels per spikelet	Kernel weight	Height	
Seed source	0.0063		-0.0000	0.0005	-0.0008	0.0270	0.0073	-0.0114	0.0043	0.0014	0.0346
Seed size	-0.0015	0.0000		0.0027	0.0002	0.0587	-0.0085	-0.0342	0.0043	-0.0017	0.0200
Stand count	0.0182	0.0002	-0.0002		0.0178	0.0159	0.0639	0.0715	0.2381	-0.0542	0.3712
% Emergence	0.0241	-0.0002	-0.0000	0.0134		-0.0120	0.0698	0.0835	0.2391	-0.0518	0.3659
Spikes per plot	0.4286	0.0004	-0.0002	0.0007	-0.0007		-0.0823	-0.1545	-0.0923	0.0043	0.1040
Spikelets per spike	0.2359	0.0002	0.0001	0.0049	0.0071	-0.1496		0.1695	0.2855	-0.0728	0.4808
Kernels per spikelet	0.5185	-0.0001	0.0001	0.0025	0.0039	-0.1277	0.0771		0.3563	-0.0520	0.7786
Kernel weight	0.5399	0.0001	-0.0000	0.0080	0.0107	-0.0733	0.1247	0.3421		-0.0883	0.8639
Height	-0.1193	-0.0001	-0.0000	0.0083	-0.0154	0.1439	0.2260	0.3995	0.0104		0.6533

R^2 = 0.96596
Residual = 0.03404

from excessive vegetative growth at early season) is therefore the factor limiting the production of optimum spikelets/spike.

Number of spikes/plot had large positive effect on yield but its effect was neutralized by its negative relationships with number of spikelets/spike, number of kernels/spikelet and kernel weight. These negative associations are also attributable to the excessive vegetative growth during the early season.

Plant height per se showed a negative relationship with yield but its overall effect was highly positive by affecting the number of spikelet/spike, spikes/plot, and most important the number of kernels/spikelet. This is probably due to the presence of the tall cultivar Moro in the experiment, a club wheat which had the highest number of spikelets/spike and kernels/spikelet among the seven cultivars tested.

Emergence percentage had a larger direct association with yield than stand count, but overall effects of these two traits were very close, the same is true for their indirect effects on grain yield. Both of these traits had larger overall effect on yield than number of spikes/plot. Neither of these traits had significant correlation with number of spikes/plot nor did they have indirect effect on yield via this trait, but both showed significant correlations with kernel weight and had noticeable indirect effects on yield via

this trait. This indirect effect of stand on yield through kernel weight which is the component of yield that develops last in the season implies that a good stand establishment early in season develops the top and root systems of the plant properly so that deep roots provide nutrients and water to the plant late in the season.

Seed source and seed size did not have either a large direct nor indirect effect on final grain yield. Indirect effects of other traits on yield via seed source and seed size did not have any notice-able magnitude either; nevertheless there were highly significant positive correlation coefficients (Table 10) between seed size and stand count and between seed size and number of spikes/plot. As it has already been mentioned the effects of these two traits especially seed size is not only dependent on locations but also to the cultivar used to study these traits. Therefore, further detailed investigations of these traits would be rewarding.

Based on these results the following conclusions can be drawn:

1. Stand establishment has direct and indirect effects on yield even under favorable conditions such as at Hyslop Agronomy Farm.

2. The effects of seed source and seed size on stand establish-ment and yield are very much dependent on locations and cultivars. Both traits were more important under favorable rather than unfavor-able conditions. Any result obtained with a given cultivar may not be extendable over other cultivars because of differential varietal responses.

3. Planting the seed on per volume bases alleviates the negative effect of small seed on stand establishment, but its effect on yield is very much location- cultivar dependent.

Study 2

A. Relationships of Coleoptile Length and Crown Depth and Yield and Yield Components Under Space Planting Conditions

Mean squares from the analysis of variance for coleoptile length, crown depth and 10 other agronomic traits calculated for each experimental site are presented on Tables 12, 13, and 14. At all three locations the deeper planting resulted in longer coleoptile and deeper crown. The differences were highly significant for both traits; however the cultivar x depth of planting interactions were also significant, implying that not all the cultivars responded similarly to the depth of sowing.

At Hyslop site, deeper seeding produced more spikes/plant (17.97 vs 16.48), higher total plant yield and grain yield (103.8 g vs 99.3 g, and 38.27 g vs 37.32 g, respectively), about the same number of spikelets per spike, kernel weight, harvest index, and the length of the first leaf (20.27 vs 20.30, 41.96 mg vs 41.74 mg, 0.376 vs 0.370, and 90.27 mm vs 89.92 mm, respectively), and shorter plants with lower number of kernels per spikelet, and narrower first leaf (87.13 cm vs 96.02 cm, 2.60 vs 2.78, and 2.08 mm vs 2.58 mm, respectively). Differences due to the depth of seeding were significant for the number of spikes/plant, number of

Table 12. Mean squares from the analysis of variance for twelve traits measured on the 7 wheat cultivars grown in 2 depths at Hyslop Agronomy Farm, Corvallis, Oregon in 1974-75.

Source of Variation	d. f.	Coleoptile length	Crown depth	No. spikes per plant	No. spikelets per spike	No. kernels per spikelet	Kernel weight	Total yield per plant	Grain yield per plant	Harvest index	Height	Length of the first leaf	Width of the first leaf
Cultivar (C)	6	160.8**	1499.4**	589.01**	95.17**	8.323**	436.38**	12192.2**	2108.13**	0.02681**	4191.3**	1448.08**	0.4314**
Seed source (S)	1	0.3	2.7	27.66	0.39	0.206	0.58	114.7	0.05	0.00000	28.0	52.48	0.0002
C x S	6	21.1	32.2	15.78	0.99	0.186	1.45	837.2	147.96**	0.00053	50.2	155.59	0.1165
Seed size (Z)	2	53.8*	8.4	25.17	0.87	0.081	5.61	321.3	150.89*	0.00193*	282.6	884.02*	0.7398**
C x Z	12	10.4	8.1	21.23*	0.64	0.076	5.11	314.9	36.52	0.00044	8.6	153.24	0.0728
S x Z	2	5.6	27.9	7.40	1.04	0.187	1.25	80.1	1.20	0.00024	51.1	137.59	0.0032
C x S x Z	12	16.1	18.1	13.08	1.00	0.123	3.65	280.9	37.92	0.00073	20.3	93.15	0.0822
Error "a"	82	16.4	15.2	8.45	0.71	0.126	2.70	285.2	40.92	0.00054	23.9	202.50	0.0719
Depth (D)	1	225183.0**	43950.7**	140.10**	0.03	2.197**	3.08	1316.5*	57.52	0.00247	4977.8**	8.03	15.8752**
C x D	6	141.7**	700.8**	20.23	2.49*	0.489*	3.66	932.7**	198.08**	0.00279**	105.1**	237.43	0.2392*
S x D	1	7.3	12.4	30.10	0.76	0.475	0.21	0.6	0.13	0.00120	29.3	16.76	0.0300
C x S x D	6	20.8	9.8	8.74	0.50	0.103	7.37*	109.7	10.12	0.00050	18.4	85.51	0.1139
Z x D	2	50.4	4.6	32.15	0.11	0.223	0.51	249.1	64.02	0.00082	90.2	241.36	0.1594
C x Z x D	12	8.9	12.7	21.16	0.55	0.084	3.17	395.4	48.42	0.00072	8.9	171.46	0.1476
S x Z x D	2	3.8	2.9	0.29	3.35	0.050	1.15	542.9	26.58	0.00061	11.1	214.38	0.1341
C x S x Z x D	12	24.7	23.1	11.92	0.88	0.106	1.84	545.7*	84.59**	0.00018	13.9	163.69	0.0696
Error "b"	84	20.2	19.9	12.81	0.74	0.208	3.23	254.5	34.19	0.00066	33.7	273.11	0.0989
Total	251												
Coefficient of variability		5.35	7.76	16.86	4.17	13.16	3.92	16.63	16.92	6.21	5.35	15.79	11.49

 * Significant at the 5% level
** Significant at the 1% level

Table 13. Mean squares from the analysis of variance for twelve traits measured on the 7 wheat cultivars grown in 2 depths at Rug Farm Pendleton, Oregon in 1974-75.

Source of Variation	d. f.	Coleoptile length	Crown depth	No. spikes per plant	No. spikelets per spike	No. kernels per spikelet	Kernel weight	Total yield per plant	Grain yield per plant	Harvest index	Height	Length of the first leaf	Width of the first leaf
Cultivar (C)	6	138.5*	468.4**	1244.2**	86.669**	5.6266**	471.15**	9807.4**	747.0**	0.03865**	3507.71**	5105.0**	8.605**
Seed source (S)	1	20.5	15.2	56.4	0.067	0.1014	1.03	414.0	64.9	0.00000	5.43	1712.8*	0.030
C x S	6	16.4	22.3	13.8	0.208	0.1531	1.60	144.1	19.1	0.00028	49.29	343.0	0.619
Seed size (Z)	2	25.9	14.8	3.5	0.622	0.0025	7.07	727.5	118.7	0.00069	21.34	7191.8*	8.787**
C x Z	12	28.6	20.4	16.9	0.713	0.1683	5.67	568.5	72.7	0.00014	26.12	378.2	0.607
S x Z	2	6.6	7.4	63.1	0.089	0.4359*	1.66	567.9	63.6	0.00035	90.29	28.2	1.531
C x S x Z	12	23.0	18.5	14.4	0.775	0.1274	3.78	431.8	79.4	0.00019	29.20	412.7	0.641
Error "a"	82	45.8	24.9	31.3	1.061	0.1082	4.68	675.8	94.8	0.00032	39.92	399.3	0.542
Depth (D)	1	110126.0**	21248.4**	72.9	71.360**	0.2640	127.57**	23567.3**	3689.9**	0.00142	522.89**	6430.6**	77.500**
C x D	6	135.0*	91.0**	82.6**	1.129	0.3617*	7.30	1006.1	76.7	0.00089	87.45	1237.5*	1.393
S x D	1	36.6	7.0	30.7	0.001	0.1548	6.25	6.6	10.8	0.00019	56.19	4.3	0.109
C x S x D	6	41.8	45.9	21.2	0.346	0.1560	7.13	1142.6	143.8	0.00101	28.46	652.3	0.687
Z x D	2	3.5	3.0	1.3	0.255	0.0517	2.02	238.7	24.9	0.00010	102.46	443.7	1.720
C x Z x D	12	14.3	12.2	32.8	1.135	0.0828	3.73	934.7	154.5	0.00033	30.83	345.9	0.770
S x Z x D	2	3.8	7.6	1.7	1.564	0.1450	11.63	13.5	16.9	0.00013	12.91	299.1	0.551
C x S x Z x D	12	33.5	12.1	23.2	0.744	0.0894	3.35	891.0	112.4	0.00066	21.15	670.8	0.590
Error "b"	84	49.1	22.0	25.3	0.896	0.1318	5.89	844.5	112.7	0.00048	42.46	509.1	0.674
Total	251												
Coefficient of variability		11.05	13.09	19.61	5.46	11.48	5.82	17.69	17.68	4.77	7.19	15.72	24.22

* Significant at the 5% level
** Significant at the 1% level

Table 14. Mean squares from the analysis of variance for twelve traits measured on the 7 wheat cultivars grown in 2 depths at Sherman Experiment Station Moro, Oregon in 1974-75.

Source of Variation	d.f.	Coleoptile length	Crown depth	No. spikes per plant	No. spikelets per spike	No. kernels per spikelet	Kernel weight	Total yield per plant	Grain yield per plant	Harvest index	Height	Length of the first leaf	Width of the first leaf
Cultivar (C)	6	288.8**	383.47**	118.67**	94.585**	4.214**	419.53**	1832.7**	262.82**	0.042**	712.00**	2031.8**	0.6805**
Seed source (S)	1	0.25	2.68	0.25	2.117	0.406	12.75	350.0*	36.19	0.0000	7.00	683.4	0.0009
C x S	6	47.42	13.21	11.28	1.609	0.341	7.75	321.5**	24.37*	0.0002	20.35	223.4	0.1722*
Seed size (Z)	2	6.05	78.36**	24.28*	1.614	0.143	3.34	666.7**	47.30*	0.0013	65.59**	4322.6**	0.4094**
C x Z	12	32.33	7.24	12.08	0.632	0.181	7.99	24.9	4.06	0.0007	10.73	327.3	0.0891
S x Z	2	20.86	18.17	3.86	1.650	0.008	0.14	0.8	5.04	0.0020	29.25	112.3	0.1743
C x S x Z	12	31.94	13.29	7.91	0.786	0.173	6.81	123.1	12.81	0.0009	14.12	358.9	0.0774
Error "a"	82	38.06	11.06	6.84	0.748	0.224	8.39	86.0	10.69	0.0012	14.93	220.1	0.0699
Depth (D)	1	187507.00**	5413.59**	666.41**	5.943**	20.450**	2076.04**	29944.5**	5227.04**	0.2833**	137.28**	12.0	0.1676
C x D	6	349.79**	325.21**	15.94*	1.617	0.411	17.35	307.2**	37.11	0.0034*	86.39**	190.9	0.0195
S x D	1	6.35	0.06	12.09	1.187	0.049	1.70	258.0	33.07	0.0003	0.57	108.0	0.0486
C x S x D	6	19.29	10.39	20.03**	1.673	0.100	7.37	191.1	14.82	0.0005	20.12	371.7	0.0300
Z x D	2	48.48	33.76	0.07	1.304	0.046	8.01	51.4	0.75	0.0006	3.94	171.8	0.0478
C x Z x D	12	45.97	11.73	5.52	1.361	0.113	7.18	70.8	6.79	0.0003	18.02	278.2	0.1071
S x Z x D	2	119.95	7.10	1.64	1.602	0.305	10.10	10.9	7.74	0.0042*	3.94	42.8	0.0329
C x S x Z x D	12	52.56	13.32	4.58	1.700	0.378	8.13	44.3	12.17	0.0013	25.19	415.2	0.1143
Error "b"	84	67.62	17.61	6.56	0.893	0.225	8.09	91.1	13.73	0.0012	15.07	366.2	0.0786
Total	251												
Coefficient of variability		8.47	7.64	18.71	5.41	23.67	10.20	21.04	25.18	12.29	6.38	18.31	12.61

* Significant at the 5% level
** Significant at the 1% level

kernels/spikelet, plant height, width of the first leaf, and total plant yield. Cultivar x depth of planting interactions were also significant for number of spikelets/spike, number of kernels/spikelet and width of the first leaf. These interactions were highly significant for total plant yield, grain yield, harvest index and plant height.

Duncan's new multiple range test comparing the performance of cultivars for five agronomic traits at each depth is shown on Table 15. Differences among cultivars for coleoptile length and crown depth were not significant under shallow seeding conditions, but were significant under deep seeding situations. Strampelli produced the longest coleoptile and the shallowest crown while Hyslop and Kirac had the shortest coleoptile and the deepest crown, respectively. The greatest total plant yield was obtained from Yamhill followed by Moro from shallow seeding, and with Hyslop followed by Moro under deep seeding. Differences in grain yield of cultivars for two depths are compared in Table 16.

Four out of seven cultivars produced higher yield when planted deeper; however none of the differences was statistically significant.

Correlation coefficients among 14 characteristics are presented in Table 17. Significant positive associations were found between depth of planting and coleoptile length, crown depth, and number of spikes per plant. Associations of coleoptile and crown depth, and of crown depth and the number of spikes per plant were positive and

Table 15. Cultivar means for five agronomical characteristics measured on the 7 wheat cultivars grown in 2 depths at Hyslop Agronomy Farm, Corvallis, Oregon in 1974-75.

Depth (cm)	Cultivar	Coleoptile length (mm)	Crown depth (mm)	Total yield per plant (g)	Grain yield per plant (g)	Height (cm)
5	Hyslop	45.00a[1]	39.00a	111.1ab	44.60a	85.72 c
	Yamhill	45.66a	38.61a	123.2a	45.18a	95.05 b
	Moro	46.00a	36.61a	113.5ab	42.13ab	112.61a
	Strampelli	45.50a	33.50a	74.6 c	31.13 bc	90.61 bc
	Sprague	46.77a	39.88a	78.3 c	31.28 bc	87.16 bc
	Kirac	46.44a	39.27a	85.1 bc	27.61 c	111.55a
	Luke	45.55a	33.61a	109.1ab	39.28abc	89.44 bc
	Average	45.84	37.21	99.2	37.32	96.02
12	Hyslop	99.27 c	60.44 bcd	129.7a	52.73a	77.88 c
	Yamhill	104.66abc	62.72 b	112.4ab	40.27 bc	83.61 bc
	Moro	109.16ab	72.00a	122.6ab	46.28ab	101.50a
	Strampelli	111.83a	46.00 d	82.1 c	32.83 c	88.77 b
	Sprague	103.77 bc	73.50a	82.4 c	29.83 c	76.11 c
	Kirac	106.55abc	75.22a	95.1 bc	30.23 c	101.00a
	Luke	104.22 bc	55.50 c	109.1abc	35.33 bc	81.05 bc
	Average	105.63	63.62	103.8	38.27	87.13

[1] DMRT; Means followed by the same letter are not significantly different at the 5% level

Table 16. Comparisons between the grain yield per plant of each cultivar under two depths of seeding.

