

A MODEL OF THE EXTENSION AND BRANCHING OF A SEMINAL ROOT OF BARLEY, AND ITS USE IN STUDYING RELATIONS BETWEEN ROOT DIMENSIONS

II.* RESULTS AND INFERENCES FROM MANIPULATION OF THE MODEL

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Abstract

A model of root growth was used to investigate why the average length (\bar{l}) of cereal root members remains roughly constant. Taking as a standard the model root which agreed with actual roots from an experiment, the nine variables in the model were altered singly to see which had greatest influence on \bar{l} .

The results showed that the constancy of \bar{l} was due primarily to the existence of ceilings to the rates at which each class of root member can extend. These ceilings are thought to be determined by a property associated with the diameter of the root member. Also of importance was the timing of the onset of each order of branching. This timing was related to that at which the parent members, as a population, began to increase roughly linearly in volume. A tentative explanation of the concomitance is put forward.

Understanding of the phenomenon was advanced by the study, but a full explanation was not achieved, mainly because of the lack of information about certain aspects of root development.

I. INTRODUCTION

The work reported in these papers was fully introduced in Part I (Hackett and Rose 1972). In brief, it was felt that the maintenance by graminaceous species of roughly constant relations between their root dimensions must reflect the existence of underlying principles of root growth which it could be profitable to discover. A model of the extension and branching of a cereal root was developed with the aim of bringing some of these principles to light. Part I presented the model and established its validity for the purpose in mind. Part II now presents the results and inferences derived from manipulation of the model.

II. METHOD

(a) Symbols

Symbols used both in Part I and the present paper are defined in Part I (see p. 671). New symbols introduced will be defined in the text.

(b) Procedure

The approach adopted was to alter the values of the variables in the model and examine the effect on the average length, \bar{l} (where $\bar{l} = L/N$). The aim was to achieve a ranking of the variables in an order of influence on \bar{l} . Since \bar{l} is roughly constant in reality, the variables which

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hypothetically induce the greatest instability in \bar{l} could be taken to be those which the plant controls most sensitively. Conversely, the variables which hypothetically have little influence on \bar{l} could be taken to be those which require little control and may contribute much to the plasticity of root form. Consideration of the means by which the plant restricts or permits the freedom deduced to exist could then lead to the identification of hitherto unsuspected properties of root growth.

The variables were manipulated in the following way. The model root which agreed in form with the average intact seminal root in the experiment of Hackett (1971) was termed the standard root (see Table 2, Part I), and the values given to the variables were termed the standard values. Working generally with one variable at a time, the effect on \bar{l} of multiplying the standard value of each variable by the factors 0.25, 0.5, 2.0, and 4.0 was determined. In this way, a quantitative assessment of the importance of each variable could be gained. Exceptions to this procedure had to be made with respect (1) to t_f and t_s , which represent events, not continuing properties of the root, (2) to v_a and v_f , because factors less than unity could not be used when v was altered alone without the length of the axis becoming less than the length of the branched region of the axis, and (3) to b_a and b_f with factors greater than unity, for the same reason as given under (2). Because of the restrictions necessary when varying v and b alone, the effect of varying them together was also examined.

To facilitate the computation, the numerical operations were written in Fortran. The program was run repetitively on the computer, varying the input as desired. Equations (9) and (12) in Part I were used to generate the information needed. Output was obtained for each day up to $t = 30$ days, t_a having been set at 1 day. Carrying the model through to $t - t_a = 29$ days was to extrapolate by 7 days past the last data against which the model had been checked. The risks involved in this extrapolation were thought to be small when weighed against the information which might be gained.

Three criticisms of the approach described above can be made. Firstly, \bar{l} can rightly be said to be an artificial parameter. A branched root bears two or more populations of root members which differ markedly in their characteristics (e.g. Table 3, Part I), so \bar{l} has little meaning in reality. This problem is considered to be of little relevance here because \bar{l} is used merely to indicate whether the roots produced by the model are structurally abnormal.

