

## Opportunities for improving crop yields through research - a physiological perspective

D.J. Chalmers

Department of Horticultural Science, Massey University  
Palmerston North, New Zealand

### Introduction

Plant functions above the ground, including growth of the plant parts of interest to the farmer, are limited by the extent to which the root system can supply healthy amounts of inorganic nutrients and water. Clearly the root environment (rhizosphere) yields these materials with widely varying "generosity" but in Australian temperate agriculture there are few farming environments that yield them as readily as the sun and the air yield light and CO<sub>2</sub>. Consequently for crops where vegetative growth is necessary to (a) provide the harvested material (e.g. forage) or (b) to occupy the space with leaves in order to intercept light energy to grow the crop; at times the plant will need to increase the size of its root system to meet the demand for resources from the soil. It follows that the faster we want the crop to grow, the faster the root system will need to grow to meet those requirements. One might argue that perennial crops have established root systems that do not need to extend. Further, other root systems may adjust root activity to meet increased demand or particular environmental conditions. Consequently a precise relation between root and top dimensions may not be required.

Nevertheless, one accepts there is a limiting root dimension, smaller than which a root system could not provide sufficient nutrients and/or water to maintain the plant. Such a root system must extend to permit further growth above the ground. The question is whether the association between root and top dimensions is approximate or specific or alternatively to what extent the root adapts to, or compensates for its environment. If the relationship is approximate and the roots do indeed adjust and compensate much could be accomplished by understanding the nature of that adjustment. If the relationship is precise and specific, however, it is axiomatic that in farming situations where production does not reach the potential indicated by water availability, it is limited by the potential for root growth.

### The Relation between Root Growth and Top Growth

Plants do not usually maintain a constant ratio between the size or weight of the top and the size of the root system. In most plants the top:root ratio increases or decreases as the plant grows. Environmental factors such as light intensity, nutrition (1) and temperature differentials between roots and shoots (2) affect top:root ratio.

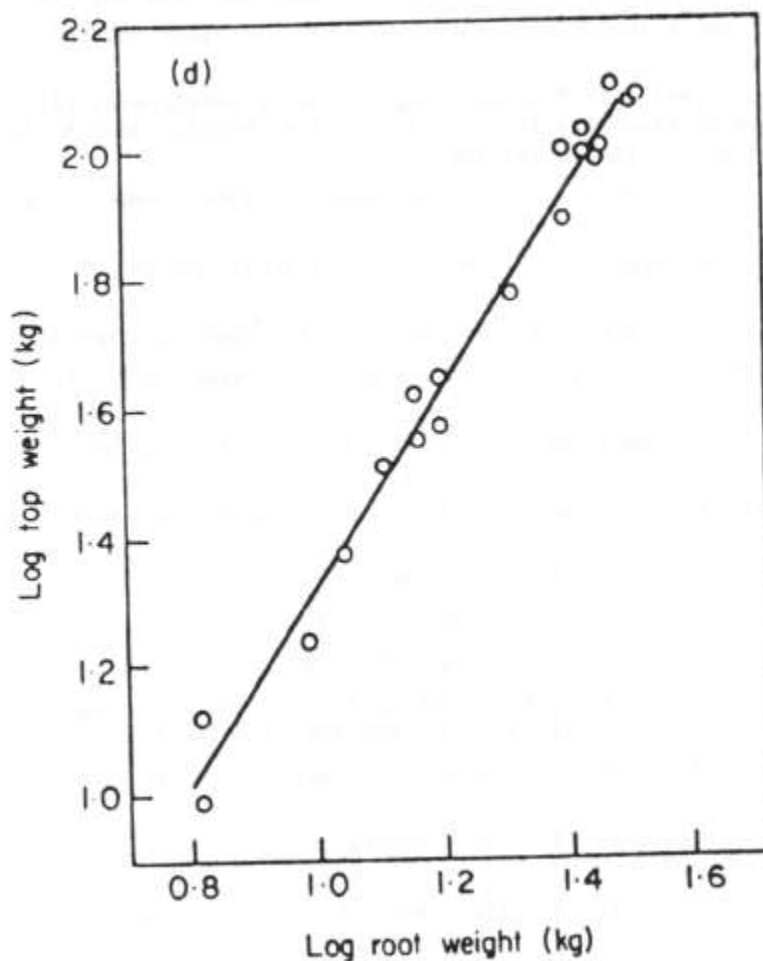
Nevertheless these data and conclusions can be misleading. A strong linear relation is found between the log the weight of the top of a plant and the log of the weight of the root system. This relationship appears to hold for vegetative growth of a wide range of plants including peach trees (3,4) loblolly pine (5) rye grass (6), turnip, carrot, pea and cotton (7). This has been described as an allometric relationship and has been interpreted to mean that a physiological relationship binds the relative growth rate (RGR) of the root system to the RGR of the top of the plant. That is, the potential yield of a crop is related to the RGR of the root system because the top of the plant cannot grow at a rate that is faster than the maximum rate that the root system can manage in that environment. If this is so we can define much more precisely experimental systems which will allow us to study the productivity of any crop in a way which will allow us to determine how yield is limited in the environment of interest.

