

DRY MATTER AND NITROGEN  
ACCUMULATION AND REDISTRIBUTION  
IN TRITICUM AESTIVUM L.  
AND AVENA SATIVA L.

by

Patrick Michael McMullan

A thesis  
presented to the University of Manitoba  
in partial fulfillment of the  
requirements for the degree of  
Master of Science  
in  
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## ABSTRACT

McMullan, P. M. M.Sc., The University of Manitoba, June, 1985. Dry Matter and Nitrogen Accumulation and Redistribution in *Triticum aestivum* L. and *Avena sativa* L. Major Professor: Dr. P. B. E. McVetty.

Dry matter (DM) and nitrogen (N) accumulation and redistribution on a per plant basis was investigated in four wheat (*Triticum aestivum* L.) genotypes and four oat (*Avena sativa* L.) genotypes. The study was conducted at the "Point" field research station of the Department of Plant Science at the University of Manitoba in 1983 and in 1984.

Simple correlations determined using raw data values of variables from all 6 replicates for all 4 treatments indicated that DM and N accumulation and redistribution in oats is similar to that of wheat. Wheat and oats appear to have similar physiological complexes in regard to these processes.

Seasonal patterns of DM and N accumulation indicated that genotypes highest for DM and grain yield per plant in wheat and oats, Glenlea and OA424-1, respectively, were not necessarily highest for total N concentration per plant. However, differences for DM often overshadowed differences for N concentrations, whereby plant N content reflected plant DM. Cultivars highest for plant N content were highest for grain N yield per plant in both crops.

Harvest index (HI) values covered a moderate range while nitrogen harvest index (NHI) values had a wide range for both crops. The wheat genotypes were generally higher for NHI while the oat genotypes were generally higher for HI. As a result, the oat genotypes were of higher grain yield per plant, due to higher DM and HI, while the wheat genotypes were of higher grain N concentration, due to higher NHI and lower grain yield per plant.

Improving HI and NHI of within a population while maintaining DM appears to be a possible method for simultaneously increasing yield and grain protein concentration.

Chapter I  
INTRODUCTION

Wheat, Triticum aestivum L., and oats, Avena sativa L., are important cereals in both Canadian and world agriculture. In terms of acreage and production, wheat ranks first in both Canada and the world while oats ranks fourth and sixth in Canada and the world, respectively (Canada Grains Industry, 1984; Food and Agriculture Organization, 1983).

For both crops, high grain protein concentration and high grain yield are the two most desired agronomic traits. These two traits, however, are frequently negatively correlated, and increases in one often leads to decreases in the other. The problem arises then as to increasing one trait while maintaining or increasing the second in face of the negative correlation between the two.

Grain yield is dependent upon dry matter produced in and translocated from vegetative tissues of the plant. Grain protein concentration is dependent in part upon the amount of nitrogen taken up from the soil, assimilated, remobilized, and then translocated from the vegetative tissues of the plant. Grain protein concentration is ultimately dependent upon the relative amounts of dry matter and nitrogen translocated to the reproductive tissue.

A better understanding of dry matter and nitrogen accumulation and redistribution is necessary to achieve simultaneous improvement in both

grain yield and grain protein concentration. This study was initiated to examine dry matter and nitrogen accumulation and redistribution in four cultivars of wheat and four cultivars of oats. Information on nitrogen accumulation and redistribution is lacking in oats. Further, information on these traits may aid in determining selection methods for wheat and oats to simultaneously increase grain yield and grain protein concentration.

Chapter II  
LITERATURE REVIEW

INTRODUCTION

The two primary objectives in wheat (Triticum aestivum L.) and oat (Avena sativa L.) improvement programs for western Canada include increased grain yield and grain protein concentration. Secondary objectives of these improvement programs include disease and insect resistance, lodging and sprouting resistance, heat and drought tolerance, and early maturity. Agronomically acceptable cultivars must contain all or nearly all of the above mentioned traits.

Both grain yield and grain protein concentration are complex characters, making it difficult to improve these traits. Consequently, both grain yield and grain protein concentration have been broken down into component parts at various levels and from various viewpoints in an attempt to simplify their improvement.

GRAIN YIELD

Relationship of Biological Yield and Harvest Index to Grain Yield

Grain yield is the seed yield adjusted to zero per cent moisture and can be equated to biological yield (BY), the total aboveground plant dry matter at zero percent moisture, and harvest index (HI), the ratio of grain yield over biological yield, as the product of these two

components (Donald and Hamblin, 1976). Biological yield is the product of growth rate and growth duration (Takeda and Frey, 1979). Biological yield at anthesis and maturity was reported by Austin et al. (1977) to be positively correlated with grain yield. Increasing biological yield may thus result in an increase in grain yield.

Harvest index is a measure of the efficiency of dry matter translocation from the vegetative tissues of the plant to the grain (Jennings and Shibles, 1968), and is a measure of the efficiency of conversion of photosynthate into economic yield (Baker and Gebeyehou, 1982). Harvest index was positively correlated with grain yield for wheat grown at normal field densities (Chaudhary et al., 1977; McVetty and Evans, 1980b). Spaced plant harvest index has also been positively correlated with plot grain yield in wheat (Fischer and Kertesz, 1976). As well, harvest index has been positively correlated with grain yield in oats (Takeda et al., 1979; Takeda et al., 1980). However, a high harvest index does not guarantee a high grain yield because biological yields can vary dramatically among cultivars.

The improvement of yield potential in cereal crops has come largely from an increase in harvest index (Donald and Hamblin, 1976; Gifford and Evans, 1981; Sims, 1963) combined with modest increases in biological yield (Helsel and Frey, 1978; Lupton, 1966). Dry matter is derived from photosynthates formed in the vegetative tissues, considered as "sources". Grain yield is the result of translocation of this dry matter to the developing grains, which are considered "sinks".

### Source-Sink Interactions

Plant physiologists consider a green plant to consist of "sources", sites of photosynthetic carbon fixation, and "sinks", all non-photosynthetic parts (Herold, 1980). Source-sink interactions deal with the provision by the sources and consumption by the sinks of photosynthetic carbon compounds in a green plant (Herold, 1980).

Wardlaw (1965) studied the wheat cv. Gabo grown in controlled environment conditions and found that  $^{14}\text{C}$  assimilates moved from the flag leaf blade, i.e. the source, to the sheath, then to the node. Thereafter, assimilates moved up the stem to the ear, i.e. the sink. Similarly, King et al. (1967) found that removing the ear of the wheat cv. Gabo decreased net photosynthesis by the flag leaf by approximately 50 percent. Similarly, reduction in photosynthate supply has been shown to reduce grain yield in both wheat and oats (Duwayri, 1984; Womack and Thurman, 1962). Duwayri (1984) found the number of kernels decreased when defoliation of wheat by removal of awns, flag leaf, or both occurred. Kernel weight decrease occurred when awns were removed, but not when the flag leaf was removed (Duwayri, 1984). Womack and Thurman (1962) also found kernel weight decreased when the flag leaf was defoliated in wheat and oats. These findings support the idea that synthesis and translocation of photosynthates are affected by both the leaf source and the ear sink. During grain development, as the requirement for assimilates by the ear increased, the rate of  $^{14}\text{C}$  photosynthate translocation increased (Wardlaw and Moncur, 1976); however, as translocation rate increased, the concentration of photosynthate decreased. Thus, the total amount of photosynthate



delivered over time may not be altered. When there was a reduction in the source size, a concurrent decrease in the sink size occurred through effects on yield components.

### Yield Components

Grain yield in cereals is the product of the number of inflorescences per unit area, the number of kernels per spike, and the average kernel weight (Engledow and Wadham, 1923), the so-called yield components of cereals. Decreases in one component may be compensated for by increases in another. Thus, comparable grain yields may be produced in several different manners because of yield component compensation (Grafius, 1956).

If adverse conditions occur early in plant development, the number of inflorescences per unit area may be affected; however, this decrease may be compensated for by an increase in either kernel weight or the number of kernels per spikelet (Evans and Wardlaw, 1976). Due partly to their compensatory ability, yield components are often negatively correlated (Darwinkel, 1980; Gebeyehou et al., 1982).

Kernel weight is the last yield component to develop (Ledent, 1982). It is the result of grain filling rate and grain filling duration (Sofield et al., 1977a), two factors which have been extensively studied in wheat and oats.

## Grain Filling

Individual kernel weight is an important yield component in both wheat and oats. Almost all of the dry matter that an individual kernel accumulates is derived from sources within the plant, outside of the kernel. The ultimate size of the mature grain is a function of the rate and duration of grain dry matter accumulation, both of which are sensitive to environmental conditions (Sofield et al., 1977a).

Kernel dry matter accumulation follows a sigmoidal path in both wheat and oats (Housely et al., 1981; Housely et al., 1982; Ohm and Peterson, 1975; Peterson and Smith, 1976). During the major phase of dry matter accumulation, kernel growth rate is often linear and can be measured with reasonable precision.

McKee et al. (1979) found positive correlations for grain yield versus grain filling rate and for grain yield versus length of the grain filling period. Further, grain weight was positively correlated with grain filling rate. Donovan et al. (1977) found that duration rather than rate of carbohydrate deposition appeared to be the critical factor affecting final carbohydrate content of the grain which, in turn, affects kernel weight. Thus, lengthening the grain filling period may increase grain dry weight, and subsequently grain yield. However, lengthening the grain filling period may result in one of two deleterious effects on grain filling. In warm, dry climates where winter crops are grown, the filling period may extend into the dry period, when high temperatures which tend to depress kernel dry weight occur (Sofield et al., 1977b). In cool climates where spring crops are

grown, the filling period may extend into the frost season, where frost can damage the maturing grain and limit grain yield (Robertson et al., 1959).

Regulation of grain dry matter accumulation has been studied to determine factors which could perhaps be altered to increase kernel weight. Jenner and Rathjen (1975) found that more  $^{14}\text{C}$  sugars, (starch precursors), entered the free space of the endosperm of 49-day-old wheat grains than 28-day-old grains, while the 28-day-old grains had greater levels of insoluble starch. This indicated that starch synthetic capacity decreased as the grains matured. The onset of the declining phase of starch accumulation as grains begin to mature is due to a decrease in the grain's capacity to synthesize starch and not due to a decrease in assimilate supply. Thus, kernel dry matter accumulation may be regulated by starch synthesis activity.

A second alternative was postulated by Sofield et al. (1977b). It was found that the accumulation of both dry matter and nitrogen by the wheat grain ceased at the time of lipid deposition in the chalazal zone. Since the chalazal zone lies between the vascular trace and the endosperm (Frazier and Appalanaidu, 1965), grain growth terminated by lipid blockage in the pigment strand, which decreases assimilate supply, is implicated in the regulation of kernel dry matter accumulation. It has not yet been determined as to which of these two possibilities of regulation of the termination of grain dry matter accumulation is correct.

## GRAIN PROTEIN

Higher grain protein concentration is the second of the two principal improvement objectives in wheat and oats, the first being grain yield previously mentioned. Grain protein concentration is the ratio of grain protein content over total grain dry matter content.

Boatwright and Haas (1961) found that the nitrogen present in the grain protein of wheat was derived primarily by translocation of previously reduced nitrogen stored in the leaves, stem, and head chaff (nongrain portions of the spike) of the plant rather than by concurrent nitrogen assimilation and movement to the grain during the period of grain filling. Similarly, Peterson and Schrader (1974) reported that a significant amount of nitrogen found in the grain of oats at maturity was present in the vegetative portion of the plant at anthesis.

Grain protein content may be increased by increasing the amount of nitrogen translocated to the grain which can then be incorporated into the protein of the grain. The amount of nitrogen translocated can be increased by increasing the nitrogen content of the plant at anthesis or by increasing the efficiency of translocation of the nitrogen. Whichever method is used, uptake of nitrogen from the soil and assimilation of the same into protein is a complex series of reactions.

### Nitrate Reductase Activity

Nitrate is removed from the soil by the roots of plants (Hageman, 1979). This nitrate is then assimilated by the plant by a sequence of reactions, which result in the formation of proteins.

Nitrate reductase is the first enzyme in the nitrogen reduction cycle, whereby nitrate is reduced to nitrite. The nitrite is then converted to ammonium by the action of nitrite reductase. The activity of nitrate reductase is the rate-limiting step in nitrogen assimilation (Cregan and van Berkum, 1984). Eilrich and Hageman (1973) found a positive relationship between nitrate concentration and nitrate reductase activity. Further, the authors found a positive relationship between seasonal nitrate reductase activity and grain nitrogen content, as well as a positive relationship with grain yield.

Nitrate reductase activity can vary between plants and between parts within a plant. Nitrate reductase activity was highest in the leaf blades of wheat plants while nitrate content was greater in the lower plant parts (Harper and Paulsen, 1967), indicating that rapid reduction of nitrate occurs in the leaf blades and that nitrate is translocated from the root to the leaf blades in the nitrate form.

Varietal differences in nitrate reductase activity exist in wheat and oats (Cataldo et al., 1975b; Dalling et al., 1975; Nair and Abrol, 1979; Rao et al., 1977). Dalling et al. (1975) found total seasonal nitrate reductase activity in wheat was closely related to total plant nitrogen at maturity. Deckard et al. (1977) found nitrate reductase activity at 28 days post-seeding, and for the entire growing season, was negatively correlated with grain protein concentration. In contrast, these authors found nitrate reductase activity at 28 days was positively correlated with yield. The negative correlations were partially explained on the basis that assimilation and remobilization of nitrogen are separate genotypic characteristics (Deckard et al., 1977).

### Plant Nitrogen Accumulation

Varietal differences exist in maximum total plant nitrogen content for both wheat and oats. In cereals, nitrogen accumulation is dependent upon the ability of the plant to take up nitrogen from the soil (Cataldo *et al.*, 1975b; McNeal *et al.*, 1966; McNeal *et al.*, 1968; Schmidt, 1960). Plants with the largest content of plant nitrogen can be considered the most efficient in nitrogen accumulation (Desai and Bhatia, 1978).

Plant nitrogen was positively correlated with plant dry matter at both anthesis and maturity in wheat (Austin *et al.*, 1977; Desai and Bhatia, 1978). At anthesis, nitrogen concentrations were similar among varieties in both wheat and oats (Halloran and Lee, 1979; Johnson *et al.*, 1967; Peterson *et al.*, 1975). As varietal differences exist for dry matter in wheat and oats (Cataldo *et al.*, 1975b; McNeal *et al.*, 1966), plants with the highest levels of dry matter would be expected to have the largest amounts of plant nitrogen, assuming similar nitrogen concentrations.

Nitrogen stored in the vegetative material of the plant is in the form of amino acids and proteins. Protease enzymes hydrolyze the proteins into amino acids. These can then be translocated from the vegetative material to the reproductive tissues of the plant after anthesis (Boatwright and Haas, 1961; Rao and Croy, 1972). The latter authors reported that a high grain protein wheat line had a higher level of leaf blade protease activity after heading than a contrasting low grain protein wheat line. The residual levels of protein in the vegetative tissue of the high protein wheat line were significantly

lower than in the low protein wheat line. It is possible, then, that higher grain protein concentrations in wheat or oats can be achieved via enhanced protease activity in conjunction with a greater degree of nitrogen translocation.

#### Efficiency of Nitrogen Translocation

Perhaps the most important factor affecting grain nitrogen and subsequently grain protein content and concentration is the amount of nitrogen translocated from the vegetative portion of the plant to the grain and the efficiency with which this is achieved (Austin et al., 1977). Two methods of expressing nitrogen translocation efficiency exist. The first is called nitrogen translocation efficiency, (Seth et al., 1960), and is expressed as:  $(\text{maximum N content} - \text{N content at maturity}) / (\text{maximum N content})$ , while the second is called nitrogen harvest index, (Austin et al., 1977), and is expressed as:  $\text{grain N content} / (\text{grain N content} + \text{vegetative N content})$ .

Nitrogen translocation efficiency represents how efficient the plant is at removing nitrogen from the vegetative portion of the plant and translocating this nitrogen to the developing kernels (McNeal et al., 1966). Nitrogen harvest index represents the proportion of total plant nitrogen present in the grain at maturity. A larger nitrogen harvest index indicates a higher translocation of vegetative nitrogen to the grain as the majority of the nitrogen comes from the nitrogen pool accumulated in the plant prior to anthesis.

Johnson et al. (1968) found that higher protein lines of wheat had a more complete translocation of nitrogen from the straw to the grain. Similarly, Peterson et al. (1975) found that two oat cultivars, both higher in groat protein concentration than the remaining cultivars, lost a greater amount of nitrogen from the vegetative portions than the others. These authors found that the leaf blades had the highest loss of nitrogen. Lal et al. (1978) found differences in nitrogen remobilization efficiency among five wheat varieties. Halloran and Lee (1979) found significant differences in values for nitrogen harvest index in five wheat cultivars of similar grain protein concentrations. These cultivars varied in nitrogen levels, and different amounts of nitrogen were translocated. It appears that translocation of stored vegetative nitrogen is important in determining the level of grain nitrogen content and concentration.

Within head nitrogen translocation efficiency, defined as grain nitrogen over grain nitrogen plus head chaff nitrogen, followed a pattern similar to nitrogen harvest index in five wheat cultivars, although differences were much larger (Halloran and Lee, 1979). In particular, two cultivars which differed by less than 0.1% in nitrogen harvest index varied by almost 12.0% in within-head nitrogen partitioning efficiency. Lal et al. (1978) also found differences in nitrogen translocation efficiency among plant parts. Lower leaves had maximum translocation efficiency while the culm had minimum translocation efficiency. Although cultivars may be similar for plant nitrogen translocation efficiency, nitrogen translocation efficiency from various plant parts may be a factor which limits the amount of nitrogen translocated to the grain of a plant.



### Nitrogen Harvest Index Relationships

Desai and Bhatia (1978) found a significant positive correlation ( $r=+.58^*$ ) between nitrogen harvest index and harvest index in fifteen durum wheat cultivars. Similar relationships in wheat were found by Austin *et al.* (1977) ( $r=+.53^*$ ) and Dubois and Fossati (1981) ( $r=+.69^{**}$ ). This indicates a relationship exists between the remobilization and translocation of carbon and nitrogen compounds from the vegetative tissue to the grain.

Desai and Bhatia (1978) and Dubois and Fossati (1981) found a significant positive correlation ( $r=+.51^*$  and  $r=+.81^{**}$ , respectively) between nitrogen harvest index and grain protein yield (grain protein concentration times grain yield) in wheat. This indicates that the amount of protein deposited in the grain is related to the amount of nitrogen translocated from the straw. Nitrogen harvest index thus represents an important factor in grain protein concentration, as altering it will alter the level of nitrogen in the grain, which will then affect grain protein content and concentration.

### Grain Nitrogen and Protein Accumulation

Nitrogen accumulation in the grain of wheat and oats is closely related to that of grain dry matter accumulation (Brunori *et al.*, 1977; Cataldo *et al.*, 1975b; Donovan *et al.*, 1977), and follows the typical sigmoidal curve of growth.

Nitrogen concentration in the grain of wheat frequently decreased during the first few days after anthesis but this was usually followed

by an increase until maturity (Sofield et al., 1977b). This trend also occurred in oats, although the decrease in nitrogen concentration occurred later in development (Peterson and Smith, 1976). Oat cultivars that were highest in groat nitrogen concentration at maturity tended to be highest throughout development (Peterson and Smith, 1976).

Lower nitrogen concentration in the mature grain of a low percent nitrogen cultivar might be due to a greater remobilization of carbohydrates into the developing grain (Cataldo et al., 1975b), in effect a carbohydrate dilution effect. The rate of grain carbohydrate accumulation may be an important factor in determining final nitrogen concentration.

Regulation of grain nitrogen and protein accumulation has been studied to determine which factors may be altered in order to increase these characters. Brunori et al. (1977) found that protein accumulation in wheat stopped suddenly as soon as the ribonucleic acid (RNA) content in the grain began a rapid decline. This suggests that the maintenance of the RNA content in the developing endosperm of the wheat kernel is essential to the process of protein formation and accumulation. However, in other crops, the role of RNA is not as clear because in maize, protein accumulated while RNA content decreased (Ingle et al., 1965), while in rice, the level of RNA in the grain remained constant while protein accumulation decreased (Cruz et al., 1970). Thus, in oats, a system similar to that in wheat may or may not operate. Selective activity of ribonuclease on RNA might also be operative in the wheat grain (Brunori et al., 1977).

The level of soluble amino acids in the grain of cereals might also play an important role in grain protein synthesis and formation. Soluble amino nitrogen level in the grain was initially high and its level progressively decreased as protein accumulated (Donovan et al., 1977; Kapoor and Heiner, 1976; Peterson and Smith, 1976). At maturity, the level of soluble amino nitrogen was very low. This indicated that the availability of amino nitrogen (in the form of amino acids) may play an important role in maintaining the ability to synthesize endosperm protein (Brunori et al., 1977; Kapoor and Heiner, 1976). Because amino acids are incorporated into proteins, when the level of amino acids decreases, protein formation also decreases.

#### GRAIN YIELD-GRAIN PROTEIN CONCENTRATION RELATIONSHIPS

In the majority of studies, grain yield and grain protein concentration have been found to be negatively correlated in both wheat and oats (Pendleton and Dungan, 1960; Sraon et al., 1975; Stanford and Hunter, 1973; Terman et al., 1969); however, some studies in wheat indicated that positive correlations do occasionally occur (Johnson et al., 1973; McNeal et al., 1971).

McNeal et al. (1968, 1971) found a significant negative correlation in wheat between grain protein concentration and grain to straw ratios, an estimate of the vegetative dry matter. As grain yield increases relative to the amount of vegetative dry matter, the amount of nitrogen in the vegetative tissue proportional to grain yield will decrease. Thus, the amount of nitrogen available to the grain will be lower and the grain protein concentration may be lower.

## SELECTION FOR GRAIN YIELD

Direct selection for yield is achieved by selecting plants believed to be of high yield potential. Selection can be by direct measurement or by visual assessment of grain yield. Indirect selection for yield is achieved via selection for plant characteristics that are easy to select for and which are correlated with yield.

### Direct Selection for Yield

It has been possible to select directly for grain yield in both wheat (Briggs and Shebeski, 1970; Nass, 1983) and oats (Eagles and Frey, 1974; Frey, 1977). However, it is difficult to identify superior-yielding single plants in early segregating generations. Yield in F<sub>2</sub> plants has low heritability (Bhatt and Derera, 1977; Fischer and Kertesz, 1976), making it difficult to effectively select for high yield in F<sub>2</sub> plants.

### Indirect Selection for Yield Through Yield Components

Yield components may serve as useful indirect selection parameters for yield. Yield components have been found to be under relatively simple genetic control (Grafius, 1956; Ibrahim *et al.*, 1983), which would make selection for these fairly easy.

McNeal *et al.* (1978) found that selection for yield components in wheat could effectively change the grain yield of a population. Kernel weight and kernel number per spike were useful parameters for indirect selection for yield, whereas spike number per plant was not. Sidwell *et*

al. (1976) found that selection for yield via selection for kernel weight was more effective in increasing grain yield in wheat than selection for other yield components or grain yield per se.

Indirect selection for yield in oats can also be effective in increasing yield. Chandhanamutta and Frey (1973) and Geadelmann and Frey (1975) both found that selection for panicle weight, the product of kernel weight and the number of kernels per panicle, was effective in increasing grain yield in oats. It was found that 80% of the grain yield increase could be attributed to increased seeds per panicle while the remaining 20% could be attributed to increased seed weight (Chandhanamutta and Frey, 1973).

The total increase in the selected yield component may not be realized in grain yield because of the negative relationships and compensatory effects of yield components (Grafius, 1956; Sidwell et al., 1976). Indirect selection for grain yield through selection for yield components may not result in the full increase in yield potential.

#### Harvest Index as a Yield Selection Parameter

Both Fischer and Kertesz (1976) and Nass (1973) found that grain yield in spring wheat was highly positively correlated with harvest index ( $r=+.65^{**}$  and  $r=+.62^{**}$ , respectively). Similarly, in oats, harvest index was found to be positively correlated with yield (Takeda et al., 1979). Genetic variation exists for harvest index in wheat (Chaudhary et al., 1977). Thus, it may be possible to use harvest index as an indirect selection parameter for grain yield.

Results using harvest index as an indirect selection parameter have been inconsistent. Nass (1983) compared six methods of selection for yield in the F<sub>2</sub> generation of two wheat crosses, one of these involving indirect selection via selection for harvest index. This selection method was found to be comparable to random selection. Whan et al. (1982) also found harvest index was an ineffective selection parameter in a wheat cross.

Harvest index may not be useful as a selection parameter in crosses involving parents of great diversity (Nass, 1983). It has been suggested that selection for yield through selection for harvest index may only be effective in populations of similar biological yield (McVetty and Evans, 1980a).

McVetty and Evans (1980b) selected for yield in crosses involving tall and semidwarf hard red spring wheats using combined indices of harvest index and plant height or biological yield and plant height. The use of the appropriate selection index on the F<sub>2</sub> populations resulted in predictions of high-yielding F<sub>4</sub> bulks which were all significantly better than those achieved through random selection. Indirect selection for yield through selection for harvest index may be the most efficient method for increasing grain yield, if other appropriate indices are used in conjunction with it.

## SELECTION FOR GRAIN PROTEIN CONCENTRATION

Direct selection for grain protein concentration is accomplished by selecting plants believed to be of high grain protein concentration potential. Selection can be by direct measurement of grain protein concentration. Indirect selection for grain protein concentration is achieved via selection for plant characteristics that are easy to select for and which are correlated with grain protein concentration.

### Direct Selection for Grain Protein Concentration

Studies have shown that direct selection for grain protein concentration in wheat and oats is possible (Cowley and Wells, 1980; Loffler and Busch, 1982). However, direct selection for protein concentration often results in the selection of wheat or oats with a decrease in grain yield (Cowley and Wells, 1980; Loffler and Busch, 1982).

### Indirect Selection for Grain Protein Concentration

Duffield et al. (1972) found nitrate reductase activity was highly heritable in wheat at later growing stages and under "favorable" conditions. This suggests that "favorable" conditions must be present to secure good heritability estimates. When these conditions are satisfied, it may be possible to use selection for high nitrate reductase activity as an indirect selection method for increasing protein concentration.

Croy and Hageman (1970) would have selected nine of the top thirteen high grain protein content varieties of wheat on the basis of high nitrate reductase activity. However, Deckard and Busch (1978) were unable to use selection for high nitrate reductase activity as a means to increase grain protein content in wheat. From the limited information available on nitrate reductase activity, it appears that it may not be useful as a selection parameter to increase grain protein content, due to its highly variable response to the environment.

Loffler and Busch (1982) compared seven selection methods for grain protein concentration increase in wheat, one of these the direct selection approach mentioned earlier and six indirect selection methods. Indirect selection through selection for biological yield or harvest index resulted in a decrease in grain protein concentration. Indirect selection through selection for protein content per kernel resulted in equal but opposite percentage changes in grain yield and grain protein concentration. Selection for grain protein yield resulted in a large grain yield increase but a small grain protein concentration decrease. Of several parameters used in the selection for grain protein concentration, it appears that selection for grain protein yield or protein content per kernel may be suitable as indirect selection parameters for grain protein concentration.



SELECTION FOR GRAIN YIELD AND GRAIN PROTEIN CONCENTRATION

Selection for simultaneous increases in both grain yield and grain protein concentration may be accomplished by selection for nitrogen harvest index. Dubois and Fossati (1981) and Loffler and Busch (1982) reported a positive correlation for nitrogen harvest index versus grain yield ( $r=+.83^{**}$  and  $r=+.62^{**}$ , respectively) and for nitrogen harvest index versus grain protein yield ( $r=+.51^{**}$  and  $r=+.71^{**}$ , respectively). Further, these authors reported a positive correlation for nitrogen harvest index versus harvest index ( $r=+.69^{*}$  and  $r=+.54^{**}$ , respectively). As grain protein concentration is the ratio of protein over dry matter in the grain, selection for nitrogen harvest index may result in increases of both dry matter and nitrogen translocation, thereby increasing both grain dry matter and grain nitrogen, without decreasing the nitrogen concentration.

Indirect selection via selection for nitrogen harvest index resulted in a fairly large grain yield increase and a slight increase in grain protein concentration in wheat (Loffler and Busch, 1982). Selection for nitrogen harvest index may be the most efficient method to simultaneously increase grain yield and grain protein concentration. However, due to the sparse amount of literature available on the use of nitrogen harvest index as an indirect selection parameter for simultaneous increases in grain yield and grain protein concentration, further study in this area should be undertaken.

Chapter III  
MATERIALS AND METHODS

MATERIALS

The materials used in this study consisted of four genotypes of wheat (Triticum aestivum L.) and four genotypes of oats (Avena sativa L.), hereafter referred to as cultivars. The wheat and oat cultivars were selected so that their relative grain yields and grain protein concentrations covered a wide range of values (Table 1).

Three of the wheat cultivars (Glenlea, UM632, and UM684) are, or would be, suitable for the utility class of hard red spring wheat while the fourth (Benito) is a bread wheat class hard red spring wheat. Fidler and Sentinel are Canadian spring oat cultivars, while OA424-1 and OA269-E are advanced breeding lines that would qualify for the spring oats class.

