2-4

Adaptive significance of the relation between root and shoot growth

MADHAV GADGIL AND SULOCHANA GADGIL
Centre for Theoretical Studies, Indian Institute of Science, Bangalore 560 012

Abstract

The partitioning of dry matter between the root and shoot tissues of a plant is regulated precisely at a constant value for a given genotype under specified environmental conditions. But individuals of different species or of the same species under different environmental conditions show characteristic variation in the root-to-shoot ratio. We postulate that this ratio is ultimately regulated not by competition between root and shoot of a plant, but by considerations of the maintenance of a proper balance between the functions of root and shoot of an integrated whole plant such that the net carbon fixation by the plant is maximised. A theoretical analysis of this problem shows that under certain conditions the root-to-shoot ratio would be expected to decrease for plants growing under better lighted or more arid conditions, in contradiction to the usually observed and expected trends. A simple mathematical model of the phenomenon is presented which delineates the critical parameters of the system and generates several testable predictions. For example, it is predicted that if the root-to-shoot ratio increases under conditions of greater availability of light, then the cost of maintenance and replacement of unit shoot tissue will be smaller than that for root tissue.

Key words: Root-to-shoot ratio, resource allocation, phenotype strategies.

1. Introduction

One of the objectives of plant ecology should be to furnish a predictive theory for the design of a plant occupying a particular environment. Such a design may be specified in a variety of ways. For example Horn[1] describes the design of a tree in terms of the number of 'layers' in which the leaves of a tree are distributed. He then develops a theoretical formulation for the photosynthetic efficiency of a tree for varying light intensities incident at the top of the tree and for varying distributions of the leaves of the tree. On the basis of this formulation, he predicts that tree species characteristic of early stages of succession will have multilayered leaves, while those characteristic of later stages of succession will have leaves disposed in a single layer.

25

We consider here, another significant parameter of the design of a plant, namely, the ratio of the weight or calorific value of the material making up its root system to that of its shoot. It is notable that this ratio is maintained at a constant value for a given genetic strain at a given growth stage under any given set of environmental conditions. The precise regulation of the value of this ratio suggests that plants are rather sensitive in their functioning to any change in this value from some optimal level. Such root-to-shoot ratios have been the subject of a number of studies comparing different plant species as well as phenotypic variation within a genetic strain. Rodin and Bazilevich[2] document the root-to-shoot ratios for plant species deriving from a variety of communities ranging from the tropical rain forest and mangrove swamps to the tundra. Troughton[3] and Brouwer[4] review the available information on the phenotypic response of the root-to-shoot ratio to a number of factors such as the moisture content of the soil, addition of fertilizers and the extent of shading. The major conclusion deriving from both kinds of studies comparing variation amongst different plant species and within a species is that the root-to-shoot ratio is higher for a plant growing under arid, in contrast to moist soil conditions, and also higher for a plant growing in well lit as opposed to shaded conditions (also see Dormer[5], Evans[6], Torrey and Clarkson[7], Whittington[8], Williams[8] and Monk[10]).

2. Physiological and adaptive explanations

These observations have been explained on the basis of two kinds of interpretations. Brouwer[4] advocates what he terms as a physiological explanation. The shoot is dependent on the root for the supply of water and minerals, while producing its own carbohydrates, whereas the root is dependent on the shoot for the supply of carbohydrates, but acquires its own supply of water and minerals through absorption. A reduction in the moisture content leads to a greater limitation in the supply of water which is felt more severely by the shoot than the root and hence leads to an increase in the root-to-shoot ratio. Analogously, a reduction in the availability of light leads to a greater limitation in the supply of carbohydrates which is felt more severely by the root than by the shoot and hence leads to a decrease in the root-to-shoot ratio. The explanation is thus based on the notion that there is a competition between the root and the shoot for the limiting factors and an increase in the extent of limitation by any factor implies a less serious limitation for the organ producing or absorbing the factor, but a more serious limitation for the organ which does not acquire the factor directly but from the other organ.

Troughton[3] advocates an alternative explanation which treats the plant as an integrated system. The flow of materials among various organs of the plant is then not determined by competitive interactions. Rather, the flow must be programmed so that a constant balance is maintained between the absorptive function of the root and the photosynthetic function of the shoot such that the overall performance of the plant is maintained at its highest level possible. Thus when the moisture content of the

soil is reduced, the root cannot supply as much water as before, while the leaves can potentially manufacture as much carbohydrates as before. The plant as a whole may then benefit if any further growth of the plant concentrates on the production of relatively more root material with the consequent shift of the root-to-shoot ratio towards a higher value. In an analogous fashion any decrease in the light availability will lead to a lowering of the root-to-shoot ratio.

Troughton's explanation[3] is obviously more appealing to anyone adopting a Darwinian approach to plant ecology. We expect the plant to have evolved to function as an integrated system, with the different components adjusted as to maximise some criterion of the overall performance of the system. The most obvious choice for such a criterion is the net amount of carbon fixed per unit time. Although the ultimate criterion of performance will be the reproductive fitness, the maximization of this reproductive fitness must be brought about through the intermediate step of maximising net carbon fixation in a given environment. Hence we now consider a model in which the relative proportions of different plant organs are assumed to be adjusted to maximise its rate of net carbon fixation. There may be, of course, special cases where what is important to maximise is not so much net carbon fixation, but, some other property, e.g., the ability of the plant to withstand strong wind. However, we ignore these possibilities for the present.

3. Optimum resource allocation

The amount of carbon fixed per unit time is a function of several variables. These include the amount of chlorophyll present in the leaf tissue and the amount of water and minerals supplied by the root to the leaf tissue. Slavik[11] cites considerable evidence showing the depression in the level of photosynthesis without any reduction in the amount of water supplied to the shoot tissue. The amount of water required by the shoot depends on the size of the shoot, while the amount of water (and minerals) supplied by the root depend on the size of the root system. The extent to which the demands for water and minerals of the shoot are satisfied will depend on the root-to-shoot ratio. For any given environment, the higher the ratio, the more complete will the satisfaction of the water requirement of the shoot be; hence the closer will the photosynthetic apparatus function to its maximal potential efficiency. This is expressed in Fig. 1 which shows carbon fixation per unit of photosynthetic tissue, or per unit of shoot tissue if the proportion of photosynthetic and supporting tissue is assumed to be given as a function of the root-to-shoot ratio.

