

## An analysis of growth of the potato crop

By E. J. ALLEN

*Department of Agriculture (Crop Husbandry), University of Wales, Aberystwyth*

AND R. K. SCOTT

*Broom's Barn Experimental Station, Higham, Bury St Edmunds, Suffolk*

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### SUMMARY

Linear relationships between both total and tuber dry-matter yields and the amount of radiation intercepted by potato crops are demonstrated. Their existence suggests that, in the absence of disease and drought, the essential objective in the production of this crop is to maximize radiation interception. This paper critically assesses the influence of factors which the grower can control on light interception and estimates potential yields for specific environments. The implications of this analysis for growers, breeders, research and the whole industry are discussed.

### INTRODUCTION

For many years the growth of crops has been analysed in terms of the size of the leaf surface, leaf area index ( $L$ ) and its efficiency, the rate of dry-matter production per unit leaf area, net assimilation rate ( $E$ ) (Watson, 1952). Generally, the results of this type of analysis have been disappointing in elucidating the causes of variation in crop yields mainly because, for much of growth,  $L$  and  $E$  are not independent. As  $E$  is measured solely through  $L$  and for much of growth varies inversely with  $L$ , it is a largely unusable measure in the analysis of growth.  $L$ , too, is subject to considerable deficiencies as it regards all leaves as equal irrespective of their age, arrangement and angle and is not directly related to growth rate for the whole of the life of the crop. This is most clearly shown in the integral of  $L$ , leaf area duration ( $D$ ) which is sometimes closely related to yield but often is not (Gunasena & Harris, 1969, 1971; Ifenkwe, 1975). The reasons for these differences have not been explained by conventional growth analysis.

Recently, Monteith (1977) has proposed a new approach in which growth is considered in terms of two independent aspects, the amount of energy intercepted by the leaf surface and the efficiency of its use. Where this analysis has been made on drought- and disease-free crops grown in the United Kingdom, variation in yields has been due almost entirely to variation in the amount intercepted rather than the efficiency of conversion, which has been remarkably constant. As recent evidence for barley (Winzeler,

Hunt & Mahon, 1976) suggests that the amount of assimilate respired during the whole season can be taken as a constant proportion of assimilated dry matter, Monteith (1979) points out that crop growth rate should be proportional to the rate of photosynthesis which depends in the first instance on the amount of radiant energy intercepted by foliage. Figure 1 shows that crop growth rates for potatoes early in the season are indeed determined by the amount of intercepted radiation. Similar linear responses have been reported for barley, wheat, maize and soya beans (Biscoe & Gallagher, 1977).

Few experiments have actually measured light interception in potatoes, but recently Scott & Wilcockson (1978) have applied this analysis using the unpublished measurements of light interception made by R. A. S. Williams. In this work and throughout the paper intercepted radiation refers to the difference in total radiation measured by tube solarimeters placed horizontally above and below the canopy. Estimates based on Williams's data show that crops grown with a wide range of treatments in several seasons at Sutton Bonington produced total dry-matter yields proportional to the amount of light intercepted (Fig. 2*a*). Further, J. N. Bean's (personal communication) data for Pentland Crown, Désirée and Arran Comet sprouted in different ways in one season fit the general relationship (Fig. 2*b*). When Sale (1973*a, b*) used shading to reduce light incidence and interception on irrigated crops in the high insolation environment of the Murrumbidgee Valley, New South Wales, Australia, dry-matter yield was reduced propor-

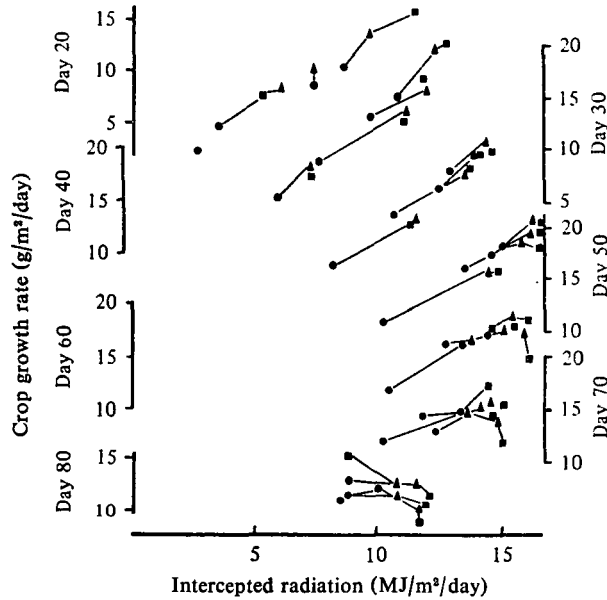


Fig. 1. The relationship between crop growth rate and intercepted radiation at 20-day intervals between 20 and 80 days after emergence. The points are means of the factorial combination of four plant population densities and three fertilizer applications.

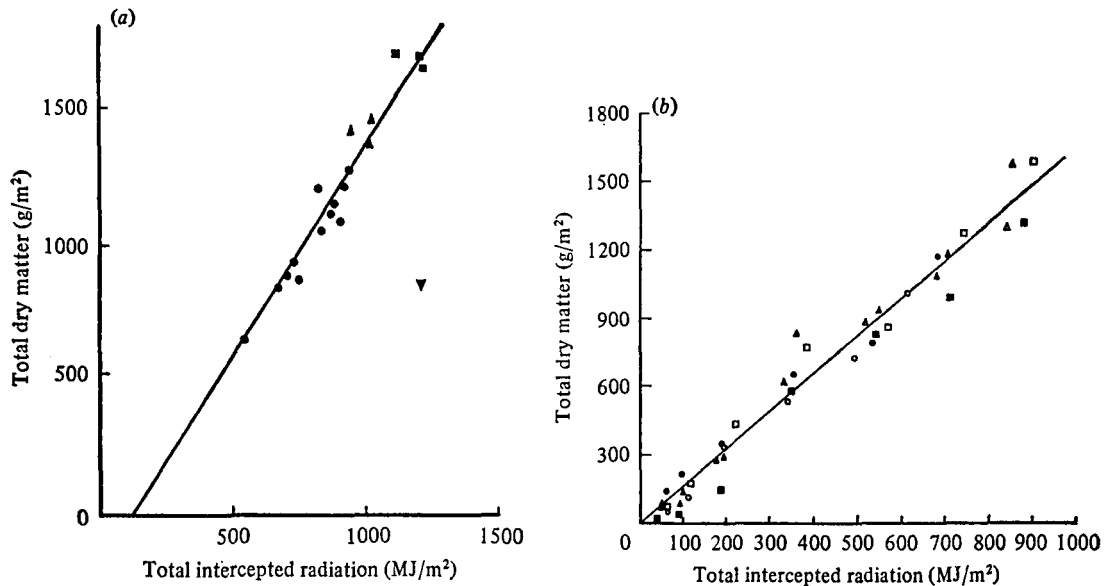


Fig. 2. The relationship between total dry matter and intercepted radiation at (a) Sutton Bonington: ●, R. A. S. Williams, unpublished data for 1964; ▲ ■, Younger (1975) for the years 1972 and 1973; ▼, Scott & Wilcockson (1978) for 1976. (b) Trefloyne (J. N. Bean, unpublished). The line is the fitted line of the Sutton Bonington data drawn through the origin. ● ○, Arran Comet; ▲ △, Désirée; ■ □, Pentland Crown. Solid symbols, storage at 6 °C; open symbols, storage at 12 °C.

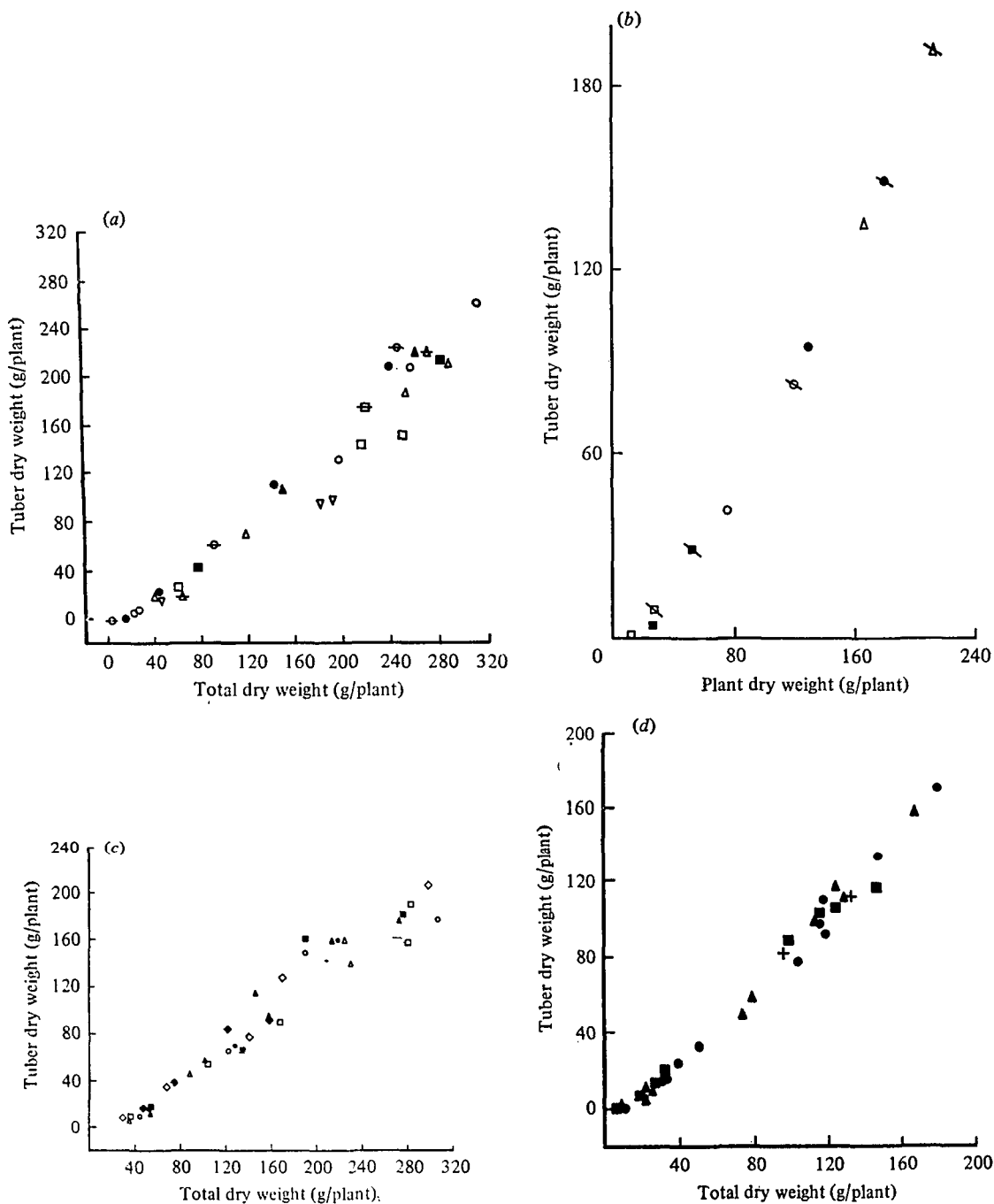


Fig. 3. The relationship between tuber dry weight and total dry weight. (a) In *Désirée* from different planting dates. Unpublished data of J. L. Jones.  $\circ$ , 16. iii. 74;  $\triangle$ , 27. iii. 74;  $\square$ , 9. iv. 74;  $\nabla$ , 18. iv. 74;  $\bullet$ , 19. iii. 75;  $\blacktriangle$ , 9. iv. 75;  $\blacksquare$ , 1. v. 75;  $\ominus$ , 1. iii. 76;  $\triangleleft$ , 30. iii. 76;  $\boxminus$ , 21. iv. 76.