FIELD STUDIES IN 1983 AND IN 1984

The four wheat cultivars and four oat cultivars were grown in 1983 and in 1984 in separate but adjacent six-replicate, randomized complete block design (RCBD) experiments, at the Winnipeg field research station of the Department of Plant Science. Four-row plots, with rows 5.0 m in length and 0.3 m apart, were used.

TABLE 1

Pedigree, relative grain yield, and relative grain protein concentration of wheat and oat genotypes

GENOTYPE	PEDIGREE <sup>1</sup>	RELATIVE GRAIN YIELD	RELATIVE GRAIN PROTEIN CONCENTRATION
Benito	Neepawa/3/RL 4255*4//Manitou/CI 7090	LOW	MEDIUM-HIGH
UM632	HPIC/Glenlea	HIGH	HIGH
UM684	HPIC/Glenlea	HIGH	MEDIUM-HIGH
Glenlea	Pembina*2/Bage//CB 100	HIGH	LOW
Fidler	Random/RL 3013	HIGH	MEDIUM-HIGH
Sentinel	Marne*2/4/Beaver/Garry//Clinton/3/Clintland	HIGH	MEDIUM-HIGH
OA424-1	<u>Avena fatua</u> /Clintland//Gemini/3/CAV2700/5872-1	MEDIUM	MEDIUM
OA269-E	CAV2700/Gemini//Kelsey	HIGH	LOW

<sup>1</sup>Pedigree written according to Purdy *et al.* (1968).

Soil samples were taken after the 1983 growing season at 0-15 cm and 15-60 cm depths, and analyzed for macronutrients. Results from these analyses indicated that soil nitrogen content did not limit growth that year. Prior to planting in 1984, soil samples were taken at these same depths, and analyzed for macronutrients. Results from these analyses indicated that fertility levels were adequate, and no fertilizer was added. Sentinel, OA424-1, and OA269-E were rust-susceptible, so plots were sprayed in 1983 with the fungicide Tilt®, when evidence of rust was observed. Plots were not sprayed in 1984. Maximum and minimum air temperatures were recorded on a daily basis, while precipitation was measured and recorded on a weekly basis.

Plots were monitored for dry matter (DM) accumulation by cutting 0.25 m (0.50 m in 1984) of the outside row of plots at ground level at the following stages of growth: four-leaf stage, anthesis (50% of plants had reached anthesis), midfilling (21 days post-anthesis), and maturity. Plants were separated into the following parts, when present: stem plus leaf sheaths (hereafter referred to as stem), leaf three, leaf two, flag leaf, inflorescence chaff (nongrain portions of the inflorescence), and grain. These were dried at 80° C for 72 hours, and then dry weights were determined. DM was determined by summing the part dry weights. Grain DM accumulation was monitored by cutting inflorescences from 0.25 m of outside row of plots at approximately weekly intervals post-anthesis. These samples were then dried at 80° C for 72 hours, then threshed. One hundred kernels from each threshed sample were then dried at 110° C overnight to determine kernel dry weight.

Nitrogen (N) accumulation was monitored by summing reduced nitrogen and nitrate nitrogen contents (nitrogen concentration times dry weight) of the DM samples, ground in a Wiley laboratory mill. Reduced nitrogen concentration was determined by Kjeldahl analysis (either micro- or macro-Kjeldahl), using titanium dioxide as a catalyst (Williams, 1973). Nitrate nitrogen was determined by a modified method of Cataldo *et al.*, (1975a), as follows. Ten mL of deionized, distilled water was added to 100 mg of dry tissue and incubated in a shaking water bath for 1 hour at 45° C. A 1 mL aliquot was removed and microfuged for 2 minutes. To 0.2 mL of the microfuged sample was added 0.8 mL of 5% (w/v) salicylic acid in concentrated sulfuric acid. After 20 minutes, 20 mL of 8% sodium hydroxide was added and the tubes were vortexed. After cooling, absorbance at 450 nm was determined. Nitrate nitrogen concentration was determined from a calibration curve, using  $\text{NaNO}_3$  as the standard. Grain N accumulation was determined as reduced nitrogen concentration in the grain DM accumulation samples times grain DM content.

Dry matter translocation indices (DMTI), the ratio of grain yield over grain yield plus vegetative DM and expressed as %, were calculated for each plant part and total plant at midfilling and maturity. DMTI on a total plant basis at maturity is equivalent to harvest index (HI). Similarly, nitrogen translocation indices (NTI), the ratio of grain N yield over grain N yield plus vegetative tissue N yield and expressed as %, was calculated for each plant part and for the total plant at midfilling and maturity. NTI on a total plant basis at maturity is equivalent to nitrogen harvest index (NHI). All index values at maturity were apparent values (Schapaugh and Wilcox, 1980), as no attempt was made to collect senesced leaves.

The amount of nitrogen translocated from vegetative tissue to the grain was measured by subtracting vegetative tissue N yield at maturity from N yield at anthesis. The majority of grain nitrogen is derived from nitrogen accumulated in the vegetative tissue prior to anthesis. Relative amounts of nitrogen assimilated after anthesis were measured by dividing grain N yield at maturity by N translocated from vegetative tissue.

At maturity, the inner two rows of the plots were cut, bagged, and dried indoors. These were threshed and then weighed for yield. Moisture content of the grain was determined. Grain protein concentration was determined on uniformly ground grain samples and expressed as reduced N concentration (see above) times 5.7 for wheat and 6.25 for oats. Thousand kernel weight was determined by weighing 200 dry seeds from each plot. The number of kernels per inflorescence was measured from the total number of seeds in 20 inflorescences selected at random from the outer rows of each plot at maturity. The number of inflorescences per plot was estimated by dividing plot yield by the product of kernels per head and kernel weight. All data obtained in both the wheat and oat experiments were expressed on a zero per cent moisture basis. A table of terms and units used throughout the thesis is presented in Appendix Table 1.

STATISTICAL ANALYSES

All data sets were analyzed as RCBD experiments, using analysis of variance (ANOVA). Means were compared using Fischer's Least Significant Difference (LSD) test at  $p=0.05$  after ANOVA gave significant F values. Correlation co-efficients between pairs of traits were determined using raw data values of variables from all 6 replicates for all 4 treatments for 1983, 1984, and for both years combined. All statistical analyses were performed using the Statistical Analysis System (Helwig and Council, 1982) on the University of Manitoba AMDAHL 580 mainframe computer.

## Chapter IV

### RESULTS AND DISCUSSION

#### GROWING SEASON CHARACTERIZATION

The 1983 and 1984 growing seasons were monitored for maximum and minimum air temperatures and precipitation. Monthly means for these environmental parameters are presented in Tables 2 and 3.

The 1983 season was characterized by normal air temperatures in May and June, combined with low precipitation (Tables 2 and 3), especially in May. July and August were hotter than normal, while precipitation was normal in July, but low in August. It should be noted, however, that rainfall occurred mainly on three days in July, with heavy rainfall occurring on the week of July 17-23 (Appendix Table 2). This caused severe lodging of the crops and subsequent limitation of plant growth.

In 1984, air temperatures similar to 1983 were observed; however, large differences in precipitation occurred (Tables 2 and 3). Rainfall was low in May, but an excess of rain in June was received. In spite of this high rainfall, lodging did not pose a problem. The low precipitation of July and August did not hinder plant growth and development, as soil moisture carryover from June provided adequate soil moisture conditions.



TABLE 2

Monthly mean maximum and minimum temperatures (°C) in the 1983 and 1984 growing seasons

MONTH	MONTHLY MEAN	1983	1984	LONG-TERM NORMAL <sup>1</sup>
MAY	MINIMUM	6.0	8.2	6.7 (5.3) <sup>2</sup>
	MAXIMUM	19.4	20.4	20.2 (18.9) <sup>2</sup>
JUNE	MINIMUM	12.2	13.7	10.5
	MAXIMUM	23.8	24.0	23.1
JULY	MINIMUM	17.1	16.0	13.3
	MAXIMUM	28.5	28.0	25.9
AUGUST	MINIMUM	17.6	16.3	11.8 (12.2) <sup>2</sup>
	MAXIMUM	31.1	29.5	24.7 (25.2) <sup>2</sup>

<sup>1</sup>From Annual Meteorological Summary, 1984.  
Environment Canada, Winnipeg.

<sup>2</sup>Normal adjusted for 1984 growing season.

TABLE 3

Monthly total precipitation (mm) in the 1983 and 1984 growing seasons

MONTH	1983	1984	LONG-TERM NORMAL <sup>1</sup>
MAY	29.1 <sup>2</sup>	24.1 <sup>2</sup>	65.7
JUNE	67.8 <sup>2</sup>	190.6+	80.1
JULY	76.4	51.8	75.9
AUGUST	21.3	15.4	75.2

<sup>1</sup>From Annual Meteorological Summary, 1984.  
Environment Canada, Winnipeg.

<sup>2</sup>Includes precipitation from the Winnipeg International Airport.

Davidson and Campbell (1984) reported dry weights and grain yields of wheat plants, cv. Manitou, decreased with intensity and duration of moisture stress. Fischer and Kohn (1966a, 1966b) found increased moisture stress resulted in higher grain protein concentration. The growing season of 1983 was therefore less conducive to plant growth, due to the high moisture stress present in that year. Allison (1966) reported that excess moisture can result in loss of nitrate from the soil by two mechanisms: (1) in a cropped soil, if precipitation is greater than evapotranspiration, leaching of nitrate will occur if the soil is at moisture levels greater than field capacity, or (2) denitrification of nitrate (nitrate is converted to nitrogen gas) if soil moisture is high, such as in rainy periods. The available soil nitrogen pool was most likely limited due to the excess precipitation in June, 1984 through the previously mentioned mechanisms.

## WHEAT

### Agronomic Characterization

Agronomic characterization of the four wheat cultivars was conducted to determine the grain yield-grain protein concentration relationships present, and to investigate the physiological basis of yield of these cultivars.

Grain yields were suppressed in 1983 while grain protein concentrations were high (Table 4), due to the low moisture conditions present in that year (Table 3), while the inverse occurred in 1984. Glenlea was high for grain yield in both years, although only significantly so in 1984, but it was lowest in grain protein

TABLE 4

Agronomic characterization of wheat cultivars for 1983 and 1984.

CULTIVAR	YIELD (KG/HA)	% PROTEIN (N x 5.7)	PROTEIN YIELD (KG/HA)	1000 KERNEL WEIGHT (g)	KERNELS PER HEAD	SPIKES PER PLOT
----- 1983 -----						
BENITO	2520.3	19.9	502.7	24.568	31	1010
UM632	2361.5	21.0	495.1	38.359	25	743
UM684	2510.8	19.9	500.5	34.309	31	717
GLENLEA	2675.9	18.9	505.3	36.050	36	626
LSD (0.05)	ns	0.8	ns	1.351	3	119
----- 1984 -----						
BENITO	2780.5	15.8	441.7	29.252	31	919
UM632	3056.4	16.5	505.6	40.706	34	669
UM684	3055.7	16.4	499.9	40.893	33	679
GLENLEA	3509.3	14.1	498.5	41.296	39	645
LSD (0.05)	177.4	1.6	43.5	1.945	3	101

concentration in both years. UM632, intermediate for grain yield, was also high for grain protein concentration in both years, although it was similar to UM684 and Benito for grain protein concentration in 1984. A negative grain yield-grain protein concentration correlation existed in 1983 ( $r=-.53^{**}$ ) but not in 1984, due to the significantly lower grain yield of Benito. With the exception of Benito in 1984, grain protein yields were similar among all cultivars as low grain yields were offset by high grain protein concentrations. The low grain yield of Benito could not be offset by its significantly lower grain protein yield. Cataldo *et al.* (1975b) concluded that low grain nitrogen concentration may arise due to a dilution of grain nitrogen by a greater remobilization of carbohydrates into the grain. Similar results were observed in this study.

Cultivars varied in yield components in both 1983 and 1984 (Table 4). Later-determined components, such as kernels per head and thousand kernel weight, were lower in 1983, due to the high moisture stress present. Glenlea was highest for kernels per head in both years and for thousand kernel weight in 1984, while Benito was lowest for thousand kernel weight in both years. UM632 and UM684 were intermediate for these components. Similar grain yields among cultivars were produced by differing levels of yield components.

#### Plant Dry Matter Accumulation

Plant DM is one of the factors determining grain yield (Takeda and Frey, 1979). Cultivar differences in DM have previously been reported in wheat, both on a per spaced plant basis (Fischer and Kertesz, 1976).

and on a per area basis (Bhatia, 1975). As DM was studied by separation into its component parts, it is reported on a per plant basis in this study.

DM accumulation was lower in 1983 than in 1984 (Figures 1 and 2), due in part to the dry soil conditions and in part to the severe lodging in 1983. Glenlea, the highest yielding cultivar, was highest for DM at all sampling dates after the four-leaf stage except at maturity in 1983, where it was similar to UM684. Benito, the low yielding cultivar, was lowest for DM at all sampling dates except at maturity in 1983, where it was similar to UM632. At all sampling dates in both years, UM684 and UM632, intermediate for grain yield, were similar to each other except at the four-leaf stage in 1984 and were second-highest for DM. DM decreased from midfilling to maturity in 1983, due to the dryness of plants at maturity, which resulted in loss of plant material through shattering and senesced leaf loss (Figure 1). In 1984, dew was present when maturity samples were taken, which aided in the prevention of shattering. As DM was studied through breakdown into its component parts, DM accumulation in plant parts could be determined. Individual plant part DM among cultivars was generally similar in trends to plant DM in both years, with Glenlea highest for DM and Benito lowest while UM632 and UM684 were intermediate (Tables 5 and 6).

Differences in DM reflect differences in growth rate, growth duration, or both (Takeda and Frey, 1979). As all cultivars were similar in phenology, differences in DM reflected differences in growth rate, with Glenlea highest and Benito lowest, while UM632 and UM684 were similar to each other and intermediate in growth rate.

Figure 1: Mean plant DM (a) at four-leaf stage and anthesis and (b) at midfilling and maturity in wheat in 1983.

Total vertical columns with the same letter above within a sampling date do not differ significantly at  $p=.05$  under Fischer's LSD.

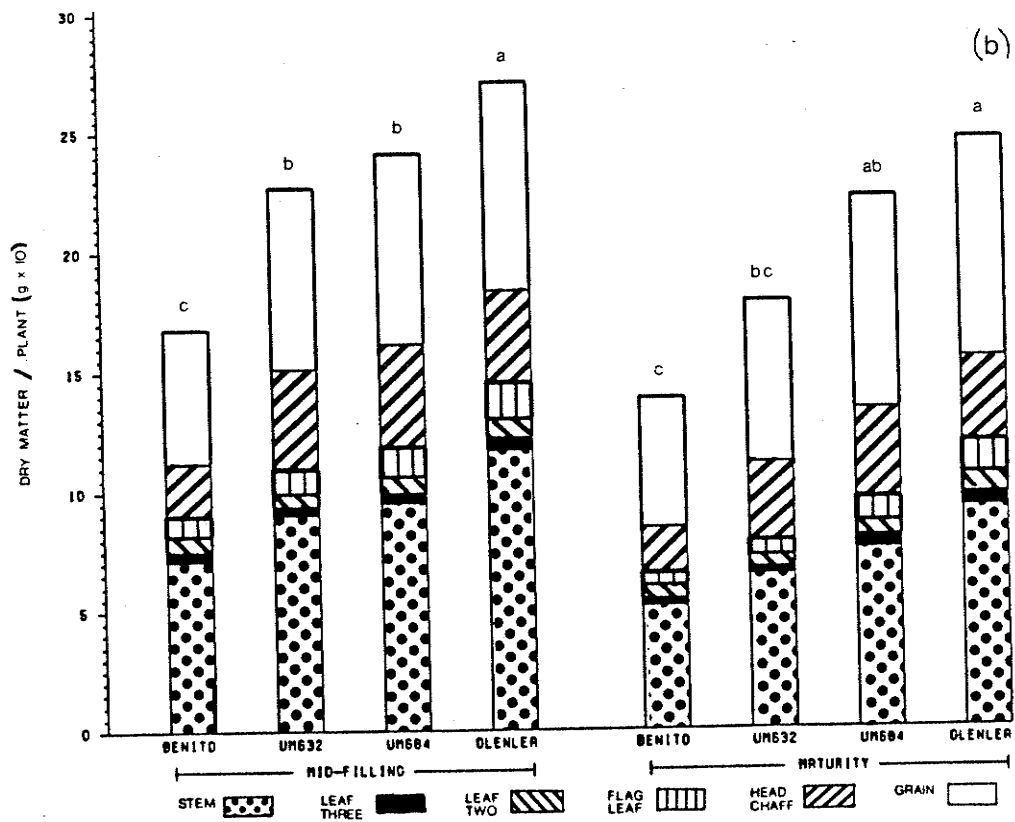
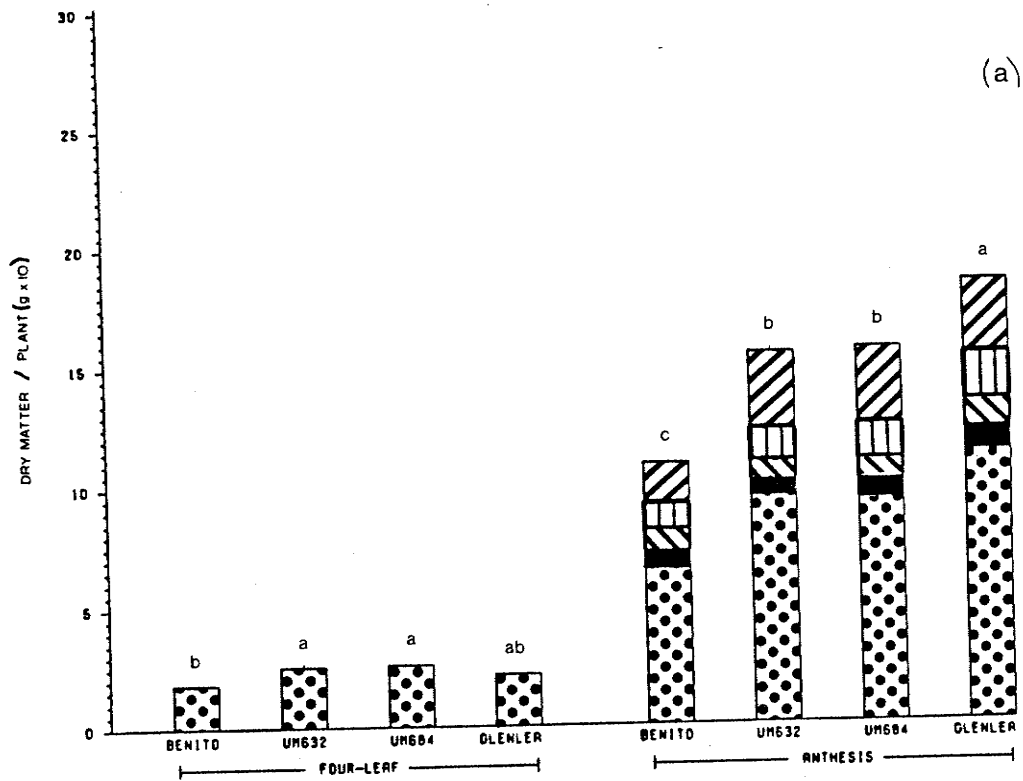


Figure 2: Mean plant DM (a) at four-leaf stage and anthesis and (b) at midfilling and maturity in wheat in 1984.

Total vertical columns with the same letter above within a sampling date do not differ significantly at  $p=.05$  under Fischer's LSD.



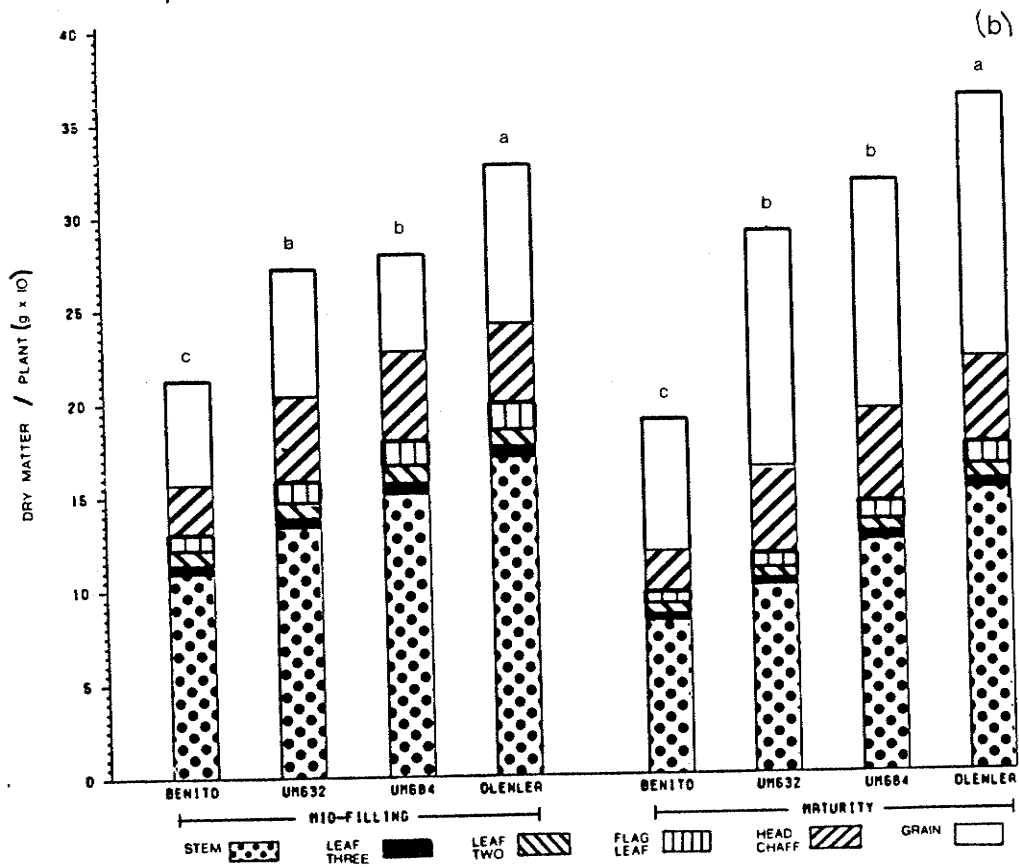
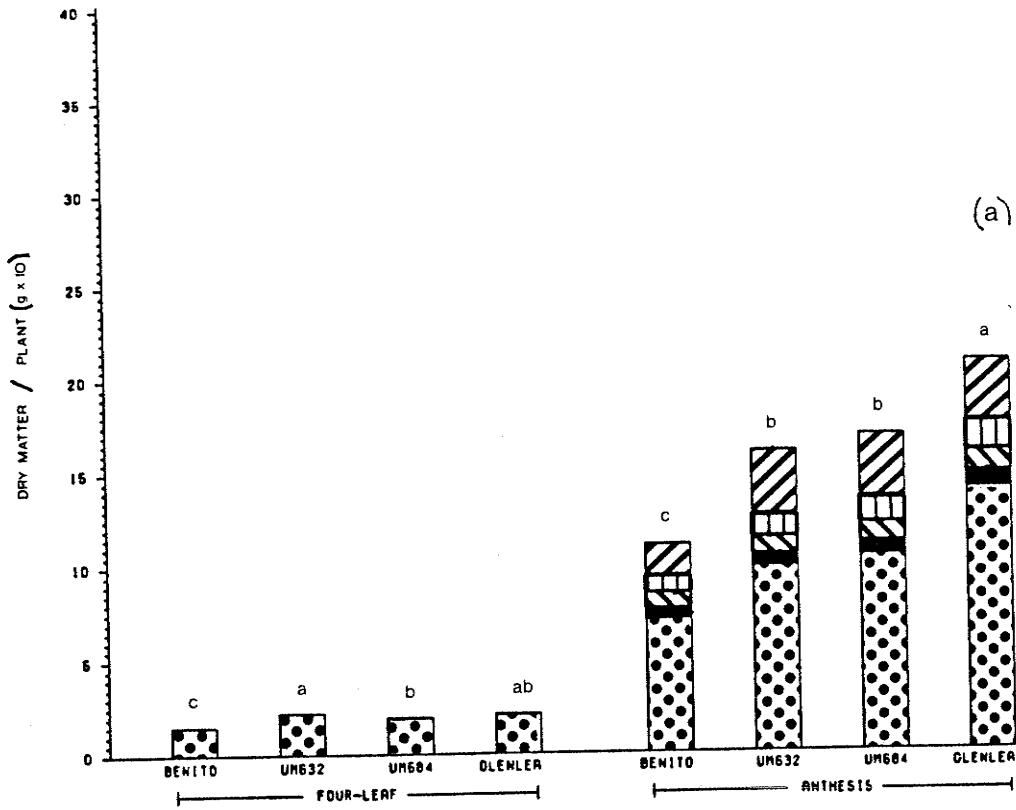


TABLE 5

Mean plant part DM (g x 10) in wheat in 1983.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	HEAD CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
BENITO	1.83					
UM632	2.54					
UM684	2.58					
GLENLEA	2.17					
LSD (0.05)	0.45					
----- ANTHESIS -----						
BENITO	6.49	0.68	0.93	1.10	1.66	
UM632	9.46	0.72	0.83	1.32	3.19	
UM684	9.33	0.75	0.91	1.48	3.15	
GLENLEA	11.26	0.96	1.19	1.94	3.02	
LSD (0.05)	1.24	0.12	0.13	0.21	0.42	
----- MIDFILLING -----						
BENITO	7.11	0.40	0.68	0.84	2.20	5.57
UM632	9.03	0.36	0.55	1.02	4.16	7.56
UM684	9.52	0.40	0.70	1.22	4.30	7.96
GLENLEA	11.70	0.50	0.80	1.50	3.81	8.74
LSD (0.05)	0.99	0.08	0.10	0.16	0.50	0.70
----- MATURITY -----						
BENITO	5.17	0.25	0.56	0.52	1.92	5.38
UM632	6.46	0.27	0.51	0.62	3.28	6.72
UM684	7.49	0.51	0.61	0.99	3.72	8.87
GLENLEA	9.21	0.56	0.82	1.32	3.54	9.16
LSD (0.05)	1.46	0.06	0.13	0.14	0.81	2.37

TABLE 6

Mean plant part DM (g x 10) in wheat in 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	HEAD CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
BENITO	1.49					
UM632	2.22					
UM684	1.96					
GLENLEA	2.10					
LSD (0.05)	0.25					
----- ANTHESIS -----						
BENITO	7.08	0.58	0.85	0.85	1.70	
UM632	9.89	0.63	0.92	1.16	3.41	
UM684	10.42	0.75	0.98	1.32	3.34	
GLENLEA	13.92	0.88	1.13	1.54	3.27	
LSD (0.05)	0.58	0.06	0.11	0.16	0.24	
----- MIDFILLING -----						
BENITO	10.91	0.49	0.77	0.86	2.63	5.59
UM632	13.32	0.53	0.82	1.11	4.57	6.82
UM684	15.10	0.60	0.92	1.34	4.79	5.21
GLENLEA	16.97	0.66	0.88	1.41	4.24	8.54
LSD (0.05)	0.88	0.05	0.06	0.12	0.29	0.83
----- MATURITY -----						
BENITO	8.21	0.36	0.54	0.60	2.17	7.03
UM632	9.98	0.40	0.57	0.77	4.61	12.65
UM684	12.34	0.46	0.65	0.96	4.96	12.24
GLENLEA	15.01	0.56	0.75	1.15	4.61	14.08
LSD (0.05)	1.69	0.04	0.07	0.11	0.67	1.85

Glenlea was high for both DM at maturity and grain yield on a per area basis. This relationship was not observed in the remaining cultivars in 1983 but was observed in 1984. However, grain yield per plant was related to DM at maturity in both years. Fischer and Kertesz (1976) found no correlation between spaced plant DM and grain yield on a per area basis, due to differences in tillering x density interactions. The similar lack of relationship between DM and grain yield on a per area basis in this study may be explained by this fact. Also, differences in grain yield on a per area basis could exist due to differences in dry matter translocation, because DM accumulation and translocation are separate physiological systems.

#### Dry Matter Translocation

The translocation of dry matter from vegetative tissue to the developing grain is another factor affecting grain yield (Takeda *et al.*, 1980). Measurement of HI is the most common method used to determine dry matter translocation efficiency.

Values for dry matter translocation index (DMTI), defined on an individual plant part and plant basis, were higher at midfilling in 1983 than in 1984 (Table 7); however, at maturity, values were similar for all cultivars between years with the exception of UM632, where DMTI was lower because of shattering. Contrarily, Baker (1982) found a highly significant cultivar x site-year interaction for HI.

