CHARLES ROGER SLACK
22 April 1937 — 24 October 2016
INTRODUCTION

Roger Slack was born and educated in the UK, but moved to Australia in 1962 and then on to New Zealand in 1970, where he spent the rest of his career. Together with Marshall (‘Hal’) Hatch (FRS 1980), he developed an essentially complete understanding of an alternative pathway of carbon flow in photosynthesis in higher plants, called the C4 pathway, extending the earlier pathway developed for C3 photosynthesis. With Grattan Roughan, he made important contributions to understanding plant lipid metabolism, and with Roger Haslemore to malting barley breeding.

As a committed experimentalist, with strong views of how research should be relevant to the users, Roger was very successful in developing an understanding of some of the basic metabolic processes in plants: photosynthesis and fatty acid synthesis. He focused on science, including both laboratory work and writing research papers, and disliked administrative duties.

* William.laing@plantandfood.co.nz
† An obituary for Roger Slack can be found at https://royalsociety.org.nz/who-we-are/our-people/our-fellows/obituaries/fellows-obituaries/charles-roger-slack/, which provides a scientific and personal perspective. Information in that obituary is contained within this memoir of Roger Slack’s life. Details of the Roger Slack Award, conferred by the New Zealand Society of Plant Biologists, can be found at http://plantbiology.science.org.nz/?pageprotect_id=38. Some information on that website is reproduced in this memoir.
EARLY LIFE

Charles Roger Slack, born on 22 April 1937 at Ashton under Lyne, near Manchester, was the only child of Albert and Eva Slack. His father, a keen gardener, involved his son in horticulturalist pursuits, including building a large glass house where Roger learned how to grow tomatoes, to propagate chrysanthemums and to debud them. Roger’s father died when he was 11 years old and he was then raised by his mother. He went to a grammar school at Audenshaw, Manchester, and, as a top-stream student, advanced rapidly to the sixth form. His horticultural experience probably influenced him to study agriculture and horticulture and then apply to the School of Agricultural Science at the University of Nottingham, although he first had to spend a year working on a farm. At the Sutton Bonnington campus, he met Pam Shaw, his future wife.

After university, Roger joined the Colonial Sugar Refinery labs at Brisbane, with Pam later joining him. They married in March 1963, and their children Andrew and Kathy were born soon after.

PROFESSIONAL CAREER, 1958–2000

Roger graduated with a BSc (Hons) from the School of Agricultural Science at the University of Nottingham in 1958 and then undertook a short course in biochemistry at University College, London, before returning to Nottingham and gaining a PhD (figure 1).

In 1962 he was recruited by the David North Plant Research Centre in Brisbane, Queensland, which was funded by the Colonial Sugar Refining Company (CSR), and began working on the biochemistry of sucrose accumulation by sugar cane (figure 2). This led to the discovery of the C4 pathway of photosynthesis. By 1970 he had transferred to New Zealand’s Plant Physiology Division (PPD) of the Department of Scientific and Industrial Research (DSIR) in Palmerston North. In New Zealand he worked on cool tolerance of C4 plants, fatty acid biosynthesis in plants and, later, on malting barley and its breeding.

Roger was transferred to Crop and Food Research (CFR) in July 1992 with the reorganization of the DSIR and the Ministry of Agriculture and Fisheries into a set of Crown Research Institutes (Government-owned research companies). This did not involve any immediate change in facilities, location or collaborators. Roger retired in 2000 and remained in Palmerston North until his death in 2016.

PHOTOSYNTHESIS: THE DISCOVERY OF THE C4 PHOTOSYNTHESIS PATHWAY

In the following, the discovery of the C4 pathway will be referred to as being by ‘Hatch and Slack’, the order most commonly used. The pathway of photosynthesis they elucidated will be referred to as the C4 pathway, because the first stable compound with $^{14}$CO$_2$ incorporated was a four-carbon acid with $^{14}$C at the C4 position. The other major pathway of photosynthesis, the C3 pathway, is so named because the first stable compound was a C3 acid, phosphoglyceraldehyde (PGA). In this case the $^{14}$C was found at the C1 carbon.

