
The Mathematical Model as an Aid to Developing Concepts concerning the Soil-Atmosphere-Crop Relation

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The mathematical model as an aid to developing concepts concerning the soil–atmosphere–crop relation

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SUMMARY

The relation between light absorption rate and crop growth rate may be deduced from the kinetics of net photosynthesis showing that for a crop, such as winter wheat, growing from winter to summer this relation must be S-shaped. Altering the soil-solution nutrient level changes, in an opposite sense, the root:shoot ratio, thereby changing light interception. Destruction of live roots by soil organisms by increasing root growth enhances the long-life organic content of the soil. The relation between growth of the plant and the growth of seeds or tubers on the plant is determined by their relative competitive strengths for attracting nutrients.

1. INTRODUCTION

Mathematical models are not only of use as correlations of observed data, but may also be employed to test concepts concerning the origin of natural phenomena. Aspects of the soil-atmosphere-crop interrelation have long been modelled, though at first glance the types of models appear to be mutually conflicting. Thus the growth of grass is often related to cumulative temperature multiplied by time; while that of wheat is related to cumulative light interception. Crop demand for soil contained nutrients is sometimes related to its growth rate and in contrast also to its development stage. Indeed the manner in which soil-solution nutrient concentration interacts with crop growth rate is unclear in all the above models. Both development and growth of the shoot is usually correlated independently of those for the root, and the growth of the seed independent to that of the plant which bears it. This paper makes tentative suggestions for resolving these conflicts in part.

2. CROP GROWTH, TEMPERATURE AND LIGHT

The interrelation between crop growth and cumulative temperature time or cumulative light-intercepted time is relatively simple as it depends directly on the measured kinetics of net photosynthesis. This is temperature limited at low temperatures, light limited at higher temperatures and respiration controlled at the highest temperatures. Typically for a growing wheat crop the net exponential growth rate follows the relation shown (figure 1). This set of graphs has been drawn assuming a crop dry mass of $1 \text{ t ha}^{-1}\dagger$, a day

length of 12 h and no water limitation (Andrew 1987). The net exponential growth rate index is obtained roughly by multiplying the net shoot growth term by the ratio shoot dry mass:plant dry mass. The pronounced maximum in the curves is caused by the falling efficiency of light energy conversion into plant mass at low temperatures and the high respiration at high temperatures. This changing energy conversion efficiency results in the line relating light absorption rate to crop growth rate being S-shaped for a crop such as winter wheat which grows from the cold of the winter to the heat of summer (figure 2). The use of a straight line correlation is thus an approximation to a flat S. For grass the popular *t-sum* can be seen to be

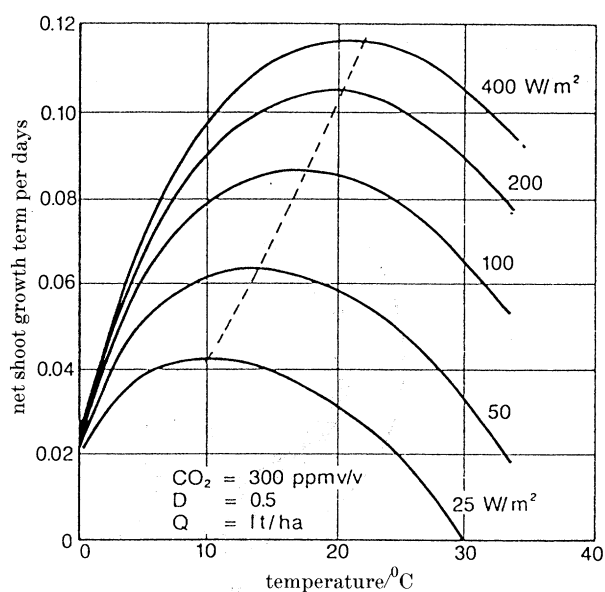


Figure 1. Effect of light intensity and of temperature on net photosynthesis.

† 1 hectare = 10^4 m^2 .

