DUNCAN JOSEPH GREENWOOD
16 October 1932 — 13 February 2010
During his 55-year career as a highly distinguished scientist, Duncan Greenwood made a major contribution to the field of soil science and plant nutrition. His early studies on soil aeration revolutionized thinking on the mechanisms by which oxygen influences the activity of microorganisms and their metabolism of organic substances in structured soil. His ideas resulted in the ‘micro-site concept of soil aeration’, which is still widely accepted today. Later he turned his attention to the nutritional requirements of vegetable crops at a time when the horticultural industry was starting to introduce inorganic fertilizers. He developed a novel static model of N, P and K response, which he used to produce the first scientifically based inorganic fertilizer recommendations for 23 different vegetable crops. Not satisfied with this major development, Duncan started to create more sophisticated dynamic models using novel widely applicable relationships that took more account of the effects of weather on nutrient behaviour in the soil and plant. He not only used these to provide important insights into many of the complex interacting processes involved, but also incorporated them into some of the first computer-based decision support systems for practical site-specific fertilizer advice for the vegetable growing industry. The application of these advances had an important effect on the efficiency of crop production and the reduction of associated environmental impacts. Duncan continued to devise new models for nutrient and water use throughout the rest of his career and to explore ways of applying them in different areas of soil and crop science.

BACKGROUND

Duncan Joseph Greenwood was born on 16 October 1932 in New Barnet, Hertfordshire, to Herbert James and Alison (née Fairgrieve), and was later followed by a younger brother,
Eric Fairgrieve Greenwood. The family moved to Fulwood in Preston when Duncan was five years old, where he attended Hutton Preparatory and Grammar Schools. His early childhood was happy, although he became increasingly concerned by the threats of World War II and the associated risks of food shortages. He started growing vegetables and by the end of the war had his own allotment, which he kept for many years. As a result, he became intensely interested in agriculture and read about it widely. A family acquaintance, Sir John Russell FRS, director of Rothamstead, was consulted about how best to embark on a career in agriculture. His advice was to take a specialist degree first, so Duncan chose to study chemistry at the University of Liverpool.

Unfortunately, he did not enjoy his time at Liverpool as many of the topics on the course failed to interest him. He also continued to live at home and travelled to the university by public transport every day, which he found particularly stressful. After graduating, he took great care in choosing his next move and eventually took up an offer from the University of Aberdeen to study for a PhD under the joint supervision of Dr Howard Lees (biochemistry) and Dr W. T. H. Williamson (soil science). His project on the effect of oxygen concentration on the breakdown of amino acids and other organic compounds in soil proved an inspired choice as it enabled him to undertake original research and to develop novel ideas and techniques.

In 1959 Duncan was offered the opportunity to continue this work in the Chemistry Section of the newly opened National Vegetable Research Station at Wellesbourne. During the next few years, he devised the ‘micro-site concept of soil aeration’, which has since become widely accepted and for which he was awarded the Sir Gilbert Morgan Medal from the Society of Chemical Industry. Duncan continued to develop his ideas and, after discussions with his colleague, Dr John Nelder (FRS 1981), came to the view that many soil and plant processes could be described by simple quantitative relationships and used for predictive purposes. After his promotion to head of the section at the early age of 34, he turned his attention to the nutrition of vegetable crops.

Over subsequent years, Duncan created a suite of mathematical models from simple chemical, biological and physical principles to interpret N, P and K response data of a wide range of vegetable and agricultural crops grown on different soils. His results formed the basis of the first nationwide fertilizer recommendations for vegetable crops in the UK. Later he was one of the first in the world to develop a more dynamic approach by devising equations to describe key processes governing nutrient uptake and crop response. He combined these into simulation models to explain how soil, plant and weather conditions interact to affect the mobility of nutrients in soil, their uptake by the crop and their influence on plant growth and environmental pollution.

His research led to him becoming an internationally renowned expert in his field, for which he received many awards, including the Research Medal of the Royal Agricultural Society of England, a Lifetime Achievement Award from the Horticultural Industry and the President’s Medal of the Institute of Horticulture. During his career he became president of the British Society of Soil Science and of the International Committee of Plant Nutrition, as well as holding several other senior offices in learned societies. He was widely acclaimed by his scientific peers, with whom he collaborated extensively, and was in great demand internationally as an invited speaker. His extensive contribution to research was recognized following his retirement with the award of a CBE in 1993 (figure 1). However, retirement did not dim his enthusiasm for research, which he continued until his untimely death in 2010.
Duncan first became interested in the effects of aeration on soil processes during his PhD studies at Aberdeen, where he compared the rates of decomposition of 23 amino acids under both aerobic and anaerobic conditions. Measurements of the mineralization of each amino acid, together with the accompanying consumption of oxygen and the release of carbon dioxide, were made during the continuous circulation of combinations of amino acid solution and air through soil aggregates using both ‘forced air’ percolators (Lees 1947, 1949) and a novel ‘rocking’ percolator, which he specifically developed for the purpose (1)*. His results showed that most amino acids decomposed rapidly under aerobic conditions, all following a similar pattern that was largely unaffected by the water content of the soil until it became visibly dry. More detailed studies with leucine suggested a two-phase decomposition process may have been occurring, with around 40% of its carbon converted into carbon dioxide and the remainder synthesized into cellular material, some of which was subsequently oxidized to produce more carbon dioxide (3). Comparative anaerobic studies showed that decomposition was typically 5 to 10 times slower than under aerobic conditions, with fatty acids and ammonia the primary products rather than carbon dioxide. Almost half of the amino acids studied were

