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# CHAPTER 1

## INTRODUCTION

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*Who publishes doubt and calls it knowledge, whose science is despair, whose pretence to knowledge is envy, whose whole science is to destroy the wisdom of ages to gratify ravenous envy.*

*-Milton Jerusalem, William Blake 1757-1827*

The work presented in this thesis is chiefly concerned with the comparison of adaptations to soil water deficits between the Brassica species, *B. napus* and *B. juncea*. Canola (*B. napus*) is an oilseed crop of increasing importance in Australia while Indian mustard (*B. juncea*) is still a minor crop but with a possible role in oilseed development. Canola grows in similar climatic regions to wheat (Buzza, 1979; 1991). It performs comparatively poorly at the climatic extremes of high or low temperatures (Buzza, 1991) and under high water deficits (Buzza, 1979). Poor adaptation to high water deficits is probably the most important of these constraints restricting the crop to the higher rainfall areas of the Australian wheat belt.

*B. juncea* is grown as an oilseed crop in India, Pakistan and China and is reputed to be well adapted to high soil water deficits. Australian evidence, while sparse, provides some confirmation for this reputation. In this regard, *B. juncea* occurs as a weed in the semi-arid regions of New South Wales (Cunningham et al., 1981) and it has yielded more than *B. napus* under high deficits in at least one study (Angus and van Herwaarden, 1989). Despite this reputation Indian mustard is almost entirely confined in Australia to a very small area grown for the production of condiment mustard. Oilseed production has been prevented because of quality problems arising from high erucic acid in the oil and high glucosinolate concentrations in the meal. The development of low erucic acid cultivars prompted Kirk and Oram (1981) to suggest that this crop may have the potential to be an alternative to *B. napus* in water limited environments. This suggestion gained further standing with the recent discovery of a low glucosinolate trait in *B. juncea* (Love et al., 1990). However, as yet very little is known about the comparative performance of the two crops either internationally or under Australian conditions.

The work reported here compared the adaptation of the two crops at different levels of soil water deficit. Specifically it aimed at determining their relative yield at different levels of soil water deficit and at identifying important traits contributing to the observed yield differences. More generally the comparisons were made to establish first if the *B. juncea* crop could replace *B. napus* under water limited conditions and further, the extent of this crops adaptation eg. would it be a viable crop under low deficit conditions.

Detailed measurements of water use efficiency and plant water relations were made together with the agronomically important parameters of growth and yield. A physiological approach was taken so that at least a preliminary understanding of the traits involved in any differences could be provided. Measurements were made predominantly under field conditions, accepting the disadvantage of high variability, in order to ensure that as far as possible the processes were assessed under realistic conditions. All cultivars used in these studies were matched for phenology and

height in order to increase the validity of the comparisons. At least three cultivars of each species were used in the field experiments.

The thesis reports one of the first detailed comparisons of these crops under field conditions including detailed measurements of plant water use and plant water relations. It follows a thematic approach, addressing growth (Chapter 4), yield and yield components (Chapter 5), water use and water use efficiency (Chapter 6), plant water relations (Chapter 7) and the interrelation of these parameters (Chapter 8).

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# CHAPTER 2

## LITERATURE REVIEW

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*"As ten millions of circles can never make a square, so the united voice of myriads  
cannot lend the smallest foundation to falsehood."*

*The Vicar of Wakefield, Oliver Goldsmith, 1728-1774*

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## **2.1. Introduction**

It is axiomatic to state that water is essential to plant life, if for no other reason than that plants are composed of between 80 to 95 % water by mass. Nor is it surprising that water deficits are a major limitation to the productivity of crop plants. Meigs (1953) suggested that water deficits are the principal limiting factor to crop growth for 40% of the earth's land surface and Boyer (1982) assessed them to be the single most important limitation to agriculture. Such critical importance has ensured that the response of plants to water deficits has been an active area of research for most of this century (see reviews by Iljin, 1957; Kozlowski, 1964; Hsiao, 1973; Hsiao et al., 1976; Bradford and Hsiao, 1982; Ludlow and Muchow, 1990). The following review, first provides some brief background on Brassica oilseeds and then proceeds to a discussion of the methods used for measuring the response of plants to water deficits and the adaptive mechanisms of plants to these deficits. Where possible discussion has been related to the crop members of the *Brassica* genus. No attempt has been made to cover all plant responses or adaptations, with the review being mainly concerned with the responses and adaptations that are important to crop productivity.

## **2.2. Brassica oilseeds**

Oilseeds from the *Brassica* genus have been in cultivation in India from as early as 2000 B.C. (Colton, 1985) and from the thirteenth century in Europe (Appelqvist, 1972). The crop was an important source of lamp oil for northern Europe from the Middle Ages until almost the end of the nineteenth century. The history of the development of this crop is reviewed in more detail elsewhere (Downey, 1966; Appelqvist, 1972; Buzza, 1973).

Commercial production of *Brassica* oilseeds began in Australia in the mid 1960s and rapidly expanded until the early 1970s when the disease *Leptosphaeria maculans* (blackleg) devastated the industry, particularly in Western Australia. From 1971 to 1985 only a small area was planted each year rarely exceeding 10000 ha in NSW (Colton, 1990). However, with the introduction of blackleg resistant and locally adapted varieties of high quality the industry greatly expanded with 130000 ha planted in NSW in 1994 and 335000 ha nationally. (R. T. Colton, pers. comm.).

Four species of the *Brassica* genus are grown to any extent as oilseed crops (Buzza, 1991). These are *B. napus* L., *B. campestris* L., *B. juncea* (L.) Czernjaczw (Indian mustard, referred to as mustard in this thesis) and *B. carinata* A. Baun (Abyssinian mustard). Of these *B. napus* and *B. campestris* are the most important, with *B. juncea* being an important crop in India and China but rarely grown in Europe, North America or Australia except as a condiment crop. *B. carinata* is a

minor oilseed crop almost entirely confined to Ethiopia (Buzza, 1991). The Australian industry is now almost entirely based on *B. napus* but in the past significant areas of *B. campestris* were also grown. All cultivars of *B. napus* currently grown in Australia meet "canola" quality standards in that their erucic acid concentrations are less than 2% of total fatty acids in the oil and glucosinolates are less than 30 micromoles per gram in the meal. As such, and in keeping with commercial practice, *B. napus* is referred to in this thesis as canola although the term can apply to any Brassica oilseed that meets the above criteria.

Cytogenetic relationships within the genus have been reviewed by Prakrash and Hinata (1980). These relationships have an important bearing on the work reported in this thesis since they indicate that, although sometimes difficult, it is possible to transfer useful genes from *B. juncea* to *B. napus* in a backcrossing program. This has already been achieved with seedling resistance to blackleg (Sacristan and Gerdeman, 1986). Hence if important adaptations to high deficit conditions are found in mustard it is at least theoretically possible that these traits can be transferred to *B. napus* should mustard appear to have limitations as a major crop in its own right.