(b) For old (864 day-degrees  $\geq 4^{\circ}\text{C}$ ) and young (0 day-degrees  $\geq 4^{\circ}\text{C}$ ) seed of *Désirée* (Ali, 1979).  $\square$   $\circ$   $\bullet$   $\triangle$ , sampling dates 2. vi., 13. vi, 27. vi, 18. vii, 5. viii; crossed symbols, old seed.

(c) In *Désirée* from different row widths and plant densities (Ifenkwe, 1975).  $\bullet$   $\blacksquare$   $\blacktriangle$   $\blacklozenge$ , 29950, 37440, 49920, 74880 plants/ha. Closed symbols, 66 cm row width; open symbols, 132 cm row width.

(d) In *Home Guard* from different planting dates in five years. Data from J. L. Jones (unpublished) and Allen (1977).  $\bullet$   $\blacktriangle$   $\blacksquare$   $+$ , 1st, 2nd, 3rd and 4th planting from February to May.

tionately. This strongly suggests that the amount of light intercepted is indeed causal in determining dry-matter accumulation. Similar relationships have recently been demonstrated in other crops: sugar beet (Scott & Jaggard, 1978), wheat and barley (Gallagher & Biscoe, 1978).

Of course, the target in potato production is tuber yield, not total dry-matter yield. Ivins & Bremner (1965) formulated a model of growth which suggested that leaf growth was determined by plant size at tuber initiation, and initiation before 'the basis of a large leaf area is established' resulted in smaller leaf surfaces which senesced earlier. A conflict between leaf and tuber growth was regarded as inherent in the growth of the crop with any factor promoting the growth of one at the expense of the other. The model was essentially descriptive, and more recent data have allowed a fuller analysis of two aspects, tuber initiation and dry-matter partitioning, believed to be crucial. The data of Ali (1979) and Raouf (1979) show that despite large differences in plant size at initiation, the subsequent distribution of dry matter was unaffected. Whilst with crops of Home Guard grown from seed of advanced physiological age, small and short-lived leaf surfaces ensued if initiation occurred when plants were small, in Désirée peak *L* values were not affected by size at initiation and in 1978 all treatments achieved complete ground cover. Thus, while

the pattern of growth which Ivins & Bremner (1965) describe does occur, it is by no means universal.

There is good evidence that in most temperate environments tuber yield is directly related to total dry-matter yield. Figure 3 shows that this holds for many varieties, dates of planting, planting densities and sprouting treatments, until leaf dry weight declines with senescence and increases in tuber dry weight account for all the increase in total weight. Extreme treatments can change the relationship, for example, heavy rates of application of N fertilizer encourage leaf and stem growth, while very long sprouting periods may favour tuber growth, but within the normal range of these cultural practices differences in dry-matter partitioning are smaller than earlier evidence suggested (Bremner & Radley, 1966). Thus, a linear relationship between tuber dry-matter yield and amount of radiation intercepted would be expected, and Fig. 4 shows that this did exist in the data from Sutton Bonington. Tuber dry-matter data from Sale's (1973*a, b*) experiments did not fit this common line although the relationship between the two factors was linear. The lower efficiency of conversion of intercepted radiation into tuber dry matter in the high-radiation environment appeared to be associated with delay in onset of tuber bulking and increased stem growth caused by the higher temperatures (Bodlaender, 1963).

The priority for crop husbandry seems clear; to

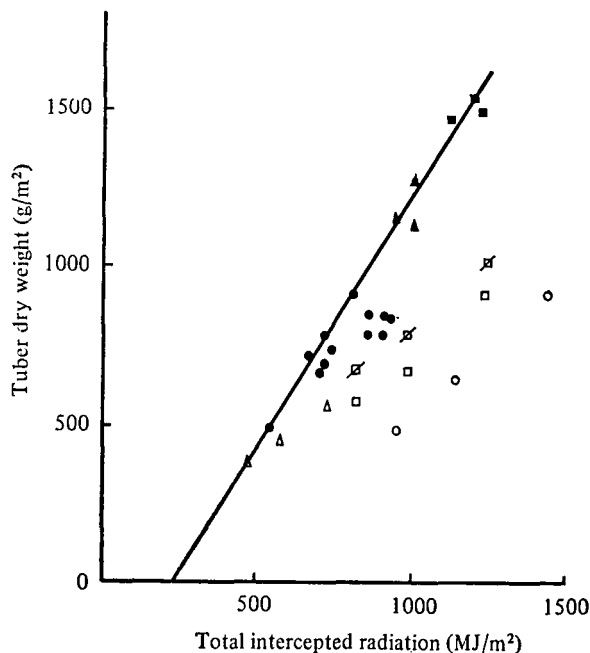


Fig. 4. The relationship between tuber dry weight and intercepted radiation; from Sutton Bonington and from Sale (1973*a, b*). ● ▲ ■, 1964, 1972, 1973; △, Summer-planted experiment 1971; □, spring-planted experiment 1970 (original data); ▣, spring-planted experiment 1970 (adjusted data, see Scott & Wilcockson, 1978); ○, spring-planted experiment 1971 (waterlogged).

maximize the amount of radiation intercepted. This may be achieved by manipulating leaf growth in relation to variation in incident radiation and/or by establishing and maintaining the leaf surface for longer periods. The identification of this principle allows agronomists (a) to examine the factors which influence leaf area and assess the scope for further improvement, and (b) to determine realistic yield potential for specific environments, which affords a real measure of the current efficiency of husbandry practices.

This paper critically assesses the influence of factors which the grower can control on light interception, and estimates potential yields for specific environments. The implications of this analysis for growers, breeders, research and for the whole industry are discussed.

#### RADIATION RECEIPTS AND INTERCEPTION

##### *Natural light regime*

Table 1 shows the way light receipts change during the growing season for sites in the east and west of the British Isles at the same latitude

(52° N). The months of April, May and June contribute approximately half of the total light receipts for the April–October period, and improvement in interception in the early part of the season would be a potent means of increasing the total amount of radiation intercepted. In any year there is little variation in total light receipts between inland sites, but coastal sites have substantially more radiation (Monteith, 1962); each month average receipts are of the order of 20% greater at Aberporth than at Broom's Barn. Although overall annual receipts are similar from year to year, values for individual months differ by 30–60%. Such differences are likely to be especially important in relation to growth by treatments such as date of planting and physiological age, which markedly displace in time the curves of leaf area index. Over longer periods values are less variable but differences can still be significant. For example, at Broom's Barn receipts for the period June–September 1969 were more than 10% greater than those of the same period in 1968 or 1972, although totals for the whole growing season were almost identical (1968) or differed by only 5% (1972).

The daylength component of the light regime may

Table 1. *Solar radiation (MJ/m<sup>2</sup>/day)*

Year	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Total Mar.–Oct.
Broom's Barn									
1966			15.3	15.3	12.5	12.1	10.7	5.2	
1967	8.6	9.9	13.3	15.9	15.1	12.0	7.4	7.0	2732
1968	8.7	13.8	15.2	16.5	13.7	10.2	9.0	5.9	2847
1969	5.5	12.7	14.3	18.9	15.6	10.9	9.1	5.8	2839
1970	6.8	9.6	16.6	19.4	13.8	12.5	10.1	5.8	2895
1971	6.8	10.5	16.4	13.3	17.1	11.1	10.3	6.2	2807
1972	8.2	9.7	14.3	15.6	13.5	12.9	8.0	5.4	2681
1973	8.0	10.9	15.3	19.3	14.1	13.4	9.8	5.0	2936
1974	6.8	10.8	15.3	16.0	13.8	12.8	9.1	4.2	2720
1975	4.8	9.9	12.8	19.0	16.3	14.4	9.4	5.7	2828
1976	6.8	11.7	14.3	19.8	17.6	14.5	8.7	4.0	2984
1977	6.2	9.7	15.2	13.5	14.8	9.6	8.9	5.8	2559
1978	7.1	9.0	14.7	14.7	11.8	11.2	9.3	5.1	2539
Lowest	4.8	9.0	12.8	13.3	11.8	9.6	7.4	4.0	2228
Highest	8.7	13.8	16.6	19.8	17.6	14.5	10.7	7.0	3331
Aberporth									
1968	9.5	14.9	17.0	19.8	19.5	15.7	9.8	5.4	3414
1969	9.2	15.9	15.6	23.2	18.4	13.0	8.8	6.7	3403
1970	8.5	13.1	16.6	19.2	16.9	14.0	10.6	5.4	3194
1971	7.7	12.9	20.5	17.5	21.0	12.8	12.0	7.2	3417
1972	9.8	15.0	16.8	17.0	17.0	16.1	12.7	6.5	3400
1973	10.2	15.0	16.3	21.5	18.1	15.0	10.4	5.8	3441
1974	8.9	16.2	17.6	19.2	18.2	14.6	10.0	5.1	3367
1975	9.1	14.0	20.4	23.0	18.7	14.8	11.6	7.4	3647
1976	9.6	15.2	16.9	20.8	18.5	19.5	8.7	5.5	3509
1977	7.9	15.2	22.2	18.7	19.4	15.3	10.3	6.4	3536
1978	9.0	14.4	18.1	17.7	15.2	14.0	11.7	5.1	3226
Lowest	7.7	12.9	15.6	17.0	15.2	12.8	8.7	5.1	2914
Highest	10.2	16.2	22.2	23.2	21.0	19.5	12.7	7.4	4061

influence the growth pattern of the crop. *Solanum andigena*, the ancestor of modern varieties, is a short-day plant, i.e. setting tubers earlier in short days. The first potato crops to be grown in these islands were often not harvested until early winter as tubers did not set until the shorter days of late summer (Hawkes, 1978). The adaptation of the species to commercial production has been facilitated by selection for tuberization in the lengthening days of spring. There is no definitive evidence that current varieties (*S. tuberosum*) exhibit marked daylength sensitivity within the range experienced during the growing season in England. J. N. Bean (personal communication) found that when daylength at plant emergence (from early April to late May) differed by up to 2 h, plants reached the same weight at the time tubers were initiated. Hay & Allen (1978) found that the variety Roslin Eburu, bred in the U.K., tuberized at the same total plant weight when grown in short (12–13 h) days in Malawi (14 °S) as do maincrop varieties in the UK (16 h).

