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Field measurements of the photosynthetic rate of potatoes grown with different amounts of nitrogen fertilizer

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SUMMARY

Three experiments are reported in which the photosynthetic rates of potatoes grown with various amounts of applied nitrogen (N) fertilizer were measured. Rates of photosynthesis in leaves of plants grown without applied N reached levels as high as those receiving N in all experiments. The rate of photosynthesis in the uppermost leaves of the variety Pentland Crown was found to increase during the season, whereas in Estima rates remained the same. Decline in the rate of photosynthesis with leaf age was more rapid in strongly shaded leaves than in less shaded leaves which were found to be photosynthetically active 8 weeks after expansion.

INTRODUCTION

The influence of mineral nutrition on photosynthesis of plants has been reviewed by Nátr (1972) wherein examples of increased rates of photosynthesis with increasing amounts of nutrients are cited, and Andreeva *et al.* (1971) reported that photosynthetic rates of potatoes increased with nutrient solution strength up to an optimum concentration. Increased photosynthetic rates with increasing amounts of applied nitrogen (N) were, however, not found in field-grown wheat by Thomas & Thorne (1975), Pearman, Thomas & Thorne (1979) and Gregory, Marshall and Biscoe (1981), and it has been suggested (Gregory *et al.* 1981) that responses to N in pot experiments result from testing much lower concentrations ($< 10^{-5}$ M) than those found in many arable soils ($< 10^{-3}$ M).

There is limited information on the factors influencing rates of leaf photosynthesis of field grown potatoes and how these may affect yield. This paper reports the effects of different amounts of applied N on the photosynthetic rates of potato leaves at different insertion points and the changes in photosynthetic rates with leaf age and plant ontogeny.

MATERIALS AND METHODS

Three experiments were carried out on the Cambridge University Farm, one in 1985 (Expt 1) and two in 1986 (Expts 2 and 3). Treatments comprised all combinations of three levels of N, 0, 90 or 180 kg/ha and two (Expts 1 and 2) or six (Expt 3) varieties. The varieties in Expts 1 and 2 were Estima and Pentland Crown with the additional varieties Pentland Dell, Diana, Cara and Maris Piper in Expt 3. Fertilizer at the rates of (kg/ha) 109 P, 207 K, 60 Mg and N according to the treatments was applied by hand over the open ridges at planting. There were four (Expt 1) or three (Expts 2 and 3) replicates in a randomized block design. Plots consisted of four rows of plants 12·5 m (Expt 1) or 7·5 m (Expts 2 and 3) long and observations were made on the centre two rows.

The net photosynthetic rate was measured using a portable infra-red gas analyser (Analytical Co.). The terminal leaflet of the selected leaf was enclosed in the leaf chamber and a reading taken after approximately 30 sec, once the relative humidity of the chamber was changing only slowly. A flow rate of 200 ml/min of air through the chamber was used for all measurements. For Expt 1 measurements were made between 11.00 and 15.00 h on days when skies were clear so that light exceeded 1300 μE/m^2 per sec (Dwelle, Hurley & Pavek, 1983) and a reading of saturated photosynthetic rate could be made. For Expts 2 and 3, an artificial light source was constructed to allow measurement of saturated photosynthetic rates between 10.00 and 13.00 even on dull days. The light was powered by an auxillary battery and heating of the chamber was reduced to +0·1 °C by use of an infra-red filter between the bulb and the chamber. Readings were taken from two mainstems in each plot and repeated observations of the same plant avoided. Measurements were made of the uppermost

Table 1. *Photosynthetic rates of upper leaves* (*mg* $CO_2/dm^2.h$) *in Expt* 1

Variety...	Estima			Pentland Crown			
N applied (kg/ha)... Date of measurement	0	90	180	0	90	180	S.E.
20.vi	20·4	15·3	26·6	21·3	24·7	22·0	2·32
2.vii	16·2	9·8	8·9	16·6	10·7	10·6	2·00
13.viii	17·8	18·8	21·0	22·3	27·9	19·4	1·88

