This is to certify that the

thesis entitled

COMBINING ABILITIES OF THREE QUALITY PARAMETERS IN FIVE SOFT WINTER WHEATS (TRITICUM AESTIVUM L. AESTIVUM)

presented by

Susan Gildehaus Aylward

has been accepted towards fulfillment
of the requirements for

M.S. degree in Crop and Soil Sciences

Everett H. Everson

Major professor

Everett H. Everson

Date May 17, 1985

COMBINING ABILITIES OF THREE QUALITY PARAMETERS IN FIVE SOFT WINTER WHEATS (TRITICUM AESTIVUM L. AESTIVUM)

by

Susan Gildehaus Aylward

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Crop and Soil Sciences

1985

ACKNOWLEDGEMENTS

I would like to extend my sincere gratitude to all those who so graciously assisted in this project. They are:

To my adviser and committee members, Everett Everson, Tom Isleib, and Barbara Sears.

To the USDA soft wheat Quality Laboratory in Wooster, Ohio; especially Patrick Finney, Charles Gaines, and John Donelson.

To Faz Haghiri, Bert Bishop, Ross Brazee, and Bob Fox of the Ohio State Agriculture and Research Development Center in Wooster, Ohio.

To Steve St. Martin and Bruce Griffing of Ohio State University.

To my helpful friend Wen for his valuable computer expertise.

TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

ABSTRACT

COMBINING ABILITIES OF THREE QUALITY PARAMETERS IN FIVE SOFT WINTER WHEATS (TRITICUM AESTIVUM L. AESTIVUM)

By

Susan Gildehaus Aylward

A five parent diallel cross between diverse parents within the soft wheat class was grown in a randomized complete block design over two locations in Michigan. Combining abilities of the traits Particle Size Index (PSI), Particle Size Analysis (PSA), and Endosperm Separation Index (ESI) were assessed on the F_2 field data. The residual greenhouse generated F_1 seed was also tested for PSA on the laser powered Microtrac Particle Size Analyzer.

Results showed highly significant general and specific combining ability effects in approximately equal ratios for PSA and PSI in the F_2 generation. The large F_1 PSA maternal effect disappeared after one round of segregation. ESI showed highly significant general combining ability only, suggesting that it is a separate genetic trait.

No F_2 hybrid combination showed greater softness than the parent cultivar Houser. Nicking for increased hardness was the main heterotic effect. A suggestion is made for PSA to replace PSI for kernel hardness determinations.

INTRODUCTION

Understanding the genetic consequences that result from breeding strategies such as inbreeding, crossbreeding and selection are the primary objectives of the plant breeder. Plant breeding programs must accommodate both simple and polygenic inheritance of desired and undesired characters. Qualitative variation is characterized by discrete classes whereas quantitative variation forms a continuous array of metric values ranging from one extreme to the other. Nearly every function or organ including the most economically relevant in crop species shows inheritance of a quantitative nature. Even the expression of those traits strictly inherited qualitatively is in most cases modified by genes with small quantitative effects.

Breeders need methods to identify good cross combinations from which to select superior genotypes even in such highly improved crops as wheat. For this purpose, the combining abilities of the parents of individual crosses are assessed with the eventual goal of channeling these better genetic combinations into the germplasm of a new economic variety.

Soft wheat has been increasingly used not for breadbaking, but for cookies, cakes, and crackers. This significant forty year trend has mandated the evaluation of breeding lines based on their performance in pastry products. It has also stimulated research into the chemistry of wheat and flour products. Soft wheat quality tests are primarily concerned with milling, baking, and hardness parameters. These parameters and total flour yield are essential factors in assessing soft wheat quality.

At all stages of the breeding program, from early generations to advanced uniform nursery trials, quality tests are performed. Early generation screening tests are performed on as little as twenty grams of wheat to determine protein content, hardness, and alkaline water retention capacity. In later test generations where the wheat is abundant, cakes are baked in duplicate as the ultimate quality evaluation.

In the soft white wheat breeding program at Michigan State University, breeding for quality has enjoyed a high priority. As a result, some of the industry's highest quality lines have been developed here. The Michigan State wheat breeding program maintains an ongoing liaison with the U.S.D.A. Soft Wheat Quality Laboratory (SWQL) at the Ohio State Agricultural Research and Development Center (OARDC) in Wooster, Ohio. The SWQL functions as the

necessary link between the breeder and the milling and baking industries. The purpose of this research project is to study the combining abilities of the quality parameter endosperm hardness, which the industry uses to grade wheat for industrial use. Three soft white wheats developed at Michigan State University, one soft white wheat developed at Cornell University, and one soft red wheat developed at Purdue University were used in this study with the ultimate breeding goal of determining which contributed superior endosperm softness to its progeny and then incorporating superior gene combinations into the ongoing wheat hybridization system.

LITERATURE REVIEW

Hardness Measurements

Wheat varieties differ in the vitreosity, hardness, and milling behavior of their mature air-dry endosperms. Biffin (10) used a subjective visual method of classification based upon the vitreousness of the kernel. The conventional wisdom was that the more vitreous, the harder the wheat. However, he found that vitreosity was not necessarily related to quality, since some soft wheats were translucent. Visual assessment, although not eliminated, has been repudiated since soft wheats of high protein content can appear at least somewhat vitreous. The reason for this vitreousness is the layer of protein rich endosperm cells just below the aleurone layer. Because of the relative lack of starch grains in that area, the protein layer appears uniform and thus vitreous. Soft wheats typically contain many starch grains in the outer endosperm cells, and these small grains scatter and absorb light which results in an opaque or floury looking grain. Since Biffin's time hardness tests have been devised that measure resistance by an individual grain to penetration by

a stylus (35) and resistance to crushing (65). However, these methods are limited by interkernel variability and nonuniform endosperm (13). Methods using bulk samples include those that measure resistance to grinding (56), time to grind a given sample (17, 57), and particle size resulting from grinding (81, 96, 97). Williams (93) and Simmonds (76) have both suggested using near infrared reflectance spectroscopy for hardness tests. O'Buchowski and Bushuk (68) compared several methods and found that some of the methods measured different properties of the grain. Those methods based on pearling the grain depended strongly on bran properties while those based on milling properties measured the endosperm characteristics. They found that bran had a definite influence on the results of grain hardness evaluation.

Particle Size Index (PSI) Test

In the PSI test, a weighted sample of grain is ground and sifted under standard conditions and the weight of the sample passing through the sieve is measured. Soft wheats produce a large number of small particles with poor packing density and poor flow properties. This results in poorly sieving wheats. Hard wheats on the other hand tend to fracture into regularly shaped particles of larger size,

which pack well and exhibit good flow properties. This results in ease of sieving.

Several grinders have been used such as the Hobart grinder, Labconco Heavy Duty mill, Quadrumat Jr., and the Brabender grinder. These grinders have varying types of grind and so it has been difficult to standardize the PSI test. Researchers have been satisfied with the rank ordering of wheats, accepting the variability of the grinder as long as the order was similar. In a PSI comparison, Williams (94) established the degree to which individual laboratories were able to differentiate classes of wheat based on the PSI test. Three methods of grinding were used, the Labconco grinder, the Falling number KT-30, and Near Infrared Analysis (NIR). The Labconco grinder provided the least differentiation between samples and had the highest test coefficient of variation. NIR showed the highest differentiation among samples and the highest correlation to PSI values. Coefficients of correlation among all collaborators showed excellent agreement (r=.99 or better). He concluded that the PSI test is a valid reproducible method of measuring hardness in wheat and of differentiating wheat types. He also pointed out that NIR is probably the most practical rapid test for wheat hardness since it has the advantage of providing protein and moisture data as well. Miller et al. (60) found that in a comparison between the Brabender grinding time method,

PSI meth
the high
Yam
stating
appreci
paramet
without
found t
(BFY) w
first
correla
laborat
increas
Quadrum
(Finney
Quadrum
propert
obtaine

M
Chauda
flour
qualit
that t

PSI method and NIR, correlations between PSI and NIR were the highest.

Yamazaki (101) summed up 40 years of PSI research by stating that the value of kernel hardness can best be appreciated when it is directly associated with a milling parameter rather than standing alone as a kernel property without any relevance to processing quality. It has been found that PSI correlates highly with break flour yield (BFY) which is the amount of flour liberated after the first set of break roles. Stenvert (81) found a correlation of r=.5 between BFY and PSI using a Buhler laboratory mill. Yamazaki (101) found the r value increased to .85 using a Labconco grinder. With a Quadrumat Jr. mill the correlation was increased to r=.95 (Finney et al., unpublished). It is concluded that the Quadrumat Jr. mill most closely approximates the milling properties relating to endosperm fracturing and the BFY obtained on an Allis Chalmers mill.

Particle Size Analysis (PSA)

Miller et al. (57), Yamazaki and Donelson (99), and Chaudary et al. (19) have reported on the relation between flour particle size and cake quality. They found that cake quality increased as flour mean particle size decreased and that this relationship was highly correlated. Methods used

to measu
Counter
spectrosc
Coulter
distribut
negative
analysis
negative
PSI in B
has cert
over se
grade, Q

An
laser li
scattere
in diame
area of
develope
the sc
distribu
This is
placed
proper
A singl
infer t
microns

to measure particle size distribution are by Coulter Counter analysis and by near infrared reflectance spectroscopy (NIR). Donelson and Yamazaki (23) used Coulter Counter procedures to analyze the particle size distributions of coarse soft wheat flours and found high negative correlation coefficients between Coulter Counter analysis and PSI. Using NIR, Williams (93) found a negative correlation of r=-.96 between particle size and PSI in Burr milled wheat. The results indicated that wheat has certain varietal fracture patterns that are consistent over several types of milling including Allis straight grade, Quadrumat, and Allis patent pin-milling.

An alternate method of measuring particle size is with laser light scattering technology (91, 92). Light which is scattered by small particles ranging from 2 to 176 microns in diameter can be used to determine the cross sectional area of those particles. A measurement technique has been developed which determines the volume mean diameter from the scattered light, and variance of the particle distribution regardless of the nature of the distribution. This is accomplished with a unique filter, which when placed in the Fraunhofer diffraction plane, transmits the proper amount of light as a function of scattering angle. A single measurement of the scattered light flux is used to infer the particles' volumes with diameters from 2 to 176 microns. For an in depth discussion of elementary

diffracti

above mer

Befo

to a s

separati

effect

endosper

flakes

separati

this sep

approxim

bran aft

wheats w

microsco

thickne

(see Fi

microns.

whether

yield,

milling.

Flour y

Jr. ar

particl

diffraction theory and spatial filter theory, refer to the above mentioned articles (91, 92).

Endosperm Separation Index (ESI) Test

Before milling wheat, the grains are usually tempered to a standard moisture content which optimizes the separation of bran from endosperm. This procedure has the effect of making the bran tougher to grind and the endosperm softer. Hence the bran is primarily removed as flakes during the milling operation. The endosperm separation index (ESI) measures the ease or difficulty of this separation on an Allis mill. It is defined as the approximate quantity of endosperm remaining attached to the bran after break and reduction passes (94). Good milling wheats will have lower ESI values. Using scanning electron microscopy, Lineback *et al.* (51) showed that bran layer thickness differed significantly in some wheat cultivars (see Fig. 1). Mean bran thickness ranged from 50 to 76 microns. They suggested further research to establish whether correlations exist between bran thickness and flour yield, cleanness of endosperm separation and ease of milling. ESI is estimated in a microtest, the "Percent Flour Yield (PFY)", in which flours ground on a Quadrumat Jr. are sieved through a 54-mesh screen. The bran particles remaining on top of the 54-mesh screen are

measured

purposes

microtest

EGI and

classed a

two diffe

and kerne

measured and then calculated as the PFY score. For our purposes of intuitive understanding, I shall refer to this microtest as the ESI test. There is no correlation between ESI and PSI indicating again that bran separation can be classed as a separate milling parameter from PSI. Hence two different traits can be measured, ie. milling potential and kernel hardness.

Figure 1.

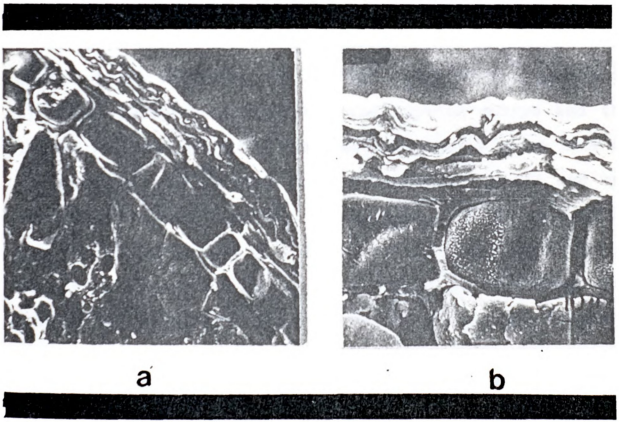

Figure 1. Electron micrographs of fractured wheat kernels at magnifications used to study bran width. Lineback et al. (1978) (51).

Kernel Ha

Ker

The
separate
male gam
sac thro
fuses wi
gamete
2). The
latter i
chromoso
from th
hybrids
genetic
whether
triploi
from th
genes c
express
ones (4
protein
1977 (7

Af
synchro

Kernel Hardness

Kernel Embryology and Tissue Development

The wheat embryo and the endosperm arise from two separate fertilization events. Fertilization occurs as two male gametes from one pollen grain penetrate to the embryo sac through the micropylar opening, whereupon one gamete fuses with the haploid egg megagamete and the other male gamete fuses with the two haploid polar nuclei (see Fig. 2). The former develops into the diploid embryo and the latter into the triploid endosperm containing three sets of chromosomes, two derived from the maternal parent and one from the paternal parent. The endosperm of reciprocal hybrids between lines with differing alleles will differ in genetic constitution a1 a1 a2 and a2 a2 a1, depending upon whether the maternal parent possessed a1 or a2. Thus the triploid inheritance adds to the genetic complexity arising from the allohexaploid nature of wheat (31). Products from genes carried on the maternally derived chromosomes are expressed in twice the dosage as the paternally derived ones (44). This has been demonstrated in gliadin storage proteins by Mecham et al. 1978 (55) and Qualset and Wrigley 1977 (74).

