Inheritance of stem solidness and its relationship to yield and other agronomic traits in spring wheat
by Mohammad Aslam Hayat

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Crop and Soil Science
Montana State University

Abstract:
The wheat stem sawfly, Cephus cinctus Norton (Hymenoptera: Cephidae), a devastating pest of wheat, has caused considerable economic damage in the Pacific Northwest. Solid-stemmed wheat varieties have provided a genetic source of resistance against the insect. However, solid-stemmed wheats tend to yield less than hollow-stemmed wheats. Some, but not all, studies have shown yield to be negatively related to stem solidness. To date, it is not clear whether solid-stemmed wheats have low yield due to a negative genetic correlation or to the poor genetic background of the original solid-stemmed selections. The cause of the negative association between solid stems and other traits was studied in spring wheat using solid-stemmed wheats released in different eras. The progeny derived from different crosses between solid and hollow parents was evaluated to determine the genetic basis for improved yield in modern solid-stemmed spring wheats. Space-planted nurseries of different crosses grown in 1990 and 1991 showed that the genetic basis of stem solidness is different between an early release (Rescue) and a later release (Lew) Additionally, larger experiments of F6 progeny derived from crosses between solid and hollow parents were grown in two different environments and agronomic data were gathered. The genetic correlation coefficients between stem solidness and grain yield were small and did not tend to be negative. Therefore, no negative genetic relationship appears to exist between stem solidness and grain yield. However, stem solidness was found negatively correlated to protein and plant height in early solid-stemmed releases. Thus, it appears that a linkage existed between the genes for solid stems and genes conferring poor percent protein and tall plants in the early releases. This linkage appears to have been broken in later releases. Stem solidness was independent of all other traits studied. Heritabilities of all traits, except yield, were high.

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Mohammad Aslam Hayat

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Date October 1, 1993

Dedicated to HOLY PROPHET MOHAMMAD
(Peace be Upon Him)
the great social reformer
and
to my beloved late parents who passed away
during my stay at Montana State University, Bozeman
and
were greatly missed

VITA

Mohammad Aslam Hayat was born to Mr. and Mrs. Malik Mian Mohammad Awan on October 1, 1957 in Sahiwal, Pakistan. He got his secondary education at Multan district. He received his Master of Science in Agronomy from University of Agriculture Faisalabad, Pakistan in December 1983.
He is married to Tanveer Hayat. They have two daughters, Jawairia (seven year) and Hafsa (five year); and a sweet baby boy Talal Mohammad Hayat.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES--Continued

LIST OF TABLES--continued

LIST OF FIGURES

ABSTRACT

The wheat stem sawfly, Cephus cinctus Norton (Hymenoptera: Cephidae), a devastating pest of wheat, has caused considerable economic damage in the Pacific Northwest. Solid-stemmed wheat varieties have provided a genetic source of resistance against the insect. However, solid-stemmed wheats tend to yield less than hollow-stemmed wheats. Some, but not all, studies have shown yield to be negatively related to stem solidness. To date, it is not clear whether solid-stemmed wheats have low yield due to a negative genetic correlation or to the poor genetic background of the original solid-stemmed selections. The cause of the negative association between solid stems and other traits was studied in spring wheat using solid-stemmed wheats released in different eras. The progeny derived from different crosses between solid and hollow parents was evaluated to determine the genetic basis for improved yield in modern solid-stemmed spring wheats. Space-planted nurseries of different crosses grown in 1990 and 1991 showed that the genetic basis of stem solidness is different between an early release (Rescue) and a later release (Lew). Additionally, larger experiments of F6 progeny derived from crosses between solid and hollow parents were grown in two different environments and agronomic data were gathered. The genetic correlation coefficients between stem solidness and grain yield were small and did not tend to be negative. Therefore, no negative genetic relationship appears to exist between stem solidness and grain yield. However, stem solidness was found negatively correlated to protein and plant height in early solid-stemmed releases. Thus, it appears that a linkage existed between the genes for solid stems and genes conferring poor percent protein and tall plants in the early releases. This linkage appears to have been broken in later releases. Stem solidness was independent of all other traits studied. Heritabilities of all traits, except yield, were high.

CHAPTER 1

INTRODUCTION

The wheat stem sawfly, Cephus cinctus Norton (Hymenoptera: Cephidae), is a destructive pest of wheat in the northwestern areas of the United States and the southern wheat growing areas of Canada (Wallace and McNeal, 1966). Wheat productivity in these areas is severely limited due to the attack of wheat stem sawfly. Developing larvae tunnel to the base of plant where they girdle the stem internally. This tunneling reduces the yield and test weight of the grain (Seamans et al., 1938). Girdling causes severe lodging of the crop resulting in serious economic losses to the farmers (Holmes,1977).

Weiss et al. (1987) reported severe sawfly infestations in Montana. The annual monetary losses in Montana were estimated to be $ 5,265,000 in 1945 and $ 7,045,500 in 1946 due to sawfly cutting (Montana Agricultural Experiment Station and Montana Extension Service Staffs, 1946). A loss of $ 17,000,000 to the combined wheat crop of Montana and North Dakota was observed in 1952 (Davis, 1955). In 1989, extensive damage was observed in winter wheat (Triticum aestivum L.) in central Montana (Morrill et al., 1992). The sawfly remains a devastating wheat pest.

Solid-stemmed wheat varieties have provided a genetic source of resistance against wheat stem sawfly. 'Rescue' was the first solid-stemmed variety with resistance to wheat stem sawfly. It was reported to have yield potential almost equal to hollow-stemmed susceptible cultivars at the time of release (Montana Agricultural Experiment Station and Montana Extension Service Staff, 1946). However, the protein quality and baking strength of Rescue were lower than hollow-stemmed, susceptible cultivars (Stoa, 1947). Later it was concluded that solid-stemmed wheats tend to yield less than susceptible hollow-stemmed varieties (Wallace and McNeal, 1966). Some, but not all genetic studies, have shown yield to be negatively correlated with stem solidness (McNeal et al., 1965).

To date, it is not clear whether solid-stemmed wheats have low yield due to a negative genetic correlation, or to the poor genetic background of the original solid-stemmed selections. A negative genetic correlation could be attributed to pleiotropy or to linkage between genes for solid stems and genes conferring low yield. In later case, one would expect the negative correlation to have lessened during breeding for improved varieties as a result of cross-overs and recombination of genes.

