The Growth

of

the Potato

Edited by

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THE POTATO

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PREFACE

THE ERA of sheer empiricism in agricultural experimentation is now drawing to a close. No longer is the plant breeder content to select purely on the basis of final yield or apparent disease resistance; he wishes to understand how the various physiological and morphological characteristics contribute to yield, their interrelationships and the possibilities and limitations of combining them to give a variety of higher yield and quality. The agronomist recognizes the costly inefficiency and strictly limited experience arising from the never-ending variety, fertilizer and cultivation trials in which the final result only is measured; he desires to study and understand his complex ecological system much more closely so that recommendations can be made with confidence and ever-increasing understanding.

Current farming practice embodies the accumulated experience of previous generations; we should be able to assume that it provides the best compromise between conflicting requirements even if we do not understand the underlying reasons. But how justified is even this assumption? How long after the need for a certain practice has disappeared does it remain within the current framework? Is, for example, the unceasing tillage of a potato field a necessary feature in an age of herbicides?

No ready answer can be confidently given to these deceptively simple questions. However, an attempt has been made at this Tenth Easter School in Agricultural Science to examine one crop, the potato, to find just how much (or little) we know about its physiology and its responses to the soil and aerial environment, to explore how current farming practice takes account of these responses, and to seek possible ways in which techniques may be modified to meet new needs and to profit by new developments. The findings should prove of interest to an audience much wider than those intimately concerned with the potato; indeed, a deliberate attempt has been made to assess those aspects which are particularly important with the potato, such as apical dominance, nutrient flow to storage organs, water relations, fertilizer responses and density relationships, within a much wider context. The stimulus and interest arising from bringing together at this School scientists from a wide spectrum of interests —from the biochemist to the processor—has prompted the suggestion that this discussion should be followed by further appraisals of contrasting types of crops. It is hoped that from the series there will emerge a clearer picture of those significant physiological and ecological responses which differ between, or are common to, all crops and

how these are or may be manipulated for greater yields and higher quality of produce.

The Tenth Easter School, of which these are the proceedings, was held at the University of Nottingham School of Agriculture on 8–11 April 1963. It owes much to the stimulating communications from the principal contributors, to those who from the floor so vigorously and ably contested many issues and added new ideas and information, and to the Chairmen of the various sessions, Mrs. N. McDermott, Dr. A. R. Wilson, Professor O. V. S. Heath, Professor E. G. Hallsworth, Professor A. H. Bunting, Dr. J. C. Holmes and H. Jackson, Esq. The University of Nottingham wishes to express its gratitude to the Ross Group, Potato Marketing Board, Unilever Ltd., Smith's Potato Crisps, J. W. Chafer Ltd. and The National Association of Seed Potato Merchants for their assistance towards meeting the expenses of this School, particularly in assisting overseas speakers to attend. Miss E. Lord bore the brunt of the detailed organization of the School and the assembly of the proceedings.

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AN INTRODUCTORY SURVEY

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DURING THE past century the study of the interrelationships within the soil–plant–atmosphere system, which comprises the very core of agronomy, has been neglected relative to the (essential) investigation of the details of its component parts. Even concerning the plant itself, plant physiologists have concentrated on elucidating the intimate details of component processes, much less attention being given to exploring the manner in which these processes are integrated within a living plant. Because of the closely interconnected mechanisms which make up the whole plant, it is rarely possible to deduce the response of the organism to a given factor, or complex of factors, from a knowledge of the separate responses of single biochemical reactions, or groups of reactions, to those factors. Concurrent investigations at all levels of organization are necessary to provide a closer understanding of the behaviour of the whole. The growing recognition of this need has led in recent years to a much wider application of the approach known as *growth analysis*—the study of the changes in the whole plant during its ontogeny. This extends in one direction, by tracing back responses of the whole plant in terms of changes in rates of processes and patterns of metabolism, to meet with the process physiologist and biochemist and, in the opposite direction, by following changes in different situations, to meet with the soil scientist and micrometeorologist in the field of analytical ecology.

As this approach is the underlying theme of this Symposium, I do not intend to list its contributions to our understanding; many of these will emerge in succeeding papers. Rather, it seems appropriate here to examine some of the underlying concepts and to explore their limitations and applicability. This will be attempted within a general description of the course of growth and development of the potato, which is needed also as a background for the succeeding detailed discussions. For a comprehensive review of the potato, the reader is referred to the handbook by Schick and Klinkowski (1961).