Although differences among cultivars in 1983 existed for various parts for DMTI, the cultivars were similar for plant DMTI at midfilling

TABLE 7

Mean DMTI (%) in wheat in 1983 and 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	UPPER LEAVES	HEAD CHAFF	TOTAL PLANT
----- 1983 -----							
----- MIDFILLING -----							
BENITO	43.7	93.2	89.0	86.7	74.1	71.9	33.0
UM632	45.5	95.4	93.1	88.0	79.5	64.5	33.3
UM684	45.5	95.2	91.9	86.5	77.3	64.9	33.0
GLENLEA	42.7	94.5	91.6	85.3	75.7	69.7	32.3
LSD (0.05)	2.2	0.9	1.0	1.3	1.8	1.8	ns
----- MATURITY -----							
BENITO	51.2	95.2	90.5	91.0	79.8	73.7	38.6
UM632	50.5	96.4	92.7	91.4	82.7	66.8	37.4
UM684	53.6	94.4	93.4	89.5	80.2	69.8	39.4
GLENLEA	49.6	94.1	91.6	87.2	76.9	72.5	37.5
LSD (0.05)	ns	1.4	2.1	2.5	4.4	ns	ns
----- 1984 -----							
----- MIDFILLING -----							
BENITO	33.8	92.0	87.8	86.6	72.4	67.9	26.3
UM632	33.8	92.7	89.3	85.9	73.4	59.8	25.1
UM684	25.6	89.7	84.9	79.6	64.5	52.0	18.6
GLENLEA	34.2	93.0	90.8	86.0	74.7	66.6	26.6
LSD (0.05)	2.3	0.7	1.2	2.1	2.4	2.5	1.9
----- MATURITY -----							
BENITO	46.1	95.0	92.9	92.1	82.3	76.3	37.1
UM632	55.9	96.9	95.7	94.3	87.9	73.3	43.6
UM684	50.6	96.3	94.9	92.6	85.4	70.9	38.5
GLENLEA	48.5	96.2	95.0	92.5	85.2	75.3	39.0
LSD (0.05)	2.4	0.5	0.5	0.7	1.3	4.1	2.5

and maturity, and were therefore similar for DM translocation efficiency (Table 7). Differences for grain yield per plant therefore reflected differences in plant DM. However, in 1984, UM684 was lowest for DMTI in all plant parts and total plant at midfilling, while the remaining cultivars were similar for DMTI values except for head chaff. At maturity, UM632 was highest for DMTI in all parts, and therefore was higher for DM translocation efficiency. Although the remaining cultivars differed somewhat for plant part DMTI, they were similar for plant DMTI and therefore similar for DM translocation efficiency. Among UM632, UM684, and Glenlea, differences for DMTI were offset by differences in plant DM, resulting in similar grain yields per plant.

HI values (DMTI values for the total plant at maturity) among cultivars ranged from 37.1 to 43.6 over both years (Table 7). These values were in the upper range of values reported by Bhatia (1975) in 21 spring wheat genotypes and by Löffler and Busch (1982) in the progeny of three crosses of hard red spring wheat. The low range of values observed for this study can be attributed to the limited range of genetic diversity.

HI was not correlated to DM in 1983 or in 1984. This is similar to results reported by Chaudhary *et al.* (1977) in 30 cultivars of wheat, Desai and Bhatia (1978) in 15 durum wheat cultivars, and Dubois and Fossati (1981) in 12 winter wheat cultivars over 7 locations. The efficiency of DM translocation was not dependent upon the level of DM and DM translocation efficiency was independent from DM accumulation.

HI was not correlated with grain yield on a per area basis nor was it correlated with grain protein yield. HI has been positively correlated with grain yield in wheat ( $r=+.65^{**}$ ,  $+.73^{**}$ ) and grain protein yield ( $r=+.53^{*}$ ,  $+.58^{**}$ ) (Desai and Bhatia, 1978; Loffler and Busch, 1982, respectively). The lack of significant correlations in this study may be due partly to the low number of cultivars studied and partly due to the limited genetic diversity among the wheat cultivars used in this study. Although HI has been shown to be positively correlated with grain yield, it does not guarantee high grain yield. Differences in HI were smaller than differences in DM, resulting in differences in grain yield.

#### Grain Dry Matter Accumulation

Grain DM accumulation is a function of the amount of DM accumulated by each grain which, in turn, is a function of the amount of DM translocated from the photosynthetic tissue.

Grain DM accumulation was over a shorter period in 1983 than in 1984 (Figure 3), due to the high moisture stress in the previous year. Consequently, accumulation was more linear in 1983 and more sigmoidal in 1984. UM632 was highest for grain DM accumulation in both years, while Benito was lowest. Glenlea and UM684 were second- and third-highest, respectively, in 1983 but were similar to UM632 in 1984.

In 1983, all cultivars except Glenlea decreased in grain DM from 28 to 35 days post-anthesis, as did Benito in 1984 from 35 to 43 days post-anthesis (Figure 3). Decreases in grain DM at the end of the grain

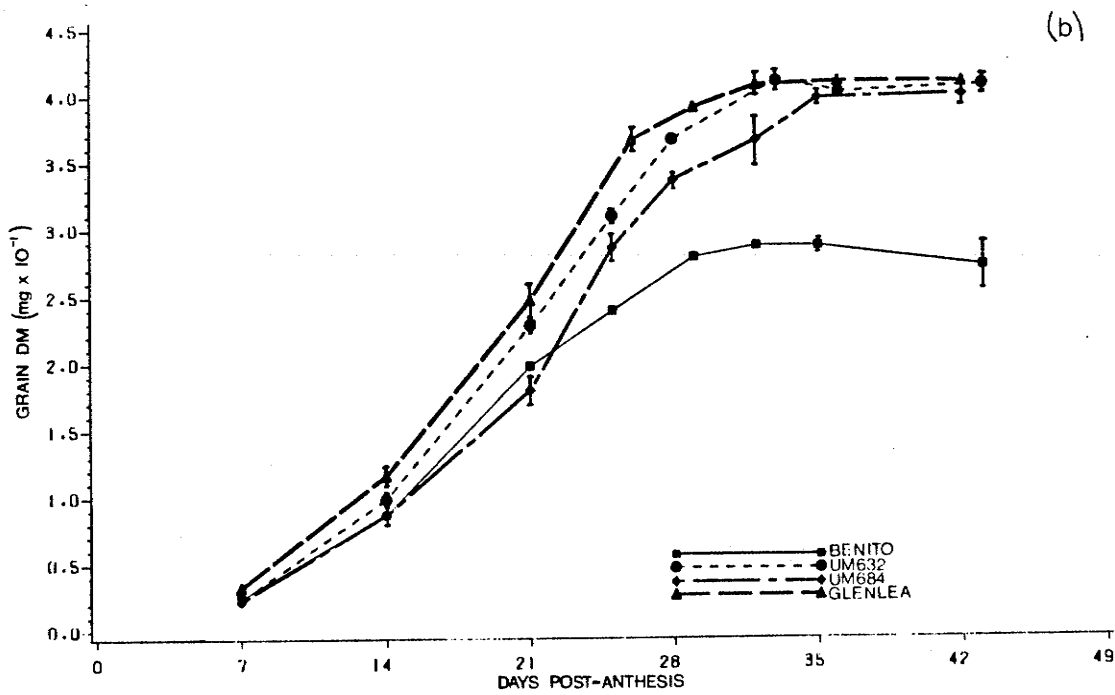
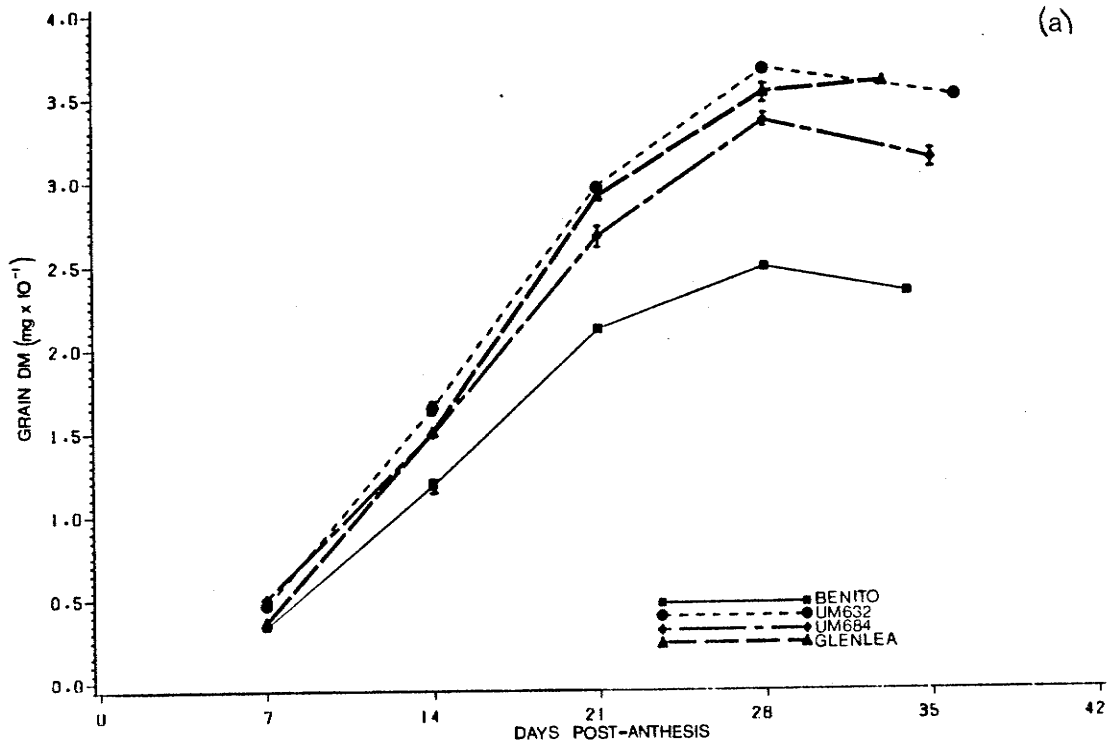


Figure 3: Grain DM accumulation as a function of days post-anthesis in wheat (a) in 1983 and (b) in 1984.



filling period in wheat have also been observed by Housely et al. (1982) and Donovan et al. (1977). This coincides with a period of rapid desiccation of the grain, when soluble materials may be moved out of the grain (Donovan et al., 1977).

When data was expressed as sampling date grain DM content over final grain DM content, all cultivars were similar in percent of final grain DM acquired at any sampling date in 1983 (Figure 4a). In 1984, differences among cultivars were evident (Figure 4b). Although cultivars differed slightly for DM accumulation as a percent of final grain DM content, differences among cultivars for grain DM accumulation reflected differences in final grain DM content.

#### Nitrogen Concentrations

Maximum nitrogen concentration represents the relative ability of the plant to store nitrogen. The stored nitrogen subsequently is translocated to the developing grain to form grain protein.

Total nitrogen concentration (hereafter referred to as N concentration) was determined by summing nitrate-N and reduced-N concentrations. Differences in nitrate-N concentrations (Appendix Tables 3 and 4) did not indicate differences among cultivars in nitrate reductase activity in each part, as reduced-N concentrations (Appendix Tables 5 and 6) did not correlate with nitrate-N.

Higher N concentrations were found in the upper leaves, while lower N concentrations were found in the stem and head chaff (Tables 8 and 9). This indicated that higher nitrate reductase activity occurred in the

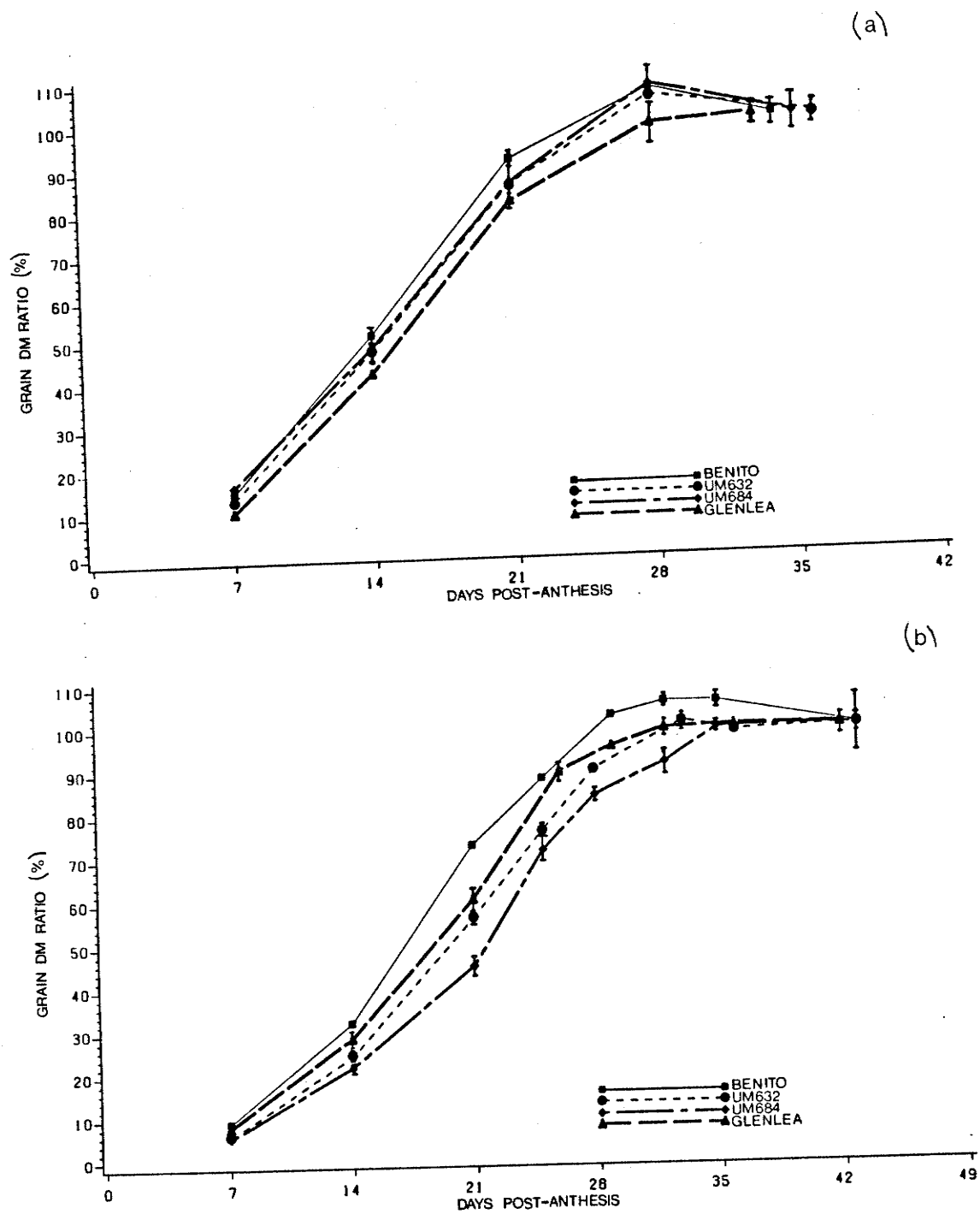


Figure 4: Ratio of sampling date grain DM content over final grain DM content (%) as a function of days post-anthesis in wheat (a) in 1983 and (b) in 1984.

TABLE 8

Mean plant part N concentrations (mg/g) in wheat in 1983.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	HEAD CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
BENITO	44.16					
UM632	47.87					
UM684	48.70					
GLENLEA	46.89					
LSD (0.05)	ns					
----- ANTHESIS -----						
BENITO	16.72	37.13	44.40	45.74	23.71	
UM632	22.72	39.24	47.54	50.93	23.22	
UM684	19.07	41.20	49.01	47.55	22.14	
GLENLEA	15.82	42.02	50.35	52.39	23.72	
LSD (0.05)	6.61	ns	ns	1.62	1.51	
----- MIDFILLING -----						
BENITO	12.14	17.00	19.69	27.46	8.84	28.88
UM632	13.50	17.29	18.33	23.93	10.27	33.04
UM684	12.20	17.30	17.81	23.31	10.16	31.95
GLENLEA	12.92	15.58	16.76	23.01	10.38	28.91
LSD (0.05)	ns	ns	ns	3.33	1.26	1.25
----- MATURITY -----						
BENITO	8.10	15.96	17.45	18.38	9.14	35.04
UM632	8.51	15.39	16.78	17.30	8.86	36.64
UM684	7.91	16.04	14.39	15.83	6.23	35.22
GLENLEA	9.64	15.39	14.31	15.25	8.45	33.07
LSD (0.05)	ns	ns	ns	ns	ns	1.53

TABLE 9

Mean plant part N concentrations (mg/g) in wheat in 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	HEAD CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
BENITO	44.86					
UM632	44.53					
UM684	45.72					
GLENLEA	43.51					
LSD (0.05)	ns					
----- ANTHESIS -----						
BENITO	11.49	26.25	34.91	40.69	19.25	
UM632	12.46	33.49	39.41	44.41	19.45	
UM684	11.10	30.07	34.19	39.63	18.46	
GLENLEA	10.62	28.75	37.30	43.94	18.52	
LSD (0.05)	1.17	3.09	3.73	2.19	ns	
----- MIDFILLING -----						
BENITO	6.05	9.61	18.10	27.63	9.21	23.87
UM632	8.19	15.28	20.97	30.67	10.17	24.83
UM684	7.21	13.42	23.72	29.75	10.67	24.99
GLENLEA	6.62	9.25	13.75	27.64	9.39	22.20
LSD (0.05)	1.02	2.45	3.35	2.34	0.97	1.51
----- MATURITY -----						
BENITO	3.08	7.89	8.38	8.87	7.54	27.15
UM632	3.14	8.56	8.53	8.60	4.23	28.64
UM684	2.47	7.31	8.33	8.12	4.79	27.07
GLENLEA	2.81	7.38	8.16	8.28	6.27	23.92
LSD (0.05)	0.52	0.86	ns	ns	0.92	2.68

leaf blades and lower activity occurred in the stem and head chaff. This is similar to results reported by Harper and Paulsen (1967), who found that nitrate reductase activity was highest in the leaf blades of wheat plants.

As N concentrations were similar among cultivars at the four-leaf stage in both 1983 and 1984 (Tables 8 and 9), cultivars were therefore similar for N accumulation capacity. N concentrations were maximal at anthesis, and represented the maximal storage capacity of the plant. At anthesis, N concentrations were higher in 1983 than in 1984, due to the lower DM and rainfall in 1983. As stem tissue constituted the largest portion of DM, cultivars differed in capacity to accumulate N due mainly to differences in stem N concentration. UM632, the high protein concentration cultivar, was highest for N concentrations and capacity to accumulate N in both years, while Glenlea, the low protein concentration cultivar, was lowest. Benito was similar to both of these cultivars for N concentrations and N accumulation capacity in both years. UM684 was similar to both UM632 and Glenlea in 1983 but was similar only to Glenlea in 1984.

Decreases in N concentration from anthesis to midfilling through to maturity indicated that N was translocated from vegetative tissue (Tables 8 and 9). Decreases observed for N concentration in vegetative tissue and increases in the grain N concentration were also reported by Johnson et al. (1967) in five winter wheat cultivars, and by McNeal et al. (1968) in five spring wheat cultivars. These studies also indicate that N is translocated from vegetative tissue to the grain. Nitrogen concentrations at maturity were higher in 1983 than in 1984, indicating plants were able to translocate N to a greater extent in 1984. In 1983,

UM632 had the largest decrease in N concentrations and appeared to translocate a greater amount of N in the period from anthesis to maturity, while Glenlea had a smaller decrease and appeared to translocate the least N. UM632 appeared to translocate a higher amount of N due to its larger decrease in N concentrations in 1984.

#### Plant Nitrogen Accumulation

Plant N content is the product of DM times N concentration. Although DM was lower in 1983 than in 1984 (Figures 1 and 2), N content was higher in the former year (Figures 5 and 6).

Glenlea, UM684, and UM632 were highest for N content in 1983 at all sampling dates except the four-leaf stage, where Glenlea was similar to Benito, and maturity, where UM632 was significantly lower than Glenlea (Figure 5). These three cultivars were again highest for N content in 1984, except at anthesis, where Glenlea was significantly higher and at midfilling, where UM684 was significantly lower than Glenlea (Figure 6). Benito was lowest for N content in both years, although it was similar to UM632 at maturity in 1983. N content reflected DM at all stages in both years while no relationship was found between N concentration and DM. Although N concentrations were not related to DM, higher N concentrations offset lower DM at various stages, whereby plants were of similar N content.

Desai and Bhatia (1978) reported that cultivars highest for N content can be considered the cultivars most efficient in N accumulation. However, as observed in this study, cultivars with the

Figure 5: Mean plant N content (a) at four-leaf stage and anthesis and (b) at midfilling and maturity in wheat in 1983.

Total vertical columns with the same letter above within a sampling date do not differ significantly at  $p=.05$  under Fischer's LSD.

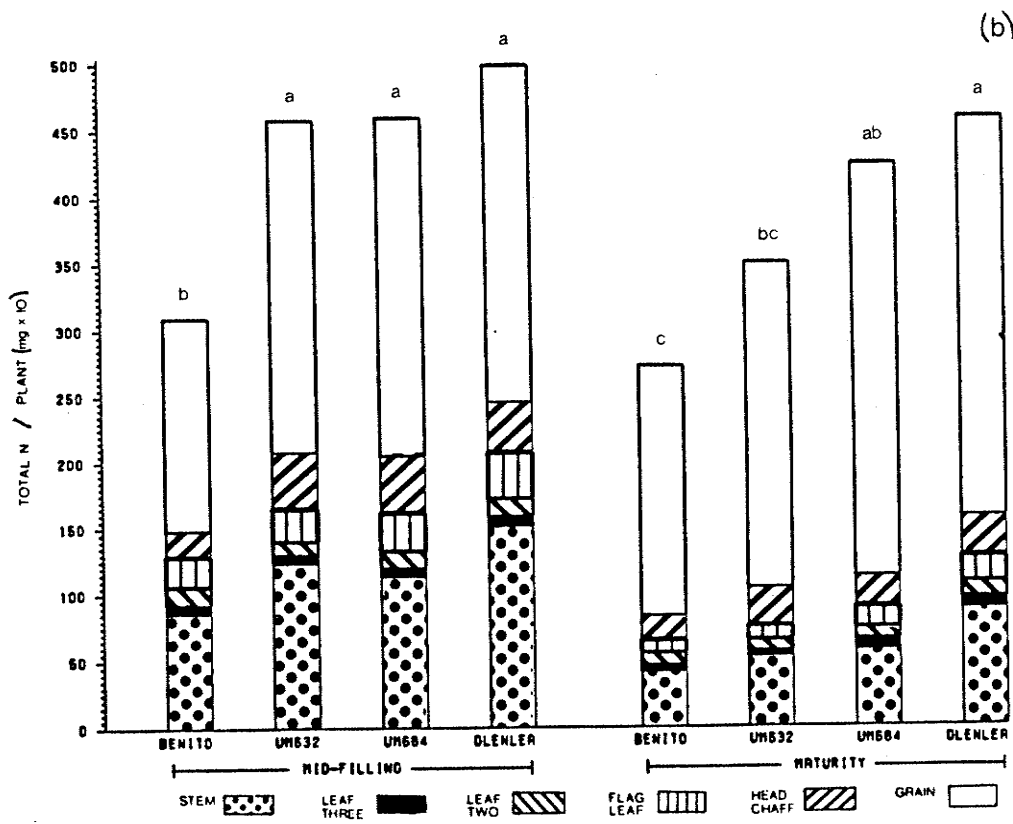
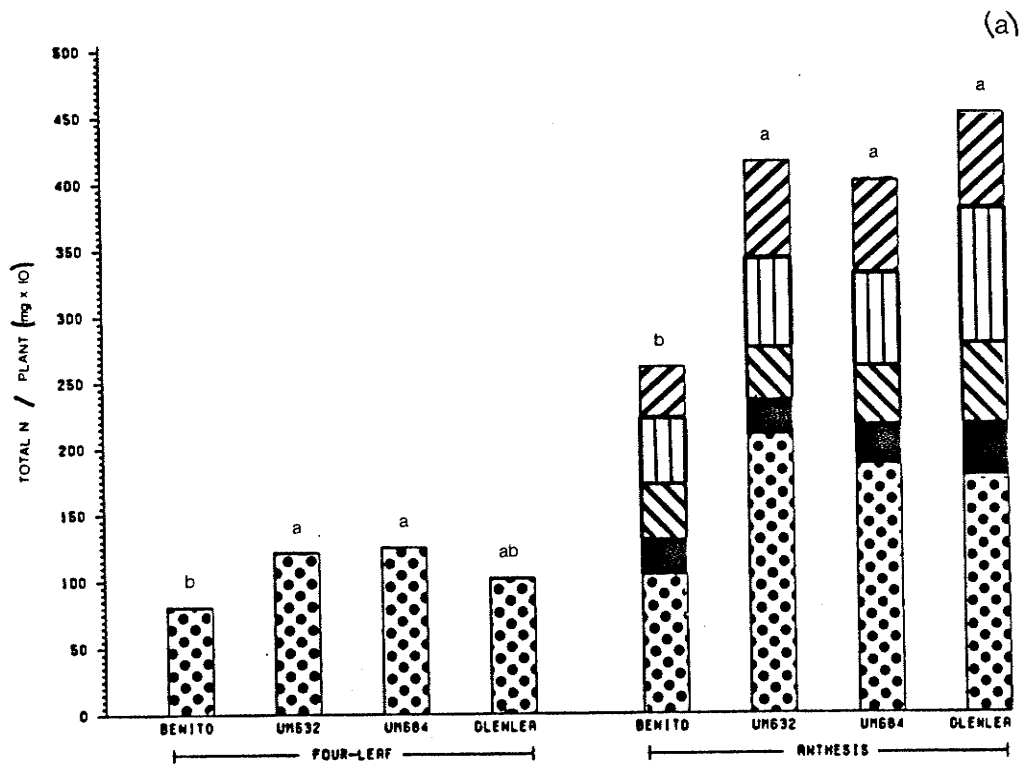
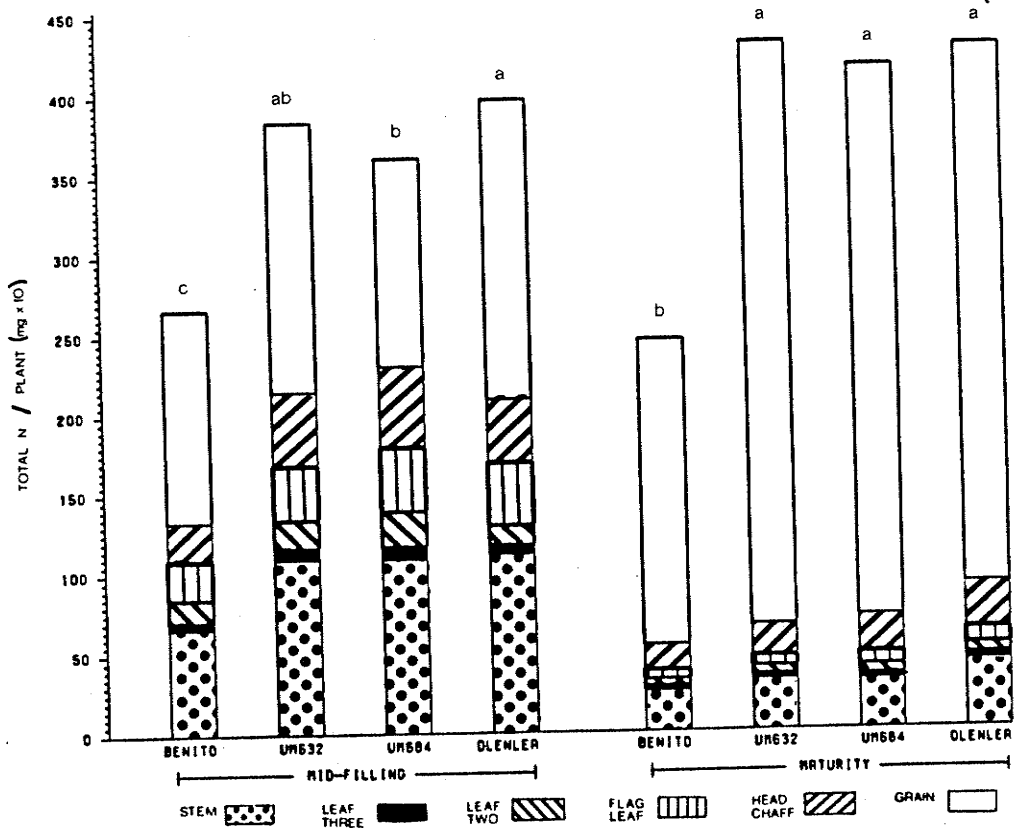
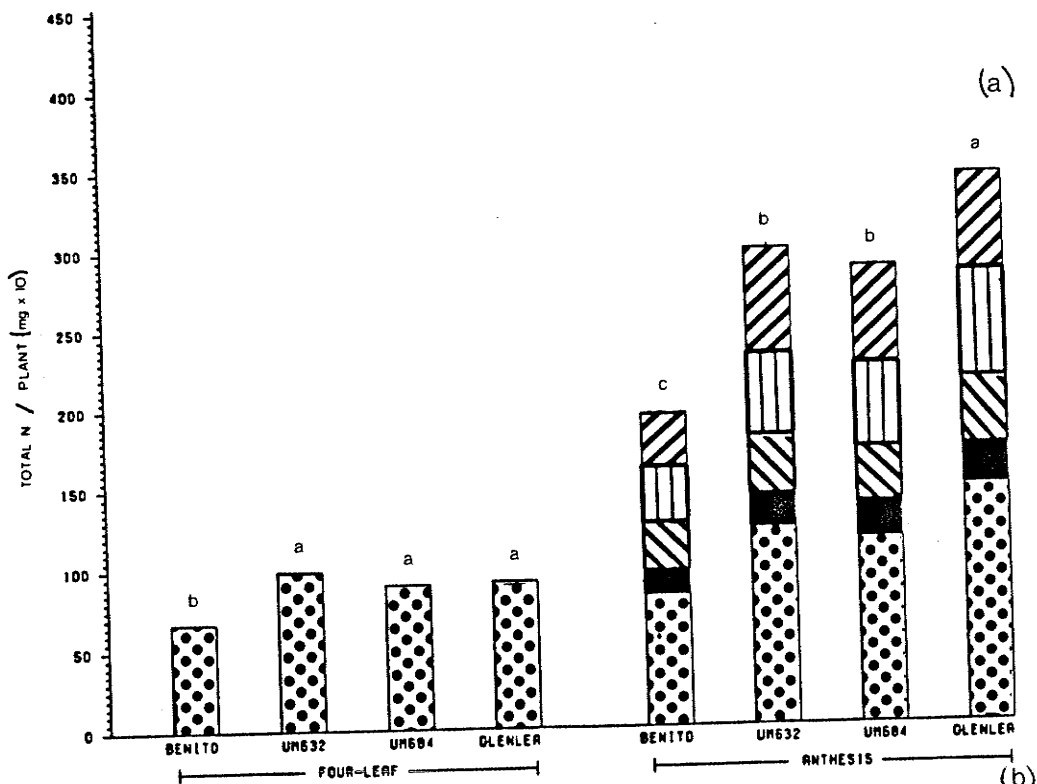




Figure 6: Mean plant N content (a) at four-leaf stage and anthesis and (b) at midfilling and maturity in wheat in 1984.

