PHOTOSYNTHETIC GAS EXCHANGE RESPONSES TO LIGHT, TEMPERATURE, CARBON DIOXIDE AND WATER STRESS, AND CHANGES IN PHOTOSYNTHETIC PIGMENTS TO LIGHT AND WATER STRESS IN TWO CULTIVARS OF *Hordeum vulgare* L.

THESIS

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TO MOM AND DAD
THANKS FOR EVERYTHING

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SUMMARY

The gas exchange responses of two cultivars of *Hordeum vulgare* L., to light, temperature, CO_2 and water stress were investigated in the laboratory. The optimum temperature for net CO_2 assimilation was found to be 25°C and 22.5°C for cv. Clipper and cv. Dayan respectively. Net CO_2 assimilation was reduced at 30°C in cv. Dayan. At low light intensity the highest quantum yield efficiency was 0.051 $mol.mol^{-1}$ at 30°C for cv. Clipper, and 0.066 $mol.mol^{-1}$ at 20°C for cv. Dayan. At the same temperature, cv. Clipper had a higher water use efficiency than cv. Dayan, but stomatal conductance for cv. Dayan was higher than cv. Clipper.

Stomatal limitation to CO_2 was lowest at the optimum temperature for CO_2 assimilation in both cultivars. Stomata limited CO_2 assimilation in cv. Clipper to a larger degree than in cv. Dayan. Relative stomatal limitation for cv. Clipper at 25°C was 0.280 ± 0.010, and for cv. Dayan at 22.5°C was 0.028 ± 0.011.

Short-term exposure to elevated CO_2 concentrations increased CO_2 assimilation in both cultivars, but more so for cv. Clipper. Transpiration rate at elevated CO_2 partial pressures were higher in cv. Dayan than in cv. Clipper. At very high CO_2 (860 $\mu mol.m^{-2}s^{-1}$) partial pressure water use efficiency in cv. Clipper was higher than cv. Dayan, but at low CO_2 partial pressures water use efficiency in cv. Dayan was higher than cv. Clipper.

Water stress reduced the relative leaf water content and net CO_2 assimilation in both cultivars. Cultivar Dayan was more tolerant to water stress, and CO_2 assimilation in this cultivar was less affected by water stress. In both cultivars water stress increased the concentration of chlorophyll *a*, chlorophyll *b*, and chlorophyll *a+b*. the chlorophyll *a:b* ratio remained relatively constant throughout the stress period. No correlation between relative leaf water content and total carotenoid concentration was observed.

ABBREVIATIONS AND SYMBOLS

Symbol	Definition	Units
A	Net assimilation rate	$\mu mol.m^{-2}s^{-1}$
E	Transpiration rate	$mmol.m^{-2}s^{-1}$
g	Stomatal conductance	$\mu mol.m^{-2}s^{-1}$
WUE	Water use efficiency	$mol.mol^{-1}$
Q	Apparent quantum use	$mol.mol^{-1}$
Vc	Carboxylation rate of Rubisco	$\mu mol.m^{-2}s^{-1}$
I	Relative stomatal limitation	--
s	Leaf area	cm^{-2}
RWC	Relative water content	%
Ci	Internal $[CO_2]$	$\mu mol.m^{-2}s^{-1}$
°C	Temperature	°C

CHAPTER 1

INTRODUCTION

In order to develop improved genotypes with higher photosynthetic rates which function successfully under stress conditions, it is necessary to determine how stress affects the relative contributions of different processes such as the light limitation, the supply of CO_2 through the stomata and the enzymatic fixation of CO_2 on net photosynthetic CO_2 assimilation. The exchange of CO_2 and water vapour between plants and the atmosphere is regulated in the long term (days to weeks) by changes in leaf area and by the development of the photosynthetic apparatus in the leaf mesophyll. In the short term (hours to days) gas exchange is regulated by adjustments of the photosynthetic capacity and stomatal aperture. Regulation of gas exchange is important in order to maintain growth without desiccation in an atmosphere in which the gradient for CO_2 uptake between the ambient air and the intercellular air spaces is maintained at about 0.1 $Mmol.mol^{-1}$, whereas the gradient in water vapour concentration is normally greater than 10 $Mmol.mol^{-1}$ (Schulze, 1986). Since nature has not evolved a membrane which is permeable to CO_2 but not water vapour (Cowan, 1977; Schönherr, 1982), CO_2 uptake for photosynthesis and water vapour loss via transpiration both take place through the stomata. This inevitably results in a proportionally greater water vapour loss than CO_2 uptake. The efflux of water vapour from the leaf to the atmosphere is thus in the category of 2 orders of magnitude greater than the influx of CO_2 (Fischer and Turner, 1978). Stomatal and photosynthetic responses to stimuli such as light, CO_2, and temperature are understood (Raschke, 1979; Ziegler, 1983) to allow useful predictions of rates of net CO_2 assimilation (Farquhar and von Caemmerer, 1982). In

contrast, our understanding of stomatal and photosynthetic responses to water and salinity stress and models of these stress functions remain somewhat mechanistic.

Light responses

Light is one of the major environmental factors regulating plant growth. Plants adapt to their environment by regulating the composition, structure and function of the thylakoid membrane, and as a result the plants overall photosynthetic capacity, in order to maintain and optimize for maximal photosynthetic activity and CO_2 assimilation (Anderson, 1986; Chow and Anderson, 1987).

Light energy that is absorbed by the leaf has several potential predestinations. The predominant fate is to drive the photochemical reactions that result in the regeneration of NADPH and ATP used for CO_2 assimilation. Measurements of gas exchange by leaves in light have demonstrated that for wavelengths in the region of 600 nm, about 9 quanta are required to fix each molecule of CO_2 (Evans, 1987). This is only possible if light is equally distributed between the two photosystems, as they operate in series and are spatially separated (Anderson, 1986). At low irradiance (< 500 μmol $m^{-2}s^{-1}$) photosynthesis uses virtually 100% of the available quanta, but in full sunlight (2000 μmol $m^{-2}s^{-1}$) more quanta are available than can be used in the photochemical process. Leaves therefore need to dissipate 60-90% of the quanta at high irradiance in orderly manner, such as non-radiative decay, if they are to avoid damaging formation of O_2 radicals from excess reduction of ferredoxin (Farquhar *et al.*, 1989). This may occur as partial uncoupling of the thylakoid to

reduce the increased pH gradient caused by the trans-thylakoid proton gradient, resulting in photoinhibition. It may also occur through the xanthophyll cycle, which has been proposed because the amount of zeaxanthin present correlates with a measure of non-radiative dissipation of energy by photosystem II (Demmig *et al.*, 1987). This non-radiative dissipation of light converts the excess energy into heat. Quanta of blue (400 nm) or red (700 nm) light contain 0.30 and 0.17 MJ mol^{-1}, while the formation of NADPH and ATP require 0.22 and 0.33 MJ mol^{-1} respectively. Thus 9 mol of quanta needed to fix 1 mol CO_2 contain 1.54-2.69 MJ and regenerate 2.25 NADPH and 3 ATP, (2.25 x 0.22 + 3 x 0.03 = 0.59 MJ) or 22-38% efficiency. The remaining 62-78% is lost as heat (Farquhar *et al.*, 1989).

The response of CO_2 assimilation to photon flux describes a curve or curvilinear progression, consisting of two distinct phases. An initial linear phases where CO_2 assimilation increases proportionally to the increase in photon flux, passing through the light compensation point, and a progressive decrease in the slope of the curve ($\delta A/\delta Ci$) with an increase in photon flux, which reaches a plateau - at which point the assimilation rate is light saturated. The curve can be approximated to that of a modified form of the Michaelis-Menton hyperbola, (Dale and Causton, 1990) described in the equation below

$$A = \frac{A_{max} - Q}{k \times Q} - Rd$$

where; A = net CO_2 assimilation ($\mu mol\ m^{-2}s^{-1}$)

A_{max} = the maximum rate of net CO_2 assimilation

Q = photon flux density ($\mu mol\ m^{-2}s^{-1}$)

k = the value of photon flux (Q) at which $A = \frac{A_{max}}{2}$

Rd = the rate of respiration occurring in the light (μmol $m^{-2}s^{-1}$)

The initial slope of the light response curve (α) may be described as the apparent maximum quantum yield. The qualification "apparent" is important here, since the estimate is based on incident light and not absorbed light, i.e. true maximum quantum yield (ϕ) is obtained only if reflected and transmitted light are taken into account.

Quantum yield (Q) is the efficiency of light utilisation by photosynthesis, the number of moles of CO_2 fixed per mole quanta absorbed by the leaf. Since light becomes of less importance as a factor limiting photosynthesis with increases in photon flux, the maximum quantum yield may only be measured at low light intensities where photosynthesis is strictly limited by light and not other factors such as Rubisco regeneration, RuDP regeneration and the availability of orthophosphate (von Caemmerer and Farquhar, 1981), using thw following equation:

$$Q = \frac{A}{PFD}$$

Individual leaves of many C_3 plants are unable to utilize photosynthetically active light above 500 μmol $m^{-2}s^{-1}$ efficiently. Thus the light saturated assimilation rate may be regarded as a measure of the photosynthetic capacity of the leaf, under the particular environmental or experimental conditions.

Temperature responses

Temperature is prominent among the major ecological variables that determine the natural distribution of plants. Habitats occupied by higher plants show dramatic differences in the prevailing temperature during the period of active growth, ranging from near freezing in the arctic and alpine regions to above 50°C in some dry deserts. Moreover, in many habitats the same individual may be subjected to a very wide seasonal variation in temperature regime and even diurnal temperature fluctuation can be considerable.

Like most other physiological processes, photosynthesis is strongly affected by temperature. In most plants, changes in photosynthetic capacity affected by changes in temperature are reversible over a considerable range (commonly 10-35°C), but exposure to temperatures below or above this range often causes irreparable injury to the photosynthetic system. Alexandrov, 1977, and Goltsev *et al.* (1987) have demonstrated that high temperature increases the electrophoretic mobility of thylakoid membranes. In air, photosynthesis is poised between limitation by Rubisco (predominantly at lower than ambient CO_2 partial pressures) and limitation by the rate of RuDP regeneration (which predominates at higher partial pressures of CO_2) (Farquhar *et al.*, 1980). The rate of RuDP regeneration is governed by the rate of electron transport, the rate at which carbon is removed from the Calvin cycle and at which orthophosphate is recycled by product synthesis, and by the occurrence of photorespiration. Growing evidence supports the view that the phosphate status of photosynthetic systems is important in determining the temperature response of photosynthetic CO_2 assimilation in the range of 2-30°C. First, in isolated chloroplasts the orthophosphate optimum increases at low temperature (Leegood and Walker, 1983; Mächler

et al., 1984). Second, leaves illuminated at low temperatures, using plants grown at higher temperatures, tend to exhibit an inhibition of photosynthesis by 2% O_2 (Jollife and Tregunna, 1968, 1973; Cornic and Louason, 1980; McVetty and Canvin, 1981). This lack of stimulation by 2% O_2 is due to the system being phosphate limited (Harris *et al.*, 1983; Leegood and Furbank, 1986; Sharkey *et al.*, 1986). Third, low temperatures promote oscillations in both chlorophyll fluorescence and CO_2 assimilation (Sivak and Walker, 1986; Leegood and Furbank, 1986), which are indicative of a limitation of *in vivo* phosphate under these conditions (Sivak and Walker, 1986).

In order to understand the underlying differences in the temperature dependence of photosynthesis, it is necessary to subdivide net CO_2 assimilation into its component processes and then to investigate the temperature dependence of each process separately.

Rubisco carboxylase/oxygenase

The enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (E.C. 4.1.1.39) catalyses two different reactions in the chloroplast stroma. It acts as a carboxylase with the substrates RuDP and CO_2 and as an oxygenase with the substrates RuDP and O_2. The former reaction results in the CO_2 uptake of photosynthesis whereas the latter results in mitochondrial CO_2 evolution, called photorespiration. Thus the rate of assimilation of CO_2 in a leaf depends on the rates of RuDP carboxylation and oxygenation. The ratio of carboxylation:oxygenation is determined by the partial pressures of the substrates CO_2 and O_2, and by the catalytic properties of the enzyme with respect to these substrates (Brooks and Farquhar, 1985).

Rubisco activity in intact leaves correlates with the rate of net CO_2 uptake over a wide range of light intensities (Kobza and Seemann, 1988). At light saturation, atmospheric CO_2 and growth regimes similar to those encountered in the field, photosynthesis can be simultaneously limited by both the capacity of RuDP regeneration and Rubisco activity (von Caemmerer and Farquhar, 1981; von Caemmerer and Farquhar, 1984; Evans and Terashima, 1988; Sage *et al.*, 1989). Short-term exposure to elevated partial pressures of CO_2 disrupts the balance between Rubisco, RuDP regeneration, and possibly orthophosphate regeneration (Sage *et al.*, 1989). In response, the capacity for those processes which are non-limiting at high CO_2 (RuDP carboxylation and RuDP regeneration) are regulated downwards so that they remain balanced with the limiting processes (orthophosphate limitation) (Sage *et al.*, 1988; Sharkey *et al.*, 1988). Short term exposure to elevated CO_2 causes the activation state of Rubisco to decline, regardless of whether orthophosphate regeneration of RuDP serves as the major limitation on photosynthesis (von Caemmerer and Edmondson, 1986; Sage *et al.*, 1988; Sage *et al.*, 1989). In intact of leaves C_3 plants, increasing temperature causes an increase in both the CO_2 compensation point and the inhibition of net photosynthesis by O_2 (Jackson and Volk, 1970; Jollife and Tregunna, 1973; Brooks and Farquhar, 1985). Such observations have led to the suggestion that the rate of photorespiration relative to the rate of photosynthesis increases with temperature. Two explanations for this increase have been offered. *In vitro* studies by Badger and Andrews (1974) and Laing *et al.* (1974) indicate that the kinetic properties of Rubisco change in such a way that the CO_2/O_2 specificity declines with temperature. Others authors have suggested that there is little effect of temperature on the CO_2/O_2 specificity and that the explanation lies in a change in the ratio of $[CO_2]/[O_2]$ dissolved in solution (Ku and Edwards, 1977).

Light activation of Rubisco has been demonstrated in leaves (Mächler and Nösberger, 1980; Perchorowicz *et al.*, 1981; Salvucci *et al.*, 1986; von Caemmerer and Edmondson, 1986) and intact chloroplasts (Bahr and Jensen, 1978; Heldt *et al.*, 1978). The light activation of Rubisco and the rate of CO_2 assimilation have been shown to proceed in tandem (Perchorowicz *et al.*, 1981; Salvucci *et al.*, 1986; von Caemmerer and Edmondson, 1986). Several enzymes involved in C_3 photosynthetic carbon metabolism in addition to Rubisco are also light activated, but unlike Rubisco these enzymes are activated by the ferredoxin/thioredoxin system (Buchanan, 1980). Rubisco, *in vivo*, is activated by the Rubisco activate system in an ATP-dependent process (Portis, 1990; Campbell and Ogren, 1990). Campbell and Ogren (1990) have demonstrated that associated with light activation of Rubisco is an apparent requirement for electron transport through PS I and the establishment of a trans-thylakoid pH gradient. The mechanism by which electron transport and the pH gradient are sensed and translated into a higher Rubisco activation state remains to be determined.

The regulation of photorespiration is determined by the rate of RuDP regeneration, the ratio of CO_2:O_2 in the chloroplast, and the amount and kinetic properties of the specific Rubisco. The magnitude of this rate is the subject of wide disagreement. It has been suggested that O_2 substitution for CO_2 in the Rubisco reaction accounts for about two-thirds of total O_2 inhibition of photosynthesis at normal atmospheric CO_2 concentrations, and photorespiratory CO_2 release accounts for the remaining third, which is equal to about 15% of the rate of net CO_2 fixation. In contrast, it has been suggested that the rates obtained underestimate

photorespiration caused by recycling of photorespiratory CO_2, and that photorespiratory CO_2 release may be as high as 50% of the rate of net photosynthesis (Zelitch, 1975; 1979)

It is well established that Rubisco may be regulated down in response to a decrease in light intensity below the photosynthetic light saturation point (Andrews and Lorimer, 1987; Woodrow and Berry, 1988; Salvucci, 1989; Sage *et al.*, 1990; Seemann *et al.*, 1990). In addition, Rubisco may be down regulated in response to increased partial pressure of CO_2 or decreased O_2 partial pressure (Schnyder *et al.*, 1986; Sage *et al.*, 1988; Sage *et al.*, 1989). As a result of this down regulation, absolute CO_2 assimilation rates are reduced at high partial pressures of CO_2, especially after long acclimation to high CO_2 (Sage *et al.* 1989). It is unclear whether the reduction in Rubisco activity results from reduced quantity of Rubisco protein *per se* or a decrease in the activity of the existing enzyme.

Water stress

Restricted water availability and the resultant development of water stress is a major factor in regulating the distribution and productivity of plants (Woodward, 1987). The nature and extent of the effects of water stress on plants are a function of the intensity and duration of the stress, as well as of the genetically determined capacity of species to cope with the environment (Chaves, 1991). It is well established that the rate of CO_2 assimilation in the leaves is depressed at moderate leaf water deficits or even before leaf water status is changed in response to a drop in air humidity (Lange *et al.*, 1971; Bunce, 1984) or in soil water potential (Davies and Sharp, 1981; Gollan *et al.*, 1986). In such cases stomatal control of CO_2 diffusion is the principal factor controlling photosynthesis. When the drought period

is lengthened, dehydration becomes more severe and changes may occur in metabolic functions (Kaiser, 1987) and/or whole plant behaviour (Schulze, *et al.*, 1987).

Given the limited water reserves in leaves compared to the potential rate of transpiration, the regulation of stomatal aperture to restrict damage to the tissues as a result of dehydration is of major importance for plants. Stomatal characters such as morphology, size, and distribution show large differences among species. However, only part of this variation is under heritable control since leaf developmental stage and environmental preconditioning exert a large influence on stomatal characteristics. On the other hand, the physiological control of stomatal aperture is presumably more important than size and frequency of stomata in determining stomatal conductance under water stress (Chaves, 1991). There is evidence which suggests that differences in stomatal response to water stress may in part be determined by genetic differences in the capacity to produce abscisic acid (ABA) (Quarrie, 1983). Quarrie and his co-workers have shown that genotypes of wheat selected from high ABA accumulation have a higher water use efficiency (WUE) in the field than low ABA genotypes (Quarrie and Lister, 1983; Innes *et al.*, 1984).

According to Wong *et al.* (1979) the strong correlation between stomatal conductance and photosynthetic rate represents an adjustment of stomatal conductance to match the intrinsic photosynthetic capacity. This interpretation agrees with the theoretical model of stomatal functioning proposed by Cowan and Farquhar (1977), so that an optimum balance between loss of water and CO_2 uptake may be maintained. Similarly, this observation would fit Farquhar and Sharkey's (1982) suggestion that stomata operate to keep the CO_2

concentration in the chloroplast close to the transition point from CO_2 to RuBP limitation of photosynthesis.

Farquhar *et al.* (1989) have suggested that the non-uniform stomatal closure under water stress might lead to an incorrect calculation of Ci.

$$Ci = Ca - \frac{1.6A}{g}$$

where; Ca = External partial pressure of CO_2

A = Net assimilation rate

g = Stomatal conductance

An overestimation of C_i occurs whenever some of the stomata are closed and A and g are non-linearly related. In these circumstances, for a given g, the average A is smaller than it would be if conductance was uniform throughout the leaf and, therefore Ci is overestimated (Terashima *et al.*, 1988 for review). However, for the purpose of this thesis, it is assumed that internal CO_2 partial pressure is consistent throughout the leaf and, that stomatal conductance is equivalent throughout the leaf.

Sensitivity of photosynthesis to water stress varies between plant species (Boyer, 1976a). Chaves (1991, *pers. comm.*) and Speer *et al.* (1988) have suggested that slowly imposed water stress may affect mesophyll photosynthesis at relative water contents higher than those which inhibit photosynthetic capacity in a rapidly applied stress. This suggestion has been confirmed by Jones (1973) where slowly applied water stress decreased both the initial slope of the CO_2 response curve and the maximal rate of photosynthesis in cotton.

Photosynthetic pigments

The photosynthetic pigments chlorophylls and carotenoids, together with sterols, prenylquinones, and prenols, belong to the group of isoprenoid plant lipids called prenyl lipids. Carotenoids as tetraterpenoids are simple prenyl lipids, the carbon skeleton made up of solely of isoprenoid units. Chlorophyll a and b are mixed prenyl lipids: they possess an isoprenoid phytyl chain which is bound to a non-isoprenoid porphyrin ring system. The possession of the phytyl side chain, which is esterified to the carboxyl group of the ring, gives the chlorophylls their lipid character.

The chlorophylls of higher plants, ferns, mosses, and green algae, as well as of the prokaryotic organism *Prochloron*, contain chlorophyll a as the major pigment and of chlorophyll b as an accessory pigment. Both chlorophylls are genuine component of the photosynthetic membranes and commonly occur in the ratio (a/b) of 3:1, but it is known that growth conditions can alter this ratio. The group of primary plants carotenoids can be divided into the oxygen-free carotenes and the xanthophylls, which contain oxygen in different forms. ß-carotene is the precursor of the xanthophylls (zeaxanthin, violaxanthin and xantherxantherin). The carotenoids of green photosynthetic active tissue which are needed for the photosynthetic function, are classified as primary carotenoids, whereas those of red fruits and flowers are termed secondary carotenoids.

