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Reduction in the efficiency of light use due to disease

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RESUMO

Foram estudados os efeitos de uma micose causada por *Ascochyta fabae* na interceptação de luz solar pelo copado e no crescimento de *Vicia faba*, durante o seu cultivo no campo (Universidade de Nottingham, Inglaterra). Infecções precoces reduziram a "duração da área foliar" e a "eficiência de utilização de luz", originando um decréscimo na produção de matéria seca da cultura.

RÉSUMÉ

Les effets d'une maladie due à *Ascochyta fabae* ont été étudiés vis-à-vis à l'interception du rayonnement solaire par les feuilles et à la croissance des plantes de *Vicia faba*. Les essais ont été faits en culture à l'air libre (Université de Nottingham, Angleterre). Des infections précoces entraînent à la réduction soit de "la durée de l'aire foliaire" soit de "l'efficacité d'utilisation du rayonnement". Par conséquence, le décroissement de la matière sèche de la culture a été constaté.

SYNOPSIS

The effects of disease and the timing of infection on light interception and growth were studied on field bean (*Vicia faba*). Early infection by *Ascochyta fabae* reduced both leaf area duration and light use efficiency and, consequently, the dry matter production of the crop.

1. INTRODUCTION

Observations of the depression of crop yields by disease are commonplace, and the control of disease outbreaks is of major concern in agriculture and forestry. However, the mechanisms of yield depression are relatively poorly quantified, despite the scientific and practical importance of the subject (BOOTE *et al.*, 1983; MADDEN, 1983; WAGGONER & BERGER, 1987; BRASSETT & GILLIGAN, 1989). The effects of disease and other stresses on the ability of vegetation to produce photosynthate (measured as dry matter production) can be considered in terms of those which reduce the quantity of solar energy intercepted by the crop and those which reduce the efficiency with which the intercepted energy is fixed in photosynthesis, or both (MONTEITH, 1977).

Much evidence suggests that the main influence of stresses on dry matter production is through consequent reductions in the size and duration of the leaf canopy, and therefore light interception (BISCOE & GALLAGHER, 1977; GALLAGHER & BISCOE, 1978; WAGGONER & BERGER, 1987; MADEIRA, CLARK & ROSSALL, 1988; RUSSELL, JARVIS & MONTEITH, 1988). However, GREEN, HEBBLETHWAITE & ISON (1985) have shown that the efficiency of light use in field bean (*Vicia faba*) may be reduced by water stress, while HUGHES (1988) suggested that similar effects may be expected due to disease.

The analysis proposed by MONTEITH (1977) identifies three factors which express the dependence of the dry matter production of vegetation on environmental and biological variables:

- (a) crop duration, the period over which green vegetation is present, t (days);
- (b) the quantity of solar radiation intercepted by the crop canopy, equal to the product fI ($\text{MJ m}^{-2} \text{d}^{-1}$), where I is the incident flux density ($\text{MJ m}^{-2} \text{d}^{-1}$) and f is the fraction of radiation intercepted;
- (c) the efficiency of light use or dry matter yield of energy, e (g MJ^{-1}), which measures the efficiency with which the vegetation converts intercepted solar energy to dry matter.

The dry matter produced by the vegetation, W (g m^{-2}) is the time integral of the product of the above terms

$$W = \int e f I dt. \tag{1}$$

The weather of a particular season determines the available solar radiation and also influences the crop duration through the temperature and water balance. Other environmental and biological factors influence dry matter production through their indirect effects on f and e . The fraction of radiation intercepted is determined by canopy leaf area and leaf geometry, and may be related to them by an equation of the form of Beer's law, where path length is replaced by leaf area index, L (MONTEITH, 1975).

WAGGONER & BERGER (1987) recently used a model similar to that of MONTEITH (1977) to analyse the published yields of a number of crops in terms of the effects on the canopy of biotic stress due to pathogen attack. If $(1-d)L$ is the leaf area index of a diseased crop (excluding defoliation d , due to a particular disease) and x is the fraction of leaf area affected by the pathogen, WAGGONER & BERGER give

$$W_1 = \int e_1 \{1 - \exp[-K(1-d)L]\} I(1-x) dt \tag{2}$$

thus

$$f_1 = (1-x) \{1 - \exp[-K(1-d)L]\} \tag{3}$$

where K is the extinction coefficient for the particular crop. A simplified approach was used in the present work, considering light interception by healthy leaf tissue only. In this case

$$W_2 = \int e_2 \{1 - \exp[-K(1-x)L]\} I dt \tag{4}$$

and

$$f_2 = 1 - \exp[-K(1-x)L] \tag{5}$$

where $(1-x)L$ is the healthy leaf area index of the diseased crop. Usually, d is negligible for the first stages of infection by disease. The difference between these two equations is associated with different methods of estimation of f for diseased crops, as the fraction of radiation intercepted is not affected by x in the equation (2). Hence, different values will be obtained for e_1 and e_2 .