The morphology and the general botany of *B. napus* are described by Buzza (1979) and the morphology of *B. juncea* by Cunningham et al. (1981). Both species are generally similar in appearance but have some distinctive differences. The laminae (leaf blades) of upper leaves of mustard do not clasp the stalk as they do in canola (Bengtsson et al., 1972; Buzza, 1979) and the leaf colour of mustard often appears to be lighter than in canola. The agronomic requirements of *B. juncea* are considered to be very similar to those of *B. napus* and *B. campestris* (Kirk and Oram, 1981). The advantages of mustard are thought not to be confined to the reputed greater drought resistance, with a review of the literature suggesting that this crop has a greater resistance to pod shattering and to certain diseases (Kirk and Oram, 1978).

*B. napus* material grown in Australia was initially derived from Canadian cultivars. The Canadian cultivars were crossed with a range of material from Europe, Japan and China providing a wide genetic diversity and lines ranging in maturity from early Chinese types to late European types (Mendham et al., 1984). *B. juncea* has been divided into two groups by Kirk and Oram (1978) on the basis of morphology, chemistry and economic use. The Indian and Pakistani form is a short early-flowering plant with seeds containing both allyl and butenyl glucosinolates. The Chinese and Eastern European form is taller later flowering with seeds containing only allyl glucosinolates.

### **2.3. Measuring the response of plants to water deficits**

Much of the literature concerning the response of plants to water deficits makes use of the concept of stress. Levitt (1980) attempted to link this concept to the relationship of stress and strain used in physics, with stress referring to the force applied to a body and strain to describe the deformation of the body resulting from the stress. In this analogy stress corresponds to water deficits and strain corresponds to the plant response. Further physical analogies can be made. In this regard elastic strain corresponds to plant responses that are completely reversible, such as happens with mild water stress that decreases photosynthetic rates at midday followed by a quick recovery with the removal of the stress later in the afternoon. Permanent strain, on the other hand, corresponds to irreversible responses such as leaf senescence and breaking point strain corresponds to plant death. These physical analogies should not be taken too far as plants are complex organisms with feedback and feedforward loops. However they are useful in that they indicate the need for careful quantification of stress in order to understand a plants response or adaptation to water deficit.

Water deficits may arise in the soil, in the plant or in the atmosphere or in combinations of these. Water potential ( $\psi$ ) is perhaps the most widely used measure of water stress in both soil and plant tissue, while vapour pressure deficit is probably the most widely used measure of atmospheric water deficit although it is equally valid to express this as atmospheric water potential. Plants act as a link between soil water and atmospheric water, and as such plant water potential can be influenced by soil water potential, the concentration of water in the atmosphere  $c_a$  and at the evaporative surface of the leaf  $c_l$  and the resistance to water flow between the soil and the atmosphere (Slatyer, 1967). These relationships can be expressed in simple terms as in equation 2.1, assuming isothermal, steady state conditions (Morgan, 1980a),

$$\psi_{plant} = \psi_{soil} - RE \quad (\text{Eqn. 2.1})$$

where R is the resistance to water flow in the soil and plant, E the evaporative rate which is proportional to  $(c_l - c_a)/(r_l + r_a)$  where  $r_l$  and  $r_a$  are the leaf and boundary layer resistances respectively. The strict form of this relationship will depend on canopy architecture (Cowan, 1968) It is clear from these relationships that, in the absence of plant adaptations, water deficits will influence plant water potential regardless of whether they arise in the soil, plant or atmosphere.

Water potential in plant tissue is often expressed as the sum of three or four components, as in equation 2.2,

$$\psi = P_i + \pi + \tau + (g) \quad (\text{Eqn. 2.2})$$

where  $P_t$  is turgor pressure,  $\pi$  osmotic potential,  $\tau$  is matric potential and  $g$  gravitational potential (Dainty, 1976; Begg and Turner, 1976). However,  $g$  can be ignored in crop plants as it involves a gradient of only  $0.01 \text{ MPa m}^{-1}$  and matric potential is not an important component for the range of  $\psi$  normally found in plants and, further, its effects are accounted for by  $P_t$  and  $\pi$  (Tyree and Jarvis, 1982; Passioura, 1982). Hence  $\psi$  in crop plants is best considered to be the sum of turgor pressure and osmotic potential. Water potential is ultimately a measure of the chemical activity of water ( $a_w$ ) as expressed in equation 2.3,

$$\psi = \frac{RT}{\bar{V}_w} \ln a_w \quad (\text{Eqn. 2.3})$$

where  $R$  is the universal gas constant,  $T$  is absolute temperature and  $\bar{V}_w$  is the partial molal volume of water.

Leaf water potential is normally measured by pressure chamber or thermocouple psychrometer techniques. Pressure chamber techniques have been recently reviewed by Turner (1986; 1988) while psychrometer techniques have been extensively reviewed in the symposia edited by Brown and van Haveren (1972) and more recently by Turner (1986). Both techniques give similar estimates of leaf  $\psi$  when used properly (Ritchie and Hinckley, 1975). Pressure chamber measurements are relatively fast and do not require careful temperature control and hence this technique is often considered the most appropriate field technique (eg. Turner, 1986). However, in the work reported in this thesis thermocouple psychrometers were used as they allow  $\psi$  and  $\pi$  to be measured from the same tissue sample thereby reducing errors involved in generating relationships of  $\psi$  with  $\pi$  and in estimating turgor which were required in these studies so that osmoregulation could be estimated.

Despite being well based in thermodynamics (Slatyer and Taylor, 1960) and being critical for water transport there are some difficulties in relating tissue  $\psi$  to physiological function (Bradford and Hsiao, 1982). These difficulties arise because a loss of 10% of a tissue's water at full turgor will markedly affect metabolism but corresponds to only, approximately, a 0.5 MPa drop in  $\psi$  depending on species or approximately a 0.4% drop in  $a_w$  (Hsiao et al., 1976). It is unlikely that such small changes will influence reactions involving water as reactants or products. Nonetheless many plant processes can be related to leaf  $\psi$  and, as such, Hsiao's (1973) summary, based on an extensive review of the literature is still valid and provides a useful indication of the sensitivity of plant processes to water stress as assessed by leaf  $\psi$  (Table 2.1).



