

Effects of Radiation, Temperature and Humidity on Photosynthesis, Transpiration and Water Use Efficiency of Oilseed Rape (*Brassica campestris* L.)

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Abstract. The net photosynthetic rate (F), transpiration rate (Q) and water use efficiency (F/Q) of oilseed rape (*Brassica campestris* L. cv. Span) was studied under a range of atmospheric conditions by gas exchange techniques. The plants were at the full bloom/pod initiation stage of development at the time of measurement. The environmental conditions consisted of various levels of photosynthetically active radiation (100 to 2800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR: 400–700 nm), air temperature (10 to 42 °C) and vapour pressure deficit (0.7 to 2.1 kPa VPD). The peak values of F were recorded at 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, 20 °C air temperature and 1.2 kPa VPD of air in the chamber.

Q increased with increasing PAR, air temperature and VPD. However, the F/Q remained high and almost constant from 600 to 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, but declined at the low and high photon flux densities. F/Q decreased progressively with increase in air temperature and VPD of air in the chamber.

The environment, especially factors of the physical environment including radiation, temperature and atmospheric humidity, may cause stresses producing anything from mild perturbations having negligible effects on yield to severe stress resulting in critical crop losses (THRESHOW 1970). Rarely in nature do plants grow under fully optimum conditions. It follows that the continued improvement in crop production, either through breeding or by adopting suitable agronomic practices, may be obtained only by determining the ideal conditions regulating the physiological processes, growth and productivity of each given species. As in many other crops, flowering and pod development are the most critical stages that affect the final grain yield of oilseed rape (ALLEN and MORGAN 1975, RICHARDS and THURLING 1978, TAYO and MORGAN 1979, THURLING and VIJENDRA DAS 1980). The results of shading experiments under controlled environmental conditions suggest that a reduction in the supply of carbon assimilates around the time of anthesis is particularly harmful since in addition to reducing the number of pods which develop, it appears to restrict the capacity for compensatory

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growth in the remaining pods when the supply returns to normal (TAYO and MORGAN 1979). Therefore, the studies reported here were conducted with the objective of assessing the effects of photosynthetically active radiation, air temperature and humidity on net photosynthetic (F) and transpiration (Q) rates and water use efficiency (F/Q) of oilseed rape. In this paper the vapour pressure deficit of air (leaf to air water vapour pressure difference) has been used to study the effects of humidity on the physiological processes in rape.

MATERIAL AND METHODS

Plant Culture

Oilseed rape (*Brassica campestris* L. cv. Span) was grown in a standard potting mixture of peat, river sand and soil in free-draining pots. A single plant that received adequate water and nutrients was grown in each pot in a naturally lit glasshouse maintained at 27/22 °C day/night temperatures. No stress symptoms were noted during the growth of the rape. At the time of measurement, the plants were at full flowering to early pod initiation.

Measurements

Prior to measurement, one fully expanded leaf attached on the mainstem was permitted to equilibrate for several hours under one set of environmental conditions; subsequent environmental conditions were imposed once a plateau in gas exchange had been maintained for at least 2 h. During the measurements, a single intact leaf was enclosed in a 17 × 20 × 2 cm water-cooled, perspex chamber. The CO₂ differential across the assimilation chamber was determined using an infrared gas analyser (Analytical Development Co., Hoddesdon, U.K.) and transpiration rate was determined using a dew point hygrometer (Cambridge International Systems, Massachusetts, U.S.A.). Leaf and air temperatures within the chamber were measured with thermocouples, and the quantum flux density within the chamber was measured with a Li-Cor quantum sensor placed adjacent to the leaves. The leaf area was measured by a portable area meter (Li-Cor Model 3000). The apparatus has been described in detail by RAWSON and WOODWARD (1976).