Depth	Hyslop	Yamhill	Moro	Strampelli	Sprague	Kirac	Luke
5 cm	44.60*	45.18	42.13	31.13	31.28	27.61	39.28
12 cm	52.73	40.27	46.28	32.83	29.83	30.23	35.33

* Grams per plant

significant as well. Significant negative correlations were obtained between seeding depth and plant height and/or width of the seedling leaf. Coleoptile length was also negatively related to the number of kernels per spikelet, plant height and width of the first leaf. Similar negative correlations were also observed between crown depth and five traits (number of kernels per spikelet, plant height, harvest index, and both length and the width of the seedling leaf).

One aspect of these correlations worth noticing is the nonsignificant relationships between seed source and all the other traits and between seed size and the rest of characteristics except length and width of the first leaf. These results are different from those observed under solid seeding conditions (study 1) and indicate that the superiority of seed source and size are evident under situations where competition for water, light, and nutrient does exist (solid seeding), but not under noncompetitive conditions of space planting. Significant positive correlations between seed size and the length and the width

Table 17. Correlation coefficients between 14 traits measured on the seven wheat cultivars space-planted in 2 depths at Hyslop Agronomy Farm, Corvallis, Oregon in 1974-75.

Character	Source	Size	Coleoptile	Crown	Spikes per plant	Spikelets per spike	Kernels per spikelet	Kernel weight	Height	Grain per plant	H.I.	Length of the first leaf	Width of the first leaf
Depth	0.00	0.00	0.98**	0.85**	0.14**	0.01	-0.15	0.03	-0.36**	0.05	-0.09	-0.01	-0.60**
Seed source		-0.00	-0.00	0.01	-0.06	0.02	0.05	0.01	-0.02	-0.00	0.00	0.03	0.02
Seed size			0.01	0.01	0.08	0.04	0.00	0.06	0.11	0.09	0.08	0.16**	0.18**
Coleop. length				0.83**	0.11	-0.00	-0.13*	0.03	-0.32**	0.02	-0.09	0.01	-0.59**
Crown depth					0.17**	0.03	-0.25**	-0.03	-0.20**	0.03	-0.19**	-0.18**	-0.51**
Spikes per plant						-0.14**	-0.58**	-0.44**	-0.25**	0.36**	-0.07	-0.19**	-0.19**
Spikelets per spike							0.17**	0.35**	0.25**	0.53**	0.04	-0.03	0.02
Kernels per spikelet								0.19**	0.12	0.33**	0.45**	0.31**	0.33**
Kernel weight									0.06	0.19**	0.08	0.10	0.17**
Height										-0.05	-0.21**	-0.16**	0.21**
Grain per plant											0.36**	0.07	0.11
H. I.												0.16**	0.17**
Length of the first leaf													0.30**

 * Significant at the 5% level
** Significant at the 1% level

of first leaf agrees with the results obtained in barley by Kaufmann
and Giutard (1967).

Direct and indirect effects of seeding depth, seed source, seed
size, coleoptile length, crown depth, length and width of the first
leaf, and plant height on grain yield were determined by path
coefficient analysis (Table 18). For the convenience of discussion
these factors are called associate factors (in contrast to components
of yield, i.e. number of spikes/plant, number of spikelets/spike,
number of kernels/spikelet, and kernel weight).

Among the associate factors, crown depth showed the highest
direct effect on yield. This trait also had positive indirect effects
especially via number of spikes/plant; however total effect of crown
depth was negligible because of the negative indirect effects via other
components such as number of kernels per spikelet and kernel weight.
Coleoptile length affected the yield indirectly through crown depth,
plant height, and number of spikes per plant but its direct and total
effects were negative and small. Total effect of seeding depth on
yield was positive despite the negative direct effect. This total
effect has come about through indirect influences via crown depth,
number of spikes/plant, kernel weight and some other small positive
and a few negative effects. Length of the first leaf influenced the yield
by positive direct and total effects however the values for direct and
indirect influences were small. Width of the first leaf had the

Table 18. Path coefficient analysis of direct and indirect influences of 12 traits on grain yield per plant of seven wheat cultivars space-planted at Hyslop Agronomy Farm, Corvallis, Oregon in 1974-75.

Relationships of yield and:	Direct effect	Indirect effects via												Total (r)
		Depth	Seed source	Seed size	Coleoptile length	Crown depth	Length of the first leaf	Width of the first leaf	Height	Spikes per plant	Spikelets per spike	Kernels per spikelet	Kernel weight	
Depth	-0.1238		0.0000	-0.0000	-0.0685	0.1661	-0.0003	0.0304	0.0080	0.1457	0.0041	-0.1236	0.0109	0.0490
Seed source	0.0097	-0.0000		0.0000	0.0000	0.0019	0.0010	-0.0010	0.0004	-0.0625	0.0083	0.0412	0.0036	0.0026
Seed size	-0.0191	-0.0000	-0.0000		-0.0007	0.0019	0.0054	-0.0091	-0.0025	0.0833	0.0165	0.0000	0.0218	0.0975
Coleoptile length	-0.0699	-0.1213	-0.0000	-0.0002		0.1623	-0.0108	-0.0005	0.0132	0.1145	-0.0000	-0.1071	0.0109	-0.0089
Crown depth	0.1955	-0.1052	0.0001	-0.0002	-0.0580		-0.0061	0.0259	0.0045	0.1769	0.0124	-0.2060	-0.0109	-0.0289
Length of the first leaf	0.0339	0.0012	0.0003	-0.0031	-0.0007	-0.0352		-0.0152	0.0036	-0.1978	-0.0124	0.2554	0.0364	0.0664
Width of the first leaf	-0.0507	0.0743	0.0002	-0.0034	0.0412	-0.0977	0.0101		-0.0047	-0.1978	0.0083	0.2719	0.0619	0.1136
Height	-0.0223	0.0446	-0.0002	-0.0021	0.0224	-0.0391	0.0034	-0.0086		-0.2602	0.1033	0.0989	0.0218	-0.0381
Spikes per plant	1.0410	-0.0173	-0.0006	-0.0015	-0.0077	0.0332	-0.0064	0.0096	0.0056		-0.0579	-0.4779	-0.1602	0.3599
Spikelets per spike	0.4133	-0.0012	0.0002	-0.0008	0.0000	0.0059	-0.0010	0.0010	-0.0056	-0.1457		0.1401	0.1274	0.5336
Kernels per spikelet	0.8239	0.0186	0.0005	-0.0000	0.0091	-0.0489	0.0105	-0.0167	-0.0027	-0.6038	0.0702		0.0692	0.3299
Kernel weight	0.3640	-0.0037	0.0001	-0.0011	-0.0021	-0.0059	0.0034	0.0086	-0.0013	-0.4580	0.1447	0.1565		0.2052

$R^2 = 0.92668$
Residual = 0.07332

highest total effect on yield among the associate factors; this effect has been achieved indirectly and mainly via depth of seeding, number of kernels per spikelet and kernel weight.

At the Pendleton site deeper seeding resulted in longer coleoptiles (82.14 mm vs 40.33 mm), deeper crown (47.38 mm vs 29.01 mm), more spikes per plant (29.04 vs 27.97), higher number of spikelets per spike (19.40 vs 18.33), heavier kernels (37.9 mg vs 36.48 mg), taller plants (89.3 cm vs 86.4 cm), larger total yields, grain yields, and harvest indices (156.6 g vs 137.2 g, 58.85 g vs 51.20 g, and 0.379 vs 0.374, respectively) and more kernels per spikelet (2.88 vs 2.82). Shallow seeding produced longer and wider seedling leaves (132 mm vs 122 mm and 3.59 mm vs 2.48 mm, respectively). Differences due to the depth of seeding were significant in all but three traits (number of spikes per plant, number of kernels per spikelet and harvest index). However cultivar x depth of planting interactions were significant for coleoptile length, number of kernels per spikelet, and length of the seedling leaf and highly significant for crown depth and number of spikes per plant (Table 13).

Duncan's new multiple range test were calculated for five traits and are presented in Table 19. Coleoptile length of cultivars were not significantly different when planted either shallow or deep; however the difference is highly significant for all cultivars when compared over two depths. Crown depth of cultivars did not differ

Table 19. Cultivar means for 5 agronomic characteristics measured on the seven wheat cultivars grown in 2 depths at Rug Farm Pendleton, Oregon in 1974-75.

Depth (cm)	Cultivars	Coleoptile length (mm)	Crown depth (mm)	Total yield per plant (g)	Grain yield per plant (g)	Height (cm)
5	Hyslop	37.11a[1]	28.50a	135.5a	50.27a	78.94 c
	Yamhill	40.27a	31.44a	146.2a	53.02a	84.61 bc
	Moro	40.05a	30.88a	143.5a	53.11a	96.05ab
	Strampelli	39.72a	24.50a	127.0a	55.43a	84.55 bc
	Sprague	40.55a	31.88a	111.8a	43.16a	80.00 c
	Kirac	43.72a	29.55a	145.1a	48.21a	100.55a
	Luke	40.88a	26.33a	151.6a	55.19a	80.33 c
	Average	40.33	29.01	137.2	51.20	86.43
12	Hyslop	84.55a	50.27a	139.0a	53.57a	80.27 b
	Yamhill	84.16a	47.66ab	172.8a	63.02a	85.00 b
	Moro	83.39a	51.05a	173.7a	61.53a	100.61a
	Strampelli	82.05a	36.94 b	133.0a	59.41a	85.77 b
	Sprague	77.88a	49.72a	134.5a	52.03a	80.44 b
	Kirac	85.83a	49.33a	164.3a	56.26a	109.61a
	Luke	77.11a	46.66ab	178.9a	66.14a	83.50 b
	Average	82.14	47.38	156.6	58.85	89.31

[1]DMRT; means followed by the same letter are not significantly different at the 5% level

significantly under shallow seeding but significant differences were detected under deep seeding. Moro and Strampelli cultivars produced the deepest and shallowest crown respectively. All cultivars had deeper crowns when planted deep, but the difference between crown depth of Strampelli planted deep and shallow was very small and nonsignificant. There were no significant differences among cultivars for total yield and grain yield per plant under either sowing depths. The cultivars yielded more in terms of total or grain when planted deep than when sown shallow.

Unlike the Hyslop site, cultivars were taller under deep seeding conditions than shallow planting. This differential response over locations can be interpreted based on the differences in soil fertility and amount of rainfall between the two sites. Cultivars produced higher total yield and grain yield per plant at the Pendleton site than at the Hyslop site indicating the higher soil fertility at the former site. The amount of rainfall during the growth period was, however, much lower at the Pendleton site; therefore deep seeded plants had a better chance of exploiting the available moisture and producing taller plants than shallow seeded ones. At the Hyslop site, moisture was not a limiting factor; hence all cultivars performed to their full capacity for plant height and hence the shallow seeded plants were taller. As a matter of fact, there would not be any difference between the height of cultivars seeded shallow or deep at the Hyslop site if plant height was

measured from the seeding site rather than the soil surface. This implies the existence of a compensation effect on the length of internodes. When the first internode is longer (due to deep seeding), the other internodes become comparatively shorter so that under no moisture stress the actual height of the plant (from the place that seed is sown to the tip of the plant) becomes independent of seeding depth.

Correlation coefficients among 14 characteristics are given in Table 20. Associations between depth of seeding and five other traits, i.e. coleoptile length, crown depth, number of spikelets/ spike, kernel weight, and grain yield per plant were all positive and highly significant. Comparing these results with those presented in Table 17 for the Hyslop site, it is evident that at Pendleton, plants seeded deeper produced more spikelets, heavier kernels and ultimately higher yields than plants seeded shallow; while at the Hyslop site such differences were not noted. This can be attributed to the differences in amount of rainfall at the two sites. At the Hyslop site moisture was abundant throughout the growing season while at the Pendleton site with much less rainfall, the moisture became less available at the late stages of growth; therefore the plants seeded deeper apparently had deeper or more developed root systems than shallow seeded plants and had a better opportunity for moisture utilization.

Table 20. Correlation coefficients between 14 traits measured on the seven wheat cultivars space-planted in 2 depths at Rug Farm, Pendleton, Oregon in 1974-75.

Character	Source	Size	Coleoptile	Crown	Spikes per plant	Spikelets per spike	Kernels per spikelet	Kernel weight	Height	Grain per plant	H. I.	Length of the first leaf	Width of the first leaf
Depth	0.000	0.000	0.953**	0.844**	0.071	0.297**	0.064	0.175**	0.129*	0.333**	0.065	-0.194**	-0.497*
Seed source		-0.000	-0.013	0.023	-0.063	-0.009	0.039	-0.016	0.013	-0.044	-0.004	0.100	0.010
Seed size			0.020	0.010	0.012	0.035	0.008	0.051	0.036	0.066	-0.013	0.280**	0.235**
Coleop. length				0.814**	0.032	0.309**	0.057	0.209**	0.176**	0.299**	0.015	-0.172**	-0.468**
Crown depth					0.089	0.373**	-0.060	0.070	0.166**	0.239**	-0.153**	-0.149**	-0.472**
Spikes per plant						-0.412**	-0.482**	-0.444**	-0.003	0.372**	-0.181**	-0.233**	-0.224**
Spikelets per spike							0.165	0.345**	0.266**	0.266**	-0.197**	0.098	0.038
Kernels per spikelet								0.095	-0.069	0.362**	0.383**	0.151**	0.051
Kernel weight									0.296**	0.202**	0.131*	0.302**	0.295**
Height										0.187**	-0.350**	-0.058	0.011
Grain per plant											0.081	0.030	-0.072
H. I.												0.220**	0.107
Lengths of the first leaf													0.640**

* Significant at the 5% level
** Significant at the 1% level

Coleoptile length was positively and significantly related to

five characteristics, namely: crown depth, number of spikelets per

spike, kernel weight, height, and grain per plant. Crown depth was

significantly correlated to the number of spikelets per spike, plant

height, grain yield, harvest index, length of the seedling leaf and

width of the seedling leaf; however the last three correlations were

negative. Seed source and seed size responded the same way as they

did at the Hyslop site, the only significant correlations being those of

seed size and length and width of the first leaf.

To gain a better insight into the relationships of these traits and

yield, path coefficient analyses were performed and the results are

shown in Table 21. The striking difference between this table and that

of the Hyslop site is the increase in the magnitude of total effects

of associate factors and the decrease in the total effects of yield com-

ponents. None of the associate factors had a high direct effect on

yield but the total effect of planting depth was higher than the effects

of kernel weight or the number of spikelets per spike. This total

effect was achieved mainly through the number of spikelets per spike,

number of kernels per spiklet and kernel weight. Direct, indirect,

and total effects of seed source and seed size were small compared

to other associate factors indicating that under space planting the

effects of these two factors are negligible. Both coleoptile length

and crown depth had a high total effect on yield accomplished mainly

Table 21. Path coefficient analysis of direct and indirect influences of 12 traits on grain yield per plant of the seven wheat cultivars space-planted at Rug Farm, Pendleton, Oregon in 1974-75.

Relationships of yield and:	Direct effect	Indirect effects via: Depth	Seed source	Seed size	Coleoptile length	Crown depth	Length of first leaf	Width of first leaf	Height	Spikes per plant	Spikelets per spike	Kernels per spikelet	Kernel weight	Total (r)
Depth of planting	0.0167		0.0000	0.0000	-0.0643	-0.0035	0.0015	0.0226	-0.0025	0.0831	0.1371	0.0516	0.0907	0.3330
Seed source	0.0104	0.0000		-0.0000	0.0009	-0.0001	0.0008	-0.0000	-0.0003	-0.0738	-0.0042	0.0314	-0.0083	-0.0432
Seed size	0.0184	0.0000	0.0000		-0.0013	-0.0000	-0.0022	-0.0107	-0.0007	0.0141	0.0162	0.0064	0.0264	0.0666
Coleoptile length	-0.0675	0.0159	-0.0001	0.0004		-0.0033	0.0036	0.0078	-0.0035	0.0375	0.1427	0.0459	0.1083	0.2877
Crown depth	-0.0041	0.0141	0.0002	0.0002	-0.0549		0.0012	0.0214	-0.0032	0.1042	0.1722	-0.0483	0.0564	0.2594
Length of the first leaf	-0.0077	-0.0032	0.0010	0.0052	0.0116	0.0006		-0.0291	0.0011	-0.2728	0.0452	0.1216	0.2432	0.1167
Width of the first leaf	-0.0454	-0.0083	0.0001	0.0043	0.0316	0.0019	-0.0049		-0.0002	-0.2623	0.0175	0.0411	0.2376	0.0130
Height	-0.0196	0.0022	0.0001	0.0007	-0.0119	-0.0007	0.0004	-0.0005		-0.0035	0.1228	-0.0556	0.2384	0.2728
Spikes per plant	1.1708	0.0012	-0.0007	0.0002	-0.0022	-0.0003	0.0018	0.0102	0.0001		-0.1902	-0.3882	-0.2302	0.3725
Spikelets per spike	0.4617	0.0050	-0.0001	0.0006	-0.0209	-0.0015	-0.0008	-0.0017	-0.0005	-0.4824		0.1329	0.1788	0.2711
Kernels per spikelet	0.8054	0.0011	0.0004	0.0001	-0.0038	0.0003	-0.0012	-0.0023	0.0014	-0.5643	0.0762	.	0.0493	0.3626
Kernel weight	0.5184	0.0029	-0.0002	0.0009	-0.0141	-0.0003	-0.0023	0.0134	-0.0058	-0.5198	0.1593	0.0765		0.2289

R^2 = 0.939892
Residual = 0.060108

due to number of spikes per plant, number of spikelet per spike and kernel weight.