For a given plant, any increase in the root-to-shoot ratio implies that the plant is allocating some of the resources to the production of root which could have been utilized for the production of shoot. We can therefore conceive of alternative constructions of a given plant such that the same total capital is divided between the root and shoot tissues in different proportions. When the root tissue acquires the major share of the

capital, the rate of carbon fixation per unit shoot tissue will be high, but the total amount of shoot tissue which can undertake carbon fixation will be small. On the other hand, when the shoot tissue is allocated a major share of the capital, the rate of carbon fixation per unit shoot tissue will be low, although the amount of shoot tissue which can photosynthesize is large (Fig. 1). The product of the rate of carbon fixation by unit shoot tissue and the total amount of shoot tissue gives us the gross amount of carbon fixed. As can be seen from Fig. 1, this will be very low at both very high and very low values of the root-to-shoot ratio, but will be at a maximum at some intermediate level.
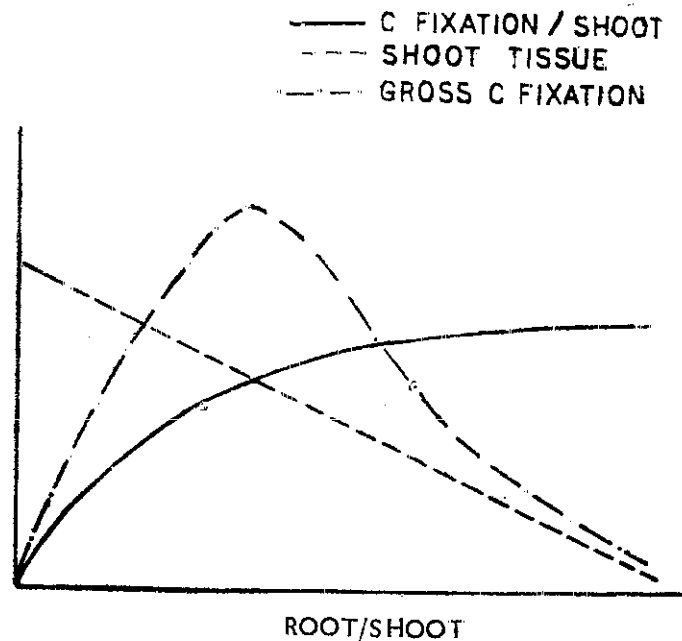

FIG. 1. Carbon fixation by unit shoot tissue, gross carbon fixation, and the amount of tissue out of a fixed total weight of plant present as shoot tissue as functions of root-to-shoot ratio.

What is to be maximised is, however, not the gross amount of carbon fixed per unit time, but the net amount, i.e., gross minus the amount used up in maintenance and replacement. This will tend to depress the curve of carbon fixation at all values of root-to-shoot ratio. If the cost of maintenance and replacement of unit root and shoot times is exactly equal, then the total cost will not be affected by the root-to-shoot ratio. This is depicted by line $r = s$ in Fig. 2. If, on the other hand, the cost of unit root tissue is greater (or less), then the total cost will increse with an increase (or decrease) in the root-to-shoot ratio (Fig. 2).

Substraction of the cost from the gross carbon fixation curve gives us the net carbon fixation curve (Fig. 3). The maximum for the net carbon fixation curve is identical with that of the gross carbon fixation curve with respect to the root/shoot ratio only if the total cost is independent of the root-to-shoot ratio. If the cost of the unit root
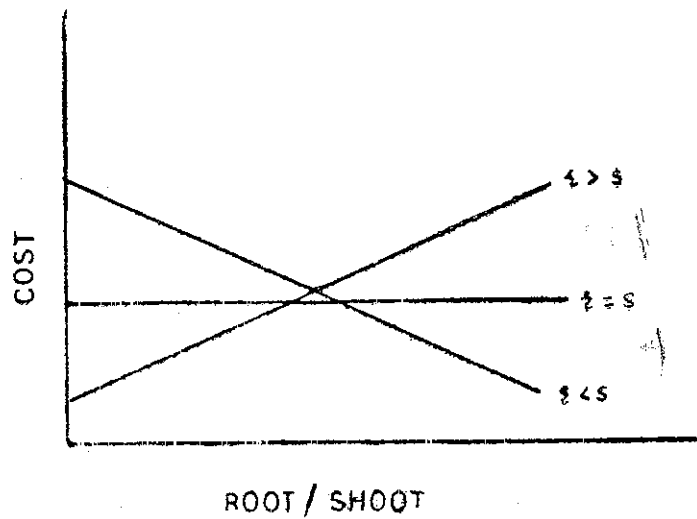
FIG. 2. The total cost of maintenance and replacement of plant tissue as a function of the root-to-shoot ratio. r and s are the cost of maintenance and replacement of unit root *and* shoot tissues respectively.
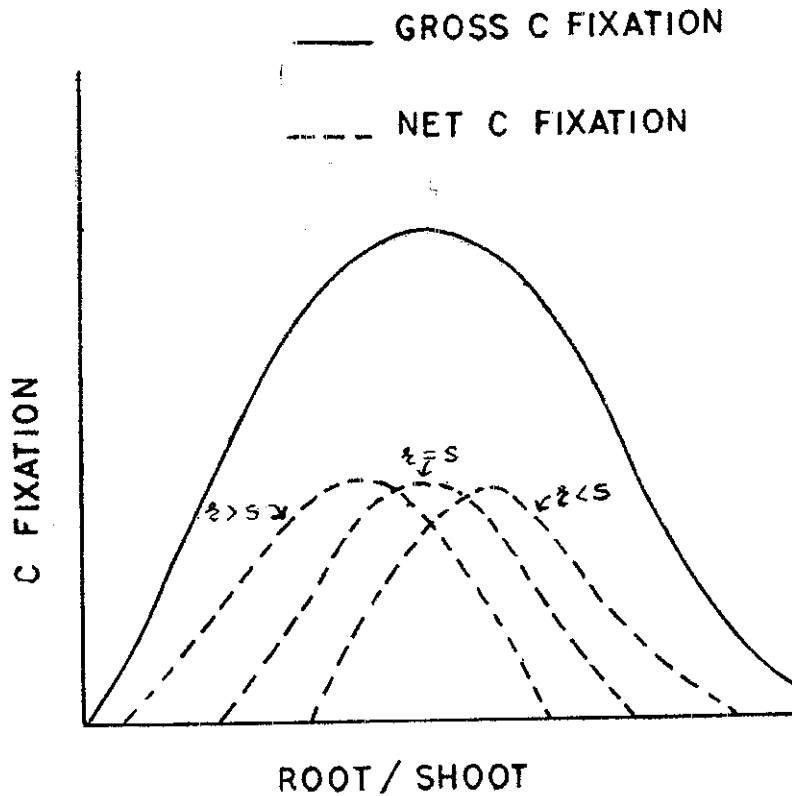