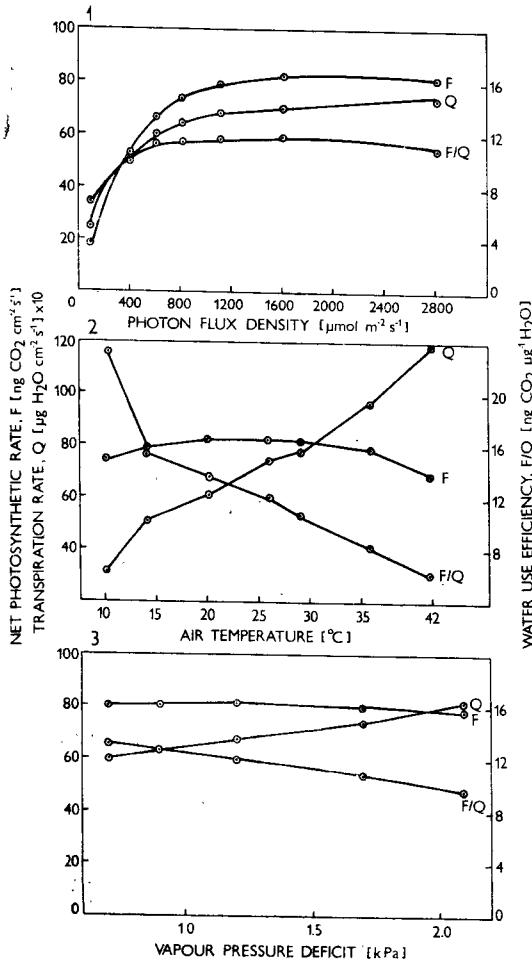
The chamber was placed horizontally alongside the plant canopy. One Philips 1800 W Quartzline light and one 400 W mercury vapour lamp together with different thicknesses of white tissue paper were used to attain six quantum flux densities (100, 400, 600, 1100, 1600, 2800 μmol m⁻² s⁻¹ PAR: 400–700 nm). Temperature control was achieved by an automatic airconditioning unit circulating water through the water jacket of the chamber. The different temperature levels maintained in the chamber were 10, 14, 20, 26, 29, 36 and 42 °C. Humidity was controlled by a dewpoint hygrometer and various vapour pressure deficits obtained by passing various proportions of humidified to dry air through the chamber (0.7, 0.9, 1.2, 1.7 and 2.1 kPa VPD). The flow rate of air passing through the chamber was maintained so that ambient CO₂ was depleted by no more than 20 cm³ m⁻³. The area of leaves enclosed in the chamber varied from 100 to 130 cm². The plants used had leaf water potentials, osmotic potentials and turgor pressures of $-7.0 \pm 0.3 \times 10^5$ Pa, $-10.0 \pm 0.4 \times 10^5$ Pa and $+3.0 \pm 0.3 \times 10^5$ Pa respectively. The rate of net photosynthesis (F) and transpiration (Q) have

been expressed on a leaf area basis as in RAWSON *et al.* (1978). The water use efficiency (F/Q) was calculated by dividing the rate of net photosynthesis with the rate of water loss obtained under a particular set of conditions.

RESULTS AND DISCUSSION

Effect of Photosynthetically Active Radiation

The response of F to quantum flux density is shown in Fig. 1. The shape of the F/PAR curve was curvilinear from flux densities of 100 to 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. However, the increases in F above 1100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR were only marginal, indicating light saturation around this quantum flux density. Similar results showing positive response to PAR have been reported for wheat and sorghum (DOWNES 1970), subterranean clover (FUKAI and SILSBURY 1977), soybean and sorghum (RAWSON *et al.* 1978) and cotton (CONSTABLE and RAWSON 1980). TAYO and MORGAN (1979) reported that the shading of leaves at flowering reduced the number of pods and seed yield



Figs. 1 to 3. Effect of photon flux density (400–700 nm) (1), air temperature (2) and vapour pressure deficit (3) of air on net photosynthetic rate (F), transpiration rate (Q) and water use efficiency (F/Q) in oil seed rape.

in rape. Their results provide the evidence that the supply of carbon assimilates regulates the number of pods which develop on the axillary racemes as well as on the terminal inflorescence.

The rate of transpiration (Q) also showed a curvilinear response to increasing PAR (Fig. 1). TURNER (1974) showed that leaf diffusive conductance to water vapour in field crops such as tobacco and sunflower was strongly dependent on light in much the same way as is transpiration in rape.

An increase in PAR from 100 to 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ increased the water use efficiency (F/Q) in rape, due to a proportionately greater increase in F than Q in this range of quantum flux density (Fig. 1). Above 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, F/Q remained almost constant and then declined above 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR due to a slight drop in F , which could be nonstomatal in nature (THRESHOW 1970, CHARTIER *et al.* 1977).

Effect of Temperature

The value of F increased slightly due to an increase in air temperature from 10 °C to 20 °C, was constant from 20 °C to 30 °C and declined at air temperatures above 30 °C (Fig. 2). Maximum rates of photosynthesis occur at 20 to 30 °C in most temperate crops and as high as 35 °C in some tropical plants (THRESHOW 1970, BAKER *et al.* 1972, FUKAI and SILSBURY 1977, SINGH *et al.* 1982). The decrease in F at high temperatures may reflect an increase in the rate of respiration at high temperatures (BAKER *et al.* 1972, FUKAI and SILSBURY 1977). Some years ago injury from high temperature was often attributed to denaturation of proteins, but recently such injuries have been reported to occur because of inactivation of enzymes and damage to cell membranes (THRESHOW 1970, TURNER and KRAMER 1980).