After the formation of the triple fusion nucleus, synchronous free nuclear division, cellularization, and

maturatic
begin dev
10-14 da
approxima
The majo
granules
soluble
leaves a
These ca
into the
cheeks t
small st
when the
Later th
whereupo
The res
cells m
then e
Finally
grains
which
practic
accumul
squeeze
and th
protei

maturation occur (see Fig. 3). Endosperm storage products begin developing when the tissue is completely formed, ie. 10-14 days after fertilization; and they continue for approximately six weeks whereupon the grain is ripe (72). The major constituents of wheat endosperm cells are starch granules and storage protein. Starch is synthesized from soluble carbohydrates which originate in the stems and leaves and which are conducted to the base of the ovary. These carbohydrates then traverse the ovary and diffuse into the endosperm (72). It is in the region of the two cheeks that starch grains are first observed. First the small starch bodies are seen near the endosperm cell nuclei when the endosperm has just filled the embryo sac cavity. Later they are seen at many cytoplasmic points of origin, whereupon they increase rapidly in number and size (72). The reserve cells are filled in varying stages. Those cells most distal to the embryo are initially filled, and then eventually those cells adjacent to the embryo. Finally, the kernels become densely packed with starch grains of various sizes except for the aleurone layer, which remains devoid of starch grains (see Fig. 4). In practically all of the endosperm cells in which starch accumulates, the protoplasmic contents die and become squeezed into the spaces between the densely packed grains, and then the cytoplasmic remnants appear embedded in a protein matrix (see Fig. 5).

Figure 2.

Figure 3

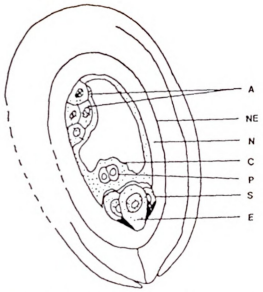

Figure 2. Structure of wheat ovule before fertilization. Antipodal cells A. Nucellar epidermis NE. Nucellar tissue N. Central endosperm mother cell C. Polar nuclei P. Synergids S. Egg cell E. (Reproduced with permission from Mares et al. 1975). Simmonds et al. 1981 (79).

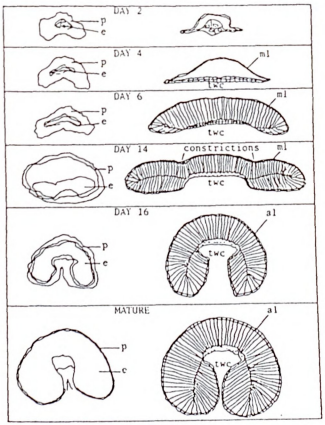

Figure 3. Changes in the shape of the developing wheat endosperm from anthesis to maturity. p = pericarp. e = endosperm. ml = meristematic layer. twc = thick-walled cells. al = aleurone. (Reproduced with permission from Fyers. 1970. 1974). Simmonds et al. 1981 (79).

Figure 4.

Figure 5.

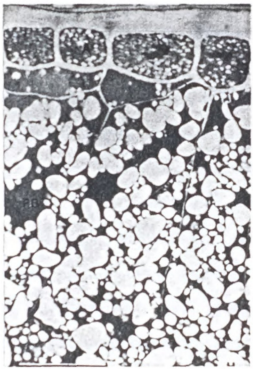

Figure 4. Mature grain has gradation in protein content from the subaleurone to the midendosperm region of the cell. Simmonds et al. 1981 (79).

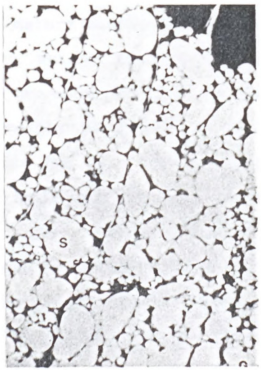

Figure 5. Thirty-six days after anthesis, A- and B- type starch granules completely fill the long prismatic endosperm cells; storage protein forms a matrix between them. Simmonds et al. 1981 (79).

Star

Star
storage
as two
develop
A-type
microns
rarely e
that amy
days of
number
starch
granule
the tot
B-type
25-50%
Fig. 7
B-type
endosp
their
experi
26).

Starch Granule (Amyloplast) Development

Starch, the principal component of carbohydrate storage in the mature seed, occurs in the mature endosperm as two populations of granules differing in size. They develop within plastids bounded by double membranes. The A-type starch (primary granules) range from 20 to 45 microns in diameter and B-type starch (secondary granules) rarely exceed 10 microns (27, 28) (see Fig. 6). It appears that amyloplasts reproduce by division during the first six days of endosperm development (18, 41), after which the number of A-type amyloplasts remains constant (14). A-type starch granules contribute 3% of the total number of granules in the mature endosperm, but account for 50-75% of the total starch weight because of their size (27, 28). B-type granules account for 97% of the numbers and from 25-50% of the weight of starch in the mature grain (see Fig. 7). Briarty *et al.* (15) estimated the numbers of B-type granules to be 900 per cell, or about 94 million per endosperm. Initially, B-type granules are spherical, but their final shape is determined by the dense packing they experience as the grain reaches physiological maturity (24, 26). They form by budding off of A-type amyloplasts.

Figure 6.

Figure 7

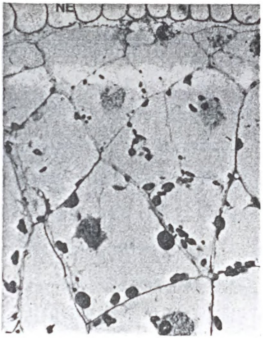

Figure 6. Five days after anthesis, intact nucellar epidermal cells (NE), large, open, and highly vacuolated endosperm cells, and early stages of A- type starch granule formation. Simmonds et al. 1981 (79).

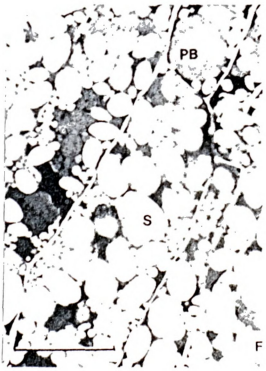

Figure 7. Twenty-seven days after anthesis, starch and protein deposits almost completely fill the cell volume. Small B- type starch granules are greatly in evidence. Simmonds et al. 1981 (79).

Pro

The
from 0.5
Their s
mature
compress
bodies a
matrix c
which th
stated
its pro
the co
lipopro
body be
endospe
amino a
still t
world.

Protein Body Development

The protein bodies in endosperm are spherical, ranging from 0.5 to 15 microns in diameter (42) (see Fig. 8). Their shape becomes extremely distorted however in the mature tissue, because of kernel desiccation and compression by starch granules. Many smaller protein bodies are fused during growth, so that the storage protein matrix of the mature wheat grain tends to be a continuum in which the starch grains are embedded (9). Adams et al. (2) stated that wheat differs from most other cereals in that its protein bodies cannot be recognized at maturity due to the compression and fusion that have occurred. The lipoprotein membranes originally surrounding the protein body become enmeshed into the general protein mass. Wheat endosperm has poor nutritional development in the essential amino acid lysine, but because of its abundance wheat is still the most important source of protein for much of the world.

Figure 8.

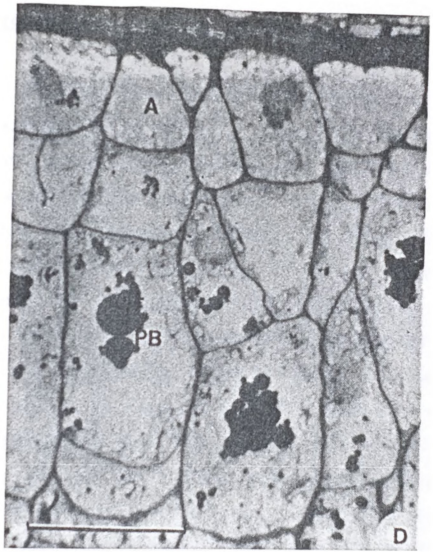

Figure 8. Fifteen days after anthesis, aleurone cells A are clearly differentiated and storage protein deposition is well under way. Simmonds et al. 1981 (79).

Sta

The
the prot
the sta
These c
derived
such as
soluble
(77) (s
and pr
membran
the pro
Barlow
desicca
dependi
hardnes
compres
the ce
remnant
9F). E
physica

It
the ma
that t
biochem

Starch/Protein Interface in the Mature Wheat Kernel

The molecular interface between starch granules and the protein matrix is complex. Carried on the surface of the starch granule are amylose and amylopectin chains. These chains are in molecular contact with components derived from the desiccated remnants of the plastid stroma such as glucose and its short polymeric chains, water soluble proteins, and remnants of the endoplasmic reticulum (77) (see Fig. 9C). This material is surrounded by lipid and protein components derived from the amyloplast membrane, and is in close contact with membrane remains of the protein bodies and the rough endoplasmic reticulum. Barlow *et al.* (7) have found that upon dehydration and desiccation, an adhesive bond forms that varies in strength depending upon the inherent and genetically controlled hardness of the grain. Simmonds (76) found that the compressed matrix consists of remnants of protein bodies, the cell nucleus, endoplasmic reticulum, and cellulosic remnants of the cell walls at cell boundaries (see Fig. 9F). Both starch granules and protein bodies are separated physically from contact by lipoprotein membranes.

It is not known how intact these membranes remain in the mature cell. It is at this starch/protein interface that the prevailing hypothesis of grain hardness offers biochemical explanations.

Figure
accumula
cells fr
days aft
reticulu
anthesis
with ro
Twenty
endoplas
D) Seve
containi
endosper
anthesis
where se
Forty da
MR and
starch g
Simmonds

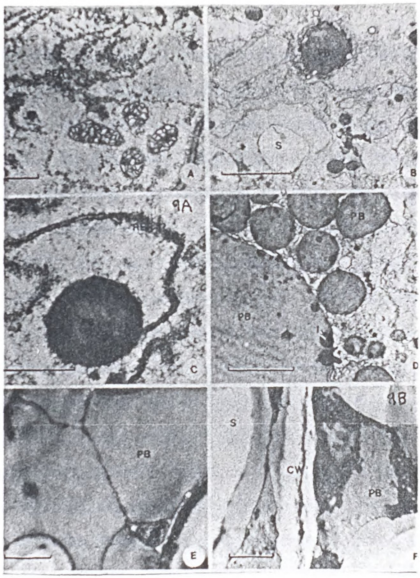

Figure 9. Development of rough endoplasmic reticulum and accumulation of storage protein in developing wheat endosperm cells from about eight days after anthesis to maturity. A) Ten days after anthesis. Extensive development of rough endoplasmic reticulum RER. Scale bar = 1 μm. B) Seventeen days after anthesis. Close association of developing protein bodies PB with rough endoplasmic reticulum. Scale bar = 10 μm. C) Twenty days after anthesis. Distended section of rough endoplasmic reticulum filled with protein. Scale bar = 1 μm. D) Seventeen days after anthesis. Numerous protein bodies containing osmiophilic inclusions I are present in the endosperm. Scale bar = 1 μm. E) Thirty-one days after anthesis. Trapped membrane remnants form osmiophilic zones where several protein bodies have fused. Scale bar = 1 μm. F) Forty days after anthesis. Mature grain shows membrane remnants MR and storage protein compressed and forming a matrix between starch granules S. CW endosperm cell wall. Scale bar = 1 μm. Simmonds et al. 1981 (79).

The

grain we

contains

10% and

conditio

endosper

amounts

However,

techniq

Th

to the

endospe

endospe

cell vo

for end

12% pro

hardnes

Or

with a

Kernel

which

Morphology of the Mature Wheat Grain

The starchy endosperm comprises roughly 80-86% of the grain weight (40). At physiological maturity, wheat grain contains about 40% water, a figure which drops to between 10% and 15% at harvest depending upon environmental conditions. Milling techniques yield between 70-80% endosperm and since these flours usually contain small amounts of bran, the theoretical purity is never achieved. However, with high quality grain and good milling techniques, it has been and continues to be improved.

There is a gradation in protein content from the outer to the inner endosperm cells, which results in a nonuniform endosperm (25). In fact, approximately 25% of the endosperm protein is contained in the 11% outer endosperm cell volume of the subaleurone region (30). Typical values for endosperm composition are 70% starch, 13% moisture, and 12% protein by weight. Whole grain density increases with hardness as reported by Stenvert et al. (82).

Physical Properties

One objective of wheat breeding is to develop kernels with appropriate hardness for the end use of the grain. Kernel hardness can best be characterized as a syndrome which encompasses a number of physical properties including

flour re
wheatmea
also re
separate
sifting
resistar
tend to
opposed
flour.
soft an
there i
residue
wheat.
during
relativ
process
more wa
convert
reason
hardnes
industr
suffic
fermen
format
granul

flour release on a single grinding, specific volume of the wheatmeal and resistance to abrasion (66). Hardness is also reflected in how cleanly the grain constituents separate, in the resulting fragment sizes, and in their sifting behavior. Harder wheats are associated with higher resistance to abrasion, grinding, and crushing and they tend to have a granular meal with a sandy texture as opposed to soft wheats which yield a characteristic fine flour. Figures 10A and 10B show starch granules from a soft and hard wheat respectively. It can be seen that there is more non starch residue in the hard wheat. This residue may contribute to the sandy texture of the hard wheat. Hard wheats incur more damaged starch granules during milling operations than do soft wheats. The relative proportion of damaged starch granules affects the processing behavior of the flour. Damaged granules absorb more water than intact granules and thus are more readily converted into sugars by beta-amylase. It is for this reason that the proportion of damaged starch and hence the hardness of the grain from which it was milled have industrial importance. Breadbakers seek a flour with sufficient starch grain damage to allow expansion during fermentation, but not enough damage to interfere with the formation of the continuous protein network around the granules (81). Soft wheat bakers seek less starch grain

damage
unferme
A
occurs
wheats
becomes
those b
content
through
content
of the
that t
from t
this d
adheri
commun
and po
bran
manipu
T
after
increa
Becaus
matrix
granul
remai

damage in their flours since their products are largely unfermented.

A significant difference in fracturing properties occurs between hard and soft wheats (see Fig. 11). In hard wheats the boundary between cell wall and cell contents becomes the line of weakness resulting in fracture along those boundaries. This occurs because their endosperm cell contents are very hard. Soft wheats tend to fracture through the cells themselves because the endosperm cell contents are not as tightly held together. Another effect of the shearing forces during milling of a hard wheat is that the subaleurone endosperm tends to separate cleanly from the aleurone cells (see Fig. 12). In the soft wheats this does not occur and so starchy endosperm is left adhering to the bran. However, Andrews (personal communication) has observed superior milling soft wheats and poor milling hard wheats leading to the hypothesis that bran separation and kernel hardness can be genetically manipulated as different traits.