* Numbers in this form refer to the bibliography at the end of the text.
resistant to degradation over a 10-day period in the absence of oxygen, except when nitrate was added as a hydrogen acceptor (2). This work represented some of the earliest quantitative investigations into the effects of aeration on the decomposition of amino acids in soil.

Duncan continued to develop his ideas on the role of oxygen in soil microbial processes after he moved to the National Vegetable Research Station at Wellesbourne, later to become the headquarters of Horticulture Research International before its integration into the School of Life Sciences at the University of Warwick. At the time, concentrations of oxygen in soil were assumed to depend on its transport through the gaseous phase. However, Duncan argued that the presence of water could make its concentration highly variable within the soil microstructure. He devised new equations using steady state kinetics to calculate the rate of oxygen diffusion into assemblages of water-saturated soil crumbs, and used these to determine its effect on the net rate of microbial decomposition of organic materials within them (4, 5). By assuming that the rate of diffusion of oxygen through the soil water inside the crumbs is governed by the oxygen concentration (partial pressure) at their surface, he showed that the crumbs could be considered as consisting of two coexisting zones: an aerated outer one where respiration proceeds at a constant rate independent of oxygen concentration, and an inner anaerobic core where respiration is zero. He also used his theory to deduce that the ‘switch’ from aerobic to anaerobic conditions within the aggregates occurs sharply at a very low oxygen concentration (less than about $3 \times 10^{-6}$ M) in widely different soils, a value which he confirmed by novel polarographic techniques. Later, he used similar theoretical approaches to show that fluxes of oxygen into an aerobic soil were always much greater than those for carbon dioxide released by respiration, and predicted the concentrations of the latter will seldom be sufficient to affect ionic concentrations in the soil solution unless anaerobic zones are present (9).

He also used similar approaches to examine the role of oxygen concentrations on nitrification and nitrate dissimilation (denitrification) in soil. Percolation measurements at different oxygen partial pressures showed that ammonium is always the preferred N source for microbial assimilation. Nitrate disappeared from the system only when oxygen partial pressures fell below a critical level at which it started to replace oxygen as a hydrogen acceptor. Drawing parallels with his previous theory of oxygen diffusion into water-filled soil crumbs, he showed that nitrification and denitrification can also occur simultaneously in sharply delineated aerobic and anaerobic zones within each crumb in much the same way as other microbial processes (6). These results led to what became known as the micro-site theory of soil aeration, a concept now widely accepted. In 1963, his work on nitrogen transformations and the distribution of oxygen in soil was recognized by the award of the Sir Gilbert Morgan Medal by the Society of Chemical Industry.

Duncan also examined the effects of poor soil aeration on root growth and function for different types of vegetable seedlings. He showed that oxygen absorbed by the leaves can be transported via the stem to their roots to help meet the demands of root respiration in anaerobic environments, in much the same way as in aquatic and bog plants. Calculations using Fick’s Law confirmed that the rates of transport depended on the gradient in oxygen concentration between the leaves and the roots, and were consistent with oxygen diffusing through continuous non-tortuous gas-filled channels located in the cortex within about 12 µm of the root surfaces (7, 8). Although the rate of transport varied between species, it appeared to be sufficient to meet at least a third of the oxygen demand of the roots growing under
anaerobic conditions and could reduce adverse effects on root respiration, at least in the early stage of growth.

CROP NUTRITION

Response of field vegetable crops to NPK fertilizer

In the years after World War II, the demand for vegetables in the UK was almost entirely met from domestic production in market gardens, with most of the nutrients applied as organic manures. However, around the time that Duncan moved to Wellesbourne, new production methods were being introduced, with vegetables increasingly grown extensively as farm crops using inorganic fertilizers as the sole source of nutrients. While crops such as cereals, sugar beet and potatoes had been grown in this way for some time, this was a new approach for the wide range of vegetable crops then being grown, and information was limited about their nutrient requirements. This was a problem to which Duncan next turned his attention.

