

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

I. THE MODEL

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Abstract

Previous papers have reported that relations between the total number, length, surface area, and volume of graminaceous root members tend to remain roughly constant during vegetative growth. Through the use of a model of the extension and branching of a seminal root of barley (*Hordeum vulgare* L.), which was developed for the purpose, an attempt has now been made to determine the properties of root growth responsible for the phenomenon.

The present paper introduces the study and describes the model. The model takes advantage of the fact that the extension and branching of cereal root members grown in homogeneous media proceeds at approximately constant rates for lengthy periods. The overall dimensions of roots can therefore be determined by reference to formulae representing time and a limited number of properties of each type of root member.

The validity of the model for the use intended is demonstrated by testing the underlying assumptions and checking the model against actual data. Other possible roles for the model are suggested.

Part II of the series (Hackett and Rose 1972) reports the results and inferences from manipulation of the model.

I. INTRODUCTION

The development of the root system of barley (*Hordeum vulgare* L.) and other graminaceous species proceeds in such a manner that relations between the total number, length, surface area, and volume of the root members remain approximately constant during the vegetative stage of growth (Shearer 1968; Hackett 1969, 1971; Evans 1970, 1971). Evidence of this has been found not only in intact plants but also in defoliated plants (Evans 1971) and ones mutilated by removal of the tips of the root axes (Hackett 1971).

The existence of this property of root development implies that the plasticity of root form so evident to the eye is achieved within a framework of some remarkably constant principles. The aim of the work now being reported was to look for these principles, the belief being that their identification could contribute to the understanding, and ultimately to the prediction, of root growth. The approach taken was to model the growth of a seminal root of barley (a root is defined as an axis with its

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associated laterals) and then to use the model to examine the properties of actual and hypothetical roots.

It seemed simplest to confine efforts first to the case of the intact root. In such roots, the axes and various orders of laterals can be regarded as distinct classes of root member. Further, the constancy of relations between length, surface area, and volume can be put down initially to the preponderance of first-order laterals and their relatively uniform diameter throughout the root system (Hackett 1969). Relations between only the number and length of root members therefore needed to be considered. Neither of these simplifications was possible when considering mutilated roots (Hackett 1971).

The first of these two papers describes the model which was developed. The assumptions underlying it are discussed and the validity of its use for the purpose intended is demonstrated. Part II of the series (Hackett and Rose 1972) reports what has been learnt from manipulation of the model.

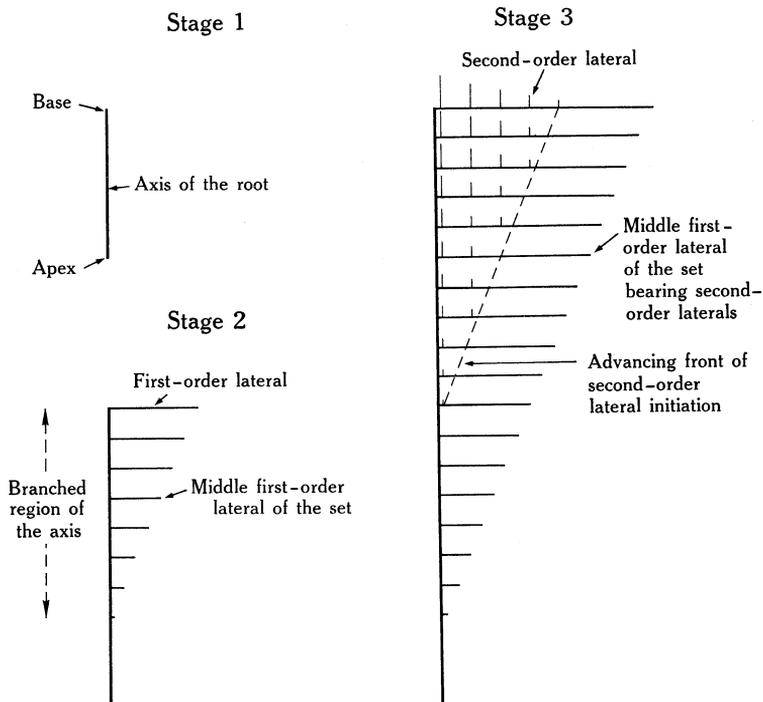


Fig. 1.—Patterns of root branching assumed for the three stages of root growth dealt with by the model.