The increase in damaged starch of hard wheats occurs after the initial splitting along the cell wall plane when increasing pressure causes fracturing across the cell. Because the starch granules are so firmly embedded in the matrix, the later cleavage results in fractured starch granules and storage protein (see Fig. 13). The cell wall remains attached to the released particles because cell

walls ar
occurrin
little a
that th
material
sieving
soft whe
break a
sufferi
through
granule
wheats
and fr
storage
firmly

walls and contents form a coherent whole with breakage occurring along the weakest point. In soft wheats there is little adhesion between cell walls and cell contents, so that the walls tend to mill into separate sheets of material which can sometimes cause problems in subsequent sieving and dressing procedures. The starch granules of soft wheats are not as tightly held in the matrix, and they break away more easily under increasing pressure, thereby suffering less damage (see Fig. 14). The fracture occurs through the cell contents and around individual starch granules. Symes (83) found that during pin-milling, soft wheats fractured into discrete particles of storage protein and free starch granules, while hard wheats yielded a storage protein fraction which contained starch granules firmly attached to the protein matrix particles.

Figure 1

Figure

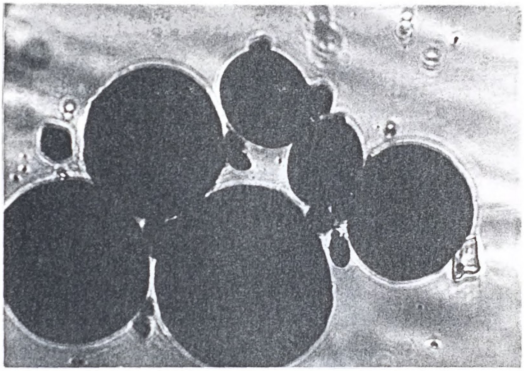

Figure 10A. Purified protein and starch preparations from the soft wheat Arthur.

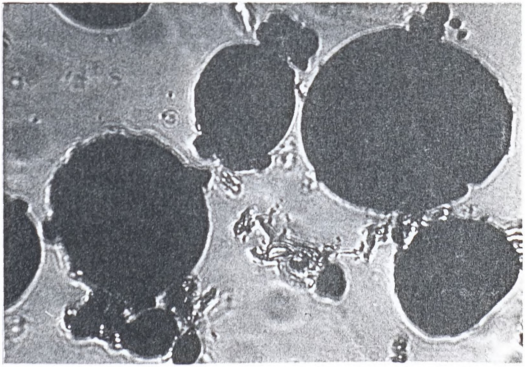

Figure 10B. Purified protein and starch preparations from the hard wheat Eagle.

Figure 1

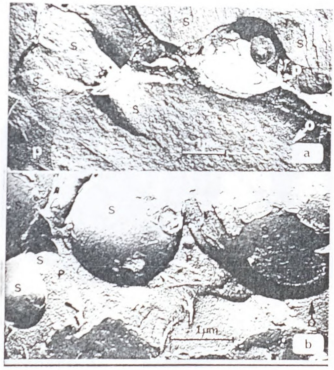

Figure 11. Freeze-etch replicas of fractured endosperm tissue. (a) Hard wheat (cr. Gabo) showing extensive cross-fracturing. (b) Soft wheat (cr. Soft Falcon) showing exposed starch granules revealed by surface fracturing. (S = starch granules; P = protein; O—► shows direction of shadowing.) Simmonds 1974 (78).

Figure 1

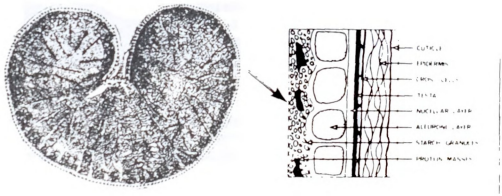

Figure 12. Transverse section of a wheat grain. MacRitchie (1980) (53).

Figure 1

Figure

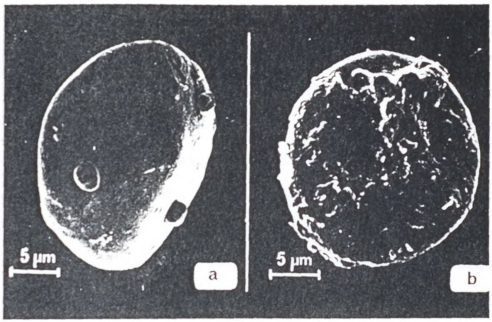

Figure 13. Scanning electron micrographs of purified starch granules prepared under non-aqueous conditions from soft (a) and hard (b) wheat varieties. Simmonds 1974 (78).

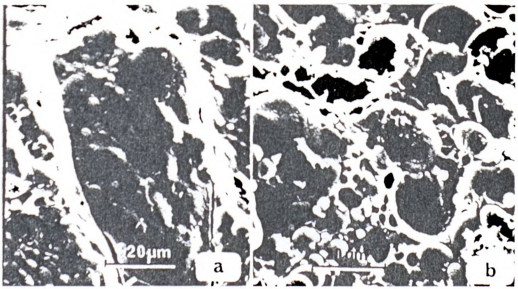

Figure 14. Scanning electron micrographs of hard (a) and soft (b) wheat kernels which have been fractured transversely. Simmonds 1974 (78).

Ma
being
differe
have lo
the p
chemica
Barlow
light
transm
micros
staini
granul
rapid
solubl
gave
evider
reticu
that
diffe
their
and t
const
sampl
cross

Biochemical Basis of Hardness

Many researchers have attempted to explain hardness as being based upon biochemical and physicochemical differences within the kernel (8, 76, 77, 82, 96). They have looked at the interrelationship between the starch and the protein constituents both microscopically and chemically in order to explain differences in hardness. Barlow (8) obtained information on this interface using light microscopy, soluble protein extraction and staining, transmission electron microscopy, scanning electron microscopy, freeze etching, and fluorescent antibody staining. He found that immediately surrounding the starch granules was a region of water soluble proteins capable of rapid swelling upon hydration (see Fig. 15). These water soluble proteins were associated with carbohydrates which gave rise to glucose upon hydrolysis. He also found evidence that amyloplast membrane, and endoplasmic reticulum residue exist around the starch granules, and that starch granules prepared from hard and soft wheats differed in the amount of protein material adhering to their surfaces. Furthermore, between the membrane remnants and the granules were spaces of varying width, relatively constant within a sample, but variable between different samples. Freeze fracturing revealed that the fracture crossed through the starch granule in proportions that

roughly
the PSI
starch
wheats
the sa
tests
floresc
surrour
demonst
in sta
than i
A
amount
by wei
protei
total
equiva
test (
al. (7
found
carbo
small
also
compo
consi
water

roughly paralleled the hardness of the wheat as measured by the PSI test (see Fig. 11). Micropenetrometer tests (8) on starch and matrix material purified from soft and hard wheats revealed that the hardness of each constituent was the same for both classes of wheat. Immunofluorescence tests on microtomed endosperm tissue stained with florescein confirmed this zone of water soluble material surrounding the starch granule. Jones and Dimler (43) demonstrated a higher proportion of water soluble proteins in starch rich fractions obtained by air classification than in the fine particle protein rich fractions.

A milled hard wheat starch granule carries large amounts of matrix resulting in protein levels of up to 8% by weight. Included are both matrix and water soluble proteins. Simmonds (78) found that extractions of the total quantity of water soluble material were roughly equivalent to the kernel hardness as measured by the PSI test (see page 5 for explanation of PSI test). Simmonds et al. (77) further examined the water soluble material. They found a carbohydrate to protein ratio of about 2:1. The carbohydrate was composed primarily of glucose, although small quantities of xylose, arabinose, and mannose were also present. Although they did not find any specific compounds at the starch protein interface that could be considered an adhesive, they found a larger amount of the water soluble material. It has been pointed out by Yamada

and Old
very st
Us
hardnes
from s
protein
the pr
either
differ
hardne
yielde
wheats
as a
starch
cleanl
wheat.
throug
geneti
T
starch
of gr
protei
compon
storag
endosp
appea

and Olden (97) that carbohydrates and glycoproteins act as very strong adhesives in biological systems.

Using nearly isogenic lines differing in kernel hardness, Wrigley (96) extracted the water soluble proteins from starch granules that had been purified from storage protein by solvent flotation. Electrophoretic analysis of the protein matrix material failed to show differences in either the gliadin or glutenin groups, ruling out differences in the matrix composition as an explanation of hardness. However, starch granules from the hard wheats yielded two to three times more material than the soft wheats. He suggested that the water soluble material acts as a cementing substance between storage protein and starch. When adhesion is weak, starch is liberated more cleanly with less adhering protein as in the case of a hard wheat. It appeared that it was a varietal trait, and that through the amount and composition of this material the genetic control of grain hardness is expressed.

The above evidence suggests that the adhesion between starch granules and the protein matrix is the determinant of grain hardness rather than the composition of the protein matrix or the intrinsic hardness of the separate components. It appears that the bonding between starch and storage protein may be stronger in hard wheat, so that the endosperm cell contents comprise a coherent whole. It appears to be a quantitative rather than qualitative

differe
materia
(65) t
sectior
compone
surrour
I
hypoth
postul
that i
then v
would
entrap
would
protei
spaces
latter
electr
starch
yet S
cemen
in ha
expla
starc
isola

difference, with the greater amount of water soluble material acting as a cementing force. According to Moss (65) the major gene discovered by Symes (85) (see next section) must control the production of one, or a group of components, in the zone of water soluble material surrounding the starch granules.

In addition to the above starch protein adhesion hypothesis of grain hardness, Stenvert and Kingswood (82) postulated that the adhesion concept is unnecessary and that if the protein matrix as a whole is not continuous, then variation in the strength of the endosperm structure would result. They stated that starch granules physically entrapped by a continuous matrix as in the hard wheats would result in a different separation of starch from protein than would a discontinuous structure with air spaces unfilled by matrix, as is found in soft wheats. The latter would release starch granules. They used scanning electron microscopy to support these suggestions.

Both hypotheses suggest variations in adhesion between starch and the protein matrix as explanations for hardness, yet Simmonds and others (8, 78, 96) postulated a specific cementing substance which is present in greater quantities in hard grain, and Stenvert and Kingswood based their explanation on the degree of physical contact between starch and matrix. This "cement" has not as yet been isolated, and further work needs to be done in this area to

estabi

and K

tentat

establish conclusive proof for this hypothesis if Stenvert and Kingswood's hypothesis is to be considered only tentative.

Figure

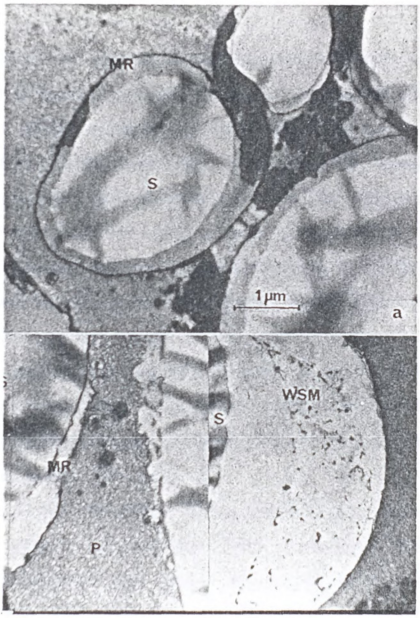

Figure 15. Electron micrographs of starch-protein interface: (a) general view showing membrane residue (MR) surrounding each starch granule (S); (b) higher magnification showing membrane residue in greater detail; and (c) micrograph illustrating network of presumed water-soluble material (WSM). Simmonds 1974 (78).

G

I
hardne
or mu
phenom
85) t
conver
This
and se
of a r
of th
genes
hardn
relat

subje
concl
betwe
unabl
subse
trait

recov
strid
signi

Genetics of Hardness

In 1908, Biffin stated that cultivars of wheat vary in hardness (10). Prior to 1935, workers postulated one, two or multiple gene differences in hardness (1). The phenomenon of grain hardness has been shown by Symes (84, 85) to be genetically controlled. By backcrossing he converted a hard cultivar into a soft one and vice versa. This effect appeared to be controlled by one major gene, and several modifying genes. He stated that grain hardness of a new wheat cultivar would be influenced by the hardness of the donor parent and by the degree to which modifying genes are carried over. Worzella (95) concluded that hardness was inherited as a quantitative character with relatively few genes involved.

Millington and Remilton (62) and Nakagawa (66) used subjective, visual inspection and reached differing conclusions. Thompson and White (88) tried to distinguish between hard and soft wheats by using percent bran but were unable to reach any conclusions. These two criteria have subsequently been shown to be independent of the genetic trait hardness.

In Syme's study (84) the exact parental type was recovered much less frequently than if the difference was strictly due to monofactorial inheritance. He found four significantly different levels in the soft class,

indica

which

that i

for th

hardne

preser

contro

chromo

Chines

posses

involv

charac

locate

Zhirov

betwee

and th

self-p

on th

chrom

envir

inter

indicating that at least two additional genes are present which influence grain hardness differences. He concluded that it is possible that the same major gene is responsible for the large effect in all cases, with different levels of hardness being the result of modifying genes. Konzak (47) presented other evidence suggesting that the genetic control of hardness is complex and involves more than one chromosome.

Using substitution lines of the cultivar "Hope" in Chinese Spring, Law et al. (50) showed that chromosome 5D possessed a single gene (Ha) for grain hardness. Lines involving ditelocentric 5D's failed to segregate for this characteristic, strongly suggesting that this gene is located on the short arm of chromosome 5D. Ternovkaya and Zhirov (87) discovered a positive functional relationship between the number of D chromosomes (from 7-14) in the seed and the density of the endosperm by studying the progeny of self-pollinated pentaploid wheat hybrids. They speculated on the possibility of creating kernels with controlled chromosome sets.