He first pioneered the use of systematically designed fertilizer experiments in which increasing levels of N, P or K fertilizer were laid out in order across adjacent rows of a crop (10). Statistical analysis showed that the effects of any trends in nutrient status across a site could be effectively eliminated by using different combinations of fertilizers in the blocks, by randomly varying the direction in which their application rates increased, and by changing the orientation of the crop rows. The design eliminated the need for extensive guard areas between adjacent treatments and allowed a more complete coverage of the response surfaces than the conventional random block approach, with considerable economy of land and labour. Duncan used this systematic approach on a low fertility site at Wellesbourne to compare the responses of over 20 different vegetable crops and potatoes to 15 levels of N, P or K fertilizer (18–20).

He also developed a response equation from stationary phase concepts of nutrient transport in soil and their effects on uptake by roots (11). It took account of the nutrient status of the soil before fertilizer was applied and the importance of adsorption–desorption reactions on their transport to plant roots, together with the beneficial effects of the nutrients on plant growth, and any detrimental osmotic effects on plant response particularly from high N levels in the soil. After making various approximations to minimize the number of parameters involved, the fresh yield ($Y$) of a crop was related to the levels of nitrogen, potassium and phosphate fertilizer ($N_f$, $K_f$ and $P_f$) applied by the equation

$$1/Y = \left[1/(1 - (N_s + N_f)/\alpha_N)\right] \left[1/A + 1/[B_N(N_s + N_f)] + 1/[B_K(K_s + K_f)] + 1/[B_P(P_s + P_f)]\right]\]$$

where $A$ is the theoretical maximum yield, $N_s$, $P_s$ and $K_s$ are the initial levels of the nutrients in the soil, $B_N$, $B_K$ and $B_P$ are measures of the ability of crops to utilize the nutrients recovered and $\alpha_N$ is the level of N in the root zone that prevents growth due to osmotic effects. Duncan validated this equation using data from his systematic fertilizer experiments for the different vegetable and potato crops grown on the low fertility site at Wellesbourne, and with separate NPK response data for potatoes from a series of trials previously carried out by ADAS on a wide range of soils throughout England and Wales.

Duncan then devised a novel method to predict how the different vegetable crops would be expected to respond on soils other than that of his experiments at Wellesbourne. To avoid
the conventional approach of an extensive series of fertilizer trials for each crop at sites across the country, he made use of an observation by Crowther & Yates (1941) that the relative responsiveness of any two agricultural crops (i.e. the ratio of their individual responses) to a specific nutrient was often approximately constant irrespective of the soil on which they were grown. Assuming the same relationship applied to vegetable crops, he compared the ratio of the responses of each of the vegetable crops with that of potato from his data at Wellesbourne with the individual responses of potato on the multiple sites in the nationwide trials, and predicted how each of the vegetable crops would respond on the different sites. Although validation experiments showed his predictions were not perfect, they were far superior to existing estimates based on farmers' experience, and they were used to create the first scientifically derived NPK fertilizer recommendations for vegetable crops in the UK (Ministry of Agriculture, Fisheries and Food 1973).

More detailed analyses of the response data from the validation experiments suggested that much of the variation in responsiveness of vegetable crops between sites originated from differences in theoretical maximum yield ($A$ in equation [1]). This was subsequently confirmed by analysing the variations in P responses of a series of brassica genotypes in both greenhouse and field environments (35). Quantitative trait locus analysis using data for doubled haploid lines also showed a greater association between shoot dry matter accumulation and various measures of P use efficiency, rather than with more efficient P accumulation or with its internal use within the plant (39).

Although the experiments at Wellesbourne provided a valuable insight into average responses of vegetable crops to fertilizer, there were considerable year-to-year variations that could not be explained by differences in the soil nutrient status or the theoretical maximum yield. Duncan surmised that these effects originated from differences in weather, and used lettuce data from the low-nutrient status site at Wellesbourne to show that 75% of the total variance from the effects of fertilizer application in nine experiments over five contrasting years could be explained by differences in precipitation (rainfall and irrigation). This was mediated through its influence on the adverse osmotic effects of N on growth, on the leaching of nitrate down the soil profile and on the dispersion of P from fertilizer granules (12). The magnitude of the effects depended on the timing of the precipitation events, with those in the early stages of growth particularly important in governing subsequent plant behaviour. These findings convinced him that a more dynamic approach was needed to gain further insight into the factors governing crop responses to nutrients.

**Simulation models of nutrient response**

Duncan first focused his attention on processes involving N in the soil and plant and, over the course of his career, he developed several mechanistic N simulation models for research and advisory purposes. Each comprised a series of core nutritional components used to calculate the potential growth of the crop and its demand for N, the development of its rooting system, the uptake of mineral N from the soil and the effects of suboptimal supplies on growth (33). Equations for many of these processes were derived from first principles, allowing incremental changes in N in the soil and plant to be updated at daily intervals throughout growth using standard soil and meteorological data. Simplifications and approximations were also introduced as appropriate to facilitate their application to field conditions in the UK, where soil and environmental conditions are seldom extreme. As a result, his models required relatively few inputs and used parameters that were either easily measured or readily available
from the literature; this made them simpler to use and applicable to a much wider range of soil and cropping situations than most other models developed for similar purposes. The following paragraphs outline some of the key equations he developed and how they were used in various versions of his models.