Table 2.1. Generalised sensitivity to water stress of plant processes or parameters<sup>a</sup>

Process or parameter affected	Sensitivity to stress			Remarks
	→			
	Very sensitive		Relatively insensitive	
	Tissue $\psi$ required to affect process <sup>b</sup>			
	0 MPa	-1.0 MPa	-2.0 MPa	
Cell growth	-----			
Wall synthesis	-----			Fast-growing tissue
Protein synthesis	-----			Fast-growing tissue
Protochlorophyll formation	-----			Etiolated leaves
Nitrate reductase level	-----			
ABA accumulation	-----	-----		
Cytokinin level		-----		
Stomatal opening	-----	-----	-----	Depends on species
CO <sub>2</sub> assimilation	-----	-----	-----	Depends on species
Respiration		-----		
Proline accumulation		-----		
Sugar accumulation			-----	

<sup>a</sup> Length of the horizontal lines represents the range of stress levels within which a process becomes first affected. Dashed lines signify deductions based on more tenuous data.

<sup>b</sup> With  $\psi$  of well-watered plants under mild evaporative demand as the reference point.

From Hsiao, 1973

The components of leaf  $\psi$  can also be used to assess water stress. In comprehensive surveys carried out early this century, leaf osmotic potential was found to be lower in xerophytic compared to mesophytic plants (Harris, 1934; Iljin, 1957). However, despite this  $\pi$  is not a very appropriate measurement of stress as it is clearly a function of solute concentration. Solute concentration can be influenced by osmoregulation (Morgan, 1984) and hence  $\pi$  may be better considered as a measure of a plants response to stress rather than a quantification of stress. Similarly turgor pressure can be influenced by solute accumulation and is thus inappropriate as an absolute measure of stress.

Relative water contents ( $\zeta$ ) are also commonly used to measure water stress. It is calculated from tissue that is rehydrated to full turgor (Barrs, 1968). However, there are difficulties in determining the end point when the tissue is fully saturated (Catsky, 1974; Turner, 1986). Substantial reductions in  $\zeta$  drastically affect plant function causing herbaceous plants to lose their shape and form and changes the spatial relationships among organelles and membranes (Bradford and Hsiao, 1982).

However, obvious differences in stress can be present without any measurable change in  $\zeta$  (Huffaker et al., 1970).

In several papers, Hsiao and others have emphasised the difficulty of relating any single one of the above parameters to differences in metabolism (Hsiao, 1973; Hsiao et al., 1976; Bradford and Hsiao, 1982; Hsiao and Bradford, 1983; Turner, 1986; Krammer, 1988). The approach taken in the work reported in this thesis was to measure  $\psi$ ,  $\pi$ ,  $P_t$  and  $\zeta$  on the same leaf as this provides details on the level of stress experienced by a plant and the response of the plant to water stress;  $\psi$  and  $\zeta$  are the best measures of stress and their interrelations with  $P_t$  and  $\pi$  indicate physiological adaptation (see 2.4.3. for details). Ultimately the most accurate and important measure of a crops response to water deficits is the level of growth, yield or survival and these were carefully measured in this work.

Less quantitative measures such as wilting and leaf rolling can also be used to assess stress. However, these measures were not used in the work reported in this thesis.

#### **2.4. Adaptation to water deficits**

Hsiao et al. (1976) state that "rarely are terrestrial plants growing in a natural environment free from water stress for a period of more than a few days". A simple consideration of the environment makes this clear. Living roots are exposed to soil water potentials mainly in the range 0 to -3 MPa while leaves are exposed to atmospheric water potentials in the range -50 to -200 MPa. The large gradient between soil and atmospheric water potential provides the driving force for transpiration and induces water flow at a rate dependent on the plant and soil resistances. As a consequence of these resistances to flow, water deficits not only occur when supply is less than demand but also, dynamically, when resistances curtail the flow rate even when roots are growing in moist soil (Begg and Turner, 1976).

A wide range of adaptations to water deficits exist. In one of the first attempts at classifying these adaptations Shantz (1927) divided xerophytic plants into four types, namely those that either escape, resist, avoid or endure drought. A similar concept underlies the recent classification by Levitt (1972;1980) who divided plant adaptations into three categories comprising drought escape and two forms of drought resistance - avoidance and tolerance. These concepts permeate much of the literature and provide a good framework for understanding plant strategies (pardon the anthropomorphism) in the face of water deficits. However, for the purposes of this review a more mechanistic classification is used dividing adaptations into three categories; phenological, morphological and physiological. Hanson and Hitz (1982) suggest that a fourth category of metabolic adaptations be considered; however, this

form of adaptation falls outside the scope of this review as no metabolic adaptations were assessed in the work reported in this thesis.

#### **2.4.1. Phenological adaptation**

Desert ephemerals are perhaps the best non-crop examples of this type of adaptation. They germinate after substantial rainfall, grow rapidly and set seed before depleting all soil moisture. Plant breeders have manipulated this adaptation in crops and, although not matching the extremes that occur naturally in the desert ephemerals, they have bred early cultivars for nearly all major crops. This allows at least partial avoidance of terminal water deficits in many environments.

In the Brassica oilseeds a wide range of maturity types are available. *B. campestris* has some of the earliest types with some lines reaching maturity in 60 days from sowing (Buzza, 1979) and up to 40 days earlier than *B. napus* lines (Armstrong et al., 1985). The earliness available in *B. campestris* was the main reason for its past use in the drier areas of the Australia wheat belt. However, early lines of *B. napus* have now been developed (Myers et al., 1982; Thurling and Kaveeta, 1992a, 1992b). In India, *B. juncea* cultivars appear to be intermediate in earliness between *B. campestris* and *B. napus* (Kumar et al., 1987).

Manipulation of maturity is normally achieved by changing flowering time. Early flowering time reduces the risk of water deficits but also limits yield by reducing the amount of assimilate available for seed filling. For example *B. campestris* had no yield advantage over *B. napus* despite flowering three to four weeks earlier under high deficit conditions in Western Australia because of its reduced dry matter accumulation (Richards and Thurling, 1978). In this same environment *B. napus* yield was found to be positively related to time to flowering until October 1 but to be negatively related after that date (Thurling and Vijendra Das, 1979a). It is important then to optimise flowering time for particular environments by achieving a balance between a long enough vegetative period to assimilate as much source as possible without being so long that seed yield (sink) is limited by water deficits. These factors are also relevant to the choice of planting dates bearing in mind that early plantings may be at risk from frost and that late plantings may have too short a vegetative phase and be exposed to water deficits (Thurling, 1974a, 1974b).

Flowering time is controlled mainly by temperature and photoperiod in the spring types of *B. napus* and *B. campestris* (Hodgson, 1978a). The temperature dependence of time to flowering and phenology in general has allowed the phase duration of various stages in *B. napus* and *B. campestris* to be predicted using degree-days (Hodgson, 1978b). More recently this approach has been used to

compare the number of degree-days to maturity between *B. juncea*, *B. napus* and *B. carinata* (Singh et al., 1989).