The most impressive aspect of allometric data is the extent to which the relationship  
 $\log W_s = \log b + k \log W_r$

where  $W_s$  is the weight of vegetative material above the ground, and  $W_r$  is the weight of roots, accounts for experimental variation observed. To illustrate, the relationship between log top weight and log root weight in Fig. 1 was obtained in a study of peach trees varying in age from 3 to 15 years (3). Although

management during the year of study was constant for all trees, there would doubtless have been many changes (of detail) in soil management, fertilizer application, pruning and cropping level during their growth. Further the populations of peach trees included trees with and without fruit which was shown to markedly alter partitioning of photoassimilate (3). Under these circumstances the relationship reported between  $\log W_t$  and  $\log W_r$  is remarkable for its strength and linearity. Comprehensive studies of vegetatively active plants (e.g. 8) report similar results prompting the conclusion that for a particular environment the RGR of the root system of vascular plants limits the potential for vegetative growth above the ground. There are many related conclusions which flow from this basic point of knowledge. Clearly plant size above the ground is a function of root size beneath the ground and finally, agronomic and horticultural productivity is related to the potential for root growth. Between these conceptual milestones, however, lies a neglected, virgin field of research opportunity and achievable progress.

**Fig. 1. The relation between the logarithm of tree top dry weight and the logarithm of tree root dry weight of peach trees between 3 and 15 years of age.**



### The Effect of Top Root Ratio

The slope  $k$  quantifies the relationship between the RGR's of the top and the roots. When the slope is greater than one the top:root ratio increases as the plant grows in that environment. For slopes less than one the top:root ratio decreases with growth. The value of  $k$  changes with environment for a given plant and this fact has adaptive and evolutionary significance. Above the ground as light and or  $CO_2$  become limiting the top:root ratio or the value of  $k$  increases and thereby the balance between the amount of plant

above and below the ground alters to suit the limiting variable in the new environment. Similarly, when a factor in the root zone, such as water or nutrients are limiting, the value of  $k$  or the top:root ratio decreases to compensate, thereby enabling the plant to bring supply of factors from the root system into balance with what can be produced by the tops (e.g. 1). These adjustments occur, however, at the cost of decreased overall growth and yield.

Changes in top:root ratio do not occur spontaneously or rapidly. The top: root ratio maintains a functional balance for a given environment and stage of development. Further, the properties of the rhizosphere and the regulatory process itself largely preclude rapid adjustment by the plant to short term changes in the environment or the top:root ratio. For example, a number of studies have observed that for a given root environment and plant size the plant maintains a constant top:root ratio. In a root pruning and defoliation experiment for example, overall growth was reduced but compensatory growth by the reduced portion of the plant restored the original top:root ratio rapidly (9). In natural systems also, episodic growth by the tops was followed by a compensating flush of growth by the roots and vice versa (5) to maintain the allometric relation between them over time. These data show that the control mechanisms are not necessarily co-ordinated in time, and individual growth events may even be inversely correlated. Considering that growth by roots and top appears to be complementary rather than co-ordinated, the constancy of the allometric relationship over time (e.g. from one season to the next) is striking and speaks for a quantitative perhaps stoichiometric link between so far undefined products of growth by the root system and subsequent, resultant shoot growth above the ground. In short the only way that the root can adapt to an increasingly hostile root environment is to decrease its top:root ratio which means to grow more root. In experimental systems this only occurs slowly at a decreased level of productivity. Down on the farm, however, in your average Australian soil, it frequently cannot happen at all, because in such an environment, for example when soil water or nutrients are depleting, additional root growth is often prevented by developing factors in the rhizosphere.