II. THE MODEL

(a) Terminology

The morphological terms used in this paper are applied in accordance with the definitions given by Hackett (1968, 1971), with the exception that, following Barley (1970), the classes of laterals are now termed first-order, second-order, and third-order instead of primary, secondary, and tertiary.

(b) Conceptual Basis of the Model

The conceptual basis of the model is illustrated in Figure 1, where a "root" is shown at three stages of development: (1) before any branching has occurred, (2) when first-order laterals have emerged, and (3) when second-order laterals have emerged. Little attention has been given to third-order laterals because these have been negligible in number on the material we have studied so far and because there is no guidance from elsewhere on the values to give to the additional variables which would be needed.

The root is considered to be healthy and undamaged, with the laterals emerging strictly acropetally. The rates of extension and branching of each class of root member are uniform throughout the root and constant with time (e.g. there is no aging).

The mathematical description of this model which now follows sums the number and length of each type of root member. A diameter term can be introduced to permit calculation of the surface area and volume of the root members (assuming that each is a smooth cylinder) but the steps required are too trivial to include in this account.

*(c) Mathematical Description**(i) Symbols*

The subscripts a , f , s , and t refer to the axis, the first-order laterals, the second-order laterals, and the third-order laterals of the root respectively.

Let n = number of root members,

N = total number of root members on the root,

v = rate of extension of root members (mm day⁻¹),

l = length of root members (mm),

L = total length of root members on the root (mm),

b = rate of extension of the branched region along a root member (mm day⁻¹),

q = density of branching (mm⁻¹),

t = time from initial wetting of the seed (day),

t_a, t_f, t_s, t_t = time from $t = 0$ at which the first representative of each class of root member appears (day).

(ii) Growth of the Root

Stage 1: Root axis present only.

$$N = n_a = 1. \quad (1)$$

$$L = v_a(t - t_a) = l_a. \quad (2)$$

Stage 2: Axis and first-order laterals present.

$$n_f = b_a q_f (t - t_f). \quad (3)$$

$$N = n_a + n_f = 1 + b_a q_f (t - t_f) \simeq b_a q_f (t - t_f). \quad (4)$$

$$\begin{aligned}
 l_f &= n_f \times (\text{the length of the middle lateral of the set}) \\
 &= n_f \times \frac{1}{2}v_f(t-t_f) \\
 &= \frac{1}{2}b_aq_fv_f(t-t_f)^2.
 \end{aligned} \tag{5}$$

$$L = l_a + l_f = v_a(t-t_a) + \frac{1}{2}b_aq_fv_f(t-t_f)^2. \tag{6}$$

Stage 3: Axis, first-order laterals, and second-order laterals present.

$$\begin{aligned}
 n_s &= (\text{the number of first-order laterals bearing second-order} \\
 &\quad \text{laterals}) \times (\text{the length of the branched region of the} \\
 &\quad \text{middle first-order lateral of the set}) \times (\text{the density of} \\
 &\quad \text{the second-order laterals}) \\
 &= b_aq_f(t-t_s) \times \frac{1}{2}b_f(t-t_s) \times q_s
 \end{aligned} \tag{7}$$

$$= \frac{1}{2}b_aq_fb_fq_s(t-t_s)^2. \tag{8}$$

In estimating the first term of equation (7) we have assumed that second-order lateral branching advances along the root axis at a rate equal to b_a .

$$\begin{aligned}
 N &= n_a + n_f + n_s \\
 &= 1 + b_aq_f(t-t_f) + \frac{1}{2}b_aq_fb_fq_s(t-t_s)^2.
 \end{aligned} \tag{9}$$