FIG. 3. Gross and net carbon fixation as a function of the root-to-shoot ratio. r and s are the cost of maintenance and replacement of unit root *and* shoot tissues respectively.

tissue is greater than that of unit shoot tissue, this maximum is shifted towards a lower value of the root-to-shoot ratio. On the other hand, the maximum of the net curve is shifted towards a greater value of the root-to-shoot ratio, as compared with the gross curve, if the cost of maintenance and replacement of unit shoot tissue is greater than that of unit root tissue.

The optimal root-to-shoot ratio is that at which the carbon fixation curve rises to a maximum. To use Troughton's terminology[3], this is the composition of the plant at which the photosynthetic function of the shoot and the absorptive function of the root are properly balanced.

The response of the optimum root/shoot ratio to a variation in environmental conditions such as those considered by Troughton[3] can be studied qualitatively by using the above analysis. Consider, for example, the effects of a change in light intensity. We shall now show that when the cost of unit shoot tissue is greater than that of unit root tissue (irrespective of the light intensity) the optimum value of the root/shoot ratios for *higher* light intensity is *less* than that for lower light intensity. An increase in light intensity may shift the entire curve of photosynthesis per unit tissue upwards unless the light is strong enough to inhibit photosynthesis. In addition, the curve may also shift laterally. The result stated above follows readily if the curve is assumed to suffer a lateral shift to the left as a result of the increase in light intensity, whereas a shift to the right tends to oppose the trend to be demonstrated. Hence we assume a lateral shift to the right. This implies that at the increased light intensity the photosynthesis is saturated at a higher value of the root-to-shoot ratio since the increased maximal photosynthesis generates a greater need of water (Fig. 4). Figure 5a shows
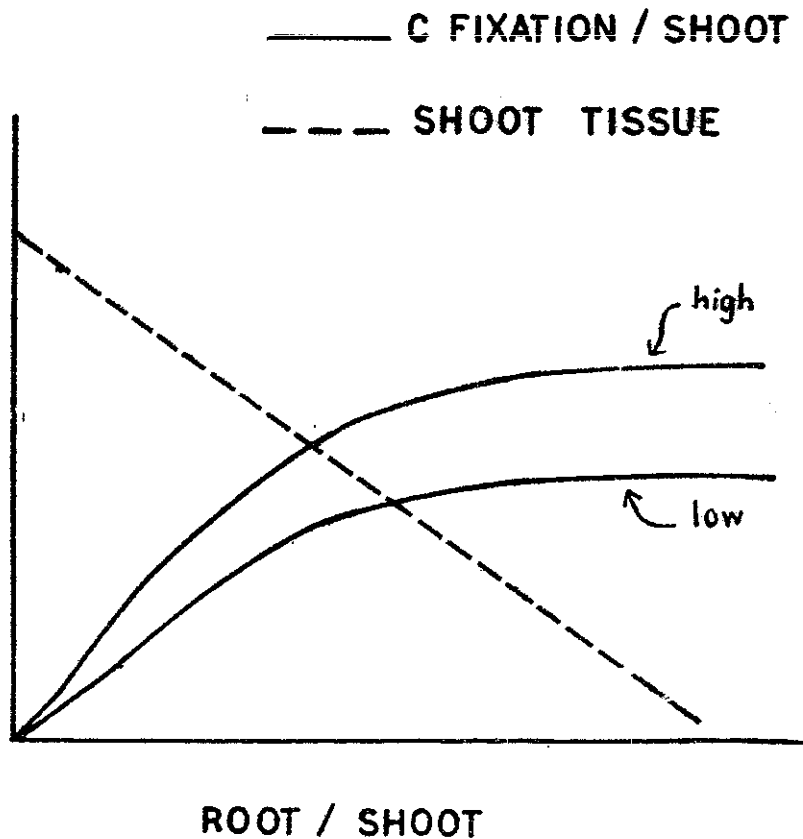
—————— C FIXATION / SHOOT

— — — SHOOT TISSUE

ROOT / SHOOT

Fig. 4 Carbon fixation by unit of shoot tissue at high and low light intensity and the amount of tissue out of a fixed total weight of plant as shoot tissue as functions of root-to-shoot ratio.

the curves of gross carbon fixation as a function of the root-to-shoot ratio for the two light intensities. Again similar to the curve of carbon fixation per unit shoot tissue, the curve for higher light intensity is shifted upwards and to the right. Figure 5a also shows the curve of the cost of maintenance and replacement. When the cost of unit shoot tissue is assumed to be greater than the cost of unit root tissue, the net carbon fixation curves obtained are as shown in Fig. 5b. As the cost of the shoot is assumed to be greater, both the net carbon fixation curves have their maxima shifted towards a higher value of the root-to-shoot ratio in comparison with the gross carbon fixation curves. It is important to notice that this shift is more marked in the case of the flatter curve of gross carbon fixation representing the condition at lower light intensity. Since the slope of the gross carbon fixation curve at higher light intensity is much more steep,