Variation in flowering time is highly heritable in *B. napus* (Thurling and Vijendra Das, 1979b); it is also under relatively simple genetic control (Thurling and Vijendra Das, 1979c) and is easy to measure. Hence, this form of adaptation is relatively easily manipulated in breeding programs using photoperiod and vernalization genes. The work reported in this thesis does not include an assessment of this form of phenological adaptation for two reasons. First, as stated above this form of adaptation is already widely used and at least empirically well understood and second, when cultivars of varying phenology are included in comparative studies phenology becomes confounded with the other traits being examined. This makes a valid assessment of the relative importance of traits and even yield differences very difficult.

The Brassica oilseeds, while morphologically determinate, have an indeterminate corymbose type raceme. Indeterminacy is considered to be a phenological adaptation to water deficits allowing continued production of flowers while water is available (Turner, 1986; Ludlow and Muchow, 1990). Reproductive plasticity is a consequence of indeterminacy allowing some crops such as cotton (*Gossypium hirsutum*), cowpeas (*Vigna unguiculata*) and peanuts (*Arachis hypogaea*) to capitalise on rainfall events during the season (Bunting, 1975; Turk and Hall, 1980). However it is not clear that this type of adaptation is an advantage under conditions of terminal water deficits. For example in lupins (*Lupinus angustifolius*) plants with fewer lateral branches were better adapted to short dry seasons producing a greater number of pods on the terminal inflorescence before the onset of severe water deficits (Hamblin et al., 1986). The benefits of indeterminacy appear to be greatest in environments with a high probability of storm rainfall a feature of much of the Australian summer cropping regions. While there may be some instances where indeterminacy is a disadvantage in winter crops, with assimilate expended on branches that are unproductive because of water stress, indeterminacy is still desirable in the oilseed Brassicas as it is thought to contribute to their better yield stability compared to cereals in Mediterranean environments (Nix, 1975).

#### **2.4.2. Morphological adaptation**

Reduced leaf area is considered to be an important adaptation to water deficits (Begg and Turner, 1976; Fischer and Turner, 1978). This can be achieved by either reducing the rate of leaf expansion or by senescence. Both are effective means of reducing water use, as transpiration and leaf area index are linearly related for leaf area indices up to approximately 3 (Ritchie, 1974).

In a study of grain legumes Morgan (1992a) found midday leaf water potentials in black gram (*Vigna mungo*) were maintained above -0.6 MPa throughout the season with a tendency to increase during the season. In contrast soybean (*Glycine max*) water potentials steadily declined through the season to values below -1 MPa. However, the leaf area duration in soybeans was three times that in black gram in which productivity was sacrificed through turgor being maintained mainly by limiting leaf area while turgor was maintained in soybeans by osmoregulation which allowed a greater leaf area to be maintained despite declining water potential. The sacrifice of productivity associated with this adaptation is its main deficiency in crop plant. However, it does not mean that this adaptation is not useful. It may allow indeterminate crops to survive until the next rainfall and thereafter resume more active growth. Clearly reduced growth rates are more reversible than leaf senescence and, in turn, leaf senescence is preferable to desiccation since at least some nutrients and carbohydrate can be recycled.

The radiation load on leaves can also be reduced by changing leaf angle and orientation. In rice there is a good correlation between leaf rolling and  $\psi$  (O'Toole and Cruz, 1980). Similarly in soybeans the angle of the terminal leaflet is related to  $\psi$  (Oosterhuis et al., 1985). These adaptations have the advantage of being far more reversible than leaf area reduction and hence are less likely to incur a yield penalty (Begg, 1980; Ludlow and Muchow, 1990).

Rapid expansion of leaf area may also be considered a form of morphological adaptation (Ludlow and Muchow, 1990; Lopez-Castaneda and Richards 1994b). Such adaptation is thought to be useful for two reasons. In the first place the foliage will increase the water available for transpiration by decreasing the amount of evaporation from the soil and secondly, it will increase water use efficiency by carrying out more photosynthesis under cooler temperature which has been shown to increase water use efficiency (Tanner and Sinclair, 1983). Detailed measurements of leaf area and leaf area development were made in the work reported in this thesis allowing an assessment of the comparative early vigour of canola and mustard.

Another approach to reducing or delaying transpiration involves selecting plants for reduced diameter in their main xylem vessels in the seminal roots thereby increasing hydraulic resistance (Passioura, 1972). This purports to restrict water supply to shoots reducing leaf area early in the season and sparing some soil water for later use. Breeding plants that differ in xylem vessel diameter has been achieved (Richards and Passioura, 1981) but the effect of this trait on plant yield under water deficits has yet to be fully assessed. Further, the scope for manipulating root anatomy and hydraulic resistance in dicotyledons is limited (Ludlow and Muchow,

1990) suggesting that this technique is not likely to be of importance in the Brassica oilseeds.

Transpiration can also be reduced by epicuticular wax (glaucousness or bloom). In wheat glaucousness increases reflectance in the PAR range and reduces transpiration and carbon assimilation. This results in increased water use efficiency (Richards et al., 1986). Over a range of environments, irrespective of the level of water deficit Richards, (1984) found an average yield increase of 7% associated with this trait. In sorghum the amount of epicuticular wax increases with increasing water deficits (Jordan et al., 1983). The transport of water across cuticles and periderms, in relation to their chemistry and structure, was reviewed in detailed by Schönherr (1982). Little is known about this trait in the Brassica oilseeds despite the obvious blue bloom that can often be observed on field grown *B. napus* crops.

Leaf pubescence has similar effects to glaucousness and has been shown to reduce water loss in soybeans (Gl orashy et al., 1971). However, in this study no differences in photosynthesis or seed yield were detected between near-isogenic lines that were densely pubescent, normal or glabrous. Densely pubescent soybean isolines were later shown to have higher water use efficiencies than normal lines (Clawson et al., 1986). My own observations suggest that *B. juncea* leaves often appear to have a higher number of leaf hairs than *B. napus* but I am not aware of any published reports on variation of this trait in the Brassica oilseeds.

Stomata regulate water loss and hence differences in stomatal size, number, and distribution (and sensitivity, see 2.4.3.) will affect water loss. Distribution of stomata differs between canola and *B. campestris* with canola having twice the stomatal frequency of *B. campestris* on the adaxial surface while having similar stomatal frequency on the abaxial surface (Major, 1975). However, *B. campestris* has a higher frequency of stomata on the stem, pedicels and pods resulting in similar total numbers of stomata. Both species have a greater frequency of stomata on the abaxial compared to the adaxial leaf surface (Major, 1975). The importance of these differences in adaptation to water deficits in the Brassica field crops has not been assessed.