DEVELOPMENT OF THE MOTHER TUBER

The life of an individual potato plant begins with the initiation of a tuber on a stolon of the mother plant. The first phase of growth is

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the growth of that tuber and the development of its buds until its increase in size ceases as a consequence of the death of the mother plant. No opportunity has been given for later detailed discussion of the general features of this phase; for completeness of the record I should therefore digress to summarize these briefly. Unfortunately, there are no adequate data concerning the pattern of growth of individual tubers with time. Krijthe (1955), on the unproven assumption that the largest tuber present had always been the largest, suggested that the weight of a tuber increased linearly with time, the rates of increase differing greatly between tubers; Plaisted (1957) found a logarithmic relationship between the *mean* tuber weight (total weight of tubers divided by number) and time over a long period. Other observations, which are also subject to criticism of experimental technique, suggest that the assumptions on which the above conclusions were based are unjustified (Sadler, 1961; Engel and Raeuber, 1961); tubers appear to follow a sigmoid course with time but the slopes and duration of this curve differ widely between tubers and are not closely related to relative times of initiation. (Tubers initiated when an appreciable number are already growing, however, often cease growing when quite small and may be resorbed.)

The increase in volume of a tuber arises from increases in the number and size of its cells; Artschwager (1924) points out in his classical descriptive paper that, although the cells of the pith and cortex are the first to divide, the main increases are in the pericycle and internal and external phloem. The proportion of internal phloem (comprising storage parenchyma and embedded phloem islets) and the pith to the external phloem and cortex, i.e. the cells inside to those outside the vascular ring, increases slightly during growth owing to the faster rate of increase in cell number, and despite the slower rate of increase in cell size, in the former than in the latter (Plaisted, 1957; Sadler, 1961). Tubers at initiation were found to have a volume of about $2 \cdot 5 \times 10^{-2}$ cm^3 and contained approximately $2 \cdot 68 \times 10^5$ cells, and tubers with a volume of 300 cm^3 contained approximately 366×10^6 cells; the 12,000-fold increase in tuber volume was accompanied by 370-fold and 90-fold increases in cell number and 40-fold and 90-fold increases in cell size in the 'internal' and 'external' tissues, respectively (Sadler, 1961).

Each tuber arises as a swelling between the terminal bud and the penultimate expanding internode of the stolon and grows by a wave of expansion which passes from the base towards the apex (Krijthe, 1946). As the tuber grows, the lower leaves of the terminal bud, each with its axillary bud, become separated from each other and from the terminal bud, which is now the apical bud of the tuber. The apical bud and the tuber itself are therefore part of the primary vegetative axis of the stolon and the main buds in the 'eyes' and the side shoots

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arising from the apical bud are secondary axes. The lateral buds in each of the 'eyes' are third-order axes—they arise as axillary buds of the central bud.

Sadler (1961) has shown that, in the variety Arran Pilot, the terminal bud at initiation contains 12 leaves. The mature tuber also possesses about 12 'eyes', suggesting that all central buds of the eyes of the mature tuber arise as axillary buds which are present already at, or else shortly after, tuber initiation. Shortly after the tuber has formed, the apical bud contains 9–10 leaves and this number is maintained until maturity; that is, the rate of differentiation of new
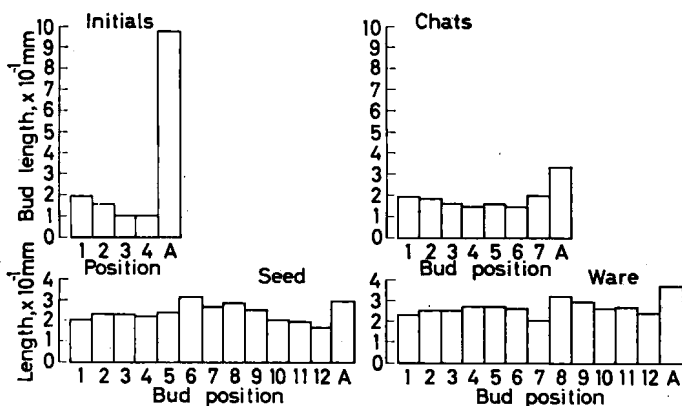