As noted earlier, the main differences in the dry matter production of vegetation are usually associated with differences in canopy leaf area and duration and therefore in intercepted radiation, and e is a relatively conservative quantity (BISCOE & GALLAGHER, 1977; MONTEITH, 1977; GALLAGHER & BISCOE, 1978; WAGGONER & BERGER, 1987; HUGHES, 1988; RUSSELL *et al.*, 1988).

This paper reports the first measurement of a reduction in the efficiency of light use by a crop (*Vicia faba* L.) due to a leaf and pod spot disease and compares the two models. The pathogen *Ascochyta fabae* Speg., responsible for this disease, induces necrotic lesions, which constitute a loss of photosynthesizing tissue. The necrotic leaf tissue may remain and affect light interception, but often falls out depending on the severity of infection and the weather conditions. Leaf senescence is also induced by *A. fabae* infection.

2. MATERIALS AND METHODS

The measurements of dry matter yield of energy reported here were obtained in an field experiment where crops of the determinate field bean cultivar "Ticol" were deliberately infected with *Ascochyta fabae*. This experiment was done in order to study the effects of the crop stage at which infection commenced and severity of infection on subsequent crop growth (MADEIRA, 1988; Madeira *et al.*, 1988). The growth, dry matter production and yield of the infected crops, grown at Nottingham in 1987, were compared with those obtained from a control crop, which was untreated, and with a crop receiving a prophylactic fungicide treatment using chlorothalonil (JELLIS, LOCKWOOD & AUBURY, 1984).

Samples for growth analysis were harvested at intervals of approximately two weeks, from six weeks after sowing to crop maturity (21 weeks). Measurements were made of canopy leaf area (Leaf Area Meter, Delta-T Devices Ltd.), above ground dry matter and the extent of infection by *A. fabae* and other diseases. Concurrent measurements were made of the solar radiation intercepted by the crops, using tube solarimeters placed above and below the canopies. Seed yields were also assessed at final harvest. The results of this work are reported in detail elsewhere (MADEIRA, 1988; MADEIRA *et al.*, 1988).

3. RESULTS AND DISCUSSION

The measurements of total dry matter production per unit area obtained at successive harvests up to 126 days after sowing are plotted against estimates of intercepted solar radiation accumulated over the corresponding periods in Fig. 1. The slopes of the lines are the values of the dry matter yield of energy e , for the particular crop treatment, expressed in g MJ^{-1} . The values of e obtained by equation (4) for the three diseased treatments were all about 1.20 g MJ^{-1} , significantly lower (at $P < 0.01$) than those of 1.45 and 1.34 g MJ^{-1} obtained for the control and fungicide treated crops, respectively, in which infection was either less severe or absent. These values are similar to those reported by MONTEITH (1978) for C3 crops (1.3 g MJ^{-1}) and to other reported values for field bean crops (TABLE 1). The mean values of dry matter yield of energy correspond to efficiencies of fixation of total solar radiation of about 2.1% for the diseased treatments, 2.35% for the fungicide and 2.55% for the control, assuming a calorific value of dry matter of 17.5 kJ g^{-1} (LEITH, 1975).