Hanson (1959) suggested that random intermating of one or more cycles in self-pollinated species should break up linkage groups and result in increased genetic recombination within the linkage group. Many other authors also suggested using random intermating to break up linkage blocks through increased genetic recombination (Miller and Rawlings, 1967; Meredith and Bridge, 1971; Redden and Jensen, 1974; Altman and Busch, 1984).

This research tested the cause of the negative relationship between solid stems and other traits in spring wheat using solid-stemmed wheats released in different eras. Rescue is the original solid-stemmed variety, released in 1945, and is a parent of Fortuna, released in 1966. Fortuna was the solid stem parent of Lew, released in 1976. Yield improvements occurred with each new release. We evaluated progeny derived from each solid-stemmed parent to determine the genetic basis for improved yield in modern solid-stemmed spring wheat varieties and to determine whether continued progress may be expected.

CHAPTER 2

LITERATURE REVIEW

History of Wheat Stem Sawfly

Wheat stem sawfly (Cephus cinctus Norton) is an insect native to North America (Ainslie, 1920; Criddle, 1922; Farstad, 1940; Callenbach and Hansmeier, 1945; Mills, 1945). The insect was present in native grasses in California and Nevada in 1890 (Ainslie, 1920). In 1895, adults were found feeding in the Canadian Northwest Territories (Ainslie, 1929). In 1906 larvae were found feeding in wheat near Kulm, North Dakota and in various grasses, chiefly Agropyron species, in Wyoming (Ainslie, 1920 and 1929) . The first reported collection of adult sawfly in Montana was in 1900, near Bozeman. Infested wheat stems were identified in 1910, in northeastern Montana near Bainville (Montana Agriculture Experiment Station and Extension Service Staffs, 1946). In 1908 larvae were found in grasses in Oregon, and from 1911 to 1915 the species was found in native grasses of Utah and other states (Ainslie, 1929).

This pest was originally a grass feeder, but larval feeding habits changed to small grains in the early 1900's (Criddle, 1922; Ainslie, 1929). Development of large scale farming resulted in movement of the insect from prairie grasses to wheat (Munro, 1945 and Davis, 1955). In 1941, the sawfly began causing economic loss in northeastern Montana counties and the western part of the Golden Triangle of Montana. By 1943, it was a major pest of wheat in Montana (Wallace and McNeal, 1966). At present, the insect remains an economic pest in Montana, North Dakota and the southern prairie provinces of Canada.

Insect Morphology

The Adult

Adult sawflies are black wasps, six to twenty millimeters long, with bright yellow markings. The wings are clear but appear to be golden in the sunlight (Wallace and McNeal, 1966).

The adults emerge from infested stubble in early summer and fly to nearby fields (Seamans et al., 1938 and Davis, 1955). Wasp emergence in June or July coincides with stem elongation of wild grasses. The date of emergence depends on temperature, soil type, and the depth that the infested wheat stubble is buried (Luginbill and McNeal, 1955). Timing of emergence is critical because stems of host plants must have developed to receive eggs. Additionally, plants must be young to provide green material during the development period of larvae. The adults fly on warm calm days, but flights may cease during cloudy weather. Wasps cling to the plants during windy conditions (Seamans, 1945 and Butcher, 1946). Wasps live for about a week, are weak fliers and generally migrate only to the nearest available host plants (Seamans, 1945 and Wallace and McNeal, 1966).

In most localities both sexes occur, but parthenogenesis is apparently common. Farstad (1938) described an area in Alberta from which no males had been found for several years and concluded that females are only produced through parthenogenesis and males can probably be produced only from fertilized eggs. However, Mackay (1955) indicated that males can be developed from unfertilized, haploid eggs and females from fertilized, diploid ones. The emerging adults are sexually mature so mating and oviposition can begin almost immediately.

Farstad and Platt (1946) noted that wheat is preferred over other small grains and Holmes and Peterson (1960) indicated that spring wheat is preferred to winter wheat. Wasps lay eggs in stems of wheat or large hollow-stemmed grasses. Large stems and plants with elongating internodes are preferred (Ainslie, 1920; Holmes and Peterson, 1958; Holmes and Peterson, 1960). Females select stems with the proper diameter and come to rest with the head oriented downward. Stems are grasped firmly with the legs, the body is arched, and the saw-like ovipositor is forced through the wall tissue of the plant. The egg passes through the ovipositor into the lumen of the stem. When the ovipositor is withdrawn the incision in the stem closes (Ainslie, 1929).

Females usually deposit a single egg in each stem and then fly to another stem (Ainslie, 1920), though other females also may deposit an egg in the same stem (Weiss et al., 1987). Ainslie (1920) and Mills (1945) found that adult females may lay 30 to 50 eggs. The number of eggs deposited in the host stems may be affected by longevity of the female, host availability, and size of the female (Wall, 1952). If more than one egg hatches in the same stem, a struggle occurs between the larvae until only one survives (Seamans et al., 1938; Munro, 1945; Davis, 1955).

The Egg

The freshly laid egg is crescent-shaped, thin, delicate and glassy in appearance (Ainslie, 1920 and Criddle, 1917). The egg can be seen under a microscope by splitting the infested stem. Ainslie (1929) stated that egg size ranges from 1.0 to 1.25 millimeters in length, varying with the size of the female. The egg always lies free within the stem of the host plant and its incubation period varies, depending on temperature and moisture (Ainslie, 1920), but is usually from four to seven days (Mills, 1945 and Roemhild, 1954).

The Larva

The newly hatched larva is nearly transparent and colorless. Later on when it starts feeding inside the stem, a greenish-yellow color develops (Wallace and McNeal, 1966). It has a very large head with chewing mouth parts (Holmes, 1954). The larva feeds on the parenchyma and vascular tissues in the interior of the stem. Seamans et al., (1938) stated that the larva feeds inside the stem by successfully tunnelling the nodes, until the stems begin to ripen. At this stage the stem is a continuous hollow tube filled with "sawdust". All nutrients required for growth, development, and reproduction of _Cephus_ _cinctus_ are obtained from feeding inside the stem during the larval stage (Holmes, 1954). There have been no reports of adult sawflies feeding (Wallace and McNeal, 1966).