#### Leaf area index ( $L$ )

Figure 5 shows the relationship between  $L$  and intercepted radiation for Majestic grown on the

square at four densities and given three fertilizer levels. The equipment used to measure photosynthetically active radiation was unreliable for part of the experiment. Interception increases with  $L$ , but with a diminishing response. The data shown are the only series published for potatoes, and are not sufficiently comprehensive to allow us to examine the extent to which cultural and other factors influence the amount of radiation intercepted by unit leaf area index. Figure 5 shows the general effects of leaf angle for a species with predominantly erect leaves, where 60% of radiation passes unintercepted through unit  $L$  ( $s = 0.6$ ), and one with predominantly prostrate leaves improve light interception considerably. The extent of differences between potato varieties has not been measured nor has the effect of lodging, which is frequent. However, there is some circumstantial evidence that observed differences in leaf disposition may be significant. At low leaf area indices varieties such as Vanessa (Allen *et al.* 1979) and Maris Bard (J. N. Bean, personal communication), which have relatively prostrate leaves, grow particularly rapidly (Table 2). Unpublished data of D. Wood (personal communi-

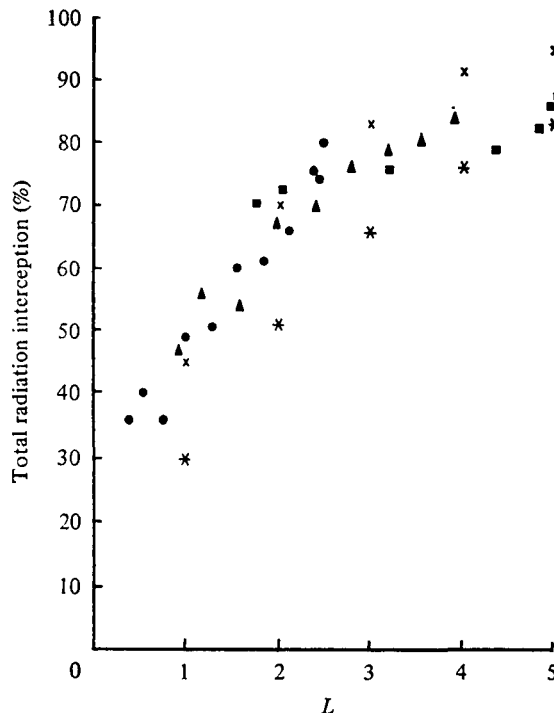


Fig. 5. The change in percentage total radiation interception with increasing leaf area index. ●, 12 000 sets/ha; ▲, 27 000 sets/ha; ■, 109 000 sets/ha from R. A. S. Williams (unpublished data);  $s$  is 0.4 (×) and 0.6 (\*) using the formula  $S_L = S_0[s + (1-s)\tau]^L$ , where  $S_L$  is irradiance for the whole solar spectrum below a total leaf area index,  $L$ ;  $S_0$  is irradiance at the top of the canopy;  $s$  is the fraction of radiation not intercepted by a foliage layer with unit leaf area index; and  $\tau$  is the transmission coefficient for total solar radiation through leaves and is assumed to be 0.25 (Monteith, 1962).

Table 2. Tuber bulking rates (t/ha/week) and mean leaf area indices (*L*)

	Period	Rate	<i>L</i>
Maris Bard	9 June–6 July 1977	8.68	2.0
Vanessa	14 June–26 June 1974	10.40	2.5
Vanessa	12 June–26 June 1979	10.50	1.9
Pentland Javelin	12 June–26 June 1979	9.40	3.4

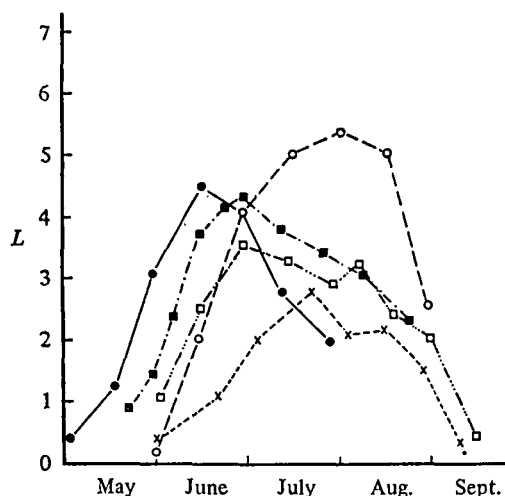


Fig. 6. A sample of leaf area index (*L*) curves. ●, Gunasena & Harris (1971), Craig's Royal; ○, Gunasena & Harris (1971), Pentland Dell; ×, Dyson & Watson (1971), King Edward; ■, Ifenkwe (1975), Maris Piper; □, Younger (1975), Pentland Crown.

cation) show that increases in *L* do not increase light interception when lodging occurs.

It is possible that the composition of the canopy in terms of the number, size and ages of the individual leaves affects the relationship shown in Fig. 5. The potato plant is one in which new leaves appear at many apices, on mainstems, secondary and axillary branches, and consequently there can be as many as 150–200 leaves on individual plants within the crop (Ifenkwe, 1975). There is large inter-plant variation in number of stems and branches, and the usual method of destructive growth analysis where groups of plants are separated into leaves and stem material does not give the information required. Unlike cereals, new leaves are produced for most of the life of the crop, so that mean leaf age may vary much less than leaf arrangement. This is important, as increasing leaf age reduces photosynthetic rate (Winkler, 1971) but it is unlikely to reduce efficiency of conversion of intercepted radiation for much of the life of the potato crop.

Although there is limited information on the

individual leaf components of the canopy, leaf area growth curves are frequently published, and typical examples from a range of sites are shown in Fig. 6. Most crops emerge and commence leaf expansion some time in May and increase their leaf area rapidly in June, reaching peak *L* values in July. Thereafter *L* usually declines steadily until some time in September, the rate of decline being similar for all treatments at a site. Few crops possess much leaf after September. There is considerable variation in peak leaf area indices, but for many crops the peak *L* value is only 3, and higher values are short lived and invariably lead to rapid subsequent decline, often associated with lodging. Thus, large peak *L* values may have little effect on total light interception. The data in Fig. 6 show clearly that potatoes are deficient in leaf area both early and late in the season, and improvements at one stage of growth seem invariably associated with deficiencies at the other. Although Ifenkwe (1975) and Gunasena & Harris (1971) have shown that considerable leaf growth can occur during April and May in some seasons, most crops intercept only 10–15% of radiation incident during May. Clearly the most important impediment to interception of available radiation (Table 1) by potatoes over the whole growing season is the absence of an adequate leaf surface early in the season. Light receipts in September and October are much lower than April and May, and improvements in early leaf growth should be more beneficial to tuber yields than prolongation of the leaf surface into late September and October. This would be especially marked if the leaf surface is lodged in the autumn, as frequently occurs.

#### *Factors affecting leaf area index*

##### *Stem density*

The most obvious means of shortening the time taken to reach complete ground cover is to increase stem density (Fig. 7). This may be achieved through the use of larger and/or more seed tubers. There is now considerable evidence (Jarvis, 1977; Allen, 1978) that for most varieties the growth and yield of individual stems is largely independent of the size of the seed tuber, which conflicts with the suggestion that large seed are necessary for the highest yields (Evans, 1975). Although the number of sprouts and stems per tuber is asymptotically related to tuber

size over the range used, the rate of increase in numbers varies with variety and seed treatment and the amount of substrate per stem does not necessarily increase with seed size. Figure 8 presents typical data for the relationship between seed tuber weight and number of above-ground stems for the variety, Pentland Crown, sprouted in two ways. Differences in the weights of substrate per stem (Table 3)

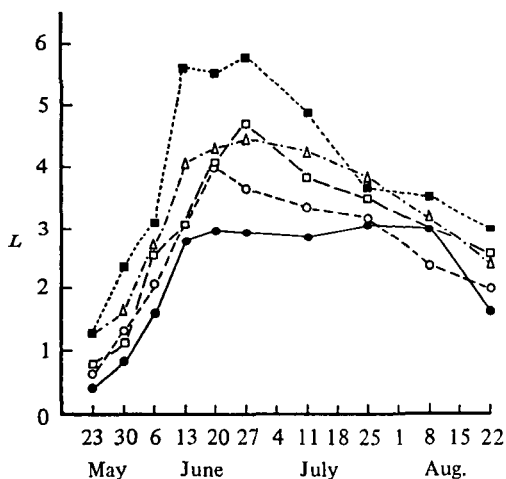


Fig. 7. The effect of density on leaf area index (Ifenkwe, 1975). ●, 24960 plants/ha; ○, 29950 plants/ha; □, 37440 plants/ha; △, 49920 plants/ha; ■, 74880 plants/ha. Data averaged over two row widths. Seed size 90–100 g.

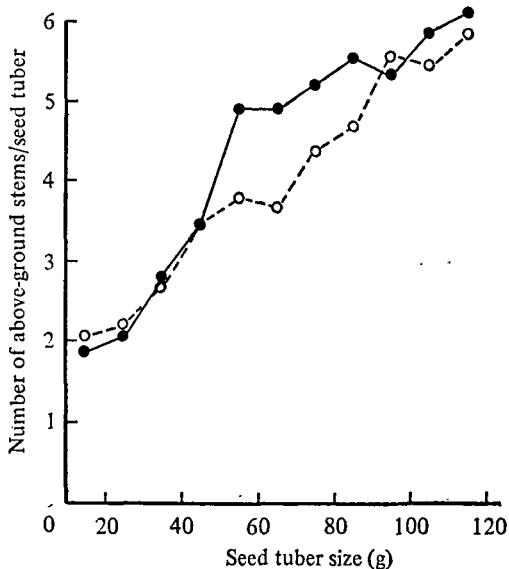


Fig. 8. Effect of seed tuber size on number of stems per tuber in Pentland Crown sprouted at two temperatures. ●, Ambient; ○, 4 °C (E. J. Allen, unpublished).

between seed sizes if all reserves were mobilized, were equivalent only to 2–3 days growth. The marked differences in early growth between large and small seed planted at the same spacing are invariably caused by differences in stem density, not by differences in 'vigour'. Visual assessment is especially misleading in such comparisons because the effect of stem clumping with larger seed usually leads to increases in mainstem length.

The effect of increasing stem density on rate of increase in  $L$  is shown in Fig. 7. Successive density increments produce progressively smaller effects on the time taken to reach  $L$  of 3. A density is reached beyond which little further improvement in rate of ground cover occurs, and effects on light interception become marginal. If density did not influence subsequent leaf growth and senescence this would be the minimum required both for the highest total and tuber dry-matter yields. Differences in peak  $L$  are not translated into differences in radiation interception; this would occur only if the high  $L$  values were linked with increased leaf persistence, but extensive data (e.g. Bremner & Taha, 1966) show that this rarely occurs. The effect of increasing stem density on leaf cover and yield is most important in short-season crops, and the optimum density is much higher for earlies than maincrops (Allen, 1978). Numerous experiments have defined the minimum stem density required for maximum tuber yields (Sharpe & Dent, 1968; Wurr, 1974a) but few have measured light interception. In Ontario, Lynch & Rowberry (1977) showed that densities above that normally recommended (40000/ha) did not increase light interception during the main period of tuber growth (Table 4). It is, therefore, very unlikely that substantial increases in rate of leaf cover and thereby tuber yields can be achieved by dramatically increasing stem density, either by increasing the size of seed or the number planted.