The importance of the balance between root and top size can be illustrated by the effect of N nutrition on the top:root ratio and the consequences for overall productivity and optimum exploitation of the soil resources by the root. Increased N levels in the presence of adequate water stimulates vegetative growth and overall productivity of *Lolium perenne* (6) but decreases the top:root ratio. That is, the improved root environment with respect to N increased overall productivity and the vegetative growth rate but the increased top:root ratio will render the plant less able to adapt to declining water availability because it taps a relatively smaller root volume.

### **Possible growth regulators produced by growth of the roots and tops**

There have been numerous hypotheses advanced to account for the regulatory mechanism involved in allometric growth. Most propose feedback control by cytokinins and/or gibberellins from growing regions in the root system (e.g. 10, 11, 12) and auxins from apices of the shoots. Richards and Rowe (12) have provided good evidence supporting involvement of cytokinin from roots in shoot growth. In their experiments shoot growth of young peach seedlings was inhibited when root growth was inhibited by physically limiting the volume available for root growth. Growth of the shoots was restored and the top:root ratio rapidly increased when the leaves were sprayed with a solution of benzyl aminopurine (BAP). Growth regulator sprays (often gibberellin) have been used to induce vegetative growth in many experiments but in this experiment BAP separated growth by the roots from vegetative growth events elsewhere in the plant which strongly indicates cytokinins are involved in that mechanism. In related studies (8, 13) the number of roots and thereby the number of growing root tips were linearly related to leaf area in peaches and tomatoes. These data also support the above hypothesis given the frequently proposed association between cytokinin synthesis and the growing root apex. At the shoot end of the allometric mechanism in vegetative plants we know that IAA is required for root initiation and growth, as demonstrated by the auxin requirement for root formation by undifferentiated callus and many other relevant studies. Thus we know with reasonable certainty the identity of two of the chemicals responsible for reciprocal control of growth by root systems and vegetative shoots, but little about other chemicals that may be involved, and nothing about the way they act. As long as this is all we understand about the mechanism regulating allometric growth, one of the most important research opportunities in the field of plant productivity goes begging.

## Effect of allometric growth on assimilate partitioning and crop yield

In the growth analysis of peach trees reported earlier Chalmers and van den Ende (3) studied assimilate partitioning during the growing season and in relation to tree age or size.

Top:root ratio declined as trees grew and their potential for vegetative vigour declined as a consequence. As a result, the proportion of the seasonal increment of dry weight allocated to vegetative growth declined from around 70% of the annual total in a growing and cropping 3 year old tree to 30% in a mature tree.

The sink potential of individual peach fruit appears to be controlled by factors within the fruit (14,15); and appears to be a constant potential (per fruit) regardless of tree size or age (16). Consequently, we can conclude that the increase in photo assimilate distribution towards fruit growth that occurred during the period peach trees aged, was due to the decrease in the competitive sink potential of vegetative growth (rather than an increase in fruit sink potential). Moreover, one could speculate with some confidence that the declining top:root ratio resulted in an increasingly unfavourable balance between roots and top which was responsible for the declining sink potential of vegetative growth.

Therefore, for any fruiting crop, where the value of  $K$  for a given environment is greater than 1 (that is top:root ratio decreases with growth) productivity measured by the harvest index, will increase with plant age, size or growth. Of course the corollary of that conclusion is that after the allocated space has been fully occupied, treatments or environments that reduce the potential for root growth will increase productivity. These conclusions predict effects of rootstocks, root restriction(8) and regulated deficit irrigation (17) all of which reduce root growth or volume, reduce vegetative growth but increase productivity by increasing the harvest index. They also predict, however, that with good soil management (e.g. 18) fruit crop productivity, particularly as measured by harvest index and precocity will be higher rather than lower on shallow and physically restricting soils.