C FIXATION
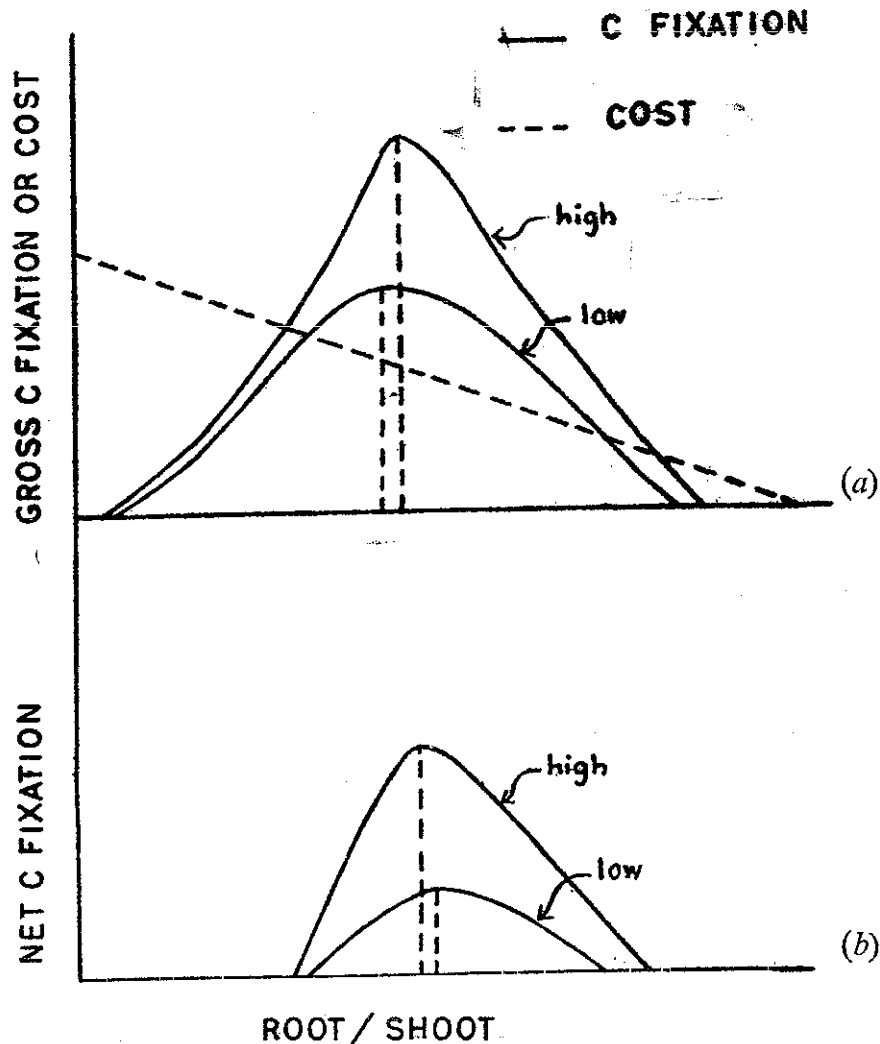
____ COST

(a)

(b)

ROOT / SHOOT

FIG. 5a. Gross carbon fixation at high and low light intensity and the total cost of maintenance and replacement of plant tissue as functions of root-to-shoot ratio.

FIG. 5b. Net carbon fixation at high and low light intensity as functions of root-to-shoot ratio. The cost of shoot tissue is assumed to be greater than that of the root tissue.

the slope of the cost curve does not affect it to that extent. The result of this is that although the maximum of gross carbon fixation curve at higher light intensity is to the right of the corresponding curve for low light intensity, its maximum for the net carbon fixation curve has actually shifted to the left of the corresponding curve for low light intensity. In other words, cost considerations being very significant at lower light intensities have driven the optimal root-to-shoot ratio towards a higher value. Since this does not happen to the same extent at higher light intensities, the optimal root-to-shoot ratio at those intensities is lower. Thus, for this particular example, it is advantageous for the plant to produce more of shoot relative to root as the light intensity increases

This conclusion is in contradiction to Troughton's[3] and also to the existing data on this problem. The conclusion, however, depends on the assumption that the cost of unit shoot tissue is greater than that of unit root tissue. The opposite assumption would reverse this conclusion. We may then postulate that for the few species for which data have been collected, the cost of shoot must be less than that of root. This is a testable conclusion.

This counter example makes obvious the necessity of an explicit and detailed analysis of an explanation such as that proposed by Troughton[3]. Such an analysis is helpful in clarifying our ideas about what the important parameters of the system are and how they are related, and of course in generating testable hypotheses. However, such qualitative analysis is only a first step towards a quantitatively predictive theory. Such quantitative prediction requires the development of more formal theory. The rest of this paper is an attempt to formalise the qualitative analysis presented above.

4. Mathematical formulation

We have noted in the previous section that the gross carbon fixation is proportional to the product of the total amount of shoot tissue and the fixation per unit shoot tissue. The latter increases with increasing availability of water and mineral resources and hence with increasing ratio of the root tissue to the shoot tissue. Thus the gross carbon fixation, G, may be expressed in terms of R, the amount of root tissue and S, the amount of shoot tissue as

$$G = aS\left(1 - e^{-dR/S}\right).$$

Here, the parameter a denotes the maximum possible value of the gross carbon fixation per unit shoot tissue (under the given conditions of moisture and mineral supply) and the parameter d specifies the extent to which the root can satisfy the demands of the shoot tissue for water and minerals. The cost, c, of maintaining the root and shoot tissues per unit time can be taken to be proportional to the amounts R and S,

$$c = uR + vS.$$

Hence net carbon fixation is

$$N = G - C = aS(1 - e^{-dR/S}) - uR - vS. \tag{1}$$

Let us assume that this net fixation N is used in further growth of root and shoot tissue, being partitioned between the shoot and the root in ratio $\theta : 1 - \theta$. Then the growth rates of the shoot and root tissues are :

$$dS/dt = N\theta \tag{2}$$

$$dR/dt = N(1 - \theta). \tag{3}$$

We assume further that this partitioning is maintained at a constant value throughout the life of the plant beginning with the partitioning of the nutritive reserves in the seed. Thus, if S_0 and R_0 are the amounts of shoot and root tissue in the seedling just germinated,

$$R_0 = S_0(1 - \theta)/\theta ;$$

$$R = S(1 - \theta)/\theta. \tag{4}$$

Combining (1), (2) and (4) we get the growth of the shoot to be

$$dS/dt = [(aS(1 - e^{-d\lambda}) - uS - v\lambda S]$$

with

$$\lambda = (1 - \theta)/\theta.$$

Hence

$$S = S_0 e^{At}; \quad R = R_0 e^{At},$$

$$S + R = (S_0 + R_0) e^{At}.$$

In this special case in which the partitioning of organic carbon is fixed throughout the life history, the growth rates of the root tissue and the shoot tissue are the same and equal to that of the total plant tissue. This growth rate, A, is maximum at the value θ given as a solution of

$$a(1 - e^{-d\lambda}) - u + v - ade^{-d\lambda}/\theta = 0. \tag{6}$$

The optimal root/shoot ratio at which the growth rate is maximum can be determined for a given set of parameters, a, d, u and v from (6). Since the optimal θ cannot be given explicitly in terms of these parameters, it was computed numerically to investigate its dependence on these parameters.