Total vertical columns with the same letter above within a sampling date do not differ significantly at  $p=.05$  under Fischer's LSD.



STEM LEAF THREE LEAF TWO FLAG LEAF HEAD CHAFF GRAIN

highest N content were not highest for N concentration. Instead, cultivars with the highest N concentration at anthesis should be considered as the most efficient for N accumulation. Thus, UM632 was the most efficient for N accumulation and not Glenlea.

Differences for individual plant part N content generally reflected differences for plant N content, with Glenlea highest, Benito lowest, and UM632 and UM684 intermediate (Tables 10 and 11). However, cultivar rankings for plant part N contents did not always reflect those for plant part DM. This was observed in the stem at anthesis in 1983 and between the flag leaf and head chaff in both years. Higher N concentrations were offset by lower plant part DM, resulting in similar N contents in these parts.

Vegetative tissue N content increased to anthesis, and then decreased to maturity in both years, while grain N content increased from anthesis to maturity. This indicated that translocation of vegetative tissue N to the grain occurred. Similar results were reported for 12 different spring wheat cultivars (McNeal et al., 1966, 1968).

Grain N yield per plant was correlated with plant N content at maturity in both 1983 and in 1984 ( $r=+.94^{**}$  and  $r=+.96^{**}$ , respectively). Increasing plant N should therefore result in higher grain N yield.

At maturity, N content was not correlated with grain protein concentration in either year. Desai and Bhatia (1978) found no correlation between these two traits ( $r=+.36$  ns). The lack of correlation could arise from differences in translocation of DM and N

TABLE 10

Mean plant part N contents (mg x 10) in wheat in 1983.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	HEAD CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
BENITO	80.74					
UM632	121.59					
UM684	125.29					
GLENLEA	101.84					
LSD (0.05)	23.69					
----- ANTHESIS -----						
BENITO	107.01	26.82	41.66	50.26	39.46	
UM632	212.87	26.64	39.64	67.30	73.60	
UM684	186.81	30.66	44.27	70.51	69.44	
GLENLEA	177.89	39.98	60.14	101.50	71.48	
LSD (0.05)	57.84	6.21	8.65	10.77	9.40	
----- MIDFILLING -----						
BENITO	85.54	6.89	13.41	22.97	19.26	161.09
UM632	123.22	6.57	10.23	25.07	42.64	250.01
UM684	113.32	6.86	12.55	28.72	43.39	254.59
GLENLEA	151.05	7.86	13.57	34.84	38.25	252.73
LSD (0.05)	25.37	ns	ns	6.88	7.36	22.62
----- MATURITY -----						
BENITO	41.64	4.24	9.81	9.54	18.09	188.74
UM632	52.63	3.84	8.57	10.46	28.69	246.01
UM684	57.39	8.15	8.59	15.53	23.04	311.39
GLENLEA	87.56	8.49	11.55	19.84	30.40	300.62
LSD (0.05)	15.25	1.22	ns	2.36	ns	78.30

TABLE 11

Mean plant part N contents (mg x 10) in wheat in 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	HEAD CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
BENITO	66.87					
UM632	98.63					
UM684	89.94					
GLENLEA	91.23					
LSD (0.05)	9.25					
----- ANTHESIS -----						
BENITO	81.48	15.19	29.72	34.82	32.72	
UM632	122.76	20.98	36.25	51.54	66.42	
UM684	115.23	22.65	34.00	52.52	61.71	
GLENLEA	147.51	25.22	42.22	67.78	60.84	
LSD (0.05)	12.64	3.48	6.77	8.48	7.59	
----- MIDFILLING -----						
BENITO	66.15	4.67	14.00	23.92	24.17	133.30
UM632	108.61	8.17	17.14	34.23	46.36	169.03
UM684	108.95	8.07	21.94	40.06	51.24	130.48
GLENLEA	111.69	6.03	12.05	39.17	39.83	187.90
LSD (0.05)	13.66	1.75	2.84	5.27	4.93	19.80
----- MATURITY -----						
BENITO	25.20	2.87	4.52	5.39	16.09	191.22
UM632	31.43	3.44	4.80	6.59	19.79	364.38
UM684	30.83	3.41	5.45	7.88	23.92	343.87
GLENLEA	42.29	4.08	6.11	9.59	28.87	336.61
LSD (0.05)	7.98	0.58	1.02	1.58	6.08	75.37

from the vegetative tissue to the grain, as these two factors help determine grain protein concentration.

### Nitrogen Translocation

The translocation of nitrogen from vegetative tissue to the grain is one of the factors influencing grain N content. Differences in the amount of nitrogen translocated can occur due to differences in the amount of plant N, the efficiency of N translocation, or both.

Values for nitrogen translocation index (NTI) were higher at midfilling in 1983 than in 1984 (Table 12), due to the more rapid grain filling of 1983. However, at maturity, values for NTI were lower in 1983, due to the low soil moisture conditions which limited N translocation.

In 1983, although differences existed for plant part NTI values, cultivars were similar for plant NTI at midfilling (Table 12). At maturity, UM684 was high for plant NTI (NHI) and Glenlea was low, while UM632 and Benito were similar to all cultivars for plant NTI. In 1984, at midfilling, UM684 was lowest for NTI, which agreed with results observed for N accumulation. Benito and Glenlea were high for plant NTI, although Glenlea was similar to UM632. At maturity, UM632 and UM684 were highest for NTI while Glenlea and Benito were lowest. UM632 and UM684 were high for nitrogen translocation efficiency over both years while Benito and Glenlea were low. Differences for NHI among UM632, UM684, and Glenlea in each year were offset by differences for plant N content, resulting in similar grain N yields per plant. Benito

TABLE 12

Mean NTI (%) in wheat in 1983 and 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	UPPER LEAVES	HEAD CHAFF	TOTAL PLANT
----- 1983 -----							
----- MIDFILLING -----							
BENITO	64.9	95.8	92.1	87.2	78.5	89.3	51.9
UM632	67.2	97.3	95.6	90.6	84.0	85.4	50.8
UM684	69.8	97.3	95.1	89.6	83.4	85.2	55.0
GLENLEA	62.6	97.0	94.8	87.8	81.8	86.3	48.7
LSD (0.05)	4.9	0.8	1.8	2.2	3.8	2.2	ns
----- MATURITY -----							
BENITO	81.8	97.7	94.9	95.1	88.7	91.5	69.3
UM632	82.0	98.4	96.4	95.7	91.1	88.9	71.1
UM684	83.6	97.4	97.1	94.9	90.2	92.9	72.6
GLENLEA	77.0	97.1	95.9	93.7	87.8	90.7	65.3
LSD (0.05)	5.1	0.9	ns	ns	ns	ns	6.0
----- 1984 -----							
----- MIDFILLING -----							
BENITO	67.0	96.6	90.5	84.8	75.8	84.6	50.2
UM632	60.8	95.5	90.8	83.1	74.0	78.4	44.2
UM684	54.4	94.1	85.8	76.5	65.1	71.7	36.2
GLENLEA	62.9	96.8	94.0	83.2	77.0	82.5	47.7
LSD (0.05)	4.5	0.8	2.0	3.2	3.1	3.3	3.8
----- MATURITY -----							
BENITO	88.3	98.5	97.7	97.3	93.7	92.1	77.8
UM632	91.6	99.0	98.6	98.1	95.9	94.6	83.9
UM684	91.7	99.0	98.4	97.7	95.3	93.2	82.5
GLENLEA	88.9	98.8	98.2	97.3	94.5	92.1	78.8
LSD (0.05)	1.7	0.2	0.3	0.4	0.8	1.8	2.7

was low in grain N yield per plant due to its lower NHI values and lower plant N content. Cultivar rankings for plant NTI changed from midfilling to maturity (Table 12). Identifying plants which are able to maintain high N translocation efficiency throughout the grain filling period on a relative basis and subsequently selecting for these plants would probably result in increased N translocation.

Values for NHI ranged from 65.3 to 83.9 over both years. Desai and Bhatia (1978) reported a slightly wider range of NHI values for 15 durum wheat cultivars, while Loffler and Busch (1982) reported a similar range of NHI values in three hard red spring wheat crosses. Values observed for NHI in this study were consistent with that of the literature.

NHI was not correlated with N content. Translocation efficiency of N from vegetative tissue was therefore a separate factor of grain N yield from uptake and assimilation of nitrogen. Similar results were reported by Desai and Bhatia (1978) for 15 durum wheat cultivars ( $r=+.15$  ns) and by Dubois and Fossati (1981) for 12 winter wheat cultivars ( $r=+.34$  ns).

NHI was not correlated with grain yield. This is in agreement with Desai and Bhatia (1978) but in contrast to Loffler and Busch (1982) who found a significant positive correlation between NHI and grain yield ( $r=+.62^{**}$ ). It is not surprising to find no correlation between these two traits, as N constitutes only a small portion of grain yield, and differences in DM translocation could account for the lack of correlation between NHI and grain yield.



Grain protein yield was not correlated with NHI. This is in contrast to the literature, where studies have shown a positive relationship between these two traits for wheat ( $r=+.58^*$ ,  $+.99^{**}$ , and  $+.71^{**}$ ) (Desai and Bhatia, 1978; Dubois and Fossati, 1981; Loffler and Busch, 1982), respectively. Differences in NHI existed in this study, and these differences offset differences in N content, thereby resulting in similar grain N contents and the lack of correlation between NHI and grain protein yield. Although NHI and grain protein yield were not correlated in this study, NHI is an important factor determining the level of grain N yield.

NHI was negatively correlated with grain protein concentration in the wheat cultivars when data was combined over both years ( $r=-.61^*$ ). The relationship observed in this study was artificial, due to the very different environmental conditions in the two growing seasons. The lack of correlation in this study in each year was probably due to the lack of correlation between NHI and grain yield and grain protein yield, as grain protein concentration is the ratio of these two traits. Desai and Bhatia (1978) found no correlation between these two traits ( $r=+.14$  ns) for 15 durum wheat cultivars, while Dubois and Fossati (1981) and Loffler and Busch (1982) also found no correlation ( $r=-.36$  ns,  $+.00$  ns, respectively).

NHI and HI were positively correlated in both 1983 and in 1984 ( $r=+.90^{**}$  and  $r=+.76^{**}$ , respectively). Desai and Bhatia (1978) reported a positive correlation between NHI and HI ( $r=+.58^*$ ) for 15 durum wheat cultivars, while Dubois and Fossati (1981) and Loffler and Busch (1982) also found positive correlations ( $r=+.69^*$  and  $+.54^{**}$ , respectively).

This indicated that HI and NHI were similar, though not identical, factors. Translocation of dry matter and nitrogen were related processes. Thus, by increasing either NHI or HI, increases in the other will most likely occur.

UM632 and Glenlea were high for amount of N translocated (Table 13); however, in 1984, Glenlea was higher than UM632. Benito was low for N translocated in both years. The amount of N translocated was positively correlated with N content at anthesis in 1983 and in 1984 ( $r=+.58^{**}$  and  $+.80^{**}$ , respectively). The amount of N translocated was therefore related to the plant N content at anthesis. Grain N yield per plant was positively correlated with the amount of N translocated in 1983 ( $r=+.52^*$ ) and in 1984 ( $r=+.55^{**}$ ). The level of grain N yield per plant was related to the amount of N translocated from the vegetative tissue of the plant.

Ratios of grain N over amount of N translocated indicated that maximum plant N content occurred very close to anthesis in 1983 (Table 13). However, the ratio for UM632 was low, due to loss of N through loss of DM (both vegetative and grain) at maturity. Ratios indicated maximum plant N content occurred after anthesis in 1984, which resulted in underestimation of the amount of N translocated.

TABLE 13

Mean N translocated (mg x 10) and ratio of grain N content over N translocated (%) in wheat in 1983 and 1984.

CULTIVAR	N TRANSLOCATED	RATIO OF GRAIN N : N TRANSLOCATED (%)
----- 1983 -----		
BENITO	176.95	102.82
UM632	321.53	76.29
UM684	290.34	108.39
GLENLEA	292.62	103.93
LSD (0.05)	30.64	33.38
----- 1984 -----		
BENITO	139.83	137.69
UM632	231.84	150.39
UM684	214.70	163.23
GLENLEA	252.57	134.51
LSD (0.05)	14.83	42.80

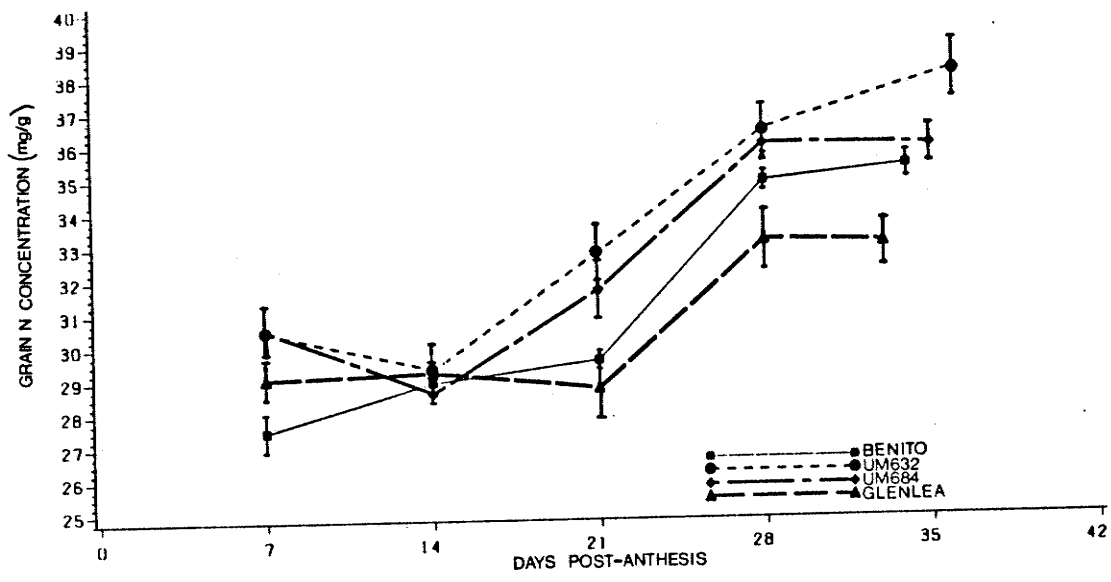
### Grain Nitrogen Concentration

Grain N concentration is the ratio of grain N over grain DM. Grain N concentration reflects DM and N translocation, whereby changes in grain N concentration occur as a result of changes in the amount of DM and/or N translocated.

In general, grain N concentrations were higher in 1983 than in 1984 (Figure 7), due to the dry soil conditions of the former year. UM632 was high for grain N concentration at all sampling dates in 1983, while Glenlea was low at all sampling dates after 14 days post-anthesis. UM684 and Benito were second-highest for grain N concentration. In 1984, UM632 and UM684 were highest for grain N concentration and Glenlea was lowest, while Benito was second-highest to 24 days post-anthesis but was high thereafter.

Grain N concentrations decreased in UM684 from 7 to 14 days post-anthesis in 1983 and in all cultivars from 7 to 21 days post-anthesis in 1984 (Figure 7). This decrease in Glenlea in 1984 was so large that it resulted in an overall decrease for its grain N concentration over the entire sampling period. These decreases most likely occurred as a result of higher DM translocation relative to N translocation. Increases in grain N concentration most likely occurred as a result of the inverse of this situation.

(a)



(b)

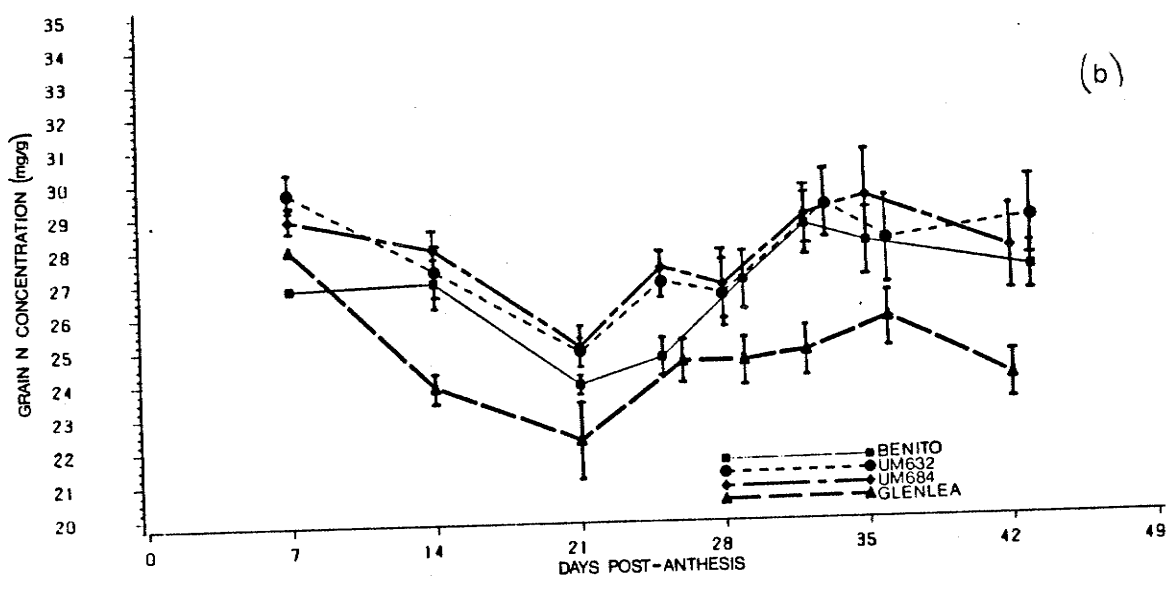


Figure 7: Changes in grain N concentration as a function of days post-anthesis in wheat (a) in 1983 and (b) in 1984.

### Grain Nitrogen Accumulation

Grain N content is the product of grain DM times grain N concentration. Differences in grain N accumulation can arise from differences in grain DM accumulation, and/or N concentration.

Grain N accumulation was higher and over a shorter period in 1983 than in 1984 (Figure 8) and, as a result, was more linear in 1983. Grain N accumulation was highest in UM632 and lowest in Benito in both years. UM684 and Glenlea were second-highest for grain N accumulation in 1983 while in 1984, Glenlea was similar to UM632 to 26 days post-anthesis and was lower thereafter while UM684 was low to 21 days post-anthesis but increased and was high at maturity.

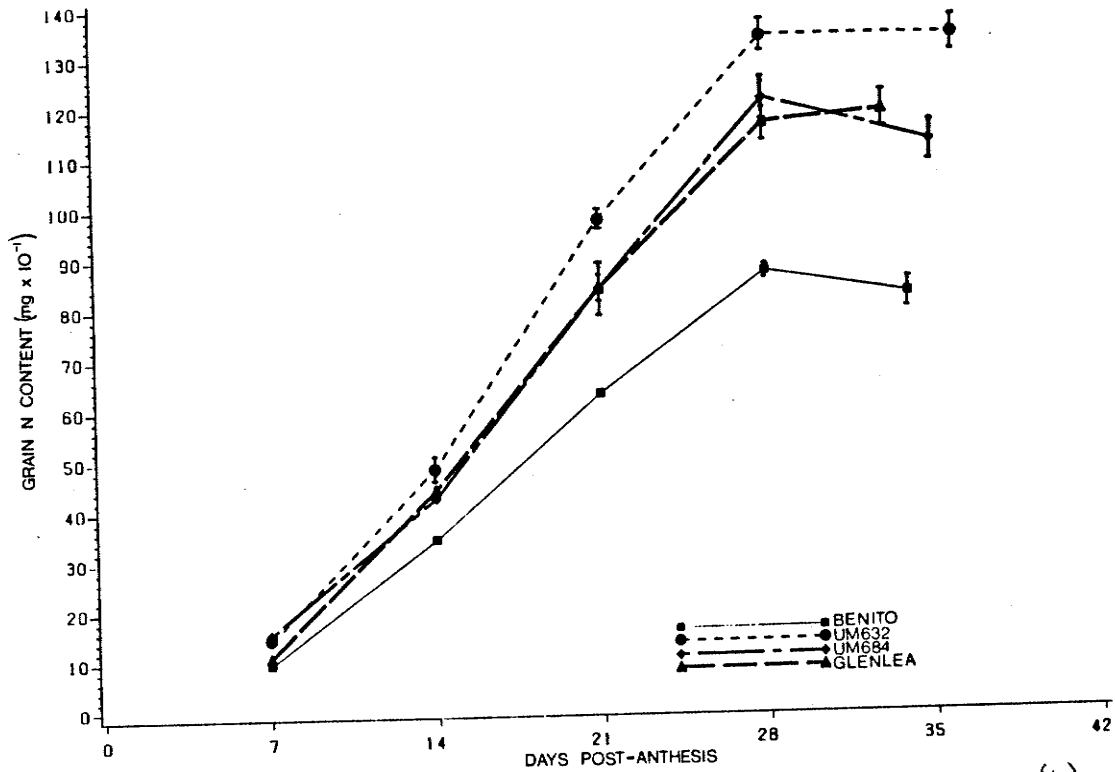
When grain N accumulation was expressed as sampling date grain N content over final grain N content, differences were very small among cultivars in 1983 and in 1984 (Figure 9), although some differences were observed at various sampling dates in 1984. However, cultivars accumulated N on a similar percent of final N content basis, whereby differences in grain N accumulation reflected differences in final grain N content.

### OATS

#### Agronomic Characterization

Grain yields and grain protein concentrations of the cultivars in this experiment were determined to identify the grain yield-grain protein concentration relationship present. Agronomic characterization was performed to determine the basis of yield of each cultivar.

(a)



(b)

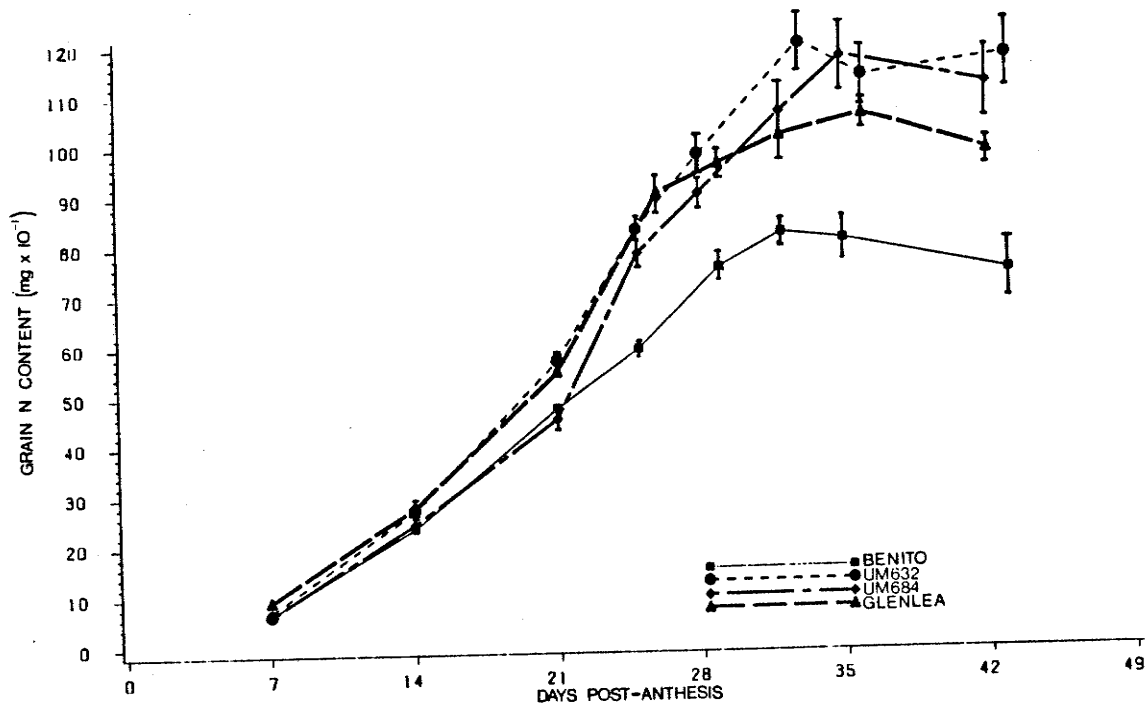


Figure 8: Grain N accumulation as a function of days post-anthesis in wheat (a) in 1983 and (b) in 1984.

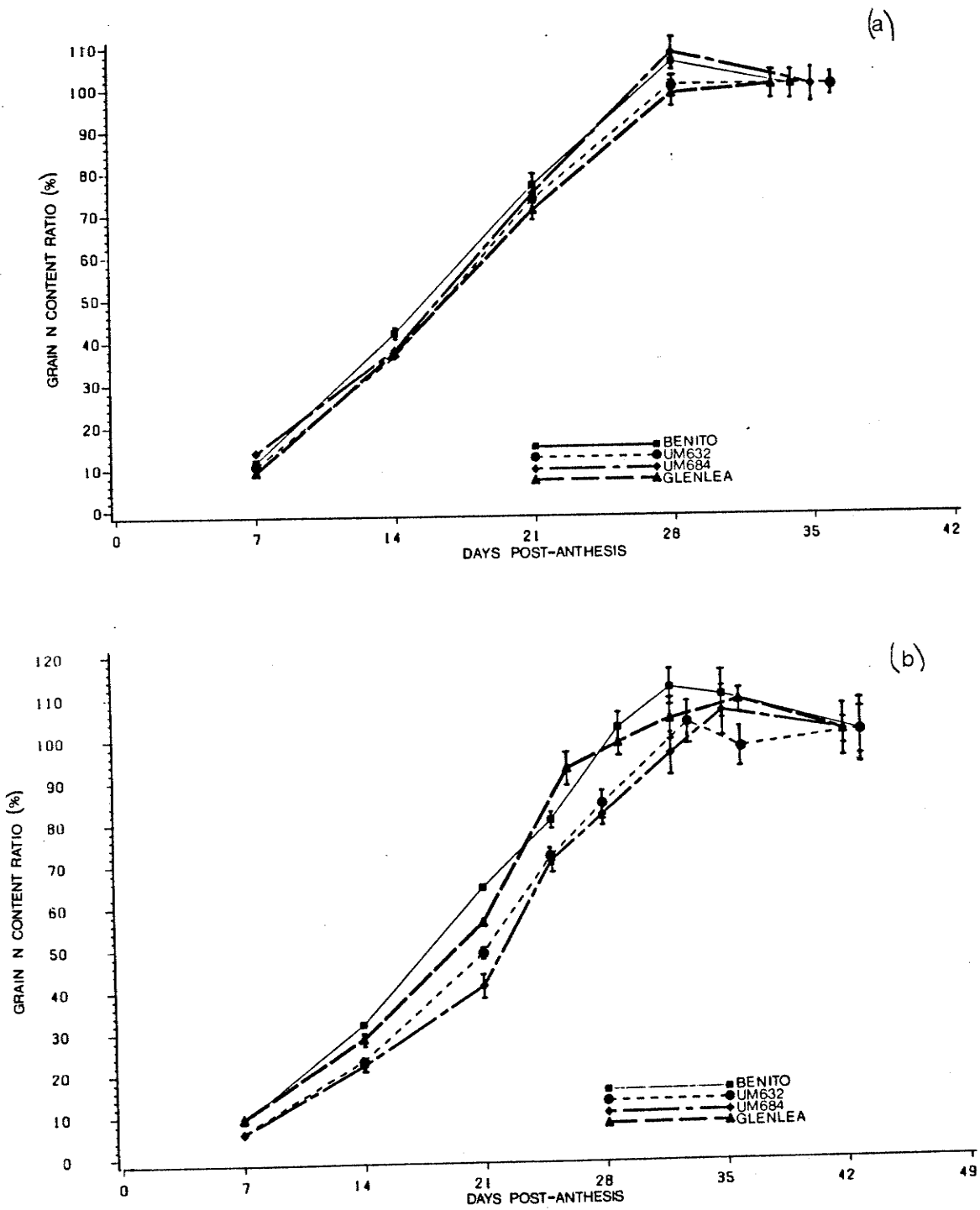


Figure 9: Ratio of sampling date grain N content over final grain N content (%) as a function of days post-anthesis in wheat (a) in 1983 and (b) in 1984.