Carotenoids are present in the thylakoid membranes of all eukaryotes, and it has been suggested for many years that they protect the photosynthetic apparatus against the destructive effects of light and O_2 (Krinski, 1971). One line of evidence supporting such a

role can be found in mutants of algae and higher plants which are deficient in carotenoid biosynthesis and which are viable only when maintained at low light (Krinski, 1971). Exposure of photosynthetic tissues to light in excess of that which can be utilized in photosynthesis results in photoinhibition, a reduction in photosynthetic activity, due primarily to a sustained reduction in the photochemical efficiency of PS II. This inhibition of photosynthetic activity by light and, in particular by the interaction of light and additional environmental stresses, has received increasing attention. Photoinhibition may result from three different processes working singly or in combination (Björkman and Demmig, 1987): (a) a decrease in the rate constant for photochemistry of PS II caused by damage to the PS II reaction centres; (b) an increase in the rate constant for non-radiative dissipation of excitation energy and (c) stomatal closure due to increased levels of endogenous ABA.

The details of the ABA biosynthetic pathway in higher plants has remained obscure even though mevalonic acid is known to be a precursor (Noddle and Robinson, 1969) and the stereochemistry of ABA formation has been shown to be identical to that of the carotenoids (Milborrow, 1983). It is not yet known whether ABA is derived directly from a cleavage product of a xanthophyll such as violaxanthin, or whether it is derived directly from a C-15 precursor such as farnesyl pyrophosphate. The initial suggestion that ABA may be derived from a xanthophyll came from observations that violaxanthin can be converted to the naturally occurring C-15 compound xanthoxin by photooxidation (Taylor and Smith, 1967; Taylor and Burden, 1970) and that radioactive xanthoxin was converted to ABA when fed to *Phaseolus* and *Lycopersicon* plants (Yamamoto and Higashi, 1978). Recently, there has been renewed interest in the possibility that xanthophylls may be ABA precursors in higher

plants. Li and Walton (1987) have demonstrated the incorporation of ^{14}C from $^{14}CO_2$, into both xanthophylls and ABA in water stressed *Phaseolus* and these results strongly suggest a role for xanthophylls as a major ABA precursor in water stressed leaves.

Aims and objectives

With the above in mind it was decided to investigate the gas exchange responses of two cultivars of *Hordeum vulgare* to some environmental factors:

The first objective was to determine the influence of light intensity on the rates of net CO_2 assimilation at different temperatures intervals. Results from this study would be used to determine the optimum temperature for each cultivar. Further, these results would be used to elucidate any difference that may exit between the two cultivars in their specific responses.

The second objective was to determine to degree to which stomata limit net CO_2 assimilation in both cultivars, and to establish to what extent temperature effects this limitation.

The third objective was to determine the effects of temperature and light intensity to short-term exposure to four different concentrations of CO_2.

The fourth and last objective was to determine the influence of water stress on the levels of photosynthetic pigments (chlorophylls and carotenoids) and the concomitant change in the rate of gas exchange over a period of twenty days.

CHAPTER 2

MATERIALS AND METHODS

Plant material

Seeds of *Hordeum vulgare* L. cv. Dayan and cv. Clipper were obtained as a gift from Mr. Koos van der Linde of Sensako, Malmesbury, Cape Province. Seeds were soaked for 2 hours in tap water and then sown onto vermiculite in 20 cm deep plastic pots.

Plants used for temperature and CO_2 response studies were germinated and grown in an EF-7 Conviron (Controlled Environments Ltd., Winnipeg, Canada) at 22.5°C, 500 ± 24.4 μmol $m^{-2}s^{-1}$ light intensity at plant height with a 10 hour photoperiod, and 55% relative humidity on a nutrient free medium. The red:farred (660:730 nm) light ratio in the Conviron was 1.9:1 (± 0.38). These plants were watered with 10% Hoaglands solution (Hoagland and Arnon, 1950; Appendix G) every two days, to ensure a full complement of nutrients and water supply. All experiments were conducted on plants that were 14-19 days old.

Plants used in the water stress investigations were grown in a Phytotron (Cleveland, RSA) at 22.5°C, a light intensity of 1318,33 ± 6.24 μmol $m^{-2}s^{-1}$ at plant height with a 10 hour photoperiod, and 50-60% relative humidity. The red:farred (660:730 nm) light ratio was 4.55:1 ± 0.04. These plants were watered with tap water every day, and after seven days the plants were divided into two groups: a control group and a stress group. The plants in the control group received water every day, whilst those in the stress group received no further water for the duration of the study.

Gas exchange measurements (See Figure 1)

Two calibrated ADC 225 Mk III CO_2 IRGAs'(Analytical Development Co. (ADC), Hoddesdon, UK) were set up for analysis in absolute mode and in open circuit. Air was supplied via a positive pressure buffer drum, fed from outside the laboratory by a high pressure pump. The air was then passed through an acidified thermoregulated-humidifier. Following humidification, the wet air was passed though a 1M H_3PO_4 acid ice-trap, to regulate the relative humidity of the air to 30-35%. The relative humidity of the air entering the cuvette was maintained at 30-35% so that additional water added to the air as a result of transpiration from the leaf in the cuvette would not increase the relative humidity to higher than 70-80%. This was necessary as the instrumentation could not accurately measure relative humidity above 85%. The thermoregulated-humidifier and ice-trap were acidified to prevent CO_2 diluting into solution. For experiments which required dry bottled gas obtained from Fedgas (Alrode, RSA), the gas was first passed through an ADC Gas Diluter (Model 006) to selectively scrub CO_2 from the gas, and then through an ADC Water Vapour Generator to humidify the gas to 30-35% relative humidity.

The humidified air was then passed through the first ADC Mk III IRGA or 'reference IRGA', and then to the first in-line thermohygrometer (Hanna Model HI 8564, Hanna Co., Spain), which measured the relative humidity and temperature of the air before it entered into the leaf chamber. The glass leaf chamber was encased in a thermostatically regulated water-jacket. The flow rate of air through the chamber was maintained at 200ml min^{-1}. On exiting the leaf chamber the air was passed through a second thermohygrometer (Hanna Model HI 8564, Hanna Co., Spain), and the relative humidity measured again. The differential value

between the relative humidities of the air leaving the leaf chamber and that entering the leaf chamber is equated to transpiration, which was calculated as mmol $m^{-2}s^{-1}$. The thermohygrometers were calibrated using an HI 7101 LiCl/NaCl calibration kit (Hanna Co, Spain). During the course of pilot investigations a residual cross-sensitivity of the CO_2 analyzers to water vapour was found, despite the

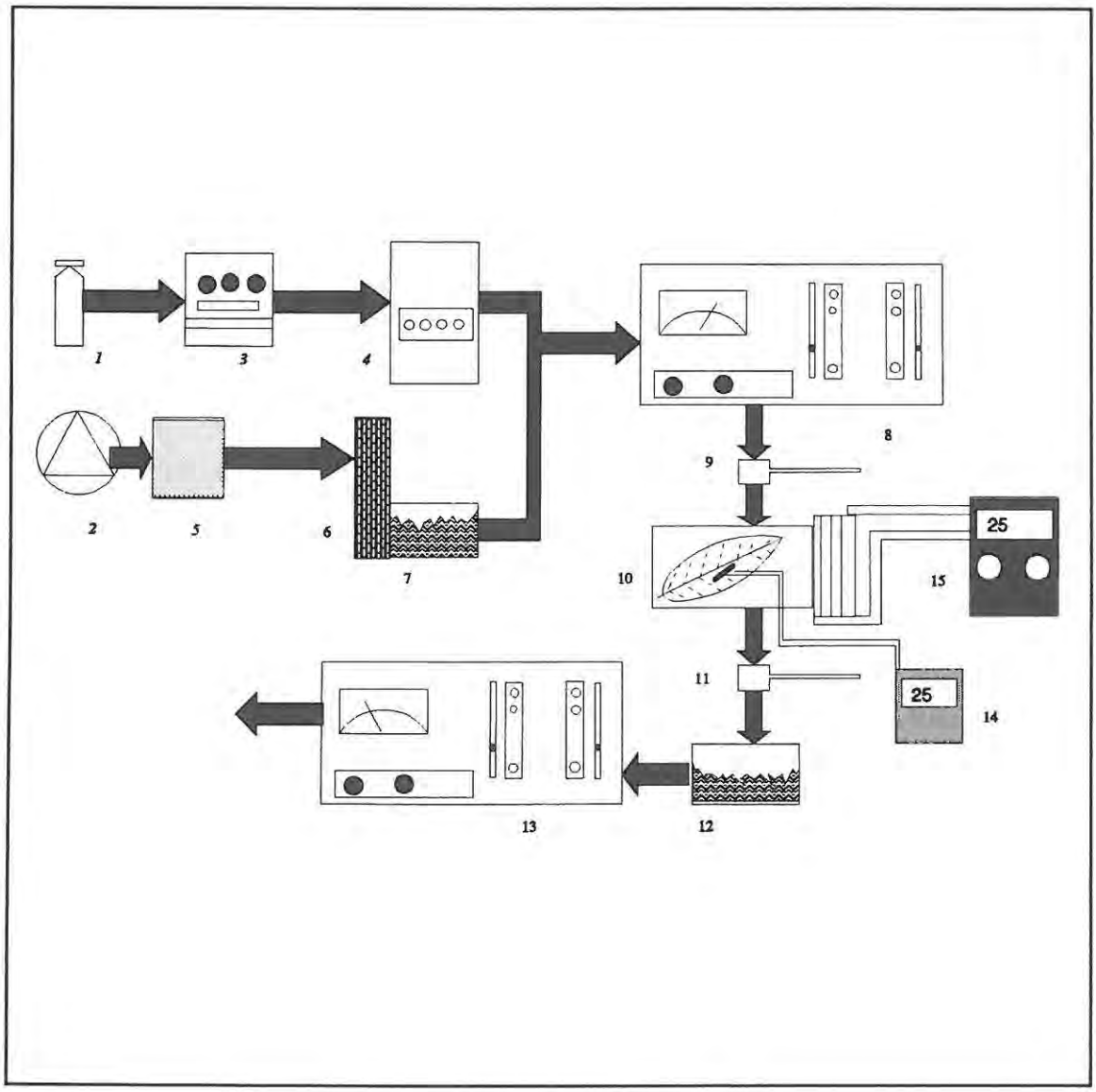

Figure 1.1. Laboratory systems setup. 1. Bottled Gas Supply; 2. External Air Supply; 3. ADC Gas Diluter; 4. ADC Water vapour generator; 5. Buffer drum; 6. Acidified Humidifier; 7.Acidified Ice-trap; 8. Reference IRGA; 9. Reference RH/Air Temperature Thermocouple; 10. Water-jacketed Leaf Chamber; 11. Analysis RH Thermocouple; 12. Acidified Ice-trap; 13. Reference IRGA; 14. Leaf Temperature Thermocouple; 15. Leaf Chamber Heat Sink. (See text for explanation)

optical interference filters in the ADC Mk III IRGAs', which are installed to reduce this cross-sensitivity. The sensitivity to water vapour depended on the partial pressure of CO_2 in the air stream such that in CO_2 free air there was no sensitivity to water vapour. However at high CO_2 partial pressures, changing the water vapour content in the analysis cell of the IRGA resulted in an increase in the differential output signal. With a known input of water vapour the resultant error of the differential output can be calculated. The error was generally small, but at high transpiration rates and high ambient CO_2 pressure the assimilation rate can underestimated by approximately 5%. Because of the fluctuating input humidity and partial pressure of CO_2 (both bottled and atmospheric), the data in this thesis have not been corrected for this effect. However to reduce the effect of this error, the airstream was passed through a second acidified ice-trap, before entering the second IRGA, or 'analysis IRGA'. This ice-trap removed excess water vapour reducing the relative humidity of the air stream so that it approximated that of the air before entering the reference IRGA.

Boundary layer resistance

The boundary layer resistance of the chamber was previously determined according to the procedure described by Parkinson (1985), whereby a double layer of filter paper of known area, moistened with distilled water and supported within a brass wire frame, was placed inside the cuvette. The filter paper was cut to approximate leaf shape. A K/J type thermocouple was placed inside the two pieces of filter paper and thermocouple voltages measured using a Fluke 51 K/J Thermometer (John Fluke, MFG Co. Ltd., Everett, Washington, USA). Magnesium perchlorate ($Mg(ClO)_4$) dried air was then passed into the cuvette at a flow rate of 200ml min^{-1}. The humidity of the air leaving the leaf cuvette was

determined using a previously calibrated thermohygrometer (Hanna Model HI 8564, Hanna Co., Spain). All measurements were made at 25°C. After the filter paper temperature had stabilized, the temperature was recorded together with the cuvette air temperature, and air flow rate. The boundary layer resistance was then calculated using the following equation,

$$r_b = \frac{[(\chi_f - \chi_o) / (\chi_o - \chi_i)]}{S/W}$$

where, r_b = boundary layer resistance;

χ_i = humidity of air entering the cuvette

χ_o = humidity of air leaving the cuvette

χ_f = saturation humidity at the filter paper temperature

S = projected area of filter paper

W = mass flow rate of air

The boundary layer was calculated at 0.1299 ± 0.000376.

Light source

Actinic light was provided by a 400 watt high pressure sodium lamp (Phillips, RSA). This lamp has spectral qualities similar to sunlight, a maximum light intensity of 2800 μmol $m^{-2}s^{-1}$ and an average red:farred (630:730 nm) ratio.of 0.67 ± 0.06. The high heat load on the lamp itself was removed by air conditioning. Infrared radiation produced by the Son-T and the deleterious effects associated with infrared radiation were removed by the water-jacket surrounding the glass cuvette.

Temperature measurement

Leaf temperature was measured with a K/J type thermocouple attached to the abaxial surface of the leaf inside the cuvette, and the thermocouple voltage measured using a Fluke 51 K/J Thermometer (John Fluke, MFG, Co. Ltd., Everett, Washington, USA).

Gas lines

Butyl rubber tubing was used for all gas circuits, except those inside the IRGA's which were stainless steel. Butyl rubber has a low water absorption and permeability factor (Bloom *et al.*, 1980) All gas lines were 0.64 cm in internal diameter, and all gas lines were kept as short as possible to reduce the total void volume.

Chlorophyll and carotenoid extraction

Immediately after gas exchange studies approximately 3g of leaf tissue was used for pigment extraction. During all steps care was taken to minimize photooxidation by light. The leaf tissue was homogenized in 15 cm^{-3} of 80% acetone with 2g of acid washed sand. The supernatant containing the extracted pigments was removed and the tissue extracted again until the tissue was white in colour. The supernatants from each extraction were combined and a 5 cm^{-3} aliquot used to read the specific absorbances in a Spectronic 20 colorimeter. The chlorophyll *a*, chlorophyll *b*, total chlorophyll (*a*+*b*), and total carotenoid concentration determined according to Lichtenthaler (1987; 1991, *pers.commun.*). The formulae are as follows:

$$C_a = 12.25A_{663.2} - 2.79A_{646.8}$$

$$\text{chlorophyll } a \text{ content} = \frac{C_a}{fw}$$

$$C_b = 21.50A_{646.8} - 5.10A_{663.2}$$

$$\text{chlorophyll } b \text{ content} = \frac{C_b}{fw}$$

$$C_{x+a} = \frac{1000A_{470} - 1.82C_a - 85.02C_b}{198}$$

$$\text{total carotenoid content} = \frac{C_{x+c}}{fw}$$

where fw is the fresh weight of tissue in grams.

Determination of relative leaf water content

Relative water content is a measure of the actual water content of a tissue with reference to the content of water in the tissue if it were fully hydrated (Bennett, 1990). RWC content was determined according to Bennett (1990). The fresh weight of excised leaf tissue was determined immediately after gas exchange studies. The excised tissue was then placed into pure water and allowed to attain full turgidity for 2 hours in low light. After two hours the tissue was dried on tissue paper and re-weighed. The tissue was then oven dried at 70°C overnight and re-weighed. Relative water content is then expressed as a percentage:

$$\%RWC = \frac{freshw. - dryw.}{turgidw. - dryw.} \times 100$$

where, RWC = Relative water content

freshw. = Fresh weight (g)

dryw. = dry weight (g)

turgidw. = turgid weight (g)

Recording of data

All measure were recorded in triplicate and all experiments were repeated three time. Thus the results presented here are the mean of nine readings.

CHAPTER 3

LIGHT AND TEMPERATURE RESPONSES[1]

Introduction

Changes in the rate of photosynthetic carbon assimilation that are occasioned by changes in environmental parameters such as light and temperature result in factors that regulate photosynthesis and require a redistribution of control between the reactions of electron transport, CO_2 assimilation and whole product synthesis. For optimal CO_2 assimilation the interaction of the various environmental factors must favour CO_2 assimilation. In C_3 plants light intensity and temperature are two of the major factors in this interaction. In this chapter the gas exchange responses to light and temperature of *Hordeum vulgare* L. cv. Clipper and cv. Dayan are investigated at ambient CO_2 concentration.

Results and discussion

Temperature

Figure 3.1. illustrates the response rates of net CO_2 assimilation for cv. Clipper, between 20°C and 30°C. The temperature at which the net CO_2 assimilation rate was highest (20.64 $\mu mol.m^{-2}s^{-1}$) was 25°C, at a light intensity of 1930 $\mu mol\ m^{-2}s^{-1}$. At light intensities below 500 $\mu mol.m^{-2}s^{-1}$, the light limiting part of the response curve, the net assimilation rate was highest at 30°C, and this is due to the higher apparent quantum yield of 0.051 $mol.mol^{-1}$, (Table 3.1.). Figure 3.2. illustrates the light response curves for net CO_2 assimilation for cv. Dayan at different temperatures. The highest rate of net CO_2 assimilation ($24.30 \pm 0.33\ \mu mol.m^{-2}s^{-1}$) was at 22.5°C, at a light intensity of 1104 $\mu mol.m^{-2}s^{-1}$. Net CO_2 assimilation at 30°C was

[1] Data for this chapter are tabulated in: Appendix A - cv. Clipper. Appendix B - cv. Dayan

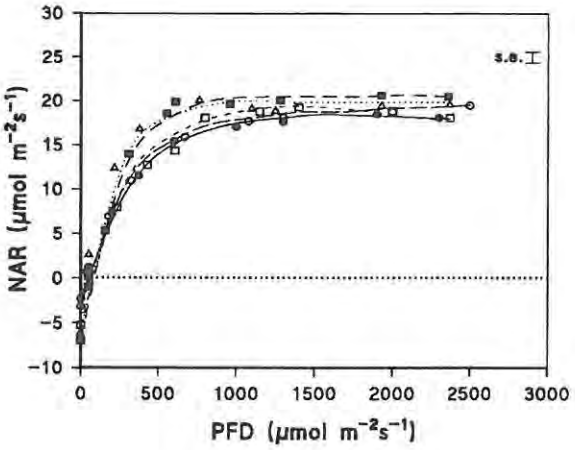

Figure 3.1. Net CO_2 assimilation (NAR) responses to light intensity and temperature in *H. vulgare* cv. Clipper at ambient CO_2 concentration (371 μmol.m^{-2}s^{-1}). 20°C (●); 22.5°C (○); 25°C (■); 27.5°C (□); 30°C (△).

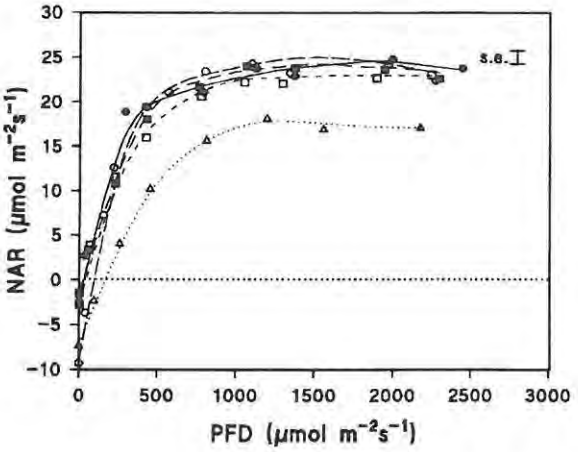

Figure 3.2. Net CO_2 assimilation (NAR) responses to light intensity and temperature in *H. vulgare* cv. Dayan at ambient CO_2 concentration (371 μmol.m^{-2}s^{-1}). 20°C (●); 22.5°C (○); 25°C (■); 27.5°C (□); 30°C (△).

markedly reduced for cv. Dayan. Reduction of photosynthesis at high temperatures is considered by most investigators to be as a results of conformational changes of proteins and their disposition in membranes (Berry and Björkman, 1980; Venediktov and Krivoshejeva, 1984; Goltsev *et al.*, 1987). In both cultivars the inflection point of the light response curves, the region between limitation by light and limitation by Rubisco, was in the region of 500 $\mu mol.m^{-2}s^{-1}$ PFD (Figures 3.1. and 3.2.). The exception was the response curve of cv. Dayan at 30°C, where the inflection occurred at a slightly higher light intensity (700-800 $\mu mol.m^{-2}s^{-1}$).