A feature of Brassica crops, not commonly found in other crops, is the interception of light by flowers. The inflorescence, particularly that of *B. napus*, creates a canopy of flowers above the leaf canopy. Hence, active leaves (and any formed pods) are shaded by the flowers. Spectral measurements indicate that flowering Brassica canopies reflect more radiation between 500 and 700 nm, giving the brilliant yellow colour, and absorb more between 400 and 500 nm than vegetative canopies (Yates and Steven, 1987). Mendham et al. (1981) speculate that this may reduce yield and they have suggested that apetalous varieties should be

developed. It is interesting to speculate that flowers may play an adaptive role similar to epicuticular wax under water deficits by decreasing radiation load by means of their increased reflectance and thereby reducing transpiration. Greater water use has been reported in an apetalous cultivar compared to the normal cultivar, Marnoo (Rao et al., 1991). However, these lines were not isolines so it is hard to establish the cause of the difference. Further, the apetalous cultivar used appears to be generally better adapted to high water deficits than Marnoo, extracting more water from depth and maintaining higher leaf turgor at low water potentials.

Increased specific leaf weight is another morphological adaptation to water deficits. It is associated with increased photosynthetic rates per unit area (Tsunoda et al., 1967; Pearce et al., 1969; Khan and Tsunoda, 1971) and hence probably also with increased water use efficiency. The wild relatives of the Brassica oilseeds, often growing under conditions of high soil water deficits, tend to have smaller and denser leaves and a larger ratio of vascular to photosynthetic tissue than the crop brassicas (Tsunoda et al., 1967).

The morphology of roots can also influence adaptation to water deficits. Root to shoot ratios are commonly found to increase with increasing water deficits (Struik and Bray, 1970; Schulze, 1974). This is commonly thought to increase water availability (Fischer and Turner, 1978; Ludlow and Muchow, 1990). However, Passioura (1982; 1983) suggests that greater root mass and deep roots may be of little value as the water transpired in producing the carbon required for more roots may offset the deeper soil moisture accessed. At high water deficits the root mass of wheat and barley may be as high as 45% of the total crop mass (Siddique et al., 1990a; Hamblin et al., 1990). However, this appears to be greatly in excess of that needed for water extraction (Siddique et al., 1990b) and probably also in excess of what is needed for harvesting nutrients under water deficit conditions. Variation between species in root length can be substantial; wheat has ten times the root length of chickpeas growing in the same environment yet they both extract the same amount of water (Gregory, 1988). This has led Richards (1991) to suggest that breeding for reduced root mass may be beneficial. However, no field evidence is available to show increased yield from crops modified in this way. Between 8 and 30 % of the mustard's crops total mass was found in the roots (Singh et al., 1990b).

Adaptations that reduce root permeability in very dry soils may exist (Passioura, 1988a). These adaptations prevent water flow from roots back into the soil at very negative soil water potentials. Reverse flows have been found in *Cynodon dactylon* (Baker and van Bavel, 1986) *Artemisia tridentata* (Richards and Caldwell, 1987) and in sorghum (Xu and Bland, 1993). However, reverse flows were not found in lucerne, *Medicago sativa* (Dirksen and Raats, 1985) perhaps reflecting a species

difference in this trait. But equally it may be a reflection of different stress duration or level. Reverse flows in sorghum were found to start at soil water potentials as high as -0.55 MPa and outflows accounted for up to 6% of daily transpiration (Xu and Bland, 1993). Root shrinking may be one way of preventing reverse flow. In cotton, diameters of large roots have been found to shrink diurnally by as much as 40% in step with diurnal changes in plant water potential (Huck et al., 1970). This scale of shrinkage would greatly increase the root/soil interfacial resistance by imposing an air gap between the root and the soil. However, shrinkage is less likely to occur for small roots under field conditions and for this reason Passioura (1988a) assessed it to be a relatively unimportant process in field plants. An adaptation more likely to increase root permeability involves increased suberization of roots (Nobel and Sanderson, 1984). However, unambiguous evidence for field variation within or between crop species is lacking for either of the above adaptations.

While the above discussion indicates that a wide range of morphological adaptations exist and that some at least have been studied in crop plants their relative impact on yield remains largely undetermined. This is especially the case for the Brassica oilseeds with very little direct work having been carried out on these adaptations in this genus. Some concluding remarks can however, be made. At a canopy or crop level reductions in leaf area though less reversible are far more effective in reducing transpiration than changes in reflectance or aerodynamic roughness (Fischer and Turner, 1978). Hence, assessing leaf area and leaf area development is more important than assessing comparative differences in epicuticular wax and pubescence in leaves. This consideration is reflected in the measurements that were made in the work reported in this thesis although an indirect assessment of epicuticular wax levels was made by measuring epicuticular conductance. There is evidence of differences in stomatal distribution between Brassica species hence stomatal frequencies were assessed in this work. Assessment of root characteristics was restricted to indirect measurements such as water use and depth of water extraction with direct measurements of root mass and distribution occurring only under glasshouse conditions.

An interesting feature of nearly all the morphological adaptations discussed above is that they are conservative, normally operating to limit transpiration. However, the normal behaviour of annual crop plants often appears to be the exact opposite, maintaining transpiration at the risk of soil water exhaustion, low water potentials and even death.



### 2.4.3. Physiological adaptation

Stomatal control of water loss is perhaps the most widely studied physiological adaptation to water deficit. Restricting stomatal apertures reduces water loss and inevitable CO<sub>2</sub> assimilation. Stomatal apertures are under complex control but appear to be regulated mainly by vapour pressure deficit, temperature and irradiance (Hall et al., 1978; Raschke, 1979; Schulze and Hall, 1982; Farquhar and Sharkey, 1982) and, more controversially, by plant water status (Bradford and Hsiao, 1982). Stomata respond to increasing vapour pressure deficit, when temperature and irradiance are held constant, by decreasing conductance and hence minimising water loss and water deficit under extreme evaporative demand. Temperature strongly interacts with vapour pressure deficit; however, when the effects are separated, leaf conductance increases with increasing temperature above the optimum for photosynthesis (Hall et al., 1976; Schulze and Hall, 1982). Leaf conductance increases with increasing radiation as does CO<sub>2</sub> assimilation (Schulze and Hall, 1982). Detailed discussion on these responses can be found in reviews by Cowan (1977), Raschke (1979) and Schulze and Hall (1982). In *B. campestris*, transpiration increases in a linear manner as air temperature increases from 10 to 42 °C and vapour pressure deficit from 0.7 to 2.1 kPa while it increases in a curvilinear manner as PAR increases from 0 to 2800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Singh et al., 1982a). Canopy transpiration in mustard under water deficit conditions is greater during the first half of the day compared to the second while in unstressed plants it is linearly related to air temperature (Kumar, et al., 1994).