Kernel weight was also the pathway through which the indirect effects of seedling leaf length and width on grain yield were exerted. Effect of the first leaf (which appears at very early stages of growth and deteriorates soon after) on grain yield via kernel weight (which is the last component of yield to develop) deserves more attention. Similar results have been reported by Kaufmann and Guitard (1967) in barley. It is hard to conceive that the seedling leaf increases kernel weight directly especially when noting that deep planting produced narrower and shorter leaves but higher kernel weight than shallow planting. Therefore, this effect seems to be an artifact resulting from other associations. It is also interesting to note that the effects of leaf length and width on yield via the number of spikes per plant are about the same magnitude as the effects via kernel weight but with opposite signs.

Climatic conditions at the Moro site were characterized by good moisture content in the soil at sowing time, but much of the soil moisture was lost by mid and late spring. Under these circumstances deep seeding resulted in highly significant differences in all the traits measured except the length and the width of seedling leaf (Table 14). Plants grown from deep-sown seeds were superior to those grown from shallow-sown seeds in coleoptile length (94.42 mm

vs 42.87 mm), crown depth (48.07 mm vs 38.80 mm), number of

spikes per plant (15.59 vs 12.34), number of spikelets/spike (16.13

vs 15.82), number of kernels/spikelet (2.29 vs 1.72), kernel weight

(31.21 g vs 25.74 g), total yield per plant (54.95 g vs 33.15 g),

grain yield per plant (17.54 g vs 8.43 g), harvest index (0.317

vs 0.250), plant height (61.27 cm vs 59.80 cm) and width of the first

leaf (2.12 mm vs 2.07 mm). Shallow seeded plants were superior

to deep seeded ones only for the length of the first leaf (8.12 vs

8.08), but the difference was negligible.

Significant cultivar x depth of seeding interactions for coleoptile

length, crown depth, number of spikes per plant, total yield per

plant, harvest index and height imply that the cultivars responded

differently to these traits when planting depth varied. These

differences were studied for five characteristics using the Duncan

new multiple range test and the results are summarized in Table 22.

Results are analogous to those obtained at the Hyslop site for coleoptile

length and crown depth, i.e. no significant differences between culti-

vars when planted shallow but differential varietal responses under deep

seeding conditions. The cultivar Moro produced the longest coleoptile

followed by Yamhill and Hyslop. Kirac crowned deeper than other

cultivars, but the differences were only significant when this cultivar

was compared to Luke or Strampelli. All cultivars, except

Strampelli crowned deeper when planted deeper. There was no

Table 22. Cultivar means for five agronomic traits measured on the seven wheat cultivars grown in 2 depths at Sherman Experiment Station, Moro, Oregon in 1974-75.

Depth (cm)	Cultivars	Coleoptile length (mm)	Crown depth (mm)	Total yield per plant (g)	Grain yield per plant (g)	Height (cm)
5	Hyslop	43.50a[1]	35.33a	37.72a	9.86ab	57.05 b
	Yamhill	43.22a	36.27a	41.27a	12.00a	56.88 b
	Moro	42.88a	39.88a	35.55a	9.26ab	60.77ab
	Strampelli	40.05a	38.00a	28.05a	8.37ab	61.88ab
	Sprague	43.77a	40.44a	24.16a	5.58 b	56.44 b
	Kirac	41.77a	41.11a	36.55a	8.36ab	65.83a
	Luke	44.88a	40.55a	28.72a	5.55 b	55.72 b
	Average	42.87	38.80	33.15	8.43	59.80
12	Hyslop	100.83ab	51.94a	58.50abc	18.67ab	59.83 bc
	Yamhill	102.50ab	47.00ab	68.94a	22.40a	57.61 c
	Moro	104.78a	52.77a	56.11abc	18.75ab	64.88ab
	Strampelli	94.50abc	37.88 c	49.83 bc	19.02ab	62.94 bc
	Sprague	91.83 bc	51.05a	40.50 c	11.78 c	56.90 c
	Kirac	98.27abc	53.11a	51.05abc	15.02 bc	71.88a
	Luke	89.27 c	42.72 bc	59.72ab	17.11abc	58.83 bc
	Average	94.42	48.07	54.95	17.54	61.27

[1]DMRT; Means followed by the same letter are not significantly different at the 5% level

difference between depth of the crown of Strampelli planted deep

or shallow. These results agree with those presented by Webbe

and Stephens (1936) and Kail et al. (1972) showing the differential

varietal responses for crown depth. When planted shallow Yamhill

produced the highest total plant yield and grain yield but the

total plant yield was not significantly better than other cultivars

indicating the capability of this cultivar to convert higher portions

of total dry matter to grain (high harvest index). This cultivar

produced the highest total and grain yield/plant under deep seeding

conditions too with even more striking differences than in shallow

seeding. When cultivars are compared for two depths, grain and

total yield were always higher under deep seeding and the differ-

ences were highly significant. Comparing these results with those

from the Hyslop and Pendleton sites, it becomes clear that as the

moisture stress increases the superiority of deep seeding becomes

more evident, and since deep planting results in deeper crown, this is

an indirect evidence of the importance of deeper crowns over shallow

crowns. Additional information for this statement can be obtained

through calculation of correlation coefficients as presented in Table

23.

Highly significant and positive correlations were obtained

between sowing depth and seven agronomic traits (coleoptile length,

crown depth, number of spikes per plant, number of kernels per

Table 23. Correlation coefficients between 14 traits measured on the seven wheat cultivars space-planted in 2 depths at Sherman Experiment Station Moro, Oregon in 1974-75.

Character	Seed Source	Seed Size	Coleoptile length	Crown depth	Spikes per plant	Spikelets per spike	Kernels per spikelet	Kernel weight	Height	Grain per plant	H. I.	Length of the first leaf	Width of the first leaf
Depth	0.000	0.000	0.959**	0.642**	0.449**	0.085	0.451**	0.553**	0.125	0.715**	0.580**	-0.011	0.084
Seed source		-0.000	-0.001	0.014	-0.009	-0.051	0.064	0.043	0.028	0.059	0.009	-0.086	-0.006
Seed size			-0.008	0.042	0.116	0.050	0.045	0.030	0.111	0.095	0.003	0.302**	0.122
Coleop. length				0.671**	0.411**	0.158**	0.466**	0.559**	0.114	0.736**	0.591**	-0.030	0.092
Crown depth					0.389**	0.170**	0.068	0.177**	0.164**	0.369**	0.216**	-0.007	-0.040
Spikes per plant						-0.101	-0.133*	0.168**	0.296**	0.438**	0.107	0.153**	0.008
Spikelets per spike							0.098	0.124	0.006	0.291**	0.188**	0.055	0.232**
Kernels per spikelet								0.402**	0.066	0.695**	0.658**	-0.038	0.049
Kernel weight									0.149**	0.713**	0.722**	0.045	0.230**
Height										0.201**	0.227**	0.253**	0.022
Grain per plant											0.737**	0.052	0.160**
H. I.												-0.033	0.117
Length of the first leaf													0.139**

* Significant at the 5% level
** Significant at the 1% level

spikelet, kernel weight, grain yield per plant and harvest index).

Similar relationships existed between coleoptile length and seven

other traits (crown depth, number of spikes/plant, number of

spikelets/spike, number of kernels per spikelet, kernel weight,

grain yield, and harvest index). Correlations between crown depth

and spikes/plant, spikelets/spike, kernel weight, grain yield,

harvest index and plant height were also positive and highly signifi-

cant. The effects of seed source and seed size were essentially the

same as at the other two sites showing that under noncompetitive con-

ditions these traits are not of value for higher yield. Correlations

between the length of the seedling leaf and seed size and number of

spikes/plant were positive and highly significant. Associations

between width of the seedling leaf and kernel weight and/or grain

yield per plant were also positive and significant at the 1% level.

It seems that as the moisture stress increases these two traits

become more important in determining the final yield. More re-

search is needed to establish the importance of these traits but if

their effects proved to be important, they provide a practical and

easy criterion for selection in populations for dry land conditions.

Response of the cultivar Strampelli in terms of total yield and grain

yield is worth more consideration. This cultivar crowned at the

same depth regardless of the planting depth; however its total yield

and grain yield per plant were much higher under deep seeding

than under shallow seeding (49.83 g/plant vs 28.05 g/plant and 19.02 g/plant vs 8.37 g/plant respectively). Increase in yield in this case can not be attributed to the crown depth. The most likely cause of yield superiority is the activity of primary roots which are formed at the planting site and apparently stay functional throughout the life of the plant.

Better assessment of the importance of different traits on grain yield can be obtained by a path coefficient analysis as shown in Table 24. Comparing this table with those calculated for the Pendleton and Hyslop sites it is evident that as the moisture stress increases, the importance of associate factors in relation to the main yield component factors increases. At the highly stressed site of Moro the total effect of planting depth and coleoptile length exceed the total effect of any other trait including the main yield components.

Depth of seeding had a negative direct effect on yield but the total effect of this factor became highly positive because of the indirect effects via coleoptile length, crown depth, number of spikes/plant, number of spikelets/spike, number of kernels/spikelet and kernel weight. The direct effect of coleoptile length was positive. This trait affected the yield indirectly through crown depth, number of spikes/plant, number of spikelets/spike, number of kernels/spikelet and kernel weight. Coleoptile length had the highest positive total effect on grain yield; however, it should also be noted that the

Table 24. Path coefficient analys: of direct and indirect influences of 12 traits on grain yield per plant of the seven wheat cultivars space-planted at Sherman Experiment Station Moro, Oregon in 1974-75.

Relationships of yield and:	Direct effect	Indirect effects via:												Total (r)
		Depth of sowing	Seed source	Seed size	Coleoptile length	Crown depth	Length of first leaf	Width of first leaf	Height	Spikes per plant	Spikelets per spike	Kernels per spikelet	Kernel weight	
Depth of sowing	-0.1394		0.0000	-0.0000	0.1194	0.0317	0.0001	-0.0005	-0.0049	0.2166	0.0189	0.2665	0.2058	0.7142
Seed source	0.0207	-0.0000		0.0000	-0.0001	0.0007	0.0011	0.0000	-0.0011	-0.0043	-0.0114	0.0378	0.0160	0.0594
Seed size	-0.0018	-0.0000	-0.0000		-0.0010	0.0021	-0.0039	-0.0007	-0.0043	0.0560	0.0111	0.0266	0.0012	0.0853
Coleoptile length	0.1245	-0.1337	-0.0000	0.0000		0.0331	0.0004	-0.0005	-0.0044	0.1983	0.0352	0.2753	. 0.2080	0.7362
Crown depth	0.0494	-0.0895	0.0003	-0.0001	0.0835		0.0001	0.0002	-0.0064	0.1877	0.0379	0.0402	0.0659	0.3692
Length of the first leaf	-0.0129	0.0015	-0.0018	-0.0005	-0.0037	-0.0003		-0.0008	-0.0098	0.0738	0.0122	-0.0225	0.0167	0.0519
Width of the first leaf	-0.0055	-0.0117	-0.0001	-0.0002	0.0115	-0.0020	-0.0018		-0.0009	0.0039	0.0517	0.0289	0.0856	0.1594
Height	-0.0389	-0.0174	0.0006	-0.0002	0.0142	0.0081	-0.0033	-0.0001		0.1428	0.0013	0.0390	0.0554	0.2015
Spikes per plant	0.4825	-0.0626	-0.0002	-0.0002	0.0512	0.0192	-0.0020	-0.0000	-0.0115		-0.0225	-0.0786	0.0625	0.4378
Spikelets per spike	0.2229	-0.0118	-0.0011	-0.0001	0.0197	0.0084	-0.0007	-0.0013	-0.0002	-0.0487		0.0579	0.0461	0.2911
Kernels per spikelet	0.5908	-0.0629	0.0013	-0.0001	0.0580	0.0034	0.0005	-0.0003	-0.0026	-0.0642	0.0218		0.1496	0.6953
Kernel weight	0.3721	-0.0771	0.0009	-0.0001	0.0696	0.0087	-0.0006	-0.0013	-0.0058	0.0811	0.0027	0.2375		0.6877

R^2 = 0.954098
Residual = 0.045902

indirect effects of seeding depth and coleoptile length are almost

identical through all the other traits. This may imply that the total

effect of coleoptile length on yield may be an artifact imposed by

the planting depth especially considering that the coleoptile length

increases almost proportionally to the seeding depth. The increase in

the crown depth due to deep seeding on the other hand is not

proportional to the increase in depth of planting. As a matter of fact,

average crown depth of cultivars increased only 9.27 mm for 70 mm

increase in sowing depth; therefore the direct and indirect effects

of this trait on grain yield are less dependent on depth of seeding

and hence they are more realistic effects than those of coleoptile

length. Crown depth had a positive direct influence on yield but

its effect was enhanced further due to the indirect effects through

coleoptile length, number of spikelets per spike, number of kernels

per spikelet, kernel weight and especially via number of spikes per

plant. Seed source and seed size had neither a large direct influence

nor great indirect influences on yield confirming the discussion

presented earlier about the importance of these traits under space

planting conditions.

Direct effect of the length of the seedling leaf on yield was

small and negative; however the total effect of this trait was positive.

Width of the seedling leaf had a much higher total effect on yield than

the length of the same leaf. This total effect was accomplished

mainly through number of spikelets per spike, number of kernels per spikelet and most importantly, kernel weight. Effects of the length and width of the seedling leaf at the Moro site are similar to those observed at Pendleton and therefore confirm the necessity of further research for these traits.

Comparing the crown depth of cultivars over three locations it is evident that cultivars did not crown at the same depth. This is in agreement with the results presented by Kail et al. (1972) and can be attributed to the differences in temperature regimes of three sites between planting and crown initiation. At the Moro site, deep planted seeds which were placed in the moist soil emerged faster than shallow planted ones and therefore encountered higher temperatures during crown initiation, hence they crowned comparatively shallower than at other sites. Shallow-seeded plants at this site did not germin-ate until late fall and therefore encountered lower temperatures and crowned relatively deeper. As a result, the difference between the depth of the crowns of shallow and deep seeded plants decreased at this site compared to the Hyslop and Pendleton sites. Actually at the Moro site, Strampelli, which was the only nonresponsive cultivar to the sowing depth, crowned shallower when planted deeper than when it was seeded shallower. These findings are also in accordance with those reported by Kail et al. (1972).

Winter survival of cultivars was not measured in this study but regardless of winter survival it was shown that the induction of the deep crown causes the better yielding ability of all cultivars especially under moisture stressed conditions. This is contrary to results reported by Ashraf and Taylor (1974) but agrees with the discussion presented by Webbe and Stephens (1936) indicating that survival ability of hardy cultivars and their higher yield is related to their ability to crown deeper than non-hardy cultivars.

The correlation coefficient between plant height and coleoptile length was influenced greatly by environment. It was negative and highly significant at the Hyslop site, positive and highly significant at Pendleton site, and nonsignificant at the Moro location. This can be explained by differences in the expression of plant height at the three locations. Plant height was reduced at Pendleton and Moro while coleoptile length was fully expressed over all locations. Since the best expression of plant height was obtained at Hyslop, the negative correlation is the most likely index relating the gene actions governing the performance of these traits. Low and nonsignificant correlations between plant height and coleoptile length were reported by Chowdhery and Allan (1963), Parodi, Patterson and Hyquist (1970), and Scarascia and Porceddu (1973), but significant negative correlations have not been reported so far. The negative correlations can be explained on three bases. First, the results presented by

various workers have been based on the correlation of greenhouse or

growth chamber data for coleoptile length with either greenhouse or

field data for plant height; therefore the field environmental conditions

were not sampled for coleoptile length. Second, plant height in those

experiments was measured under moisture stress conditions; there-

fore the full potential of cultivars was not revealed. Third, the

negative associations in the present study are due to the inclusion of

certain semidwarf cultivars (Hyslop, Luke, Sprague) which were

preselected for dryland cultivation and therefore have long coleoptiles.

B. Inheritance of Coleoptile Length and Crown Depth

Information obtained from the first part of this study indicated

that there is no difference between coleoptile length and crown depth

of different cultivars when planted shallow. Therefore, to study the

inheritance of these traits only the data obtained from deep-seeded

plots were used.

Heritability in the narrow sense was estimated for each location

by regression of F_1's on midparents. Data were further combined

over all locations and H_{ns} were calculated in the combined data.

Phenotypic correlation coefficients between midparents and F_1's

were also calculated for each location and over all locations. Results

are presented on Table 25.

Table 25. Parent-progeny regression and correlation coefficients for coleoptile length and crown depth of six wheat cultivars and their F_1 diallel crosses planted at three locations, in Oregon in 1974-75.

Location:	Hyslop		Pendleton		Moro		All sites combined	
Character	Regression Coefficient	Correlation Coefficient	Regression Coefficient	Correlation Coefficient	Regression Coefficient	Correlation Coefficient	Regression Coefficient	Correlation Coefficient
Coleoptile length	-0.0534	-0.0360	0.14140	0.1010	0.1320	0.1485	0.7846**	0.7169**
Crown depth	0.7198**	0.7030**	0.7019**	0.7050**	0.3580*	0.5642**	0.7740**	0.8141**

* Significant at the 5% level
** Significant at the 1% level

When data were analyzed for each location separately, coleoptile length had small and nonsignificant H_{ns} and correlation coefficient values implying the genes governing the inheritance of this trait do not act additively. When data were combined over three locations results differed considerably; both H_{ns} and correlation coefficient values increased dramatically and became highly significant indicating that genes behave largely in an additive manner.