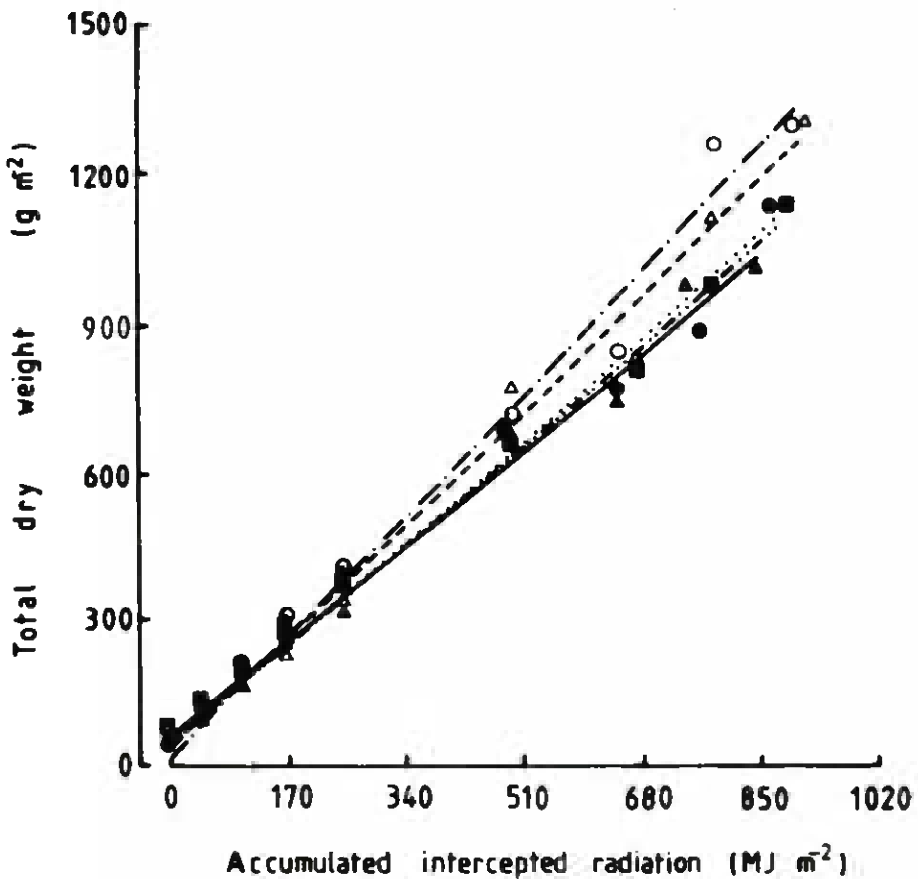
TABLE 1 - *Published values of the mean crop growth rates and the dry matter yield of energy for field beans.*

Crop growth rate ($\text{g m}^{-2} \text{ d}^{-1}$)	Dry matter yield of energy (g MJ^{-1})	Reference
8.9-14.9	0.54-1.03	FASHEUN & DENNETT (1982)
-	1.35-1.53	THOMPSON (1983)
6.4-12.9	0.91-1.45	GREEN <i>et al.</i> (1985)
-	0.74-1.41	KASIM & DENNETT (1986)
13.3-17.1	1.19-1.45	Present work

FIGURE 1 - *Total dry matter per unit area vs corresponding estimates of accumulated solar radiation intercepted for field bean crops, using equation (4). Data from 44 to 126 days after sowing.*

Key: Control, untreated, \circ ($y = 1.45x + 14$, $r^2 = 0.98$);
 Fungicide treatment, \triangle ($y = 1.34x + 24$, $r^2 = 0.99$);
 Diseased treatments inoculated at different crop growth stages (MADEIRA, 1988):

- 1, \bullet ($y = 1.19x + 44$, $r^2 = 0.99$);
 2, \blacktriangle ($y = 1.19x + 49$, $r^2 = 0.99$);
 3, \blacksquare ($y = 1.21x + 38$, $r^2 = 0.99$).



There are evident differences between the predictions of equations (3) and (5): the former will underestimate the total light interception by the canopy, but overestimate the light interception by healthy leaves because shading by damaged leaf tissue is ignored. The latter assumes a uniform proportion of disease damage, and therefore underestimates the light interception by healthy leaves in the (common) case when disease and senescence are more severe on old leaves low in the canopy than on young leaves high in the canopy, which applied to cv. Ticol. In the present work, comparison of the estimates of light interception (f_1 and f_2) shows that values of f_1 (from eq. 3) are higher by between 2 to 13% than those of f_2 obtained using equation (5). The values of dry matter yield of energy estimated using equation (4) were therefore re-calculated using equation (2). Assuming K is constant, the values of e estimated for the diseased treatments by the analysis proposed by WAGGONER & BERGER are higher, about 1.22 g MJ^{-1} compared with 1.19 g MJ^{-1} obtained by equation (4), a difference of 2.5% but well within the limits of experimental error. The true values of e for the diseased crops are likely to lie between those estimated by the two methods. For the disease/crop combination studied here, the measured proportion of disease leaf area x was about 15% and lesions quickly became necrotic and were "lost" in partial defoliation. In this case, equation (4) gives simpler analysis and similar results when x is small or when infection results in lesions which are "lost" from the leaf area. However, large errors may be introduced if this equation is applied to crops with severe disease symptoms (large x).

4. CONCLUSION

In the current work, significant differences in canopy area developed only at the end of the period of vegetative growth, and the differences in e were therefore responsible for the majority of the depression in dry matter production in the diseased treatments (MADEIRA, 1988). This finding contrasts both with those of WAGGONER & BERGER (1987) and that of previous work on Ticol by the present authors (MADEIRA *et al.*, 1988), in which only differences in

canopy duration were significantly associated with depression of dry matter production due to disease. The present measurements therefore provide the first evidence in support of HUGHES expectations (HUGHES, 1988), that examples would be found of disease depressing the efficiency of light use in a field crop.

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