The role of plant water status in stomatal control is more controversial. Evidence exists showing that stomata close when plants are stressed beyond a threshold  $\psi$  measured on a bulk tissue basis (see reviews by Boyer, 1976; Hsiao, 1973, Hsiao et al., 1976; Bradford and Hsiao, 1982). This closure is likely to be mediated by ABA (Raschke, 1970; Pierce and Raschke, 1980) at least under conditions of slowly developing water stress. However, the control of stomatal closure by leaf water potential or turgor pressure has been challenged (Schulze and Hall, 1982; Schulze, 1986). In summary the argument against this control is based on three main types of evidence. In the first place, stomata can remain open in wilted leaves (Henson et al., 1982a; Turner et al., 1984). Second, in the course of a day maximum conductance often occurs at minimum  $\psi$  (Küpper, 1984). Finally, plants growing in drying soil can influence leaf conductance via root signals in the absence of any loss in turgor (Zhang and Davies 1989a, 1989b; Davies and Zhang, 1991; Tardieu et al., 1992). However, the evidence is not consistent. For example in broad-leaved lupins (*Lupinus cosentini*) evidence is lacking for regulation of stomatal conductance by root signals (Gallardo et al., 1994). In field grown maize,

experimental data (Tardieu et al., 1993) fit a model of stomatal control that includes both leaf water status and root signals (Tardieu and Davies, 1993). The mechanism of stomatal control is unresolved but it is clear that closure does occur in response to water deficits regardless of how they are sensed.

In the short term, control of stomatal conductance probably provides the plant with its most powerful means of controlling transpiration rate (Passioura, 1982). Over the long term morphological adaptations such as reduced leaf area and leaf movements will also reduce transpiration particularly so at leaf area indices below 3 as LAI and transpiration are linearly related up to 3 (Ritchie, 1974).

One advantage of stomatal closure as an adaptation is its reversibility. However, as noted earlier, stomatal closure, inevitably reduces CO<sub>2</sub> assimilation and for that reason productivity. The optimization of these two processes, so that plants have the maximum CO<sub>2</sub> assimilation rates (A) for minimum transpirational water loss (E) and thus the largest possible transpiration efficiency (A/E), is of clear benefit to a plant.

At the leaf level Cowan and Farquhar (1977) hypothesised that stomatal conductance ( $g_s$ ) is optimised when  $\partial A / \partial E$ , the slope of the relationship between E and A when conductance is the chief source of variation, remains constant over short periods as this maximises A/E for the period (see Farquhar and Sharkey 1982; Cowan, 1982 for detailed discussion of the theory). Some experimental evidence is consistent with this hypothesis (Farquhar et al., 1980). However, this approach is conservative when in fact most crop plants appear to be prodigal in their use of water. It may be more appropriate that crop plants maintain  $g_s$  as large as possible to ensure high A. Further, by so doing A/E may be maximised because there is an upper limit to E in crop canopies beyond which further stomatal opening will not influence E but may increase A. In these circumstances A/E is maximised by stomata being wide open (Passioura, 1982). It is also a consideration that canopy temperature increases with stomatal closure further restricting the predicted increase in A/E at a canopy level (Ludlow and Muchow, 1990).

Two reviews, Fischer and Turner (1978) and Sinclair et al. (1983), suggest that variation in transpiration efficiency is limited within species and that variation between species is based mainly on differences in their biochemical pathway (ie. C<sub>3</sub> versus C<sub>4</sub>). Recent studies, however, have shown within species variation in wheat (Condon et al., 1993), barley (Hubick and Farquhar, 1989) peanuts (Hubick et al., 1988; Wright et al., 1988a) and cowpeas (Ismail and Hall, 1992, 1993). Few studies are available on the variation in this efficiency in the Brassica oilseeds. It varies diurnally with variation in vapour pressure deficit in *B. campestris* (Singh et al., 1982a) and mustard (Singh et al., 1986) declining with increasing vapour pressure

deficit. Transpiration efficiency also declines with increasing temperature (Singh et al., 1982a). In mustard it has been found to increase from sunrise reaching a peak between 8.00 and 10.00 h depending on growth stage and temperature (Kumar et al., 1994).

In the only field study that I am aware of that compares mustard and canola Lewis (1992) found no differences in water use efficiency (total dry matter production divided by total evapotranspiration). However, this assessment was based on only one cultivar of mustard and two of canola and further, under glasshouse conditions, he did find greater water use efficiency in the mustard. Water use efficiency differs from transpiration efficiency in that it is based on evapotranspiration rather than just transpiration. Water use efficiency can not be used to predict differences in transpiration efficiency as differences in water use efficiency may be entirely due to differences in soil evaporation. Both transpiration efficiency and water use efficiency were assessed in the work reported in this thesis.

Osmoregulation is another important physiological adaptation to water deficits. It has been known for some time that xerophytic plants have much lower leaf  $\pi$  than mesophytic plants (Harris, 1934; Iljin, 1957). Morgan (1984) cites levels of  $\pi$  of approximately -0.5 MPa for mesophytic shade plants, -1.0 to -2.0 MPa for most crop plants, -3.0 to -4.0 MPa for xerophytes and near -10 MPa for some halophytes. The accumulation of solutes in response to water deficits allows plants to partially or fully maintain turgor pressure as water potential decreases. The accumulation of solutes is often assumed to be passive resulting from growth being inhibited to a greater extent than photosynthesis (Munns and Weir, 1981; Li et al., 1993). Turner (1986) suggests that the term osmotic adjustment is more appropriate than osmoregulation, reflecting passive rather than active control. However, wheat plants with high osmoregulation maintain greater growth rates under water deficits than those with low osmoregulation (Morgan, 1983) and the capacity to osmoregulate appears to be under single gene control in wheat (Morgan, 1983; Morgan, 1991) suggesting an active accumulation. Hence, this adaptation is referred to as osmoregulation in this thesis.

The main benefit of osmoregulation is in maintaining turgor. Turgor pressure has long been thought to be the major parameter controlling growth during water deficits (Hsiao, 1973; Hsiao et al., 1976). In his extensive review of the literature, Hsiao (1973) states that "the direct effect of turgor change can be taken as proven in the case of reduced cell growth". Recently however, evidence that leaf growth, leaf conductance and photosynthesis all decline in drying soil when  $P_t$  is maintained has led to the suggestion that hormones produced in the roots are responsible for reduced leaf conductance (Gollan et al., 1985; Turner et al., 1985; Blackman and

Davies, 1985; Zhang et al., 1987) and leaf growth (Munns, 1987; Passioura, 1988b). This has led to a belief that  $P_t$  does not control leaf elongation (Passioura, 1988c; Kuang et al., 1990).