Light intensity

At low light intensities both cultivars exhibit the typical crossing over of the response curves due to the different light compensation points reached at each of the temperatures. This has also been found by several other investigators (von Caemmerer and Farquhar, 1981; Kirschbaum and Farquhar, 1984). This crossing over of the response curves has also been attributed to increases in the rate of RuBP regeneration at higher temperatures (Labate and Leegood, 1988).

The results shown in Figures 3.1. and 3.2. shows little evidence of a reduction in net CO_2 assimilation at high light intensities, with the exception of some degree of photoinhibition at very high light intensities for cv. Dayan. This lack of photoinhibition at high light intensities, which is a common characteristic of C_3 plants, is due to the growth conditions of the plants, where all nutrients were supplied in the water. A similar effect was found by

Labate and Leegood (1988) when these authors grew *Hordeum vulgare* L. cv. Sonja in vermiculite and watered with nutrient solution.

Table 3.1. Low light intensity apparent quantum use efficiencies (mol.mol^{-1}) for *Hordeum vulgare* cv. Clipper and cv. Dayan at five leaf temperatures.

Temp °C	Quantum yield (mol.mol^{-1})	
	Clipper	Dayan
20.0	0.030 ± 0.005	0.07 ± 0.002
22.5	0.036 ± 0.003	0.052 ± 0.006
25.0	0.039 ± 0.006	0.053 ± 0.004
27.5	0.032 ± 0.002	0.054 ± 0.003
30.0	0.051 ± 0.005	0.016 ± 0.001

The occurrence of photoinhibition at these very high light intensities, even when the plants are grown under non-stressed conditions, suggest that cv. Dayan favours a lower light environment than cv. Clipper.

At light intensities close to compensation point, the maximum apparent quantum use efficiency of cv. Clipper, was 0.051 mol.mol^{-1} at 30°C, and for cv. Dayan, 0.07 mol.mol^{-1} at 20°C, (Table 3.1). Ehleringer (1978) has attributed reduction of apparent quantum use efficiency of C_3 plants directly to temperature, in CO_2 free air. Monson *et al.* (1982) have shown that apparent quantum use efficiency of C_3 plants to be temperature dependent in normal atmospheric air. Ludlow (1981) has questioned the validity of assuming equal relationships between the apparent quantum use efficiency and leaf temperature for monocotyledons and dicotyledons, as actual quantum use efficiency can not be measured.

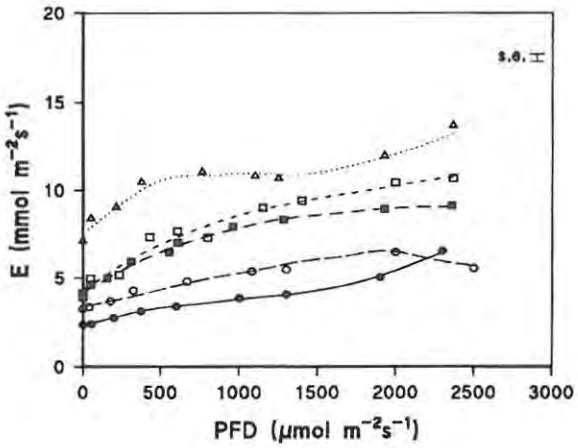

Figure 3.3. Rate of transpiration (E) (mmol.m^{-2}s^{-1}) to light and temperature for *H. vulgare* cv. Clipper at ambient CO_2 concentration (371 μmol.m^{-2}s^{-1}). 20°C (●); 22.5°C (○); 25°C (■); 27.5°C (□); 30°C (△).

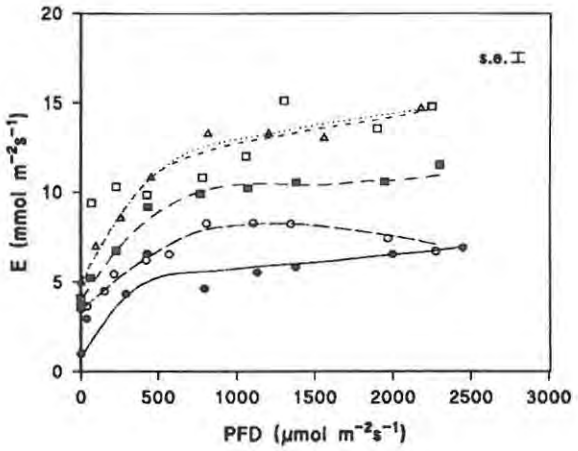

Figure 3.4. Rate of transpiration (E) (mmol.m^{-2}s^{-1}) to light and temperature for *H. vulgare* cv. Dayan at ambient CO_2 concentration (371 μmol.m^{-2}s^{-1}). 20°C (●); 22.5°C (○); 25°C (■); 27.5°C (□); 30°C (△).

Recently Chow *et al.* (1990), have suggested that changes in photosystem stoichiometry may compensate to correct for uneven absorption of light by the two photosystems induced by temperature.

The results of this study indicate that with increasing temperature, apparent quantum use efficiency increases for cv. Clipper and decreases for cv. Dayan. This has important implications for growth in low light, high temperature environments, in that cv. Dayan would be less competitive than cv. Clipper in such environments.

The highest light compensation point achieved by cv. Clipper was obtained at 25°C, followed by 30, 27.5, 22.5°C and the lowest compensation point at 20°C (Figure 3.1). For cv. Dayan, the highest light compensation point was achieved at 30°C followed by 22.5°C and then 20, 25, and 27.5°C with the same compensation value (Figure 3.2). The compensation points for cv. Clipper were all close together (i.e. had a low range), whereas the range for cv. Dayan was wider. The light compensation point is symptomatic of the rate of respiration, as it represents the point at which the rate of net CO_2 assimilation is in equilibrium with the rate of CO_2 evolution by respiration. From the results presented here it is clear that the light compensation point is not drastically affected by the range of temperatures examined in these two cultivars of barley, except for cv. Dayan at high temperature.

Transpiration

Initially transpiration increased with increasing light intensity in both cultivars investigated (Figure 3.3. and 3.4.). However, at high light intensities the rate of transpiration decreased

at 22.5°C in both the cultivars. Transpiration at 22.5°C in cv. Clipper was reduced at light intensities above 1950 $\mu mol.m^{-2}s^{-1}$, and in cv. Dayan above light intensities of 1200 $\mu mol.m^{-2}s^{-1}$. Sharkey (1984) has shown that high rates of transpiration from leaves results in a reduced mesophyll capacity for assimilation of CO_2, and has suggested that the effect of transpiration induced stress on CO_2 assimilation is similar to the effects observed after withholding water. Sharkey (1984) has also proposed that large water potential gradients within the areoles of leaves, between xylem and the sites of evaporation, are responsible for the decline in photosynthesis. Therefore the large decline in CO_2 assimilation of cv. Dayan at 30°C could be partly as a results of a higher transpiration rate at high light intensities.

Rubisco

The rate of carboxylation of Rubisco for cv. Clipper showed little variation except at very high light intensities and light intensities between 450-900 $\mu mol.m^{-2}s^{-1}$ (Figure 3.5.). The highest overall rate of carboxylation was achieved at 25°C whilst the lowest rate was achieved at 30°C. For cv. Dayan there was a larger range of carboxylation rates over the five temperatures investigated (Figure 3.6.). The highest carboxylation rate for cv. Dayan was reached at 20°C, and the lowest at 30°C. In all cases there was a slight depression in carboxylation rate of Rubisco at very high light intensities. It has been suggested that changes in the kinetic parameters of oxygenase relative to carboxylase and changes in the CO_2/O_2 solubility ratio with increasing temperature, affects the rate of carboxylation of Rubisco (Badger and Andrews, 1974; Laing *et al.*, 1974; Ku and Edwards, 1977; Hall and Keys, 1983; Jordan and Ogren, 1984).

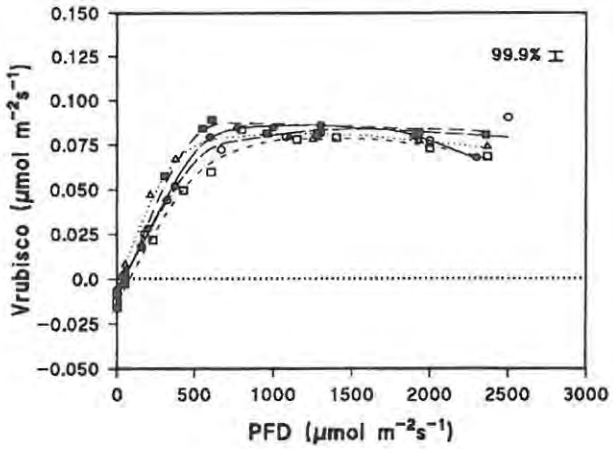

Figure 3.5. Rate of carboxylation of ribulose-1,5-bisphosphate carboxylase/oxygenase for *H. vulgare* cv. Clipper to light intensity and temperature, at ambient CO_2 concentration (371 μmol.m^{-2}s^{-1}). 20°C (●); 22.5°C (○); 25°C (■); 27.5°C (□); 30°C (△).

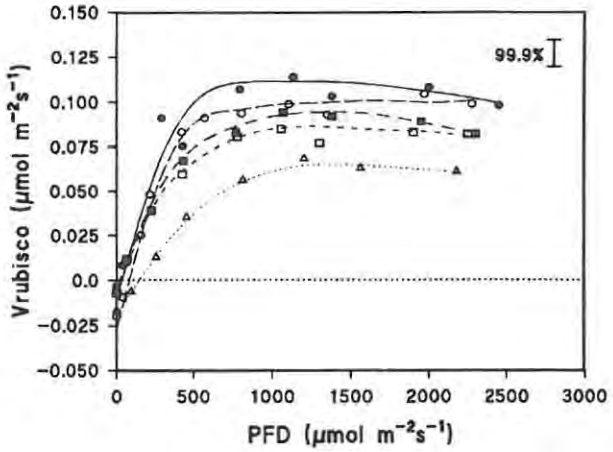

Figure 3.6. Rate of carboxylation of ribulose-1,5-bisphosphate carboxylase/oxygenase for *H. vulgare* cv. Dayan to light intensity and temperature, at ambient CO_2 concentration (371 μmol.m^{-2}s^{-1}). 20°C (●); 22.5°C (○); 25°C (■); 27.5°C (□); 30°C (△).

Water use efficiency

High light intensity markedly reduced the WUE at 20°C, and to lesser extent at 25, 27.5, and 30°C for cv. Clipper (Figure 3.7). A similar trend was found for the WUE of cv. Dayan (Figure 3.8). For cv. Clipper, WUE was highest at 20°C (0.0046 $mol.mol^{-1}$, 600 $\mu mol.m^{-2}s^{-1}$) and was lowest 30°C, at which a maximum of 0.0018 $mol.mol^{-1}$ at both 765 and 110 $\mu mol.m^{-2}s^{-1}$. WUE was highest for cv. Dayan at 793 $\mu mol.m^{-2}s^{-1}$ PFD and 20°C at 0.0046 $mol.mol^{-1}$, and lowest at 30°C where the maximum WUE achieved was 0.0014 $mol.mol^{-1}$ at 1202 $\mu mol.m^{-2}s^{-1}$. In all cases the WUE initially increases with light intensity until ± 500 $\mu mol.m^{-2}s^{-1}$ above which it maintained a plateau and then started to decline with increasing light intensity. At high temperatures (25, 27.5 and 30°C) cv. Dayan has a lower WUE than cv. Clipper. However at the two lower temperatures the WUE of both cultivars is comparable. From these results it is clear that at lower temperatures both cultivars are more efficient in water usage.

Stomatal conductance

In cv. Clipper, stomatal conductance increased with increasing temperature at light intensities below 1000 $\mu mol.m^{-2}s^{-1}$ (Figure 3.9). At light intensities between 1000 and 2000 $\mu mol.m^{-2}s^{-1}$ stomatal conductance at 30°C was exceeded by the rate of conductance for 25 and 27.5°C. At light intensities in excess of 2000 $\mu mol.m^{-2}s^{-1}$ the rate was highest at 20°C followed by 30°C, 27.5, 25 and lastly 22.5°C. The highest stomatal conductance was reached at 2300 $\mu mol.m^{-2}s^{-1}$ and was 618.6 $\mu mol.m^{-2}s^{-1}$ at 20.0°C. This high stomatal conductance is due an increase in the transpiration rate which occurred without drastic change in the net CO_2 assimilation rate (Figure 3.1 and 3.3). However, the overall stomatal conductance at

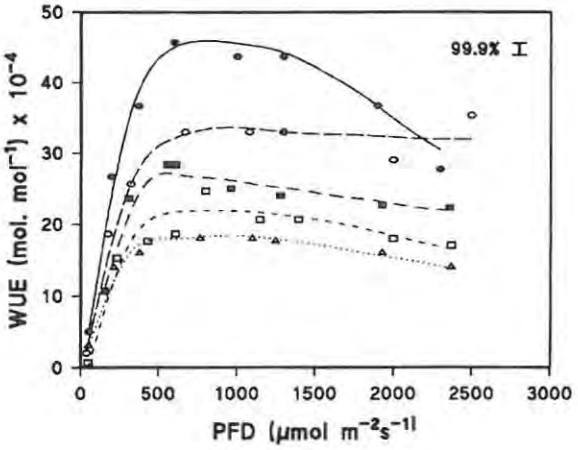

Figure 3.7. Water use efficiency (WUE) (mol.mol^{-1}) for *H. vulgare* cv. Clipper to light and temperature, at ambient CO_2 concentration (371 µmol.m^{-2}s^{-1}). 20°C (●); 22.5°C (○); 25°C (■); 27.5°C (□); 30°C (△).

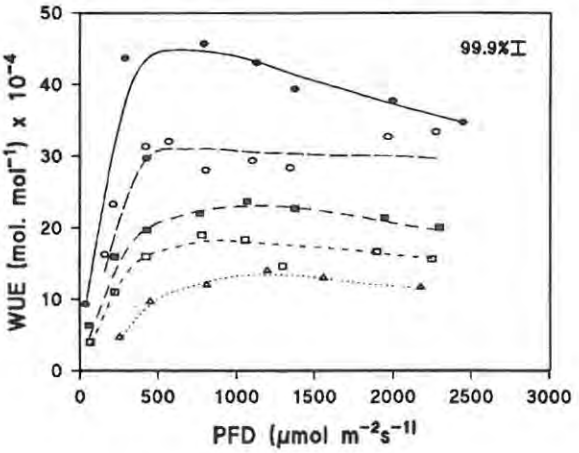

Figure 3.8. Water use efficiency (WUE) (mol.mol^{-1}) for *H. vulgare* cv. Dayan to light and temperature, at ambient CO_2 concentration (371 µmol.m^{-2}s^{-1}). 20°C (●); 22.5°C (○); 25°C (■); 27.5°C (□); 30°C (△).

20°C was lower than that recorded at the other temperatures. The stomatal conductance responses for 22.5, 25, and 27.5°C all followed similar patterns.

The stomatal conductance for cv. Dayan increased with increasing light and temperature, except at high light intensities at 22.5°C where a substantial drop occurred (Figure 3.10). The well documented effect of changes in atmospheric humidity on stomata (Wong, *et al.*, 1979; Bradford, *et al.*, 1980; Beyschlag, *et al.*, 1990; Inoue, *et al.*, 1990) would have had little effect on the changes in stomatal conductivity as throughout all experiments the relative humidity was maintained between 30-35%. Therefore the calculated changes in stomatal conductance result from changes in the transpiration:assimilation ratio, and are in accordance with the views put forward by Raschke (1970), Cowan and Farquhar (1977), Farquhar (1978), Hall and Schulze (1980).

Conclusion

The experiments reported here demonstrate that net CO_2 assimilation is dependent on temperature and light in both cultivars of barley (Figure 3.1. and 3.2.). The temperatures at which net CO_2 assimilation was consistently highest were 25 and 22.5°C for cv. Clipper and cv. Dayan respectively. The maximum apparent quantum use efficiency for the two cultivars was realised at 30°C for cv. Clipper and at 20°C for cv. Dayan (Table 3.1). Elevated temperature severely reduced assimilation at 30°C in cv. Dayan, possibly as a result of an inhibition of enzyme carboxylation due to a change in the solubility ratio of CO_2:O_2, concomitant with partial conformational change of photosystem stoichiometry in the chloroplasts.

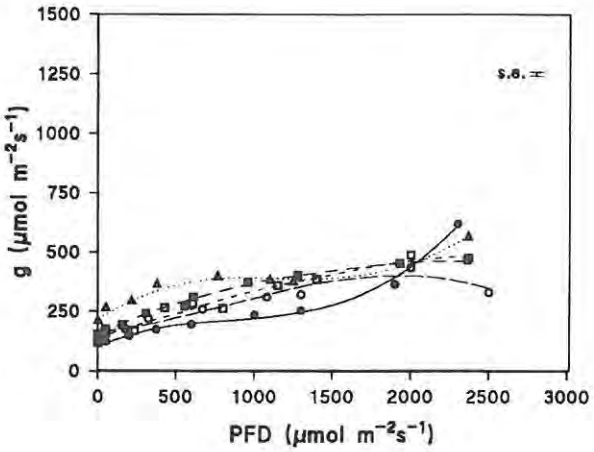

Figure 3.9. Stomatal conductances (g) (µmol.m^{-2}s^{-1}) for *H. vulgare* cv. Clipper to light intensity and temperature, at ambient CO_2 concentration (371 µmol.m^{-2}s^{-1}). 20°C (●); 22.5°C (○); 25°C (■); 27.5°C (□); 30°C (△).

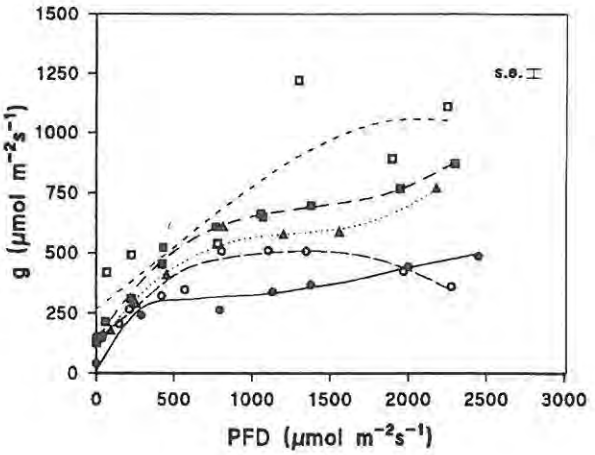

Figure 3.10. Stomatal conductances (g) (µmol.m^{-2}s^{-1}) for *H. vulgare* cv. Dayan to light intensity and temperature, at ambient CO_2 concentration (371 µmol.m^{-2}s^{-1}). 20°C (●); 22.5°C (○); 25°C (■); 27.5°C (□); 30°C (△).

It is well known that transpiration rates of C_3 plants increase with temperature as a mechanism to partially release the heat load of the leaf. This increase of transpiration with temperature was clearly demonstrated in this study, however the reason for the decline in transpiration at 22.5°C at high light intensities in both cultivars is not known. This decline may be associated with the growth temperature which was 22.5°C. The decrease in transpiration at 22.5°C had direct affect on decreased WUE at this temperature. Whereas WUE at high light intensities at the other temperatures decreased, the WUE at 22.5°C and high light intensities maintained an increase. The general pattern of WUE was that it declined with increasing temperature.

From these results it was decided that further studies on these two cultivars of barley would be carried out near their optimal temperatures for net CO_2 assimilation, i.e. 25°C for cv. Clipper and 22.5°C for cv. Dayan. However due to lack of growth facilities both cultivars had to be grown at 22.5°C as stated in Materials and Methods.

CHAPTER 4

STOMATAL LIMITATIONS AND TEMPERATURES

Introduction

Farquhar and Sharkey (1982) developed a simple method of separating stomatal and mesophyll limitations using the response of the CO_2 assimilation rate and the mole fraction of CO_2 at the mesophyll cell surface. Assimilation rate measured at normal atmospheric CO_2 concentration, is subtracted from the rate of assimilation that would occur if there was no stomatal limitations (Figure 4.1.). The relative limitation which stomata impose may then be calculated:

$$I = \frac{A_o - A}{A_o} \qquad (4.1.)$$

I is the proportionate decrease in assimilation that may be attributed to the stomata and other gas phase limitations. *I* has no units.