It can also be said that placing reliance on the standard root as the point of reference is to assume that the standard values of the variables are typical of barley grown without any serious environmental limitation. Since the plants were grown in a favourable environment and received adequate nutrient supply from an aerated solution, the assumption has been made with reasonable confidence.

Finally, concentration on the effect of altering one variable at a time leaves open the question of the effect of altering the variables in combination. When work with the model began, there was no basis on which to select combinations of variables for study, except perhaps conservation of mass or volume. Even with this constraint, the range of possible combinations was large. Reliance was therefore placed on making wide alterations to one variable at a time. Since even this limited approach proved the need for more experimental information, the restriction is believed to have been appropriate.

III. RESULTS

The results are reported uniformly by reference to plots of \bar{l} against t (Figs. 1 and 2). Some of the trends in the figures can be predicted by examining equations in Part I, but a standard form of presentation is thought to be helpful to the reader.

(a) *The Standard Root*

Figure 1(a) shows \bar{l} plotted for the standard root (the curve is referred to as \bar{l}_{st} . below).* \bar{l}_{st} is seen to fall very rapidly after t_f but soon begins to rise linearly.

* Events close to the origin in Figures 1 and 2 were thought to be unimportant enough to permit \bar{l} to be omitted for short periods of t to help improve the clarity of the figures.