Grain yields were suppressed and grain protein concentrations elevated in 1983, due to the high moisture stress present in that year, while the inverse occurred in 1984 (Table 14). Sentinel was highest for grain yield in both years and OA424-1 was lowest, but both were high in grain protein concentration (Table 14). OA269-E, which was similar to Sentinel for grain yield in 1983 and was similar to all cultivars in 1984, was lowest for grain protein concentration for both years. Fidler, which was similar to OA424-1 in 1983 for grain yield but was higher than it in 1984, was intermediate for grain protein concentration. A negative grain yield-grain protein concentration relationship was observed in 1983 ( $r=-.46^*$ ) but a positive correlation was observed between these two traits in 1984 ( $r=+.44^*$ ). Previous reports, such as that of Sraon et al. (1975), indicates that a negative relationship exists in oats between these two traits. The differences in correlations observed in this study is most likely due to the limited number of cultivars studied. As Sentinel was highest for both grain yield and grain protein concentration, it was therefore highest for grain protein yield. The remaining cultivars were similar for this trait in 1983, as grain yields were offset by grain protein concentrations. In 1984, however, the lower grain protein concentration of OA269-E could not offset its grain yield. Therefore, its grain protein yield was lower than that of Fidler and OA424-1, which were similar to each other.

Cultivars varied in yield components, whereby similar grain yields were composed of different levels of each component (Table 14). OA424-1, which was highest for thousand kernel weight in both years was

TABLE 14

Agronomic characterization of oat cultivars for 1983 and 1984.

CULTIVAR	YIELD (KG/HA)	% PROTEIN (N x 6.25)	PROTEIN YIELD (KG/HA)	1000 KERNEL WEIGHT (g)	KERNELS PER HEAD	PANICLES PER PLOT
----- 1983 -----						
FIDLER	2597	14.7	382	29.9	47	570.3
SENTINEL	3014	15.6	470	28.9	54	592.1
OA424-1	2413	15.8	380	36.0	61	335.8
OA269-E	3060	12.9	396	27.5	36	965.9
LSD (0.05)	244	0.3	34	2.0	8	144.9
----- 1984 -----						
FIDLER	4228	11.6	490	24.9	83	622.4
SENTINEL	4209	12.6	530	30.2	73	582.4
OA424-1	3802	12.4	474	36.9	76	409.0
OA269-E	3979	10.6	422	27.9	53	803.1
LSD (0.05)	285	0.5	39	2.2	6	79.8

also highest for number of kernels per panicle while Sentinel was second-highest. Fidler, which was similar to Sentinel for thousand kernel weight in 1983, was lowest in 1984, while OA269-E was lower than Fidler in 1983, and the inverse occurred in 1984. The dry soil conditions of 1983 decreased the number of kernels per panicle as compared to 1984. The increases in number of kernels per panicle resulted in similar thousand kernel weights between years except in Fidler, which decreased in thousand kernel weight due to its large increase in kernels per panicle. This was expected, because kernel weight is determined after total potential number of kernels has been determined (Ledent, 1982).

#### Plant Dry Matter Accumulation

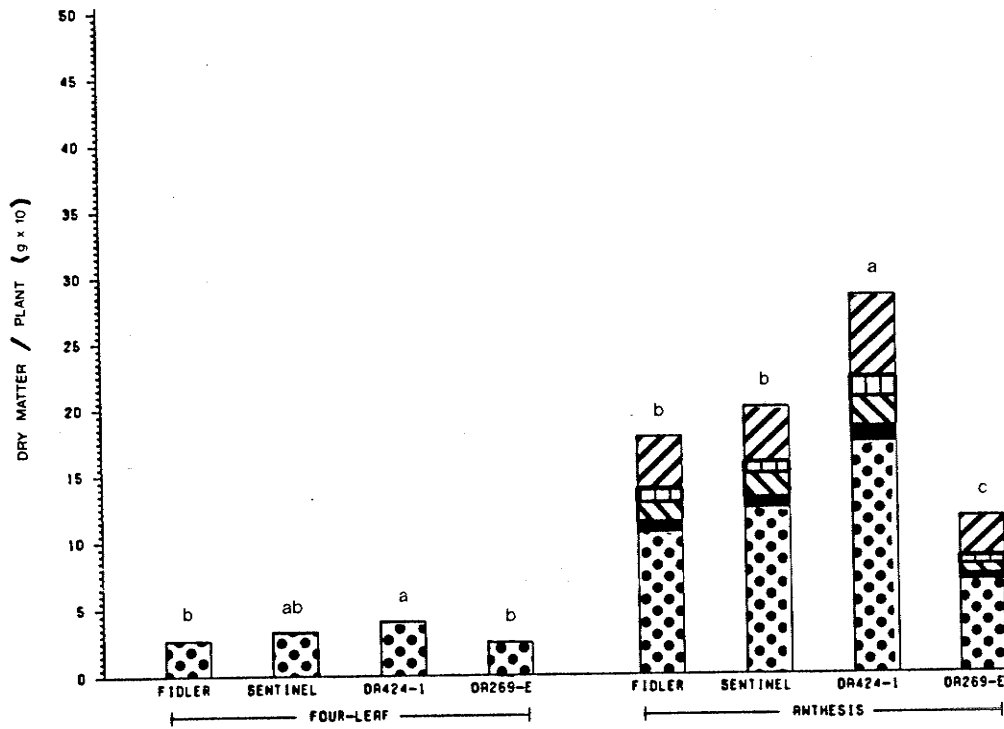
Plant DM accumulation is the product of growth rate times growth duration (Takeda and Frey, 1979). As grain yield is the product of DM and DM translocation efficiency, DM accumulation is an important factor of grain yield.

DM was lower in 1983 than in 1984 (Figures 10 and 11), due in part to the soil moisture stress of 1983 and in part to the severe lodging which occurred in that year. OA424-1 was highest for DM in both years, although it was similar to Sentinel at the four-leaf stage and at midfilling in 1983. OA269-E was lowest for DM in both years but was similar to Fidler and Sentinel at the four-leaf stage in 1983. Sentinel was second-highest for DM although it was similar to Fidler at various stages of plant growth in both years. Fidler and OA269-E decreased in DM from midfilling to maturity in 1983 due to a loss of plant material

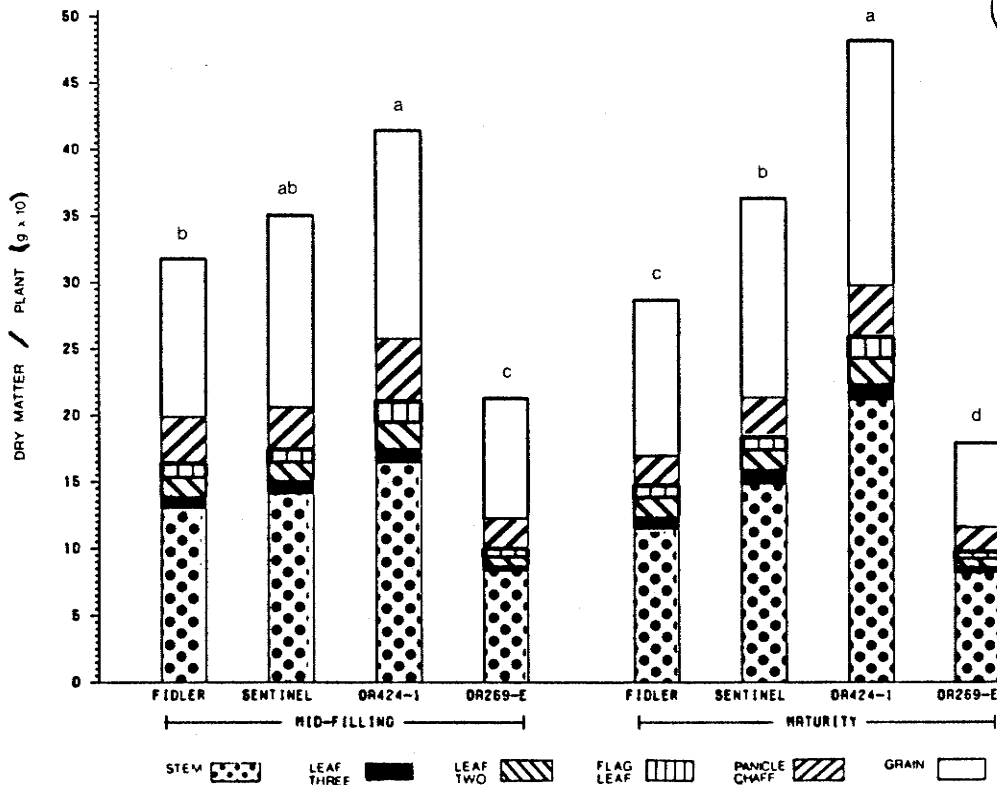
Figure 10: Mean plant DM (a) at four-leaf stage and anthesis and (b) at midfilling and maturity in oats in 1983.

Total vertical columns with the same letter above within a sampling date do not differ significantly at  $p=.05$  under Fischer's LSD.

(a)



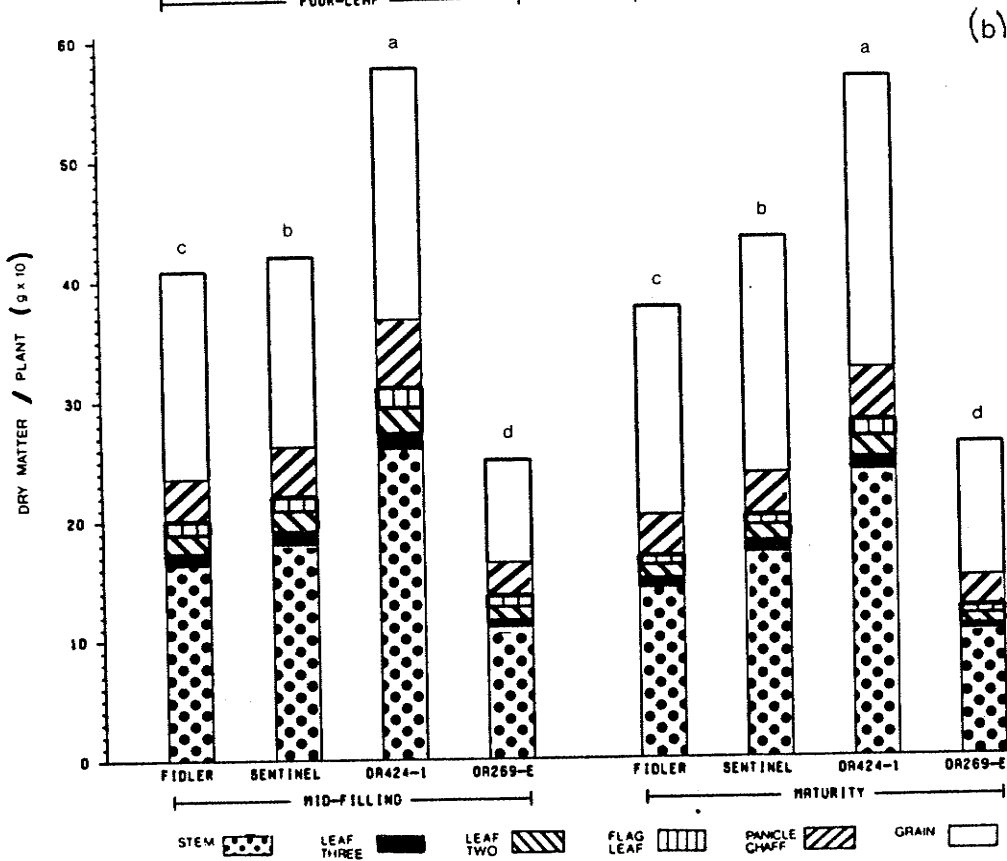
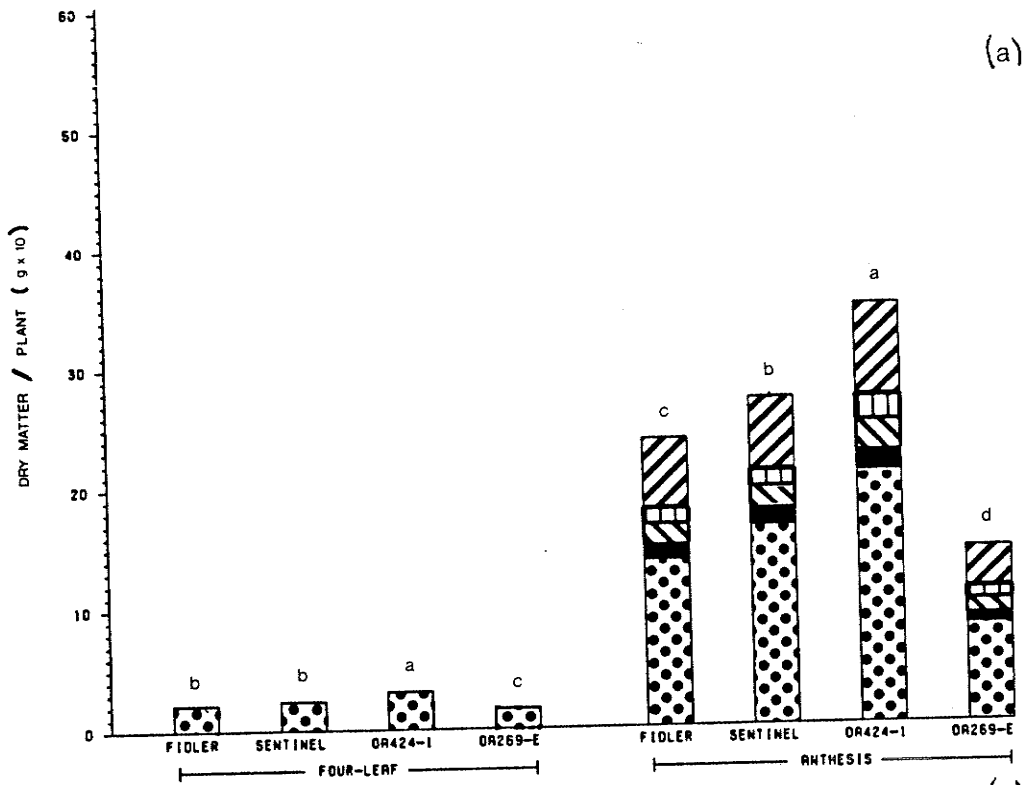
(b)



STEM (dots) LEAF THREE (solid black) LEAF TWO (diagonal lines) FLAG LEAF (horizontal lines) PANICLE CHAFF (diagonal lines) GRAIN (white)

Figure 11: Mean plant DM (a) at four-leaf stage and anthesis and (b) at midfilling and maturity in oats in 1984.

Total vertical columns with the same letter above within a sampling date do not differ significantly at  $p=.05$  under Fischer's LSD.



through shattering while loss of plant material was not a problem in 1984. Individual plant part DM differences among cultivars were generally similar to those for plant plant DM in each year (Tables 15 and 16), with OA424-1 highest and OA269-E lowest, while Sentinel was second-highest and Fidler was third-highest.

As cultivars were similar in phenology, differences in DM accumulation reflected differences in growth rate, as DM is defined as growth rate times growth duration (Takeda and Frey, 1979). OA424-1 was therefore highest for growth rate and OA269-E was lowest, while Fidler and Sentinel were intermediate for growth rate.

DM was negatively correlated with grain yield on a per area basis in 1983 ( $r = -.50^*$ ), but no correlation was found in 1984. DM was positively with grain yield per plant in 1983 and in 1984 ( $r = +.65^{**}$  and  $r = +.94^{**}$ , respectively). Increasing plant DM should increase grain yield per plant. The lack of correlation between DM and grain yield on a per area basis most likely arose from tillering x density interactions (Fischer and Kertesz, 1976).

#### Dry Matter Translocation

HI represents the efficiency of DM translocation of the plant at maturity, while DMTI represents the translocation efficiency of DM from a particular tissue at any stage of plant growth post-anthesis.

In 1983, although differences existed at midfilling for plant part DMTI values among cultivars, plant DMTI values were similar among cultivars (Table 17). Therefore, cultivars were similar for DM translocation efficiency at this stage. At maturity, cultivars were



TABLE 15

Mean plant part DM (g x 10) in oats in 1983.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	PANICLE CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
FIDLER	2.66					
SENTINEL	3.27					
OA424-1	4.05					
OA269-E	2.43					
LSD (0.05)	0.88					
----- ANTHESIS -----						
FIDLER	10.59	0.78	1.46	1.01	3.95	
SENTINEL	12.31	0.87	1.75	0.86	4.15	
OA424-1	17.23	1.23	2.17	1.51	6.21	
OA269-E	6.83	0.42	0.77	0.57	3.00	
LSD (0.05)	2.08	0.27	0.25	0.21	1.17	
----- MIDFILLING -----						
FIDLER	12.97	0.85	1.53	1.04	3.47	11.94
SENTINEL	14.10	0.95	1.44	0.97	3.17	14.40
OA424-1	16.42	1.09	1.97	1.60	4.73	15.66
OA269-E	8.35	0.30	0.76	0.57	2.31	9.01
LSD (0.05)	3.98	0.25	0.42	0.22	1.22	3.36
----- MATURITY -----						
FIDLER	11.44	0.91	1.47	0.89	2.23	11.73
SENTINEL	14.78	1.13	1.49	0.93	3.02	15.00
OA424-1	21.10	1.25	1.92	1.63	3.85	18.44
OA269-E	8.18	0.36	0.67	0.50	1.85	6.33
LSD (0.05)	2.69	0.22	0.27	0.22	0.50	3.94

TABLE 16

Mean plant part DM (g x 10) in oats in 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	PANICLE CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
FIDLER	2.18					
SENTINEL	2.40					
OA424-1	3.17					
OA269-E	1.70					
LSD (0.05)	0.23					
----- ANTHESIS -----						
FIDLER	13.77	1.23	1.75	1.26	5.85	
SENTINEL	16.45	1.45	1.81	1.35	6.01	
OA424-1	20.85	1.66	2.55	2.06	7.68	
OA269-E	8.11	0.70	1.25	0.96	3.45	
LSD (0.05)	0.78	0.08	0.24	0.17	0.45	
----- MIDFILLING -----						
FIDLER	16.39	1.01	1.53	1.16	3.52	17.24
SENTINEL	18.02	1.16	1.68	1.18	4.22	15.80
OA424-1	25.99	1.35	2.08	1.67	5.67	21.04
OA269-E	11.00	0.59	1.16	0.90	2.80	8.56
LSD (0.05)	1.60	0.06	0.12	0.13	0.46	2.24
----- MATURITY -----						
FIDLER	14.19	0.84	1.09	0.74	3.42	17.47
SENTINEL	17.09	0.96	1.31	0.81	3.62	19.66
OA424-1	23.88	1.12	1.72	1.38	4.37	24.33
OA269-E	10.41	0.48	0.85	0.65	2.55	11.25
LSD (0.05)	1.26	0.07	0.12	0.09	0.87	2.48

TABLE 17

Mean DMTI (%) in oats in 1983 and 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	UPPER LEAVES	PANICLE CHAFF	TOTAL PLANT
----- 1983 -----							
----- MIDFILLING -----							
FIDLER	47.9	93.2	88.5	91.8	77.5	77.9	37.8
SENTINEL	50.4	93.7	90.9	93.7	81.0	81.8	41.1
OA424-1	49.2	93.4	88.6	90.5	76.7	76.3	37.2
OA269-E	51.9	96.7	91.1	94.0	84.6	79.5	42.3
LSD (0.05)	ns	1.6	3.2	1.8	4.2	ns	ns
----- MATURITY -----							
FIDLER	50.3	94.3	88.4	92.6	77.6	83.8	40.7
SENTINEL	50.3	93.0	91.0	94.1	80.8	83.2	41.1
OA424-1	46.4	93.6	90.4	91.6	79.0	82.4	38.0
OA269-E	42.6	94.3	89.6	92.1	79.3	76.0	34.5
LSD (0.05)	ns	ns	ns	ns	ns	3.9	ns
----- 1984 -----							
----- MIDFILLING -----							
FIDLER	51.9	94.6	92.1	94.0	82.8	83.7	42.9
SENTINEL	47.9	93.4	90.8	93.4	80.4	79.4	38.6
OA424-1	44.7	93.9	90.9	93.0	80.4	78.7	36.4
OA269-E	43.7	93.4	87.9	90.4	76.1	75.2	34.1
LSD (0.05)	1.8	0.7	0.8	0.9	1.7	2.0	1.8
----- MATURITY -----							
FIDLER	55.1	95.4	94.1	95.9	86.7	83.7	46.2
SENTINEL	53.4	95.3	93.7	96.0	86.4	84.4	45.2
OA424-1	50.4	95.6	93.4	94.6	85.2	84.7	42.8
OA269-E	51.7	95.8	92.9	94.4	84.9	81.4	42.7
LSD (0.05)	2.5	ns	0.6	0.7	1.3	ns	2.6

similar for DMTI in all parts except panicle chaff, and were therefore similar for plant DMTI (HI) and efficiency of DM translocation. Differences for grain yield per plant, therefore, reflected differences for plant DM. At midfilling in 1984, Fidler was highest for DMTI values in all parts and in the total plant. Sentinel and OA424-1 were second-highest for plant DMTI in the upper leaves and panicle chaff, but differences for stem DMTI resulted in a higher plant DMTI value for Sentinel. OA269-E was lowest for plant DMTI, due mainly to leaves and panicle chaff. Fidler and Sentinel were highest for plant part DMTI at maturity, but on a total plant basis, only Fidler was higher than OA424-1 and OA269-E. The higher HI values of Fidler offset its lower DM value relative to Sentinel, resulting in similar grain yields per plant between these two cultivars. However, the DM of OA424-1 more than offset its lower HI, resulting in its higher grain yield per plant. HI values ranged from 34.5 to 46.2 over both years. These values fall within a range of HI values reported by Rosielle and Frey (1977) in progeny from three oat crosses.

HI was not correlated with DM in 1983 or in 1984. Thus, DM translocation efficiency was independent from DM accumulation and increases in HI may be achieved independently of DM.

HI was not correlated to grain yield on a per area basis in any one year, but was positively correlated with grain yield on a per area basis over both years combined ( $r=+.43^*$ ). Similarly, Takeda *et al.* (1980) found positive correlations between these two traits ( $r=+.35^{**}$  and  $+.42^{**}$ ) in two years of study of 1200 oat lines. Grain yield per plant was positively with HI in 1983 and in 1984 ( $r=+.80^{**}$  and  $r=+.94^{**}$ ,

respectively). Grain yield was positively related to the efficiency of DM translocation.

HI was not correlated with grain protein yield in the oat experiment. Jalani *et al.* (1981) found a positive correlation between grain protein yield and HI ( $r=+.59^{**}$ ) in 790 oat lines. The lack of correlation between HI and grain protein yield observed in this study may be due to the limited number of cultivars studied.

#### Grain Dry Matter Accumulation

Grain DM accumulation is dependent upon the amount of DM translocated from the vegetative tissue to the developing grains, and the number of kernels per head.

Grain DM accumulation was over a shorter period in 1983 than in 1984, due to the low soil moisture conditions of the former, and accumulation was subsequently more linear in 1983 (Figure 12). OA424-1 was highest for grain DM accumulation in both years and Sentinel was second-highest, although it was similar to Fidler in 1983. OA269-E was lowest for grain DM accumulation in both years but was similar to Fidler in 1984. All cultivars decreased in grain DM over the final two sampling dates in both years, except Fidler in 1983. As previously discussed, soluble materials in the grain may be lost in the transpirational stream of the grain, as this is a period of rapid desiccation of the grain.

When data was expressed on a percent of final grain DM content (Figure 13), cultivars were generally similar for grain DM accumulation

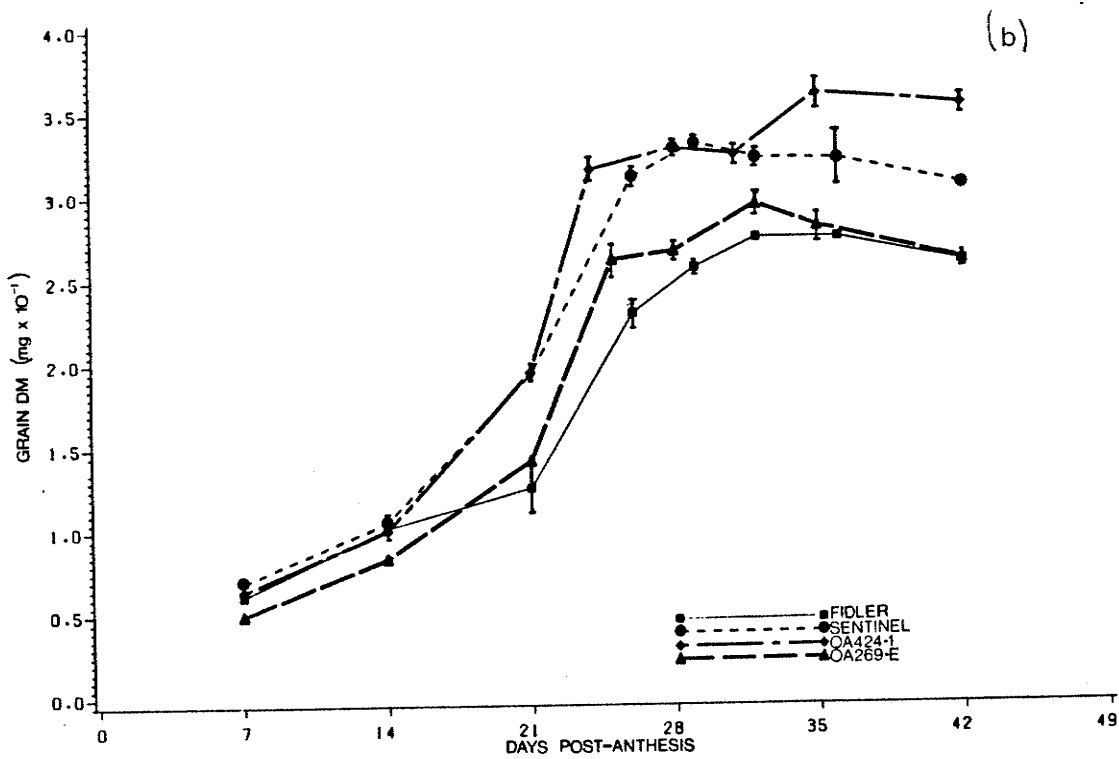
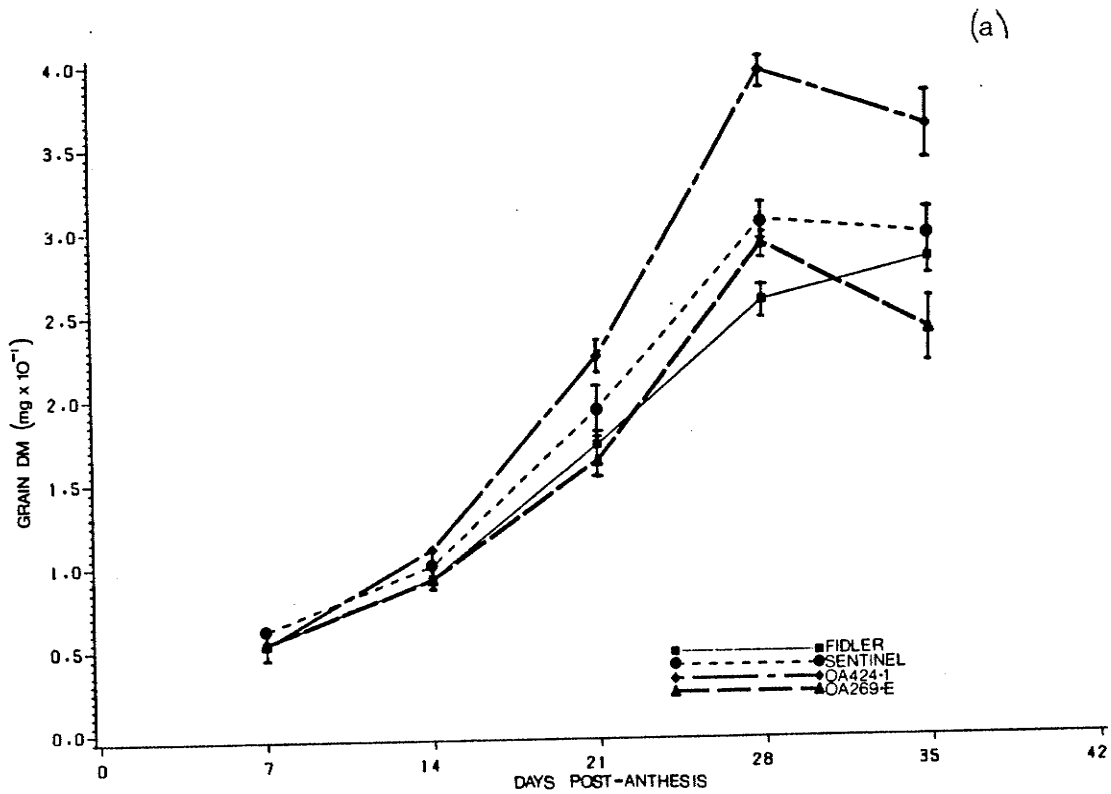


Figure 12: Grain DM accumulation as a function of days post-anthesis in oats (a) in 1983 and (b) in 1984.

