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Report for 1971

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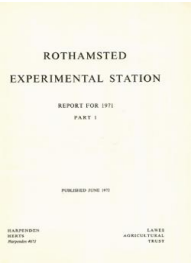
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Physics Department

H. L. Penman

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PHYSICS DEPARTMENT

H. L. PENMAN

Respiration. The physics of plant growth involves three kinds of interlocking balances: in mass, in energy, and in water. The first, as growth, is very much an out-of-balance of two opposing processes of assimilation and respiration, and much of the department's work is concerned with the physics and plant physiology of carbon dioxide movement to the crop, into the leaves and thence to the seats of fixation, and with movements from the crop and the soil in the process of respiration. In the simple growth equation $G = A - R$, the respiration term is inescapably real and positive—the plant has to burn some of its dry matter to provide energy for growth—but it is fair to ask if any sort of control of it is possible, either from the start, by plant genetics, or, with plants as they are in the field, by soil or crop management. There are important differences between 'tropical' and 'temperate' plants in their light and carbon dioxide response curves (such that maize, for example, is a much more efficient plant than wheat) and one source, if not unique, of the differences is thought to be in the intensity of respiration in illuminated plants. With Professor Tregunna in the department for a year, the main use of the controlled environment chambers was in respiration studies on leaves, keeping the roots in the most favourable environment they need, and modifying the leaf environment by changing the oxygen content of air moving through the chambers. In this problem of identifying the sources and causes of leaf respiration there is as much biochemistry as there is biophysics, and at least we have been introduced to some of the ideas and the language.

Soil respiration. The problem of what happens around the roots is, in some ways, easier because there is no simultaneous assimilation to be independently estimated, but in other ways it is more difficult, notably because the environment is not inert, for other organisms in the soil are respiring too, and old root residues stimulate them. Basically, the simplest description of the physics is that diffusive interchange carries oxygen down into the soil and carbon dioxide up out of it, and previous reports have summarised work on the relative importance of void spaces between soil crumbs, and the pore structure of the crumbs themselves in controlling rates of gas movement to and from centres of biological activity. In recent years respirometers have been used in the field to measure the sizes of these fluxes and their dependence on soil, plant and weather factors, first at Wrest Park, Silsoe, by the staff of the National Institute of Agricultural Engineering, then, on the same equipment, by the Physics Department, working inconveniently far from base. The results were valuable, and a new set of eight respirometers (just under 1 metre cube) was installed at Rothamsted, in the meteorological enclosure, in time for use in 1970. During this first year, and in the intervening winter, control and monitoring were improved, but unfortunately lack of assistance at some critical periods prevented full exploitation of the better technique, and some of the results from the second full year of use have a blur of uncertainty about them.

The six respirometers cropped in 1970 were cropped again, and the other two remained fallow. Dwarf beans were grown, chosen because their stem geometry permits a good gas-tight and water-tight seal where they come through the lid. Differences in vigour of plant growth gave corresponding differences in oxygen uptake and carbon dioxide emission, with a greater spread than in 1970, mainly because management produced a wide range of water regimes in the soil. Use of the neutron soil moisture meter during the

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winter showed that water was leaking into two of the tanks. They were emptied, the leaks repaired, and the soil was restored by flooding it in: when it had settled down part of the surplus water was drained off to leave one tank with a water-table at 30 cm depth (a), and the other with a water-table at 60 cm depth (b). Thereafter there was no attempt to replace water lost by evaporation (a slight amount, into the circulating air) or transpiration in any of the tanks, one of which, (c), had been excessively dried by the most vigorous of the plants in 1970. The effects of the contrast in water regime are equally clear in the final yields and in the respiration rates during the peak rate of growth in August. The yields, as freshweight (with 19% dry matter) were: (a) 1·25; (b) 1·15; (c) 0·14 kg per tank. The carbon dioxide productions in August were: (a) 251; (b) 236; (c) 94 g per tank (100 g per tank = 1·2 tonnes per hectare).

