Neth. J. agric. Sci. 31 (1983) 287-289

Introduction to the theme

Marinus J. A. Werger

Department of Plant Ecology, University of Utrecht, Lange Nieuwstraat 106, 3512 PN Utrecht, Netherlands

Key-words: functional equilibrium, root/shoot ratio

It is general knowledge that the plant's root and shoot are at least partly complementary in function and are interdependent: the shoot needs the water and mineral nutrients absorbed by the root, while the root needs the carbohydrates produced in the shoot. Consideration of this interdependence, as well as some empirical evidence, led, already more than half a century ago, to the statement that the ratio of root mass to shoot mass remains constant for a specific plant of a certain age and under constant environmental conditions (Turner, 1922; Crist & Stout, 1929). With progressing age and, more importantly, a change in the plant's phenological state, the root/shoot ratio alters: it usually decreases (e.g. Brouwer,1962b; Troughton, 1978).

Brouwer (1962a, b, 1965), Troughton (1977a) and others also showed that after a sudden change in environmental conditions to a new stable situation, the plant reacts with a rapid change of its root/shoot ratio to a new stable ratio, apparently attuned to the new situation. In brief, experimental evidence has shown that in most cases the plant's root/shoot ratio shows the following correlation to environmental conditions (see e.g. Brouwer, 1962a, b; Troughton, 1977b; Schulze, 1982 for references): root/shoot ratios generally increase with increasing deficiency of nitrogen; within limits, root/shoot ratios also increase with reduced water supply in soils which are not permanently moist, with increase of light intensity and length of photoperiod in the shoot's environment, and if temperatures in the root zone are below or above the optimal temperature for root-functioning. Under conditions of increased oxygen supply in the root zone, root/shoot ratios also tend to increase. However, for some of these environmental factors (e.g. oxygen supply, length of photoperiod, temperature) there are also some observations to the contrary (see the same sources for references).

To explain the observations on an apparent regulation of root/shoot ratios a number of hypotheses have been put forward, which were recently summarized very ably by Troughton (1977b). These hypotheses mainly start from the idea, already mentioned above, that root and shoot are interdependent, and that both parts must maintain a minimum supply towards each other as otherwise at least part of the plant will die. Thus, under conditions of growth there should be a homeostatic mechanism to preserve a constant relationship between root and shoot. This relationship was termed 'functional equilibrium' by Brouwer (1962b).

According to this theory the relationship is maintained by what can be understood as a sort of competition between root and shoot for water and minerals at the one hand, and carbohydrates at the other. That organ that is nearest to the source of supply will be served first when the supply is limited and thus can maintain its growth at a higher rate resulting in a relatively higher mass value. Thus, carbohydrates more often limit root growth than shoot growth, and consequently, treatments that cause an increase of carbohydrate supply, either through increased photosynthesis output, or through a reduction of the utilization of carbohydrates in the shoots themselves, are likely to augment root growth. Similarly, supply levels of minerals and water are more often limiting for shoot growth than for root growth, and consequently a stimulated uptake of minerals and water is likely to result in a relative increase in shoot growth. In this way relative mass increase in each organ is controlled by the supply from the other organ (Brouwer, 1962b; Loomis, 1953; Troughton, 1977b).

Several slight variations on this basic hypothesis have been proposed by Troughton (1977b), together with a more strongly deviating hypothesis, which states that not the supply with carbohydrates by the shoot is limiting root growth, but the root's ability to utilize the carbohydrates supplied.

Apart from this diversity of ideas on the nature of the relationship that attunes root and shoot growth, quantitative knowledge on the processes operational in maintaining such a relationship is very limited (see Wareing & Patrick, 1975 for a brief review).

The following five papers discuss various aspects of the root/shoot problem as introduced here. The first paper deals with the ecological side, emphasizing the importance of the plant's carbon balance in determining and maintaining characteristic root/shoot ratios in different life forms and in different habitats. It discusses the carbon balance with reference to maximal growth and the plant's water and nutrient demand, and deals with the ecological implications of evergreen and deciduous foliage in various life forms.

The second paper deals with the way in which a functional equilibrium between root and shoot may be regulated. It is suggested that this regulation is effected in a more complicated way than simply by limitation of carbohydrate or nutrient supply, respectively.

The third paper discusses how dynamic simulation models of plant and crop growth based on the state-variable approach are constructed. It is argued that there is no need for exact knowledge on the plant's hormonal status to construct dynamic simulation models: not the exact nature of the regulating system between root and shoot needs to be revealed to construct such a model, but the exact level at which the various organs operate in direct response to exogenous (environmental) variables at any moment should be known.

Additionally, the fourth paper describes in detail the results of a series of experiments on the genetically determined differences in root growth at various nitrogen levels and its significance for the competitive ability of the population.

In the final paper Brouwer gives a reappraisal of the concept of a functional equilibrium between root and shoot.

Together these five papers provide an in-depth discussion on the functional equilibrium between root and shoot from various points of view. In this they significantly contribute to an integration of our knowledge on various aspects of this problem, though the contributions in this bundle of essays make it clear that the problem as yet is far from being solved.

References

Brouwer, R., 1962a. Distribution of dry matter in the plant, *Neth. J. agric. Sci.* 10: 361-376.

Brouwer, R., 1962b. Nutritive influences on the distribution of dry matter in the plant. *Neth. J. agric. Sci.* 10: 399-408.

Brouwer, R., 1965. Root growth of grasses and cereals. In: The growth of cereals and grasses. University of Nottingham, pp. 153-166.

Crist, J. W. & G. J. Stout, 1929. Relation between top and root size in herbaceous plants. *Plant Physiol.* 4: 63-85.

Loomis, W. E., 1953. Growth and differentiation of plants. Iowa State College Press, Ames, Iowa.

Schulze, E. D., 1982. Plant life forms and their carbon, water and nutrient relations. Encyclopaedia Plant Physiology N.S. Vol. 12b, pp. 615-676. Springer Verlag, Berlin, Heidelberg, New York.

Troughton, A., 1977a. The rate of growth and partitioning of assimilates in young grass plants: a mathematical model. *Ann. Bot.* 41: 553-565.

Troughton, A., 1977b. Relationship between the root and shoot systems of grasses. In: J. K. Marshall (Ed.), The belowground ecosystem. Range Sc. Dept. Sc. Ser. No. 26: 39-51. Colorado State University, Fort Collins.

Troughton, A., 1978. The influence of reproductive development upon the root system of perennial ryegrass and some effects upon herbage production. J. agric. Sci., Camb. 91: 427-431.

Turner, J. W., 1922. Studies on the mechanism of the physiological effects of certain mineral salts in altering the ratio of top growth to root growth in seed plants. *Am. J. Bot.* 9: 415-445.

Wareing, P. F. & J. Patrick, 1975. Source-sink relations and the partition of assimilates in the plant. In: J. P. Cooper (Ed.), Photosynthesis and productivity in different environments. IBP 3: 481-499. Cambridge University Press.