By analogy with the argument leading to equation (5), the total length of the second-order laterals on the most basal branched first-order lateral is

$$\frac{1}{2}b_fq_s v_s(t-t_s)^2 = \beta(t-t_s)^2 \text{ with } \beta = \frac{1}{2}b_fq_s v_s.$$

Now, for all branched first-order laterals (numbering n'_f laterals)

$$l_s = \beta(t-t_s)^2 + \beta[(t-t_s)-t_i]^2 + \beta[(t-t_s)-2t_i]^2 + \dots + \beta[(t-t_s)-n'_f t_i]^2,$$

where $t_i = 1/b_aq_f$ is the time interval between the emergence of successive first-order laterals, and $n'_f t_i = t-t_s$. Thus

$$l_s = \beta(t-t_s)^2 + \beta \sum_{m=1}^{n'_f} [(t-t_s) - (m/b_aq_f)]^2,$$

where m is an integer. Expanding the contents of square bracket and summing the series yields

$$l_s = \beta(n'_f + 1)(t-t_s)^2 - [2\beta(t-t_s)/b_aq_f] \cdot \frac{1}{2}n'_f(n'_f + 1) + (\beta/b_a^2q_f^2) \cdot \frac{1}{6}n'_f(n'_f + 1)(2n'_f + 1). \tag{10}$$

On substituting $b_aq_f(t-t_s)$ for n'_f , the first and second terms of equation (10) become equal and cancel. l_s is thus equal to the third term of equation (10), which, written in full, is

$$l_s = \frac{1}{6}b_aq_fb_fq_s v_s(t-t_s)^3 + \frac{1}{4}b_fq_s v_s(t-t_s)^2 + b_fq_s v_s(t-t_s)/12b_aq_f. \tag{11}$$

The size of the various terms of equation (11) can be estimated using $b_a = 25$ and $q_f = 0.4$ which are common values for cereal roots. The ratio of the third term to the first term is $1/[2(b_aq_f)^2(t-t_s)^2] = 1/[200(t-t_s)^2]$. Therefore the third term is negligible when $(t-t_s) > 0.5$ day. The ratio of the second term to the first term is

$1.5/b_a q_f(t-t_s) = 0.15/(t-t_s)$. Thus the importance of the second term falls as $(t-t_s)$ increases, being 10% of the first term when $(t-t_s) = 1.5$ days and 1% when $(t-t_s) = 15$ days.

Neglecting the third term in equation (11), but otherwise writing in full

$$L = l_a + l_f + l_s \\ = v_a(t-t_a) + \frac{1}{2}b_a q_f v_f(t-t_f)^2 + \frac{1}{6}b_a q_f b_f q_s v_s(t-t_s)^3 + \frac{1}{4}b_f q_s v_s(t-t_s)^2. \quad (12)$$

Stage 4: Third-order laterals present. Although third-order laterals will not be considered in detail in these papers, an estimate of their importance is of interest. Their number and length are given, to a first approximation, by

$$n_t \simeq \frac{1}{6}b_a q_f b_f q_s b_s q_t(t-t_t)^3,$$

and

$$l_t \simeq \frac{1}{24}b_a q_f b_f q_s b_s q_t v_t(t-t_t)^4.$$

Assuming values used in Table 2, and letting $b_s = v_s$, $q_t = 0.1$, and $v_t = 0.5$, then $n_t \simeq 180$ and $l_t \simeq 225$ mm when $(t-t_t) = 10$ days, i.e. third-order laterals will form a relatively insignificant part of the root system (cf. Table 2).

III. DISCUSSION

Of prime importance in considering this model is whether cereal roots actually conform in their extension and branching to the conceptual basis of the model. A check is made in Table 1.

The references listed in Table 1 are unfortunately few. Very little quantitative information of the kind needed for the comparison is available. Moreover, consideration had to be confined to experiments in which the root medium was reasonably homogeneous and environmental conditions were roughly constant. Rates of extension and branching are not uniform and constant with time when the soil profile is markedly layered or when changes occur in environmental conditions. This restriction, however, does not rule out any large body of data.