However, the strength of this conclusion seems unwarranted. It is clear that mechanisms are present that allow shoots to respond to root signals (Munns and King, 1988; Munns, 1992) at least in very young plants in controlled environments. But it is not clear that these signals totally override  $P_t$ . Passioura (1988b), concluded from pressurised root studies that the relative leaf expansion rate was controlled by soil signals rather than by turgor. However, in this study, where neither turgor nor root signals were measured, the stress levels were minimal with no effect on shoot dry weight and in fact the total dry weight of the dry pressure treatment was largest of all treatments. Suggesting, if anything, that turgor affects are more important than root drying. Further, pressurising the soil may have wide ranging effects on the plant including changing leaf shape (Passioura and Gardner, 1990) and while the nexus between soil and shoot water relations is broken it is replaced by a confounding of soil pressure and hence strength with leaf turgor.

A more satisfactory experimental system involves the use of splitting root systems and growing some portion of the root system in moist soil and some in dry soil. Some evidence from these type of studies do show soil water deficit effects which appear to override tissue turgor (Davies and Zhang, 1991) though these studies are almost entirely based on single genotypes. However, the evidence is far from uniform. Sadras et al. (1993) showed that under field conditions leaf expansion rates in sunflower are better described by leaf  $\psi$  than by soil moisture; further, they showed that split root plants behaved the same as the moist controls rather than as the dry controls as would be expected if root signals were the controlling factor (Davies and Zhang, 1991). Similarly in broad-leaved lupins, split root plants behaved like wet controls rather than like dry controls (Gallardo et al., 1994) with no evidence of root signals influencing stomatal conductance and leaf gas exchange. Further, in a series of field experiments between 1980 and 1988 Morgan (1995) found no evidence that soil water contents control wheat dry matter production but evidence of a leaf turgor effect that was in turn related to the capacity of the lines to osmoregulate. Clearly cell enlargement and hence leaf expansion are complex processes involving the physical actions of turgor on the cell wall and the biochemically controlled cell loosening processes (Boyer, 1987; Cleland, 1987; Ray, 1987; Li et al., 1991) and root signals may also play a role. However, the importance of this last mechanism has yet to be established under field conditions. Given these uncertainties and the compelling evidence for a linear relationship between leaf expansion and turgor pressure (Bunce, 1977), it appears unwarranted to dismiss

leaf turgor as the primary control mechanism of leaf growth under water deficit conditions.

A more balanced view, perhaps, is that the control of stomatal conductance depends on both root and shoot signals (Tardieu et al., 1992; Tardieu and Davies, 1993; Tardieu et al., 1993) in at least some species and that leaf expansion, while influenced by root signals, is still predominantly controlled by turgor. As such the maintenance of turgor by adaptations such as osmoregulation should be beneficial to crop growth and yield under water deficit conditions.

Osmoregulation needs to be distinguished from the passive concentration of solutes that occurs with water deficits as a result of decreasing cell volume (normally assessed as relative water content). Two main approaches are available. The first involves measuring changes in  $\zeta$  and  $\pi$  over a wide range of values allowing the proportion of  $\pi$  due to solute accumulation ( $\pi_a$ ) for a given  $\psi$  to be calculated using equation 2.4,

$$\pi_a = \pi_v - \frac{\pi_t \zeta_t}{\zeta} \quad (\text{Eqn. 2.4})$$

where  $\pi_v$  is the osmotic potential at  $\zeta$ ,  $\pi_t$  the osmotic potential at full turgor and  $\zeta_t$  the relative water content at full turgor (often assumed to be 1) with  $\frac{\pi_t \zeta_t}{\zeta}$  being the osmotic potential due to concentration with water loss (Morgan, 1991). Osmoregulation is then expressed as the change in osmotic potential due to solute accumulation, i.e.  $\Delta\pi = -\pi_a$ . The second approach involves rehydrating tissue to a relative water content of one and measuring  $\pi$  and then comparing this with  $\pi$  of tissue rehydrated from well watered control plants; the osmotic adjustment is calculated as the difference between the two i.e.  $\Delta\pi_1 = \pi_t \zeta_t - \pi \zeta$ , ignoring bound water estimates (Turner et al., 1986; Andersen and Aremu, 1991). The two measurements differ as  $\Delta\pi_1 = \Delta\pi \zeta$  thus the osmotic adjustment calculation will underestimate the actual solute accumulation if  $\zeta$  declines with stress (Morgan, 1995). Both approaches have been used in the work reported in this thesis but the field measurements were predominantly carried out using the first method.

Osmoregulation has been identified in wheat (Morgan, 1977a), barley (Blum, 1989), sorghum (Wright et al., 1983b; Santamaria et al., 1990; Basnayake et al., 1993), millet (Henson et al., 1982b), cotton (Karami et al., 1980), pigeonpeas (Flower and Ludlow, 1986), rice (Turner et al., 1986), chickpeas (Morgan et al., 1991) and in *B. juncea* (Singh et al., 1990b) and *B. carinata* (Kumar et al., 1984). Positive associations have been shown between osmoregulation and yield in wheat, with high osmoregulating lines averaging 11% more yield over 56 field trials carried out over 4 years (Morgan et al., 1986). Further, when isopopulations were tested under extreme stress, yield increases of up to 50% were found (Morgan, 1983). Similarly in

sorghum, high osmoregulating lines yielded up to 34% and 24% more than low osmoregulating lines when water deficits occurred preanthesis or postanthesis respectively (Ludlow et al., 1990; Santamaria et al., 1990). A greater capacity for osmoregulation in chickpea genotypes, measured under glasshouse conditions, was associated with increased grain yield in the field under water deficits (Morgan et al., 1991). In the Brassica oilseeds *B. carinata* was found to have greater osmoregulation than canola and a grain yield more than twice that of canola (Kumar et al., 1984). However, only one cultivar of each species was used in that study and no indication of the maturity type of the two cultivars was given.

An important benefit of this adaptation is that no yield penalty appears to be incurred in high osmoregulating lines when grown under low deficits. In such conditions no adverse effects on grain yield were found between low and high osmoregulating groups in chickpea (Morgan et al., 1991), wheat (Morgan and Condon, 1986; Morgan, 1995) or sorghum (Tangpremsri et al., 1995). In barley, Grumet et al. (1987) found that high osmoregulating lines, selected in response to salt stress, had smaller yields than low lines. However, the difference in  $\pi$  between the lines of only 0.1 MPa suggests that there was little or no difference in osmoregulation between the lines and no measurements of  $\pi$  were made in the field experiments from which the yield data was collected.

Osmoregulation influences growth and yield in a number of ways. It has been shown to maintain harvest index in wheat (Morgan and Condon, 1986) and sorghum (Ludlow et al., 1990; Santamaria et al., 1990) subjected to water deficits and to increase it in wheat under severe water deficits (Morgan and Condon, 1986). The maintenance of harvest index in high osmoregulating lines of wheat is associated with better seed set, increased tiller and floret survival and reduced leaf senescence (Morgan, 1980b; Morgan and King, 1984). It is also associated with increased seed set in sorghum attributable to reduced spikelet abortion (Santamaria et al., 1990; Tangpremsri et al., 1995) and increased use of preanthesis assimilates in grain filling (Ludlow et al., 1990). The maintenance of seed set in high osmoregulating lines of wheat is thought to be a consequence of turgor maintenance acting to delay the increase in concentration of ABA a process associated with turgor declining to zero (Morgan, 1980b; Morgan, 1984; Morgan and King, 1984). High concentrations of ABA have been reported to increase abortion of reproductive tissue (Morgan, 1980a, 1980b; Saini and Aspinall, 1982).