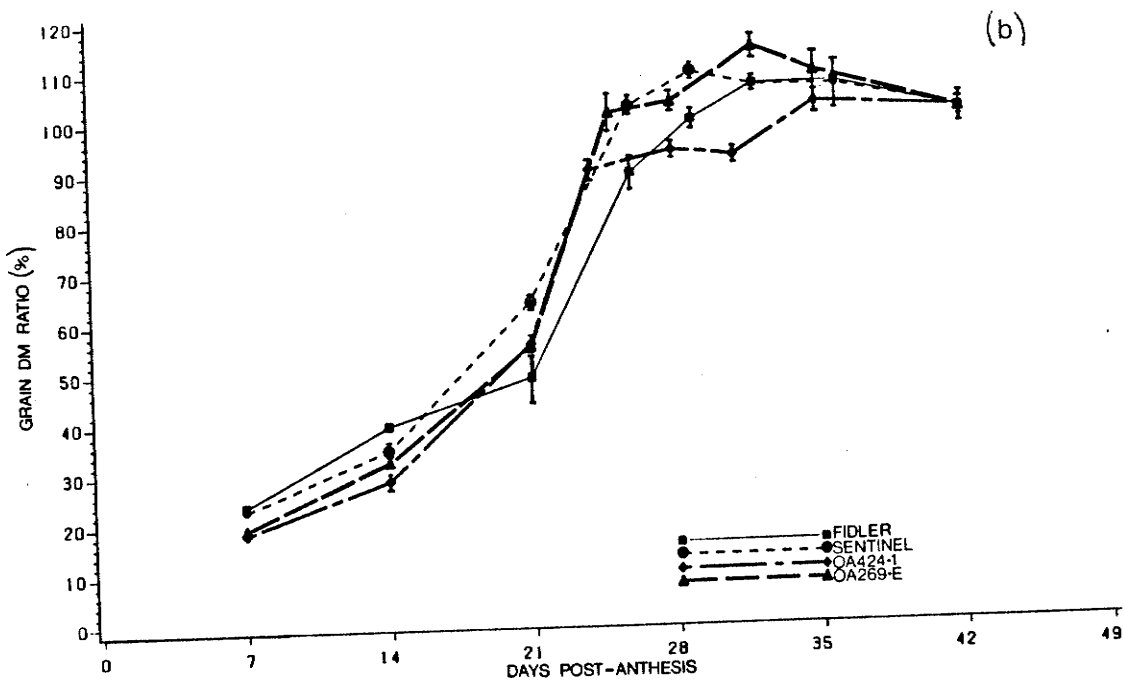
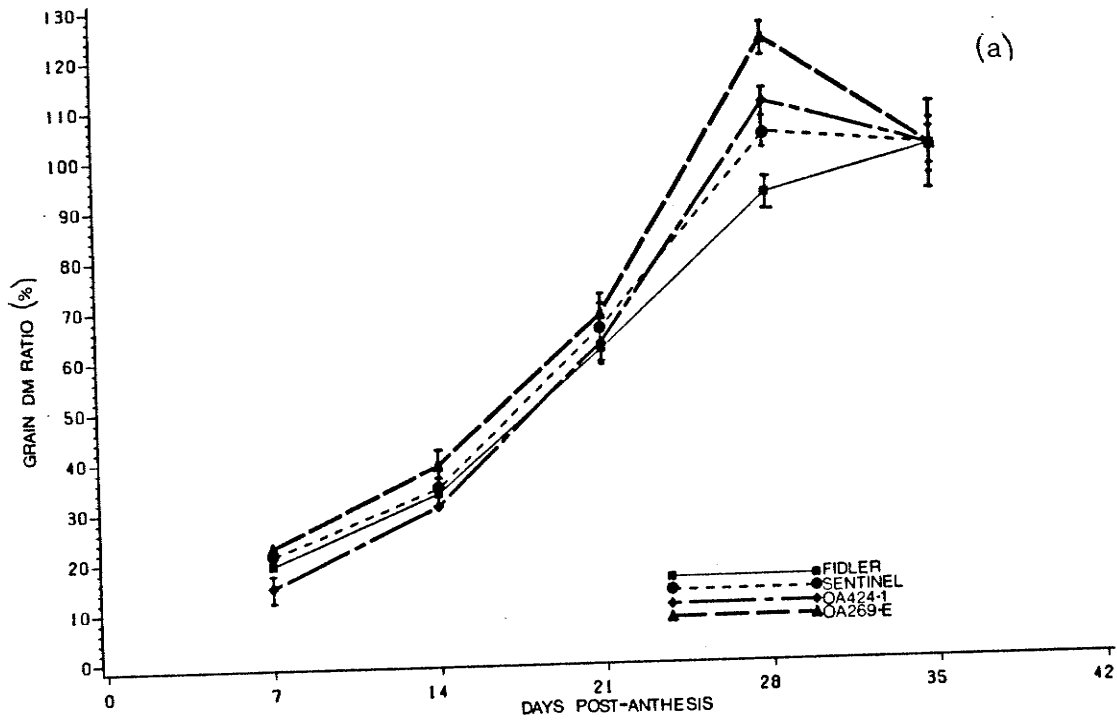


Figure 13: Ratio of sampling date grain DM content over final grain DM content (%) as a function of days post-anthesis in oats (a) in 1983 and (b) in 1984.

in 1983 and in 1984, although differences among cultivars were evident at various sampling dates. Grain DM accumulation reflected differences in final grain DM content, as all cultivars were generally similar for accumulation as percent of final grain DM content.

### Nitrogen Concentrations

N concentration represents the capacity of N storage in the plant at any one time. N concentrations at anthesis represent maximal N storage capacity and decreases in N concentrations post-anthesis indicate N translocation.

Differences in nitrate-N concentrations (Appendix Tables 7 and 8) did not indicate differences in nitrate reductase activity, as reduced-N concentrations (Appendix Tables 9 and 10) did not correlate with nitrate-N concentrations. Higher N concentrations were found in the upper leaves, as in the wheat experiment, while lower N concentrations were found in the stem and head chaff (Tables 18 and 19). Although the second leaf was higher for DM than the flag leaf, the latter had higher N concentrations and was most likely higher for nitrate reductase activity.

Cultivars were similar for capacity to accumulate N at the four-leaf stage in 1983, as they were similar for N concentration (Table 18). In 1984, Sentinel was highest for capacity to accumulate N while Fidler was lowest, as these two cultivars were highest and lowest, respectively, for N concentrations (Table 19). OA424-1 and OA269-E were similar to both of these cultivars for N accumulation capacity, as they were similar to both for N concentration. At anthesis in 1983,



TABLE 18

Mean plant part N concentrations (mg/g) in oats in 1983.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	PANICLE CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
FIDLER	48.52					
SENTINEL	51.34					
OA424-1	47.80					
OA269-E	48.90					
LSD (0.05)	ns					
----- ANTHESIS -----						
FIDLER	28.79	36.87	45.15	51.97	23.90	
SENTINEL	29.68	42.04	49.34	58.36	24.45	
OA424-1	28.36	40.81	45.81	50.98	23.66	
OA269-E	25.53	38.65	44.81	54.70	22.39	
LSD (0.05)	2.39	ns	2.90	4.20	ns	
----- MIDFILLING -----						
FIDLER	18.88	24.47	27.78	27.36	15.96	24.96
SENTINEL	21.76	25.22	28.27	26.83	18.92	25.25
OA424-1	17.91	23.80	29.19	31.80	15.71	22.75
OA269-E	18.33	22.44	28.13	35.47	19.11	19.55
LSD (0.05)	3.30	ns	ns	4.35	2.20	1.72
----- MATURITY -----						
FIDLER	17.84	21.76	20.12	15.22	10.70	23.44
SENTINEL	17.90	22.57	23.02	19.88	12.95	25.39
OA424-1	18.11	23.79	21.65	17.99	10.49	23.76
OA269-E	20.36	25.48	26.40	25.68	14.64	23.57
LSD (0.05)	ns	ns	3.22	2.75	2.81	1.47

TABLE 19

Mean plant part N concentrations (mg/g) in oats in 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	PANICLE CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
FIDLER	48.81					
SENTINEL	53.75					
OA424-1	52.67					
OA269-E	49.95					
LSD (0.05)	3.84					
----- ANTHESIS -----						
FIDLER	10.11	25.32	33.33	42.15	18.71	
SENTINEL	10.37	26.89	34.30	43.03	19.84	
OA424-1	10.35	26.22	29.95	39.64	19.01	
OA269-E	11.63	24.37	33.84	44.88	19.75	
LSD (0.05)	1.25	ns	2.85	2.88	ns	
----- MIDFILLING -----						
FIDLER	6.18	9.72	16.24	21.99	13.15	16.40
SENTINEL	6.34	9.90	19.55	25.13	15.59	19.57
OA424-1	4.23	13.24	18.41	22.42	12.70	16.72
OA269-E	8.74	13.05	23.31	32.83	14.78	14.08
LSD (0.05)	1.77	2.80	3.42	3.16	1.15	0.94
----- MATURITY -----						
FIDLER	4.90	9.22	8.63	8.20	9.92	18.24
SENTINEL	4.23	8.82	12.14	10.82	10.62	20.24
OA424-1	5.45	10.60	13.52	13.58	8.76	19.15
OA269-E	6.14	10.74	12.35	14.41	10.03	17.44
LSD (0.05)	0.97	1.80	1.85	2.11	1.36	0.83

Sentinel, one of the high grain protein concentration cultivars, was highest for N concentration in all plant parts, and was therefore highest for N accumulation capacity. OA269-E, the low grain protein concentration cultivar, was lowest for N accumulation capacity due to its generally low N concentrations, particularly in the stem, while Fidler and OA424-1 were intermediate for N concentration and N accumulation capacity. In 1984 at anthesis, OA269-E was highest for N concentration in the stem and was therefore highest for N accumulation, because the stem constituted the largest portion of plant DM. Sentinel and Fidler were higher than OA424-1 for N concentration in leaf two and flag leaf (Table 19) and were second-highest for N accumulation capacity.

Decreases in N concentration from anthesis to midfilling through to maturity (Tables 18 and 19) indicated that N was translocated from vegetative tissue. Decreases for N concentration were also reported by Peterson et al. (1975) in three cultivars of oats. Sentinel appeared to translocate the most N in 1983, as it had the highest N concentrations at anthesis and was low at maturity. OA269-E appeared to translocate the least N, because it was low for N concentrations at anthesis and was high for the same at maturity. Fidler and OA424-1 were intermediate for N concentration decreases, indicating they were intermediate for N translocation. In 1984, Fidler appeared to translocate the highest amount of N, as it had the lowest N concentrations at maturity, while Sentinel was second-highest. OA269-E was followed by OA424-1 in decreasing amounts of N concentration, indicating that they were the second-lowest and lowest, respectively, for amount of N translocated.

### Plant Nitrogen Accumulation

Plant N accumulation is the product of DM times N concentration. Differences in N content can occur as a result of differences in DM, N concentration, or a combined effect of the two.

Although DM was lower in 1983 than in 1984, N content was higher in 1983 (Figures 14 and 15), resulting from possible loss of soil nitrogen through leaching, caused by the high rainfall in June, 1984. This was due to the high level of precipitation received in June, 1984. OA424-1, one of the high protein concentration cultivars, was highest for N content in both years, but was similar to Sentinel at the four-leaf stage and midfilling in 1983. Sentinel, the other high protein concentration cultivar, was second-highest for N content in both years, but was similar to Fidler at all stages in 1983 except maturity. Fidler, in 1984, was second-lowest for N content. OA269-E, the low protein concentration cultivar, was lowest for N content in both years, but was similar to Fidler at the four-leaf stage in 1983.

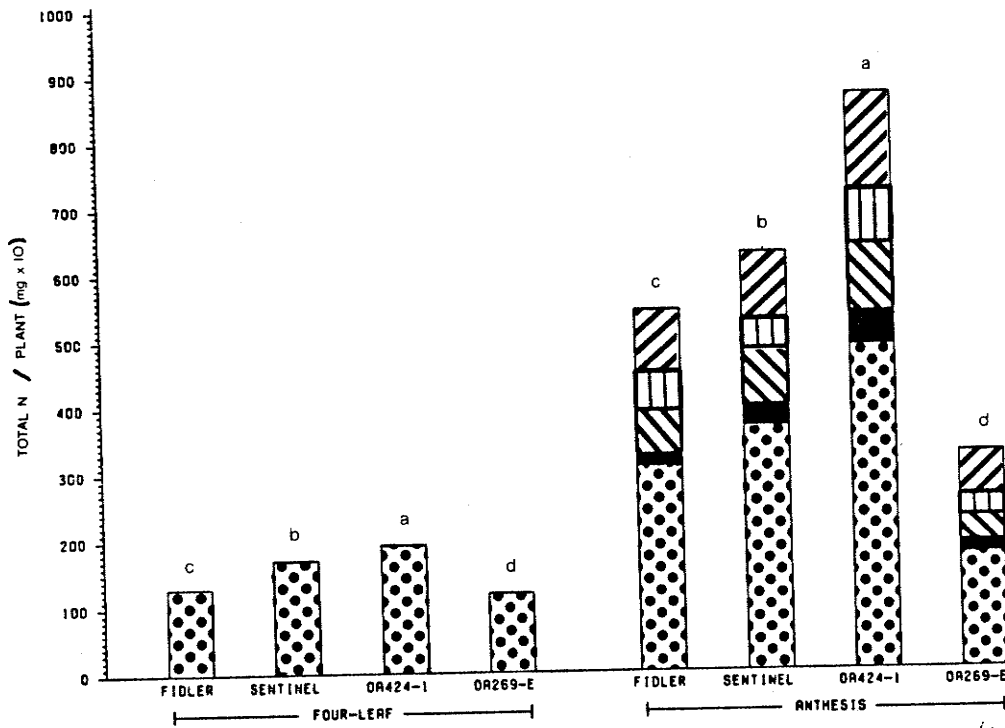
N content was related to DM at all stages in both years. However, N concentration was not related to DM. Differences for N concentration could not offset differences for DM, whereby N content reflected DM.

A positive correlation was found between N content at maturity and grain N yield per plant in 1983 ( $r=+.92^{**}$ ) and in 1984 ( $r=+.95^{**}$ ). However, this relationship was not observed between grain protein yield on a per area basis and N content. The lack of relationship between N content at maturity to grain protein yield on a per area basis is most likely caused by differences in tillering x density interactions, as N content was measured on a per plant rather than a per area basis.

Figure 14: Mean plant N content (a) at four-leaf stage and anthesis and (b) at midfilling and maturity in oats in 1983.

Total vertical columns with the same letter above within a sampling date do not differ significantly at  $p=.05$  under Fischer's LSD.

(a)



(b)

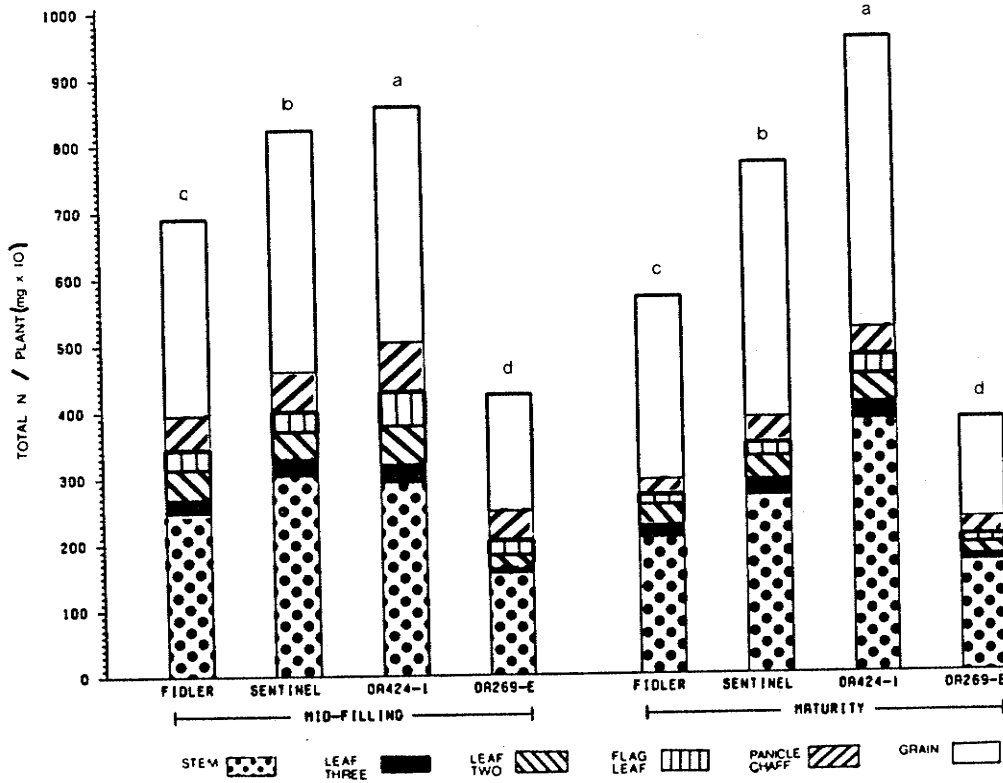
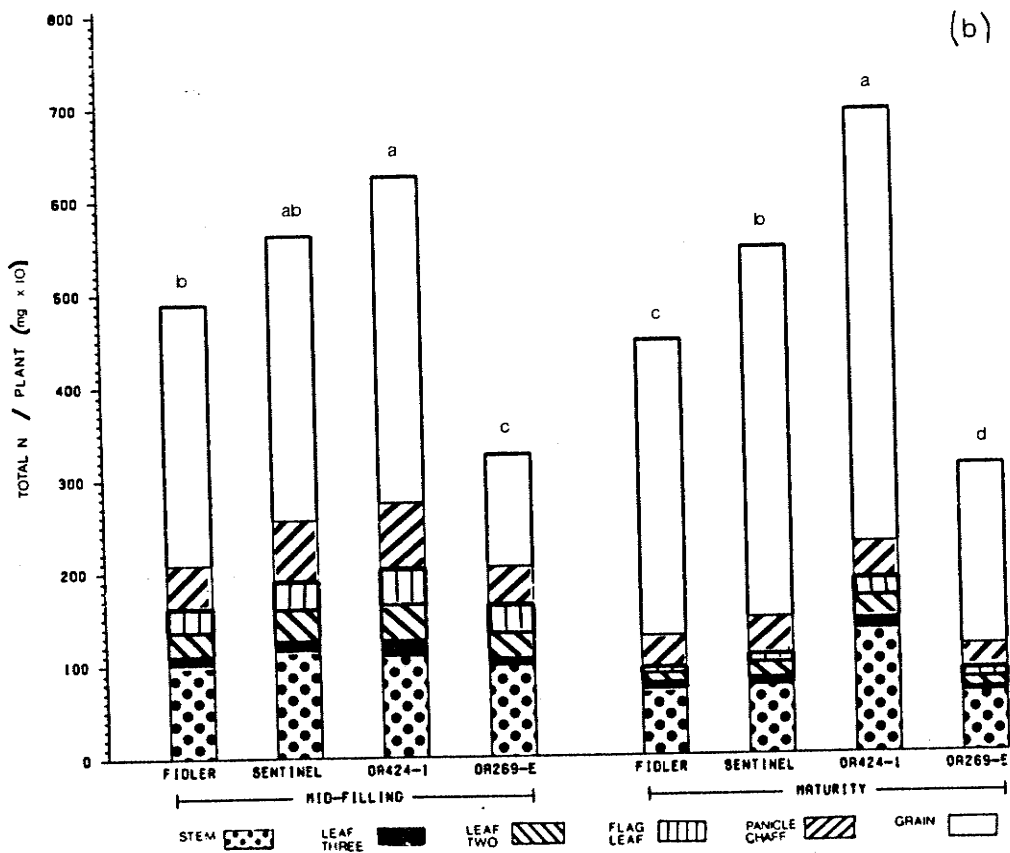
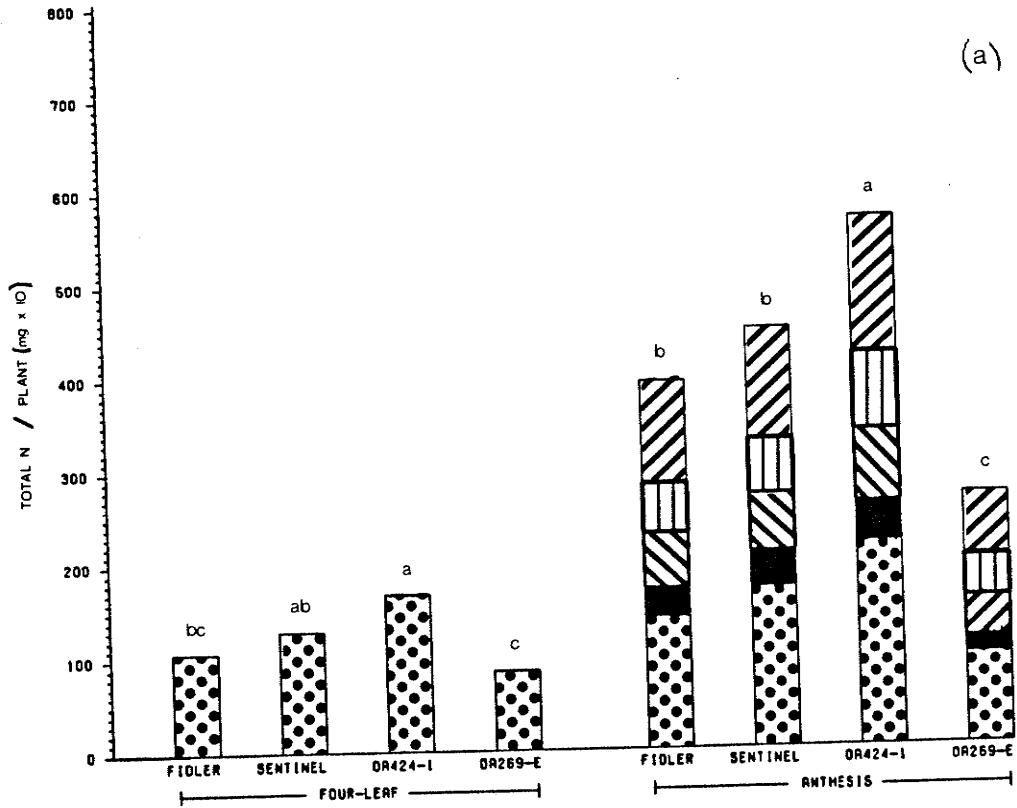


Figure 15: Mean plant N content (a) at four-leaf stage and anthesis and (b) at midfilling and maturity in oats in 1984.

Total vertical columns with the same letter above within a sampling date do not differ significantly at  $p=.05$  under Fischer's LSD.





N content at maturity was positively correlated with grain protein concentration in 1983 ( $r=+.76^*$ ) and in 1984 ( $r=+.64^*$ ). Similarly, Dubois and Fossati (1981) found a positive correlation between these two traits in twelve winter cultivars ( $r=+.58^*$ ). The level of grain protein concentration was related to the level of N stored in the plant. This relationship may not be observed if plant N content is expressed on a per area basis.

Individual plant part N contents (Tables 20 and 21) generally reflected individual plant part DM and plant N contents, with the exception of leaf three and panicle at midfilling in 1983, and leaf two and the flag leaf at anthesis and midfilling in 1984. In these plant parts, lower DM was offset by higher N concentrations, resulting in similar N contents.

#### Nitrogen Translocation

Grain N yield is dependent upon the amount of N translocated to the grain. This is, in turn, dependent upon the amount of N stored in the plant and the efficiency of N translocation.

NTI values were generally lower in 1983 than in 1984, due to the dry soil conditions in 1983. Although differences for plant part NTI values were observed in 1983 (Table 22), cultivars were similar for plant NTI at midfilling and maturity. Thus, cultivars were similar for N translocation efficiency and differences for grain N yield per plant existed due to differences for plant N content. In 1984, OA269-E was low for NTI values at both midfilling and maturity, and was low for N

TABLE 20

Mean plant part N contents (mg x 10) in oats in 1983.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	PANICLE CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
FIDLER	129.09					
SENTINEL	169.92					
OA424-1	192.61					
OA269-E	118.86					
LSD (0.05)	46.55					
----- ANTHESIS -----						
FIDLER	306.37	18.19	65.75	57.01	94.21	
SENTINEL	365.40	30.98	84.76	44.71	101.23	
OA424-1	485.53	49.76	102.76	81.03	145.57	
OA269-E	172.40	16.53	37.70	30.60	66.58	
LSD (0.05)	74.19	14.06	13.13	ns	23.74	
----- MIDFILLING -----						
FIDLER	247.19	21.19	44.44	30.55	51.27	295.76
SENTINEL	303.75	24.71	41.04	30.60	60.22	362.40
OA424-1	292.32	27.80	57.19	51.50	74.38	353.42
OA269-E	153.03	6.70	21.20	22.16	44.26	175.98
LSD (0.05)	83.79	8.42	15.70	10.00	15.90	65.47
----- MATURITY -----						
FIDLER	205.38	19.46	30.84	13.98	23.70	274.08
SENTINEL	266.23	25.88	34.30	20.33	38.98	381.59
OA424-1	379.73	26.55	41.21	29.43	40.49	436.76
OA269-E	165.49	8.41	18.16	12.16	26.62	149.83
LSD (0.05)	72.11	6.43	6.47	6.68	6.81	95.38

TABLE 21

Mean plant part N contents (mg x 10) in oats in 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	PANICLE CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
FIDLER	106.37					
SENTINEL	128.66					
OA424-1	167.48					
OA269-E	84.80					
LSD (0.05)	16.37					
----- ANTHESIS -----						
FIDLER	139.47	31.01	58.57	53.34	109.63	
SENTINEL	169.54	38.95	61.56	58.82	118.78	
OA424-1	216.46	43.45	76.62	82.61	146.16	
OA269-E	95.29	17.02	42.90	43.67	68.17	
LSD (0.05)	22.76	5.07	11.47	8.55	12.83	
----- MIDFILLING -----						
FIDLER	100.85	9.779	24.96	25.83	46.15	281.58
SENTINEL	114.79	11.43	33.08	30.28	65.59	306.76
OA424-1	108.44	17.79	38.32	37.97	71.30	351.16
OA269-E	97.59	7.68	27.13	29.96	41.41	120.79
LSD (0.05)	ns	3.24	6.20	6.29	6.23	31.43
----- MATURITY -----						
FIDLER	70.06	7.70	9.42	6.13	34.33	317.84
SENTINEL	72.96	8.54	16.06	8.91	39.33	398.07
OA424-1	131.90	11.98	23.60	19.04	39.00	464.55
OA269-E	63.38	5.10	10.43	9.34	25.66	194.04
LSD (0.05)	23.94	2.12	4.42	4.07	13.34	49.86

TABLE 22

Mean NTI (%) in oats in 1983 and 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	UPPER LEAVES	PANICLE CHAFF	TOTAL PLANT
----- 1983 -----							
----- MIDFILLING -----							
FIDLER	55.1	93.3	87.1	91.1	76.2	85.1	43.9
SENTINEL	54.5	93.9	89.9	92.7	79.7	85.7	44.4
OA424-1	55.1	93.2	85.8	87.2	72.3	82.2	41.6
OA269-E	53.4	96.4	89.4	89.2	78.2	79.8	41.3
LSD (0.05)	ns	2.1	ns	2.9	ns	4.8	ns
----- MATURITY -----							
FIDLER	57.3	92.9	89.5	94.8	79.7	91.8	48.1
SENTINEL	59.1	93.7	91.7	95.6	83.2	90.6	50.0
OA424-1	53.3	94.0	91.1	93.5	81.2	91.3	45.9
OA269-E	46.3	93.9	88.6	92.5	79.8	83.4	40.3
LSD (0.05)	10.3	ns	ns	ns	ns	4.4	ns
----- 1984 -----							
----- MIDFILLING -----							
FIDLER	74.2	96.7	91.9	91.6	83.5	85.8	60.2
SENTINEL	73.8	96.5	90.2	91.0	82.5	82.3	58.7
OA424-1	76.5	95.2	90.1	90.3	79.0	83.0	56.5
OA269-E	56.7	93.9	81.3	80.3	64.8	74.4	38.6
LSD (0.05)	5.6	1.0	1.8	2.3	2.9	2.3	4.5
----- MATURITY -----							
FIDLER	82.3	97.6	97.1	98.1	93.2	90.4	72.1
SENTINEL	84.8	97.9	96.1	97.8	92.3	91.0	73.6
OA424-1	78.6	97.5	95.2	96.1	89.7	92.2	68.2
OA269-E	75.6	97.4	94.9	95.3	88.6	88.4	63.4
LSD (0.05)	3.4	ns	0.8	1.0	1.8	ns	3.8

translocation efficiency. The remaining cultivars were generally similar for plant part NTI values and were similar for plant NTI; however, at maturity, OA424-1 was lower than Fidler and Sentinel and was similar to OA269-E for all NTI values. Fidler and Sentinel were highest for NTI values. Fidler and Sentinel were therefore highest for N translocation efficiency, while OA424-1 was second-highest and OA269-E was lowest. No individual plant part was limiting to N translocation in either OA269-E or OA424-1. OA424-1 decreased in N translocation efficiency from midfilling to maturity relative to Sentinel and Fidler (Table 22). Increasing the level of N translocation in the latter period of grain filling would likely increase its grain N yield. Although OA424-1 was lower than Sentinel for NHI, its plant N content more than offset this, resulting in its higher grain N yield per plant. OA269-E was lowest for both NHI and plant N and was therefore lowest for grain N yield per plant.