Table 1 indicates that most of the assumptions are acceptable within the limits mentioned above or can be accepted as first approximations. The exception is the assumption that first- and second-order laterals have constant rates of extension which are uniform throughout the root. Hackett and Bartlett (1971) and Hackett (1971) have published root profiles showing the change in length of first-order laterals along undamaged root axes of barley at various times from germination. If v_a and v_f had been constant in these experiments, the profiles would have had the appearance of sets of similar right-angled triangles. They did not. The angle nearest the apex of the root axis changed with time; the "hypotenuse" was always curvilinear; and the curvature of the hypotenuse also changed with time.

Faced with such evidence, it was necessary to consider very carefully the extent to which conclusions from use of the model could be influenced by weakness in the assumption that rates of extension are constant and uniform.

Two checks were made. First, using rounded values of the appropriate variables determined from the primary data of the experiment of Hackett (1971), predicted and actual profiles of the first-order laterals at 8, 13, and 23 days from seed wetting

TABLE 1

ANALYSIS OF THE ASSUMPTIONS UNDERLYING THE MODEL: A COMPARISON WITH EXPERIMENTAL DATA RELATING TO THE VEGETATIVE STAGE OF TEMPERATE CEREALS

Assumption	Validity	Evidence*	Conclusion
1. (a) The axis bears first-order laterals up to its very base	Untrue. Commonly there is a bare zone of about 10 mm, even in water culture	(1),(2)	Often negligible, but assess likely errors carefully
(b) First-order laterals when branched bear second-order laterals up to their very base	Untrue. Commonly there is a bare zone of about 10 mm	(3)	Often negligible, but assess likely errors carefully
2. Laterals emerge in acropetal sequence along root members	First-order laterals: not absolutely correct. In the region where first-order laterals are emerging, the distal of an adjacent pair often emerges before the proximal Second-order laterals: no information	(3),(4)	Neglect Assume to be correct
3. v_a , v_f , and v_s are uniform throughout the root and constant with time	v_a : approximately correct for a homogeneous root medium† v_f : not true, even in a homogeneous root medium v_s : no information. Unlikely to be correct	(2),(5),(6) (1),(2)	Assume to be correct Assess likely errors carefully Assess likely errors carefully
4. (a) b_a does not always equal v_a	Correct	(3)	Retain both b_a and v_a in model
(b) b_f does not always equal v_f	No information		Retain both b_f and v_f in model
5. (a) b_a is constant with time	Some variation can be observed	(2)	Assume to be correct
(b) b_f is uniform throughout the root and constant with time	No information. Characteristics may be similar to v_f		Assess likely errors carefully
6. q_f and q_s are uniform throughout the root and constant with time	High variability is common when examined on a small scale (i.e. 10 by 10 mm), but approximately true on a larger scale (i.e. 50 by 50 mm). Can observe trends in q_f along axes	(3)	Assume to be correct
7. Spread of second-order lateral branching along root axis proceeds at rate b_a	What little information there is suggests that this is approximately so	(3)	Assume to be correct

* References: (1) Hackett and Bartlett (1971); (2) Hackett (1971); (3) Hackett, unpublished results; (4) May, Chapman, and Aspinall (1965); (5) Brouwer and Loen (1962); (6) Weaver, Kramer, and Reed (1924).

† The model is not concerned with rates of growth of root members between the time of their initiation and the time of their emergence. During this time, the rates are of course unlikely to be arithmetic, but this is considered unimportant in the present context.

were compared (Fig. 2). The error due to v_f not being uniform and constant was large only over the basal 40 mm of the axis, from which would have emerged about 12 first-order laterals. We are concerned about this error but have concluded that it can be neglected for the purposes of Part II of this series. There are no data with which to compare estimated profiles of second-order laterals, but the errors here must be small up to 23 days. The error due to the existence of bare regions at the base of the axis was noticeable, but as judged by the results of the second check these regions could be neglected for present purposes (they are simple to allow for when desired).