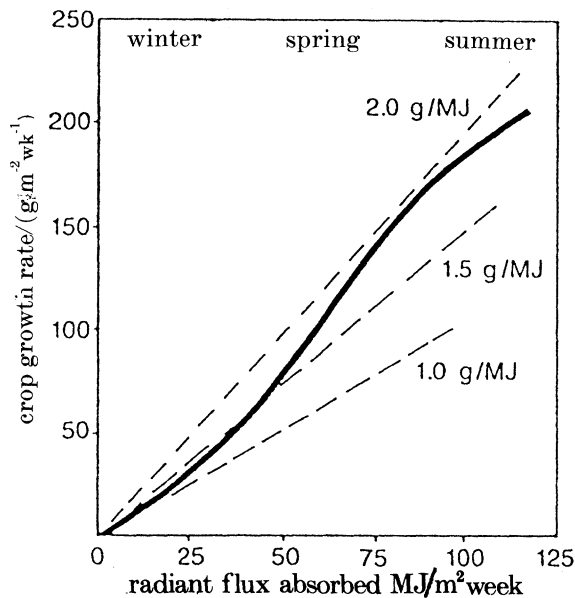


Figure 2. Typical measured crop growth rate as a function of light absorption rate during growth of winter wheat.

legitimate simplification for growth during early spring when the growth rate index is very low being temperature limited.

3. ROOT:SHOOT RATIO

During the period of growth of a crop the root:shoot ratio changes markedly. Particularly noticeable is the continuation in growth of the canopy during the constant rate period of crop growth while the root mass remains roughly constant. I suggest that speculation on the cause of this phenomenon throws light on the whole subject of the manner in which fertilizers operate and on the relative accumulation rates of long-life organic matter in soils beneath different crops in addition. A comparison of the distribution in plant dry mass for a crop such as winter wheat during the period of exponential growth with that during the later constant growth rate period shows the marked fall in root:shoot

ratio (figure 3). However if the comparison is made using the active root:active shoot ratio then the change is insignificant between the two periods of crop growth. During the exponential growth period the leaves are in the sunlight and are all actively photosynthesizing, but during the constant rate period of crop growth the lower leaves in the canopy are shaded and primarily act as food stores. Hence it is evident that active root mass is roughly proportional to active shoot mass. The role of fertilizer as a means of increasing the concentration of nutrients in the soil solution may be postulated by an extension of the above concept. It is not solely to enable crop growth to continue when soil reserves of nutrient run out but also to boost growth rate at a much earlier period in the crop's history by increasing the shoot:root ratio. Less roots are required to absorb nutrients when this is more available and in consequence more leaves are deployed to intercept light per unit plant mass. The process of vegetative development is equally a method by which a plant is enabled to deploy its mass more effectively as it grows in intercepting both light and soil nutrients. The growth of new leaves does not, in a direct manner, influence the conversion efficiency of light energy into dry crop mass. Rather vegetative development of the plant structure mitigates the inevitable fall of light interception per unit plant mass as the plant grows caused by a falling surface:volume ratio, employing the universal technique of increasing convolution. Leaves are increased in number rather than just in size and roots similarly increase in number as well as length. A further consequence of the above concept of a law controlling the root:shoot ratio is the deduction that if roots are continuously destroyed by the attack of other soil dwelling organisms then, providing the destruction rate is not too rapid, the plant will devote more of its growth to root maintenance and less to shoot growth. Dead root matter should therefore accumulate at a greater rate in the soil than in the absence of such predatory organisms. Permanent grass, under which it has long been known that long-life organic matter accumulates at some two to three times the rate of that for a rotated crop is, I suggest, the chief example of this phenomenon (figure 4).