So, in a single month, the soils of (a) and (b) produced about the same weight of carbon dioxide as the final dry matter yield of the crop. Some, of course, came from biological sources other than the roots, and it is not safe to identify the extra amount with what was measured from the uncropped tanks. The August outputs for these were 81 and 88 g per tank, after July maxima (the hottest month) of 94 and 108 g per tank. For all tanks the minima occurred in February, with a range from 22 g (uncropped in 1970) to 30 g for the tank, (c), that yielded most crop in 1970, a difference attributable to the persistent stimulus by root residues from the 1970 crop.

Results in 1971 confirmed the known diurnal and seasonal patterns of respiration in the dependence of the rate of oxygen uptake on temperature, but attempts to get corresponding short period assays of carbon dioxide emission were not consistently successful. At present, the length of time for which the system can be left unattended is too short, and some change in technique is needed to achieve whole-season continuity. (Currie)

Plant respiration. The controlled environment chambers were used for experiments on beans with the leaves exposed to normal or small concentrations of oxygen (0·21 and 0·05 cm^0), expected to produce important differences in photo-respiration that might be detected by biochemical assay of glycolic acid oxidase, an important enzyme in photo-respiration. Measurements on extracts of leaves showed no detectable difference. Nor was there any difference in the $^{13}C/^{12}C$ ratio of organic carbon in the plants. (We are grateful to Dr. Bruce Smith, University of Texas, for this assay.) The carbon ratio differs among plant species—e.g. it is greater for maize than for wheat—and, hitherto, differences have often been attributed to differences in photo-respiration. Failure to make a temperate plant behave like a tropical plant by an imposed change in photo-respiration suggests that some other reason must be sought to account for maize having a carbon ratio greater than wheat. (Tregunna)

The conditions for these experiments are now standardised, with roots and aerial parts of the plants in separated environments. The roots are in a Hoagland culture solution, vigorously stirred and aerated with air free from carbon dioxide. The tops are in a measured air stream at constant temperature, controlled carbon dioxide content is continually monitored at input and exhaust, and, by suitable dilution with nitrogen, the input oxygen content is adjustable. The bean plants were sampled twice, to give dry weight gains, and for amino-acid analyses. (Marjorie Byers, Biochemistry Department, p. 124.) The continuous monitoring of carbon dioxide gave continuous estimates of rates of net assimilation, and as the integrated values agreed well with the measured dry weight gain, the detailed history of the growth is known with some confidence: short period differences between treatments can be discussed as real. In the whole period, a change in oxygen concentration, in ratio 1/4, produced a change in growth in ratio 2/1, at constant carbon dioxide concentration (270×10^{-6} cm^0). Perhaps too simple in plant physiology, if it is assumed that respiration rate is proportional to oxygen concentration, then this

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suggests a ratio of respiration/assimilation of 4/7. Doubling the carbon dioxide concentration at normal oxygen concentration increased growth in ratio 3/2. In two experiments, the maximum efficiencies of fixing of light energy were near 10 and 5% of the visible component from the mercury vapour lamps (about 90 W m^{-2} inside the leaf chambers). (Parkinson)

Field measurements (canopy enclosure). Physical observations on plants, either in controlled environments in the laboratory, or on managed—and measured—environments in the field, yield numbers for water vapour and carbon dioxide fluxes associated with known gas concentrations around the leaves (and roots) and the incident light intensity. Statistical regression equations yield little of interpretative value, but informed guesses at 'model' functional relationships can be very useful in attempts to link the field and laboratory experience even though they contain some 'mathematical' constants. Ultimately, all the constants needed to get good fits between model and reality should be plant or environment parameters capable of independent measurement or assessment. One of these is the resistance to gas transport across the leaf surface, called the stomatal resistance, r_s, for a single leaf, and the surface resistance, r_S for a canopy. In the late summer of 1967 Szeicz calculated, from aerodynamic theory applied to his measurements, the surface resistance of a kale crop and got a range from 0·34 to 0·60 s cm^{-1} for r_S. This year, with kale under the field canopy enclosure (*Rothamsted Report for 1970*, Part 1, 34) the measured transpiration rates and humidity differences gave a range 0·32 to 0·58 s cm^{-1}. Laboratory measurements on individual leaves gave minimum values of r_s between 0·8 (August) and 1·6 s cm^{-1} (October), showing that several leaf layers take part in transpiration and photosynthesis.