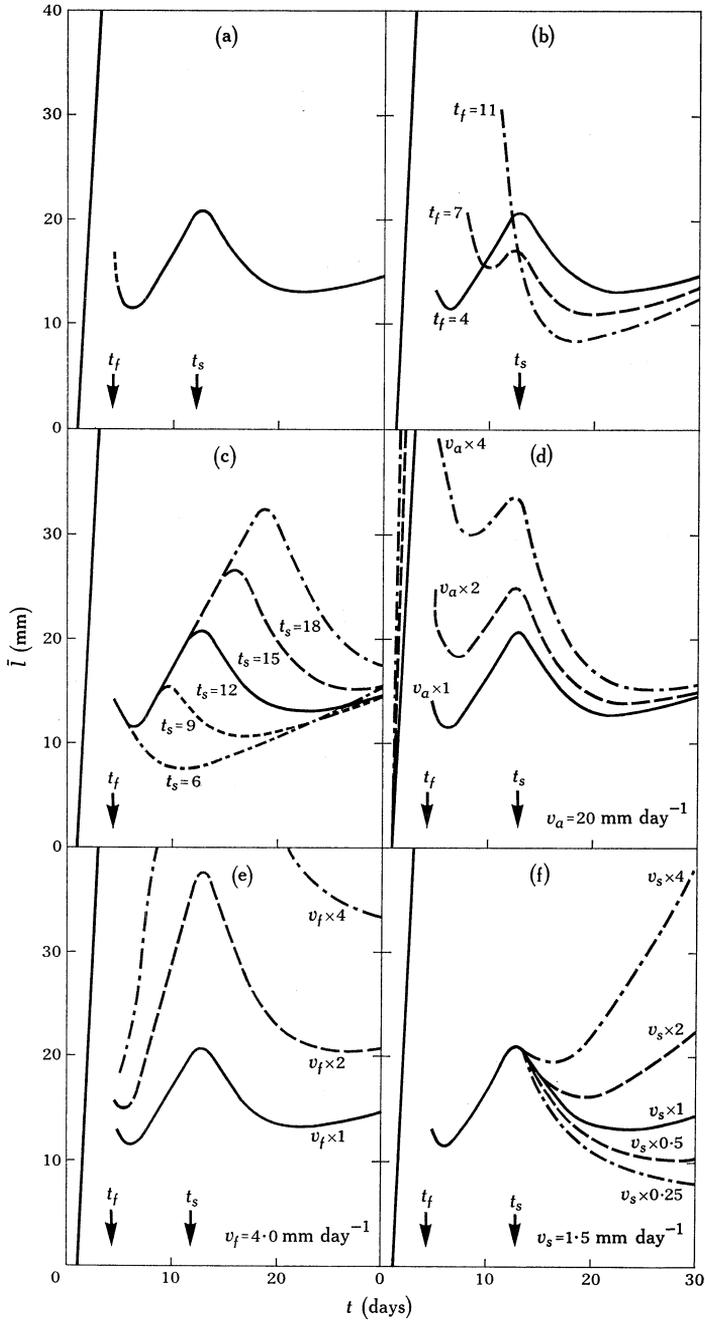


Fig. 1.—Average length \bar{l} (mm) of the root members of hypothetical roots grown by use of the model: (a) the standard root, (b)–(f) a comparison of the standard root (solid line) with roots grown when t_f , t_s , v_a , v_f , and v_s (broken lines) were varied.

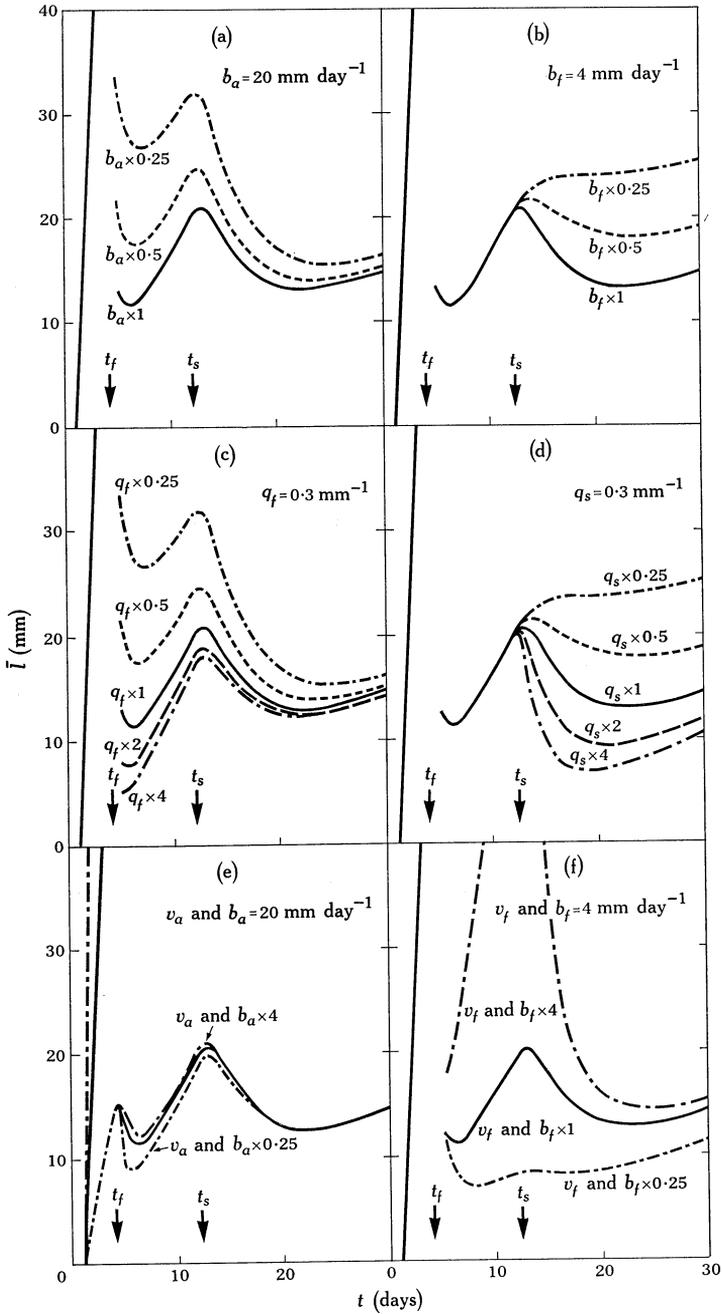


Fig. 2.—Average length \bar{l} (mm) of the root members of hypothetical roots grown by use of the model; (a)–(f) a comparison of the standard root (solid line) with roots grown when b_a , b_f , q_f , q_s , v_a and b_a , and v_f and b_f (broken lines) were varied.