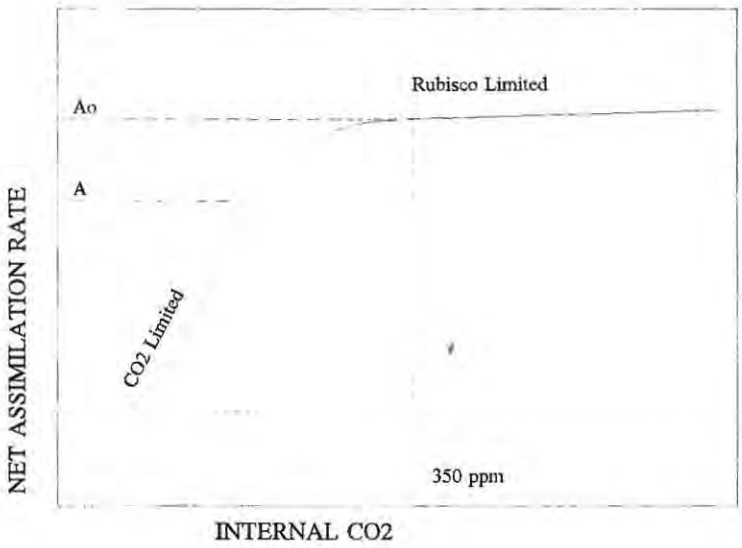

Figure 4.1. A generalised response of CO_2 assimilation rate to internal CO_2 mole fraction. Ao is the rate at which CO_2 assimilation would proceed in the absence of any stomatal limitations; A is the actual rate of CO_2 assimilation. (Pammenter, *pers. commun.*, 1989).

Results and discussion

The data in Table 4.1. shows that at the optimum temperature for net CO_2 assimilation, the relative stomatal limitations were lowest for both cultivars. For cv. Clipper, the relative stomatal limitation at 25°C was 0.280, and for cv. Dayan, at 22.5°C, was 0.028. Above and below the temperature optimum of both cultivars the relative rate of stomatal limitation to net CO_2 assimilation increases. Stomatal limitations were highest in cv. Clipper at 27.5°C. The range of the relative stomatal limitations for cv. Clipper was 0.051. A much larger range existed for cv. Dayan, 0.290. This larger range implies that stomata may play a more direct role in the regulation of net CO_2 assimilation in cv. Dayan. This may be explained in that at the optimal temperature the relative stomatal limitation is near to zero, whilst at non-optimal (high) temperatures when the trade off between CO_2 uptake for assimilation and H_2O efflux via transpiration favours the loss of H_2O. Stomatal resistance is then increased to reduced excess loss of water which, would otherwise result in desiccation of the leaf. In cv. Clipper this regulatory effect of stomata occurs to a lesser degree, as the range of the relative stomatal limitations is less.

Table 4.1. Relative limitations imposed on net CO_2 assimilation in cv. Clipper and cv. Dayan at five temperatures, by stomata and other gas phase limitations.

Temperature (°C)	cv. Clipper	cv. Dayan
20.0	0.290 ± 0.017	0.111 ± 0.010
22.5	0.312 ± 0.013	0.028 ± 0.011
25.0	0.280 ± 0.010	0.138 ± 0.010
27.5	0.331 ± 0.018	0.278 ± 0.012
30.0	0.291 ± 0.018	0.318 ± 0.011

In their model of stomatal limitations and photosynthesis, Farquhar and Sharkey (1982) have shown that there is an temperature optimum for net CO_2 assimilation which is dependent on CO_2 partial pressure and irradiance. Farquhar and Sharkey (1982) have also suggested that low temperatures reduce assimilation rate because of the reduced activity of Rubisco and of the capacity for electron transport. Furthermore, these authors have also suggested that high temperatures also reduce electron transport capacity and increase the rates of CO_2 evolution from photorespiration, again causing a decline in the assimilation rate. Optimal stomatal behaviour leads to only a small benefit in terms of water saved when compared to the situation which would occur if stomata were uniformly open all day under all environmental conditions, with the same carbon gain (Cowan and Farquhar, 1977). Nevertheless, such savings represent a significantly increased rate of growth or reduced probability of mortality.

Conclusion

From these results it may be concluded that CO_2 assimilation *H. vulgare* cv. Clipper is limited to a larger degree by stomata than in cv. Dayan. In both cultivars stomatal limitation to CO_2 assimilation is lowest at the temperature at which net CO_2 assimilation is optimal. This correlation between optimal CO_2 assimilation and stomatal limitation to assimilation suggests that stomata are a dominant factor in limiting assimilation in these two cultivars. This does not however, suggest that at temperatures which are not optimal for CO_2 assimilation, that other factors such as enzyme stability or CO_2:O_2 solubility do not play a role in reducing the capacity for CO_2 assimilation.

CHAPTER 5

EFFECT OF TEMPERATURE AND HIGH CO_2 ON NET ASSIMILATION[1]

Introduction

Earth's atmospheric CO_2 concentration is increasing on an annual basis due to human activities, and it is expected that the present annual mean concentration (*ca.* 350 $\mu mol.m^{-2}s^{-1}$) will be doubled during the next century (Amthor, 1991; Marston, *et al.*, 1991). Concern regarding this increase in global CO_2 concentration has prompted a great deal of research on responses of plants to CO_2 enrichment. Literature surveys of Kimball (1983 a,b), Cure (1986) and Mott (1990) suggest that doubling of the atmospheric CO_2 concentration increases the growth rates of nearly all agronomic C_3 plants by a similar amount. In this study the effects of hypo- and hyper-atmospheric levels of CO_2 on net assimilation in two cultivars of *H. vulgare* are compared.

Results and discussion

Light responses

Figure 5.1. and 5.2. illustrates the net CO_2 assimilation response of *H. vulgare* cv. Clipper and cv. Dayan to light intensity at four different CO_2 partial pressures respectively. At saturating light intensity the assimilation increased with increasing CO_2 partial pressure. This increase of net CO_2 assimilation to short term changes in partial pressure of CO_2 is well documented (Leegood and Furbank, 1986; Sage and Sharkey, 1987; Labate and Leegood, 1988; Sage *et al.*, 1989) and is thought to occur through partial inhibition of photorespiration

[1] Data tabulated in: Appendix C; cv. Clipper. Appendix D; cv. Dayan.

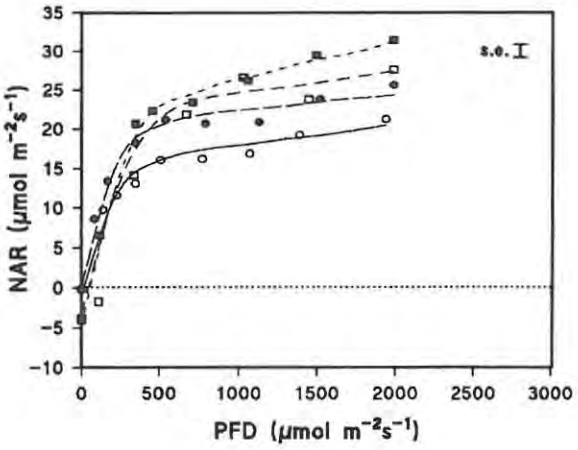

Figure 5.1. Net CO_2 assimilation response to light intensity, at CO_2 partial pressures of 260 ± 6.5 (●); 352 ± 25 (○); 634 ± 14 (■); 860 ± 13 (□) $\mu mol.m^{-2}s^{-1}$, for *H. vulgare* cv. Clipper. Leaf temperature 25°C.

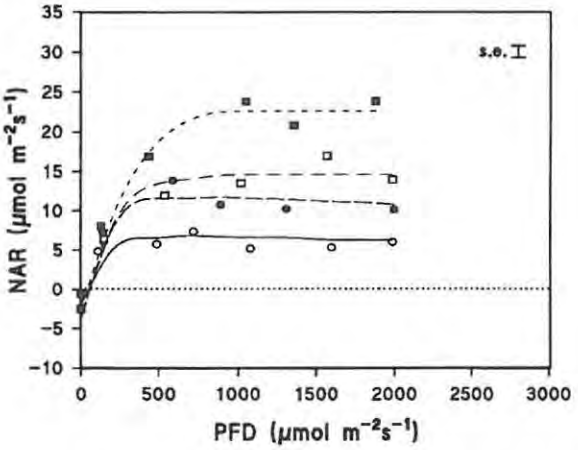

Figure 5.2. Net CO_2 assimilation response to light intensity, at CO_2 partial pressures of 260 ± 6.5 (●); 352 ± 25 (○); 634 ± 14 (■); 860 ± 13 (□) $\mu mol.m^{-2}s^{-1}$, for *H. vulgare* cv. Dayan. Leaf temperature 22.5°C.

(Pearcy and Björkman, 1983; Long and Drake, 1991). In the short term, assimilation may be limited by the capacity to regenerate inorganic phosphate (Pi) from phosphorylated photosynthetic intermediates (Leegood and Furbank, 1986; Sage and Sharkey, 1987; Sivak and Walker, 1986; Labate and Leegood, 1988; Sage *et al.*, 1989). Limitation of assimilation may be reduced by feeding or supplying inorganic phosphate, (Sivak and Walker, 1986) or increased by limiting Pi by feeding compounds which sequester cytosolic Pi as phosphorylated compounds, which are not readily metabolized (Cockburn *et al.*, 1967a,b; Herold and Lewis, 1977). It is known that the chloroplast maintains a one-to-one stoichiometry between imported orthophosphate and exported triose phosphate and that the total phosphorus concentration of the chloroplast remains more or less constant, in the short-term (Sivak and Walker, 1986). In cv. Clipper this limitation by Pi apparently is not reached as the rate of net CO_2 assimilation sustains an increase even at high light intensities.

Quantum use efficiency

The light limitation, or initial slope of the response curve, can be equated to quantum efficiency. In both cultivars, the initial slopes of the four response curves increase with increasing CO_2 partial pressure (Figure 5.1. and 5.2.), thus indicating that apparent quantum efficiency increases with increasing CO_2 partial pressure. In low light and high partial pressures of CO_2, electron transport will be lower than the capacity for carbon assimilation. In contrast under saturating light and low CO_2 partial pressure, the situation will be reversed (Lilley and Walker 1975; von Caemmerer and Farquhar, 1981; Edwards and Walker, 1983).

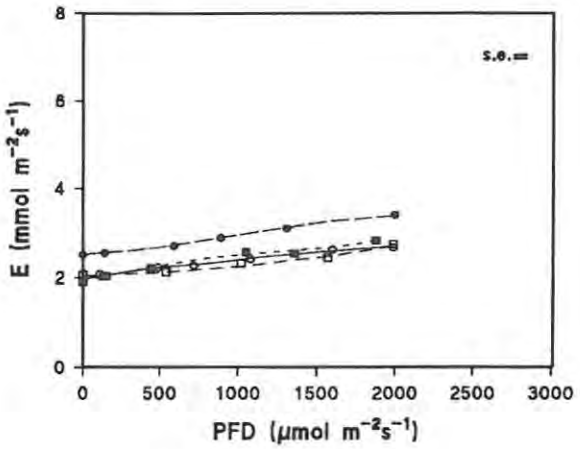

Figure 5.3. Rate of transpiration to light intensity, at CO_2 partial pressures of 260 ± 6.5 (●); 352 ± 25 (○); 634 ± 14 (■); 860 ± 13 (□) $\mu mol.m^{-2}s^{-1}$, for *H. vulgare* cv. Clipper. Leaf temperature 25°C.

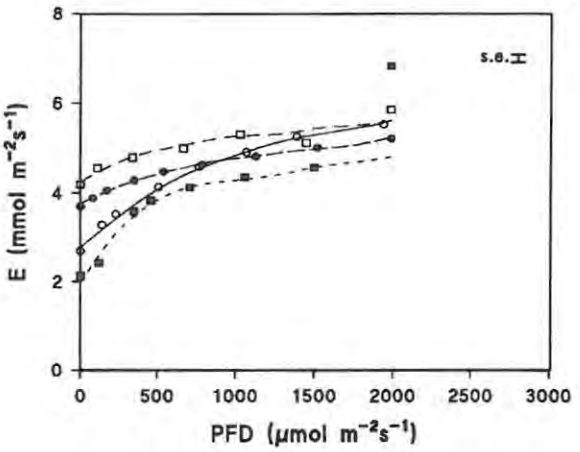

Figure 5.4. Rate of transpiration to light intensity, at CO_2 partial pressures of 260 ± 6.5 (●); 352 ± 25 (○); 634 ± 14 (■); 860 ± 13 (□) $\mu mol.m^{-2}s^{-1}$, for *H. vulgare* cv. Dayan. Leaf temperature 22.5°C.

Therefore as the CO_2 partial pressure increases at low light the capacity for CO_2 assimilation increases, even though the rate of electron transport is not increased. This ultimately results in an increase in the apparent quantum efficiency, as illustrated in Figure 5.1. The maximum rate of CO_2 assimilation in plants is assumed to be equal to the maximum rate of electron transport (von Caemmerer and Farquhar, 1981). It is clear from Figure 5.1. that with increasing partial pressure of CO_2 the rate of assimilation, and therefore the rate of electron transport increases.

Interactive effects of light and CO_2 on assimilation

The response of cv. Dayan to CO_2 partial pressures of 260, 325 and 634 $\mu mol.m^{-2}s^{-1}$ there was slight inhibition of assimilation at high light intensities. Inhibition of assimilation by high partial pressure of CO_2 in the absence of O_2 has been observed in a number of studies (Laing, *et al.*, 1974; Viil, *et al.*, 1977; Woo and Wong, 1983). CO_2 serves both as an activator and substrate for Rubisco (Lorimer *et al.*, 1976). In leaves, carboxylation of Rubisco is activated by light, CO_2 and O_2 (Perchorowicz *et al.* 1981; von Caemmerer, *pers. commun.*, 1991), however high levels of CO_2 (> 400 $\mu mol.m^{-2}s^{-1}$) have been found to cause a reduction (40-50%) in carboxylase activity *in vivo* in spinach (von Caemmerer, *pers. commun.*, 1991). Woo and Wong (1983) have suggested that the inactivation may be due to a decrease in RuDP and a build up of phosphoglycerate and fructose diphosphate at high partial pressures of CO_2. However, such a mechanism suggests that the decrease in assimilation would be independent of internal CO_2 partial pressure. Woo and Wong (1983) have also suggested that the inhibition may be as a result from an effect on the electron transport activity, although the exact nature of this effect is not known. The occurrence of inhibition

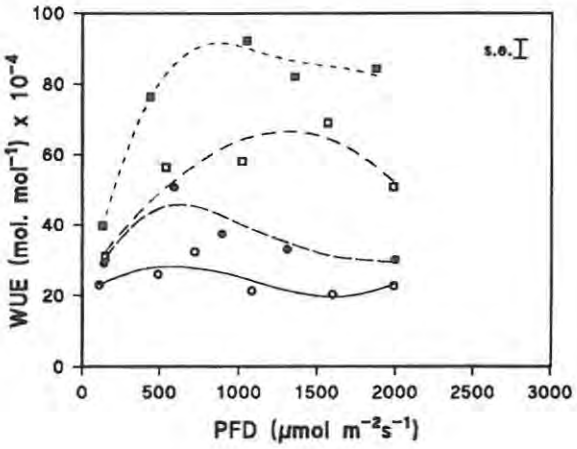

Figure 5.5. Response of water use efficiency to light intensity, at CO_2 partial pressures of 260 ± 6.5 (●); 352 ± 25 (○); 634 ± 14 (■); 860 ± 13 (□) μmol.m^{-2}s^{-1}, for *H. vulgare* cv. Clipper. Leaf temperature 25°C.

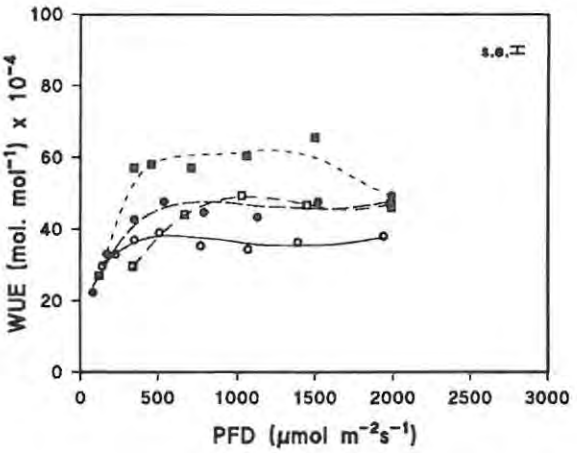

Figure 5.5. Response of water use efficiency to light intensity, at CO_2 partial pressures of 260 ± 6.5 (●); 352 ± 25 (○); 634 ± 14 (■); 860 ± 13 (□) μmol.m^{-2}s^{-1}, for *H. vulgare* cv. Clipper. Leaf temperature 25°C.

is dependent on environmental conditions, growth history of the plant and varies from species to species (Woo and Wong, 1983).

Transpiration

Transpiration rates differed widely between the two cultivars (Figure 5.3. and 5.4.). Transpiration rates in cv. Clipper at the four CO_2 partial pressures, varied little and showed a gradual increase with increasing light intensity. The highest rate of transpiration was observed at a partial pressure of 352 $\mu mol.m^{-2}s^{-1}$, and this was at all light intensities. At the other three partial pressures investigated, transpiration rates were clustered together over the full range of light intensities investigated (Figure 5.3.). Transpiration rates for cv. Dayan showed wide variation within CO_2 partial pressures and over the range of light intensities (Figure 5.4.). At all CO_2 partial pressures, transpiration rates increased with light intensity up to 500 $\mu mol.m^{-2}s^{-1}$, after which the rate of increase declined. The highest rate of transpiration occurred at 634 $\mu mol.m^{-2}s^{-1}$ CO_2 and over the full range of light intensities.

Water use efficiency

The significance of the different rates of transpiration become apparent upon examination of the calculated WUE. For both cultivars, the highest and lowest WUE were obtained CO_2 partial pressures of 860 and 260 $\mu mol.m^{-2}s^{-1}$ respectively (Figure 5.5. and 5.6.). However, the maximum efficiency for cv. Clipper was almost 33% higher than that for cv. Dayan at 860 $\mu mol.m^{-2}s^{-1}$ CO_2, and was also higher at 260 $\mu mol.m^{-2}s^{-1}$ CO_2. The WUE of the two cultivars was similar at 352 $\mu mol.m^{-2}s^{-1}$ CO_2, but only at low light. WUE in cv. Clipper declined at

higher light intensities, at which point the WUE of cv. Dayan exceed that of cv. Clipper. At 634 $\mu mol.m^{-2}s^{-1}$ CO_2 cv. Clipper again had a higher WUE than cv. Dayan.

Conclusion

Net CO_2 assimilation in cv. Clipper was higher than that in cv. Dayan at all the CO_2 concentrations examined. Although the rate of transpiration in cv. Clipper was higher that in cv. Dayan, WUE in cv. Clipper was always better than cv. Dayan, except at a CO_2 partial pressure of 260 $\mu mol.m^{-2}s^{-1}$. However, these short-term responses to increased CO_2 concentration can not be extrapolated to long-term acclimation responses, as acclimation by C_3 plants to elevated levels of CO_2 often results in inhibition of net CO_2 assimilation. It is thought that excessive carbohydrate loading of leaves and physical distortion of the chloroplasts by enlargement of starch grains may result in a decline in assimilation from either feedback inhibitions, or physical damage to the chloroplast (Sage, *et al.*, 1989). Further studies are needed to clarify similarities and dissimilarities to long-term responses to CO_2 concentration in these two cultivars.

CHAPTER 6

WATER STRESS AND ITS EFFECT ON PHOTOSYNTHETIC PIGMENTS AND GAS EXCHANGE[1]

Introduction

Improving our understanding of plant water use has been a long standing goal of plant scientists. Water stress induces severe reductions in net CO_2 assimilation, which are manifested in diminished growth and yield. The ultimate cause of this breakdown in plant productivity is still controversially discussed. Several researchers have described an inhibition of the light reactions in response to water stress (Boyer, 1971; Björkman and Powles, 1984; Boyer *et al.*, 1987). Metabolic adaptations, such as increased photorespiration and reassimilation of photorespiratory CO_2, are not sufficient to consume the total amount of excess radiant energy. To avoid photoinhibition, the light reactions have to contribute to a diminution of quantum yield for CO_2 assimilation besides these two dark reaction. Within the leaf, rearrangement of photosynthetic pigments would be such a possibility, especially when the ratio between antenna and reaction centre pigments is diminished. In this study the effect of water stress on photosynthetic pigments and gas exchange is investigated.

Results and discussion

Gas exchange responses

The decline in relative leaf water content (RWC) for cv. Clipper over the fifteen day period of the water stress study is illustrated in Figure 6.1. There was a marked drop in RWC from 98.53% on the first day of the imposition of water stress after five days to 74.89%. By ten

1 Data tabulated in: Appendix E; cv. Clipper. Appendix F; cv. Dayan.

days, the RWC of the stressed plants had reduced to 59.24%, after which a marginal increase in RWC was observed (1.21% increase to 60.45%). The control plants showed little variation in RWC, although a slow decline from 98.72% to 91.37% over the experiment period was measured.