As the crop ripens, the larva moves downward. Holmes (1975) suggested that the light penetrating the stem walls of maturing host plants may initiate the downward movement. The larva cut a groove with its mandibles around the inside of the stem near the ground level. Cutting begins when the stems contain approximately 50% moisture (Holmes, 1975) and the kernel is 40 to 50% moisture (Holmes and Peterson, 1965). At this point, the larva plugs the top of the stub with frass and moves down in the stub of the stem that remains below ground. Here it forms a cocoon in which it overwinters and pupates the next spring. When wind blows, the stem breaks off at the groove, and the adult is able to emerge in summer by pushing through the plug of frass.

Host Plants

Wallace and McNeal (1966) stated that _Cephus_ _cinctus_ Norton is able to attack several plant species. _C_. _cinctus_ may infest nearly all cultivated grains but wheat is a preferred host (Farstad and Platt, 1946). Larvae may feed on

Hordeum vulgare L. (barley), Secale cereale L. (rye), Triticum aestivum , Triticum durum L., Triticum monococcum L., Triticum polonicum L., Triticum timopheevii Zhuk., and Triticum turanicum Jakubz, but most of larvae may not survive in H. vulgare and S. cereale (Wallace and McNeal, 1966). Triticum durum, T. polonicum and T. timopheevii appear to be resistant to larval development (Wallace and McNeal, 1966). Although barley is more resistant to cutting than wheat, the amount of cutting in barley appears to vary between cultivars (Farstad and Platt, 1946). Farstad (1940) reported that oat (Avena sativa L.) is entirely resistant to the wheat stem sawfly and speculated that this is due to lack of essential nutrients required for the growth and development of the insect. Farstad (1944) found that sawflies may lay eggs in the stems of Linum usitatissimum L. (flax), however, larval development was stunted, and almost all of the larvae died before harvest. In addition to cultivated hosts, wheat stem sawfly may also infest many wild grasses, especially Agropyron species, which according to Criddle (1917), were the preferred host prior to wheat.

Crop Damage

The wheat stem sawfly affects yield both physiologically and physically. Yield of the infested stems is decreased by cutting vascular bundles and thus reducing nutrients and water flow to the developing kernels (Austin et al., 1977 and Weiss and Morrill, 1992). Infested stems may produce fewer kernels that are lower in dry weight than those produced by non-infested plants (Seamans et al., 1938; Holmes, 1977).

McNeal et al. (1955) conducted replicated trials with four wheats, seeded on three dates, and found a mean loss of 5.7% in the weight of the kernel due to sawfly tunnelling. They concluded that losses could range from 5% to over 20%. Holmes (1977) found a range in yield reduction of 10.8 to 22.3% attributable to reduction in the number and size of the kernel. He further found a mean loss of 11.5% in kernel weight caused by sawfly cutting and a 6.2% loss in kernel weight due to larval tunnelling. The loss in protein content ranged from 0.6 to 1.2%. Three factors appear to affect the magnitude of crop losses: rainfall in July and August, date of infestation, and larval cutting dates (Holmes, 1977).

The greatest economic loss is attributed to the physical damage. The larva girdles the stem at the base and cuts a V-shaped notch, resulting in severe lodging and yield loss. The amount of loss due to fallen heads is mediated by infestation rate, plant density, wind, and pre-harvest rainfall (Wallace and McNeal, 1966). Farstad and Jacobson (1945) estimated losses, due to lodging caused by larvae, at 800-1600 Kg/ha. The overall losses caused by wheat stem sawfly were estimated at 133,805 Megagram for Montana and North Dakota in 1951 and 61,252 Megagram for Montana alone in 1952 (Montana Agriculture Experiment Station and Montana

Extension Service, 1946; Davis, 1952). In Canada, 544,200 Megagrams of wheat were lost annually (Platt and Farstad, 1946).

Control Strategies

Methods used to control wheat stem sawfly include altering tillage practices (Criddle, 1922; Farstad et al., 1945; Munro et al., 1949; Weiss et al., 1987), using trap crops (Seamans, 1926), swathing (Holmes and Peterson, 1965), changing planting date (Jacobson and Farstad, 1952; McNeal et al., 1955; Holmes and Peterson, 1963; Weiss et al., 1987), and using resistant crops such as flax, oat, and barley in rotation (Butcher, 1946). Other factors may influence sawfly number, such as parasitism from parasitoids, field size (Holmes, 1982), fertilizer application (Luginbill and McNeal, 1954a), and resistant wheat cultivars (Callenbach and Hansmeier, 1945; Butcher, 1946; Agricultural Research Service Staff, 1955; Kasting and McGinnis, 1963). Disease and predators have little effect on _C. cinctus_ although birds may destroy a small part of the population (Davis et al., 1955).

Chemicals generally have not been effective for sawfly control because the adults feed very little and the eggs and larvae are inside the host stem. Munro et al. (1949) studied five insecticides for control of wheat stem sawfly and concluded that none of the chemicals produced satisfactory control. Gall and Dogger (1967) concluded that application of 2,4-D directly to the insect or the wheat plant was ineffective. Contact insecticides such as parathion and malathion kill wasps which are active in the field, but do not provide protection throughout the oviposition period (Holmes and Hurtig, 1952; Wallace, 1962). To date, no foliage spray is recommended for the control of wheat stem sawfly (W. L. Morrill, Personal Communication, 1993).

Attempts at biological control have been unsuccessful. One study suggested that use of parasitoids to control _C. cinctus_ was not successful because sawflies mature too early in wheat (Holmes et al., 1963). Wheat stem sawfly originally occurred in wild grasses (Ainslie 1920; Agricultural Research Service Staff, 1955) at comparatively low population densities, where populations were suppressed by parasitoids. Although sawflies quickly adapted to wheat (Ainslie, 1920), parasitoids were slower to follow. Davis et al. (1955) stated that the rate of parasitism was nearly 100% in wild grasses but seldom was above 2% in wheat. Parasitism rates vary from year to year (Holmes, 1982). Rates may be lower due to unfavorable environmental conditions such as shorter growing seasons (Beirne, 1972). Seven hymenopterous species of native parasitoids, all of them wasp like, attack wheat stem sawfly (Davis et al., 1955). The species are _Bracon lissogaster_ Muesebeck, _B. cephi_ Gahan, _Eupelmella vesicularis_ Retzius, _Eupelmus allynii_ French, _Eurytoma atripes_ Gahan, _Pleurotropis_ utahensis Crawford, and Scambus detritus Holmgren (Holmes, 1953; Agricultural Research Service Staff, 1955; Davis et al., 1955). Attempts to establish foreign parasitoids such as Collyria calcitrator Gravenhorst and Bracon terebella Wesmeal (Agricultural Research Service Staff, 1955; Luginbill and McNeal, 1955) were unsuccessful.