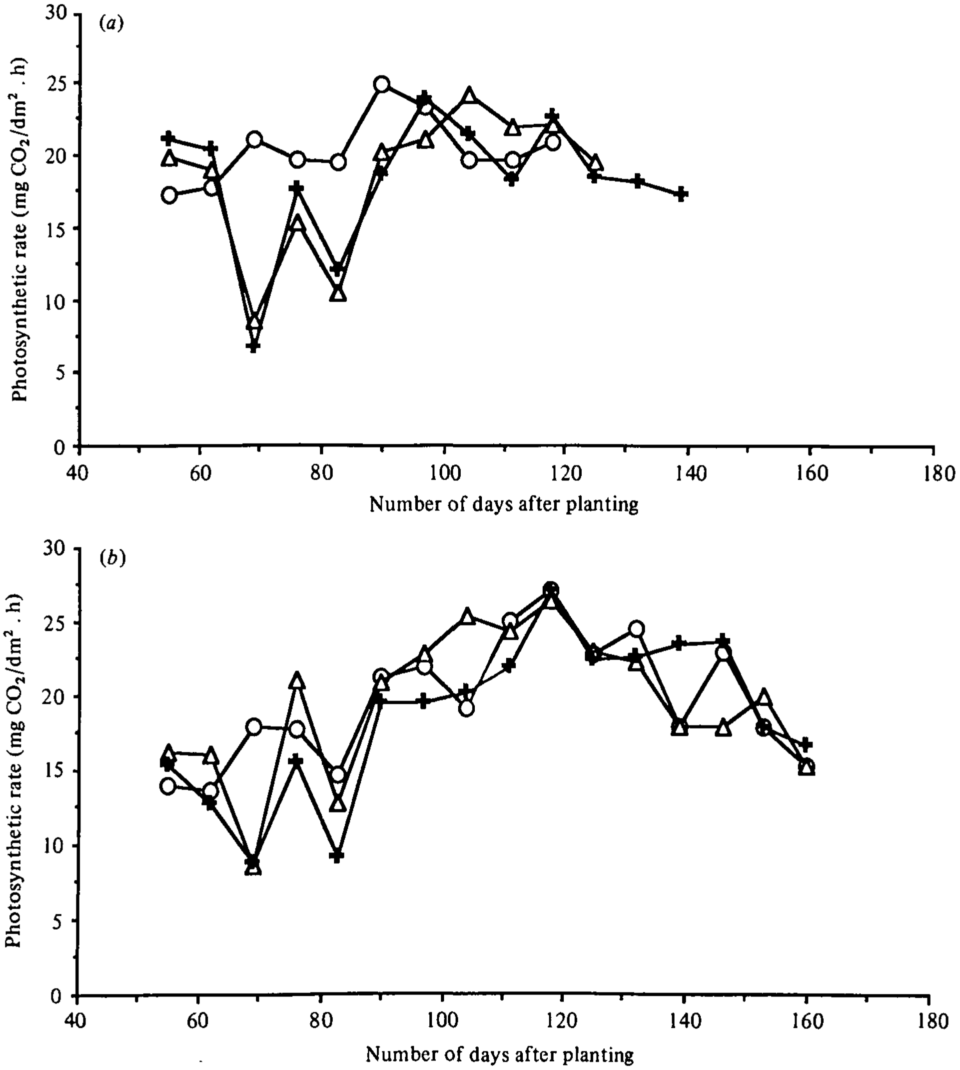

Fig. 1. Photosynthetic rate of the upper leaf: (*a*) Estima and (*b*) Pentland Crown in Expt 2. ○, 0 kg N/ha; △, 90 kg N/ha; +, 180 kg N/ha.

expanded leaves (diameter of terminal leaflet > 25 mm) in all experiments and additional measurements of the 5th and 10th leaves (numbered acropetally) are reported for Expt 2. For the 5th and 10th leaves, readings were taken from expansion (diameter of terminal leaflet > 25 mm) until senescence (50% yellow). Experiments were irrigated by an overhead sprinkler system and deficits were maintained below 30 mm for much of the season, although in 1986 deficits increased beyond this later in the season in some treatments.