The yield of seed crops will be similarly affected by root growth and top:root ratio. Major differences between annual seed crops and perennial fruit crops however, are that they are annual and determinate. Consequently, an extended period of vegetative growth is required first to fill the space to obtain maximum light interception. Growth during this period is a key determinant of grain yield and it is significant that crops that are not capable of rapid growth during the vegetative phase do not appear to be able to provide a high grain yield. Nevertheless with respect to developing management systems to maximise yield of grain crops, it is noteworthy that virtually all yield improvements obtained from breeding grain crops has come from improving the harvest index (19,20). That is, plant breeders so far have been unable to modify the allometric relation between roots and shoots.

The change from the vegetative phase to the cropping phase (where crop growth requires a high proportion of current photoassimilate) is accompanied by a large change in the value of  $k$ . For example, in fruiting tomato plants Richards (4) found  $k$  increased from 1.02 to 1.85 after fruit growth became a significant proportion of total growth. Richards, however, demonstrated, as Chalmers and van den Ende (3) found with peach trees, that if fruit growth was eliminated from the calculation that the allometric relation between roots and vegetative growth was preserved unaltered. Pasture and hay grasses also show a change in the value of  $k$  when inflorescences are emerging (6) if the event is well coordinated amongst the population of tillers being studied. These latter observations, however, were not supported by a plant component analysis which would have established whether the change in  $k$  caused, or resulted in, a change in partitioning priorities within the plant as occurs with peach and tomato.

Nevertheless the foregoing data is best accounted for by assuming that the allometric relation is confined to the association between root growth and vegetative forms of growth above the ground. The increase in the value of  $k$  reflects the breaking of the nexus between growth of above ground parts and the roots, and highlights the fact that root growth is not a prerequisite for growth by the non vegetative organs.

Furthermore the data clearly indicate in what crops and conditions, root growth will and will not be required to increase the yield of the harvested crop. Sink strength of non vegetative organs such as fruit and seeds to a large extent may be controlled by mechanisms originating within the organ (16). This

competitive potential on a whole plant basis is a function of seed or fruit number and independent plant size or age. On the other hand, competitive potential generated by vegetative growth is linked to the growth rate and the relative size of the root system. As the growth rate of the root system declines as the top:root ratio increases, growth by the fruit or seed would be favoured by decreasing competition from vegetative growth.

### **Possible role of root growth in the source-sink controversy**

Plants with fruit accumulate dry weight more rapidly than non-fruiting plants. In the 1920's Chandler and Heinecke (21,22) showed that grape vines and apple trees bearing fruit accumulated 40-80%, more dry weight over a 5-10 year period than plants that had not been permitted to crop. More recently, non-vegetative sinks have frequently been found to increase rates of photosynthesis. Nevertheless, although feedback inhibition of photosynthesis which these data indicate, is now generally accepted to occur, the data remains equivocal (25). For example, in a similar study with peach trees to that carried out by Chalmers et al (26) at Tatura, Victoria De Jogn and Doyle (27) at Davis, California, were unable to show that the presence or growth stage of fruit affected the rates of photosynthesis. Soil conditions, peach root distribution, root growth and consequent tree vigour, however, are demonstrably superior at Davis compared to Tatura (cf 28, 29 and 30). Under the conditions at Davis, peach shoot growth may not be limited by the allometric constraint imposed by poor root environment and potential for total photosynthesis may not be enhanced when fruit growth relieves the plant of that soil restraint. Similar reasoning could be applied to other results where sink effects have not been detected. Clearly experimental conditions will often (by design) have a non-limiting root environment. Sink effects would not be detected in those instances if the above hypothesis is correct. On the other hand, in agriculture we know that the rhizosphere is far from ideal. Consequently it is very likely that sink strength often limits agronomic productivity.

### **The link between root size and function**

It is tempting to interpret the link between the RGR of roots and vegetative growth in terms of the function of supplying essential nutrients and water from the soil to the top of the plant. In other words root size and top: root ratio may adjust in order to keep the capacity of the root system in balance with the functions of the above ground parts. It has been shown quite unequivocally, however, (1,13) that root functions such as nutrient and even water uptake are related to the growth increment and can be independent of root dimensions. For example in experiments where high and low N and light levels have been used to vary top:root ratio (1) the root activity with respect to uptake of K was a function of the total dry weight increment for that treatment.