Wheat stem sawfly populations can be reduced by tillage systems. Reduced tillage and no-till management systems may increase wheat stem sawfly survival rate (Farstad et al., 1945; Weiss et al., 1987). Sawfly larvae overwinter in wheat stubble (Agricultural Research Service Staff, 1955), therefore tillage practices which push infested stubble to the soil surface increase sawfly larval mortality by reducing overwinter survival (Holmes and Farstad, 1956; Holmes, 1982; Weiss et al., 1987). Infestations generally are more severe on field borders, therefore entire fields need not be tilled.

Luginbill and McNeal (1954a) studied the effect of fertilizers on sawfly damage in 'Rescue' (solid stem) and 'Thatcher' (hollow stem) spring wheat, and 'Yogo' winter wheat. They concluded that application of phosphorus alone or in combination with nitrogen increased sawfly cutting in both spring and winter wheats. They indicated that phosphorus caused better growth and development of the plant making it more susceptible to sawfly infestation. Amount of sawfly cutting in winter wheat was reduced when potassium was applied together with nitrogen and phosphorus, whereas nitrogen alone had little effect on the amount of sawfly cutting. It was suggested that this was a result of the interaction of the three fertilizers (Luginbill and McNeal, 1954a).

Use of narrow strips instead of wide fields increase the severity of wheat stem sawfly damage. Holmes (1982) found that in larger fields, damage was confined mostly to edges of the fields, and resulting damage was not as severe.

Delayed spring planting were found to reduce sawfly damage. Since adults require stems for egg laying, plants which are still tillering avoid attack. Weiss et al. (1987) found that the earliest planting of hollow-stemmed wheat resulted in the highest crop damage. As planting was delayed, sawfly infestations decreased and yield increased. However, they suggested that solid-stemmed spring wheats planted earlier in the severely infested areas will reduce the sawfly damage and increase profits. McNeal et al. (1955), studying four spring wheat varieties, reported that later seeding reduced sawfly cutting significantly. Later, Morrill (unpublished data 1989-1992) concluded that delayed planting reduces efficient use of spring soil moisture, and should not be recommended for wheat stem sawfly control.

Girdled stems do not break immediately, therefore, lodging losses increase as harvest is delayed (Luginbill and McNeal, 1954b). Swathing reduces lodging losses but increases harvest costs (Holmes and Peterson, 1965). Swathing does not reduce sawfly populations because larvae have retreated to stem bases (Holmes and Peterson, 1965) and does not prevent the losses in yield and quality caused by the tunnelling of the larvae (Holmes, 1977).

The most effective control is to grow wheat varieties resistant to sawfly attack (Luginbill, 1969; Luginbill and Knipling, 1969). If a plant is resistant, it is capable of suppressing or retarding the development of a pest. Resistance in wheat to the wheat stem sawfly is positively correlated with stem solidness (Kemp, 1934; Farstad, 1940; Platt and Farstad, 1946; Platt et al., 1948; Luginbill and Knipling, 1969). The resistance results from the hinderance of egg development, first-instar larval development, or older larval development (Roberts, 1954). Population levels of the wheat stem sawfly are greatly reduced by the use of solid-stemmed spring wheat cultivars (Holmes and Peterson, 1957). EcKroth and McNeal (1953) studied morphological characteristics of 180 varieties of spring wheat in relation to sawfly resistance. Only stem solidness appeared to contribute resistance. Solid stems offer protection from damage by the larvae, but not protection from oviposition by the female (Holmes and Peterson, 1960). McNeal et al. (1955) reported that after sawfly larva tunnelling, solid-stemmed wheats were more resistant to being cut than hollow-stemmed wheats. EcKroth and McNeal (1953) studied maturity, height, and stem diameter and determined that these characters had little relation to infestation and cutting by the wheat stem sawfly.

Stem Solidness

Stem solidness is caused by the development of pith (undifferentiated parenchymous cells) inside the stem. Although it has never been demonstrated that pith is the only factor causing a variety to be resistant, many observations show that when a variety is less solid it is also less resistant (Wallace and McNeal, 1966). Roemhild (1954) reported a direct relationship between thickness of parenchyma cell walls and larval mortality in solid-stemmed spring wheat. Adults lay eggs in solid stems but many eggs and larvae die. The pith appears to cause stems to dry out earlier, and larvae have difficulty in migrating to the stub prior to maturity.

Kemp (1934) attempted to locate the source of wheats resistant to the wheat stem sawfly infestations and found that solid-stemmed wheats had less sawfly cutting than hollow-stemmed wheats. He found the wall of the stem at the nodes was thicker in solid-stemmed wheats than those of hollow-stemmed wheats.

Environmental Effect

Environmental conditions affect the degree of stem solidness in wheat. Platt (1941) found that stem solidness of *T. aestivum* cultivars was affected by variation in height, temperature, moisture supply, and spacing of plants. Under greenhouse conditions the solidness of S-615, a solid-stemmed wheat from Portugal, was almost completely inhibited. Artificial shading in the field inhibited the expression of stem solidness. Holmes et al. (1960) also showed that shading the plants reduced stem solidness. Similar results were obtained by Holmes (1984). Luginbill and McNeal (1958) found that the stem solidness of Rescue decreased as seeding rate was increased and as row spacing was narrowed.

Inheritance of Stem Solidness

Stem solidness is a highly heritable character. Lebsock and Koch (1968) reported that heritability estimates for stem solidness ranged from 60 to 95%.

Biffen (1905), in one of the first recorded reports on the inheritance of stem solidness, studied crosses of 'Rivet' (Triticum aestivum), which is solid in the top internode, with hollow-stemmed cultivars of T. aestivum. He reported a ratio of three hollow segregates to one solid in the F_2 generation and concluded that hollow stem was dominant. He also suggested that stem solidness is not morphologically a simple character.

Engledow and Hutchinson (1925) studied crosses of 'Rivet' with 'Chinese Spring' and concluded stem solidness was dominant and did not appear to be associated with any other character of the wheat plant. The difference between solid and hollow stems was hypothesized to be controlled by one gene.