NHI was not correlated with N content in either 1983 or in 1984. This demonstrated that N uptake and assimilation is a separate physiological process from N translocation. Cultivars with the highest levels of plant N may not, therefore, be highest for N translocation efficiency and grain N yield. Similar results in wheat have been reported by Desai and Bhatia (1978) for 15 durum wheat cultivars and by Dubois and Fossati (1981) for 12 winter wheat cultivars ( $r=+.15$  ns and  $+.34$  ns), respectively. Oats and wheat appear to be similar in the relationship of N assimilation and N translocation.

NHI was not correlated with grain yield over both years. Desai and Bhatia (1978) reported a similar lack of correlation between these two

traits while Loffler and Busch (1982) ( $r=+.62^{**}$ ) reported a positive correlation. This indicated that N translocation efficiency was not associated with grain yield, which can be expected, as grain N yield constitutes only a small portion of grain yield.

NHI was positively correlated with grain protein yield in the oat experiment over both years ( $r=+.37^{*}$ ). Similar results have been reported in wheat, such as those of Desai and Bhatia (1978), Dubois and Fossati (1981), and Loffler and Busch (1982) ( $r=+.58^{*}$ ,  $+.99^{**}$ , and  $+.71^{**}$ ), respectively. The level of N, and subsequently protein, in the grain was related to the efficiency of N translocation to the grain. As efficiency of N translocation increases within a cultivar, grain protein yield will then increase.

NHI was not correlated with grain protein concentration in the oat experiment in either year. Desai and Bhatia (1978), for 15 durum wheat cultivars, Dubois and Fossati (1981), for 12 winter wheat cultivars, and Loffler and Busch (1982), for three hard red spring wheat crosses, reported similar results ( $r=+.14$  ns,  $-.36$  ns, and  $+.00$  ns), respectively. As grain protein concentration is the ratio of grain protein content over grain DM, the lack of correlation can arise from differences in DM and N translocation. To ensure a high grain protein concentration, a plant should be high for both DM and N translocation efficiency, as can be seen in Sentinel.

HI and NHI were positively correlated in the oat experiment in 1983 ( $r=+.90^{*}$ ) and in 1984 ( $r=+.81^{**}$ ). Similar results in wheat have been reported by Desai and Bhatia (1978), Dubois and Fossati (1981), and Loffler and Busch (1982) ( $r=+.58^{*}$ ,  $+.69^{*}$ , and  $+.54^{*}$ ), respectively. The

correlation between these two traits indicated that DM and N transfer from vegetative tissue to the grain were closely related, but not identical, processes. Thus, it may be possible to select for increased DM or N translocation efficiency and increase both traits simultaneously.

OA424-1 translocated the highest amount of N in 1983, but was similar to Sentinel and Fidler for this in 1984 (Table 23). As cultivars were similar for NHI in 1983, differences in the amount of N translocated occurred due to differences for plant N content. In 1984, differences for NHI were offset by differences for N content among OA424-1, Fidler, and Sentinel, resulting in similar amounts of N translocated. OA269-E, low for both NHI and N content, was therefore lowest for the amount of N translocated. The amount of N translocated was positively correlated with N content at anthesis in 1983 and in 1984 ( $r=+.71^{**}$  and  $+.50^{*}$ , respectively). The amount of N translocated was therefore dependent upon the level of plant N content at anthesis. Grain N yield per plant was positively correlated with the amount of N translocated in 1983 ( $r=+.77^{**}$ ) and in 1984 ( $r=+.53^{**}$ ). The level of grain N yield per plant was related to the amount of N translocated from the vegetative tissue.

Ratios of grain N over the amount of N translocated indicated that maximum vegetative N content most likely occurred after anthesis in both years (Table 23). As maximum vegetative N content occurred after anthesis, the amounts of N translocated were consequently underestimated.

TABLE 23

Mean N translocated (mg x 10) and ratio of grain N content over N translocated (%) in oats in 1983 and 1984.

CULTIVAR	N TRANSLOCATED	RATIO OF GRAIN N : N TRANSLOCATED (%)
----- 1983 -----		
FIDLER	250.79	111.52
SENTINEL	268.75	136.25
OA424-1	370.72	117.44
OA269-E	96.35	208.05
LSD (0.05)	73.09	ns
----- 1984 -----		
FIDLER	264.37	124.31
SENTINEL	301.90	135.89
OA424-1	292.02	173.65
OA269-E	153.13	131.94
LSD (0.05)	36.42	33.97



### Grain Nitrogen Concentration

Grain N concentration is the ratio of grain N content over grain DM content. Changes in grain N concentration occur as a result of changes in DM translocation relative to N translocation.

Grain N concentrations were higher in 1983 than in 1984 (Figure 16), due to the dry soil conditions of 1983. Sentinel was highest for grain N concentration in both years, while OA269-E was lowest. Fidler and OA424-1 were similar to each other for grain N concentration in both years. Differences in concentration between these results and that reported for the agronomic data occur due to differences in sampling technique.

Grain N concentrations increased in 1983 in cultivars to 28 days post-anthesis and then decreased, except OA269-E, which increased throughout the sampling period (Figure 16a). In 1984, grain N concentrations increased in all cultivars throughout the sampling periods except OA269-E, which decreased from 7 to 14 days post-anthesis (Figure 16b). As a result, OA269-E showed a net decline in grain N concentration over the sampling period. Decreases in grain N concentration occurred as a result of higher DM translocation relative to N translocation, while the opposite of this, high N and low DM translocation, resulted in increases in grain N concentration.

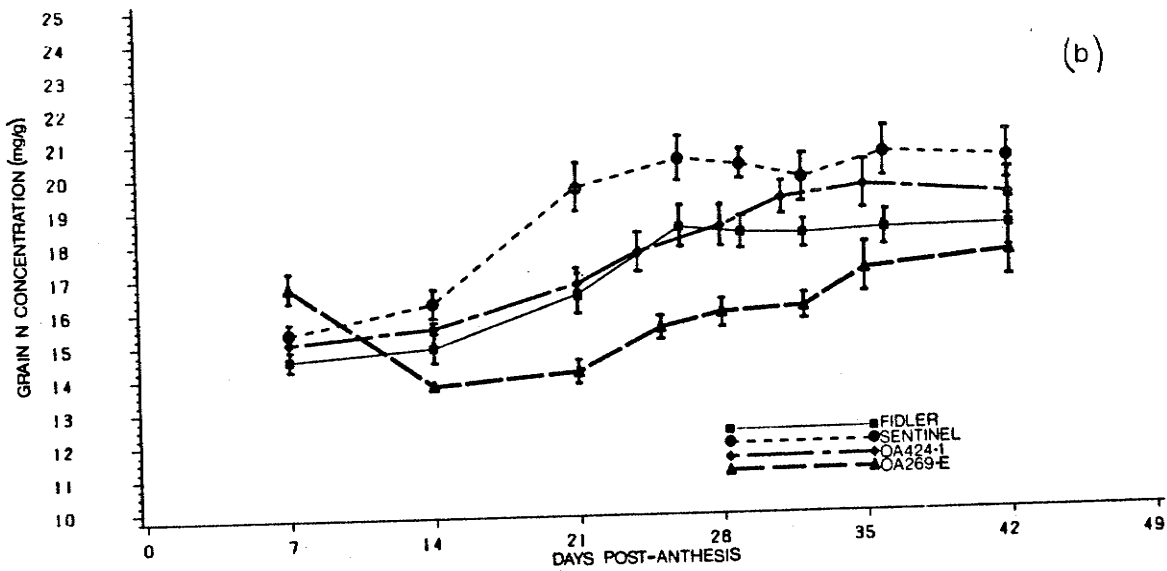
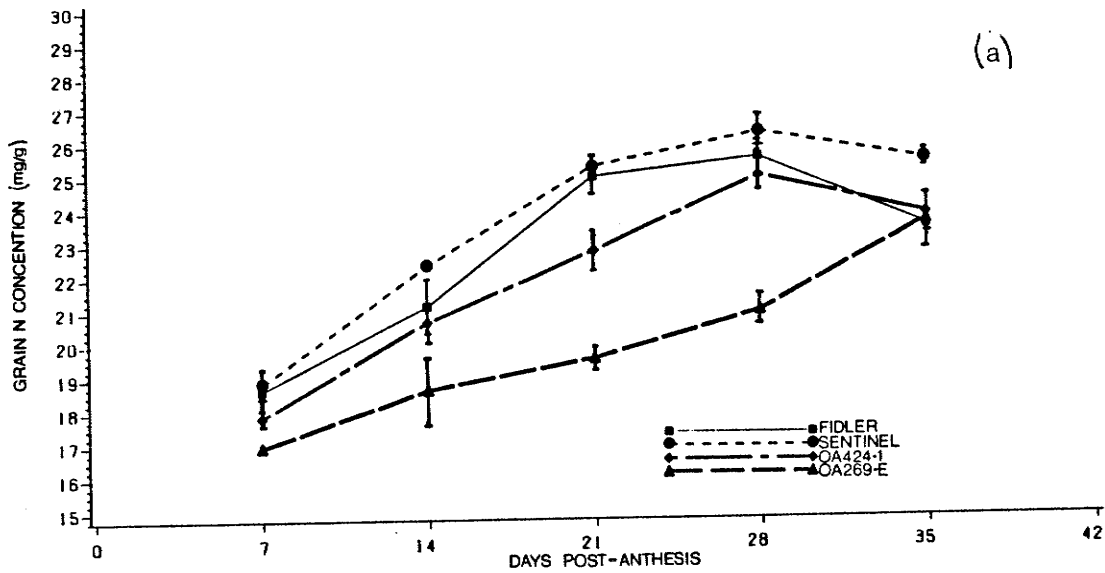


Figure 16: Changes in grain N concentration as a function of days post-anthesis in oats (a) in 1983 and (b) in 1984.

### Grain Nitrogen Accumulation

Grain N accumulation is the product of grain DM accumulation times grain N concentration. Differences in grain N accumulation reflect differences in grain DM accumulation, grain N concentration, or both.

Grain N accumulation was higher and over a shorter period in 1983 than in 1984 (Figure 17), due to the dry soil conditions in 1983. OA424-1 was highest for grain N accumulation in both years, but was similar to Sentinel in 1984. OA269-E was lowest for grain N accumulation in both years, but was similar to Fidler in 1984. Sentinel and Fidler were second- and third-highest, respectively, for grain N accumulation in 1983.

When grain N accumulation was expressed on a percent of final grain N content (Figure 18), cultivars were similar for grain N accumulation in 1983. In 1984, Sentinel was slightly higher in percent of final grain N content in the period from 14 to 28 days post-anthesis, but otherwise all cultivars were similar.

Differences in grain N accumulation reflected differences in grain DM accumulation, although grain N concentrations tended to increase differences among cultivars. Further, grain N accumulation tended to reflect final grain N contents, as cultivars were similar in percent of final grain N content accumulated.

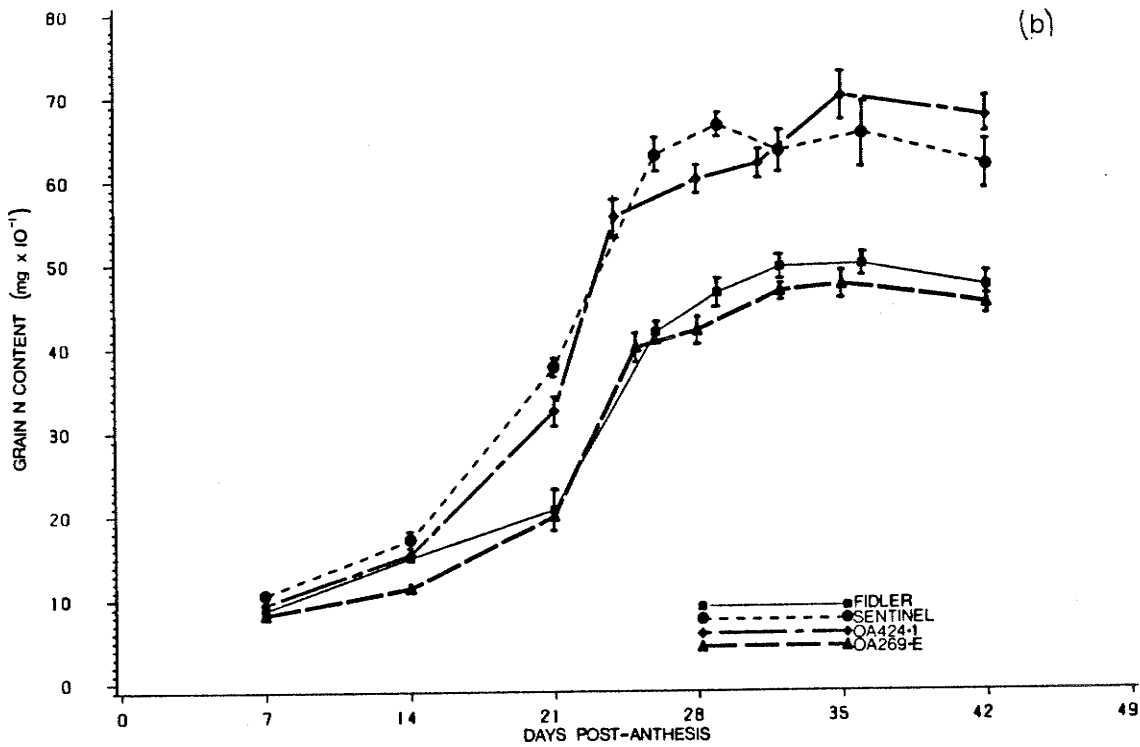
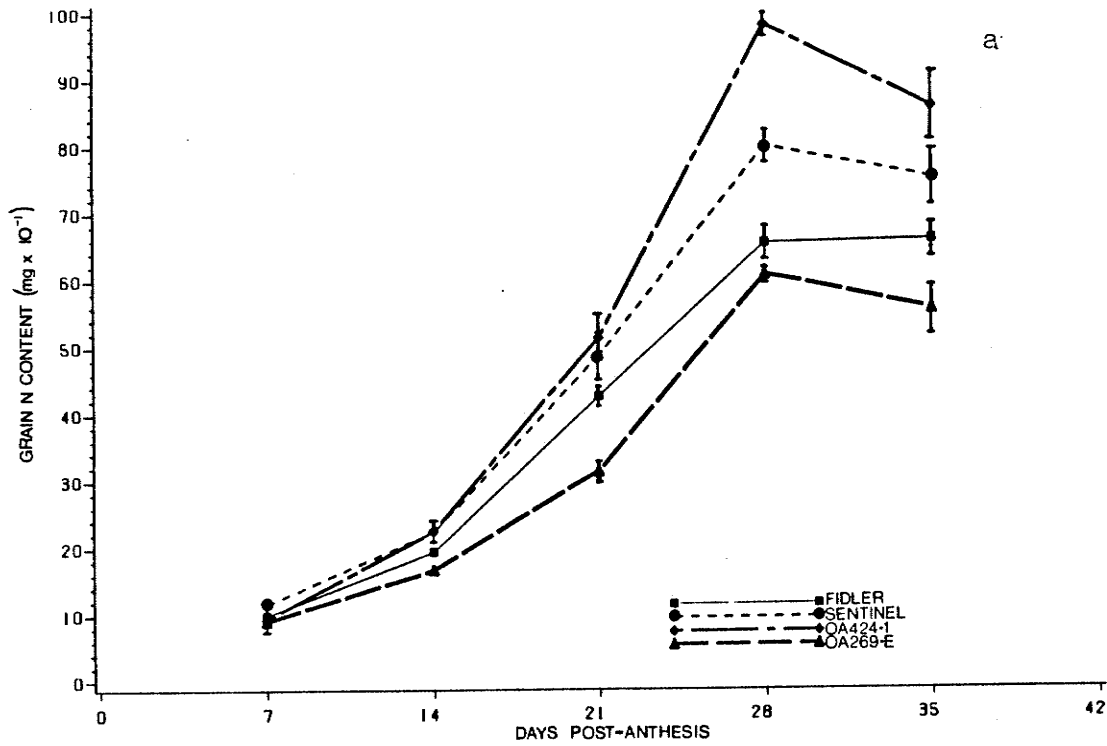


Figure 17: Grain N accumulation as a function of days post-anthesis in oats (a) in 1983 and (b) in 1984.

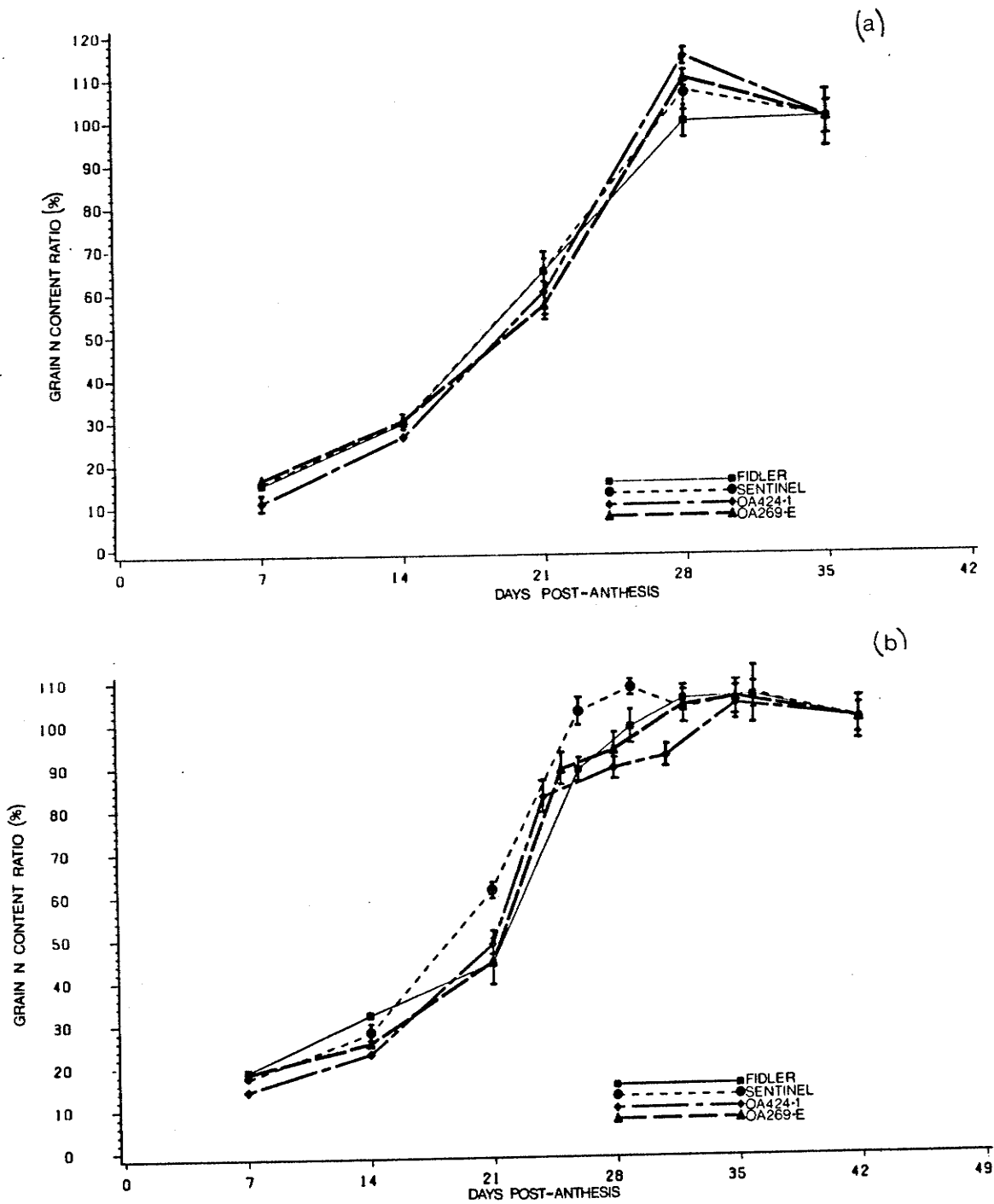


Figure 18: Ratio of sampling date grain N content over final grain N content (%) as a function of days post-anthesis in oats (a) in 1983 and (b) in 1984.

## Chapter V

### GENERAL DISCUSSION AND CONCLUSIONS

From the various simple correlations determined among the cultivar means in both crops and from reports in the literature, wheat and oats appear to have similar physiological complexes in respect to DM and N accumulation and redistribution. Thus, methods of selection using HI and NHI simultaneously should be effective in increasing both grain yield and grain protein concentration in wheat and oats.

The results of this study revealed that Glenlea and OA424-1, the cultivars with the highest DM were highest for grain yield per plant, while the contrasting low DM cultivars, Benito and OA269-E, were lowest for this trait. However, in both experiments, this relationship was not observed when grain yield was expressed on a per area basis. Differences in tillering x density interactions most likely caused the lack of relationship. Increasing DM would, in theory, increase grain yield, providing HI is maintained.

HI values of the oat cultivars were higher than those of the wheat cultivars. HI was not related to grain yield, either on a per plant or a per area basis for either growing season, or either crop. DM translocation efficiency was thus a separate physiological complex from DM accumulation, indicating that increases in HI can be achieved without a decrease in DM. Increasing HI within a population while maintaining its DM would result in grain yield increases.

N concentrations at anthesis represent the near-maximal N storage capacity of a plant. In both experiments, cultivars with the highest levels of DM did not have the highest N concentrations. In the wheat experiment, differences for N concentration were high enough to offset DM, resulting in similar N contents among UM632, UM684, and Glenlea. Although a similar DM-N concentration relationship was observed in the oat cultivars, differences for DM were large enough to offset N concentration, resulting in different N contents for all oat cultivars.

Plant N content was related to grain N yield per plant but not to grain protein yield on a per area basis in either the wheat or oat cultivars. Tillering x density interactions, which have dramatic effects on plant DM, most likely caused the lack of relationship between N content and grain protein yield, as plant N content was determined on an individual plant basis in this study. Selecting individual plants high for N content would not therefore guarantee high grain protein yield.

As with HI, cultivar differences were observed for NHI in both crops. However, NHI values were higher in the wheat cultivars than in the oat cultivars. NHI was not related to N content in either experiment, as N assimilation and N translocation efficiency were shown to be separate, physiological complexes. Thus, N translocation efficiency is independent of N accumulation, and increases in NHI can be achieved without decreasing plant N content. In wheat, differences for NHI were able to offset N content, resulting in similar grain N yields among UM632, UM684, and Glenlea. However, in oats, differences for NHI were not great enough to offset differences for N content, due to the

large differences for N content. Similar amounts of N translocated occurred as a result of two factors: (a) higher N accumulation or (b) higher NHI. Differences in NHI were offset by differences for N content, whereby similar amounts of N were translocated among UM632, UM684, and Glenlea in 1983 and OA424-1 and Sentinel in 1984. Increasing NHI would result in increased grain N yield, if N content and DM were maintained at their present level within the cultivar.

As grain protein concentration is the ratio of grain protein content over grain DM, increasing the efficiency of dry matter and nitrogen translocation should result in grain yield increases while at least maintaining grain protein concentration. However, DM should be maintained to realize the full increase in grain yield and grain protein concentration.



#### LITERATURE CITED

- ALLISON, F. E. 1966. The fate of nitrogen applied to soils. Adv. Agron. 18: 219-258.
- AUSTIN, R. B., FORD, M. A., EDRICH, J. A. and BLACKWELL, R. D. 1977. The nitrogen economy of winter wheat. J. Agric. Sci. Camb. 88: 159-167.
- BAKER, R. J. 1982. Effect of seeding rate on grain yield, straw yield and harvest of eight spring wheat cultivars. Can. J. Plant Sci. 62: 285-291.
- BAKER, R. J. and GEBEYEHOU, G. 1982. Comparative growth analysis of two spring wheats and one spring barley. Crop Sci. 22: 1225-1229.
- BHATIA, C. R. 1975. Criteria for early generation selection in wheat breeding programmes for improving protein productivity. Euphytica 24: 789-794.
- BHATT, G. M. and DERERA, N. G. 1977. Response to two-way selection for harvest index in two wheat (Triticum aestivum L.) crosses. Aust. J. Agric. Res. 28: 29-36.
- BOATWRIGHT, G. O. and HAAS, H. J. 1961. Development and composition of spring wheat as influenced by nitrogen and phosphorous. Agron. J. 53: 33-36.
- BRIGGS, K. G. and SHEBESKI, L. H. 1970. Visual selection for yielding ability of F<sub>3</sub> lines in a hard red spring wheat breeding program. Crop Sci. 10: 400-402.
- BRUNORI, A. A., MANNINO, G. A. and BOZZINI, A. 1977. Protein accumulation, RNA and soluble amino nitrogen content in developing endosperm of two varieties of Triticum aestivum with high and low protein seed. Theor. Appl. Genet. 50: 73-77.
- CANADA GRAINS INDUSTRY. 1984. Canadian grains industry statistical handbook 84. Canada Grains Council. Winnipeg. pp. 11-13.
- CATALDO, D. A., HAROON, M., SCHRADER, L. E. and YOUNGS, V. L. 1975a. Rapid colorimetric determination of nitrate in plant tissue by nitration of salicylic acid. Commun. Soil Sci. Plant Analysis. 6: 71-80.
- CATALDO, D. A., SCHRADER, D. M., PETERSON, D. M. and SMITH, D. 1975b. Factors affecting seed protein concentration in oats. I. Metabolism and distribution in two cultivars that differ in groat protein concentration. Crop Sci. 15: 19-23.

- CHANDHANAMUTTA, P. and FREY, K. J. 1973. Indirect mass selection for grain yield in oat populations. *Crop Sci.* 13: 470-473.
- CHAUDHARY, B. D., LUTHRA, O. P. and SINGH, V. P. 1977. Studies on harvest index and related characters in wheat. *Z. Pflanzenzuchtg.* 79: 336-339.
- COWLEY, C. R. and WELLS, D. G. 1980. Inheritance of seed protein in crosses involving 'Hand': a hard red winter wheat. *Crop Sci.* 20: 55-58.
- CREGAN, P. B. and VAN BERKUM, P. 1984. Genetics of nitrogen metabolism and physiological/biochemical selection for increased grain crop productivity. *Theor. Appl. Genet.* 67: 97-111.
- CROY, L. I. and HAGEMAN, R. H. 1970. Relationship of nitrate reductase activity to grain protein production in wheat. *Crop Sci.* 10: 280-285.
- CRUZ, L. J., CAGAMPANG, G. B. and JULIANO, B. O. 1970. Biochemical factors affecting protein accumulation in the rice grain. *Plant Physiol.* 46: 743-747.
- DALLING, M. J., HALLORAN, G. M. and WILSON, J. H. 1975. The relation between nitrate reductase activity and grain nitrogen productivity in wheat. *Aust. J. Agric. Res.* 26: 1-10.
- DARWINKEL, A. 1980. Ear development and formation of grain yield in wheat. *Nether. J. Agric. Sci.* 28: 156-163.
- DAVIDSON, H. R. and CAMPBELL, C. A. 1984. Growth rates, harvest index and moisture use of Manitou spring wheat as influenced by nitrogen, temperature and moisture. *Can. J. Plant Sci.* 64: 825-839.
- DECKARD, E. L. and BUSCH, R. H. 1978. Nitrate reductase assays as a prediction test for crosses and lines in spring wheat. *Crop Sci.* 18: 289-293.
- DECKARD, E. L., LUCKEN, K. A., JOPPA, L. R. and HAMMOND, J. J. 1977. Nitrate reductase activity, nitrogen distribution, grain yield and grain protein of tall and semidwarf near-isogenic lines of *Triticum aestivum* and *T. turgidum*. *Crop Sci.* 17: 293-296.
- DESAI, R. M. and BHATIA, C. R. 1978. Nitrogen uptake and nitrogen harvest index in durum wheat. *Euphytica* 27: 561-566.
- DONALD, C. M. and HAMBLIN, J. 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. *Adv. Agron.* 28: 361-405.
- DONOVAN, G. R., LEE, J. W. and HILL, R.D. 1977. Compositional changes in the developing grain of high- and low-protein wheats. I. Chemical composition. *Cereal Chem* 54: 638-645.