The demand of a crop for $N$

The rate of demand of a crop for $N$ is the product of its potential growth rate and the fraction of $N$ in its tissues needed for maximum growth. Most vegetable crops are harvested prior to senescence, so Duncan developed a growth equation based on the proportion of incoming radiation intercepted by the leaves between May and September when the plants are actively growing (15). As the average monthly radiation in the UK does not vary greatly over this period, he deduced that

$$k_2(t - t_0) = W + k_1 \ln W - (W_0 + k_1 \ln W_0)$$  \[2\]

where $W$ is the dry mass of the plants (excluding fibrous roots) per unit area at time $t$, and $W_0$ is the mass at the start ($t_0$); $k_1$ and $k_2$ are constants, each with a similar value for 17 different vegetable crops, cereals and potatoes, with little variation between years. This simple equation accounted for the increases in the weight of a crop, from initially isolated plants at their commercial spacing in the field through the formation of complete canopies and up to the onset of senescence, assuming there were no shortages of nutrients or water. Its merit is that it shows that the potential growth curves of a wide range crops can be described by an exponential and linear phase, with the differences between crops largely explained by the effects of $W_0$ due to different seed or transplant weights and planting densities.

The average organic $N$ concentration in the dry matter of whole plants declines during growth even when they are adequately supplied with $N$. Duncan found that an empirical equation described how the critical $N$ concentration $N_c$ (the minimum % organic $N$ in vegetable plants needed for maximum growth) changed with the dry mass of a crop in t ha$^{-1}$:

$$N_c = 1.35 \left(1 + 3ce^{-0.26W}\right),$$  \[3\]

where $c$ is a crop-specific coefficient, which often approximates to unity. This equation gave excellent agreement with data for 16 different vegetable crops, potatoes and winter wheat up to the onset of senescence (23, 25, 26), although $N_c$ can normally be expected to remain constant during the exponential growth phase (Caloin & Yu 1984). The decline in organic $N$ during growth occurs because an increasing proportion of photosynthate is diverted to the production of the low-$N$ structural and storage material at the expense of that used to produce proteins for photosynthesis. To understand this relationship better, Duncan devised a simple model of $C$ and $N$ assimilation to predict the changes in protein concentration in crops during growth (16, 17), from which he derived an alternative relationship between $N_c$ and $W$ for field-grown vegetable crops

$$N_c = aW^{-b},$$  \[4\]

where $a$ and $b$ are crop-specific coefficients, with the mean value of $b$ approximating to 0.5 (29). Predictions from equations [3] and [4] are very similar when $W > 1$ t ha$^{-1}$, although the latter tends to overestimate $N_c$ when crops are small. Nevertheless, both equations were in excellent agreement with independent data over much of the range, showing that critical $N$ concentrations in the dry matter of a wide range of crops are determined largely by their
dry mass per unit area rather than by their species. The same equation was found to apply equally well to the vegetative growth phase of forage crops, although the mean value of a differed between C3 and C4 crops, reflecting their different photosynthetic efficiencies. This demonstrated for the first time that C4 crops require an average of only 72% of the N required by C3 crops at the same weight for optimum growth (29).

Reductions in growth from suboptimal concentrations of plant N

Caloin & Yu (1984) showed that the decline in relative growth rate of N-sufficient plants during growth could be described by the changing proportions of photosynthetic and metabolic components in their tissues, if each had a different fixed N concentration. Duncan extended this approach to include the effects of a suboptimal N supply on the relationship between the concentration of N in the plant and its growth (30), and showed that to a first approximation

\[ R_N / R_c = (N - N_o)/(N_c - N_o), \]  

where \( R_N \) and \( R_c \) are the relative growth rates of plants with suboptimal and optimum N supplies respectively, \( N \) and \( N_c \) are the N concentrations in these two sets of plants, and \( N_o \) is their minimum N concentration when they become so N-deficient that growth stops; \( N_o \) is assumed to remain constant throughout growth. Equation [5] accurately described the changes in relative growth rate of vegetable, potato, cereal and forage crops over the range of plant N concentrations observed in the field when fertilizer treatments increased from zero to the optimum level.