Yamashita (cited by Platt et al., 1941) used an extensive series of crosses involving several species of *Triticum* to study the genetics of the solid stem character. He indicated the presence of several genes that varied in number and effect with each species.

Putnam (1942) studied the inheritance of stem solidness in tetraploid wheats. He split the stems length-wise and recorded them as solid, intermediate, or hollow. His results in crosses of *T. durum* and *T. turgidum* varieties to 'Golden Ball' (solid-stemmed wheat) indicated that the inheritance of stem solidness was unifactorial. The solid stem character was partially dominant.

Holmes (1984) reported that the Portuguese spring wheat 'S-615' is a parent of all currently grown solid-stemmed bread wheats. Wallace et al. (1969) listed a group of spring wheat selections from Portugal that were both solid-stemmed and resistant to *C. cinctus*. They stated that these selections may possess different or additional genes from those found in 'S-615'.

Platt et al. (1941), in a study of inheritance of solid stem, crossed the hollow varieties 'Renown' and 'Thatcher' with solid-stemmed selections of 'S-615-9' and 'S-633-3'. They reported that three genes were involved in the expression of solidness and that the solid condition resulted when all three genes were recessive. The authors suggested that the genes act cumulatively, and that four or more dominant genes would produce phenotypically hollow plants.

McNeal (1956) studied inheritance of stem solidness in a cross of 'Rescue' by 'Thatcher'. He found that the hollow-stemmed 'Thatcher' and solid-stemmed 'Rescue' were differentiated by one major gene and several modifying genes for stem solidness. The major gene was found to have an effect equal to two and one-half times that of all minor modifying genes.

McNeal et al. (1957) examined F_2 plants from crosses between 'Rescue' and four solid-stemmed wheat introductions from Portugal. They concluded that each of the Portuguese wheats possessed the same major gene, or genes, for stem solidness that occur in Rescue. However three of the Portuguese wheats differed slightly from Rescue. This was ascribed to the action of minor genes affecting stem solidness.

McKenzie's findings (1965) agreed with the study by McNeal (1956) in 'Rescue' x 'Thatcher' material concerning the presence of a single major gene. McKenzie (1965) studied inheritance of stem solidness in two hollow-stemmed ('Red Bobs' and 'Redman') by two solid-stemmed ('C.T.715' and 'S-615') spring wheats and hypothesized that the varieties in each cross differed by four genes for stem solidness. One major gene was indicated in both crosses and the other three genes within each cross were similar in their influence on solidness.

Several cytogenetic studies of stem solidness have been reported by Larson. Larson and MacDonald (1959) found in monosomic lines of S-615 that top and bottom internode solidness was controlled by genes at different loci. After examining aneuploids of Rescue it was found that chromosome 3D had genes on the long arm for a solid top internode and genes for solid lower internode on the short arm (Larson and MacDonald, 1962). Larson (1959) also found that chromosome 3D of Rescue had a gene, or genes, inhibiting the production of pith, especially in the top internode, but in S-615, a parent of Rescue, the 3D chromosome promoted pith production in the top internode (Larson, 1959). Larson and MacDonald (1959) showed that an aneuploid of Rescue has fewer chromosomes influencing solid stem than has its solid-stemmed parent, 'S-615'.

Relationship of Solid-Stems to Other Traits

Resistant varieties of wheat offer the best means of controlling wheat stem sawfly. Most solid-stemmed spring wheats have lower yield potential (McNeal et al., 1965; Wallace and McNeal, 1966) and poorer milling and baking values than hollow-stemmed cultivars (Stoa, 1947). The reduced yield potential of solid-stemmed cultivars relative to hollow-stemmed cultivars have caused a decrease in the acceptance of solid-stemmed cultivars by the growers of Montana (Weiss and Morrill, 1992).

Recent reports and cultivar releases suggest that the production of solid-stemmed cultivars with high yield should be possible (Lebsock et al., 1967; Lebsock and Koch, 1968; McNeal and Berg, 1977a; McNeal and Berg, 1979).

CHAPTER 3

MATERIALS AND METHODS

The material used to study the inheritance of stem solidness and its correlation with other agronomic traits was derived by crossing solid-stemmed parents, released in different eras (Table 1), with hollow-stemmed parents. Crosses were made to obtain F1, F2 and backcross progeny in 1990 and 1991 in the greenhouse, using Rescue (CI 12435) and Lew (CI 17429) as solid stem parents, and Thatcher (CI 10003) and Newana (CI 17430) as hollow stem parents. F1 progeny of the crosses were selfed and backcrossed. Spikes were bagged to avoid contamination. Space-planted parents, F1, F2 and backcross progeny were grown in a randomized complete block design with four replications at Bozeman, Montana in 1990 and 1991. A replication contained two rows of each F2, one row of each parent, each F1 and each backcross in the experiment grown in 1990. In 1991, the same experiment was repeated except that there were four rows of each F2 and the F1's were crossed to both of the parents (Table 2).

Tillers per plant (no), plant height (cm), stem solidness, grain yield (gm) and kernel weight (gm) were recorded on a single plant basis. Individual plant ratings for stem solidness were made, near plant maturity, using a 1-5 scale where 1 designates complete hollowness and 5 designates complete solidness (McNeal, 1956) as shown in Figure 1. At maturity plants were threshed individually to measure the grain yield.

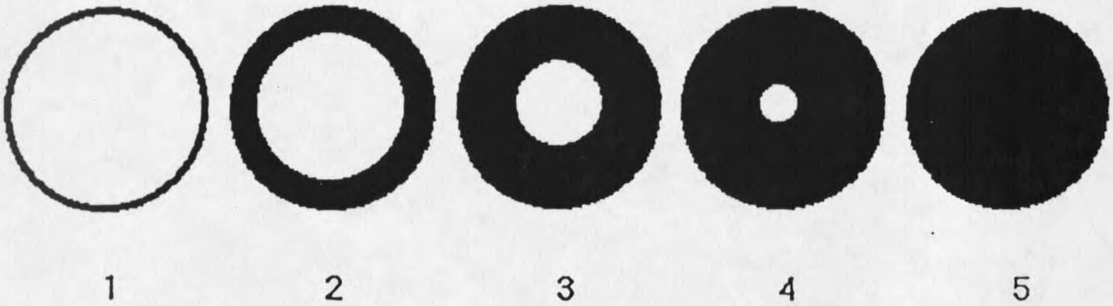

Figure 1. Diagram showing categories for stem solidness rating. 1 = hollow, 5 = solid (McNeal, 1956).