PHOTOSYNTHESIS

While all photosynthesis in higher plants follows the C3 pathway at some stage in the process, this pathway as a stand-alone pathway suffers from several problems that reduce
the rate of photosynthesis, especially at higher temperatures (e.g. above 25°C). First, the CO₂-fixing enzyme ribulose bisphosphate carboxylase/oxygenase (RuBisCO) has a low affinity for CO₂ and a low maximum rate of reaction (low turnover number). A lot of this enzyme is required to maximize photosynthesis. Second, this enzyme is competitively inhibited by O₂, again significantly reducing the rate of CO₂ fixation. Third, O₂ can react with ribulose bisphosphate instead of CO₂ and form phosphoglycolate, a serious inhibitor of the C₃ cycle. This phosphoglycolate must be removed and plants use the recovery pathway called photorespiration to convert two molecules of phosphoglycolate to PGA with the loss of one molecule of CO₂. These three factors reduce photosynthesis significantly in ambient air (ca 320 ppm CO₂ in 1966). C₄ photosynthesis (Furbank 2016; Sage 2016a), which evolved around 20 million years ago, is an add-on pathway which negates these problems, by effectively driving up the CO₂ concentration around RuBisCO and speeding its rate of reaction, thus reducing the amount of RuBisCO needed, preventing oxygen inhibition of CO₂ fixation and phosphoglycolate production, and so removing photorespiratory CO₂ production.

C₄ photosynthesis uses two major methods to avoid these problems. It uses a different fast O₂-insensitive CO₂-fixing enzyme called phosphoenolpyruvate carboxylase to initially fix CO₂ and produce a C₄ acid. While this enzyme does not produce a product that can be easily converted into reduced carbon (e.g. glucose) of use to the plant, the C₄ acid is transported to a second set of cells called the bundle sheath cells where RuBisCO is sequestered in
Roger’s achievement, along with Hatch, was to identify this C4 pathway and describe the detailed biochemistry, thus explaining how tropical C4 plants can grow faster in warm temperatures than their C3 cousins.

**Discovery of the C4 pathway**

Roger, with Hal Hatch, recognized several requirements for establishing a new biochemical pathway, especially in photosynthesis, where it was believed that the pathway had already been described. First, the proposed pathway had to be sufficiently general to show importance. Initially, the fixation of CO₂ into C₄ acids was regarded as resulting in no net fixation of CO₂, something done for biosynthetic reasons rather than carbon accumulation. The fixation of CO₂ by a C₃ acceptor resulted in a C₄ acid that was part of the tricarboxylic acid cycle. Thus, any further metabolism of the C₄ acid would result in release of the CO₂. Second, the kinetics of label transfer through the pathway had to be consistent with the pathway. Precursor compounds had to incorporate the label before later products. Third, all proposed reactions needed to have associated enzymes that could be measured and characterized. Fourth, extractable enzyme activities had to be compatible with the overall rates of the
pathway. Lastly, rates of reaction in isolated cells or organelles had to match those of the intact tissue. The requirements were necessary to avoid artefacts and false trails.

**Laying out the C4 photosynthetic pathway**

In 1966, a paper published by Hatch and Slack in the *Biochemical Journal* (1) provided strong evidence that the pathways of CO₂ fixation proposed by Calvin (ForMemRS 1959) and his group (*Bassham et al. 1950*) were incomplete, or did not describe the pathway of photosynthesis in all species of plants. In a review in 1964 discussing anomalies in labelling and kinetics, Bassham reviewed results observed with algae, barley and soybean, the pathways in the latter two higher plants (C3 in retrospect) having been shown compatible with the initial algal results, namely, the C5 sugar phosphate ribulose bisphosphate (RuBP) was carboxylated to form two molecules of the C3 phosphoglyceric acid (PGA) as the first product of photosynthesis (*Bassham 1964*). PGA was then reduced and interconverted to pentose phosphate, which was then phosphorylated to regenerate RuBP, completing the cycle. Excess carbon was either stored as starch or exported. All reported alternatives and anomalies could be satisfactorily explained, and photosynthesis by what later became known as C4 plants was not discussed. A brief mention was made on the role of malic acid as the first CO₂ fixation product, but this was dismissed as an insignificant pathway.

In their 1966 paper (1), Hatch and Slack worked with sugar cane and extended the work reported earlier by Kortschak and colleagues (*Kortschak et al. 1965*). These authors had reported that in sugar cane CO₂ appeared first in a C4 acid (malic acid) and only later in PGA and then hexoses. The Hatch and Slack paper reported detailed kinetics using ¹⁴CO₂ feeding and pulse–chase techniques and proposed a pathway whereby either phosphoenolpyruvate (PEP) or pyruvate was initially carboxylated to a C4 acid (oxaloacetic, malic or aspartic acids). They identified oxaloacetate as an initial product was labile and had to be identified using special techniques. The fixed carbon was then transferred into C3 intermediates, either by decarboxylation/refixation or by a hypothetical transcarboxylation. This paper added significantly to the original Kortschak *et al.* paper in terms of detail and validation, and Hatch and Slack then went on to fully establish and describe the C4 pathway. The conclusion of this paper was that fixed CO₂ first entered the C4 acid in the C4 position, and then moved to the C1 of PGA. They proposed the transfer occurred by a transcarboxylation reaction of unspecified form.