5. Results

A number of computations for optimal, θ, over a wide range of parameters were carried out. Some of the results are illustrated in Figs. 6, 7, 10 and 11. The major conclusions from these computations are :

(1) The optimal root-to-shoot ratio (θ) increases with an increase in the carbon fixation by unit shoot tissue (a), if the cost of maintenance of unit shoot tissue (u) is lower than that of unit root tissue (v) (Fig. 6). The reverse holds if the cost of maintenance of unit shoot tissue (u) is greater than that of unit root tissue (v) (Fig. 6). This result has been interpreted in detail in section 2 above. The first trend may be interpreted to represent the increase in the root-to-shoot ratio with an increased availability of light intensity as reported by Troughton[6] and Brouwer[4]. The second trend has never been observed, possibly because the cost of shoot tissue is generally lower than that of the root tissue.

(2) The optimal root-to-shoot ratio (θ) again exhibits a variable behaviour in response to variation in the relative amount of root tissue required to keep the supply of water and minerals to the shoot tissue at some specific level (Fig. 6). When the cost of
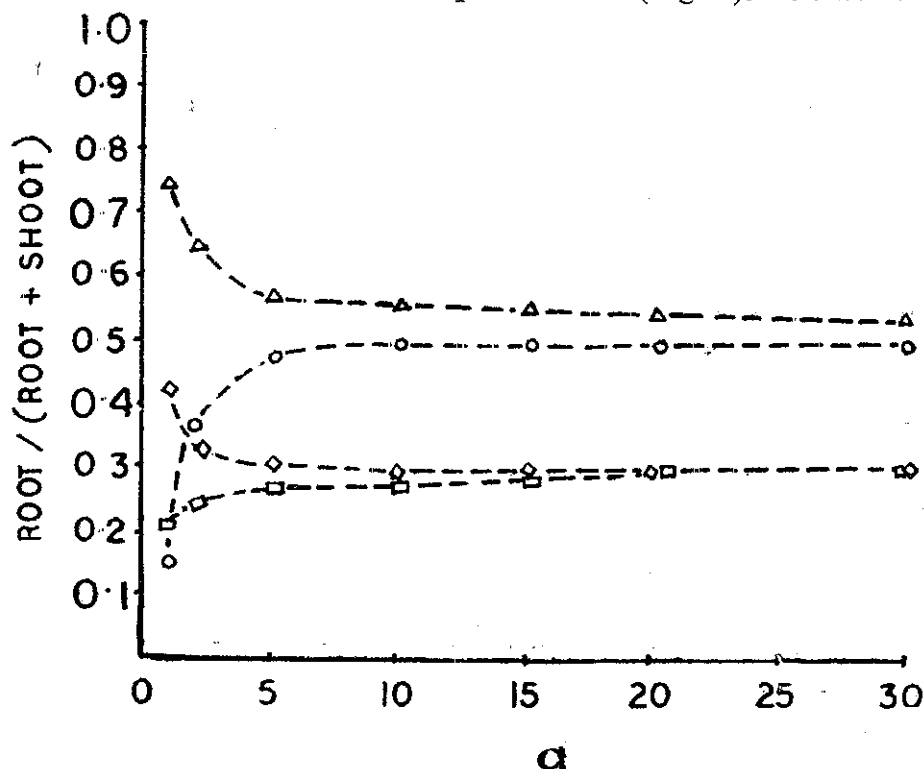

FIG. 6. Optimal root/root plus shoot ratios (θ) as functions of the parameter a for four different sets of values of other parameters.

(1) 0 $\cdots$ 0 : $d = 1$, $u = 0.2$, $v = 1$ (3) $\triangle$ $\cdots$ $\triangle$: $d = 1$, $u = 1$, $v = 0.2$

(2) $\square$ $\cdots$ $\square$: $d = 5$, $u = 0.2$, $v = 1$ (4) $\langle\rangle$ $\cdots$ $\langle\rangle$: $d = 5$, $u = 1$, $v = 0.2$.

maintenance and replacement of shoot tissue (u) is much less, by about a factor of five, than the cost of root tissue (v), then the optimal root-to-shoot ratio (θ) first increases as less and less root tissue is required to keep the supply of water and minerals at a given level, i.e., as d increases, and then declines with a further increase in the value of d. When the cost of shoot (u) approaches or exceeds the cost of root (v), then the optimal root-to-shoot ratio (θ) decreases as less and less root is required to maintain the supply of water and minerals at a given level, i.e, as d increases (Fig. 7).