Figures 6.2. - 6.5. illustrate the net CO_2 assimilation rates for the control and stressed treatments for cv. Clipper. The control plants showed a constant decrease in net CO_2 assimilation, which may be in part be attributed to a lack of nutrients in the potting medium. The control plants were watered with tap water only, (see Materials and Methods) to eliminate any additional effects that may have been brought on by changing nutrient levels. A reduction of about 10 $\mu mol.m^{-2}s^{-1}$ in the assimilation rate was observed for the control plants over the 15 day period. An even greater reduction in assimilation was observed in the water stressed plants, where it decreased from 15 to 1.5 $\mu mol.m^{-2}s^{-1}$ after 10 days, but increased slightly at day 15. The initial slope of the CO_2 response curve represents the light limiting part of the response curve, and the slope of this part of the curve represents the apparent quantum use efficiency. The apparent quantum use efficiency in the control plants (Figures 6.2. - 6.5.) remains relatively constant for days 0 and 5, and then declines and remains constant for days 10 and 15. In the stressed plants quantum use efficiency showed an immediate decline once water was withheld (Figures 6.2. - 6.5.). The major impact of water stress on net CO_2 assimilation was manifested after five days of stress, where a difference of approximately 10 $\mu mol.m^{-2}s^{-1}$ was observed at light intensities above 500 $\mu mol.m^{-2}s^{-1}$.

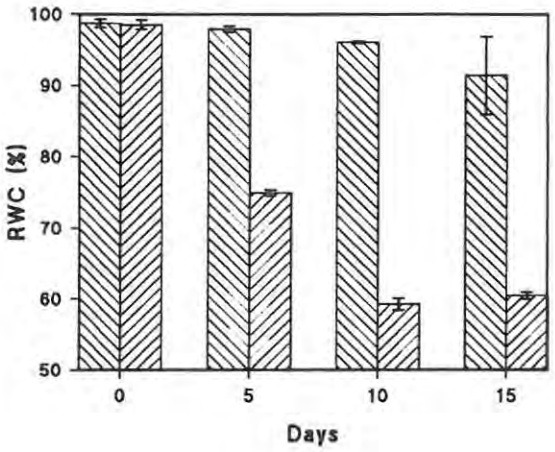

Figure 6.1. Relative leaf water content (RWC) of *H. vulgare* cv. Clipper. Control (▨); Stress (▨). Bars represent the s.e. of three replicate readings.

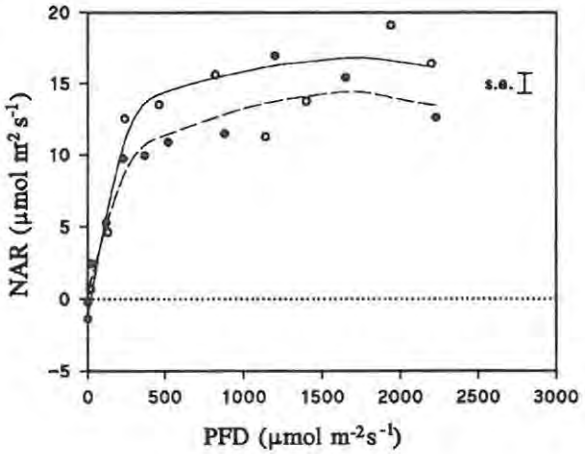

Figure 6.2. Response of net CO_2 assimilation rate to light intensity of day 0, control (o), and stressed (●), *H. vulgare* cv. Clipper. 25°C leaf temperature and ambient CO_2 concentration 371 $\mu mol.m^{-2}s^{-1}$.

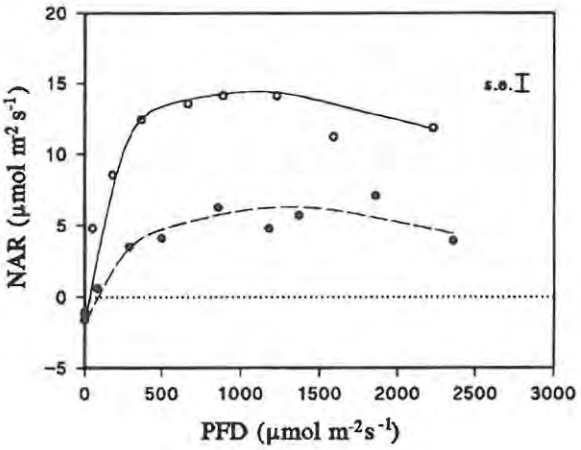

Figure 6.3. Response of net CO_2 assimilation rate to light intensity of day 5, control (o), and stressed (•), *H. vulgare* cv. Clipper. 25°C leaf temperature and ambient CO_2 concentration 371 μmol.m^{-2}s^{-1}.

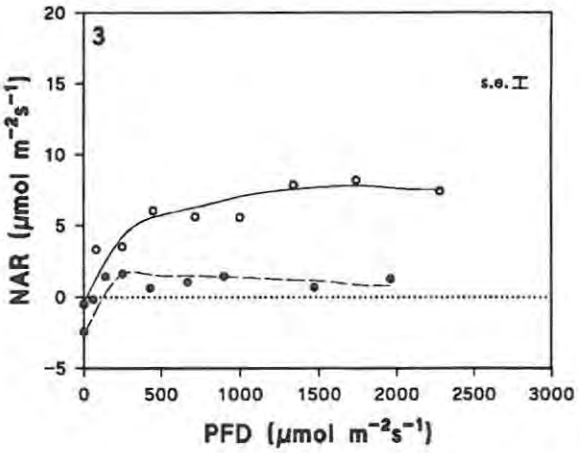

Figure 6.4. Response of net CO_2 assimilation rate to light intensity of day 10, control (o), and stressed (•), *H. vulgare* cv. Clipper. 25°C leaf temperature and ambient CO_2 concentration 371 μmol.m^{-2}s^{-1}.

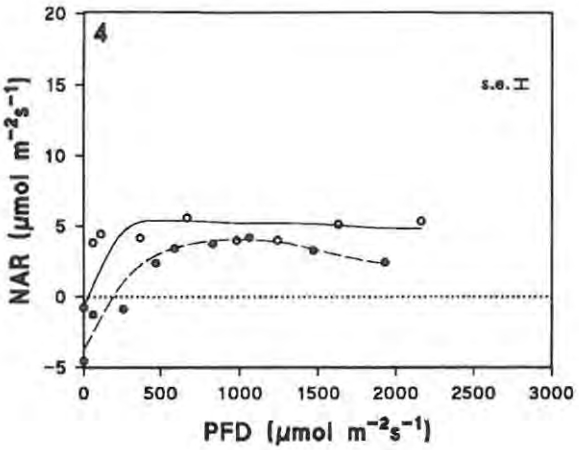

Figure 6.5. Response of net CO_2 assimilation rate to light intensity of day 15, control (o), and stressed (●), *H. vulgare* cv. Clipper. 25°C leaf temperature and ambient CO_2 concentration 371 $\mu mol.m^{-2}s^{-1}$.

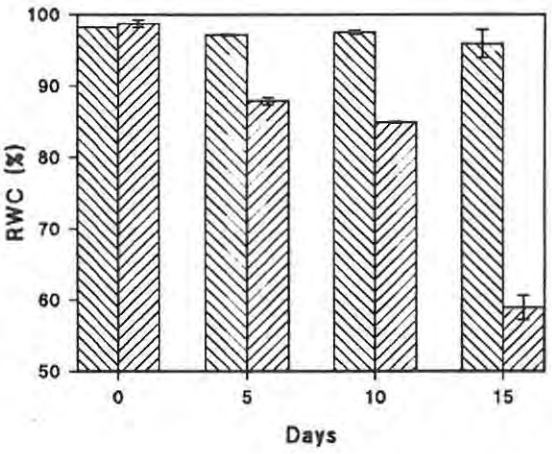

Figure 6.6 Relative leaf water content (RWC) of *H. vulgare* cv. Dayan. Control (▨); Stressed (▨). Bars represent the s.e. of three replicate readings.

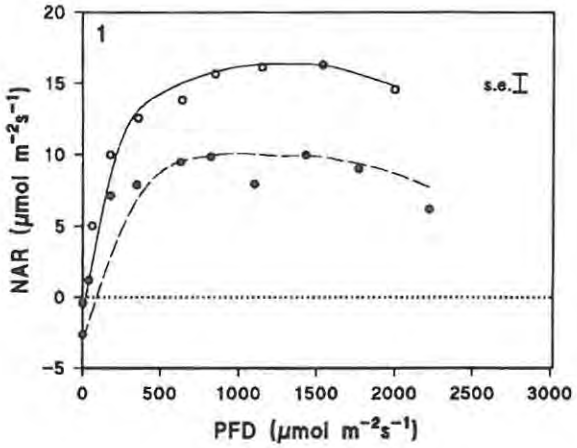

Figure 6.7. Response of net CO_2 assimilation rate to light intensity of day 0, control (o), and stressed (•), *H. vulgare* cv. Dayan. 22.5°C leaf temperature and ambient CO_2 concentration 371 μmol.m^{-2}s^{-1}.

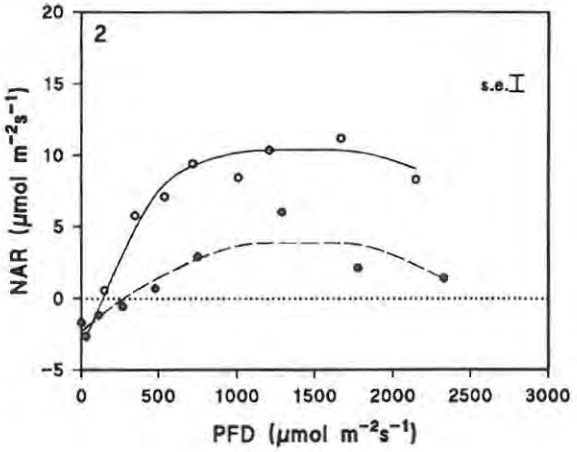

Figure 6.8. Response of net CO_2 assimilation rate to light intensity of day 5, control (o), and stressed (•), *H. vulgare* cv. Dayan. 22.5°C leaf temperature and ambient CO_2 concentration 371 μmol.m^{-2}s^{-1}.

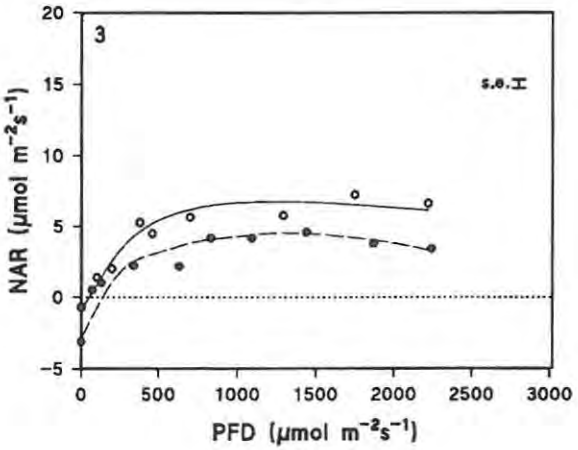

Figure 6.9. Response of net CO_2 assimilation rate to light intensity of day 10, control (o), and stressed (•), *H. vulgare* cv. Dayan. 22.5°C leaf temperature and ambient CO_2 concentration 371 μmol.$m^{-2}s^{-1}$.

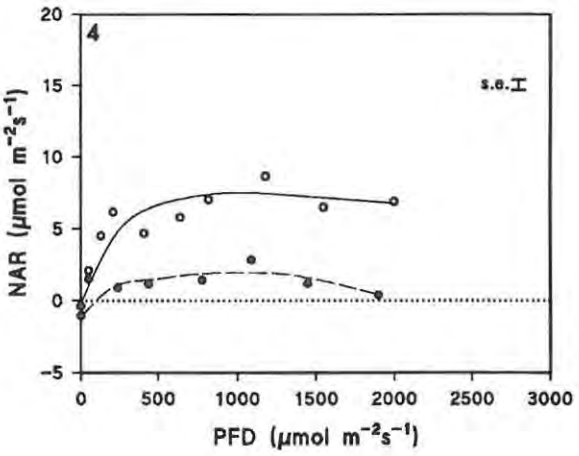

Figure 6.10. Response of net CO_2 assimilation rate to light intensity of day 15, control (o), and stressed (•), *H. vulgare* cv. Dayan. 22.5°C leaf temperature and ambient CO_2 concentration 371 μmol.$m^{-2}s^{-1}$.

Figure 6.6 shows the changes in RWC of cv. Dayan due to the imposition of water stress. The control plants maintained leaf RWC, although there was a slightly decrease from 98.25% to 95.91% over the experimental period. As with cv. Clipper, RWC declined from 98.71% to 58.98% over the stress period, which resulted in a change of 38.17%.

The net CO_2 assimilation rates for cv. Dayan, control and stressed plants, are shown in Figures 6.7 - 6.10. There was an overall decline in assimilation with time, and this is again attributed to the lack of any nutrients in the potting medium. However, there was a slight increase in the assimilation over the last 5 days. There was a decline in quantum use efficiency in both the control and stress plants, but to a much larger extent in the latter (Figures 6.7. - 6.10.). The largest decline in CO_2 assimilation by the stress plants was after 5 days (Figure 6.8).

When water stress developed in cv. Clipper, WUE decreased (Figure 6.11.), whereas in the non stressed plants little change occurred and overall the WUE in these plants increased. The decrease in WUE over the drought period was 0.0013 $mol.mol^{-1}$ in the water stressed plants. In the control plants, WUE increased by 0.0007 $mol.mol^{-1}$ from 0.0025 to 0.0032 $mol.mol^{-1}$. The lowest WUE obtained for water stressed plants was 0.009 $mol.mol^{-1}$ after 10 days without water, and the lowest WUE obtained for the non stressed plants was 0.0021 $mol.mol^{-1}$ after the same period of days.

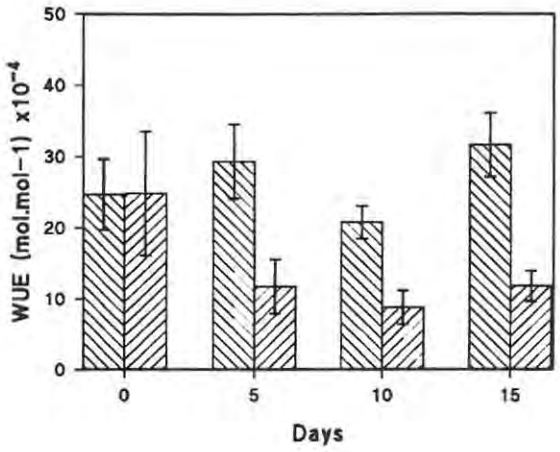

Figure 6.11. Water use efficiency (WUE) for control ▨ and stressed ▨ *H. vulgare* cv. Clipper. Bars represent the s.e. of nine replicate readings.

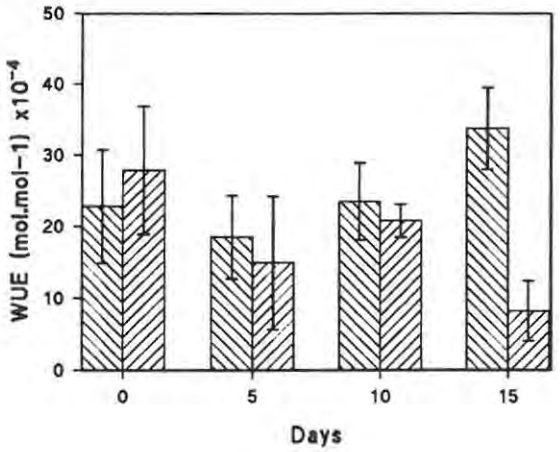

Figure 6.12. Water use efficiency (WUE) for control ▨ and stressed ▨ *H. vulgare* cv. Dayan. Bars represent the s.e. of nine replicate readings.

Water stress resulted in a general decreased WUE in cv. Dayan (Figure 6.12.). Unlike cv. Clipper, water stressed cv. Dayan sustained a relatively constant WUE for the first 10 days, after which WUE decrease. The Dayan control maintained a relatively constant WUE for the first 10 days after which an increase in WUE occurred. This may be due to a decline in stomatal conductance.

Photosynthetic pigments

In cv. Clipper, water stress increased chlorophyll *a* concentration from 1.49 mg.g.fw^{-1} to 2.04 mg.g.fw^{-1}, but remained below the concentration of chlorophyll *a* in the control plants except for day 5 (Table 6.1.). After 15 days the chlorophyll *a* concentration had increased by 0.59 mg.g.fw^{-1} in the stressed plants, but by 1.14 mg.g.fw^{-1} in the control plants; a difference of 0.55 mg.g.fw^{-1}. There was a increase in chlorophyll *b* concentration in both stressed and control plants of cv. Clipper. However this increase was comparable for both series of plants (Table 6.1.). Total chlorophyll concentration also showed no significant difference between stressed and non stressed plants, although after water stress was imposed the control plants always maintained a slightly higher total chlorophyll concentration. The overall increase in total chlorophyll concentration in the control plants was 1.87 mg.g.fw^{-1} and in the water stressed plants was 1.48 mg.g.fw^{-1}. After the imposition of stress (day 5) the concentration of total chlorophyll increased by 44.6%. Measurement of total carotenoid concentrations over the experiment period, shows that in the control plants the carotenoid concentration increased from 1.69 mg.g.fw^{-1} to 2.69 mg.g.fw^{-1} (Table 6.1.). In the stressed plants the total carotenoid concentration declined to 1.07 mg.g.fw^{-1} after an increasing from 1.45 on day 0 to 1.719 mg.g.fw^{-1} on day 5 (Table 6.1.).

Chlorophyll *a* concentration in cv. Dayan increased in the control plants throughout the experiment period, initially from 2.25 mg.g.fw^{-1} to 3.12 mg.g.fw^{-1} (Table 6.2.). In the water stressed plants the chlorophyll *a* concentration increased from 2.09 mg.g.fw^{-1} to 3.35 mg.g.fw^{-1} after 10 days, whereafter it declined to 2.43 mg.g.fw^{-1} (Table 6.2.). The concentration of chlorophyll *b* in both the control and stressed plants followed a similar pattern (Table 6.2.). There was an increase from 2.48 mg.g.fw^{-1} to 3.27 mg.g.fw^{-1} over the 15 day period in the control plants, and from 2.09 mg.g.fw^{-1} to 4.05 mg.g.fw^{-1} in the stressed plants over the first 10 days.

Table 6.1. Concentration (mg. g. fw^{-1}) of chlorophyll *a*, chlorophyll *b*, chlorophyll *a:b* and total carotenoids in *H. vulgare* cv. Clipper.

Day	Chlorophyll *a*		Chlorophyll *b*		Chlorophyll *a:b*		Total Carotenoids	
	Control	Stress	Control	Stress	Control	Stress	Control	Stress
0	1.7 ± 0.07	1.5 ± 0.01	1.7 ± 0.12	1.5 ± 0.32	0.98 ± 0.01	0.98 ± 0.03	1.7 ± 0.05	1.4 ± 0.04
5	1.9 ± 0.05	2.4 ± 0.11	1.4 ± 0.07	1.9 ± 0.03	1.30 ± 0.04	1.27 ± 0.05	1.4 ± 0.01	1.7 ± 0.06
10	2.8 ± 0.18	1.7 ± 0.07	3.9 ± 0.27	2.2 ± 0.18	1.09 ± 0.03	0.75 ± 0.05	1.7 ± 0.14	1.1 ± 0.10
15	4.1 ± 0.11	2.0 ± 0.02	5.7 ± 0.19	2.4 ± 0.19	1.15 ± 0.03	0.84 ± 0.04	2.6 ± 0.06	1.1 ± 0.04

The chlorophyll *b* concentration in the water stressed plants decreased to 2.57 mg.g.fw^{-1} on the fifteenth day (Table 6.2.). The total chlorophyll concentration in the control plants increased throughout the study, and the total increase was 1.67 mg.g.fw^{-1}. In the stressed plants the total chlorophyll concentration increased rapidly over the first 10 days, from 4.11 to 7.40 mg.g.fw^{-1}, after which it declined to 5.00 mg.g.fw^{-1}. Total carotenoid concentration in the stressed plants of cv. Dayan increased over the first five days from 1.86 mg.g.fw^{-1} to 3.46 mg.g.fw^{-1}. The concentration the declined to 3.21 mg.g.fw^{-1} and then on day 15 to 2.07

mg.g.fw^{-1} (Table 6.2.). In contrast the total carotenoid concentration in the control plants remained relatively constant for the first five days and then decreased to a lower plateau at day 10 at which it stabilized (Table 6.2.).

Table 6.2. Concentration (mg. g. fw^{-1}) of chlorophyll *a*, chlorophyll *b*, chlorophyll *a:b* and total carotenoids in *H. vulgare* cv. Dayan.

Day	Chlorophyll *a*		Chlorophyll *b*		Chlorophyll *a:b*		Total Carotenoids	
	Control	Stress	Control	Stress	Control	Stress	Control	Stress
0	2.3 ± 0.06	2.0 ± 0.05	2.4 ± 0.05	2.1 ± 0.09	0.53 ± 0.02	0.51 ± 0.04	2.0 ± 0.21	1.9 ± 0.10
5	2.6 ± 0.02	2.1 ± 0.08	2.6 ± 0.09	2.1 ± 0.14	1.27 ± 0.04	0.50 ± 0.03	2.2 ± 0.01	3.5 ± 0.01
10	2.7 ± 0.07	3.4 ± 0.18	3.2 ± 0.14	4.0 ± 0.30	0.75 ± 0.02	0.55 ± 0.05	1.5 ± 0.01	1.7 ± 0.09
15	3.1 ± 0.34	2.4 ± 0.07	3.3 ± 0.36	2.6 ± 0.11	0.84 ± 0.02	0.51 ± 0.04	1.4 ± 0.20	2.1 ± 0.04

The relationship between water stress and leaf water status shown in Figure 6.1. and 6.6., has be demonstrated for a number of species (Fry, 1972 (*Gossypium*); Leach, 1980 (*Hordeum vulgare*); von Caemmerer and Farquhar, 1984 (*Phaseolus vulgaris*); Weber and Gates, 1990 (*Quercus rubra*); Ramalho *pers. commun.*, 1991(*Lupinus albus*); Marur, 1991, (*Gossypium*)). The decrease in gas exchange is one of the earliest effects of water stress and coincides with stomatal closure (Boyer, 1976b; Bradford and Hsiao, 1982; Weber and Gates 1990). The decline in gas exchange is also affected by other environmental factors such as light intensity, temperature, nutrient status, and plant acclimation to drought.