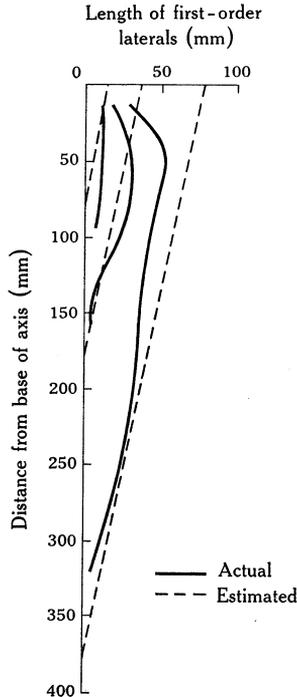


Fig. 2.—Change in length of first-order laterals along the seminal root axis of barley at 8, 13, and 23 days from seed wetting: comparison between data of Hackett (1971) and output from the model when $b_a = 20$, $v_f = 4$, and $t_f = 4$.

The second check was more embracing. Drawing again on rounded values obtained from the same experiment, N and L were calculated for each day up to day 23 and were compared with the actual data (Table 2). The agreement was quite good. It was noticed especially that the model adequately reproduced (1) the 50-fold increase in number of second-order laterals during the final 10 days of the experiment and (2) the small fluctuations of L/N with time. It was concluded that the model could be used for the purpose for which it was developed.

It would have been satisfying to have been able to establish the generality of the model by showing that data from independent experiments can be fitted in the same way, but no other data exist in sufficient detail. Some independent verification was obtained, however, from the experiments of May, Chapman, and Aspinall (1965) and May *et al.* (1967) who analysed the growth of the root system of barley in terms of the four growth measures listed in Table 3. Using the symbols adopted for the model, and considering one root only, it can be shown that their growth measures are expressed by the model in the form shown in columns 3–6 of Table 3. These expressions, albeit for a single root, explain a prominent feature of their results. May *et al.* (1967) stated

that for the whole root system, the mean extension rate declined with time, particularly over the first 4 days of growth. We show in Figure 3 and Table 3 that the magnitude of all four growth measures of a root system will tend to that of the dominant order of lateral, so it is not surprising that the mean extension rate fell in the manner reported.

TABLE 2
NUMBER AND LENGTH OF THE SEMINAL ROOT MEMBERS OF BARLEY

Comparison between actual measurements from the experiment of Hackett 1971 (values in bold type) and the output from a model of root growth (values in normal type) based on the following values of the input variables (see the text for units and explanation of the symbols): $t_a = 1$; $t_f = 4$; $t_s = 12$; $v_a = 20.0$; $v_f = 4.0$; $v_s = 1.5$; $b_a = 20.0$; $b_f = 4.0$; $q_f = 0.3$; $q_s = 0.3$

Time from seed-wetting (days)	Axis length (mm)	First-order laterals		Second-order laterals		Total		Average length (mm)
		No.	Length (mm)	No.	Length (mm)	No.	Length (mm)	
2	20					1	20	20
3	40					1	40	40
4	60					1	60	60
5	80	6	10			7	90	13
6	100	12	50			13	150	11
7	120	18	110			19	230	12
8	140	24	190			25	330	13
8	150	25	170			26	320	12
9	160	30	300			31	460	15
10	180	36	430			37	610	16
11	200	42	590			43	790	18
12	220	48	770			49	990	20
13	240	54	970	4	0	59	1210	21
13	220	53	890	9	100	63	1120	18
14	260	60	1200	14	20	75	1480	20
15	280	66	1450	32	50	99	1780	18
16	300	72	1730	58	120	131	2150	16
16	300	62	1810	87	320	150	2430	16
17	320	78	2030	90	240	169	2580	15
18	340	84	2350	130	400	215	3100	14
19	360	90	2700	176	640	267	3700	14
20	380	96	3070	230	950	327	4400	13
21	400	102	3470	292	1350	395	5220	13
22	420	108	3890	360	1840	469	6150	13
23	440	114	4330	436	2450	551	7220	13
23	380	121	3390	405	2530	543	6330	12