In practice, the usefulness of increased stem densities to increase early leaf cover is restricted by the associated effects on the number and hence size distribution of tubers. Numbers of tubers increase more rapidly with increase of stem density than yields, so that increases in stem density reduce the proportion of ware tubers within the total yield and may reduce the ware yield. This may not apply to Pentland Crown which, as Fig. 9 shows, does not increase in number of tubers when the number of above-ground stems is doubled, beyond a relatively low stem density. This pattern of behaviour may allow the use of very high stem densities without loss of ware yield. In other varieties, especially those with large numbers of tubers per stem, e.g. King Edward, large increases in stem density are likely to reduce ware yield.

An obvious approach to advancing the time when



Table 3. Effect of seed size on substrate per stem and relationship to known crop growth rates (g/plant/day) in May and June. Variety Pentland Crown

Seed weight (g)	No. of stems	Fresh wt./stem (g)	Dry wt./stem (g)	Difference (g)
170	7	24.3	4.86	1.86
30	2	15.0	3.00	

Growth rates		
	Plant (4 stems) (g)	Stem (g)
15-25 days	2.0-4	0.5-1
25-35 days	2.5-5	0.6-1.25

Table 4. Effect of plant density on PAR ( $MJ \times 10^{-2} / m^2/min$ ) at different levels in the canopy of Russet Burbank measured between 12.30 and 14.40 h (Lynch & Rowberry, 1977)

Number of plants/ha ( $\times 10^4$ )	At canopy surface	One-third below canopy surface	Two-thirds below canopy surface
6 August 1973			
4.0	1.67	0.67	0.46
6.3	1.67	0.67	0.42
11.1	1.67	0.67	0.33
11 August 1973			
4.0	2.09	0.79	0.46
6.3	2.09	0.63	0.42
11.1	2.09	0.96	0.33

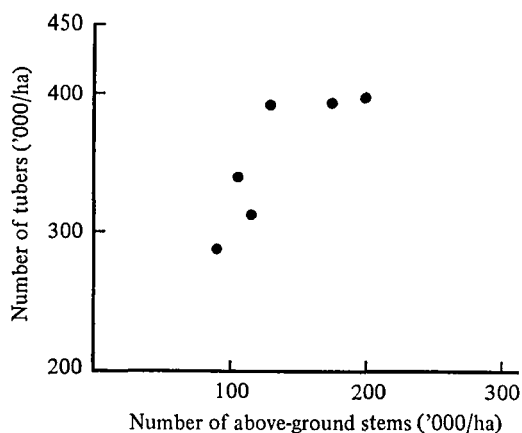


Fig. 9. The relationship between number of tubers and number of above-ground stems in Pentland Crown (Allen, 1979).

leaf cover is complete is to grow in close rows or beds. An added advantage is that at any stem density closer rows lessen the extent of mutual shading when  $L$  is small. There are no data for the extent of differences in radiation interception between beds and traditional practice, nor has leaf area index been measured. In the most extensive comparisons Jarvis & Shotton (1968) obtained similar yields of tubers from beds and conventional rows, but saleable yields were much less from the beds due to greening associated with inadequate soil cover. It is notable that in districts where there is a tradition for early potato growing row widths of less than 50 cm are common and in Jersey, where much hand cultivation is still done, rows are 40 cm or less apart.

At first sight the general trend in maincrop production to wider rows seems to conflict with the principle that yield is related to radiation interception. Ifenkwe & Allen (1978) have shown that even rows 138 cm apart do not reduce saleable yield at final harvest, although at the earliest harvests

yields were affected. These experiments were carried out where rainfall was plentiful and leaf growth both rapid and extensive, so that even on the wide rows complete ground cover was achieved by the end of June. Later in the season plants on the conventional row widths lodged but those on the wide rows did not. Thus, compensatory differences in light interception probably occurred.

#### Date of planting

There is abundant good evidence that early planting, while advancing emergence and early leaf growth, usually restricts the peak and persistence of the leaf surface (Fig. 10). Early planting occurs when soil and air temperatures are low, and this will affect rates of leaf production and expansion, and may restrict final leaf size, as has been found in sugar beet (Milford & Riley, 1980). Delay in planting is often a very effective means of maintaining a leaf canopy into the autumn, and such

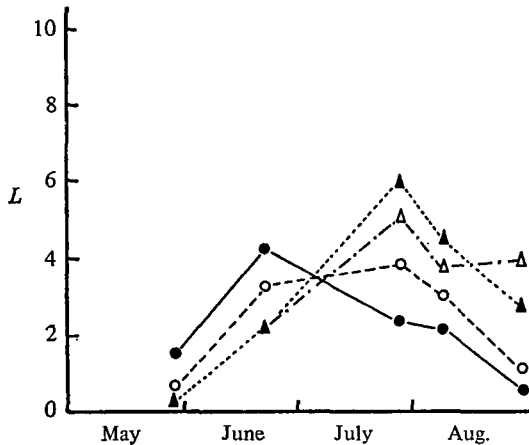


Fig. 10. Effect of date of planting on leaf area index ( $L$ ) in Désirée (Allen, 1977). ●, 21. iii; ○, 4. iv; ▲, 18. iv; △, 2. v.

canopies are composed of relatively young leaves.

Early planting is likely to increase tuber yields if the improvement in light interception in May and June more than offsets the loss associated with earlier senescence. In Allen's (1977) experiments with maincrop varieties in Pembrokeshire, early planting (March and early April) was more effective in advancing early leaf growth than in Bremner & Radley's (1966) experiments in the East Midlands; yield increases were also more substantial. Early planting is more advantageous in mild environments because growth proceeds immediately after planting whereas in colder environments the delay in onset of growth, the restricted peak leaf area and persistence lead to no advantage. Inevitably in these colder environments planting over the period March–mid-April has little effect on yield, but further delay results in progressively greater reductions in yield. As many potatoes are still planted after mid-April it is clear that there is still scope for improvement, but in most seasons this would not have a major effect on the national average yield.

The major factor restricting the effectiveness of early planting in the United Kingdom is the inability of many varieties to grow at the temperatures prevailing when soil conditions allow planting to begin. Observation suggests that varieties may differ markedly in the interval between planting and emergence even where sprout lengths at planting are similar. Unpublished data of T. C. Gillison and P. F. Wareing show that the base temperature for growth of Home Guard is lower than for other varieties. Knowledge of the base temperatures for different varieties should allow prediction of their response to date of planting.

#### *Sprouting (physiological age) of seed*

Like early planting, the use of sprouted seed generally hastens emergence and early leaf growth, then leads to an earlier onset of senescence (Madec & Perennec, 1955). Table 1 indicates that in general, unit leaf area will be more effective in May and June than in August and September. However, there are variations, and sprouting has not invariably improved yield if crops have been allowed to reach maturity (Younger, 1975). The merits of the practice are still debated, particularly in relation to mechanization of the planting operation. One factor contributing to the inconsistency of performance of 'sprouted' crops and a major hindrance in interpretation of experimental results is the lack of definition of the term 'sprouting'. As a consequence of variations in the end of natural dormancy, the temperatures prevailing in store and the duration of the sprouting period, treatments based on weeks of sprouting in ambient conditions are likely to produce differing numbers of sprouts of differing length and morphology. As the effects on early growth and senescence may well be progressive from the unsprouted to the heavily sprouted condition, some quantitative measure of the state of sprouting is required to understand better and, more importantly, to predict its effects.

Recently, it has been shown for several varieties that the extent of sprout growth (the length of the longest sprout) may be related to a scale of accumulated day-degrees above a base temperature experienced by the seed tuber from the onset of sprout growth to planting (Allen *et al.* 1979; O'Brien & Allen, 1978; Wurr, 1978) and that this scale can be related to field growth and yield. As more day-degrees accumulate from onset of sprout growth, emergence, early leaf growth, tuber initiation and leaf senescence are advanced (O'Brien *et al.* 1980). The magnitude of the effect and the number of day-degrees required to produce a particular response are specific to individual varieties. The significance of these effects is greatest in early varieties in which very large effects on leaf area and leaf longevity can be produced (Allen *et al.* 1979; O'Brien *et al.* 1980). Responses are also demonstrable in many maincrop varieties but fewer data are available (see Wurr, 1978; Ali, 1979). At early harvests taken before the onset of senescence, increases in early leaf growth through sprouting are usually beneficial as light interception is improved. As harvesting is delayed the effects of sprouting are likely to become dependent upon the relative values of early and late light interception in relation to the different leaf growth patterns. If the crop from aged seed senescences considerably in advance of the intended harvest date, it may give less yield than a crop from younger seed, despite improved early light

interception. Conversely prolongation of the leaf surface into October through the use of very young (possibly unsprouted) seed will increase yields only if more light is intercepted in autumn than was sacrificed in the early part of the season. Thus the correct sprouting condition at planting is a function of the variety and the planned date of harvest. In general, as the date of harvest is delayed, seed with less sprout growth is required. The progress through various sprouting conditions has been likened to an ageing process and the term 'physiological age' used to describe the state of the seed tuber (Madec & Perennec, 1955). The accumulated day-degree scale provides a quantitative measure of the 'ageing' process and the terms 'old' and 'young' can be directly related to that scale.

It seems likely that for each environment, variety and planned harvesting date there is a correct physiological age at planting which will lead to senescence when the maximum possible yield within the available growing season has been achieved. For the early varieties, e.g. Home Guard, the optimum ages for the early harvesting period have been demonstrated (Fig. 11). Similar effects have been shown in maincrop varieties (Fig. 12). This aspect of growth is of enormous potential

benefit to growers, for it would suggest that maximizing yield for much of the season may be achieved while producing naturally mature tubers which are fit for harvest and, if necessary, storage. What is quite clear is that no single sprouting treatment is optimal for the many varieties, locations and harvesting programmes used by growers. The correct physiological ages must be determined and then growers may significantly improve their control of leaf growth through this factor.

The large effects of physiological age on early leaf growth suggest that crops planted with unsprouted (i.e. physiologically very young) seed may, on average, have a lower yield potential than crops from sprouted seed, this being especially so in mild environments and seasons in which interception of light in May and June is achieved. The reduction in potential will increase if the growing season is shortened through late planting or early defoliation (Baldwin, 1964). The practical advantages of mechanized systems of seed handling and planting may, of course, make the yield penalty acceptable to some growers.

More fundamentally it should be clear that the growth and yield of a variety is very dependent upon the age of the seed used and timing of the harvesting

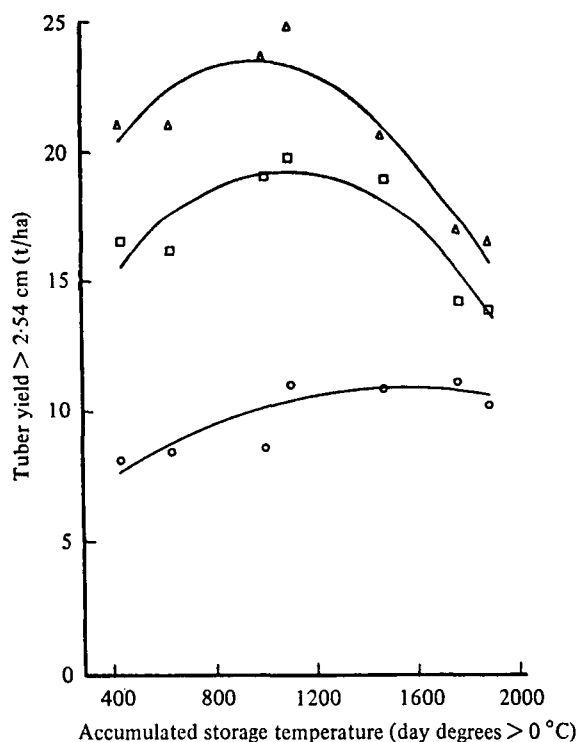


Fig. 11. The relationships between tuber yield and accumulated storage temperature on three dates of harvesting. Variety Home Guard (O'Brien & Allen, 1978). ○, 15. vi. 77; □, 29. vi. 77; △, 18. vii. 77.