As it was mentioned previously, environmental conditions during early stages of growth were favorable at all sites, allowing the coleoptile of cultivars and crosses to develop to their full potential. Therefore the failure of the data from each location to predict the same gene actions as the combined data can be attributed to the small number of samples to account for all the genes involved in governing the inheritance of this trait. Once the data were combined, sufficient samples became apparently available. The inheritance of the trait, therefore, seems to be polygenic with most of the genes behaving additively. This conclusion is also supported by the almost identical average length of midparents and F_1's (97.07 mm vs 97.42 mm) and is in accordance with the results reported by Allan, et al. (1961) and Parodi, et al. (1970).

Correlation and regression coefficients for crown depth were about the same at Hyslop and Pendleton site but smaller at the Moro site. Nevertheless all values were highly significant in all locations and in

combined data indicating the additive gene action. Comparing the

crown depth of F_1's with those of midparent as in the following table

provides additional support for this conclusion.

Table 26. Comparison of average crown depth (mm) of midparents and F_1's in three locations and combined over locations.

Generation	Location			All locations combined
	Hyslop	Pendleton	Moro	
MP	66.08	46.93	50.48	54.50
F_1	63.02	46.04	52.73	53.95

Detection of the same mode of gene action in each location and

in the combined data may imply that the number of genes involved

in conditioning the inheritance of crown depth is fewer than those

governing the inheritance of coleoptile length. This conclusion

however needs further confirmation through studying the F_2 popula-

tions.

Based on the results presented in this study the following

conclusions can be drawn:

1. All cultivars crown at about the same depth and their

coleoptiles are about the same length when planted shallow.

2. Coleoptile length increases almost proportionally to the

increase in sowing depth however varietal differences do exist and

can be observed under a deep seeding situation.

3. The increase in crown depth of cultivars is not proportional to the increase in planting depth; furthermore, varietal responses differ: cultivar Strampelli crowns at about the same depth regardless of the planting depth.

4. Responses of cultivars to planting depth in terms of total yield and grain yield is highly influenced by environmental conditions. As the moisture stress increases, differences between the yield of shallow seeded and deep seeded cultivars increases.

5. Direct and indirect effects of coleoptile length and crown depth on yield increases as the moisture becomes less available.

6. The influence of coleoptile length on yield can be attributed to the effect of planting depth, but the effects of crown depth are probably real effects independent of seeding depth.

7. Deep crowned plants produced higher yield than shallow crowned ones under moisture stressed conditions. This increase in yield was cultivar-independent, but as the climatic conditions become more favorable differential varietal responses become more evident.

8. Length and width of the first leaf (seeding leaf) show an indirect effect on yield especially under less favorable climatic conditions. More research is needed to clarify the importance of these traits.

9. Seed source and seed size have negligible effects on yield under space planting conditions regardless of the degree of environmental stress.

10. Genes governing the inheritance of coleoptile length and crown depth appear to act additively therefore selection for both traits is possible.

Study 3. Relationships Between Adenosine Phosphates and Energy Charge, and Stand Establishment and Yield

Differential varietal responses to seed source and seed size and relationships of these components of seed quality to stand establishment and yield were demonstrated in study 1. It was also shown that coleoptile length and crown depth of cultivars affect the grain yield especially under limited moisture condition. Effects of these factors were manifested through the direct and indirect influences on grain yield by affecting the growth of the roots and tops of the plants.

Differential growth potential of cultivars at early stages of growth was attributed to the differences in efficiency of the mitochondrial oxidative phosphorylation of cultivars (McDaniel, 1969 and 1973b, McDaniel and Sarkisian, 1966). Differential yield potential of cultivars was explained based on the differences in

synthesis and utilization of adenosine triphosphate of cultiv rs

(Ching and Kronstad, 1972).

The purpose of this study was to determine whether differences

in varietal performance in the field can be explained by variations

in ATP level of the cultivars. It was also intended to investigate

the possibilities of using this biochemical property as a tool to screen

or breed cultivars with high growth potential. Experiments consisted

of three parts and the results are discussed for each part separately.

Part A. Effect of Temperature and Imbilition Periods on Biochemical Properties of Wheat Seeds

Ching and Kronstad (1972) demonstrated that under unfavorable

climatic conditions in Eastern Oregon, the wheat cultivar Yamhill

outyielded cultivar Hyslop while the reverse took place when these

two cultivars were planted in Western Oregon with favorable climatic

conditions and high fertility. The superiority of Yamhill in Eastern

Oregon was attributed to the ability of this cultivar to produce and utilize

more ATP at early stages of growth than Hyslop resulting in better

growth under unfavorable conditions which ultimately was translated

to higher yield. It is generally believed that the club wheat Moro, a

widely adapted cultivar in Eastern Oregon, produces better stand

than the other cultivars if it is planted early in the season, but if the

sowing is delayed, this superiority vanishes.

If ATP content of the seed is the prime cause of better stand, one should be able to demonstrate differential varietal responses in ATP content under situations similar to those encountered in the field under normal seeding conditions. Furthermore, it should be possible to show that the difference in ATP content of the cultivars decreases as the planting is delayed. The purpose of this study was to investigate this problem by subjecting the seeds of various cultivars to two different temperatures and three different periods of imbibition. For the convenience of discussion, temperature x imbibition period is referred to as temperature regime in the rest of this section.

Adenosine triphosphate (ATP), adenosine diphosphate (ADP), and adenosine monophosphate (AMP) were measured in a laboratory. Total adenosine phosphates (AP), energy charge (EC), and ATP per miligram of seed weight (ATP/mg) were calculated. To be able to compare these biochemical properties under different temperatures and various lengths of imbibition, ATP, ATP/mg and EC were converted to ATP/heat unit, EC/heat unit and ATP/mg/heat unit. Heat unit as used in this experiment is defined as: Imbibition period (days) x (temperature during imbibition-base). Base in this calculation was taken as 4.45° C, below which presumably there is negligible growth. Mean squares from the analysis of variance and means

of cultivars and temperature regimes for seven traits are given in Tables 27, 28 and 29.

Significant differences were found among the cultivars and temperature regimes for all the traits studied. Cultivar by temperature interactions were also significant in every case. Duncan's new multiple range test revealed no significant differences between cultivars for ATP content of the seeds per unit of seed weight (ATP/mg), but it showed significant differences for all the other traits. Cultivar Yamhill had the highest ATP and total adenosine phosphate (AP) content as well as ATP/heat unit but the highest EC and EC/heat unit were observed in Strampelli and Sprague respectively, both with rather low ATP content.

Differences between various temperature regimes were found to be significant in all the traits, however, differences between two temperature regimes namely 192 hours and 10° C (equal to 44.4 heat units) and 72 hours, 20° C (equal to 46.65 heat units) were not significant in any trait except EC/heat unit; nevertheless, the former temperature regime produced higher ATP, EC, ATP/mg, ATP/heat unit, EC/heat unit and ATP/mg/heat unit than the latter regime. This may imply the time dependence of these biochemical activities, i. e. given about the equal heat unit the activities are accomplished better if that heat unit is obtained during longer periods of time (comparable to late seeding) than if it is obtained during short

Table 27. Mean squares from the analysis of variance for seven biochemical properties of seven wheat cultivars grown under five temperature regimes.

Source of variation	d. f.	ATP	AP	EC	ATP/mg	ATP/heat unit	EC/heat unit	ATP/mg/heat unit
Replication	3	26. 31	78. 6	0. 0008	0. 0314	0. 0219	0. 000001	0. 0000194
Temperature	4	898. 09**	2082. 6**	0. 0097**	0. 5157**	0. 0293**	0. 005034**	0. 0000081**
Cultivar	6	19. 47**	64. 5**	0. 0056**	0. 0107**	0. 0171**	0. 000011**	0. 0000168**
Temp x Cult.	24	8. 11**	19. 7**	0. 0028**	0. 0080**	0. 0074**	0. 000007**	0. 0000102**
Error	102	2. 00	5. 0	0. 0006	0. 0019	0. 0014	0. 000001	0. 0000013
Total	139							
Coefficient of variability		12. 24	12. 25	3. 25	15. 26	12. 58	3. 40	14. 87

 * Significant at the 5% level
** Significant at the 1% level

Table 28. Cultivar means for seven biochemical traits measured under five temperature regimes.

Cultivars	ATP	AP	EC	ATP/mg	ATP/heat unit	EC/heat unit	ATP/mg/ heat unit
Hyslop	10.71 b[1]	17.10 bc	0.727ab	0.275	0.263 bc	0.0236 d	0.0068 b
Yamhill	12.98a	21.03a	0.737ab	0.309a	0.330a	0.241 b	0.0077ab
Moro	12.24ab	18.86abc	0.755ab	0.331a	0.322ab	0.0249 b	0.0091a
Strampelli	11.17ab	17.26 bc	0.763a	0.270a	0.284abc	0.0250 b	0.0068 b
Sprague	10.96ab	17.20 bc	0.753ab	0.287a	0.306abc	0.052a	0.0083ab
Kirac	12.44ab	20.22ab	0.720 b	0.276a	0.322ab	0.0236 c	0.0071 b
Luke	10.39 b	16.26 c	0.726ab	0.270a	0.259 c	0.0234 c	0.0070 b
Mean	11.56	18.28	0.740	0.288	0.298	0.0234	0.0075

[1] DMR T; means followed by the same letter in the same column are not significantly different at the 5% level.

Table 29. Temperature means for seven biochemical traits measured on the seven wheat cultivars.

Temperature Regime	ATP (n mole/seedling)	AP (n mole/seedling)	EC	ATP/mg (n mole)	ATP/heat (n mole/seedling)	EC/heat Unit	ATP/mg/heat unit (n mole)
72 hours, 10° C	4.46 d[1]	7.35 c	0.720 b	0.121 c	0.267 c	0.0432a	0.0072a
96 hours, 10° C	6.53 c	10.57 b	0.741ab	0.170 c	0.294ab	0.0334 b	0.0076a
192 hours, 10° C	15.49ab	23.70a	0.755ab	0.373ab	0.349a	0.0170 c	0.0084a
72 hours, 20° C	14.29 b	23.90a	0.722 b	0.345 b	0.306ab	0.0155 d	0.0074a
96 hours, 20° C	17.01a	25.86a	0.761a	0.434a	0.273 bc	0.0122 e	0.0070a
Mean	11.56	18.28	0.740	0.288	0.298	0.0243	0.0075

[1]DMRT; Means in the same column followed by the same letter are not significantly different at the 5% level.

periods of time (early seeding). However this may also indicate the accumulation of ATP, ADP, and AMP; i.e., under low temperature the rate of synthesis is higher than the rate of utilization. The largest ATP, AP, EC and ATP/mg values were obtained under conditions of 96 hour germination in 20° C (equal to 62.2 heat units) but the amount of ATP and ATP/mg produced per each heat unit received were highest under 192 hours, 10° C regime.

Significance of the cultivar by temperature regime interactions could provide insight into the differential varietal responses. Differences in ATP content of cultivars are delineated in Figure 11. Generally ATP content of all cultivars increases for the first three temperature regimes, but they decrease in the 4th regime and again increase in the 5th temperature regime. Yamhill is the only one cultivar with a different pattern of response where its ATP content increases consistently. Differential varietal responses are evident under all the temperatures used for this study but the difference between lowest and highest cultivars in ATP content is greatest under 96 hours, 20° C followed by 72 hours, 20° C and it decreases under the other regimes. This indicates that the procedure that is most widely used during imbibition (72-96 hours, 20° C) is the most suitable treatment to differentiate the cultivars. Yamhill had higher ATP than Hyslop under all situations, however, its superiority was negligible over the first three regimes. This cultivar also was superior to all the other cultivars in the last two regimes. Kirac,
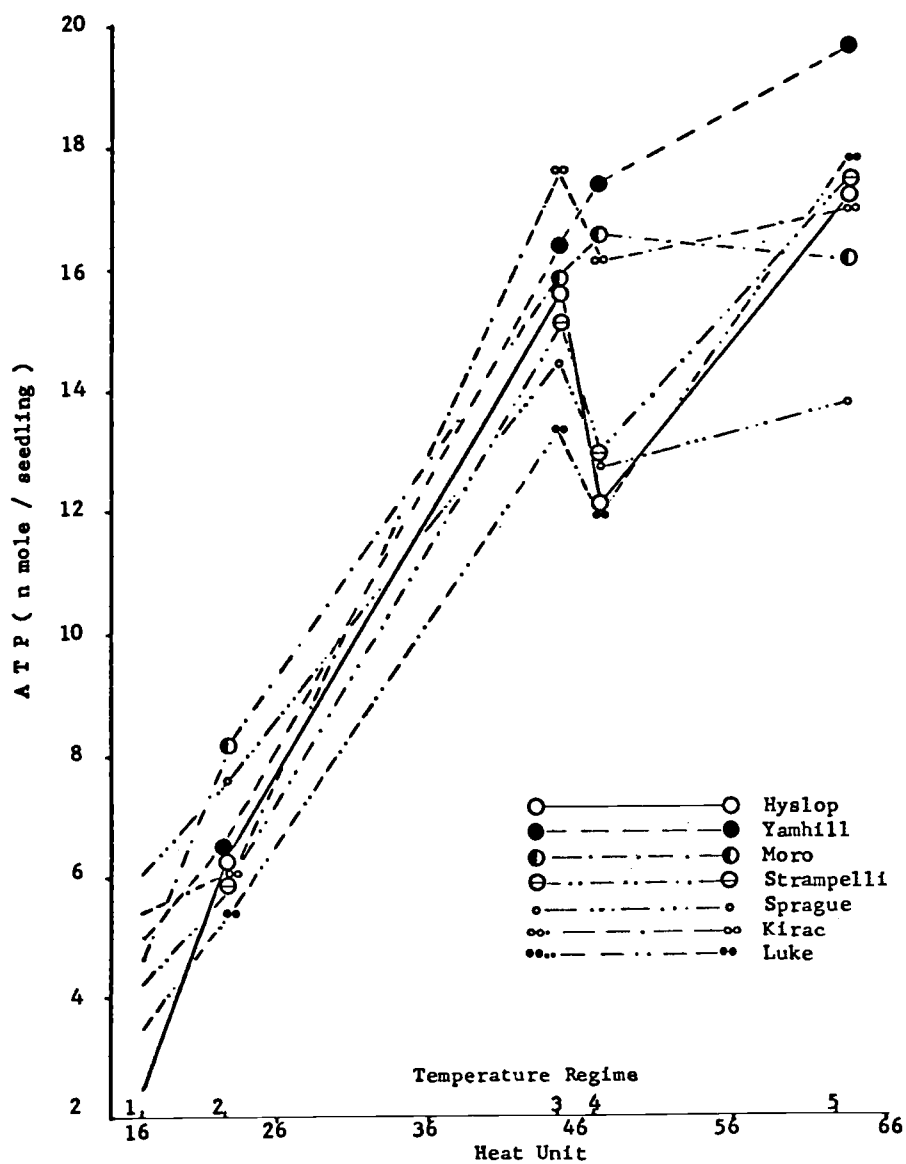
Figure 11. ATP content of seven wheat cultivars at various heat units and temperature regimes.

a well known cultivar in Turkey for its ability to emerge well under deep seeding and limited moisture conditions, had the highest ATP among all cultivars under the third temperature regime denoting that its ability to germinate fast might be due to maintenance of high ATP level under unfavorable conditions. Moro is not different from other cultivars in the pattern of response for the first three temperatures, but its ATP content remains at a constant level at temperatures 4 and 5 resulting in its superiority to all the cultivars except Yamhill at the 4th regime. However, in the 5th regime this preponderance is maintained only over Sprague. General belief about the superiority of this cultivar in early planting can be explained by its ability to maintain the high ATP level under the normal seeding situations; however, it might also be true that the belief originates from comparing Moro with other old cultivars not investigated in this study.

Cultivar by temperature interactions for five biochemical properties other than ATP can be depicted in Table 30. Energy charge of the cultivars changes little over different temperatures and with an inconsistent pattern. Differences within cultivars are smallest for Moro followed by Yamhill, and largest for Luke followed by Strampelli and Hyslop. Since EC is a ratio its magnitude varies by changing either numerator (influenced mostly by ATP) or dominator (influenced by ATP, ADP and AMP), therefore, a cultivar

Table 30. Cultivar means for five biochemical traits measured under 5 temperature regimes.

