WATER STRESS AND REMOBILIZATION OF DRY MATTER AND NITROGEN IN WHEAT AND BARLEY GENOTYPES

by

Zeinolabedin Tahmasebi Sarvestani

(B.Sc. Agronomy, University of Shiraz, Iran)

(M.Sc. Agronomy, Esfahan University of Technology, Iran)

A thesis submitted to the University of Adelaide

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Department of Plant Science,

Waite Agricultural Research Institute,

Glen Osmond, South Australia.

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STATEMENT

I hereby declare that the thesis here presented contains no work which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan or photocopy.

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LIST OF PUBLICATIONS

Part of the work described in this thesis has been presented at scientific conferences and published in proceedings.

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Tahmasebi, Z., Jenner, C.F., and McDonald, G. (1994). Effects of water stress on remobilization efficiency of dry matter and nitrogen from the shoot of two cultivars of wheat during grain filling. Wheat Breeding Society of Australia. Proceedings of the Seventh Assembly, Adelaide, South Australia. 237-240.

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LIST OF ABBREVIATIONS

ABA.....abscisis acid

cv.....cultivar

day 24.....day 24 after anthesis

DM.....dry matter

ESS.....ethanol soluble sugar

et al.....and others

HI.....harvest index

NHI.....nitrogen harvest index

N.....nitrogen

M.....molar

mM.....millimolar

µM.....micromolar

2-ME.....2-mercaptoethanol

nm.....nanometer

N.S.....not significant

p.a.....Post anthesis

SP.....soluble protein

TSC.....total soluble carbohydrates

ppm.....parts per million

v/v.....volume by volume

WSS.....water soluble sugars

°C.....Degree Centigrade

SUMMARY

1. The effects of the availability of water during grain filling on the accumulation of dry matter (DM) and nitrogen (N) in the grain and also on the remobilization of these components from the shoot to the grain has been examined in two wheat (*Triticum aestivum* L.) and three barley (*Hordum vulgare* L.) genotypes.

2. The information available on the effects of water stress grain yield and the remobilization of both N and DM from the shoot of wheat and barley plants has been reviewed.

3. The assumption made in this investigation is that the effects of water stress on remobilization of N and DM are mediated through the severity of water stress and also the behaviour of the genotypes. Accordingly, remobilization of soluble carbohydrates and soluble protein from different parts of the shoot in well-watered (control) conditions and water stress conditions has been determined. It seems that the remobilization of N and DM from the shoot to the grain is limited by the availability of water during grain filling.

4. In both species leaves were the most important part of the shoot in relation to the contribution of N to the grain, while the stem (internodes + peduncle) was the most important part in relation to contribution of DM to the grain.

5. Imposing water stress to the shoot during the grain filling phase reduced grain yield in both species at maturity and the response increased with the severity of the water stress which was mainly due to an effect of water stress on individual grain weight.

6. Grain nitrogen concentration was significantly higher under severe water stress than under conditions of adequate water in the grain of both species at maturity, because DM accumulation in the grain was more sensitive than N accumulation in the grain under water stress conditions.

7. Depriving the upper section of the root system of water resulted in different responses for the two species in terms of the remobilization of DM and N from the shoot.

8. It is concluded that :

(a) Remobilization of N and DM from the shoot of both wheat and barley plants are affected by water stress during the grain filling phase. The amount of N and DM remobilized is reduced under water stress.

(b) The remobilization of N and DM from different parts of the shoot to the grain in both wheat and barley respond differently under water stress and well watered conditions during grain filling.

(c) Differential responses to the treatments between cultivars and also in different parts of the shoot suggest that the remobilization of DM and N are controlled through different mechanisms.

(d) Reduction in final grain weight and grain protein concentration under water stress could possibly be mediated either through effects on the size of the grain or through effects of water stress on the availability of reserves and assimilates for grain growth.

(e) Water stress during the grain filling phase not only reduced DM and N accumulation in the grain, but also generally increased the grain N concentration in both wheat and barley grain.

Chapter 1. General introduction

In Australia wheat production represents 13% of the total farm production and over the last decade 11.4 Mha have been sown annually to wheat with production averaging 15.3 Mt each year. Barley occupies about 2.8 Mha and production has averaged 2.8 Mt (Bolt 1989).

Water is a fundamental component of plant life. It comprises approximately 85 to 90% of the total fresh weight in physiologically active herbaceous plants. When the amount of water is unfavourable for optimum plant growth the plant is said to be under water deficit. Water deficit has long been recognised as one of the major factors reducing crop yields in drought-prone areas of the world. The periodic droughts that are a feature of the climate in many parts of the world must be factored into any strategy for improving food security. For example, over the last 100 years in Australia there have been at least eight major, widespread droughts and numerous severe regional droughts (Fig. 1.1).

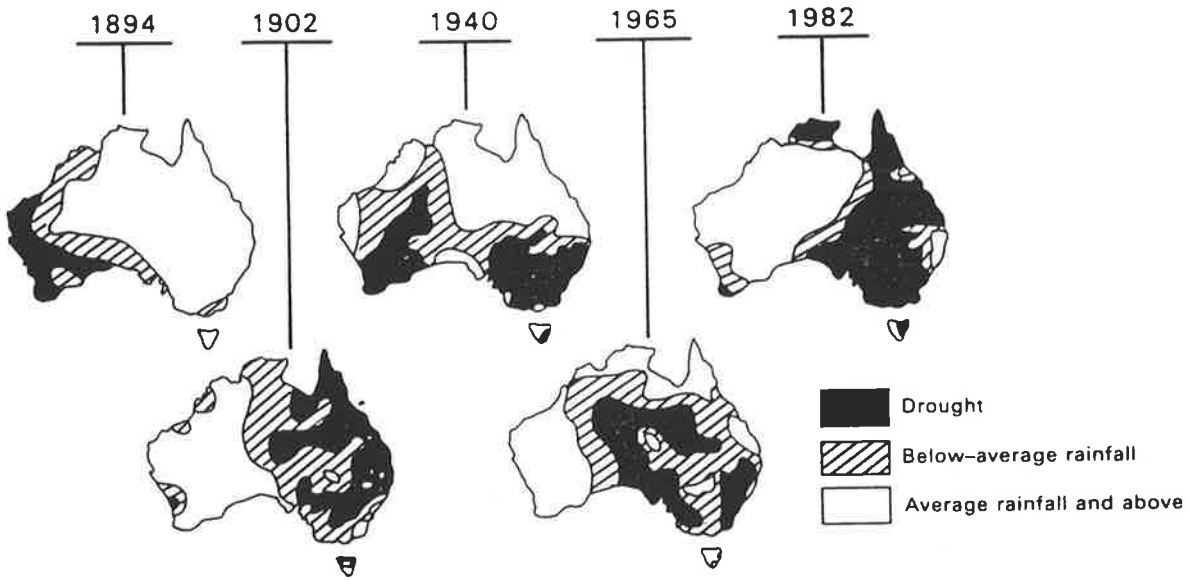

Fig. 1.1. Areas of Australia affected during a series of major droughts during the last 100 years (from McWilliam 1986).

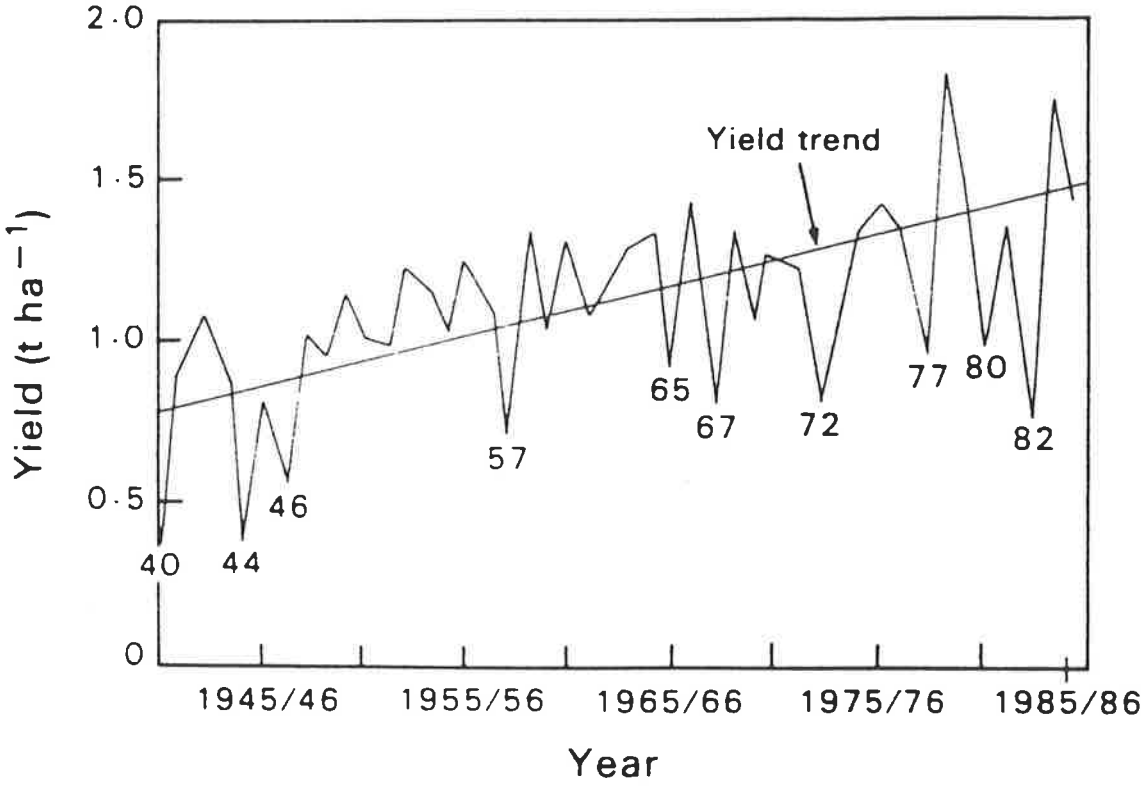

Fig. 1.2. Effect of drought on average yields of wheat in Australia from 1940/41 to 1984/85 Major drough years are indicated (from McWilliam 1986).

A comparable analysis of the impact of drought on the average yield of Australian wheat is given in Fig. 1.2. This shows the yield of wheat in Australia over the period from 1940 to 1985 and the impact of 10 droughts made up of six major drought years (1940, 1944, 1957, 1967, 1972, 1982) and four less serious drought years (1946, 1956, 1977, 1980). The absolute reduction in average yield during a particular drought year is confounded with the steady increase in average wheat yield over the period, as indicated by the trend line. The figure clearly indicates the frequency of drought in the Australian cereal belt, and the significant effect it has on national wheat yields.

The cereal zone in southern Australia lies broadly in an area receiving between 250 and 500 millimetres of annual rainfall (Fig. 1.3). Most of this rain (approx. 75 per cent) falls during the growing period for winter cereals (April to October) but it is unreliable. It has been calculated (Cornish 1950) that 65 per cent of the annual yield variation can be attributed to the rainfall during the growing season.

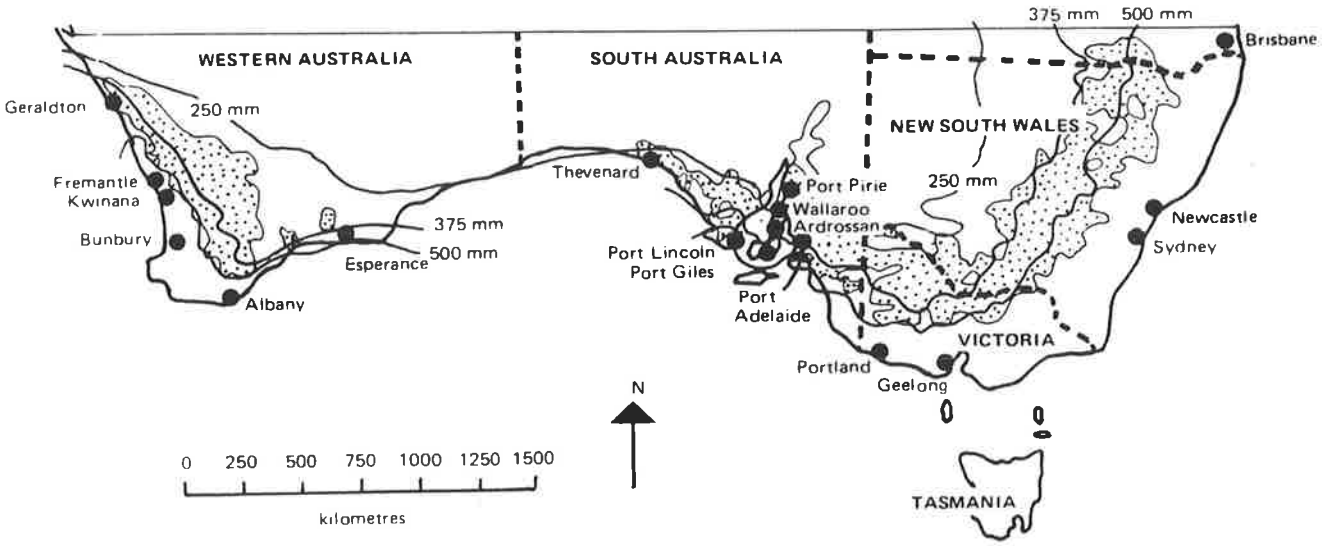

Figure 1: Cereal zone of southern Australia

Fig. 1.4. Cereal zone of southern Australia From Rathjen and Krause (1980).

In southern Australia the top soil is frequently wet after sowing when there is little crop cover. Exposure of the soil surface to sunshine and wind results in a large loss of water from the soil surface by evaporation and often half of the rainfall received during the growth of the crop is lost in this way (Richards 1994). The benefits of early leaf canopy growth (vigour) of wheat or barley result from covering the soil surface more quickly which reduces loss of water, and from additional growth during the winter at almost no cost in terms of water because of the low evaporative demand at this time.

According to Milborrow (1981) the effects of water and thermal stress on different developmental (1), metabolic (2) and regulatory (3) processes are the same (Table 1.1). When post-anthesis stress is low, most of the grain carbohydrate is derived from CO_2 fixed during the grain filling period (Evans *et al.* 1975). This period is considerably influenced by the environment and can be resolved into two components, rate and duration; both components are variable and display genetic and environmental influence (Sofield *et al.* 1977). Drought during grain filling reduces the duration of grain filling and reduces the mean weight of the grain.

Table 1.1. Effects of water and thermal stress on different processes

	Process	Water stress	Heat stress
(1)	Senescence	accelerate	accelerate
(1)	Growth	reduced	reduced
(2)	Chlorophyll degradation	enhanced	enhanced
(2)	Cellulose synthesis	reduced	reduced
(2)	Respiration	enhanced	enhanced
(2)	Amylolytic activity	enhanced	enhanced
(2)	CO_2 Fixation	reduced	reduced
(3)	Cytokinin metabolism	enhanced	enhanced
(3)	Cytokinin activity	reduced	reduced
(3)	Abscisic acid	increase	increase

(From Milborrow 1981).

Empirically the responses in the grain to developing water stress are similar to the response to elevated temperature (Milborrow 1981; Jenner *et al.* 1991).

Reserves in the vegetative parts of the shoot can be mobilized to sustain grain growth during limitation of photosynthetic supply induced by environmental factors such as drought. Investigations into the contribution of plant parts to grain protein show that the increase in grain N after heading can exceed losses from the leaves and stems throughout the grain development period. The remaining grain N content therefore is being supplied by soil N absorbed by the roots after anthesis and to a lesser extent remobilization of N from the roots.

The importance of shoot reserves in the last (reproductive) stage of cereal crops was described by Beaven (1920) more than 70 years ago as follows: " Some time ... before the grain is ripe the plant ceases to gain in weight of solid matter. Its last effort is to transfer its accumulated reserves into the grain. But all the dry matter of the grain is first stored up in the leaves and stems of the plant... It is mainly ... on the extent to which this "uplift" takes

place that plenty or scarcity of the staple food of man depends". On this view of crop development several factors, such as differences in stem height and in the extent of N remobilization from different parts of the shoot , could possibly determine inter varietal and inter specific differences in the contribution of shoot reserves to grain filling.

Different cereal species are grown using similar management practices in a large range of environments in southern Australia. When grown under the same levels of management, barley yields are about 25% more than wheat (Richards 1994). In addition Bidinger *et al.*. (1977) concluded that pre-anthesis reserves contributed 27% and 17% respectively for wheat and barley under drought conditions but under irrigated conditions there was less remobilization and little difference between the two cereals. The situation common to most of Australia's wheat and barley-growing areas is an environment where the post-anthesis supply of soil N and moisture is low and root activity is reduced. This results in little uptake of N from the soil and increasing levels of plant water deficits. Since there is a lack of information in the literature in relation to remobilization of nitrogen (N) and dry matter (DM) of the shoot of wheat and barley under post anthesis water stress it is very important to improve the knowledge related to this area. Accordingly, a number of questions can be raised:

(i) Are there any differences between accumulation of N and dry matter in the grain of wheat and barley under water stress during grain filling?

(ii) Are there any differences between remobilization of N and dry matter from the shoot of wheat and barley under water deficit during grain filling?

(iii) Do different cultivars show similar responses in terms of the remobilization of N and dry matter from the shoot ?

(iv) Do wheat and barley show different responses under similar levels of water stress related to remobilization of N and carbohydrate from the shoot ?

(v) Do different parts of the shoot make similar contributions to remobilization of N and carbohydrate under normal and water deficit conditions ?

(vi) Are there differences in response of grain filling to water stress and non-water stress conditions between wheat and barley ?

The study reported in this thesis was therefore undertaken to investigate the responses of wheat and barley cultivars under water deficit during grain filling. The objective was to gain a better understanding of the effects of water deficit on the accumulation of N and DM in the grain and also remobilization of reserves from vegetative parts of the shoot and its contribution to the accumulation of dry matter and N in the grain of wheat and barley cultivars. To achieve these goals firstly, the influence of water deficit on the accumulation of N and dry matter in the grain and remobilization of these components from the vegetative parts of the shoot to the grain of two wheat cultivars were investigated. Secondly, a similar experiment was carried out for barley cultivars differing in protein content. Thirdly, the remobilization of soluble sugars and soluble protein in wheat cultivars under water deficit was studied. Finally the influence of water stress on the accumulation of N and dry matter in the grain and the remobilization of these components from the vegetative parts of the shoot of wheat and barley was examined. The related points mentioned in this chapter will be described in more detail in Chapter 2.

Chapter 2. Literature review

2.1 Introduction

This review considers the importance of grain development and remobilization of DM and N from the shoot and genetic variation related to the mobilization of N. The influence of water deficit on some aspects of the physiology and metabolism of cereals (wheat and barley) is then discussed.

Cereal growth is generally divided into pre-anthesis and post anthesis stages. Pre-anthesis growth refers to the phases of seedling establishment, tillering and stem elongation up to flowering, while post-anthesis growth refers to the period from flowering to maturity which includes grain development and growth. Grain growth occurs when vegetative growth is essentially complete and occurs under conditions of increasing water and heat stress.

Wheat and barley crops in the Mediterranean environment are not generally subjected to severe water stress before anthesis. However, grain growth, which occurs post-anthesis, is generally completed under conditions of increasing water and heat stress. In this environment the major abiotic factors limiting grain growth are low soil moisture and N availability which can influence growth duration of the plant and also grain growth. Therefore, improvement in agronomy and early crop growth have favoured a trend for the date of anthesis to be earlier in more recently bred varieties (Siddique *et al.* 1989b; Richards 1991). The shorter time from sowing to ear emergence has been coupled with a longer interval from ear emergence to maturity, and therefore for grain filling. An understanding of morphology and anatomy of a plant is important because these characteristics may be associated with agricultural productivity in many ways. For example, straw length and strength, components of yield, response to various diseases, photosynthesis, time and amount of water requirements, fertilizer and pesticides applied, and effects of environmental stresses such as drought and so on are all related in part to plant morphology and anatomy, and all affect productivity. In the following part the morphology, yield and composition of wheat and barly plant will be briefly explained.

2.2 Morphology of wheat and barley plant

2.2.1 Wheat

Wheat has received considerable morphological and anatomical study because of its economic importance. The summary of the accumulated knowledge of both vegetative and reproductive parts of wheat plant were by Musick and Porter (1990). The shoot of wheat is a short rhizome bearing several axillary leafy culms (tillers) that may each grow to about a meter in height. The number of culms varies with cultivar, planting depth, density, and external conditions. Each culm has five to seven nodes. The number of leaves that develops depends on the rate and pattern of the development of the apex, and may vary from 3-4 to more than 8 leaves per culm. The uppermost, or flag leaf, subtends the inflorescence.

2.2.2 Barley

The barley plant has been described in detail by Nilan and Ullrich (1993). The stem or culm of the barley plant, is cylindrical, consisting of hollow internodes separated by solid nodes (joints) with transverse septa. Typically there are five to seven internodes, of which the basal internode is the shortest. They increase in length and are progressively smaller in diameter toward the top. Length of the culm depends on genetic and environmental factors and ranges from 70 cm in dwarf types to more than 150 cm. Likewise, strength of the stem is dependent upon genes as well as environmental factors. The distance from the flag leaf to the base of the spike varies greatly between tillers on the same plant and is influenced by environmental conditions. Barley cultivars differ in the size and shape of their leaves and in the position in which they are held on the plant. The uppermost blade, called the flag leaf, is often the smallest, other than the seedling leaf (Nilan and Ullrich (1993) and references cited therein.)

2.3 Grain development of the cereal grain

Grain growth after anthesis can be divided into two stages: grain enlargement and grain filling. Grain enlargement commences at fertilisation and under normal conditions of growth is completed within 20 days. Grain filling commences 10-15 days after anthesis and

continues for 20-30 days until the grain ripens. However the duration of grain growth depends on environmental conditions, particularly related to temperature and water. Growth of the grain, from initiation to maturity, follows a complex course of several phases. These phases are described in more detail.

In wheat cellularization occurs at about 3 days post anthesis (p.a.) by which time the endosperm mother cell consists of about 1000 nuclei. The process of cellularization which takes 1-2 days has been studied extensively (Morrison 1975). After cellularization is complete nuclear division is no longer synchronous. The majority of cells divide by both radial and tangential divisions. Within the endosperm the rate of cell division decreases from about day 13 p.a. and would have stopped completely by day 20 p.a. (Briarty *et al.* 1979).

Fresh weight growth of the endosperm from day 14 p.a. to day 35 p.a. is due primarily to cell expansion. Commonly, cell size doubles from day 13 p.a. to day 20 p.a. and doubles again by day 35 p.a. (Briarty *et al.* 1979). During the final stages which commences at about 35 days p.a., the fresh weight of the kernel declines as water is lost. At about the same time deposition of DM stops, and there appears to be a loss of DM prior to maturity. Although difficult to quantify, the loss of DM seems to amount to about 3% of the grain dry weight (Donovan *et al.* 1977). By the end of this stage the grain would now have reached harvest-ripeness.

In general, at elevated temperatures the rate of DM accumulation is increased but the duration of grain filling is reduced, and mature grain weights may be less than those at lower temperatures. For example, Ellis and Kirby (1980) have compared yield and components in barley grown in Scotland and Eastern England. Yield, as well as weight per grain, was greater in Scotland over two seasons. It was considered that the cooler temperatures in Scotland may have contributed to increased dry weight per grain because at lower temperatures maturation was delayed and a longer period was available for grain filling. In one experiment, barley plants (cv. Triumph) were grown in a glasshouse (approximately 20° / 15°C day/ night) and transferred to controlled growth rooms at either 30°/25°C or 20°/15°C at two to three days pre anthesis. The results of this experiment confirm the observations

above, i.e., that the duration of grain filling was reduced and final grain starch content was significantly less at the higher temperatures.

2.4 Accumulation of DM and protein in the grain

2.4.1 DM accumulation and harvest index

When post-anthesis stress is low, most of the grain carbohydrate is derived from CO_2 fixed during grain filling (Evans *et al.* 1975). Therefore the limit to yield could be either source-limited or sink limited. Since most of the wheat and barley grown in Australia is grown in arid or semi arid zones, the major limiting factor in these zones is water. Final yield depends on the effect of environmental stress on the balance between sink size (kernel numbers) and source (the amount of photosynthesis and remobilisation).

In detailed studies encompassing a wide range of locations, environmental conditions and cultural practices, Shanahan *et al.*. (1984, 1985) found that there was a close correlation between grain yield and kernel number per unit area. Photosynthetic activity of the ear and the blade of the flag leaf alone can provide all the photoassimilate required by the plant (Evans and Rawson 1978) and the rate of photosynthesis of the flag leaf varies throughout the season in response to assimilate demand by the developing ear (Evans and Rawson 1978). Since at harvest about half of the above ground DM of modern wheat and barley cultivars is located in the grain, the total dry weight of the non-grain parts is usually less than their weight at anthesis (Austin *et al.* 1980). These relationships indicate that most of the photosynthate produced during the post-anthesis period, and probably some photosynthate produced before anthesis also is used for grain filling.

There is evidence that not all the DM remobilized during grain filling makes a direct contribution to grain growth. In a series of experiments examining responses to N fertilizer, McDonald (1992) found that kernel weight in small plot experiments was generally lower at high rates of N despite greater apparent remobilization and there was no consistent relationship between the amount of DM remobilized and grain yield. This suggests that in this experiment the increase in remobilized DM at the higher rates of N made little direct contribution to kernel growth and consequently to grain yield. Increased remobilization of

DM may not contribute proportionately to kernel growth and grain yield because part of the remobilized DM could be utilised in dark respiration (Bell and Incoll 1990). Notwithstanding this, Siddique *et al.* (1989b) have argued that the high proportion of grain yield derived from remobilized DM is one reason why DM production at anthesis should be maximised. The direct contribution of remobilisation to kernel weight will vary according to environmental stress, but its exact importance perhaps needs further examination.

Potential yield in wheat is established early in the life cycle at the stage when the terminal spikelet has been initiated (Siddique *et al.* 1989a). Physiological studies suggest that stem and ears grow rapidly at this stage and as a result these two organs compete with each other for a limited supply of assimilate (Siddique *et al.* 1989a; Slafer and Andrade 1993). DM accumulation during head development preceeding anthesis influences grain number (Fischer 1985); the more pre-anthesis DM produced, the more grain there is to be filled and the more critical the post-anthesis water supply and DM accumulation becomes in preventing grain shrivelling and a low harvest index (HI).

Like grain yield and biological yield, HI is the end product of the interaction of genetic, environmental and agronomic factors. It is highly influenced by environment (Siddique *et al.* 1989a), generally being higher under favourable conditions and lower under terminal drought. Provision of water usually raises the HI, whereas provision of N fertilizer tends to lower it. The lowering of the HI at higher N levels can be more pronounced when water is in short supply and when varieties are tall or later maturing (Donald and Hamblin, 1976).

Gifford and Evans (1981) indicated the best wheats now have a harvest index around 50%. The highest HI found in the literature was 60% for early planted spring wheat cultivar "Twin" in Utah (Hanks and Sorensen 1984), while the lowest values of slightly less than 20% were found for wheat growing under severe water deficit in southern Iran (Poostchi *et al.* 1972), and for wheat growing after anthesis under severe stress in Australia (Passioura 1977). A linear relationship between HI and the percent of the seasonal water use after anthesis was found by Passioura (1977). The results demonstrate grain filling as a critical

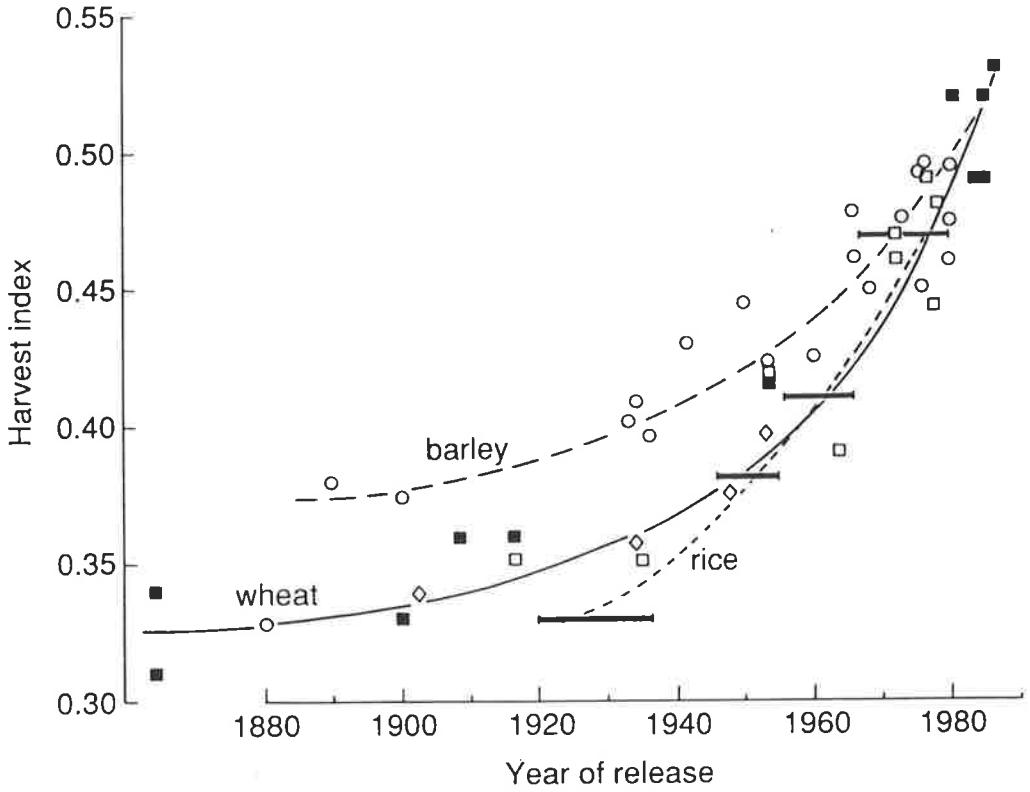

Fig. 2.1 Rise in the harvest index of wheat, barley and rice varieties with year of their release (from Evans 1993).

stage for water deficit effects on HI, generally being higher under favourable conditions and lower under terminal drought. British winter varieties released at various times are illustrated in Fig. 2.1, along with data for barley and rice which indicate a pronounced rise in the HI, particularly among varieties released since 1950. Many comparisons of old and new wheat varieties in other environments indicate a similar rise in HI in recent varieties, such as those of Hucl and Baker (1987) and Siddique *et al.* (1989b). Barley lines with high shoot weight have been identified (Hanson *et al.* 1985), but all are tall and it remains to be seen how readily high HI and high shoot weight can be combined.

2.4.2 Protein accumulation in the grain and NHI

Wheat proteins are classified into various groups depending on their solubility. The major storage protein group in the endosperm of wheat is gluten protein. The gluten protein

is subdivided into two distinct groups, gliadin and glutenin. Glutenin is quite different from gliadin, occurring as large disulphide-linked molecules or aggregates. These aggregates dissociate into approximately 15 subunits classified as HMW or LMW (Payne *et al.* 1980). The glutenin proteins are rich in hydrophobic amino acid residues capable of promoting associations between subunits, such as leucine (hydrophobic interactions) and glutamine (hydrogen bonding) (Bushuk *et al.* 1980).

Storage protein first appears in wheat endosperm at about 10 days p.a. and is located within spherical membrane-bound bodies. At about 20 days p.a. only about 50% of the final amount of storage protein has been synthesised (Donovan *et al.* 1977; Jennings and Morton 1963). Synthesis of storage proteins stops approximately 35 days after anthesis and evidence suggests this may be due to low grain water content (Wrigley and Bietz 1988). Given that synthesis of most wheat storage protein occurs between 10 to 35 days after anthesis, environmental stresses during grain development are likely to have some effect on final storage protein content and on protein composition.

In barley grain protein is also the major nitrogenous reserve. There is a number of proteins in the endosperm at maturity which have a range of physiological roles during germination. With such a variety of complex macromolecules, studying the deposition of individual proteins is difficult, and in practice it has proved preferable to study the deposition of proteins more generally.

Grain protein concentration is determined by the amount of both protein and starch within the grain and starch makes up between 70-80% of the total dry weight of grain (Jenner *et al.* 1991; Gleadow *et al.* 1982). The amount of non-protein N (mostly free amino acids) per grain is almost constant during development (Jennings and Morton 1963).

The soluble cytoplasmic proteins, the water-soluble albumins and salt-soluble globulins, make up most of the protein present during the cell division phase in the endosperm (Jennings and Morton 1963).

The quantity of protein deposited in the grain, and its concentration are influenced by several factors during grain filling. For instance percentage of N (protein) in grains varies greatly depending on grain position in the ear. Grains from the upper- and lower- most

spikelets and from the more distal florets tend to be lower in N than grains from the central region of the spike (Bremner 1972). Results of these experiments suggest that the process of protein synthesis is not the limiting step in distal grains and that differences in N (protein) content between grains reflect regional differences in N supply within the ear.

There is well documented evidence of a positive relationship between the rate of N fertilizer application and grain protein percentage (Hucklesby *et al.* 1971; Hunter and Stanford 1973; Benzian and Lane 1981). A possible mechanism behind this relationship is suggested by Dalling (1985). High N nutrition late in development increases N imported by the grain relative to carbohydrate so that grain N concentration increases over time. Under low N nutrition, however, N imported to the grain parallels carbohydrate import throughout development and grain N concentration remains fairly constant over the grain filling period.

Inverse relationships between grain yield and protein percentage have been widely reported (McNeal *et al.* 1968. Loffler *et al.* 1985). These were found when all the N fertilizer was applied at seeding. Enhanced vegetative growth in the favourable high N environment early in the developmental period may lead to greater yields being obtained, but the same amount of N is distributed amongst a larger number of grains during grain filling, leading to a lower protein percentage overall. McNeal *et al.* (1968) suggested that the negative correlation coefficients between grain N percentage and grain weight they obtained in their experiments indicate that grain N percentages decrease as grain weight makes up a larger proportion of the above ground plant weight (i.e. as HI increases). Therefore as the grain to straw ratio narrows the grain N percentage decreases because there is proportionately less top growth, and therefore less N is available for translocation to the grain.

N Harvest Index (NHI; which is amount of N in the grain at maturity divided by the amount of N in above ground parts of plant at the same time) in bread wheats rarely exceeds 80%. According to McNeal *et al.* (1966) N in the roots appears to have little influence on the efficiency of N partitioning, so it is usually acceptable for NHI values to refer only to the above ground parts. Spiertz and deVos (1983) measured NHI values in healthy crops and reported that they lie between 74-78%. Loffler and Busch (1982) also reported values

between about 55 and 74%. Durum wheats possibly can return higher NHI values, exceeding 80% (Desai and Bhatia 1976). However, the NHI values in wheat decrease with increasing N nutrition (Halloran 1981; Whitfield *et al.* 1989). In the experiments of Withfield *et al.* (1989) NHI values decreased from a mean of 0.77 in treatments without added N fertilizer to 0.70 in treatments with 150 kg N per hectare applied at sowing. Restricting available water and increased fertilization reduced NHI to 0.64. The decline in NHI seen with increasing N nutrition is a physiological response to an increased supply of N within the plant and appears to be mitigated by water stress.

2.5 Hormonal changes and grain growth

During grain development the level of the plant hormone abscisic acid (ABA) increases until maximum grain fresh weight is reached and then decreases rapidly as the grain begins to desiccate. ABA changes in the embryo during grain development are essentially the same as for the whole grain, though the ABA levels are 2-3 times higher in the embryo than in the remaining part of grain. Ober *et al.* (1991) hypothesized that water deficit during early endosperm development might inhibit kernel growth by decreasing endosperm cell division, and this response might be mediated by changes in endosperm ABA levels. To test this hypothesis they subjected maize (cultivar Pioneer 3925) to water deficit from 1 to 15 days after pollination. Water deficit increased ABA concentration in the endosperm of kernels taken from the apical region of the cob by four-fold compared to controls. ABA concentrations were also increased in the middle and basal regions of the ear, but to a lesser extent. Based on correlative changes in ABA concentration and cell division they suggest that ABA may play a role in inhibiting endosperm cell division during water limitation.

The content of ABA in wheat grains has been shown to change during development (King 1976; Radley 1976; Goldbach and Michael 1976). King (1976) reported that application of ABA to wheat ears had no effect on the rate of grain growth but, instead, led to an earlier cessation of grain growth and hastened the drying of the grain. Goldbach and Goldbach (1977) observed that exposing the leaves of barley to a stream of warm air increased the concentration of ABA in all plant parts including the grains. It was found that

because plant organs differed in their intensity of ABA metabolism, the final ABA content in the various organs differed. To explain the observations that ABA applied to young barley plants had almost no effect on grain growth whereas application to older plants hastened grain maturation, these authors suggested that the ability of grains to metabolize ABA decreases as the grain ages. More recently, studies related to ABA in plants and drought resistance have been summarised by Kirkham (1990). It is suggested that "since plants cope with drought in various way, it is unlikely that particular ABA response will be the same for all drought-resistant plants"

Wheeler (1972) found that the content of cytokinins, gibberellins and auxins in wheat grains changed greatly during grain growth. Cytokinin activity was highest early in development, gibberellins reached a peak at about three weeks after anthesis and auxins were at a maximum later. It was suggested that cytokinins have a role in regulating endosperm cell division. Wardlaw (1971) made the suggestion that reduced cytokinin production may be an important factor in the premature senescence of grains from water stressed plants, and Michael *et al.* (1972) found that the cytokinin content of barley grains was reduced by low soil moisture.

Cytokinins may also influence N partitioning in plants. Cytokinins are produced in root tips and the amount exported from roots is responsive to N nutrition (Salma and Wareing 1979; Sattelmacher and Marschner 1978). They are translocated to the shoot in the transpiration stream and are presumed to influence protein synthesis in leaves. It has been hypothesized therefore that cytokinins may affect partitioning of N within the plant by influencing accumulation of N in leaves; more cytokinin produced in root tips may increase N accumulation in leaves. Control of N partitioning by translocation of cytokinins to the shoot would consequently be responsive to the supply of N to the plant. N, which has been demonstrated to increase cytokinin synthesis and the export from root to shoot, and cytokinins, both applied to plant at anthesis, increased grain set in disadvantageous positions on the ear (Herzog 1986). Increases of final grain weight due to cytokinin applications also have been obtained with wheat (Michael *et al.* 1972).

2.6 Source of assimilate for grain growth

2.6.1 Sources of carbon assimilates

The main sources of carbon assimilates for the developing wheat grain are the flag leaf, the ear and the penultimate stem internode (peduncle) (Carr and Wardlaw 1965; Rawson and Hofstra 1969). Several other foliage leaves may concurrently contribute photosynthate to grain filling. Due to their greater distance from the ear, current photosynthate from these leaves may go preferentially to closer competing sinks rather than to the developing grains which are a major sink for photosynthate from the ear.

Considerable amounts of soluble carbohydrates, such as sucrose and fructans, accumulate in the peduncle and the internodes below it , shortly after anthesis, at a time when leaf area is maximal and the active phase of grain growth has not commenced (Lopatecki *et al.* 1962; Stoy 1965). The estimated amount of sugars stored in the peduncle and contributing to grain growth under non-stressed conditions is about 7% of final grain weight (Wardlaw and Porter 1967). Assimilates formed before anthesis contribute no more than 10-12% of the final grain weight under non stressful conditions (Wardlaw and Porter 1967; Rawson and Evans 1970; Austin *et al.* 1977).

Reserves accumulated immediately after anthesis are more readily remobilizable and are usually involved in yield formation to a larger extent than pre-anthesis reserves, which are considered to compensate for insufficient current photosynthesis only in the case of severe environmental stress, and to be relevant for yield stability (Herzog 1986). Normally relocation is confined to short periods during the linear growth or maturation phase in response to deficits between the actual source capacity and the (sink) demand of grains. To some degree, relocation from leaves depends on senescence, on the genotypic source/sink relation at anthesis, and on the effects of environmental conditions during the reproductive period (Herzog 1986).

Under conditions of stress, post-anthesis stored reserves contribute significantly to grain yield (Pheloung and Siddique 1990). The mobilization of stem reserves occurs late in the grain filling period and the cost of assimilate transfer to the grains appears to be covered by products from current photosynthesis (Stoy 1979; Bell and Incoll 1990) . In well-

watered plants photosynthates from the penultimate leaf and those beneath are utilized largely in the basal parts of the plant, while most of the carbon fixed in the flag leaf is supplied to the ear (Evans *et al.* 1975). Varietal differences exist in the extent of the contribution to grain growth of ear photosynthesis (Carr and Wardlaw 1965; Birecka *et al.* 1968). The presence of awns can double the rate of net photosynthesis by ears (Evans and Rawson 1978; Teare *et al.* 1972).

Jenner and Rathjen (1972) who measured the concentration of sucrose in the flag leaf blade of wheat grown in the field, found that the concentration increased greatly during the morning and middle of the day, and then decreased through the latter part of the afternoon and the following dark period. The findings of Jenner and Rathjen (1972) are in accordance with more recent detailed investigations on leaf blades of a number of *Poa* spp. and barley during vegetative growth (Schnyder 1993). Results are consistent in showing that the diurnal storage of carbohydrates occurs mainly in the form of sucrose.

The fructan content of mature leaf blades is usually low except when photosynthate export is inhibited, e.g., at low temperature, and does not exhibit a clear diurnal variation. Throughout grain filling a relatively low amount of carbohydrate is found in leaf blades of wheat; thus leaf blades do not usually contain other (long term) carbohydrate storage pools (Schnyder 1993).

Fructans constitute most of the mass of water soluble carbohydrate stored in the stem. There are a number of remarkable differences in fructan metabolism between the stem and the leaves and other organs of the wheat and barley plant, such as the timing of fructan synthesis and breakdown , the mass of fructan accumulated and the turn-over time of the pool. Under adequate moisture conditions the storage of this carbohydrate in the stem is at its maximum during the lag phase period of grain filling (Blacklow *et al.* 1984; Borrell *et al.* 1989; Pheloung and Siddique 1991).

Although fructan concentration in growth zones of leaves and in the ear and grain can be very high, the actual mass of fructan accumulating in these regions is small, and most of the fructan is rapidly lost when expansion growth ceases. The large concentration of fructans observed in the internodes of wheat and barley suggests that most, if not all, is

stored in the vacuoles of the parenchyma cells rather than in other tissues which comprise only a small fraction of the total volume of the internodes (Schnyder 1993). There is good evidence to suggest that temporary storage is very important under stress conditions (Bidinger *et al.* 1977; Austin *et al.* 1980). Respiration in the stem and in the developing grain is an important factor to take into account when considering the fate of carbohydrate reserves. According to Rawson and Evans (1971) respiratory losses could account for about one third of the loss of carbohydrate from the stem of wheat during grain filling. However estimates of respiratory losses based on ^{14}C-labelling of stem reserves range from 39% (Wardlaw and Porter 1967) to almost zero (Bell and Incoll 1990) depending on environmental conditions.

There is a lack of information about reserve carbohydrate metabolism of the glumes. Glume weight changes little during the grain-filling period (Bonnet and Incoll 1992) indicating that longer term storage of carbohydrates is not important. In recent experiments the total concentration of non-structural carbohydrates was usually less than 10% of the dry weight of glumes, with most being in the form of sucrose (Schnyder 1993).

Reports of the composition of, and the changes in, grain carbohydrates during the development of wheat and barley show that both species have much in common (Jennings and Morton 1963 ; Ueyama 1964; MacGregor *et al.* 1971; Baxter and Duffus 1973; Cerning and Guilbot 1973; Donovan *et al.* 1977). These studies indicate the fructans which were most abundant were non-sucrose ethanol-soluble carbohydrates. Glucosan, galactan, glucodifructose, raffinose and maltose have been reported to occur in smaller quantities, and although substantial amounts of glucose and fructose may be present at the beginning of grain growth they fall to very low levels in the later stages of the grain's development. Both sucrose and total ethanol-soluble carbohydrates (expressed as concentrations or per grain) increase to a maximum at about 8-15 days after anthesis, then maintain a relatively constant level or gradually decline.

The synthesis of fructans appears to occur only after a critical concentration of sucrose is reached in the tissue (Smouter and Simpson 1991) and involves the transfer of fructose from one sucrose molecule to another under the action of the enzyme sucrose-

sucrose-fructosyl transferase with the formation of a trisaccharide (glucose-fructose-fructose) and glucose. Further polymer formation may involve the enzyme fructan-fructan-fructosyl transferase. The residual glucose is also available as a substrate for fructan synthesis (Winzeler *et al.* 1990).

2.6.2 Sources of N assimilates

There are two main sources of N for grain growth : uptake from soil, and remobilization from vegetative organs. N uptake after anthesis depends on growth conditions (water and temperature), the nutrient status of the soil and the genotype (Austin and Jones 1975). More than 50% of grain protein may come from N taken up during grain filling in a well fertilized crop grown under ample water. However, in semi-arid and Mediterranean environments the fertility of the soil and soil water are usually low and soil N is greatly depleted by the time of anthesis . In such conditions very little uptake occurs during grain filling and nearly all N in the grain is derived through remobilization from leaves as indicated in Figure 2.2 and stems (Dalling *et al.* 1976; Blacklow and Incoll, 1981). Although assimilates formed before anthesis contribute no more than 10-12% of the final grain weight under non stress conditions (Wardlaw and Porter 1967; Rawson and Evans, 1970; Austin *et al.* 1977), according to Dalling *et al.* (1976) and Spiertz (1977) about 50-80% of N present in vegetative organs before anthesis accounts for 70 to 100% of the total N content of the grain due to remobilization. Differences in the efficiency of N redistribution to the grain have been shown in wheat (Johnson *et al.*. 1967; Halloran, 1981). Pate (1980) reported that most of the mineral N (NO_3^-, NH_4^+) absorbed by the root is assimilated into amino acids in the leaves and, to a lesser extent, in the roots themselves. The N composition of the phloem sap differs markedly from the xylem sap. The major amino acid of xylem sap is glutamine whereas glutamate and aspartate are the main amino acids in phloem sap (Simpson 1986).

More than 50% of the N absorbed by roots is transported to the ear in the xylem stream. Before entering the grain much of this N is first transferred from xylem to phloem in the glumes. Thus the glumes play an important role in the transfer of N within the ear

(Simpson *et al.* 1983) and may also be an active site for the inter-conversion and synthesis of amino acids suitable for protein formation (Donovan and Lee 1978).

An investigation into the contribution of plant parts to grain protein was carried out by Neales *et al.* (1963). They were able to show that the increase in grain N after heading exceeded losses from the leaves and stems throughout the grain development period. The remaining grain N content therefore was being supplied by soil N absorbed by the roots after anthesis and to a lesser extent remobilization of N from the roots.

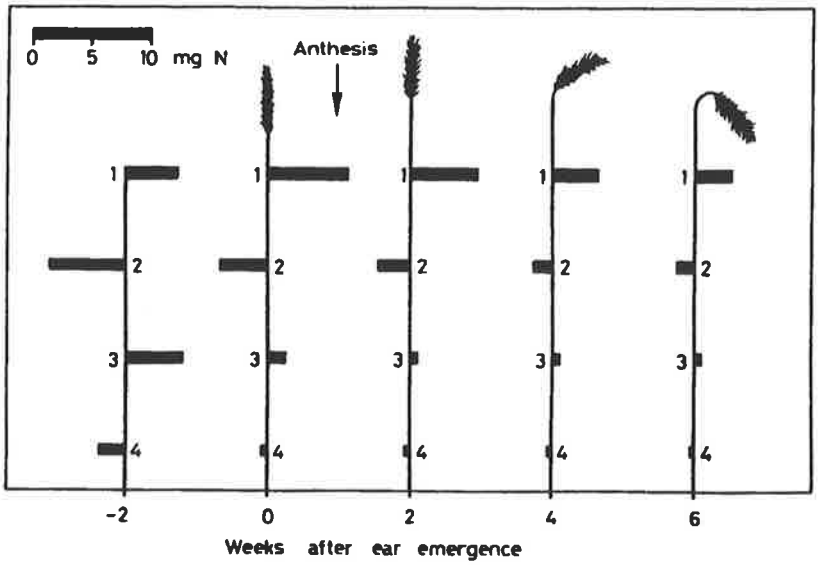

Fig. 2.2. N remobilization from individual leaves of field grown winter wheat. The leaves are numbered from the top downwards and their N contents are represented by the horizontal bars (from Feller 1991)

The significance of these results however depends on the environment (soil water and N level status) in which the plants are grown. Neales *et al.* (1963) suggested that the role of green leaves in the supply of N to the wheat plant is twofold. Firstly the leaves provide carbohydrate to the roots as a source of energy for the uptake of N, and secondly they act as a direct N source to the grains during the senescence of the leaf. The first role is enhanced if

the level of soil N in the root environment during grain growth is high. However, if the N requirement of the grains exceeds the N uptake of the plant, then the N reserves in the vegetative tissue are utilised as the source. Since most of the N in the green leaves is contained in the proteins of the photosynthetic system, particularly ribulose 1,6 diphosphate carboxylase, detrimental effects on the ability of the remaining vegetative tissue to photosynthesize will shorten grain filling and reduce yield.

Spiertz and Ellen (1978) reported that 48% of the grain N yield was taken up and assimilated during the grain filling period in conditions where the soil N was not limited after flowering. In their experiment a high supply of organic N meant that the N uptake was maintained. This allowed the continued function of leaves to provide carbohydrates for the assimilation of N by the roots, thus high yields of high protein wheat were obtained. A study by Dalling *et al.* (1976) reported that an average of 79% of the N harvested in the grain was already present at anthesis for the two varieties studied.

Chloroplasts represent the major proteinaceous compartment in photosynthetic tissues, containing as much as 50% of the total protein (Dalling 1986). Because most of the protein catabolized during leaf senescence is derived from the chloroplasts, much attention has been given to understanding how proteins are degraded. Originally vacuoles were thought to degrade chloroplast proteins, mainly because so little of the proteolytic activity measured (in vitro) originated from chloroplasts (Dalling 1986).

2.7 Genotypic and species differences in contribution of reserves to the grain

A number of investigations have been concerned with genotypic differences in the potential contributions of reserves to grain filling in wheat and barley and its relationship to yield. In a comparison of wild progenitors and cultivated wheats the loss in dry weight of the stems between the attainment of maximum mass and maturity was larger in the modern wheats than in the wild progenitors (Evans and Dunstone 1970). However, investigations of genotypic differences within a species indicate that there is no simple relationship between

Table 2.1 Grain yields of spring barley genotypes, according to height, and the calculated contributions to grain yields from assimilation up to five days after anthesis

				Contribution to grain yield from assimilation during the period 18 days before anthesis to five days after anthesis	
Year		Height to base of ear (cm)	Grain yield (g/m^2)	Contributed amount (g/m^2)	Percent
1976	tall	45	318	173	54
	single dwarf	36	286	180	61
	double dwarf	30	291	178	61
1977	tall	90	715	107	15
	single dwarf	68	654	89	14
	double dwarf	49	659	91	14

From Austin (1980).

grain yield and the amount of reserves remobilized during grain filling (Evans and Dunstone 1970).

The contributions to grain yield of pre-anthesis reserves in the hot, dry year of 1976 and cool, wet year of 1977 of tall, single dwarf and double dwarf cultivars in the United Kingdom are shown in Table 2.1. Grain yields were much lower in 1976 than in 1977. The contribution to grain yield from assimilation derived from pre-anthesis assimilates was less in tall cultivars than in single dwarf or double dwarf cultivars in 1977 while it was similar in 1976 for all of them (Austin *et al.* 1980).

For some genotypes of wheat (Halloran and Lee 1979) there is no close relationship between the proportion of total plant N in the grain at harvest and the total amount of N accumulated in plants. It has been reported that high protein genotypes of wheat generally

translocate more N to the grain from the vegetative plant parts than do normal cultivars (Lal *et al.* 1978). Some high protein genotypes of wheat also require continued assimilation of N by leaves during grain development (Mikesell and Paulsen 1971). McNeal *et al.* (1972) found genotypic differences in N translocation, but there were no differences for high compared to low grain protein concentration groups.

In a study of two high and two low protein wheat varieties Seth *et al.* (1960) reported that prior to heading, the vegetative N concentration was alike for both high and low protein lines. After heading the high protein lines increased in grain N percentage more rapidly than low protein lines. Seth *et al.* (1960) also found that by the milk stage and at maturity the level of root protein was lower in the high protein lines than in the low protein lines. Foliar applications of nitrate N and urea were also tested after heading. The protein content of the grains in the high protein lines was found to have increased to a greater extent than that in the low protein lines. According to these results the difference in grain N content is possibly due to more efficient translocation of N from the vegetative parts to the grain, and/or a more efficient mechanism of protein deposition within the grain.

Halloran and Lee (1979) reported differences between cultivars in N harvest index and total grain N as a percentage of total head N. They also noticed that highly significant differences existed between cultivars in the percentage of dry weight and N in the glumes and culms at maturity. This would seem to suggest there is genotypic variation for translocating N from the glumes and culms presumably to the grain. However, Mikesell and Paulsen (1971) found quite different results. In their investigation of the movement of N from the culms to the heads of selected high and low protein wheat lines they found that the efficiency of translocation of ^{14}C-labelled amino acids from the culm to the grain did not differ between lines tested. However this may be due to variation in the rate or extent of the breakdown of protein in glumes and culms rather than to differences in translocation of the resulting amino acids. This possibility does not seem to have been investigated.

Given the problems of determining the magnitude of the contribution of pre-anthesis reserves to grain yield, it is difficult to say whether they play a greater or smaller role in modern, high-yielding varieties than in older wheats. Even comparisons between crops are

uncertain. Thus there is no clear answer to the question at issue whether or not the rise in HI of modern varieties derives to some extent from either (1) more complete use of reserves during grain growth or (2) reduced partitioning to reserves in the early stages of the life cycle.

2.8 Remobilization of assimilates

Temporary storage in the stem occurs almost exclusively in the form of water-soluble carbohydrates (Austin *et al.* 1977). Usually the weight of extended internodes increases until about 2-3 weeks after anthesis and this weight increase is due mostly to the accumulation of water soluble carbohydrate (Bonnett and Incoll 1992). Internodes can lose up to 50% of their dry weight (Blacklow and Incoll 1981), and water soluble carbohydrate accounts for 90-100% of this weight loss in internodes of barley and wheat (Austin *et al.* 1977).

Fructans can be stored at different sites within the plant, and very different patterns of synthesis and degradation occur under the influence of a range of external and internal factors. The principal distinction that can be made is between storage in primary heterotrophic organs, such as leaf sheaths, shoots, roots, stems, and grains, and in autotrophic organs such as leaves (Pollock 1986; Pollock and Chatterton 1988). Storage in leaves is intimately connected with the synthesis and export of sucrose, and consequently with chloroplast carbon metabolism; in heterotrophic sinks on the other hand, synthesis is from imported carbon and thus is less affected by short-term environmental fluctuations (Pollock and Chatterton 1988). It is tacitly assumed that, within the leaf, fructans accumulate predominantly in mesophyll cells. Non-uniformity of distribution of fructans along the length of the leaf has been observed (Wagner and Wiemken 1989). Such non-uniform patterns of distribution have generally been ignored when carbohydrate determinations have been made (Pollock *et al.* 1989).

Accumulation of fructan in cereal and grass stems during flower development is the most readily detected physiological correlate of fructan metabolism. Final fructan concentration can be as high as 30% of the dry weight (Smith 1973), with a gradient of

accumulation from the apex increasing towards the base of the stem (Pollock and Jones 1979; Smith 1973). Accumulation continues during stem growth, flowering, and anthesis; fructan contents then fall during the later stages of grain filling (Blacklow *et al.* 1984; Borrell *et al.* 1989). Disappearance of fructan is almost complete in cereal stems (Blacklow *et al.* 1984) . It is probable that some, at least, can be used to sustain grain growth during periods where flag leaf photosynthesis is limited (Blacklow *et al.* 1984; Borrell *et al.* 1989; Hendrix *et al.* 1986).

It appears that the amount of DM remobilized depends on cultivar and prevailing growth conditions, and genetic variability in DM translocation has been reported (Austin *et al.* 1977). The few studies of the regulation of fructan metabolism in such tissues have been concerned principally with fructan breakdown (Smith 1976). The remobilization of water soluble carbohydrate from the stem generally starts during the period of near constant rate of DM accumulation in grains and coincides with a marked decrease in the net assimilation rate (Blacklow *et al.* 1984). However, the redistribution of DM and water soluble carbohydrate from stems can also be induced at an earlier stage. For instance, water stress resulted in a rapid remobilization of water soluble carbohydrate in wheat after anthesis (Pheloung and Siddique 1991). Bonnett and Incoll (1992) demonstrated that the loss of dry weight from the individual internodes of the barley stem started at the same time in all the internodes although the duration of reserve storage differed greatly between internodes. The onset of reserve mobilization in individual internodes and the maintenance of high rates of DM accumulation in grains at a time of rapidly decreasing net assimilation rate all suggest that fructan remobilization is induced in response to a deficiency in current photosynthate supply to grains.

2.9 Remobilization of N and proteolytic activities

Wheat varieties with high seed protein percentage either absorb more N from the soil or translocate a greater proportion of vegetative N to the grain than is the case with low protein varieties (Seth *et al.* 1960). Peterson *et al.* (1975) observed that two oat (*Avena sativa* L.) genotypes with high groat protein concentration remobilized a greater amount of

vegetative N to the developing panicle than did four lines with lower groat protein. Seth *et al.* (1960) suggested the presence of genetic variation for N Remobilization Efficiency (NRE) which is defined as:

$$\frac{\text{(Maximum vegetative N - final vegetative N)}}{\text{(Maximum vegetative N)}} \times 100\%$$

In wheat, the mean NRE of five varieties ranged from 49.5% for the spike chaff to 82.7% for the leaves (Lal *et al.* 1978). Varietal differences in the NRE of the culm, flag leaf, lower leaves and spike chaff were also found among the five varieties.

Although the presence of genetic variability for N remobilization has been established in a number of crops, its exploitation for plant improvement has yet to be reported. The nature of genetic control of N remobilization is not known. In part this may be due to difficulties in the measurement of N remobilization, which requires N determinations at a number of times during the plant growth cycle to estimate maximum and final vegetative N.

Proteases are enzymes responsible for the degradation of polypeptides to amino acids and high protease activity may be associated with plant genotypes with a high potential for N remobilization from the vegetative tissue to the grain. The relationship between protease activity and N remobilization is indicated by the reported higher post-anthesis protease levels in the leaf blades of high grain protein wheat as compared to lower grain protein wheat (Rao and Croy 1972). Estimates of N remobilization from the measurement of protease activity assume that enzyme activity is the rate limiting step of N movement from the vegetative tissue. A high correlation between observed N loss from the vegetative tissue and the rate of protease activity has been reported in two wheat varieties (Dalling *et al.* 1976).

Two major classes of enzymes which have been implicated in general protein breakdown are endopeptidases and exopeptidases. Exopeptidases include aminopeptidases, carboxypeptidases and dipeptidases (Waters *et al.* 1980). In general aminopeptidase and carboxypeptidase activities decrease in senescing leaves of cereals and neutral endopeptidase activity increases or remains unchanged (Feller *et al.* 1977). These results suggest that the

loss of activity of aminopeptidase and the increase in endopeptidase activity in the neutral pH range are related to N remobilization from senescing plant parts (Fig. 2.3.).

Increased productivity of protein per unit area requires enhanced translocation of vegetative N to the seed, thereby leaving less N in the unharvested crop residue. Although the genetic control of N remobilization is poorly defined, available evidence suggests that genetic improvement is possible. Protease activity measurement in the vegetative tissue or estimates of amino N or total N movement to the developing grain could be useful to identify genotypes having enhanced remobilization potential.

2.10 Transport of assimilates into and within the grain

All sucrose entering the endosperm is transported in the phloem of the vascular bundle running within the crease from the base to the tip of the grain . From an anatomical point of view it is not possible to tell whether or not there is lumen continuity between the phloem of the plant and the phloem of the grain. However, from physiological studies Jenner (1985a, 1985b, 1985c) has proposed that the flow of sucrose into the grain is not accompanied by mass flow of water, thereby suggesting that the two phloem systems are not continuous. In wheat grains sucrose travels down a concentration gradient from the phloem to its destination within the cells of the endosperm (Jenner 1974a).

Nitrogenous compounds of the xylem sap must first be transferred to the phloem before they enter the grain. Specialized transfer cells in the vascular tissue at the base of each grain may be involved in this transfer process (Zee and O'Brien 1971). Assimilate moves from the endosperm cavity across the aleurone layer into the endosperm, taking an apoplastic route as well as a symplastic route (Niemietz and Jenner 1993). Assimilate is taken up from the apoplastic space of the endosperm by the endosperm cells where the sucrose is converted to starch and amino acids to protein during the active phase of storage in the grain.

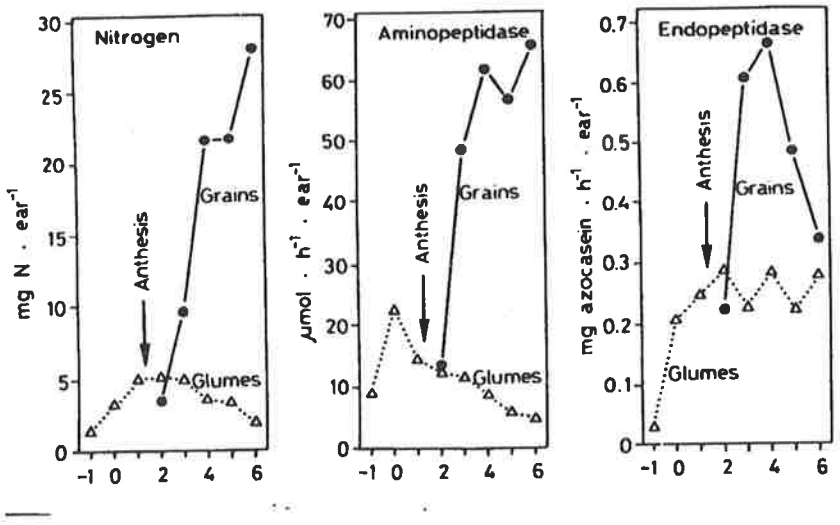

Figure 2.3. Nitrogen and peptide hydrolase activities in wheat ears (from Feller 1991)

2.11 Plant growth and water deficit

2.11.1 Definition of water deficit

Biological stress was defined by Levitt (1972) as "any environmental factor capable of inducing a potentially injurious strain in living organisms". Since stress due to a deficiency of water is more common than that due to excess of water , water deficit stress is commonly referred to as water stress. The definition is recognized in terms of the plant's reaction to its own water status. Water status can be measured in both the soil and the plant. In the study of plant reaction to water stress, measurement of plant water status is more valuable (Slatyer 1967).

Water potential as a measure of water status in plants has become widely accepted (Boyer 1969; Hsiao 1973; Turner and Jones 1980). It is best understood as the capacity of the water to do work, i.e. to move from a higher to a lower potential energy (Taylor and Slatyer 1961; Kramer 1969). The total water potential (Ψ) under equilibrium conditions at a particular point in the plant can be partitioned into its components: Ψs the osmotic (solute)-

potential component, Ψp is the pressure (turgor)-potential component, Ψm is the matric component and Ψg is the component due to gravity (Kirkham 1990). As the gravitational component of the total water potential is low it can be neglected, except in very tall trees (Turner and Jones 1980).

2.11.2 Water deficit and root hydraulic and chemical signals

2.11.2.1 Hydraulic signals

In the past 50 years progress in our understanding of plant water relations has shifted the emphasis away from the soil to the plant (Kramer, 1988). Most recent evidence suggests that in doing so some important mechanisms that allow the plant to regulate development as a function of soil water status may have been overlooked. Current thinking in this area is summarized in Fig. 2.4.

It has been generally accepted that as soil dries, water uptake is reduced and leaf water status declines. Leaf water potential is the most commonly used indicator of shoot water status. However variation in shoot physiology can often be linked more closely to changes in soil water status than to changes in leaf water status (Turner *et al.*. 1986). Therefore plants must "sense" the drying of the soil around the root and communicate this information to the shoot by some means other than a reduction in the flux of water to the shoots. Although it may seem likely that leaf growth rate and stomatal functioning are finely attuned to the water relationship of the plant (Boyer, 1989), the literature contains many data suggesting that leaf water status was not always play a central role in the regulation of drought responses.