Two model equations have been tried, the more complex containing a term that automatically imposes a limiting rate of photosynthesis as light intensity and carbon dioxide concentration are increased without limit. It will be needed only in extreme conditions rarely met in the field, and probing of the simpler variant will be more profitable. This, already in use elsewhere, takes the form

$$\frac{\phi - \phi_0}{F} = r + \frac{\phi - \phi_0}{\epsilon(I - I_0)}$$

where ϕ is the external concentration of carbon dioxide

ϕ_0 is the 'compensation point' concentration of carbon dioxide

F is the net flux to the canopy of carbon dioxide

r is a 'resistance' to uptake of carbon dioxide with aerodynamic, stomatal and mesophyll components: it will be less than ϕ/F

I is the light intensity

I_0 is a light 'compensation intensity'

and ϵ is an efficiency of photosynthesis: it will be greater than the usual value F/I.

The field leaf canopy enclosure was set out on several days over a complete cover of irrigated kale. Air was circulated at controlled temperature, humidity and carbon dioxide content (160 to 380 $\times 10^{-6}$ cm^0). The transpiration rate was found from the rate of condensation at the humidity control and, with the leaf temperature known, the vapour pressure difference causing transpiration was derived, to give the resistance to water vapour transport (0·32 to 0·58 s cm^{-1}, already quoted). This was mainly stomatal in origin, because the air was stirred. Light intensity, monitored inside the enclosure, changed naturally in the course of a day. The flux, F, to the crop was estimated from the amount of carbon dioxide that had to be added to the input air to maintain a chosen

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concentration in the canopy. With a range of values of F, I, and ϕ for the day, the constants that give the best fit to the equation were calculated. Two values will illustrate, as averages for two days late in October and early in November. The value of ϵ was near 4%, as the ratio of energy content of the carbon dioxide fixed to the total solar radiation received. This is a mathematical constant: the noon value of the agronomic ratio (F/I, in the same units) on one day was near 2%. The value of r, on both days, was 1·5 s cm^{-1}. The relevant value of stomatal resistance to carbon dioxide was 0·5 s cm^{-1} (derived from the water vapour value) leaving 1·0 s cm^{-1} as a measure of the apparent crop mesophyll resistance to carbon dioxide transport. As indicated in the definitions, this will be less than the conventional value given in previous reports, but this is a difference, not a discrepancy, attributed to respiratory activity that increases with oxygen concentration (1.4). (Lake and Tregunna)

A new resistance porometer. Including the diffusion porometer described last year, none can be used to give continuous readings of stomatal resistance, and calibration is indirect and of uncertain accuracy. A new design (1·8) seems better in all three respects. It was used on the irrigation experiment, and for occasional measurements on sugar beet (for Botany Department) and on potatoes at Woburn (for Nematology Department). Lake took the instrument out to Israel and used it successfully in some glasshouse experiments on roses of Dr. Z. Plaut. In full sunlight, leaves on detached shoots in water had the same value of r_s as those on the plants in irrigated soil, implying that the root and rhizosphere resistances in the soil were not imposing any detectable restriction on the supply of water to the plants. (Parkinson and Legg)

Agricultural meteorology

Instruments. Six sets of Kent–Harrison logging equipment were modified in time for installation on the macro-plots of Great Field, under kale in 1971. In spite of troubles, 95% of the records are safely on paper tape and the remainder can be taken from charts, as in the past. A computer programme for retrieval of records is being worked out in the Computer Department. The field equipment, partly automated, partly recording as usual, was run from June to November, including a few frosty nights. (Long and French)

A new sampler for water vapour and carbon dioxide, almost complete, is expected to be in use in 1972: it will give more detailed records in a form compatible with the Kent–Harrison logging equipment. (Legg)

Experiments: Rothamsted. Field beans and potatoes were grown on the irrigation experiment, and on some plots of both there was detailed growth analysis. To produce a range of plant cover, two planting densities were used, and two dates of planting attempted: the first sowing of beans was ruined by pigeons.