Factors Influencing Hardness

Baenziger et al. (4) found highly significant environmental, genotype and genotype by environment interaction components of variance for hardness as measured

by the
12 env
enviro
cultiv
qualit
suffic
Parish
temper
They
atmosp
wheat
was hi
hardne
grain
kernel
softe
increa
microp
conte
respo
Becau
endos
Yamaz
shoul

by the PSI test. They tested 22 soft wheat cultivars over 12 environments and found that the cultivar means from an environment were significantly correlated with the regional cultivar means. They concluded that for preliminary quality evaluations, data from one environment is sufficient for ranking cultivars with respect to PSI. Parish and Halse (70) have shown the influence of temperature and humidity during ripening on grain hardness. They found that hard wheat became harder in a more humid atmosphere during the later stages of ripening, while all wheat became harder if the temperature during this period was higher. They found that even light rain affected grain hardness with especially dry sites and years producing grain lower in PSI than other sites.

Several workers have found PSI to be affected by kernel moisture content (30, 35, 45, 63). In each case, softening of the grain was reported as moisture levels increased. Grosh and Milner (35) found by micropenetrometer tests that hardness decreased as moisture content increased. Orth (69) found that soft wheats responded more to moisture content than did hard wheats. Because moisture affects the PSI test, with higher endosperm moisture content resulting in a softer wheat, Yamazaki et al. (101) recommended that PSI measurements should be made at similar grain moisture. Alternatively,

data s

making

H

wheats

for t

found

granul

hardne

soft

wheat

corre

of a

incre

urea

data should be adjusted to a uniform moisture basis before making measurements.

Historically, it was generally accepted that hard wheats were higher in protein and that this was the reason for their hardness. However, researchers (89, 95, 101) found no correlation between protein content and granularity. Trupp (89) concluded that protein content and hardness have different genetic causes. Symes (84) found soft wheats of higher protein content than some hard wheats. Sampson (75) showed the absence of any significant correlation between hardness and protein content in lines of a soft by hard hybrid. Altman et al. (3) found that increasing grain protein percentage with foliar applied urea did not affect kernel hardness.

Dialle

widesp
dialle
crosse
can b
elemer
diago
full
where
recip
full
the r

inher
popul
parer
quant
the
prim
pare
perf
abil
inte
rela

Diallel Mating Design

Perhaps no other mating design has enjoyed the widespread use and controversy in plant breeding as has the diallel cross. A diallel is the set of all possible crosses between a given number, p, of parental lines. It can be represented by an p x p matrix, where the ijth element represents the hybrid between and the leading diagonal (ii) elements represent and selfed parents. A full diallel includes the parental lines, a set of crosses where for each ijth element $i<j$, and a set of crosses reciprocal to the first. A partial diallel is either the full diallel excluding the reciprocals or excluding both the reciprocals and parental lines.

Traditionally, diallels are used to assess the mode of inheritance of quantitative genetic characters within a population and to isolate individual variations between parents in the diallel. This genetic component of a quantitative character can be divided into three effects: the general combining ability (gca) which reflects primarily the additive genetic effect of each of the parents involved in the cross as measured by its average performance in hybrid combinations; the specific combining ability (sca) which is the specific effect caused by the interaction of certain hybrid combinations in which they do relatively better or worse than would be expected on the

basis
regard
and a
the ma
accoun
error,
charac

Pij =

be co
(Yi.
cross
vario
diffe
varia
the
If th
be o
proge
parer
the
gca
indi

basis of the average performance of the lines and is regarded as an estimate of the non-additive gene effects; and a reciprocal effect (r) which is due to the reversal of the male and female parents. If a term (e) is added which accounts for the environmental effects and observational error, then we have the following model for a quantitative character:

$$Pij = m + gca_i + gca_j + sca_{ij} + r_{ij} + e_{ij} \qquad 1.1$$

In selecting a cross, there are two important items to be considered: $\bar{Y}ij$, the desired cross character; and $\frac{1}{2}$ ($\bar{Y}i.$ + $\bar{Y}.i$), the total average of the character of all crosses having line i as a parent. Differences between the various $\frac{1}{2}$ ($\bar{Y}i.$ + $\bar{Y}.i$) values will reflect mainly differences in the gca's of the p parental lines. If the variance of gca's is small and that of sca's large, then the emphasis in selection will be on individual crosses. If the variance of sca's is small, then the emphasis will be on identifying superior parents and examining their progenies. It is the relative positioning, or ranking, of parental gca's which is of importance to the breeder, since the assumption is made that two individuals ranking high in gca have greater breeding potential than two low ranking individuals.

Va
genetic
102).
from
equati
crosse
estima
Pij =
S
analy
the
speci
resu
para
most
line

Various methods have been designed to estimate these genetic effects from the diallel cross (22, 33, 34, 39, 46, 102). The value of a particular cross may be predicted from a diallel analysis using the right hand side of equation 1.1 to predict the left hand side. If not all crosses are observed, then the missing ones may be estimated by the following:

$$Pij = m + gca_i + gca_j \qquad 1.2$$

Several assumptions must be met in the diallel analysis before modes of gene action can be construed from the above estimates. These are the assumptions first specified by Hayman (39):

a) diploid segregation
b) no differences between reciprocal crosses
c) independent action of non-allelic genes
d) no multiple alleles
e) homozygous parents
f) genes independently distributed between the parents

One weakness of diallel analysis is extrapolation of results within a diallel subset of a population to a large parametric population (46). But as Gilbert (32) noted, most breeders are primarily interested in the parental lines and their crosses and not with their

repres

words,

the r

The qu

the cr

from

Cocke

(wher

rando

from

apply

gener

are i

the i

a d

assur

domi

cova

(Wr)

(Vr)

the

requ

from

domi

Bart

representativeness of the population as a whole. In other words, the interpretation of diallel results depends upon the reference population with which the breeder started. The question to be answered is whether the parents used in the crosses are the reference genotypes or random genotypes from some reference population. Griffing (34) and Cockerham (21) discussed both analyses with fixed effects (where the parental genotypes are the population) and with random effects (where the parents are a sample of genotypes from a reference population). Fixed effects estimates apply only to the included genotypes and can not be generalized to some universal population. Random effects are interpreted relative to a reference population of which the included genotypes are a random sample.

Criticism of the analysis of information obtained from a diallel deals with violations of two statistical assumptions. The first is in Hayman's estimation of dominance and epistasis using the regression of the covariance between offspring and their nonrecurrent parents (Wr) on the variance of all the offspring of the rth parent (Vr). Gilbert (32) has noted that Wr and Vr do not fulfill the basic assumptions of independence and normality required for regression analysis, so that any departure from simple linearity may not actually reflect parental dominance as Hayman contends. Gilbert suggested applying Bartlett's test for homogeneity of variance to Vr to test

this, s
Mayo (5
Vr and
that t
assess
stated
assess
V
determ
popula
diffe
the p
are a

criti
assum
gene
pare
conc
esti
et
anal
obta
pos
com
gra

this, since it is sensitive to departures from normality. Mayo (54) noted that heteroscedasticity, ie. dependence of Vr and Wr on each other, is inherent in the regression and that therefore significance testing cannot be used in assessing the significance of the regression line. He stated that inspection for outliers is a valid use for assessment of Hayman's Wr-Vr graph.

Variety cross evaluations are important in breeding to determine the relative potential of varieties as breeding populations and to evaluate the response of varieties to different recurrent selection schemes (37). Hence, gca of the parents and sca of the crosses of promising varieties are appropriate for a fixed effects diallel analysis.

Sokal and Baker (80) and Baker (6) have also addressed critical issues in the diallel analysis; specifically that assumptions of no epistasis and independent distribution of genes are unrealistic especially for the small number of parents usually included in a diallel analysis. Baker concluded that most diallel experiments are restricted to estimation of gca and sca mean squares and effects. Tandon et al. (86) compared the graphic and combining ability analysis techniques of diallel crosses by using data obtained from the F_1, F_2, and F_3 generations of all possible combinations of five varieties of wheat. The combining ability analysis was found to be better than the graphic analysis in predicting the prepotency of crosses,

especi

domina

identi

giving

degree

Heter

expre

can

compl

defi

comm

cros

hete

hete

(64)

dist

spec

feas

gene

effe

bee

cou

How

especially so in later generations when the expression of dominance effects is reduced. Graphic analysis failed to identify small but significant non-allelic effects, while giving consistent results only in the presence of a high degree of dominance.

Heterosis and Maternal Effects

Heterosis is defined as the enhancement of trait expression manifested in a cross over each parent. This can result from increased heterozygosity or from complementary additive gene action. Economic heterosis is defined as the superiority of the F_1 hybrid over the best commercial variety released for cultivation. In cross-pollinated species such as maize, the species where heterosis was first exploited with great success, maximum heterosis occurs at an optimum level of genetic diversity (64), and not necessarily in crosses between the most distantly related individuals. In a self-pollinated species such as wheat, the exploitation of heterosis is feasible since the necessary components, male sterility, genetic restoration of fertility, and instances of effective cross pollination under field conditions have been established. Lines showing high gca and high sca could be used successfully in a F_1 hybrid wheat program. However, the fixation of heterotic genes in advanced

genera

geneti

additi

behave

can be

been

16, 1

actio

found

varia

cross

found

wheat

to t

high

yiel

did

cros

abil

qual

esti

Mil

gra

generations can utilize only that segment of the total genetic variability which results from the action of additive genes and those epistatic gene interactions which behave additively, because only these types of gene action can be retained by subsequent inbreeding.

Heterosis for yield and yield components in wheat has been well established in both F_1 and F_2 generations (5, 12, 16, 17, 38, 49, 52, 56, 90). These investigations of gene action and combining abilities by diallel analysis have found a preponderance of additive (gca) genetic variability. Baily (5) demonstrated this in three way crosses where high parent heterosis was seen. Bitzer (12) found that developing successful high yielding hybrid wheats came from high yielding x high yielding crosses due to the large amount of gca. He found that low yielding x high yielding crosses that increased genetic diversity for yield did not result in unusual levels of sca effects, and did not result in greater heterosis than high x high crosses.

Gyawali (36) and Pearson (71) have conducted combining ability analyses on pearling resistance as a softness quality parameter, but as stated before, this is a dubious estimate of endosperm hardness.

Maternal effects have also been established in wheat. Millet and Pinthus (61) demonstrated maternal control of grain weight, presumably through the supply of nutrients to

growth

obtain

by th

freque

F_1 sp

exert

signi

hybri

addit

deter

growth substances to the spike. The weight of F_1 grain obtained from the maternal plants was controlled primarily by the genotype of the maternal tissues. However, the frequency distribution of the F_2 grain weight obtained from F_1 spikes indicated the presence of genotypic effects exerted by the endosperm or embryo. Bingham (11) found a significant paternal effect in the backcrosses of F_1 hybrids, and concluded that genotype of the grain in addition to the assimilative capacity of the plant was the determinant of grain size.

'Augu
culti
aesti
exper
homoz
on t
They
Univ
bree
Mich
beer
PSI
Ped

pos
of
sub
see
one
re

METHODS AND MATERIALS

Three soft white winter ('Houser', 'Tecumseh', 'Augusta') and two soft red winter ('Arthur', 'Hillsdale') cultivars of diverse ancestries of Triticum aestivum L. aestivum were used as parents in a full diallel cross experiment. Each parent was assumed to be homogeneous and homozygous. The cultivars were selected as parents based on their diverse PSI scores within the soft wheat class. They represent cultivars developed in the Michigan State University, Cornell University, and Purdue University wheat breeding programs and are all adapted cultivars for Michigan. PSA and ESI for these five cultivars had not been previously determined. The three year averages for PSI and cultivar parentages are given in Table 1. Pedigrees are written in the style of Purdy et al. (73).

The five parents were crossed in the greenhouse in all possible combinations (including reciprocals) in the spring of 1983. The F_1 seed from each cross was bulked for subsequent fall planting, and there was enough residual seed for PSA analysis (5 mg). The seed borne on a plant is one generation ahead of the plant, so that whenever reference to a generation is made, it is to the seed

generati

in rand

at each

in rows

experim

Saranac

rows w

Augusta

possibl

experi

and to

F

were e

three

sample

and ES

of in

in a

weigh

54-me

After

remai

weigh

was

20/o

ESI

generation. In the fall of 1983, the F_1 seed was planted in randomized complete block designs with two replications at each of two locations. The seed was spaced 15 cm apart in rows 4.6 m long. Rows were spaced 45 cm apart. The experiments were located in East Lansing, Michigan and Saranac, Michigan. The randomly distributed experimental rows were interspersed with check rows of the cultivar Augusta in order to minimize wind chill and subsequent possible winter kill. Check alleys 1.8 m wide bordered the experimental plots on all four sides for the same purpose and to minimize edge effects.

F_2 seed was harvested in August of 1984. The samples were equilibrated in a room at 60% humidity and 70°C for three weeks to a uniform moisture level of 11.5 ± .4. The samples were then tested for PSI, ESI, and PSA. The PSI and ESI measurements were determined from 4 random samples of individual plants in each plot. Five grams were ground in a Quadrumat Jr. mill at 40°C. The coarse meal was weighed and placed in a Sonic Sifter with two sieves, a 54-mesh screen on top and a 106M screen on the bottom. After two minutes at a sift amplitude of 8, the meals remaining on top and on the bottom of the two screens were weighed. The sample weight on top of the 54-mesh screen was adjusted to a 20 gram sample by the formula: 20/original sample weight x sifted sample weight. Then the ESI determination was calculated with the formula:

20-adjus
sample h
sample w
sample w
random s
the Mic
series o
non-aqu
scatter
For the
the sam

A

the F_2
observa
statis

Y_{ijklm}

where
replic
locat
L, R,

compo
cross
the p
locat

20-adjusted sample weight/20. The weight of the remaining sample below the 106M screen was divided by the initial sample weight for the PSI determination. This remaining sample was bulked for each of the 4 cross samples. Three random samples of this bulked meal were analyzed for PSA on the Microtrac Particle Size Analyzer (see Fig. 16). A series of three five mg samples were suspended in 200 ml of non-aqueous methanol over a 200 second time period for scatter angle detection and mean volume diameter analysis. For the F_1 PSA analysis, the residual F_1 seed was tested in the same way as the F_2 samples.

A conventional analysis of variance was performed on the F_2 data from the diallel. Total variation among observations was partitioned according to the following statistical model:

$$Y_{ijklm} = M + L_i + R_{ij} + G_{kl} + (LG)_{ikl} + E_{ijkl} + w_{ijklm}$$

where M is the mean; L is the location effect; R is the replication effect; G is the genotypic effect; (LG) is the location by genotype interaction; E is the error term over L, R, and G; and w is the sampling error term.