Cultivar	Temp. regime	EC	EC/heat unit	ATP/mg (n mole)	ATP/heat unit (n mole/seedling)	ATP/mg/heat unit (n mole)
Hyslop	1	0.652	0.0392	0.068	. 0.146	0.0041
	2	0.765	0.0344	0.165	0.284	0.0074
	3	0.744	0.0167	0.358	0.351	0.0080
	4	0.739	0.0158	0.320	0.259	0.0068
	5	0.732	0.0117	0.462	0.275	0.0074
Yamhill	1	0.728	0.0437	0.119	0.299	0.0071
	2	0.711	0.0320	0.146	0.290	0.0065
	3	0.749	0.0168	0.372	0.368	0.0083
	4	0.736	0.0157	0.381	0.373	0.0081
	5	0.759	0.0122	0.527	0.316	0.0084
Moro	1	0.748	0.0449	0.146	0.273	0.0087
	2	0.759	0.0341	0.284	0.368	0.0127
	3	0.744	0.0167	0.382	0.355	0.0086
	4	0.740	0.0158	0.382	0.355	0.0081
	5	0.780	0.0125	0.459	0.259	0.0073
Strampelli	1	0.740	0.0444	0.104	0.254	0.0062
	2	0.772	0.0347	0.130	0.263	0.0058
	3	0.791	0.0178	0.374	0.342	0.0084
	4	0.716	0.0153	0.302	0.277	0.0064
	5	0.796	0.0128	0.440	0.282	0.0070
Sprague	1	0.787	0.0473	0.187	0.365	0.0112
	2	0.763	0.0343	0.218	0.343	0.0098
	3	0.761	0.0171	0.353	0.325	0.0079
	4	0.714	0.0153	0.299	0.277	0.0064
	5	0.737	0.0118	0.378	0.221	0.0060
Kirac	1	0.702	0.0421	0.118	0.325	0.0071
	2	0.723	0.0325	0.114	0.265	0.0051
	3	0.742	0.0167	0.422	0.399	0.0095
	4	0.687	0.0147	0.381	0.344	0.0081
	5	0.747	0.0120	0.345	0.274	0.0055
Luke	1	0.682	0.0409	0.100	0.210	0.0060
	2	0.698	0.0314	0.130	0.245	0.0058
	3	0.753	0.0169	0.344	0.299	0.0077
	4	0.719	0.0154	0.348	0.257	0.0074
	5	0.775	0.0124	0.425	0.285	0.0068

with rather low ATP level may have a comparatively high EC level if the amount of AMP is very low; therefore, this parameter does not reflect the growth and energy potential in the higher organisms especially if the rapid turnover of the ATP at the early stages of growth is also taken into consideration.

Energy charge/heat is highest at the first temperature regime (when limited heat units are received by the cells) for all the cultivars and it drops sharply and steadily as more and more heat units are received. The largest range of variability was observed in cultivar Strampelli which also had the largest EC. The interesting point is that in each of the last three temperature regimes there is practically no difference between the EC/heat unit of different cultivars.

The pattern of dispersion of ATP/mg is very similar to that of ATP. Averaging ATP/mg over five temperature regimes, cultivar Moro had the highest value followed by Yamhill, Sprague, Kirac, Hyslop, Strampelli, and Luke (0.331, 0.309, 0.287, 0.276, 0.275, 0.270, and 0.270 n mole, respectively). ATP/mg may provide a better index for comparing the seeds of different sizes than ATP, especially if the differences in seed size are imposed by the external environmental conditions such as F_1 seeds produced by hand immasculation and pollination. However, the fact that embryo growth is confined to a very short time after anthesis while endosperm growth is achieved during much longer period of time may cause an artifact

if the varietal differences in growth are interpreted on the basis of their ATP per unit of seed weight. Similar arguments can be set forward for the ATP/mg/heat unit.

ATP/heat unit shows a great variation depending on cultivars and temperature regimes as it is shown in Figure 12. All the cultivars showed a decline in ATP/heat unit over the last two temperatures except Yamhill which declined only at the last temperature, but it had the highest value at this point. Sprague was the only cultivar which started with very high level, but unlike all the other cultivars, its ATP/heat unit content fell down sharply as more heat units were received. The reason for this differential response is not known but it could be explained assuming the accumulation of ATP at lower temperatures and disability of this cultivar to utilize the synthesized ATP at these temperatures.

Comparing Figures 11 and 12 it can be seen that despite the large variation among cultivars in Figure 12, the relative performance of cultivars are the same in ATP/heat unit and ATP content. The wide variation of cultivars in ATP/heat unit content under first two temperature regimes may be due to accumulation of ATP. This can be verified with high EC/heat unit values in these temperature. Therefore ATP/heat unit does not seem to provide a better index of growth than ATP per se. In the rest of this study only values of ATP, EC, and ATP/mg measured under 20° C temperature
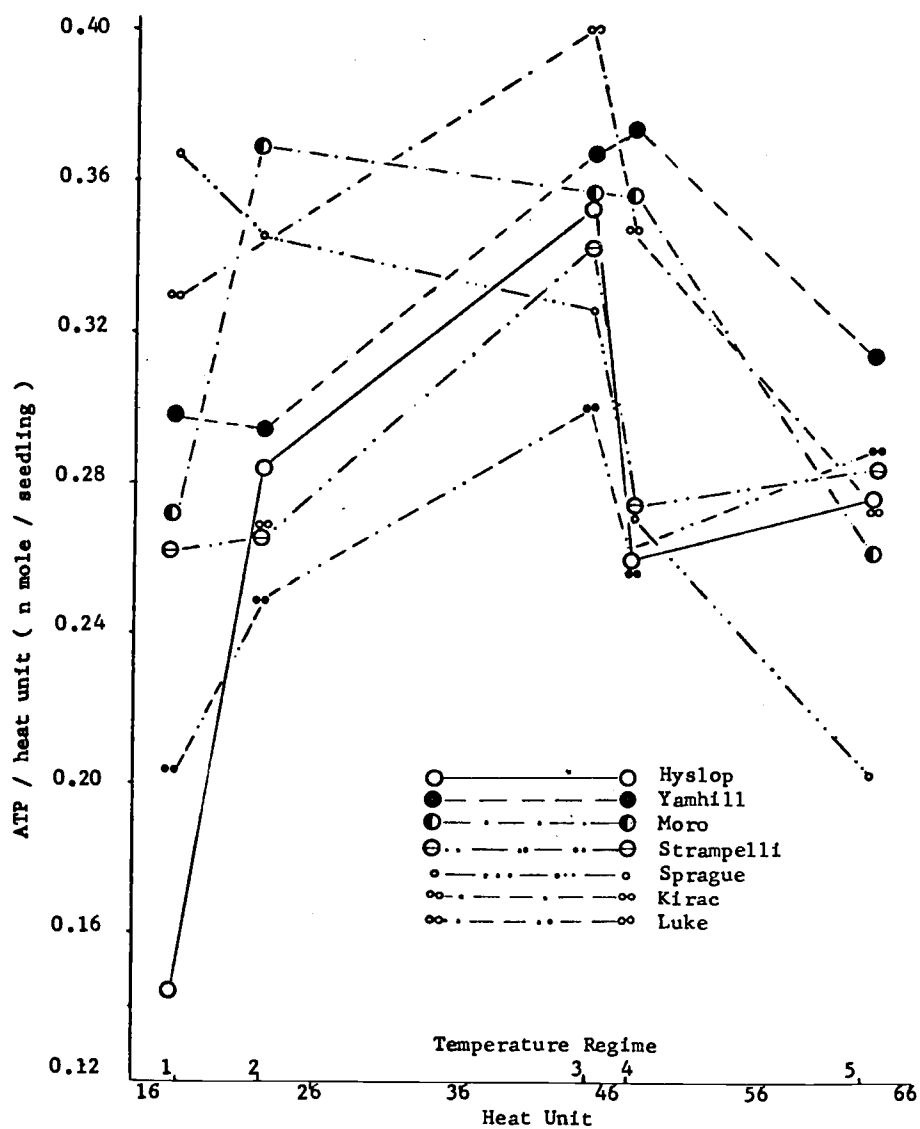
Figure 12. ATP/heat unit content of seven wheat cultivars at various
heat units and temperature regimes.

and 72 hours incubation period were used. This temperature regime was chosen because Ching and Ching (1973) demonstrated that under 20° C temperature synthesis and utilization of ATP are balanced. In addition, the results of the present experiment indicate that differential varietal responses are most pronounced under this temperature regime.

Part B

1. Effects of Seed Source and Seed Size on
Biochemical Properties of the Seed

Mean squares from the analysis of variance show highly significant differences among seed sizes, seed sources, and cultivars as well as seed source by cultivar interactions for ATP, EC, and ATP/mg (Table 31). Duncan's new multiple range test given on Table 32 indicates significant differences among cultivars for seed size, ATP, EC and ATP/mg. Differences between seed sources were also significant for all traits except EC. Differences in seed size among cultivars are inherent differences; average kernel weights of the cultivars over three locations are very close to mean seed sizes presented in this table, but differences in size due to seed source are due to environmental effects imposed by planting seeds in different locations.

Highest ATP, EC and ATP/mg were measured on Yamhill, Moro, and Kirac respectively. Differences within ATP and ATP/mg

Table 31. Mean squares from the analysis of variance for seed size, ATP, EC, and ATP/mg measured on seven wheat cultivars from three sources.

Source of variation	d.f.	ATP	EC	ATP/mg
Size	9	165.9**	0.0045**	0.300**
Source	2	84.8**	0.0055**	0.589**
Cultivar	6	73.7**	0.0083**	0.087**
Source x cultivar	12	13.8**	0.0064**	0.024**
Error	180	2.7	0.0008	0.006
Total	209			
Coefficient of variability	10.94	11.58	4.01	17.26

 * Significant at the 5% level
** Significant at the 1% level

Table 32. Cultivar and seed source means for seed size, ATP, EC and ATP/mg.

Cultivars	Seed Size	ATP (n mole per seedling)	EC	ATP/mg (n mole)
Hyslop	34.73 b[1]	13.99 bc	0.710 bc	0.453abc
Yamhill	39.00a	15.99a	0.720ab	0.476ab
Moro	33.37 bc	15.78a	0.746ab	0.529a
Strampelli	34.92 b	12.39 cd	0.692 c	0.421 bc
Sprague	30.90 c	13.32 cd	0.723ab	0.480ab
Kirac	32.84 bc	15.15ab	0.726ab	0.531a
Luke	33.53 bc	11.79 d	0.724ab	0.385 c
Seed Source				
Hyslop	38.11a	12.87 b	0.713a	0.369 b
Pendleton	33.78 b	14.76a	0.730a	0.485a
Moro	30.66 b	14.79a	0.717a	0.550a

[1]DMRT, means followed by the same letter are not significantly different at the 5% level

of cultivars were more evident than within EC of cultivars.

Seeds from the Hyslop source were heavier than seeds from Pendleton and Moro but the latter two sources produced higher ATP and EC than the former source. ATP/mg was also higher in seeds from Pendleton and Moro than those from Hyslop which indicates that differences in ATP and EC are not only due to seed size but origin of seed also affects these properties.

Significant seed source x cultivar interactions impede the above generalizations about seed source, therefore ATP, EC and ATP/mg were compared by DMRT for each source and each cultivar separately. Results are summarized on Tables 33 and 34. EC of cultivars showed little discrepancies using seeds from the Hyslop source, with cultivar Kirac being the only one significantly inferior to the rest and cultivar Yamhill having the highest value. Utilizing the Pendleton source, Hyslop and Strampelli cultivars were significantly subordinate to the rest and again Yamhill had the highest quantity. Differences between EC of cultivars were more pronounced when seeds were obtained from the Moro Station; cultivars Moro and Strampelli were significantly superior and inferior to the rest respectively and cultivar Yamhill was next to the lowest. Considering the EC of individual cultivars there were not significant differences among sources for Hyslop, Sprague, and Luke cultivars but other cultivars showed meaningful differences: one having the highest value when the Hyslop

Table 33. Mean of cultivars from three sources for ATP, EC, and ATP/mg..

Seed source	Cultivars	ATP (n mole/seedling)	EC	ATP/mg (n mole)
Hyslop	Hyslop	11.39 c[1]	0.715a	0.329 b
	Yamhill	15.89a	0.726a	0.425a
	Moro	13.92 b	0.720a	0.387a
	Strampelli	11.94 c	0.717a	0.342 b
	Sprague	11.35 c	0.714a	0.327 b
	Kirac	15.31ab	0.682 b	0.441ab
	Luke	10.29 c	0.719a	0.331 b
	Average	12.87	0.713	0.369
Pendleton	Hyslop	14.38 bc	0.701 b	0.486ab
	Yamhill	15.05 b	0.747a	0.453 bc
	Moro	17.50a	0.742a	0.567a
	Strampelli	13.27 c	0.679 b	0.393 c
	Sprague	14.80 bc	0.739a	0.545a
	Kirac	14.83 b	0.765a	0.510ab
	Luke	13.51 bc	0.739a	0.441 bc
	Average	14.76	0.730	0.485
Moro	Hyslop	16.19ab	0.712 bc	0.543 b
	Yamhill	17.03a	0.686 c	0.550 b
	Moro	15.93ab	0.777a	0.634a
	Strampelli	13.70 d	0.679 d	0.528 b
	Sprague	13.82 cd	0.717 b	0.569ab
	Kirac	15.32 bc	0.730 b	0.644a
	Luke	11.57 e	0.715 b	0.384 b
	Average	14.79	0.717	0.550

[1]DMRT; means followed by the same letter are not significantly different at the 5% level

Table 34. Cultivar means for ATP, EC, and ATP/mg from three sources.

Cultivar	Source[1]	ATP (n mole/seedling)	EC	ATP/mg (n mole)
Hyslop	1	11.39 c[2]	0.715a	0.329 b
	2	14.38 b	0.701a	0.486a
	3	16.19a	0.712a	0.543a
Yamhill	1	15.89a	0.726a	0.425 b
	2	15.05 b	0.747a	0.453 b
	3	17.03a	0.686 b	0.550a
Moro	1	13.92 c	0.720 b	0.387 b
	2	17.50a	0.742 b	0.567a
	3	15.93 b	0.777a	0.634a
Strampelli	1	11.94 b	0.717a	0.342 b
	2	13.27ab	0.679 b	0.393 b
	3	13.70a	0.679 b	0.528a
Sprague	1	11.35 b	0.714a	0.327 b
	2	14.80a	0.739a	0.545a
	3	13.82ab	0.717a	0.569a
Kirac	1	15.31a	0.682 c	0.441 b
	2	14.83a	0.765a	0.510 b
	3	15.32a	0.730 b	0.644a
Luke	1	10.29 b	0.719a	0.331 b
	2	13.51a	0.739a	0.441a
	3	11.57 b	0.715a	0.384ab

[1] 1 = Hyslop source   2 = Pendleton source   3 = Moro source

[2] DMRT; means of three sources followed by the same letter are not significantly different at the 5% level

source was used, two responding better to the Pendleton source, and one performing better with seeds from the Moro source.

ATP/mg was found to be different among cultivars from the same source as well as within each cultivar from different sources. Highest and lowest values of ATP/mg were produced respectively by cultivars Hyslop and Sprague for the Hyslop source, by Yamhill and Strampelli cultivars for the Pendleton source, and by Moro and Luke for the Moro source. Referring to individual cultivars, in no case did seeds from the Hyslop source give significantly higher ATP/mg than other sources. Except for Luke which produced higher ATP/mg when the seed originated from Pendleton, all the cultivars had the highest quantity of ATP/mg when seeds were obtained from the Moro station.

Significant differences were also found for ATP among cultivars from the same seed source and within each cultivar over three sources. The patterns of cultivar x seed source interaction for ATP are plotted in Figure 13. Luke, Sprague and Moro cultivars have similar patterns; the highest and the lowest responses being observed from seeds from Pendleton and Hyslop respectively. Seeds from the Moro station were the source of high ATP involving the cultivars Hyslop, Yamhill and Strampelli. Kirac was the only cultivar which did not respond to seed source, this may mean this cultivar is stable over these environments or it may have happened because this
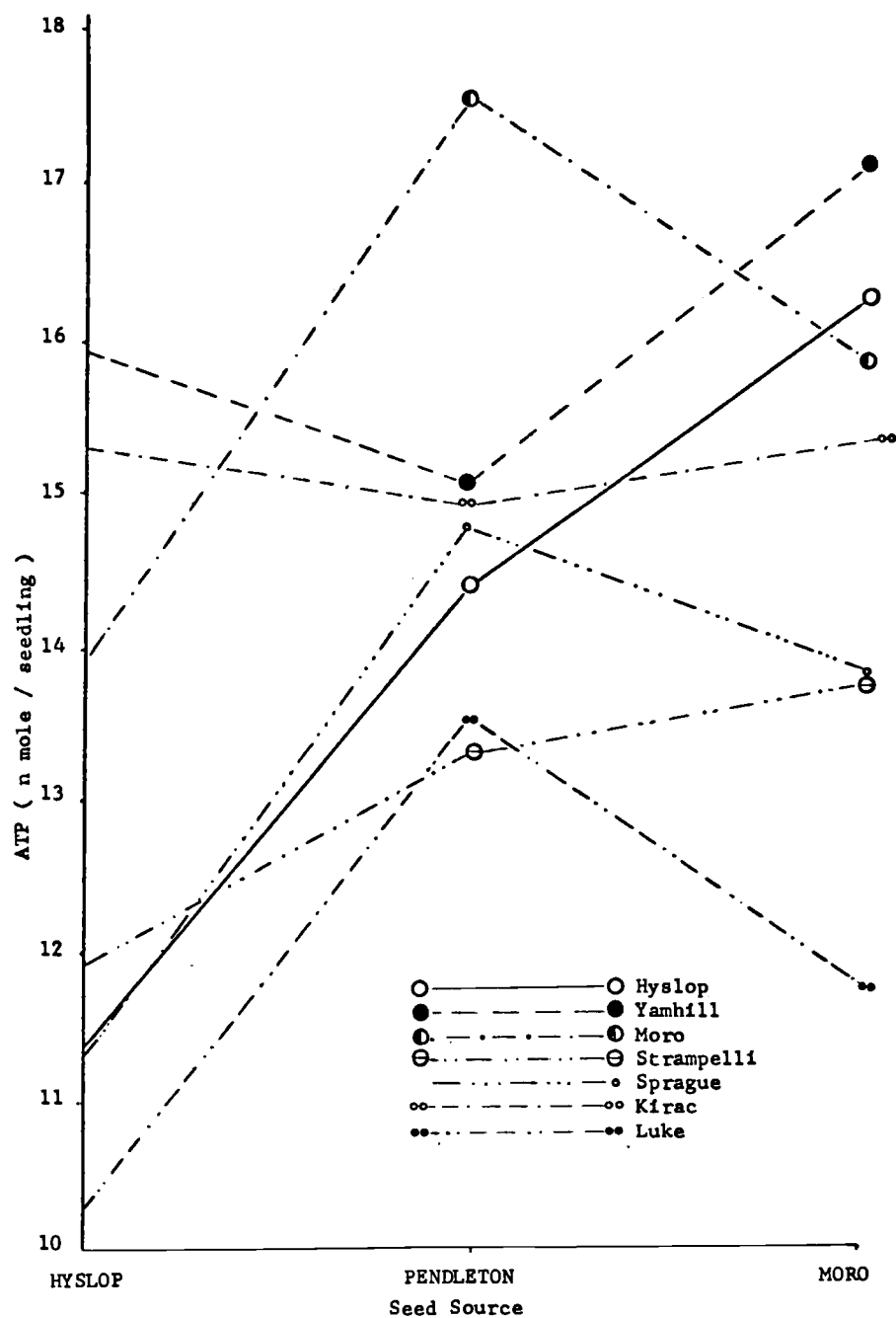
Figure 13   Effect of seed source on ATP content of seven wheat
cultivars.

cultivar is from very diverse genetic source and differs from the
other cultivars in not having been developed for the Oregon climate
therefore, exerting its minimum capacity. The highest average ATP
was obtained by variety Yamhill followed by Moro and Kirac cultivars.
The lowest average ATP was observed in cultivar Luke followed by
Strampelli and Sprague.