Potassium uptake was not related to root size or weight and varied almost 10 fold per unit root weight between the extremes of growth treatments. Similarly the activity of peach roots for uptake of macro nutrients (N + P + K + Ca + Mg) was found to be linearly related to the dry weight increment of the plant and independent of root size (13). In the latter experiments also, treatments had resulted in widely varying top:root ratio which meant that root activity varied up to 5 fold per unit root weight. After accounting for variations in the vapour pressure deficit due to environmental effects, water use by plants is proportional to growth and in the above experiments was also shown to be independent of root size.

It is clear, therefore, that plant roots can readily adjust function to meet demand for nutrients and water for growth by other organs. Nevertheless, growth by the roots is strongly linked to growth by the shoots or top. This apparent contradiction can be explained by assuming that the rhizosphere was adequate for supply of the measured nutrients and/or water from the root environment provided by the experimental conditions. In contrast, in the same experimental conditions reported above, since ryegrass root dimensions were affected by N treatments, the rhizosphere and therefore the root system had become limiting with respect to N uptake. In the study of peach root function root growth was prevented by a physical barrier which according to Richards and Rowe (12) inhibited root initiation, thereby resulting in an experimental system in which top growth was limited by cytokinin. When cytokinin was applied to the leaves, growth and root function with respect to nutrients and water uptake were restored.

One needs to consider in what ways these experimental systems are relevant to the agronomic rhizosphere. First, the agronomic rhizosphere is often unable to supply minerals or water at non-limiting rates. Thus a soil may bind essential nutrients, have a highly buffered unsuitable pH, may leach severely or may have physical deficiencies that prevent plants from using water that would otherwise be available from the environment. The specific mechanism of deficiency in each instance may be well understood but agronomic production cannot be increased (at an economic cost) by simply adding or overcoming the deficient component. Secondly the roots of agronomic plants and the rhizosphere interact dynamically as the plant grows. Stored water and nutrients are depleted and become deficient. In temperate agronomic situations in Australia the root system is often functioning at the margin of deficiency. Consequently in most agricultural situations during the growing season roots have little or no capacity to adapt to better exploit the rhizosphere except by growing and extending the rhizosphere. On the other hand, the capacity of the root to vary uptake of water and nutrients in relation to need may be extremely relevant for intensive agricultural or horticultural crops where water and nutrients are in full control.

## Conclusions

There is a precise and specific relation between growth by the roots and vegetative growth by the top of a plant.

Top:root ratio does not remain constant. In non-root crops the ratio usually increases with growth or plant age and/or favourable rhizosphere conditions. It decreases when conditions in the rhizosphere deteriorate. This adjustment, however, is slow and occurs at a lower overall level of productivity.

The root system has considerable capacity to adapt or vary essential functions such as nutrient and water uptake to meet demands for growth. Roots must grow, however, to adapt to most temperate agronomic situations because the rhizosphere is depleted or depleting with respect of water and essential nutrients.

Auxins, cytokins and probably gibberellins are key regulators of the allometric relation between roots and tops but little is known about how they act or what other chemicals may be involved.

Growth by non-vegetative organs such as seed and fruit are not affected by the allometry of vegetative growth. Fruits and seeds therefore grow independently of direct effects of the rhizosphere on root growth but compete with the resultant vegetative sink potential. Assimilate partitioning between crop and non-crop plant components and the harvest index are largely determined by this dichotomy between mechanisms of growth regulation.

While there has been increased interest in the rhizosphere and root function, knowledge still lags far behind what is known about other aspects of agronomy and physiology. In a recent symposium on crop productivity (31) the rhizosphere was accorded appropriate emphasis but like so much other research on soil and root function it largely ignored root growth per se. This paper establishes unequivocally that root growth is a prerequisite for agronomic productivity where the crop is vegetative material. For annual grain crops root growth is necessary to enable plants to grow a canopy that can make optimum use of space and incident radiation. Given the established shortcomings of rhizosphere conditions on farms in temperate areas of Australia, it is safe to conclude that the potential for root growth is the limiting factor in many if not most situations where optimum productivity is not achieved.

It follows therefore, that where vegetative growth is concerned, research workers should be studying and assessing mechanisms, treatment effects, breeding, selection, adaptation, and so on in terms of what happens to root growth. There is no point in intercepting 100% of incident radiation if it cannot be converted into growth. Equally there is no point in amending or improving the soil if roots do not grow into it to exploit its additional resources of water and/or nutrients. Where vegetative growth is the issue, treatments, cultivars or management systems that do not meet the root growth criteria will be a failure. On the other hand, when the interest is in growth of non-vegetative parts of the plant, root function and the factors that affect it should be examined. These issues will be important during grain filling and fruit growth in horticultural crops especially where they can be grown intensively using irrigation.