The increase, however, is arrested immediately after t_s . l_{st} then declines somewhat until a new and slower rate of increase is struck. l_{st} remained between 11 and 21 mm.

The pattern is one of negative inflexions occurring at the onset of a higher order of branching, and positive inflexions occurring as the system readjusts. Confidence can be placed in these inflexions (1) because the coefficient of variation of l in the actual data was only 11%, so at least the first two inflexions can be regarded as experimentally observed phenomena, and (2) because it can be deduced from Table 3, Part I, that after t_a , t_f , and t_s , dl/dt will tend to v_a , $\frac{1}{2}v_f$, and $\frac{1}{3}v_s$ respectively, so inflexions of the type seen in Figure 1(a) must occur, using the standard values of the variables.

(b) *Effect of t_f and t_s* [Figs. 1(b) and 1(c)]

Delaying t_f had relatively small effects on l after t_f [Fig. 1(b)], and after t_s , l converged on l_{st} . The effect of $t_f \ll 4$ days was not examined because it was considered unrealistic.

The influence of t_s on l was more impressive [Fig. 1(c)]. The longer t_s was postponed, the higher l rose, but after t_s , l fell quickly and converged on l_{st} . Varying t_s between 6 and 18 days caused l to vary between 7.5 and 32.5 mm.

(c) *Effect of v_a , v_f , and v_s* [Figs. 1(d)–1(f)]

The influence of v_a on l was quite large until several days after t_s [Fig. 1(d)]. When v_a was increased fourfold, l lay between 30 and 40 mm until 14 days and then approached l_{st} .

Increasing v_f had a more powerful effect than increasing v_a [Fig. 1(e)]. The twofold increase put l above 37 mm, whilst the fourfold increase put it off scale (to 70 mm). Some recovery occurred after t_s , but by 30 days, the values for l for both levels of v_f were well above l_{st} . The influence of v_s on l was also large [Fig. 1(f)], though the effects of course were not seen until after t_s .

(d) *Effect of b_a , b_f , q_f , and q_s* [Figs. 2(a)–2(d)]

Altering b_a and b_f had equivalent effects on l to altering q_f and q_s . The influence of all four variables on l was noticeably smaller than that of the variables associated with v , the maximum value of l reached being only 34 mm.

(e) *Effect of v and b Varied Together* [Figs. 2(e) and 2(f)]

The curves are best read by comparing them with the curves in which only one of the variables was altered at a time.

Study of Figures 1(d), 2(a), and 2(e) shows that when v_a is larger than normal, the first-order laterals soon swamp its effects on l if b_a has approximately the same value as v_a . Figures, 1(e), 2(b), and 2(f) convey the same impression with respect to v_f , b_f , and the formation of second-order laterals. A conclusion from these comparisons is that t_f and t_s assume more importance the greater are the rates of extension of the parent root members.

IV. DISCUSSION

We now present and develop our inferences from the results.

(a) *The Variables v_a , v_f , and v_s*

Figures 1(e), 1(f), and 2(f) strongly suggest that the plant places a ceiling on the rate at which its lateral root members can extend. If this were not so, it would be unlikely that \bar{l} would in reality be roughly constant with time.

We therefore considered how the plant might be setting this ceiling and believe a clue to the mechanism may lie in the positive correlation between the diameter (d) of each class of root member and its characteristic rate of extension.

The literature gives a variety of examples of this correlation, both within and between classes of root member (Wilcox 1962a, 1962b, 1967; Hackett 1969a; Mason, Bhar, and Hilton 1970), but no special significance has been attributed to these observations so far. One possible reason for this is that the meristem of the root axis has been thought to exert dominance over the branching pattern of the root (Street 1969), so any relationship with d would be expected to be confounded with the influence of growth substances originating in the axis. However, the evidence most quoted relates only to growth in the immediate vicinity of the apical meristem of the root axis (Street 1969), and now that indoleacetic acid has been found to move largely acropetally in the roots of intact plants (Morris, Briant, and Thomson 1969), the likelihood that there is a direct analogy between root and shoot systems with respect to apical dominance seems small.