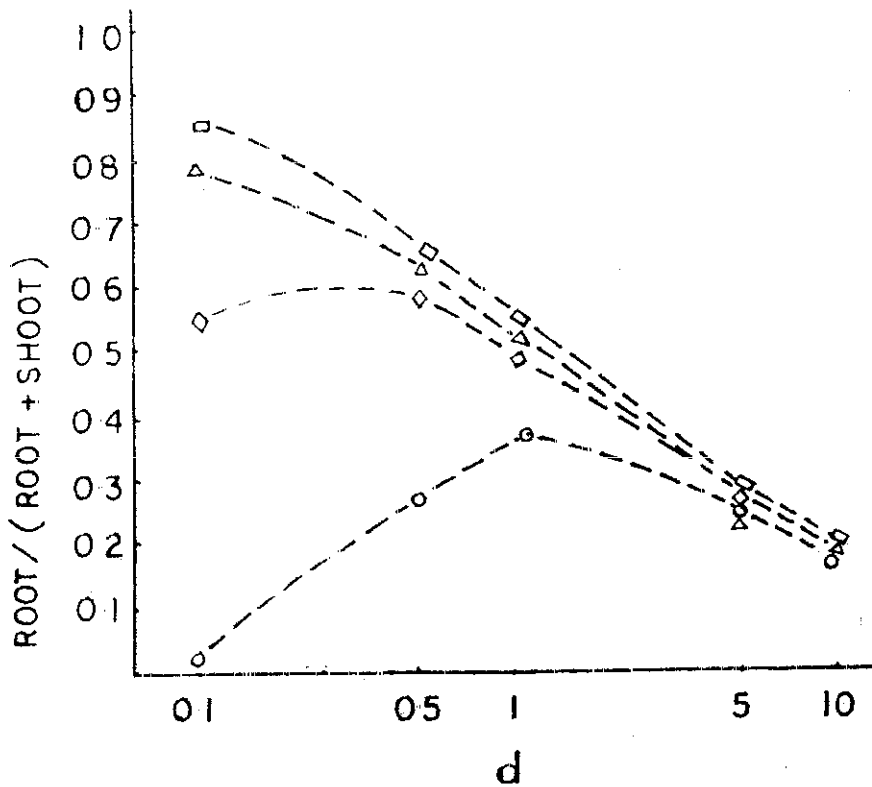FIG. 7. Optimal root/root plus shoot ratios (θ) as functions of the parameter d for four different sets of values of other parameters.

(1) 0 ··· 0 : $a = 2,$ $u = 0.2,$ $v = 1$ (3) △ ··· △ : $a = 2,$ $u = 0.2,$ $v = 1$

(2) □ ··· □ : $a = 10,$ $u = 1,$ $v = 0.2$ (4) ⟨⟩ ··· ⟨⟩ : $a = 10,$ $u = 0.2,$ $v = 1.$

This result is amenable to an interpretation analogous to that provided for the response of optimal root-to-shoot ratio (θ) to changes in light intensity. An increase in the value of d does not affect the asymptote of the curve of photosynthesis per unit shoot tissue, but will affect the rate at which this asymptote is approached (Fig. 8). We can then compute the curves for gross carbon fixation by taking the product of this with the amount of shoot tissue at different values of root-to-shoot ratio (Fig. 9a). The maxima of these curves shift towards a lower value of the root-to-shoot ratio with an increase
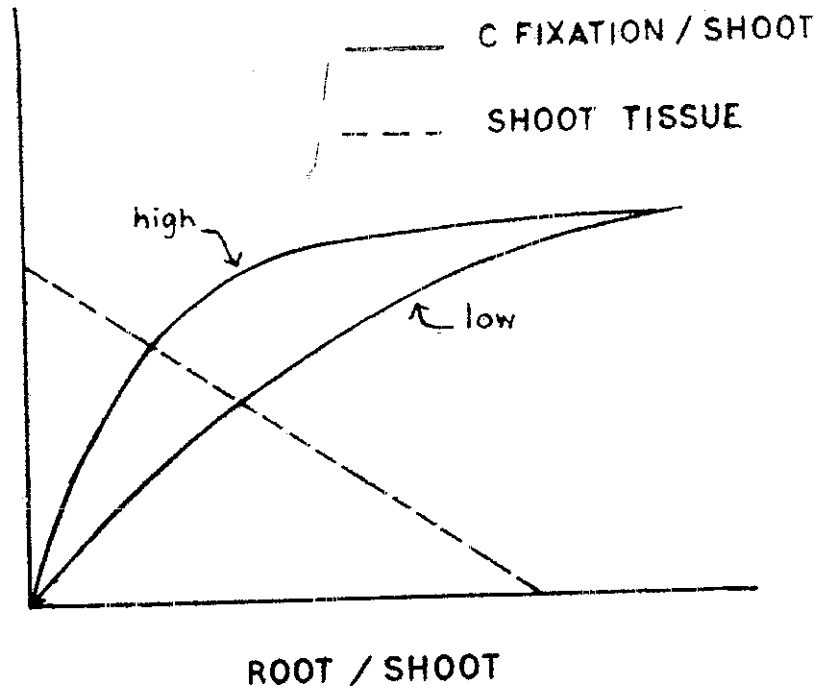
FIG. 8. Carbon fixation by unit of shoot tissue at different values of d and the amount to tissue out of a fixed total weight of plant as shoot tissue, as functions of root-to-shoot ratio.

in d. There would therefore be a tendency for the optimal root-to-shoot ratio to decrease with any increase in the value of d. However, as shown above for the analysis of the effect of light intensity, this tendency may be upset when the total cost $(uS + vR)$ is subtracted from the gross carbon fixation curve to obtain the net carbon fixation curve. The reversal of the tendency may occur because cost considerations are more important for the curves with lower values of d. If shoot is more expensive than root, then the cost considerations shift the maxima of net carbon fixation curves towards a greater value of root-to-shoot ratio. This shift would be more important for the lower values of d. This would merely reinforce the tendency for the optimal root-to-shoot ratio to decrease with any increase in the value of d. On the contrary, if shoot is less expensive than root, then the cost considerations shift the maxima of net carbon fixation curves towards a lower value of root-to-shoot ratio. This shift would be more important for the lower values of d (Fig. 9b). This would conflict with the tendency for the optimal root-to-shoot ratio to increase at lower values of d, and depending on the exact shapes of the curves could lead to the variable behaviour generated by our mathematical model (Figs. 7 and 9b).