The genotype sum of squares was partitioned into three components: an overall contrast between parents and crosses with a single degree of freedom, variation among the parents themselves, and variation among crosses. The location by genotype sum of squares was partitioned in a

fashi
envir
aggre
denom
Inter
exper

in or
squa
1 (f
exte
reci

C_{kl}

wher
the
is
the
effe
Gri
as

per
the
cro
di

fashion analogous to that used for genotypes. Because environmental effects were assumed to be random, the aggregate location by genotype mean square was used as the denominator in F-ratios to test genotypic effects. Interaction effects were tested using the mean square for experimental error.

The F_1 data was analyzed as a completely random design in one block for gca and sca effects. The F_2 cross sums of squares was further partitioned using Griffing's (34) model 1 (fixed) method 3 analysis of combining ability with the extensions proposed by Cockerham (20) pertaining to reciprocal effects:

$$G_{kl} = g_k + g_l + s_{kl} + m_k - m_l + r_{kl}$$

where g_k and g_l are the gca's of the parents involved in the cross; s_{kl} is the sca of the particular cross; $m_k - m_l$ is the maternal effect between the two parents, and r_{kl} is the reciprocal effect of the particular cross. Reciprocal effects were calculated for each cross according to Griffing (34) where $m_k - m_l + r_{kl}$ were pooled and treated as one effect.

Mean squares for diallel effects were expressed as percentages of the among cross mean squares to estimate their relative importance in accounting for variation among crosses. Parent heterosis, h_k, was estimated by taking the difference between the single cross hybrid and their

midpar

observ

their

was e

midpa

midparent value. If P_k and $P_{k'}$, and SCF2 represent the observed PSA, PSI and ESI values of parents k and k' and their mean reciprocal crosses respectively, then heterosis was estimated as $\sum_{i=1}^{5}$ (SCF2 - MPSC) where MPSC is the midparent value or $(P_k + P_{k'})/2$.

Table

Cultiv Code	
MO201	
MO280	
MO284	
MO295	
MO300	
Pedic	
Arth	
3/Wa	
2/Ho	
Farm	
Tecu	
W38/	
Vigo	
427a	
Hou	
Als	
Hil	
Vah	
14.	
Aug	
Bre	

Table 1. Parental lines and 3 year averages (1979-1981) for the endosperm trait Particle Size Index (PSI).

Cultivar Code	Cultivar Registration Name	No. in Diallel	Type	PSI
MO201	Arthur	1	soft red	35.1
MO280	Tecumseh	2	soft white	37.8
MO284	Houser	3	soft white	41.3
MO295	Hillsdale	4	soft red	34.8
MO300	Augusta	5	soft white	37.8

Pedigrees of cultivars:

Arthur = Minhardi/Wabash/5/Fultz Selection/Hungarian/2/38/3/Wabash/4/Fairfield/6/Redcoat sib/Wis, CI12633/7/Vigo/4/T/2/Hope/Hussar/3/Fulhio/Purkof (Purdue 427a-1-3)*3/5/Kenya Farmer.

Tecumseh = Minhardi/Wabash/5/Fultz Selection/Hungarian/2/W38/3/Wabash/4/Fairfield/6/Redcoat sib/Wis, CI12633/7/Vigo/4/Trumbull/2/Hope/Hussar/3/Fulhio/Purkof (Purdue 427a-1-3)*3/5/Kenya Farmer.

Houser = N10B/NY-W-Rye/2/HCPE-HS/YW/3/Genesee/2/CI12658/Als/3/Avon-I2205.

Hillsdale = Asosan/Genesee*4/6/Purdue F4126A9-32-2/5/Vahart/Frondoso/Vahart/CI12658/3/Asosan/4/Norin 10/Brevor 14.

Augusta = Genesee/Redcoat/4/Genesee*5/3/Yorkwin//Norin 10/Brevor 14.

Figur

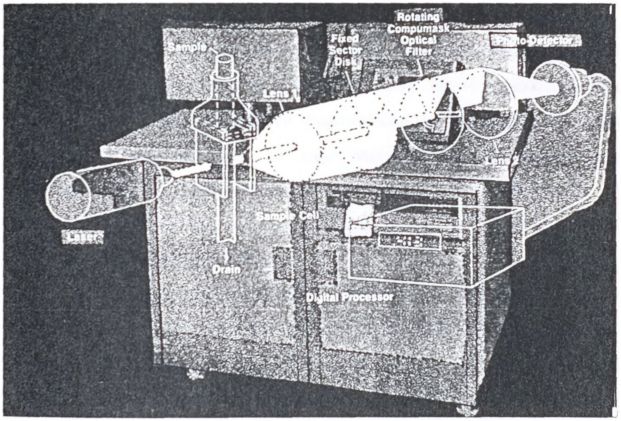

Figure 16. The Microtrac Particle Size Analyzer.

two

Inde

in T

valu

comb

15,

valu

wit

fin

Cou

usi

PSI

PSI

Par

det

adv

th

Co

av

RESULTS AND DISCUSSION

The means of the raw data over the two replications in two environments for F_2 Particle Size (PSA), Particle Size Index (PSI), and Endosperm Separation Index (ESI) are given in Tables 10, 11, and 12 (see Appendix). The pooled mean values for F_1 PSA, F_2 PSA, PSI, and ESI from which the combining analyses were made are given in Tables 13, 14, 15, and 16 (see Appendix).

Pearson's correlation coefficient between the raw values of F_2 PSA and PSI was highly significant at r=-0.70 with 398 degrees of freedom. This is consistent with the findings of Donelson and Yamazaki (23), using the Coulter Counter and with both Williams (93) and Miller et al. (60), using NIR. In the two latter studies, NIR correlated with PSI at an average value of -0.94. The results suggest that PSA measured by NIR and by the laser powered Microtrac Particle Size Analyzer give sufficiently precise determinations of particle size. NIR does have the advantage in supplying additional moisture data. However, the Microtrac Particle Size Analyzer can be used confidently for hardness determinations where NIR is not available. The lower correlation of -0.70 between PSI and

PSA i

in pa

secon

PSI's

exper

(5 mg

howev

sift

PSA in this study compared with those previously cited may in part be due to the breakdown of particles over the 200 second test period in the non-aqueous methanol, to the PSI's environmental component as will be shown, to experimental error secondary to the small PSA sample size (5 mg), or to any combination of the above. It is clear however, that both NIR and PSA can replace the grind and sift method of PSI determination where applicable.

F_2 Ge

envir

in T

cross

but

hete

char

valu

pare

8 on

thre

genc

sig

ins

PSI

int

is

may

gra

ove

coe

the

ch

F_2 Generation Analysis of Variance

All three F_2 characters showed highly significant environmental and genotypic components of variation as seen in Table 2. The mean difference between parents and crosses show highly significant variation for PSI and PSA but not for ESI, meaning that there was a significant heterotic effect over the parents for the two specified characters. This effect can be observed in the heterotic values where the greatest mean performance change over any parent is -3.29 for PSI and 5.65 for PSA (see Tables 7 and 8 on pages 70 and 74, respectively).

Variation among parents was highly significant for all three characters. Although PSI and ESI showed significant genotype by environment interactions, PSA did not exhibit significance for this interaction. Moreover, PSA exhibited insignificant among parent by environment interaction while PSI and ESI showed highly significant and significant interactions, respectively. These results suggest that PSA is less sensitive to the environment than PSI, and that it may be a more heritable character from which to assess grain hardness. The larger environmental component in PSI over PSA may assist in explaining why their correlation coefficient was not higher. The results also suggest that there was considerable genetic diversity for all three characters among the parents and the crosses.

Table

Sour
Envi
Reps
Genc
Pa
Ar
Ar
G*E
(
(
G
S
M
I
G*I

*,

Table 2. ANOVA including Combining Ability Analysis (34) for the 3 traits Particle Size Analysis (PSA), Particle Size Index (PSI), and Endosperm Separation Index (ESI) from a randomized complete block experiment in 2 locations in a 5 x 5 diallel cross of winter wheat for the F_2 generation: Mean Squares.

Source	df	PSI	ESI	PSA
Environment	1	148.73**	1045.97**	288.66**
Reps/env	2	35.44	5.77	2.95
Genotypes	24	147.18**	12.06**	179.72**
Parents vs. crosses	1	246.11**	.009	780.56**
Among Parents	4	97.64**	24.14**	94.37**
Among Crosses	19			
GCA	4	340.94**	35.43**	325.118**
SCA	5	267.96**	3.21	317.85**
Maternal	4	14.46	3.90	36.82
Reciprocal	6	22.35	3.90	19.70
G*E	24	18.42*	4.28*	25.25
(P vs. C)*E	1	12.24	0.66	1.81
(Among P)*E	4	32.09**	6.97*	4.83
GCA*E	4	38.41**	8.83**	75.49*
SCA*E	5	10.15	1.70	4.87
M*E	4	7.50	2.62	23.56
R*E	6	11.17	3.34	27.41
G*E*R	48	8.39	1.99	22.02
	300	3.50	1.13	(200) 1.95

*,** Denote significance at the .05 and .01 α-levels, respectively.

F_1 Pa

mater

midpa

not k

the

here

dire

vers

abil

to a

sign

comp

For

was

effe

tri

to

eff

dif

was

for

di

co

pe

F_1 Particle Size Analysis (PSA)

Since a partial diallel was performed on the F_1 material, direct comparison between the hybrids and the midparent values to identify the amount of heterosis could not be made. Therefore the difference in heterosis between the F_1 and the F_2 generations could not be established here. Also, since the F_1 material was greenhouse grown, direct comparisons between values of the F_1 generation versus the F_2 generation could not be made. The combining ability analysis for PSA in the F_1 was performed according to a diploid and a triploid model. Results showed highly significant general, specific, maternal, and reciprocal components of variation for both models as seen in Table 3. For the diploid model, 16% of the variance accounted for was due to gca, 20% was due to sca, 40% was due to maternal effects, and 24% was due to reciprocal effects. For the triploid model, 14% of the variance accounted for was due to gca, 20% was due to sca, 42% was due to maternal effects, and 24% was due to reciprocal effects. The difference between the diploid model and the triploid model was 2% less in gca effects and 2% more in maternal effects for the triploid model. Hence, using the triploid model did not change the proportion of combining ability components to any appreciable extent. According to the percentages of variance accounted for, the maternal

varia

other

genom

two m

genom

ratio

compo

effe

show

Indi

exhi

0.53

and

domi

high

comb

pre

amo

dom

whe

at

1.

thi

in

an

variance accounted for approximately twice as much as the other effects. It is in this generation that the maternal genome exerts its most profound effects on the kernel since two maternal copies are translated for every one paternal genomic copy. The ratio between the estimated gca and sca ratios is 1:1.3 indicating that secondary to the maternal component for this trait, the additive and non-additive effects are equally important in its inheritance, with sca showing slightly more effect.

Table 4 gives the gca estimates for this character. Individually, Hillsdale at 1.30 and Houser at 1.42 exhibited greater gca than the other three with Arthur at 0.53 intermediate between them and both Tecumseh at -1.44 and Augusta at -1.82. This means that located within the dominant maternal effects in this F_1 generation, there is highly significant genetic variability due to additive gene combinations and/or additive by additive epistasis. Also present is highly significant sca, which indicates the amount of dominant, additive by dominant, and dominant by dominant genetic variability. This can be seen in Table 5 where the crosses (order does not denote sex) Houser/Arthur at 2.33, Hillsdale/Tecumseh at 2.34, Augusta/Arthur at 1.17, and Augusta/Tecumseh at 2.12 exhibited greater sca than the remaining crosses. The reciprocal effects as seen in Table 6 showed that the crosses Tecumseh/Arthur at 7.98 and Houser/Arthur at 5.82 where Arthur was used as female

were

The i

page

femal

Augus

had

tive

in m

will

Augu

in

desi

test

dete

were considerably greater than the remaining crosses. The individual mean values for the crosses in Table 13 on page 85 reveal that the softest hybrids are (male first/ female second) Arthur/Tecumseh with a PSA of 61.83 and Augusta/Hillsdale with a PSA of 69.61. These two hybrids had among the lowest sca's at -3.27 and -2.14, respectively. This suggests that a higher amount of sca results in more hardness, not more softness. That this is the case will be seen in the next section. Arthur/Tecumseh and Augusta/Hillsdale are the combinations that could be used in a hybrid wheat program where optimum softness was desired, using Tecumseh and Hillsdale as A lines. Yield testing of these two hybrids would be the next step in determining their usefulness in a hybrid wheat program.

Table 3. *Mean squares for general (gca), specific (sca), maternal, reciprocal combining abilities, and error for the* F_1 *and* F_2 *hybrids of the endosperm*

Table 3. Mean squares for general (gca), specific (sca), maternal, reciprocal combining abilities, and error for the F_1 and F_2 hybrids of the endosperm trait Particle Size Analysis (PSA), F_2 hybrids of the endosperm trait Particle Size Index (PSI), and F_2 hybrids of the bran trait Endosperm Separation Index (ESI), all involving a 5 parent diallel of winter wheat.

Source	df	PSI	ESI	F_2 PSA	F_1 PSA Triploid Model	F_1 PSA Diploid Model
Among Crosses	19					
GCA	4	340.94**	35.43*	325.118**	43.43**	47.45**
% Var		47%	78%	41%	14%	16%
SCA	5	267.96**	3.21	317.85**	47.21**	47.21**
% Var		46%	7%	50%	20%	20%
Maternal	4	14.46	3.90	36.82	125.72**	118.69**
% Var		2%	6%	5%	42%	40%
Reciprocal	6	22.35	3.90	19.70	48.81**	48.81**
% Var		5%	8%	4%	24%	24%
G*E (F_2)	24	18.42**	4.28*	25.25		
Error (F_1)					3.401	3.401

*,** Denote significance at the .05 and .01 α-levels, respectively.

% Var = Percent of the variance accounted for.

Table

G^1	
G^2	
G^3	
G^4	
G^5	
SE(d	
LSD	

$^{+}$St

Table 4. Estimates of general combining ability effects (gca) for the 3 characters Particle Size Analysis (PSA) in the F_1 generation in 1 location and F_2 generation in 2 locations, Particle Size Index (PSI) in the F_2 generation in 2 locations, and Endosperm Separation Index (ESI) in the F_2 generation in 2 locations from all possible crosses involving 5 winter wheat parents.