There is no doubt that water loss from leaves precedes water movement from the roots and uptake from the soil, but the soil moisture profile affects from where the moisture needs to be exploited to maintain the plants transpirational demands (Passioura 1988). When the surface soil dries very substantially roots in this soil layer may dehydrate, but the leaves can be well supplied with water from other roots growing in wet soil and may therefore show no dehydration relative to leaves of well watered plants. Dehydration of the shallow roots could influence metabolism in the root tips greatly and thereby provide some chemical

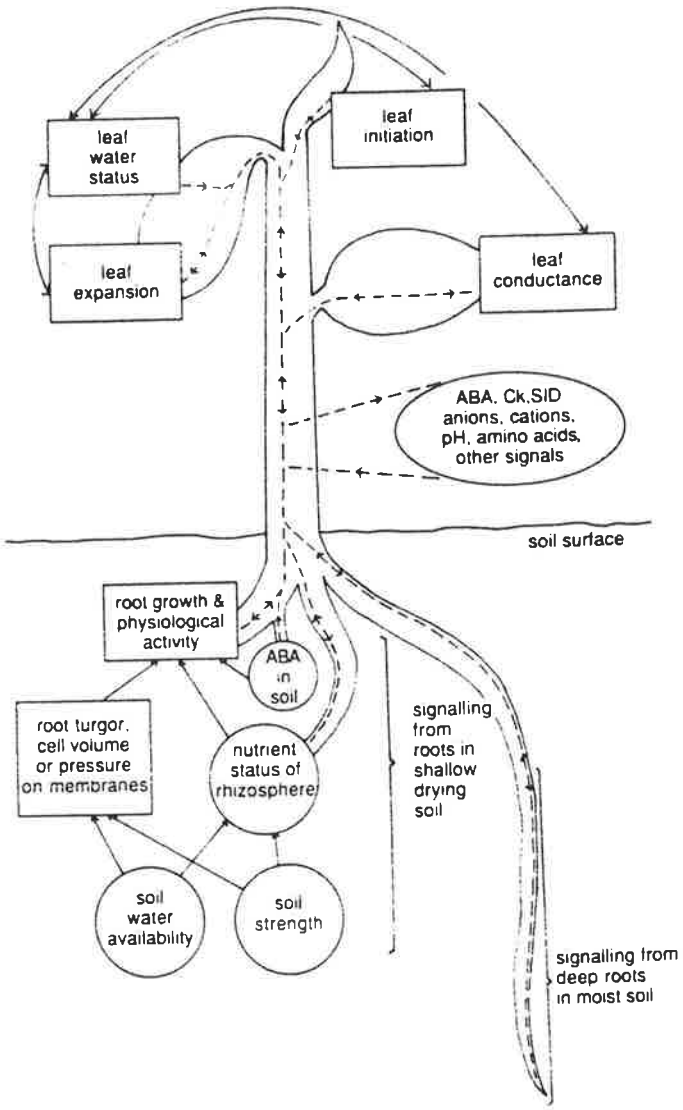

Fig. 2.4. Diagramatic representation of factors influencing the generation of chemical information (dotted lines) in roots in a drying soil, the transfer of this information to leaves, and its effects on shoot processes. Soil effects are shown as circles and plant physiological and developmental processes are shown as rectangles (from Davies and Zhang 1991).

indication of soil drying under circumstances where the supply of water to the shoots would not be a sensitive indicator of changes in the soil. Although there are other possibilities which may be involved in the coordination of whole plant responses to other stresses such as wounding, pathogens, or cold (Davies 1987; Jones 1990; Pickard 1973) current evidence suggests that these signals are chemical in nature.

2.11.2.2 Chemical signals

Abscisic acid

The relationship between root water status and root ABA content described by Zhang and Davies (1987) suggests that accumulation of ABA by the root may be a sensitive measurement of water status. Strong evidence that ABA is synthesised in increased quantities in roots in drying soil is provided by several studies. For example (i) In split-root experiments, the half of the root system in drying soil contains substantially increased concentrations of ABA compared to the other half of the root system in wet soil (Zhang and Davies 1987). (ii) A small proportion of the root system separated from the main soil mass and allowed to dehydrate partially in air contains higher concentrations of ABA within a few hours (Neales *et al.* 1989). (iii) Comprehensive analysis of the ABA content of roots in different parts of the soil profile shows significant differences in concentration through the profile. These differences reflect the water status of the soil surrounding the individual roots (Zhang and Davies 1989).

If roots are loaded with ABA, increased concentrations of this compound can be detected in the leaves of transpiring plants soon after the light has been switched on. Covering leaves with tin foil prevents transpiration, and enhanced ABA concentrations are not detected, suggesting that this compound moves from roots to shoots primarily through the xylem stream (Zhang and Davies 1987). It is well known that ABA fed into the xylem can substantially affect leaf gas exchange (Kriedemann *et al.* 1972) and this suggests that xylem ABA may have a role in controlling stomatal behaviour of plant.

Cytokinin

Itai and Vaadia (1965) showed that drought stress reduced the production and transport of cytokinin from sunflower roots. It seems possible that in drying soil a reduction in cytokinin supply, perhaps acting in concert with other signals, could reduce stomatal conductance. High concentrations of cytokinin can override the effects of ABA on stomata (Blackman and Davies 1983; Radin 1984). One could therefore argue that as the soil dries, a reduction in cytokinin supply would amplify shoot responses to increasing concentrations of ABA. In this respect there may also be a role for inorganic ions, as the sensivity of stomata of sunflower to ABA in the xylem sap can vary enormously, largely as a function of a reduced supply of nitrate and calcium through the xylem of plants in drying soil. The influence of the ionic status of the soil on stomatal sensivity to ABA has also emphasized by Radin(1984). It thus seems possible that positive and negative signals may combine and interact in their effects on shoot processes, perhaps with positive signals dominating in plants in moist soil and negative signals increasing in importance as the soil dries .

2.11.3 Water deficit and grain growth

Grain set may be reduced if plants experience water stress during ear-emergence and flowering (Wardlaw 1971). If grain set is not reduced, water deficit during the early stages of grain development usually results in a reduction of grain dry weight at maturity (Asana and Saini 1958; Wardlaw 1971; Brocklehurst *et al.* 1978; Brooks *et al.* 1982). The reduction in grain dry weight at maturity is related to a reduction in endosperm cell numbers (Brocklehurst *et al.* 1978) or to a reduction in the number and size of starch granules (Brooks *et al.* 1982). During early (up to 26 days after anthesis) development the DM of wheat grains was unaffected by water stress. From 36 days after anthesis, however, grain from non-stress plants was significantly heavier than that from stressed plants. After 29 days the DM of stressed grains remained constant, whereas control grains continued to accumulate DM up to 44 days after anthesis (Brooks *et al* . 1982) .

2.11.4 Water deficit and carbon supply

Net photosynthesis of leaves is reduced by water deficit. This can result from a decrease in leaf area and/or a decrease in rate of net photosynthesis per unit area. The reduction in leaf area is due to either a slower rate of leaf expansion (Boyer 1970; Turner and Begg 1978) or an increased rate of leaf senescence (Fischer and Kohn 1966; Ludlow 1975) in droughted plants. Leaf expansion is more sensitive to water deficit than leaf senescence (Ludlow 1975). However, cereal leaves are fully expanded at anthesis and the reduction of leaf area by post-anthesis drought is entirely due to accelerated leaf senescence. Fischer and Kohn (1966) showed that the yield of wheat under dry land conditions was positively related to the leaf area duration after anthesis.

Photosynthesis of the ear seems to be less affected by water stress than that of the leaves. Wardlaw (1971) found that the rate of ear photosynthesis in wheat plants was not reduced by stress until after leaf photosynthesis declined, and subsequently showed that a temporary water deficit during the first seven days after anthesis reduced photosynthesis of the flag leaf and stem more than that of the ear structures. Under conditions of water stress, the relative contribution of the ear to grain filling was therefore increased. Evidently in the absence of leaves, ear photosynthesis and mobilization of pre-anthesis assimilates were adequate to maintain a supply of assimilate to the grain equal to that in unstressed plants which still had green leaves.

When drought was allowed to develop from the beginning of the grain filling period, post-anthesis water soluble carbohydrate accumulation in stems was suppressed, whereas water soluble carbohydrates were accumulating in the stems of irrigated plants (Pheloung and Siddique 1991). Again, the initial rate of DM accumulation in grains differed little between droughted and irrigated plants . Imposition of water stress on wheat (Virgona and Barlow 1991) at the time of maximum stem water soluble carbohydrate content failed to accelerate the loss of water soluble carbohydrate from the stems.

The contribution to grain growth of assimilates from glumes and awns increases relative to that of leaf assimilates in droughted wheat plants (Evans *et al.* 1972). The better

osmotic adjustment of glumes than of leaves may be one reason for maintained photosynthesis in wheat spikes (Morgan 1980). Rapid and severe water deficit may affect the non stomatal component particularly if high light intensity coincides with severe water deficit, resulting in photoinhibition (Powles and Osmond 1978). However, when water deficit develops slowly, both stomatal and non stomatal components decline together so that the intercellular $C0_2$ concentration remains constant (Osmond *et al.* 1980).

Previous studies have shown that contributions of stem water soluble carbohydrates (WSC) to grain yield are greater when plants are under drought stress than when under irrigation (Bidinger *et al.* 1977; Wardlaw 1967), while others have reported that water deficits do not enhance the translocation of stem sugars to the grain (Davidson and Chevalier 1992). Plants in irrigated treatments had more stem WSC, on a per plant basis than plants in non-irrigated treatments both at the time of peak WSC content and at physiological maturity. In both cases WSC from the stems was depleted, either by remobilization or respiration . The absolute amounts of WSC that were stored and lost from the stems were greater in the irrigated than non-irrigated plants (Davidson and Chevalier 1992). The stem may then have served as an important carbohydrate storage site for both the irrigated and non-irrigated wheat plants.

2.11.5 Water deficit and leaf senescence

A common plant response to water stress is leaf senescence (Radin 1981). Protein and chlorophyll loss also accompany senescence of leaves on well-watered plants, which is called natural senescence (Thimann 1980). In the leaves of Gramineae it starts at the tip, progresses towards the base and finally reaches the leaf sheath (Feller and Keist 1986).

N deficiencies cause protein deficiencies in leaves, which reduce photosynthesis, leaf area expansion and DM accumulation and accelerate senescence. It has been shown that N application increases the N content of leaves and delays senescence which, in the absence of water deficit and high temperatures, extends the grain filling period (Spiertz and Ellen 1978). After anthesis, N compounds are relocated from vegetative parts to the filling grains (Gregory *et al.* 1981).

Although water deficit and senescence result in similar visual symptoms of loss of chlorophyll, catabolic aspects of water stress-induced senescence and natural senescence may differ. Naturally-senescing leaves display a falling chlorophyll a/b ratio (Sestak 1977) but the ratio rises in maize leaves under water deficit (Alberte *et al.* 1977).

Metabolism of protein appears similar in water stressed and naturally senescing leaves. Large proteins and long-lived proteins (Dungey and Davies 1982) are more sensitive to stress than others which suggests that RubPcase is one of the first proteins lost in response to water stress as it is in senescence. Protein synthesis is dramatically reduced in both senescing and water stressed leaves (Dungey and Davies 1982). Protein hydrolysis is accelerated in water stressed leaves (Dungey and Davies 1982) and probably also in naturally senescing leaves.

2.12 Water deficit and remobilization of assimilate

The mobilization of stem reserves occurs during the grain filling period (Stoy 1979). In non-stressed plants, photosynthesis from the penultimate leaf and those below are utilized mainly in the basal parts of the plant (Evans *et al.* 1975). Varietal differences exist in the extent of the contribution of ear photosynthesis (Birecka *et al.* 1968) and of stem reserves (Asana and Mani 1950; Bidinger *et al.* 1977) to grain growth. It has long been known that the stems of species of cereal grains contain considerable amounts of soluble carbohydrates at anthesis, but that at maturity, these substances have disappeared. The contribution of pre-anthesis assimilate to grain yield depends on growing conditions. When stress is not a factor, this contribution is around 10% and consists of mobilized N compounds (Austin *et al.* 1980).

When stress occurs, particularly during grain filling, current photosynthate supply is reduced and grain growth depends more on mobilized assimilates, both carbohydrates and N compounds, from the stem and other vegetative organs. Under severe drought conditions, a contribution as high as 50% may be possible (Austin *et al.* 1980).

It is commonly supposed that environmental factors influence the amount of labile materials which accumulate in stems , and the extent to which they are lost, giving the plants

some ability to compensate for the effects of unfavourable weather during grain filling (Austin *et al.* 1977).

Recently chemical desiccation has been used to stimulate the effects of post-anthesis stress. Hossain *et al.* (1990) conducted an experiment to assess the feasibility of chemical desiccation to identify post-anthesis stress resistance among genotypes of hard red winter wheat and to determine the relationship between tolerance to chemical desiccation and carbohydrate and N partitioning in wheat. They reported that a greater proportion of the soluble carbohydrates than of the total DM in the stem, sheath, and blade was translocated to the kernel. Soluble carbohydrate translocation from the stem was significantly reduced by desiccation. Loss of DM and soluble carbohydrate from the stem and sheath under desiccation was generally associated with genotype tolerance to kernel weight injury.

2.13 Water deficit and remobilization of N

The growing wheat seedling absorbs N from the soil in the form of nitrate, most of which is transported to the leaves where it is finally reduced to glutamate in the chloroplast (Dalling 1985). In order for the plant to utilise the stored N held within various vegetative organs for grain filling these organs must first senesce. There are significant differences between individual organs with regard to translocation efficiency of their stored N. While leaves are able to remobilize nearly 80 percent, and stems up to 65 percent of their N present at anthesis, the roots may only remobilize 20-30 percent by the time of maturity (Dalling 1985).

Progressive development of the wheat plant regulates the turnover of stored protein within the tissue. As old plant parts senesce, protein is remobilised and utilised in the growth of younger material. This movement of N occurs continuously throughout the development of the plant. The amount of protein in a plant organ at any time is a reflection of the balance between its synthesis and degradation. All proteins within the wheat plant are in a state of continual turnover. This gives the plant a flexible mechanism whereby a cell or organ can quickly adjust to the changing environmental or seasonal circumstances around it (Dalling 1985).

Ultimately the bulk of the protein is deposited in the maturing ear, with the leaves and stems acting as temporary storage sites. The leaves and stems may in fact each contribute as much as 30 percent of the protein deposited in the grain while an additional 10 percent is obtained from the roots (Dalling *et al.* 1976). The glumes are capable of supplying a further 15 percent of the protein but more importantly seem to be involved in temporary deposition of N early in grain filling, and as a site for transfer of N from the xylem to the phloem (Jenner *et al.* 1991).

Water deficit reduces the concentration of N in maize leaves due to reduced nitrate flux to the leaves under drought stress (Shaner and Boyer 1976). When developing kernels are deprived of N, both carbohydrate and protein deposition in the kernels are reduced (Singletary and Below 1989).

N uptake is reduced under drought conditions (Rehatta *et al.* 1979; Van Keulen 1981). This reduction of uptake is the result of reduced growth and/or reduced N transport in the soil (Van Keulen 1981). Water deficit during grain filling accelerates leaf senescence, and relocation of N contributes to grain protein deposition at the time when wheat starch accumulation has slowed. Thus low yields from water deficits during grain filling are generally accompanied by high protein contents, which are mostly in the range of 12 to 16%.

The proportion of N translocated from the shoot to the roots is influenced by the physiological status of the plant. Plant leaves begin to senesce soon after they have fully expanded. N exported from senescing lower leaves will partly be imported by the roots (Fig. 2.5) from where it may be remobilised to the shoot. Low soil N increases the proportion of N cycled through the shoot to the roots, very likely reflecting increased senescence of lower leaves (Nicolas *et al.* 1985). Results of this experiment showed that the uptake of N was markedly reduced under drought conditions. Possibly soil N was less available to the droughted plants because a smaller surface of the soil was available for diffusion and the soil solution eventually became discontinuous when soil moisture content decreased (Van Keulen 1981). However, two varieties, Warigal and Condor differed markedly in their capacity to take up N from the soil under drought. The uptake of N was

reduced under drought by 50 and 94 percent, whereas transpiration rate was reduced by 33 and 36 percent for Warigal and Condor, respectively. The difference in uptake of N between cultivars and treatments during early grain growth did not result in marked differences in grain N yield per ear at maturity because it was compensated by a greater remobilization of N from vegetative organs. However the remobilization of N from the culm (stem + leaves) was increased by less than 7 percent relative to control during the drought treatment and most of the redistribution of N occurred after rewatering.

2.14 Water deficit and yield components

In wheat and barley, ear initiation occurs during the tillering phase and the development of spikelets and florets takes place during the time that stem elongation and the death of tillers is occurring. The number of grains per ear is thus subject to environmental influences, including drought, during this time and is often the yield component which varies most in response to season-to-season variation in water supply.

Yield component analysis regards yield as the product of plants per unit area, heads per plant, spikelets per head, grains per spikelet, and weight per grain. The number of grains per head can be influenced by water deficit just before, and until a few days after, anthesis. Thereafter, only grain size is affected by water deficit. Grain yield can be considered to consist of two basic components: grain number per unit area and single grain weight. The grain number component establishes the yield potential that is realized if conditions after anthesis are favourable for grain filling. Conceptually, water deficit after anthesis could limit yield by reducing the photosynthetic rate and duration. As photosynthesis continues to decline during the later phase of grain filling, relocation of pre-anthesis DM could contribute to the grain filling process. Grain weight often exceeds post-anthesis DM increase, sometimes by as much as 50% under water deficits (Gallagher and Biscoe 1978).

The results of total aboveground biomass and grain yield of barley, durum and bread wheat across five Mediterranean environments in northern Syria showed that barley produces more than wheat where the average rainfall is less than 300 mm (Acevedo 1992).

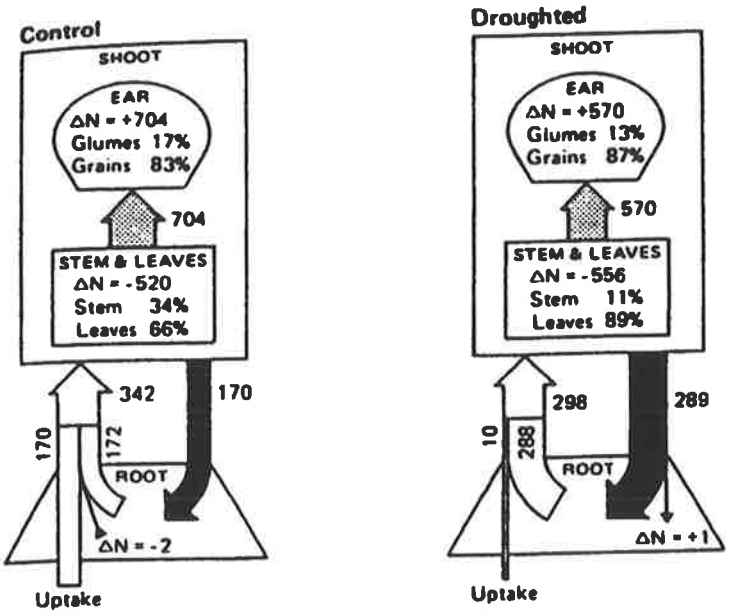

Fig. 2.5. Model of translocation and partitioning of N in *Triticum aestivum* (cv. Condor) on the seventh day after anthesis. The open arrow represents translocation of N in the xylem whilst the black arrow represents translocation of N in phloem and the shaded arrow represents the net flux of N to the ear. Values of ΔN represent increments or decrements of N in plant parts. Units are μg N $day^{-1}plant^{-1}$. The droughted plants did not receive water from one day after anthesis until nine days after anthesis (from Nicolas *et al.* 1985).

Table 2.2 Phenological development, yield and yield components for barley and wheat as means from five environments in northern Syria (adapted from Acevedo 1992)

Variable	Barley	Wheat
Phenological development (days)		
From emergence to heading	90	102
From emergence to maturity	126	144
Grain filling period	36	42
Yield (t/ha)		
Biological	4.92	4.69
Grain	1.91	1.65
Straw	3.01	3.04
Harvest Index	**0.39**	**0.35**
Yield component		
Spikes/m^2	285	204
Grain/spike	17.5	25.5
Grains/m^2	4996	5215
Mean grain mass (mg)	38.2	31.6

(From Acevedo 1992).

At 290 mm rainfall, both cereals had a biological yield of about 5.5 t /ha. The phenological trait which enabled barley to yield better than wheat in the stressful environment was earliness in flowering associated with shorter grain filling (Table 2.2). The increase grain yield of barley comes essentially from an increased mean grain mass, as the grain number per unit area is similar to, or slightly lower than, that of wheat.

2.15 Water deficit and N metabolism of the grain

The decreases in N content of different parts of the wheat plant can be directly attributed to the gain of N in the caryopses (Herzog 1986). Water deficit at the time of grain filling is often associated with premature cessation of starch deposition. Increased percentage of grain N is thus usually the result of reduction in carbohydrate content of the grain. There is no evidence that stress causes more protein to accumulate because stress has no significant or consistent effect on the absolute amount of protein in wheat or barley grains, but protein as a percentage of DM is often higher in stressed than in watered plants.

The storage capacity of the grains might be less affected for N than for carbon. Grain amino acid concentration was increased by stress in wheat, but in barley this occurred only 37 days after anthesis and was due solely to the lower water content of stressed grains at this time (Brooks1980). Grain protein synthesis, however, was apparently not influenced by these changes in amino acid concentration. The available evidence suggests that water deficit does not reduce the supply of sucrose to the grain as the concentration of sucrose within the endosperm is not reduced by drought (Brooks *et al.* 1982 ; Nicolas *et al.* 1985).

2.16 Concluding remarks

Concepts of DM and N remobilization in plants have been expanded in recent years by the development of techniques for the construction of whole-plant models of N remobilization. The combination of these models and ^{15}N studies of N movement has provided a more dynamic understanding of N transport and partitioning in plants and is providing a new base from which the factors that control N partitioning may be investigated. However, there are a number of areas in which our knowledge is limited and which would benefit from further research. Amongst these are the control of remobilization of DM and N from different parts of the shoot of wheat and barley plant particularly under conditions of water deficit . A better understanding of these areas would seem important if we wish to be able to manipulate the partitioning of reserves and increase the yield and quality of

economically important plants. This study is therefore undertaken to improve our understanding of the control of remobilization of DM and N in wheat and barley plants.

Chapter 3. Materials and methods

3.1 Choice of genotype

Two genotypes of wheat (*Triticum aestivum* L.) and three genotypes of barley (*Hordeum vulgare* L.) were used for the experiments in this investigation (Table 3.1). Wheat genotypes (Sun 92A and Vasco) were chosen because they had been used in the studies of Stoddard and Marshall (1990) and barley genotypes (Forrest, W.I. 2808 and W.I.2692) because they had been used in a study of genotype response to agronomic manipulation by South Australia Research Development Institute (SARDI) programs (Jeffries 1991).

Table 3.1. Wheat and barley genotypes used in this investigation

Species	Genotype	Protein percentage	Maturity	Height
Wheat	Sun 92A	high (18%)*	Early - Medium	Short- Medium
Wheat	Vasco	moderate (12.5%)*	Early Medium	Medium-Tall
Barley	Forrest	moderate (13.2%)**	Medium	Medium - Tall
Barley	W.I.2692	moderate (12.8%)**	Medium	Medium- Tall
Barley	W.I.2808	moderate-low (12.1%)**	Medium	Medium - Tall

* : Glass house conditions

**: Field conditions

3.2 Environment

Plants were grown in pots in a glasshouse (except for the last experiment which was conducted in a growth cabinet). The experiments were conducted under natural light and controlled temperature (25±2 °C during the day and 16±2°C at night) conditions. A layer (2 cm) of wood chips to assist drainage was placed in the bottom of a 20 cm deep pot, and the pot filled to within 2 cm of the rim with sterilized, recycled soil (approx. 3.5 kg dry weight). All pots were watered to maintained approximately field capacity until 10 days

after anthesis by weighing the pots two times per week and adding water to make up for the loss in weight. The pots were re-randomised weekly throughout each experiment. Tillers were removed as they emerged in all of the experiments. All the measurements were made therefore on plants with a single shoot.

3.3 Plant water status

A pressure bomb was used to estimate the pre-dawn water potential of the plant. The flag leaf to be measured was excised from the plant at the junction of the lamina and sheath with a sharp blade and was enclosed in a plastic bag and immediately inserted through a slit in a rubber stopper and placed in the pressure bomb which was sited close to the plants. The leaf blade extended about 2 cm through the rubber stopper. Pressure was then applied at a rate of less than 0.1 MPa s^{-1} (Hsiao 1990) from a compressed-air cylinder until the xylem sap was just visible on the cut surface of the leaf. The sap on the cut end was observed with a 10 x magnification hand lens. The pressure reading was recorded at predawn and expressed as the flag leaf water potential.

3.4 Establishment of water treatments

Ten seeds per pot were sown and seedlings thinned to 6 plants per pot after emergence and plants were restricted to a single culm by removing all tillers as they emerged. Plants were watered daily by hand to maintain a soil water content close to field capacity until day 10 after anthesis to minimise the possibility of pre-anthesis moisture stress and were supplied with 200 mL of soluble fertiliser containing 2.6 g Hortico 'Aquasol' (23% N) every second week until anthesis. All pots were watered under the same water regime (around field capacity) until the start of grain filling (10 days after anthesis). Water treatments were imposed from 10 days after anthesis by withholding water and monitoring the water potential of the flag leaf of the plants (in the first and second experiments) or based on soil water content in other experiments. In the first and second experiments the following treatments were established:

1) Not watered: Water was withheld completely .

2) Medium stress: Water was withheld at day 10 after anthesis and pots were rewatered when the water potential of the flag leaf fell to -2 MPa (-2.5 MPa for barley). This cycle was repeated until maturity.

3) Mild stress: Water was withheld from day 10 after anthesis but pots were rewatered when the water potential of the flag leaf fell to -1 MPa (-1.5.MPa for barley), and this cycle was repeated until maturity.

4) Divided root: Plants were grown in pots with a barrier consisting of 2-3 cm gravel (see Fig. 3.1) which divided the root system horizontally; the lower section was watered but the upper part was not watered from day 10 after anthesis. This treatment was used to stimulate the top soil drying which occurs commonly in Mediterrian environments.

5) Control : Pots were watered throughout the experiment.

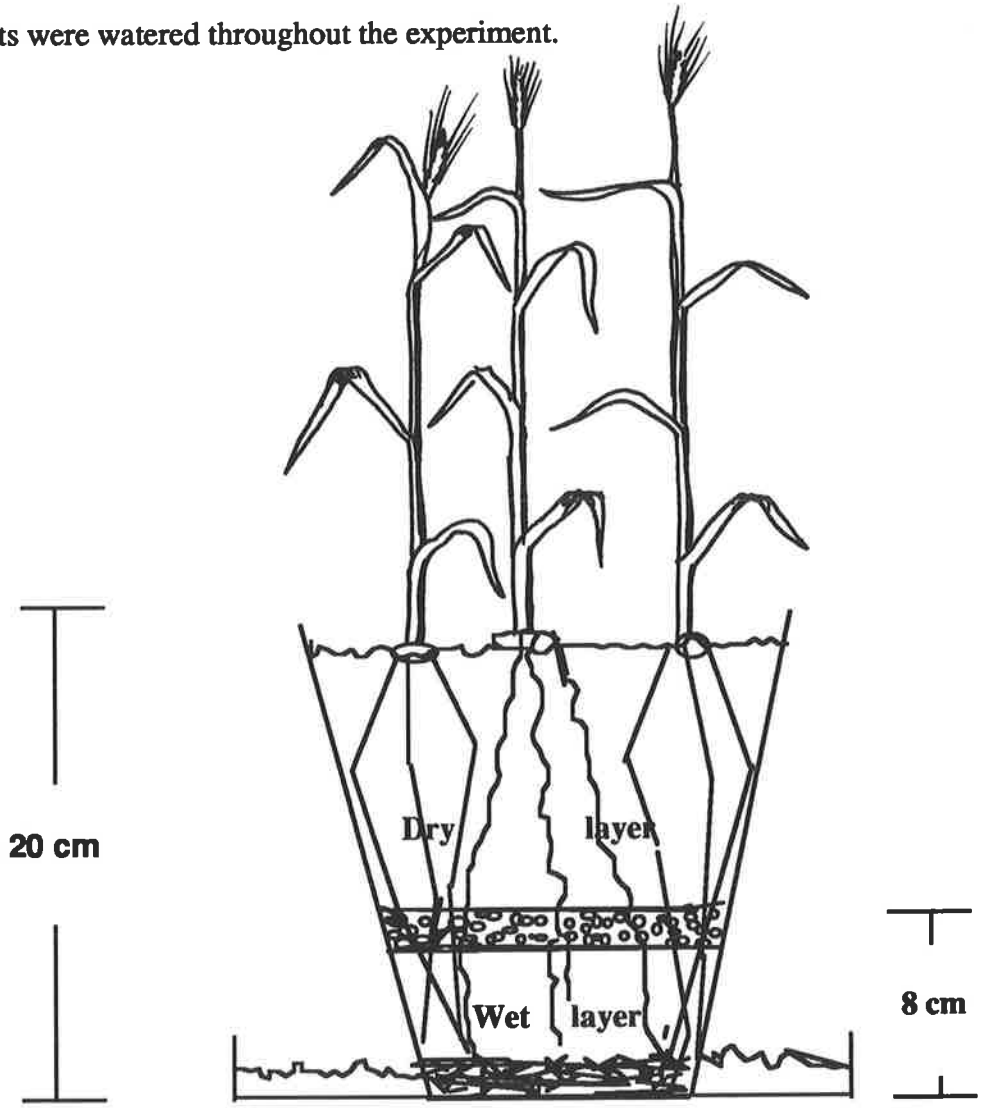

Fig. 3.1. Diagramatic representation of divided root treatment in this study.

In the third and fourth experiments, which had only two watering treatments (well-watered and water-stressed) the water stress treatment was based on the water holding capacity of the soil as follows: six pots containing the same soil in the previous experiments (recycled soil RS) were saturated with water, covered with black plastic and allowed to drain to a constant weight. The pots were then weighed and the moisture content of the soil measured. The moisture content of the soil at this stage (25%) (w/w) was assumed to represent the field capacity of the soil in the pots. All pots were watered to field capacity 3 times per week until day 10 after anthesis and the water stress treatment imposed at day 10 after anthesis. Pots in the well watered treatment were maintained around field capacity by frequent weighing and the addition of water to return them to field capacity, while pots in the water stress treatment were allowed to dry and then were maintained at approximately 50% field capacity until maturity.

3.5 Measurement of dry weight and related attributes

In all experiments the plants were harvested at day 24 after anthesis and at maturity. The measurements were based on these two harvests because the major purpose of the experiments was to examine the effects of post-anthesis stress on the processes associated with grain filling, protein deposition in the grain and remobilisation of dry matter and N. Some remobilisation is likely to occur prior to day 24, especially when stress is imposed, but the main purpose of the measurements was to examine the physiological responses to stress rather than provide an accurate quantification of the amount of DM and N remobilised and its contribution to yield. Consequently, the values of remobilized dry matter and N estimated from these experiments are likely to underestimate the true values.

Plants were separated into grain, chaff, peduncle, lower internodes, flag leaf and other leaves, dried in an oven at 85 °C for 48 hours, then put in desiccator and allowed to cool to room temperature. The dry weights of the different parts of the shoot were recorded. The various attributes relating to DM and N movement in the shoot that are discussed in this study were evaluated as follows:

(i) DM remobilization (mg per shoot)

= (DM at day 24 after anthesis in the organ) - (DM at maturity in the same organ).

(ii) DM remobilization efficiency (%)

$$= \frac{\text{DM remobilized}}{\text{DM at day 24}} \times 100.$$

(iii) Apparent contribution of reserves of assimilate to grain (%)

$$= \frac{\text{DM remobilized}}{\text{grain DM accumulation between day 24 and maturity}} \times 100$$

(iv) Harvest index (HI; %)

$$= \frac{\text{grain yield per shoot}}{\text{total DM content of aboveground plant}} \times 100.$$

(v) N remobilization (mg per shoot)

= (N content at day 24 after anthesis)-(N content at maturity).

(vi) N remobilization efficiency (%)

$$= \frac{\text{N remobilization}}{\text{N content at day 24 after anthesis}} \times 100.$$

(vii) N and DM decrement (-) or increment (+) in the grain (mg per shoot)

= (N or DM content in the grain at maturity) - (N or DM content at day 24).

(viii) Apparent contribution of vegetative N to grain N (%)

$$= \frac{\text{N remobilized}}{\text{grain N accumulation between day 24 and maturity}} \times 100.$$

(ix) N harvest index (NHI; %)

$$= \frac{\text{grain N per shoot}}{\text{total N content of above ground plant}} \times 100$$

(x) Percentage senescence of the leaves

$$= \frac{\text{dry weight of senesced leaves}}{\text{dry weight of total leaves}} \times 100.$$

3.6 Plant biochemical measurements

3.6.1 Measurement of total N concentration using the Kjeldahl method with the Auto 1030 Analyzer.

A sample (0.5g dry weight) was digested with 7.5 ml of concentrated sulphuric acid at 390 °C which converted the N in the sample into ammonium sulphate ($(NH_4)_2SO_4$). A catalyst tablet was added to promote the oxidation of the organic matter. The catalyst tablet also contained potassium sulphate which raised the temperature of the digest and

thereby increased the rate of the reaction. After digestion, 25 mL H_2O was added and the ammonium was released from the digest by steam distillation with alkali (NaOH). Ammonium was collected in a 2% boric acid solution which was titrated with 0.1 M HCl with 1% of methyl red/ bromocresol green as indicator (Bremner 1965).

3.6.2 Determination of total ethanol soluble carbohydrate.

Ethanol soluble carbohydrates were extracted by boiling the samples in 80% ethanol / water (v/v) based on the method of Dubois *et al* . (1956). To extract the tissue, 500 mg of fresh tissue was cut into small pieces, then dropped into 10 ml of 80% ethanol which was boiling. After boiling for 15 minutes the tissue was ground to a fine pulp, using a mortar and pestle. The slurry was decanted into a 50 ml centrifuge tube and the mortar and pestle were washed with a further 5 ml of 80% ethanol, and the washings were added to the same centrifuge tube which was centrifuged for 10 minutes at 2000 r.p.m. The pellet was extracted another two times and all the extracts were pooled into a 50 ml volumetric flask and made to volume. To remove the chlorophyll, 10 ml of the extract was decanted into a 50 ml centrifuge tube and 10.7 ml distilled water and 3.3 ml chloroform were added and after vigorous shaking the suspension was centrifuged at 2000 r.p.m for 5 minutes. The supernatant was transferred using a Pasteur pipette into a 25 ml volumetric flask and made up to volume with 80% ethanol. The chloroform layer was discarded.

A portion (0.1ml) of the 80% ethanol extract was added to 0.9 ml of water followed by 1 ml of 5% aqueous phenol. A jet of concentrated sulphuric acid (5 ml) was pumped into the centre of the sample and the optical density was measured at 490 nm when the tubes had cooled. The assay was calibrated with a standard curve of sucrose (5 to 70 µg per tube) and the data were expressed as equivalent to sucrose.

3.6.3 Determination of fructan

The final pellet of ethanol insoluble material was dried at 50°C. The pellet was suspended in 5 ml of water, boiled for 15 minutes and centrifuged at 2000 r.p.m. The

supernatant was poured into a volumetric flask and the pellet was re extracted twice more with boiling water. Finally the pooled supernants were made to volume and centrifuged as above. Fructans were measured using the phenol test as described above, and the data were expressed as sucrose equivalents.

3.6.4 Soluble protein

Soluble protein content was estimated by the dye-binding method of Bradford (1976). One volume of dye-reagent concentrate was diluted with four volumes of distilled water. The diluted dye-Bradford reagent was filtered through Whatman no. 1 filter paper and the filtrate used for analysis. An aliquot of the tissue extracts containing 0-100 microgram protein was mixed with 5.0 ml of diluted dye-reagent. After about five minutes the absorbance of the mixture at 595 nm was determined. The assay was calibrated using a standard solution of bovine serum albumin (fraction II, Sigma).

3.6.5 Determination of chlorophyll

Chlorophyll content of the tissues was determined based on the method of Bruinsma (1963). The tissue (leaf) was cut it into pieces (1 cm) with a pair of scissors and mixed. A subsample of 0.5 g fresh weight of mixed pieces was transferred to a pestle and ground with about 0.5 g of sand (acid washed) and a small amount of magnesium carbonate in 10 ml of cooled 80% acetone. The slurry was poured onto a sintered glass filter and the extract was filtered by suction into a flask covered with foil to exclude light. The residue on the filter was washed with another 5 ml cooled acetone. The combined extracts were made up to volume in a 25 ml stoppered flask. If necessary the concentration of the chlorophyll extract was diluted with known amounts of cool 80% acetone. The optical density at 663 and 645 nm was read, and the chlorophyll content calculated using the following formula:

Chl a (mg/L) = (12.7 x A663) - (2.7 x A645)

Chl b (mg/L) = (22.9 x A645) - (4.7 x A 663)

Chl a+b (mg/L) = (20.2 x A645) + (8.0 x A 663)

3.6.6. Endopeptidase activity

Endopeptidase activity was extracted from the flag leaf and the other leaves. Leaf material was cut into 1 cm pieces and mixed, and a subsample of 0.5 gram fresh weight was ground in a mortar with a pestle on ice with 3 - 5 ml (depending on the moisture content of the leaf) of sodium acetate buffer (0.1M pH 5) and some acid-washed sand. The suspension was centrifuged for 10 minutes at 10, 000 r.p.m. at 4°C, and the supernatant was decanted and kept on ice. Endopeptidase activity was assayed by the azocasein method (Guerin 1993). Enzyme extract (150 µl) was incubated with 0.3 ml of azocasein (10 mg/ ml of distilled water) and 0.5 ml citrate - phosphate buffer pH 5.5 and 0.05 ml 2-mercaptoethanol (0.1M) for two hours at 37°C. The reaction was stopped with the addition of 1 ml Hagihari reagent [(acetic acid (0.3M), trichloroacetic acid (0.1M) and sodium acetate (0.2M)]. The tubes were centrifuged for 10 minutes at 10,000 g. For each sample one zero time reference was included using the same procedure at the same time except that 1 ml Hagihari reagent was added before adding the enzyme extract. The supernatant was decanted into a fresh tube and the absorbance was read at 340 nm (A340) against the zero time reference for each sample, and the units of activity are given as A340 nm / minute / g fresh weight of leaf. Specific activity, (A340/ mg soluble protein / minute) was also calculated.

3.7 Statistical analyses

In all the experiments a minimum of 3 replicates were used. Standard analysis of variance was used for the analysis of all data. All experiments were set up as a factorial in a randomised complete block design. Treatment means were compared using the LSD (Steel and Torrie 1960) procedure at the 5% and 1% level of significance or using the standard errors.

Chapter 4. Effects of water stress on remobilization of DM and N from vegetative parts of the shoot

4.1 Introduction

Reserves accumulated before anthesis play an important role in grain growth, but the extent of their contribution depends on prevailing environmental conditions such as nutrient level (Daigger *et al.* 1976), temperature, and water stress (Campbell and Davidson 1979) and is also under genetic control (Van Sanford and Mackown 1987; Halloran 1981). This is particularly important for wheat growing under a Mediterranean-type environment because the weather after anthesis is usually hot and dry and photosynthesis is low. Water stress during grain filling is one of the important factors that may result in an increase in the contribution of stored reserves to grain filling relative to current assimilate. Yield, therefore, depends partly on the translocation of reserves to the grain.

The calculated proportion of yield provided by translocation of pre-anthesis assimilates for wheat is estimated at between 7 and 57% (Austin *et al.* 1977; Bidinger *et al.* 1977; Gallagher *et al.* 1975, 1976). Genetic variability in DM remobilization has been reported (Davidson and Birch 1978) and the extent of this remobilization is subject to genotype x year interaction (Wych *et al.* 1982). Several studies have indicated that grain N in wheat primarily originates as a result of translocation from vegetative parts after anthesis (Boatwright and Haas 1961; Simmons and Moss 1978). McNeal *et al.* (1966) and Bhatia and Rabson (1976) have reported that grain protein concentration might be improved by selecting genotypes that translocate a higher percentage of N from vegetative organs to the grain. Others have shown, however, that the relationship between grain protein concentration and N translocation or N translocation efficiency is not consistent (Mikesell and Paulsen 1971).

Field evaluation of growth and yield during or following stress is difficult because the stress can not be controlled. This is particularly true where different genotypes are being compared, because they are usually at different stages of development at any one time and therefore comparisons at the later stages are not meaningful. It is also difficult to ensure similar stresses for genotypes with different growth habits. Although environmental

conditions in the glasshouse and growth room are unlike those in the field in some respects, at least the level of water stress can be controlled, and the other difficulties avoided. The purpose of this experiment was four fold:

(i) To determine the effects of different levels of water stress on the accumulation of DM and N and also DM harvest index (DMHI) and N harvest index (NHI) in the grain during grain filling.

(ii) To identify the effects of different levels of water stress on the remobilization of DM and N from the shoot and also to examine the responses to drought in the upper section of the root while the lower section was watered.

(iii) To investigate the importance of different parts of the shoot as sources of remobilized N and DM available for contribution to the grain under water stress and well watered conditions.

(iv) To improve knowledge related to the differential effects of water deficit on the remobilization of DM and N during grain filling in two different wheat cultivars.

4.2 Materials and methods

The experiment was conducted in pots in the glasshouse using two wheat genotypes differing in yield and protein content. The plants were stressed at similar stages of development (10 days after anthesis) and treatments consisted of Non watered, Medium stress, Mild stress, Divided root and Control (see Chapter 3). Soil water potential was maintained around field capacity in all pots until 10 days after anthesis, when treatments were imposed. At day 24 and at maturity three pots from each treatment were harvested and the above ground parts separated into chaff, flag leaf, other leaves, internodes, peduncle and grain. These were dried at 85° C for 48 hours and weighed. N concentration was determined by the standard macro-Kjeldahl procedure. Calculated parameters were as described in Chapter 3 and standard statistical procedures were used for analysis of variance.

4.3. Results

4.3.1 Flag leaf water relations

Total water potential of the flag leaf of Sun 92A (Fig. 4.1) declined from day 12 in water stressed plants, then decreased rapidly from day 18 in severe stress (non-watered) conditions. On day 21 water potential in the medium stress treatment increased because the plants were rewatered. Under non watered conditions, water potential declined throughout the experiment until day 31 after anthesis when the flag leaf under this treatment completely senesced. After rewatering in the medium stress treatment flag leaf water potential recovered, and then declined again. Under medium stress the flag leaf had completely senesced by day 41, and in the other treatments the flag leaf had senesed by day 55. The response of Vasco was similar.

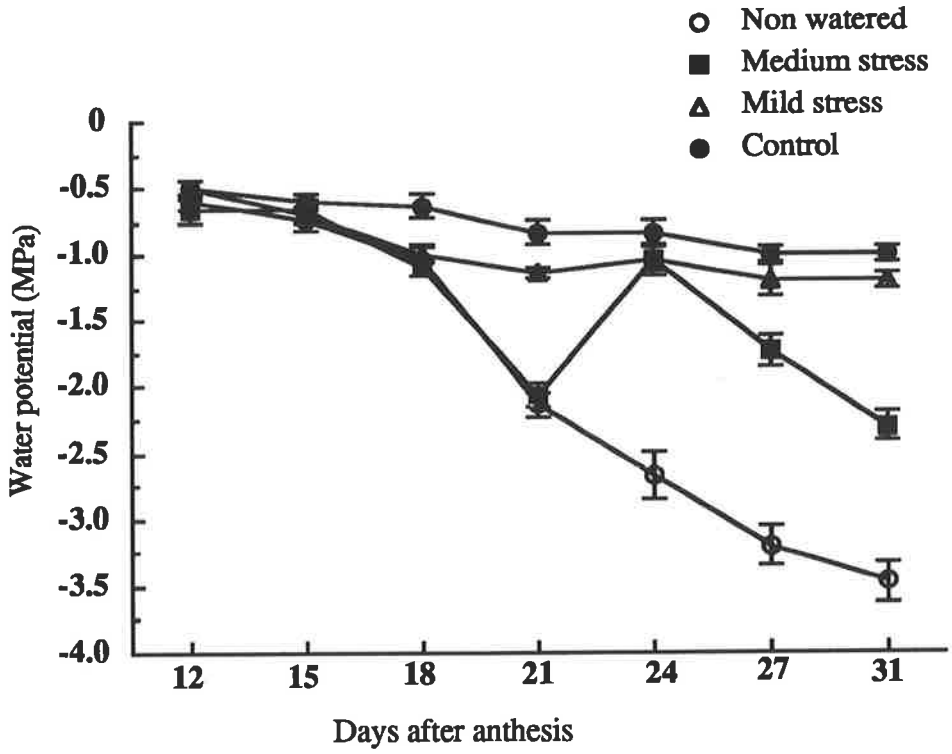

Fig. 4.1. The total water potential of the flag leaf of Sun 92A under different levels of water stress between days 10 and 31 after anthesis. Error bars are standard errors of the means.

4.3.2 Chlorophyll content

The total chlorophyll content of the flag leaf of both cultivars was measured at day 24 (Fig.4.2). Severe stress reduced total chlorophyll content in Sun 92A and Vasco by about 27% and 15%, respectively. In Vasco the chlorophyll content was similar under medium and mild stress and under the divided root system, but all treatments significantly reduced chlorophyll content in Sun 92A.

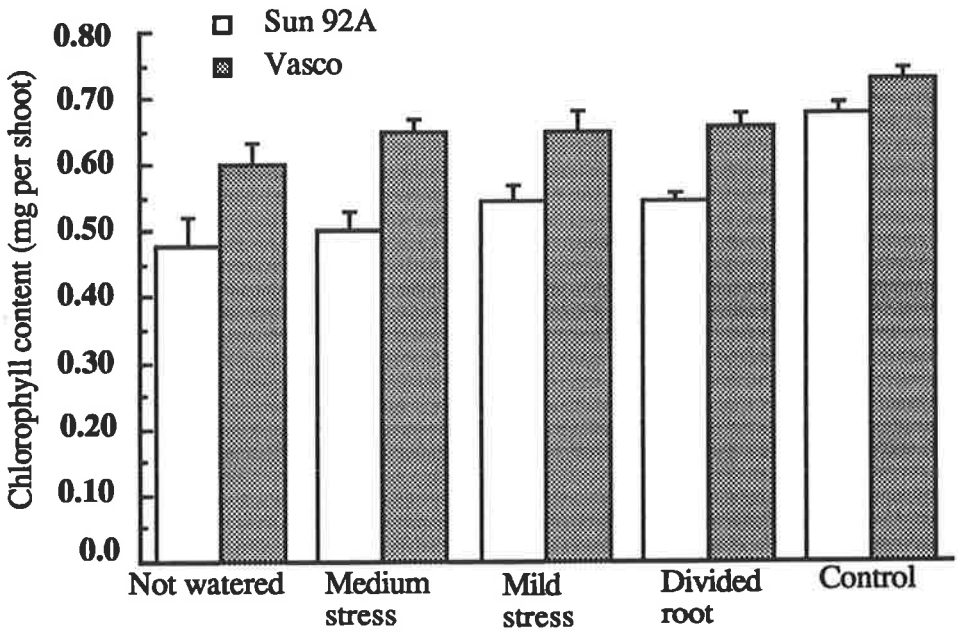

Fig. 4.2. The chlorophyll content of the flag leaf in both wheat cultivars at day 24. Error bars are standard errors.

4.3.3 Senescence of the leaves

The assessment of senescence of the leaves was measured based on the procedure of Nicolas (1985) (see Chapter 3). The proportion of the leaves which were senescent in Sun 92A increased with time and was related to the severity of the treatments (Fig. 4.3a). For instance, under non-stressed conditions it slowly increased with time, but under severe stress senescence was rapid and 21 days after imposition of this treatment the leaves had completely senesced. When watering ceased 10d after anthesis, the senescence of the flag

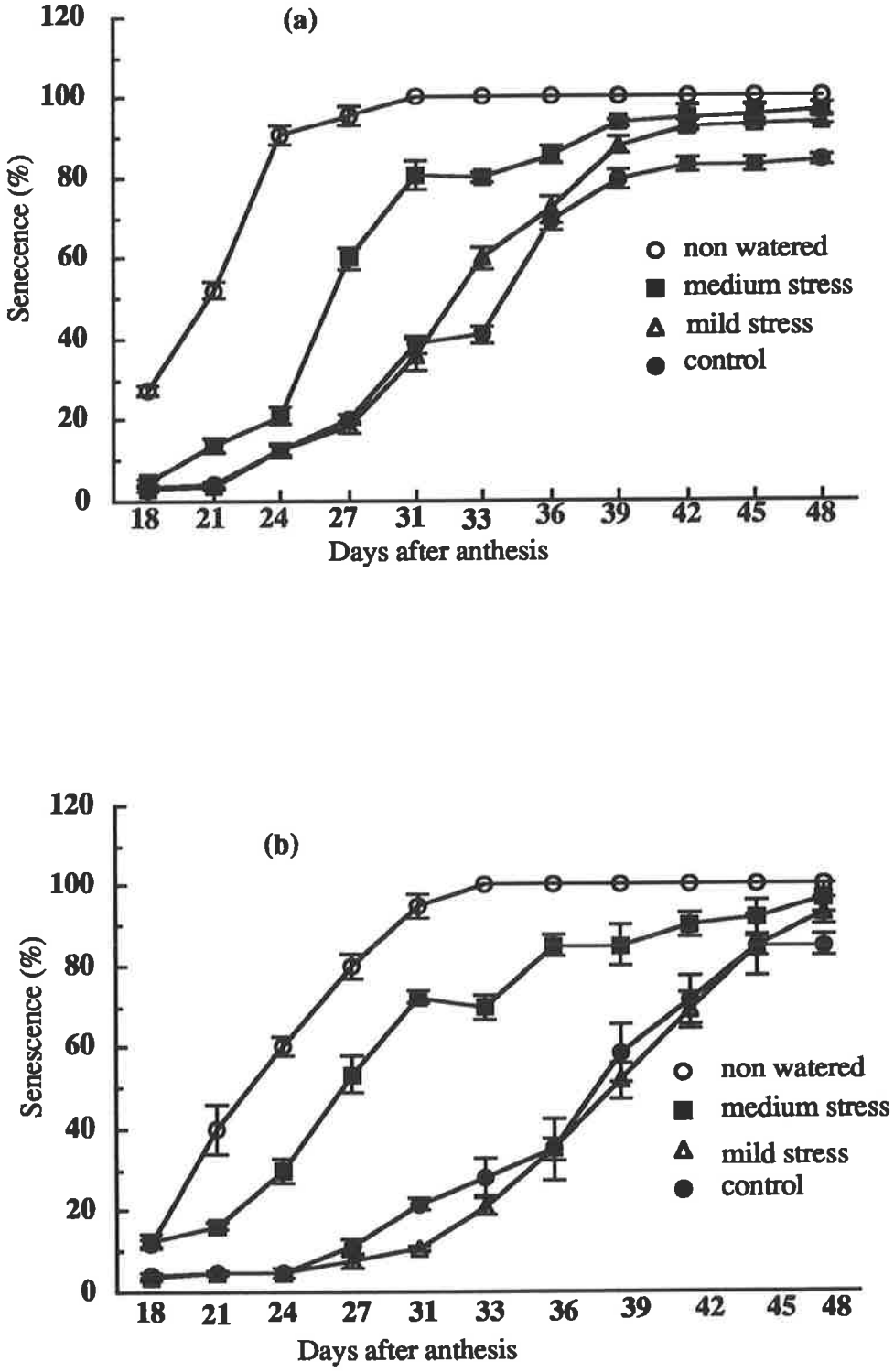

Fig. 4.3. The senescence of the leaves in Sun 92A (a) and Vasco (b) between days 18 and 48 after anthesis. Error bars are standard errors.

leaf of Vasco was slower than Sun 92A and this also occurred in the control and mild-stress treatments (Fig. 3b). No data were gathered for the divided root treatment.

4.3.4 Grain DM accumulation

The effects of water stress treatments on the grain of wheat cultivars are presented in Table 4.1. There were significant interactions ($P< 0.05$) between water stress treatments, cultivars and harvests. Both cultivars had significantly more DM at maturity than at day 24. Grain yield was significantly higher in Vasco than in Sun 92A under all conditions except the non watered treatment at day 24 (Table 4.1). Water stress reduced grain DM increment in both cultivars between day 24 and maturity and in general the extent of the reduction was related to the level of stress (Fig. 4.4) although the effect was greater in Sun 92A.

Table 4.1. Grain DM accumulation as affected by different treatments of water stress in two cultivars of wheat during grain filling

	Day 24		Maturity	
Treatment	Sun 92A	Vasco	Sun 92A	Vasco
	mg per shoot			
Not watered	404	312	480	636
Medium stress	412	577	715	1404
Mild stress	620	761	1062	1555
Divided root	471	935	1124	1648
Control	415	704	1130	1827

LSD 5% of interactions of Treatments x Harvests x Cultivars: 156; Treatments x Harvests : 110 ; Harvests x Cultivars : 67

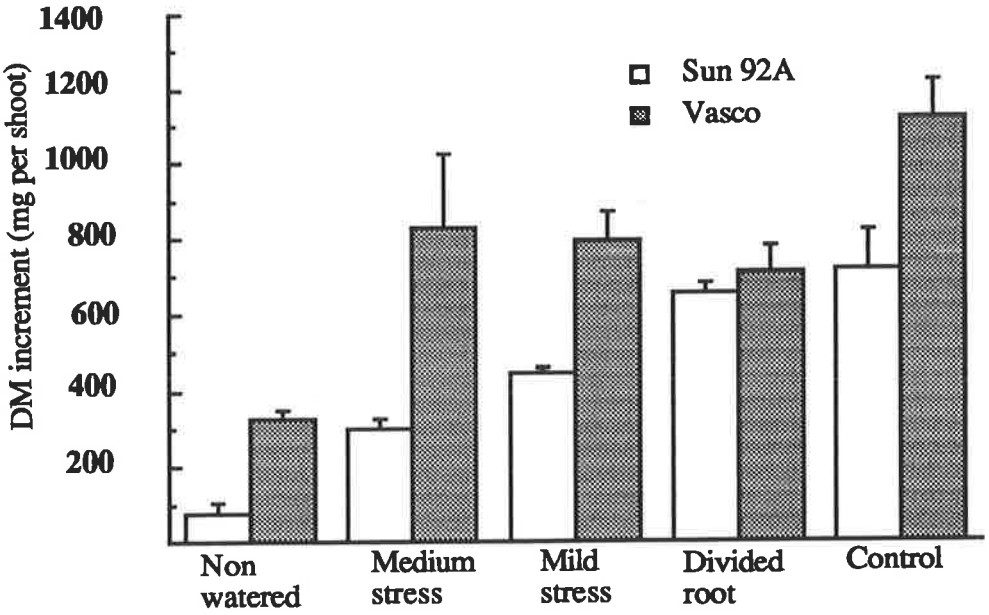

Fig. 4.4. Grain DM accumulation between day 24 and maturity under water deficit treatments. Error bars are standard errors.

Since yield varied between the two cultivars for the unstressed control, the significant water stress interaction with cultivars was evaluated by calculating the percentage reduction in yield. Percent reductions in grain yield at maturity for Sun 92A under not watered, medium stress, mild stress and divided root treatments were 58% , 55%, 7% and 1% respectively compared with 66%, 29%, 15 % and 14% for Vasco. The results of this experiment showed that final grain dry weight in Sun 92A under the divided root system did not differ from controls. In addition DM accumulation between the two harvests under divided root conditions was reduced in Vasco but not in Sun 92A. This response in Vasco however was due to a significant increase in grain dry weight at day 24 associated with a decrease at maturity relative to the control treatment. In general under all situations the DM increment between day 24 and maturity was significantly greater for Vasco than Sun 92A (Fig. 4.4). At maturity Sun 92A showed a significantly higher HI than Vasco under all conditions except the medium stress condition (Fig. 4.5).

4.3.5 Grain N accumulation

The interaction between water stress treatment and cultivar on N accumulation in the grain is presented in Table 4.2. At day 24, N accumulation in the grain of both cultivars under control, mild and medium water stress was similar (Table 4.2). At maturity however significantly more N had accumulated in the grain of Vasco than in Sun- 92A under all conditions except the most severe stress (non watered) treatment. The pattern of N accumulation between day 24 and maturity (Fig. 4.6) was generally similar to that of grain yield accumulation in both cultivars between day 24 and maturity (Fig. 4.4).

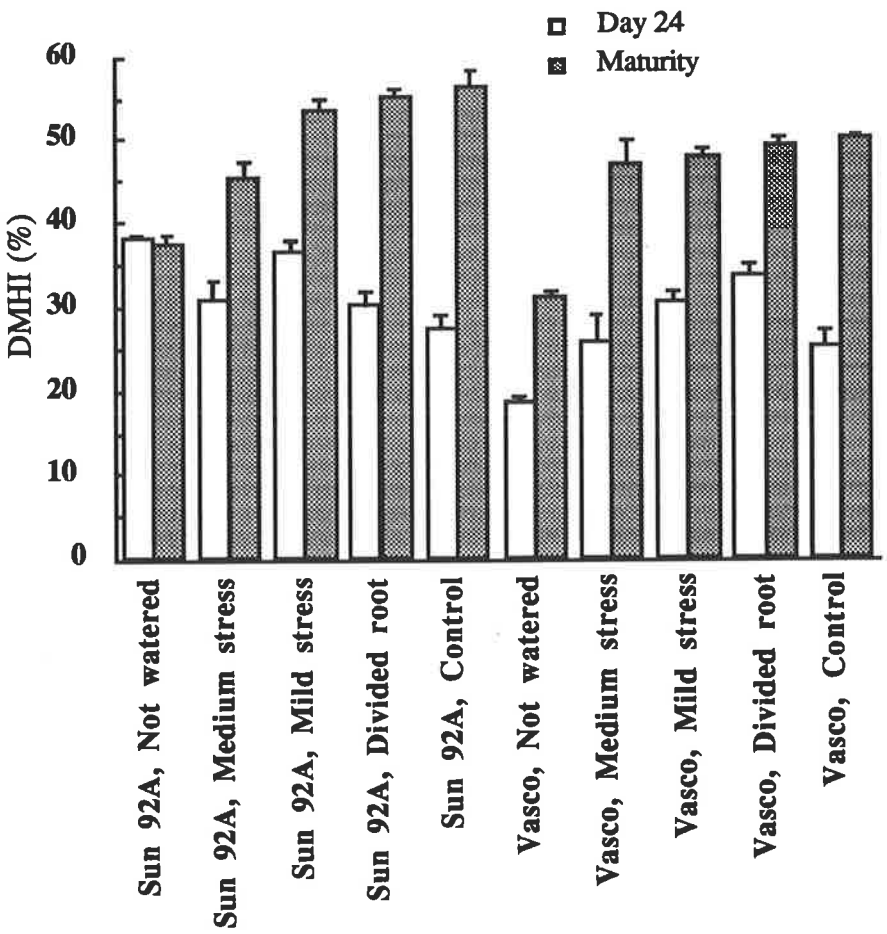

Fig. 4.5. The effect of water stress on the HI of 2 varieties of wheat at day 24 and maturity. Error bars are standard errors.

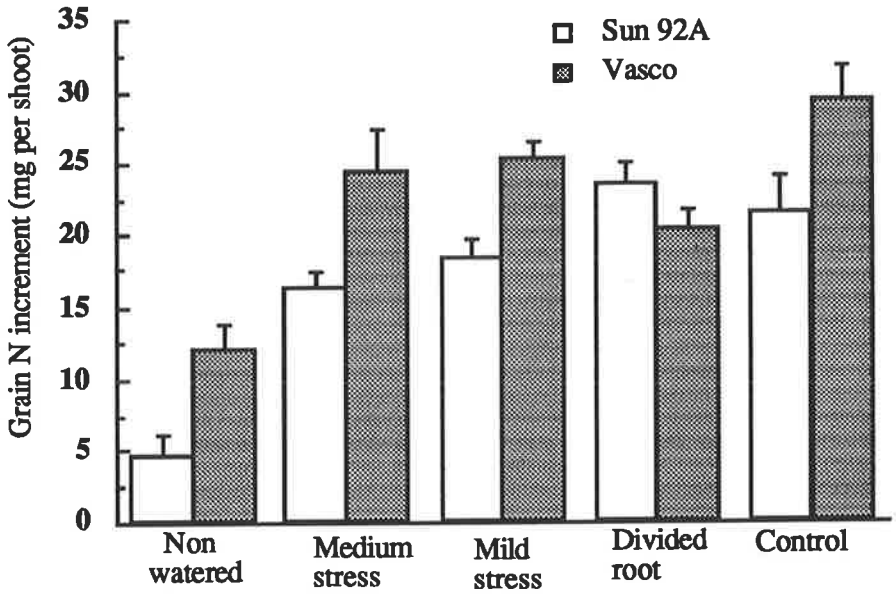

Fig. 4.6. Grain N accumulation between day 24 and maturity in two wheat cultivars growth under different water stress treatments. Error bars are standard errors.

Table 4.2. Grain N accumulation as affected by different treatments of water stress in two cultivars of wheat during grain filling

Day 24			Maturity	
Treatments	Sun 92A	Vasco	Sun 92A	Vasco
		mg per shoot		
Not watered	16	10	21	22
Medium stress	13	15	29	39
Mild stress	19	17	37	43
Divided root	14	22	37	43
Control	14	15	35	44

LSD 5% for interactions of Treatments x Harvests x Cultivars : 3.8; Treatments x Harvests : 2.7; Harvests x Cultivars : 1.7

Since cultivars varied for grain yield and N, the effects of water stress on yield and N in the grain, expressed as a percentage of controls are shown in Table 4.3. Grain yield per shoot was more sensitive than grain N in response to water stress. Under non-watered conditions grain yield reductions in Sun 92A and Vasco were 58% and 66%, respectively, while the corresponding values of N were 40% and 50%, respectively.

At maturity, grain from plants exposed to water stress had a significantly higher percentage of N than that from plants grown under conditions of adequate water in both cultivars. Imposition of the most severe water deficit treatment resulted in a significant increase of the N concentration in both cultivars at day 24. Also at maturity water stress treatments resulted greater in grain N concentrations . It was notable that N concentration under all conditions was greater in Sun 92A than Vasco at both harvests (Fig. 4.7). Also medium stress had a greater effect on raising grain N in Sun 92A than in Vasco. The NHI was significantly higher at maturity than at day 24 under all treatments in both cultivars (Fig.4.8).

Table 4.3. Grain N content and yield as a percentage of control at maturity

Treatments	Grain N		Grain Yield	
	Sun 92A	Vasco	Sun 92A	Vasco
	percent			
Control	100	100	100	100
Divided root	106	96	99	90
Mild stress	105	96	93	85
Medium stress	83	89	45	71
Not watered	60	50	42	34

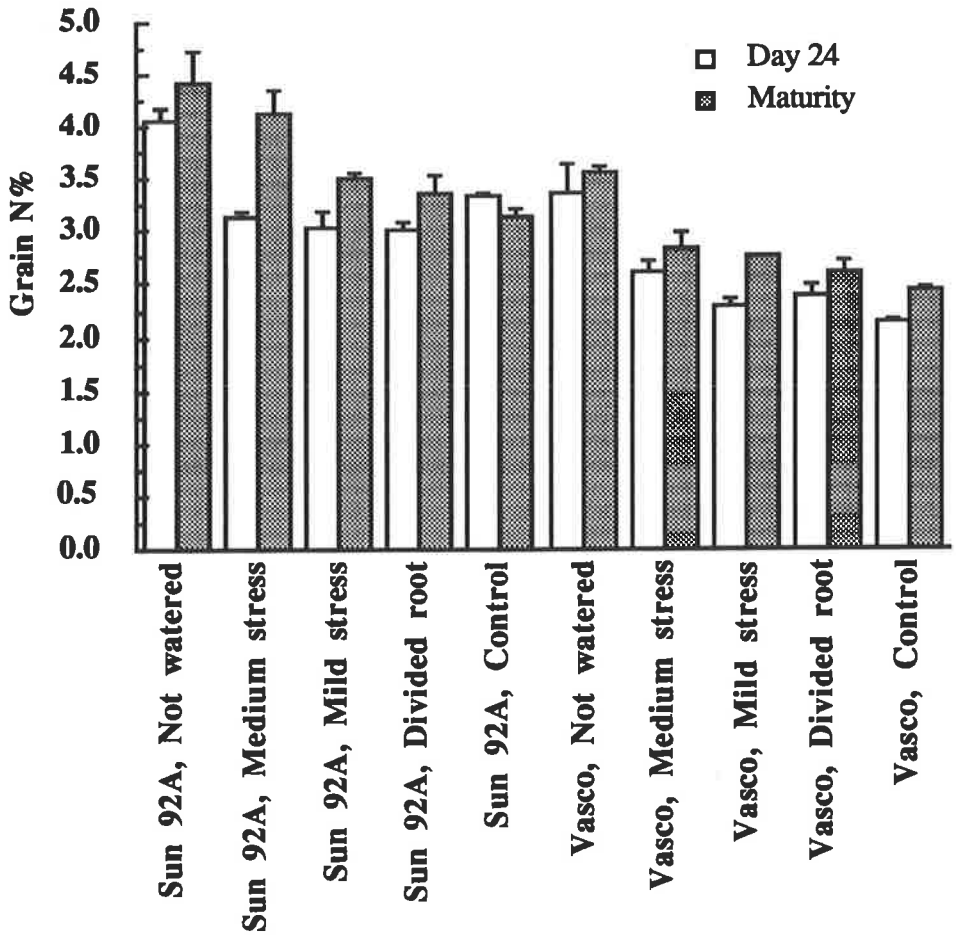

Fig. 4.7. The effects of water stress on the grain N percentage of two wheat cultivars at day 24 and at maturity. Error bars are standard errors.

It was noticeable that the NHI at maturity significantly decreased with increasing severity of water stress, and there was a highly significant difference between the two cultivars under the water stress treatments.

4.3. 6 DM, N content and their remobilization from the shoot

4.3.6.1 DM and N content in the whole shoot (vegetative parts + grain)

In general, water stress reduced the accumulation of DM in the whole plant and the interaction of harvest and treatments and cultivars was significant ($P< 0.05$; Fig. 4.9).