RESULTS

In all experiments, rates of photosynthesis of leaves on plants grown without applied N were as high as on those receiving applied N. In Expt 1, only three measurements of saturated photosynthesis in the upper leaves were made before the appearance of new leaves ceased and there was no clear trend of change in the rates from the first measurement soon after emergence of the plants until the upper leaves began to age (Table 1). Readings from Expt 1 on 2 July showed lower rates of photosynthesis with applied N than with no N, this was probably due to higher evapotranspirative demand by the large canopies of the applied N treatments causing increased stomatal resistance despite relatively low soil moisture deficits. In Expt 2, the photosynthetic rate of the upper leaves was maintained at similar levels throughout the season in Estima (Fig. 1*a*) although on days of high evapotranspirative demand, rates of applied N treat-

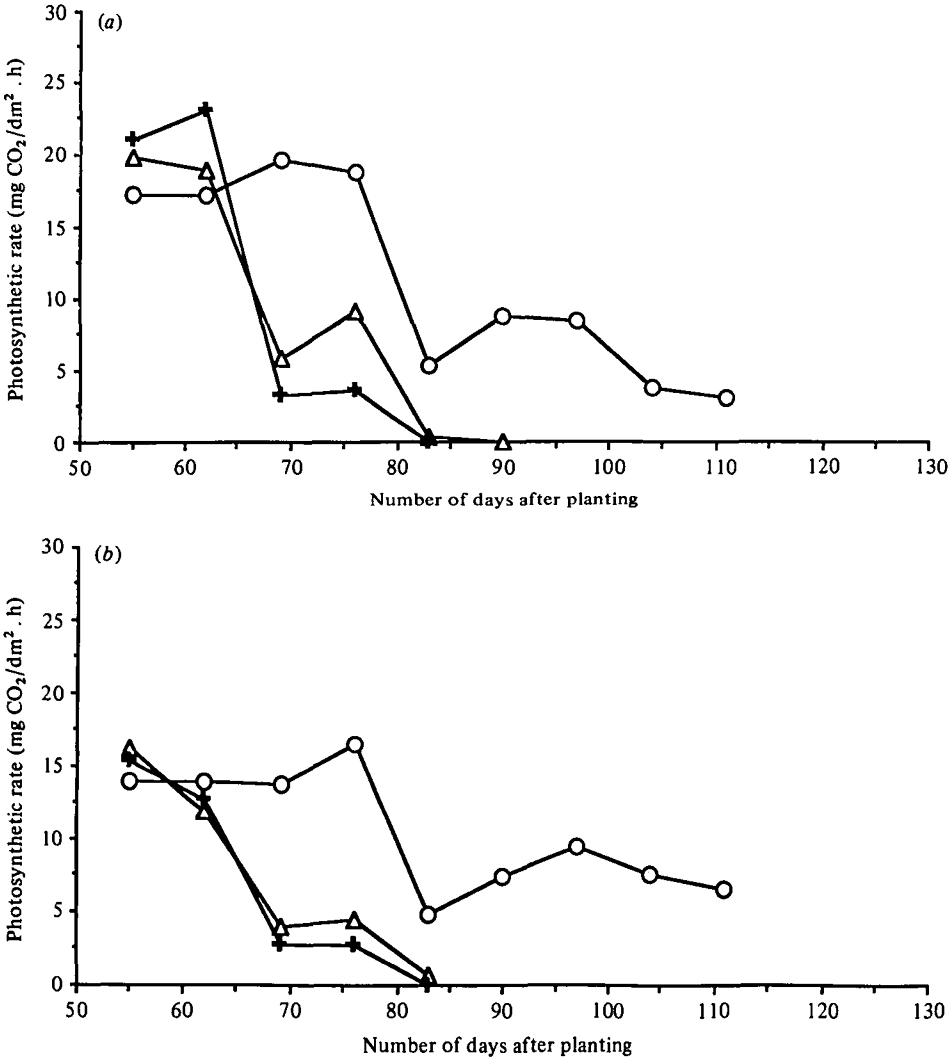

Fig. 2. Photosynthetic rate of the 5th leaf: (*a*) Estima and (*b*) Pentland Crown in Expt 2. ○, 0 kg N/ha; △, 90 kg N/ha; +, 180 kg N/ha.

ments were depressed as in Expt 1. Expansion of more apical leaves with increasing amounts of applied N in Estima allowed photosynthetic rates of the upper leaves to be maintained for longer than with no applied N. The photosynthetic rate of the upper leaves in Pentland Crown in Expt 2 was lower than in Estima at the first measurements but tended to increase over the season (Fig. 1*b*) and was maintained at higher rates for longer than in Estima even in plots with no applied N.