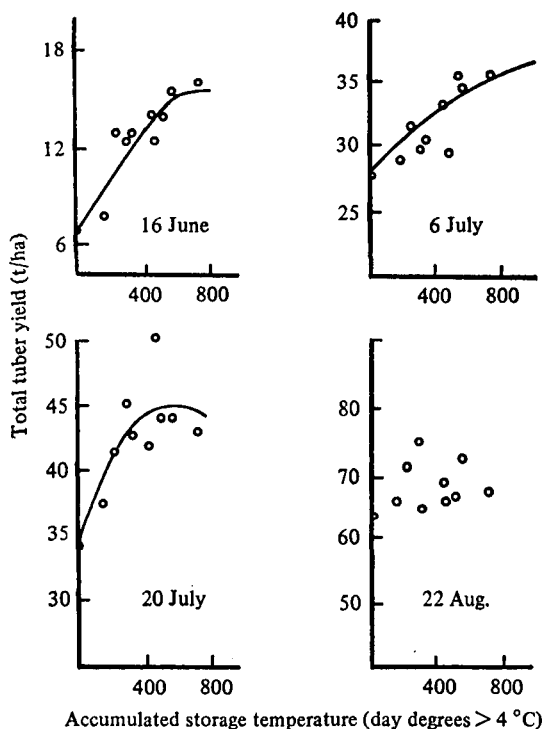


Fig. 12. The relationship between total tuber yield and accumulated storage temperature in Désirée (Ali, 1979) on four harvest dates.

programme. Furthermore, it is known that physiological age affects root growth (O'Brien, 1980), water uptake (J. N. Bean, unpublished) and optimum stem densities (Bean & Allen, 1975), so this factor, which has hitherto been largely unrecognized and certainly uncontrolled, is likely to influence the effects of most husbandry factors on leaf growth and yields.

#### Nitrogen and water

As the amount of nitrogen fertilizer applied to potato crops increases a decreasing proportion is taken up (Table 5), and the incremental effect on leaf growth also decreases. Thus, in terms of advancing leaf growth a limit, which is within the currently recommended range, is soon reached in the amount of N which will produce a response (Fig. 13). Increases in peak  $L$  values do occur with rates of N which exceed that which is recommended, but such effects can add only marginally to the amount of radiation which is intercepted. Perhaps surprisingly, the time when the leaf surface senesces is hardly affected. As many maincrops given standard N dressings, especially those planted late, are defoliated while still actively growing, it is unlikely

Table 5. Nitrogen uptake by potatoes\* in relation to level of applied nitrogen fertilizer (P. M. Harris, personal communication)

N applied	N recovered in tubers	N recovered from fertilizer	N recovered as % of applied
0	160.2		
50	203.7	43.6	87.1
100	233.9	73.7	73.7
150	272.4	112.2	74.8
200	288.2	128.1	64.0
250	316.2	156.0	62.4

\* Averaging varieties King Edward and Désirée, 1978.

that any increased leaf persistence which might accompany higher peak  $L$  values would materially affect radiation interception. Very high yields have been produced without altering conventional N applications; Ifenkwe (1975) has shown that such crops are capable of extracting about twice the quantity of N as was applied as fertilizer. It is also clear that high rates of N application stimulate leaf rather than tuber growth, and the onset of bulking may be delayed by 7–10 days (Fig. 14). Any improvements in light interception achieved by increasing N above current recommendations are likely to be at least counterbalanced by unfavourable alteration in the partitioning of assimilates.

Although there seems no good reason to apply more nitrogen the gradual upward trend in usage continues (Table 6). Moreover, there is considerable interest in and increased use of foliar applications of N to supplement the available N, which already appears more than adequate. Unless they lead to the interception of more radiation, or the more efficient use of that which is intercepted, high rates of N application cannot produce this effect. We have already shown that there is little scope for increasing the former and recently, for cereals, Marshall (1978) concluded that above a minimum N application, which is small compared with current use, photosynthetic rate was not affected.

It is often suggested that increases in rate of early leaf growth through increased stem density are associated with earlier senescence caused by depletion of soil nitrogen. Consequently, considerable emphasis has been given to the possibility of offsetting this by addition of more N. There is no convincing evidence that high stem densities require more nitrogen.

The water requirement of any crop is determined by the evaporative demand created by the prevailing incident radiation and the saturation vapour pressure deficit of the air. Evaporation of water occurs through the stomata which also allow  $CO_2$

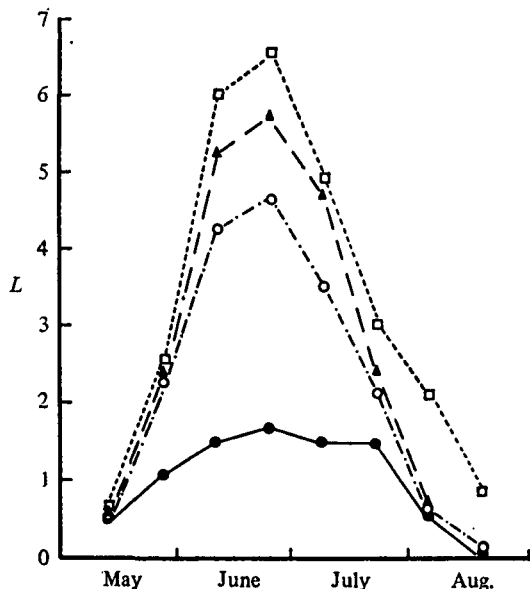


Fig. 13. The effect of nitrogen on leaf area index ( $L$ ). P. M. Harris, personal communication. ● ○ ▲ □: 0, 100, 200 and 300 kg N/ha.

exchange. When the plant is unable to meet the evaporative demands of the atmosphere, the leaves lose turgor and stomata close, which restricts both photosynthesis and water loss. From a field with a closed crop surface about one-quarter of the sun's energy is reflected: of the non-reflected energy, about half is used in evaporating water and the other half is used in various processes of energy transfer from the surface to the atmosphere. Increases in dry-matter yields require the interception of more radiation, which inevitably means increased water demand. Penman (1970) has shown that yields of grass and potatoes are proportional to accumulated evapotranspiration which is itself closely related to intercepted radiation. Thus an inevitable consequence of aiming for the highest dry-matter yields is a water demand in excess of that which can consistently be met by the plant from natural sources. The production of the highest yields demands large increases in the water available to the plant in addition to the supply from soil and rainfall; the same principle does not necessarily apply for N. In the year 1976 when irradiance was exceptionally great but there was little rain, the very high potential dry-matter yield was not obtained because water stress was so severe. Both leaf expansion and longevity were seriously curtailed, restricting both the interception of radiation and the efficiency of its use (Fig. 2). Although there is no direct evidence from irrigation experiments, it is likely that in that year the elimination of water stress would

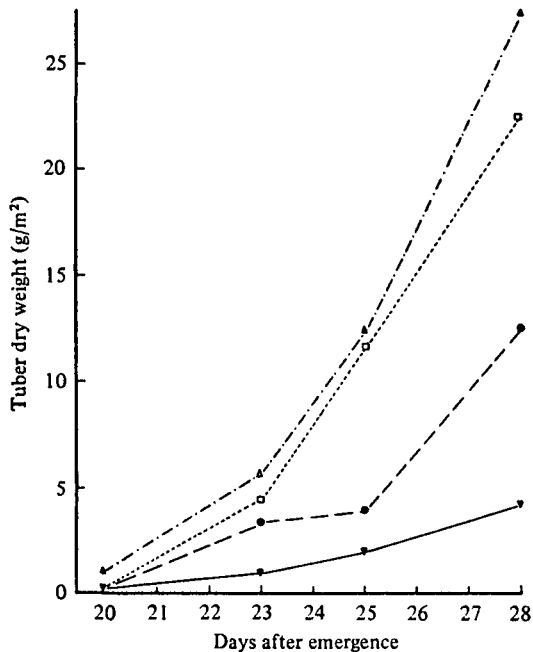


Fig. 14. Effect of nitrogen on changes with time of tuber dry weight soon after tuber formation. Dyson & Watson (1971). △ □ ● ▼: 0, 94, 118 and 376 kg N/ha.

have produced record yields. However, the evaporative demand was so great that very frequent irrigation would have been required to maintain growth. In a recent publication on the analysis of the effects of drought on barley, Legg *et al.* (1979) applied this analysis and also showed that drought reduced both the amount of light intercepted (the major effect) and the efficiency of conversion. Decreased efficiency was due to a combination of a larger proportion of the foliage of stressed crops being light-saturated, stomatal closure and increased respiratory losses.

#### Variety

From a wide range of experiments it is clear that many varieties are capable of producing and maintaining for much of the season a leaf surface which can intercept at least 85% of the incident radiation. The data in Fig. 2 and unpublished data of J. N. Bean and E. J. Allen suggest that the efficiency with which different varieties convert intercepted radiation into dry matter is similar. Thus, the major effect of variety on leaf growth and thereby yield potential is likely to be on the rate at which a complete leaf cover can be attained. Few data have been found on temperature minima for growth of different varieties or on the effects of temperature

Table 6. Actual average rates of application of NPK applied as inorganic fertilizer (kg/ha) to maincrop potatoes\*

Year	N	P <sub>2</sub> O <sub>5</sub>	K <sub>2</sub> O	FYM	
				% acreage	Rate (t/ha)
1972	166	181	242	32	45
1973	176	189	244	27	?
1974	176	185	245	?	?
1975	174	179	245	47	?
1976	179	178	254	37	?
1977	181	186	251	51	?

\* Excludes crops which were not given any fertilizer (B. M. Church, personal communication).

on rates of leaf differentiation, emergence or expansion, so that the fundamental causes of any differences between them cannot be examined. As suggested earlier, there is evidence from early varieties that temperature minima for growth do differ.

The available data on early leaf growth in the field do not allow meaningful conclusions to be drawn as the varieties are usually emerging at different times, and soil and air temperatures are not recorded. On theoretical grounds, varieties which have high optimum stem densities (as a consequence of low numbers of tubers per stem) should have an advantage in early leaf cover over varieties grown at lower stem densities, given that rates of emergence and expansion of individual leaves were the same. Pentland Crown is just such a variety.

#### Site

Small differences in soil and air temperatures between sites in spring may have a crucial influence on early leaf growth and radiation interception. The earlier and more consistent rise in temperatures in spring (Table 7) in western parts of the UK confers upon the arable soils of these areas an intrinsic advantage. This is, of course, the principal reason for the early potato industry in these areas. For sugar beet, Scott & Jaggard (1978) have estimated that a reduction of 1 °C in the mean temperature for each week from April to July would, in a season of average radiation, reduce interception and, by implication, sugar yield by 10%. Temperature differences of this magnitude exist between many areas. The relative freedom from frost in the west ensures that the advantages in early leaf growth so obtained are not vitiated by frost damage. Frost in May can be a major impediment to early light interception by potatoes in the eastern parts of the U.K. (Radley, 1963). The potential of westerly environments for producing consistent heavy-yielding potato crops has been demonstrated for Pembrokeshire by Allen (1977) and Ifenkwe & Allen (1978).