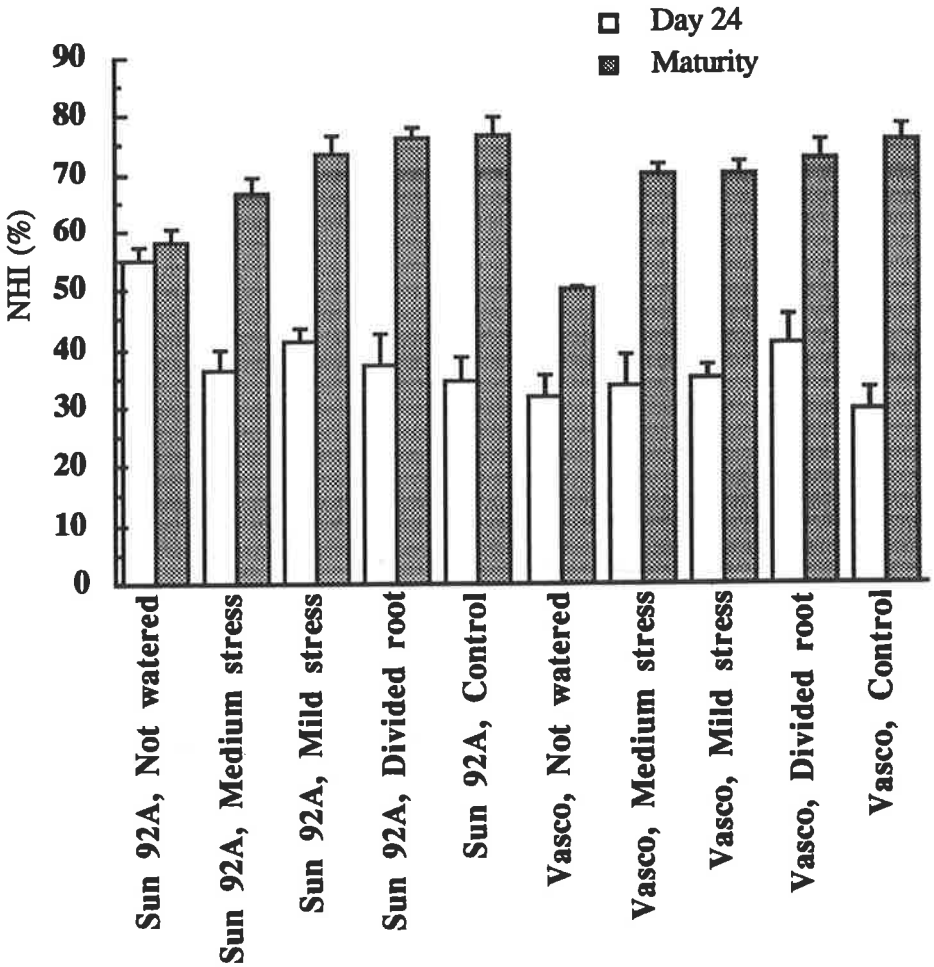

Fig. 4.8. The interactions between harvests and water stress and cultivars on NHI during grain filling. Error bars are standard errors.

There was an increase in DM in the whole shoot between day 24 and maturity for both cultivars under all treatments. Vasco produced considerably more DM than Sun 92A under all watering treatments (Fig. 4.9). The divided root treatments reduced total shoot DM at the final harvest in Vasco but not in Sun 92A. Dry matter production in Sun 92A was reduced only by medium stress and severe (not watered) stress.

The average total shoot N contents over all harvests and cultivars, harvests and treatments, and cultivars and treatments are presented in Figs. 4.10, 4.11 and 4.12 respectively. Mild stress did not affect the N content of the shoot (Fig. 4.10) but the medium and more severe stresses significantly reduced it.

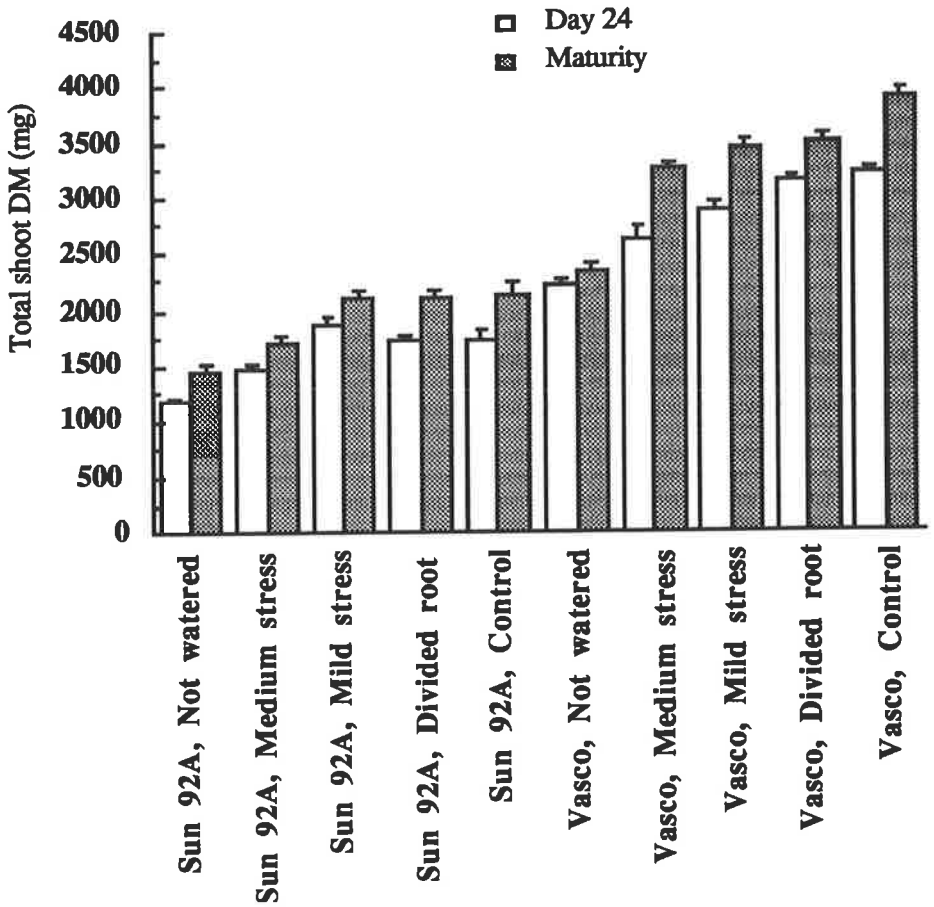

Fig. 4.9. The effects of water stress treatments on total shoot DM content during grain filling in two wheat cultivars. Error bars are standard errors.

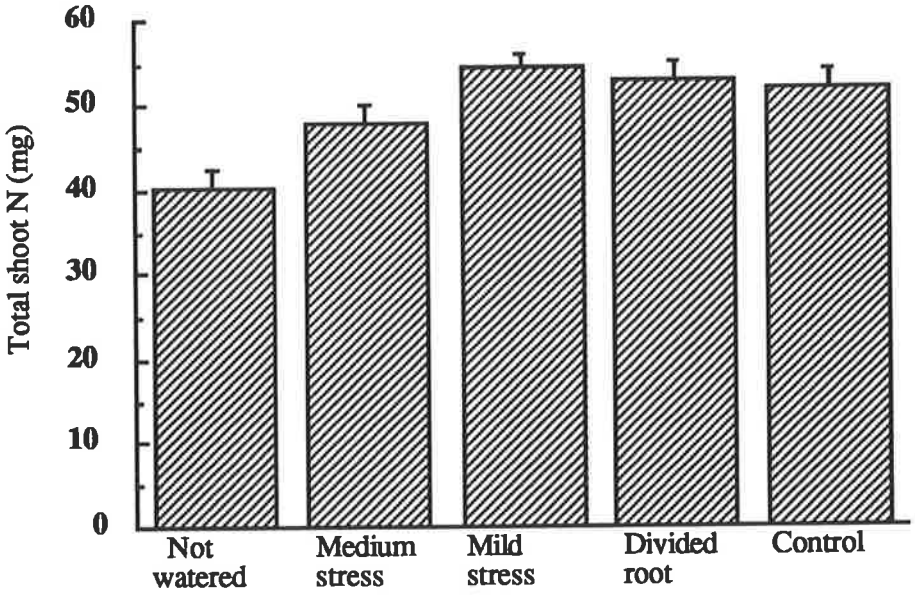

Fig. 4.10. Total shoot N content over all harvests and cultivars during grain filling under water stress. Error bars are standard errors.

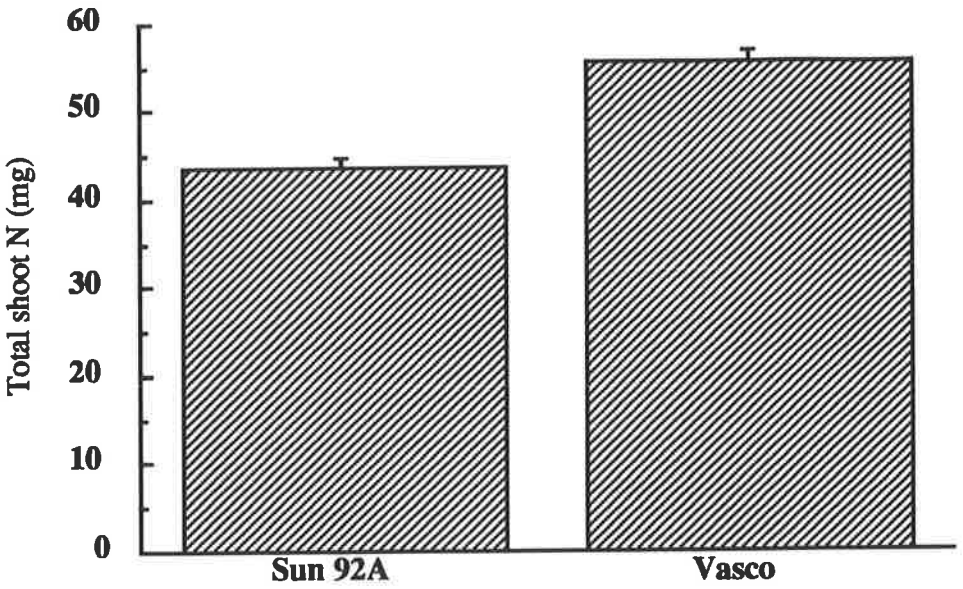

Fig. 4.11. Total shoot N content of two wheat cultivars over all water stress treatments and harvests. Error bars are standard errors.

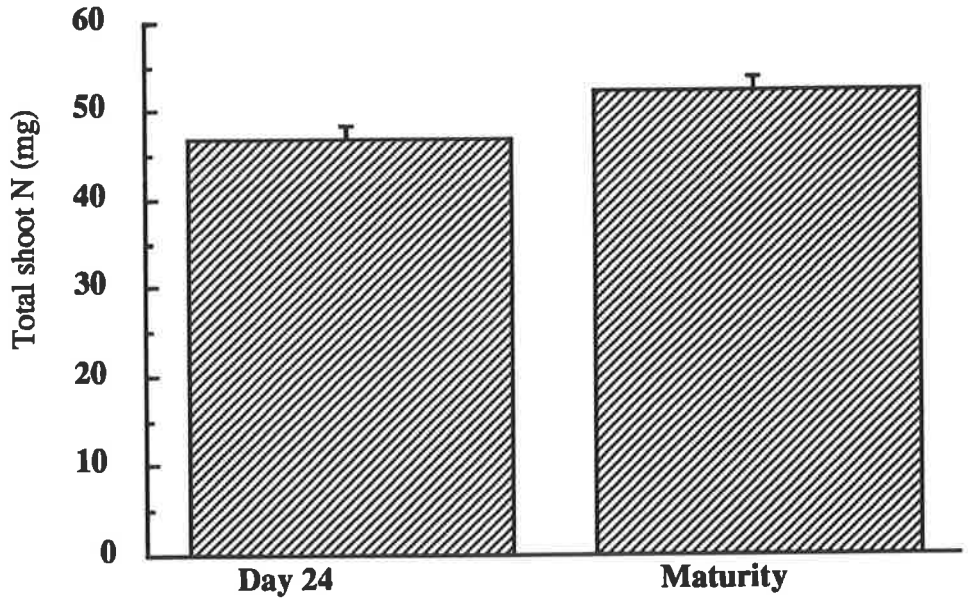

Fig. 4.12. Total shoot N content at day 24 and maturity over all treatments and cultivars . Error bars are standard errors.

4.3.6.2 DM and N content and remobilization from the shoot (vegetative parts)

4.3.6.2.1 DM content and remobilization

Average DM contents of the vegetative parts in the two wheat cultivars was significantly greater at day 24 than at maturity except for the non-watered treatment. DM content was significantly ($P < 0.001$) greater in Vasco than Sun 92A at both harvests and also under water stress treatments. Water stress treatments reduced the remobilization of DM from the shoot of both cultivars between day 24 and maturity: remobilization of DM was highest under the control treatment and lowest in the medium stress treatment. The divided root treatment remobilized more DM than medium stress and less than control. In non watered plants however an increase in shoot DM between the two harvests was observed. Although the interactions between treatments x cultivars on remobilization of DM was not significant (Fig. 4.13) over both cultivars, differences in DM remobilization from the shoot among water stress treatments were highly significantly different (Fig. 4.14). Remobilization efficiency and the apparent contribution of DM to the grain was greater in Sun 92A than Vasco under almost all conditions (Table 4.4).

Table 4.4. DM content and remobilization efficiency of vegetative parts under different levels of water stress at day 24 and maturity

	Day 24		Maturity		Remobilization efficiency		Apparent contribution to grain	
Treatments	V1	V2	V1	V2	V1	V2	V1	V2
	mg per shoot				percent			
Not watered	696	1337	793	1399	0	0	0	0
Medium stress	917	1582	857	1531	7	3	19	6
Mild stress	1031	1710	909	1647	12	4	28	8
Divided root	1042	1820	896	1700	14	7	22	17
Control	1054	2026	867	1799	18	11	26	20

V1: Sun 92A V2: Vasco, LSD 5% for Treatments x Harvests: 71; Harvests x Cultivars: 45; Treatments x Harvests x Cultivars : N.S.

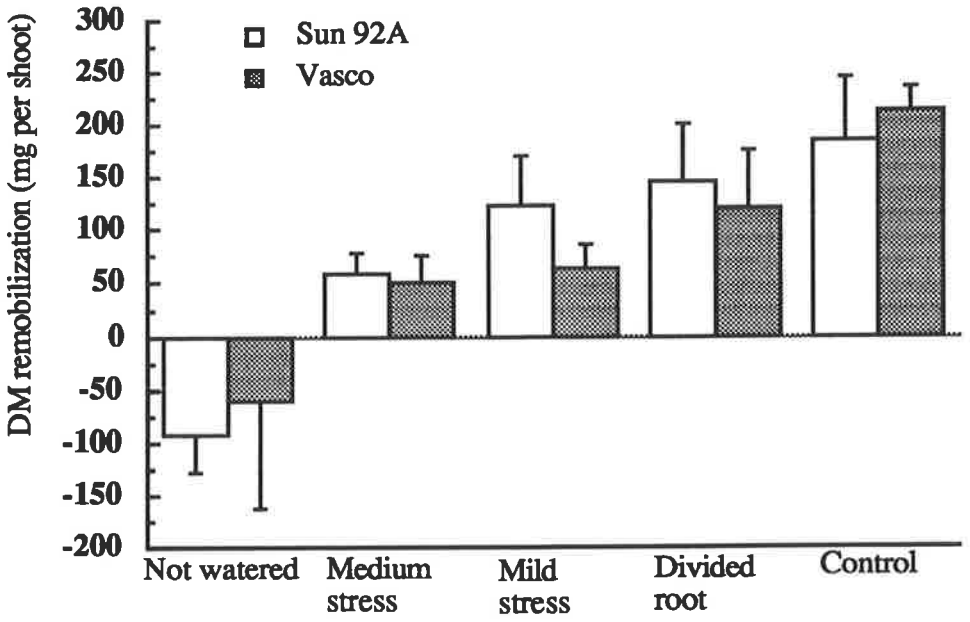

Fig.4.13. The remobilization of DM from the vegetative parts of the shoot under water stress treatments between day 24 and maturity. Error bars are standard errors.

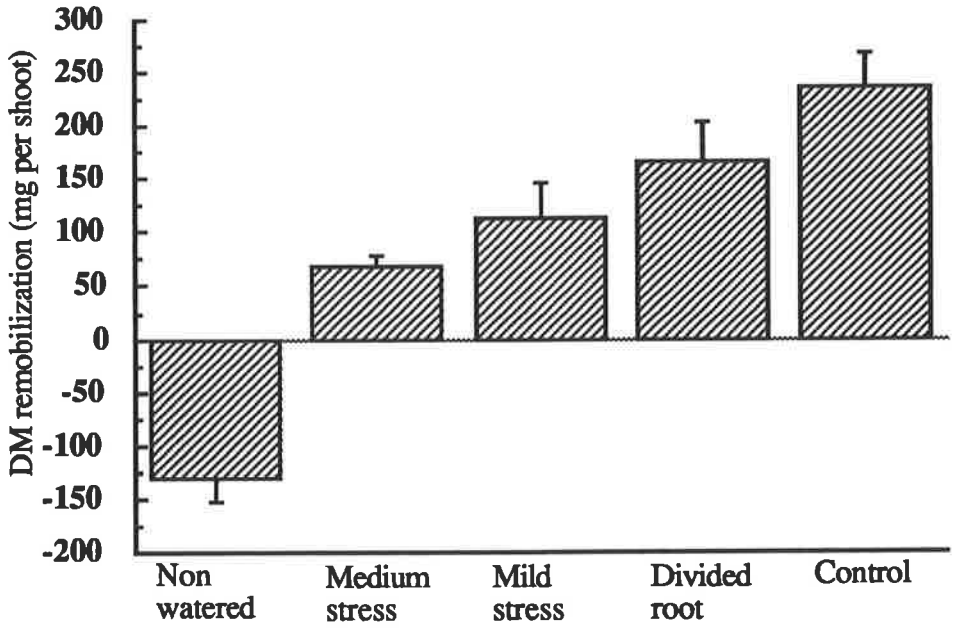

Fig. 4.14. The remobilization of DM from the shoot under water stress over both cultivars during grain filling. Error bars are standard errors.

4.3.6.2.2 N content and remobilization

N contents of the vegetative parts of the shoot in the two wheat cultivars under water stress treatments and at both harvests are presented in Table 4.5. N content was significantly greater at day 24 than at maturity. N content was also significantly ($P < 0.001$) greater in Vasco than Sun 92A at both harvests and also under water stress conditions.

N was remobilized from the shoot between day 24 and maturity in both cultivars. Remobilization of N was significantly greater under the control conditions than under all water stress treatments (Fig. 4.15). Although only part of the root system in the divided root treatment was stressed, it appeared to reduce the remobilization of N from the shoot of Vasco. Although severe stress appeared to have abolished the loss of N from the shoot (Fig.4.15), it did not result in increased N content of the shoot between the two harvests, unlike DM (Fig. 4.14). In the following sections the responses of each part of the shoot to different levels of water stress will be presented separately. DM and N are also considered separately.

4.3.6.3 Lower stem Internodes

4.3.6.3.1 DM content and remobilization

Lower stem internode DM was significantly greater at day 24 than at maturity under control and divided root conditions (Fig. 4.16), but in the other three treatments there was no significant difference between the two harvests. Internodes in Vasco were longer and heavier than Sun 92A at day 24 and at maturity; therefore DM content of internodes of Vasco over both harvests was significantly greater than Sun 92A (Fig. 4.17). DM was remobilized from the internodes of both cultivars between day 24 and maturity (Fig. 4.18). More DM was remobilized in control plants than in plants under stress (Fig. 4.19). Sun 92A appeared to remobilize more DM than Vasco under the medium and mild stress treatments but the differences were not significant (Fig.4.19). It was of interest, however,

Table 4.5. N content and remobilization efficiency of N from the vegetative parts of the shoot in two wheat cultivars under different levels of water stress at day 24 and maturity

	Day 24		Maturity		Remobilization efficiency *		Apparent contribution to grain %	
Treatments	V1	V2	V1	V2	V1	V2	V1	V2
	mg per shoot				percent			
Not watered	14.4	22.3	15.2	22.6	0	0	0	0
Medium stress	22.9	29.2	15.0	16.9	34	42	49	51
Mild stress	26.6	32.4	13.5	18.3	49	43	72	54
Divided root	24.4	32.4	11.8	16.2	52	50	55	77
Control	26.0	35.8	10.7	14.2	59	60	73	74

V1: Sun 92A V2: Vasco, LSD 5% for Treatments x Harvests: 2.01; Harvests x Cultivars: 1.2; Treatments x Harvests x Cultivars : N.S. *(N difference between day 24 and maturity / N at day 24) x 100

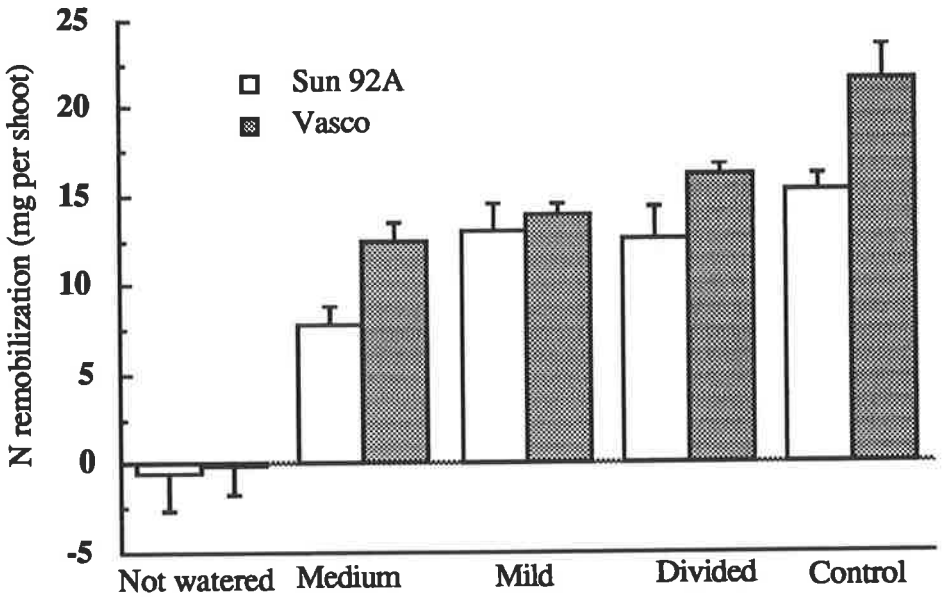

Fig. 4.15. N remobilization from the shoot under different levels of water stress between day 24 and maturity. Error bars are standard errors.

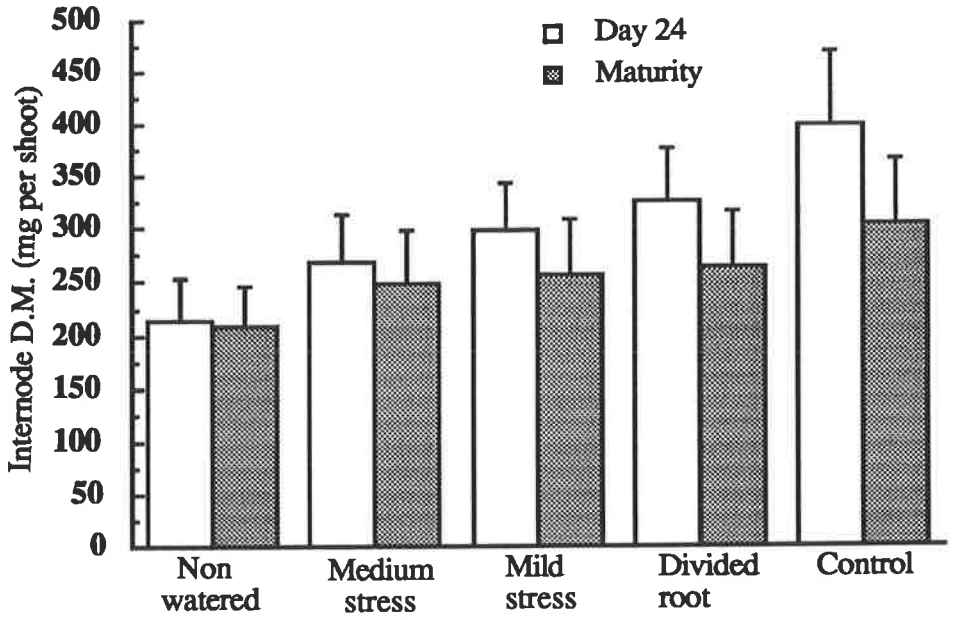

Fig. 4.16. The interaction of water stress and harvests on lower stem internode DM content averaged over both cultivars during grain filling. Error bars are standard errors.

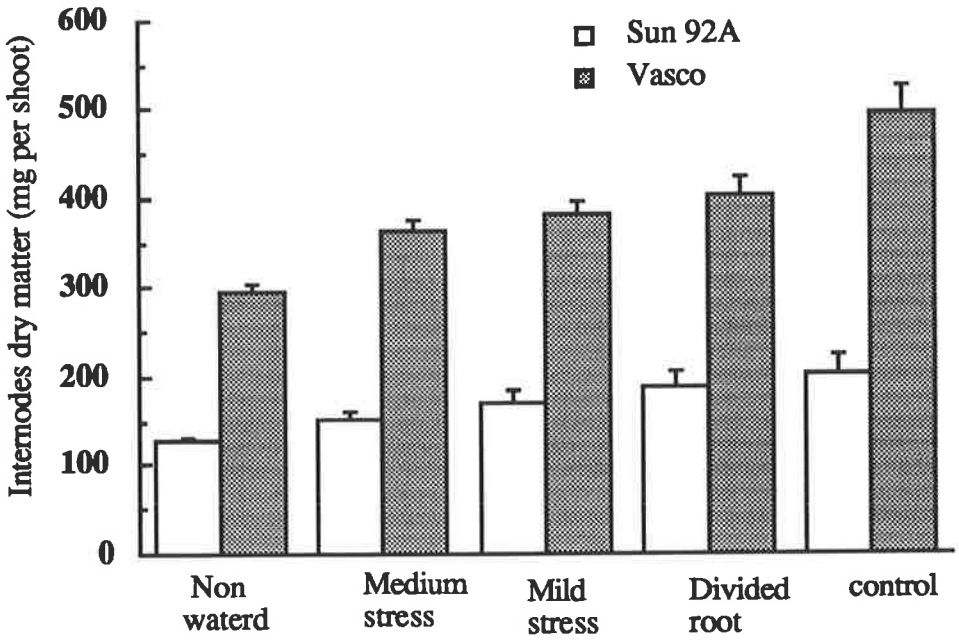

Fig. 4.17. The interaction of water stress and cultivars on lower stem internode DM content over both harvests during grain filling. Error bars are standard errors.

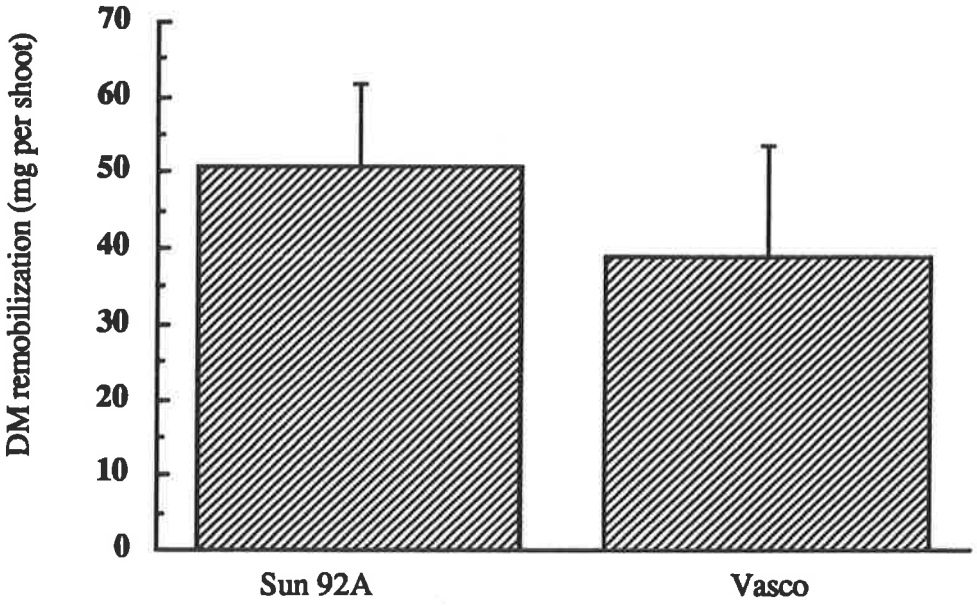

Fig. 4.18. Remobilization of DM from the lower stem internodes in two wheat cultivars over all water treatments during grain filling. Error bars are standard errors.

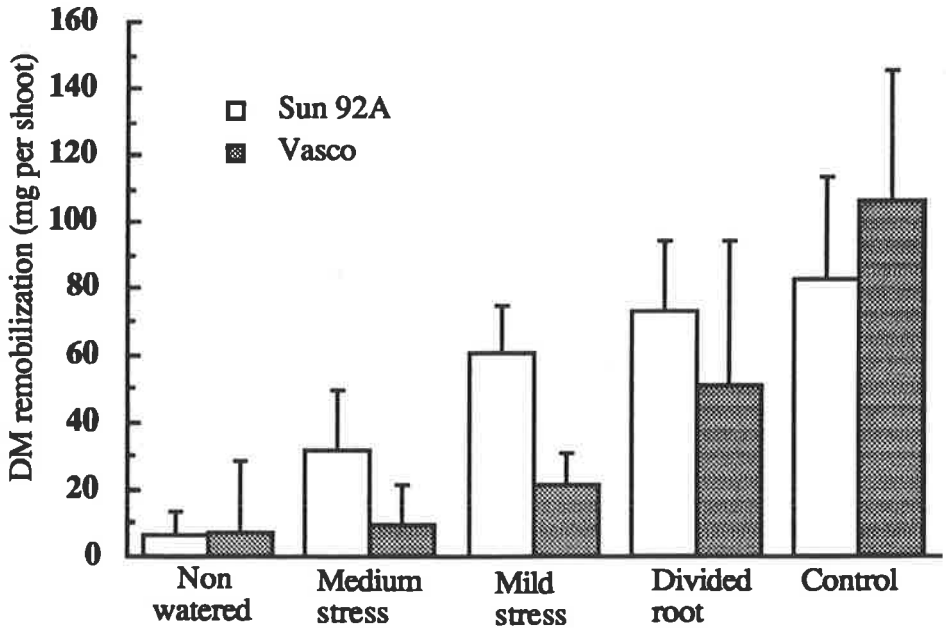

Fig.4.19. The interaction of treatments and cultivars on remobilization of DM during grain filling. Error bars are standard errors.

Table 4.6 DM content and remobilization efficiency of lower internodes in two wheat cultivars under different levels of water stress at day 24 and maturity

	Day 24		Maturity		Remobilization efficiency		Apparent contribution to grain %	
Treatments	V1	V2	V1	V2	V1	V2	V1	V2
	mg per shoot				percent			
Not watered	130	300	124	293	4	2	7	2
Medium stress	168	369	136	359	16	3	10	1
Mild stress	201	394	140	372	30	5	14	3
Divided root	224	429	151	378	32	12	11	7
Control	245	549	163	443	33	19	11	9

V1: Sun 92A V2: Vasco Interactions of treatments x cultivars x harvests: N.S.

LSD 5% for Treatments x Harvests : 33; Harvests x Cultivars : 21

that all stress treatments generally reduced the remobilization of DM from the internodes of Vasco, but only the most severe stress did in Sun 92A (Fig.4.19). Remobilization efficiency of the internodes (Table 4.6) was greater in Sun 92A than in Vasco; remobilization efficiency was reduced significantly under conditions of water stress in the internodes of both cultivars .

In the well watered plants DM remobilization efficiency was 33% and 19% for Sun 92A and Vasco respectively, whereas the corresponding values were 4% and 2% under the most severe water deficit treatment . Remobilization from the internodes could have made a contribution to grain DM in Sun 92A. Vasco however appeared to contribute little of its internode DM to the grain under any condition.

4.3.6.3.2 N content, percentage and remobilization

Compared to their effects on total DM, the water stress treatments had reduced the N content in the internodes by day 24 to a lesser extent. Internodes in Vasco were longer and

Table 4.7. Internode N remobilization as affected by different treatments of water stress in Sun 92A (V1) and Vasco (V2) during grain filling

	Day 24		Maturity		Remobilization efficiency		Apparent contribution to grain N	
Treatments	V1	V2	V1	V2	V1	V2	V1	V2
	mg per shoot				percent			
Not watered	1.5	3.2	1.2	2.9	20	9	6	3
Medium stress	1.8	3.7	0.9	1.8	50	51	6	9
Mild stress	2.0	4.0	0.6	1.4	70	65	7	10
Divided root	2.8	4.0	0.6	1.3	78	67	10	13
Control	2.1	4.3	0.6	1.6	71	62	7	9

V1: Sun 92A V2: Vasco Interactions of Cultivars x Treatments x Harvests : N.S.

LSD 5% for Treatments x Harvests : 0.38; Harvests x Cultivars : N.S.

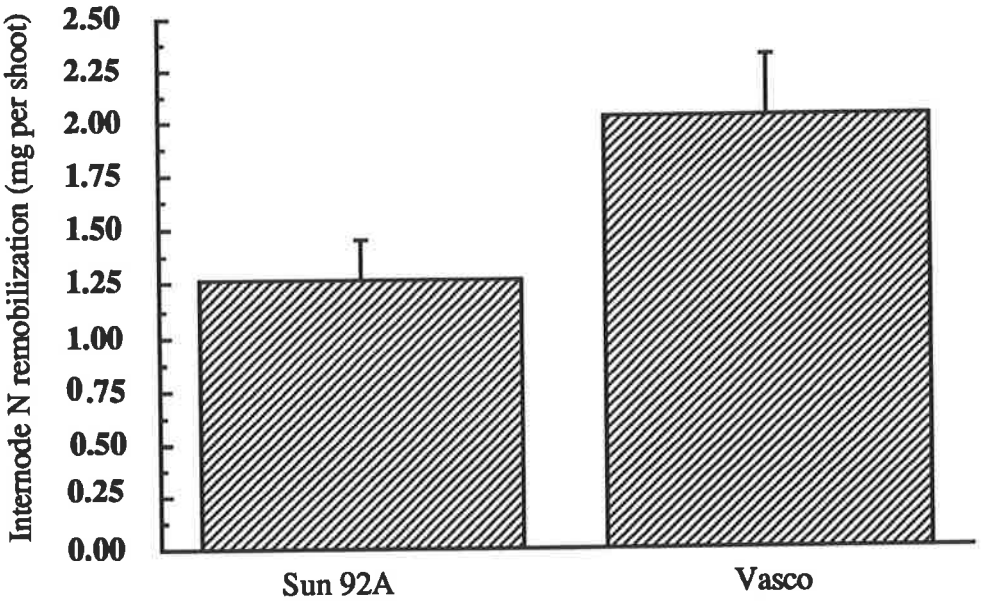

Fig. 4.20. Remobilization of N from internodes of two wheat cultivars over all treatments between day 24 and maturity. Error bars are standard errors.

heavier, and contained more N than those of Sun 92A (Table 4.7). There were no significant differences in response between the two cultivars to water stress treatments at day 24 or at maturity. Internodes of Vasco generally remobilized more N than Sun 92A (Fig.4.20) and more N was remobilized from the internode in control, divided root and mild stress treatments between day 24 and maturity than under more severe stresses (Fig. 4.21).

It appeared that the amount of N remobilized from the internodes was not simply related to the amount of DM remobilized from the internodes (Fig. 4.19). Comparatively more N than DM was remobilized, and the remobilization efficiency of N in Vasco was as great as that for Sun 92A under most conditions. Internodes appeared to contribute comparatively little N (< 13%) for grain filling under any conditions in either cultivar (Table 4.7). N as a percentage of dry weight fell by about 50% in the internodes of watered plants between day 24 and maturity (Fig. 4.22). The interactions between harvests and water treatments over both cultivars were highly significant ($P < 0.001$). At day 24 except under control conditions the N percentage of other treatments was similar, but at maturity, N percentage differed between water stress treatments (Fig. 4.22). The N concentration of the internodes increased with the severity of the stress, which is consistent with the reduction in N remobilization that occurred (Fig. 4.21).

4.3.6.4 Flag leaf

4.3.6.4.1 DM content and remobilization

The interaction of water stress treatments and harvests on the flag leaf DM content was significant ($P < 0.001$). At day 24 DM content was greatest in the mild stress and the divided root treatments in Sun 92A, and in the divided root and control treatments in Vasco. At maturity DM content of the flag leaf was generally greater under non watered than control conditions in both cultivars (Table 4.8).

The amounts of DM remobilized from the flag leaf between day 24 and maturity over both cultivars are presented in Fig. 4.23. The amounts remobilized were not significantly different between control, divided root, and mild stress, but significantly lower in medium

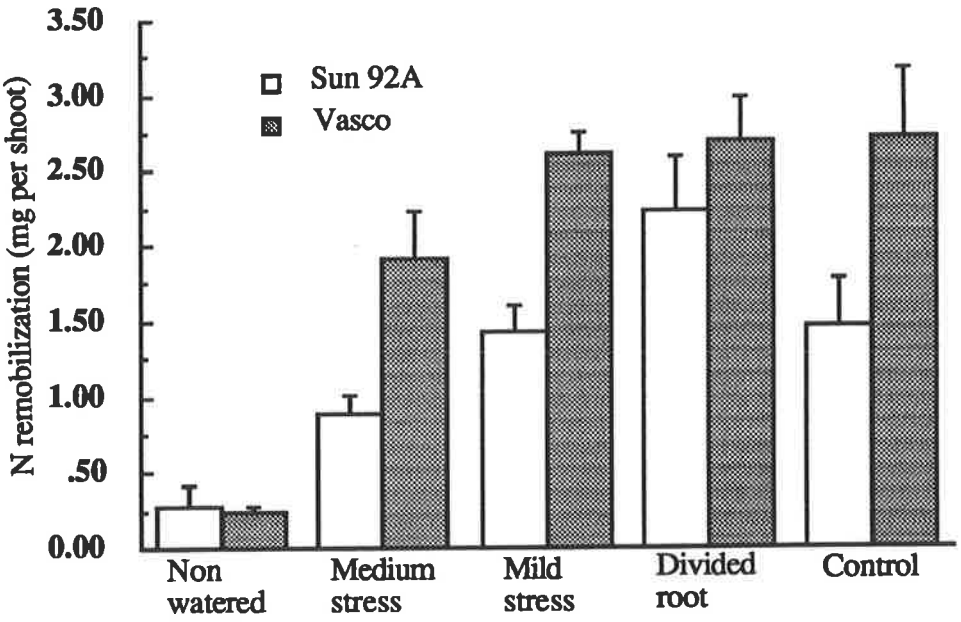

Fig. 4.21. Remobilization of N from internodes of two wheat cultivars under different levels of water stress during grain filling. Error bars are standard errors.

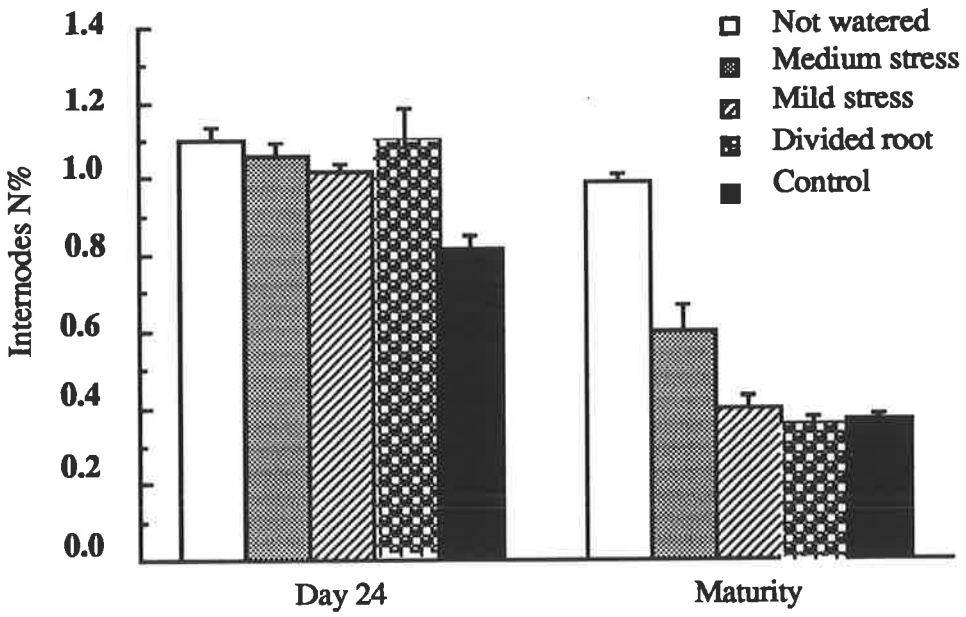

Fig. 4.22. Interactions between water stress and harvests over both cultivars on N percentage of internode. Error bars are standard errors.

Table. 4.8. Flag leaf DM as affected by different treatments of water stress in two cultivars of wheat during grain filling

	Day 24		Maturity		Remobilization efficiency		Apparent contribution to grain	
Treatments	V1	V2	V1	V2	V1	V2	V1	V2
	mg per shoot				percent			
Not watered	115	163	156	191	- 36	- 17	0	0
Medium stress	188	174	170	167	10	4	6	1
Mild stress	219	195	166	188	24	3	12	1
Divided root	218	216	152	188	30	13	10	4
Control	188	225	149	175	20	22	5	4

V1: Sun 92A V2: Vasc[illegible]nteraction of Harvests x Treatments x Cultivars: N.S.; Treatments x Harvests : 31.4; Treatments x Cultivars : N.S.

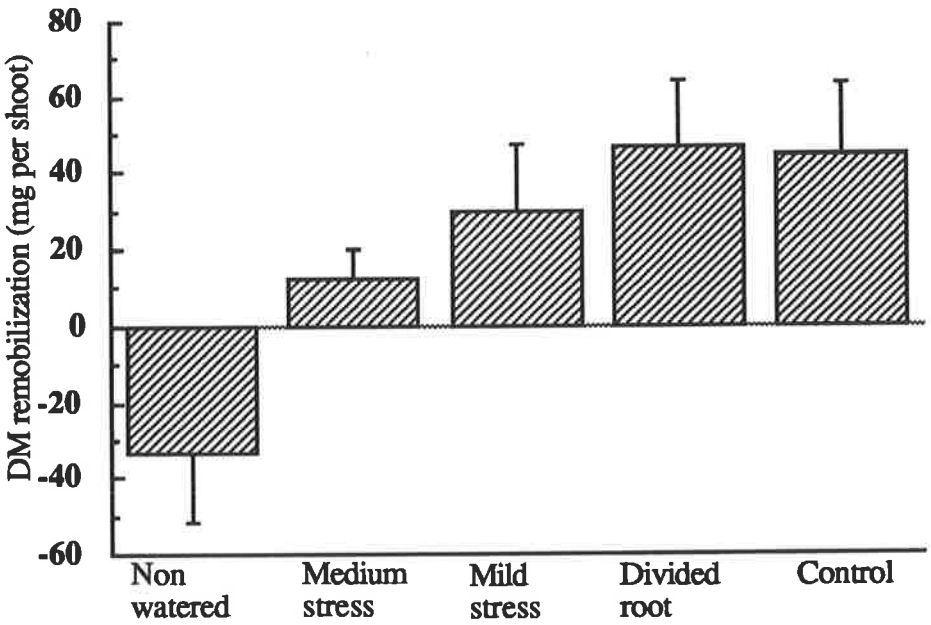

Fig. 4.23. Remobilization of DM from the flag leaf over both cultivars during grain filling. Error bars are standard errors.

and severe stress. Remobilization of DM was generally higher in Sun 92A than in Vasco under water stress conditions except for the non watered treatment where the leaves of both cultivars increased in weight. Even though severe stress reduced flag leaf DM by day 24 (Table 4.8), there was more DM in these leaves at maturity than there was at day 24. As a result the calculated values for remobilization efficiency of DM from the flag leaf were negative in this treatment. Little contribution of DM from the flag leaf to the grain was apparently made under all conditions.

4.3.6.4.2 Flag leaf N content, remobilization and concentration

Except in the non watered treatment (Table 4.9) N content of the flag leaf of both cultivars was significantly greater at day 24 than at maturity. At both harvests N content of the flag leaf was similar under mild stress, divided root and control conditions. However under severe stress N content of both cultivars increased between day 24 and maturity and the N content was greater under severe stress at maturity than in the other treatments. The remobilization of N was significantly higher in the control, divided root and mild stress treatments than under medium stress conditions (Fig. 4.24). Under non watered conditions there was no N remobilization from the flag leaf in either cultivar and the flag leaf contained more N at maturity than at day 24 . The contribution of flag leaf N for grain filling could have been greater in Sun 92A than Vasco under water stress conditions (Table 4.9). The decrease in the N concentration of the flag leaf (Fig. 4.25) between day 24 and maturity in both cultivars was significant ($P< 0.05$) in all except the non watered plants.

4.3.6.5 Other leaves (all leaves except the flag leaf)

4.3.6.5.1 DM content and remobilization

Withholding water completely reduced the DM content of the other leaves at day 24 (Table 4.10). Even so, there was an increase in weight of the other leaves in the non-

Table 4.9. Flag leaf N content of wheat cultivars as affected by four levels of water stress during grain filling

	Day 24		Maturity		Remobilization efficiency		Apparent contribution to grain	
Treatments	V1	V2	V1	V2	V1	V2	V1	V2
	mg per shoot				percent			
Not watered	3.1	3.8	3.7	4.2	- 19	-10	0	0
Medium stress	6.3	5.2	2.4	2.1	62	60	24	13
Mild stress	7.8	6.1	2.1	1.8	73	70	32	17
Divided root	6.3	6.9	1.8	1.4	71	80	20	26
Control	6.6	7.1	1.7	1.3	74	81	23	20

V1: Sun 92A V2: Vasco Interactions of Cultivars x Treatments x Harvests: N.S.
Harvests x Treatments : 0.86; Harvests x Cultivars : 0.54

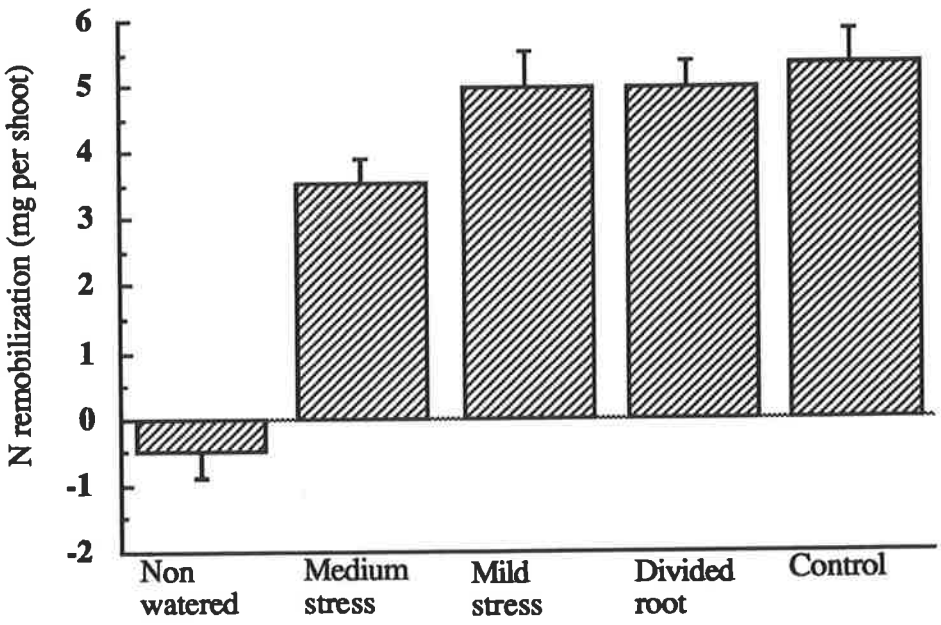

Fig. 4.24. The remobilization of N from the flag leaf over all cultivars under different levels of water stress during grain filling. Error bars are standard errors.

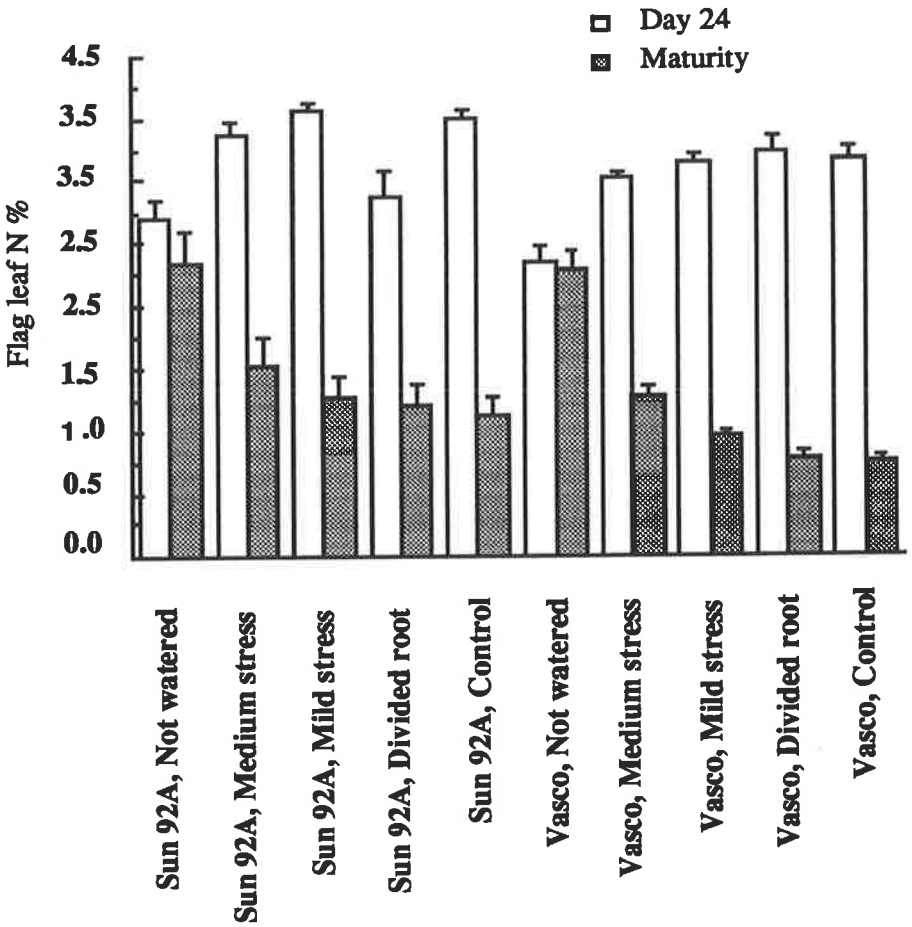

Fig. 4.25. Flag leaf N percentage of two wheat cultivars under water treatments at day 24 and at maturity. Error bars are standard errors.

watered plants during grain filling, unlike the leaves in all other treatments where dry weight decreased.

Up to 33% of the DM from the other leaves was remobilized under watered conditions. Medium stress reduced remobilization, especially in Sun 92A. These responses were similar to those which appeared in the flag leaves (Table 4.8). As in the case of the flag leaf (Fig. 4.24) stress reduced the amount remobilized, and under the most severe stress (Not watered) the other leaves gained weight between day 24 and maturity (Fig 4.26).

Table 4.10. DM content of all leaves except the flag leaf as affected by different treatments of water stress during grain filling

	Day 24		Maturity		Remobilization efficiency		Apparent contribution to grain	
Treatments	V1	V2	V1	V2	V1	V2	V1	V2
	mg per shoot				percent			
Not watered	138	315	161	352	-16	-11	0	0
Medium stress	204	468	193	426	5	8	4	5
Mild stress	238	430	175	409	26	4	14	3
Divided root	232	492	180	420	22	14	8	10
Control	217	535	144	442	33	17	10	8

V1: Sun 92A; V2: VascoInteractions of Treatments x Cultivars x Harvests: N.S.; Treatments x Harvests : 40 ; Harvests x Cultivars : N.S.

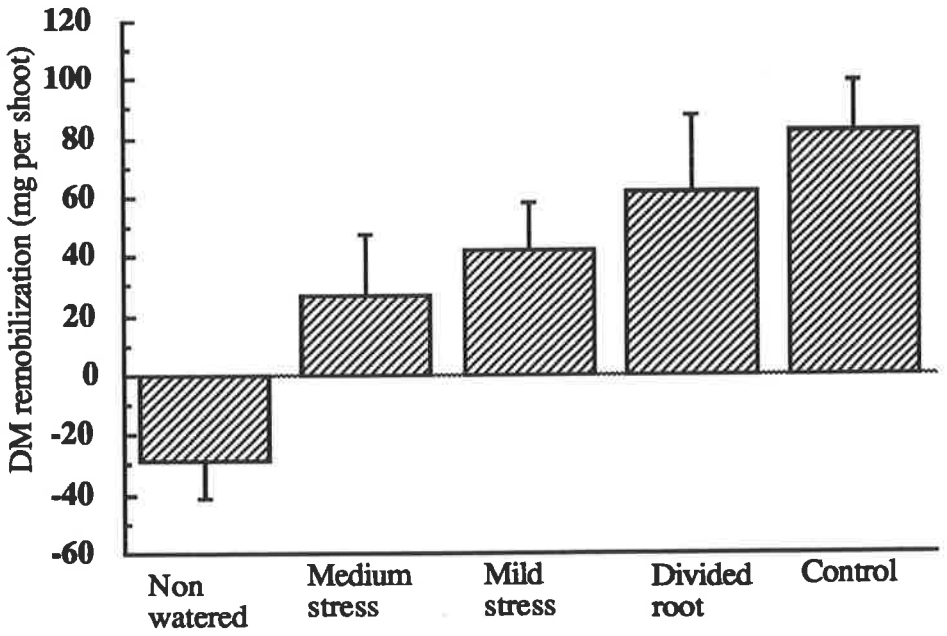

Fig. 4.26. Remobilization of DM from other leaves under water stress treatments over two wheat cultivars between day 24 and maturity. Error bars are standard errors.

4.3.6.5.2 N content and remobilization

More N was found in other leaves of both cultivars under non stressed conditions than under stress of conditions at day 24 (Table 4.11). Generally N content of other leaves in both cultivars was greater at day 24 than maturity in all treatments except for the severe water stress treatment. The fact that there was substantially more N in the other leaves of Vasco than Sun 92A at day 24 accounts for the findings that more N was remobilized from Vasco than Sun 92A (Fig. 4.27). More N was remobilized also in well watered plants than under stress conditions (Fig. 4.28). However N increased, rather than decreased, in the other leaves of plants under non watered conditions between day 24 and maturity. Remobilization efficiency of N from the other leaves (Table 4.11), and the effects of stress were similar in both cultivars.

Mild stress and divided root treatments reduced the remobilization of N from the other leaves of Vasco, but had no effects on Sun 92A (Fig. 4.29). Under medium water stress the remobilization of N in both cultivars was affected to a similar extent. Under severe water stress the other leaves of both cultivars continued to gain N between day 24 and maturity .

Withholding water decreased N concentration in the other leaves at day 24 (Fig.4.30) while less severe water stress had no effect. The N concentration in the leaves fell between day 24 and maturity. However at maturity the concentration of N in the leaves was greater than the control, and in the most severe treatment the concentration of N was about double that of watered plants.

4.3.6.6 Peduncle

4.3.6.6.1 DM content and remobilization

The two cultivars responded differentially under water stress treatments at day 24 and maturity. For instance at day 24, DM content of both cultivars significantly decreased under non watered treatments, while at maturity the responses were different. At maturity DM content of Sun 92A under the non watered treatment decreased, in contrast in Vasco under the

same conditions it increased (Table 4.12). The amount of DM remobilized from the peduncle of Vasco decreased with increasing severity of water stress (Fig. 4.31). However in Sun 92A similar amounts , or more DM was remobilized under stress as in watered plants.

Table 4.11. N content of all leaves except the flag leaf as affected by different treatments of water stress of two varieties of wheat during grain filling

	Day 24		Maturity		Remobilization efficiency		Apparent contribution to grain	
Treatments	V1	V2	V1	V2	V1	V2	V1	V2
	mg per shoot				percent			
Not watered	3.6	5.6	3.9	6.8	-8	-18	0	0
Medium stress	7.1	10.8	4.4	5.9	38	45	17	20
Mild stress	8.7	11.2	2.9	3.9	68	63	32	28
Divided root	8.4	10.9	2.5	4.2	70	61	26	32
Control	8.4	13.7	2.2	3.6	73	73	30	35

V1: Sun 92A V2: Vasco N: N Interactions of Treatments x Cultivars x Harvests : N.S. ; Harvests x Treatments : 1.3; Treatments x Cultivars : N.S.

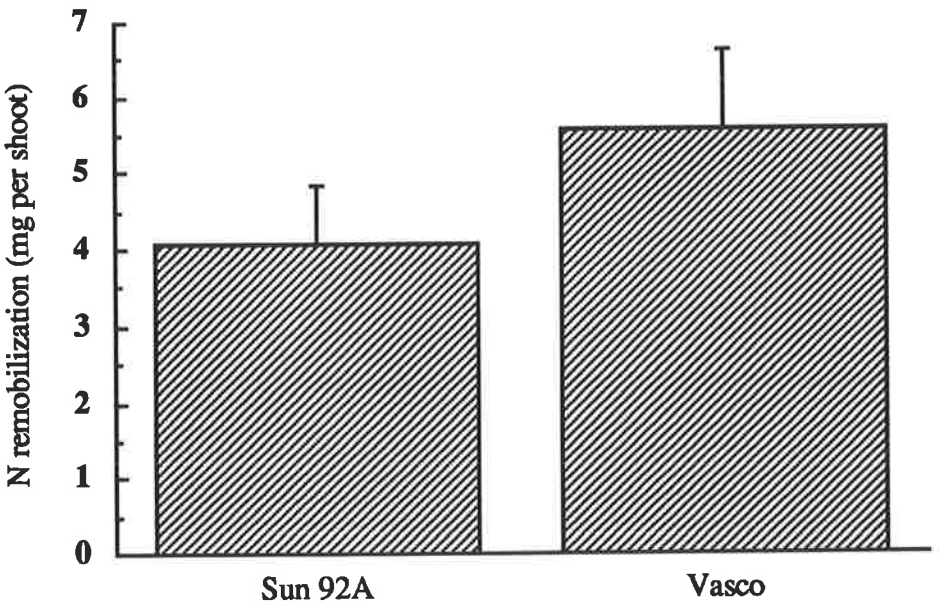

Fig. 4.27. Remobilization of N from other leaves in two wheat cultivars over all treatments during grain filling. Error bars are standard errors.

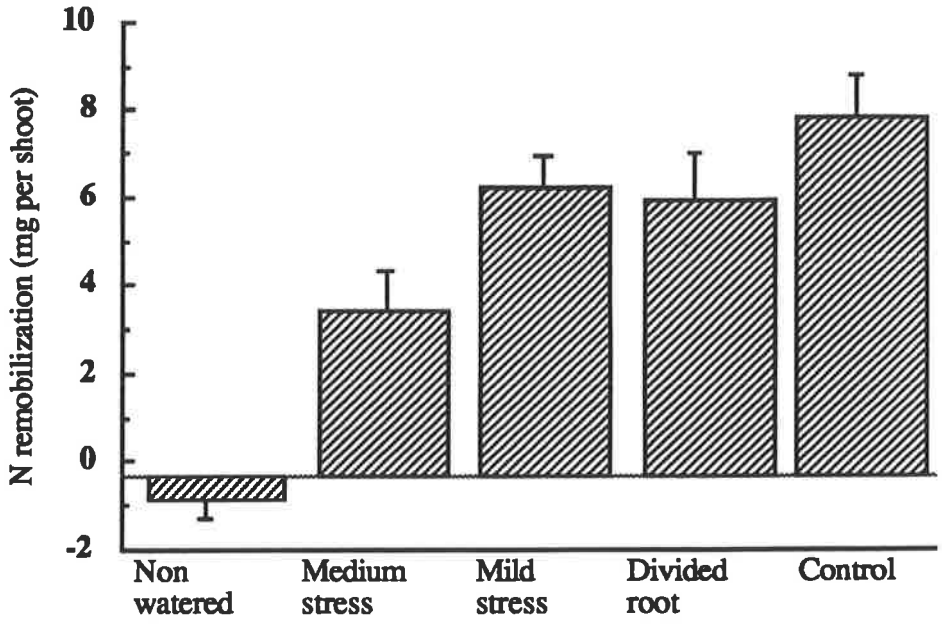

Fig. 4.28. Remobilization of N from other leaves under water stress treatments over both cultivars during grain filling. Error bars are standard errors.

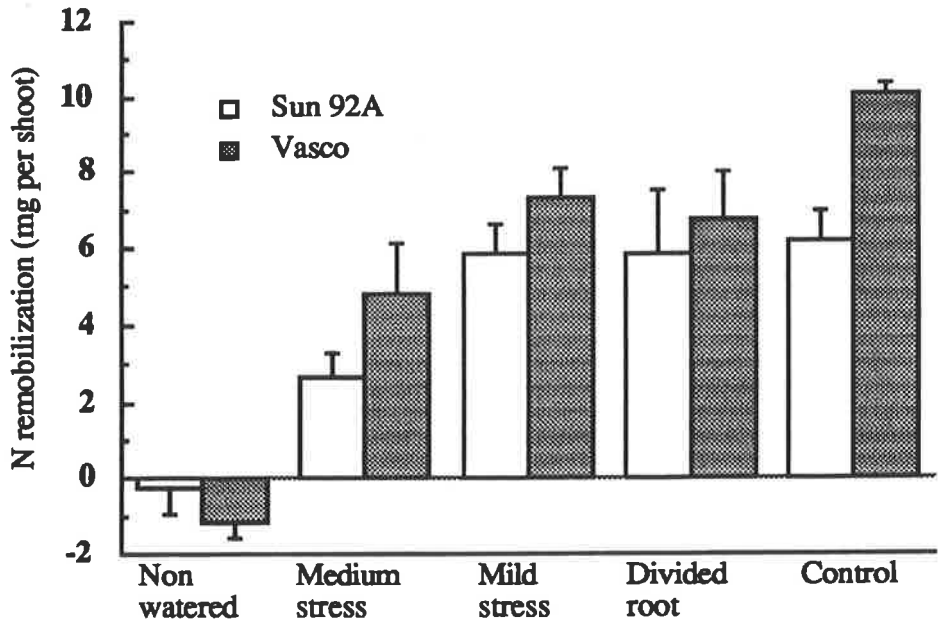

Fig. 4.29. The remobilization of N from other leaves in different levels of water stress during grain filling. Error bars are standard errors.

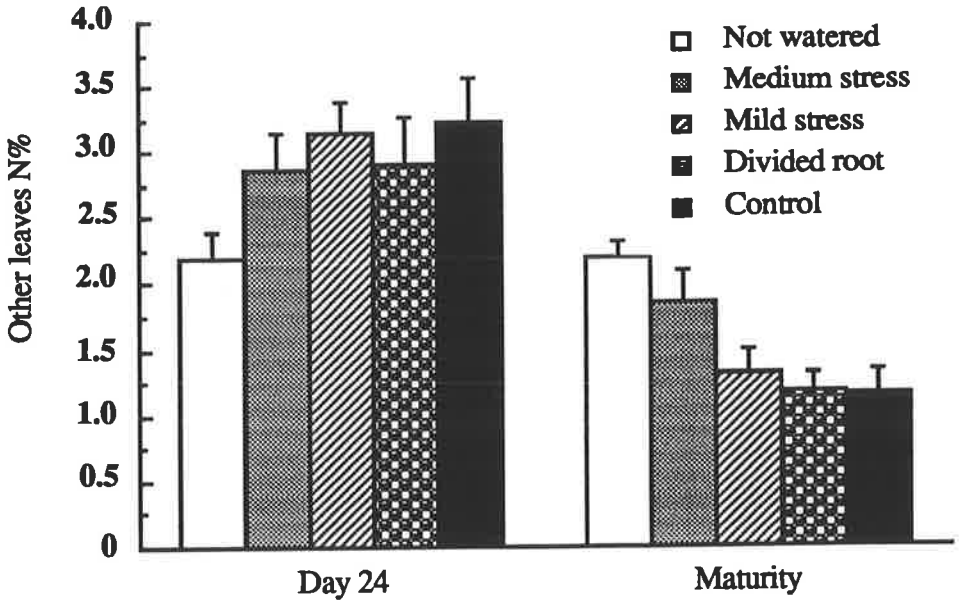

Fig. 4.30. Interactions of harvest time and water treatments overall cultivars on other leaves N percentage during grain filling. Error bars are standard errors.

Table 4.12. DM content and remobilization efficiency of the peduncle in two wheat cultivars as affected by different levels of water stress during grain filling

	Day 24		Maturity		Remobilization efficiency		Apparent contribution to grain	
Treatments	V1	V2	V1	V2	V1	V2	V1	V2
	mg per shoot				percent			
Not watered	133	224	101	213	24	5	42	3
Medium stress	142	243	90	214	36	12	17	4
Mild stress	143	239	124	207	13	13	4	4
Divided root	140	253	125	195	10	23	2	8
Control	157	256	125	199	20	22	4	6

V1: Sun 92A V2: Vasco LSD 5% for Treatments x Cultivars x Harvests: 18

Treatments x Harvests : 13; Harvests x Cultivars : N.S.

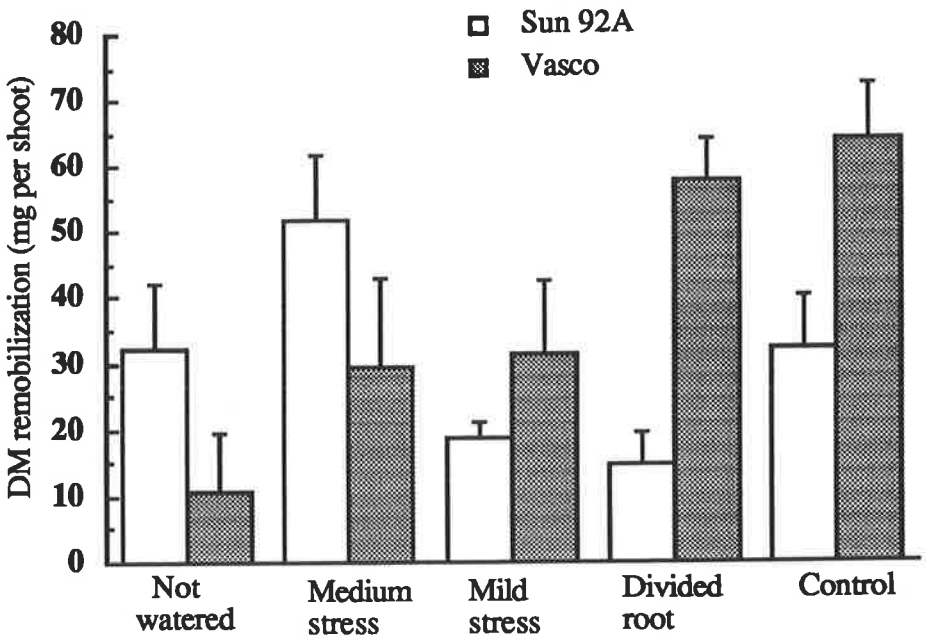

Fig. 4.31. Peduncle DM remobilization in two wheat cultivars between day 24 and maturity under water stress treatments. Error bars are standard errors.