Development of the rooting system

Consideration of a simple conceptual model of the partition of photosynthetically fixed C between plant shoots and their fibrous roots, and an assumption that the rate of turnover of these roots occurs at a rate \((m)\) that is a constant fraction of their live root mass, allowed Duncan to deduce that total root length per unit area \((L)\) is related to the weight of shoot plus storage organs per unit area of the crop \((W)\) at time \(t\) by the equation

\[ \ln L = c + d \ln W - mt, \]  

where \( c \) and \( d \) are crop-specific coefficients (21). Estimates of rooting depth can then be calculated from the values of \( L \) using the exponential root distribution equation of Gerwitz & Page (1974). Equation [6] accurately described data for different vegetable crops and showed that root lengths of pea and broad bean were about half of those of non-leguminous crops at the same weight. He also deduced that approximately 3.5% of a root system is likely to be destroyed each day, a figure not dissimilar to independent estimates for cereals and grass. The corresponding estimates of rooting depth were also well-defined for most vegetable crops, suggesting that simple relationships can be used to describe the rooting patterns of a wide range of crops, and that the depth of root penetration of quite different species is largely determined by the total weight of their dry matter per unit area.

Dynamic models of N in the soil–crop system

A common feature of these models was the assumption that the soil profile can be treated as a series of horizontal 5 cm layers to allow for changes in soil properties and rooting densities with depth during growth. In most, redistribution of water and nitrate are calculated from daily rainfall and evaporation data using the cascade model of Burns (1974), modified to
include transpiration from areas covered by the crop (after Siddig 1982). The amounts of nitrate in each layer are adjusted each day for uptake by the roots, and for the temperature-dependent release of nitrate by microbiological metabolism of crop debris, soil organic matter and ammonium fertilizer. All of the soil nitrate above a minimum concentration within the current depth of rooting is considered to be available to the crop, and is extracted sequentially until either the total daily demand of the crop is satisfied or the nitrate contents of the rooted layers are depleted. When the soil is moist and there is adequate nitrate in the profile, the demand will normally define the total amount taken up on any one day, but luxury uptake is permitted for some crops.

The potential daily increase in crop dry weight per unit area is estimated from simple growth curves defined by equation [2] and is used to calculate the corresponding N demand of the shoot plus any storage organs using equation [3], to which a contribution for the N content of its fibrous roots is added. The vertical expansion of the rooting system is calculated from equation [6], assuming an exponential decline in root density with depth and its horizontal spread from the canopy cover. If the nitrate in the rooted zone is suboptimal, N uptake is reduced using equation [5], resulting in a reduction in growth rate for that day. These equations are repeated sequentially for each day during the growing season until the crop weight reaches a predefined maximum or the duration of growth is completed.

Although the models were initially designed for analysing the responses of vegetable crops to soil and fertilizer N in field trials (13, 14, 28), they proved equally applicable for agricultural crops such as sugar beet (22). Furthermore, in collaboration with colleagues in The Netherlands and Belgium, Duncan incorporated additional routines for the partition of assimilates within the plant, allowing estimates of the yields and N contents of potato tubers (24) and cereal grain (27) to be made. Rigorous statistical tests for evaluating the performance of models were developed, which showed that they provided a sound basis for examining how optimum fertilizer levels varied from year to year and from soil to soil owing to differences in weather across the UK and northern Europe. Furthermore, with the increasing awareness of the role of N in environmental issues, the models were also used to assess the impacts of different fertilizer and rotational cropping practices on the uptake and losses of N from the soil–plant system (31). Such scenario testing was used to inform the Nineteenth Report of the Royal Commission on Environmental Pollution on the sustainable use of soil (Royal Commission on Environmental Pollution 1996) and the Code of good agricultural practice for the protection of soil (Ministry of Agriculture, Fisheries and Food 1998).

As it had long become clear that there was no single measure of N-supplying power of the soil that could be reliably used to estimate crop N requirement prior to fertilizer application, Duncan incorporated his research model, later known as N_ABLE (33), into a stand-alone decision support system (DSS) to provide practical site-specific N fertilizer advice directly to the industry. Run on a desktop computer, the DSS included parameter values for seven soil types and 23 vegetable crops and potatoes, together with typical weather data for different regions of the country. The DSS estimated the optimum fertilizer rate for the selected site prior to fertilizer application by automatically running the research model with different levels of N fertilizer (which could be applied as either single or split dressings) to identify that predicted to give maximum yield on the date of harvest. There was also an option for incorporating actual weather data to calculate any additional top-dressing requirements in years with excessive rainfall early in growth. This world-first model-based N fertilizer recommendation system was tested extensively by ADAS in independent trials before being released to the industry.
under the brand-name of WELL_N in 1994. From then on it was widely used by advisors and vegetable growers, and proved to be a great success at improving the efficiency of N fertilizer use and reducing nitrate pollution. One large brassica producer in the UK estimated that by following WELL_N he made significant savings in N fertilizer with no loss of yield, while increasing the proportions of crop in marketable grades. A modified version of the DSS was later created on the Internet—where it was freely available to the general public and widely used for teaching.