Larger experiments of F6 lines derived from solid by hollow crosses were planted in 1992 at Bozeman, Montana U.S.A. Two experiments with lattice designs, one a 12-by-12 and the other a 13-by-13, were planted in three replications on both dryland and irrigated environments. Each plot was a 3.04 meter row. Seeding rate was 10 grams per row at a planting depth of 3.80 cm with rows spaced 30.5 cm apart.

Experiment 1, contained the five parents and 139 F6 lines, derived from six different crosses; Rescue/Newana, Fortuna/Newana, Lew/Newana, Rescue/Thatcher, Fortuna/Thatcher, Lew/Thatcher. Each replication contained one line of each parent and 21-24 lines of each cross. A total of 144 entries were planted in each of two environments.

Experiment 2 was comprised of crosses derived from Fortuna/Pondera and Lew/Pondera including reciprocal crosses, and was also planted in single rows with the same planting specifications. Each replication contained one row of each parent and 37-43 lines of each cross. A total of 169 entries per replication were planted in each of two environments.

Days to heading (number of days from January 1 to 50% of the heads emerging from the boots), plant height (cm), grain yield (Mg ha^{-1}), test weight (kg m^{-3}) and stem solidness data (McNeal, 1956) were gathered. For stem solidness rating, two stems per row were cut at random, near crop maturity. A cross section was cut through the center of each internode, beginning with the bottom internode (internode 1). A total of five internode ratings were recorded. Most of the plants examined had five internodes, but in a few plants that had only four internodes the rating for the fourth was doubled to provide comparable ratings. Internode scores were summed to give the stem a single score. Finally, score for both stems was averaged and noted as one final stem solidness score. Average plant heights were collected by measuring two plants (height in centimeters from soil surface to the estimated average height of 2 or 3 main tillers, excluding awns) per plot at random. Finally each row was harvested separately with a plot combine to obtain grain yield and test weight. Test weight was measured on a

Seedburo test weight scale using kg m^{-3} scale. Percent protein was recorded for six crosses of experiment one, using Near-infrared Reflectance (NIR) in the cereal quality laboratory, Montana State University, Bozeman.

Table 1. Different solid-stemmed wheats released in different eras with their pedigrees.

cultivars	year of release	pedigree
Rescue	1945	Apex/S-615*
Fortuna	1966	Rescue/3/Chinook/4/ Frontana//Kenya58/ Newthatch
Lew	1976	Fortuna/S6258

* = original solid-stemmed wheat from Portugal.

Table 2. Number of plants studied per generation.

cross and generations		1990	1991
Rescue/Newana	**P1	39	6
	P2	43	14
	F1	46	19
	F2	93	59
	B1	@	11
	B2	42	15
Lew/Newana	P1	37	12
	P2	41	9
	F1	44	22
	F2	84	29
	B1	@	@
	B2	47	12
Rescue/Thatcher	P1	35	4
	P2	32	16
	F1	40	20
	F2	88	53
	B1	@	13
	B2	44	23
Lew/Thatcher	P1	38	9
	P2	40	7
	F1	44	44
	F2	89	96
	B1	@	14
	B2	46	17

@ = Seed was not available for these generations.

** = Parent 1, parent 2, their F1 and F2 progeny and progeny of the backcrosses of F1 to P1 and P2, respectively.

Statistical Analysis

For the 1990 and 1991 experiments, analysis of variance was computed to test the significance of differences between the generations and a generation means analysis was used to quantify the genetic effects (Rowe and Alexander, 1980). Generation means analysis, as outlined by Mather and Jinks (1977), was used to estimate the types of gene action and the conformity of the genetic system governing the expression of stem solidness to a simple additive-dominance genetic model. Lack of fit of the genetic model to the data, as indicated by the χ^2 test, implied the existence of epistatic effects. These were accommodated by increasing the complexity of the model to include the additive by additive, nonallelic interaction component. Simple correlations were determined to study the relationship of stem solidness with other agronomic traits in the 1990 and 1991 experiments.

For 1992 experiments analysis of variance was computed, combined over dryland and irrigated environments because the interaction over environments were non-significant. Heritability estimates, and genetic and phenotypic correlations were also computed.

Expected mean squares for a given cross were computed as follows:

source	df	Expected (mean square)
Experiment	e-1	
Rep(Expt)	(r-1)e	
Genotype	(g-1)	$\sigma^2 + r\sigma^2GE + re\sigma^2G$
Genotype(Expt)	(g-1)(e-1)	$\sigma^2 + r\sigma^2GE$
Error	r(g-1)(e-1)	σ^2

e,g,r = Number of experiments, genotypes and replicates, respectively.
σ^2G, σ^2GE, σ^2 = Genotypic, genotypic by expt. and error variances, respectively.

Observed mean squares were equated to expected mean square and mean product (MP) was obtained from SSCP matrices for each source of variation.

The following variance components were estimated:

σ^2G = genotypic component due to genetic differences among lines.

σ^2GE = component arising from the interaction of lines with experiment.

σ^2e = component arising due to plot-to-plot environmental variation.

Equivalent components of covariance were estimated by equating mean cross product to their expectations.

Heritability estimates for each trait were calculated as:

$$h^2 = \sigma^2G / \{\sigma^2G + (\sigma^2GE/e) + (\sigma^2/re)\}$$

The phenotypic correlation between two traits, i and j, was estimated as:

$$\text{Phenotypic } r = \text{MCPG}_{ij} / (\text{MSG}_i \cdot \text{MSG}_j)^{1/2}$$

where MCPG_{ij} is the line mean cross product, and MSG_i and MSG_j are the line mean squares for trait i and trait j.

The genotypic correlation between two traits, i and j, was estimated by:

$$\text{Genotypic } r = \sigma^2 g._{ij} / (\sigma^2 g._i \times \sigma^2 g._j)^{1/2}$$

where $\sigma^2 g._{ij}$ is the line component of covariance (mean product) between traits i and j, and $\sigma^2 g._i$ and $\sigma^2 g._j$ are the line components of variance of the two traits.