There was a tendency therefore for a higher remobilization under stress in Sun 92A than in the absence of stress. Thus only in Sun 92A, and under severe stress, was there a substantial apparent contribution of DM from the peduncle to the grain (Table 4.12).

4.3.6.6.2 N content, concentration and remobilization

There was more N in the peduncle of Vasco than Sun 92A at day 24 and at maturity (Table 4.13) but similar amounts were remobilized in both cultivars except under non watered conditions (Fig. 4.32). Withholding water completely almost abolished the remobilization of N from the peduncle of Vasco but had only a small effect on Sun 92A. The concentration of N in the peduncle fell between day 24 and maturity, and at maturity it was significantly higher under stress conditions (Fig. 4.33). Sun 92A showed a significantly higher ($P< 0.01$) N concentration than Vasco at day 24 but not at maturity.

Table. 4.13. Peduncle N content of two wheat cultivars as affected by different levels of water stress during grain filling

	Day 24		Maturity		Remobilization efficiency		Apparent contribution to grain	
Treatments	V1	V2	V1	V2	V1	V2	V1	V2
	mg per shoot				percent			
Not watered	1.9	2.7	1.1	2.6	42	3	16	1
Medium stress	2.2	3.0	0.9	2.0	59	33	8	4
Mild stress	2.2	2.9	1.1	2.0	50	31	6	3
Divided root	2.2	3.0	1.1	1.8	50	40	5	6
Control	2.0	2.3	1.0	1.3	50	43	5	3

V1: Sun 92A V2: Vasco LSD 5% for Treatments x Cultivars x Harvests: N.S. Treatments x Harvests: 0.26 ; Treatments x Harvests : 0.25

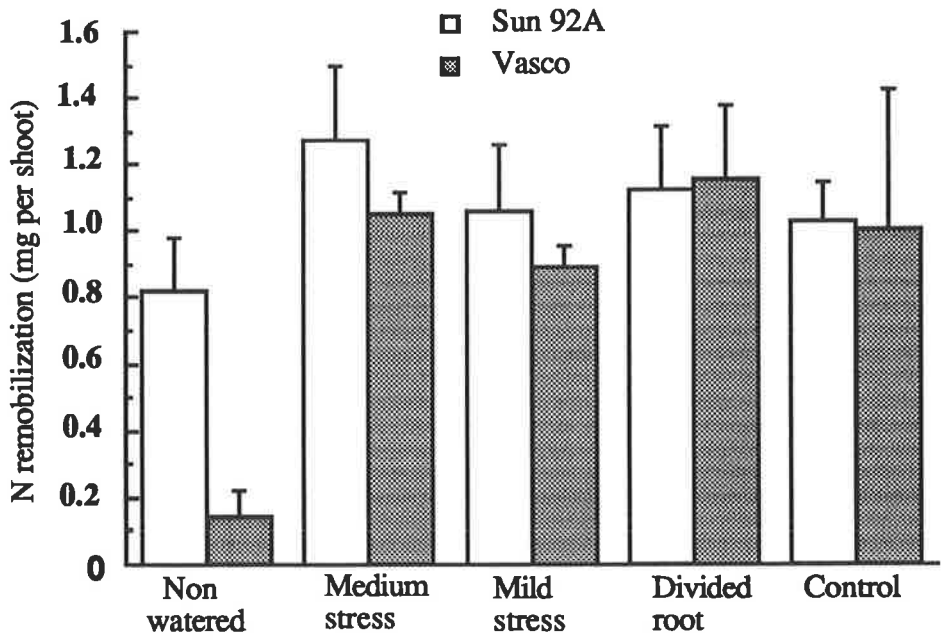

Fig. 4.32. N remobilization from the peduncle between day 24 and maturity in two wheat cultivars under water stress treatments. Error bars are standard errors.

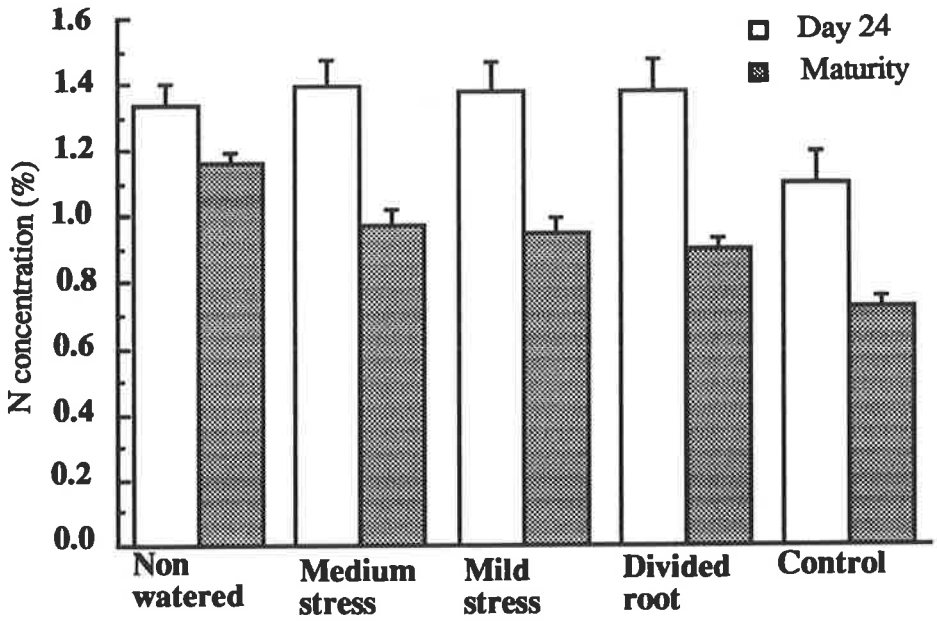

Fig. 4.33. N concentration of the peduncle at day 24 and maturity over both cultivars under water stress during grain filling. Error bars are standard errors.

Table 4.14. Chaff DM content in wheat cultivars under water stress at day 24 and at maturity

	Day 24		Maturity	
Treatments	Sun 92A	Vasco	Sun 92A	Vasco
	mg per shoot			
Not watered	180	335	251	350
Medium stress	215	329	284	395
Mild stress	231	453	303	511
Divided root	228	430	305	517
Control	247	454	286	527

LSD 5% for Treatments x Cultivar x Harvest: N.S. ; Treatments x Cultivars: Harvests x Treatments : N.S.

4.3.6.7 Chaff

4.3.6.7.1 DM content and remobilization

Chaff DM was greater at maturity than at day 24 but the difference was not significant (Table 4.14). Vasco (over both harvests) contained more DM in the chaff than Sun 92A under most treatments and severe stress reduced the net increase in DM between day 24 and maturity in Vasco. The results of this experiment indicated that chaff did not appear to remobilize DM between day 24 and maturity and therefore appeared to make no contribution to the grain DM.

4.3.6.7.2 N content and remobilization

N content of the chaff in Vasco was significantly greater than in Sun 92A under all conditions except medium stress (Table 4.15). Remobilization of N from the chaff was not observed between day 24 and maturity. Therefore the chaff of both cultivars did not appear to contribute to grain N in any stress condition. However under control conditions both cultivars appeared to contribute a small amount of N from the chaff to the grain (8% and 6% for Sun 92A and Vasco respectively). In terms of N concentration, it was significantly ($P< 0.05$) decreased between day 24 and maturity and the decrease in N concentration over both cultivars varied between 7% and 34% (Fig. 4.34). The decline appeared to be due mainly to an increase in DM rather than substantial losses in N.

4.4 Discussion

The main aims of this experiment were to examine the effects of water stress on grain yield, grain N content, DMHI and NHI, and also to determine the effects of water stress on DM and N remobilization from different parts of the shoot of two different wheat cultivars during grain filling. Water stress imposed on the plants clearly affected the accumulation of N and DM in the grain of both cultivars as well as the DMHI and NHI (summarized in Table 4.15). Several studies have found that protein, as a percentage of grain DM, increases with drought (Salter and Goode 1967; Brooks *et al.* 1982). Results

Table 4.15 Chaff N content in wheat cultivars under water stress at day 24 and at maturity

	Day 24		Maturity	
Treatments	Sun 92A	Vasco	Sun 92A	Vasco
	mg per shoot			
Not watered	4.3	7.0	5.2	6.0
Medium stress	5.4	6.4	6.1	6.6
Mild stress	5.9	8.1	6.7	9.3
Divided root	4.7	7.5	5.9	7.5
Control	6.9	8.3	5.2	6.4

Interactions of treatments x cultivar x harvest: N.S.

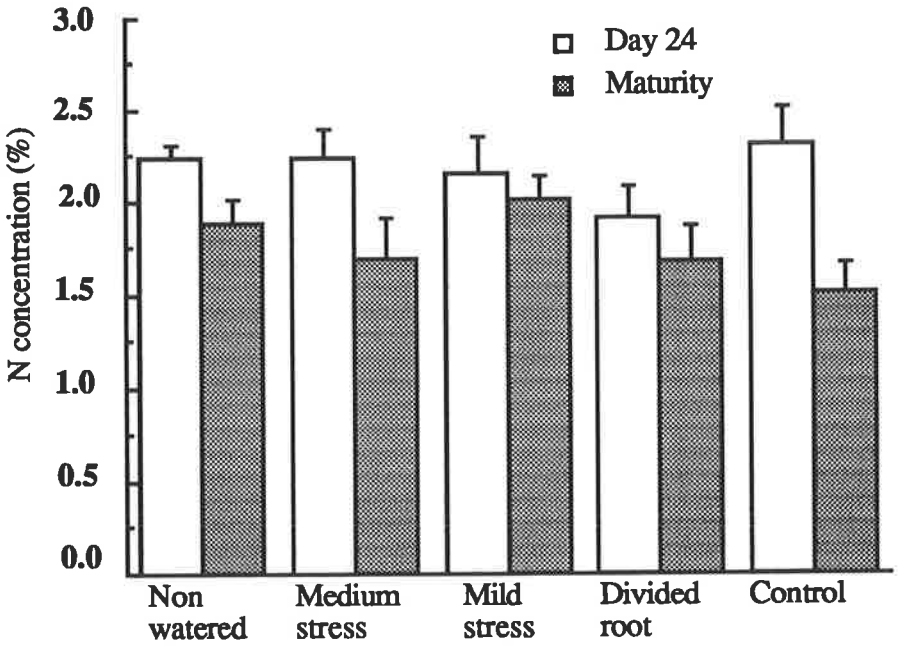

Fig. 4.34. Interaction of water treatments and harvests on N concentration of the chaff over both cultivars at day 24 and at maturity. Error bars are standard errors.

from this study also showed a significant increase of grain N percentage (GNP) under water stress conditions during grain filling (Table 4.16).

The grain DM and N yield per shoot were lower under water stress than in non-stressed conditions, while GNP was higher , indicating that the higher percentage N of grains was due to the small size of the grain under stress. Grain protein concentration is determined by the amount of both protein and starch within the grain, and starch makes up between 70-80% of the total dry weight of grain (Jenner *et al.* 1991; Gleadow *et al.* 1982).

Table. 4.16. Summary of grain parameters under well watered, divided root and water stress conditions (means of 3 treatments) in two wheat cultivars at maturity

	Control		Divided root		Stress	
Parameter	Sun 92A	Vasco	Sun 92A	Vasco	Sun 92A	Vasco
DM(mg per shoot)	1130	1827	1124	1648	752	1198
N (mg per shoot)	35	44	37	43	29	34
N (%)	3.1	2.4	3.4	2.6	4.0	3.0
DMHI(%)	56	51	55	49	45	41
NHI (%)	77	76	76	73	66	63

Comparatively, stress decreased DM accumulation more than N accumulation in the grain under water stress, indicating differences in the relative sensitivity of the two processes to water stress. Biochemical processes concerned with protein accumulation have been observed to be more heat tolerant than the process of starch deposition (Bhullar and Jenner, 1985; Tashiro and Wardlaw, 1991). Nicolas (1985) also found GNP was significantly higher under drought than under well-watered conditions. Grain dry weight is an expression of the rate of DM accumulation and grain growth duration (Brocklehurst 1977). Water stress in this experiment may have reduced grain dry weight in both cultivars by reducing the duration of DM accumulation in the grain.

HI is the end product of the interaction of genetic, environmental and agronomic factors, and is highly influenced by environment (Siddique *et al.* 1989a). Results of the present study showed that HI reached the highest value under non water stressed conditions and was lowest under water stress (Table 4.16). The highest DMHI in this experiment was found in the control treatment in Sun 92A (about 56%) and the lowest value around 30% under the severe stress treatment in Vasco (see Fig.4.5). The highest HI found in the literature was 60% for early planted spring wheat cultivar "Twin" in Utah (Hanks and Sorensen 1984), while the lowest values of slightly less than 20% were found for wheat growing under major water deficit in southern Iran (Poostchi *et al.* 1972), and for wheat growing under severe stress after anthesis in Australia (Passioura 1977). HI generally is higher under favourable conditions and lower under terminal drought.

NHI also reached its highest value (about 80% in Sun 92A) under control conditions and its lowest value (around 50%) in Vasco under the non watered treatment (Fig. 4.6). According to Spiertz and Devos (1983) NHI values in healthy crops lie between 74-78%, and Loffler and Busch (1982) reported values between about 55 and 74%. Therefore it seems that at least for the grain filling attributes observed, the results of this study in the glasshouse and other experiments in the field are comparable.

The potential contribution to grain yield from material stored in different vegetative parts calculated by differences in dry mass between day 24 and maturity gives no direct measure of the amount of stored material actually reaching the grains. Respiration has been measured in the stems of cereals and it has been proposed that this respiration would reduce the contribution to grain yield of material stored in the stem by up to 14-49% (Rawson and Evans 1971). These figures were calculated on the assumption that all of the respiratory substrate was stored carbohydrate. Some respiratory substrate could, of course, have been provided by current assimilation. In this experiment remobilization was calculated from the loss of DM and N between day 24 and maturity, however, remobilization may occur before day 24. Also, leaves and other organs could still be producers or importers of DM between day 24 and maturity, so the estimation of the amount remobilized or contributed to the grain during this time may be an under estimate

of the actual amount. Thus the terms 'apparent remobilization' and 'apparent contribution' to the grain are used in this experiment. Even though the estimates may not be accurate in absolute terms, it is reasoned that the measured responses to the treatments do reflect the effects of stress on remobilization, at least in relative terms. It has been suggested that the ability to remobilize large amounts of assimilate and translocate it to the grain is a desirable trend for cereals in dryland environments (Gale and Youssefian 1985).

Grain yield per shoot of Vasco was considerably greater than that of Sun 92A (Table 4.16). However, for the shoot as a whole, DM remobilization efficiency was lower in Vasco than Sun 92A (Tables 4.4 and 4.17). Therefore it can be concluded that heavier grain yield per shoot in Vasco is not due to a greater remobilization efficiency of DM from the shoot but in absolute terms more DM was remobilized from the shoot of Vasco than Sun 92A.

There were differences between cultivars in the remobilization of N from different parts of the shoot (Table 4.18). The loss of N from other leaves between day 24 and maturity in Vasco was around 40% greater than Sun 92A under water stress and about 60% greater under non stress conditions. In the case of the flag leaf the corresponding differences between the two cultivars were smaller and under stress Sun 92A flag leaves lost more N than did those of Vasco. In both cultivars leaves remobilized far more N than any other organ, and N was apparently not remobilized from the chaff in either cultivar under stress. It appears therefore that the amount of N remobilized depends on cultivar and prevailing growth conditions, and upon the part of the shoot under consideration. Under non stress conditions and stress conditions alike, the gain in grain N from day 24 to maturity exceeded the loss from the rest of the plant.

Somewhat surprisingly, the whole shoot (vegetative parts + grain) gained as much N between day 24 and maturity under stress as in well watered conditions (Fig. 4.15) even though drought reduced uptake of N into the above ground portions of the plant prior to day 24. How much of this N taken up after day 24 might have been remobilized from the roots was not estimated.

Table. 4.17. DM increment (+) and apparent remobilization (-) from vegetative parts in two wheat cultivars under divided root, water stress (mean of 3 treatments) and well watered conditions between day 24 and maturity

	Increment (+) and remobilization (-) (mg per shoot)						Apparent remobilization efficiency (%)					
	Control		Divided root		Stress		Control		Divided root		Stress	
	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2
Grain	+715	+1123	+653	+713	+273	+649	-	-	-	-	-	-
Low. internodes	-82	-106	-73	-51	-33	-13	33	19	32	12	16	3
Peduncle	-32	-67	-15	-58	-34	-24	20	22	10	23	36	12
Flag leaf	-39	-50	-66	-28	-10	+5	20	22	30	13	10	4
Other leaves	-73	-93	-52	-72	-17	-9	33	17	22	14	5	0
Chaff	+39	+73	+77	+87	+70	+46	-16	-16	-33	-20	-34	-12

V1: Sun 92A V2: Vasco

Table. 4.18. Grain N increment (+) and vegetative parts remobilization (-) in two wheat cultivars under divided root, water stress (mean of 3 treatments) and non stress control between day 24 and maturity

	Increment (+) and remobilization (-) (mg per shoot)						Apparent remobilization efficiency (%)					
	Control		Divided root		Stress		Control		Divided root		Stress	
	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2
Grain	+21	+29	+24	+20	+13	+21	-	-	-	-	-	-
Low. internodes	-1.5	-2.7	-2.2	-2.7	-0.9	-1.6	71	62	78	67	47	42
Peduncle	-1.0	-1.0	-1.1	-1.2	-1.0	-0.7	50	43	50	40	50	22
Flag leaf	-4.9	-5.8	-4.5	-5.5	-3.0	-2.3	74	81	71	80	39	40
Other leaves	-6.2	-10.1	-5.9	-6.2	-2.7	-3.7	73	73	70	61	32	30
Chaff	-1.7	-1.9	1.2	0	+0.8	+0.2	24	23	-25	0	-15	-11

V1: Sun 92A V2: Vasco

By maturity, the N content in vegetative parts had declined considerably more, in relative terms, than did DM. Non stressed plants remobilized more N than stressed plants. This result confirms that water stress is an important factor affecting the accumulation of DM and N in the grain and also remobilization of DM and N from the shoot during grain filling. The apparent contribution of assimilates from different parts of the shoot to the grain was estimated by calculating the percentage contribution of remobilized material to the mass of grain accumulated by the grain between day 24 and maturity rather than to total grain mass. If all the mass lost from the vegetative organs was remobilized to the grains it is clear that after day 24 the vegetative organs are the major source of assimilate for grain filling under both water stress and non water stress conditions. In this experiment the proportion of DM apparently contributed from all vegetative parts of the shoot to the grain was 30% and 27% for Sun 92A and Vasco under control conditions, 31% and 29% under divided root conditions and 60% and 10% under stress conditions, respectively (Table 4.19). Water stress appeared to increase the contribution of DM, especially from the internodes and peduncle of Sun 92A but to diminish it from all parts of the shoot of Vasco.

Chaff did not appear to contribute DM to the grain possibly because chaff senescence was later than other parts of the shoot.

Gallagher *et al.* (1975) and Daniels *et al.* (1982) observed that high yielding crops had both a greater increase in total crop dry mass after anthesis and a smaller loss of mass from the vegetative organs and hence a lower pre-anthesis contribution to grain growth than lower yielding crops. In this experiment, Vasco with a higher total grain mass than Sun 92A also accumulated more DM in vegetative parts and lost proportionately less under drought.

Water stress reduced the fraction of the N content of the shoot remobilized (Table 4.18) in both cultivars alike, and had the greatest effects on the leaves which made the largest contribution to grain N. Estimates for the contribution under stress (Table 4.19) reflect the fact that accumulation of N in the grain under stress is reduced relatively more than the loss of N from the vegetative organs.

Table. 4.19. Apparent contribution of DM and N (as a percentage of the total amounts in the grain) from different parts of the shoot to the grain in two wheat cultivars under divided root, water stress (mean of 3 treatments) and non stress control between day 24 and maturity

	DM						N					
	Control		Divided root		Stress		Control		Divided root		Stress	
	V1V1	V2	V1	V2	V1	V2	V1	V2	V1	V2	V1	V2
	%											
Low. internode	11	9	11	7	27	2	7	9	10	13	7	7
Peduncle	4	6	2	8	21	4	5	3	5	6	10	3
Flag leaf	5	4	10	4	6	1	23	20	20	26	16	10
Other leaves	10	8	8	10	6	3	30	35	26	32	16	16
Chaff	-	-	-	-	-	-	8	6	-	-	-	-
Total	30	27	31	29	60	10	73	73	61	77	49	36

V1: Sun 92A V2: Vasco

It is concluded that water stress during grain filling reduced grain yield, N yield, DMHI and NHI. Water stress also reduced DM and N remobilization from the shoot and the reduction was related to the severity of the water stress. Remobilization of DM was more sensitive than N indicating differences in the relative sensitivity of the two processes to water stress. Depriving the upper section of the root to the water had no major effects on remobilization of DM and N from the shoot to the grain of both wheat cultivars. Leaves made the largest contribution to grain N and internodes the largest contribution to grain DM.

Chapter 5. Effects of water stress on remobilization of N and other DM from the shoot of three cultivars of barley during grain filling

5.1 Introduction

Malting barley is an important and high value crop in southern Australia. Many farmers who grow barley do not apply N fertiliser because of the risk of increased grain protein levels. On the other hand, as the intensity of cropping increases and soil fertility, in general, declines, N deficiency is becoming a major factor limiting both grain yield and grain protein in winter cereals grown in South Australia (McDonald 1989).

In South Australia, areas where malting barley can be grown successfully year after year are relatively small. There is also a significant problem with fluctuations in the malting performance of barley in those areas of South Australia where growing conditions can vary widely from season to season. The rainfall and temperature during the growing season affect a number of components of malting quality (e.g. Stuart *et al.* 1988; Logue *et al.* 1994) , of which grain protein concentration is one. One of the main requirements for acceptable malting quality is a low (< 10%) grain protein concentration. Water stress during grain filling not only reduces grain yield but also increases GNP, which is not desirable for malting quality.

In many areas with a Mediterranean-type climate, the fertility of the soil and soil water after anthesis are usually low, and soil N and water are greatly depleted by the time of anthesis. Under such conditions very little uptake of N occurs during grain filling and nearly all N in the grain is derived from remobilization from the vegetative parts of the shoot. Reserves of C and N accumulated immediately after anthesis are more readily remobilizable, and are usually involved in yield formation to a larger extent, than pre-anthesis reserves. Assimilates accumulated before anthesis are considered to compensate for insufficient current photosynthesis only in the case of severe environmental stress, and to contribute to yield stability (Herzog 1986).

There are significant differences between individual organs with regard to translocation of their stored N. Leaves are able to remobilize nearly 80 percent, and

stems up to 65 percent of their N present at anthesis (Herzog 1986). The responses of different species under different water deficit environments (severe stress and mild stress) differ markedly and the environmental effects on gas exchange are much less for barley than for wheat (Herzog 1986). There are also reports that the N translocated from vegetative parts to the developing grain after anthesis is under genetic control (Van Stanford and Mackown 1987; Halloran 1981).

The development of a more detailed knowledge of the interaction between genotype and environment (water stress) in relation to remobilization of DM and N storage in the vegetative parts of the shoot to the grain and also N content and concentration in the grain will aid breeders in the improvement of malting varieties.

This study examined the genetic variability in responses to water stress among three barley cultivars. It also examined remobilization of DM and N from the shoot in three different cultivars subjected to water stress during grain filling. The study aimed at the following:

i) To determine the effects of post-anthesis water stress on grain DM, DMHI, N content, GNP and NHI among three barley cultivars differing in protein content.

ii) To evaluate differences in post-anthesis N and DM remobilization among barley cultivars under different levels of water stress.

iii) To investigate the importance of different parts of the shoot as sources of remobilized N and DM under water stress.

iv) To estimate the apparent remobilization of N and DM from different parts of the shoot and also the apparent contribution of them to the grain during grain filling.

5.2 Materials and methods

The experiment was conducted in the glasshouse under natural light and controlled temperature (25±2 °C during the day and 16±2°C at night) conditions. Three barley cultivars, Forrest (moderate protein), W.I.2692 (moderate protein) and W.I.2808 (low protein) were grown under 4 levels of water stress and well watered conditions as control. Ten seeds per pot were sown and seedlings thinned to 6 plants per pot after

emergence and plants were restricted to a single culm by removing all tillers as they emerged. The plants were watered regularly until day 10 after anthesis to minimise the possibility of pre-anthesis moisture stress. Stress was imposed from day 10 after anthesis as described in Chapter 3. Harvests were made at 24 days after anthesis and at maturity. Different parts of the shoot, including the chaff, peduncle, internodes, flag leaf, other leaves and grain from each replicate were oven dried at 85°C for 48 h, weighed and the N concentration determined by Kjeldahl analysis (see Chapter 3 for details).

5.3 Results

5.3.1 Grain DM content, accumulation and HI

In all three barley cultivars, grain DM was significantly ($P < 0.001$) higher at maturity than at day 24, and greater under control condition than under all water stress treatments both at day 24 and at maturity (Table 5.1). On day 24 the divided root treatment resulted in lower grain DM than withholding water in two of the three cultivars. At maturity under withholding water condition, grain yield decreased in all

Table 5.1. Grain DM of barley cultivars at day 24 and at maturity under different levels of water stress

	Day 24			Maturity		
Treatments	V1	V2	V3	V1	V2	V3
	mg per shoot					
Not watered	626	537	630	712	644	727
Medium stress	516	565	611	866	668	761
Mild stress	729	725	748	1072	953	968
Divided root	531	532	556	961	933	1040
Control	837	819	950	1085	1052	1234

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5%:Cultivar x Harvest : 16; Treatment x Harvest : 21; Treatment x Harvest x Cultivar : 36

Table 5.2. Grain yield under water stress as a percentage of control in three barley cultivars at day 24 and maturity

	Day 24			Maturity		
Treatments	V1	V2	V3	V1	V2	V3
Not watered	75	66	66	66	61	59
Medium stress	73	69	64	80	63	62
Mild stress	87	69	79	99	91	78
Divided root	63	65	59	89	89	84
Control	100	100	100	100	100	100

V1: Forrest V2: W.I.2692 V3: W.I.2808

three cultivars. Among the three barley cultivars, W.I.2692 had the lowest grain yield under all conditions. The grain yield under each treatment as a percentage of control is shown in Table 5.2.

At day 24, percentage reductions in grain yield did not differ greatly between the three cultivars. At maturity, Forrest was relatively less sensitive than the other two cultivars under all water stress treatments. It was also noted that the divided root treatment had no greater effect at maturity than did mild stress.

The interaction between cultivars and water stress was significant ($P< 0.01$) for grain yield accumulation between day 24 and maturity (Fig. 5.1). The accumulation was greatest in W.I.2692 and W.I.2808 under the divided root treatment, and severe stress significantly reduced it. In Forrest however, all treatments except the most severe stress resulted in greater gain in grain DM between the two harvests than was observed in well watered plants.

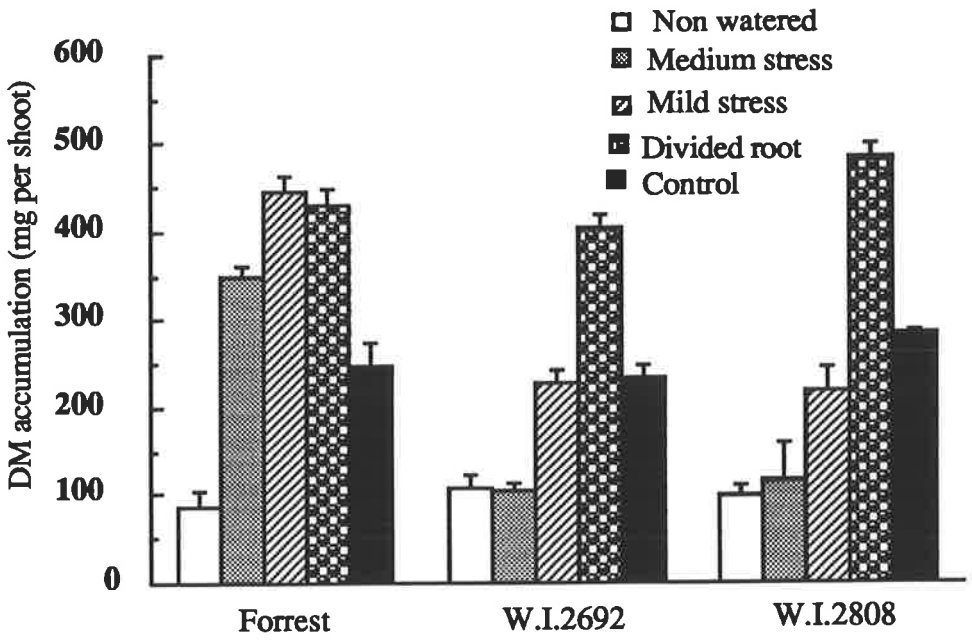

Fig. 5.1. The effect of water stress in three barley cultivars on grain DM accumulation between day 24 and maturity. Error bars are standard errors.

The Harvest Index (HI) of the three barley cultivars differed significantly in response to water stress. Under control conditions, HI in all cultivars was significantly ($P< 0.001$) greater than under non-watered conditions or medium water stress (Fig. 5.2). W.I.2808 had the highest HI at both harvests.

5.3.2 Grain N accumulation and NHI

Grain N content differed between cultivars at day 24. W.I.2692 and W.I.2808 accumulated more N in the grain under well-watered conditions than under stress, while Forrest accumulated the highest level of N under non-watered conditions (Table 5.3). Also at day 24, all cultivars accumulated less N in the grain in the divided root treatment. At maturity, the yield of N in the grain was greater in non-stressed than in stressed plants, and there was little difference between any of the water stress treatments. Forrest was less affected by the stress treatments than the other two cultivars.

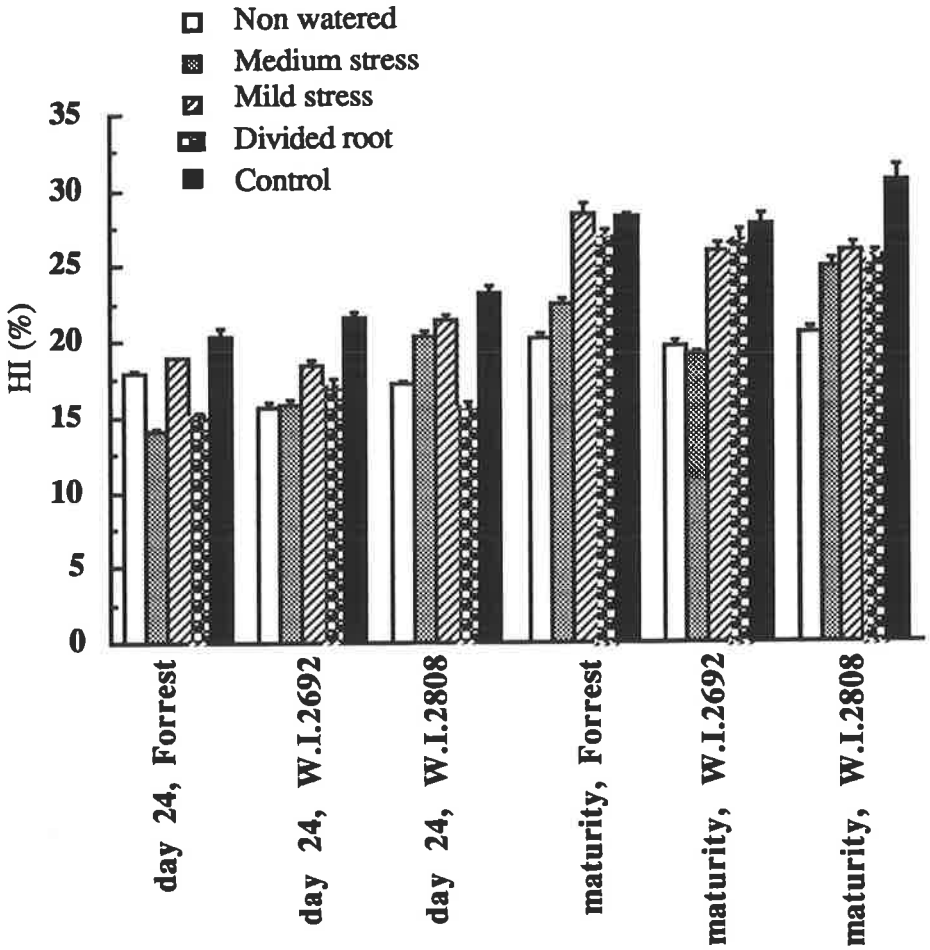

Fig. 5.2. The effects of water stress on DM HI of three barley cultivars at day 24 and at maturity. Error bars are standard errors.

Table 5.3. Grain N yield of three barley cultivars under water stress treatments at day 24 and maturity.

	Day 24			Maturity		
Treatments	V1	V2	V3	V1	V2	V3
	mg per shoot					
Not watered	21	16	16	23	19	19
Medium stress	12	14	15	21	18	18
Mild stress	17	16	18	25	22	23
Divided root	12	14	11	22	21	24
Control	17	21	20	25	25	28

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% Cultivar x Harvest x Treatment: 2.1

N accumulation between day 24 and maturity was generally greater in Forrest than in the other two cultivars. It was of interest that significantly more N accumulated in the grain of the divided root treatment than in any other treatment (Fig. 5.3). Severe water stress reduced the increment in all three cultivars. Grain N percentage (GNP) was significantly ($P < 0.001$) higher in all three barley cultivars under severe water stress than under conditions of adequate water at both harvests. Under the severe water stress (non-watered) treatment Forrest at day 24 had the highest GNP, 3.38% (Fig. 5.4). Although the well-watered treatments resulted in the lowest GNP in the grain (Fig. 5.4), NHI (Fig.5.5) was greatest under well-watered conditions in all three barley cultivars except Forrest where NHI was highest under the non-watered treatment at day 24. NHI increased from day 24 to maturity; there did not appear to be a consistent effect of stress on NHI; there was little difference between cultivars.

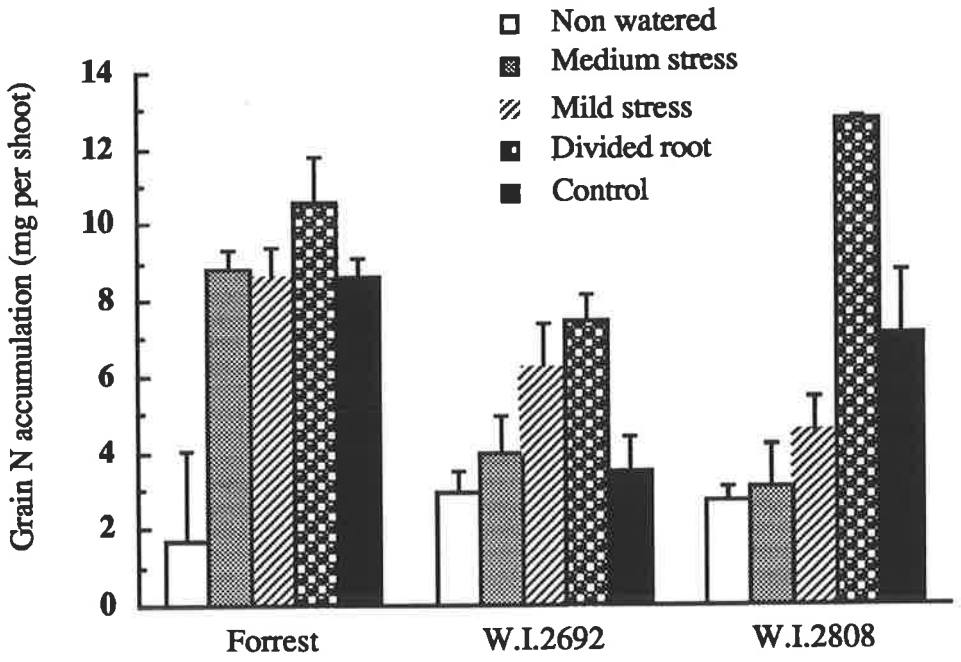

Fig. 5.3. The effect of water stress on the accumulation of N in the three barley cultivars between day 24 and maturity. Error bars are standard errors.

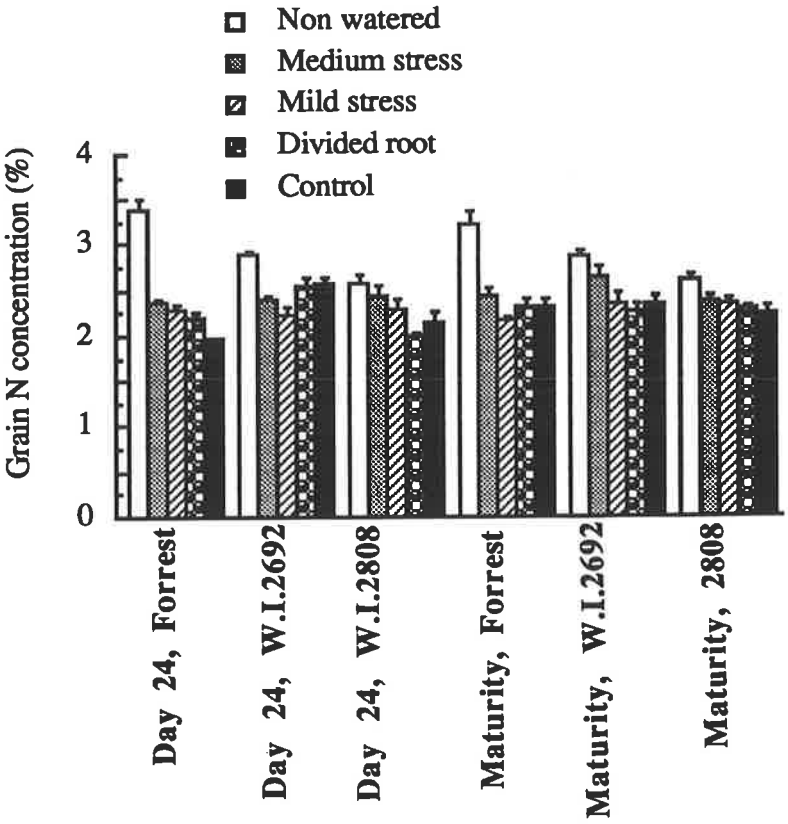

Fig. 5.4. The interaction between water stress, cultivars and harvests on grain N percentage during grain filling. Error bars are standard errors.

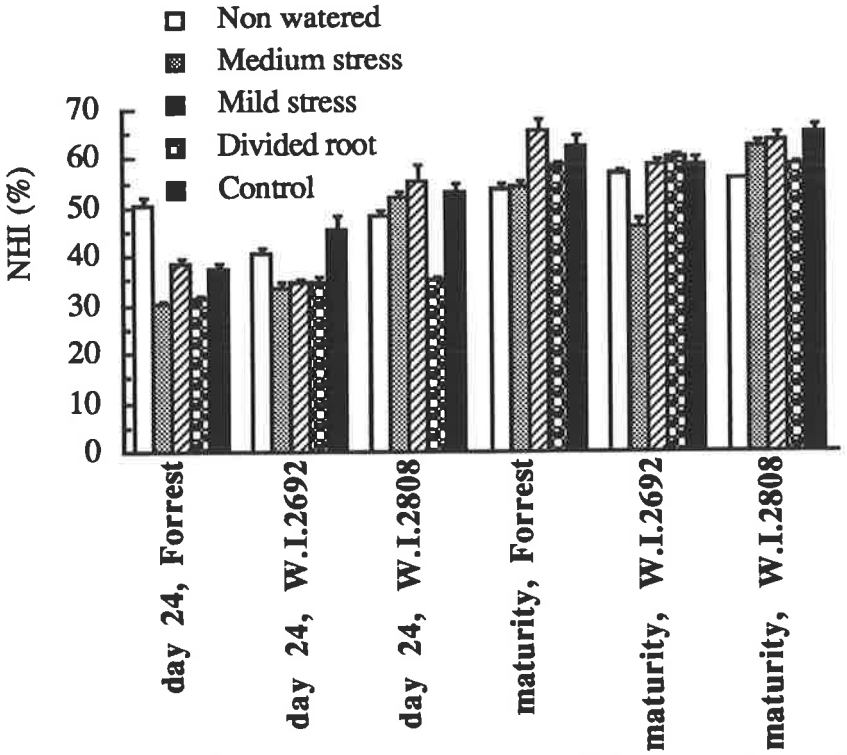

Fig. 5.5. The interaction between treatments, cultivars and harvests on NHI of the grain. Error bars are standard errors.

5.3.3 DM and N content in the whole shoot (vegetative parts + grain)

5.3.3.1 DM content in the whole shoot

DM content significantly decreased under water stress. Water stress generally reduced DM content of the shoot at both harvests but the response of cultivars differed under the water stress treatments and between harvests (Fig. 5.6). At day 24, the divided root treatment significantly reduced DM of the shoot in all cultivars, but at maturity shoot DM was unaffected by this treatment in W.I.2808. With Forrest and W.I.2692, the more severe the stress the greater was the reduction in shoot DM, whereas with W.I.2808 withholding water reduced DM to a lesser extent than did the medium stress treatment.

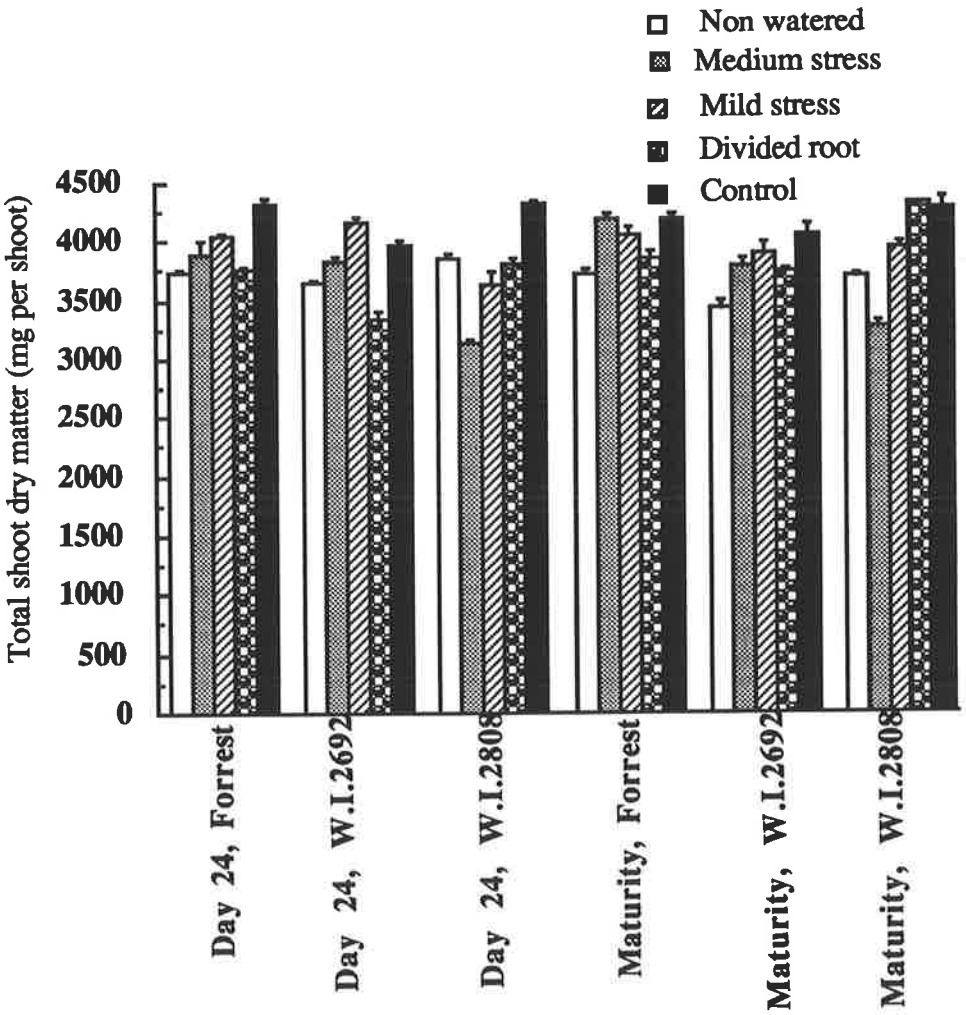

Fig. 5.6. The effect of water stress on total shoot DM at day 24 and at maturity in 3 varieties of barley. Error bars are standard errors.

5.3.3.2 N content in the whole shoot (vegetative parts + grain)

There was no increase in the amount of N in the shoot between day 24 and maturity in Forrest and W.I.2692. However in W.I.2808 there was an increase in shoot N in well-watered and under mild stress conditions. In the other two cultivars (Forrest and W.I.2692), there was a decrement in the amount of N at maturity compared to day 24 in several of the stress treatments. Forrest under non-watered conditions, contained significantly more N in the shoot than all other treatments at the final harvest (Fig. 5.7).

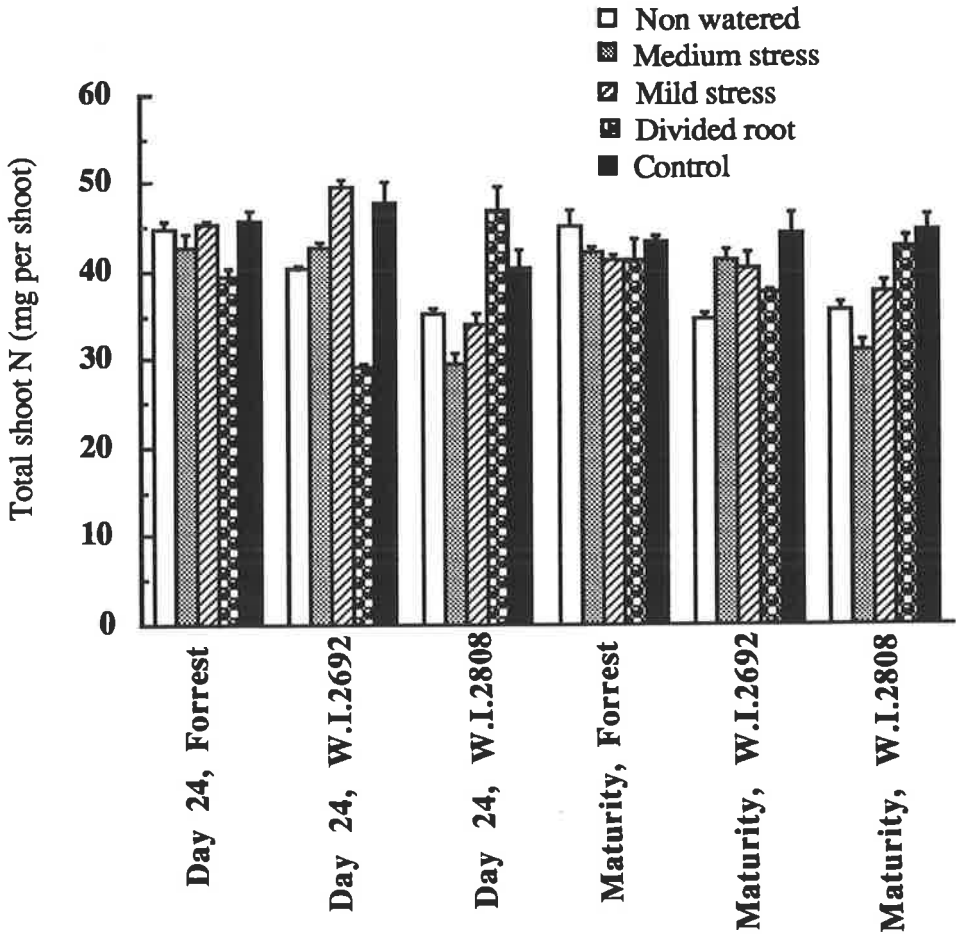

Fig.5.7. Effects of water stress on total shoot N content at day 24 and maturity. Error bars are standard errors.

5.3.3.3 Dry matter, N content and their remobilization from the vegetative parts of the shoot.

5.3.3.3.1 Dry matter content and remobilization from the vegetative organs

DM contents of the shoot (less the grains) in the three barley cultivars under water stress treatments and at both harvests are presented in Table 5.4. DM content of the shoot was generally greater at day 24 than at maturity. A small proportion of the total DM (10-16%) appeared to have been remobilized in the watered control, and stress seemed to have reduced remobilization in all cultivars.

DM was remobilized from the shoot of all three barley cultivars between day 24 and maturity. Significantly more DM was remobilized from the shoot in the moderate protein cultivars (Forrest and W.I. 2692) than in W.I. 2808. Among treatments, DM remobilization (averaged over all cultivars) was greatest under control and mild stress, and a smaller and similar amount was remobilized from the divided root, non-watered and medium stress treatments. The interaction between cultivars and treatments on shoot DM remobilization was significant (Fig. 5.8). In Forrest more DM was remobilized from the shoot under control, mild stress and divided root conditions than under non watered or medium stress. In W.I.2692 however, remobilization of DM was similar under control, severe stress (non watered) and medium stress, and more DM was remobilized under mild stress. In W.I.2808 no remobilization of DM was found under mild stress. Also in W.I.2808 and W.I. 2692 the divided root treatment appeared to have stopped remobilization.

5.3.3.3.2 N content and remobilization from the vegetative organs

At day 24, N content of the shoot (less the grain) in the Forrest and W.I.2692 was similar under control, mild stress and medium stress conditions (Table 5.5). N content was similar under divided root and non-watered conditions and was significantly lower than the control. N content of the low protein cultivar (W.I.2808) was significantly

Table 5.4. DM (mg/shoot) content in the vegetative parts of the shoot of three barley cultivars under water stress at day 24 and maturity.

	Day 24			Maturity			Remobilization efficiency %		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
Not Watered	2848	2868	3051	2706	2627	2816	5	9	8
Medium Stress	3135	3043	2399	2996	2846	2301	4	6	4
Mild stress	3125	3170	2736	2708	2685	2726	13	15	0
Divided root	2982	2590	2996	2550	2545	3001	14	2	0
Control	3270	2955	3170	2740	2681	2816	16	10	11

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Cultivar x Harvests x Treatments:142; Treatments x Harvests : 82; Harvests x Cultivars : 63

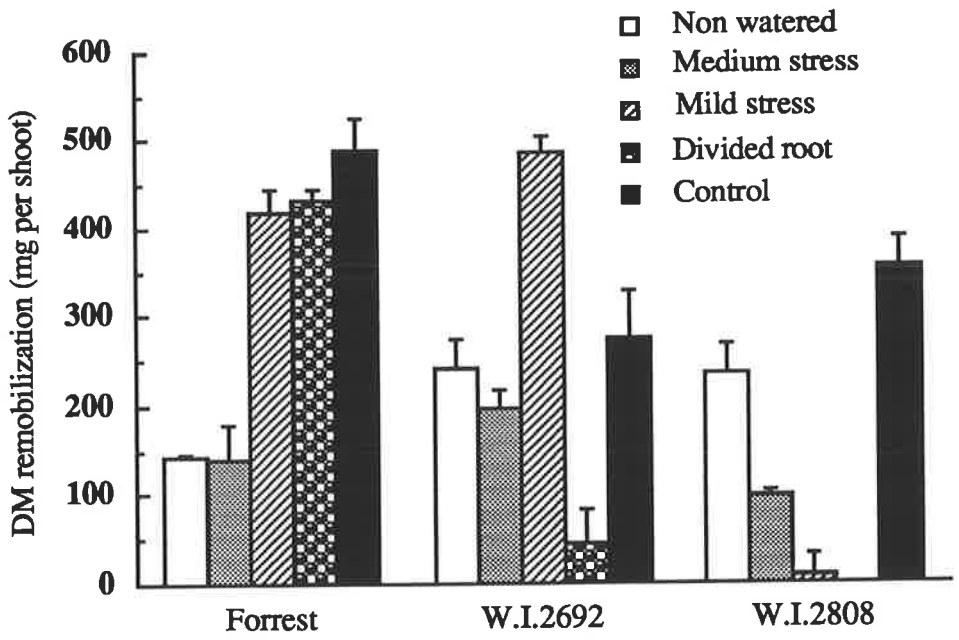

Fig. 5.8. The remobilization of DM from the shoot of three barley cultivars under water stress treatments between day 24 and maturity. Error bars are standard errors.

lower than the other 2 cultivars under all water stress conditions at the first harvest. At maturity also, except in the divided root treatment, N content of the two moderate protein cultivars was greater than the low protein one (Table 5.5). The N remobilization efficiency also differed between cultivars (Table 5.5). For instance, moderate protein cultivars (Forrest and W.I.2692) had a higher efficiency than the low protein cultivar (W.I.2808). The ranking of cultivars in terms of the amount of N remobilized from the shoot was: W.I.2692 > Forrest >W.I. 2808. The remobilization of N from the shoot of barley cultivars differed in response to the different levels of water stress (Fig.5.9).

Table 5.5. N content of the shoot in barley cultivars under different levels of water stress during grain filling

	Day 24			Maturity			Remobilization efficiency (%)		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
	mg per shoot								
Not Watered	20.6	22.7	17.3	18.0	14.1	15.1	13	37	13
Medium Stress	28.1	28.8	13.6	18.0	20.3	12.2	36	30	10
Mild stress	25.8	28.8	17.1	15.2	15.5	13.2	41	46	23
Divided root	25.3	25.5	21.0	15.7	13.8	16.7	38	46	20
Control	28.0	29.9	18.2	15.1	17.4	14.7	46	42	19

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Cultivars x Treatments x Harvests:2.5; Treatments x Harvests : 1.4 ; Harvests x Cultivars : 1.1

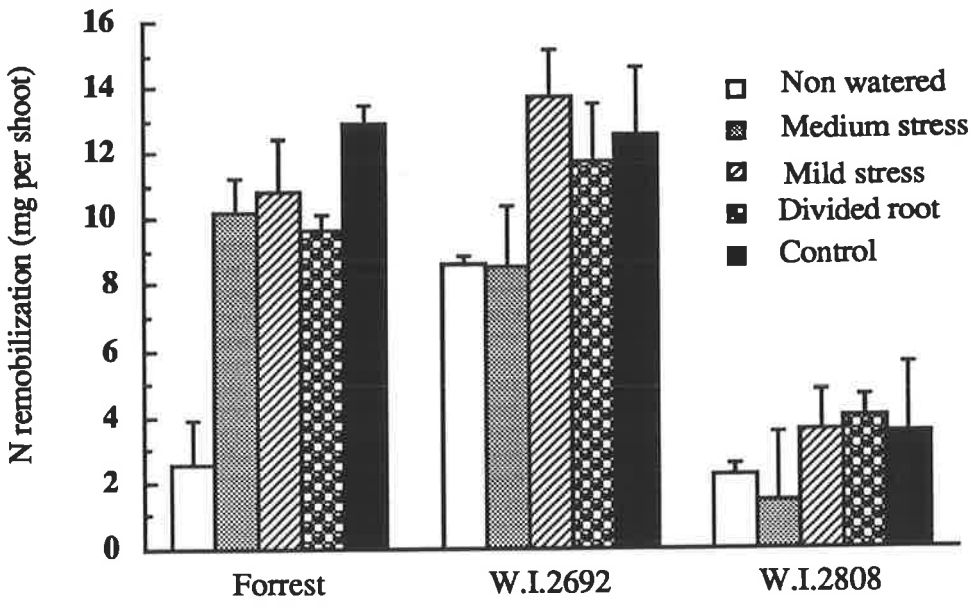

Fig. 5.9. The remobilization of N from the shoot in barley cultivars under water stress treatments between day 24 and maturity. Error bars are standard errors.

Approximately the same quantities of N (10-14 mg) were remobilized from Forrest and W.I.2692 under well watered or mild stress conditions. Severe stress greatly reduced remobilization in Forrest, but not in W.I.2692. Compared to the other two cultivars, much less N was remobilized from W.I.2808, and stress had little effect.(Fig. 5.9).

5.3.3.3.3. Lower stem internode DM and remobilization

Over all water stress treatments more DM was accumulated in thelower internodes of W.I.2692 than in Forrest and W.I. 2808 at both harvests (Table 5.6). A greater amount of DM also accumulated in the internodes under control conditions than under non watered conditions (Table 5.6). DM content was also greater under divided root treatment than medium stress and mild stress at both harvests.

Table 5.6. DM content of the lower internodes in barley cultivars under different levels of water stress at day 24 and maturity

	Day 24			Maturity			Remobilization efficiency %		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
	mg per shoot								
Not watered	1376	1528	1500	1256	1258	1309	9	18	13
Medium stress	1529	1559	1364	1449	1454	1178	5	5	14
Mild stress	1536	1590	1419	1319	1343	1239	18	16	8
Divided root	1412	1404	1454	1180	1295	1387	16	8	5
Control	1510	1595	1615	1327	1314	1313	12	18	19

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Harvest x Cultivar : N.S. ; Harvest x Treatment : 55; Treatment x Harvest x Cultivar : 95

In terms of remobilization less than 20% of the DM appeared to have been remobilized from the lower stem internodes under any conditions. The response of the different cultivars to water stress was significantly different (Fig. 5.10). In Forrest, DM remobilization was significantly greater under mild stress than all other treatments. The severe and medium stress conditions reduced the remobilization of DM from the lower internodes of this genotype. However in W.I.2692, DM remobilization was similar under severe and mild stress and control conditions while it was reduced under medium stress and divided root conditions. In W.I.2808, DM remobilization was similar under water stress treatments, while it was less under divided root treatment.

5.3.3.3.4 N content and remobilization

N content of the lower internodes, averaged over all water stress treatments, was greater at day 24 than at maturity in all cultivars (Table 5.7). At day 24, mild stress conditions significantly increased the N content of the internode compared to control

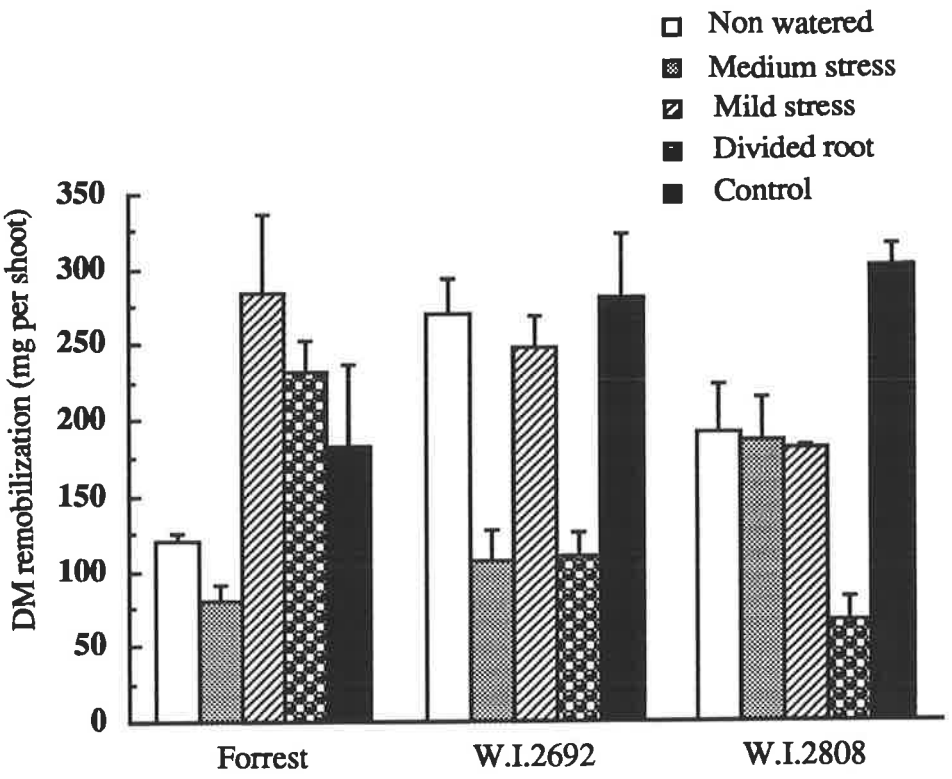

Fig.5.10. The remobilization of DM from lower internodes in three barley cultivars under different levels of water stress between day 24 and maturity. Error bars are standard errors.

conditions but no other treatment had any significant effect, either at day 24 or at maturity. Both Forrest and W.I.2692 (moderate GPC) remobilized more N from the internodes than W.I.2808, a cultivar with low GPC, especially under water stress (Table 5.7). Although the responses of the cultivars to the different levels of water stress were not similar (Fig.5.11), all cultivars remobilized more N from the internode under mild stress than under other conditions.

Table 5.7. N content and remobilization efficiency of N in the internodes of barley cultivars under different levels of water stress.

	Day 24			Maturity			Remobilization efficiency %		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
	mg per shoot								
Not watered	5.6	4.7	3.8	3.8	4.1	3.9	32	13	-3
Medium stress	5.4	5.4	3.6	4.3	5.2	2.8	20	4	22
Mild stress	5.7	6.6	3.6	3.7	4.1	2.9	35	38	19
Divided root	4.5	5.8	4.4	3.4	4.0	4.0	24	31	9
Control	4.3	5.7	3.9	4.1	4.6	3.7	5	19	5

V1: Forrest V2: W.I.2692 V3: W.I.2808 L.S.D 5% for Cultivar x Treatments x Harvests: NS; Harvests x Treatments:0.52; Harvests x Cultivars: 0.15

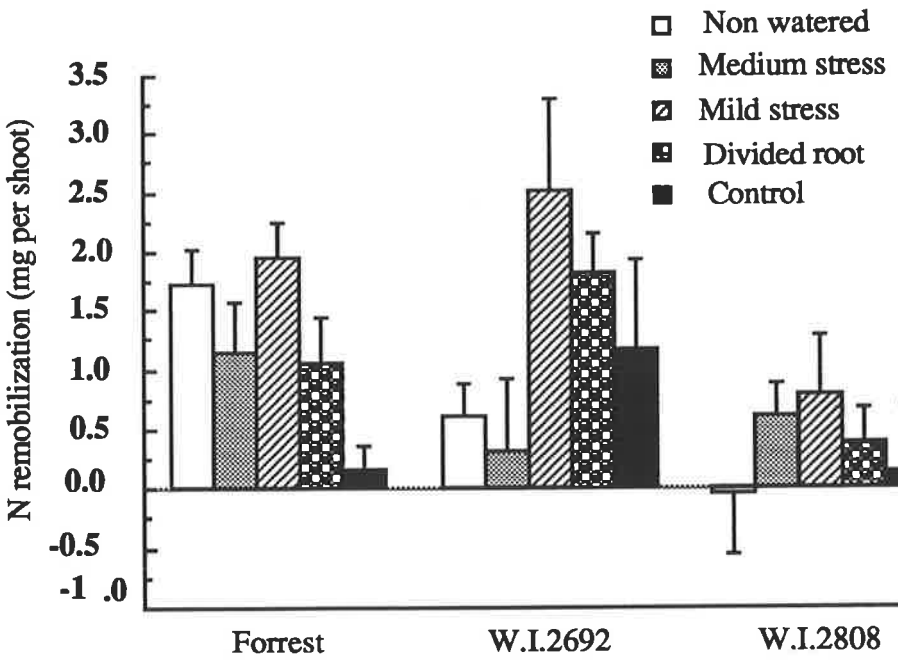

Fig. 5.11. The remobilization of N from lower internodes in three barley cultivars under water stress between day 24 and maturity. Error bars are standard errors.

5.3.3.3.5. Peduncle DM content and remobilization

Peduncle DM content at day 24 was significantly greater (about 2 times) than at maturity in all cultivars and over all water stress treatments (Table 5.8). However the interaction between cultivar and water stress treatments was significant at the two harvests. For example at day 24, W.I.2808 under medium stress showed a lower amount of DM than the control but at maturity medium stress had no effect.

About 50% of the DM was remobilized in the peduncle between day 24 and maturity and except for mild and medium stress in W.I.2808, stress had little effect on the amount of DM remobilized (Fig.5.12).