Dynamic models of K and P in the soil–crop system

The mobility of potassium and phosphate in soil are at least an order of magnitude less than that of nitrate owing to interactions with the soil surfaces. Duncan’s models for K and P response therefore differ from those for N in that all relevant soil and uptake processes are assumed to occur from within a single cultivated layer (usually 20–30 cm in depth) in which nutrients from both soil and fertilizer are uniformly distributed at the start.

The K model (POTAS) assumed that the sole ionic constituents in the soil are K, Ca and Mg, with nitrate and bicarbonate used to maintain electro-neutrality (32). Active soil K is partitioned between solution and exchangeable forms according to the standard activity ratio. Each day solution K moves to each of the root surfaces by mass flow and diffusion, from where it can be taken up by the plant subject to total uptake not exceeding the demand defined by the potential growth and critical K concentration in the crop at the time. Solution K in the resulting depletion zone around each root then re-equilibrates with the exchangeable form prior to the next increment in growth. With few exceptions, the model was in good agreement with weight and K concentration data for both spring wheat and 12 different vegetable crops in multi-level fertilizer experiments, and provided useful predictions of soil K levels above which no response would be expected under average UK conditions.

In the P model (PHOSMOD), the cultivated layer of soil is treated as three separate regions: one consisting of the total volume enriched by P diffusing from individual fertilizer granules, another enriched by any liquid starter fertilizer, and the remainder consisting of soil unaffected by any P applications (34). The model assigns each new increment in root growth to one or more of these regions. Soil P in each region is divided into solution, extractable and non-extractable fractions, with the Freundlich isotherm used to partition the solution and extractable forms. The instantaneous effects of the non-extractable fractions are small but can play a role in predicting long-term changes in soil P status. As uptake proceeds, solution and exchangeable P diffuse towards the root surfaces, creating cylindrical zones of depletion, the radii of which increase over successive days. These diffusive fluxes are estimated by Fick’s Law, and depend strongly on the water contents and tortuosity of the soil. In a later modification the fluxes are based on an ‘effective root radius’ to accommodate the enhancing effects of root hairs and mycorrhiza on P uptake. As with the other models, uptake is restricted if the total amount of P extracted by the roots exceeds demand on any one day, with an additional overarching constraint that no more than 20% of P from granular fertilizer can be recovered by the time of maturity to ensure consistency with observation. The model was validated using crop weight data from P response experiments for seven different vegetable crops in the UK, and for barley in Norway, although the corresponding predicted plant P concentrations tended to deviate somewhat. Scenario testing with the model confirmed previous observations that crops were most vulnerable to P deficiency during the early stages of growth when they were growing exponentially; that maximum responses of mature crops
to fresh granular applications of P fertilizer were always smaller on soils with a low P status; and that, in the long term, levels of extractable P will eventually equilibrate at a value specific for any particular soil (34).

Duncan published slightly simplified versions of both K and P models on the Internet, where they could be run interactively for different crops grown on a wide range of soil types under typical weather conditions for different parts of the world.

Interactions between N, P and K

A new model examining the interactive effects of N, P and K on the growth and nutrient contents of crops was developed by integrating routines from the separate N, P and K models described above (36). This used the principle of the Law of the Minimum to calculate actual daily increments in plant weight and uptake of each nutrient based on the one least able to meet the requirements of the plant for that day. Routines describing the inter-dependence of K and nitrate concentrations in the soil solution and other interactions between nutrients in the rooting zone that affect their availability to the crop were also included. Despite being based on the Law of the Minimum, the model was adaptable enough to predict the shapes of other types of response curve, including the Mitscherlich equation or the Multiple Limitation hypothesis, depending on soil and weather conditions. Tests showed that it accurately predicted the dry weights and N contents of four different vegetable crops grown with multiple combinations of N, P and K fertilizer levels at different stages of growth, but the corresponding P and K contents were somewhat less reliable. Despite these limitations, the model demonstrated that there was a strong relationship between the N and P contents of the crops over a wide range of fertilizer levels and that K uptake was suppressed at high plant P and low N contents, all of which were consistent with observation.