The photosynthetic rates of the 5th leaves declined rapidly in both varieties with applied N and had fallen to negligible levels within 2 weeks whereas with no applied N, high rates were maintained for 2 weeks longer and even after 8 weeks were photosynthetically active although at much lower rates (Fig. 2). Decline in the photosynthetic rates of the 10th leaves was also rapid with applied N but rates of about half those of the upper leaves were maintained for some 5 weeks (Fig. 3). With no applied N, high photosynthetic rates were maintained for longer in Pentland Crown than with applied N, but in Estima leaf senescence reduced rates earlier than in Pentland Crown for all N treatments simultaneously. Measurements on the 10th leaves of plants with no applied N could not be taken as early as with applied N because expansion of the terminal leaflet was less rapid: however, these leaves appeared at similar times so that the chrono-

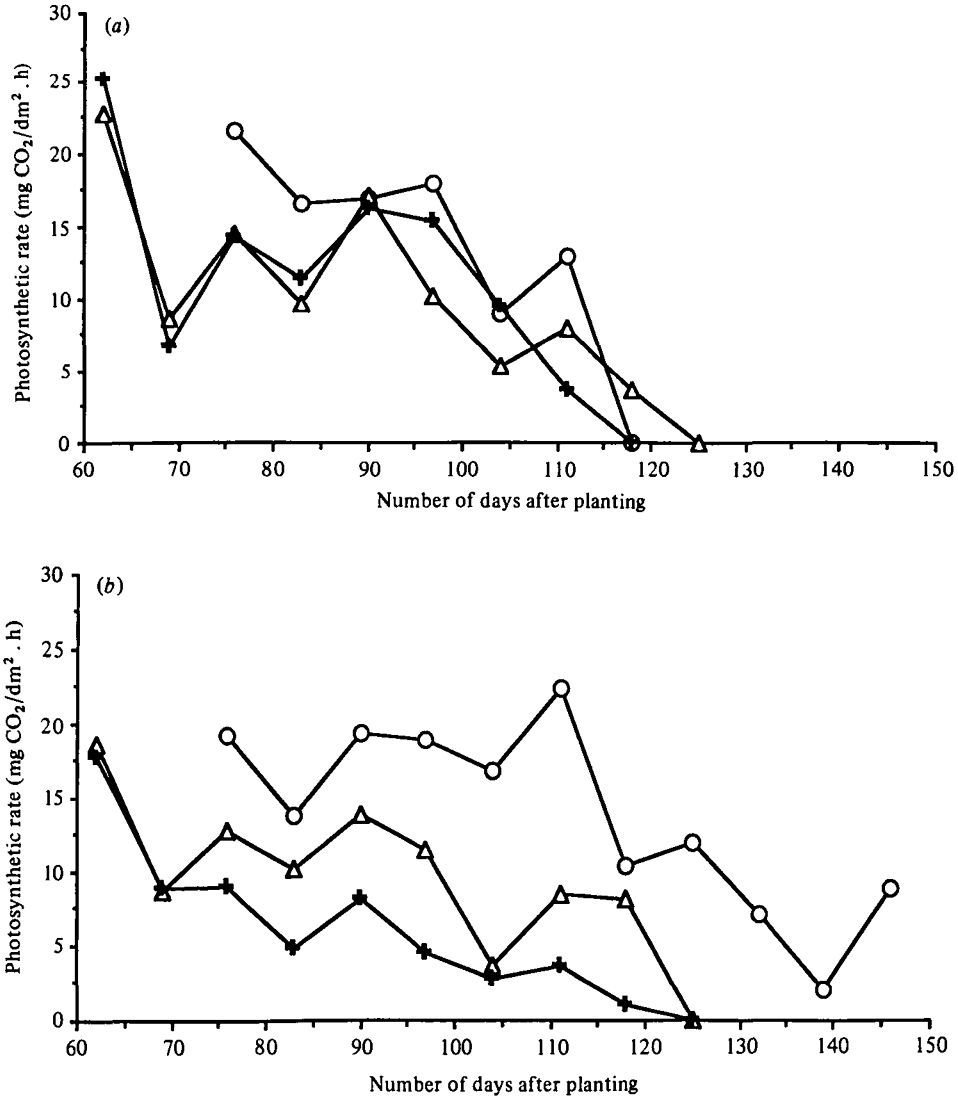

Fig. 3. Photosynthetic rate of the 10th leaf: (*a*) Estima and (*b*) Pentland Crown in Expt 2. ○, 0 kg N/ha; △, 90 kg N/ha, +, 180 kg N/ha.

Table 2. *Photosynthetic rates of upper leaves ($mg\ CO_2/dm^2.h$) on* 8.viii *in Expt* 3

Cara	19·0
Diana	25·7
Estima	21·1
Maris Piper	16·3
Pentland Dell	20·4
Pentland Crown	20·7
S.E.	1·36

logical ages of leaves were comparable and prolonged photosynthetic activity was not the result of delayed leaf appearance.

A single measurement of photosynthetic rates in Expt 3 showed no differences between levels of applied N but there were large varietal differences with higher rates in Diana than other varieties and lower rates in Maris Piper (Table 2); however, the range of values was not outside that recorded in Expt 2 and a single observation is insufficient to establish any real varietal differences.

DISCUSSION

The results reported here are in agreement with the assertion of Gregory *et al.* (1981) that available N in many arable soils is not low enough to limit leaf photosynthesis of crop plants directly. The maximum rates recorded were the same for all levels of applied N and were similar to rates reported by Dwelle *et al.* (1983) in the field. Any increase in dry-matter production by N application is therefore achieved through effects on leaf area duration rather than on the efficiency of conversion of incident radiation.