#### Pests and diseases

The effects of pests and diseases can be analysed in the same way as the factors previously mentioned. Perhaps the most obvious example is the effect of the Colorado Beetle, which certainly affects light interception and may affect the efficiency of the diminished canopy. Potato blight remains probably the most important factor determining the persistence of the canopy, and many other diseases affect foliage longevity, e.g. black scurf, skinspot and *Verticillium* wilt. Other diseases, of which the most important are the virus diseases, leaf roll and the various mosaics, almost certainly affect both interception and the efficiency of conversion. Nematodes will reduce water and nutrient uptake and thus may restrict both components of the analysis.

#### TUBER BULKING AND POTENTIAL YIELDS

A consideration of incident radiation and published leaf area indices would suggest that because tubers form a constant fraction of total weight, bulking rates would increase to a maximum and then gradually decrease as the amount of intercepted radiation increased and then decreased. This appears in conflict with much published data, for tuber bulking rates are usually taken as constant over much of the life of the crop and mean bulking rate, obtained by dividing final yield by the period of tuber growth, is used to define tuber growth. A figure of 5 t/ha/week, i.e. 1 t dry matter/ha, is accepted as the 'normal' bulking rate for potatoes. Wurr (1974b) and Carlsson (1970) have both shown that bulking rates are not constant but decline over time. Figure 15 presents the bulking rates for six crops grown at different sites and giving a wide yield range, which clearly shows that bulking rates generally decline with time. The highest rates were found with early varieties in Pembrokeshire, where the canopy was sufficiently complete for advantage

Table 7. (a) Mean temperatures ( $^{\circ}\text{C}$ ) for Aberporth and Broom's Barn in spring 1972-8. (b) Maximum and minimum temperatures (monthly averages,  $^{\circ}\text{C}$ ) for Broom's Barn (BB) and Aberporth (A)

(a)	Year	Feb.	Mar.	Apr.	May
		Aberporth			
	1972	4.9 (2)*	6.5 (2)	7.9 (0)	9.4 (0)
	1973	5.2 (4)	6.3 (0)	7.4 (2)	10.1 (0)
	1974	5.5 (0)	5.8 (0)	8.8 (0)	10.0 (0)
	1975	5.8 (0)	5.1 (3)	7.7 (1)	9.6 (0)
	1976	4.9 (5)	5.2 (5)	7.5 (0)	10.6 (0)
	1977	5.8 (2)	7.3 (0)	7.0 (0)	10.2 (0)
	1978	3.5 (13)	6.5 (3)	6.6 (2)	10.9 (0)
	1979	2.4 (12)			
		Broom's Barn			
	1972	4.0 (4)	6.7 (3)	8.0 (1)	11.0 (0)
	1973	3.7 (13)	6.4 (4)	7.0 (4)	11.7 (0)
	1974	5.3 (3)	5.7 (4)	8.1 (1)	11.2 (0)
	1975	4.5 (7)	4.5 (8)	8.1 (6)	9.7 (0)
	1976	4.2 (9)	4.6 (12)	8.0 (3)	12.5 (0)
	1977	5.0 (6)	6.7 (4)	7.1 (5)	10.4 (0)
	1978	2.1 (15)	6.7 (5)	6.3 (5)	11.0 (0)
	1979	0.9 (20)	4.7 (5)		

\* Number of days with air frosts.

(b)		1969		1970		1971		1972	
Month		Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Jan.	BB	7.9	3.2	5.5	1.1	6.5	1.9	5.2	1.1
	A	7.9	4.1	7.5	3.1	7.7	3.5	6.8	2.8
Feb.	BB	2.8	-2.2	5.7	-0.2	7.4	1.5	6.4	1.6
	A	4.4	0.1	6.2	1.9	7.4	2.7	7.0	2.7
Mar.	BB	5.9	0.5	6.3	-0.2	8.1	1.2	11.1	2.3
	A	7.4	2.0	6.6	2.0	7.5	3.0	9.1	3.8
Apr.	BB	12.3	2.9	10.1	3.1	10.9	3.9	11.5	4.5
	A	10.5	4.5	8.8	4.2	10.7	4.7	10.2	5.6
May	BB	16.0	7.6	18.3	7.9	16.8	6.4	15.2	6.8
	A	13.1	7.5	14.5	8.5	14.2	7.4	12.0	6.8
		1973		1974		1975		1976	
Jan.	BB	6.4	1.8	8.5	2.7	9.1	3.9	7.3	2.5
	A	7.4	3.5	8.6	3.7	9.1	5.0	8.0	4.9
Feb.	BB	6.8	0.6	8.1	2.6	7.5	1.4	6.8	1.6
	A	7.1	3.2	7.9	3.1	8.7	2.8	7.1	2.6
Mar.	BB	10.5	2.3	9.2	2.1	6.9	2.0	7.8	1.4
	A	9.0	3.5	8.5	3.0	7.2	3.0	8.1	2.2
Apr.	BB	11.1	2.9	12.6	3.5	11.8	4.4	12.1	3.9
	A	9.2	4.5	12.4	5.2	10.3	5.0	10.5	4.4
May	BB	16.1	7.2	16.9	6.5	13.5	5.9	17.3	7.8
	A	14.2	7.9	13.0	6.9	12.5	6.6	13.5	7.6
		1977		1978		1979			
Jan.	BB	4.6	0.5	5.2	0.5	2.0	-3.2		
	A	5.9	1.8	6.6	2.5	4.6	-0.4		
Feb.	BB	7.7	2.3	4.6	-0.3	3.0	-1.2		
	A	8.2	3.4	5.4	1.6	4.5	0.3		
Mar.	BB	10.0	3.5	10.2	3.1	7.9	1.5		
	A	9.8	4.7	9.0	4.0				
Apr.	BB	11.1	3.1	9.8	2.8	11.7	4.1		
	A	9.3	4.7	9.4	3.7				
May	BB	14.7	6.1	15.7	6.3	15.5	6.5		
	A	13.6	6.8	13.9	7.9				

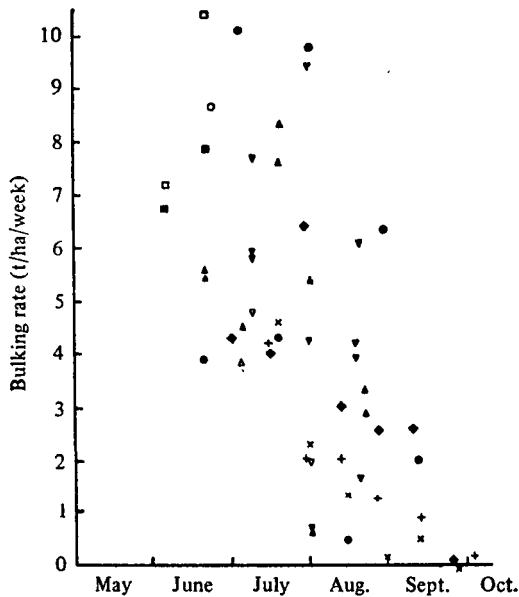


Fig. 15. The relationship between bulking rates and time. ●, Darby (1974), Pentland Crown; ▲ △, Ifenkwe (1975); ▲, Maris Piper 1973; △, Maris Piper 1974; ■ □, Allen *et al.* (1979); ■, Home Guard; □, Vanessa; × +, Dyson (1965) King Edward (2 seasons); ▼ ▽, Allen (1977); ▼, Désirée; ▽, Maris Piper (two dates of planting); ○, J. N. Bean (unpublished), Maris Bard; ◆, Wurr (1971), Pentland Crown.

to be taken of the high irradiance in May and early June; values were considerably in excess of 5 t/ha/week. Negative bulking rates are often recorded in September and October (Dyson, 1965).

Because of inadequacies in frequency of sampling, attributes recorded and lack of radiation data, it is not possible to plot tuber growth against radiation intercepted, the most discriminating test of the relationship. During July and August when leaf cover is complete and the average changes in light receipts from week to week are small, changes in bulking rate will be gradual. Thus, many sets of data may be adequately represented by linear regressions of yield on time. However, this does obscure the fundamental pattern of tuber growth.

In principle, if radiation interception can be estimated, the relationships in Figs 2 and 4 offer a means of predicting yields in different environments. It is clear that accurate prediction relies heavily on knowing the slope of the relationship, i.e. the efficiency term. A small over- or under-estimate will have a large effect on predicted values; in absolute terms the more so the greater the amount of radiation intercepted. In neither figure does the line of best fit pass through the origin. For the relationship

Table 8. Effects of the interval between defoliation and harvest on tuber yield (t/ha) of Désirée\* (D. C. E. Wurr, personal communication)

Harvested at	Date of defoliation		
	19 July	16 Aug.	13 Sept.
Defoliation	6.05	14.24	18.13
After 2 weeks	6.68	14.92	18.77

\* Means of two spacings.

with tuber yield this may not be entirely due to error, but clearly the true line for the relationship in Fig. 2 must pass through the origin; the transfer of reserves from seed tubers to the young plant can account for but a trivial fraction of total plant weight. At final harvest all crops had intercepted at least 500 MJ and the lack of definition lower on the scale limits the accuracy. On Fig. 1 the data for crop growth rate during the early stages clearly do conform to theory. J. N. Bean's more comprehensive data show that the relationship between crop dry weight and intercepted radiation from tuber initiation onwards passes close to the origin.

Regarding the line for tuber weight, initiation occurs some time after the interception of radiation has begun. However, there are also difficulties late in the season. Because of the errors involved in measuring total dry weight once senescence begins, and the lodging of some treatments which invalidates radiation measurements, tuber yields are those which treatments had achieved on the date coinciding with the onset of senescence of the majority. Differences in senescence may reflect differences in translocation of assimilate from stems to tubers, enhancing tuber yield per MJ intercepted in the more advanced treatments. The extent to which differences in efficiency correspond with the extent of translocation needs examining. There is evidence from experiments in which the interval from defoliation to harvest has been lengthened that tuber yields may increase significantly in the absence of current photosynthesis (Table 8).

Given these limitations the slope of the line in Fig. 4 has been used as a measure of efficiency to calculate potential yields for a range of environments. The first attempt to calculate potential yield was by Alcock (1967), and his value for dry matter produced per unit light intercepted is similar to that in Fig. 4. Alcock estimated the potential tuber yield for a crop intercepting all incident radiation during a tuber growth period of 1 June to 10 September at Bangor, N. Wales, to be 92.5 t/ha. In making this calculation he assumed that all leaves were equally illuminated, every 0.42 MJ/m<sup>2</sup>/day produced 6.73 kg dry matter/ha/day, and this dry matter was partitioned in a similar way to known potato crops.



More recent data clearly show that tuber initiation occurs early in growth, some 3–4 weeks in advance of full leaf cover, so that complete light interception throughout tuber bulking does not occur. None the less this tuber bulking period is appropriate for many maincrop potatoes in England and Wales and, allowing for failure to intercept all the June radiation, the best crops are close to this estimate of their potential. Many crops have produced 80 t/ha but few have exceeded 90 t/ha.