	PSI	ESI	F_2 PSA	F_1 PSA
G^1	-2.98	0.83	3.15	0.53
G^2	-0.68	0.39	1.19	-1.44
G^3	1.59	-0.32	-2.17	1.42
G^4	0.86	-0.67	-0.97	1.30
G^5	1.20	-0.21	-1.20	-1.82
SE(gi-gj)†	.62	.29	.83	.53
LSD	1.54	.74	2.08	2.60

†Standard error of the difference between two effects.

Table

Pare

1

2

3

4

St

SE

SE

L

†

Table 5. Estimates of Specific Combining Ability (SCA) effects for the traits Particle Size Analysis (PSA) measured from F_1 hybrids in one location and F_2 hybrids over 2 locations; and for the trait Particle Size Index (PSI) measured from F_2 hybrids in two locations from all possible crosses involving 5 winter wheat parents.

Parents		2	3	4	5
1	F_1 PSA	-3.27	2.33	-0.25	1.17
	F_2 PSA	-5.45	2.82	2.37	0.24
	PSI	4.22	-1.90	-1.37	-0.97
2	F_1 PSA		-1.22	2.34	2.12
	F_2 PSA		1.84	1.72	1.86
	PSI		-2.42	-0.74	-1.08
3	F_1 PSA			0.03	-1.17
	F_2 PSA			-3.34	-1.34
	PSI			2.18	2.11
4	F_1 PSA				-2.14
	F_2 PSA				-0.78
	PSI				-0.08
Standard Error†			F_1 PSA	F_2 PSA	PSI
SE(sij-sik)			.75	1.18	0.87
SE(sij-skl)			.53	.83	0.62
LSD			2.60	2.08	1.54

†Standard error of the difference between two effects.

Tabl

Par						
1						
2						
3						
4						
5						
Mea						

Table 6. Estimates of reciprocal combining ability effects for the endosperm trait Particle Size (PSA) measured from F_1 hybrids, from all possible crosses involving 5 winter wheat parents where maternal and reciprocal degrees of freedom are pooled, df = 10, according to Griffing (33).

Parents	1	2	3	4	5	Mean
1		7.98	5.82	-0.37	1.24	3.67
2	-7.98		-1.11	-2.14	-0.45	-2.70
3	-5.82	1.11		1.04	0.76	-0.73
4	0.37	2.14	-1.04		-1.73	-0.07
5	-1.24	-0.45	-0.76	1.73		-0.18
Mean	-3.67	2.70	0.73	0.07	0.18	0

mate
Sinc
of r
inhe
cont
con
gen
eff
and
Fig
bet
ger
sca
mo
co
ro
ha

Pe
a
t
w
i

F_2 Particle Size Analysis (PSA)

Table 3 shows that in the second generation the maternal and reciprocal effects have all but disappeared. Since the large F_1 maternal effect vanishes after one round of random segregation, this effectively rules out maternal inheritance for this endosperm trait. Hence the genotypic contribution of the endosperm trait particle size is controlled predominantly by the triploid endosperm tissue genotype. Selection for PSA would be correspondingly more effective in this generation than in the F_1 since more gca and sca are apparent after the first round of segregation. Figure 17 shows visually that there is no relationship between the gca's of the two generations. In the F_2 generation, the gca variance is again almost equal to the sca variance (see Table 3), with the sca having slightly more effect. This suggests that the character is controlled by additive and non-additive gene effects in roughly equal proportion, with non-additive gene action having slightly more effect.

In the F_2 generation, Table 4 reveals that the largest PSA gca effects were exhibited at 3.15 by Arthur, which had also shown the largest maternal and reciprocal effects in the F_1 (see Table 6). Along with Arthur, Tecumseh at 1.19 was the only other parent exhibiting positive gca as seen in Table 4. The fact that parents exhibit negative gca

sugg
alle
nega
5 r
Hill
sca
at
at
thi

mid
com
lar
fiv
exh
hov
in
a
PS
th
co
sc
Ho
4,
cr
Hi

suggests that they had a higher proportion of negative alleles for this character. Houser had the highest negative gca at -2.17 followed by Augusta at -1.20. Table 5 reveals that the crosses Houser/Arthur at 2.82 and Hillsdale/Arthur at 2.37 exhibited the greatest amount of sca. An intermediate amount was shown by Houser/Tecumseh at 1.84, Hillsdale/Tecumseh at 1.72, and Augusta/Tecumseh at 1.86. The reciprocal effects were not significant for this trait and therefore will not be discussed further.

When mean performance was measured against the midparent for an estimate of heterosis as in Table 7, the combinations using Arthur, Tecumseh, and Houser had the largest positive change, with Arthur predominating. All five cultivars had relatively large effects with Hillsdale exhibiting the least amount of change. Positive heterosis however, a term typically associated with yield components in wheat, is not in fact reflected in these results. Since a higher value reflects a harder wheat as in this case for PSA, what is reflected is actually negative heterosis. In this case the additive and non-additive effects are combining to nick for greater hardness, not softness. The softest wheat according to mean parental performance is Houser at a PSA of 56.7 which shows a positive change of 4.1 in hybrid combination. The next softest wheat was the cross Hillsdale/Houser with a mean PSA value of 58.9. Hillsdale show the least amount of negative heterosis with

a ch
relat
soft
tend
hete
effe
of a
be
Tecu

a change of 2.53, but even in spite of Hillsdale's high relative negative heterotic value, Houser remains the softest wheat. This is due to the hybrids' greater tendency toward hardness as measured by the amount of heterosis over the midparent. Moreover, according to gca effects, Houser would be a good choice due to the absence of additive genes for hardness. Negative sca effects would be desirable for soft wheats also as in the case for Tecumseh/Arthur at -5.45 and Hillsdale/Houser at -3.34.

Figu

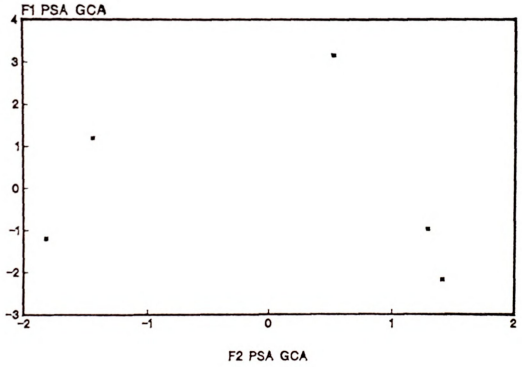

Figure 17. F_1 vs. F_2 Particle Size (PSA) general combining ability effects (gca).

Table

Pare	
1 SC	
	ME
2 SC	
	MI
3 S	
	M
4 S	
	M
5 S	

Table 7. Heterosis for the endosperm trait Particle Size Analysis (PSA) in the F_2 generation when measured by the sum of the single cross hybrid (SC F_2) - midparental differences (MPSC) for each parent.

Parents	1	2	3	4	5	Σ(SC F_2-MPSC)
1 SC F_2	63.2	64.3	69.2	69.9	67.5	+5.65
MPSC		63.0	60.0	63.3	62.0	
2 SC F_2		62.7	66.2	67.3	67.2	+4.38
MPSC			59.7	63.0	61.8	
3 SC F_2			56.7	58.9	60.6	+4.10
MPSC				60.0	58.8	
4 SC F_2				63.3	62.4	+2.53
MPSC					62.1	
5 SC F_2					60.8	+3.25

F_2 Pa

effec
mate
sign
gene
Tabl
exhi
Tecu
4.2
Hou
bet
see
mic
het
ne
th
te
th
ha
A
s
s
a
c

F_2 Particle Size Index (PSI) Analysis

The F_2 PSI showed highly significant gca and sca effects in a gca:sca ratio of 1:1 and showed nonsignificant maternal and reciprocal effects. This means that there are significant sources of both additive and non-additive genetic variability for the trait in equal importance. Table 4 reveals that Augusta at 1.20 and Houser at 1.59 exhibited the greatest gca effects and Arthur at -2.98 and Tecumseh at -0.68 showed the least. Tecumseh/Arthur at 4.22 exhibited the greatest sca effects, with Hillsdale/Houser at 2.18 and Augusta/Houser at 2.11 intermediate between the former combination and the remaining crosses as seen in Table 5. The mean performance measured against the midparent values for this trait also showed negative heterosis, as did PSA (see Table 8). In this case, a negative value actually reflects negative heterosis, so that the least negative result reflects the maximum tendency toward softness. Again, Arthur at -3.29 showed the greatest tendency toward lower PSI values and hence harder wheats. Tecumseh at -1.98, Houser at -2.02, and Augusta at -1.72 were intermediate with Hillsdale at -0.70 showing the least amount of negative heterosis. The softest performing wheats were the parent cultivar Houser at 40.95 with the highest gca value of 1.59 followed by the crosses Hillsdale/Houser at 40.25 with an sca of 2.18 and

Aug
of
the
Tec
whe

pla
imp
be
cor
in
co
in
fa
hy
in
an
wi
ad
hi
ni
ce
th
a
h
h

Augusta/Houser at 40.51 with an sca of 2.11. The low value of Arthur decreases the softness of the hybrids in spite of the fact that the highest sca occurred in the cross Tecumseh/Arthur at 4.22. Augusta was the fourth softest wheat at 39.33.

Characters normally dealing with the fitness of the plant are those most likely to exhibit heterotic improvement, such as yield and yield components. It might be expected that a harder endosperm would be more likely to contribute to the overall evolutionary fitness of the plant in terms of greater hardiness under adverse environmental conditions and resistance to pest damage and other tissue invasions that would render soft endosperm less fit. In fact the tendency toward harder endosperm as a result of hybridization has been established. Perhaps selection for increasingly soft wheats over years of breeding for cake and cookie quality has resulted in the development of lines with reduced combining abilities for additive and non-additive gene combinations. In other words, breeding for high PSI wheats has meant selecting lines with poor genetic nicking for the character endosperm hardness. If the cement hypothesis is correct, then perhaps the amount of this hypothetical substance has in fact been selected against since the time that breeding for soft wheat quality has been emphasized. Consistent with diallel theory, hybrid combination between diverse parents resulted in

hybr

incr

cros

be m

by w

took

Hous

comb

hybrid vigor for hardness. Perhaps it represents an increase in the amount of this alleged cement in those crosses exhibiting the highest sca effects. Efforts should be made to analyze the material according to Simmonds (77), by which a thorough chemical analysis of the material which took several years to develop would be made.

Again, according to the mean performance, the cultivar Houser at 40.95 remains the softest wheat with all hybrid combinations resulting in harder wheats.

Table

Parent	
1 SC F	
MPSC	
2 SC I	
MPSC	
3 SC	
MPSC	
4 SC	
MPSC	
5 SC	

Table 8. Heterosis for the endosperm trait Particle Size Index (PSI) in the F_2 generation when measured by the sum of the single cross hybrid (SC F_2) - midparental differences (MPSC) for each parent.

Parents	1	2	3	4	5	Σ(SC F_2-MPSC)
1 SC F_2	35.18	36.16	32.32	32.12	32.85	-3.29
MPSC		35.72	38.08	35.58	37.25	
2 SC F_2		36.26	34.10	35.05	35.04	-1.98
MPSC			38.60	36.12	37.79	
3 SC F_2			40.95	40.25	40.51	-2.02
MPSC				38.47	40.14	
4 SC F_2				35.99	37.59	-0.70
MPSC					37.66	
5 SC F_2					39.33	-1.72

F_2 Endo

Si
was exe
diversi
accord
parent
among
signif
and r
varian
endosp
additi
relati
an in
posit
at 0.

extre
effec
in Ta
chara
Three
at 0
Arthu
effe

F_2 Endosperm Separation Index (ESI) Analysis

Since it was decided to run ESI after the experiment was executed, the parents were not selected based on their diversity as were those of the other two traits. However, according to the Anova in Table 2, the differences between parents was highly significant. Table 3 shows that the among crosses combining ability analysis revealed significant gca effects, but nonsignificant sca, maternal, and reciprocal effects. Gca accounted for 78% of the variance. This suggests that bran separation from endosperm is largely controlled by additive and additive by additive epistatic variability. Hence, finding the relative gca's of the lines would be useful in breeding for an increase or decrease in this character. The only positive gca values as seen in Table 4 are those for Arthur at 0.83 and Tecumseh at 0.39.

Because parents were not chosen to represent the extremes of expression for this character, the heterotic effect based upon hybrid mean performance was small as seen in Table 9. However, positive heterosis is seen for this character in that higher values in fact reflect higher ESI. Three cultivars exhibit this positive effect, with Houser at 0.17 exceeding the others. This was followed by both Arthur and Augusta at 0.10 which exhibited less positive effects. Arthur also showed the highest parent mean

perfor
and th
higher
perfor
also o
develo
upon
its ne
effect
sca e

Howev
was
obser
chara
effec

by u
Highe
addit
used
due
as
pare
exhi
gca

performance at 76.58 when compared with the other parents and the hybrids. Obviously, breeders wishing to develop higher ESI varieties would select Arthur based on its mean performance, on its relatively high heterotic effect, and also on its highest gca value of 0.83. Breeders wishing to develop low ESI varieties would select Hillsdale, based upon its relatively low mean performance value of 74.05, its negative heterotic value of -0.08, and its negative gca effect of -0.67. Since this trait did not show significant sca effects, the individual crosses will not be considered.

The F_2 PSA correlated significantly with PSI. However, the association between ESI and both PSA and PSI was not significant. This reinforces the previous observations that bran separation is a genetically separate character from endosperm hardness. Its different genetic effects also reinforces this hypothesis.

The results suggest that this trait could be improved by using varieties such as Arthur that are high in gca. Higher ESI lines could be developed on the basis of additive genetic variability, where high ESI cultivars are used in a recurrent selection crossing system. However, due to the absence of non-additive components of variation as evidenced by non-significant sca, heterosis between parents of diverse ancestry would not be expected to exhibit superior combinations other than those based upon gca alone.

Table

Parent
1 SC
MPSC
2 SC
MPSC
3 SC
MPSC
4 SC
MPSC
5 SC

Table 9. Heterosis for the bran trait Endosperm Separation Index (ESI) in the F_2 generation when measured by the sum of the single cross hybrid (SC F_2) - midparental differences (MPSC) for each parent.

Parents	1	2	3	4	5	Σ(SC F_2-MPSC)
1 SC F_2	76.58	75.94	75.69	75.68	75.75	+.10
MPSC		76.47	75.33	75.31	75.53	
2 SC F_2		76.36	75.31	74.93	75.57	-.14
MPSC			75.22	75.20	75.42	
3 SC F_2			74.08	73.95	74.63	+.17
MPSC				74.06	74.28	
4 SC F_2				74.05	73.96	-.08
MPSC					74.27	
5 SC F_2					74.49	+.10

1. P
M
d
a
n
:

2.