**C4 photosynthesis is found in a wide range of plants**

In a second paper (3), Hatch and Slack showed that what they had observed with sugar cane was a general phenomenon over different leaf ages (positions), and environmental conditions (CO₂ and light intensity) and also that initial fixation into C4 acids occurred in a range of other species in addition to sugar cane. Of the dicotyledonous species they examined, none showed C4 photosynthesis. In the case of monocotyledonous Gramineae, some were C4 (e.g. sugar cane, corn and *Paspalum dilatatum*), while others were clearly C3 (e.g. wheat and bamboo), separating the Gramineae into tropical and temperate species. Only one other non-gramineaceous species from the monocotyledons was observed to show C4 photosynthesis, namely sedge grass (*Cyperus* spp). Hatch and Slack observed that the C4 pathway was
Hatch and Slack then addressed the issue of how the detailed biochemistry of the pathway functioned (figure 3) (4). They established that PEP carboxylase was most likely the primary CO₂-fixing enzyme, and that enzymes from the C3 pathway of photosynthesis were also involved. However, they observed a low amount of ribulose 1,5-bisphosphate carboxylase (RuBisCO) in C4 plants compared with that in C3, but a large quantity of the enzyme that generated RuBP. They thus rationalized that a transcarboxylase was involved in passing the carbon from the C4 acid to PGA, with RuBP as the acceptor. They also identified that when the C4 acid lost its carbon, it probably generated pyruvate, and so a mechanism to generate PEP from pyruvate was needed. In this paper, they did not yet recognize that classical C4 plants have a different anatomy from C3 plants, and that the biochemistry of the C4 and the C3 aspects of photosynthesis were sequestered in different parts of the leaf.

The next step was the identification of the enzyme that converted pyruvate, the product of the decarboxylated C4 acid, to PEP. The sensitivity of this enzyme to extraction conditions and temperature explained why it had not been previously discovered; unusually it did not survive low-temperature extraction. This new enzyme, named phosphopyruvate synthetase (now known as pyruvate Pi dikinase) (2, 5), was purified and characterized, and the reaction shown to be pyruvate + ATP + Pi = PEP + AMP + PPI. While this reaction would thermodynamically be favoured in the reverse direction, removal of the products by PEP
carboxylase, pyrophosphatase and adenylate kinase (enzymes enriched in C4 plants (11)) would ensure that sufficient PEP was produced to sustain C4 photosynthesis. Amounts of the enzyme were similar to the rates of photosynthesis, and the enzyme was light-activated (6, 7). This discovery provided a firm footing for the C4 pathway, allowing for the regeneration of the original C4 CO₂ acceptor. Furthermore, physiological studies established the importance of light activation of other enzymes in the C4 pathway (8), providing further proof of the pathway. What was needed was the understanding of how the carbon flowed from the C4 acid to the C3 photosynthetic carbon reductive cycle. This came with the realization that C4 plants’ anatomy was distinct from that of C3 plants.

**DISCOVERY OF TWO INTERLOCKING PATHWAYS**

It was known that leaves of tropical grasses had a different anatomy, called the Kranz anatomy, from other leaves from temperate plants. Kranz anatomy plants show a distinct bundle sheath of cells around the vascular bundle. About this time, it was also observed by others that the chloroplasts in the bundle sheath cells of tropical grasses were different from the mesophyll chloroplasts. Among other differences, the bundle sheath chloroplasts contained starch, the mesophyll chloroplasts did not. Roger partially isolated these chloroplasts (10) and effectively showed that the bundle sheath chloroplasts were enriched in C3 enzymes, including RuBisCO, while the C4 enzymes were not chloroplast-associated. This suggested that there were different roles for the two types of chloroplasts.