Table 5.8. DM content and remobilization efficiency of the peduncle in three barley cultivars under different levels of water stress at day 24 and maturity

	Day 24			Maturity			Remobilization efficiency (%)		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
	mg per shoot								
Not Watered	263	246	244	163	156	156	38	36	36
Medium Stress	263	272	138	135	137	99	49	50	28
Mild stress	277	249	123	141	122	112	57	51	20
Divided root	247	182	241	113	117	113	50	32	53
Control	324	196	248	185	115	107	43	35	57

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Harvest x Treatment : N.S.; Harvest x Cultivar 14.1; Harvest x Cultivar x Treatment : 32

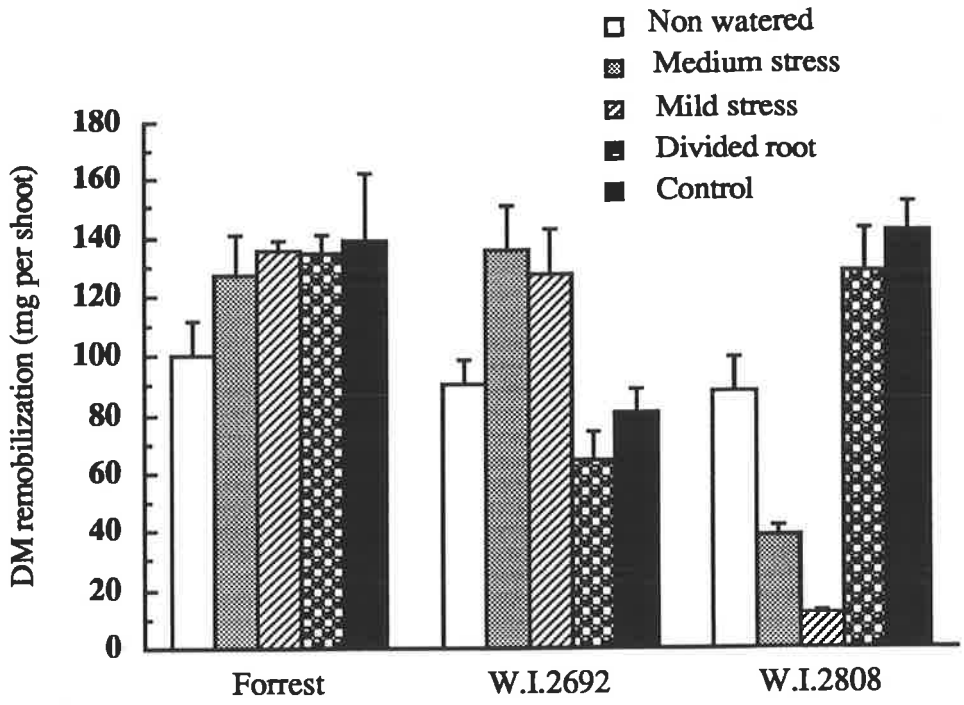

Fig. 5.12. The remobilization of DM from the peduncle between day 24 and maturity in three barley cultivars under water stress treatments. Error bars are standard errors.

5.3.3.3.6. Peduncle N content, remobilization, and concentration

N content in the peduncle of the high protein barley cultivars (averaged over all water stress treatments) was significantly greater than in the low protein cultivar at day 24 and at maturity (Table 5.9). At day 24, the N content was lower under all water stress treatments than the control value. At maturity, however, stress had no significant effect on the N content of the peduncle except for medium stress which increased the amount of N. There was substantial remobilisation of N from the peduncle in the well-watered control, but much less N was mobilised in the other treatments. The remobilization of N from the peduncle of the moderate protein cultivars, Forrest and W.I.2692 was greater than from W.I.2808 (low protein). Indeed, severe and medium stress resulted in a net accumulation of N between the two harvests in two moderate barley cultivars, while in W.I.2808 a similar response was found under all stress conditions (Fig.5.13).

Table 5.9. N content and remobilization efficiency of the peduncle in barley cultivars under different levels of water stress at two harvests

	Day 24			Maturity			Remobilization efficiency (%)		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
	mg per shoot								
Not watered	0.41	0.51	0.27	0.44	0.65	0.40	-10	-30	-48
Medium stress	0.54	0.96	0.17	0.62	1.25	0.38	-15	-35	-12
Mild stress	0.45	0.79	0.17	0.36	0.47	0.26	20	41	-32
Divided root	0.37	0.65	0.28	0.35	0.63	0.35	5	3	-25
Control	2.10	2.00	1.40	0.49	0.37	0.33	76	82	76

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Harvests x Cultivars x Treatments: NS ; Treatments x Harvests : 0.13; Cultivars x Harvests : 0.10

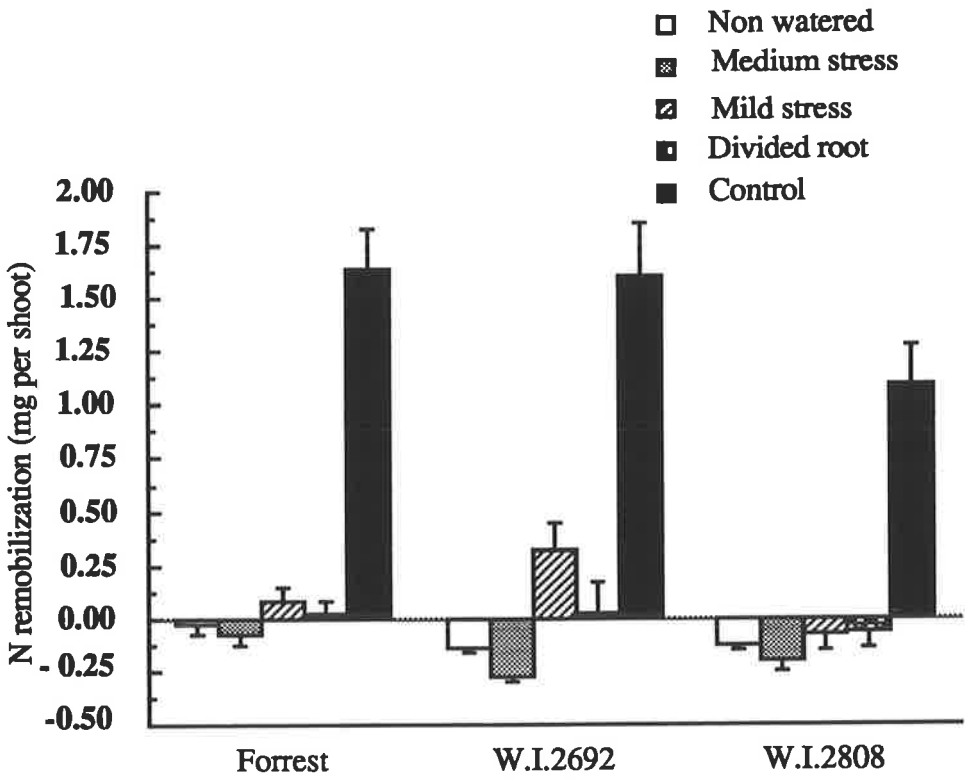

Fig. 5.13. The remobilization of N from the peduncle in three barley cultivars under water stress between day 24 and maturity. Error bars are standard errors.

In terms of the N concentration of the peduncle, there were significant ($P < 0.001$) interactions between cultivars and water stress treatments. For instance at day 24 it was significantly greater in the control than in all water stress treatments (Fig. 5.14). However, at maturity the peduncle in plants grown under stress had a higher concentration of N than those grown under well watered conditions, and in a number of treatments the N concentration increased between day 24 and maturity.

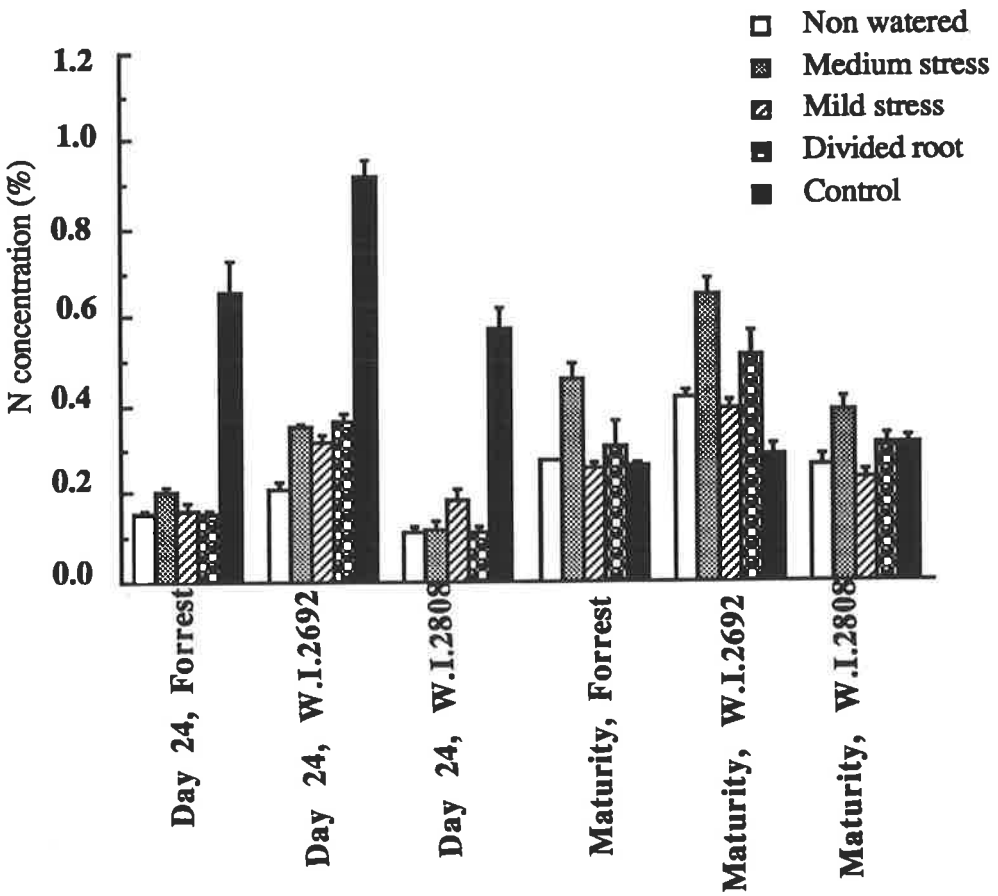

Fig. 5.14. N concentration of the peduncle in three barley cultivars under water stress at day 24 and maturity. Error bars are standard errors.

5.3.3.3.7. Flag leaf DM content and remobilization

DM content of the flag leaf (averaged over all treatments) in Forrest and W.I.2692 was greater than in W.I.2808 at both harvests (Table 5.10). At day 24, the average of DM content of the flaf leaf was greater in control condition than in severe stress condition but at maturity the average was greatest under severe stress than under control condition.

The remobilization of DM from the flag leaf differed significantly ($P< 0.01$) between cultivars . Forrest did not remobilize DM except when well watered, (Table 5.10) while W.I.2692 remobilized 27% of the DM content of the flag leaf under mild stress. Less DM was remobilized from the flag leaf under water stress treatments than under watered conditions. ($P< 0.001$). The cultivars responded differentially to water stress treatments (Fig. 5.15). All cultivars remobilized DM from the flag leaf under well watered conditions while in the divided root treatment, remobilization occurred only in W.I.2692 and W.I.2808, and in mild stress only W.I.2692 remobilized DM from the flag leaf. In other water stress conditions, there was a net increase in DM in the flag leaf between day 24 and maturity .

Table 5.10. DM content of the flag leaf in barley cultivars under different levels of water stress at day 24 and maturity

	Day 24			Maturity			Remobilization efficiency (%)		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
	mg per shoot								
Not watered	247	241	308	278	259	320	-13	-7	-4
Medium stress	306	283	152	347	331	186	-13	-17	-22
Mild stress	291	339	207	297	246	238	-2	27	-15
Divided root	292	273	290	319	226	232	-9	17	20
Control	317	277	311	266	243	238	16	12	23

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Harvest x Treatment : 21.8; Harvest x Cultivar : 16.8; Harvest x Cultivar x Treatment : 37.7

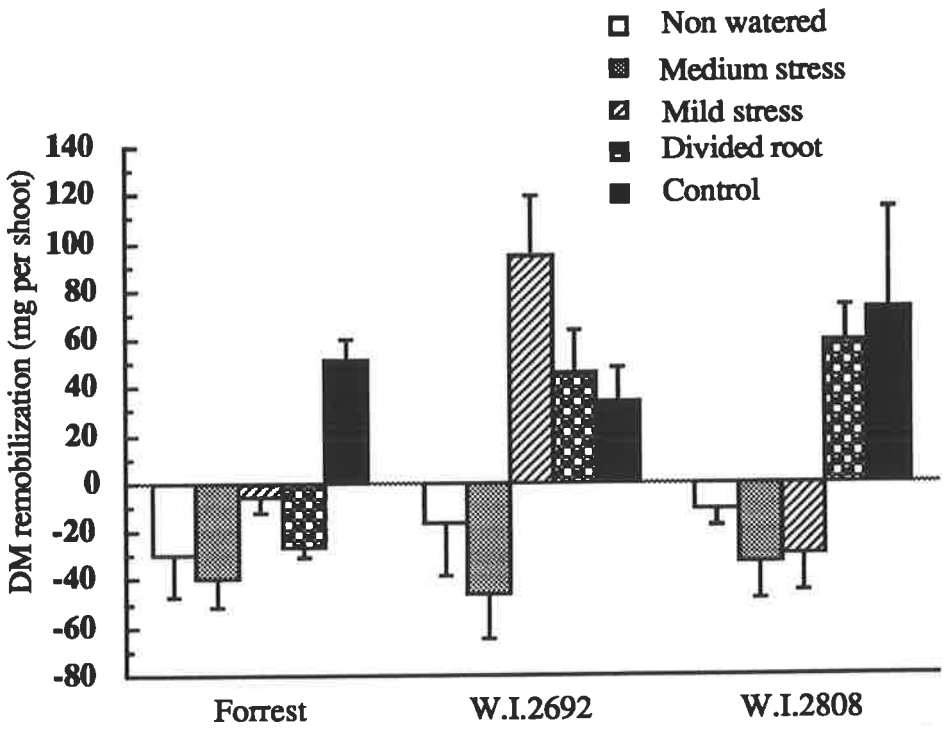

Fig. 5.15. The interaction of cultivars and treatments on DM remobilization from the flag leaf between day 24 and maturity. Error bars are standard errors.

5.3.3.3.8. Flag leaf N content, remobilization and concentration

N content in the flag leaf (over all water stress treatments) was significantly ($P < 0.001$) greater at day 24 than maturity in all three barley cultivars (Table 5.11). Water stress reduced N content at day 24 but not at maturity. Sixty nine to 72% of the N present at day 24 was apparently remobilized by the time of maturity when the plants were kept well-watered.

Table 5.11. N content and remobilization efficiency of the flag leaf in barley cultivars under different levels of water stress at two harvests

	Day 24			Maturity			Remobilization efficiency (%)		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
	mg per shoot								
Not Watered	2.5	5.1	3.0	2.1	1.8	2.1	16	65	30
Medium Stress	6.3	7.1	2.2	2.3	3.0	1.1	63	58	50
Mild stress	6.2	6.2	3.0	2.0	2.2	1.1	68	64	63
Divided root	5.5	7.0	3.9	2.2	1.5	1.5	60	79	62
Control	6.1	7.1	3.6	1.7	2.1	1.1	72	70	69

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Cultivars x Harvests x Treatments : 0.76; Harvests x Cultivars : 0.34 ; Harvests x Treatments : 0.44

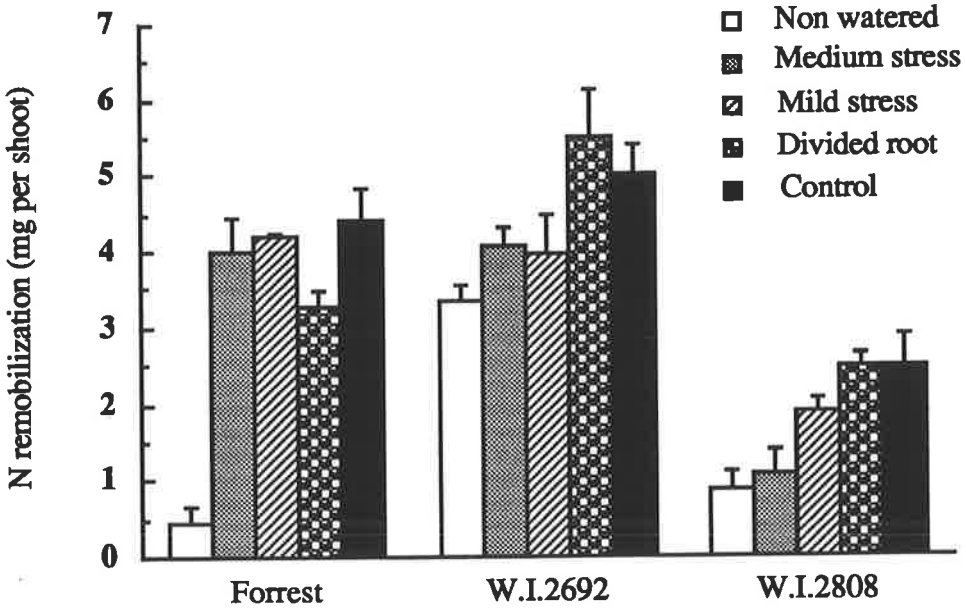

Fig. 5.16. The interaction of cultivars and treatments on remobilization of N from the flag leaf between day 24 and maturity. Error bars are standard errors.

Only the most severe stress reduced the apparent remobilization efficiency, and then in two of the three cultivars. W.I.2692 remobilized significantly more N from the flag leaf than did Forrest. Cultivars showed significantly different responses under the different water stress treatments (Fig. 5.16). For instance only W.I.2692 remobilized a greater amount of N under the divided root treatment than all water stressed plants while in Forrest, the only treatments which significantly reduced remobilization were severe water stress and the divided root treatment. Compared to W.I.2692, W.I.2808 remobilized significantly less N in all treatments.

N concentration (%) of the moderate protein cultivars in the flag leaf was significantly ($P< 0.001$) greater than in the low protein cultivar at both harvests (Fig. 5.17). At day 24, W.I.2692 (over all water stress treatments) showed the highest N concentration in the flag leaf, and W.I.2808 the lowest. N concentration at maturity was significantly lower under all water stress treatments in all three barley cultivars.

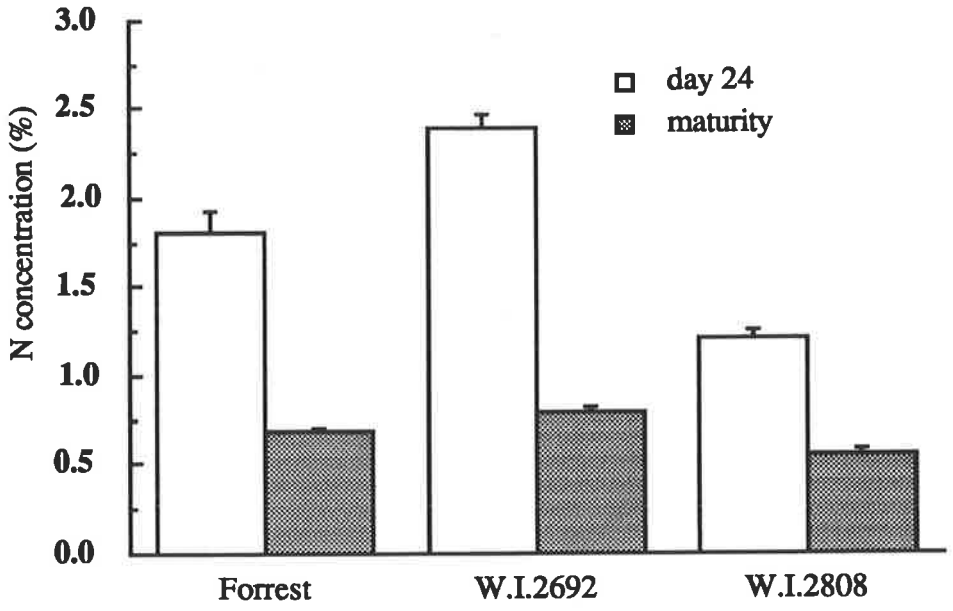

Fig. 5.17. The concentration of N in the flag leaf of barley cultivars at day 24 and maturity. Error bars are standard errors.

5.3.3.3.9 Other leaves (all leaves except the flag leaf) DM content and remobilization

At day 24, the DM content of the other leaves was greater in Forrest than in W.I.2692 and W.I.2808 (Table 5.12), but at maturity it was significantly less than the other two cultivars. DM in the other leaves did not decrease between day 24 and maturity, thus there did not appear to be any remobilization of DM over all treatments between the two harvests . In fact, in W.I.2692 and W.I.2808 there was a net increase in DM between the two harvests, under all conditions (Fig. 5. 18).

Table 5.12. DM content and remobilization efficiency of other leaves in barley cultivars under different levels of water stress in both harvests

	Day 24			Maturity			Remobilization efficiency (%)		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
Not watered	629	616	685	679	728	761	-7	-18	-11
Medium stress	691	617	553	739	631	686	-7	-2	-24
Mild stress	692	720	792	677	731	923	2	-1	-17
Divided root	720	453	723	700	671	1028	3	-48	-42
Control	792	657	657	723	828	890	9	-26	-35

V1: Forrest V2: W.I.2692 V3: W.I.2808LSD 5% for Treatments x Cultivars x Harvests :82; Treatments x Harvests : 48; Treatments x Cultivars : 37

It was however of interest that the responses of Forrest in the three least stressful treatments differed from those W.I.2692 and W.I.2808 (Fig. 5. 18). While W.I.2692 and W.I.2808 continued to gain DM between day 24 and maturity, Forrest remobilized a small proportion of its DM (about 10%) under mild stress, divided root and control conditions.

5.3.3.3.10 Other leaves N content, remobilization and concentration

At day 24, N content in the other leaves of the moderate protein cultivars (averaged over all water stress) was significantly greater than in the low protein genotype (Table 5.13). At maturity however, it was similar in all three barley cultivars. N content at day 24 and at maturity was lower under non-watered conditions than in the other treatments (Table 5.13). At maturity, it was not significantly different to medium and mild stress treatments.

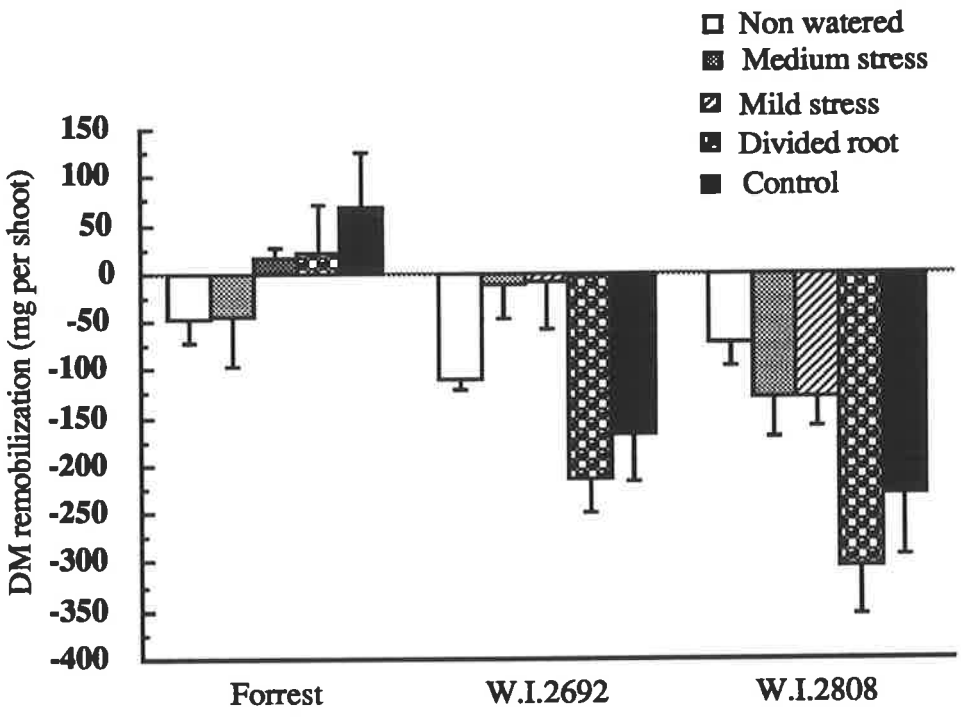

Fig. 5.18. The remobilization of DM from the other leaves in barley cultivars under different levels of water stress. Error bars are standard errors.

The two moderate protein cultivars remobilised significant amounts of N from the lower leaves (Fig.5.19). Forrest and W.I.2692 remobilized similar amounts of N (about 2.5 mg per shoot), but W.I.2808 (low protein) did not remobilize any N from the other leaves between day 24 and maturity. The interaction between cultivars and treatments on N remobilization was significant ($P< 0.01$) (Fig. 5.19). Forrest and W.I.2692

remobilized a considerable proportion of the N from the other leaves but W.I.2808 did not remobilize any amount of N under any condition.

N concentration of the other leaves in the moderate protein barley cultivars (the average) was greater than in the low protein cultivar at day 24 (Table 5.14) and at maturity. Although there were no significant Cultivar x Treatment x Harvest interactions, it was of interest that at day 24, N concentration was greatest under the divided root condition in all three barley cultivars (Table 5.14).

Table 5.13. N content and remobilization efficiency of other leaves in three barley cultivars under different levels of water stress in both harvests

	Day 24			Maturity			Remobilization efficiency (%)		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
mg per shoot									
Not watered	7.8	7.9	6.2	6.95	5.8	6.2	11	27	0
Medium stress	9.5	10.1	4.9	7.9	7.6	5.1	17	25	-4
Mild stress	10.8	10.3	6.9	7.4	6.6	7.6	31	36	-10
Divided root	9.5	6.7	7.9	7.7	6.0	8.8	19	10	-11
Control	10.0	10.0	5.4	6.9	8.1	7.8	31	19	-44

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Treatments x Harvests: 0.92; Cultivars x Harvests : 0.71; Treatments x Harvests x Cultivars: 1.6

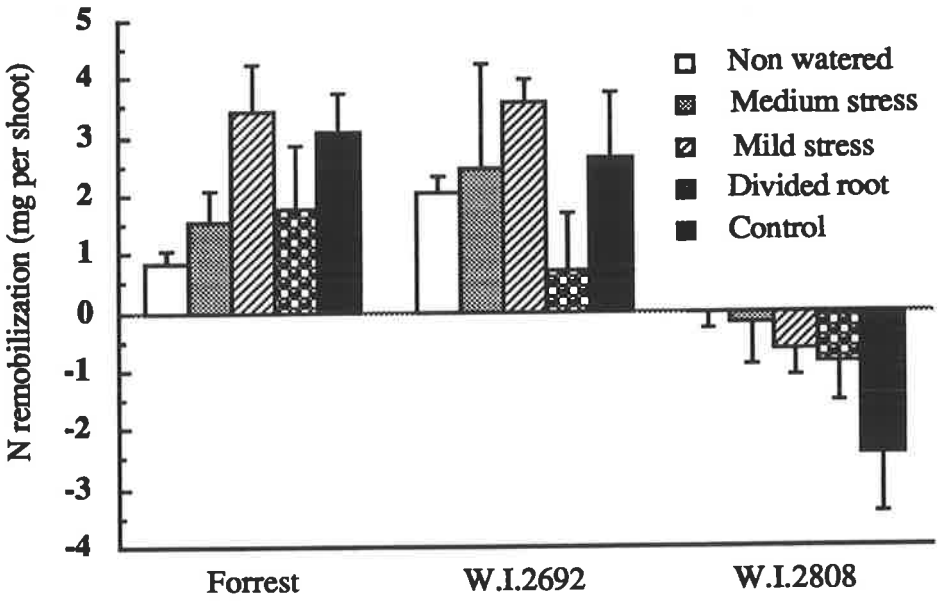

Fig. 5.19. The effects of water stress on remobilization of N from other leaves in barley cultivars between day 24 and maturity. Error bars are standard errors.

Table 5.14. N concentration of the other leaves in barley cultivars under different levels of water stress at day 24 and maturity

	Day 24			Maturity		
Treatments	V1	V2	V3	V1	V2	V3
			mg per shoot			
Not watered	1.24	1.28	0.90	1.02	0.80	0.82
Medium stress	1.37	1.27	0.88	1.07	1.20	0.74
Mild stress	1.27	1.26	0.85	1.09	0.90	0.82
Divided root	1.31	1.48	1.10	1.10	0.89	0.86
Control	1.27	0.97	0.81	0.96	0.97	0.88

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Cultivar x Harvest x Treatment: N.S.; Cultivar x Harvest :0.8; Treatment x Harvest : N.S.

5.3.3.3.11. Chaff DM content and remobilization

DM content of the chaff was significantly greater at day 24 than at maturity (Table 5.15). It was greater in Forrest than than in W.I.2692 and W.I.2808 at both harvests. Under water stress (averaged over all cultivars) at day 24, DM under all conditions was similar, but at maturity it was greater under severe stress (non-watered) than in all other treatment .

The average remobilization of DM from the chaff in the three barley cultivars was similar. Only the non-watered treatment in Forrest resulted in significantly less DM than the control (Fig.5.20).

Table 5.15. DM content and remobilization efficiency of chaff in barley cultivars under different levels of water stress at two harvests

	Day 24			Maturity			Remobilization efficiency (%)		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
	mg per shoot								
Not watered	343	253	301	327	226	270	4	11	10
Medium stress	346	311	183	309	261	151	11	16	17
Mild stress	330	287	228	285	251	214	14	13	6
Divided root	295	282	283	265	236	241	10	16	15
Control	320	251	319	259	232	268	19	8	16

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Harvest x Treatments : N.S.; Harvests x Cultivars : N.S.; Harvests x Cultivars x Treatments : 17.8

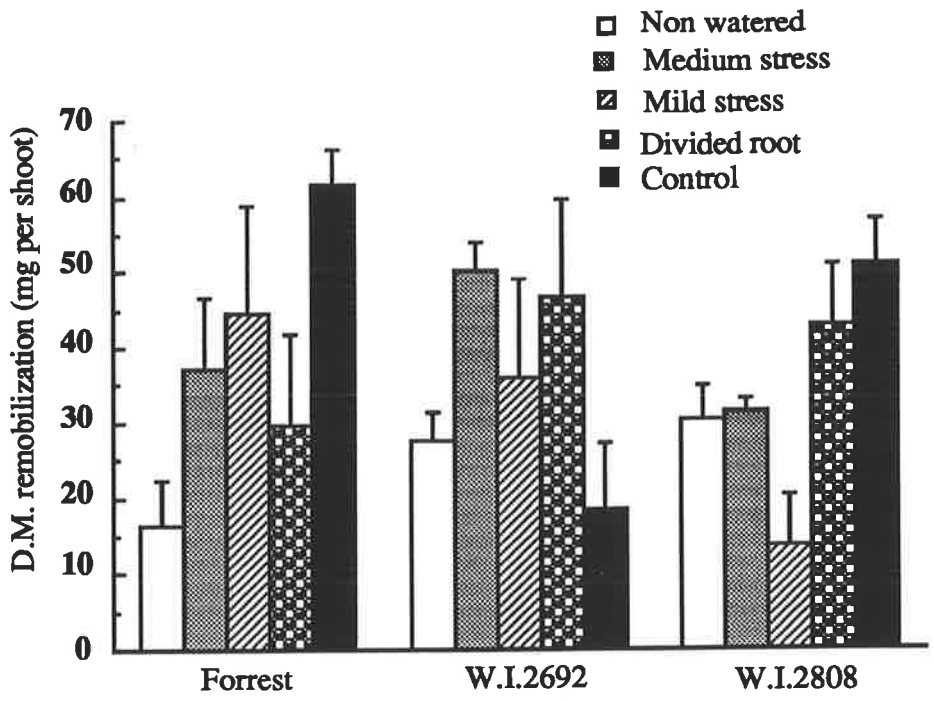

Fig. 5.20. The remobilization of DM from chaff in barley cultivars under water stress treatments between day 24 and maturity. Error bars are standard errors.

Table 5. 16. N content and remobilization efficiency of chaff in barley cultivars under different levels of water stress at two harvests

	Day 24			Maturity			Remobilization efficiency %		
Treatments	V1	V2	V3	V1	V2	V3	V1	V2	V3
	mg per shoot								
Not watered	4.3	4.6	4.1	3.6	1.8	2.4	16	60	41
Medium stress	6.4	5.2	2.8	2.9	3.2	1.4	55	38	50
Mild stress	5.8	4.9	3.5	1.7	2.1	1.3	71	57	63
Divided root	5.5	5.3	4.0	2.0	1.8	2.1	64	66	48
Control	5.4	4.3	4.0	1.8	2.3	1.7	66	47	58

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Harvests x Cultivars : 0.20; Harvests x Treatments : 0.26; Cultivars x Harvests x Treatments : 0.46

5.3.3.3.12 Chaff N content, remobilization and concentration

N content of the chaff in the moderate protein cultivars (over all water stress) was greater than in the low protein genotype at both harvests (Table 5.16). At day 24, except for the severe stress, N content in the chaff was similar under all water stress conditions. At maturity, greater amounts of N were found in the chaff under mild and severe water stress than in other conditions. In Forrest, N remobilization was reduced only under the

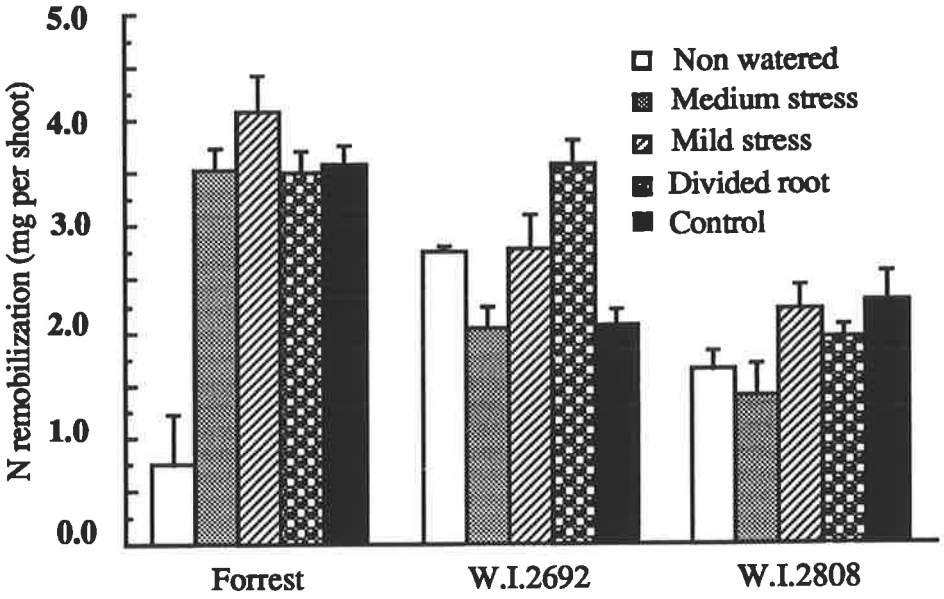

Fig. 5.21. The remobilization of N from chaff in barley cultivars between day 24 and maturity. Error bars are standard errors.

non-watered treatment. In W.I.2692 however, N remobilization under this treatment was greater than in control conditions. In W.I.2808 N remobilization was similar under all conditions. (Fig. 5.21).

N concentration of the chaff at day 24 was greater, on average, in Forrest than in W.I.2692 and W.I.2808 (Table 5.17) but at maturity it was similar in all three barley cultivars. The responses of chaff N % to water stress were different at the two harvests. At day 24, it was similar under all treatments except the non watered treatment, but at maturity N% of the chaff was increased under severe stress (non watered) or medium

stress conditions. There was also highly ($P < 0.001$) significant Treatment x Cultivars x Harvests interaction in N% . At day 24, the lowest N% among water stress treatments was found in Forrest under severe water stress , while in W.I.2692 and W.I.2808 it was similar for all treatments. At maturity, N% in the chaff of Forrest was significantly greater under non watered conditions than in all other treatments (Table 5.17).

Table 5.17. N concentration of the chaff in three barley cultivars under different levels of water stress between day 24 and maturity

	Day 24			Maturity			
Treatments	V1	V2	V3	V1	V2	V3	**Mean**
			(%)				
Not watered	1.26	1.80	1.36	1.09	0.80	0.91	
Medium stress	1.86	1.68	1.56	0.94	1.22	0.95	
Mild stress	1.76	1.71	1.45	0.60	0.85	0.62	
Divided root	1.87	1.89	1.42	0.76	0.75	0.86	
Control	1.69	1.74	1.26	0.71	0.97	0.65	

V1: Forrest V2: W.I.2692 V3: W.I.2808 LSD 5% for Cultivar x Harvest x Treatment :0.2; Cultivar x Harvest : 0.1; Treatment x harvest: 0.1

5.4. Discussion

The major aim of this experiment was to examine whether there were any genetic differences in remobilization of DM and N from vegetative parts of the shoot among three barley cultivars. It was also of interest to determine the effects of water stress on grain yield, grain N content, DMHI and NHI in the three barley cultivars.

Water stress imposed on the plants affected the accumulation of N and DM in the grain of three barley cultivars as well as the DMHI (Table 5.18). Water stress reduced the accumulation of DM and N in the grain and also DMHI (but not NHI) of all three barley cultivars, however, it increased substantially N concentration in the grain.

Grain yield in this experiment decreased under stress (divided root and water stress treatments combined) in all three cultivars to approximately the same extent. It is necessary to note that the level of water stress and the rate of its development may not be "typical" of those encountered in the field. The pattern of responses of the barley cultivars used in this study in terms of yield and N% under well watered conditions were consistent with the results of the field experiments in South Australia (South Australia Research and Development Industry Annual Review 1991 and 1992; Table 5.19) indicating that in each year Forrest and W.I.2692 produced lower yield than W.I.2808 and greater N% than W.I.2808.

Table 5.18. Grain DM and N content, HI under divided root, stress (mean of three treatments) and non stress control in three barley cultivars at maturity

	Control			Divided root			Stress		
Parameter	V1	V2	V3	V1	V2	V3	V1	V2	V3
DM(mg)	1085	1052	1234	961	933	1040	866	668	761
N (mg)	25	23	29	22	21	24	21	16	20
N (%)	2.3	2.3	2.2	2.3	2.3	2.3	2.4	2.6	2.4
DMHI (%)	28	28	31	27	27	26	22	19	25
NHI (%)	63	59	65	59	60	59	66	59	63

V1 = Forrest V2 = W.I.2692 V3 = W.I.2808

Table 5.19. Grain yield and protein concentration (mean of about 20 sites in South Australia) of three barley cultivars under field conditions.

Parameter	Forrest		W.I.2692		W.I. 2808	
	1990	1991	1990	1991	1990	1991
Yield (kg/ha)	2243	3089	2248	3067	2414	3267
Protein yield (kg/ha)	296	376	287	355	292	346
Protein (%)	13.2	12.2	12.8	11.6	12.1	10.9

The increased grain N concentration may possibly be explained by two other mechanisms. The grain under water stress may have a limited number of sites for carbohydrate accumulation, and once these sites are saturated no more carbohydrate is accumulated, or the synthesis of starch may be more sensitive to stress than is the synthesis of protein.

Remobilization of stored assimilate from the shoot contributes to grain growth, especially under stressed conditions when photosynthesis is greatly reduced (Bidinger *et al.* 1977; Gallagher *et al.* 1975; Pheloung and Siddique 1991). It has been suggested that the ability to remobilize large amounts of assimilate and translocate it to the grain is a desirable trait for cereals in dryland environments (Gale and Youssefian 1985). Herzog (1986) reported that to some degree, relocation from leaves depends on senescence, on the genotypic source/sink relation at anthesis, and on the effects of environmental conditions during the reproductive period.

Substantial amounts of DM were remobilized from internodes and peduncle (Table 5.20), the total quantity from these organs exceeding the grain DM increase during the second half of grain filling. The difference may reflect respiratory loss - see Chapter 4. Water stress reduced remobilization only in the peduncle of W.I.2808. Little or no DM was lost from the flag leaf and the other leaves of W.I.2692 and W.I. 2808 actually gained significant amounts of DM. Clearly, remobilization of DM occurred in barley on a substantial scale from some organs but not from others, and cultivars differed in their patterns of DM remobilization. Under stress, the net gains in DM in the other leaves of W.I.2808 numerically almost matched remobilization from the internodes and peduncle, possibly accounting for the reduced DMHI (Table 5.18) under stress in this cultivar.

The divided root treatments resulted in substantial responses in terms of grain filling and some aspects of remobilization. Less DM had accumulated by day 24 in the grain under this treatment than in watered or stressed plants, but at maturity there was

Table. 5.20. DM increment (+) and apparent remobilisation from vegetative parts (-) in three barley cultivars under control, divided root and stress (mean of three treatments) conditions between day 24 and maturity

	Control			Divided root			Stress		
Parameter	V1	V2	V3	V1	V2	V3	V1	V2	V3
Grain	+248	+233	+284	+430	+402	+484	+293	+146	+144
Internode	-183	-281	-302	-232	-109	-67	-139	-208	-186
Peduncle	-139	-81	-142	-134	-64	-128	-122	-118	-46
Flag leaf	-51	-47	-39	+27	-28	-40	+30	+49	+6
Other leaves	-56	+153	+178	-63	+204	+282	+27	+50	+120
Chaff	-62	-18	-51	-30	-47	-43	-33	-41	-25

V1 = Forrest V2 = W.I.2692 V3 = W.I.2808

little difference between divided root and mild stress (Table 5.1); there were similar effects on N deposition in the grain (Table 5.3). Some parts of the plants however responded in other ways to the effects of exposing parts of the root system to dry soil. DM accumulation in the internodes for example (Table 5.6) was reduced by this treatment at day 24 to a greater extent than in plants suffering mild or medium water stress, and this effect was observed in two of the cultivars but not in W.I.2808. N accumulation in the internode on the other hand (Table 5.7) was not affected by the divided root treatment. The divided root treatment had no effect on the remobilization of DM from the peduncle (Fig. 5.11) but abolished the remobilization of N from the peduncle (Fig. 5.13).

Besides indicating that DM and N remobilization are controlled by different mechanisms, it is also clear that the roots of barley plants growing (in pots) in dry soil are affecting the metabolism of the shoot Which may occur independently of the water status of the plant. However, without measurements of the water status of the plants, this can not be confirmed, although the reductions in grain yield that occurred in the

experiment strongly suggest significant increases in water stress above the control in all treatments.

In two of the three cultivars (Forrest and W.I.2692), more than enough N was remobilized from the vegetative organs to account for accumulation in the grain, under stress as well as in well watered conditions (Table 5.21). Remobilization of N did not appear to account for all of the gain of N in the grain of the low protein genotype W.I. 2808 under well watered conditions, but did under stress. Water stress increased grain N% in W.I.2692 more than in either of the other two cultivars (Table 5.18).

In southern Australia, crops commonly grow under stress during the last stages of grain filling. However, these results do not suggest that selection for reduced N remobilization under water stress would be a useful selection criterion for high malting quality barley (lower grain N%) in crops growing under stress. More N was remobilized from the chaff than from the internodes, peduncle or other leaves individually, and the chaff appeared to match remobilization of N from the flag leaves (Table 5.21). Clearly in barley the chaff is an important source of N for grain filling (Table 5.21). As a potential source of DM however the chaff is much less important than the peduncles or internodes (Table 5.20).

The remobilization of DM and N from the various parts of the plant appears to be under different types of control. Support for this view comes from comparison of the apparent remobilization efficiency of N and DM from the individual parts of the shoot. For example, in the peduncle, stress had little effect on the remobilization of DM (Table 5.8) but appeared to abolish remobilization of N (Table 5.10). In the flag leaf on the other hand the responses to water stress treatments were reversed (Table 5.10 and 5.11).

Estimates of apparent contribution to grain filling were calculated on the assumption that all of the remobilized material was available for grain filling. Therefore the term of "apparent contribution" was used in this study. The apparent contribution of DM (Table 5.22) from the shoot was greater in Forrest under control and divided root

Table. 5.21. Grain N increment (+) and vegetative parts remobilization (-) in three barley cultivars under control, divided root and stress conditions between day 24 and maturity

	N increment (+) or remobilization (-) mg per shoot								
	Control			Divided root			Stress		
Parameter	V1	V2	V3	V1	V2	V3	V1	V2	V3
	mg per shoot								
Grain	+8.6	+3.5	+7.1	+11.0	+11.0	+10.0	+6.0	+4.3	+4.0
Internode	-0.2	-1.2	-0.1	-1.1	-1.8	-0.4	-1.5	-1.2	-1.5
Peduncle	-1.6	-1.6	-1.1	-0.1	-0.1	-0.1	+0.1	+0.1	+0.2
Flag leaf	-4.4	-5.2	-2.3	-3.3	-5.1	-2.2	-2.8	-4.3	-1.3
Other leaf	-2.9	-2.7	+2.0	-2.3	-0.9	+0.7	-2.0	-2.7	+0.4
Chaff	-3.6	-2.0	-2.3	-3.5	-3.6	-1.9	-2.8	-2.5	-1.8

V1 = Forrest V2 = W.I.2692 V3 = W.I.2808

conditions while it was greater in W.I.2692 under stress conditions. In all three barley cultivars the stem (internodes + peduncle) appeared to contribute DM, but leaves of two of three barley cultivars did not contribute DM to the grain. On the other hand leaves (other leaves + flag leaf) demonstrated the greatest apparent contribution of N to the grain in all three barley cultivars (Table 5.23). In both cases, apparent contribution was greater under control than stress conditions. However the chaff of all three barley cultivars apparently contributed N to the grain and its contribution was greater under stress than control or divided root conditions particularly in moderate protein cultivars.

Since the apparent contribution of vegetative stored DM (Table 5.22) and N (Table 5.23) to the grain is calculated from changes in dry mass, the value obtained may not indicate the amount of material actually reaching the grains because of the respiration of the stem in barley plant.

Table. 5.22. Apparent contribution (%) of DM from different parts of the shoot to the grain in three barley cultivars under control , divided root and stress (mean of three treatments) conditions between day 24 and maturity

	Control			Divided root			Stress		
Parameter	V1	V2	V3	V1	V2	V3	V1	V2	V3
Internode	74	120	107	54	27	14	47	142	129
Peduncle	56	35	50	31	16	26	42	80	32
Flag leaf	21	20	14	0	7	8	0	0	0
Other leaves	23	0	0	15	0	0	0	0	0
Chaff	25	8	18	7	12	9	11	28	17

V1 = Forrest V2 = W.I.2692 V3 = W.I.2808

Respiration has been measured in the stems of cereals and it has been proposed that the substrate for this respiration would reduce the contribution of grain yield of material stored in the stem by 61% (Austin *et al.*1977) and 83% (Austin *et al* 1980). There is no reason to suppose, however, that carbohydrate substrate provided from remobilized material is preferentially utilized in respiration. Thus, remobilized DM is no less available for grain filling than is currently assimilated carbon. The N lost from the vegetative parts (internodes, peduncle,leaves and chaff) was quite substantial (between 9.0 and 12.7 mg/pot) and was often greater than the N increase in the grain. A positive cause of this discrepancy is the gaseous loss of N from the leaves and other green tissues. Recently, Palta *et al.* (1994) found that significant amounts of N may be lost from the shoots of wheat during grain filling, and this loss was greater when plants grew in well-watered conditions. They suggested that the loss of N occurred as NH_3 volatilized from the shoots.

Table. 5.23. Apparent contribution (%) of N from different parts of the shoot to the grain in three barley cultivars under control, divided root and stress (mean of three treatments) conditions between day 24 and maturity

	Control			Divided root			Stress		
Parameter	V1	V2	V3	V1	V2	V3	V1	V2	V3
Internode	2	34	1	10	16	4	25	28	38
Peduncle	19	46	15	0	0	1	0	0	0
Flag leaf	51	149	32	30	46	22	47	100	33
Other leaf	34	77	0	21	9	0	33	63	0
Chaff	42	57	32	32	33	19	47	58	45

V1 = Forrest V2 = W.I.2692 V3 = W.I.2808

In summary, water stress during the post-anthesis period was unfavourable for the assimilation of CO_2. Thus yield was determined to a great extent by the availability of other sources of assimilate including remobilized material. Differences between cultivars and also between DM and N remobilization from different parts of the shoot support the idea that the remobilization of N and other DM are controlled through different mechanisms. These findings have prompted further investigation of the process of remobilization of non structural carbohydrates and soluble protein within vegetative parts of the shoot in the next chapter (Chapter 6).

Chapter 6. The remobilization of carbohydrates and proteins from the shoot of two wheat cultivars in response to water stress during grain filling

6.1 Introduction

The importance of non-structural carbohydrates stored in the stem and leaves of cereals prior to kernel development has been under discussion for many years. Early views suggested that storage significantly contributed to DM deposition in the grain (Archbold 1945). Recent studies suggest that under well-watered conditions this storage continues well into the period of grain filling (Pheloung and Siddique 1991; Bonnett and Incoll 1992a; Borrell *et al.* 1993). Therefore the subsequent decline in stored carbohydrates during the later stages of grain growth could indicate that they were supplying a high proportion of grain's requirements for carbohydrate (Bell and Incoll 1990; Bonnett and Incoll 1992). On the other hand, the overall contribution of stored carbohydrates to final kernel dry weight under near optimal conditions appears to be only around 5-15% (Austin *et al.* 1977; Bell and Incoll 1990). There is good evidence to suggest, however, that temporary storage is very important under stress conditions (Bidinger *et al.* 1977; Austin *et al.* 1980). Knowledge of these carbohydrates is important not only for their potential to contribute directly to grain DM, but also because wheat cultivars that produce better quality under drought conditions by utilizing these carbohydrates could be developed.

Young leaves which become the major site of N assimilation prior to grain filling, depend on N imported from other parts of the plant and protein content of the leaves peaks when the leaves are fully expanded. As senescence sets in, assimilation of N as well as other inorganic nutrients declines. During this period, leaf metabolism changes from N assimilation to remobilization, and in addition nitrate reductase activity declines (Kar and Feierabend 1984). One of the obvious characteristics of senescence is the loss of proteins. This allows the remobilization of N reserves from leaves or other areas and translocation into the reproductive parts (seeds). In the field under a Mediterranean climate where both N and water during grain filling are the main growth-limiting factors, the processes occurring during senescence allow the plants to complete their life-cycles and produce seed

by remobilization of stored N to reproductive parts (Huffaker 1990). Since the major protein in the leaves is RuBP carboxylase (Wittenbach 1979; Dalling and Nettleton 1986), this is the major source of N for redistribution. During senescence, this protein is rapidly degraded (Peoples *et al.* 1980; Wittenbach 1982). Endoproteolytic activities of leaf cells from many plants species are located mainly in vacuoles (Huffaker 1990 and references cited in this review). The proteolytic enzymes are mainly found in the vacuoles of the wheat leaf (Wagner *et al.* 1981; Wittenbach *et al.* 1982). The two main endoproteases (EP) of barley leaves were predominantly localized in vacuoles isolated from barley leaves. Evidence for the localization of EP activity in chloroplasts and subparticles of chloroplasts is presented in Huffaker (1990). A sequential degradation of chloroplast in the vacuole has been proposed for wheat (Wittenbach 1979). Some investigators found increased proteolytic activity correlated with protein loss, while others found no correlation or a negative one (Feller and Keist 1986). Species differences are important in determining hydrolysis of specific proteins during stress-induced senescence. Under conditions of total nutrient deprivation, RuBPCase was degraded but not as rapidly as other soluble protein (SP) in *Lemna* fronds. In the cereal leaves, RuBPCase behaves similarly to a storage protein during N deprivation, whereas in *Lemna,* it apparently does not. The difference in proteolysis between cereal leaves and *Lemna* raises intriguing questions about regulation (Huffaker 1990).

Differential effects of environmental conditions (water stress) on remobilization of DM and N from different parts of the shoot have been noted in both wheat and barley (Chapters 4 and 5). These effects were quantified as a change in the amounts of DM or N in the shoot between day 24 and maturity. It is possible that the amounts of remobilizable DM or N might differ from one part of the shoot to another, or between different varieties. Also, the actual proportion remobilized of the potential amounts remobilizable may be affected by stress, or differ in response to stress in the different parts of the shoot.

The objectives of this experiment were to examine how post-anthesis water stress influences the amount of total soluble carbohydrates (TSC) and SP in different parts of the shoot during grain filling. Thus the aims of this experiment were as follows:

(i) To examine the effects of water stress on TSC, and also on the remobilization of two fractions of TSC, ethanol soluble sugars (ESS) and water soluble sugars (WSS) from different parts of the shoot during grain filling.

(ii) To estimate the changes of SP and total N as the result of stress from different parts of the shoot during grain filling.

(iii) To compare the responses of two cultivars differing in protein content.

6.2 Materials and methods

The experiment was conducted in a glasshouse. Plants were watered regularly until day 10 after anthesis to minimise the possibility of pre-anthesis moisture stress. Two cultivars of wheat were grown in pots 20 cm deep containing recycled soil. Ten seeds per pot were sown and seedlings thinned to 6 plants per pot after emergence and plants were restricted to a single culm by removing all tillers as they emerged. Plants were grown with the natural photoperiod for Adelaide in the months of January - May and controlled temperature (25°±2°C during the day and 16°± 2°C at night) and were regularly watered with a commercial liquid plant food (Aquasol). Aphids when present were controlled using a pyrethrum spray. Only one level of stress which was 50% of field capacity (assuming that mean of moisture content of the soil in three stress treatments in previous experiments was around 50% of field capacity) was imposed at 10 days after anthesis. This level of water stress, which was assumed to correspond with the medium water stress treatment in previous experiments, was maintained by rewatering the pots twice per week until maturity. Harvesting was done at 24 days after anthesis and at maturity. Different parts of the shoot (chaff, peduncle, lower internodes, flag leaves and other leaves) were extracted for the assay of ESS, WSS, TSC and SP as described in Chapter 3. The N concentration was determined by Kjeldahl analysis. Standard statistical procedures were used for analysis of variance.

6. 3 Results

6.3.1 Grain

6.3.1.1 Grain DM and HI

Grain DM content was greater at maturity than at day 24 in both cultivars under both treatments (Fig. 6.1) It was also significantly ($P < 0.05$) greater in Vasco than Sun 92A in both treatments and both harvests. Thus grain DM accumulation between day 24 and maturity was also significantly ($P < 0.001$) higher in Vasco than Sun 92A (Fig. 6.2). HI was significantly ($P < 0.05$) greater at maturity than at day 24 in both cultivars and in both treatments (Fig. 6.3). At maturity, water stress had reduced the HI in both conditions.

6.3.1.2 Grain N content, N concentration and NHI

Grain N yield was greater at maturity than at day 24 in both cultivars but N yield of Vasco in the grain was greater than Sun 92A (Fig. 6.4). Stress reduced the grain N yield in Sun 92A but not in Vasco. The accumulation of N between day 24 and maturity was

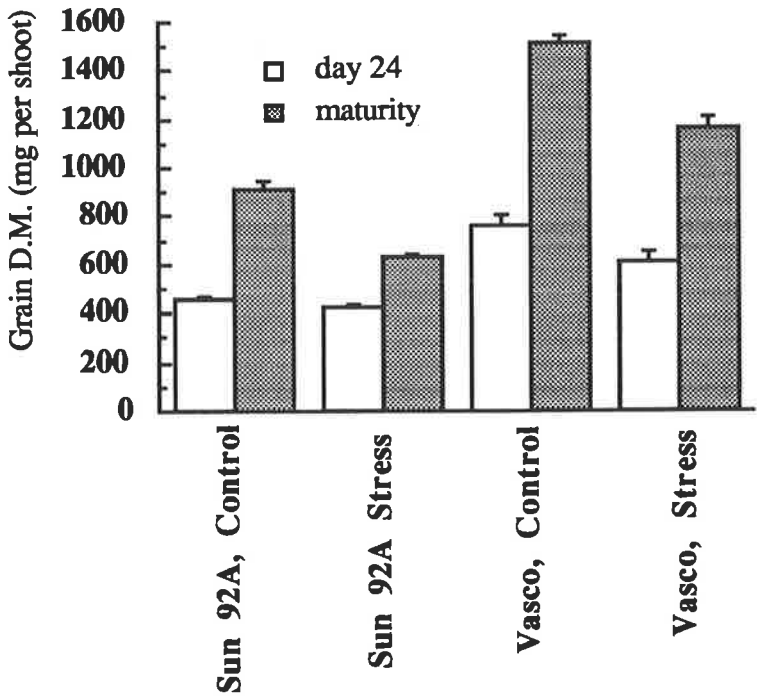

Fig. 6.1. Grain DM content in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

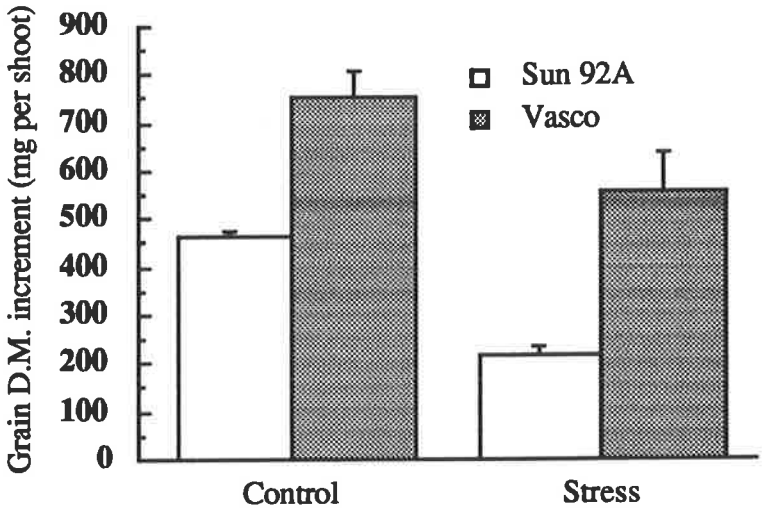

Fig. 6.2. Grain DM increment between day 24 and maturity in two wheat cultivars under stress and control. Error bars are standard errors.

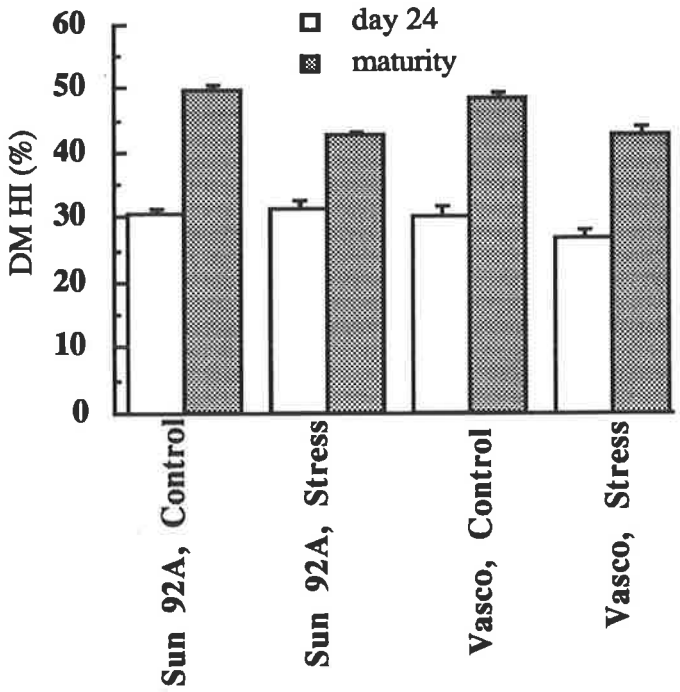

Fig. 6.3. Grain DM HI in two wheat cultivars at day 24 and maturity. Error bars are standard errors.

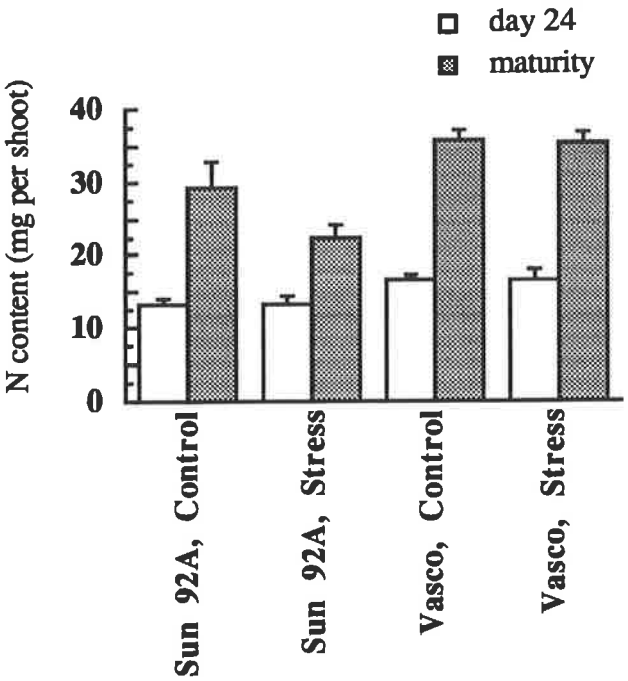

Fig.6.4. Grain N yield in two wheat cultivars under stress and control conditions at day 24 and maturity. Error bars are standard errors.

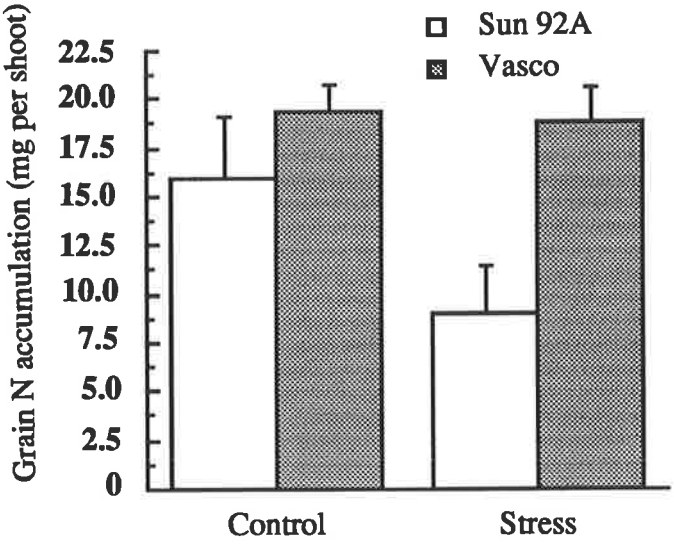

Fig. 6.5. Grain N accumulation between day 24 and maturity in two wheat cultivars under stress and control. Error bars are standard errors.

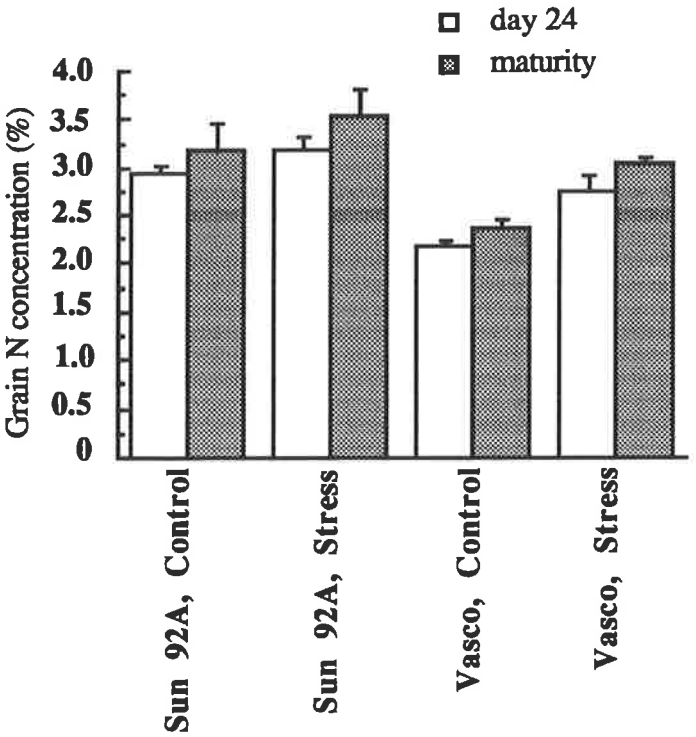

Fig. 6.6. The N% in the grain of two wheat cultivars under stress and control conditions at day 24 and maturity. Error bars are standard errors.

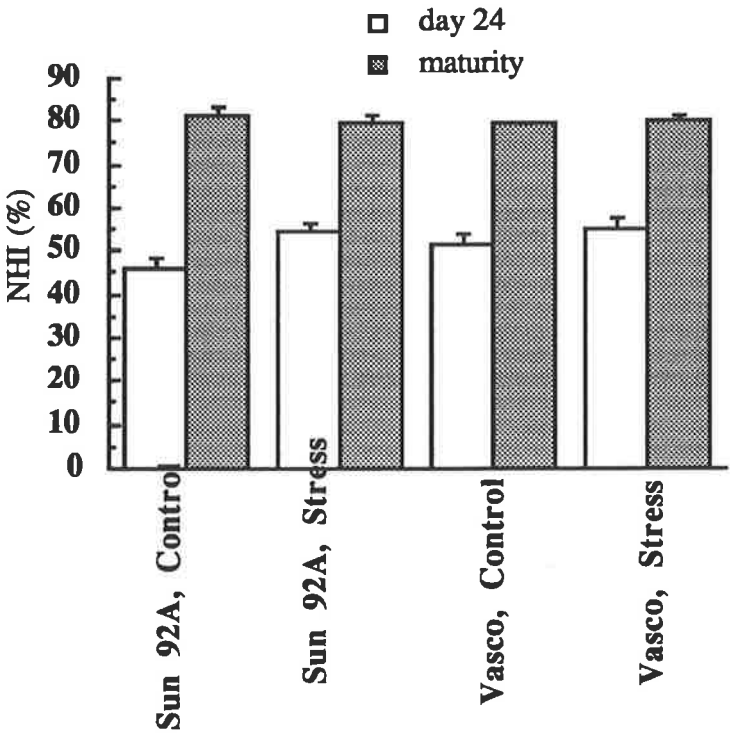

Fig. 6.7. Grain NHI in two wheat cultivars under stress and control conditions. Error bars are standard errors.

also greater in Vasco than Sun 92A in both conditions (Fig. 6.5), and stress reduced the accumulation of N only in Sun 92A. On the other hand N% in the grain of Sun 92A at maturity was greater than Vasco (Fig. 6.6) and stress increased the concentration of N in the grain of both cultivars at day 24 and at maturity of both cultivars. Despite these differences, grain NHI at maturity was similar in both treatments and in both cultivars (Fig. 6.7).