For some areas the earlier rise in spring temperatures results in an earlier onset of leaf growth, and experiments at Trefloyne show that tuber bulking can commence before 1 June, and in view of this the yields obtained for milder environments in the south-west should be at least equal to Alcock's figure.

Table 9 presents calculation of potential yield for an environment in which leaf growth began on 1 April and proceeded to achieve complete light interception by 1 June; a not unreasonable assumption for the south-west as the data of Ifenkwe & Allen (1978) show. If growth continued until 31 August with average radiation this leaf growth pattern would intercept approximately 1705 MJ/m<sup>2</sup> which, using the relationship in Fig. 4, would produce on a dry-weight basis 2300 g/m<sup>2</sup> or 23 t/ha of tubers. On a fresh-weight basis this represents a yield of 115 t/ha assuming 20% dry matter or

105 t/ha if the dry-matter content were 22%. This latter value is very similar to the 100 t/ha reported by Van der Zaag & Burton (1978) which was calculated from the data of Sibma (1970), for a crop which achieved maximum light interception by early June. If account is taken of the higher light intensities at coastal sites which is of the order of 20%, potential yields increase to between 125 and 140 t/ha. tubers Few attempts to grow large (let alone maximal) yields in such environments have been made, but available data suggest that the calculation is not unrealistic nor unattainable.

The light interception predicted by 10 June would be 510 MJ/m<sup>2</sup> for average receipts or 615 MJ/m<sup>2</sup> at a coastal site, which would produce fresh yields of 25 or 31 t/ha respectively, and the tuber yields in Table 10 show that several varieties almost achieved this on an irrigated, coastal site in North Pembrokeshire in 1978. As Ifenkwe's (1975) crops reached yields of 70 t/ha by 7 August at Trefloyne in 1974 where *L* values were then 2–3, it seems likely that yields exceeding 100 t/ha are possible in these environments. Conversely, environments in which early leaf growth is poor, for example much of Scotland, will not be able to produce yields of even 80 t/ha. Leaf growth may not begin until mid-May and complete light interception is not achieved until late June or early July, which is likely to reduce total light interception by 300–400 MJ/m<sup>2</sup> and reduce maximum yields by 15–21 t/ha, to a figure of 71–77 t/ha.

All these estimates are based on average radiation values and in any one year actual radiation receipts will determine potential yield. The relative potential of sites is unlikely to alter. However, no single figure should be taken as the potential for an environment, for in dull years the reduced radiation will lower potential yield and in bright years the potential yield will be increased. Similar yields at a site from year to year are often the consequence of quite different growth patterns and represent quite different proportions of the potential. In dull, wet years yields are restricted by radiation but are unaffected by water stress and often may be close to the potential of the environment. Similar yields in dry, bright years may be the result of severe water

Table 9. *Light interception for environment with onset of leaf growth on 1 April*

	% Light intercepted	Incident radiation (MJ/m <sup>2</sup> )	Intercepted radiation (MJ/m <sup>2</sup> )
April			
1st half	10	360	{ 18
2nd half	25		
May			
1st half	50	446	{ 110
2nd half	75		
June	100	510	510
July	100	465	465
August	100	390	390
		Total	1705

Table 10. *Yields (t/ha) of a range of varieties grown at Trefn, N. Pembrokeshire in 1978*

Date	Variety						
	Arran Comet	Maris Bard (once grown)	Maris Bard*	Home Guard	Pentland Crown	Désirée	S.E.
30 May	20.6	11.6	16.8	19.2	16.7	17.8	0.91
7 June	30.5	16.8	24.7	24.8	25.9	22.4	0.94
16 June	35.1	21.4	32.0	27.3	30.9	28.8	1.49

\* Certified seed.

Table 11. Yields from crops grown with conventional husbandry

Site and author	Year	Variety	N fertilizer (kg/ha)	Mean seed wt. (g)	Planting date	Harvest date	Total yield (t/ha)
N.V.R.S.	1973	Maris Piper	200	{ 62	28 Mar.	1 Oct.	78.3 (86.3)*
Wellesbourne	1973	Désirée		{ 60	28 Mar.	24 Sept.	78.1 (90.6)
D. C. E. Wurr (personal communication)	1974	Pentland Crown	160	{ 38	18 Apr.	24 Sept.	65.2 (72.2)
	1974	King Edward		{ 39	18 Apr.	24 Sept.	66.5 (69.5)
Trefoyne	1974	Maris Piper	151	{ 45	21 Mar.	28 Aug.	71.6 (85.2)
Allen, 1977	1974	Désirée		{ 45	21 Mar.	28 Aug.	79.4 (79.4)
Ifenkwe, 1975	1974	Maris Piper	160	{ 85	27 Mar.	7 Aug.	70.0 (70.5)
		Désirée		{ 85	27 Mar.	7 Aug.	66.2 (72.1)
Sutton Bonington (Darby, 1974)	1973	Pentland Crown	75†	93	12 Apr.	16 Sept.‡	87.8 (96.2)
Reading P. M. Harris (personal communication)	1978	King Edward	200	33	12 Apr.	21 Sept.	89.0 (93.3)

\* Yield values in parentheses are highest single plot yields within the quoted treatment.

† Also received an application of pig slurry.

‡ Effective date due to blight infection.

stress and represent a much smaller fraction of the potential.

## IMPLICATIONS

### For growers

Achievement of maximum yield was the objective of the Agricultural Development and Advisory Service 'blueprint' for maximizing potato yields (Evans, 1975). The inputs for the blueprint were chosen, apparently arbitrarily, so that no controllable input limited yield, and large increase in seed size, seed rate, fertilizers and length of growing season were included in the implicit belief that previous experiments had not explored a sufficiently wide range of these factors to achieve 'maximum' yields. This suggests a pronounced conflict in the methods of research and advice to growers necessary to achieve continuing increases in yields. Our analysis would suggest that very heavy yields of potatoes may be produced without significantly raising inputs, and this is confirmed by the highest annual yields of some of our collaborators shown in Table 11. Such yields are not new, for Delaney (1941) reported a yield of 87 t/ha in Donegal and there are other examples in the literature.

Although the blueprint has produced some high yields, > 80 t/ha, many examples of more modest yields are found and some growers have achieved a similar range of yields to blueprint crops without altering their conventional inputs. As the blueprint approach to experimentation has not discriminated between factors as to their importance in determining yields (Evans, 1975; Nield, 1977; Evans, 1978), the reasons for this variation in yield would remain unclear without the type of analysis undertaken here.

It is clearly unnecessary to raise inputs above current recommendations in order to achieve high yields. With irrigation, yields of 70–80 t/ha should be attained by maincrop growers in England and Wales in most years. In all areas there seems little doubt that, in the absence of irrigation, variation in yields between sites and seasons. Growers who are unable to irrigate must accept both lower potential yields and much greater variation from year to year. Growers in areas such as Scotland in which spring temperatures are often low late into May, so that early leaf growth is slow, must accept that this reduces their yield potential and they will rarely achieve yields above 60 t/ha, despite similar radiation receipts (Table 12). Attempts to maximize yield in Scotland using the blueprint approach did not produce any yields in excess of 65 t/ha. Table 12 illustrates dramatically the extent to which indiscriminate use of the blueprint may reduce rather than enhance yields. In Expt 5 severe water shortage occurred in late June and July and in the absence of

Table 12. Comparison of yields of crops grown according to the ADAS 'Blueprint' with those grown with conventional inputs in the east of Scotland (Lang &amp; Rodger, 1978)

Yield from conventional combination (t/ha)	58.70	44.35	64.15	55.50	63.14	54.94	56.80
Response to Blueprint combination (t/ha)	+5.52	-9.16	-2.66	+9.89	-17.67	+10.49	-0.66
Response to individual components							
Year	1975	1974	1976	1976	1977	1977	
Experiment no.	1	2	3	4	5	6	
Site	Bush Estate	County	Bush Estate	County	Bush Estate	County	Mean
Fertilizer	+3.91	-3.16	-0.75	+4.57	+8.59	+3.75	+2.82
Seed size	-6.25	-6.02	0	-2.48	+3.09	-1.48	-2.19
Seed rate	+8.66	+1.61	+1.00	+1.76	-33.31	+2.48	-3.00
Chitting	+1.03	+4.42	+1.25	+2.33	-1.47	+6.20	+2.29
S.E.	1.10	1.05	1.20	0.93	2.05	0.92	

Table 13. Yield components and other characteristics at harvest of 7 varieties of winter wheat (Austin, 1978)

	Height to base of ear (cm)	Grain yield (g/m <sup>2</sup> dry wt.)	Straw yield (g/m <sup>2</sup> dry wt.)	Harvest* index (%)	Number of ears/m <sup>2</sup>	Number of grains/ear	1000-grain dry wt. (g)
Little Joss	130	403	918	30	365	32.8	33.7
Holdfast	112	394	856	31	524	22.7	31.9
Maris Widgeon	115	486	923	34	323	31.0	49.1
Maris Huntsman	95	657	985	40	428	32.4	43.0
Kinsman	82	638	1019	38	457	30.2	44.9
Hobbit	67	757	925	45	429	45.6	33.6
Mardler	73	761	930	45	469	39.5	35.5

\* Yield of dry grain expressed as a percentage of the yield of dry grain and straw.

irrigation the higher seed rate plots senesced. In all the experiments in Scotland no consistent responses to the individual components of the blueprint were detected, and Lang & Rodger (1978) concluded that there was no evidence that the yield of farm crops was likely to be limited to any extent by current recommendations relating to seed size, seed rate and fertilizer rate.

Growers in the S.W. parts of the U.K. where early growth is achieved regularly may achieve much higher yields than the currently accepted maximum of 80-90 t/ha if they grow the crop throughout the season free from disease and water stress. Failure to achieve the predicted yields is a measure of management failure and results from the inability of the crop to intercept incident radiation. This is especially important in the failure to establish the recommended full stem population, which may be compounded by the irregularity of the planted sets. Aerial photographs of many crops, including

potatoes, have shown that even in apparently well-grown crops much light is wasted because gaps exist.

#### For plant breeders

With wheat it is possible to show how variety has contributed to the progressively increasing yields during this century (Table 13). Increases have arisen because of greater total dry-matter production associated with the use of more nitrogen, and an increasing ratio of grain to straw. The variety Pentland Crown has certainly contributed to the increasing national potato yield, but in the absence of drought and disease it does not greatly outyield varieties bred 70 years ago (Steckel & Gray, 1979). The majority of varieties recommended in the last 15 years do not outyield Pentland Crown, and owe their acceptance to other improved characteristics.

There is considerable difficulty in obtaining accurate measures of the yield potential of different

Table 14. *Total tuber yields (t/ha) (Allen, 1977); physiologically 'young' seed*

Date of planting	Home Guard	Désirée	Maris Piper
18 April	65.9	62.3	58.4
2 May	55.9	48.6	52.4

S.E. 7.88.

potato varieties caused by the long period over which the crop is harvested, and the large effect of physiological age of the seed on growth patterns in the field. Allen (1977) showed that with physiologically old seed Home Guard produced substantially lower yields than either Désirée or Maris Piper. However, with physiologically young seed planted in April, growth patterns were similar and yield reached similar high levels (Table 14).