1. Hunt, R. 1975. *Ann. Bot.* 39, 745-755.
2. Davidson, R.L. 1969. *Ann. Bot.* 33, 561-569.
3. Chalmers, D.J. and van den Ende, B. 1975 *Ann. Bot.* 39, 423-432.
4. Richards, D. 1981. In *Structure and function of plant roots*, eds R. Brouwer et al. Martinus Nijhoff/Dr. W. Junk Publishers. The Hague, pp 373-380.
5. Drew, A.P. and Ledig, F.T. 1980. *Ann. Bot.* 45, 143-148.
6. Troughton, A. 1956. *J. Brit. Grasslands Soc.* 11, 56-65.
7. Pearsall, W.H. 1927. *Ann. Bot. Lond.* 163, 549-556.
8. Richards, D. 1986. *Acta Horticulturae*, 175, 27-36.
9. Brouwer, R. 1963. *Jaarb I.B.S. (Wageningen)* 11, 31-39.
10. Wareing, P.F. (1970). In *"Physiology of tree crops"*. Eds. L.C. Luckwill and C.V. Cutting. Academic Press London and New York pp 1-21.
11. Sachs, T. 1972. *J. theor Bio.* 37, 353- 361.
12. Richards, D. and Rowe, R.N. 1977. *Ann. Bot.* 41, 729-740.
13. Richards, D. and Rowe, R.N. 1977. *Ann. Bot.* 41, 1211-1216.
14. Chalmers, D.J. and van den Ende, B. 1977. *Ann. Bot.* 41, 707-714.
15. Jerie, P.H. and Chalmers, D.J. 1976. *Austral. J. Plant Physiol.* 3, 429-434.
16. Chalmers, D.J. 1985. In *"Hormonal regulation of development III"* *Encyclopaedia of Plant Physiol.* Vol 11 Eds R.P. Pharos and D.M. Reid Springer Verlag, Berlin pp 169-192.
17. Chalmers, D.J., Mitchell, P.D. and van Heek, L. 1981. *Amer. J. Hort Soc.* 106, 307-312.
18. Olsson, K.A. and Cockcroft, B. 1980. *proc. Austral. Agron. Soc.* 1, 30-39.
19. Sims, H.T. 1963. *Austral. J. Exp. Agric. Anim. Husb.* 3, 198-202.
20. Evans, L.T. and Dunstone, R.S. 1970. *Austral. J. Biol. Sci.* 23, 245-254.
21. Chandler, W.H. and Heinecke, A.J. 1925. *Proc. Amer. Soc. Hort. Sci.* 22, 74-80.
22. Chandler, W.H. and Heinecke, A.J. 1926. *Proc. Amer. Soc. Hort. Sci.* 23, 36-46.
23. Hansen, P. 1970. *Physiol. Plant.* 23, 805-810.
24. Maggs, D.H. 1963. *J. Hort. Sci.* 38, 119-128.
25. Geiger, D.R. 1976. *Can. J. Bot.* 54, 2337-2345.
26. Chalmers, D.J., Canterford, R.L., Jerie, P.H., Jones, T.R. and Ugalde, T.D. 1975. *Austral. J. Plant Physiol.* 2, 635-645.

27. De Jong, T.M. and Doyle, J.F. (1984). J. Amer. Soc. Hort. Sci. 109, 878-882.
28. Richard, D. and Cockcroft, B. 1974. Austral. J. Exp. Agric. Anim. Husb. 14, 103-107.
29. Richard, D. and Cockcroft, B. 1975. Austral. J. Agric. Res. 26, 173-180.
30. Veihmeyer, F.J. and Hendrickson, A.H. 1938. Plant Physiol. 13, 169-177.
31. Paul, E.A., Bauer, W.D. and Tinker, P.B. In "Crop productivity Research imperatives revisited". Eds. M. Gibbs and C. Carlson. An international conference held at Boyne Highlands Inn, October 13-18, 1985 and Airlie House, December 11-13, 1985.