Means of the parents and crosses were identified to study the mean comparisons as follow:

$$t = \bar{x}1 - \bar{x}2 / \{(\text{MSE}/\text{reg1}) + (\text{MSE}/\text{reg2})\}^{1/2}$$

where $\bar{x}1$ and $\bar{x}2$ are the means of the variable one and two, respectively; MSE is the mean square error; r,e,g are number of replications, experiments and genotypes, respectively. TPROB program of MSUSTAT was used to find the probabilities for given t-value. All the means were assigned letters according to Student t-test (Steel and Torrie, 1960).

CHAPTER 4

RESULTS AND DISCUSSION

Genetic Effects

The analysis of variance of generation means for different crosses in 1990 and 1991 is given in Appendix 15 and 16, respectively. Parents and their progenies differed significantly ($P \leq 0.01$) for stem solidness for all crosses in both years. Therefore genetic effects for all the crosses were calculated (Mather and Jinks, 1977; Rowe and Alexander, 1980). Significant additive effects in the year 1990 were detected in the crosses where Rescue was used as a solid-stemmed parent, while significant additive, dominant and additive by additive effects were found in the crosses involving Lew as a solid stem parent (Table 3).

In 1991, significant additive effects were present in crosses of Rescue/Thatcher and Lew/Thatcher. The cross of Rescue/Newana showed additive effects, and both additive and additive by additive effects were found in the Lew/Newana cross (Table 4).

In all cases in which Rescue (an older solid-stemmed wheat) was the solid-stemmed parent, only additive effects were observed. However, in the crosses where Lew (a newer solid-stemmed wheat) was the solid-stemmed parent, additive, dominant and epistatic effects were observed. This may indicate that the genetic basis of stem solidness is

Table 3. Estimates of genetic effects for stem solidness for different crosses in 1990.

Effect	Rescue/Newana	Lew/Newana	Rescue/Thatcher	Lew/Thatcher
a	7.71*	5.90**	9.65*	6.23**
d	NS	2.46*	NS	9.10*
aa	NS	3.47*	NS	7.18*

a,d,aa = Additive, dominant and additive by additive, respectively.

*,** = Significant at the 0.05 and 0.01 probability levels, respectively.

NS = Non-significant.

Table 4. Estimates of genetic effects for stem solidness for different crosses in 1991.

Effect	Rescue/Newana	Lew/Newana	Rescue/Thatcher	Lew/Thatcher
a	5.70^{**}	4.89^{*}	6.05^{**}	5.41^{*}
d	NS	NS	NS	NS
aa	NS	5.20^{*}	NS	NS

a,d,aa = Additive, dominant and additive by additive, respectively.

*,** = Significant at the 0.05 and 0.01 probability levels, respectively.

NS = Non-significant.

different between the early release (Rescue) and the later release (Lew), although the source of stem solidness in Lew traces back to Rescue. These results are compatible with results of other workers. Yamashita (cited by Platt et al., 1941), in crosses of several species of Triticum, indicated the presence of several genes for stem solidness that varied in number and effect with each species. Wallace et al. (1969) stated that a group of solid-stemmed spring wheat selections from Portugal may possess different or additional genes from those found in S-615. Larson and MacDonald (1959) showed that Rescue has fewer chromosomes influencing solid stem than has its solid-stemmed parent, 'S-615'.

Comparison of Means

Comparison of means of different wheats used in Experiment 1 are given in Table 5. A comparison between the solid-stemmed parents released in different eras showed that all three of them differed significantly from each other for mean days to heading. Fortuna was the earliest followed by Lew. Rescue was the latest among all the parents. Newana and Thatcher, both hollow-stemmed parents, did not differ for mean days to heading, but were later than the solid stem parents with the exception of Rescue.

All the parents differed significantly for mean plant height except Rescue versus Thatcher and Fortuna versus Lew. Solid-stemmed wheats Fortuna and Lew did not differ for mean test weight and were of significantly higher mean test

Table 5. Comparison of means of different wheats released in different eras*.

parents	days to heading	plant height (cm)	test weight (kg/m^3)	grain yield (Mg/ha)	stem solidness	protein (%)
Rescue	188d	108c	729a	4.46ab	20c	14.56d
Fortuna	180a	98b	778c	5.15b	20c	14.04bc
Lew	184b	97b	775c	4.98ab	15b	13.96b
Newana	185c	80a	728a	6.12c	8a	13.18a
Thatcher	184bc	110c	744b	4.20a	8a	14.46cd

* = Means followed by the same letter are not significantly different at the 0.05 probability level.

weight than all other parents studied. Fortuna (Lebsock et al., 1967) and Lew (McNeal and Berg, 1977a) are improved solid-stemmed cultivars, therefore, it is supposed that these are better grade wheats. Rescue and Newana did not differ for mean test weight and their average test weight was the smallest among all the parents studied. Although test weight of Rescue was comparable to other cultivars from 1945 to 1947 (Stoa, 1947), this cultivar is no longer competitive with current cultivars and therefore is not accepted by Montana farmers.

The solid-stemmed parents did not differ for mean yield in this study. However, data from state wide yield trials has shown that, in general, Rescue has low yields, Fortuna is intermediate and Lew is the highest yielding solid-stemmed wheat (e.g. Bowman et al., 1992). Hollow-stemmed wheats differ significantly from each other. Newana, a hollow-stemmed wheat, was the highest yielding parent among all the cultivars studied.

The solid-stemmed parents, Rescue and Fortuna, did not differ significantly from each other for mean stem solidness score, while Lew differed significantly from Rescue and Fortuna. On the average Rescue was the most solid, Fortuna being less and Lew was the least solid-stemmed wheat. It seems that in improved varieties certain genes conferring stem solidness were lost while breeding for improved yield potentials. Hollow-stemmed cultivars did not differ from each other for mean solid stem score. Older solid-stemmed parents differ significantly for mean protein percentage from the newer ones. Mean protein percentage of older solid-stemmed wheats was greater than the newer releases. A previous study has shown that Rescue has certain deficiencies in milling and baking value (Stoa, 1947).

Comparison of means of F6 progeny derived from various crosses of different solid-stemmed wheats with Newana as hollow-stemmed wheat are given in Table 6. All the crosses differ significantly for mean days to heading. Lew/Newana was the latest, while Rescue/Newana being intermediate and Fortuna/Newana was the earliest. Rescue and Lew are mid season maturity (Stoa, 1947; McNeal and Berg, 1977a). Fortuna is early maturing (Lebsock et al., 1967) and Newana is of mid-late maturity (McNeal and Berg, 1977b). These investigations agree with this study in which the cross involving Fortuna as a solid stem parent headed earlier than the crosses involving Rescue or Lew as a solid stem parent. Crosses with Newana behaved different than expectations, in that, Lew/Newana was the latest and Rescue/Newana was intermediate. This may be surprising in that Rescue is of later maturity than Lew.