Thus, the 1969 papers that described the distribution of enzymes in the mesophyll and the bundle sheath of maize were particularly significant in understanding C4 photosynthesis. The first, by Slack alone (9), established a method based on non-aqueous density gradient fractionation of the two types of chloroplasts in maize and showed the bundle sheath chloroplasts were enriched in traditional C3 cycle enzymes RuBisCO and the RuBP biosynthetic enzyme phosphoribulokinase, while the mesophyll chloroplasts contained C4 enzymes, pyruvate Pi dikinase and adenylate kinase. At this stage it was not yet recognized that the C4 pathway fed CO₂ to RuBisCO in the C3 pathway, raising the CO₂ concentration in the bundle sheath cells, and that separation of the biochemistry between two cell types was integral to the pathway. This paper was rapidly followed up by a second paper (10), in which the authors concluded ‘that the operation of the C4-dicarboxylate acid pathway requires the concerted function of the mesophyll and parenchyma-sheath chloroplasts. Enzymes that catalyse the formation of the carbon dioxide acceptor, phosphoenolpyruvate, and the incorporation of carbon dioxide into C4 dicarboxylate acids are present in mesophyll chloroplasts, whereas the parenchyma-sheath chloroplasts contain enzymes operative in the conversion of triose phosphates into fructose 6-phosphate’. The authors still considered the possibility of a transcarboxylation reaction to transfer carbon from the C4 acids, but were also willing to consider that malic enzyme decarboxylated malic acid to release CO₂ (and pyruvate, which was transferred back to the mesophyll chloroplasts) which would be fixed by RuBisCO in a bundle sheath located in the C3 cycle. However, the authors still did not regard this as a major route for carbon, mainly on the basis that the amount of RuBisCO was too low. It should be remembered that while oxygen inhibition of photosynthesis and stimulation of photorespiration had been established, the role of RuBisCO in this was not ascertained for another couple of years (Bowes et al. 1971; Ogren & Bowes 1971). This led
to an understanding that a major function of the C4 photosynthesis is to pump up the CO₂ concentration in the bundle sheath site of RuBisCO and thus prevent oxygen inhibition of photosynthesis and reduce photorespiration, as well as stimulating CO₂ fixation by saturating RuBisCO. This paper did recognize that the bundle sheath would be relatively inaccessible to CO₂ and that metabolites would need to be transferred rapidly between the two cell types. It is possible that the emphasis on a transcarboxylase activity came from Hal Hatch’s early PhD work on fat metabolism in plants and his discovery of a transcarboxylase activity associated with acetyl CoA carboxylase (Hatch & Stumpf 1961).

REVIEWING C4 PHOTOSYNTHESIS

In 1970, Hatch and Slack (12) reviewed the photosynthetic CO₂-fixation pathways and examined issues apparent with the C3 pathway, including the \( K_M(\text{CO}_2) \) for RuBisCO being unphysiologically high compared with the CO₂ concentration in equilibrium with the ambient atmosphere, carbon transport to and from the chloroplast, regulation of photosynthetic enzymes, the origin of glycolate in photorespiration and its metabolism. All these issues would be cleared up soon afterwards. They also reviewed the C4 pathway and its status in a long Progress in Phytochemistry article (13) in 1970. In that review (as of March 1969), they described the C4 pathway as consisting of two interconnecting pathways, but did not identify the exact mechanism of how the carboxyl carbon of the C4 dicarboxylic acid is transferred into the second cycle or the identity of the acceptor. Interestingly, they recognized that the evidence collectively supported their proposed model, but any one experiment only tentatively supported the model. They also credited others (Kortschak, Hart and Burr as well as Tarchevskii and Karilov) for making preliminary observations identifying C4 dicarboxylic acids as the initial products of photosynthesis. In this review they described the principles of identifying a metabolic pathway using radioactive CO₂ and analysed their published data in this light.

The review (13) analysed published data in terms of the path of the radiocarbon. At this stage there was still uncertainty on how the carbon was transferred from the C4 dicarboxylic acid to phosphoglyceric acid, and the authors argued ‘The fact that there are no significant losses of \(^{14}\text{CO}_2\) from leaves during pulse chase experiments would appear to be inconsistent with the possibility that transfer of radioactivity from the C-4 of dicarboxylic acids to 3-phosphoglycerate proceeds by decarboxylation then refixation of the released \(\text{CO}_2\)’. However, later they stated ‘a pool of bicarbonate derived by decarboxylation of C-4 dicarboxylic acids may be totally inaccessible to external CO₂’, thus leaving open the later true method of carbon transfer. Some discussion continues in this review on the possible acceptors and the transcarboxylation reaction. However, quantitatively, the transfer of carbon from the ‘C4-dicarboxylic acid accounts for essentially all the radioactivity entering 3-phosphoglycerate from \(^{14}\text{CO}_2\)’.