It seems probable that a number of current varieties are able to intercept radiation for much of the available growing season and in the absence of any possibility of changing the photosynthetic pathway, the efficiency of this process will not be markedly altered by breeding. The question may, therefore, be asked whether varieties are likely to be produced with much higher yield potentials than those currently available. The aspect of growth which might be improved to lead to greater light interception is the rate at which a full leaf cover is produced by selecting for either growth at lower temperatures or more rapid growth at prevailing temperatures, or both. To assess the existing genetic variation in the former character it is essential that selection is carried out in environments in which temperatures remain close to the threshold for some weeks after planting. Neither character can be assessed in Continental-like environments in which the spring rise in temperatures is very rapid.

Alternatively the rate of leaf cover may be improved either by mixing varieties or seed of differing physiological ages of a single variety. In maincrop varieties such as Désirée where large effects of age on early growth can be demonstrated the use of a proportion of old seed may improve early leaf growth and not prejudice the maintenance of a complete leaf cover for the remainder of the season (Schepers & Sibma, 1976). The use of such mixtures of seed ages within a variety would not interfere with the commercial harvesting and sale of the produce. If varieties were mixed it would be necessary to have separation at harvest as the sale of mixed varieties is unlikely to be acceptable. Alternate row planting of an early and a maincrop variety would allow mechanical harvesting of individual varieties.

Some improvement in light interception early in growth may be achieved in varieties having large,

prostrate leaves. The theoretical advantages of such leaves for light interception at low  $L$  values are well known (Fig. 5) but no data for potatoes have been found. Allen *et al.* (1979) have reported high tuber bulking rates (see Table 2) for Vanessa which has very prostrate leaves, and relatively low rates for Pentland Javelin which has more erect leaves, but no direct measurements of light interception were made. As later-formed leaves in Pentland Javelin are relatively prostrate it is not inconceivable that advantageous changes in leaf angle during growth may be obtained through breeding.

In attempts to increase the yield potential of varieties the relationship between number of tubers and yield is crucial. When yields are low, varieties which are naturally prolific in their number of tubers often produce low ware yields because of the large fraction of undersize tubers. However, this may be an essential characteristic of varieties bred for the highest yielding environments. On the other hand varieties which set fewer tubers but do increase in numbers per unit area over the increasing stem range could be used in high-yielding environments provided stem densities were in excess of the minimum required for total yield in order to control tuber size. Pentland Crown is exceptional in that the number of tubers does not increase beyond a low stem density, and increases in yield beyond 80 t/ha may be associated with the production of more and more oversize tubers. This trait would become increasingly unacceptable as yield increased.

The analysis allows an explanation of why varieties whose seasonal patterns of leaf production and death conform to the second early type frequently outyielded maincrops whose leaf area curves are displaced later in the season (Gunasena & Harris, 1971). Looking to the future it seems that there are other reasons why breeders should select for second early characteristics. The earlier onset of harvesting will permit the operation to be completed in generally better conditions with less tuber damage and less loss during storage. This analysis indicates that these characteristics and the associated practical advantages can be obtained without sacrificing yield.

#### *For the industry*

For long the potato industry has been based on a marked division into the coastal districts which specialize in first early production, more inland sites in the west and parts of central England where second earlies are grown, and the eastern parts where late-harvested crops for storage predominate. The analysis showed that as well as being early, the western coastal sites, with 20% more radiation, are potentially higher yielding on any harvest date. Clearly one way to increase the national average yield would be to redistribute existing acreage

towards the more favoured sites. Any factor such as cheap imports which reduces the premium on earliness and leads growers to harvest later will also increase overall average yield. Cole (1973) has shown that even at the earliest sites the first harvested crops are not the most profitable. Any major shift towards later harvest in the earliest districts will most severely affect those growers aiming at the second early market on unirrigated sites in central England. Growth on such sites may be impeded by low temperatures early in the season and water shortage later. Consequently yields will be much lower than achieved further west.

There is a lack of data which characterize the coastal environment in relation to crop growth. The extra radiation will not be exploited if plants are more water stressed. We need detailed meteorological data for a series of coastal sites and most importantly a characterization of the extent to which the advantages of the coastal site diminish with distance inland. For this purpose fuller data than are available at the standard agro-meteorological station are necessary.

The analysis provides a mechanism for predicting yields of irrigated crops and thereby affords some control of a major element of the calculations on which a harvesting strategy must be based. This applies both to the individual grower in organizing his harvesting operations and especially to the processor, whose requirement for a continuous supply of a standard commodity is the most important factor determining the efficiency of his operation. As is discussed more fully in the next section, even where growth is restricted by a known factor, and actual efficiencies of conversion of intercepted radiation are measured, the analysis can be used predictively when the particular factor, for example drought or blight, is known to operate. This does offer a predictive capability for the industry as a whole, although the information presently available is from non-stressed crops.

#### *For research*

In his discussion of the ideas on which this analysis is based Monteith (1979) stated 'The concept of intercepted radiation as a major discriminant of crop growth therefore provides both a baseline and a framework for analysing crop yields... Properly applied such a principle could reduce by at least an order of magnitude the amount of effort devoted by the Agricultural Research Service to multi-factorial field trials, currently analysed in purely statistical terms and without reference to the basic physical concepts.'

Irrespective of discipline the research worker can analyse whether the effects of treatments on growth and yield occur through effects on radiation interception or the efficiency of conversion. Where

growth is unaffected by constraints such as water stress, pests or diseases, growth proceeds with an almost constant maximum efficiency for much of the season and yield is determined by the amount of light intercepted. Where growth is restricted by any factor, the actual efficiency can be measured and compared with the maximum which represents the target.

At first sight the dependence of yields on radiation interception is perhaps surprising, because it is known that year-to-year and site-to-site variations in solar energy receipts are much smaller than variations in yield. The crucial step in accepting the result of the analysis is to realize that it is intercepted, not incident, radiation which is the discriminant of growth, and that when this is measured in different crops at neighbouring sites in the same season or at the same site in different seasons, differences are large because of differences in the extent and persistence of the leaf surface.

Associated with the reluctance to accept these ideas is the intuitive feeling that because yields change with soil type where differences in the aerial environment are negligible, differences in intercepted radiation cannot be a major discriminant of yields. There is a lack of data relating to the growth of potato crops at different sites which could provide the basis of the analysis. As water and nutrient availability differ from site to site, it seems likely that both the extent of interception and the efficiency of conversion would differ. The important point is that if the analysis were made the researcher would then be able to identify and quantify the deficiencies of the whole environment and provide a measure of the potential for improvement by amelioration. Comparisons of wheat grown on adjacent but markedly different soils (Sargeant, 1978) which gave yields on a clay soil almost double those on a sand, showed differences both in radiation interception and efficiency, the sandland crops being less efficient (1.02 g/MJ) than the clayland crops (1.30 g/MJ).

As pointed out in the introduction, meaningful analysis of growth is not possible when done on factors which are not independent of each other. There is a fundamental difference between the efficiency term in the present analysis and the net assimilation rate term in conventional growth analysis. While at this stage it cannot be claimed that changes in the efficiency with which intercepted radiation is converted into plant material have precise physiological meaning, they are basically independent of the size of the leaf surface, which is certainly not true of net assimilation rate. Changes in the amount of radiation intercepted can occur both through changes in the extent of leaf cover and through changes in incident radiation. Where crops are drought- and disease-free the efficiency term is

maintained almost constant, and this applies over a wide range of  $L$  and light environments, i.e. a wide range of values of intercepted radiation. Thus it is possible to have low  $L$  values and high crop growth rates and high  $L$  values and low crop growth rates without any change in the efficiency term. However, the slope of the relationship between growth rate and intercepted radiation can change at any value of  $L$  if plants are affected by disease or drought.

If the crop canopy were frequently light saturated then the efficiency of conversion of intercepted radiation would decrease and direct proportionality would be lost. Sale (1974) has shown that light saturation of potato crops does occur in the high insolation conditions of the Murrumbidgee. However, Biscoe & Gallagher (1977) have examined the response of winter wheat to absorbed radiation and shown that net photosynthesis of the canopy as a whole increased almost linearly with irradiance between 50 and 300 W/m<sup>2</sup> PAR. This represents the greater part of the range in the United Kingdom. Monteith (1965) has calculated from first principles that at high levels of irradiance and  $L$  canopy photosynthesis is increased by erect leaves. From this we might expect that efficiency of conversion of intercepted radiation would change with leaf angle. However, a study of published leaf area growth curves shows that few crops maintain a sufficiently high  $L$  value (in excess of 3–4) for very long and some crops never achieve these values. Thus, for most if not all of the life of a potato crop, differences of photosynthetic rate between crop canopies are likely to be determined by differences in the amount of light intercepted rather than in the efficiency of its conversion, and dry-matter yield at the end of any growth period is likely to be determined by the total amount of radiation intercepted.

The discovery that differences in yields are strongly related to the amount of radiation intercepted rather than in the efficiency of conversion indicates that the conversion of a photon of light intercepted in March at low temperatures is at the same efficiency as a photon intercepted in May or June at higher temperatures. There is now evidence that once a closed canopy is formed, rates of crop photosynthesis are largely independent of temperature over the range 10–25 °C (Monteith & Elston, 1971; de Vos, 1977). Similar data do not exist for crop growth rate, but circumstantial evidence from comparison of data of Sale (1973*a, b*) and Ifenkwe (1975) indicates that the same is true, certainly that any effects of temperature are subordinate to those of radiation interception. Before a full leaf cover is formed, temperature affects growth by increasing the rate of growth of the leaf surface and thereby the amount of light intercepted. It may be that the

Table 15. *Effect of date of planting on specific leaf areas (cm<sup>2</sup>/g) of three varieties (Allen, 1977)*

Variety	Date of planting	Dates of sampling	
		17 May	25 July
Red Craigs Royal	21 March	229.5	203.0
	11 April	225.3	248.8
	2 May	—	311.1
Désirée	21 March	219.9	245.1
	11 April	248.8	306.4
	2 May	—	337.2
Maris Piper	21 March	230.5	281.5
	11 April	283.1	317.0
	2 May	—	386.5

changes in the form of the leaf canopy associated with delayed planting indicate the way in which increasing temperature increases leaf area and radiation interception. Late plantings both of sugar beet and potatoes, which usually pass through most of their development in warmer conditions, produce larger leaves with smaller specific weights. Thus an increase of the leaf area:leaf weight ratio may be a general response to warm conditions (Table 15), and facilitate increased radiation interception. We lack direct evidence on the relationship between specific leaf weights and radiation interception.

Where the analysis has been applied to all the major crops grown in Britain, attention is immediately focused on the importance of the seasonal pattern of leaf production and death. A decade ago Watson (1968) wrote, 'It seems to me that of all topics in crop physiology the internal and external factors controlling leaf production, growth and longevity are most in need of further study... It is obvious that much of the future effort of crop physiologists must be directed to studies of morphogenesis and towards understanding how plant form is determined...'. Now that we recognize more clearly how to analyse the growth of crops the importance of Watson's suggestions for research is all the more urgent. Very little of such information has been published for potatoes.

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