Another reason for the neglect of the positive correlation between v and d is probably that negative correlations have been observed in some circumstances (e.g. Barley 1962, 1963; Waddington and Baker 1965; Isensee, Berger, and Struckmeyer 1966). In all of the instances we are aware of, however, the effect was the result of some physical or physiological impedance to growth. These reports are therefore largely irrelevant to the present case because we are here concerned with what plant characteristic limits v .

In considering whether the maximum rate of extension of root members is dependent on their diameter, strong evidence in support of the hypothesis would be a demonstration that over all classes of root member the relationship between v and d was approximately the same. Data for the intact plants from the experiment of Hackett (1971) allowed this to be tested.

Using the total number and total length of each class of root member present at each harvest, it was possible to calculate the mean extension rates for the intervening periods. The method of calculation was that applied to root systems by May, Chapman, and Aspinall (1965). Values of d were available from the direct measurements made on the material.

Since the relationship between v and d appeared from rough calculation to be of the type $v = d^x$ (where $x > 1$), $\log_e v$ was plotted against $\log_e d$ (Fig. 3). With the data in this form, there was a highly significant linear relationship between the variables ($\log_e v = 1.63 \log_e d + 4.08$; $P < 0.001$), and the points for all three periods seemed to belong to the same population. It was therefore concluded that v and d had been related uniformly throughout the root system in this experiment and that the influence of apical dominance, if any, was negligible in the present context.

If this type of correlation is found in other material, it could come to be regarded as one of the themes which help determine root form. Awareness of it might assist considerably in the interpretation of root development. Admittedly, the reason why v is related to d in the manner observed is not yet clear, but the mechanism is probably to be sought in the root meristem. Van't Hof and Ying (1964), Van't Hof (1967), and Burholt and Van't Hof (1971) have shown that v_a can be profitably expressed in terms of the length of the mitotic cycle, the number of files of cells, the rate of cell proliferation per file of cells, and the length of the mature cells. If a comparison of v_a , v_f , and v_s could be made in these terms, a satisfying explanation of the correlation between v and d might emerge.

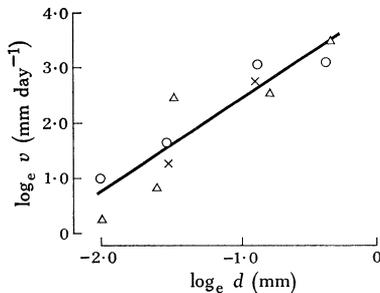


Fig. 3.—Relationship between the logarithm of the diameter d (mm) of root members of barley and the logarithm of the mean extension rate v (mm day⁻¹) for three periods of growth (days from germination). × 8–13 days (from the left, seminal (S) first-order (1°) laterals and S axes (A) respectively); ○ 13–16 days (S², S¹, SA, and nodal (N) A respectively); Δ 16–23 days (S², S¹, N¹, SA, and NA respectively).

(b) The Variables t_f and t_s

The results also showed that \bar{l} was sensitive to t_f and t_s , so we were led to ask how the plant controls them. The literature on the initiation and outgrowth of lateral root members is almost entirely concerned with t_f , and it explains the phenomena mainly in terms of the action of growth substances (Street 1969). Many of the experiments are difficult to interpret, however, because the growth substances were applied externally. Often, too, excised roots were used, which eliminated any possible influence of translocation from the shoot. We find it difficult to derive from this work any principle which might explain the timing of all orders of branching in intact plants, and in an attempt to develop an alternative line of thinking, the implications of the following simple observation were explored.