6.3.2. Lower internodes

6.3.2.1 Lower internode DM, ESS and TSC content and remobilization

In both wheat cultivars in both treatments, DM content of the lower internodes was significantly ($P< 0.001$) greater at day 24 than maturity, but DM content of Vasco was much greater than Sun 92A at both harvests (Fig. 6.8). However remobilization of DM from the internodes between the two harvests was similar in both wheat cultivars under control conditions, while the amount of DM remobilized was greater in Vasco than in Sun 92A under water stress conditions (Fig. 6.9). Postanthesis water stress significantly reduced the amount of DM remobilized between day 24 and maturity. ESS content of the internodes was similar in both cultivars in each treatment at day 24 and very little ESS remained at maturity (Fig. 6.10). More ESS was remobilized under control than under water stress conditions in both cultivars (Fig. 6.11). In terms of TSC content (Fig.6.12), the amount was similar to ESS (Fig.6.10) content in the internode under all conditions. Evidently, all (or most) of the TSS in the internodes was present as ESS (compare Figs. 6.11 and 6.13).

6.3.2.2 Lower internodes N, SP content and remobilization

N content of the lower nternodes was greater in Vasco than Sun 92A at both harvests and both conditions (Fig. 6.14). It was also greater at day 24 than at maturity in both cultivars; however, the response of Sun 92A and Vasco at day 24 to stress was different. In

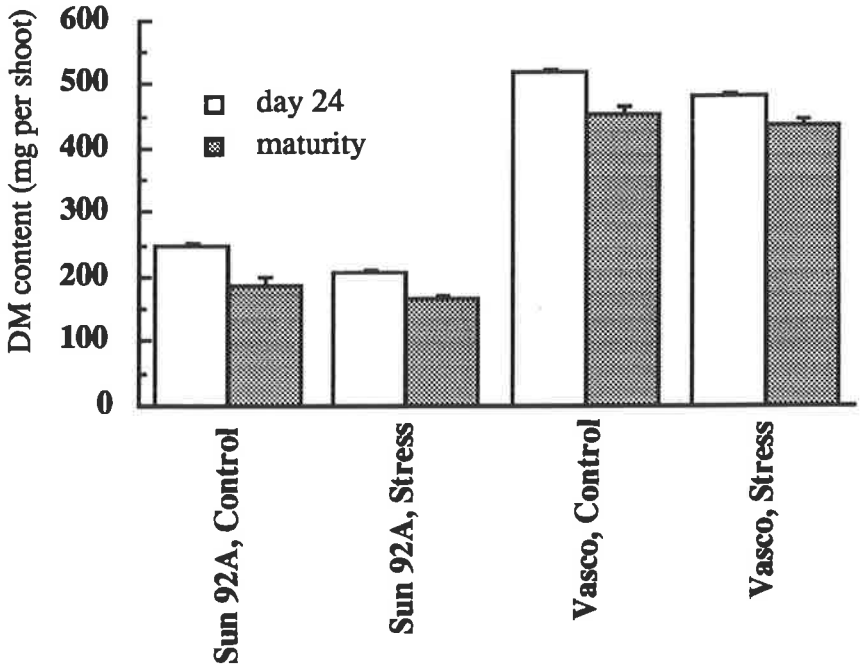

Fig. 6.8. DM content of lower stem internodes in two wheat cultivars under two water stress treatments at day 24 and maturity. Error bars are standard errors.

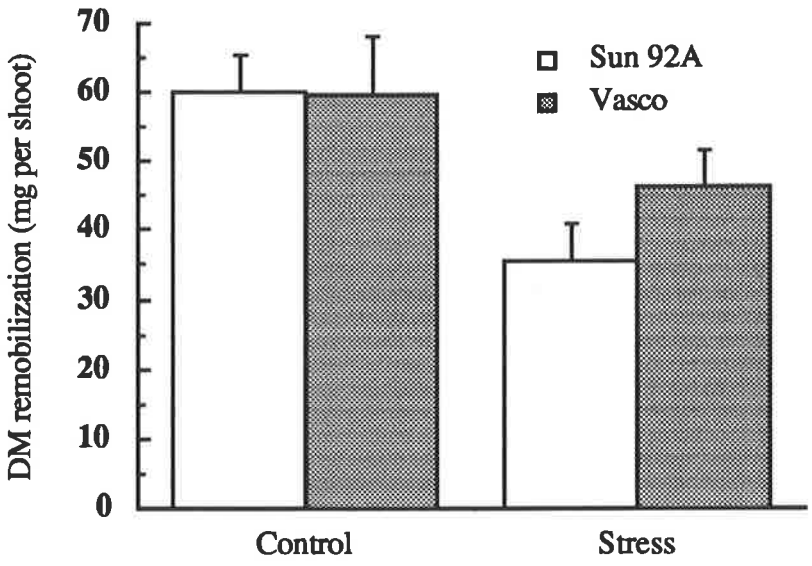

Fig. 6.9. The remobilization of DM from the lower internodes in two wheat cultivars between day 24 and maturity. Error bars are standard errors.

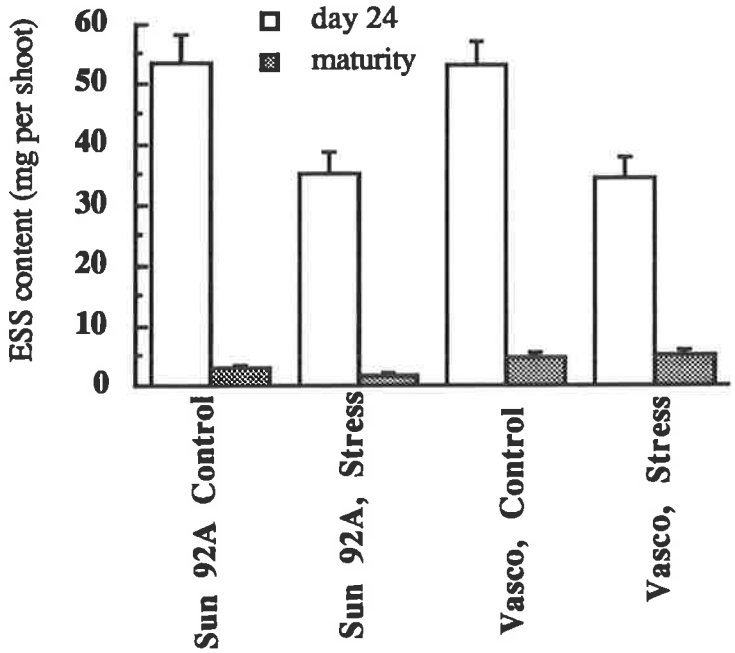

Fig. 6.10. ESS content of the lower internodes in two wheat cultivars at day 24 and maturity under stress and control conditions. Error bars are standard errors.

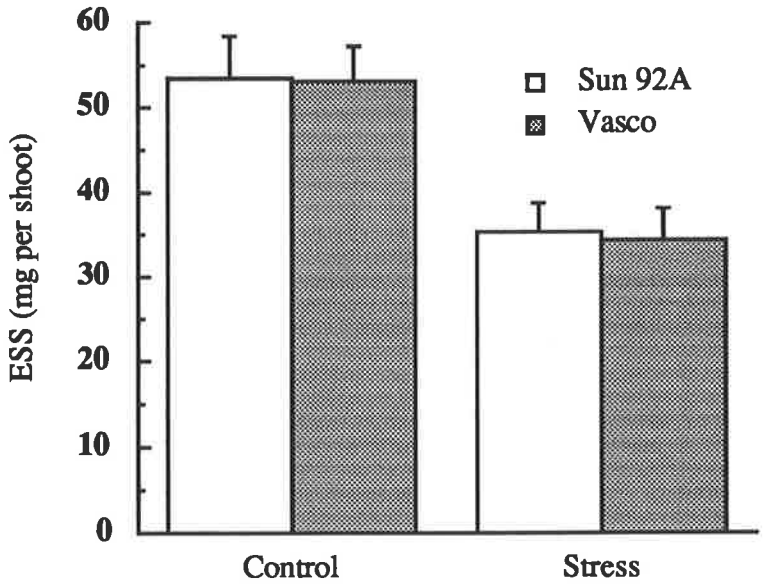

Fig. 6.11. The remobilization of ESS from lower internodes of two wheat cultivars between day 24 and maturity. Error bars are standard errors.

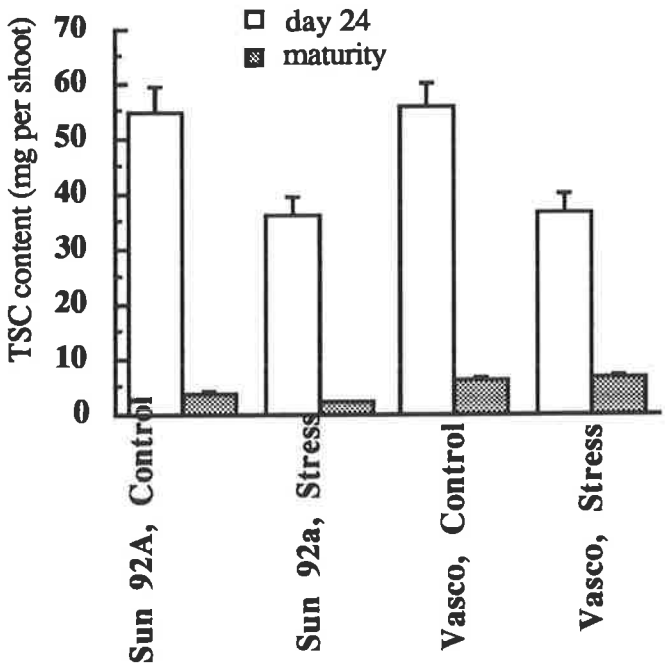

Fig. 6.12. TSC content in the lower sinternodes of two wheat cultivars under control and stress conditions and two harvests. Error bars are standard errors.

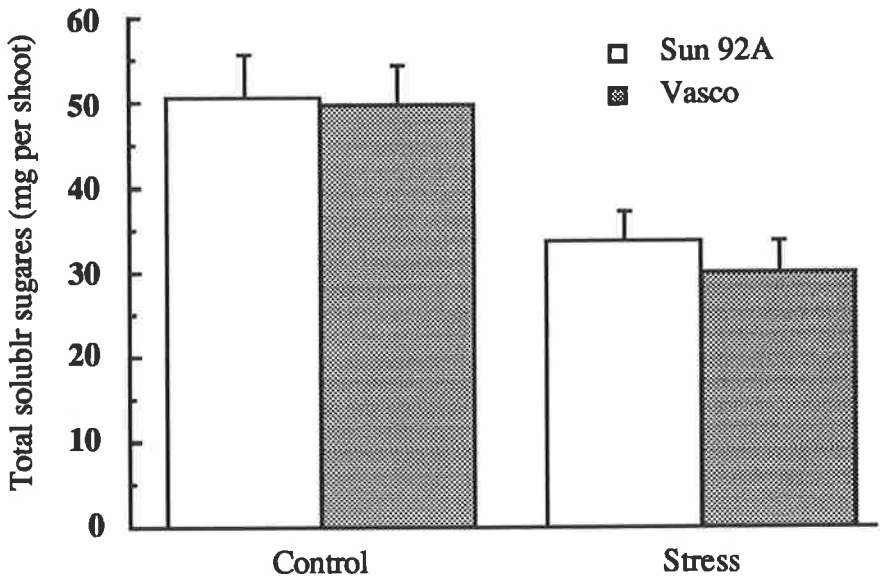

Fig. 6.13. The remobilization of TSC from the lower internodes in two wheat cultivars between day 24 and maturity. Error bars are standard errors.

Sun 92A water stress reduced N content compared to control conditions while in Vasco, N content was similar under both conditions. Despite a greater amount of N in the lower internodes of Vasco than Sun 92A at day 24, N remobilization was greater in Sun 92A than in Vasco under control conditions but less under stress (Fig. 6.15).

N concentration of the internodes was also significantly ($P< 0.001$) greater at day 24 than at maturity in both cultivars (Fig. 6.16) and over both harvests it was higher in Sun 92A than in Vasco. The amount of SP in the internodes of Sun 92A under well-watered and stress conditions was greater at day 24 than maturity (Fig. 617). This was also the case in well-watered Vasco, but under water stress there was no significant difference. At day 24 Sun 92A contained significantly ($P < 0.01$) greater amounts of SP than Vasco, while at maturity Vasco contained greater amounts than Sun 92A (Fig. 6.17). As a result the remobilization of SP from the internodes in Sun 92A was significantly ($P< 0.001$) greater than in Vasco (Fig. 6.18) and it was greater in control than stress conditions (Fig.6.19).

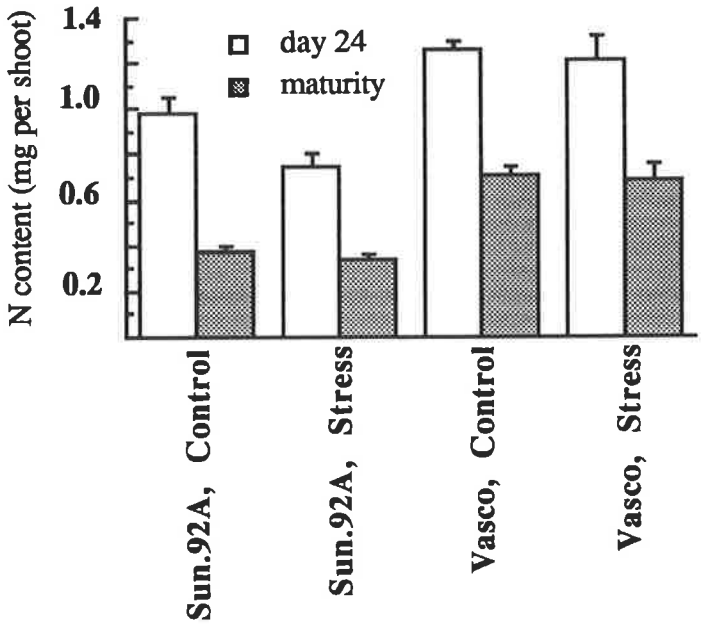

Fig. 6.14. The N content of the lower nternodes in two wheat cultivars at day 24 and maturity under control and stress conditions. Error bars are standard errors.

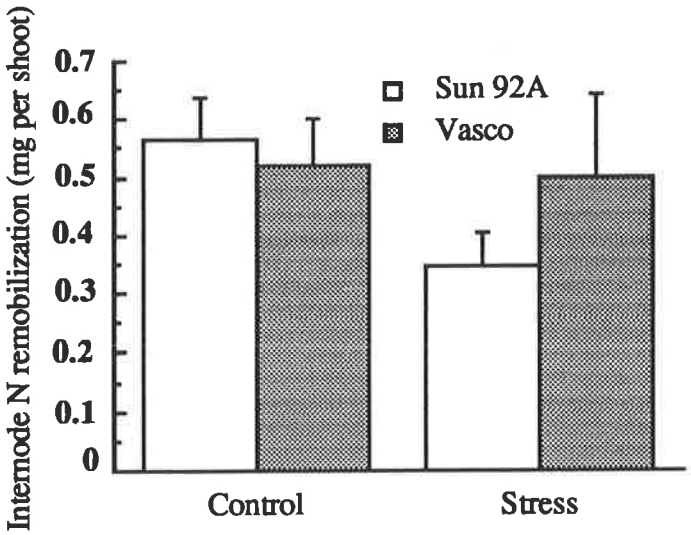

Fig. 6.15. The remobilization of N from the ilower nternodes in two wheat cultivars between day 24 and maturity. Error bars are standard errors.

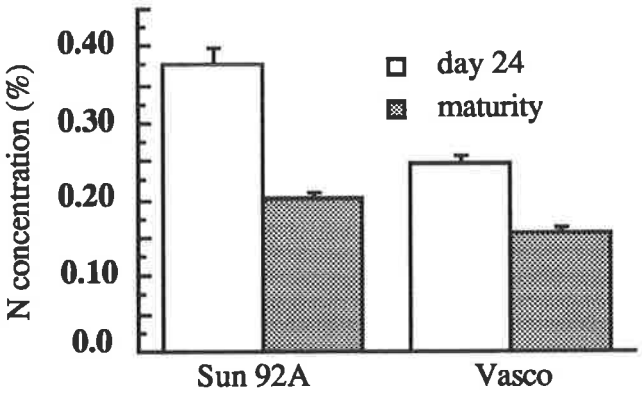

Fig. 6.16. The concentration of N in the lower nternodes of two wheat cultivars (over control and water stress) at day 24 and maturity. Error bars are standard errors.

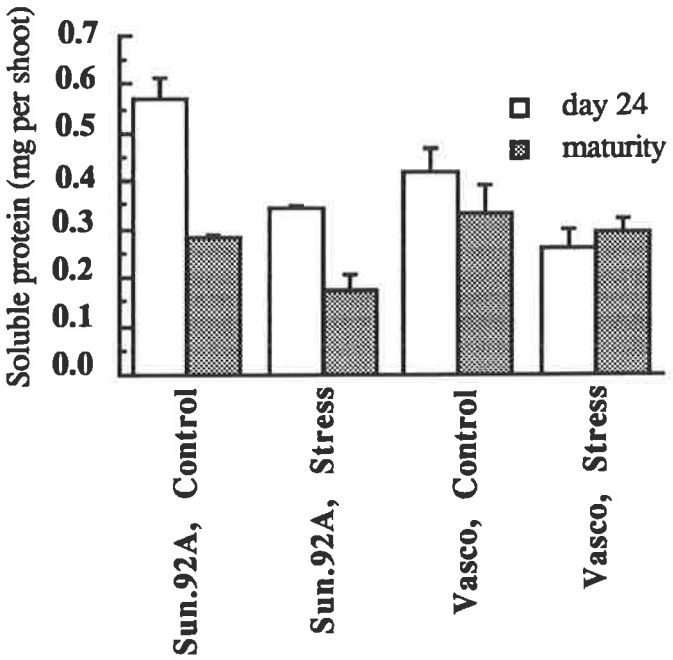

Fig. 6.17. SP content of internodes in two wheat cultivars under stress and control conditions at day 24 and maturity. Error bars are standard errors.

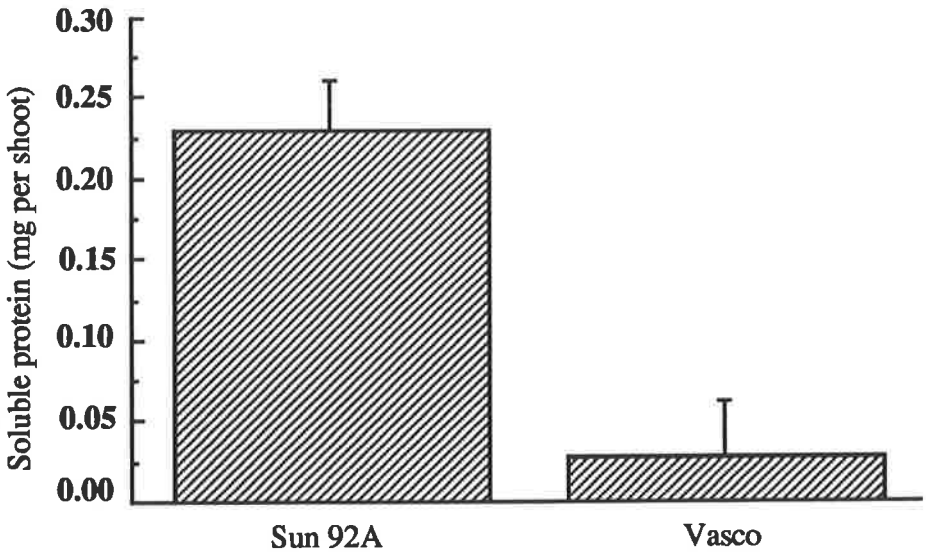

Fig. 6.18. The remobilization of SP from the lower stem internodes between day 24 and maturity. Error bars are standard errors.

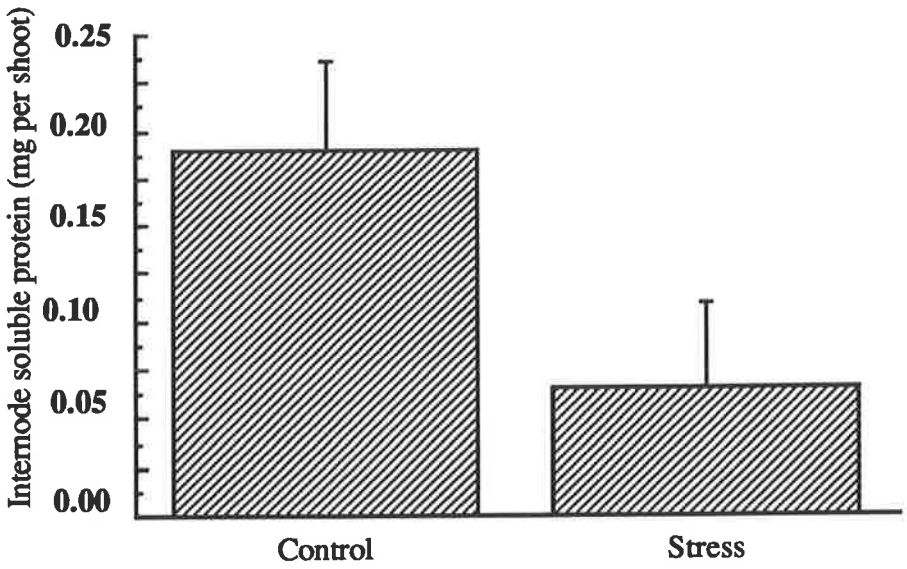

Fig. 6.19. The remobilization of SP from the lower stem nternodes of two wheat cultivars under stress and non stress conditions. Error bars are standard errors.

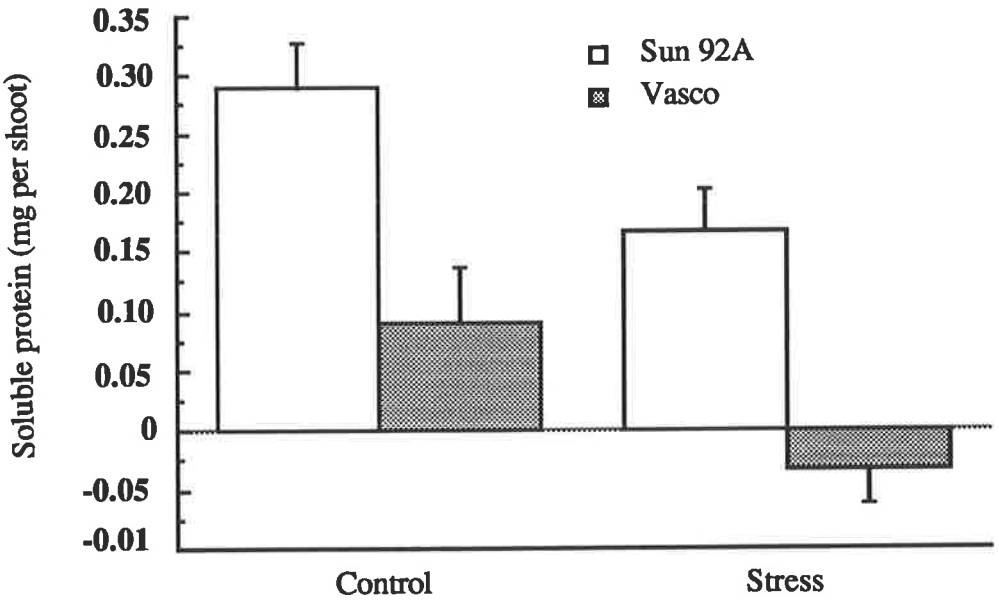

Fig. 6.20. The remobilization of SP from the lower stem internodes in two wheat cultivars between day 24 and maturity. Error bars are standard errors.

Although the interaction of cultivars and treatments statistically was not significant, the remobilization of SP from the internodes of Vasco appeared to differ from Sun 92A under water stress (Fig. 6.20).

6.3.3. Peduncle

6.3.3.1 DM, ESS and TSC content and remobilization

DM content of the peduncle in Vasco was significantly greater than in Sun 92A in all conditions (Fig. 6.21) but the remobilization of DM between day 24 and maturity was not significantly different for both cultivars in the two treatments (Fig. 6.22). Although the DM content of Vasco was significantly greater than Sun 92A, ESS content of the peduncle in Sun 92A at day 24 was significantly ($P< 0.001$) greater than Vasco (Fig. 6.23). At day 24, stress had reduced the amount of ESS in the peduncle of Sun 92A but not in Vasco, but at maturity, the amount of ESS was lower in the stress treatment of both cultivars. The remobilization of ESS from the peduncle between the two harvests (Fig. 6.24) was also greater in Sun 92A than in Vasco under control conditions while it was similar for the two cultivars under stress conditions. However, by maturity there was very little ESS in the peduncle.Thus stress reduced the amount of ESS remobilized between day 24 and maturity and DM in Sun 92A but not in Vasco, but in both cultivars there was more complete use of ESS under stress.

The pattern of TSC content of the peduncle was similar to the pattern of ESS (compare Fig. 6.23 and Fig. 6.25) and the remobilization of TSC from the peduncle also was similar to the remobilization of ESS in both cultivars and both treatments (Fig. 6.26).

6.3.3.2 Peduncle N and SP content and remobilization

The N content of the peduncle in Vasco was greater than Sun 92A under stress or non-stress and at both harvests (Fig. 6.27), and in both cultivars N content was greater under control conditions than stress conditions. Water stress reduced N remobilization from the peduncle, and under stress the remobilization of N was greater in Vasco than Sun 92A (Fig.6.28).

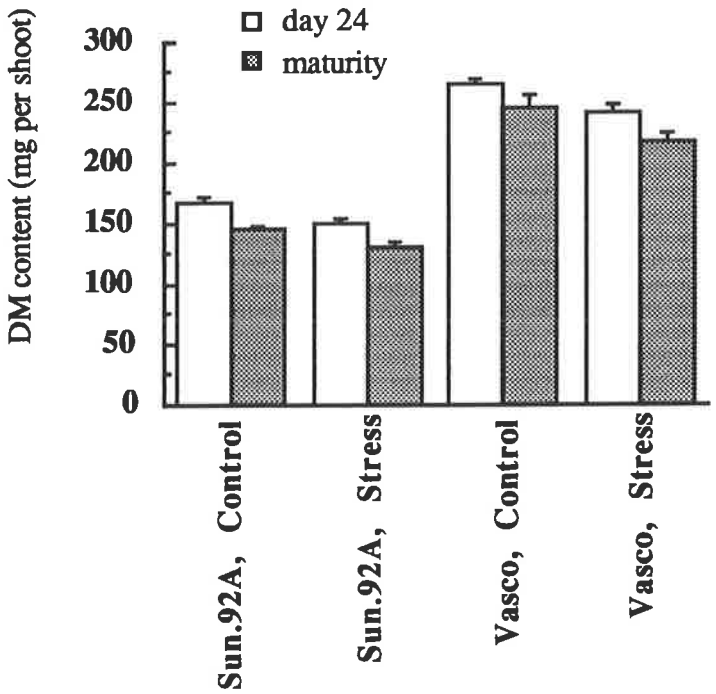

Fig. 6.21. DM content of peduncle in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

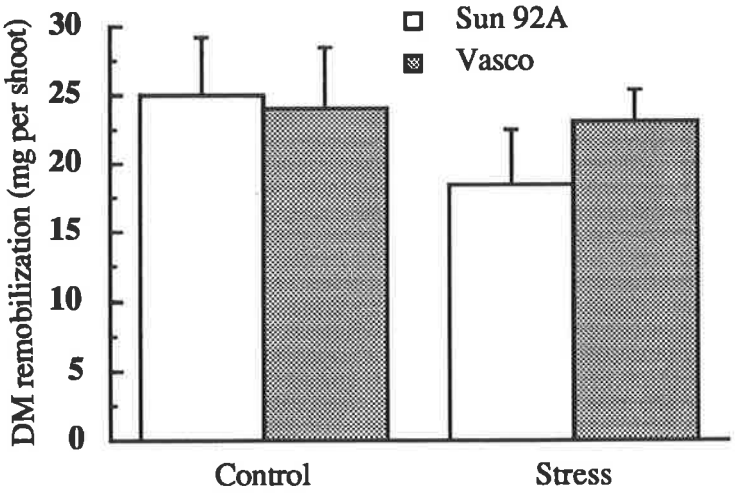

Fig. 6.22. The remobilization of DM from the peduncle in two wheat cultivars between day 24 and maturity. Error bars are standard errors.

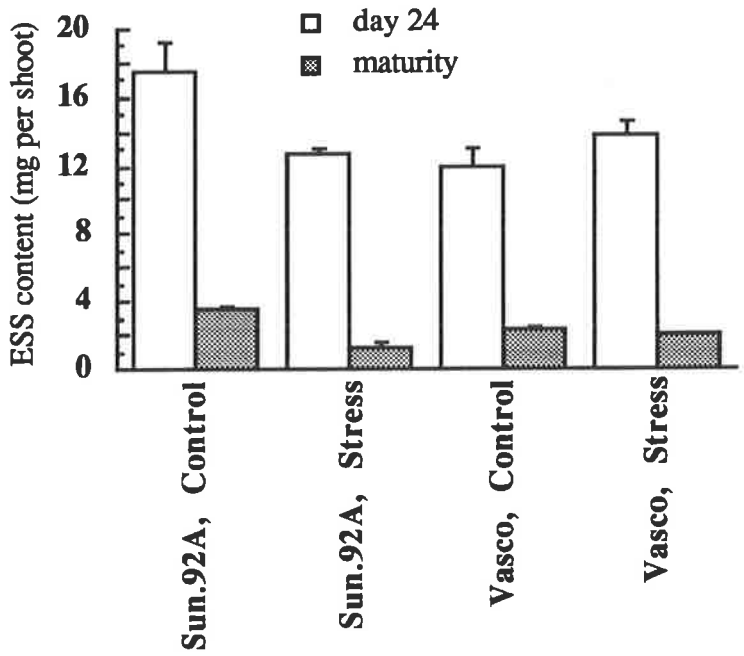

Fig. 6.23. ESS content of peduncle in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

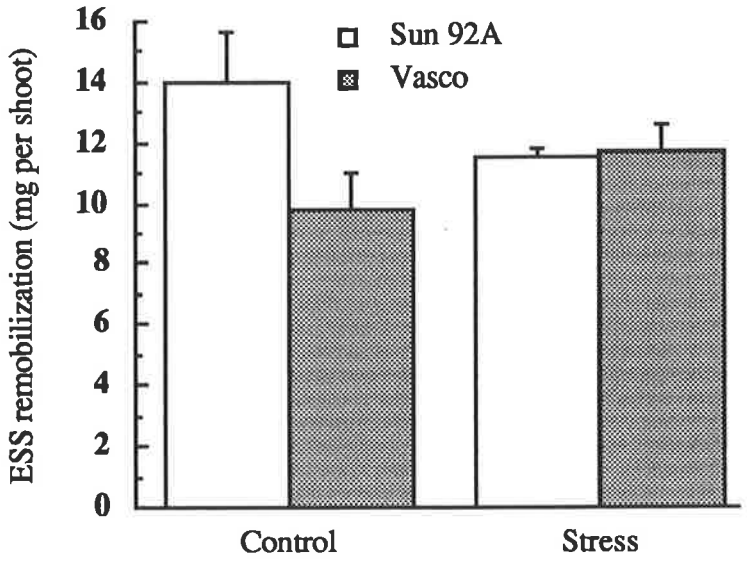

Fig. 6.24. The remobilization of ESS from the peduncle in two wheat cultivars between day 24 and maturity. Error bars are standard errors.

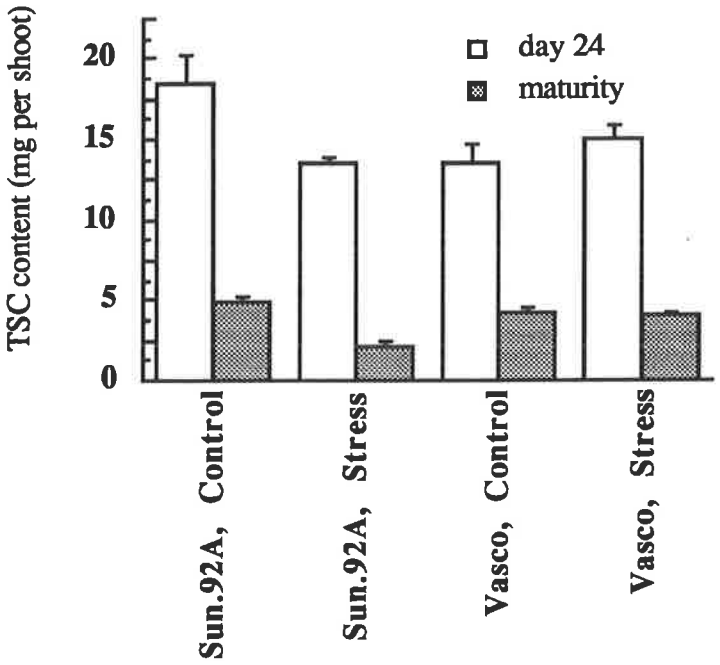

Fig. 6.25. The TSC content in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

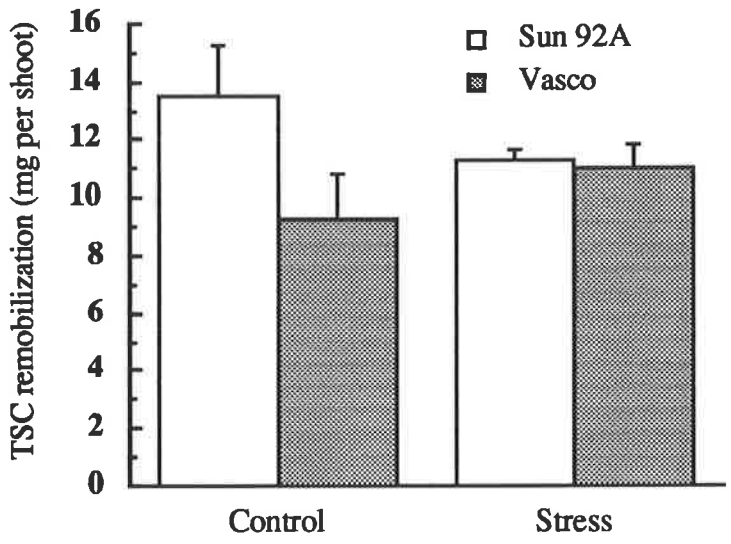

Fig. 6.26. The remobilization of TSC from the peduncle in two wheat cultivars under stress and non stress conditions. Error bars are standard errors.

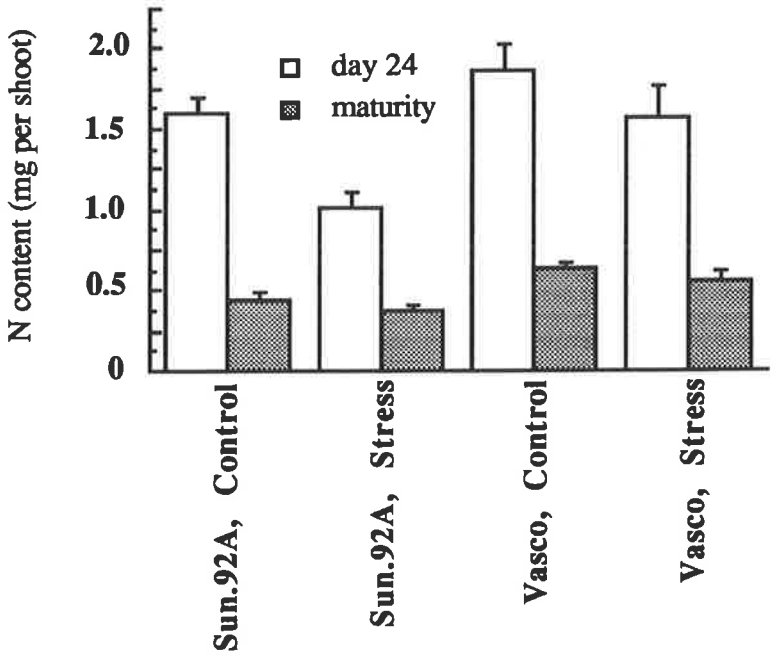

Fig. 6.27. N content in the peduncle of two wheat cultivars under control and stress at day 24 and maturity. Error bars are standard errors.

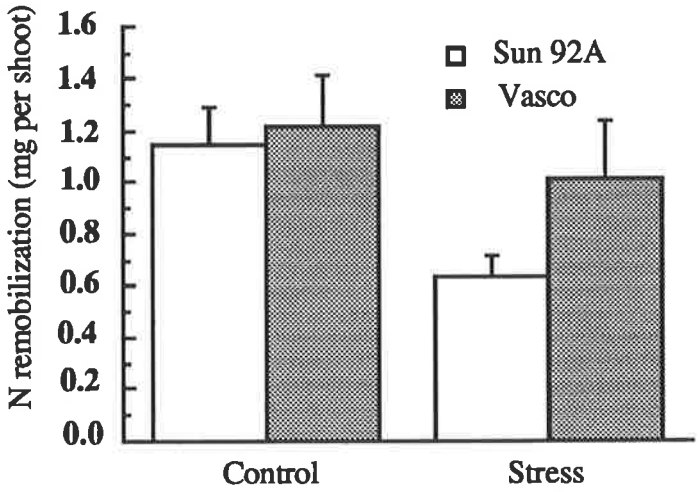

Fig. 6.28. The remobilization of N from the peduncle in two wheat cultivars under stress and non stress conditions. Error bars are standard errors.

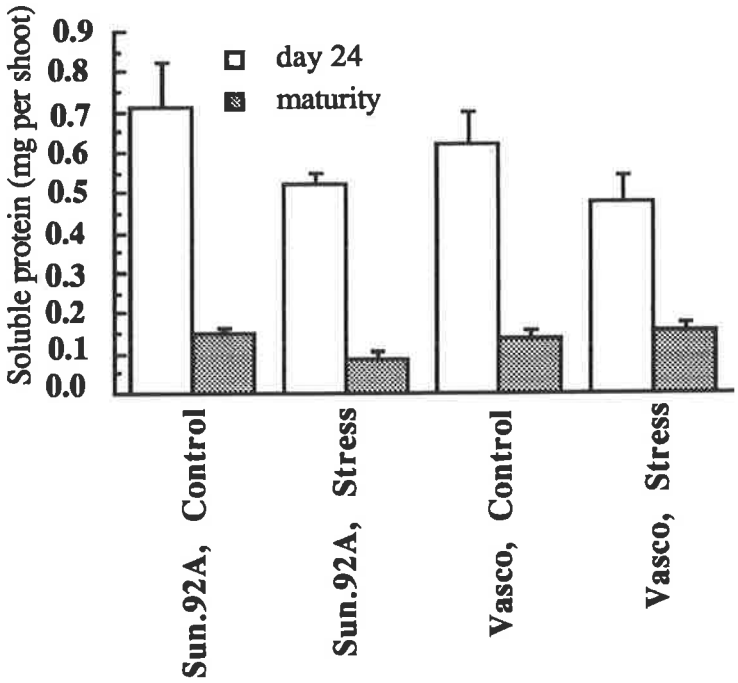

Fig. 6.29. SP content of peduncle in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

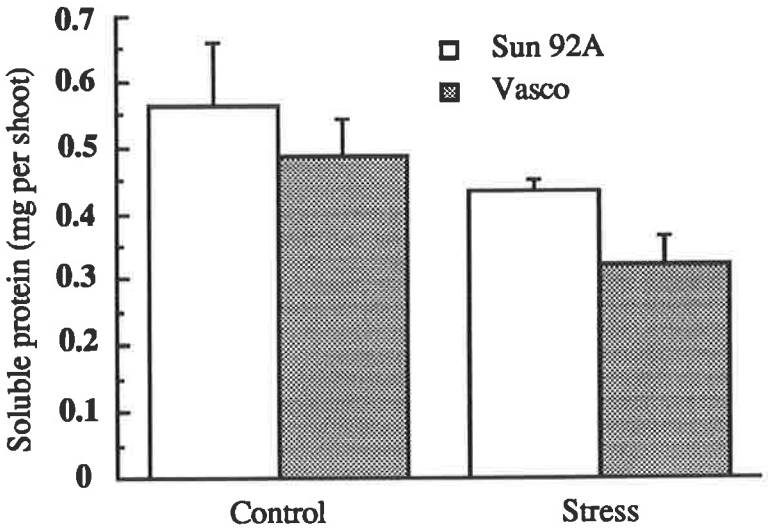

Fig. 6.30. The remobilization of SP from the peduncle between day 24 and maturity in two wheat cultivars under stress and control conditions. Error bars are standard errors.

SP content in the peduncle was not significantly different in both cultivars at day 24 under control and stress conditions (Fig. 6.29). The amount of SP remobilized from the peduncle was greater in Sun 92A than Vasco and in both cultivars remobilization was reduced by stress (Fig. 6.30).

6.3.4 Flag leaf

6.3.4. 1. Flag leaf DM, ESS and TSC content and remobilization

DM content of the flag leaf in both cultivars decreased between day 24 and maturity under both conditions (Fig. 6.31). DM content of the flag leaf in Vasco was greater than Sun 92A at both harvests under control conditions and also it was greater than Sun 92A at maturity in the stress treatment.

Water stress increased the remobilization of DM from the flag leaf of Sun 92A, but decreased it in Vasco, and significantly more DM ($P < 0.01$) was remobilized from the flag leaf of Sun 92A than Vasco under water stress (Fig. 6.32). On the other hand at day 24 ESS content in the flag leaf of Vasco was significantly greater than Sun 92A under both water stress and control conditions, while at maturity it was similar in both cultivars and in the two treatments (Fig. 6.33).

Remobilization of ESS from the flag leaf of Vasco was significantly ($P < 0.001$) greater than in Sun 92A and water stress stress reduced remobilization of ESS only in Vasco (Fig. 6.34). A similar pattern was found for remobilization of TSCs from the flag leaf (Fig. 6.35).

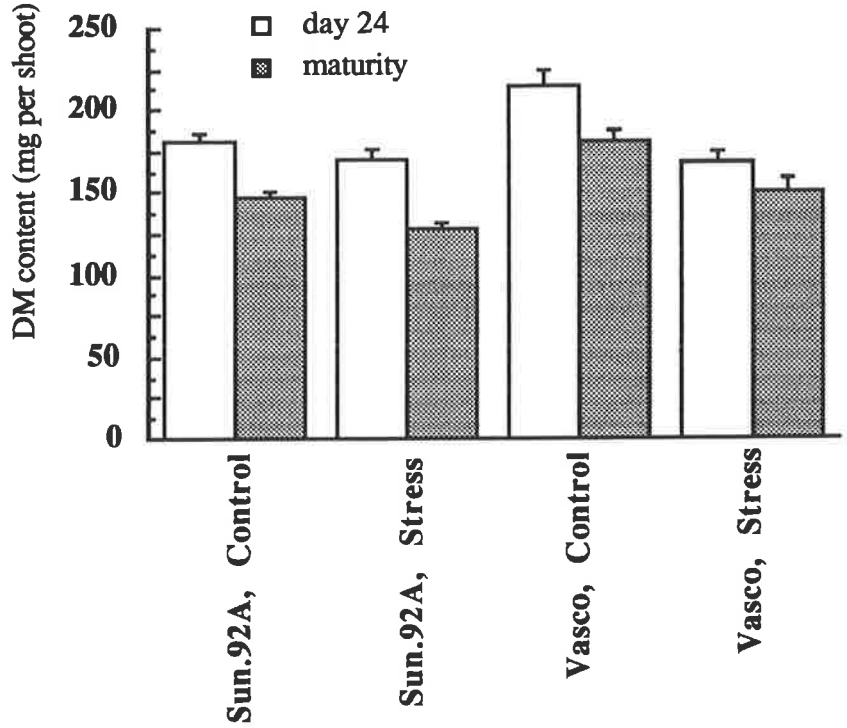

Fig. 6.31. DM content in the flag leaf in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

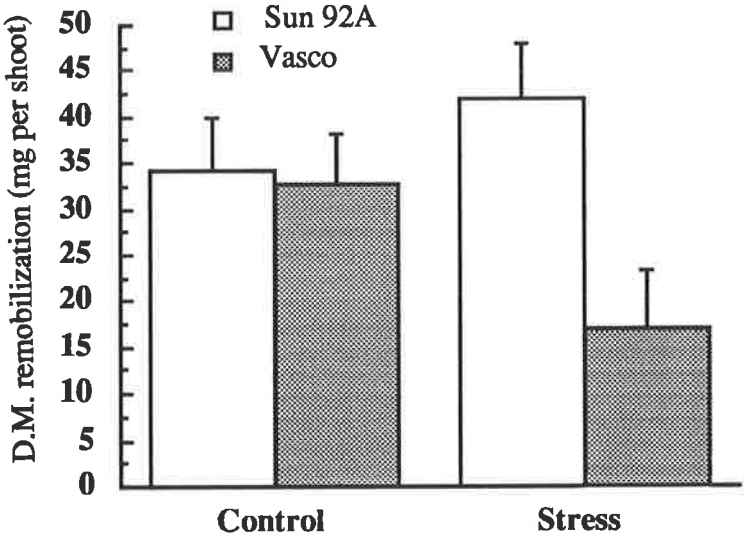

Fig. 6.32. The remobilization of DM from the flag leaf in two wheat cultivars under stress and non stress conditions between day 24 and maturity. Error bars are standard errors.

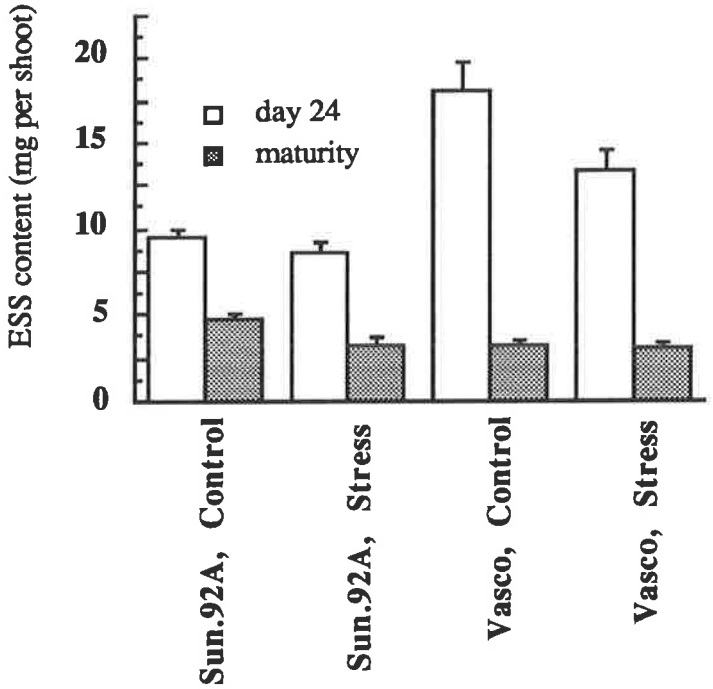

Fig. 6.33. ESS content in the flag leaf of two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

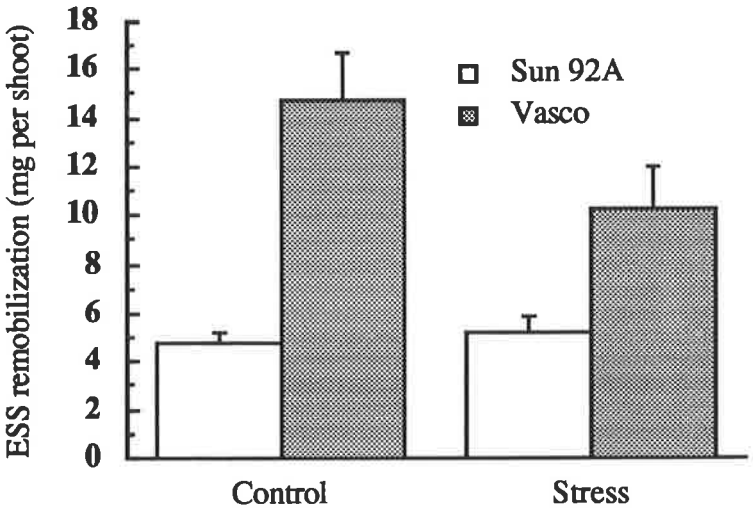

Fig. 6.34. The remobilization of ESS from the flag leaf in two wheat cultivars under stress and control conditions. Error bars are standard errors.

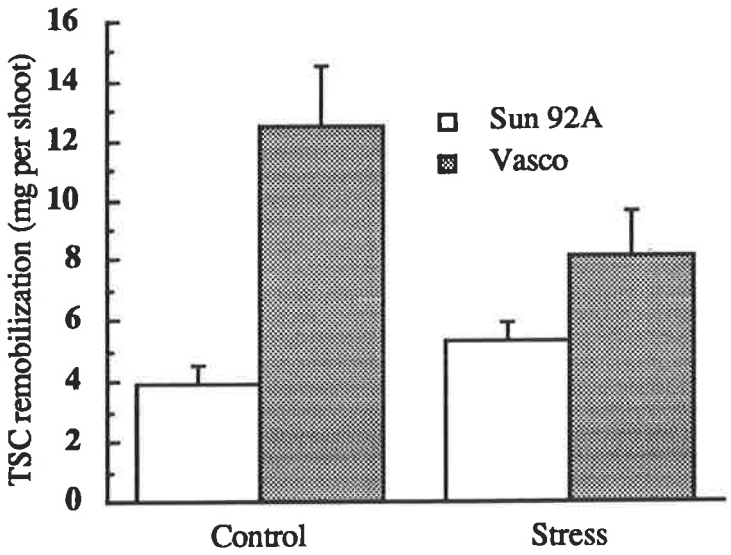

Fig. 6.35. The remobilization of TSC from the flag leaf in two wheat cultivars under stress and non stress conditions. Error bars are standard errors.

6.3.4.2 Flag leaf N content, N concentration and SP content and remobilization

Despite a greater amount of DM (Fig. 6.31) in the flag leaf of Vasco than Sun 92A, N content in the flag leaf of Sun 92A was greater than in Vasco in both treatments at day 24, while N content of both cultivars was similar at maturity (Fig. 6.36). As a result N remobilization from the flag leaf was significantly ($P < 0.01$) greater in Sun 92A than in Vasco in both water stress and control conditions, and stress reduced remobilization of N from the flag leaf (Fig. 6.37). The pattern for N% in the flag leaf (Fig. 6.38) was similar to N content in the flag leaf.

At day 24 SP content of the flag leaf was greater in Sun 92A than in Vasco under both conditions (Fig. 6.39). Sun 92A remobilized similar amounts of SP from the flag leaf in both watering treatments, while Vasco remobilized greater amounts of SP under control conditions than stress conditions (Fig. 6.40). Sun 92A remobilized considerably more SP than Vasco.

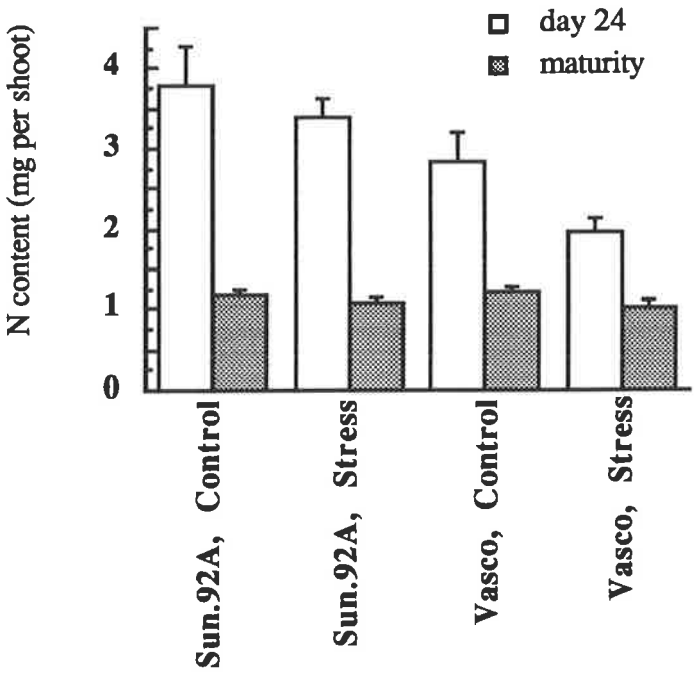

Fig. 6.36. N content in the flag leaf of two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

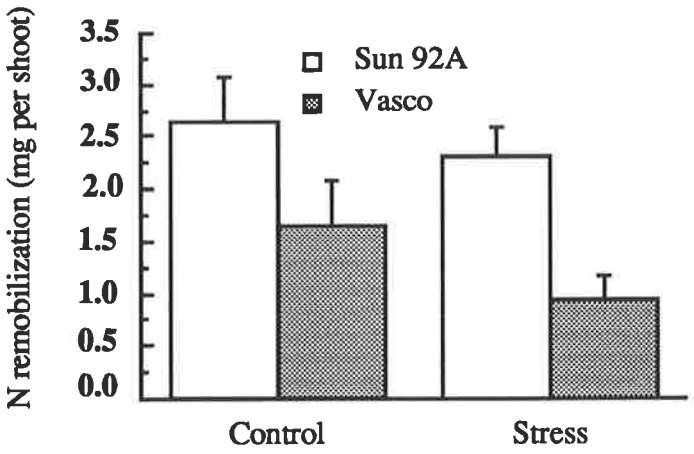

Fig. 6.37. N remobilization from the flag leaf in two wheat cultivars under stress and control conditions. Error bars are standard errors.

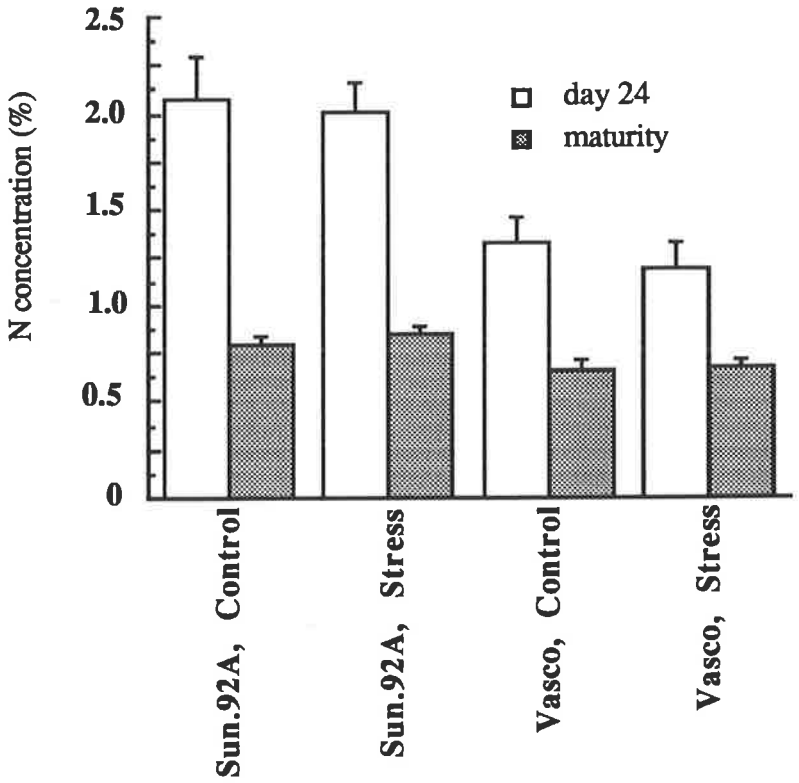

Fig. 6.38. The N % in the flag leaf of two wheat cultivars at day 24 and at maturity under stress and control conditions. Error bars are standard errors.

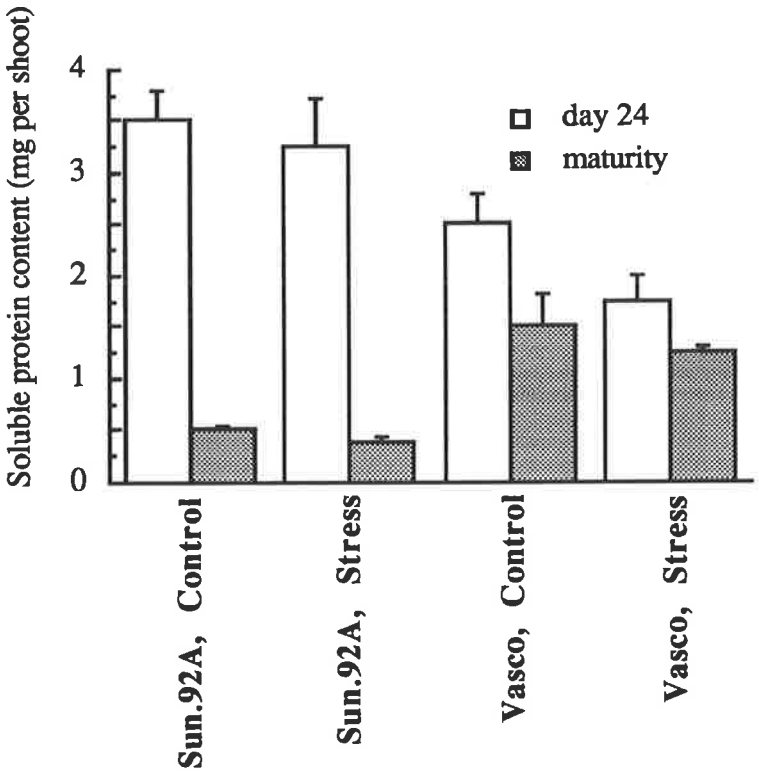

Fig. 6.39. Soluble protein content of the flag leaf in two wheat cultivars in two wheat cultivars at day 24 and maturity. Error bars are standard errors.

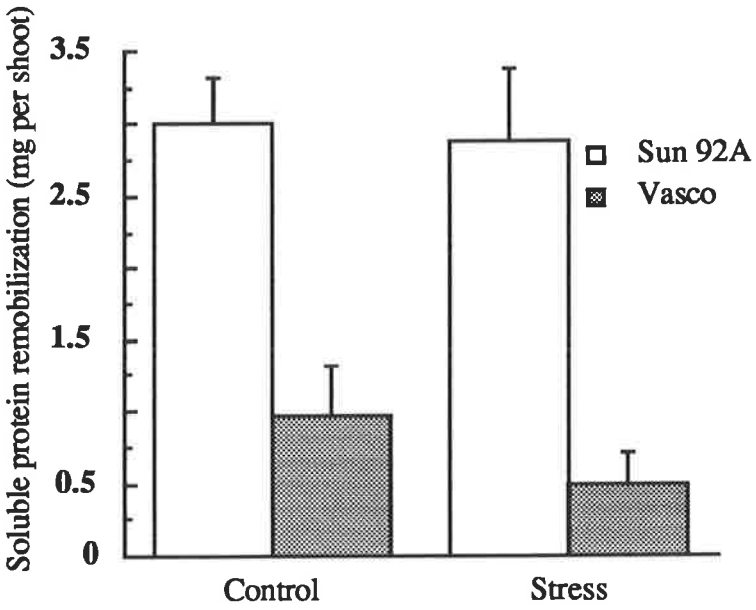

Fig. 6.40. SP remobilization from the flag leaf in two wheat cultivars under stress and control conditions. Error bars are standard errors.

6.3.5. Other leaves

6.3.5.1 Other leaves DM, ethanol-soluble and total soluble sugars content and remobilization

DM content of the other leaves in Vasco was significantly ($P<0.001$) greater than in Sun 92A in both harvests and both conditions (Fig. 6.41). The remobilization of DM was similar in both cultivars under control and stress conditions separately (Fig. 6.42). The pattern of ESS content of the other leaves (Fig, 6.43) was similar to DM content (Fig. 6.41); therefore, ESS was significantly ($P<0.01$) greater in Vasco than Sun 92A under both conditions and both harvests (Fig. 6.43). The remobilization of ESS from other leaves was also greater in Vasco than Sun 92A under well-watered and stress conditions (Fig. 6.44), and the pattern did not reflect DM remobilization.

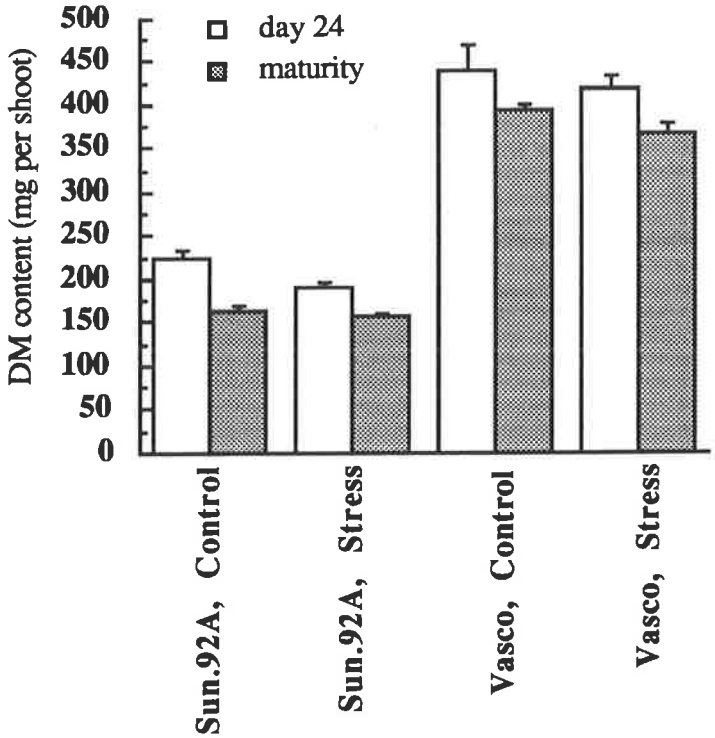

Fig. 6.41. DM content of the other leaves in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

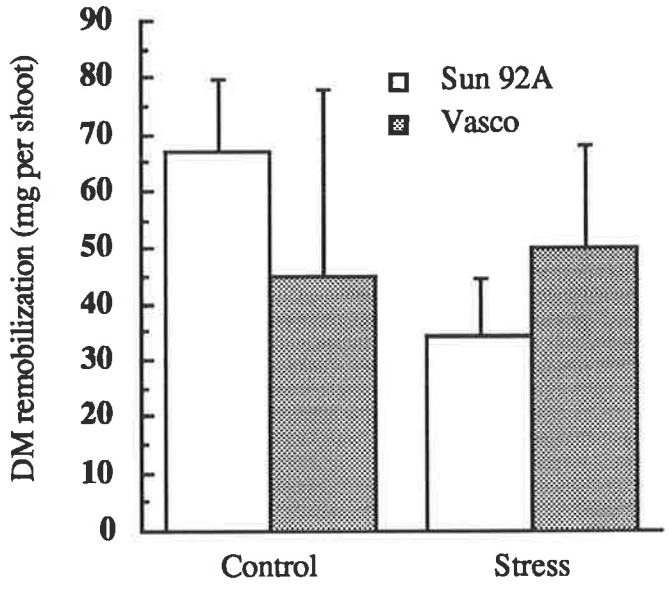

Fig. 6.42. The remobilization of DM from other leaves in two wheat cultivars under stress and non stress conditions. Error bars are standard errors.

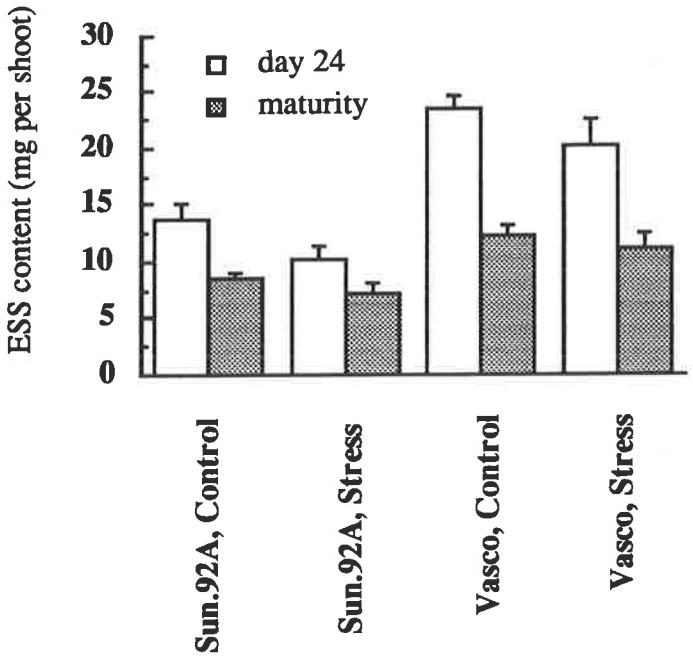

Fig. 6.43. ESS content of the other leaves in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

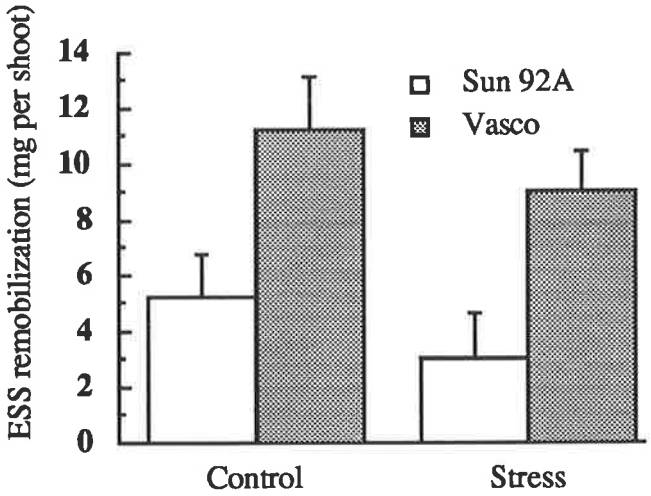

Fig. 6.44. The remobilization of ESS from the other leaves of two wheat cultivars under stress and non stress conditions. Error bars are standard errors.