3.

CONCLUSIONS

1. Particle Size Analysis (PSA) as measured by NIR or the Microtrac Particle Size Analyzer is a precise determination of wheat endosperm particle size showing advantages over Particle Size Index (PSI) measurements. PSA exhibits less environmental interaction, shows a greater range of gca, and only requires small sample amounts. These findings support the adoption of PSA for kernel hardness determinations.

2. The three characters Particle Size Analysis (PSA), Particle Size Index (PSI), and Endosperm Separation Index (ESI) exhibit considerable genetic diversity as revealed by the Anova.

3. Particle Size Analysis (PSA) and Particle Size Index (PSI) show combining ability gca:sca ratios of 1:1.2 and 1:1 respectively, indicating that both additive and non-additive genetic variability are important to the inheritance of these traits in roughly equal proportion.

4. A triploid genetic model shows no advantages over a diploid model for combining ability analysis in the triploid endosperm trait, hardness.

5. The F_1 maternal effect for Particle Size Analysis (PSA) dominates other combining ability effects, but this disappears after one round of segregation. Arthur/Tecumseh and Augusta/Hillsdale are the choice hybrids to generate in a hybrid wheat program based upon their superior softness in hybrid combination. Yield testing should be considered next for these hybrids to determine their usefulness in a hybrid wheat program.

6. The F_1 Particle Size Analysis (PSA) maternal and reciprocal effects disappear in the F_2 generation, indicating that this trait is controlled by the triploid endosperm tissue genotype. Selection for lines in which the genes are to be fixed should begin in the F_2 generation. However, subsequent inbreeding of lines would fix only the additive and epistatic gene interactions which behave additively. Hence, the gca of a line would be more important than the sca in generations after the F_1.

7. Because of the heterotic tendency to nick for increased hardness, no hybrid combinations were softer than the parent cultivar, Houser, for the trait Particle Size Analysis (PSA). Hillsdale/Houser was second in softness in this generation. Parents with low gca and hybrid populations exhibiting low sca or low average heterosis should be selected when developing wheats for softer PSA.

8. Particle Size Index (PSI) also exhibited the tendency toward harder wheats when hybridized. The softest wheat again was the parent cultivar, Houser, with the crosses Augusta/Houser and Hillsdale/Houser following closely. Parents with high gca and hybrid populations exhibiting high sca or high average heterosis should be selected when developing wheats for softer PSI.

9. It is possible that endosperm hardness is a fitness character, subject to hybrid vigor. Endosperm softness has resulted from years of selecting out those gene combinations that nick for greater hardness because the emphasis was upon increasing cake and cookie quality. That is, it is possible that higher quality was developed at the expense of evolutionarily fit endosperm.

10.

11.

10. Further chemical analyses should be made to verify the cement hypothesis of endosperm hardness.

11. It is indicated that Endosperm Separation Index (ESI) is controlled by additive and additive epistatic genetic variability and hence fixation of these effects could be expected to be fixed into pure lines. Lack of correlation with both PSA and PSI in addition to different patterns of genetic variability as evidenced by the absence of non-additivity point to the separateness of this trait as a genetic character. Therefore, one could increase or decrease ESI while keeping PSI or PSA constant. For an increase in ESI, Arthur would be a good choice based upon its relatively high heterotic effect, and high gca value. Hillsdale would be used to decrease ESI, based upon its relatively low heterotic effect and its low gca value. Finally, finding the gca's of lines would be useful when trying to increase or decrease this character. In a hybrid wheat program, a high x high ESI combination or low x low combination should be selected due to the additive gene effects and lack of sca effects.

APPENDIX

Table

Male Female	
MO201	
MO280	
MO284	
MO29	
MO30	

Table 10. Parent and hybrid mean values where n = 3 for the endosperm trait Particle Size Analysis (PSA) measured in the F_2 generation over 2 replications in 2 environments.

Male / Female	env/rep	MO201	MO280	MO284	MO295	MO300
MO201	1/1	64.47	65.81	70.06	71.35	65.71
	1/2	58.61	59.09	65.84	70.49	63.81
	2/1	67.88	64.65	68.52	69.88	72.88
	2/2	61.73	61.65	68.62	72.46	65.94
MO280	1/1	63.39	62.52	64.38	64.33	66.01
	1/2	59.46	59.70	68.45	70.22	67.83
	2/1	71.97	64.30	70.91	63.87	68.41
	2/2	68.03	64.47	70.41	72.68	68.19
MO284	1/1	67.10	61.85	56.44	60.40	61.36
	1/2	66.58	64.54	55.12	59.38	59.84
	2/1	74.93	63.65	57.57	55.58	59.82
	2/2	71.58	65.58	57.49	61.33	64.30
MO295	1/1	67.68	64.63	56.23	61.89	62.25
	1/2	66.95	68.55	62.83	61.97	66.38
	2/1	68.79	67.30	55.42	62.64	58.98
	2/2	71.63	66.81	59.76	66.80	61.41
MO300	1/1	66.36	66.87	60.04	61.33	60.89
	1/2	66.98	58.89	58.72	64.30	60.53
	2/1	72.27	70.07	60.62	60.48	62.19
	2/2	66.46	71.40	60.34	64.04	59.80

Table

Male Femal
MO201
MO280
MO28
MO29
MO3

Table 11. Parent and hybrid mean values where n = 4 for the endosperm trait Particle Size Index (PSI) measured in the F_2 generation over 2 replications in 2 environments.

Male / Female	env/rep	MO201	MO280	MO284	MO295	MO300
MO201	1/1	34.30	36.70	31.26	31.15	31.11
	1/2	37.24	34.79	33.36	33.16	32.67
	2/1	34.58	38.05	33.14	32.68	30.26
	2/2	34.63	36.76	33.12	30.48	32.45
MO280	1/1	37.23	36.68	33.97	34.11	34.86
	1/2	35.59	35.39	34.10	32.98	34.05
	2/1	36.44	36.84	33.76	34.81	38.85
	2/2	33.79	36.14	32.76	34.57	32.45
MO284	1/1	33.47	34.77	40.06	39.03	39.36
	1/2	33.37	34.05	37.48	36.97	42.54
	2/1	29.47	35.81	41.86	40.28	42.94
	2/2	31.41	33.64	44.41	40.26	42.48
MO295	1/1	32.20	36.11	39.69	36.94	36.54
	1/2	31.65	34.49	37.39	34.56	36.33
	2/1	34.50	36.47	47.87	36.35	40.12
	2/2	31.06	36.92	40.55	36.14	37.82
MO300	1/1	34.06	34.61	38.83	36.16	36.81
	1/2	32.87	36.23	37.72	34.09	36.41
	2/1	35.22	35.91	40.41	41.39	40.83
	2/2	34.23	33.55	39.85	38.35	43.27

Table 12. Parent and hybrid mean values where n = 4 for the bran trait Endosperm Separation Index (ESI) measured in the F_2 generation over 2 replications in 2 environments.

Male / Female	env/rep	MO201	MO280	MO284	MO295	MO300
MO201	1/1	77.39	75.30	76.39	76.02	77.84
	1/2	77.58	77.94	77.13	76.44	77.77
	2/1	74.53	74.87	75.63	74.69	74.48
	2/2	76.83	74.91	74.98	73.91	74.46
MO280	1/1	77.56	77.46	77.30	77.02	77.53
	1/2	77.90	77.75	76.50	76.36	77.44
	2/1	75.18	75.33	75.42	75.32	73.33
	2/2	73.88	74.90	73.53	73.51	73.86
MO284	1/1	76.83	76.70	76.58	76.49	77.27
	1/2	76.71	76.87	76.75	76.33	75.89
	2/1	74.72	72.86	71.16	72.25	72.54
	2/2	73.14	73.37	71.86	71.98	72.83
MO295	1/1	77.76	76.21	75.55	75.43	75.30
	1/2	77.13	76.24	75.34	76.00	74.82
	2/1	75.37	72.50	72.24	72.06	71.86
	2/2	74.18	72.36	71.46	72.74	73.33
MO300	1/1	76.91	77.23	76.68	76.64	75.44
	1/2	77.06	77.47	77.43	76.41	77.20
	2/1	74.02	74.22	73.38	72.30	74.29
	2/2	73.55	73.51	71.05	71.11	71.04

Table 13. Hybrid mean values where n = 4 for the endosperm trait Particle Size Analysis (PSA) measured in the F_1 generation as a randomized complete block design over 1 replication.

Male / Female	MO201	MO280	MO284	MO295	MO300	TYi.
MO201		77.79	84.10	75.22	75.11	312.22
MO280	61.83		71.65	74.05	73.29	280.82
MO284	72.46	73.86		77.79	73.18	279.29
MO295	75.95	78.33	75.71		69.61	299.60
MO300	72.63	72.40	71.67	73.07		289.77
TY.j	282.87	302.38	303.13	300.13	291.19	1479.70
Yi.+Y.j	595.09	583.20	600.42	599.73	580.96	

Table 14. Parental and hybrid mean values pooled over 2 replications in 2 environments, where n = 12, for the endosperm trait Particle Size Analysis (PSA) in the F_2 generation.

Male / Female	MO201	MO280	MO284	MO295	MO300	TYi.
MO201	63.17	62.79	68.26	71.04	67.08	269.17
MO280	65.71	62.74	68.53	67.77	67.61	269.62
MO284	70.04	63.90	56.65	59.17	61.33	254.44
MO295	68.76	66.82	58.56	63.32	62.25	256.39
MO300	68.01	66.80	59.93	62.53	60.84	257.27
TY.j	272.52	260.31	255.28	260.51	258.27	1306.89
Yi.+Y.j	541.69	529.93	509.72	516.90	515.54	

Table 15. Parent and hybrid mean values pooled over 2 replications in 2 environments, where n = 16, for the endosperm trait Particle Size Index (PSI) in the F_2 generation.

Male / Female	MO201	MO280	MO284	MO295	MO300	TYi.
MO201	35.18	36.57	32.72	31.89	31.62	132.80
MO280	35.76	36.26	33.64	34.11	35.02	138.53
MO284	31.93	34.56	40.95	39.13	41.83	147.45
MO295	32.35	35.99	41.37	35.99	37.70	147.41
MO300	34.09	35.07	39.20	37.49	39.33	145.85
TY.j	134.13	142.19	146.93	142.62	146.17	712.04
Yi.+Y.j	266.93	280.72	294.38	290.03	292.02	

Table 16. Parent and hybrid mean values pooled over 2 replications in 2 environments, where n = 16, for the bran trait Endosperm Separation Index (ESI) in the F_2 generation.

Male / Female	MO201	MO280	MO284	MO295	MO300	TYi.
MO201	76.58	75.75	76.03	75.26	76.13	303.17
MO280	76.13	76.36	75.68	75.55	75.54	302.90
MO284	75.35	74.95	74.08	74.26	74.63	299.19
MO295	76.11	74.32	73.64	74.05	73.82	297.89
MO300	73.38	75.60	74.63	74.11	74.49	299.72
TY.j	302.97	300.62	299.98	299.18	300.12	1502.87
Yi.+Y.j	604.14	603.52	599.17	597.07	599.84	

BIBLIOGRAPHY

BIBLIOGRAPHY

1. Aamodt, O. S. and J. H. Torrie. 1935. Studies on the inheritance of and the relation between kernel texture and protein content in several spring wheat crosses. Can. J. Res. Sect. C. 13:202.

2. Adams, C. A., Norveillie, L., and N. Liefenberg. 1976. Biochemical properties and ultrastructure of protein bodies isolated from selected cereals. Cereal Chem. 53:1-12.

3. Altman, D. W., McCuiston, W. L. and W. E. Kronstad. 1983. Grain protein percentage, kernel hardness, and grain yield of winter wheat in foliar applied urea. Agron. J. 75:87-91.

4. Baenziger, P. S., Clements, R. L., McIntosh, M.S., Yamazaki, W. T. Starling, T. J., Sammons, D. J., and J. W. Johnson. 1984. Effect of cultivar, environment, and their interaction and stability analyses on milling and baking quality of soft red winter wheat. Crop Sci. 25:5-8.

5. Baily, T. B., Qualset, C. O., and D. F. Cox. 1980. Predicting heterosis in wheat. Crop Sci. 20:339-342.

6. Baker, R. J. 1978. Issues in diallel analysis. Crop Sci. 18:533-536.

7. Barlow, K. K., Buttrose, M.S., Simmonds, D. H., and M. Vesk. 1973a. The nature of the starch-interface in wheat endosperm. Cereal Chem. 50:443-454.

8. Barlow, K. K., Buttrose, M.S., Simmonds, D. H., and V. Vesk. 1973b. The nature of the starch-protein interface in wheat endosperm. Cereal Chem. 50:443-454.

9. Bechtel, D. B., Gaines, R. L., and Y. Pomeranz. 1980. Changes in protein bodies of maturing wheat. (Abstr.) Cereal Foods World 25:516-517.

10. Biffin, R. H. 1908. On the inheritance of strength in wheat. J. Agric. Sci. 3:86.

11. Bingham, J. 1966. Paternal effect on grain size in wheat. Nature 209:940-941.

12. Bitzer, M. J. and S. H. Fu. 1972. Heterosis and combining ability in sourthern soft red winter wheats. Crop Sci. 12:35-37.

13. Blum, P. H., Panos, G., and Smith, R. J. 1960. Measurement of hardness of barley and malt with the Brabender Hardness Tester.II. Modification during malting. Am. Soc. Brew. Chem. Proc. 18:95.

14. Briarty, L. G. 1978. The mechanisms of protein body deposition in legumes and cereals. In: Plant Proteins. G. Norton, ed. Butterworths: London, Boston. pp. 81-106.

15. Briarty, L. G., Hughes, C. E., and A. D. Evers. 1979. The developing endosperm of wheat--A stereological analysis. Ann. Bot. 44:641-658.

16. Briggle, L. W. 1963. Heterosis in wheat--A review. Crop Sci. 3:407-412.

17. Brown, C. M., Weibel, R. O., and R. D. Seif. 1966. Heterosis and combining ability in common winter wheat. Crop Sci. 6:382-383.