Figure 1. *Number and lengths of buds on tubers in size classes Initials, 0·025–0·49; chats, 0·50–19·99; seed, 20–89·9; ware, 90 cm³. Data from Arran Pilot planted in April, measurements made on July 18. Buds numbered from base to apex; A = apical bud (after Sadler, 1961)*

leaves from the apical meristem keeps pace with the expansion of internodes on the tuber. It seems likely that the *second-order buds* (the main buds of the eyes) continue to increase in volume and to differentiate leaves, but at a continually decreasing rate, for an appreciable time after they have separated from the apical bud. Development is suspended first in the basal bud—possibly soon after tuber initiation—and then progressively in the succeeding second-order buds. The apical bud does not cease growing until the tuber ceases growing with the death or destruction of the haulm. At lifting, all second-order buds are of much the same length but shorter than the apical bud (*Figure 1*); however, all have about 9–10 leaves. The onset of dormancy in the various buds is therefore very much a progressive phenomenon. Because of its different morphological origin and history, the apical bud would be expected to behave differently from the lateral buds in the succeeding period of growth.

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There is little information concerning the influence of the lifting of tubers while still immature on the development of buds. It seems likely that growth of the tuber and its buds stops on separation from the haulm and, apart from small influences arising from differences in the amount of tuber tissue and number of buds, subsequent behaviour will be much the same as with mature tubers.

THE STORAGE PHASE OF GROWTH

The second phase of growth, the storage phase, extends from lifting until the tubers are planted some months later. This extremely important phase is the subject of several communications (cf. the following section). Physiological investigations are concerned with understanding the interrelationships between the nutritional, metabolic and hormonal components of the growing sprouts and the mother tuber while the agronomic object is to manipulate these so as to ensure that the tubers at planting have the required number of sprouts of the desired size.

GROWTH IN THE FIELD

The final and most prominent phase of growth, that in the field with the production of daughter tubers, is also discussed by a number of contributors in subsequent sections. Here, attention is drawn to the general ecological picture (*Figure 2*). Three phases may be recog-
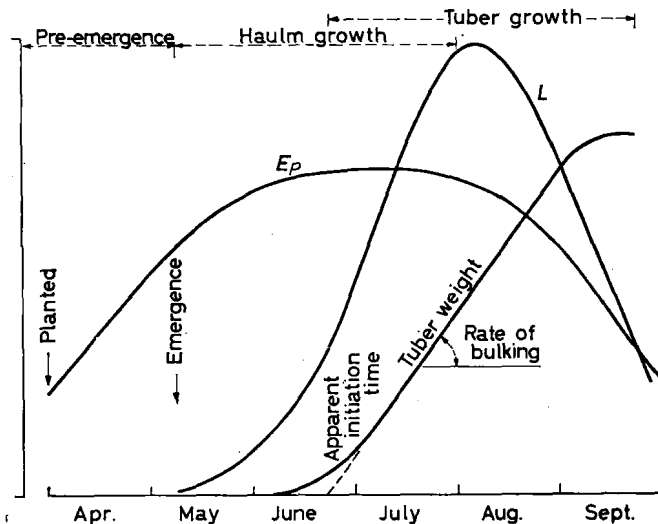
Figure 2. *Relationships of the main components of potato growth during the growing season in the English Midlands*
$L = leaf$ *area index,* $E_p = potential$ *rate of net assimilation during an average growing season*

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nized: (*i*) pre-emergence, which involves the establishment of root and leaf surfaces from materials stored within the mother tuber, and which occurs at a rate determined mainly by the soil temperature and size of sprout at planting; (*ii*) that in which haulm growth is predominant, and (*iii*) that of tuber growth—a stage closely interrelated, and overlapping, with that of haulm growth. The growth of main-crop varieties in most cool–temperate zones occurs within a growing season which is strictly limited in duration; planting is determined by the need for temperatures adequate for growth and the probability of escape from late frosts, and the end of the season is often determined by late blight or early autumn frosts. Understanding of the reasons for variation in the final resultant, the yield of tubers, may be sought by the approaches described below.