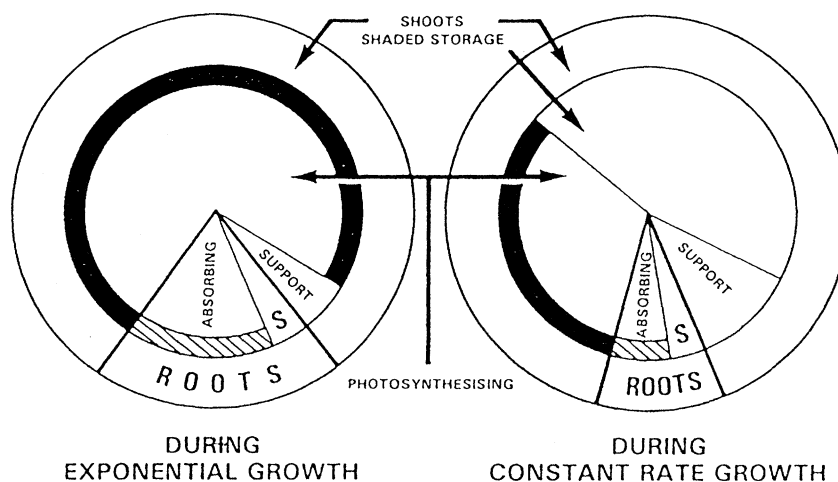


Figure 3. Typical distribution of dry mass for a wheat crop during exponential and constant rate growth periods.

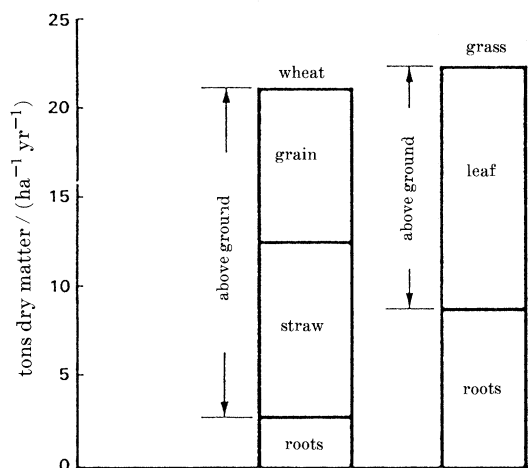


Figure 4. Comparative distribution of dry mass for a wheat crop and a cut permanent grass crop.

4. GRAIN, TUBERS AND THE PLANT

As the commercially valuable harvest is often only a fraction of the total plant mass, such as the grain or the tubers, it is necessary to construct a mathematical model in which this fraction can be estimated for the relevant crop growing under differing environmental conditions. The use of an empirical 'harvest index', the ratio of valuable product to total, usually, above ground plant mass merely begs the question of what determines this quantity. Modelling approaches for obtaining the harvest index fall into two types. Those that seek to estimate the yield, for instance of grain or other seeds by attempting to compute the number of inflorescences, pods and seeds in pods. This is essentially a photosynthate sink centred analysis. The

second type embraces those models that assume, with normal plant development, there are an over-supply of sinks and that the extent of filling of these sinks in total and the distribution of their filling is determined by the strength and content of the source of photosynthate, the plant and the relative strength of the sinks. My view is that the latter approach is both more likely to be in accordance with natural behaviour, it appears to fit the experimental data better with fewer empirical constants and is also simpler to employ.

An example of the elements of such a sink based analysis is to compare the growth of grain on the wheat plant with that of tubers on the potato plant (figure 5.). In a sink based analysis the plant and the grain or tuber are treated as separate but interacting organisms, the former supplying nutrients to the latter. The similarities and differences between the wheat and the potato are made clearer if the respective growths of the plants and of the grain and tubers are compared on a timebase by using the start of grain formation and of tuber initiation as the common zero. Before this zero both wheat plant and potato plant are steadily growing, a process that continues for *ca.* 15 days after initiation. By that time both grain and tuber have attained a high growth rate. Further accelerated growth of both grain and tubers occurs between 15 and 20 days accompanied by a cessation in growth of their respective plants. From 20–40 days the grain continues its rapid fill but the living fraction of the wheat plant equally rapidly shrinks. The tubers also continue to grow rapidly and this process lasts until day 60, though it is to be noted that the tubers only grow at roughly half the rate of the grain. Unlike the wheat plant the potato plant remains roughly at a constant size. Grain growth ceases after some 50 days coinciding with the death of