Other roles for the model can be envisaged apart from that developed in Part II, although its adoption would first require careful checking of assumptions as was carried out in Table 1. Firstly, the model could be valuable for estimating data for interpolation between actual data obtained from well-spaced harvests of root material. A need for such a facility is now emerging from investigations of the nutrient uptake

TABLE 3
 EXPRESSIONS OF SOME GROWTH MEASURES OF THE STANDARD ROOT
 Expressions after May, Chapman, and Aspinall (1965) and May *et al.* (1967)*

Growth Measure	Units	Estimate of growth measure from the model			
		Axis	First-order laterals	Second-order laterals	General formula†
Relative multiplication rate = $(1/n)(dn/dt)$	root member/root member/day	0	$1/(t-t_f)$	$2/(t-t_s)$	$m/(t-t_m)$
Relative extension rate = $(1/l)(dl/dt)$	mm/mm/day	$1/(t-t_a)$	$2/(t-t_f)$	$3/(t-t_s)$	$(m+1)/(t-t_m)$
Mean extension rate = $(1/n)(dL/dt)$	mm/root member/day	v_a	v_f	v_s	v_m
Mean root length (or average length) = (l/n)	mm/root member	$v_a(t-t_a)$	$\frac{1}{2}v_f(t-t_f)$	$\frac{1}{3}v_s(t-t_s)$	$v_m(t-t_m)/(m+1)$

* Note that these authors used a different terminology: thus their primary roots correspond to our axes, their secondary roots to our first-order laterals, etc.

† The general formula contains m , the order of the laterals, reckoning the axis as a lateral of order zero.

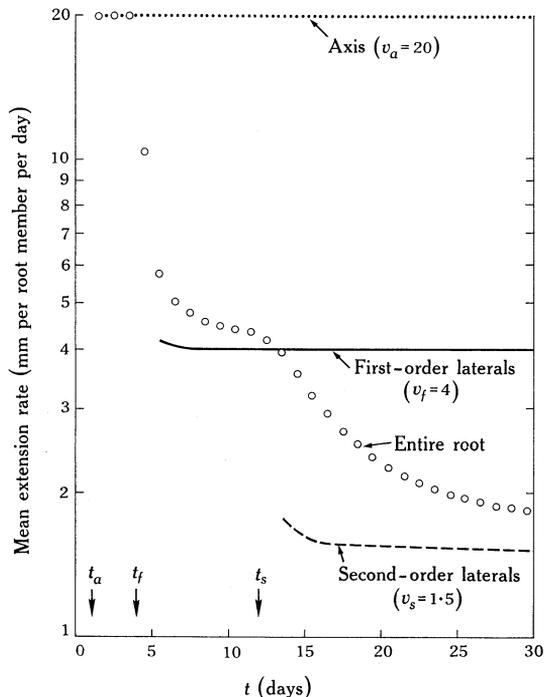


Fig. 3.—Mean extension rate $(1/N)(dL/dt)$ for the standard root using the data of Table 2 continued forward to $t = 30$ days.

characteristics of different types of root member (e.g. Russell and Sanderson 1967; Rovira and Bowen 1968, 1970; Clarkson and Sanderson 1971). These studies are moving towards the preparation of continuing balance sheets of uptake which will estimate the contributions made by each type of morphological component of the root system as it develops. It could be tiresome in this work to have to make frequent measurements of root dimensions. The model provides adequate estimates very economically.

Another use for the model might be in helping to interpret measurements of rooting density obtained from fragments of root material extracted from the field. At present this can be envisaged only for tap-rooted species, but were they found to conform to the model, it might be possible to extract whole root systems of seedlings daily from soil for up to say 10 days and then via the model predict rooting densities in different soil layers for up to 30 days. Comparisons could then be made with actual densities determined from fragments, and conclusions could be drawn about how the root system had developed.