Correlation coefficients were found to be highly significant
between ATP and cultivar, seed source or seed size, and significant
at the 5% level between EC and seed size but not between EC and seed
source nor between EC. and cultivar (Table 35).

Table 35. Correlations between cultivar, seed source, and seed
size; and ATP and EC.

Variable	ATP	EC
Cultivar	-0.2118**	0.0586
Seed Source	0.2167**	0.0332
Seed Size	0.5720**	0.1437*

* Significant at the 5% level
** Significant at the 1% level

Multiple regression analyses with standardized values were
performed to find the relative importance of seed source, seed size,
and cultivars on ATP and EC. Results are given on Table 36 indicate
that for ATP, seed size is the most important independent variable
followed by seed source and finally cultivar. All the independent

Table 36. Analysis of variance table from the stepwise regression analyses of ATP and EC as the function of seed source, seed size and cultivar.

Source of Variation	d. f.	ATP Mean squares	EC Mean squares
Regression	3	42. 24**	2. 10*
Residual	206	0. 40ns	0. 98ns
Total	209		

	S. E. of Regr. coefficient	T	S. E. of Regr. coefficient	T
Source	0. 055	8. 30**	0. 085	0. 96ns
Size	0. 003	16. 40**	0. 005	2. 33*
Cultivar	0. 022	-3. 30**	0. 034	1. 06ns

* Significant at the 5% level
** Significant at the 1% level
ns Not Significant

variables possessed significant T values. For EC, seed size was the variable which entered the regression equation first (significant T at the 5% level), followed by cultivar and source (both nonsignificant).

2. Correlations Between Agronomical and Biochemical Traits

Phenotypic correlations were calculated using combined data obtained in the experimental sites (study 1) and in laboratory (Table 37). ATP/seedling showed significant positive correlations with number of spikelets per spike and significant negative correlation with harvest index. Association between ATP and stand count, and ATP and grain yield were very small, negative, and nonsignificant. Lack of associations between ATP and stand count can be attributed to the fact that environmental conditions during emergence time were very favorable, consequently all the cultivars emerged well regardless of their ATP content and hence yield production was not hindered by poor stand. The nonsignificant differences between stands counted from small, unsized and large seeds in all locations (Tables 2, 4, 6) confirms the environmental suitabilities. Negative significant relationships between ATP and harvest index may be due to the fact that high ATP promotes vegetative growth of the crop thereby causing low grain to total ratio, but it may also be just an artifact imposed by the height of the plants because the taller cultivars

Table 37. Correlation coefficients between agronomical traits measured on seven wheat cultivars grown at three sites in Oregon, in 1974-75, and biochemical traits measured in the laboratory.

Biochem trait	Agron. trait Stand count	Spikes per plot	Spikelets per spike	Kernels per spikelet	Kernel Weight	Grain per plot	Total per plot	Harvest Index
ATP	-0.008	-0.077	0.145**	-0.060	0.027	-0.028	0.044	-0.132*
ADP	0.013	-0.029	0.057	-0.123*	0.050	-0.055	0.021	-0.139**
AMP	0.041	0.029	0.014	-0.041	0.007	-0.018	0.018	-0.065
AP	0.002	-0.045	0.125*	-0.085	0.029	-0.035	0.042	-0.140**
EC	0.031	-0.088	0.122*	0.007	0.006	0.006	0.023	-0.033
ATP/mg	-0.075	-0.125*	0.090	-0.043	-0.058	-0.098	-0.075	-0.092
AP/mg	-0.054	-0.077	0.078	-0.057	-0.051	-0.084	-0.060	-0.081

* Significant at the 5% level
** Significant at the 1% level

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usually have lower harvest index and in the laboratory experiments all three tall cultivars (Yamhill, Moro, and Kirac) had high average ATP. Positive correlation of ATP and number of spikelets/spike too can be ascribed to the high number of spikelet/spike of Moro and Yamhill cultivars.

Total adenosine phosphate and EC does not seem to provide a better criteria for relating the agronomic and biochemical characteristics, neither does any other trait presented in Table 37, and occasional significant correlations lack any biological meaning.

To assess a better understanding of the role of ATP on the grain yield components, path coefficient analysis was performed and the results are given in Table 38. ATP had negligible direct effects on yield but the total effect of ATP in yield is larger in magnitude than the total effect of seed source, seed size, cultivar, and even number of spikes/plot. This total effect is the result of initial negative direct effect plus positive indirect effects via seed source, seed size, cultivars, spikelets/spike and kernel weight and plus negative indirect effects via stand count, number of spikes/plot and number of kernels/spikelet. Most important indirect effects of ATP was through seed size and this confirms the effect of seed size on ATP content of the seed as was obtained in part B. 1 of this chapter. Negative indirect effects were smaller in magnitude than positive ones; the highest one being through number of spikes/plot which can

Table 38. Path coefficient analysis of direct and indirect influences of nine traits on grain yield per plot of seven wheat cultivars planted over three locations in Oregon in 1974-75.

| Relationships of yield and: | Direct effect | Indirect effects via | | | | | | | | | Total (r) |
		Seed source	Seed size	Cultivar	Stand count	Spikes per plot	Spikelets per spike	Kernels per spikelet	Kernel weight	ATP	
Seed source	0.0268		-0.00000	0.00000	-0.00067	0.00810	0.00846	-0.01189	0.00145	-0.01150	0.02075
Seed size	0.0395	-0.00000		0.00000	0.00101	0.05182	-0.00263	-0.03867	0.00194	-0.02622	0.02675
Cultivar	-0.0375	-0.00000	0.00000		0.00049	0.19030	-0.06531	-0.11354	-0.08478	0.00673	-0.10361
Stand count	0.0247	-0.00072	0.00162	-0.00075		-0.02065	0.07238	0.10065	0.28052	0.00035	0.45810
Spikes per plot	0.4049	0.00053	0.00505	-0.01762	-0.00126		-0.06166	-0.13535	-0.06395	0.00335	0.13399
Spikelets per spike	0.1880	0.00121	-0.00055	0.01309	0.00951	-0.13281		0.17006	0.26066	0.00634	0.51551
Kernels per spikelet	0.4958	-0.00064	-0.00308	0.00859	0.00501	-0.11054	0.06448		0.30669	0.00262	0.77163
Kernel weight	0.4845	0.00008	0.00016	0.00656	0.01430	-0.05344	0.10114	0.31384		-0.00118	0.86596
ATP	-0.0437	0.00678	0.23700	0.00577	-0.00020	-0.03117	0.02726	-0.02975	0.01308		0.18507

R^2 = 0.96807

Residual = 0.03193

be attributed to the fact that high ATP cultivars had low tillering capacity.

To find out how the less favorable climatic conditions influences the direct and indirect effects of ATP, path coefficient analysis was performed for the Moro station separately (Table 39). Results show that while there was not much difference in the direct effect of ATP, its total effect on yield was reduced considerably compared to the effects observed in combined path coefficient analyses. The most important indirect effect of ATP on yield was the negative effects via number of kernels/spike and kernel weight. As it was discussed in Study I, the small seeds (low ATP) yielded as good as large seeds (high ATP) at the Moro site and this was ascribed to the luxurious growth of large seeds in early stages of growth which caused the stressing of these plants at later stages when drought was wide spread. The negative effects of ATP in the path analysis could also be explained by similar reasoning.

Part C. Inheritance of ATP and EC

In discussing the mode of inheritance of EC it should be noticed that energy charge is a ratio not a trait, therefore it can not be inherited per se but its mode of inheritance is determined by the gene actions and interactions that govern the inheritance of components of EC namely ATP, ADP, and AMP. However, the

Table 39. Path coefficient analysis of direct and indirect influences of nine traits on grain yield per plot of seven cultivars grown at Sherman Experimental Station, Moro, Oregon, in 1974-75.

Relationship of yield and:	Direct Effect	Indirect Effects via									Total (r)
		Seed Source	Seed Size	Cultivars	Stand Count	Spikes per plot	Spikelets per spike	Kernels per spikelet	Kernel Weight	ATP	
Seed source	0.01337		-0.00000	0.00000	-0.00263	0.00749	0.02131	0.02641	-0.04025	-0.00935	0.01635
Seed Size	-0.00540	0.00000		0.00000	0.01564	0.08085	-0.00749	-0.11923	-0.01421	-0.02193	-0.07177
Cultivar	-0.07486	0.00000	0.00000		-0.00519	0.27997	-0.14458	-0.11923	-0.23262	0.00620	-0.29031
Stand Count	0.06109	-0.00058	-0.00138	0.00633		0.23731	-0.02390	0.01520	0.02900	-0.00211	0.32096
Spikes per Plot	0.74858	0.00013	-0.00058	-0.02786	0.01937		-0.11866	-0.44971	-0.11720	0.00019	0.05426
Spikelets per Spike	0.28802	0.00099	0.00014	0.03740	-0.00507	-0.30842		0.08722	-0.04972	-0.00761	0.04295
Kernels per Spikelet	0.80018	0.00044	0.00080	0.01110	0.00116	-0.42071	0.03139		0.14679	0.00679	0.57794
Kernel Weight	0.59189	-0.00091	0.00013	0.02928	0.00299	-0.14822	-0.02419	0.19845		0.00126	0.65068
ATP	-0.03709	0.00338	0.00319	0.01224	0.00348	-0.00374	0.05904	-0.14644	0.02012		-0.08582

R^2 = 0.94439
Residual = 0.05561

heritability values can be computed for this ratio in the same way that they are customarily calculated for grain yield which is a product rather than a trait.

Narrow sense heritability estimates for ATP, EC and ATP/unit calculated by regression of F_1 on midparent (method 1), reciprocal F_1 on midparent (method 2), and F_2 on F_1 (method 3) accompanied by the respective correlation coefficients are given in Table 40. Calculations were made for two sets of data, one set based on observations on 4 seeds (set of 4 seeds for F_2) where the average seed weights were equal or were very close to the kernel weight of the respective parents or progenies as they were harvested from the field. The other set was based on 10 observations (4 sets of 10 observations for F_2) making use of the possible range of seed size for each treatment.

When estimates were based on 10 observations, H_{ns} and correlation coefficients for ATP were highly significant regardless of the method used to obtain the estimates, however the differences between methods did exist; the highest heritability was obtained by regressing reciprocal F_1 on midparent and the lowest estimate was observed when F_2 was regressed on F_1. When estimates were based on average seed weight of the treatments, H_{ns} and correlation coefficients were not significant using the first method of estimation,

Table 40.   Narrow sense heritability estimates for three biochemical traits determined by the regressions of F_1 on midparent, reciprocal F_1 on midparent and F_2 on F_1 on 4 and 10 observations per treatment, and respective correlation coefficients.

Character	10 Observations		4 Observations	
	Regression	Correlations	Regression	Correlations
ATP:				
(F_1 on MP)	0.7367**	0.5955**	0.3164ns	0.1824ns
(Rec. F_1 on MP)	0.8243**	0.5049**	1.0921**	0.3715**
(F_2 on F_1)	0.6286**	0.6115**	0.4034**	0.3439**
EC:				
(F_1 on MP)	-0.0374ns	-0.0324ns	0.0711ns	-0.0561ns
(Rec. F_1 on MP)	-0.0992ns	-0.1084ns	-0.1586ns	-0.1702ns
(F_2 on F_1)	0.1876*	0.1997*	0.1480ns	0.1465ns
ATP/mg:				
(F_1 on MP)	0.8047**	0.6341**	0.8207**	0.3723**
(Rec. F_1 on MP)	0.7691**	0.4310**	0.3248ns	0.1000ns
(F_2 on F_1)	0.3955**	0.3671**	0.0172ns	0.0204ns

  * Significant at the 5% level
** Significant at the 1% level
ns Not significant

but they were significant in other cases. The difference between

H_{ns} estimates especially between method one and two are very well

pronounced.

Significant H_{ns} estimate and correlation coefficients for EC

were obtained only when regression was based on 10 observations and

the third method (F_2 on F_1) was applied. This method also gave the

highest H_{ns} estimate in second set of data though the value was not

significant.

ATP/mg had highly significant regression and correlation

coefficients on the first set of data using any method but the first

method (F_1 on midparent) and estimated the H_{ns} twice as large as the

third method did. The first method also indicated significant

regression and correlation coefficients in second set of data while the

other methods failed to yield significant results.

A drawback of estimating heritabilities in this study is related

to the seed size of F_1 which are produced by hand-immasculation and

pollinations and it is difficult to assign an average kernel weight to

these seeds, therefore ATP calculated on per miligram of seed

weight may provide a better insight to the mode of gene action than

ATP per se however as it was mentioned earlier this calculation

ignores the inherent differences in seed size of treatments.

Comparing the H_{ns} values with those of H_{bs}, which are presented

in Table 41, provides some information about the real magnitude of

Table 41. Broad sense heritability estimates for three biochemical traits measured on 4 and 10 observations per treatment.

Character	10 Observations			4 Observations		
	MP Variance	F_2 Variance	H_{bs}	MP Variance	F_2 Variance	H_{bs}
ATP	9.030	14.597	0.3814	2.383	9.868	0.7585
EC	0.00098	0.00115	0.1478	0.00075	0.00123	0.3902
ATP/mg	0.0092	0.0172	0.4651	0.00229	0.00793	0.7112

H_{ns} estimates. When estimations are based on the range of seed

sizes, H_{ns} for ATP calculated by any method exceed the H_{bs},

therefore these values of H_{ns} are over estimation. When .

H_{ns} is estimated on the average seed weight of generations the value

of H_{ns} calculated by the second method surpasses the H_{bs} value but

the estimates based on first and third methods are lower than H_{bs}

although it is still not clear which of these two estimates are more

meaningful.

Comparing the values of H_{ns} and H_{bs} for ATP/mg, it is shown

that in the first set of data the third method of estimating H_{ns} provided

a better index of the gene action than other methods, but in the second

set of data both second and third methods appear to be satisfactory.

Energy charge of the seed is little influenced by the seed size

therefore H_{ns} values obtained using average seed size are all lower

than H_{bs} value. Utilizing the range of seed sizes only regression of

F_2 on F_1 overestimated the H_{ns}.