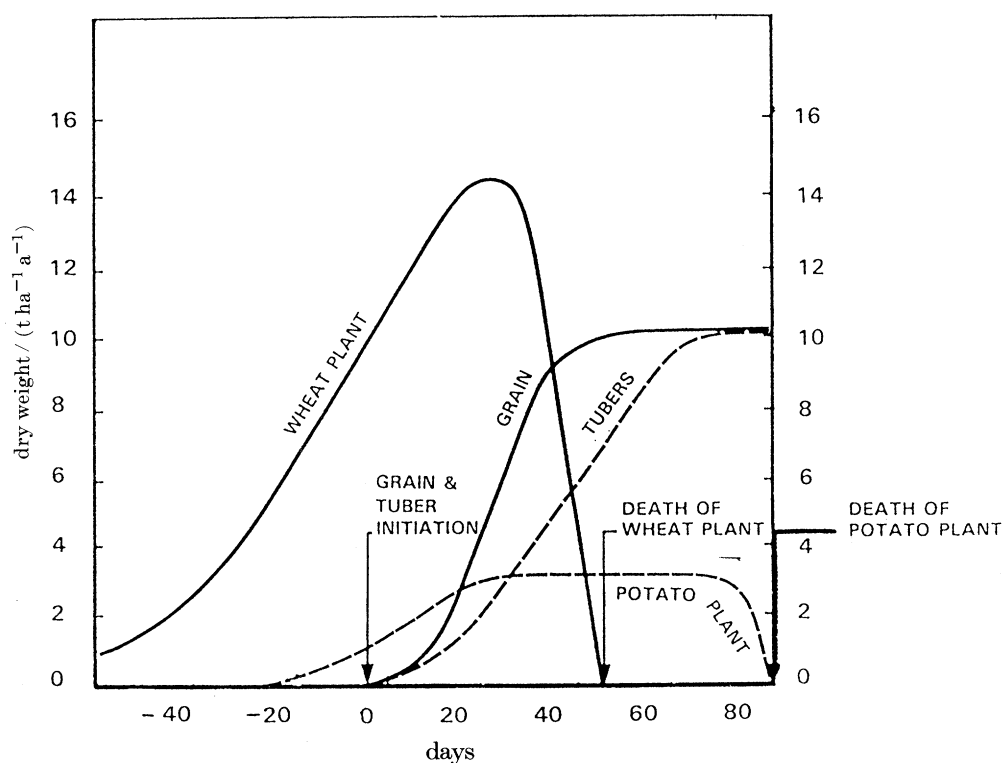


Figure 5. Comparative course of growth of wheat and potato.

the wheat plant while tuber growth ceases after about 80 days.

The slower maximum growth rate of the tubers compared with grain and the ability of the potato plant to maintain its mass throughout the period of tuber growth whereas the wheat plant shrinks and dies suggest that the tubers have a markedly lower strength of demand for photosynthate than the grain. Indeed it can be argued that the wheat plant respire to death, starved of its own fresh photosynthate by the growing grain. On this interpretation the harvest index of the wheat is a measure of the ratio of the remobilisable photosynthate store of the plant to its respiration rate. Short stalk varieties having a lower fraction of immobilizable mass and low temperatures during grain fill should therefore both lead to a higher harvest index. In the case of the potato the somewhat precarious balance between plant demand for maintenance and tuber demand for growth has to be held for as long as possible to obtain a high harvest index as tipping the balance against the plant by stressing it could lead to its premature death together with cessation of tuber growth.

5. CONCLUSIONS

This short paper is an attempt by a mathematical modeller to bring together some of the rather diverse strands that make up current crop growth models.

These strands have been brought together not at the detailed level of numerics but at the level of broad concepts as it must be at this level at which integration must first be achieved and conflict eliminated. One of the most significant strands yet to be unravelled, it appears to me, are the determinants of the vegetative development process. Although it seems clear how these stages affect the ability of a crop to intercept light, correlations of the timing of these stages is currently entirely empirical and, for justification, supposes the existence of a set of as yet unknown chemical clocks. Though the existence of chemical triggers produced as a result of phenomena occurring over a span of days is proven in connection with the initiation of flowering and tuber initiation, the application of Occam's Razor suggests to me that there is an excessive proliferation of hypothetical long running clocks in current modelling. In conclusion I make a plea for mathematical models to be used to tie together diversity of phenomena and of behaviour by their being founded on unifying principles. In the absence of such an approach diversity is the enemy of understanding.

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