- DUBOIS, J. B. and FOSSATI, A. 1981. Influence of nitrogen uptake and nitrogen partitioning efficiency on grain yield and grain protein concentration of twelve winter wheat genotypes (*Triticum aestivum* L.). *Z. Pflanzenzuchtg.* 86: 41-49.
- DUFFIELD, R. D., CROY, L. I. and SMITH, E. L. 1972. Inheritance of nitrate reductase activity, grain protein and straw protein in a hard red winter wheat cross. *Agron. J.* 64: 249-251.
- DUWAYRI, M. 1984. Effect of flag leaf and awn removal on grain yield and yield components of wheat grown under dryland conditions. *Field Crops Research* 8: 307-313.
- EAGLES, H. A. and FREY, K. J. 1974. Expected and actual gains in economic value of oat lines from five selection methods. *Crop Sci.* 14: 861-864.
- EILRICH, G. L. and HAGEMAN, R. H. 1973. Nitrate reductase activity and its relationship to accumulation of vegetative and grain nitrogen in wheat (*Triticum aestivum* L.). *Crop Sci.* 13: 59-66.
- ENGLEDOW, F. L. and WADHAM, S. M. 1923. Investigations on yield in the cereals. I. *J. Agric. Sci. Camb.* 13: 390-439.
- EVANS, L. T. and WARDLAW, I. F. 1976. Aspects of the comparative physiology of grain yield in cereals. *Adv. Agron.* 28: 301-359.
- FISCHER, R. A. and KERTESZ, Z. 1976. Harvest index in spaced populations and grain weight in microplots as indicators of yielding ability in spring wheat. *Crop Sci.* 16: 55-59.
- FISCHER, R. A. and KOHN, G. D. 1966a. The relationship between evapotranspiration and growth in the wheat crop. *Aust. J. Agric. Sci.* 17: 255-267.
- FISCHER, R. A. and KOHN, G. D. 1966b. The relationship of grain yield to vegetative growth and post-flowering leaf area in the wheat crop under conditions of limited soil moisture. *Aust. J. Agric. Res.* 17: 281-295.
- FOOD AND AGRICULTURE ORGANIZATION. 1983. 1982 FAO production yearbook. Vol. 36. Food and Agriculture Organization of the United Nations-Rome. pp. 108-120.
- FRAZIER, J. C. and APPALANAIIDU, B. 1965. The wheat grain during development with reference to nature, location and role of its translocatory tissues. *Am. J. Bot.* 52: 193-198.
- FREY, K. J. 1977. Protein of oats. *Z. Pflanzenzuchtg.* 78: 185-215.
- GEADELMANN, J. L. and FREY, K. J. 1975. Direct and indirect mass selection for grain yield in bulk oat populations. *Crop Sci.* 15: 490-494.

- GEBEYEHOU, G., KNOTT, D. R. and BAKER, R. J. 1982. Relationships among durations of vegetative and grain filling phases, yield components, and grain yield in durum wheat cultivars. *Crop Sci.* 22: 287-290.
- GIFFORD, R. M. and EVANS, L. T. 1981. Photosynthesis, carbon partitioning and yield. *Annu. Rev. Plant Physiol.* 32: 485-509.
- GRAFIUS, J. E. 1956. Components of yield in oats: A geometrical interpretation. *Agron. J.* 48: 419-423.
- HAGEMAN, R. H. 1979. Integration of nitrogen in relation to yield. In: Nitrogen Assimilation of Plants. Hewitt, E. J. and Cutting, C. V. Ed. Academic Press, New York. pp. 591-611.
- HALLORAN, G. M. and LEE, J. W. 1979. Plant nitrogen distribution in wheat cultivars. *Aust. J. Agric. Res.* 30: 779-789.
- HARPER, J. E. and PAULSEN, G. M. 1967. Changes in reduction and assimilation of nitrogen during the growth cycle of winter wheat. *Crop Sci.* 7: 205-209.
- HELSEL, D. B. and FREY, K. J. 1978. Grain yield variations in oats associated with differences in leaf area duration among oat lines. *Crop Sci.* 18: 765-769.
- HELWIG, J. T. and COUNCIL, K. A. (editors) 1982. *SAS User's Guide: Statistics*. 1982 Edition. SAS Institute Ins., Cary, N.C., 494 pp.
- HEROLD, A. 1980. Regulation of photosynthesis in sink activity-the missing link. *New Phytologist* 86: 131-144.
- HOUSELY, T. L., KIRLEIS, A. W., OHM, H. W. and PATTERSON, F. L. 1981. An evaluation of seed growth in soft red winter wheat. *Can. J. Plant Sci.* 61: 525-534.
- HOUSELY, T. L., KIRLEIS, A. W., OHM, H. W. and PATTERSON, F. L. 1982. Dry matter accumulation in soft red winter seeds. *Crop Sci.* 22: 290-294.
- IBRAHIM, O. E., OHM, H. W., NYQUIST, W. E. and CANTRELL, R. P. 1983. Inheritance of kernel number per spikelet and its association with kernel weight in two winter wheat crosses. *Crop Sci.* 23: 927-931.
- INGLE, J., BEITZ, D. and HAGEMAN, R. H. 1965. Changes in composition during development and maturation of maize seeds. *Plant Physiol.* 39: 835-839.
- JALANI, B. S., FREY, K. J. and BAILEY, T. B. 1981. Variation in protein yield and its relationship to growth rate, harvest index, grain yield, and groat-protein content of oats (*Avena sativa* L.) following selfing and outcrossing of M<sub>1</sub> plants. *Z. Pflanzenzuchtg.* 86: 89-98.
- JENNER, C. F. and RATHJEN, A. J. 1975. Factors regulating the accumulation of starch in ripening wheat grain. *Aust. J. Plant Physiol.* 2: 311-322.

- JENNINGS, V. M. and SHIBLES, R. M. 1968. Genotypic differences in photosynthetic contributions of plant parts to grain yield in oats. *Crop Sci.* 8: 173-175.
- JOHNSON, V. A., DREIER, A. F. and GRABOUSKI, P. H. 1973. Yields and protein responses to nitrogen fertilizer of two winter wheat varieties different in inherent protein content of their grain. *Agron. J.* 65: 259-263.
- JOHNSON, V. A., MATTERN, P. J. and SCHMIDT, J. W. 1967. Nitrogen relations during spring growth in varieties of *Triticum aestivum* L. differing in grain protein content. *Crop Sci.* 7: 664-667.
- JOHNSON, V. A., SCHMIDT, J. W. and MATTERN, P. J. 1968. Cereal breeding for better protein impact. *Econ. Bot.* 22: 16-25.
- KAPOOR, A. C. and HEINER, R. E. 1976. Biochemical changes in developing wheat grains. I. Changes in proteins, carbohydrates, and nucleic acids. *Can. J. Plant Sci.* 56: 385-391.
- KING, R. W., WARDLAW, I. F. and EVANS, L. T. 1967. Effect of assimilate utilization on photosynthetic rate in wheat. *Planta* 77: 261-276.
- LAL, A. B., PYARE, C. D., REDDY, G. G. and MODI, M. S. 1978. Accumulation and redistribution pattern of dry matter and N in triticale and wheat varieties under water stress conditions. *Agron. J.* 70: 623-626.
- LEDENT, J. F. 1982. Morphology and yield in winter wheat grown in high yielding conditions. *Crop Sci.* 22: 1115-1120.
- LOFFLER, C. M. and BUSCH, R. H. 1982. Selection for grain protein, grain yield and nitrogen partitioning efficiency in hard red spring wheat. *Crop Sci.* 22: 591-595.
- LUPTON, F. G. H. 1966. Translocation of photosynthetic assimilates in wheat. *Ann. Appl. Biol.* 57: 355-364.
- McKEE, H. J., LEE, H. J., KNIEVEL, D. P. and HOFFMAN, L. D. 1979. Rate of fill and length of the grain fill period for nine cultivars of spring oats. *Agron. J.* 71: 1029-1034.
- McNEAL, F. H., BERG, M. A., BROWN, P. L. and McGUIRE, A. B. 1971. Productivity and quality response of five spring wheat genotypes, *Triticum aestivum* L., to nitrogen fertilizer. *Agron. J.* 63: 908-910.
- McNEAL, F. H., BERG, M. A. and WATSON, C. A. 1966. Nitrogen and dry matter in five spring wheat varieties at successive stages of development. *Agron. J.* 58: 605-608.
- McNEAL, F. H., BOATWRIGHT, G. O., BERG, M. A. and WATSON, C. A. 1968. Nitrogen in plant parts of seven spring wheat varieties at successive stages of development. *Crop Sci.* 8: 535-537.

- McNEAL, F. H., QUALSET, C. O., BALDRIDGE, D. E. and STEWART, V. R. 1978. Selection for yield and yield components in wheat. *Crop Sci.* 18: 795-799.
- McVETTY, P. B. E. and EVANS, L. E. 1980a. Breeding methodology in wheat. I. Determination of characters measured on F<sub>2</sub> spaced plants for yield selection in spring wheat. *Crop Sci.* 20: 583-586.
- McVETTY, P. B. E. and EVANS, L. E. 1980b. Breeding methodology in wheat. II. Productivity, harvest index and height measured on F<sub>2</sub> spaced plants for yield selection in spring wheat. *Crop Sci.* 20: 587-589.
- NAIR, T. V. R. and ABROL, Y. P. 1979. Physiological studies on the leaf blades of wheat (*Triticum aestivum* L.) in relation to nitrate assimilation and grain protein accumulation. *J. Agric. Sci. Camb.* 93: 473-484.
- NASS, H. G. 1973. Determination of characters for yield selection in spring wheat. *Can. J. Plant Sci.* 53: 755-762.
- NASS, H. G. 1983. Effectiveness of several selection methods for grain yield in two F<sub>2</sub> populations of spring wheat. *Can. J. Plant Sci.* 63: 61-66.
- OHM, H. W. and PETERSON, D. M. 1975. Protein composition in developing groats of an *Avena sativa* L. cultivar and an *A. sativa* x *Avena sterilis* L. selection. *Crop Sci.* 15: 855-858.
- PENDLETON, J. W. and DUNGAN, G. H. 1960. The effect of seeding rate and rate of nitrogen application on winter wheat varieties with different characteristics. *Agron. J.* 52: 310-312.
- PETERSON, D. M. and SCHRADER, L. E. 1974. Growth and nitrate assimilation in oats as influenced by temperature. *Crop Sci.* 14: 857-861.
- PETERSON, D. M., SCHRADER, L. E., CATALDO, D. A., YOUNGS, V. L. and SMITH. 1975. Assimilation and remobilization of nitrogen and carbohydrates in oats, especially as related to groat protein concentration. *Can. J. Plant Sci.* 55: 19-28.
- PETERSON, D. M. and SMITH, D. 1976. Changes in nitrogen and carbohydrate fractions in developing oat groats. *Crop Sci.* 16: 67-71.
- PURDY, L. H., LOEGERING, W. Q., KONZAK, C. F., PETERSON, C. J. and ALLAN, R. E. 1968. A proposed standard method for illustrating pedigrees of small grain varieties. *Crop Sci.* 8: 405-406.
- RAO, S. C. and CROY, L. I. 1972. Protease and nitrate reductase seasonal patterns and their relation to grain protein production of "high" vs. "low" protein wheat varieties. *J. Agr. Food Chem.* 20: 1138-1141.

- RAO, K. P., RAINS, D. W., QUALSET, C.O. and HUFFAKER, R. C. 1977. Nitrogen nutrition and grain protein in two spring wheat genotypes differing in nitrate reductase activity. *Crop Sci.* 17: 283-286.
- ROBERTSON, D. W., HAUS, T. E. and HOFF, J. C. 1959. Frost injury to maturing barley. *Agron. J.* 51: 658-660.
- ROSIELLE, A. A. and FREY, K. J. 1977. Inheritance of harvest index and related traits in oats. *Crop Sci.* 17: 23-28.
- SCHAPAUGH, W. T. and WILCOX, J. R. 1980. Relationships between harvest indices and other plant characteristics in soybeans. *Crop Sci.* 20: 529-533.
- SCHMIDT, D. R. 1960. Dry matter and nitrogen content of oats harvest at various stages. *Crop Sci.* 1: 8-10.
- SETH, J., HEBERT, T. T. and MIDDLETON, G. K. 1960. Nitrogen utilization in high and low protein wheat varieties. *Agron. J.* 52: 207-209.
- SIDWELL, R. I., SMITH, E. L. and McNEW, R. W. 1976. Inheritance and interrelationships of grain yield and selected yield-related traits in a hard red winter wheat cross. *Crop Sci.* 16: 650-654.
- SIMS, H. J. 1963. Changes in hay production and harvest index of Australian oat varieties. *Aust. J. Exp. Agric. Anim. Husb.* 3: 198-202.
- SOFIELD, I., EVANS, L. T., COOK, M. G. and WARDLAW, I. F. 1977a. Factors influencing the rate and duration of grain filling in wheat. *Aust. J. Plant Physiol.* 4: 785-797.
- SOFIELD, I., WARDLAW, I. F., EVANS, L. T. and ZEE, S. Y. 1977b. Nitrogen, phosphorous and water contents during grain development and maturation in wheat. *Aust. J. Plant Physiol.* 4: 799-810.
- SRAON, H. S., REEVES, D. L. and RAMBAUGH, M. D. 1975. Quantitative gene action for protein content of oats. *Crop Sci.* 15: 668-670.
- STANFORD, G. and HUNTER, A. S. 1973. Nitrogen requirements of winter wheat (*Triticum aestivum* L.) varieties 'Blueboy' and 'Redcoat'. *Agron. J.* 65: 442-447.
- TAKEDA, K. and FREY, K. J. 1979. Protein yield and its relationship to other traits in backcross populations from an *Avena sativa* x *A. sterilis* cross. *Crop Sci.* 19: 623-628.
- TAKEDA, K., FREY, K. J. and BAILEY, T. B. 1980. Contribution of growth rate and harvest index to grain yield in F<sub>9</sub>-derived lines of oats (*Avena sativa* L.). *Can. J. Plant Sci.* 60: 379-384.
- TAKEDA, K., FREY, K. J. and HELSEL, D. B. 1979. Growth rate inheritance and associations with other traits and contributions of growth rate and harvest index to grain yield in oats (*Avena sativa* L.). *Z. Pflanzenzuchtg.* 82: 237-249.

- TERMAN, G. L., RAMIG, R. E., DREIER, A. F. and OLSON, R. A. 1969. Yield-protein relationships in wheat grain, as affected by nitrogen and water. *Agron. J.* 61: 755-759.
- WARDLAW, I. F. 1965. The velocity and pattern of assimilate translocation in wheat plants during grain development. *Aust. J. Biol. Sci.* 18: 269-281.
- WARDLAW, I. F. and MONCUR, L. 1976. Source, sink and hormonal control of translocation in wheat. *Planta* 128: 93-100.
- WHAN, B. R., KNIGHT, R. and RATHJEN, A. J. 1982. Response to selection for grain yield and harvest index in F<sub>2</sub>, F<sub>3</sub>, and F<sub>4</sub> derived lines of two wheat crosses. *Euphytica* 31: 139-150.
- WILLIAMS, P. C. 1973. The use of titanium dioxide as a catalyst for large-scale Kjeldahl determination of the total nitrogen content of cereal grains. *J. Sci. Food Agric.* 24: 343-348.
- WOMACK, D. and THURMAN, R. L. 1962. Effect of leaf removal on the grain yield of wheat and oats. *Crop Sci.* 2: 423-426.



APPENDIX TABLES

TABLE 1  
Terms and units used.

TERM USED	DEFINITION	UNITS
GRAIN YIELD	seed at 0% moisture	g/plant kg/ha
PROTEIN CONCENTRATION	grain N concentration times correction factor	%
PROTEIN YIELD	grain protein yield	kg/ha
GRAIN N YIELD	grain N content per plant	mg N/plant
DM	total plant dry matter	g/plant
DMTI	$\frac{\text{grain yield}}{\text{grain yield} + \text{vegetative tissue DM}}$	%
HI	$\frac{\text{grain yield per plant}}{\text{DM at maturity}}$	%
N CONCENTRATION	total n concentration	mg N/g tissue
N CONTENT	total n content per plant	mg N/plant
NTI	$\frac{\text{grain N content per plant}}{\text{grain N content} + \text{vegetative tissue N content}}$	%
NHI	$\frac{\text{grain N content}}{\text{plant N content}}$	%

TABLE 2

Total weekly precipitation (mm) received in 1983 and 1984  
at the University of Manitoba.

WEEK ENDING	PRECIPITATION	
	1983	1984
MAY 07	nm <sup>1</sup>	nm
MAY 14	nm	6.2
MAY 21	nm	15.4
MAY 28	nm	2.5
JUNE 04	nm	3.3
JUNE 11	9.0	74.2
JUNE 18	19.8	69.0
JUNE 25	32.1	44.1
JULY 02	34.6	30.0
JULY 09	0.0	17.1
JULY 16	0.0	4.6
JULY 23	37.5	0.0
JULY 30	4.3	0.0
AUG. 06	1.6	2.8
AUG. 13	0.0	6.6
AUG. 20	19.7	6.0

<sup>1</sup>nm = not measured

TABLE 3

Mean plant part nitrate-N concentrations (mg/g) in wheat in 1983.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	HEAD CHAFF
----- FOUR LEAF STAGE -----					
BENITO	5.63				
UM632	9.89				
UM684	8.71				
GLENLEA	6.88				
LSD (0.05)	1.95				
----- ANTHESIS -----					
BENITO	3.86	8.02	6.40	2.74	2.32
UM632	3.58	3.68	3.87	2.55	2.19
UM684	4.40	6.23	5.61	2.21	1.06
GLENLEA	3.04	5.59	5.16	2.79	2.09
LSD (0.05)	1.10	2.39	1.19	ns	0.98
----- MIDFILLING -----					
BENITO	2.17	2.81	2.59	0.98	0.36
UM632	2.62	2.25	1.96	1.11	0.40
UM684	2.06	2.26	2.32	1.15	0.42
GLENLEA	2.87	1.82	1.48	0.82	0.38
LSD (0.05)	ns	ns	0.47	ns	ns
----- MATURITY -----					
BENITO	2.13	2.61	3.21	2.27	0.41
UM632	2.03	1.43	1.34	1.48	0.70
UM684	2.34	1.97	1.67	2.02	0.25
GLENLEA	2.31	1.91	1.76	1.70	0.56
LSD (0.05)	ns	ns	0.91	ns	ns

TABLE 4

Mean plant part nitrate-N concentrations (mg/g) in wheat in 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	HEAD CHAFF
----- FOUR LEAF STAGE -----					
BENITO	2.59				
UM632	2.02				
UM684	2.44				
GLENLEA	1.94				
LSD (0.05)	0.44				
----- ANTHESIS -----					
BENITO	0.79	0.89	0.59	0.66	0.53
UM632	0.94	0.77	0.43	0.73	0.65
UM684	0.91	1.06	0.33	0.67	0.70
GLENLEA	0.64	0.78	0.31	0.57	0.74
LSD (0.05)	ns	ns	0.11	0.08	0.07
----- MIDFILLING -----					
BENITO	0.72	0.94	0.74	0.62	0.28
UM632	1.34	0.82	0.76	0.75	0.41
UM684	1.13	0.70	0.57	0.57	0.38
GLENLEA	0.91	0.64	0.58	0.68	0.35
LSD (0.05)	0.26	0.08	0.09	0.06	0.05
----- MATURITY -----					
BENITO	0.12	0.23	0.32	0.28	0.12
UM632	0.18	0.21	0.21	0.33	0.12
UM684	0.20	0.19	0.25	0.30	0.15
GLENLEA	0.20	0.12	0.16	0.28	0.14
LSD (0.05)	0.04	0.04	0.06	ns	0.02

TABLE 5

Mean plant part reduced-N concentrations (mg/g) in wheat in 1983.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	HEAD CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
BENITO	38.54					
UM632	37.97					
UM684	40.00					
GLENLEA	40.01					
LSD (0.05)	ns					
----- ANTHESIS -----						
BENITO	12.86	29.11	37.99	43.00	21.39	
UM632	19.14	35.56	43.67	48.37	21.02	
UM684	15.00	34.97	43.40	45.34	21.08	
GLENLEA	12.78	36.94	45.19	49.60	21.75	
LSD (0.05)	6.07	ns	6.14	1.67	ns	
----- MIDFILLING -----						
BENITO	9.97	14.19	17.09	26.48	8.48	28.88
UM632	10.88	14.49	15.81	22.35	9.87	33.04
UM684	9.87	15.04	15.39	22.19	9.73	31.95
GLENLEA	10.05	13.76	15.28	22.16	10.00	28.91
LSD (0.05)	ns	1.21	ns	3.21	1.07	1.25
----- MATURITY -----						
BENITO	5.97	13.35	14.24	16.10	8.72	35.04
UM632	6.91	13.96	15.43	15.82	8.16	36.64
UM684	5.57	14.06	12.96	13.81	5.97	35.22
GLENLEA	7.33	13.49	12.45	13.55	7.89	33.07
LSD (0.05)	ns	ns	ns	ns	2.74	1.53

TABLE 6

Mean plant part reduced-N concentrations (mg/g) in wheat in 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	HEAD CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
BENITO	42.27					
UM632	42.51					
UM684	43.28					
GLENLEA	41.57					
LSD (0.05)	ns					
----- ANTHESIS -----						
BENITO	10.69	25.36	34.32	40.03	18.72	
UM632	11.52	32.72	38.99	43.68	18.80	
UM684	10.19	29.01	33.87	38.96	17.79	
GLENLEA	9.97	27.97	36.99	43.36	17.76	
LSD (0.05)	0.89	2.92	3.70	2.26	ns	
----- MIDFILLING -----						
BENITO	5.33	8.67	17.36	27.01	8.93	23.87
UM632	6.85	14.21	20.21	29.92	9.76	24.83
UM684	6.08	12.72	23.15	29.17	10.29	24.99
GLENLEA	5.71	8.61	13.17	26.96	9.04	22.20
LSD (0.05)	0.93	2.40	3.36	2.37	0.95	1.51
----- MATURITY -----						
BENITO	2.96	7.65	8.05	8.59	7.41	27.15
UM632	2.96	8.35	8.32	8.27	4.11	28.64
UM684	2.27	7.12	8.08	7.81	4.64	27.07
GLENLEA	2.61	7.25	8.00	8.00	6.13	23.92
LSD (0.05)	0.50	0.86	ns	ns	0.93	2.68

TABLE 7

Mean plant part nitrate-N concentrations in oats in 1983.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	PANICLE CHAFF
----- FOUR LEAF STAGE -----					
FIDLER	8.88				
SENTINEL	9.49				
OA424-1	10.18				
OA269-E	9.28				
LSD (0.05)	ns				
----- ANTHESIS -----					
FIDLER	9.48	5.35	3.48	2.61	1.37
SENTINEL	9.71	7.05	5.82	3.64	1.67
OA424-1	9.21	8.07	5.23	3.86	1.82
OA269-E	7.59	5.25	3.26	2.38	1.11
LSD (0.05)	ns	ns	0.70	0.08	0.88
----- MIDFILLING -----					
FIDLER	5.98	5.96	4.58	2.66	1.25
SENTINEL	8.00	8.19	6.96	2.94	1.11
OA424-1	5.59	6.15	4.07	1.69	0.80
OA269-E	5.93	5.83	7.01	3.83	2.07
LSD (0.05)	1.68	ns	2.14	ns	0.61
----- MATURITY -----					
FIDLER	6.21	5.12	3.99	2.61	0.65
SENTINEL	5.63	6.12	5.69	4.20	1.03
OA424-1	6.08	5.95	3.25	1.72	0.60
OA269-E	7.24	7.30	7.46	3.28	2.27
LSD (0.05)	1.15	ns	1.76	1.12	0.95



TABLE 8

Mean plant part nitrate-N concentrations (mg/g) in oats in 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	PANICLE CHAFF
----- FOUR LEAF STAGE -----					
FIDLER	4.97				
SENTINEL	6.18				
OA424-1	6.53				
OA269-E	4.85				
LSD (0.05)	1.44				
----- ANTHESIS -----					
FIDLER	1.23	0.95	0.84	0.71	0.68
SENTINEL	0.95	0.81	0.81	0.63	0.87
OA424-1	1.15	0.83	0.99	0.82	0.80
OA269-E	1.41	0.85	0.93	0.72	0.92
LSD (0.05)	0.45	ns	ns	ns	ns
----- MIDFILLING -----					
FIDLER	1.62	1.69	2.00	0.92	0.17
SENTINEL	1.48	1.23	1.92	1.02	0.21
OA424-1	0.39	1.21	0.99	0.66	0.22
OA269-E	2.56	1.43	1.49	1.04	0.36
LSD (0.05)	0.95	ns	0.82	ns	0.06
----- MATURITY -----					
FIDLER	1.03	0.98	0.77	0.33	0.48
SENTINEL	0.61	0.48	0.48	0.26	0.46
OA424-1	1.23	0.65	0.69	0.43	0.40
OA269-E	1.57	0.66	1.01	0.81	0.91
LSD (0.05)	0.65	0.33	0.23	0.25	0.46

TABLE 9

Mean plant part reduced-N concentrations (mg/g) in oats in 1983.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	PANICLE CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
FIDLER	39.65					
SENTINEL	41.85					
OA424-1	37.62					
OA269-E	39.62					
LSD (0.05)	ns					
----- ANTHESIS -----						
FIDLER	19.31	31.73	41.97	49.01	22.53	
SENTINEL	19.97	34.48	44.24	53.31	22.77	
OA424-1	19.15	33.60	40.11	47.36	21.84	
OA269-E	17.98	34.60	41.15	53.23	21.28	
LSD (0.05)	1.32	ns	2.96	1.92	1.17	
----- MIDFILLING -----						
FIDLER	12.91	18.51	23.20	24.34	14.35	24.96
SENTINEL	13.76	18.27	21.31	25.86	17.81	25.25
OA424-1	12.32	16.45	25.12	30.37	14.91	22.75
OA269-E	12.40	16.77	21.23	31.92	17.04	19.55
LSD (0.05)	ns	ns	3.45	4.38	1.86	1.72
----- MATURITY -----						
FIDLER	11.63	16.53	16.77	12.51	10.05	23.44
SENTINEL	12.27	16.43	17.33	14.27	11.92	25.39
OA424-1	12.03	17.76	18.40	16.27	9.89	23.76
OA269-E	13.12	17.63	18.56	22.03	12.37	23.57
LSD (0.05)	ns	ns	ns	2.97	2.08	1.47

TABLE 10

Mean plant part reduced-N concentrations (mg/g) in oats in 1984.

CULTIVAR	STEM	LEAF THREE	LEAF TWO	FLAG LEAF	PANICLE CHAFF	GRAIN
----- FOUR LEAF STAGE -----						
FIDLER	43.84					
SENTINEL	47.57					
OA424-1	46.13					
OA269-E	45.09					
LSD (0.05)	2.63					
----- ANTHESIS -----						
FIDLER	8.88	24.37	32.48	41.44	18.03	
SENTINEL	9.41	26.08	33.49	42.40	18.96	
OA424-1	9.20	25.39	28.96	38.83	18.21	
OA269-E	10.21	23.52	32.91	44.16	18.83	
LSD (0.05)	0.89	ns	2.80	2.83	ns	
----- MIDFILLING -----						
FIDLER	4.56	8.67	14.24	21.07	12.99	16.40
SENTINEL	4.85	8.67	17.63	24.11	15.39	19.57
OA424-1	3.84	12.03	17.41	21.76	12.48	16.72
OA269-E	6.19	11.62	21.82	31.79	14.43	14.08
LSD (0.05)	0.97	2.36	2.83	3.25	1.11	0.94
----- MATURITY -----						
FIDLER	3.87	8.24	7.87	7.87	9.44	18.24
SENTINEL	3.63	8.35	11.65	10.56	10.21	20.24
OA424-1	4.21	9.95	12.83	13.15	8.29	19.15
OA269-E	4.61	10.08	11.33	13.60	9.12	17.44
LSD (0.05)	0.60	1.65	1.80	1.99	1.33	0.83