It was noted that a seedling begins root growth by throwing out an organ which grows approximately arithmetically whilst the plant as a whole is tending to grow exponentially. The branching of root members, therefore, can be thought of as a response to the restriction placed on the growth rate of the individual members. One might think that the first order of branching would suffice to cope with this "problem", but we found that the rate at which the first-order lateral population increases in volume (which has been assumed to be directly related to mass) becomes almost linear after a period of time in the standard root [Fig. 4(a)]. The same is true of the second-order laterals. Moreover, the time at which each rate approaches constancy is associated with the rise to importance of the next higher order of branching. For the onset of second-order lateral branching this is evident in Figure 4(a); with respect to third-order lateral branching, Hackett (1971) reported that this began at about 23 days. Without having the model, and without some understanding of

the properties of v , it would be possible to argue that the onset of each higher order of branching slowed the growth of the lower order, but v_f and v_s were set constant with time in the model, so this cannot be the explanation. Rather, it seems as though the root is developing new growth points to match the exponential increase in assimilation by the shoot system.

Further data on the barley root system (Hackett 1968, 1969*b*) were examined by the same means, though it was of less value since only two harvests (at 14 and 28 days) could be referred to. Once more the second-order laterals became noticeable when the first-order laterals began to increase linearly in volume [Fig. 4(*b*)]. No third-order laterals were observed in the experiment, and the volume of the second-order laterals did not begin to increase linearly by 30 days.

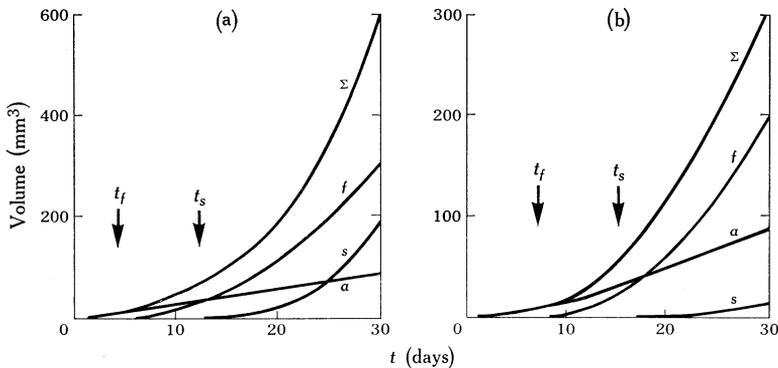


Fig. 4.—Increase in total volume (mm^3) of the axis, first-order laterals, and second-order laterals of (a) the standard root and (b) a model root derived from the experiment of Hackett (1968).

Support for the view that the onset of branching in roots is related to assimilation by the shoot can be drawn from work on other aspects of branching and root initiation in plants (Gautheret 1969; Hess 1969; Lovell and Moore 1969; McIntyre 1969, 1971*a*, 1971*b*), but before the inferences drawn from Figure 4 can be treated as a firm hypothesis much more experimentation will be required. However, the inferences do lead to a unifying explanation of why t_f , t_s , and t_t occur when they do and hence contribute to the stability of \bar{l} .

(c) Conclusion

Means by which the plant exerts control over v_a , v_f , v_s , t_f , and t_s can now be envisaged but it is still necessary to know how the limits to b and q are determined to explain the stability of \bar{l} . Unfortunately, the literature and the properties of the model are of little help in this regard. Nevertheless, a useful conclusion can still be reached.

Because published data imply that b_a and q_f vary within quite narrow limits (Weaver, Kramer, and Reed 1924; May, Chapman, and Aspinall 1965; Hackett and Bartlett 1971), and because b_f and q_s were found from manipulation of the model to have small effects on \bar{l} when v_f was at or below the standard value, it can be suggested that the constancy of \bar{l} in intact roots is due primarily to the existence of ceilings

to v_a , v_f , and v_s , and secondarily to the characteristic expression of t_f , t_s , b_a , and q_f . Within these constraints, wide variation in root form is obviously possible, and most of it would be expected to give roughly constant values of \bar{l} . Thus it can be perceived why the phenomenon has been observed in experiments where the relevant data have been collected, and it can be expected that it will be commonly observed in the future. It is still unclear, however, why the phenomenon is seen too in mutilated roots.

The general impression of root growth gained from this study is that the plasticity of form so often remarked on is due to quite small ranges of variation in a large number of variables. Similar helpful insights might be obtained by identifying and investigating other constant qualities of root systems.

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