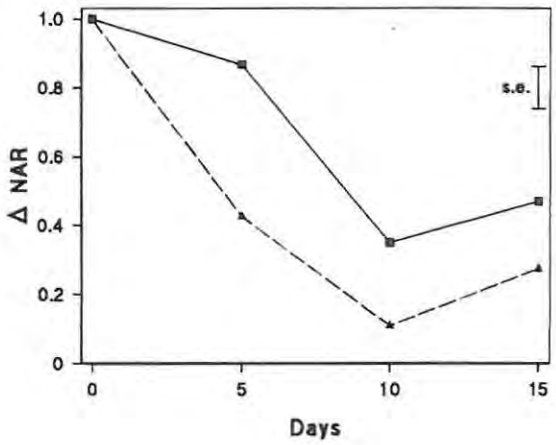

Figure 6.13. Relative assimilation rate (Δ NAR) for control and stressed treatments for *H. vulgare* cv. Clipper.

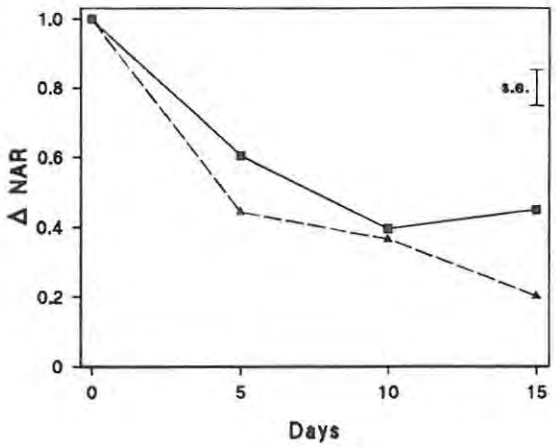

Figure 6.14. Relative assimilation rate (Δ NAR) for control and stressed treatments for *H. vulgare* cv. Dayan.

In the present study, the decline in RWC was higher for cv. Clipper than cv. Dayan over the first ten days. The relative decline in RWC (θ) for this period for cv. Clipper was 0.399 and for cv. Dayan was 0.140 (Figure 6.1. and 6.6.), where θ has no units and is calculated as:

$$\theta = \frac{RWC_0 - RWC_1}{RWC_0}$$

At the end of the drought period the θ for cv. Clipper was 0.386 and for cv. Dayan was 0.402, and at this stage drought induced senescence had progressed to such a magnitude that plants died three days later. Figures 6.13. and 6.14. illustrate the relative changes in net CO_2 assimilation rate at 1000 $\mu mol.m^{-2}s^{-1}$ for cv. Clipper and cv. Dayan respectively. The relative change in net CO_2 assimilation is calculated as;

$$\Delta A = 1 - \frac{A_0 - A_1}{A_0}$$

It is clear in Figure 6.13. that water stress decreases the relative rate of CO_2 assimilation of cv. Clipper within the first five days of stress, and that with plant age the relative rate of assimilation also decreases. However, the rate of decline in the water stress plants was much higher than in the controls plants. There is little doubt that water stress induces the photosynthetic system to photoinhibition (Björkman *et al.*, 1972; Björkman and Powles, 1984; Ludlow and Bjorkman, 1984; Kirschbaum, 1987; Sharkey and Seemann, 1989; Vassey and Sharkey, 1989; McCoy *et al.*, 1990). The increase in the relative rate of net assimilation over the last five days is most likely due to the a lengthy power failure experienced during this time, resulting in a break in the 24h photoperiod and a decline in the air temperature. Björkman and Powles (1984) have shown that the rate of recovery from inhibition is affected

by light intensity and water stress, but that this recovery is slow indicating that photoinhibition is an important component of the damage to the photosynthetic system when plants are exposed to water stress. The overall greater change in net CO_2 assimilation of the stressed plants compared to the control plants, may be as a result of increased photoinhibition induced by water stress.

Cultivar Dayan responded to water stress better than cv. Clipper. The greatest decline in relative CO_2 assimilation was first noted after fifteen days (Figures 6.13. and 6.14.). At a point between days ten and fifteen these plants were also subjected to an uncontrolled power failure. The control plants responded to the drop in temperature and break in the twenty four hour photoperiod by a increase in the relative change in assimilation. However, the relative change in assimilation of the water stressed plants continued to increase.

These results suggests that water stressed cv. Clipper was able to recover CO_2 assimilation from stress conditions more rapidly than cv. Dayan, but that cv. Dayan is less affected by the imposition of water stress than cv. Clipper, as the differences in relative change in net CO_2 assimilation in this cultivar are not as great as those for cv. Clipper (Figures 6.13. and 6.14.).

There was little change in the ratio of chlorophyll *a:b* in the control plants of cv. Clipper (Table 6.1.), but there was a slight decline in the ratio in the water stressed plants which indicates that the radiation absorption and energy transfer capacity from the antenna to PS II was reduced by stress. At the same time the amount of total carotenoids in the stressed

plants decreased relative to the control plants (Table 6.1.), which suggests that consumption of the reduction equivalents in the total carotenoid pool were diminished. This could occur through two possible avenues; first carotenoids may be utilized to quench triplet states, singlet oxygen and inhibit free radical reactions induced by water stress (Goodwin, 1980; Höffer *et al.*, 1987; Röder, 1987), and at the same time it is possible that increased abscisic acid biosynthesis may be drawing on the pool of carotenoids, specifically neoxanthin and violaxanthin. There is now considerable evidence to support such an indirect 'apo-carotenoid' pathway for abscisic acid biosynthesis (Li and Walton, 1987; Parry and Horgan, 1991). Both of these possible reasons for a decline in carotenoids are known to occur during stress (Krinski, 1979; Turkendorf *et al.*, 1980; Tuba, 1984a; Li and Walton ,1987; Stuhlfauth *et al.*, 1990; Parry and Horgan, 1991).

Unlike cv. Clipper, there was little change in the chlorophyll *a:b* ratio in either the control or water stressed plants of cv. Dayan (Table 6.1. and 6.2.). This suggests that the capacity for radiation absorption and energy transfer from the antenna to the PS II reaction centre P680 were not significantly altered by the stress. It is possible that water stress in this cultivar decreased the amount of oxygen-containing carotenoids and increased the amount of ß-carotene, in a similar manner to that which occurred in *D.lanata* (Stuhlfauth *et al.*, 1990). This would result in the total carotenoid concentration remaining unchanged. If this is the cases, one may then conclude that an hydroxylation step in carotenoid biosynthesis which leads to the synthesis of xanthrophylls is inhibited by water stress, and that the protection of the reaction centres with ß-carotene is more important than perfect radiation trapping for the consumption of reducing equivalents in the xanthophyll cycle (Tuba, 1984b).

Conclusion

The most significant result from this investigation is that in both cultivars net CO_2 assimilation decreased as the relative leaf water content declined due to the imposition of root water stress. Gas exchange in cv. Clipper was more affected by water stress than cv. Dayan, with the result that cv. Clipper had a lower WUE than cv. Dayan after the imposition of stress. The relative assimilation rate in cv. Clipper declined more rapidly than in cv. Dayan with the onset of water stress. These results suggest that cv. Dayan is more tolerant to water stress than cv. Clipper.

In water stressed plants of both cultivars, the chlorophyll *a* and chlorophyll *b*, contents increased with the imposition of water, but did not increase at the same rate as the control plants. Although the overall concentration of these pigments in the water stressed plants was less than that in the control plants, the overall ratio of chlorophyll *a:b* did not change notably. This suggests that water stress may induce an orderly deactivation of chlorophyll to reduce excessive light harvesting, thereby reducing the energy available for CO_2 assimilation. Such a mechanism would not act alone to combat the effects of water stress, but would have to act in unison with other mechanisms such reduced stomatal conductance and photoinhibition. Extra light energy (heat) gained by the leaf at high light intensities could be dissipated by increasing transpiration or by energy dissipation via the xanthophyll cycle. This proposal complies with the general belief that excess excitation energy during stress results in an increased susceptibility to photoinhibition. The discrepancy between the carotenoid concentration for cv. Clipper and cv. Dayan after water stress is currently under

investigation in further studies where individual xanthophyll concentrations are being examined and in relation to abscisic acid production.

This study indicates that there are specific effects of water stress that are independent of the photoinhibitory effects, and may come in to play before any observable reduction in plant performance.

CHAPTER 7

CONCLUDING REMARKS

Primary production and crop yield is the overall result of complex processes that are influenced by many interactions between the genetic properties of the plant and its environment. Over the past three decades attention has been focused on plant performance in an environment which is becoming less favourable for optimal plant productivity (Lyons and Asmundson, 1965; Powell, 1976; Levitt, 1980; Lakso, 1990). One of the major factors affecting plant productivity is the increase in atmospheric levels of CO_2 and related climatological changes associated, such increasing temperature. It is well known that the concentration of CO_2 in the atmosphere has increased dramatically since the industrial revolution, and a large amount of attention is being focused on the possible consequences this may have on plant performance. There have been many studies on consequences of short-term exposure to elevated CO_2 concentrations (Björkman *et al.*, 1972; Grub and Mächler, 1990), and these have generally shown that net CO_2 assimilation under these conditions increases. However, recent research has shown that long-term acclimation to elevated CO_2 partial pressures results in inhibition to CO_2 uptake by C_3 plants (Sage *et al.*, 1989). The actual mechanism of this inhibition is still widely debated.

The resultant increase in global temperature, primarily because of increasing CO_2 partial pressure (Marston *et al.*, 1991), posses another restraint to plant productivity, especially the major food crops of the world. The majority of these crops are C_3-photosynthetic types

which generally have a temperature optimum in the below 30°C. Furthermore, in many regions of the world primary productivity is determined by moisture availability. The determinant factors are the total amount of water available to the plant and the efficiency of water use for dry matter production. As the demand for food increases due to an ever increasing human population, the demand to grow crops in less arable, desert like environments increases. Restricted water availability, higher temperatures and the possibility of inhibition on net CO_2 assimilation by high CO_2 partial pressure present a dilemma with far reaching consequences.

In spite of the need to simplify the plant-environment complex experimentally, understanding plant responses to multiple stresses in the field requires a very broad perspective. The important plant processes of interest and the organisational level (ie. molecular, cellular, tissue, organ, plant, and crop level) must be clearly defined. Physiological adaptations to multiple stresses in the environment are central to the variations seen in plant responses to stress.

Time constraints and the lack of suitable equipment for long-term multiple stress studies resulted in only short-term response to single stresses being investigated in this thesis. It is hoped that the short-term single stress responses presented in this thesis will help form a basis for a multiple stress study. Such a study should involve long-term acclimation to multiple stress responses (elevated CO_2, high temperature, high light intensity, and water

stress) so that a holistic understanding of the performance and productivity of these two cultivars of *H. vulgare* L. to future environments in gained.

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APPENDIX A

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 20.0°C.

PFD	A	E	g
2300	18.11 ± 0.07	6.53 ± 0.21	618.8 ± 47.17
1900	18.52 ± 0.26	5.04 ± 0.08	363.8 ± 10.13
1300	17.62 ± 0.01	4.06 ± 0.05	254.4 ± 4.60
1000	17.06 ± 0.22	3.86 ± 0.01	235.8 ± 0.99
600	15.43 ± 0.02	3.39 ± 1.39	194.8 ± 2.30
375	11.56 ± 0.01	3.12 ± 0.04	173.6 ± 2.44
200	7.26 ± 0.94	2.75 ± 0.03	146.8 ± 1.76
52	1.23 ± 0.25	2.39 ± 0.05	122.2 ± 3.31
0	-2.31 ± 0.01	2.36 ± 0.03	120.5 ± 2.05

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2300	7796 ± 73.33	27.67 ± 1.25	266.8 ± 3.83
1900	9662 ± 111.21	36.67 ± 1.25	231.9 ± 3.78
1300	13282 ± 39.16	43.67 ± 0.47	205.1 ± 2.04
1000	17065 ± 224.80	43.67 ± 0.47	201.5 ± 1.51
600	25514 ± 373.40	45.67 ± 0.47	194.3 ± 1.57
375	30934 ± 115.10	36.67 ± 0.47	222.2 ± 1.53
200	36307 ± 38.90	26.67 ± 0.47	258.2 ± 1.01
52	23698 ± 4718.60	5.00 ± 1.41	332.5 ± 4.15
0			386.0 ± 0.31

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 22.5°C.

PFD	A	E	g
2500	19.49 ± 0.01	5.55 ± 0.06	329.1 ± 5.56
2000	18.75 ± 0.03	6.48 ± 0.06	434.4 ± 8.45
1300	18.14 ± 0.01	5.47 ± 0.02	319.9 ± 1.93
1080	17.70 ± 0.01	5.37 ± 0.02	310.2 ± 2.07
669	15.91 ± 0.01	4.80 ± 0.04	259.3 ± 3.24
325	10.98 ± 0.23	4.29 ± 0.05	219.0 ± 4.17
177	6.92 ± 0.02	3.68 ± 0.06	176.4 ± 3.80
39	0.72 ± 0.02	3.36 ± 0.06	155.9 ± 4.00
0	-3.12 ± 0.01	3.25 ± 0.03	149.7 ± 2.05

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2500	7797 ± 4.97	35.33 ± 0.47	215.2 ± 1.69
2000	9373 ± 14.82	29.00 ± 0.00	242.3 ± 1.48
1300	13952 ± 7.26	33.00 ± 0.00	222.3 ± 0.60
1080	16385 ± 8.96	33.00 ± 0.00	222.7 ± 0.67
669	23783 ± 13.22	33.00 ± 0.00	219.6 ± 1.28
325	33783 ± 713.80	25.67 ± 0.47	247.5 ± 2.82
177	39120 ± 100.84	18.67 ± 0.47	273.1 ± 1.54
39	18243 ± 758.61	2.00 ± 0.00	340.4 ± 0.50
0			388.4 ± 0.28

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C.

PFD	A	E	g
2360	20.47 ± 0.67	9.14 ± 0.01	466.9 ± 1.14
1930	20.64 ± 0.34	8.94 ± 0.03	451.6 ± 2.60
1280	20.04 ± 0.36	8.32 ± 0.06	402.4 ± 4.12
960	19.67 ± 0.01	7.92 ± 0.04	372.9 ± 3.20
610	19.88 ± 0.38	7.02 ± 0.10	309.4 ± 7.07
555	18.55 ± 0.67	6.47 ± 0.01	274.4 ± 0.52
310	14.00 ± 0.91	5.92 ± 0.05	242.4 ± 2.97
158	5.32 ± 0.02	4.99 ± 0.06	193.5 ± 2.70
49	-1.00 ± 0.56	4.63 ± 0.06	175.7 ± 2.69
0	-7.00 ± 0.32	4.12 ± 0.04	152.1 ± 1.53

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2360	8663 ± 301.9	22.33 ± 0.47	254.5 ± 1.69
1930	10675 ± 162.2	22.67 ± 0.00	251.5 ± 1.91
1280	15741 ± 253.2	24.00 ± 0.00	245.8 ± 2.69
960	20492 ± 14.7	25.00 ± 0.00	241.5 ± 0.80
610	29333 ± 1677.4	28.33 ± 0.00	223.0 ± 4.28
555	32886 ± 831.8	28.33 ± 0.47	220.4 ± 4.73
310	45264 ± 3041.3	23.67 ± 0.47	242.5 ± 8.10
158	33674 ± 123.3	10.67 ± 0.00	297.8 ± 0.80
49			362.7 ± 5.92
0			434.1 ± 4.44

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 27.5°C.

PFD	A	E	g
2370	18.07 ± 0.01	10.68 ± 0.03	474.1 ± 2.37
2000	18.86 ± 0.03	10.45 ± 0.07	487.6 ± 5.16
1400	19.28 ± 0.04	9.41 ± 0.09	384.9 ± 5.61
1150	18.81 ± 0.04	9.01 ± 0.10	359.0 ± 6.01
800	18.08 ± 0.03	7.30 ± 0.09	263.4 ± 4.49
607	14.37 ± 0.69	7.67 ± 0.34	282.7 ± 18.45
430	12.74 ± 0.32	7.33 ± 0.02	265.2 ± 1.33
235	7.94 ± 0.05	5.18 ± 0.12	168.3 ± 4.91
50	0.29 ± 0.03	4.96 ± 0.08	159.1 ± 3.13
0	-5.23 ± 0.30	3.92 ± 0.11	119.8 ± 4.15

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2370	7626 ± 44.8	17.00 ± 0.00	264.0 ± 0.35
2000	9431 ± 14.7	18.00 ± 0.00	257.9 ± 0.87
1400	13818 ± 9.6	20.67 ± 0.47	243.4 ± 1.36
1150	16345 ± 51.8	20.67 ± 0.47	240.7 ± 1.58
800	22515 ± 413.7	24.67 ± 0.47	216.3 ± 2.06
607	23692 ± 1175.7	18.67 ± 1.25	239.3 ± 18.70
430	29984 ± 1465.8	17.67 ± 0.47	256.3 ± 2.10
235	33725 ± 151.0	15.33 ± 0.47	364.4 ± 2.60
50	5929 ± 662.2	0.67 ± 0.47	346.1 ± 0.41
0			424.7 ± 6.53

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 30.0°C.

PFD	A	E	g
2370	19.55 ± 0.03	13.69 ± 0.09	561.6 ± 7.18
1930	19.41 ± 0.01	11.98 ± 0.03	445.3 ± 1.92
1250	18.83 ± 0.34	10.68 ± 0.04	370.8 ± 1.94
1100	19.10 ± 0.30	10.81 ± 0.08	379.5 ± 4.50
765	20.06 ± 0.02	11.05 ± 0.06	393.9 ± 3.37
380	16.77 ± 0.01	10.45 ± 0.06	360.4 ± 3.39
217	12.38 ± 0.01	9.05 ± 0.02	290.3 ± 0.98
50	2.62 ± 0.02	8.39 ± 0.06	260.8 ± 2.50
0	-6.17 ± 0.03	7.10 ± 0.07	208.2 ± 2.86

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2370	8236 ± 28.9	14.00 ± 0.00	265.0 ± 0.84
1930	10055 ± 5.3	16.00 ± 0.00	251.3 ± 0.35
1250	15225 ± 240.3	17.67 ± 0.47	240.7 ± 1.61
1100	17328 ± 312.6	18.00 ± 0.00	240.9 ± 0.80
765	26208 ± 45.2	18.00 ± 0.00	238.4 ± 0.80
380	44013 ± 105.3	16.00 ± 0.00	250.1 ± 0.80
217	56957 ± 81.8	14.00 ± 0.00	262.6 ± 0.30
50	52408 ± 421.4	3.00 ± 0.00	327.5 ± 0.32
0			397.8 ± 0.37

APPENDIX B

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 20.0°C.

PFD	A	E	g
2450	23.70 ± 0.03	6.88 ± 0.06	486.2 ± 7.46
2000	24.77 ± 0.02	6.54 ± 0.07	442.4 ± 7.77
1378	22.89 ± 0.01	5.83 ± 0.03	367.6 ± 3.39
1131	23.73 ± 0.00	5.52 ± 0.02	338.2 ± 1.43
793	21.05 ± 0.01	4.63 ± 0.01	262.7 ± 0.78
429	19.36 ± 0.45	6.57 ± 0.33	450.2 ± 39.78
292	18.87 ± 0.01	4.34 ± 0.04	240.6 ± 2.84
36	2.69 ± 0.32	2.94 ± 0.04	145.9 ± 2.38
0	-2.49 ± 0.02	0.97 ± 0.05	41.8 ± 2.54

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2450	9769 ± 144.4	34.67 ± 0.47	241.7 ± 1.31
2000	12580 ± 28.2	37.67 ± 0.47	228.9 ± 1.64
1378	16581 ± 16.9	39.33 ± 0.47	221.9 ± 0.99
1131	20996 ± 18.2	43.00 ± 0.00	208.3 ± 0.50
793	26475 ± 61.7	45.67 ± 0.47	196.6 ± 0.33
429	45978 ± 1650.2	29.67 ± 2.05	256.8 ± 7.92
292	64632 ± 26.4	43.67 ± 0.47	207.2 ± 1.51
36	67959 ± 754.1	9.33 ± 1.25	325.7 ± 3.46
0			454.7 ± 4.80

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C.