Beans. Irrigation (80 mm in July) had no effect on crop yield. Plant densities in ratio 3/1 produced crop yields in ratio 2/1. Measurements of leaf area and leaf water content gave a ratio of 35 mg cm^{-2} in small plants, decreasing to 20 mg cm^{-2} when plants had reached half their final size, and not changing thereafter.

Potatoes. The treatments included spacing, normal and 2 × 2 × normal; early (and chitted) and late (and unchitted) planting; two fertiliser rates; and irrigation (80 mm in July). There was no effect of planting date, doubling the fertiliser (F) increased average yield from 30 to 35 t ha^{-1}, wide spacing (at 4 × normal) only halved the yields, and at normal spacing irrigation increased yield from 34 to 45 t ha^{-1} at F, and from 42 to 51 t ha^{-1}

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at 2 F. At wide spacing the corresponding responses were from 16 to 24, and 20 to 27, t ha^{-1}. The average response to irrigation for the close spacing was 1·3 t ha^{-1} cm^{-1} (or tons per acre per inch), and for the wide spacing was 0·9 t ha^{-1} cm^{-1}. Relatively, irrigation increased yield more at wide spacing than at normal spacing (compare 24/16 with 45/34; 27/20 with 52/41), and increased tuber size at wide spacing. The differences have parallels in other relative measurements: using the new porometer, the stomatal resistance of widely spaced plants was greater than that of those normally spaced; a measurement of leaf water potential at the time of maximum water stress (mid-day) gave − 10·6 bar on the widely spaced irrigated plots and − 9·0 bar on the normal crop.

Growth analyses were done on early and late plantings, with and without irrigation, at close planting only. When the periodic increment in dry matter is divided by the corresponding value of the potential evaporation for the period the ratio, with considerable scatter, shows no clear difference between irrigated and unirrigated plots, but seems to be uniquely and linearly dependent on fraction of ground cover up to 100% cover, where it was about 0·8 + t ha^{-1} cm^{-1}—on the same scale as the measured irrigation response.

The ratio of leaf water content to leaf area had the same initial and final values as for beans, but it decreased linearly with plant size throughout the season. (Legg, Rao, Lake and French)

Experiments: Woburn. Early irrigation (May for barley, June for barley and potatoes) was probably wasted: there was heavy rain in June, and, in accord with previous experience, irrigation of barley in July (62 mm) gave no response in grain (2·8 t ha^{-1}), and a small response in straw (2·6 to 2·9 t ha^{-1}).

The potatoes had 12 mm in June and 90 mm in July. As ever, the complex interactions of other treatments, current and past, produced a great range of crop yields. On the worst plots, there was no response to irrigation (average yield 4·3 t ha^{-1}); on the best, the response to irrigation was from 32 to 48 t ha^{-1}; and the average response from all the fumigated plots was from 29 to 38 t ha^{-1}, or just under 0·9 t ha^{-1} cm^{-1}, somewhat less than the Rothamsted value for normally spaced plants. (Legg)

Soil water: 1971. Eighteen access tubes were installed, at Rothamsted, measuring to 150 cm depth. Eight (2 × 4) were in the kale on the macro-plots, two sets of four (2 × 2) in potatoes and beans, and two were set under the short grass of the meteorological enclosure. Readings were taken at about weekly intervals and, under the kale, will continue until all the crop is harvested. All the irrigation need occurred in July. The potatoes and beans had 80 mm in four applications: the kale had 75 mm in three. The response of the kale was good, from 8·2 to 12·6 t ha^{-1} of dry matter. (Long and French)

Soil water: 1970 and before. Previous reports compared the total water use by the crop (E_A) as measured by the neutron moisture meter, with the estimated potential evaporation (E_T) for the same period. Invariably, for the irrigated plots, E_A exceeded E_T, a result expected for everything other than short grass because of the greater aerodynamic roughness of the other crops, but the size of the difference has remained open to question, subject to a close study of the records. This study is almost complete back to 1967, with 1966, 1965 and 1964 remaining. Very detailed examination of results in 1970 and 1969 showed that, in ideal conditions, the meter is accurate, and that during the main part of the growing season plotting E_A against E_T gives a very good straight line with a slope greater than unity, though, depending on the crop, it may be less than unity early in the season and during ripening phases before harvest. Departure from 'ideal' conditions is frequent, partly because of soil factors—cracking near the top of the access tube, smearing at the bottom so that water may be temporarily perched

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there for weeks at a time; partly because of plant factors—wide spacing giving non-uniform drying in the horizontal, non-uniform shedding of rain and irrigation, roots growing towards the access tubes; and partly because of the inherent defect of the meter—its response is determined by the water content of the soil within a few centimetres of the access tube. In short: the neutron meter is a very valuable tool in research but only when there is very careful quality control on the readings obtained.