All the crosses with Newana differed significantly for mean plant height. The progeny of the Rescue/Newana cross were tallest. The progeny derived from the cross of Fortuna/Newana was intermediate and Lew/Newana was the

Table 6. Comparison of means of F6 progeny derived from various crosses of different wheats released in different eras*.

cross	days to heading	plant height (cm)	test weight (kg/m^3)	grain yield (Mg/ha)	stem solidness	protein (%)
Rescue/Newana	184b	97c	735a	4.66a	15c	14.18ab
Fortuna/Newana	183a	93b	748c	5.05b	10b	14.22b
Lew/Newana	185c	89a	745b	5.25c	9a	14.11a

* = Means followed by the same letter are not significantly different at the 0.05 probability level.

shortest. Reduction in plant height which might increase resistance to lodging and facilitate harvesting should not be difficult given heritability of 0.96 to 0.99 found in this study.

For mean test weight all the crosses with Newana differed significantly from each other (Table 6). Crosses where Fortuna was used as a solid-stemmed parent were of higher test weight (748.11), followed by cross involving Lew (745.32) as a solid-stemmed parent. Progeny of crosses with Rescue had the lowest test weight (735.05). This trait, a criterion for establishing market grade, is of such economic impact that low test weight cultivars are unacceptable to the trade. Since the heritability of test weight found in this study was high, selection for this trait is possible.

In all the Newana crosses, means for grain yield differed significantly from each other. Smallest grain yield was observed in the cross with Rescue (released 1945); Fortuna (released 1966) crosses yielded more than those with Rescue, while the cross with Lew (released 1976) was the highest yielding of all the three solid-stemmed parents. These results were expected, since Lew is a high yielding solid-stemmed variety, and Rescue is a lower yielding solid-stemmed variety.

In the crosses where Rescue was used as a solid-stemmed parent, progeny were more solid, while progeny of Fortuna crosses were less solid. Progeny derived from Lew were least solid. Solid stems are desired for the ability to control wheat stem sawfly cutting, and it seems that in improved varieties certain genes conferring stem solidness may have been lost while breeding for improved yield potential. However, stem solidness scores of improved solid-stemmed varieties investigated in this study are consistent with those Wallace et al. (1973) suggested as necessary for the effective control of wheat stem sawfly. The Fortuna/Newana cross differed significantly from Lew/Newana for mean percent protein, while other comparisons were non-significant.

Comparison of means of F6 progeny derived from various crosses of different solid-stemmed wheats crossed with a hollow-stemmed wheat, Thatcher, are presented in Table 7. All crosses differed significantly for mean days to heading. Fortuna/Thatcher cross was the earliest. Lew/Thatcher was intermediate, while Rescue/Thatcher was the latest.

All crosses differed significantly for mean plant height. The Rescue/Thatcher cross was the tallest, because of the fact that the parents were the tallest among all studied. This cross indicates a poor combining ability for lodging resistant and higher yields. The difference between Fortuna/Thatcher versus Lew/Thatcher cross means for plant height was not large. Both are improved solid-stemmed wheats and seem suited for plant height and days to heading.

Mean test weight for the Rescue/Thatcher cross differed

Table 7. Comparison of means of F6 progeny derived from various crosses of different wheats released in different eras[*].

cross	days to heading	plant height(cm)	test weight (kg/m^3)	grain yield (Mg/ha)	stem solidness	protein (%)
Rescue/Thatcher	186c	108c	737a	4.26a	10b	14.53a
Fortuna/Thatcher	181a	101a	761b	4.69b	11c	14.57a
Lew/Thatcher	184b	102b	762b	4.78b	9a	14.56a

* = Means followed by the same letter are not significantly different at the 0.05 probability level.

significantly from other crosses. The Fortuna/Thatcher versus Lew/Thatcher did not differ from each other. The smallest average test weight was observed in the crosses where Rescue was used as a parent. Crosses involving Fortuna as a solid-stemmed parent were of higher test weight, while the crosses with Lew were of the highest test weight among all the solid-stemmed parents used. This indicates that Rescue is of poor grade, Fortuna being better and Lew is of the best grade. Since heritability of this trait was found high in this study, selection for this trait is possible.

The Rescue/Thatcher cross had significantly lower mean grain yield when compared with the other two crosses. The crosses involving Fortuna or Lew as a solid-stemmed parent did not differ significantly from each other. The cross with Lew (released 1976) gave the highest yielding progeny. It seems that genetic yield potential was improved with each new release. In previous crosses where Newana was used as a hollow-stemmed parent (Table 6), the grain yield was higher as compared to crosses where Thatcher was used as a hollow-stemmed parent. Newana was shorter in stature and higher yielding than Thatcher in this study. The crosses involving Newana as a hollow-stemmed parent yielded more than those with Thatcher as a hollow-stemmed parent. Therefore, it may be concluded that Newana will work better than Thatcher while breeding for sawfly resistance, but further studies may be needed on combining abilities.

Mean stem solidness scores of all the crosses differed significantly from each other. Progeny derived from Rescue and Fortuna crosses were more solid than the progeny derived from the Lew crosses. This may indicate that in improved cultivars certain genes conferring stem solidness were lost while breeding for improved yield potentials. Over all it seems that Newana is a better hollow-stemmed parent than Thatcher, since crosses with Newana were more solid than the Thatcher.

Means for internodes involving various crosses from Experiment 1 and Experiment 2 are presented in Table 8. In almost all the crosses the first internode was the most solid, followed by the second internode . The fifth internode was least solid. The first two internodes are desired to be solid because larvae must pass through these to girdle the stem at the base, near ground level.

Comparison between Reciprocal Crosses

The difference between reciprocal crosses is usually attributed to the cytoplasmic difference between the parents. Mean comparison of reciprocal crosses in Experiment 2 derived from F6 progeny of different solid-stemmed wheats with Pondera, a hollow-stemmed wheat, are given in Table 9.

Significant differences were observed between reciprocals of Fortuna/Pondera for heading date, test weight and grain yield, while differences were non-significant for plant height and stem solidness. Significant reciprocal