Q increased almost linearly with increasing air temperature, while F/Q showed the reverse trend; *i.e.*, F/Q decreased almost linearly with increasing air temperature. It is now widely accepted that low temperatures reduce transpiration due to an increase in the viscosity of water and a decrease in membrane permeability to water movement at low temperatures (KRAMER 1969). This may be the reason for the low rate of transpiration at 10 °C.

Effect of Humidity

F was not affected markedly by VPD over the whole range of VPD's studied in this experiment. However, the peak values of F were recorded at 1.2 kPa VPD (Fig. 3). RAWSON *et al.* (1977) observed that changes in VPD from 0.5 to 2.9 kPa had no significant effect on photosynthesis in several crop species. They suggested that the exposure to high VPD of only a single leaf or small portion of a whole plant may not allow water stress to develop as the stressed portion may draw water from other portions of the plant not so similarly stressed. At greater values of VPD than those imposed in this study, stress conditions (decrease in leaf water potential and stomatal closure) are likely to develop even when only part is exposed to high VPD (BOYER 1975). The second effect of low humidity is a partial closure of stomata independent of the bulk leaf water potential (LANGE *et al.* 1971); this results in reduced rates of photosynthesis. WOODWARD and BEGG (1976) in soybean, RAWSON *et al.* (1977) in barley and SINGH *et al.* (1982) in chickpea also observed a drop in the rate of photosynthesis at high VPD.

The rate of transpiration increased almost linearly and F/Q decreased linearly with increase in VPD. The difference in vapour pressure between the leaf and air is known to be a major driving force for transpiration (PENMAN 1955, KRAMER 1969). The rate of transpiration increased linearly with increasing VPD in several crop species (RAWSON *et al.* 1977).

GENERAL DISCUSSION AND CONCLUSIONS

In conclusion, the maximum rate of net photosynthesis was attained at 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, 20 °C air temperature and 1.2 kPa VPD when oilseed rape was studied at the flowering stage of development. The plants can also maintain reasonably high rates of net photosynthesis and water use efficiency even if quantum flux density varies from 800 to 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, air temperature from 14 to 30 °C and VPD from 0.7 to 1.7 kPa. If this also applies in the field, these conditions occur for 3 to 4 h around midday in January and for 4 to 5 h around midday in February during the growing season for rape in northern India.

Brassica campestris L. and *Brassica juncea* L. are the two most common species of *Brassica* cultivated in India. They enter the stem elongation phase (flower initiation to anthesis) in the month of January. At this stage a greater part of the leaf area remains under sub-optimal radiation because of shading by the developing inflorescence. The day/night temperatures also remain sub-optimum except for a few hours around midday. The supply of assimilates during flowering regulates the number of pods per plant (TAYO and MORGAN 1979). This character is a major determinant of grain yield in *Brassica* species (CAMPBELL *et al.* 1978, YADAV *et al.* 1978, TAYO and MORGAN 1979, THURLING and VIJENDRA DAS 1980). In Indian mustard, the number of siliqua per plant is positively correlated with the maturity time (YADAV *et al.* 1978). However, the long maturing cultivars of rape and mustard are undesirable since not only are they susceptible to frost injury in January, but they are also susceptible to water deficits and high temperatures during grain filling. Indeed, there are reports from Canada and Australia that the correlation of days to first flower and maturity against yield is negative due to severe water shortage limiting yield in late cultivars (CAMPBELL *et al.* 1978, THURLING and VIJENDRA DAS 1980). *Brassica napus* L. cv. Altex, which was selected for early first flower under sub-optimal atmospheric conditions, is a frost resistant, short duration (110 days) cultivar that possesses a high flowering rate and dry matter accumulation under the cooler growing conditions of Canada (CAMPBELL *et al.* 1978). Genotypic variation for duration of stem elongation has also been observed among cultivars and F_1 hybrids of *Brassica napus* L. by THURLING and VIJENDRA DAS (1980). Thus, the chances of combining a shorter vegetative phase with a longer stem elongation phase in order to provide an optimum time for flowering and high grain yield appear good in *Brassica napus* L., a species that is frost resistant, rich in oil and a high yielder. A similar selection programme would be needed in *Brassica campestris* to better suit it to the climate of northern India.

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