PFD	A	E	g
2276	22.36 ± 0.01	6.70 ± 0.04	360.8 ± 3.35
1970	24.15 ± 0.02	7.41 ± 0.04	424.3 ± 3.51
1348	23.23 ± 0.02	8.23 ± 0.07	506.8 ± 8.04
1104	24.30 ± 0.33	8.27 ± 0.03	509.5 ± 3.22
805	23.41 ± 0.01	8.26 ± 0.02	507.4 ± 2.50
570	21.04 ± 0.01	6.54 ± 0.02	347.7 ± 1.14
423	19.42 ± 0.33	6.21 ± 0.03	321.9 ± 2.56
215	12.61 ± 0.31	5.44 ± 0.05	265.9 ± 3.70
150	7.27 ± 0.64	4.49 ± 0.08	205.2 ± 4.79
39	-3.68 ± 0.32	3.63 ± 0.05	156.5 ± 2.75
0	-9.27 ± 0.31	3.49 ± 0.06	149.2 ± 3.21

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2276	9821 ± 17.9	33.33 ± 0.47	226.2 ± 0.97
1970	12257 ± 55.9	32.67 ± 0.47	231.3 ± 1.00
1348	17223 ± 39.3	28.33 ± 0.47	250.2 ± 1.24
1104	22003 ± 285.0	29.33 ± 0.47	245.9 ± 1.15
805	29064 ± 2.4	28.00 ± 0.00	249.8 ± 0.41
570	36863 ± 61.9	32.00 ± 0.00	230.5 ± 0.31
423	45872 ± 672.3	31.33 ± 0.47	233.2 ± 1.65
215	58663 ± 1432.9	23.33 ± 0.47	260.8 ± 1.29
158	45964 ± 3393.9	16.33 ± 1.25	287.6 ± 4.60
39			396.0 ± 4.18
0			465.6 ± 5.85

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 25.0°C.

PFD	A	E	g
2300	22.57 ± 0.01	11.51 ± 0.01	870.8 ± 1.98
1950	23.56 ± 0.05	10.97 ± 0.16	766.6 ± 26.58
1380	23.80 ± 0.01	10.53 ± 0.04	696.0 ± 4.97
1070	23.95 ± 0.03	10.21 ± 0.07	649.4 ± 10.33
768	21.66 ± 0.01	9.90 ± 0.01	607.8 ± 2.03
433	18.02 ± 0.26	9.17 ± 0.09	522.7 ± 9.81
227	10.82 ± 0.29	6.73 ± 0.09	309.6 ± 6.90
60	3.37 ± 0.34	5.21 ± 0.17	214.2 ± 9.73
0	-1.48 ± 0.28	3.57 ± 0.19	131.9 ± 8.70

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2300	9815 ± 1.41	20.00 ± 0.00	275.0 ± 0.11
1950	12106 ± 51.5	21.33 ± 0.47	264.7 ± 1.91
1380	17173 ± 57.9	22.67 ± 0.47	259.0 ± 0.42
1070	22415 ± 154.4	23.67 ± 0.47	254.5 ± 1.06
768	28239 ± 36.5	22.00 ± 0.00	260.5 ± 0.21
433	41541 ± 623.9	19.67 ± 0.47	268.6 ± 0.62
227	49209 ± 1441.5	16.00 ± 0.82	279.8 ± 2.52
60	56720 ± 5440.9	6.33 ± 0.94	322.2 ± 4.04
0			374.4 ± 4.36

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 27.5

PFD	A	E	g
2250	23.00 ± 0.18	14.77 ± 0.45	1108.9± 96.80
1900	22.65 ± 0.06	13.54 ± 0.18	891.0 ± 29.32
1300	22.02 ± 0.06	15.11 ± 0.17	1219.7± 44.16
1057	22.19 ± 0.01	11.99 ± 0.43	663.0 ± 5.07
780	20.61 ± 0.02	10.79 ± 0.08	538.2 ± 7.31
427	15.96 ± 0.03	9.84 ± 0.07	454.4 ± 6.30
228	11.56 ± 0.03	10.29 ± 0.07	491.9 ± 6.01
68	3.90 ± 0.07	9.40 ± 0.19	418.8 ± 14.86
0	-2.74 ± 0.02	4.08 ± 0.04	129.0 ± 1.65

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2250	10178 ± 118.4	15.67 ± 0.47	279.9 ± 2.62
1900	11942 ± 20.6	16.67 ± 0.47	272.7 ± 1.58
1300	16963 ± 26.4	14.67 ± 0.47	285.6 ± 1.25
1057	21005 ± 43.8	18.33 ± 0.47	260.9 ± 0.46
780	26450 ± 5.7	19.00 ± 0.00	255.7 ± 0.93
427	37402 ± 21.4	16.00 ± 0.00	268.5 ± 0.89
228	50688 ± 348.8	11.00 ± 0.00	294.5 ± 0.59
68	57336 ± 104.9	4.00 ± 0.00	329.7 ± 0.95
0			386.8 ± 0.18

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 30.0°C.

PFD	A	E	g
2180	17.06 ± 0.44	14.66 ± 1.35	763.2 ± 170.08
1560	16.88 ± 1.70	13.00 ± 0.04	580.3 ± 3.78
1202	18.06 ± 0.00	12.87 ± 0.03	569.9 ± 2.64
814	15.60 ± 0.02	13.26 ± 0.05	601.8 ± 4.74
453	10.19 ± 0.54	10.79 ± 0.67	402.1 ± 27.93
257	4.04 ± 0.28	8.54 ± 0.06	284.7 ± 3.29
93	-2.38 ± 0.29	6.95 ± 1.57	172.5 ± 6.45
0	-7.34 ± 0.07	4.97 ± 0.20	137.5 ± 6.82

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2180	7827 ± 206.1	11.67 ± 0.00	279.4 ± 8.98
1560	10844 ± 1111.0	13.00 ± 0.47	268.6 ± 4.79
1202	15024 ± 28.6	14.00 ± 0.47	264.2 ± 0.26
814	10293 ± 263.9	12.00 ± 0.47	277.7 ± 0.40
453	22503 ± 1173.8	9.67 ± 0.00	287.9 ± 0.62
257	15680 ± 1066.6	4.67 ± 0.47	314.7 ± 1.99
93			379.2 ± 14.27
0			437.5 ± 3.03

APPENDIX C

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C at 273 ppm CO_2.

PFD	A	E	g
1940	21.22 ± 0.83	5.52 ± 0.21	221.5 ± 8.86
1390	19.23 ± 0.34	5.25 ± 0.01	205.8 ± 0.70
1070	16.88 ± 0.59	4.91 ± 0.03	188.7 ± 1.19
770	16.23 ± 0.60	4.58 ± 0.03	173.1 ± 1.10
510	16.09 ± 0.34	4.13 ± 0.03	152.1 ± 1.36
350	13.09 ± 0.68	3.55 ± 0.04	126.7 ± 1.54
230	11.64 ± 0.30	3.52 ± 0.14	125.5 ± 6.19
140	9.76 ± 0.33	3.28 ± 0.05	115.7 ± 1.85
0	-0.25 ± 0.34	2.69 ± 0.02	92.1 ± 0.94

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1940	10972 ± 376.3	38.00 ± 0.00	78.9 ± 0.02
1390	13731 ± 104.9	36.33 ± 0.47	86.3 ± 2.87
1070	15921 ± 503.5	34.33 ± 1.25	96.0 ± 4.86
770	20978 ± 667.9	35.33 ± 1.25	90.2 ± 7.23
510	31349 ± 583.3	39.00 ± 0.82	71.7 ± 3.52
350	37401 ± 1933.9	37.00 ± 1.41	80.1 ± 7.53
230	50606 ± 1328.0	33.00 ± 0.82	98.4 ± 2.84
140	69706 ± 2354.8	29.67 ± 0.47	114.4 ± 2.99
0			264.2 ± 6.23

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C at 350 ppm CO_2.

PFD	A	E	g
1990	25.60 ± 1.73	5.20 ± 0.01	205.3 ± 0.71
1520	23.80 ± 1.18	5.00 ± 0.01	195.2 ± 0.71
1130	20.84 ± 0.87	4.81 ± 0.00	185.5 ± 0.00
790	20.67 ± 0.57	4.63 ± 0.00	176.9 ± 0.00
540	21.17 ± 0.66	4.47 ± 0.05	169.5 ± 2.17
350	18.22 ± 0.33	4.28 ± 0.01	160.4 ± 0.66
170	13.42 ± 0.65	4.05 ± 0.01	149.6 ± 0.66
80	8.61 ± 0.66	3.88 ± 0.02	142.1 ± 1.06
0	-0.10 ± 0.57	3.69 ± 0.01	133.4 ± 0.61

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1990	12862 ± 870.7	49.33 ± 3.30	100.1 ± 15.30
1520	15620 ± 791.4	47.67 ± 2.50	107.2 ± 10.76
1130	18503 ± 847.0	43.33 ± 2.05	126.5 ± 8.62
790	26055 ± 852.4	44.67 ± 1.25	119.8 ± 5.87
540	39204 ± 1222.2	47.67 ± 1.70	106.5 ± 8.62
350	52053 ± 944.1	42.67 ± 0.94	128.4 ± 4.46
170	78935 ± 3829.7	33.00 ± 1.41	173.2 ± 7.19
80	107587± 8194.8	22.33 ± 1.70	225.8 ± 8.22
			331.7 ± 7.45

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C at 620 ppm CO_2.

PFD	A	E	g
1990	27.56 ± 0.01	5.85 ± 0.03	189.8 ± 0.98
1450	23.75 ± 1.03	5.11 ± 0.04	193.9 ± 1.51
1030	26.56 ± 0.03	5.30 ± 0.50	167.6 ± 1.86
670	21.83 ± 0.01	4.99 ± 0.01	155.8 ± 0.52
340	14.16 ± 0.37	4.79 ± 0.01	148.6 ± 0.49
110	-1.75 ± 0.39	4.55 ± 0.03	139.6 ± 1.01
0	-3.88 ± 0.37	4.19 ± 0.01	105.2 ± 0.21

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1990	13849 ± 3.3	47.00 ± 0.00	323.4 ± 1.13
1450	11934 ± 667.6	46.67 ± 2.05	366.7 ± 12.58
1030	25492 ± 345.6	49.33 ± 0.47	307.6 ± 2.83
670	32587 ± 407.0	44.0 ± 0.00	339.0 ± 0.79
340	41648 ± 1095.0	29.67 ± 0.94	418.7 ± 4.18
110			606.7 ± 4.75
0			644.9 ± 5.02

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C at 874 ppm CO_2.

PFD	A	E	g
1990	31.42 ± 1.40	6.83 ± 0.05	233.2 ± 1.96
1500	29.48 ± 0.80	4.56 ± 0.03	168.7 ± 1.23
1060	26.13 ± 0.38	4.35 ± 0.00	159.3 ± 0.00
710	23.38 ± 0.01	4.12 ± 0.01	149,0 ± 0.59
460	22.28 ± 1.00	3.83 ± 0.02	136.7 ± 0.80
350	20.62 ± 0.00	3.59 ± 0.01	127.0 ± 0.28
120	6.56 ± 0.02	2.42 ± 0.02	80.9 ± 0.82
0	-4.02 ± 0.35	2.13 ± 0.04	70.2 ± 1.35

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1900	15787 ± 533.6	46.00 ± 2.49	594.6 ± 12.64
1500	19729 ± 429.9	65.33 ± 1.70	537.7 ± 7.13
1060	24578 ± 314.3	60.33 ± 0.94	561.3 ± 4.18
710	33076 ± 221.6	57.00 ± 0.00	576.2 ± 1.12
460	48442 ± 2184.6	58.00 ± 2.94	568.2 ± 14.29
350	58372 ± 769.3	57.00 ± 0.00	571.1 ± 0.54
120	54651 ± 153.2	27.00 ± 0.00	716.1 ± 1.65
0			944.6 ± 9.43

APPENDIX D

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C at 260 ppm CO_2.

PFD	A	E	g
1990	6.02 ± 0.66	2.68 ± 0.00	109.6 ± 0.00
1600	5.34 ± 0.65	2.63 ± 0.02	107.4 ± 0.87
1080	5.19 ± 0.33	2.42 ± 0.05	97.1 ± 2.28
720	7.34 ± 0.33	2.27 ± 0.01	90.3 ± 0.28
490	5.75 ± 0.00	2.23 ± 0.01	84.4 ± 0.67
110	4.84 ± 0.33	2.08 ± 0.02	81.9 ± 0.70
0	-0.73 ± 0.34	1.92 ± 0.06	75.0 ± 2.62

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1990	3027 ± 329.0	22.67 ± 2.36	154.3 ± 10.31
1600	3344 ± 403.4	20.33 ± 2.62	163.4 ± 10.35
1080	4790 ± 314.4	21.33 ± 1.25	157.9 ± 5.76
720	10245 ± 432.9	32.33 ± 1.89	111.2 ± 6.63
490	11727 ± 8.9	26.00 ± 0.00	139.1 ± 0.86
110	43963 ± 2979.3	23.00 ± 1.41	149.7 ± 6.21
0			265.1 ± 7.20

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C at 300 ppm CO_2.

PFD	A	E	g
1999	10.12 ± 0.01	3.41 ± 0.01	144.8 ± 0.62
1310	10.20 ± 0.01	3.10 ± 0.02	129.6 ± 0.85
890	10.72 ± 0.32	2.89 ± 0.01	118.8 ± 0.66
590	13.79 ± 0.57	2.71 ± 0.01	110.3 ± 0.57
140	7.34 ± 0.33	2.55 ± 0.02	102.9 ± 0.94
0	-2.63 ± 0.34	2.52 ± 0.05	101.1 ± 0.04

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1999	5064 ± 1.9	30.00 ± 0.00	162.9 ± 0.50
1310	7809 ± 26.9	33.00 ± 0.00	148.9 ± 1.01
890	11869 ± 236.7	37.33 ± 0.94	130.4 ± 3.97
590	23493 ± 809.4	50.67 ± 2.05	71.7 ± 9.37
140	52444 ± 2373.5	29.00 ± 1.41	164.8 ± 6.54
0			331.6 ± 4.94

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C at 648 ppm CO_2.

PFD	A	E	g
1990	13.91 ± 0.35	2.75 ± 0.03	112.6 ± 1.55
1570	16.92 ± 1.66	2.45 ± 0.02	98.8 ± 0.71
1020	13.47 ± 0.33	2.32 ± 0.01	92.3 ± 0.28
540	11.91 ± 0.01	2.12 ± 0.01	83.5 ± 0.49
150	6.36 ± 0.00	2.04 ± 0.01	79.8 ± 0.33
0	-2.49 ± 0.33	2.07 ± 0.00	81.2 ± 0.00

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1990	6991 ± 177.3	50.67 ± 1.70	401.2 ± 7.91
1570	10750 ± 999.0	69.00 ± 7.07	321.4 ± 30.67
1020	13334 ± 138.1	58.00 ± 1.41	367.1 ± 5.43
540	22055 ± 12.51	56.33 ± 0.47	347.4 ± 1.39
150	4241 ± 23.10	31.00 ± 0.00	480.8 ± 0.57
0			665.9 ± 6.78

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C at 847 ppm CO_2.

PFD	A	E	g
1880	23.80 ± 0.34	2.83 ± 0.02	116.8 ± 0.87
1360	20.78 ± 0.57	2.54 ± 0.00	102.8 ± 0.00
1050	23.76 ± 2.16	2.58 ± 0.02	104.6 ± 0.79
440	16.87 ± 0.58	2.21 ± 0.01	87.9 ± 0.57
130	8.03 ± 0.01	2.03 ± 0.01	79.7 ± 0.45
0	-0.50 ± 0.33	1.91 ± 0.03	74.4 ± 1.18

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1880	12636 ± 168.9	84.33 ± 1.70	483.5 ± 7.12
1360	15315 ± 421.8	82.00 ± 2.45	490.7 ± 9.48
1050	22404 ± 1913.6	92.33 ± 8.73	446.7 ± 37.14
440	38628 ± 1375.9	76.33 ± 2.87	512.3 ± 12.92
130	61735 ± 104.3	39.67 ± 0.47	667.8 ± 1.17
0			847.8 ± 7.43

APPENDIX E

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C. Drought Control 1.

PFD	A	E	g
2200	16.37 ± 1.30	6.41 ± 0.01	232.0 ± 0.73
1940	19.10 ± 1.70	6.32 ± 0.02	228.2 ± 0.85
1400	13.75 ± 2.29	6.16 ± 0.05	22.1.2 ± 2.29
1140	11.25 ± 1.25	5.63 ± 0.12	198.7 ± 4.79
820	15.60 ± 0.61	5.03 ± 0.11	174.7 ± 4.40
460	13.52 ± 1.14	4.47 ± 0.12	152.6 ± 4.75
240	12.53 ± 2.21	3.45 ± 0.14	114.4 ± 5.28
130	4.63 ± 0.04	2.46 ± 0.10	79.6 ± 33.5
20	0.67 ± 0.42	1.90 ± 0.11	60.6 ± 3.66
0	-1.37 ± 0.65	1.30 ± 0.01	40.8 ± 0.37

PFD	Q x 10^{-8}	WUE x 10^{-4}	Ci
2200	7488 ± 634.2	25.33 ± 1.19	209.3 ± 10.14
1940	9863 ± 878.7	30.33 ± 2.49	177.6 ± 4.65
1400	9582 ± 1787.9	22.33 ± 3.40	224.8 ± 17.24
1140	19092 ± 635.0	20.00 ± 2.16	235.5 ± 8.77
820	29592 ± 2248.7	31.00 ± 0.82	181.0 ± 3.12
460	52197 ± 9211.6	30.33 ± 3.40	183.5 ± 15.31
240	35651 ± 267.1	19.00 ± 0.82	152.7 ± 27.52
130	3565 ± 271.0	19.00 ± 0.82	165.2 ± 99.48
20			350.0 ± 0.00
0			385.2 ± 24.89

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C. Drought 1.

PFD	A	E	g
2230	12.06 ± 1.60	4.45 ± 0.02	155.3 ± 0.98
1650	15.41 ± 0.93	4.55 ± 0.00	159.4 ± 0.00
1200	16.93 ± 2.14	4.57 ± 0.02	160.4 ± 0.81
880	11.47 ± 1.41	4.16 ± 0.04	143.8 ± 1.68
520	10.87 ± 1.43	2.79 ± 1.45	129.1 ± 1.67
370	9.93 ± 1.95	3.25 ± 0.05	108.9 ± 1.85
230	9.73 ± 1.07	2.78 ± 0.05	91.6 ± 1.80
120	5.26 ± 1.40	2.45 ± 0.08	80.00 ± 2.82
20	2.44 ± 0.53	1.73 ± 0.05	55.30 ± 1.61
0	-0.22 ± 0.54	1.43 ± 0.02	45.03 ± 0.53

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2230	5358 ± 734.3	27.33 ± 3.30	200.4 ± 16.67
1650	9632 ± 385.8	33.67 ± 2.05	167.4 ± 9.94
1200	14071 ± 1810.3	37.00 ± 4.97	152.1 ± 23.22
880	12981 ± 1614.8	27.67 ± 3.30	197.8 ± 15.57
520	20794 ± 2906.4	26.67 ± 2.05	191.3 ± 19.83
370	26839 ± 5267.2	30.67 ± 6.24	181.5 ± 29.82
230	41654 ± 4242.1	35.00 ± 3.56	158.7 ± 16.39
120	43836 ± 11688.3	21.33 ± 4.99	226.4 ± 24.81
20	122151± 26327.2	14.00 ± 2.83	261.9 ± 14.00
0			

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C. Drought Control 2.

PFD	A	E	g
2230	11.83 ± 0.46	4.25 ± 0.00	150.2 ± 0.00
1590	11.23 ± 0.79	4.09 ± 0.01	143.7 ± 0.52
1230	14.12 ± 0.01	4.17 ± 0.01	146.8 ± 0.47
890	14.13 ± 0.47	4.10 ± 0.02	143.9 ± 0.98
670	13.56 ± 0.44	3.87 ± 0.04	134.5 ± 1.92
370	12.44 ± 0.02	3.08 ± 0.49	115.3 ± 2.57
180	8.55 ± 0.46	2.48 ± 0.01	81.9 ± 0.47
50	4.79 ± 0.45	2.07 ± 0.02	67.4 ± 0.71
0	-1.56 ± 0.47	1.73 ± 0.02	55.6 ± 0.78

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2230	5304 ± 189.3	28.00 ± 1.41	189.6 ± 5.26
1590	7193 ± 415.4	27.67 ± 2.05	191.2 ± 9.46
1230	11478 ± 5.2	34.00 ± 0.00	159.9 ± 0.54
890	15946 ± 85.5	34.67 ± 0.47	156.7 ± 1.11
670	20348 ± 607.5	34.00 ± 0.82	153.4 ± 3.88
370	33334 ± 467.3	37.00 ± 0.82	143.5 ± 4.14
180	47478 ± 2557.7	34.67 ± 1.89	153.6 ± 9.27
50	95892 ± 9096.3	23.00 ± 2.16	209.4 ± 10.49
0			370.1 ± 0.37

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C. Drought 2.