Water use in high osmoregulating lines of wheat has been found to be 50% greater than in low lines (Morgan and Condon, 1986). However, greater yield in high osmoregulating lines compared to low lines can occur with no differences in water use (Tangpremsri et al., 1995). Increased water use by plants with this trait arise

from turgor maintenance which reduces leaf senescence, promotes stomatal adjustment and increases the uptake of water from the soil profile (Ludlow and Muchow, 1990). For example, under high deficits, leaf area indices at anthesis of high osmoregulating lines of wheat were found to be statistically greater than those of low lines in two out of three years and were numerically greater in all years (Morgan, 1995). The increased leaf area indices found in a high osmoregulating line of sorghum were due mainly to a decreased rate of leaf senescence (Wright et al., 1983a; Wright et al., 1983b). Stomatal adjustment allows stomata to remain open to progressively lower  $\psi$  as water deficits increase and osmoregulation appears to be the main mechanism by which this occurs (Ludlow and Muchow, 1990). Since stomatal closure is responding to turgor rather than leaf water potential. In both wheat and sorghum, lines with a high capacity for osmoregulation have greater root biomass and root length densities than low osmoregulating lines allowing more water to be extracted from the soil profile, particularly from depth (Morgan and Condon, 1986). In wheat (Morgan and Condon, 1986) and sorghum (Ludlow et al., 1990; Santamaria et al., 1990) there is no evidence of osmoregulation affecting water use efficiency. However, Singh et al. (1986) report increased water use efficiency in high osmoregulating lines of mustard and associated this with greater transpiration rates.

Potassium, amino acids and sugars account for approximately 90% of leaf or sap osmotic potential in wheat (Munns et al., 1979; Morgan, 1992b). When measured during water deficits potassium is the most important solute in high osmoregulating lines accounting for 78% of sap  $\Delta\pi$ , with amino acids accounting for 22% (Morgan, 1992b). In contrast, when solutes are measured after partial or full relief of the stress, potassium accumulation appears to be relatively small (Munns and Wier, 1981; Johnson et al., 1984). This may result from changes in solute composition that occur with rewatering or it may even occur because low osmoregulating lines were used (Morgan, 1992b). It is of interest that large potassium accumulations are also associated with turgor regulation in bacteria (Sutherland et al., 1986). Regardless of the exact nature of the solutes involved, as noted earlier, there does not appear to be a yield penalty from growing high osmoregulating lines and hence the metabolic cost of accumulating solutes does not outweigh the benefits. In fact the metabolic cost of storing assimilate and using it for osmoregulation has been shown to be less than the cost of converting it to biomass (Richardson and McCree, 1985; McCree, 1986).

Ludlow and Muchow (1990) in a review article state that for osmoregulation, in contrast to many other physiological and morphological traits, "the association with components of yield, determinants of survival, and yield have been

demonstrated rather than merely postulated". This trait is important in crop plants in that it does not adversely influence their productivity under good conditions and is also compatible with the general prodigal rather than conservative water use found in crop plants. As such detailed field measurements of osmoregulation were made in the work reported in this thesis.

Tissue elasticity also influences the way in which turgor changes with declining water potential as described in equation 2.5,

$$\frac{dP_t}{d\psi} = \frac{\epsilon}{\epsilon - \pi} \quad (\text{Eqn. 2.5})$$

where  $\epsilon$  is the bulk modulus of elasticity (Wenkert et al., 1978). At a given water potential plant tissue with high elasticity (low  $\epsilon$ ) will have higher turgor. In sorghum (Jones and Turner, 1978) and wheat (Melkonian et al., 1982)  $\epsilon$  increased with increasing stress while the opposite was found in field beans (Elston et al., 1976). In the Brassica oilseeds Kumar and Elston (1992) found mustard to have an average  $\epsilon$  of 3.5 MPa compared to 8.2 MPa in canola. Interpreting tissue elasticity is however relatively difficult as  $\epsilon$  is both turgor pressure and water content dependant (Tyree and Jarvis, 1982). Measurements of  $\epsilon$  were restricted to glasshouse conditions in the work reported in this thesis.

The desiccation tolerance of tissue has been reviewed by Bewley and Krochko (1982). This adaptation allows plants to survive protoplasmic dehydration without permanent injury. However, its significance to crop plants is probably limited as it is generally considered that plants with this adaptation forfeit productivity for survival (Bewley and Krochko, 1982; Turner, 1986). Ludlow and Muchow (1990) suggest that it may have a role in crop plants by allowing time for preanthesis dry matter to be translocated thereby improving harvest index. Given the limited number of traits that it was feasible to examine in this work desiccation tolerance was not assessed; besides it is unlikely to be present in the Brassica oilseeds as in higher plants this adaptation is predominantly found in the monocotyledonae.

There is a wide range of other physiological adaptations documented or hypothesised, some being quite novel. They include the possible exudation of surfactant compounds from roots changing the surface tension of soil water and thus allowing roots to extract water from smaller pore sizes than otherwise possible (Passioura, 1988a). However, the significance of such adaptations in crop plants has received very little attention and it is not possible to assess their importance to the Brassica oilseeds.

## **2.5. Conclusion**

While mustard has a reputation for being well adapted to water deficits the comparative adaptation of canola and mustard has received scant attention in the



literature. However, from this review, several pertinent conclusions for the project can be made.

First, if important adaptations to water deficits are found in mustard it is at least theoretically possible that these can be transferred to canola in a backcrossing program. Hence it is worth while characterising mustards response to water deficits even if this crop should prove to be in itself agronomically unsuitable.

Second, while phenology provides a powerful means of avoiding water deficits it is not feasible to examine the impact of other adaptations on dry matter production and yield in comparisons where phenology is not matched. However, phenological adaptations such as early vigour can be assessed.

Third, a vast number of morphological adaptations have been proposed yet few have been shown to influence yield under field conditions. However, it is clear that canopy development, crop water use and water use efficiency require careful characterisation as most of the proposed morphological adaptations influence some or all of these parameters directly or indirectly. Some evidence exists showing wide variation in stomatal distribution in the Brassica oilseeds this should be documented in mustard and canola.

Fourth, of the physiological adaptations the most important to characterise are transpiration efficiency and osm regulation.

These conclusions provide the rationale for the approaches taken in this work in pursuit of the aims outlined in Chapter 1.