The principles underlying the relationship between the N and P contents of plants were further examined using a new model to characterize how their N:P ratios decline during growth under conditions of near-optimal nutrition (38). Using the assumption that plants consist only of separate growth-related and storage plus structural components, each with their own N:P ratios ($R_g$ and $R_s$ respectively), Duncan used his growth equation [2] to show that the N : P ratio for the whole plant ($R_w$) is related to plant weight according to

$$R_w = R_s + (R_g - R_s)/(1 + W),$$  \[7\]

with $R_w$ also linearly related to relative growth rate. Regression analysis showed that although $R_g$ and $R_s$ differ, their respective values are similar across a wide range of vegetable crops at all stages of growth. This indicates that the decline in the N : P ratios of whole plants can largely be explained by increases in the proportion of the storage plus structural-related component as they get bigger. The model also provided a good approximation of the relationships between leaf N and P concentrations in actively growing immature leaves of a wide range of wild species in independent surveys. Furthermore, the average values of $R_g$ were also close to those for terrestrial and freshwater autotrophs, suggesting that the same cellular processes may underlie the relationships between the N : P ratios of growing cells and their growth rates.
OTHER RESEARCH

Improving bedding plant production systems

Commercial production of bedding plants in individual peat plugs often relies on the use of environmentally harmful plant growth regulators. These are applied to create compact transplants with strong root systems that keep the plugs intact during robotic transplanting. Duncan devised a novel alternative method for enhancing the root : shoot ratio of the transplants by manipulating their liquid feed to maintain near-constant suboptimal nutrient concentrations in their tissues during pre-transplant growth. He developed a protocol based on equations [2], [3] and [5] for calculating the required changes in the N, P and K concentrations in their liquid feed, which was tested successfully (37). Implementation of the protocol in commercial production systems has allowed the quality of transplants to be maintained, while improving nutrient efficiency, reducing runoff and eliminating the use of many of the plant growth regulators previously used to manipulate the root : shoot architecture of the transplants.

Agro-hydrological modelling

Duncan maintained his interest in computer modelling throughout the later stages of his career and contributed to the development and improvement of several new models of water and nitrogen cycling in the soil–crop system. These included a novel dynamic model of water transfer in cropped soil that used a small time-step (0.001 day) to decouple the processes of evaporation, redistribution of water in the soil profile and its uptake by the roots (40). This allowed an integrated Richards equation approach to be used to calculate the changes in water content in any given layer in the profile solely from the corresponding changes in the layers immediately above and below it—a much simpler but equally accurate approach to the more complex spatial–temporal routines used conventionally. The required soil hydraulic properties can be measured directly, estimated from soil textural data using pedo-transfer functions, or derived by inverse modelling techniques (42). Opportunities for improving irrigation efficiency by using such models in conjunction with soil water sensors linked by wireless technology were subsequently described.

Finally, a new model (SMCR_N) for predicting the effects of N supply on the weight and N content of multiple arable and vegetable crops was also devised using many of the principles established in N_ABLE (33) and in EU-ROTATE_N, a related model for optimizing N use over crop rotations (Rahn et al. 2010). SMCR_N addressed many of the processes largely omitted in the earlier dynamic models, including the partition of N into fibrous roots and the damaging osmotic effects of excessive mineral N on crop growth, as well as simplifying the treatment of N mineralization in the soil (41). Further improvements were made by the replacement of the previous cascade algorithm for water transfer with that using the integrated Richards equation approach described above. The updated model consistently out-performed N_ABLE in predicting both the water and N dynamics in different soil–crop systems, providing an excellent balance between accuracy, simplicity and robustness. As such, it is an ideal tool for optimizing N and water use in different cropping environments and for providing reliable assessments of the impacts of different management strategies on nitrate leaching where diverse crops are grown. The model provides an important legacy to Duncan’s work on understanding and describing the complex interacting processes of N and water in the
soil–crop system and represents a fitting and highly successful culmination to an exceptional scientific career.

PRIVATE AND PROFESSIONAL LIFE

Duncan delighted in all aspects of soil science and plant nutrition and was an acknowledged expert in the discipline throughout the world. He had the enviable ability to analyse and disassemble complex problems into their component parts and to devise simple equations to explain the underlying processes involved. His models were always based on sound scientific principles and were never over-complicated, invariably relying on easily measured input data. This made them invaluable predictive tools for improving commercial practice, something recognized by ADAS soil scientists when they worked with Duncan to develop the first scientifically based fertilizer recommendations for vegetable crops in the UK. The open architecture of his models also encouraged leading international scientists to spend time at Wellesbourne adapting them to their own specific requirements. He was also an excellent communicator and was regularly invited to lecture on his work in countries all over the world (figure 2). The success of his work and his exceptional publication record led to the award of several prestigious medals for the outstanding quality of his academic work and for his contribution to the horticultural industry.
Outside the public eye, Duncan lived a quiet life in Stratford-upon-Avon, where he valued his privacy. He was never married—except to his research, which he pursued with passion and intensity. He had no time for holidays and seldom took time off for personal reasons. However, in company, Duncan took on a larger-than-life persona that was often described as mischievously eccentric. He was an outrageous gossip, regularly relaying deliberately exaggerated versions of the latest institute news. He had a special aversion to administration, which he believed was an unnecessary distraction, and his views on administrators often did not bear repeating! To fellow scientists, Duncan was a kind and generous colleague who demanded high standards but was always happy to credit their good work. He was a source of great encouragement to his colleagues, and particularly enjoyed mentoring young and up-and-coming scientists. He was always quick to befriend visitors from foreign countries; he loved learning about their experiences and cultural background, and he was always ready to support them from his own pocket if they got into financial difficulties. Throughout his lifetime, he was also a generous donator to many different charities, particularly those supporting homelessness.