PFD	A	E	g
2360	3.89 ± 0.54	2.97 ± 0.02	97.6 ± 0.53
1860	7.08 ± 0.55	4.95 ± 0.06	173.6 ± 2.17
1370	5.70 ± 0.53	4.53 ± 0.07	156.8 ± 2.84
1180	4.77 ± 0.54	3.87 ± 0.01	130.9 ± 0.16
860	6.25 ± 0.54	3.88 ± 0.01	131.6 ± 0.24
500	4.09 ± 0.53	3.49 ± 0.03	116.6 ± 1.19
290	3.48 ± 0.01	3.04 ± 0.02	100.2 ± 0.75
80	0.59 ± 0.52	2.67 ± 0.06	86.9 ± 2.29
0	-1.06 ± 0.54	1.96 ± 0.04	62.2 ± 1.39

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2360	1647 ± 229.3	13.33 ± 1.89	265.0 ± 9.43
1860	3811 ± 286.9	14.33 ± 0.94	257.7 ± 5.99
1370	4160 ± 383.7	12.67 ± 0.94	266.9 ± 5.11
1180	4052 ± 450.1	12.00 ± 1.41	271.2 ± 1.38
860	7264 ± 625.3	16.00 ± 1.41	248.1 ± 6.98
500	8180 ± 1065.3	12.00 ± 1.41	270.0 ± 7.16
290	11991 ± 22.6	11.33 ± 0.47	271.5 ± 0.51
80	7369 ± 6436.9	2.33 ± 1.89	317.7 ± 9.30
0			354.8 ± 13.81

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C. Drought Control 3.

PFD	A	E	g
2280	7.40 ± 0.45	2.29 ± 0.09	74.6 ± 3.02
1740	8.17 ± 0.45	2.91 ± 0.03	97.1 ± 0.93
1340	7.83 ± 0.75	2.04 ± 0.01	65.7 ± 0.37
1000	5.57 ± 0.45	2.06 ± 0.01	66.5 ± 0.24
720	5.60 ± 0.45	2.09 ± 0.02	67.5 ± 0.61
450	6.04 ± 0.78	1.75 ± 0.01	55.9 ± 0.22
250	3.51 ± 0.44	1.67 ± 0.47	53.0 ± 0.25
80	3.31 ± 0.67	1.33 ± 0.35	42.0 ± 11.46
0	-0.51 ± 1.54	1.46 ± 0.01	46.0 ± 0.37

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2280	3246 ± 195.9	32.33 ± 2.05	169.9 ± 12.28
1740	4705 ± 229.8	28.33 ± 1.70	192.6 ± 8.55
1340	4473 ± 1391.0	38.33 ± 3.68	138.9 ± 18.69
1000	5609 ± 437.7	27.33 ± 2.36	196.2 ± 11.37
720	7773 ± 628.7	27.00 ± 2.16	197.4 ± 11.50
450	13412 ± 1726.1	34.67 ± 4.50	158.3 ± 22.18
250	13896 ± 1904.2	21.00 ± 2.83	225.7 ± 13.45
80	41364 ± 8337.9	25.33 ± 4.11	201.6 ± 21.42
0			349.9 ± 53.27

Gas exchange data of the response of *Hordeum vulgare* cv. Cilpper to light intensity at 25.0°C. Drought 3.

PFD	A	E	g
1960	1.24 ± 0.36	1.81 ± 0.04	59.8 ± 1.76
1470	0.66 ± 0.32	1.46 ± 0.01	47.5 ± 0.14
900	1.42 ± 0.66	1.33 ± 0.01	42.9 ± 0.33
670	1.03 ± 0.42	1.47 ± 0.01	47.8 ± 0.14
430	0.61 ± 0.33	1.63 ± 0.00	53.8 ± 0.14
250	1.60 ± 0.01	1.46 ± 0.01	47.4 ± 0.48
140	1.41 ± 0.32	1.36 ± 0.02	43.8 ± 0.74
60	-0.17 ± 0.66	1.17 ± 0.03	37.5 ± 1.05
0	-2.44 ± 0.01	0.92 ± 0.01	29.2 ± 0.39

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1960	63 9 ± 192.0	7.00 ± 2.16	353.6 ± 10.13
1470	44 6 ± 220.3	4.33 ± 2.36	307.3 ± 11.05
900	1570 ± 724.6	10.67 ± 5.18	276.4 ± 24.65
670	2047 ± 495.5	9.33 ± 2.36	283.2 ± 11.20
430	1412 ± 773.8	3.67 ± 1.89	311.2 ± 10.15
250	64.14 ± 21.7	11.00 ± 0.00	274.9 ± 0.74
140	10050 ± 2321.3	10.33 ± 2.36	278.0 ± 11.34
60			337.5 ± 28.60
0			461.9 ± 1.50

Gas exchange data of the response of *Hordeum vulgare* cv. Cipper to light intensity at 22.0°C. Drought Control 4.

PFD	A	E	g
2160	5.33 ± 0.33	2.27 ± 0.01	76.7 ± 0.48
1630	5.12 ± 0.33	2.29 ± 0.02	77.4 ± 0.62
1240	3.98 ± 0.28	2.22 ± 0.16	75.2 ± 5.55
980	3.98 ± 0.28	2.18 ± 0.16	73.6 ± 5.47
670	5.59 ± 0.01	2.31 ± 0.00	78.4 ± 0.20
370	4.16 ± 0.00	2.28 ± 0.01	77.3 ± 0.24
110	4.44 ± 1.67	2.11 ± 0.02	70.8 ± 1.50
60	3.82 ± 0.34	1.85 ± 0.04	61.3 ± 0.49
0	-0.79 ± 0.33	1.59 ± 0.02	52.0 ± 0.82

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2160	2472 ± 150.6	23.33 ± 1.70	216.9 ± 7.74
1630	3113 ± 224.9	22.33 ± 1.89	222.7 ± 8.09
1240	3179 ± 206.9	18.00 ± 0.00	244.7 ± 0.41
980	4096 ± 305.5	18.00 ± 0.00	242.6 ± 0.33
670	8334 ± 5.0	24.00 ± 0.00	213.9 ± 0.35
370	11237 ± 2.1	18.00 ± 0.00	243.2 ± 0.27
110	40391 ± 15196.9	21.33 ± 80.1	228.5 ± 39.81
60	63675 ± 5710.3	21.00 ± 2.16	230.2 ± 11.17
0			353.7 ± 10.13

Gas exchange data of the response of *Hordeum vulgare* cv. Clipper to light intensity at 25.0°C. Drought 4.

PFD	A	E	g
1930	2.42 ± 0.60	2.68 ± 0.45	87.2 ± 14.90
1470	3.28 ± 0.06	2.82 ± 0.18	91.7 ± 6.28
1060	4.18 ± 0.67	2.95 ± 0.00	96.0 ± 0.00
830	3.73 ± 0.66	2.88 ± 0.03	93.5 ± 0.99
590	3.40 ± 0.00	2.45 ± 0.00	78.7 ± 0.00
470	2.37 ± 0.67	2.71 ± 0.02	87.6 ± 0.62
260	-0.90 ± 0.01	2.64 ± 0.02	85.3 ± 0.62
60	-1.29 ± 0.67	2.39 ± 0.02	76.8 ± 0.71
0	-4.55 ± 0.66	2.29 ± 0.02	73.5 ± 0.66

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1930	1258 ± 318.0	9.33 ± 2.36	278.7 ± 11.46
1470	2247 ± 41.9	11.67 ± 0.94	266.4 ± 5.14
1060	3914 ± 609.5	14.33 ± 2.36	254.1 ± 11.30
830	4493 ± 800.9	13.00 ± 2.16	260.0 ± 11.48
590	5762 ± 0.0	14.00 ± 0.00	255.2 ± 0.00
470	5074 ± 1407.6	8.67 ± 2.36	280.9 ± 12.69
260			342.0 ± 0.00
60			351.8 ± 13.89
0			424.6 ± 15.72

APPENDIX F

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C. Drought Control 1.

PFD	A	E	g
2000	14.56 ± 0.40	4.05 ± 0.06	175.3 ± 3.10
1540	16.27 ± 0.02	4.61 ± 0.07	206.5 ± 3.96
1150	16.12 ± 0.38	4.23 ± 0.02	185.0 ± 1.18
850	15.64 ± 0.01	4.03 ± 0.01	174.4 ± 0.61
640	13.81 ± 0.38	3.83 ± 0.02	163.6 ± 1.18
360	12.55 ± 0.01	3.56 ± 0.03	149.9 ± 1.50
180	9.97 ± 0.37	3.19 ± 0.04	131.9 ± 2.00
60	5.03 ± 0.40	2.61 ± 0.06	104.2 ± 3.11
0	-0.41 ± 1.61	1.97 ± 0.18	76.5 ± 7.59

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2000	7278 ± 199.5	36.00 ± 1.41	182.5 ± 6.14
1540	10750 ± 130.2	35.33 ± 0.47	186.9 ± 2.54
1150	14016 ± 328.1	37.00 ± 0.82	174.2 ± 3.35
850	18397 ± 4.2	39.00 ± 0.00	170.9 ± 0.51
640	21698 ± 686.5	36.00 ± 0.82	181.5 ± 3.76
360	34857 ± 27.1	35.33 ± 0.47	184.2 ± 1.40
180	53452 ± 2913.1	31.33 ± 0.94	200.4 ± 3.38
60	83893 ± 6677.0	19.33 ± 1.89	249.2 ± 8.59
0			343.2 ± 36.46

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C. Drought 1.

PFD	A	E	g
2220	6.18 ± 1.39	3.30 ± 0.11	134.7 ± 5.02
1770	8.98 ± 1.36	3.02 ± 0.11	121.2 ± 4.48
1430	9.96 ± 1.40	2.87 ± 0.16	114.4 ± 6.94
1100	7.93 ± 1.19	2.77 ± 0.01	109.7 ± 0.17
820	9.83 ± 0.89	2.71 ± 0.01	107.0 ± 0.66
630	9.45 ± 0.01	2.79 ± 0.01	110.8 ± 0.71
350	7.87 ± 0.44	2.73 ± 0.02	108.2 ± 0.65
180	7.12 ± 1.17	2.09 ± 0.02	80.5 ± 0.70
40	1.22 ± 0.02	1.94 ± 0.05	74.0 ± 2.12
0	-2.64 ± 0.45	1.19 ± 0.02	44.2 ± 0.86

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2220	2776 ± 617.6	19.00 ± 4.90	255.8 ± 20.23
1770	5070 ± 737.2	29.67 ± 3.40	209.8 ± 14.87
1430	6785 ± 758.6	33.67 ± 2.87	192.9 ± 12.31
1100	7505 ± 1391.7	28.67 ± 4.11	213.4 ± 18.33
820	11989 ± 1088.5	36.33 ± 3.91	180.8 ± 13.64
630	15081 ± 121.5	34.00 ± 0.00	191.4 ± 0.95
350	22580 ± 1402.6	29.00 ± 1.41	212.9 ± 6.26
180	39570 ± 6505.7	33.67 ± 5.44	189.3 ± 23.55
40	30415 ± 456.0	6.33 ± 0.47	307.9 ± 1.14
0			430.9 ± 17.73

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C. Drought Control 2.

PFD	A	E	g
2150	8.29 ± 0.45	3.67 ± 0.09	153.3 ± 4.37
1670	11.18 ± 0.73	3.86 ± 0.01	162.9 ± 0.68
1210	10.34 ± 1.47	2.81 ± 1.39	153.8 ± 0.61
1010	8.43 ± 0.86	3.56 ± 0.01	147.6 ± 0.52
720	9.40 ± 0.42	3.38 ± 0.05	138.9 ± 2.05
540	7.10 ± 0.73	2.96 ± 0.04	119.1 ± 1.90
350	5.76 ± 1.11	2.36 ± 0.03	92.5 ± 1.52
150	0.56 ± 0.83	1.81 ± 0.05	69.4 ± 1.89
30	-2.66 ± 1.13	1.65 ± 0.04	62.3 ± 1.55

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2150	3854 ± 209.9	22.33 ± 1.70	240.8 ± 7.25
1670	6817 ± 439.3	29.00 ± 1.63	214.7 ± 7.44
1210	8542 ± 1215.4	28.00 ± 4.08	217.9 ± 17.13
1010	8343 ± 850.1	23.67 ± 2.36	236.1 ± 10.24
720	13112 ± 495.0	28.00 ± 0.82	218.5 ± 3.82
540	13294 ± 1276.4	24.33 ± 2.49	220.5 ± 3.93
350	16348 ± 3305.7	24.33 ± 4.19	231.4 ± 18.59
150	6476 ± 1653.3	2.67 ± 4.71	322.1 ± 19.76
30			404.2 ± 27.92

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C. Drought 2.

PFD	A	E	g
2330	1.38 ± 0.90	1.84 ± 0.11	69.5 ± 4.25
1780	2.10 ± 0.00	2.14 ± 0.01	81.7 ± 0.24
1290	6.01 ± 0.01	1.94 ± 0.02	73.3 ± 0.95
750	2.87 ± 0.44	1.78 ± 0.01	66.9 ± 0.45
480	0.69 ± 0.45	1.62 ± 0.01	60.7 ± 0.50
270	-0.56 ± 0.00	1.60 ± 0.01	59.4 ± 0.28
110	-1.17 ± 0.45	1.53 ± 0.02	56.8 ± 0.70
0	-1.69 ± 0.45	1.25 ± 0.01	45.8 ± 0.46

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2330	1025 ± 229.1	12.67 ± 2.36	279.0 ± 10.30
1780	1179 ± 5.1	10.00 ± 0.00	292.5 ± 0.20
1290	4668 ± 56.0	31.67 ± 0.47	200.5 ± 1.79
750	3843 ± 608.3	16.33 ± 2.36	265.5 ± 10.09
480	2664 ± 1439.3	4.00 ± 2.83	316.5 ± 12.21
270			350.0 ± 0.00
110			367.8 ± 12.62
0			393.9 ± 15.21

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C. Drought Control 3.

PFD	A	E	g
2220	6.63 ± 0.39	3.48 ± 0.01	144.7 ± 0.36
1750	7.25 ± 0.38	3.34 ± 0.01	137.6 ± 0.36
1290	5.78 ± 0.38	2.97 ± 0.02	120.0 ± 0.85
700	5.65 ± 0.01	2.61 ± 0.02	103.3 ± 0.95
460	4.48 ± 0.38	2.05 ± 0.01	78.8 ± 0.20
380	5.27 ± 0.77	2.04 ± 0.02	78.4 ± 0.56
200	1.99 ± 0.33	1.30 ± 0.96	76.3 ± 0.35
100	1.38 ± 0.38	1.53 ± 0.03	57.4 ± 1.28
0	-0.71 ± 0.38	1.26 ± 0.02	46.4 ± 0.70

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2220	2983 ± 171.4	19.00 ± 1.41	254.0 ± 4.87
1750	4137 ± 222.8	21.67 ± 0.94	242.5 ± 4.73
1290	4472 ± 304.6	19.33 ± 1.25	251.5 ± 5.22
700	8148 ± 43.3	21.67 ± 0.47	241.5 ± 0.92
460	9734 ± 837.5	22.00 ± 2.16	239.7 ± 8.13
380	13649 ± 2086.0	26.00 ± 4.24	222.4 ± 17.07
200	9948 ± 1673.0	9.00 ± 0.00	295.9 ± 0.23
100	13758 ± 3778.1	9.00 ± 2.16	294.9 ± 10.05
0			358.7 ± 13.70

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C. Drought 3.

PFD	A	E	g
2240	3.40 ± 0.28	1.32 ± 0.01	50.6 ± 0.42
1870	3.79 ± 0.01	1.35 ± 0.01	51.9 ± 0.59
1440	4.58 ± 0.29	1.38 ± 0.01	53.2 ± 0.60
1090	4.16 ± 0.28	1.38 ± 0.01	53.2 ± 0.17
830	4.16 ± 0.28	1.35 ± 0.01	51.8 ± 0.19
630	2.15 ± 0.28	1.36 ± 0.01	52.2 ± 0.64
340	2.19 ± 0.30	1.28 ± 0.01	48.9 ± 0.56
130	1.02 ± 0.30	1.18 ± 0.03	44.7 ± 1.38
70	0.51 ± 0.28	0.87 ± 0.02	32.6 ± 0.98
0	-3.10 ± 0.75	0.77 ± 0.02	28.7 ± 0.76

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2240	1516 ± 128.2	25.33 ± 1.89	224.9 ± 8.36
1870	2021 ± 11.3	28.33 ± 0.47	211.1 ± 1.45
1440	3186 ± 210.7	33.00 ± 2.16	189.5 ± 9.48
1090	3818 ± 262.3	30.00 ± 2.16	203.3 ± 8.69
830	4999 ± 367.0	34.00 ± 2.83	199.9 ± 8.49
630	3390 ± 460.5	16.00 ± 2.16	264.6 ± 8.44
340	6575 ± 928.5	17.00 ± 2.83	258.8 ± 10.61
130	7794 ± 229.5	9.00 ± 2.83	294.7 ± 12.17
70	7257 ± 4094.0	5.67 ± 3.09	306.9 ± 14.09
0			508.9 ± 45.47

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C. Drought Control 4.

PFD	A	E	g
2000	6.85 ± 0.37	3.96 ± 0.11	177.1 ± 6.41
1550	6.48 ± 0.33	2.96 ± 0.02	123.8 ± 1.08
1180	8.63 ± 0.33	3.01 ± 0.01	126.3 ± 0.65
820	7.01 ± 0.33	3.02 ± 0.03	126.6 ± 1.51
640	5.79 ± 0.33	2.44 ± 0.04	99.0 ± 1.88
410	4.68 ± 0.33	2.09 ± 0.01	82.8 ± 0.24
210	6.16 ± 0.65	1.81 ± 0.05	70.4 ± 2.01
130	4.52 ± 0.33	1.78 ± 0.00	69.4 ± 0.00
50	2.09 ± 0.34	1.42 ± 0.04	54.4 ± 1.50
0	-0.37 ± 0.01	0.97 ± 0.01	36.2 ± 0.45

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
2000	3393 ± 160.2	17.33 ± 1.70	264.7 ± 5.84
1500	4172 ± 192.9	22.00 ± 1.41	246.2 ± 4.95
1180	7273 ± 297.7	29.00 ± 1.41	215.9 ± 5.18
820	8481 ± 422.2	23.00 ± 0.82	238.9 ± 3.62
640	8944 ± 578.4	23.67 ± 0.94	235.6 ± 4.26
410	11322 ± 919.2	22.00 ± 1.41	240/3 ± 6.44
210	29358 ± 3095.5	34.00 ± 2.23	189.9 ± 11.46
130	34819 ± 2546.5	25.33 ± 1.89	226.6 ± 7.92
50	41866 ± 6720.3	14.67 ± 2.62	318.6 ± 0.38
0			

Gas exchange data of the response of *Hordeum vulgare* cv. Dayan to light intensity at 22.5°C. Drought 4.

PFD	A	E	g
1900	0.37 ± 0.01	1.41 ± 0.02	52.9 ± 0.82
1450	1.15 ± 0.01	1.62 ± 0.01	61.2 ± 0.47
1090	2.82 ± 0.01	1.67 ± 0.01	63.6 ± 0.52
780	1.41 ± 0.40	1.66 ± 0.00	62.9 ± 0.00
440	1.13 ± 0.01	1.63 ± 0.01	61.9 ± 0.47
240	0.87 ± 0.40	1.59 ± 0.02	60.2 ± 0.66
50	1.46 ± 0.40	1.51 ± 0.04	56.9 ± 1.75
0	-1.04 ± 0.40	1.38 ± 0.01	51.9 ± 0.47

PFD	Q x 10^{-6}	WUE x 10^{-4}	Ci
1990	192 ± 3.68	2.67 ± 0.01	315.9 ± 0.38
1450	789 ± 2.83	7.00 ± 0.00	296.8 ± 0.33
1090	2581 ± 13.14	17.00 ± 0.00	254.7 ± 0.62
780	1811 ± 512.9	8.67 ± 2.36	290.6 ± 10.39
440	2585 ± 9.2	7.00 ± 0.00	297.3 ± 0.33
240	3625 ± 1644.9	5.33 ± 2.36	303.8 ± 10.54
50	20895 ± 5773.2	9.67 ± 3.09	285.3 ± 11.99
0			359.7 ± 12.52

APPENDIX G

Hoaglands nutrient solution

Macronutrients			
Compound	Molecular Weight	Element	Concentration (μM)
KNO_3	101.10	N	16000.0
$Ca(NO_3)_2$ $4H_2O$	236.16	K	6000.0
$NH_4H_2PO_4$	115.08	Ca	4000.0
$MgSO_4$ $7H_2O$	246.49	P	2000.0
		S	1000.0
		Mg	1000.0

Micronutrients			
Compound	Molecular Weight	Element	Concentration (μM)
KCl	74.55	Cl	50.0
H_3BO_3	61.84	B	25.0
$MnSO_4$ H_2O	169.01	Mn	2.0
$ZnSO_4$ $7H_2O$	287.55	Zn	2.0
$CuSO_4$ $5H_2O$	249.71	Cu	0.5
H_2MoO_4 (85% MoO_3)	161.97	Mo	0.5
Fe-EDTA	346.08	Fe	20.0