Finally, it is possible to envisage the model as the starting point for a physiological model of root growth. Several models of plant growth have been published which estimate the assimilate transported to the root system (e.g. Brouwer and de Wit 1969; C. W. Rose *et al.* 1972), but this assimilate cannot confidently be given morphological expression. It is only a step further experimentally to determine both the assimilate allocated to the root system and the root form, and with this information it should be possible to develop a model of root growth which is based on environmental and physiological inputs.

IV. ACKNOWLEDGMENT

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V. REFERENCES

- BARLEY, K. P. (1970).—The configuration of the root system in relation to nutrient uptake. *Adv. Agron.* **22**, 159–201.
- BROUWER, R., and LOEN, E. A. (1962).—Growth and uptake of individual crown roots of *Zea mays* L. *Jaarb. Inst. biol. scheik. Onderz. LandbGewass.* for 1962, pp. 19–25.
- BROUWER, R., and WIT, C.T. DE (1969).—A simulation model of plant growth with special attention to root growth and its consequences. In "Root Growth." (Ed. W. J. Whittington.) pp. 224–42.
- CLARKSON, D. T., and SANDERSON, J. (1971).—Relationship between the anatomy of cereal roots and the absorption of nutrients and water. A. Rep. agric. Res. Coun., Letcombe Lab., for 1970. pp. 16–25.
- EVANS, P. S. (1970).—Root growth of *Lolium perenne* L. I. Effect of plant age, seed weight, and nutrient concentration on root weight, length, and number of apices. *N.Z. J. Bot.* **8**, 344–56.
- EVANS, P. S. (1971).—Root growth of *Lolium perenne* L. II. Effects of defoliation and shading. *N.Z. J. Agric. Res.* **14**, 552–62.
- HACKETT, C. (1968).—A study of the root system of barley. I. Effects of nutrition on two varieties. *New Phytol.* **67**, 287–300.
- HACKETT, C. (1969).—A study of the root system of barley. II. Relationships between root dimensions and nutrient uptake. *New Phytol.* **68**, 1023–30.
- HACKETT, C. (1971).—Relations between the dimensions of the barley root system: effects of mutilating the root axes. *Aust. J. biol. Sci.* **24**, 1057–64.

- HACKETT, C., and BARTLETT, B. O. (1971).—A study of the root system of barley. III. Branching pattern. *New Phytol.* **70**, 409–13.
- HACKETT, C., and ROSE, D. A. (1972).—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. *Aust. J. biol. Sci.* **25**, 681–90.
- MAY, L. H., CHAPMAN, F. H., and ASPINALL, D. (1965).—Quantitative studies of root development. I. The influence of nutrient concentration. *Aust. J. biol. Sci.* **18**, 25–35.
- MAY, L. H., RANGLES, F. H., ASPINALL, D., and PALEG, L. G. (1967).—Quantitative studies of root development. II. Growth in the early stages of development. *Aust. J. biol. Sci.* **20**, 273–83.
- ROSE, C. W., BEGG, J. E., BYRNE, G. F., TORSSELL, B. W. R., and GONCZ, J. H. (1972).—A simulation model of growth-field environment relationships for Townsville stylo (*Stylosanthes humilis* H.B.K.) pasture. *Agric. Met.* (In press.)
- ROVIRA, A. D., and BOWEN, G. D. (1968).—Anion uptake by the apical region of seminal wheat roots. *Nature, Lond.* **218**, 685–6.
- ROVIRA, A. D., and BOWEN, G. D. (1970).—Translocation and loss of phosphate along roots of wheat seedlings. *Planta* **93**, 15–25.
- RUSSELL, R. S., and SANDERSON, J. (1967).—Nutrient uptake by different parts of the intact roots of plants. *J. exp. Bot.* **18**, 491–508.
- SHEARER, R. C. (1968).—Water flux and ion uptake by wheat seedlings. Ph.D. Thesis, University of Adelaide.
- WEAVER, J. E., KRAMER, J., and REED, M. (1924).—Development of root and shoot of winter wheat under field environment. *Ecology* **5**, 26–50.