Our meter is outstanding in having a much more powerful neutron source than any other in general use, the technical advantage being that it gives greater precision: experience is that this extra precision is needed to detect second order differences of a few per cent in the comparisons of net-drying of soil profiles. The logistic disadvantage is that it must not be taken from Rothamsted, so, elsewhere, safer but less sensitive equipment has to be used. (Penman)

Tillage. In the comparison of cultivated *v* uncultivated sites at Woburn, major effort went into studying water regime and soil temperature. *Water content* was measured at intervals using a 'Wallingford' neutron meter. There are doubts about the adequacy of the holes prepared for the access tubes, and the precision is less than is obtained with the Rothamsted probe. However, if the Wallingford probe cannot detect a difference in response to treatment it is probably too small to matter. Some effects were detected, e.g. in mid-May the wettest area was uncultivated and uncropped, whereas the driest was under the barley on cultivated soil. Other measurements were made on the eelworm/irrigation experiment on potatoes. Against a promise that switching gear and ancillary electronic equipment would be delivered in spring 1971 (ordered autumn 1970), 160 units to monitor soil *water potential* were made and buried in the field, with a 10 cm diameter cable conduit from site to recording hut at a depth below the limit of penetration of cultivation implements. All this work was wasted—the necessary linking gear is still undelivered (December 1971)—and a new site is used each year.

Basic site preparation (in autumn 1970 for 1971) attempts to remove any layers compacted by previous management. Penetrometer measurements in 1970 confirmed success for 1971. At the end of the 1971 experimental period bulk density profiles showed some residual decrease in the 0 to 5 cm layers of the cultivated soil relative to the uncultivated, and below this depth the only detectable difference was evidence of a compacted layer, from 12 to 20 cm, on the cultivated plot. The crop yields were 4·7 (cultivated) and 3·9 (uncultivated) t ha^{-1} of barley grain. (Brown)

Miscellany

With D. Lawlor (Botany), energy balance measurements were made in the new growth rooms to test uniformity of environment, and variability of leaf/air equilibria. Some of the effects measured may be important in some contexts. One, unexpected, is that the Perspex ceiling was about 4°C warmer at the air outlet side of the room than at the side where the air came in, and this warmed the leaves, but not the air, below. (Lake)

A start was made on setting up some laboratory soil columns and samples at fixed water potentials, for calibration of sensors for water potential. (Brown and Eka-Singh)

Staff and visiting workers

After over 44 years on the staff George Cashen retired in March. His work on cultivation (with B. A. Keen) earned the Bessemer Premium of the Society of Engineers; for several years he studied gas adsorption by clays; and, in the final phase, he became a world authority on the electrical charges on clay surfaces and their effects on the physical

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and chemical properties of soils. This work will be continued by the Pedology Department, and Cashen's successor—Dr. P. F. North, who joined us in September—will work on the physics of soil structure. Professor Bruce Tregunna went back to the University of British Columbia in August, and G. Szeicz returned from his post-doctoral fellowship in Texas. L. ter Veer left.

Visiting workers included two sandwich course students. S. Rao (University of Bradford) helped with field work, April to September, and then M. Derry (Hatfield Polytechnic) took over, for a year. M. Eka Singh (Thailand), a student at the College of Agricultural Engineering, Silsoe, C. J. Wheatley and J. M. Hopwood were here for a few weeks each in university vacation.

J. V. Lake spent four weeks in Israel for the FAO High Value Crops Project. B. J. Legg also visited Israel and contributed a paper (1.7) at the symposium on Soil Water Physics and Technology, arranged by the International Society of Soil Science.

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