

Quantitative Studies in the Physiology  
of Plant Growth

Being the published work submitted for the  
Degree of Doctor of Science in the  
University of Adelaide

by

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THE PAPERS

1. "Physiological ontogeny in plants and its relation to nutrition.  
2. The effect of phosphorus supply on the growth of the plant and its parts." Australian Journal of Experimental Biology and Medical Science, 14, 165-85, 1936.
2. "Physiological ontogeny in plants and its relation to nutrition.  
4. The effect of phosphorus supply on the total-, protein-, and soluble-nitrogen contents, and water content of the leaves and other plant parts." Ibid., 16, 65-83, 1938.
3. "Physiological ontogeny in plants and its relation to nutrition.  
5. The effect of nitrogen and phosphorus supplies on the respiration rate of the leaves." Ibid., 16, 347-60, 1938 (with A.H.K. Petrie).
4. "Physiological ontogeny in plants and its relation to nutrition.  
6. Analysis of the unit leaf rate." Ibid., 17, 123-32, 1939.
5. "The effects of phosphorus supply on the rates of intake of phosphorus and nitrogen and upon certain aspects of phosphorus metabolism in gramineous plants." Australian Journal of Scientific Research, Series B, 1, 333-61, 1948.
6. "The physiology of plant growth with special reference to the concept of net assimilation rate." Annals of Botany, N.S. 10, 41-72, 1946.
7. "Redistribution of mineral elements during development." Annual Review of Plant Physiology, 6, 25-42, 1955.
8. "Studies in soil fertility with special reference to organic manures. 2. Plant growth and nutrition in the field." Australian Journal of Agricultural Research, 5, 198-223, 1954.
9. "Studies in soil fertility with special reference to organic manures. 3. Residual effects of the organic matter." Ibid., 5, 224-34, 1954 (with K. Spencer).
10. "Studies in citrus nutrition. 1. Leaf growth and composition." Ibid., 7, 1956 (with C.T. Gates).

11. "An analysis of the effect of phosphorus supply on transpiration ratio in plants." Australian Journal of Experimental Biology and Medical Science, 13, 49-66, 1935.
12. "Studies of the flax plant. 2. The effect of artificial drought on growth and oil production in a linseed variety." Ibid., 21, 201-9, 1943 (with N.S. Tiver).
13. "A comparative study of growth and nutrition in barley and rye as affected by low-water treatment." Australian Journal of Biological Sciences, 8, 435-66, 1955 (with R.E. Shapter).
14. "Determination of the permanent wilting percentage of soils." Journal of the Australian Institute of Agricultural Science, 8, 109-11, 1942 (with T.J. Marshall).
15. "The estimation of nucleic-acid phosphorus in plant material." Australian Journal of Experimental Biology and Medical Science, 23, 213-19, 1945.
16. "Improving the accuracy of growth indices by the use of ratings." Australian Journal of Scientific Research, Series B, 2, 319-45, 1949 (with G.A. McIntyre).
17. "Estimation of leaf area for agronomic and plant physiological studies." Australian Journal of Agricultural Research, 5, 235-46, 1954.

## Comments on the Papers

The papers submitted herewith, except where indicated to the contrary, are based on original experimental work which was designed, conducted, and interpreted by the candidate. Seven of the seventeen papers were published with others. In four of the seven (Nos. 9, 10, 12, and 13), the candidate was the senior worker, and was responsible for the interpretation of the data and the writing of the papers.

The papers fall into four groups:

- I. Numbers 1-7 are concerned with plant growth and nutrition.
- II. Numbers 8-10 are applications to field problems.
- III. Numbers 11-13 deal with plant-water relations, though basically they too are growth studies.
- IV. Numbers 14-17 describe techniques which were developed or modified for the furtherance of the growth studies.

### I. Plant Growth and Nutrition

The first three papers describe experimental work done under the guidance of the late Dr. A.H.K. Petrie at the Waite Institute. Some of this data, particularly that of the first paper, was used as the basis of a thesis submitted for the degree of Master of Science in the University of Adelaide. The published papers followed from a more mature assessment of the implications of the work, and are included in support of the candidature.

In the fourth paper the candidate proposed a new basis for the expression of net assimilation rates, and drew attention to the approximate nature of the formula in general use for computing such rates.

Papers five, six, and seven are major items of the thesis, the sixth being widely recognised by British plant physiologists as a critical evaluation of the concept of net assimilation rate.

The fifth paper includes further results from the growth experiments of papers one to three. These results did not appear in the Master's thesis. The paper includes much descriptive material which is entirely new, and it attempts an integration of the factors which determine the rates of intake of phosphorus and nitrogen by the growing plant, and the redistribution of phosphorus within the plant. For phosphorus-deficient seedlings it was

shown that the transition from dependence on seed-reserve phosphorus to that in the medium was critical for seedling establishment, and this study provided an explanation of the well-known effect of phosphorus nutrition on the balance between root and shoot growth in plants. There is little doubt that it was this paper that prompted the editors of the Annual Review of Plant Physiology to solicit the review article (paper 7) on the redistribution of mineral elements during development. This review draws very considerably on the second and fifth papers for evidence and ideas.

## II. Applications to field problems

Papers eight and nine are the second and third of a series of papers describing a crop physiological study of a problem in soil fertility. The first paper, by K. Spencer alone, is included for the information of the examiners and not in support of the candidature. Soil fertility problems have rarely been approached in this way and never with such detailed attention to the quantitative evaluation of crop response and nutrient intake. The work has progressed from field trials through numerous pot culture experiments to studies in soil chemistry and microbiology, and promise to throw considerable light on the obscure but important problem of phosphate release by organic matter in soil.

The tenth paper, also a study in crop physiology, establishes phosphorus deficiency as a significant problem for the citrus industry, and has led, in a subsequent paper by D. Bouma of Griffith\* to the establishment in the field of the relation between phosphorus nutrition and fruit quality.

## III. Plant-water relations

The three papers on plant-water relations (11-13) appear widely spaced in time. The first attempts a physiological analysis of the agronomic concept of transpiration ratio. This concept has since fallen into disrepute, even among agronomists, but it is felt that the paper served a useful purpose in drawing attention to the complex and rather arbitrary character of that concept.

Paper twelve records a war-time study of the effects of dry finishing condition on the production of oil in a linseed variety of flax.

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\* (Australian Journal of Agricultural Research, 7, No.4)

The thirteenth paper supplies much new information on the effects of water stress on plant growth and nutrition.\* This study is basic to the current research programme of C.T. Gates at Griffith, N.S.W., whose work promises to be a major contribution to the study of plant-water relations.

#### IV. Techniques

Paper fourteen is relevant to the studies of plant-water relations.

The method of estimation of nucleic acid was developed at a time when biochemists were showing little interest in the quantitative estimation of this substance. The method was successfully applied in the fifth paper, and was adequate for the description of treatment effects during early stages of growth.

The statistical procedure described in the sixteenth paper made it possible to achieve a high degree of accuracy for the quantitative analysis of growth and a field-grown crop (see paper 8). G.A. McIntyre was responsible for the mathematical section of the paper (pp. 320-29) and for the theoretical comments elsewhere. The candidate was responsible for all the experimental work, and for that part of the presentation which seeks to make a difficult procedure comprehensible and therefore usable by other experimentalists.

The estimation of leaf area by the use of photographic standards (paper 17) is here given a precision which it formerly lacked. Evidence is also presented concerning the presence and extent of subjective bias in the use of the method. The method is entirely satisfactory as a rating procedure (papers 8 and 16), and leaf area data can be collected rapidly and without damage to the experimental plants.