18. Buttrose. M. S. 1960. Submicroscopic development and structure of starch granules in cereal endosperm. J. Ultrastruct. Res. 4:231-257.

19. Chaudhary, V. K., Yamazaki, W. T., and W. A. Gould. 1981. Relation of cultivar and flour particle size distribution to cake volume. Cereal Chem. 58(4):314-317.

20. Cockerham, C. C. and B. S. Weir. 1977. Quadratic Analyses of Reciprocal Crosses. Biometrics 33(3):187-203.

21. Cockerham, C. C. 1980. Random and fixed effects in plant genetics. Theor. Appl. Genet. 56:119-131.

22. Dickinson, A. G., and J. L. Jinks. 1956. A generalized analysis of diallel crosses. Genetics 41:65-78.

23. Donelson, D. H. and W. T. Yamazaki. 1972. Soft wheat flour particle-size analysis by integrated sieve and coulter counter procedures. Cereal Chem. 49(6):641-648.

24. Evers, A. D. 1969. Scanning electron microscope observations on the gross structure of wheat starch granules. Chem. Ind. Berlin. 1969:200-201.

25. Evers. A. D. 1970. Development of the endosperm of wheat. Ann. Bot. 34:547-555.

26. Evers, A. D. 1971. Scanning electron microscopy of wheat starch. III. Granule development in the endosperm. Staerke 23:157-162.

27. Evers, A. D. 1973. The size distribution among starch granules in wheat endosperm. Staerke 25:303-304.

28. Evers, A. D. and J. Lindley. 1977. The particle size distribution in wheat endosperm starch. J. Sci. Food agric. 28:98-102.

29. Falconer, D. S. 1981. Introduction to Quantitative Genetics. 2nd Ed. Longman Grp. Lmt., p. 251.

30. Farrand, E. A. and J. J. Hinton. 1974. Study of relationships between wheat protein contents of two U.K. varieties and derived flour protein contents at varying extraction rates. II. Studies by hand dissection of individual grains. Cereal Chem. 51:66.

31. Favret, E. A., Manghers, Li, Solari, R., Avila, A., and Monesiglio, J. C. 1970. Gene control of protein production in cereal seeds. In: Improving Plant Proteins by Nuclear Techniques. IAEA Proc. Series STI/PUB/258, Vienna. pp. 87-95.

32. Gilbert, N. E. G. 1958. Diallel crosses in plant breeding. Heredity 12:477-492.

33. Griffing, B. 1956a. A generalized treatment of the use of diallel crosses in quantitative inheritance. Heredity 10:31-50.

34. Griffing, B. 1956b. Concept of general and specific combining ability in relation to diallel crossing systems. Austr. J. Biol. Sci. 9:463-493.

35. Grosh, G. U. 1959. Water penetration and internal cracking in tempered wheat grains. Cereal Chem. 36:260.

36. Gyawali, K. K., Qualset, C. O., and W. T. Yamazaki. 1968. Estimates of heterosis and combining ability in winter wheat. Crop Sci. 8:322-324.

37. Hallauer, A. R. and J. B. Miranda. 1981. Quantitative Genetics in Maize Breeding. Iowa State U. Press. Chapter 4, Hereditary variance: mating designs.

38. Harrington, J. B. 1940. Yielding capacity of wheat crosses as indicated by bulk hybrid tests. Canad. J. Res. 18:578-584.

39. Hayman, B. I. 1954. The theory and analysis of diallel crosses. Genetics 39:789-809.

40. Hinton, J. J. C. 1955. Resistance of the testa to entry of water into the wheat kernel. Cereal Chem. 32:296.

41. Hughes, C. E. and L. G. Briarty. 1976. A quantitative analysis of some ultrastructural aspects of seed development. Natl. Bar. Stand. U.S. Special Publ. 431. Proc. 4th Int. Congr. Stereol. Natl. Bur. Stand. Gaithersburg, MD. pp. 385-388.

42. Jennings, A. C., Morton, R. K. and B. A. Palk. 1963. Cytological studies of protein bodies of developing wheat endosperm. Aust. J. Biol. Sci. 16:366-374.

43. Jones, R. W. and R. J. Dimler. 1962. Electrophoretic composition of glutens from air-classified flours. Cereal Chem. 39-336.

44. Kasarda, D. D., Bernardin, J. E., and Nimmo, C. C. 1976. Wheat proteins. In: Advances in Cereal Science and Technology. Vol. 1. Y. Pomeranz, ed. Am. Assoc. Cereal Chem., St. Paul, MN. pp. 158-236.

45. Katz, R., Collins, N. D., and A. B. Cardwell. 1961. Hardness and moisture content of wheat kernels. Cereal Chem. 38:364-368.

46. Kempthorne, O. 1956. The theory of the diallel cross. Genetics 41:451-459.

47. Konzek, C. F. 1977. Genetic control of the content, amino acid composition, and processing properties of proteins in wheat. In: Advances in Genetics, Vol. 19. E. W. Caspari, ed. Academic Press, Inc., New York. pp. 407-482.

48. Kosmolak, F. G. 1978. Grinding time--screening test for kernel hardness in wheat. Can. J. Plant Sci. 58:415.

49. Kronstad, W. E. and W. H. Foote. 1964. General and specific combining ability estimates in winter wheat. Crop Sci. 4:616-619.

50. Law, C. N., Young, C. F., Brown, J. W. S., Shape, J. W., and A. J. Worland. 1978. The study of grain protein control in wheat using whole chromosome substitution lines. In: Seed Protein Improvement by Nuclear Techniques. IAEA Proc. Series STI/PUB/479. Vienna. pp. 483-502.

51. Lineback, D. R., Cashman, W. E., Hoseney, R. C., and A. B. Ward. 1978. Note on measuring thickness of wheat bran by scanning electron microscopy. Cereal Chem. 55(3):415-419.

52. Lupton, F. G. 1961. Studies in the breeding of self-pollinated cereals. 3. Further studies in cross predictions. Euphytica 10:209-224.

53. MacRitchie, F. 1980. Physiochemical aspects of some problems in wheat research. From: Advances in Cereal Science & Technology. Vol. III. AACC St. Paul, Minn. Y. Pomeranz ed. 271-325.

54. Mayo, O. 1983. Problems of significance tests in diallel analysis. Sabrao Journal 15(2):147-149.

55. Mecham, D. K., Kasarda, D. D., and C. O. Qualset. 1978. Genetic aspects of wheat gliadin proteins. Biochem. Genet. 16:831-853.

56. Mirjana, I., Vulic, B., and Virginia Djolai. 1979. Expression of heterosis and combining ability for grain protein in a diallel wheat cross. Wheat Info. Serv. 49:1-4.

57. Miller, B. S., Trimbo, H. B., and K. R. Powell. 1967. Effects of flour granulation and starch damage on the cake-making quality of soft wheat flour. Cereal Sci. Today 12:245.

58. Miller, B. S., Hughes, J. W., Afework, S., and Y. Pomeranz. 1981a. A method to determine hardness and work of grinding wheat. J. Food Sci. 46(1):851.

59. Miller, B. S., Afework, S., Pomeranz, Y., and L. Bolte. 1981b. Wheat hardness: time required to grind wheat with the Brabender automatic microhardness tester. J. Food Sci. 46(1):863.

60. Miller, B. S., Pomeranz, Y. and S. Afework. 1984. Hardness (texture) of hard red winter wheat grown in a soft wheat area and of soft red winter wheat grown in a hard wheat area. Cereal Chem. 61(2):201-203.

61. Millet, E. and M. J. Pinthus. 1980. Genotypic effects of the maternal tissues of wheat on its grain weight. Theor. Appl. Genet. 58:247-252.

62. Millington, A. J. and E. Remilton. 1954. The flour strength of Australian wheat varieties. J. Aust. Inst. Agric. Sci. 20:24-35.

63. Milner, M. and J. A. Shellenberger. 1953. Physical properties of weathered wheat in relation to internal fissuring detected radiographically. Cereal Chem. 30:202-212.

64. Moll, R. H. Lonnquist, J. H., Fortuno, J. V. and E. C. Johnson. 1965. The relationship of heterosis and genetic divergence in maize. Genetics 52:139-144.

65. Moss, H. J. 1978. Factors determining the optimum hardness of wheat. Aust. J. Agric. Res. 29:1117-1126.

66. Nakagawa, N., Soga, Y., Watanabe, S., Gocho, H., Nishio, K., and Kurata, H. 1959. Genetical studies on kernel texture of wheat and barley. Bull. First Agron. Div., Tokai-Kinki Nat. Agric. Exp. Sta. No. 6.

67. Newton, R., Cook, W. H., and Malloch, J. G. 1927. The hardness of the wheat kernel in relation to protein content. Sci. Agric. 8:205.

68. Obuchowski, W., and Bushuk, W. 1980. Wheat hardness: effects of debranning and protein content. Cereal Chem. 57:426.

69. Orth, R. A. 1977. Determination of kernel hardness of Australian wheats by a rapid grinding procedure. Aust. J. Exp. Agric. Anim. Husb. 17:462.

70. Parish, J. A., and N. J. Halse. 1968. Effects of light, temperature, and rate of desiccation on translucency in wheat grain. Aust. J. Agric. Res. 19:365.

71. Pearson, D. C., Rosielle, A. A., and W. J. R. Boyd. 1981. Heritabilities of five wheat quality traits for early generation selection. Aust. J. Exp. Agric. Anim. Husb. 21:512-515.

72. Percival, J. 1921. The Wheat Plant 1974. A monograph. Duckworth, London.

73. Purdy, L. H., W. Q. Loegering, C. F. Konzak, C. J. Peterson, and R.E. Allan, 1968. A proposed standard method for illustrating pedigrees in small grain varieties. Crop Sci. 8:405-406.

74. Qualset, C. O., and C. W. Wrigley. 1977. Chromosomal control of gliadin proteins: The practical implications. (Abstr.). Cereal Foods World 22:475.

75. Sampson, D. R. 1982. Lack of correlation between kernel hardness and protein content in a winter wheat progeny. Can. J. Plant Sci. 62:797-799.

76. Simmonds, D. H. 1972. The ultrastructure of the mature wheat endsperm. Cereal Chem. 49:212-222.

77. Simmonds, D. H., Barlow, K. K., and C. W. Wrigley. 1973. The biochemical basis of grain hardness in wheat. Cereal Chem. 50:553-562.

78. Simmonds, D. H. 1974. Chemical basis of hardness and vitreosity in the wheat kernel. Bakers Dig. 10:16-29.

79. Simmonds, D. H. and T. P. O'Brien. 1981. Morphological and biochemical development of the wheat endosperm. From Advances in Cereal Science and Technology. Vol. IV. AACC St. Paul, MN. Y. Pomeranz, Ed., pp. 5-55.

80. Sokol, M. J. and R. J. Baker. 1977. Evaluation of the assumptions required for the genetic interpretation of diallel experiments in self-pollinated crops. Canada J. Plant Sci. 57:1185-1191.

81. Stenvert, N. L. 1974. Grinding resistance. A simple measure of wheat hardness. Flour Anim. Feed Milling. 7:24.

82. Stenvert, N. L. and Kingswood, K. 1977. The influence of the physical structure of the protein matrix on wheat hardness. J. Sci. Food Agric. 28:11-19.

83. Symes, K. J. 1961. Classification of Australian wheat varieties based on the granularity of their whole meal. Aust. J. Exp. Agric. Anim. Husb. 1:18.

84. Symes, K. J. 1965. The inheritance of grain hardness in wheat as measured by the particle size index. Aust. J. Agric. Res. 16:113.

85. Symes, K. J. 1969. Influence of a gene causing hardness on the milling and baking quality of two wheats. Aust. J. Agr. Res. 20:971.

86. Tandon, J. P., Joshi, A. B., and K. B. L. Jain. 1970. Comparison of graphic and combining ability analyses of diallel crosses in wheat. Indian J. of Genetics and Plant Breeding. 30(1):91-103.

87. Ternovskaya, T. K. and E. G. Zhirov. 1979. Heritability of chromosomes of the D genome in the progeny of pentaploid wheats. II. Analysis of endosperm density in seeds with different chromosome numbers. Genetika, USSR. 15(4):701-707.

88. Thompson, J. B. and R. N. H. Whitehouse. 1962. Studies on the breeding of self-pollinating cereals. 4. Environment and the inheritance of quality in spring wheats. Euphytica 11:181-196.

89. Trupp, C. R. 1976. Particle size index - breeding behavior and association with protein percentage in wheat. Crop Sci. 16:618.

90. Verma, P. K. and O. P. Luthra. 1983. Heterosis and combining ability analysis for yield and its attributes in macaroni wheat. Indian J. Agric. Sci. 53(6):385-389.

91. Weiss, E. L. and H. N. Frock. 1976. Rapid analysis of particle size distribution by laser light scattering. Powder Technology 14:287-293.

92. Wertheimer, A. L., and W. L. Wilcock. 1976. Light scattering measurements of particle distributions. Applied Optics 15(6):1616-1620.

93. Williams, P. C. 1979. Screening wheat for protein and hardness by near infrared reflectance spectroscopy. Cereal Chem. 7:24.

94. Williams, P. C. 1983. Physical methods for grain testing. Cereal Foods World 28(9):593.

95. Worzella, W. W. 1942. Inheritance and interrelationship of components of quality, cold resistance, and morphological characters in wheat hybrids. J. Agric. Res. 65:501.

96. Wrigley, C. W. 1972. The biochemistry of the wheat protein complex and its genetic control. Cereal Sci. Today 17(12):370-375.

97. Yamada, K. U. and K. Olden. 1978. Fibronectins - adhesive glycoproteins of cell surface and blood. Nature 275:179-184.

98. Yamazaki, W. T. 1972a. A modified particle-size index test for kernel texture in soft wheat. Crop Sci. 12:116.

99. Yamazaki, W. T. and D. H. Donelson. 1972b. The relationship between flour particle size and cake-volume potential among eastern soft wheats. Cereal Chem. 49(6):649-653.

100. Yamazaki, W. T. and L. C. Andrews. 1982. Small scale milling to estimate the milling quality of soft wheat cultivars and breeding lines. Cereal Chem. 59(4):270-272.

101. Yamazaki, W. T. and J. R. Donelson. 1983. Kernel hardness of some U.S. wheats. Cereal Chem. 60(5):344-350.

102. Yates, F. 1947. Analysis of data from all possible reciprocal crosses between a set of parental lines. Heredity 1:287-301.