The empirical results reported so far correspond to our second result, i.e., the optimal root-to-shoot ratio (θ) decreases as less and less root is required to maintain the supply of water and minerals at a given level (as d increases). A decrease in the root-to-shoot ratio with an increase in the water or fertilizer supply is abundantly documented by Troughton[3] and Brouwer[4]. The former result is unexpected and should be explored further.
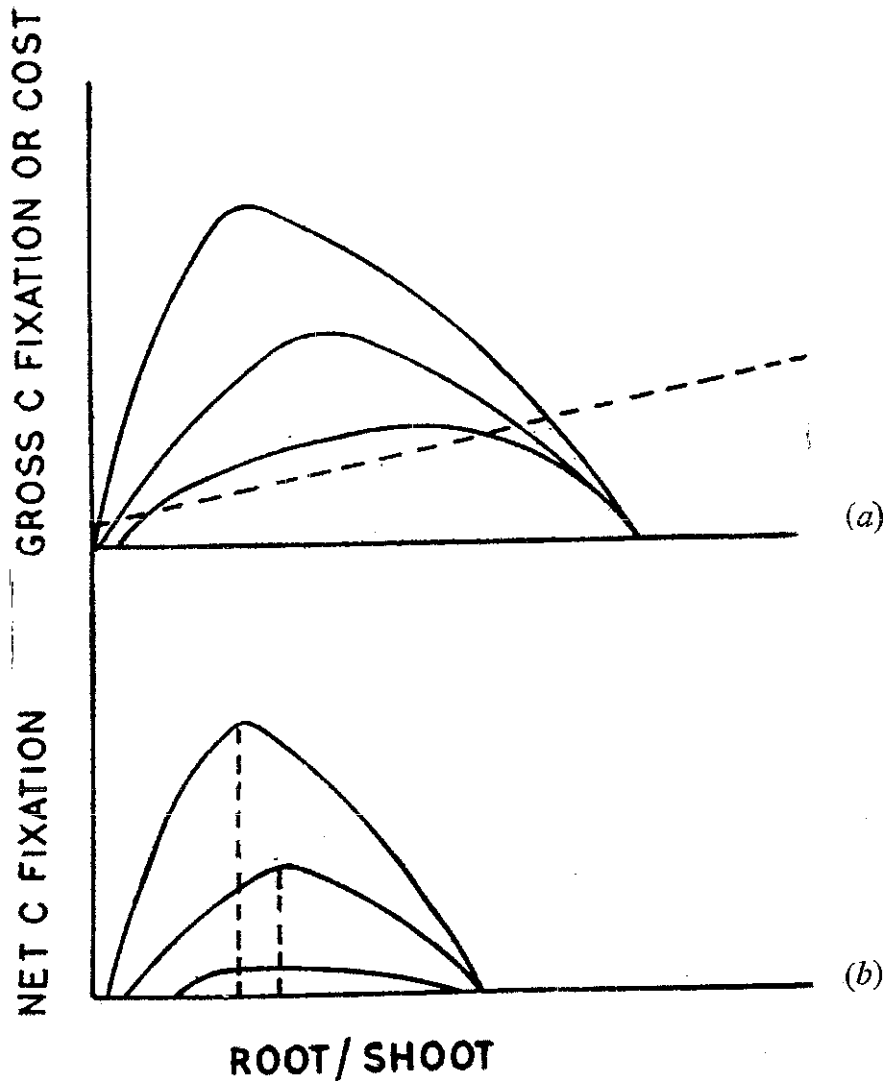
FIG. 9a. Gross carbon fixation at different values of d and the total cost as functions of root-to-shoot ratio.

FIG. 9b. Net carbon fixation at different values of d as functions of root-to-shoot ratio. The cost of shoot tissue is assumed to be much less than that of the root tissue.

(3) Root-to-shoot ratio increases as the cost of maintaining unit shoot tissue (u) increases, other parameters including the cost of maintaining unit root tissue (v) being kept constant (Fig. 10).

(4) The root-to-shoot ratio decreases when the cost of root (v) is increased, keeping other parameters, including the cost of shoot (u) constant (Fig. 11). There is no data in the literature pertaining to the last two results.

Existing literature also contains much data on the effect of temperature on the root-to-shoot ratio (e.g., Brouwer[4]). The results are complex and conflicting as would be
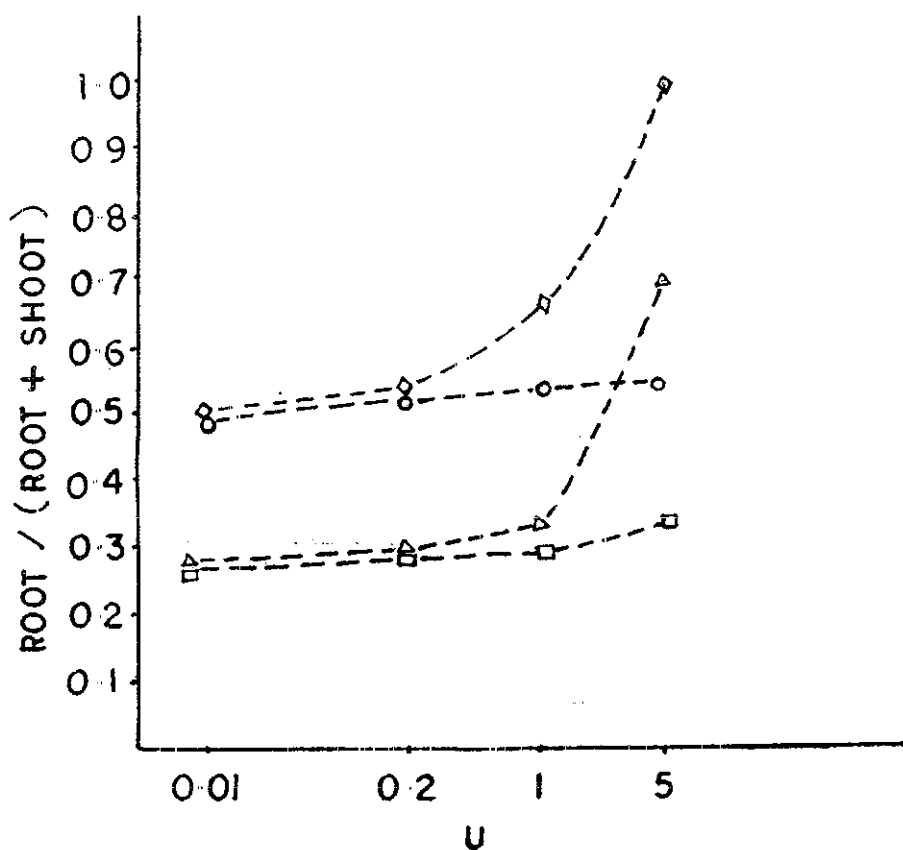
FIG 10. Optimal root/root plus shoot ratios (θ) as functions of parameter u for four different sets of values of other parameters.