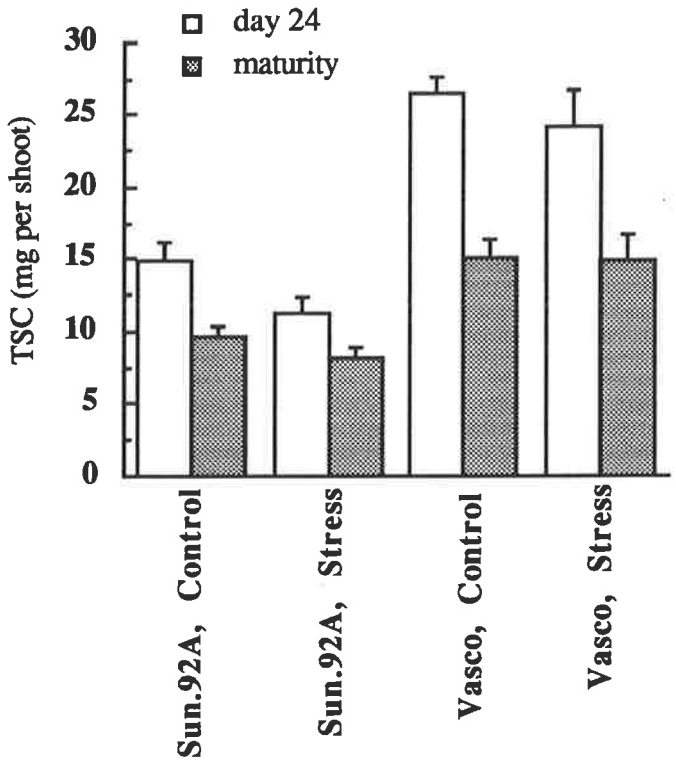

Fig. 6.45. TSC of other leaves in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

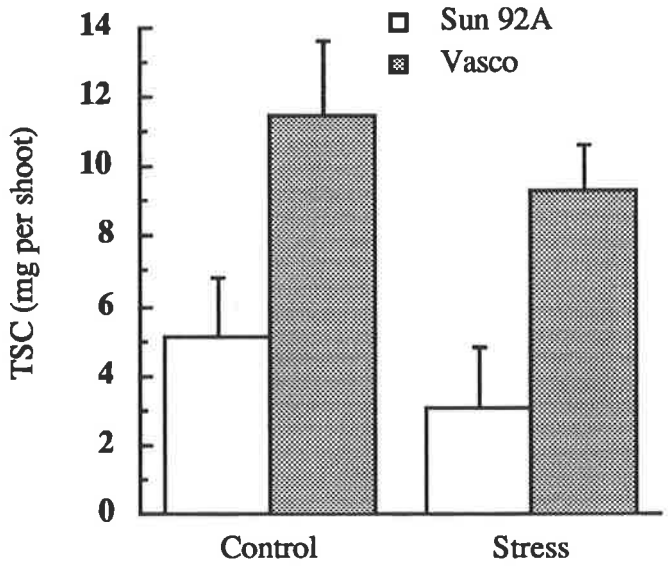

Fig. 6.46. The remobilization of TSC from the other leaves in two wheat cultivars under two treatments between day 24 and maturity. Error bars are standard errors.

TSC content of the other leaves (Fig. 6.45) was similar to ESS content (Fig. 6.43) and a similar pattern was found for the remobilization of TSC from the other leaves (Fig. 6.46).

6.3.5.2 Other leaves N concentration, content and SP content and remobilization.

At day 24 N content of the other leaves in the well-watered treatment was significantly ($P<0.001$) greater than at maturity (Fig. 6.47). N remobilization from other leaves in Sun 92A was highly significantly ($P < 0.001$) more than in Vasco in control conditions, but it was similar under water stress conditions where little N was remobilized (Fig.6.48). A similar response was found for the N% of the other leaves. The N% of the other leaves under well watered conditions was significantly ($P < 0.001$) greater at day 24 than at maturity in both cultivars, but under stress conditions N concentration of the other leaves was similar at day 24 and maturity (Fig. 6.49). The amount of SP was significantly ($P< 0.001$) greater at day 24 than at maturity in both cultivars (Fig. 6.50). Although at day 24 the SP content of other leaves under control

conditions was greater than in stress conditions, at maturity the corresponding values were all much lower and not affected by stress. The remobilization of SP was similar in Sun 92A and Vasco under control conditions, while Vasco remobilized greater amounts than Sun 92A under stress conditions (Fig. 6.51).

6.3.6 Chaff

6.3.5. 1 Chaff DM, ethanol soluble and TSCs content and remobilization.

DM content of the chaff increased between day 24 and maturity under well-watered and stress conditions, and there was greater DM in the chaff in Vasco than in Sun 92A (Fig. 6.52). Thus chaff did not appear to remobilize any amount of DM. In contrast to DM, ESS content of the chaff was significantly ($P< 0.001$) decreased between the two harvests in both cultivars and both conditions (Fig. 6.53). At day 24, the amount of ESS in the chaff of Vasco was significantly greater under stress conditions than under control conditions. Remobilization of ESS from the chaff of Vasco was greater than in Sun 92A

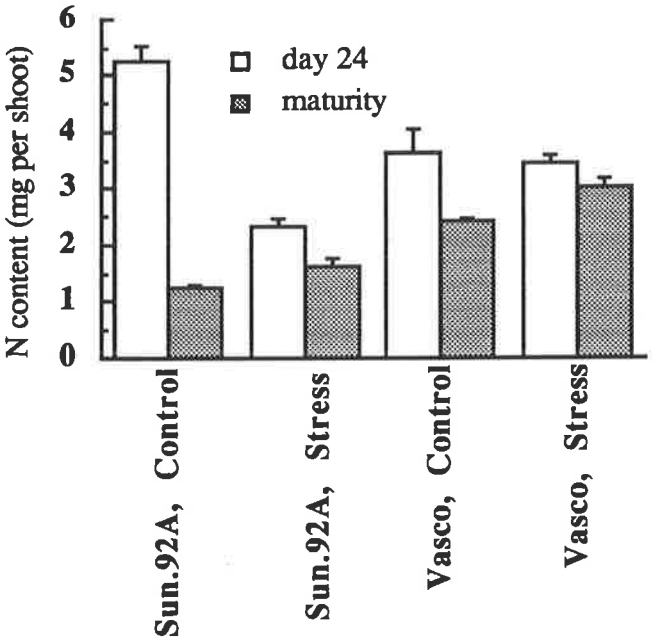

Fig. 6.47. N content of other leaves in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

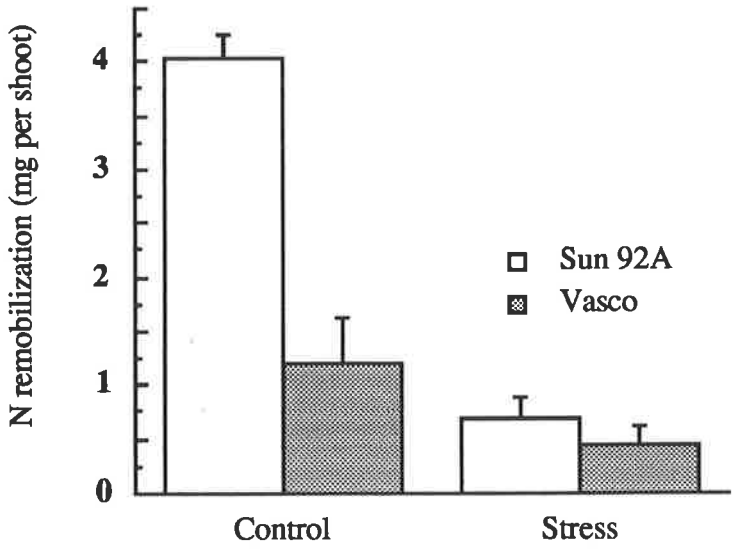

Fig. 6.48. The remobilization of N from the other leaves in two wheat cultivars under control and stress conditions. Error bars are standard errors.

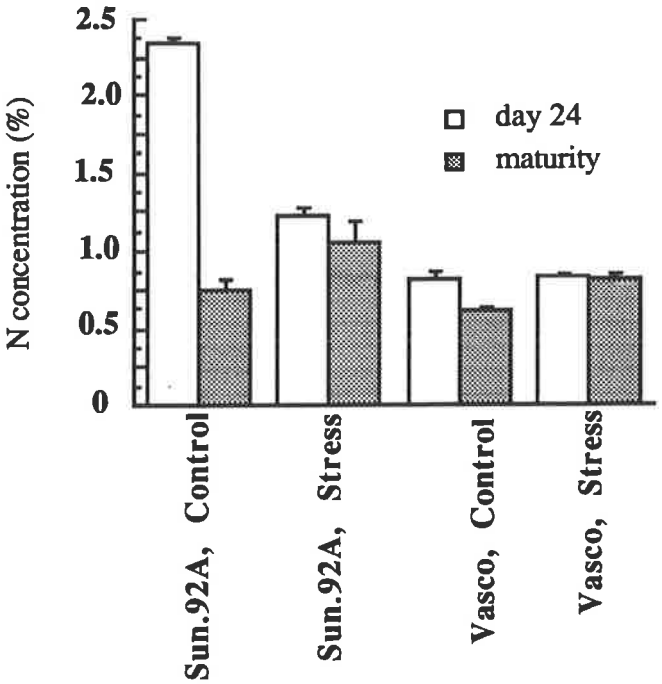

Fig. 6.49. N concentration in the other leaves of two wheat cultivars at day 24 and maturity. Error bars are standard errors.

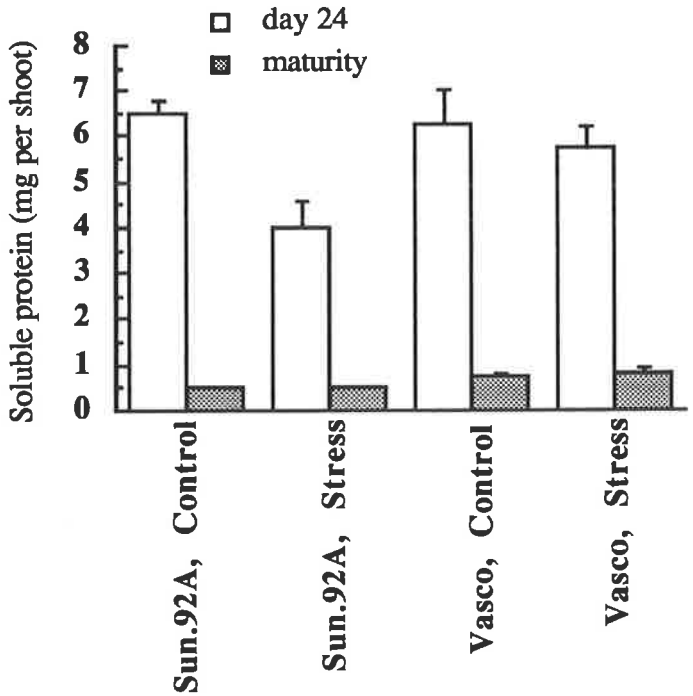

Fig. 6.50. Soluble protein content in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

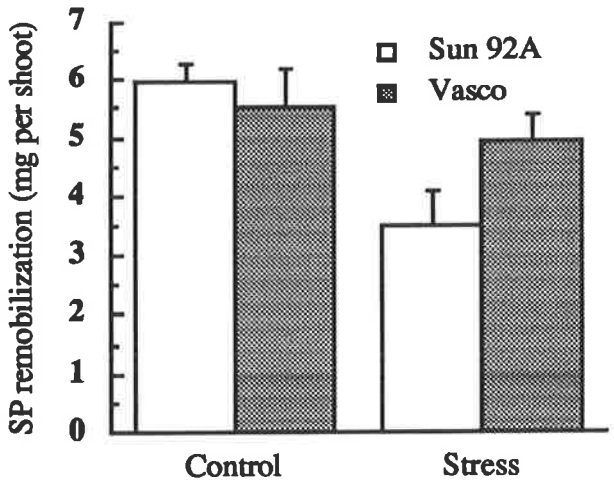

Fig. 6.51. The remobilization of SP from the other leaves in two wheat cultivars between day 24 and maturity. Error bars are standard errors.

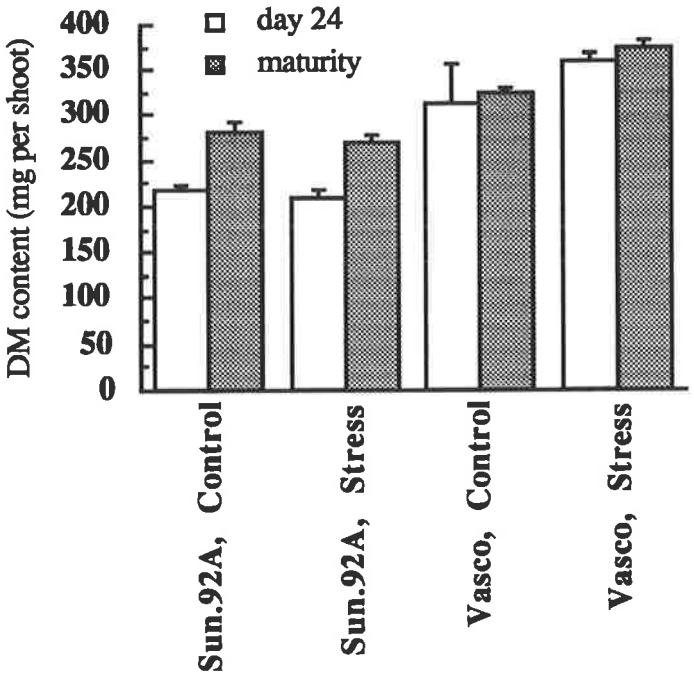

Fig. 6.52. DM content of the chaff in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

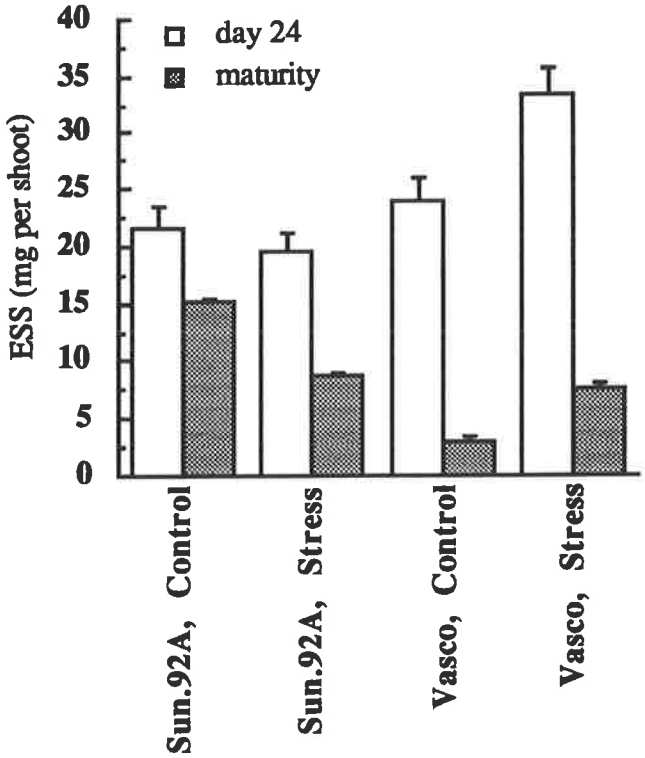

Fig. 6.53. ESS in two wheat cultivars under two treatments at day 24 and maturity. Error bars are standard errors.

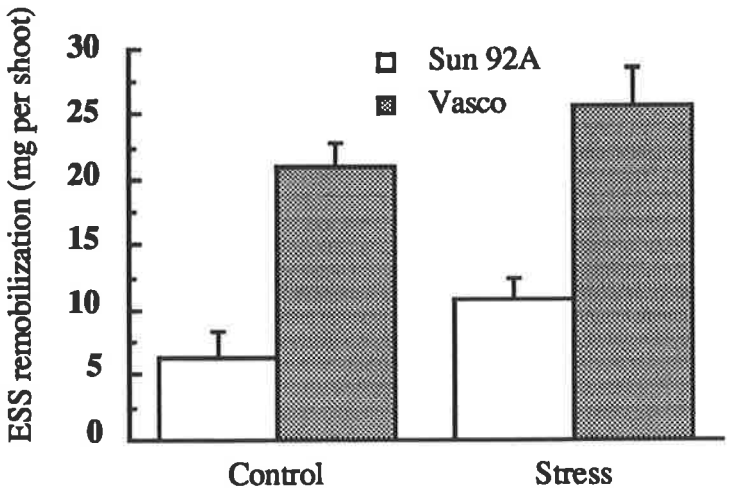

Fig. 6.54. The remobilization of ESS from the chaff in two wheat cultivars under stress and control conditions. Error bars are standard errors.

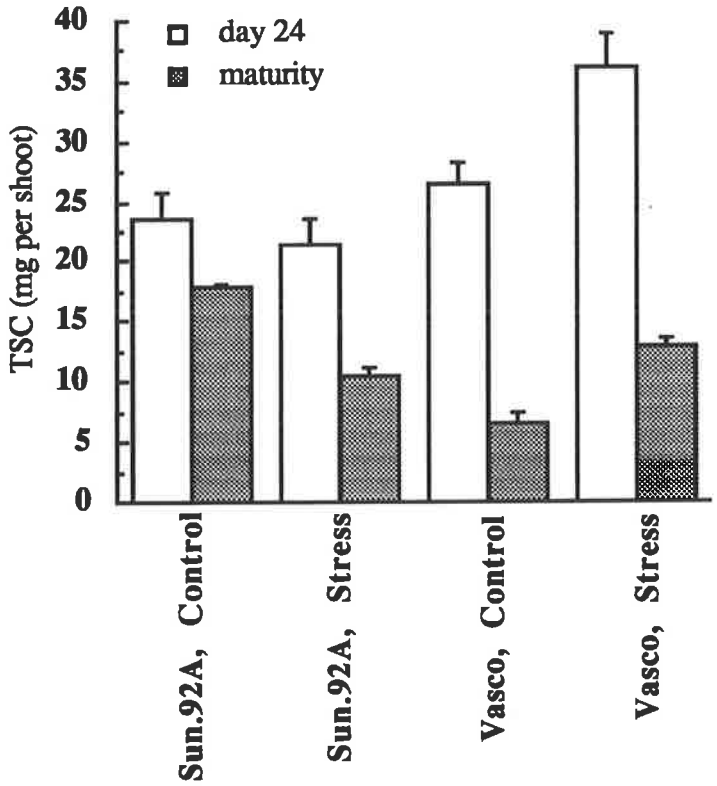

Fig. 6.55. TSC content in the chaff of two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

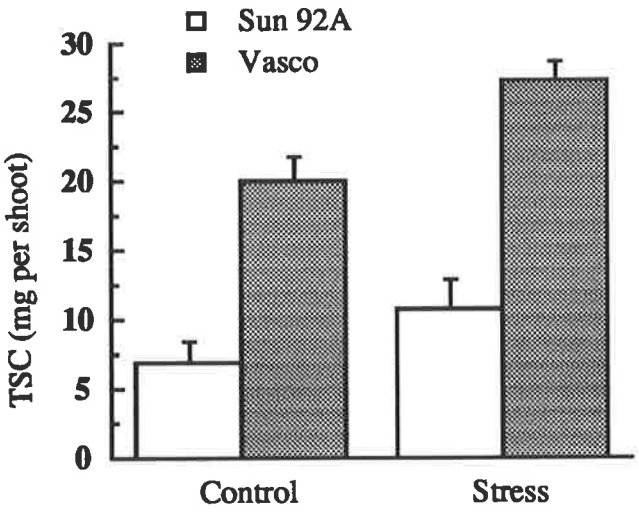

Fig. 6.56. The remobilization of TSCs in two wheat cultivars under stress and non stress conditions. Error bars are standard errors.

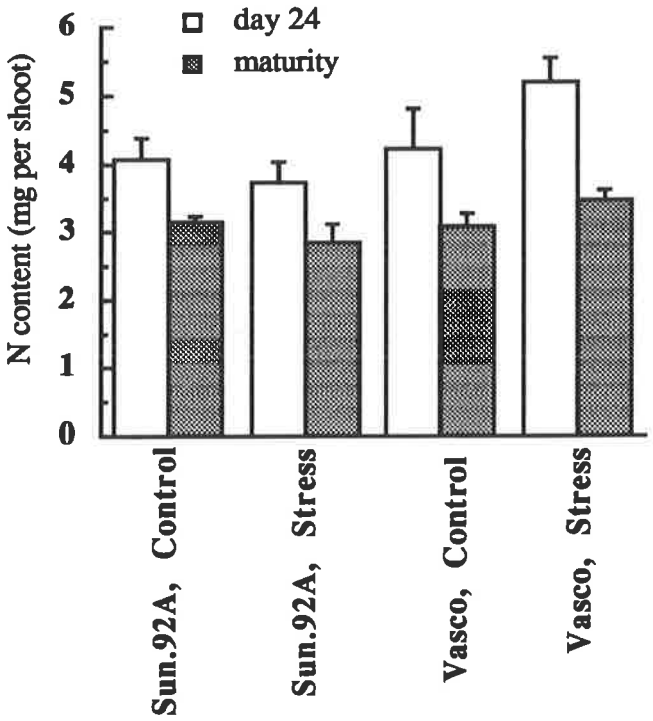

Fig. 6.57. N content of the chaff in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

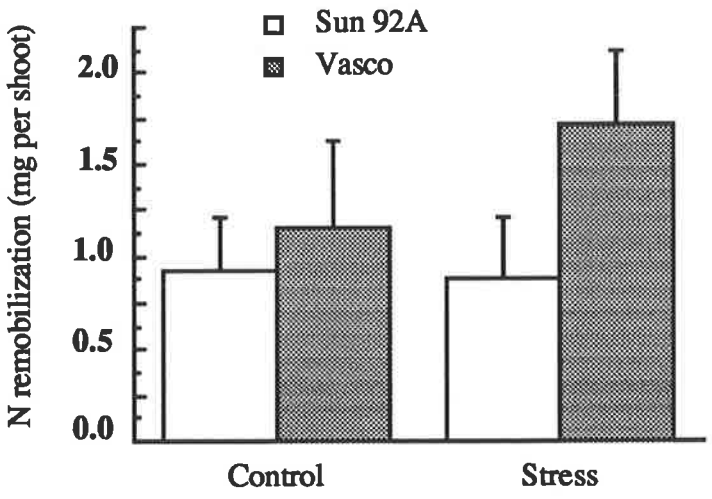

Fig. 6.58. The remobilization of N from the chaff of two wheat cultivars under control and stress conditions. Error bars are standard errors.

and stress increased remobilization of ESS in both cultivars (Fig. 6.54). The pattern of TSC content of the chaff (Fig. 6.55) was similar to the pattern of ESS. Since the TSC content of the chaff was equal to the amount of ESS, the remobilization of TSC (Fig. 6.56) was also similar to the remobilization of ESS (Fig. 6.54).

6.3.5. 2 Chaff N content and concentration (%) and SP content and remobilization

N content of the chaff was significantly ($P < 0.001$) greater at day 24 than at maturity in both cultivars and both conditions (Fig. 6.60). Remobilization of N from the chaff of each cultivar was similar in control and stress conditions (Fig. 6.58).

N concentration of the chaff was significantly greater in Sun 92A than Vasco at both harvests and both conditions (Fig. 6.59) and stress had little effect. SP content of the chaff was significantly ($P <0.001$) higher in Vasco under stress than in any other treatment at day 24 (Fig. 6.60), while at maturity it was greatest in Sun 92A under control conditions. As a result, SP remobilization from the chaff of both cultivars was greater under stress than under control conditions, and Vasco remobilized greater amounts than Sun 92A (Fig. 6.61).

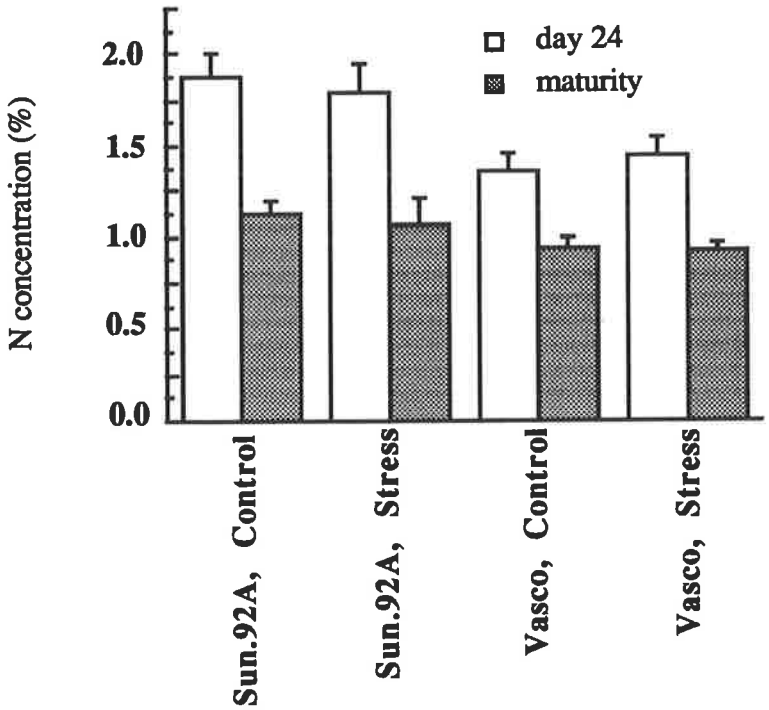

Fig. 6.59. N concentration of two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

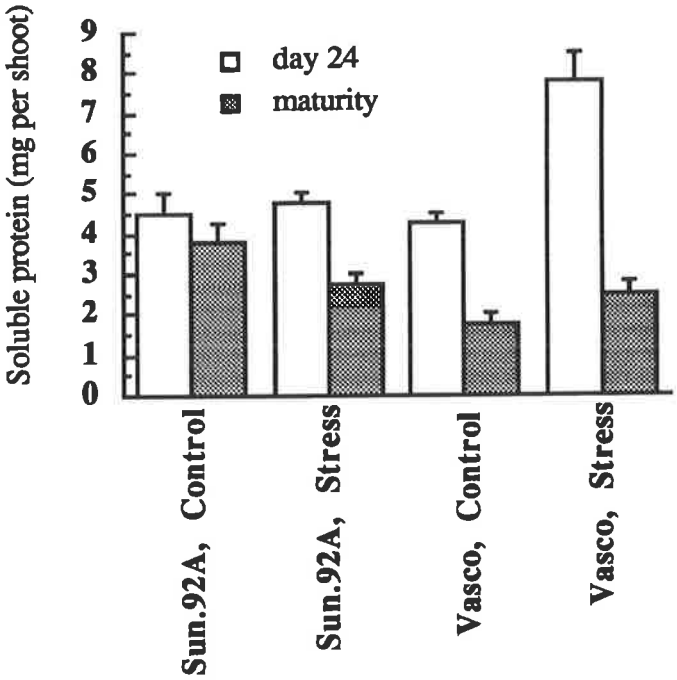

Fig. 6.60. SP content in two wheat cultivars under control and stress conditions at day 24 and maturity. Error bars are standard errors.

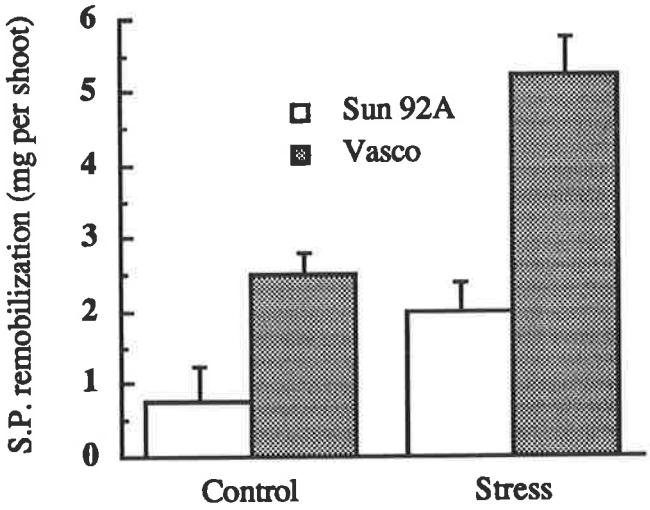

Fig. 6.61. The remobilization of SP from the chaff in two wheat cultivars under water stress and non stress conditions. Error bars are standard errors.

6.4 Discussion

The major aim of this experiment was to improve knowledge related to the accumulation and remobilization of DM, N, soluble carbohydrates and proteins from different parts of the shoot under water-stress and non-stress conditions. Results of this experiment agreed with previous experiments which showed that grain DM increased between day 24 and maturity, and the increment was greater under control than stress conditions. Also, Vasco accumulated greater DM in the grain than Sun 92A under both conditions. However in this experiment, in absolute terms DM and DM HI were different compared to the results of the earlier experiment (Chap. 4). Results from the present experiment showed that in Sun 92A DMHI was 40% and 37% and in Vasco 39% and 35% under control and water stress respectively. The corresponding values in the previous experiment (Chapter 4) were 56% and 45% in Sun 92A and 51% and 41% in Vasco. Differences in grain DM and DM HI, in part, perhaps were due to differences in anthesis date in the two experiments. Anthesis occurred 74 days after sowing and 80 days after sowing respectively for Sun 92A and Vasco in 1992 . The corresponding figures were 63 days after sowing and 72 days after sowing in 1993.

Table 6.1. The remobilization of DM, ESS and TSC from different parts of the shoot under water stress and non stress conditions between day 24 and maturity (negative values indicate net gains)

	Sun 92A control			Vasco control			Sun 92A stress			Vasco stress		
Organs	DM	ESS	TSC	DM	ESS	TSC	DM	ESS	TSC	DM	ESS	TSC
	mg per shoot											
Flag leaf	34	5	4	33	15	13	42	5	5	17	10	8
Other leaves	67	5	5	45	11	11	35	3	3	50	9	9
Chaff	-67	6	6	-16	21	20	-59	11	11	-20	26	23
Peduncle	25	14	19	24	10	9	19	12	19	23	12	32
Lower Internode	60	54	51	59	54	50	35	31	34	45	27	30
Total	119	84	85	145	111	103	72	62	72	115	84	102

In all of the vegetative organs, almost all of the soluble carbohydrate fraction was soluble in ethanol indicating that little carbohydrate was deposited as starch, and that most of it consisted of compounds of low molecular weight, probably disaccharides and oligosaccharides. In some tissues, e.g. leaves and chaff, more DM appeared to have been remobilized than can be accounted for by the net loss of soluble carbohydrates (Table 6.1). This could indicate that remobilization of the bulk of the DM from these organs depends first upon the conversion of insoluble DM to soluble and translocatable forms of material i.e. sugars. In the peduncle, and lower internodes, the net losses between the two harvests of DM and soluble carbohydrate are more nearly equal to each other indicating that most carbohydrate may be accumulated in these organs in readily mobilizable forms.

The remobilization of DM from the lower internodes was as great as from the flag leaf or the other leaves (Table 6.1), so the stem may act as a temporary storage organ to correct partially the apparent imbalance between source and sink during grain filling. Readily available stem carbohydrate reserve could contribute to grain filling or energy requiring processes within the plant. Evidence for this concept has previously been presented and discussed by Stoy (1979). This function would be especially important when plants are subjected to water stress during grain filling. However, the amount of soluble sugar remobilized from the lower internodes between day 24 and maturity appeared to have been reduced by stress, while remobilization from the chaff (and from the peduncle in Vasco) appeared to have increased slightly under stress (Table 6.1). The amount of TSC in the lower internodes was also lower at day 24 in the stress treatments, which may be due to earlier remobilisation (before day 24) or to less production. Although the total amount remobilized between the two harvests was reduced by stress, there was in fact less TSC at maturity, suggesting remobilization may have been more complete.

Blacklow *et al.* (1984) and Borrell *et al.* (1989) reported that accumulation of fructan continues during stem growth, flowering, and anthesis; fructan contents then fall during the later stages of grain filling. Disappearance of fructan is almost complete in cereal stems by the time the grains have matured (Blacklow *et al.* 1984). It is probable that some, at least,

Table 6.2. Grain total DM and N accumulation in two cultivars of wheat under water stress and non stress conditions during grain filling

	Grain DM (mg per shoot)		Grain N (mg per shoot)	
Treatments	**Mean**	**SE**	**Mean**	**SE**
Sun.92A, Control	687	89	21	3
Sun.92A, Stress	528	42	18	2
Vasco, Control	1133	145	26	4
Vasco. Stress	886	109	26	4

can be used to sustain grain growth during periods where flag leaf photosynthesis is limited (Blacklow *et al.* 1984; Borrell *et al.* 1989; Hendrix *et al.* 1986). More information is needed on the role of soluble carbohydrates remobilized from different parts of the shoot from different genotypes of wheat to understand the complex interrelationship among the mechanisms controlling remobilization of soluble carbohydrates from different parts of the shoot under favourable and water stress conditions. This kind of information would be useful to improve management practices and to select for increased economic yield of wheat plants.

According to Penning de Vries *et al.* (1974), 1.0 g of glucose produced by photosynthesis can be used by the crop to produce 0.83 g of carbohydrate or 0.40 g of protein (assuming nitrate to be the N source). This implies that increases in protein content would use more photosynthate thus ultimately leading to decreases in DM yield. This interpretation however does not explain why Vasco produced more DM per shoot in the grain than Sun 92A in both water stress and control conditions in addition to a higher amount of grain N per shoot (Table 6.2). Sun 92A showed greater DMHI and NHI than Vasco implying that remobilization efficiency of DM and N from the shoot to the grain in Sun 92A was greater than Vasco under both conditions.

Table 6.3 The remobilization of N and SP (SP expressed as N) from different parts of the shoot under water stress and non stress conditions between day 24 and maturity

	Sun 92A control		Vasco control		Sun 92A stress		Vasco stress	
Organs	N	SP	N	SP	N	SP	N	SP
	mg N per shoot							
Flag leaf	2.6	0.50	1.7	0.00	2.3	0.50	0.9	0.04
Other leaves	4.0	1.15	1.6	0.75	0.7	0.70	1.0	0.50
Chaff	0.9	0.14	1.2	0.44	0.9	0.40	1.7	0.93
Peduncle	1.2	0.10	1.2	0.08	0.6	0.07	1.0	0.05
Internode	0.6	0.05	0.5	0.02	0.4	0.04	0.5	0.00
Total	9.3	1.86	6.2	1.59	4.9	1.71	5.1	1.52

Net loss of N from an organ between day 24 and maturity is perhaps more closely related to remobilization of N than is the net change in SP. SP is an estimate of the level of RuBP carboxylase which is being turned over in the organ from amino acids derived internally or imported. Imports of amino acids after day 24 will result in an underestimate of the actual amount remobilized.

Although parts of the shoot of Vasco were heavier than Sun 92A, total remobilization of N from of the shoot was about two times greater in Sun 92A than Vasco when plants were not stressed, but about the same as Vasco under water stress (Table 6.3). In the present experiment among the different parts of the shoot, the flag leaf and other leaves were the most important parts as sources of N and remobilized a high proportion of their N and their SP in well watered conditions (Table 6.3). Previous investigation suggested that the arrival of N in the developing grains of wheat is closely related to the export of N from senescent leaves (Nair *et al.* 1978; Simpson *et al.* 1983). A few investigators have tried to identify the attributes in the developing grains that are associated with high and low N concentration. Some studies with wheat (Nair *et al.* 1978)

show that differences in grain N concentration may be due to the distribution of the same amount of N to differing amounts of DM, and other investigations point out that "high protein" can be attributed partly to a higher amount of N per kernel and partly to lower weight per kernel (Donovan *et al.* 1977). This may be a causative factor for higher grain protein concentration in Sun 92A than in Vasco. Leaf proteases are responsible for breakdown and translocation of the N to the developing grains. A comparison of the activities of these enzymes in the flag leaf of Sun 92A than Vasco is conducted in Chapter 7.

In summary, among different parts of the shoot the remobilization of TSC was greater from the internode than other parts of the shoot (Table 6.3) and there were comparatively small amounts of these components remobilized from the leaves. On the other hand, leaves were the most important parts of the shoot in terms of remobilization of N. Although the majority of the grain N and carbohydrates may come from N accumulated and CO_2 assimilated before anthesis, these results demonstrate the importance of the stem and leaves in relation to remobilization of C and N from them in wheat plants. Further studies on the environmental and genetic determinants of C and N assimilation and remobilization are needed to provide a more rational basis for the prediction of grain protein concentration, for altering it to desired levels by crop management practices, and also for breeding high-protein wheat cultivars.

Chapter 7. DM and N remobilization from different parts of the shoot: A comparison between wheat and barley in response to water stress during grain filling

7.1 Introduction

When grown side by side using identical management practices, barley yields about 25% more than wheat in a large range of environments in southern Australia (Lopez-Castaneda and Richards 1994). In another study the results of total aboveground biomass and grain yield of barley, durum and bread wheat across five Mediterranean environments in northern Syria showed that barley produces more than wheat where the average rainfall is less than 300 mm (Acevedo 1992). The phenological trait which enabled barley to yield better than wheat in the stressful environments was earliness in flowering associated with a shorter period of grain filling . The increased grain yield of barley comes essentially from an increased mean grain mass, as the grain number per unit area is similar to, or slightly lower, than that for wheat.

Several authors (Richards 1987; Turner and Nicolas 1987) have suggested that wheat yield can be increased by increasing biomass production. Certainly, there is potential for increased biomass production in Mediterranean environments in some circumstances. For instance, barley is capable of producing more biomass and grain than wheat using the same amount of water (Gregory *et al.* 1992). Early growth is particularly important for wheat and barley grown under dryland conditions in Mediterranean-type regions such as south-western Australia, where light-textured surface soils predominate. Water deficits develop after flowering when rainfall decreases and evaporation increases (Turner and Nicolas 1987). Under these conditions, early DM production, which is associated with higher leaf area and higher DM at anthesis, will maximise the water use by the crop through a reduction in soil evaporation. However, as with increased biomass caused by agronomic manipulation, genetically-increased biomass is not always translated into increased grain yield. Also, increased vegetative growth in cereals may not always be beneficial since it has been linked with premature depletion of soil moisture and the "haying off" of crops in some environments and years (Fisher and Kohn 1966).

A comparison of bread wheat and barley showed that barley had a 17% higher grain

yield than the other species when averaged over five rainfed environments in south-eastern Australia (Lopez-Castaneda 1992). A yield difference of 39% was found when the highest yielding barley was contrasted with the highest yielding wheat.

It has been shown in previous experiments (Chapters 4, 5 and 6) that remobilization of C and N from vegetative parts of the shoot depends on environmental conditions and is also under genetic control (Chapter 6). It was suggested that the different parts of the shoot from different species (wheat and barley) did not show similar responses to stress. However, wheat and barley were not grown under identical conditions. Therefore to improve knowledge about assimilation and remobilization of C and N from different parts of the shoot in wheat and barley it is necessary to compare wheat and barley under the same conditions. This experiment was conducted to compare the effect of water stress on grain N content, HI and NHI of wheat and barley during grain filling. A secondary objective was to compare the extent of remobilization of DM and N from vegetative parts of the shoot of wheat and barley under water stress and non stress conditions during grain filling.

7.2 Materials and methods

The experiment was conducted in the growth cabinet with a 14h, 21°C day and a 8h 16°C night. Light was provided by high-pressure sodium lamps supplemented with fluorescent tubes providing 560μmol m^{-2} s^{-1} PAR at ear level. Two cultivars of wheat (Sun 92A and Vasco) and one barley cultivar (Forrest) were grown in pots 20 cm deep containing recycled soil (3.5 kg oven dry). Ten seeds per pot were sown and seedlings thinned to 6 plants per pot after emergence and plants were restricted to a single culm by removing all tillers as they emerged. Plants were watered daily by hand to maintain a soil water content close to field capacity until day 10 after anthesis to minimise the possibility of pre-anthesis moisture stress and were supplied with 200 mL of soluble fertiliser containing 2.6 g Hortico 'Aquasol' (23% N) every second week until anthesis. Only one level of water stress, which was approximatly 50% of field capacity, was imposed at 10 days after anthesis. This level of water stress was kept by rewatering the pots twice per

week until maturity. Pots were weighed regularly two times per week and after each weighing the pots were re-randomised to reduce any possible effects related to position within the growth cabinet. Harvesting was done at 24 days after anthesis and at maturity. Different parts of the shoot (chaff, peduncle, lower internodes, flag leaf and other leaves) and grain were separated and were dried at 85°C for 48 hours and weighed. N concentration was determined by Kjeltec Auto analyzer 1030. Attributes calculated were as described in Chapter 3 and standard statistical procedures were used for analysis of variance.

7.3 Results

7.3.1 Grain DM content and H.I.

In both species (wheat and barley) grain DM was significantly ($P< 0.05$) greater at maturity than at day 24. In both species yield at maturity was also greater under control than water stress conditions (Fig.7.1). The accumulation of grain DM per shoot at maturity was greater in both wheat cultivars than barley under both conditions. The accumulation of DM between the two harvests under control conditions was greater in Vasco than in Sun 92A and Forrest (Fig. 7.2). Under stress conditions, however, it was similar in Sun 92A and Vasco and greater than Forrest . In terms of HI, at maturity, Sun 92A was greater (50%) than Vasco (40%) and Forrest (45%) (Fig. 7.3).

Grain number per shoot was significantly greater in Vasco than Sun 92A and Forrest (Fig. 7. 4) in both treatments. It was also greater in control than stress conditions in Vasco, whereas grain number in Sun 92A and Forrest was similar under water stress and control conditions.

The barley cultivar Forrest had significantly ($P<0.001$) greater grain weight than both wheat cultivars in both the non-stress and stress treatments and there was no significant difference between the two cultivars of wheat (Fig. 7.5).

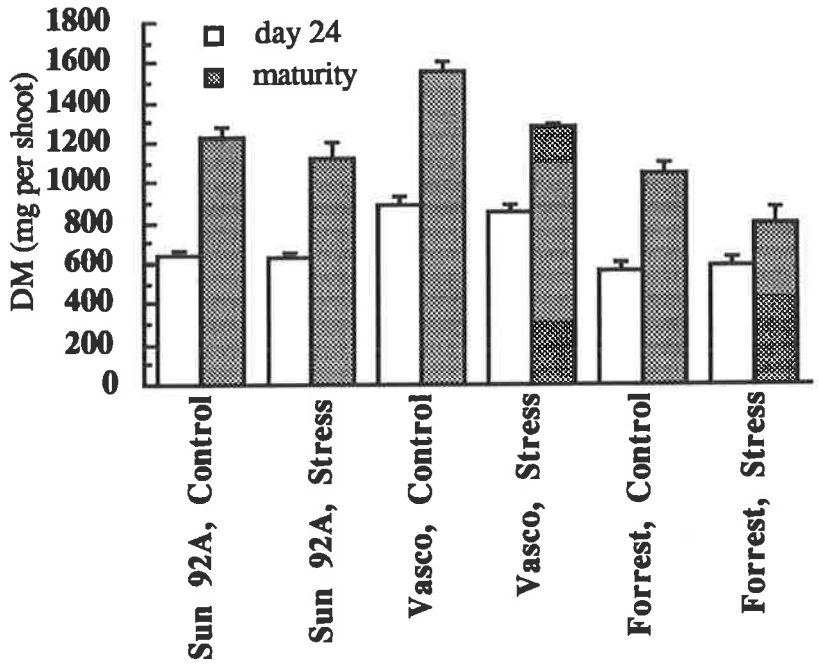

Fig. 7.1. Grain DM in two wheat cultivars and one barley cultivar under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

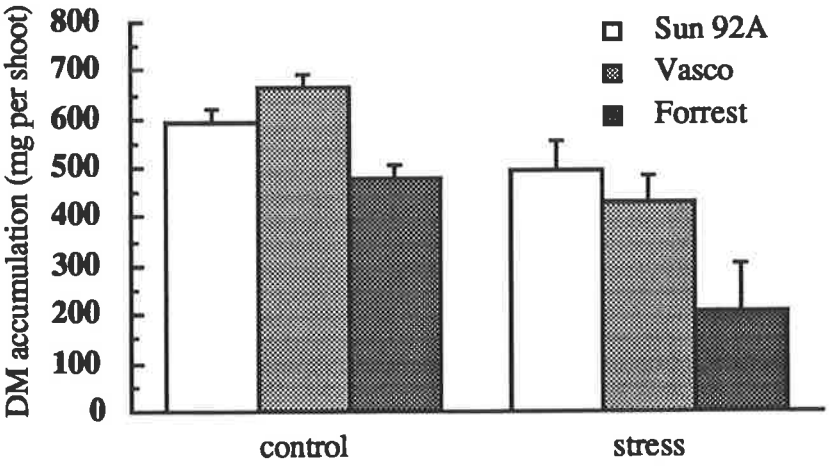

Fig. 7.2. Grain DM accumulation between day 24 and maturity in wheat and barley under control and water stress conditions. Error bars are standard errors.

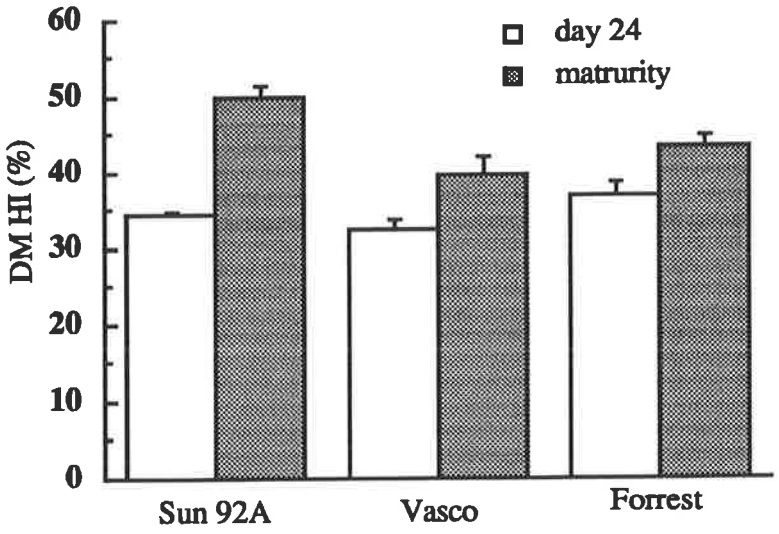

Fig. 7.3. HI of wheat and barley at day 24 and maturity (over both treatments). Error bars are standard errors.

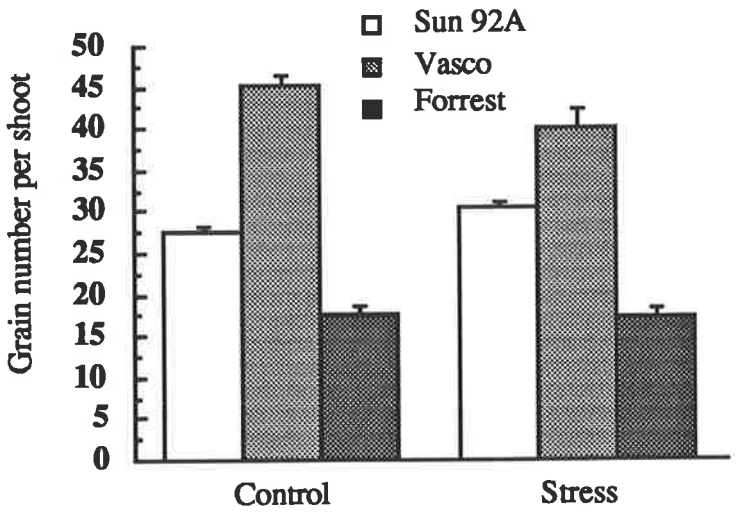

Fig. 7.4. Grain number of wheat and barley under control and water stress conditions. Error bars on selected points are standard errors.

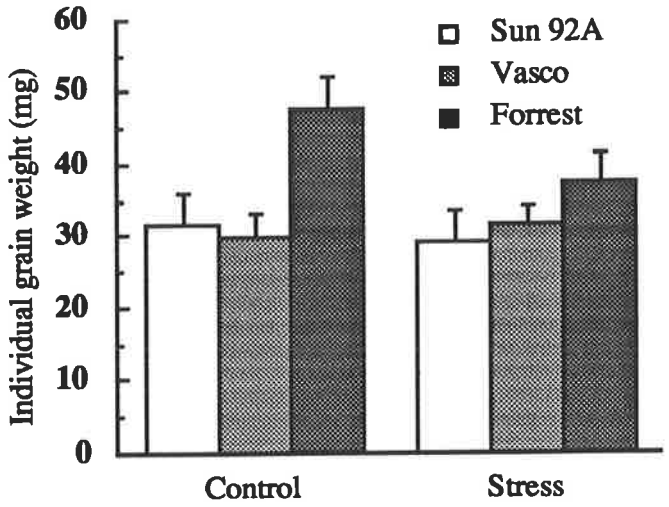

Fig. 7.5. Individual grain weight in wheat and barley under water stress and control conditions (averaged over both harvests). Error bars are standard errors.

7.3.2 Grain N content, concentration and NHI

Both species accumulated significantly greater amounts of N at maturity than at day 24, but N accumulation was significantly ($P< 0.001$) greater in wheat than barley particularly at maturity (Fig. 7. 6). N concentration (%) in the grain of both species was greater under water stress than control conditions (Fig.7.7). A similar response was found for NHI of both species at day 24 (Fig. 7.8). At maturity NHI of Forrest was greater in control than stress but stress had no effect on the NHI in either wheat cultivar.

7.3.3 DM and N content in the whole shoot (vegetative parts + grain)

7.3.3.1 DM content

DM content of the whole shoot increased between day 24 and maturity in all treatments (Fig.7.9). In all three genotypes, DM content in the whole shoot was greater under control conditions than under water stress conditions and the DM of Vasco was greater than Sun 92A and Forrest under both stress and non-stress conditions.

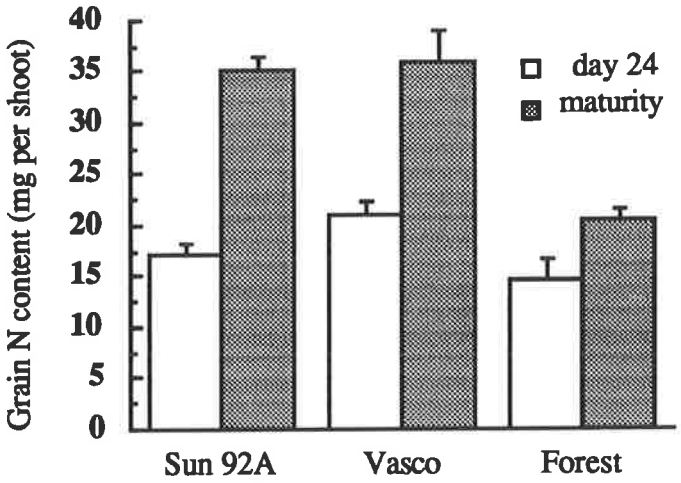

Fig. 7.6. Grain N content of wheat and barley over control and stress conditions at day 24 and maturity. Error bars are standard errors.

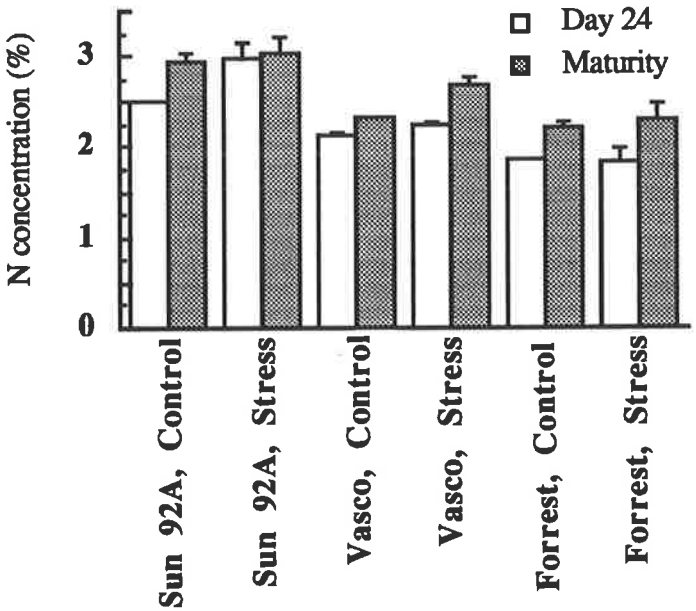

Fig. 7.7. Grain N% in wheat and barley under control and stress conditions at day 24 and maturity. Error bars are standard errors.

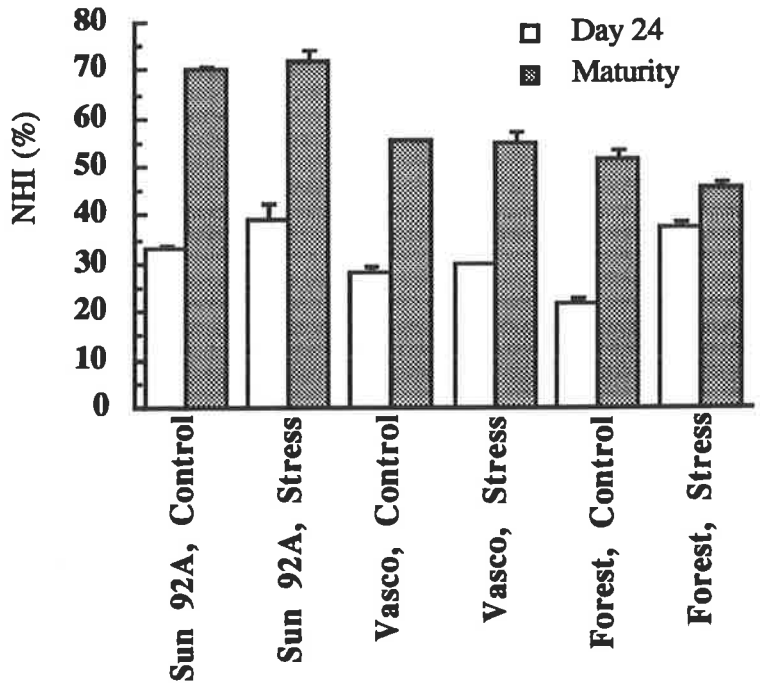

Fig. 7.8. NHI in wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

7.3.3.2 Whole shoot N content

The whole shoot N content was significantly greater in Vasco under both conditions and both harvests than in Sun 92A and Forrest (Fig. 7.10). But in each genotype the whole shoot N content was generally similar at day 24 and at maturity. This indicates little post anthesis N uptake, remobilization from the roots, or gaseous loss of N.

7.3.4 Shoot (vegetative parts only) DM and N content and remobilization

7.3.4.1 Shoot DM content and remobilization

Shoot DM content was significantly greater in Vasco than Sun 92A and Forrest in both treatments and at both harvests. Sun 92A and Forrest had similar shoot DM in the individual treatments (Fig. 7.11).

There were no significant differences between the two species on remobilization of DM from the shoot; however, the patterns of DM remobilization under water stress and non water stress conditions were different (Fig. 7.12).

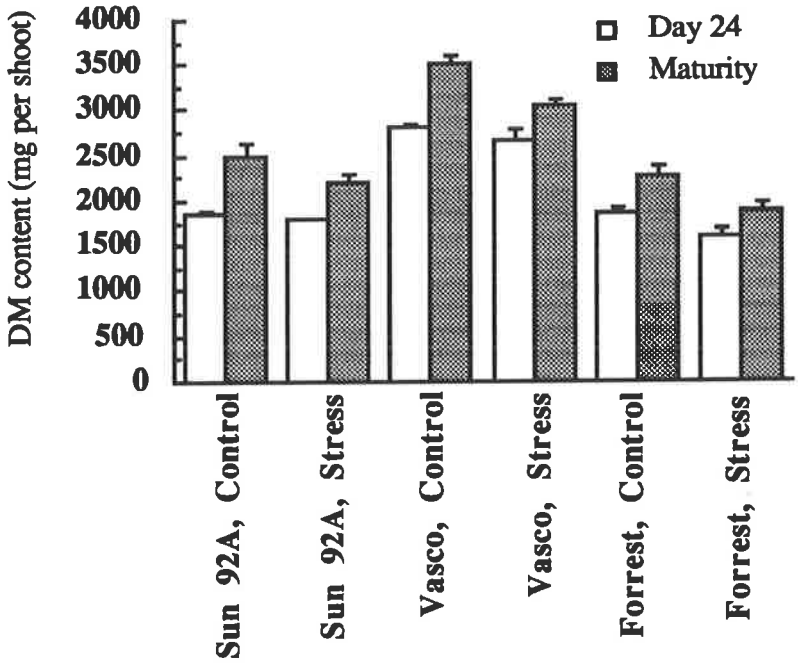

Fig. 7.9. The whole shoot (grain + vegetative parts) DM content in wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

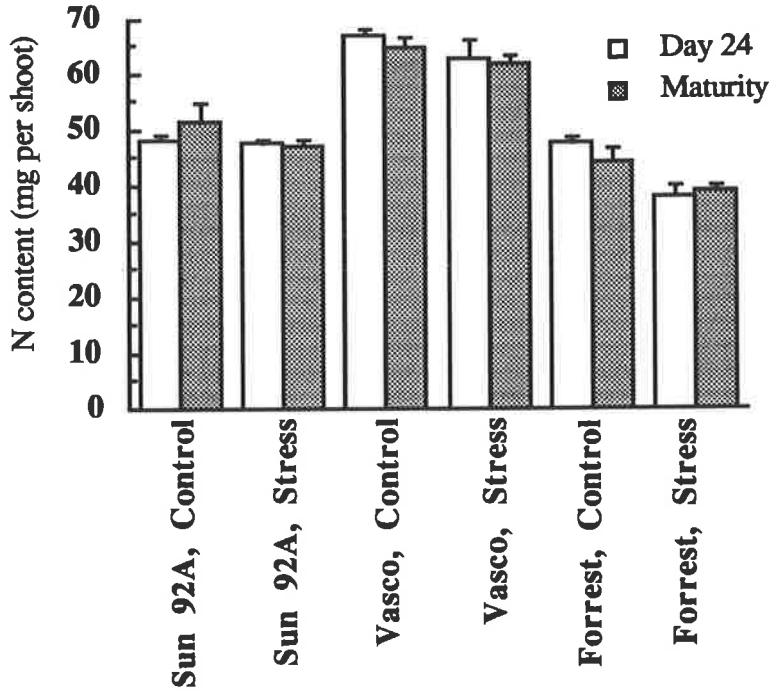

Fig. 7.10. The whole shoot (grain + vegetative parts) N content in wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

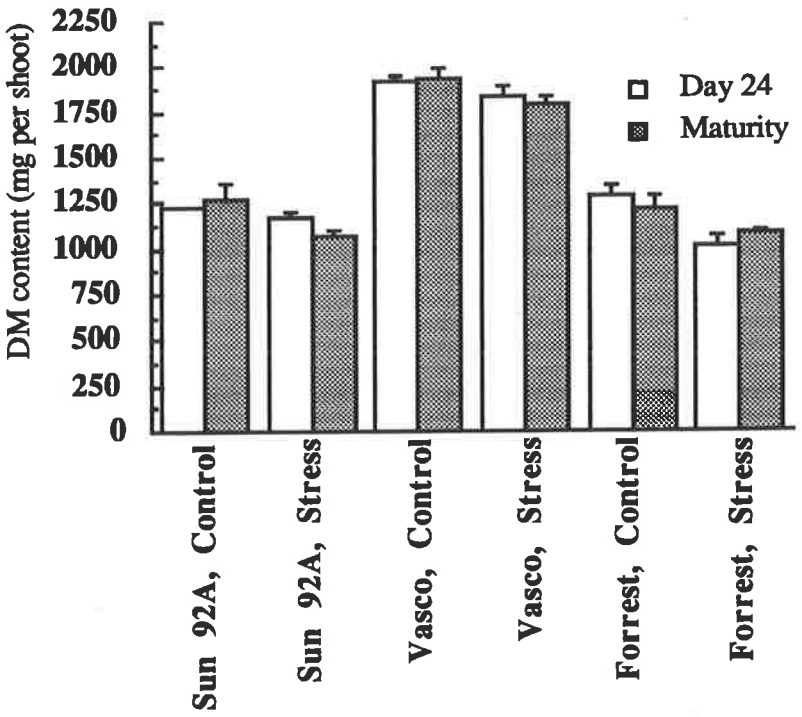

Fig. 7.11. DM content of the shoot in wheat and barley under control and stress conditions at day 24 and maturity. Error bars are standard errors.

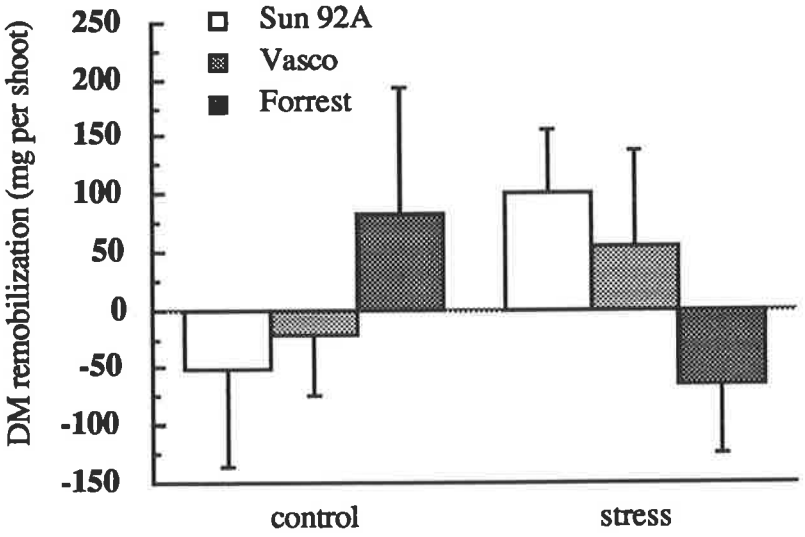

Fig. 7.12 The remobilization of DM from the shoot in wheat and barley between day 24 and maturity under water stress and control conditions. Error bars are standard errors.

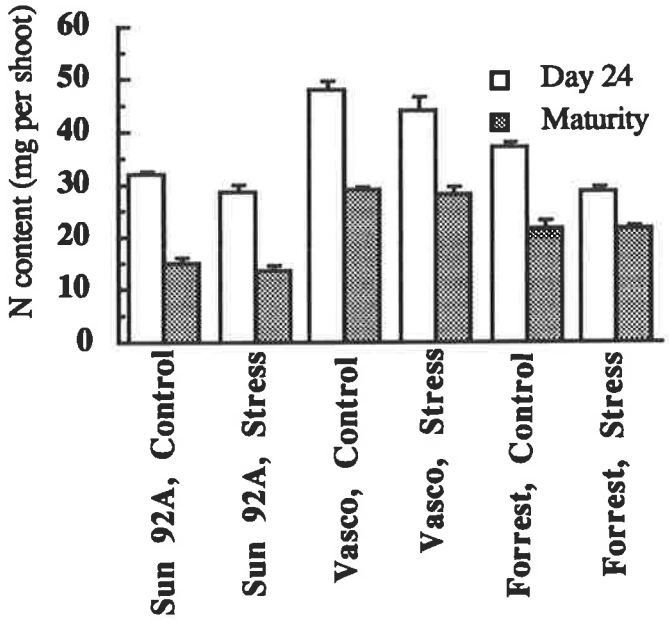

Fig. 7.13. The shoot N content in wheat and barley under control and stress conditions at day 24 and maturity. Error bars are standard errors.

7.3.4.2 Shoot N content and remobilization

The shoot N content was significantly ($P<0.001$) greater in both wheat and barley at day 24 than at maturity (Fig. 7.13). Since Vasco contained a greater amount of DM in the shoot than Sun 92A and Forrest (Fig. 7.11), this cultivar had also a greater N content in the shoot than the other two cultivars. However the pattern of N remobilization (Fig.7.14) from vegetative parts of the shoot was not comparable to DM remobilization (Fig. 7.12). N was remobilized in both species in both the stress and non-stress treatments, and remobilisation was greater in the wheat cultivars than in barley under stress conditions. Since the pattern and proportion of DM and N remobilization from the shoots of wheat and barley differed, in the following sections the remobilization of these two components from different parts of the shoot will be described in more detail.

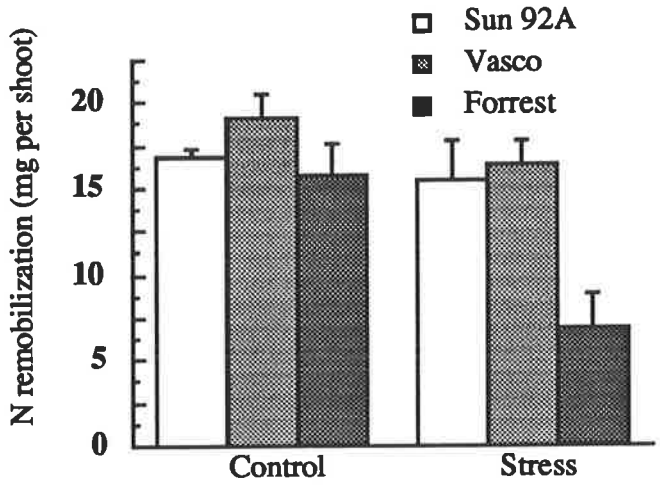

Fig. 7.14. The remobilization of N from the shoot of wheat and barley between day 24 and maturity under water stress and control conditions. Error bars are standard errors.

7.3.5 DM, N content and their remobilization from different parts of the shoot between day 24 and maturity.

7.3.5.1 Lower internodes

7.3.5.1.1 DM content and remobilization

DM content of the internode at day 24 was decreased under water stress conditions in Vasco and Forrest but not in Sun 92A (Fig. 7.15). At maturity DM content of Vasco and Forrest was similar in both treatments while it was decreased in Sun 92A under stress treatment at maturity. Under well watered conditions (Fig. 7.16), DM was remobilized from the lower internodes of Forrest and Vasco but not apparently from Sun 92A , while under stress conditions, significant amounts of DM were remobilized only in Sun 92A.

7.3.5.1.2 N concentration, content and remobilization

N concentration of the lower internodes was significantly ($P<0.001$) greater at day 24 than maturity in all conditions, but it was greater in the lower internodes of barley than both wheat cultivars (Fig. 7.17). N content of the internodes was also greater at day 24 than at maturity in all three genotypes (Fig. 7.18).