An interesting pattern of photosynthetic rate over time was found in Expt 2 with a difference in photosynthetic rates between Estima and Pentland Crown in the upper leaves early in the season, which disappeared as the photosynthetic rate in Pentland Crown increased steadily over time. There is no obvious explanation for this effect and it is unlikely to result from differences in sink strength as the difference in time of tuber initiation between Estima and Pentland Crown was small. Reduced rates in the first formed leaves were not found by Frier (1977) but the data of Dwelle, Kleinkopf & Pavek (1981*a*) with potato, Hodanova (1981) with sugar beet and Rawson *et al.* (1983) with wheat indicate that rates may increase with subsequent leaves early in the season. The difference in early rates of photosynthesis is consistent with the early and late growth pattern of the two varieties and a possible explanation is that the early leaves of Pentland Crown are of a more juvenile form (Scaramella Petri, 1959) than Estima and do not develop the full photosynthetic capacity of later mature leaves.

Apparent varietal differences were also found in Expt 3 but the variation in photosynthetic rates with ontogeny observed in Expt 2 indicates that any inherent genetic differences in photosynthesis between the varieties would require investigation throughout the season and that a single observation cannot establish any real varietal differences. Differences between the photosynthetic rates of potato clones have been reported by Dwelle *et al.* (1981*b*) and Moll (1983) but photosynthetic rates were found to be poor determinants of yields as leaf cover development and persistence were more important.

Prolonged photosynthetic activity in the lower leaves with no applied N compared with applied N indicates the importance of the light regime experienced by the leaf rather than the leaf age *per se* on the duration of photosynthetic capacity. Heavily shaded leaves at the base of the canopy may lose photosynthetic capacity within 2 weeks whereas relatively unshaded leaves may continue to produce photosynthate 8 weeks after expansion. These observations indicate that loss of photosynthetic capacity may frequently be a consequence of the environment and that the photosynthetic potential of a leaf cannot be predicted as a simple function of time. Further investigation of the decline in photosynthetic capacity under differing shade conditions would give some insight into the optimum leaf area index (LAI) for the potato crop. Above an LAI of 3, light interception in the potato increases very little (Allen & Scott, 1980; Burstall & Harris, 1983) and comparison of photosynthetic rates of individual leaves under canopies of differing LAI would be of interest as this study has shown that relatively young leaves under a dense canopy may not be net producers of photosynthate.

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