Analysis of the increase in dry weight

Two variants of the classical analysis of growth in terms of increase in dry weight (Gregory, 1917, 1926; Blackman, 1919; Briggs, Kidd and West, 1920) may be recognized. The first purports to describe the crop growth rate, i.e. the increase in weight, w, with time, t, in terms of the *efficiency*, i.e. the increase in dry weight per unit area per unit time or the net assimilation rate, and of the *size* of the leaf surface, i.e. the area of leaf per unit area of soil, or the leaf area index, L

$$\frac{dw}{dt} = \frac{1}{L} \cdot \frac{dw}{dt} \times L \qquad . \quad . \quad . \quad . \quad . \quad (1)$$

The second purports to describe the relative growth rate, or efficiency of existing material in adding new material, in terms of the net assimilation rate and the ratio of the leaf area to the total dry weight (the leaf-area ratio)

$$\frac{1}{w} \cdot \frac{dw}{dt} = \frac{1}{L} \cdot \frac{dw}{dt} \times \frac{L}{w} \qquad . \quad . \quad . \quad . \quad . \quad (2)$$

The contributions of Watson and his colleagues (Watson, 1952; Watson and French, 1962), using the approach of eqn. (1), and those of Blackman and his school (cf. Blackman and Black, 1959), using eqn. (2), have greatly increased our understanding of variation in yield and responses of crops to the environment and stimulated a wide use of these techniques. Although the still wider application of this approach should be encouraged, a reminder of its limitations and of the need to explore more deeply, wherever possible, would seem to be appropriate here.

a) Growth rates

The typical asymmetrical sigmoid curve which describes the course of dry weight with time and much other data suggest that the growth

rate is a changing function of the weight itself, i.e. $dw/dt = kw^a$ where a varies from ~ 1 at emergence to ~ 0 at maturity and k is a function of the environment and the weight. That is, the response of a plant to its environment varies greatly with its size. However, the crop growth rate may be empirically described as a function of time

$$\frac{dw}{dt} = b + 2ct + 3dt^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad (3)$$

Eqn. (3) may be obtained from the polynomial describing the change of weight with time $(w = a + bt + ct^2 + dt^3 \ldots)$. The relative growth rate may be similarly obtained from the polynomial of $\ln w$ with time, in a form suitable for use in the analysis of variance, as

$$\frac{d}{dw}(\ln w) = \frac{1}{w}$$

Changes in growth rate with time may also be obtained from the four-parameter generalized logistic function (Richards, 1959; Nelder, 1961)

$$\frac{dw}{dt} = kw\left[1 - \left(\frac{w}{A}\right)^{1/\ell}\right] \quad . \quad . \quad . \quad . \quad (4)$$

which, on integration, gives

$$w = A/[1 + e^{-(\lambda + kt)/\theta}]^\theta$$

where A is the limiting value of w and λ, k and θ are constants.

b) *The net assimilation rate, E*

As pointed out by Williams (1946), the average value of E over a finite time interval, $t_2 - t_1$, is

$$\frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{1}{L} \cdot \frac{dw}{dt} \, dt$$

If it is assumed that $w = a + bL^\alpha$ where $b \neq 0$ and $\alpha = 1$

$$E = \frac{w_2 - w_1}{t_2 - t_1} \cdot \frac{\ln L_2 - \ln L_1}{L_2 - L_1} \quad . \quad . \quad . \quad . \quad (5)$$

This is the usual expression by which E is calculated. The above assumption rarely holds, however (e.g. *Figure 3*), and more appropriate methods of estimation are required (Williams, 1946; Evans and Hughes, 1961). Evans and Hughes give a general solution of the equation $w = a + bL^\alpha$ allowing accurate calculation of E for all values of α, but possibly the most appropriate method is to take $E = (1/L)(w_2 - w_1)/(t_2 - t_1)$ and obtain the mean leaf area, L, graphically from frequent measurement or, particularly in a constant environment, obtain $(dw)/(dt)$ from eqn. (3) or (4) for points of time at which L has been measured and estimate $(1/L)(dw)/(dt)$ at such times.