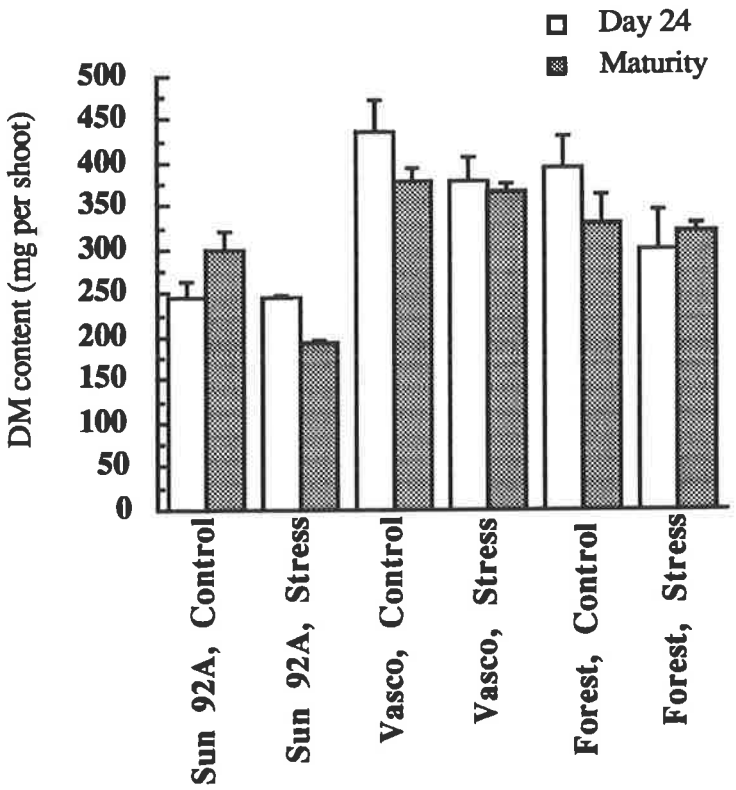

Fig. 7.15. DM content of lower internodes in wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

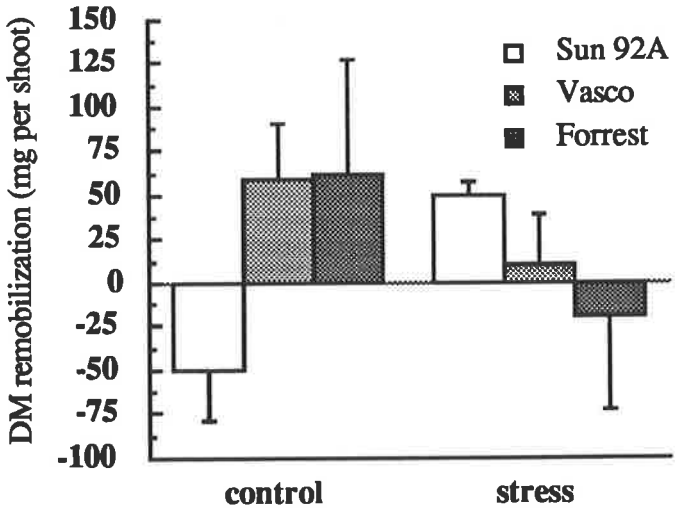

Fig. 7.16. The remobilization of DM between day 24 and maturity from lower internodes in wheat and barley under stress and control conditions. Error bars are standard errors.

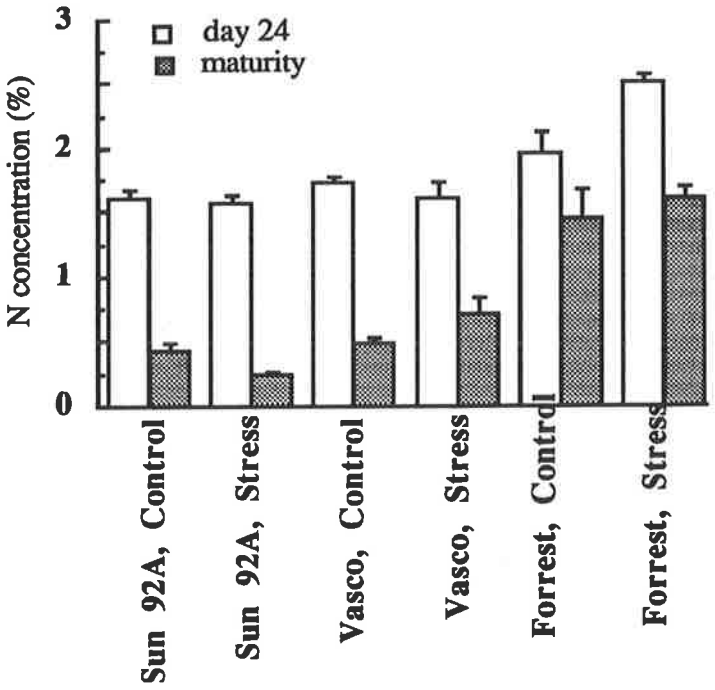

Fig. 7.17. N concentration of the lower internodes in wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

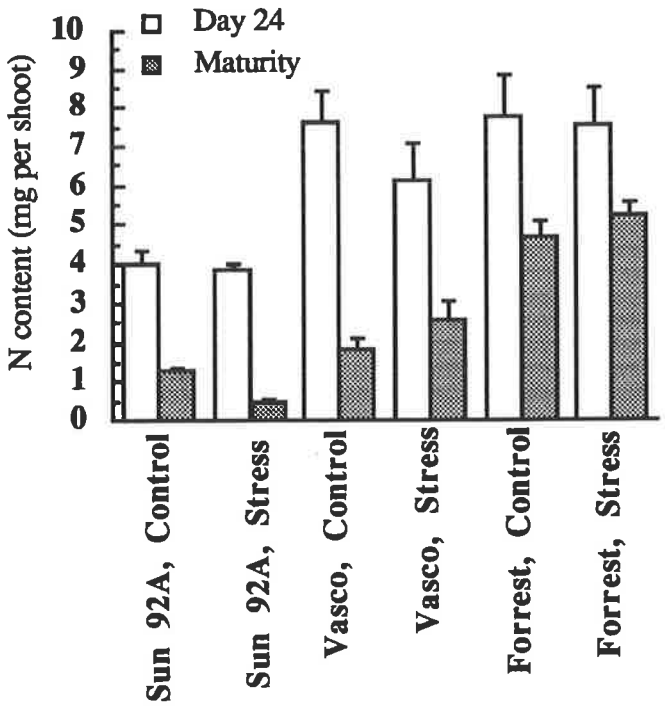

Fig. 7.18. N content of lower internodes in wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

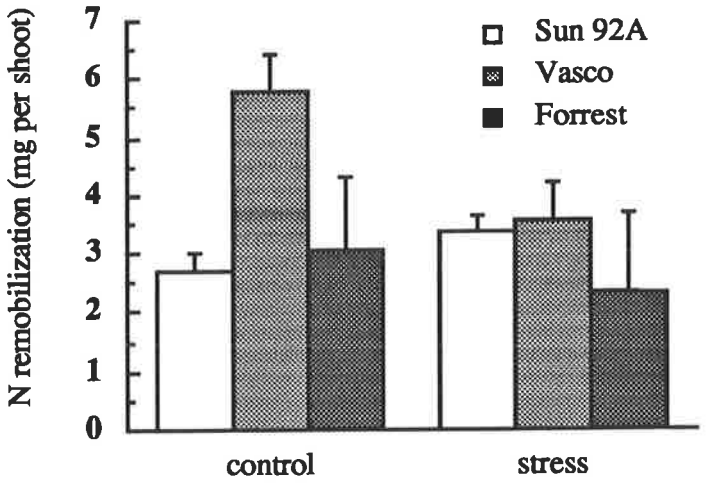

Fig. 7.19. The remobilization of N from the lower internodes between day 24 and maturity under water stress and control conditions. Error bars are standard errors.

N contents of Forrest and Vasco were approximatly the same at day 24, especially in non-stress treatment. However greater N remobilization resulted from the internodes of Vasco than from Sun 92A and Forrest in control conditions (Fig. 7.19), but it was similar in all three genotypes under stress conditions.

7.3.5 2 Peduncle

7.3.5.2.1 DM content and remobilization

DM content in the peduncle of the two wheat cultivars increased between the two harvests under non-stress conditions but decreased under stress conditions (Fig.7.20). In barley however, DM content of the peduncle was much smaller than in the wheat cultivars, and it slightly decreased between day 24 and maturity under stress conditions. Although DM content of the peduncle in wheat cultivars was significantly ($P< 0.001$) greater than barley, wheat cultivars did not appear to remobilize any DM from the peduncle in the control treatment (Fig. 7.21).

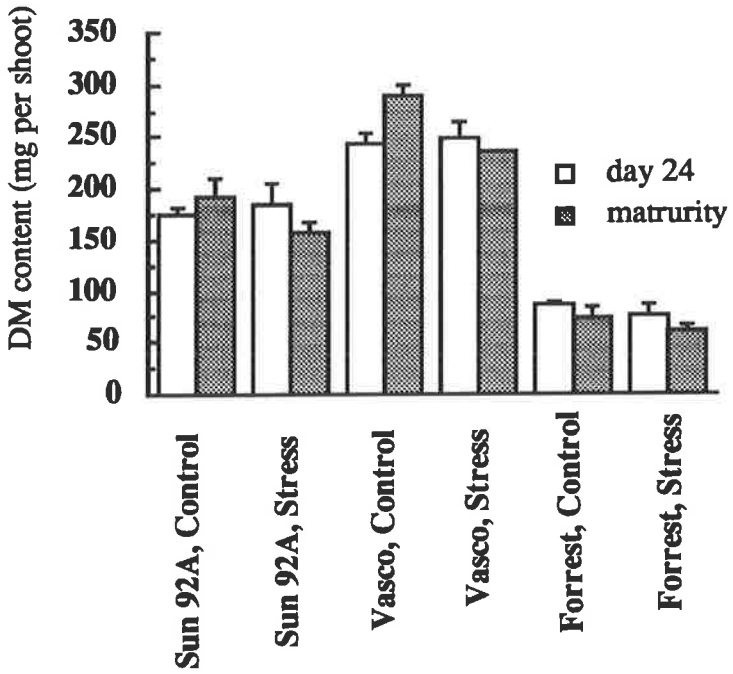

Fig. 7.20. DM content in the peduncle of wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

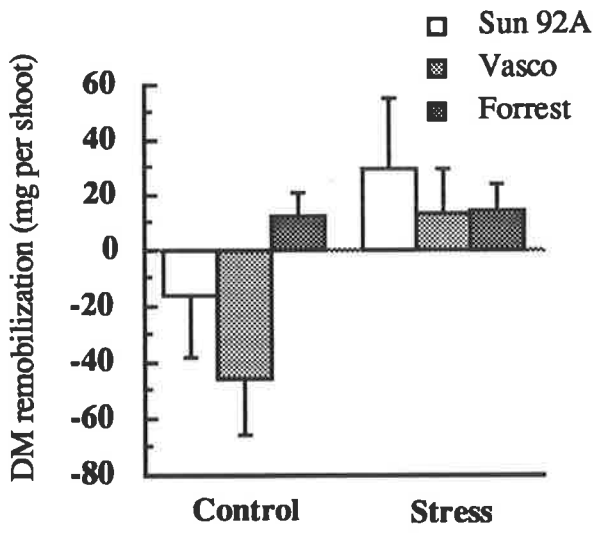

Fig. 7.21. The remobilization of DM from the peduncle in wheat and barley under stress and control conditions between day 24 and maturity. Error bars are standard errors.

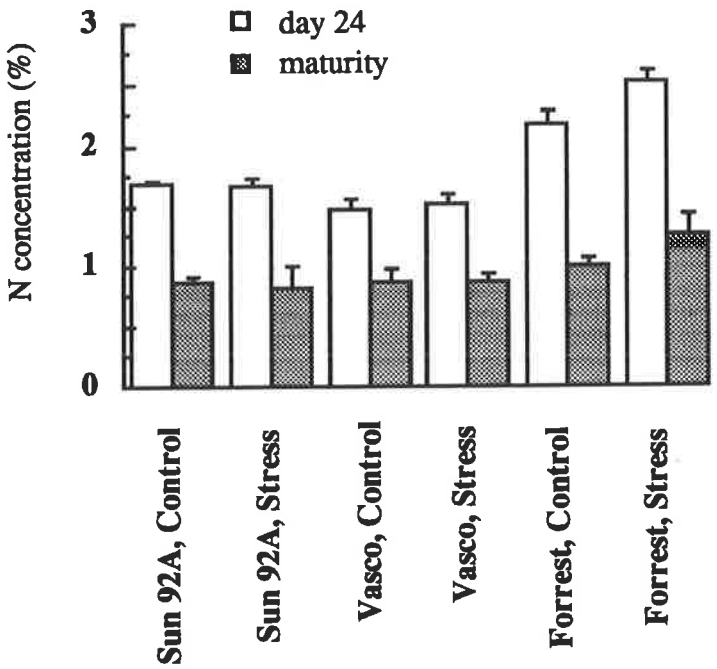

Fig. 7. 22. The concentration of N in the peduncle of wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

7.3.5.2.2 N concentration, content and remobilization

N concentration of the peduncle (Fig.7.22) decreased in wheat and barley between day 24 and maturity and the decrement was similar for each cultivar under water stress and control conditions. It was notable that at day 24, N% of the peduncle in barley was greater than wheat genotypes, whereas the N content (Fig.7.23) in the peduncle was significantly lower in barley, due to the differences in peduncle DM. Despite significant differences in the N content of the peduncle, similar amounts of N were remobilized from the peduncle of both species under well watered conditions. N remobilization was greater in the two wheat cultivars than in barley under water stress conditions (Fig. 7.24).

7.3.5.3 Flag leaf

7.3.5.3.1 DM content and remobilization

DM of the flag leaf of the two wheat cultivars was greater than Forrest (Fig. 7.25). A small amount of DM was remobilized (Fig.7.26) from the flag leaf under control conditions in Vasco and Forrest while the DM of the flag leaf increased under stress.

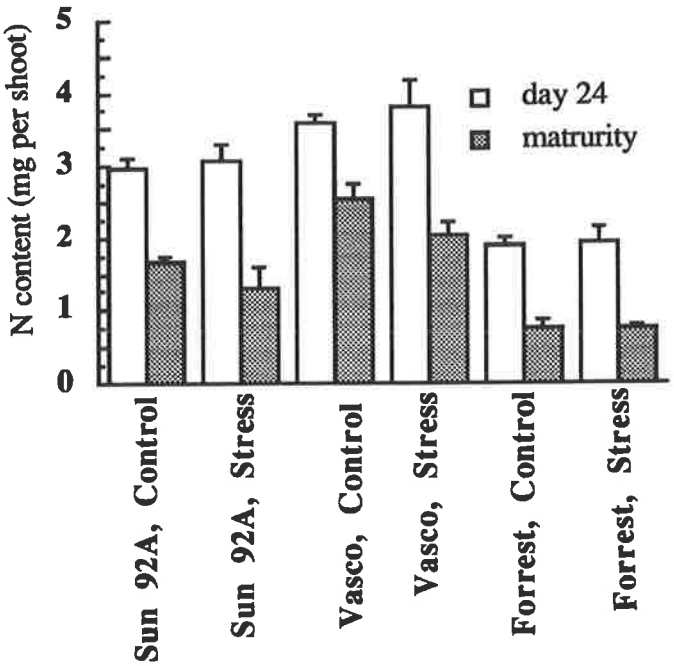

Fig. 7.23. N content in the peduncle of wheat and barley under water stress and control conditions at day 24 and maturity.

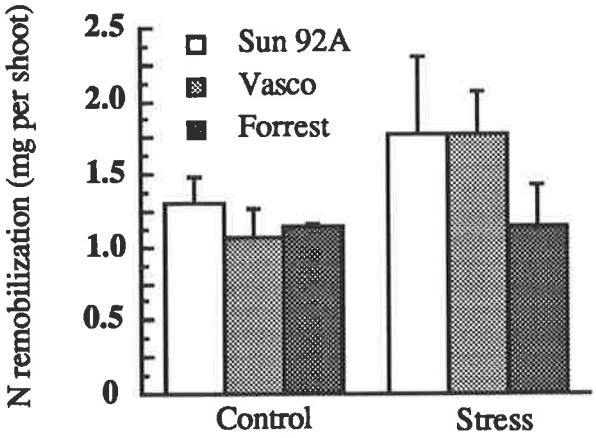

Fig. 7.24. The remobilization of N from the peduncle in wheat and barley cultivars between day 24 and maturity under water stress and control conditions. Error bars are standard errors.

7.3.5.3.2 N concentration, content and remobilization

N concentration of the flag leaf was significantly ($P< 0.001$) greater at day 24 than maturity in all conditions (Fig. 7.27). Stress did not reduce N% in either Sun 92A or Vasco, but in Forrest N% of the flag leaf was greater under control conditions than under stress conditions in both harvests . N content of the flag leaf (Fig.7.28) in contrast to DM see Fig. 7.25) was significantly ($P< 0.01$) greater at day 24 than at maturity under both water stress and control conditions in wheat and barley. N content in the flag leaf of the two wheat cultivars were significantly greater than that of barley, and significantly greater amounts of N were remobilized from the flag leaf of the two wheat cultivars compared with barley (Fig. 7.29).

7.3.5.4 Other leaves

7.3.5.4.1 DM content and remobilization

DM content of the other leaves was greater in Vasco than Sun 92A and Forrest at both harvests and in both treatments. In both wheat and barley there were similar changes of DM content between day 24 and maturity (Fig. 7.30). As a result the apparent remobilization of DM from the other leaves was similar in all three genotypes under both conditions (Fig. 7.31).

7.3.5.4.2 N content, concentration, and remobilization

N content of the other leaves was significantly greater at day 24 than at maturity under both water stress and control conditions (Fig. 7.32). Stress reduced the N content of the other leaves at day 24, but by maturity there was no difference between stress and non-stress treatments. N remobilization from the other leaves was reduced by stress. The amounts remobilized between the two harvests reached between 25%-40% of their N

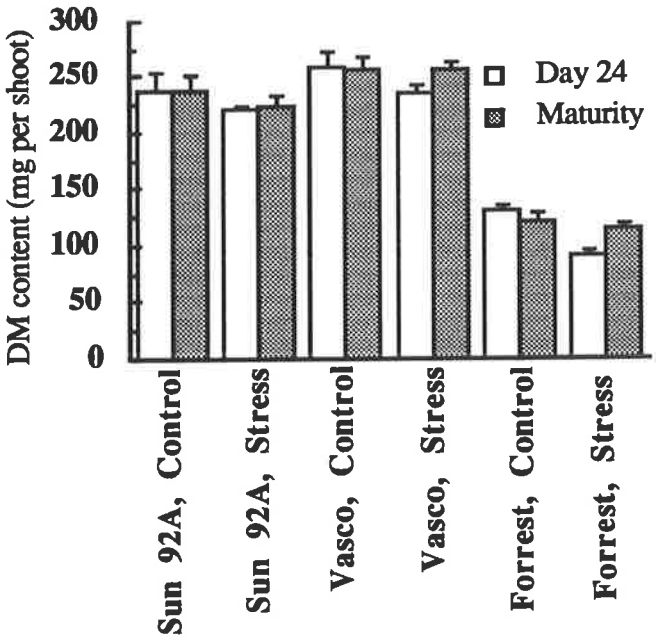

Fig. 7.25. DM content of the flag leaf in wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

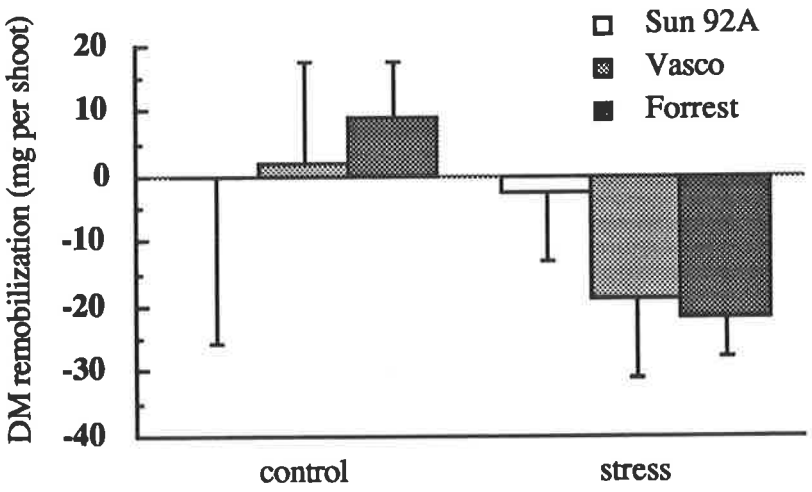

Fig. 7.26. Remobilization of DM from the flag leaf between day 24 and maturity in wheat and barley under stress and non-stress conditions. Error bars are standard errors.

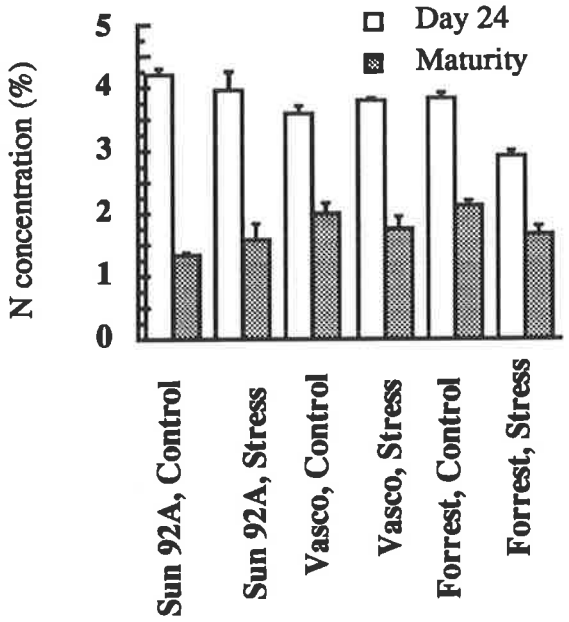

Fig. 7. 27. The concentration of N in the flag leaf of wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

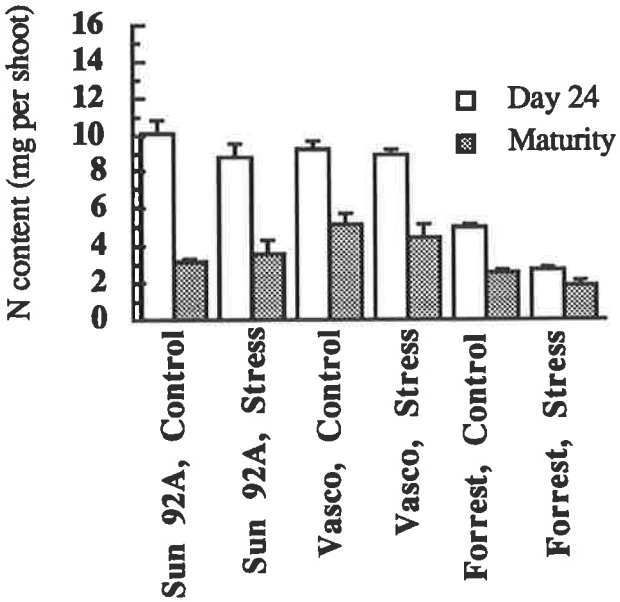

Fig. 7.28. N content in the flag leaf of wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

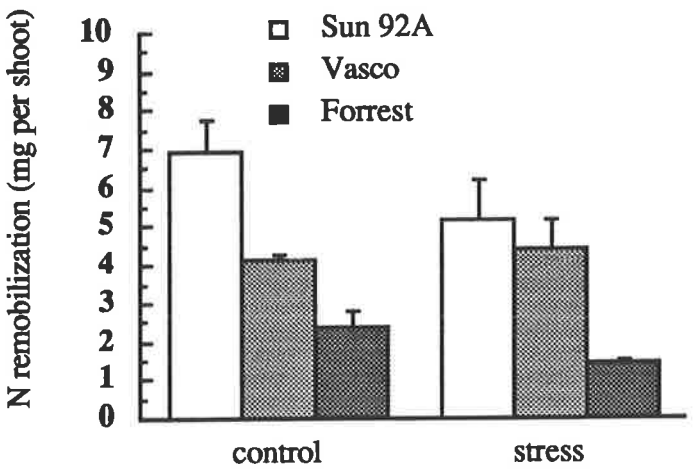

Fig. 7.29. N remobilization from the flag leaf in wheat and barley between day 24 and maturity under water stress and control conditions. Error bars are standard errors.

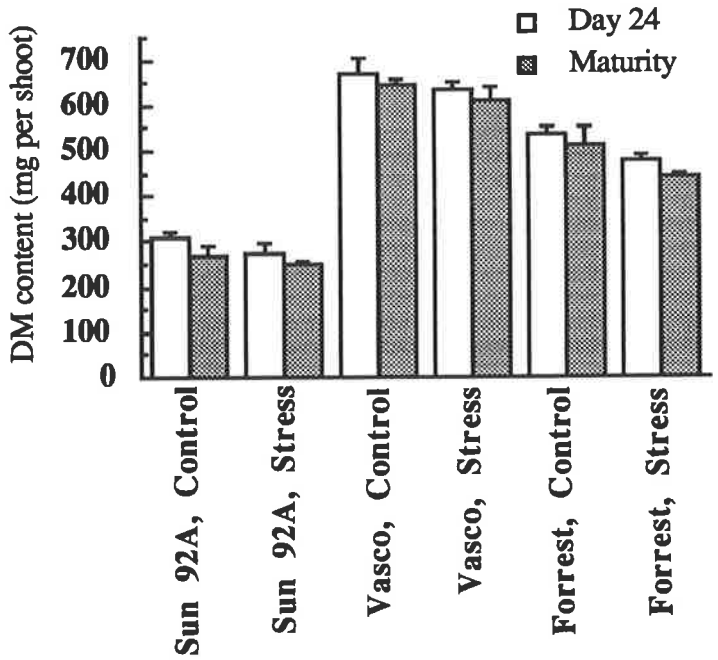

Fig. 7.30. DM content of the other leaves in wheat and barley at day 24 and maturity under water stress and control conditions. Error bars are standard errors.

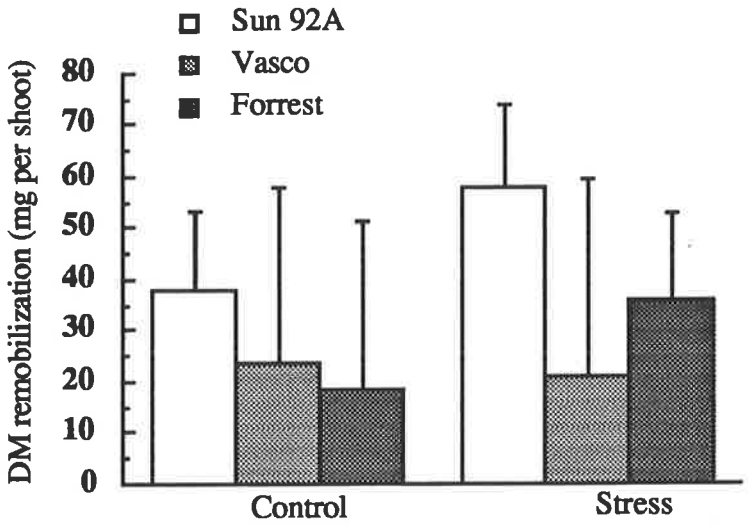

Fig. 7.31. DM remobilization from the other leaves between day 24 and maturity from wheat and barley under control and stress conditions. Error bars are standard errors.

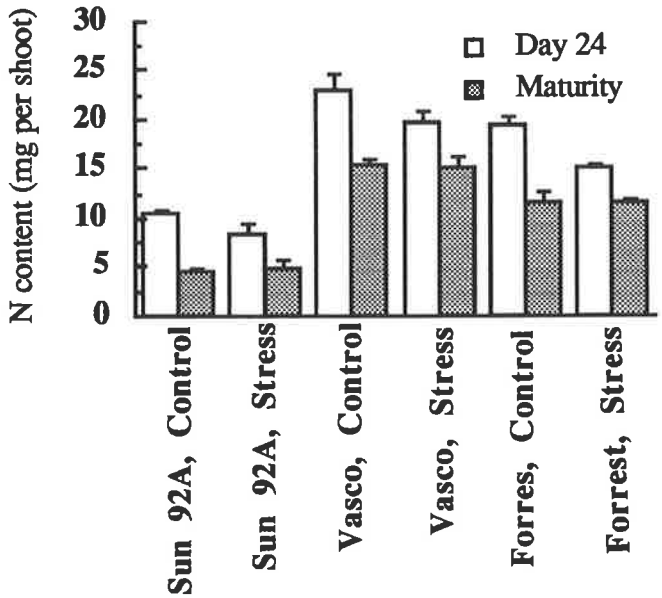

Fig. 7.32. N content in the other leaves of wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

content at day 24 (Fig. 7.33). It was notable that N remobilization from Vasco and Forrest was greater than Sun 92A. N concentration at day 24 was similar under control and stress conditions, while at maturity (Fig. 7.34) in all three genotypes N concentration of the other leaves was slightly greater under stress conditions.

7.3.5.5 Chaff

7.3.5.5.1 DM content and remobilization

DM content of the chaff of wheat and barley between day 24 and maturity increased under control conditions, but the responses differed between them under stress conditions (Fig. 7.35). The chaff was heavier in both wheat cultivars than in barley and, except in Vasco under water stress, no DM appeared to be remobilized between day 24 and maturity.

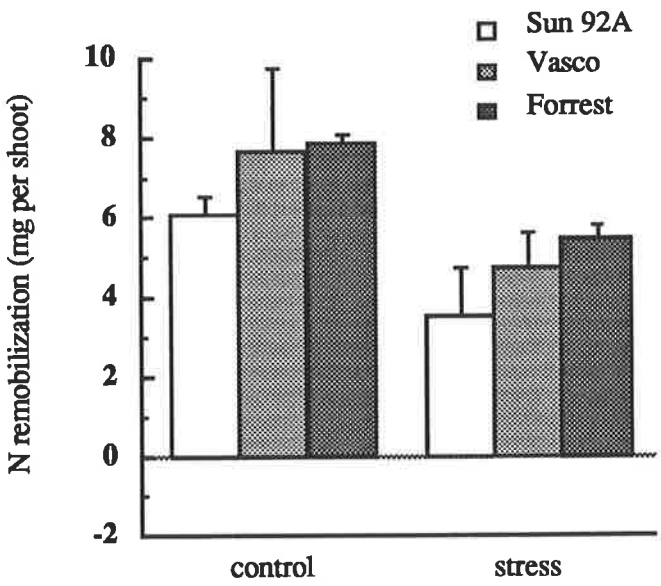

Fig. 7.33. N remobilization from other leaves between day 24 and maturity in wheat and barley under water stress and control conditions. Error bars are standard errors.

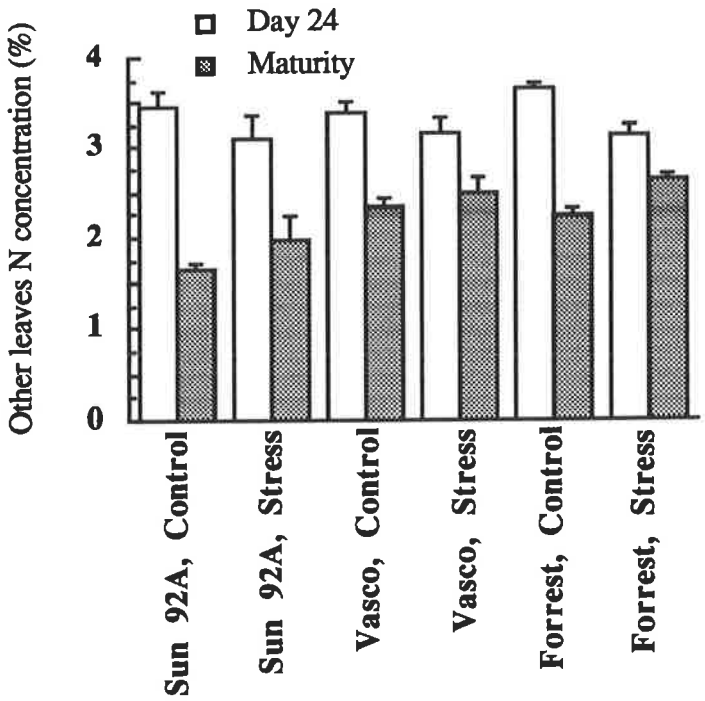

Fig. 7.34. N concentration of wheat and barley under water stress and non stress conditions at day 24 and maturity. Error bars are standard errors.

7.3.5.5.2 N concentration, content and remobilization

Although the DM of the chaff increased between day 24 and maturity, at the same time N concentration decreased in both treatments and both species (Fig. 7.36). At day 24, N% was significantly greater in the chaff of Forrest than in Vasco and Sun 92A under control conditions but it was similar under stress conditions.The chaff N content (Fig.7.37) decreased between day 24 and maturity except in Sun 92A (under control) and Forrest (under stress). It was notable that N content in the chaff was significantly greater in wheat than in barley due to greater chaff DM.

Despite the greater N content in the chaff of wheat cultivars than barley, no N appeared to have been remobilized from the chaff of Sun 92A in well watered conditions, while under stress Forrest appeared not to remobilize any N (Fig. 7. 38).

7.3.5.6 Endopeptidase activity of the flag leaf

Species and environmental differences are important in determining hydrolysis of specific proteins during stress induced senescence. Since some investigators found increased proteolytic activity correlated with protein loss (see Chapter 6), in this experiment endopeptidase activity of the flag leaf of different genotypes during grain filling were estimated (Figs 7.39 and 7.40). The developmental patterns of endopeptidase activity was different in different genotypes (Fig. 7.39). In Vasco, little activity was detectable at anthesis and activity increased progressively with time. In Sun 92A and Forrest, a high level of activity at anthesis was followed by a decline to minimum values between days 10 and 24, and a rise in activity to day 34.

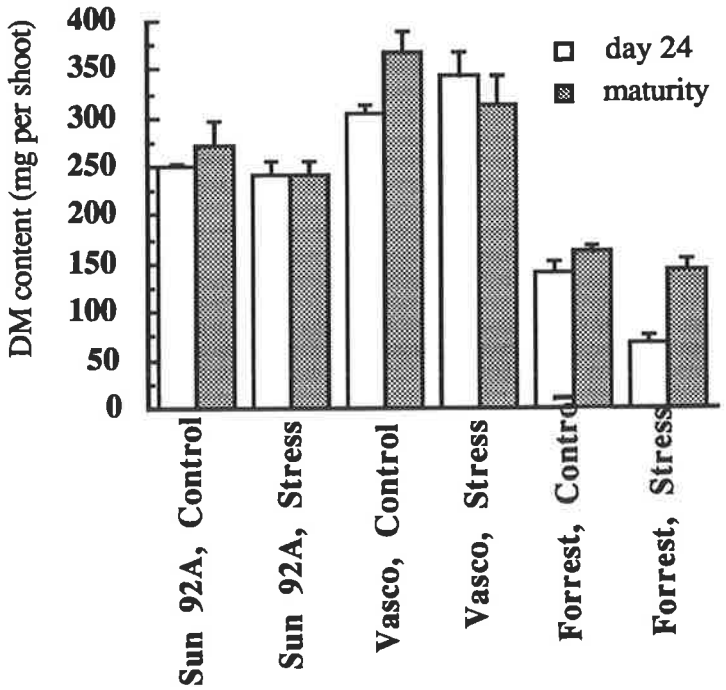

Fig. 7.35. DM content in the chaff of wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors

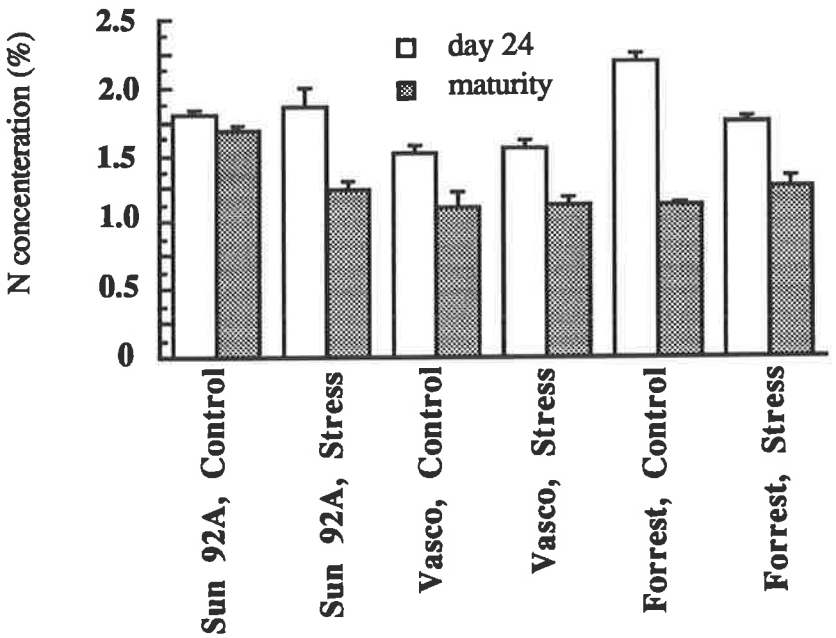

Fig. 7.36. N concentration of the chaff in wheat and barley under water stress and control conditions at day 24 and maturity. Error bars are standard errors.

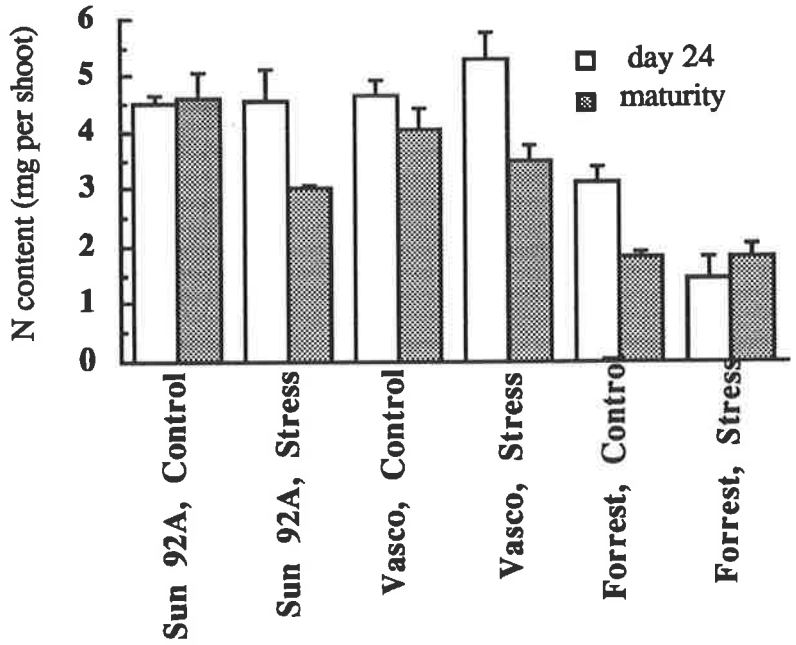

Fig. 7.37. N content in the chaff at day 24 and maturity in wheat and barley under stress conditions and control.

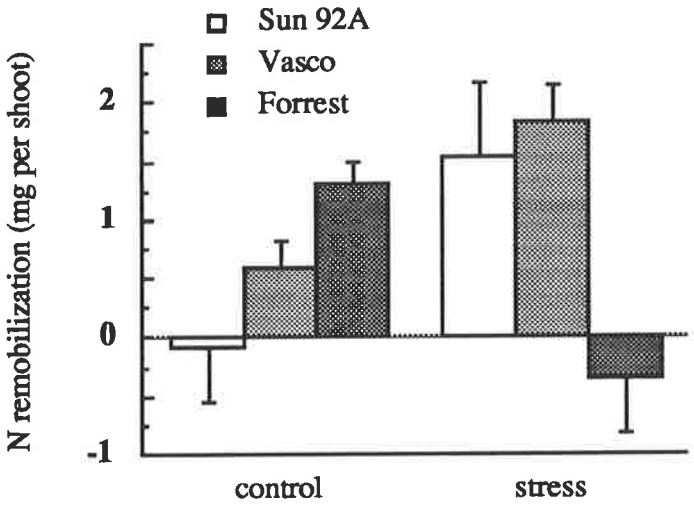

Fig. 7.38. N remobilization from the chaff of wheat and barley between day 24 and maturity under water stress and non water stress conditions. Error bars are standard errors.

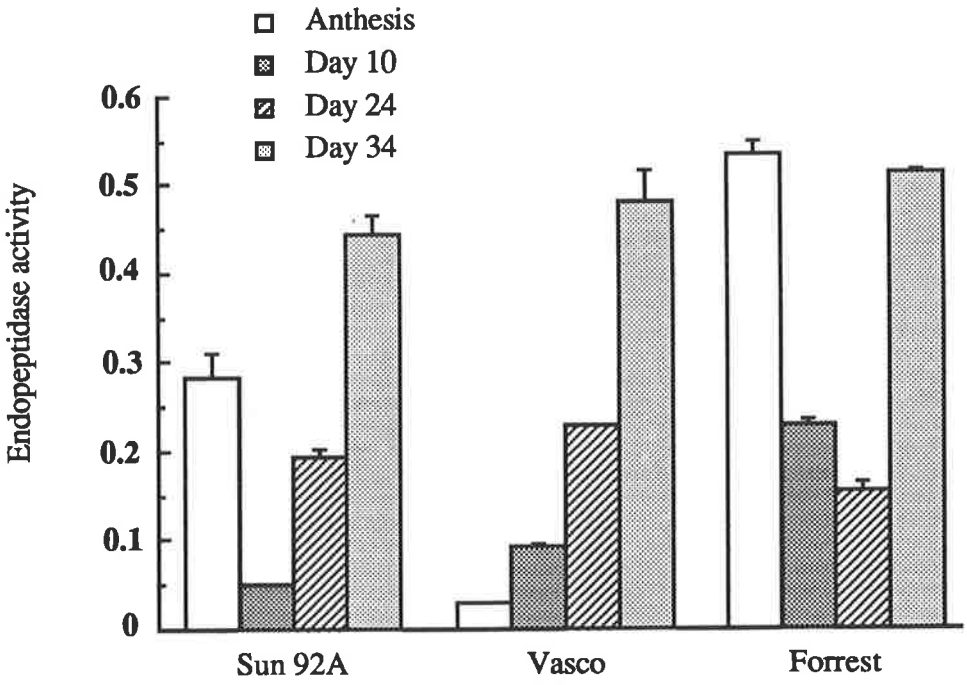

Fig. 7.39. Endopeptidase activity (Δ 340 nm/h/g dry wt) of the flag leaf in different genotypes under well watered conditions at different times during grain filling. Error bars are standard errors.

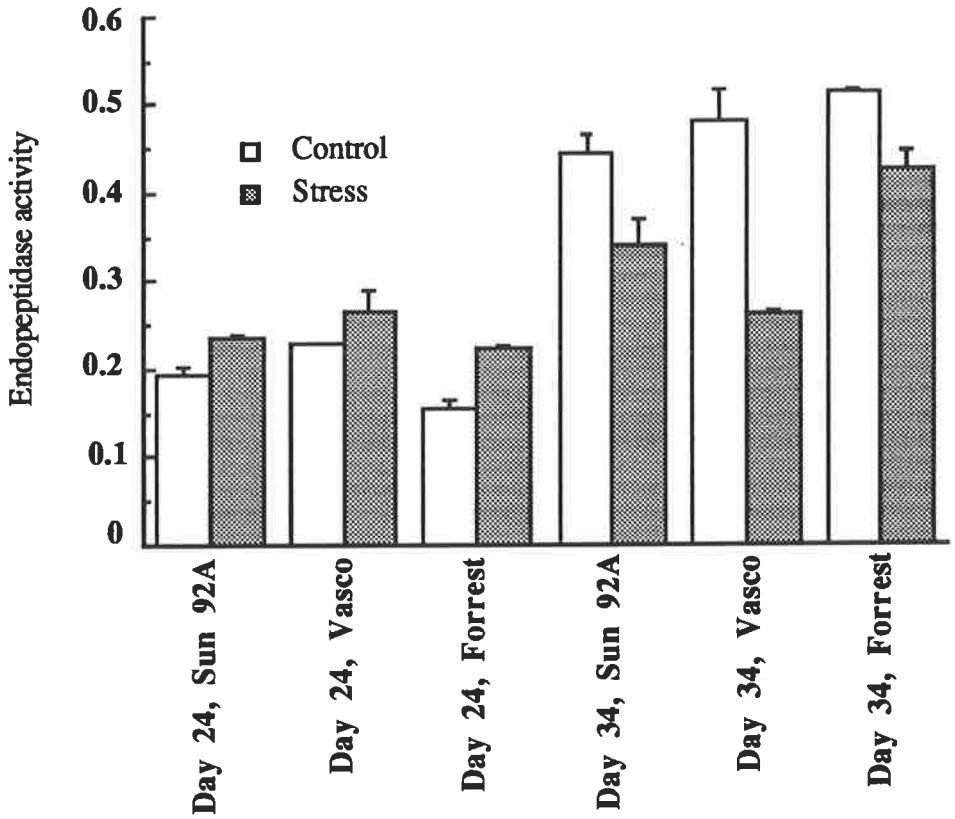

Fig. 7.40. Endopeptidase activity (Δ 340 nm/h/g dry wt) of the flag leaf of wheat and barley under well watered and stress conditions. Error bars are standard errors.

The responses to stress conditions in relation to endopeptidase activity was also different (Fig. 7.40). At day 24 after anthesis endopeptidase activity was greater under water stressed than well-watered, whereas at day 34 the activity of this enzyme was greatest under watered conditions.

7.4 Discussion

The main aims of this experiment were to compare the effects of water stress on grain DM and grain nitrogen content, HI and NHI of wheat and barley under identical conditions, and also to compare the effects of water stress on DM and N remobilization from different parts of the shoot of wheat and barley during grain filling. In this

Table. 7.1. Summary of grain parameters under well watered, and stress conditions in two wheat cultivars and in barley at maturity

	Control			Stress		
Parameter	Sun 92A	Vasco	Forrest	Sun 92A	Vasco	Forrest
DM(mg per shoot)	1268	1555	1044	1029	1273	790
N (mg per shoot)	37	36	22	31	34	18
N (%)	2.9	2.3	2.2	3.0	2.7	2.3
DMHI(%)	50	44	46	49	42	42
NHI (%)	71	56	52	70	55	46
Grain number (per shoot)	31	45	19	29	40	17
1000 grain weight	42	37	57	38	37	44

experiment, grain yield, N, HI, NHI, grain number and individual grain weight per shoot were lower under water stress than in non-stressed conditions in both wheat and barley plants. However N concentration was greater under stress conditions than control conditions in both species (Table 7.1). Results of the present study confirmed previous results indicating that HI reached greater values under well-watered conditions than in water stress conditions (Table 7.1).

In the present experiment, comparatively little DM was remobilized from any organ, and stress did not alter the remobilization very much. Apparent DM remobilization from different parts of the the shoot differed between the two treatments and two species. Although Vasco had a greater grain DM accumulation between the two harvests than Sun 92A and Forrest, it can not be concluded that this was due to a greater remobilization of DM from the shoot (Table 7.2).

The amounts of DM remobilized from the different plant parts, for barley in particular, are quite different to those measured in the previous glasshouse experiments. Whereas there was considerable apparent remobilization from the chaff in the glasshouse (Table 5.20) there was a net accumulation in the current experiment (Table 7.2).

Remobilization from other plant parts was also much lower in current experiment compared with the remobilization in the glasshouse. Total plant dry matter of Forrest was much lower in the current experiment than in the previous experiment although final grain yield was similar and the increase in grain DM between day 24 and maturity was greater than in the glasshouse. There are a number of possible reasons for the difference, although none are completely satisfactory.

The lower light intensity of the growth room may have resulted in lower accumulation of reserves within the plant and lowered the amount of reserves that could be remobilized. However, this does not explain why there should be such a big difference in the change in DM in the chaff between the two experiments or the difference between wheat and barley. The average daily temperatures in the glasshouse were higher than those in the growth room (16°/26° cf. 16°/21°) which may have resulted in a greater proportion of the DM being remobilized to meet the respiratory demand of the plant. The total stem dry matter of Forrest grown in the glasshouse was almost twice than of Forrest grown in the growth room, so the maintenance requirement for this material would also have been greater. With lower day temperatures and a smaller amount of DM the need to remobilize DM to meet this demand may have been considerably lower in the growth room. The difference in DM between the glasshouse and the growth room was greatest in Forrest which may help explain the considerable difference between the responses in wheat and barley.

Gain of N in the grain (Table 7.3) was approximately matched with loss of N from the vegetative organs, and the reduction in the grain N increment attributable to stress was also equivalent to the reduction in remobilization of N under stress. The apparent remobilization efficiency (Table 7.3) of N from flag leaves and other leaves of Sun 92A was greater than that of Vasco and Forrest in both stress and non-stress conditions and contributed most to grain N accumulation.

According to Feller *et al.* (1977) the increase in endopeptidase activity in the neutral pH range is related to nitrogen remobilization from senescing plant parts during post anthesis. A test of this proposition is provided by three types of comparisons:

Table. 7.2. DM increment (+) and apparent remobilization (-) from vegetative parts in wheat and barley between day 24 and maturity

	Control			Stress			Control			Stress		
	V1	V2	V3	V1	V2	V3	V1	V2	V3	V1	V2	V3
	Increment (+) and remobilization (-) (mg per shoot)						Apparent remobilization efficiency (%)					
Grain	+635	+664	+477	+400	+430	+255	-	-	-	-	-	-
Internode	+52	-58	-62	-50	-10	+21	-	13	15	20	3	-
Peduncle	+17	+46	-12	-29	-14	-15	-	-	14	16	6	20
Flag leaf	+0.3	-2	-9	+3	+19	+22	-	1	6	-	-	-
Other leaves	-38	-22	-18	-58	-21	-36	12	3	3	21	3	12
Chaff	+22	+62	+19	+0.7	-30	+75	-	-	-	-	4	-

V1: Sun 92A V2: Vasco V3: Forrest

Table. 7.3. Grain nitrogen increment (+) and vegetative parts remobilization (-) of N from wheat and barley between day 24 and maturity

	Control			Stress			Control			Stress		
	V1	V2	V3	V1	V2	V3	V1	V2	V3	V1	V2	V3
	Increment (+) and remobilization (-) (mg per shoot)						Apparent remobilization efficiency (%)					
Grain	+20	+17	+12	+15	+15	+8	-	-	-	-	-	-
Internode	-2.7	-5.8	-3.1	-3.4	-3.6	-2.3	67	75	40	89	59	30
Peduncle	-1.3	-1.1	-1.1	-1.8	-1.8	-1.2	44	31	58	58	47	76
Flag leaf	-6.9	-4.1	-2.4	-5.2	-4.4	-1.4	69	44	48	59	53	45
Other leaves	-6.1	-7.9	-7.6	-3.6	-4.7	-5.4	58	33	40	42	23	36
Chaff	+0.1	-0.6	-1.3	-1.5	-1.8	+0.4	-	12	42	33	34	-

V1: Sun 92A V2: Vasco V3: Forrest

(i) Prior to day 24, endopeptidase activity in the flag leaf of the three cultivars (Fig. 7.40) is ranked in order Forrest > Sun 92A > Vasco. Grain N content at day 24 is ranked Forrest < Sun 92A < Vasco (Fig. 7.6) and in terms of flag leaf N% (Fig.7.28) the order is Sun 92A > Forrest > Vasco, results which are almost the opposite of what would be expected.

(ii) There was little difference between the cultivars in flag leaf endopeptidase activity (Fig. 7.40) in watered plants, but far more N was remobilized from the flag leaf of Sun 92A than from Vasco or Forrest (Table 7.3).

(iii) Stress appeared to have reduced endopeptidase activity in Vasco to a greater extent between day 24 and maturity than in the other two cultivars (Fig. 7.41) although stress did not reduce the remobilization of N from the flag leaf of Vasco while stress appeared to have reduced remobilization a little in Sun 92A and Forrest (Table 7.3).

In both species (Table 7.3) the leaves in total remobilized more N than any other organ although the internodes also made a significant contribution in this experiment. N was apparently not remobilized from the chaff of Sun 92A under control conditions or from the chaff of Forrest under stress conditions. However, depending upon the conditions, the chaff of either species remobilized N to the grain. It appears therefore that the amount of nitrogen remobilized depends on cultivar and prevailing growth conditions, and also upon the part of the shoot under consideration.

Chapter 8. General discussion

8.1 Introduction

The growth of wheat and barley plants passes through three main developmental stages. The vegetative stage is the first stage when leaf growth, root growth, and tillering will be completed. Environmental conditions during this phase determine, among other things, the number of tillers. The reproductive period, which extends from floral induction to anthesis and fertilization is the second main stage. During this phase environmental conditions determine the rate and the duration of floral differentiation which affect the number of grains per plant. Grain filling is the third stage and the actual grain yield is determined during this phase. It is pertinent here to make a comment about the selection of the timing for the imposition of water stress treatments. Grain development after anthesis can be divided into two stages; grain enlargement and grain filling. Grain filling commences 10-15 days after anthesis and occupies at least 20-30 days until the grain ripens. So day 10 after anthesis was selected as the time for the imposition of water stress treatments, the effects of which would became manifest later during grain filling.

Moisture deficits are usually encountered late in the growing season in southern Australia and this may impact strongly on grain yield and grain protein concentration. According to Cornish (1950) 70-80% of the variation of yield in South Australia was due to variation in annual rainfall, and similar relationships exist in North Africa and Western Asia (Srivastava 1987; Blum and Pnule 1990). In Mediterranean environments, the period of crop growth is usually restricted by lack of rainfall, and water stress at the end of the season reduces growth and total dry matter yield.

Remobilisation of N from vegetative tissues is the principal source of N in water-limiting environments for the developing grain, although some studies have reported that where water is in ample supply N uptake during grain filling accounts for as much as 50% of grain N at maturity (Spiertz and Ellen 1978; Gregory *et al.* 1981). As well, the remobilization of dry matter formed during the pre-anthesis period makes a significant contribution to final yield, especially when post-anthesis photosynthesis is reduced by stress (Pheloung and Siddique 1991).

In order to explain the variable effects of water on the remobilization of the reserves from vegetative parts of the shoot in wheat and barley under dry-land conditions, information on the magnitude of moisture stress and its effect on remobilization of reserves is needed. Thus the main purposes of this investigation were as follows: (i) To establish whether or not the remobilization of N and DM from different parts of the shoot of wheat and barley plants under water stress is affected by the severity of water stress during grain filling. (ii) To investigate the behaviour of different parts of the shoot under water stress and non stress conditions in terms of the remobilization of N and DM during grain filling, and which parts of the shoot make the greatest contribution to grain filling. (iii) To determine how water stress during grain filling affects DM and N content, DMHI and NHI in wheat and barley cultivars differing in protein content . (iv) To enquire whether or not there are differences between wheat and barley. Results of the previous chapters related to the above aims have been discussed separately. In the following section the most important points will be discussed in general terms.

8.2 Responses to water stress

Water stress imposed on the plants decreased accumulation of nitrogen and dry matter in the grain of both species as well as the DMHI and NHI. The grain N yield per shoot was lower under water stress than in non-stressed conditions, while grain nitrogen percentage was greater. Water stress decreased dry matter accumulation more than N accumulation in the grain. As more than 70% of the DM of the grain is provided by starch (Jenner 1991), DM accumulation under water stress decreased presumably because water stress decreased starch accumulation in the grain.

Water stress reduced the remobilization of dry matter and nitrogen from the shoot, and in general the greater severity of the stress the greater was the inhibitory effect. In fact, the most severe treatment (total deprivation of water) not only appeared to abolish remobilization but instead to have resulted in net accumulation of dry matter in the leaves of wheat (Fig. 4.23 and Fig. 4.26). In two of the three cultivars of barley (Fig. 5.15) even mild water deficit resulted in a net increase in DM in the flag leaves during the second half

of grain filling. Thus not only does water deficit reduce carbon assimilation, but it also renders unavailable potential sources of material for grain filling in the shoot which might otherwise be remobilized.

HI at maturity under most conditions was greater in the semidwarf cultivar (Sun 92A) than in the medium height cultivar (Vasco) in wheat (Fig.4.5). Remobilization efficiency (Table 4.4) was also greater, under all conditions, in Sun 92A than in Vasco. This was consistent with the observations of Pheloung and Siddique (1991) that modern semidwarf cultivars are more efficient at remobilizing dry matter assimilated before and after anthesis compared to old tall cultivars, and that under irrigated conditions the old tall cultivars retained some of the stored assimilate in the stem at maturity. Several authors (Austin *et al.* 1980; Perry and D'Antuomo 1989) have suggested that a high HI is essential for obtaining high water use efficiency in water limited conditions. Selection of wheat for Western Australia and south western Iran has favoured cultivars that produce fewer main stem leaves and fewer tillers than the old cultivars (Siddique *et al.* 1989). Siddique *et al.* (1989b) suggested that additional increases in yield in Mediterranean environments may result from further decreases in tiller number and increase in tiller survival, particularly in low rainfall areas where biomass production is low.

Under field conditions as the soil dries the surface layers become depleted of water while water is still available deeper in the profile. Even though the plant may be amply supplied with water from roots deep in the soil, roots in the surface layer of dry soil produce signals which influence the growth and development of the shoot (see review by Davies and Zhang 1991). In barley DM deposition in the grain in the period between day 10 after anthesis and harvest 1 (Table 5.1) was not only reduced, but reduced to a greater extent by the divided root treatment than by severe water stress, even though the plants showed no signs of water deficit. Dry matter accumulation in the shoot (Table 5.4) was also decreased by the divided root treatment at day 24, but was affected to a lesser extent than was the grain. By the time the grains had matured (Table 5.2) they had almost completely recovered from the effects of this treatment, even though it was imposed throughout the experiment. These responses in the grain of cereals (barley) according to

the best of our knowledge have not been reported in the literature. Whether the root signals act by altering the delivery of assimilates to the grain, or through more direct hormone action on grain growth and development cannot be answered with the information available in this work. As the divided root treatment did not reduce the accumulation of nitrogen in the grain (even at day 24- see Table 5.3) the effects of the treatments appear to be confined to the metabolism and/or movement of carbon assimilates.

One other feature of this response is of interest. Withholding water from part of the root system has greater effects than allowing the whole root system to become dry (day 24 -Table 5.2). There are basically two alternative explanations: either root signals are produced in drying soil only when another part of the same root system is in wet soil, or the action of these root produced signals in the shoot is dependent upon the water status of the shoot.

8.3 Responses of different parts of the shoot

In wheat as well as barley, leaves (flag leaf and other leaves) remobilized far more N than any other organ (Tables 4.17 and 5.21). In terms of DM remobilization, the stem (lower internodes + peduncle) was the most important part of the shoot under almost all conditions in either species (Table 4.16 and 5.20).

In wheat the remobilization of ESS and TSC was greater from the lower internodes than from other parts of the shoot under both water stress and well-watered conditions (Table 6.3). Little remobilization of TSC appeared to take place from the leaves, so the stem was the most important part of the shoot in this respect. A readily available stem carbohydrate reserve could contribute to grain filling or energy requiring processes within the plant. Evidence for this concept has previously been presented and discussed by Stoy (1979). This function would be especially important when plants are subjected to water stress during grain filling. Jenner *et al.* (1991) concluded that the rate and duration of both starch and protein deposition in the grain are essentially independent events, controlled and influenced by different factors. In this study the accumulation of N and DM in the grain and also the remobilization of these components from different parts of the shoot were

affected by the severity of post-anthesis moisture stress, although the responses in DM and N remobilization to stress differed and the importance of different plant parts as sites of DM and N remobilization was aslo different. These differential responses support the idea that remobilization of nitrogen and other dry matter may be controlled through different mechanisms. The greater remobilization of DM in barley in the glasshouse experiment compared with the growth room experiment suggested that perhaps growth conditions, other than water stress, influence the amount of DM remobilized. It was suggested that one possibility could be the demand from maintenance respiraation.

In summary the remobilization of total soluble carbohydrates was greater from the lower internodes than other parts of the shoot while there were comparatively small amounts of these components remobilized from the leaves. On the other hand leaves were the most important parts of the shoot related to remobilization of N and soluble protein (Table 6.5).

These results demonstrate the importance of the stem and leaves as sources of remobilized C and N in both wheat and barley plants under water stress. Further studies on the environmental and genetic determinants of C and N assimilation and remobilization are needed to provide a more rational basis for prediction of grain protein concentration, for controlling it to desired levels by crop management practices, and also for breeding wheat and barley cultivars.

8.4 High and low protein genotypes and remobilization of DM and N

Previous studies suggested that the arrival of nitrogen in the developing grains of wheat is closely related to the export of nitrogen from senescent leaves. A few investigators have tried to identify the attributes of the developing grains that are associated with different grain N concentrations. Halloran and Lee (1979) reported differences between cultivars in nitrogen harvest index and total grain nitrogen as a percentage of total head nitrogen. They also noticed that highly significant differences existed between cultivars in the percentage of dry weight and nitrogen in the glumes and culms at maturity. This would seem to suggest there is genotypic variation for

translocating nitrogen from the glumes and culms presumably to the grain. Although remobilization of leaf protein, translocation of the resulting substrate, and incorporation of the substrate into endosperm protein are sequential events, and leaf proteases are responsible for the breakdown and translocation of the N to the developing grains, there is little evidence for mechanisms coordinating these processes(Jenner *et al.* 1991).

The apparent remobilization efficiency of N from both flag leaf and other leaves of Sun 92A was greater than that of Vasco and Forrest under the same conditions (Table 7.3). These results possibly suggest that the high protein cultivar of wheat was more efficient than the medium protein cv. of wheat, or than barley, at remobilizing N from the leaves into the developing grain. This idea is consistent with the work of Johnson *et al* . (1967) and Mikesell and Paulsen (1971) who noted that high protein cultivars have a greater proportion of their shoot N in the grain at maturity than do low protein cultivars.

8.5 Comparison between wheat and barley

Despite the lower 1000 grain weight in wheat than barley, grain yield of wheat (mg per shoot) was greater than barley. This was possibly because barley had a significantly lower number of grains per shoot (39% lower than Vasco and 58% lower than Sun 92A). In terms of comparison between wheat and barley, these results were unexpected as previously published values for grain yield grown side by side in the field using similar management practices, barley yield was about 25% more than wheat (Lopez-Castaneda and Richards 1994). The most likely explanation is that the experiments were carried out on plants which were reduced to a single shoot rather than on fully tillered plants. Other studies which have grown wheat and barley under the same conditions reported that in development and in pre and post - anthesis growth barley was the first to reach double ridge formation, anthesis and physiological maturity (Lopez-Castaneda 1992). Barley also produced leaves and tillers faster, leaf area and crop growth rate was greater and grain growth was also faster than wheat (Lopez-Castaneda 1992).

In quantitative terms, less N was remobilized from the flag leaf of barley than from the two wheat cultivars (Table 7.3). This however is likely to be a reflection of differences

in the size of the flag leaf as remobilization efficiency was not greatly different between the two species. What is striking is the similarity between Forrest and the medium protein wheat genotype Vasco in the values for apparent remobilization efficiency of nitrogen from the leaves (Table 7.3). Perhaps the same physiological or biochemical traits that determine grain protein concentration are operative in wheat and barley alike.

8.6 Conclusions

The most important conclusions from all of the above and previous discussion in this study were as follows:

1. Imposing water stress to the shoot during the grain filling phase reduced grain yield in both species at maturity and the response increased with the severity of the water stress.

2. Grain nitrogen concentration was significantly higher under severe water stress than under conditions of adequate water in the grain of both species at maturity, probably because starch accumulation in the grain was more sensitive than N accumulation in the grain under water stress conditions.

3. Depriving the upper section of the root system of water resulted in different responses between the two species in terms of the remobilization of DM and N from the shoot .

4. Remobilization of N and DM from the shoot of both wheat and barley plants are affected by water stress during the grain filling phase. The amount of N and DM remobilized is reduced depending on genotypes and environmental conditions.

5. The remobilization of N and DM from different parts of the shoot to the grain in both wheat and barley respond differently under water stress and well watered conditions during grain filling.

6. Differential responses to the treatments between species and also in different parts of the shoot suggest that the remobilization of DM and N are controlled through different mechanisms

7. Reduction in final grain parameters under water stress could possibly be mediated either through effects on the size of the grain or through effects of water stress on the availability of reserves and assimilates for grain growth.

8. Water stress during the grain filling phase not only reduced DM and N accumulation in the grain, but also affected the the grain N percentage which determines the quality of the wheat and barley grain.

8.7 Future work and comments

Future research topics that can be suggested include:

1. Further study on the physiology of remobilization of DM and N from the shoot of different cultivars is needed, to help understand the inter-relationship between DM and N remobilization in high and low protein and also in tall, semidwarf and short cultivars.

2. In this thesis, plants were reduced to a single shoot without any tillers. It is necessary to look at the whole plant under controlled conditions and field conditions to find out if the presence of tillers influences the results in terms of remobilization of DM and N from the shoot during grain filling.

3. Recent studies in wheat (Palta and Fillery 1995) concluded that applied N generated differences in early growth and dry matter at anthesis mainly through the effects of N on tiller number and tiller size. It was also concluded that increased growth due to high nitrogen nutrition led to increased severity of water deficit, particularly after flowering. Recent studies on N applied on barley genotypes (Fathi 1994), with and without postanthesis water stress, found that N remobilization was generally similar in a glasshouse experiment and in a field experiment. Of the six genotypes compared, the high tiller genotype (Skiff) showed the highest effect of N on DM remobilization, while the low tiller (Weeah) showed low dry matter remobilization and there was no response to N. It would

be useful to examine the influence of nitrogen nutrition on remobilization of N and DM in different types of the soil with different genotypes under post anthesis water stress. Further work over a more extensive set of environments and using other new wheat and barley cultivars is needed to improve this knowledge.

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