In contrast, Duncan never saw the need to spend money on himself. His diet was basic to say the least, although in later years he did discover the delights of a local Thai restaurant (figure 2) even though he always claimed he only frequented it because the food was cheap. He seldom spent money on new clothes, and always felt more comfortable in his crumpled slacks and sports coat with ‘Dr Martens’ shoes, all of which he purchased in local markets. Indeed, when he was elected president of the International Committee of Plant Nutrition, two of his young female assistants had to drag him along to a well-known gentleman’s outfitter in Stratford to purchase a new suit for the presentation.

During his postgraduate studies in Aberdeen, Duncan had contracted a mild dose of TB, but thereafter enjoyed reasonable health until he started having problems with his heart. Just short of his ‘official’ retirement in 1992, he suffered a massive heart attack, but eventually recovered after ground-breaking open-heart surgery and continued to pursue his research up until the day before he died. In February 2010 his failing heart finally gave out, leaving soil science and plant nutrition much poorer.

**Honours, degrees and awards**

*Civic honour*

1993  Commander of the Most Excellent Order of the British Empire (CBE)

*Degrees*

1954  BSc (Chemistry), University of Liverpool
1957  PhD, University of Aberdeen
1972  DSc, University of Aberdeen

*Fellowships*

1977  Royal Society of Chemistry
1985  Royal Society
1986  Institute of Horticulture
Awards

1962 Sir Gilbert Morgan Medal, Society of Chemical Industry
1979 Research Medal, Royal Agricultural Society of England
2000 Lifetime Achievement Award, Grower of the Year Awards
2004 President’s Medal Winner, Institute of Horticulture

Other distinctions

1975 Chairman, ARC Modelling Group
1975–1977 Chairman, Agriculture Group of the Society of Chemical Industry
1978–1982 President, International Committee of Plant Nutrition
1990–1992 President, British Society of Soil Science
2004 Honorary Member, Association of Applied Biologists

Notable invited lectures

1982 Twelfth Blackman Lecture, University of Oxford
1982 Distinguished Scholars Lecture, Queen’s University Belfast
1985 Hannaford Lecture, University of Adelaide
1988 Shell Lecture, University of Kent
1989 Fortieth Amos Memorial Lecture, Wye College, University of London
1992 Presidential Address to the British Society of Soil Science, Silsoe

Appointments

1957 Research Fellow, University of Aberdeen
1959 Scientific Officer, National Vegetable Research Station
1966 Head of Chemistry, National Vegetable Research Station
1969 Honorary Lecturer in Chemistry, University of Birmingham
1973 Senior Principal Scientific Officer and Head of Soil Science, National Vegetable Research Station
1975 Honorary Lecturer in Plant Sciences, University of Leeds
1985 Visiting Professor of Plant Sciences, University of Leeds
1986 Honorary Professor of Agricultural Chemistry, University of Birmingham
1987 Individual merit promotion to Deputy Chief Scientific Officer (Unified Grade 5)

Other contributions

1974–1979 Technical Secretary and member of the Soil Science Committee of the Joint Consultative Organisation for Research and Development in Agriculture and Food
1975–1977 Member of Council of the Society of Chemical Industry
1975–1977 Member of various committees for the Royal Society
1979–1984 Member of the Royal Society Study Group on the Nitrogen Cycle
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AUTHOR PROFILE

Ian G. Burns

Having received his honours BSc chemistry degree in 1966 and his PhD in soil chemistry in 1971 at the University of Birmingham, Ian Burns started his research career in the Chemistry Section of the National Vegetable Research Station at Wellesbourne, where Duncan Greenwood was section head. His early work focused on predicting the losses of nitrate from vegetable and agricultural production systems at field to catchment scales, and he developed various models of nitrate leaching for this purpose. He also collaborated with Duncan on an occasional basis in these early years; some of his routines for water and nitrate transport in the soil became an integral part of the models on crop response to N that Duncan had started to develop at this time.

Thereafter he switched his attention to the physiological aspects of N nutrition and its effect on crop quality, while at the same time expanding his interests from field vegetables to glasshouse and ornamental crops, including nursery stock. In 1993, following the retirement of Duncan, he was appointed head of the new Soil and Environmental Sciences Department in the recently created Horticulture Research International at Wellesbourne. He became visiting professor in the Department of Horticultural Science at the University of Perugia in 2000, and professor in the School of Life Sciences at the University of Warwick in 2004. Since his retirement he continues to maintain close contacts with the university, where he mentors research students and contributes to ongoing research.

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