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The early expectation for the net assimilation rate was that it would be mainly dependent on external factors and remain independent of internal components, at least during vegetative growth (Gregory, 1926; Heath and Gregory, 1938; Watson, 1952). This is not so; experience in constant environments has shown that the net assimilation rates of sugar beet, barley and cucumber fall continually with age (Thorne, 1960, 1961; Borah and Milthorpe, 1963; Milthorpe,
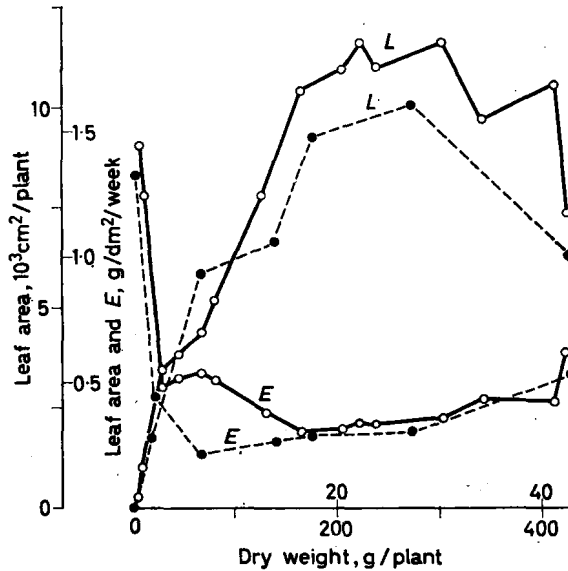

Figure 3. Relationships (i) between leaf area, L, and dry weight of plants grown in the field (○ ; outer scales) and from single bud in pots (● ; inner scales); (ii) between net assimilation rates, E (inner scale), and dry weight of the same plants. Field data kindly supplied by R. W. Radley

1959; Newton, 1963). This change with age arises in part from the increasing proportion of respiring to photosynthetic tissue, from the decreasing capacity for photosynthesis per unit leaf area (cf. *Figure 4*) and from shading of the less efficient lower leaves by the upper leaves. Components working in the opposite direction include a decreasing mean rate of respiration per unit dry weight and appreciable photosynthesis by organs other than leaves. Moreover, there is some evidence that the rate of photosynthesis is appreciably influenced by the intensity of 'sinks' elsewhere in the plant (e.g. Moss, 1961), the degree of activity in these being frequently related to components other than the supply of carbohydrate. These factors all contribute to variations of the net assimilation rate of the potato (*Figure 3*) which

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generally follows a broad U shape with plant size (and also, with time). The high net assimilation rates soon after emergence and the subsequent decrease are associated with transfer of materials from the
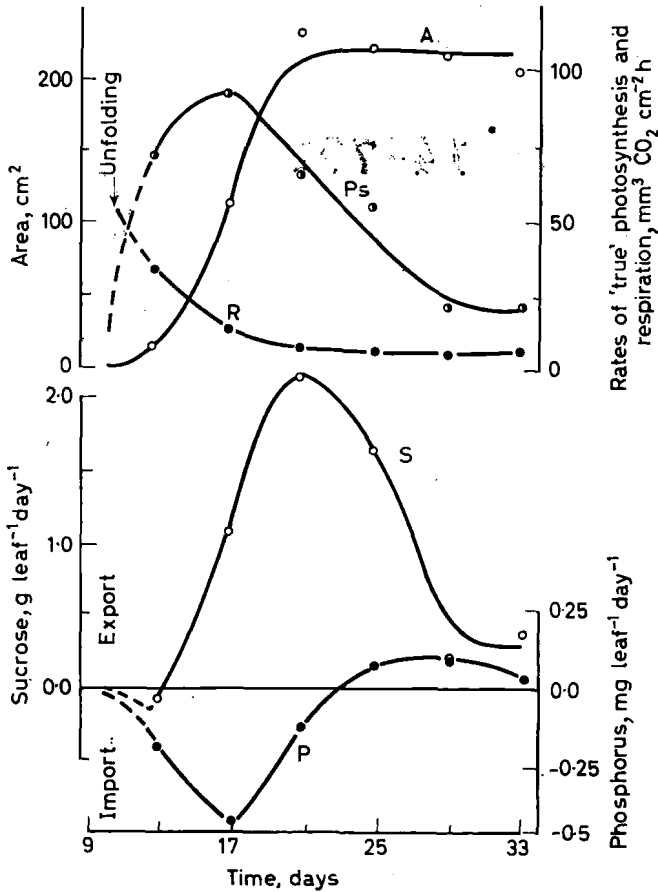

Figure 4. Relationships with time of the area (A) of the second leaf of cucumber plants grown under constant conditions, together with rates of photosynthesis (Ps) and respiration (R) per unit area, and flow of sucrose (S) and phosphorus (P) from the leaf. (After Hopkinson, 1964)

tuber and with decreasing rates of photosynthesis per unit of leaf surface; with time, an increasing number of leaves reach maturity and exhibit a much lower photosynthetic rate. The increase in the net assimilation rate, towards the end of the season, occurs because a very high proportion of photosynthate is transferred to the tubers

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