Average ATP, ATP/mg, and EC values of F_1's reciprocal

F_1's and F_2's in relation to the percentage of midparents are graphed

in Figure 14, which shows that energy charge values for all genera-

tions exceeded the midparent consistently but differences were not

significant therefore the genes governing the performance of this

ratio seem to act additively and hence H_{ns} estimate of 0.1876* is

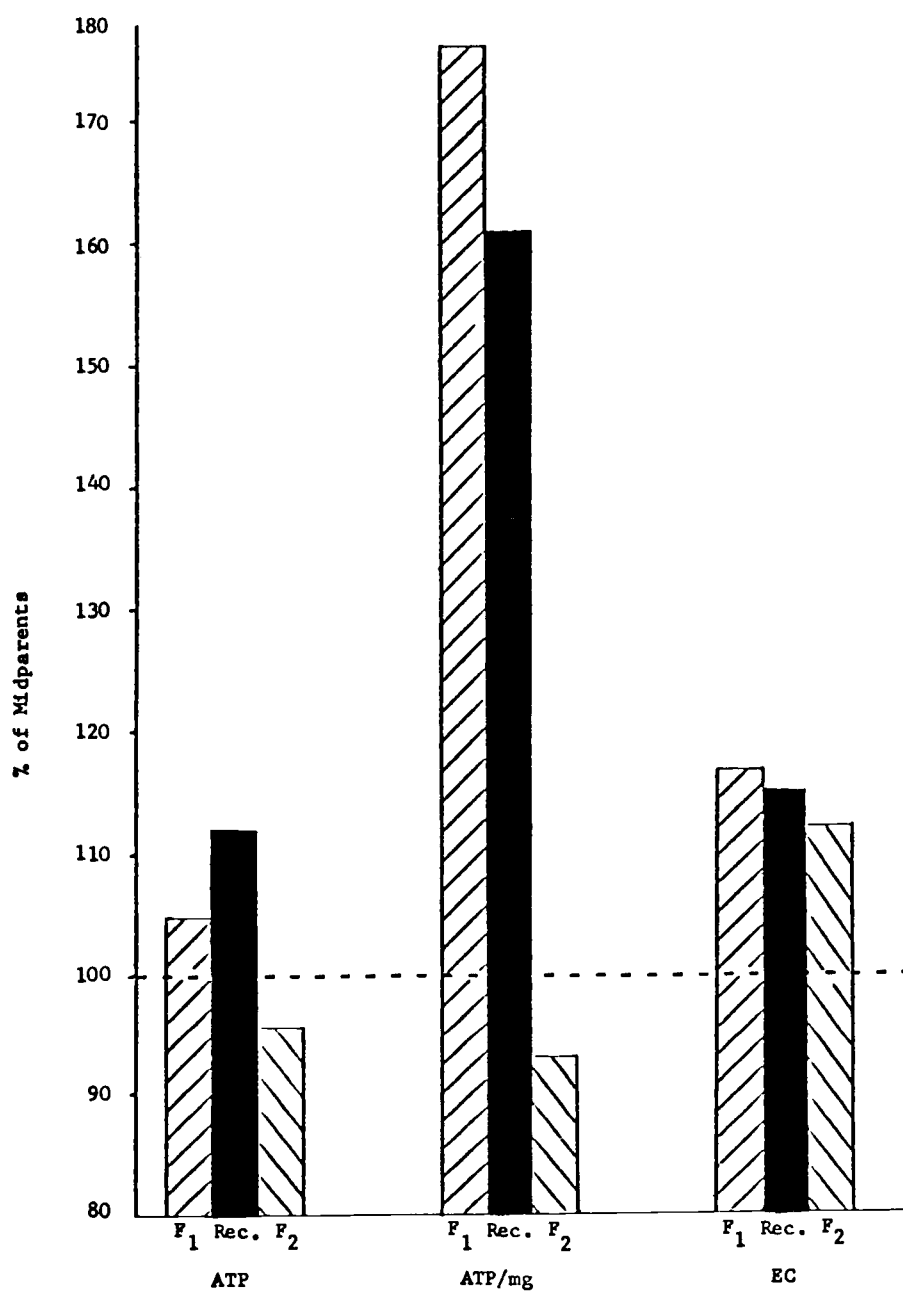the best candidate to represent the graph of EC. ATP of reciprocal

Figure 14. Average ATP, ATP/mg, and EC values of F_1's, reciprocal F_1's, and F_2's in relation to the % of midparents.

F_1 excelled the midparent, but the main cross F_1 was about the midparent and F_2 showed inbreeding depression. For the reason given below no attempt will be made here to identify a specific gene action. ATP/mg showed significant heterobeltiosis in both F_1's and reciprocal F_1 and great inbreeding depression in F_2. This may be attributed to over dominance gene actions but it is also a good indication of mitochondrial complementation which will be discussed later.

Significant generation x within generation interactions for ATP, EC, and ATP/mg as are given in Table 42 indicate that not all the parents and offspring behaved similarly in their mode of gene actions for these traits. Calculations in this table are based on two sets of data and significant differences were observed in both sets for all the traits and the interaction. To have a better insight into the differential parental performances, Duncan's new multiple range test was used to detect the significant differences for each cross making use of the second set of data for comparing ATP and EC and both first and second sets for evaluating the ATP/mg. Results are presented in Table 43.

Energy charge of F_1 and reciprocal crosses exceeded the midparent values in all crosses except for Hyslop/Yamhill F_1 and reciprocal F_1 and Yamhill/Moro F_1. Superiority of the F_1's over midparents were significant in six out of 15 crosses indicating hybrid

Table 42. Mean squares from the analysis of variance for three biochemical traits of diallel crosses of six wheat cultivars based on 4 and 10 observations per treatment.

Source of Variation	d. f. 10 Observ.	4 Observ.	ATP 10 Observ.	4 Observ.	ATP/mg 10 Observ.	4 Observ.	EC 10 Observ.	4 Observ.
Replications	9	3						
Generations	3	3	147. 18**	4871. 4**	2. 4560**	1. 2607**	0. 1622**	0. 0476**
Within generations	14	14	70. 54**	39. 5**	0. 0583**	0. 0282**	0. 0051**	0. 0023**
Gener. x w/n gener.	42	42	63. 94**	50. 5**	0. 0676**	0. 0350**	0. 0038**	0. 0022**
Error	531	177	3. 51	7. 0	0. 0054	0. 0038	0. 0007	0. 0006
Total	599	239						
Coefficient of variability			13. 49	12. 30	15. 45	13. 50	3. 55	3. 14

Table 43. Cultivar and generation means for ATP, EC and ATP/mg measured on the diallel crosses of six wheat cultivars.

Cultivar and Generation	ATP	%	EC	%	ATP/mg			
					4 Observ.	%	10 Observ.	%
(ST + KR)/2 [1]	14.52 b[2]	100	0.701 b	100	0.341 c	100	0.407 c	100
ST/KR F$_1$	13.92 b	96	0.822a	117	0.599 b	176	0.612 b	150
Kr/ST F$_1$	17.62a	118	0.788a	112	0.849a	249	0.731a	180
ST/KR F$_2$	10.76 c	74	0.815a	116	0.252 c	74	0.316 d	78
(ST + HY)/2	12.52ab	100	0.726a	100	0.310 c	100	0.335 c	100
ST/HY F$_1$	12.21ab	98	0.767a	106	0.587a	189	0.534a	159
HY/ST F$_1$	13.05a	104	0.768a	106	0.453 b	146	0.473 b	141
ST/HY F$_2$	11.38 b	91	0.760a	105	0.260 c	84	0.331 c	99
(ST + YM)/2	14.52a	100	0.732a	100	0.352 bc	100	0.382 c	100
ST/YM F$_1$	9.79 b	67	0.770a	105	0.481 b	137	0.521 b	136
YM/ST F$_1$	14.54a	100	0.775a	106	0.646a	184	0.710a	186
ST/YM F$_2$	11.27 b	78	0.786a	107	0.272 c	77	0.285 d	75
(ST + SP)/2	12.95a	100	0.717 b	100	0.300 b	100	0.334 b	100
ST/SP F$_1$	12.08ab	93	0.810a	113	0.533a	178	0.512a	153
SP/ST F$_1$	14.07a	109	0.793a	111	0.558a	186	0.576a	172
ST/SP F$_2$	9.68 b	75	0.742ab	103	0.235 b	78	0.264 c	79
(ST + MO)/2	14.76 bc	100	0.728a	100	0.341 b	100	0.365 c	100
ST/MO F$_1$	16.18 b	110	0.748a	103	0.700a	205	0.658 b	180
MO/ST F$_1$	24.01a	163	0.769a	106	0.709a	208	0.719a	197
ST/MO F$_2$	12.75 c	86	0.766a	105	0.335 b	98	0.356 c	98
(KR + HY)/2	14.09 c	100	0.713a	100	0.350 b	100	0.385 b	100
KR/HY F$_1$	17.87a	127	0.777a	109	0.606a	173	0.570a	148
HY/KR F$_1$	15.19ab	108	0.759a	106	0.514a	147	0.512a	133
KR/HY F$_2$	15.02 bc	107	0.759a	106	0.366 b	105	0.418 b	109

Table 43. Continued.

Cultivar and Generation	ATP	%	EC	%	ATP/mg			
					4 Observ.	%	10 Observ.	%
(KR + YM)/2	16.30a	100	0.706 b	100	0.415 b	100	0.438 b	100
KR/YM F$_1$	13.07 b	80	0.764ab	108	0.803a	193	0.773a	176
YM/KR F$_1$	18.88a	116	0.763ab	108	0.680a	164	0.677a	155
KR/YM F$_2$	12.21 b	75	0.780a	110	0.275 c	66	0.290 c	66
(KR/SP)/2	13.73a	100	0.672 b	100	0.371 b	100	0.384 b	100
KR/SP F$_1$	16.01a	117	0.776a	115	0.616a	166	0.632a	165
SP/KR F$_1$	7.39 b	54	0.787a	115	0.307 b	83	0.303 c	79
KR/SP F$_2$	14.85a	108	0.787a	115	0.314 b	85	0.307 c	80
(KR + MO)/2	16.26a	100	0.714 b	100	0.381 b	100	0.414 b	100
KR/MO F$_1$	13.17 b	81	0.799a	112	0.565a	148	0.588a	142
MO/KR F$_1$	17.72a	109	0.819a	115	0.581a	152	0.604a	146
KR/MO F$_2$	9.54 c	59	0.749ab	105	0.214 c	56	0.285 c	69
(HY + YM)/2	14.49 c	100	0.744a	100	0.365 c	100	0.377 c	100
HY/YM F$_1$	16.79 b	116	8.745a	100	0.469 b	128	0.516 b	137
YM/HY F$_1$	20.43a	141	0.736a	99	0.674a	185	0.688a	182
HY/YM F$_2$	14.85 c	102	0.776a	104	0.326 c	89	0.345 c	92
(HY + SP)/2	12.50 b	100	0.726a	100	0.309 b	100	0.327 b	100
HY/SP F$_1$	14.59 b	117	0.731a	101	0.505a	163	0.537a	164
SP/HY F$_1$	13.32 b	107	0.784a	108	0.469a	152	0.510a	156
HY/SP F$_2$	17.90a	143	0.795a	110	0.498a	161	0.532a	163
(HY + MO)/2	13.38 b	100	0.742a	100	0.353 b	100	0.358 c	100
HY/MO F$_1$	16.64a	124	0.799a	108	0.546a	155	0.540 b	151
MO/HY F$_1$	18.95a	142	0.789a	106	0.631a	179	0.643a	180
HY/MO F$_2$	13.64 b	102	0.801a	108	0.331 b	94	0.335 c	99

Table 43. Continued.

Cultivar and Generation	ATP	%	EC	%	ATP/mg			
					4 Observ.	%	10 Observ.	%
(YM + SP)1/2	14.16a	100	0.728 b	100	0.353 b	100	0.380 b	100
YM/SP F$_1$	15.72a	111	0.812a	112	0.682a	193	0.639a	168
SP/YM F$_1$	10.53 b	74	0.763ab	105	0.382 b	108	0.442 b	116
YM/SP F$_2$	14.17a	100	0.803a	110	0.342 b	97	0.397 b	100
(YM + MO)1/2	15.63ab	100	0.734a	100	0.373 bc	100	0.406 c	100
YM/MO F$_1$	17.25a	110	0.718a	98	0.682a	183	0.633a	156
MO/YM F$_1$	12.86 c	82	0.787a	107	0.439 b	118	0.493 b	121
YM/MO F$_2$	13.18 bc	84	0.748a	102	0.334 c	90	0.375 c	92
(SP + MO)1/2	14.74ab	100	0.727 b	100	0.340 b	100	0.357 c	100
SP/MO F$_1$	12.83 b	87	0.802a	110	0.590a	174	0.572a	160
MO/SP F$_1$	17.19a	117	0.811a	112	0.615a	181	0.631a	177
SP/MO F$_2$	14.62ab	99	0.762ab	105	0.343 b	101	0.429 b	120

[1] Abbreviations stand for: ST = Strampelli; KR = Kirac, HY = Hyslop, YM = Yamhill, SP = Sprague, and MO = Moro

[2] DMRT; means followed by the same letter are not significantly different at the 5% level

vigor for EC in those crosses. In 11 crosses the F_2 values were not significantly different from those of midparents indicating the additive gene actions, but in the other four F_2's superiority of the F_1's were maintained in F_2. Maintenance of superiority of F_1's may represent a special case of complementation which could be named additive complementation which acts similar to additive gene actions the only difference being that the offspring are compared to F_1 rather than to midparents.

The variations between ATP of midparents, F_1's, reciprocal F_1's and F_2's of individual crosses are graphed on Figure 15 and the results are summarized below:

Nine and 11 out of 15 F_1's and reciprocals excelled the midparents respectively, from which four differences in F_1 and five differences in reciprocal F_1's were significant indicating heterosis for ATP.

Differences between F_1's and reciprocal crosses were significant in 10 cases which implies the cytoplasmic type of inheritance.

Only four F_2's surpassed their midparents but a significant difference was observed in only one cross (Hyslop/Sprague). This F_2 was also significantly superior to its F_1 parent. Accepting the F_1 rather than midparent as the basis of comparison one could explain this behavior as the dominance complementation action.

Figure 15. Comparison of ATP of midparents and progenies in a 6-parent diallel cross measured under 20 C temperature and 72 hr imbibition period.

ST = Strampelli, KR = Kirac, HY = Hyslop, YM = Yamhill, SP = Sprague, MO = Moro.

——— ——— = High parent, --------- = Midparents, 1 = F_1, R = Reciprocal F_1, 2 = F_2.

Calculating the ATP/mg values of progenies as the percentage of midparents no large differences between the values in two sets of data were noted therefore only the values on 10 observations are graphed on Figure 16. Differences among generations are more clear in this figure than in previous ones. All the F_1's exceeded their midparents significantly. All but one reciprocal F_1's surpassed its midparents and 13 of them did so significantly. Differences between F_1 and reciprocal crosses were significant in nine cases, seven of them were the same crosses that had significant differences in their ATP content also. Inbreeding depression in F_2's are more evident in this trait than on ATP per se; only in one cross (Hyslop/Sprague) the heterotic effects of F_1 was maintained in F_2. This is the same cross that had higher ATP in F_2 than in F_1. It is worth noticing that virtually there was no difference in ATP and ATP/mg between the two parents of this cross. However, this does not mean that better complementation can be obtained by crossing the parents which have similar ATP content because there were several other instances where parents had about equal ATP but crosses showed quite different kinds of complementation from the Hyslop/Sprague cross.

Heterosis of F_1 and reciprocal crosses, significant differences between F_1's and reciprocals and the maintenance of heterotic effect in F_2 in some of the crosses for ATP and ATP/mg all indicate the cytoplasmic effects on this trait. Mitochondria in cytoplasm are the
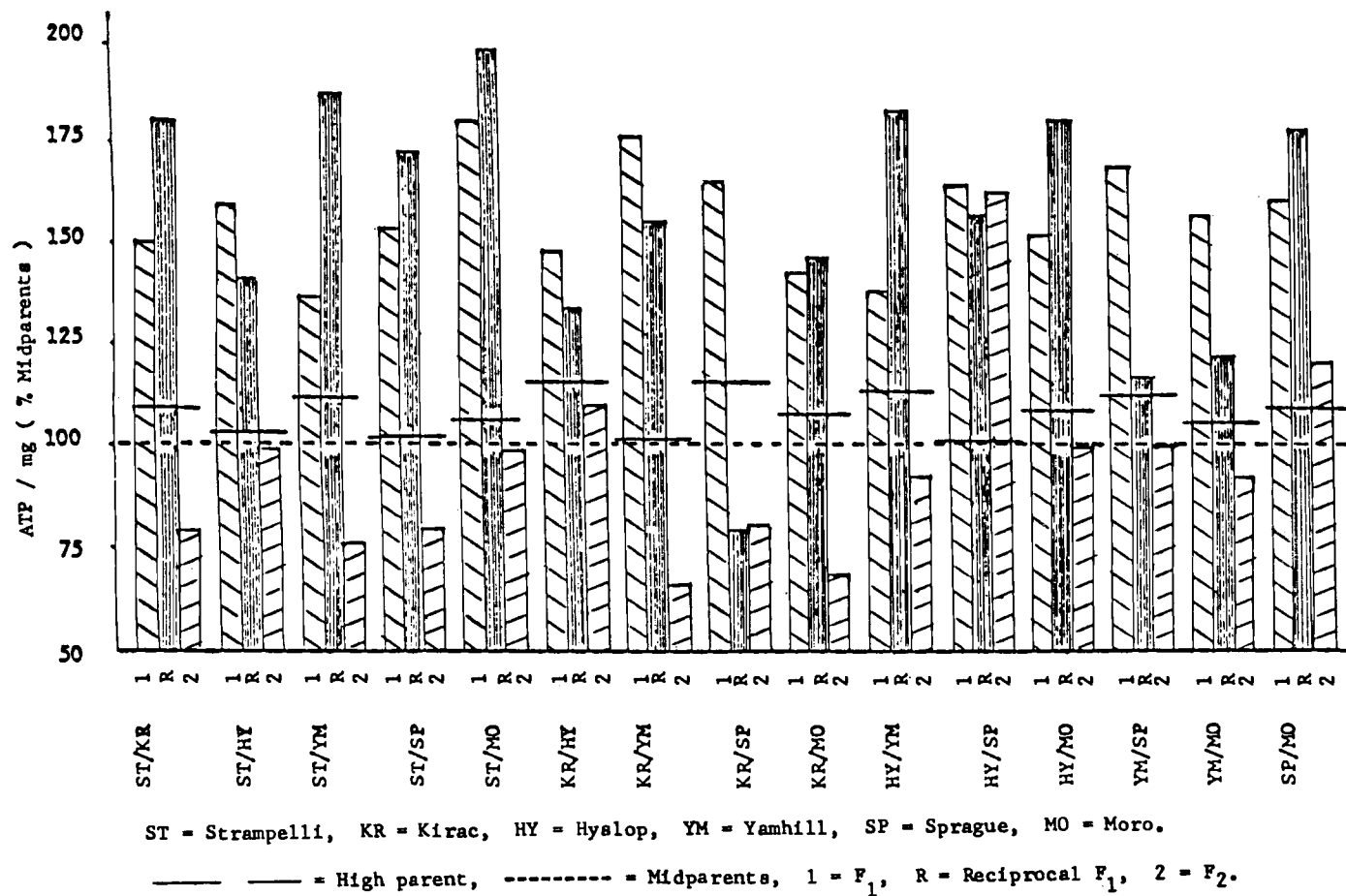
Figure 16. Comparison of ATP/mg of Midparents and Progenies in a 6-parent diallel cross.