(1) O $\cdots$ O : $a = 10$, $d = 1$, $v = 1$,   (3) $\triangle$ $\cdots$ $\triangle$: $a = 2$, $d = 5$, $v = 0 \cdot 2$,

(2) $\square$ $\cdots$ $\square$: $a = 10$, $d = 5$, $v = 1$ (4) $\langle\rangle$ $\cdots$ $\langle\rangle$: $a = 2$, $d = 1$, $v = 0 \cdot 2$.

expected from the fact that temperature would simultaneously affect the four parameters involved in determining optimal root-to-shoot ratios. An analysis of the effect of temperature on the root-to-shoot ratio (through its effect on the various individual parameters along the lines suggested above) alone can lead to a proper appreciation of this phenomenon.

6. Discussion

The model presented here is obviously not complex enough to be totally realistic. For example, it does not consider the effect of the variation in carbohydrate supply on the absorptive function of the root system, and assumes all the parameters to be constant throughout the life history. However, it has been successful in explaining some of the observations and generating a few interesting and testable predictions. It should therefore be considered as a first step in the building of a complex realistic theory. However, any attempt to build a very complex, but more realistic theory without having
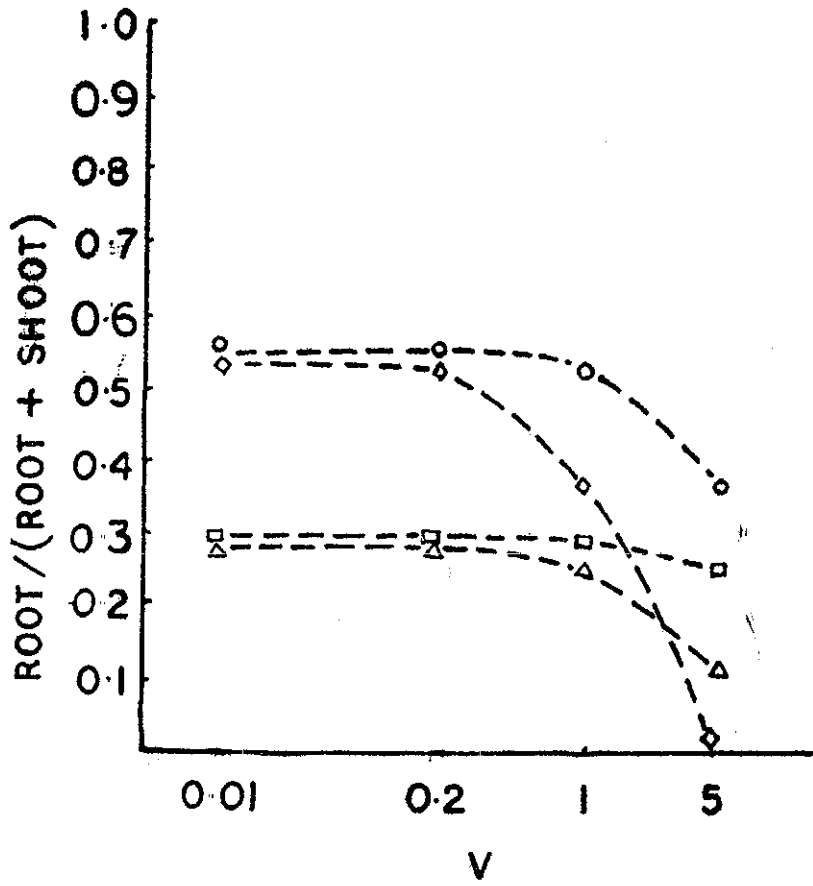
FIG. 11. Optimal root/root plus shoot ratios (θ) as functions of the parameter v for four different sets of values of other parameters

(1) 0 ⋯⋯ 0 : $a = 10$, $d = 1$, $u = 1$,

(2) □ ⋯⋯ □ : $a = 10$, $d = 5$, $u = 1$,

(3) △ ⋯⋯ △ : $a = 2$, $d = 5$, $u = 0.2$,

(4) ◇ ⋯⋯ ◇ : $a = 2$, $d = 1$, $u = 0.2$.

explored such simple models first is likely to lead to confusion. We, therefore, believe that the next step towards the development of a predictive theory of the root-to-shoot ratio would be a critical examination of the possibilities of simple theory at the level of the present one by the experimentalists. At present no data exist where all the four parameters of the theory as presented here have been simultaneoulsy determined for a single experimental system. Nor do we have detailed enough data on any system to determine if the form of the relationship between the extent of saturation of photosynthesis and the root-to-shoot ratio postulated in the theory here approximates reality. We feel that the collection of such data motivated by theoretical considerations will prove to be highly fruitful in furthering our understanding of this problem. Further elaborations of the theory to make it more realistic would most profitably follow such experimental studies.

References

1. HORN, H.

   Adaptive geometry of trees. Princeton University Press, Princeton, N.J. 1971.

2. RODIN, L. E. AND BAZIL. VICH, N. I.

   Production and mineral cycling in terrestrial vegetation Olivei and Boyd, Edinburgh, 1967, p. 288

3. TROUGHTON, A

   Growth correlations between the roots and shoots of grass plants *Proc. 8th Int. Grassland Congress*, 1960, pp. 280–283.

4. BROUWER, R.

   Root growth of grasses and cereals in *The growth of cereals and grasses*, edited by F. D. Milthorpe and J. D. Ivins. Butterworth, London, 1966, pp. 153–166.

5. DORMER, K. J

   Shoot organisation in vascular plants. Syracuse University Press, 1972.

6. EVANS, G C

   The quantitative analysis of plant growth Blackwell Scientific Publications, Oxford, 1972.

7. TORREY, J. G. AND CLARKSON, D. T. (EDS.)

   The development and function of roots. Academic Press, London, 1975.

8. WHITTINGTON, W. J. (ED.)

   Root growth. Plenum Press, New York, 1968

9. WILLIAMS, R. F.

   The shoot apex and leaf growth in *A study in quantitative biology*, Cambridge University Press, 1975.

10. MONK, C.

    Ecological importance of root/shoot ratios *Bull. Torr. Bot. club*, 1966, **93**, 402–406.

11. SLAVIK, B.

    Response of grasses and cereals to water in *The growth of cereals and grasses*, edited by F. L. Milthorpe and J. D. Ivins. Butterworth, London, 1966, pp. 227–240.