ST = Strampelli, KR = Kirac, HY = Hyslop, YM = Yamhill, SP = Sprague, MO = Moro.

——— ——— = High parent, --------- = Midparents, 1 = F_1, R = Reciprocal F_1, 2 = F_2.

major sites for ATP synthesis in growing seedlings. Mitochondria contain their own DNA which encodes a limited number of mitochondrial components. Reproduction of mitochondria requires the cooperation of nuclear messages and cytoplasmic ribosomes, tRNA's and proteins (Sage, 1972). Most of the mitochondria of hybrid seeds originate from maternal parent, but a small number may have been carried over by the sperm nuclei during fertilization resulting in mitochondrial complementation (Ching, 1976, personal communication). The differences in ATP content of F_1's and reciprocals may be explained by the different quantity or quality of the paternal and maternal mitochondria involved. Heterotic effects of F_1's as the result of mitochondrial complementation has been demonstrated by McDaniel (1969, 1970, 1972, 1973a, 1973b), and McDaniel and Sarkisian (1966 and 1968). Complementation, however, was not observed in all cases which indicates that the cause of complementation is not the proximity of maternal and paternal mitochondria in hybrid seed _per se_ but the properties or the components of different mitochondria will affect the complementation. In fact in this study negative complementation of ATP and ATP/mg was observed in some crosses (Kirac/Sprague, Yamhill/Sprague, Yamhill/Moro) and in one case (Kirac/Sprague) the reciprocal cross was significantly inferior to its midparent.

From the plant breeding point of view maintenance of high ATP in F_2 is a desirable characteristic in breeding wheat for dryland areas. Selection among these populations is more likely to result in cultivars with good emergence capabilities. However, further observations in Hyslop/Sprague cross should be continued to discern whether F_3 and later generations maintain a large ATP pool at the seedling stage.

Based on the results presented in this study, the following conclusions can be drawn:

1. ATP, EC, and ATP/mg seed weight of cultivars vary based on temperature during imbibition and the length of the incubation period.

2. Differential varietal response for ATP, ATP/mg and EC were observed in all the temperature regimes but the relative performance of cultivars was not the same over all temperature regimes.

3. Temperature of 20° C and incubation of 72 hours appeared to be the best temperature regime capable of differentiating the ATP and AP content of cultivars.

4. ATP and EC of wheat cultivars vary among as well as within cultivars depending on the seed source and the seed size.

5. Effect of seed source on ATP varies in different cultivars; Kirac cultivar was found to be non-responsive to seed source.

6. In a given cultivar larger seeds have higher ATP but the differences in ATP among cultivars can not be attributed only to their seed size differences. Calculating the ATP/mg of seed weight, significant differences among cultivars were observed.

7. Correlations between ATP or EC and agronomic traits were not large in magnitude. ATP seemed to have relatively better associations with field performance than EC.

8. Path coefficient analysis of data combined over locations showed better contribution of ATP to yield than did the similar analysis using data from the Moro Station. This was attributed to excessive early growth and spring drought at this site.

9. Mode of inheritance of ATP, ATP/mg and EC can be explained based on the mitochondrial complementation assuming negative, additive and dominant complementation.

10. Selection in crosses capable of maintaining high ATP level in F_2 and later generations is more apt to result in cultivars with high ATP content and therefore suitable for dryland area.

11. Ability of crosses to maintain a high level of ATP in F_2 depend more on the maternal rather than paternal parent; therefore making the crosses in both ways increases the chance of finding proper F_2 populations.

SUMMARY AND CONCLUSIONS

The objectives of these investigations were as follows: 1) to

determine the importance of seed source and seed size on stand

establishment, yield and yield components of cultivars grown under

different environmental conditions; 2) to gain information about the

influence of coleoptile length and crown depth on yield and yield

components of cultivars; 3) to research the mode of inheritance of

coleoptile length and crown depth; 4) to determine possible relation-

ships between agronomic properties of cultivars measured in the

field and some biochemical characteristics of seedling measured in

the laboratory; and 5) to study the mode of inheritance of adenosine

triphosphate and adenylate energy charge contents of the seedling

and possible use of these biochemical properties in breeding wheat

cultivars for dryland areas.

Seven genetically different wheat cultivars: Hyslop,

Yamhill, Moro, Strampelli, Sprague, Kirac, and Luke were utilized

in these investigations. Crosses were made among six cultivars

(Hyslop, Yamhill, Moro, Strampelli, Sprague and Kirac) in a diallel

fashion including reciprocals. F_1 and F_2 seeds were obtained.

Field experiments were conducted at Hyslop Agronomy Farm,

Corvallis (minimum moisture stress), Rug Farm, Pendleton

(intermediate moisture stress), and Sherman Experiment Station,

Moro (maximum moisture stress). Measurements were taken on coleoptile length, crown depth, length and width of the seedling leaf, percentage of emergence, number of spikes per plot, number of spikelets per spike, number of kernels per spikelet, kernel weight, plant height, total plant yield, and grain yield. Adenosine phosphates (ATP, ADP, and AMP) and adenylate energy charge (EC) were measured in the laboratory.

Heritability estimates in narrow sense (H_{ns}) and broad sense H_{bs}) were determined. Path coefficient analysis was performed to determine the direct and indirect effects of various traits on grain yield.

The following conclusions were drawn:

1. Stand establishment effects the grain yield directly and indirectly even under high rainfall conditions such as at Hyslop Agronomy Farm.

2. The effects of seed source and seed size on stand establishment and yield vary depending upon the cultivar used and the site of the experiment. These effects were more pronounced under favorable rather than unfavorable conditions.

3. The farmer's practice of planting the seed on a per volume basis overcomes the negative effect of small seed on stand establishment, but its effect on yield depends on the genotypes used as well as the environmental conditions.

4. Coleoptile length and crown depth of cultivars are about the same under shallow seeding conditions. Coleoptile length increases almost proportionally to seeding depth and varietal differences become evident under a deep seeding condition. Crown depth also increases as the seeding depth increases, but this increase is not proportional. Furthermore increase in crown depth due to increase in sowing depth depends on cultivars and environmental conditions between sowing and crown initiation.

5. Environmental conditions also affect the varietal responses to planting depth. As the moisture stress increases, the difference between total plant yield and grain yield of shallow seeded and deep planted crops increases.

6. Direct and indirect influences of coleoptile length and crown depth on grain yield are more pronounced under unfavorable climatic conditions. Effects of coleoptile on yield can be ascribed to the effect of sowing depth, but the effects of crown depth are less influenced by the depth of planting.

7. Depth of planting per se has both direct and indirect effects on grain yield. These effects are more pronounced under moisture stress conditions and can be attributed to the prolonged activities of primary roots.

8. When plots are space planted, the effects of seed source

and seed size on yield become negligible regardless of the degree
of environmental stress.

9. Considerable genetic variabilities were found among
genotypes for coleoptile length and crown depth. These variabilities
were largely due to genetic factors which were additive, therefore
effective selection for these traits could be initiated in the F_2 genera-
tion.

10. Adenosine triphosphate and EC of wheat cultivars vary
among as well as within cultivars depending on the seed source and
the seed size. In a given cultivar larger seeds have higher ATP,
but the differences in ATP content of seed among cultivars can not
be attributed only to the differences in seed size. Effect of seed
source in ATP is cultivar dependent.

11. Correlations between ATP or EC and agronomic traits
were not large in magnitude, however ATP appeared to have better
associations with agronomic traits than EC.

12. Adenosine triphosphate affected the yield directly and indirectly.
These effects were more pronounced when data were combined over loca-
tions than when data from the Moro site were utilized. This was
associated with excessive early vegetative growth and subsequent
drought at mid and late spring at the Moro site.

13. Adenosine triphosphate and EC appear to be cytoplasmically
inherited; performance of F_1's and F_2's can be explained by different

kinds of mitochondrial complementations. Mitochondria of parents were assumed to interact with each other in different ways resulting in three kinds of complementation (negative, additive, and dominant mitochondrial complementations).

14. Additive and dominant mitochondrial complementations are important in breeding high ATP-content cultivars which are capable of fast emergence and therefore suitable for dryland areas.

15. Reciprocal crosses behave differently in the degree of complementation. Therefore in breeding programs for dryland areas, crosses should be made in both ways.

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APPENDICES

APPENDIX I

PEDIGREE AND DESCRIPTION OF CULTIVARS

Luke: (P. I. 178 38 3/Burt) * Sel 101. A semidwarf, high tillering
cultivar released by Washington State University. Luke is
resistant to the races of common smut and some of the races
of dwarf bunt in the Pacific Northwest. This cultivar is recom-
mended for dryland areas with 450 mm rainfall. In the present
study the kernel weight, coleoptile length and crown depth of
Luke ranked 4th, 7th, and 6th respectively*, among the seven
cultivars studied.

Hyslop: (Nord Despre/sel 101^2). A semidwarf, high yielding
cultivar released by Oregon State University for dryland areas
with about 400 mm of rainfall. This cultivar is resistant to
common smut. Kernel weight, coleoptile length, and crown
depth of Hyslop ranked 2nd, 5th, and 4th respectively, in the
present study.

Kirac: (Florensa-Yayla 305). This is a tall cultivar released
by Eskisheher breeding station of Turkey for dryland areas of

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*Rankings are based on the average values of cultivars over three
sites. Kernel weight is ranked based on the data obtained from
solid seeding experiments. Coleoptile length and crown depth are
ranked based on the data obtained from deep seeding parts of space-
planted nurseries.

Central Anatolia. Kirac is known to have the ability of fast

emergence under deep seeding or late seeding conditions in

Central Anatolia. It had the deepest crown but both kernel

weight and coleoptile length of this cultivar ranked 3rd among

the seven cultivars in the present study.

<u>Moro</u>: (P.I. 178383/Omar^2). A tall, fast emerging club wheat

cultivar developed by Oregon State University for dryland areas

of the Pacific Northwest with about 300 mm of rainfall. Moro

had the longest coleoptile, second deepest crown and sixth

heaviest kernel in this study.

<u>Sprague</u>: (P.I. 181268/Gains). A semidwarf but weak straw cultivar

released by Washington State University for dryland areas

where snow mold is a problem and rainfall is about

250 mm. Kernel weight, coleoptile length, and crown depth of

this cultivar ranked 7th, 6th, and 3rd, respectively.

<u>Strampelli</u>: (Libero x San Pastore - Iacometti 49). This is a soft

red facultative. Italian cultivar very well adapted to the

Mediterranean climatic conditions. This cultivar had the shallow-

est crown among seven cultivars in the present study. Kernel

weight and coleoptile length of Strampelli ranked 4th and 5th

respectively.

<u>Yamhill</u>: (Heines VII/Redmon (Alba)). A low tillering, mid tall,

high yielding cultivar released by Oregon State University for

areas which have about 450 mm of rainfall. Yamhill had the heaviest kernel, second longest coleoptile and the third shallowest crown among the seven cultivars studied in this investigation.

APPENDIX II

SUMMARY OF CLIMATIC DATA FOR CORVALLIS, MORO,
AND PENDLETON, OREGON DURING THE 1974-75
GROWING SEASON

Location and soil type	Month	Precipitation (mm)	Temperature (c)		
			Max.	Min.	Mean
Corvallis,	October	35.8	20.1	2.8	11.5
(wood burn	November	174.8	11.9	3.6	7.8
silt loam)	December	207.0	9.5	2.8	6.2
	January	118.4	8.9	2.7	5.8
	February	139.2	8.9	1.1	5.0
	March	117.8	11.1	2.1	6.1
	April	61.0	12.5	1.7	7.2
	May	52.6	18.6	5.7	12.2
	June	29.0	22	8.1	15.1
	July	15.7	26.6	10.6	18.6
	Total	951.35			
Pendleton,	October	8.9	19.4	0.0	9.7
(Walla Walla	November	39.6	10.6	1.1	5.4
silt loam)	December	44.7	7.8	-0.5	3.2
	January	94.7	5.6	-3.9	1.3
	February	42.7	6.1	-2.8	1.7
	March	24.6	11.1	-1.1	5.0
	April	43.7	12.2	0.0	6.1
	May	17.3	21.1	5.0	13.1
	June	17.5	23.3	7.8	15.6
	July	1.3	32.2	12.8	22.5
	Total	335.00			
Moro	October	9.4	18.0	2.0	10.0
(Walla Walla	November	25.9	9.3	0.4	4.8
silt.loam)	December	35.3	6.2	-1.3	2.5
	January	51.1	4.1	-3.5	0.3
	February	37.3	3.9	-3.7	0.1
	March	31.8	8.1	-0.2	3.9
	April	11.7	11.1	0.7	5.9
	May	13.5	17.9	4.7	11.3
	June	2.1	21.8	8.0	14.9
	July	10.2	29.0	14.1	21.5
	Total	219.12			

APPENDIX III

ENZYME PREPARATION AND ADENOSINE PHOSPHATES MEASUREMENT

1. BUFFERS:

HEPES buffer for enzyme reactions:

HEPES	.025M	2.98 gr.
Mg(Ac)2	.025M	2.67 gr.
H_2O		400 ml.

pH was adjusted to 7.5 adding 1N NaOH. Water was added to make the total volume of 500 ml. Buffer was kept in the cold room (temperature about 40 F).

Dialysis buffer:

HEPES	.025M	2.98 gr.
EDTA	.001M	0.17 gr.
H_2O		400 ml.

pH was adjusted to 7.0 by adding 1N NaOH. Water was added to make the total of 500 ml. Buffer was kept in the cold room and was cooled in ice before using.

Arsenate buffer:

Mg(Ac)2	.025M	0.49 gr.
Arsenate	.050M	0.90 gr.
H_2O		90 ml.

pH was adjusted to 6.95. Water was added to make the total of 100 ml, then kept in the cold room.

2. Myokinase dialysis:

In cold room, enzyme was delivered into a dialya-POR TM tube. Membrane was washed with buffer before pouring the enzyme in it. Tube was placed in a beaker containing 250 ml of dialysis buffer for 3.5-6 hours, during which the buffer was renewed once. Dialyzed myokinase was kept in refrigerator for the rest of the experiment period.

3. Extraction of luciferin-luciferase:

In cold room 200 mg of freeze-dried firefly tail (Sigma FLE-50) was ground in 1 ml of arsenate buffer. Then 2 more ml of buffer was added and mixture was ground more. Mixture was transferred to a polyethylen tube, mortar and pestle was washed with 17 ml more of arsenate buffer and wash was added to the tube. Tube was centrifuged with a balancer at 10,000 g for 10 minutes. Supernatant was kept in cold room for about 16 hours before using.

Procedure was repeated every day to prepare the enzyme for next day.

4. PEP preparation:

Samples of 8 mg of Phospho Enol Pyruvate (PEP) were weighed and kept in freezer for using in the rest of experiment period.

5. Preparation of reaction mixtures (RM):

A. One set of 3 tubes was prepared for each extract and was marked

as O, P., M.

B. R M were prepaid as follows:

R M	Assay for	HEPES-Mg buffer	PEP	Pyruvate kinase	Dialyzed Myokinase
O	ATP	2.40 ml	0	0	0
P	ATP + ADP	2.32 "	8 mg	80 ml	0
M	ATP + ADP + AMP	2.00 "	8 "	80 "	320 ml*

* Since dialyzed myokinase was diluted to 1/2 X, the amount used
was 2X

C. 100 μl R M was pipeted into respective tubes labeled O, P, and

M. 900 μl of diluted extract was added to each tube.

D. Tubes were incubated at 30 C for 15 min, then were cooled and

kept in ice.

6. ATP Standards:

ATP standard solutions were prepared of 10^{-3} M in 0.025 M

HEPES-MgAc2 buffer and kept in the freezer. Each day further

dilutions to 10^{-5}, 10^{-6}, and 10^{-7} M were prepared by adding glass

distilled water.

7. Assay light emission:

A. Light emission was assayed from standards (0.2 ml) after adding

100 μ enzyme preparation. Peak height of light emission at 3

seconds was recorded as percent intensity from an Aminco

Chem-Glow Photometer. The limearity of standards with respect to light emission was checked.

B. Two replications of 0.2 ml of incubated R M from step 5-D were delivered into 2 small reaction tubes. Light emission was assayed and recorded as original intensity (Io).

C. Another two replications of 0.2 ml of R M was taken, 10 μl of ATP standard of 10^{-6} was added to each tube, light emission was assayed and intensity was recorded as I+.

8. Calculations:

ATP, ADP, AMP, and EC were calculated as follows:

$$ATP \text{ (n mole/ml)} = \frac{(ave. \ Io)}{(ave. \ I+) - (ave. \ Io)} * \frac{0.01}{0.21} * \frac{1}{0.9}$$

ATP in O tube = ATP in extract

" " P " = ATP + ADP   in extract. Therefore P-O = ADP in extract

" " M " = ATP + ADP + AMP in extract. Therefore M-P = AMP in extract

EC = (ATP) + 1/2 (ADP) / (ATP) + (ADP) + (AMP)