The authors also carefully analysed enzyme activities to ensure that their activity could explain the measured rates of photosynthesis, and concluded that all enzymes except for RuBisCO had more than sufficient activity. The low RuBisCO activity partially reflected the fact that tough cell walls of the inner bundle sheath are difficult to break to extract this enzyme, as well as later-to-be-discovered factors that control RuBisCO activity (e.g. RuBisCO activase). It also reflected the fact that less RuBisCO was needed in C4 plants compared with C3 plants, as the high CO₂ concentration in the bundle sheath chloroplast would drive the
carboxylation reaction at a faster rate than observed in C3 plants, with no competition from oxygen.

Acceptance of their discoveries in C4 photosynthesis

Roger was a fastidious biochemist, who carefully tested different options and methods to verify his work. It would not take long for the current decarboxylation/carboxylation model of C4 photosynthesis to be understood and accepted. However, the fact that the enzymes that generated RuBP were at a level sufficient to support photosynthesis and that these enzymes were located in the bundle sheath cells supported the idea that the C3 cycle was involved in C4 photosynthesis.

The solution to this conundrum was already at hand. Others (Bjorkman & Gauhl 1969) had reported sufficient RuBisCO activity and explained the difference as due to insufficient extraction and sub-optimal assay conditions. Hatch and Slack addressed two possibilities of a transcarboxylation and a decarboxylation/carboxylation using RuBisCO, both with RuBP as the acceptor, and came down in favour of the former, but were still open to the possibility of the latter. For example, high amounts of malic enzyme, which would decarboxylate malate and produce CO₂, were found in the bundle sheath cells, favouring the decarboxylation/carboxylation reactions. The regeneration of RuBP in the bundle sheath remained to be explained.

In their Progress in Phytochemistry review (13) Hatch and Slack also described fractionation data for separation of chloroplasts from the mesophyll and bundle sheath cells and how these data were consistent with the two sections of the C4 photosynthesis being separated. This was based on both extracted enzyme data and metabolite data. They also comprehensively drew in data from chloroplast anatomy, photorespiration, carbon isotope discrimination, oxygen inhibition of photosynthesis, light saturation and maximum rates of photosynthesis, CO₂ response curves of photosynthesis and the CO₂ compensation point to identify clear differences between C4 and C3 plants. All in all, this is a very comprehensive review, summarizing the state of knowledge about C4 (and C3) photosynthesis in 1970. Importantly they identified that the C4 pathway must have evolved separately in different families, something that is well accepted today. They also recognized that C4 plants were more tolerant of low water availability and were found in warmer regions because they transpire less per unit of CO₂ fixed (high water use efficiency).

They identified future work needed in several areas, including the transfer of the C4 carbon to the carbon acceptor, the mechanism of transport of metabolites between different cell types (mesophyll and bundle sheath cells), and the balance of adenosine 5'-triphosphate (ATP) to nicotinamide adenine dinucleotide phosphate (NADPH) production in the light reactions in the two cell types. This work was soon achieved in other laboratories.

Within a year things had changed. In a summarizing report of a conference held in Canberra in late 1970, Slack (14) reported: ‘In essence, the pathway consists of two interlinked cycles, one containing phosphoenolpyruvate (PEP) carboxylase, the other ribulose-1,5-phosphate (RuDP) carboxylase which are joined by a decarboxylation reaction’ and ‘It is recognised that the successful operation of this pathway is largely dependent upon the spatial separation of these two carboxylases, and on a Kranz type leaf anatomy’. Thus, in the short period between their first publication in 1966 and 1970, the full outline of the sugar cane C4 pathway was
established and accepted. The rest was filling in the details (Hibberd & Furbank 2016), in which Slack did not participate; he had moved to New Zealand.

Roger and Hal Hatch both moved on to new jobs in research after 1970, and while Hatch continued work in C4 photosynthesis at CSIRO in Canberra, Roger diverged into new fields. However, their initial elucidation of the C4 pathway was a very significant beginning of a new field that is culminating in serious efforts to develop a C4 pathway in rice, a C3 plant (von Caemmerer et al. 2012; Ermakova et al. 2020).

The importance of the C4 pathway of photosynthesis

To put the work of Hatch and Slack in historical context, it was only a few years previously, in the late 1940s and early 1950s, that the pathway of carbon in photosynthesis had been elucidated by Calvin’s group. This was regarded as the definitive pathway of photosynthesis, and criticism was not lightly entertained (Bassham 1964). Concerted efforts had been made to exclude the C4 acid malic acid as a possible pathway intermediate (Bassham et al. 1950). The enzyme RuBisCO had been identified as fraction I protein, purified and its catalysis of the reaction between CO2 and ribulose bisphosphate (RuBP) described (e.g. Weissbach et al. 1956). The Nobel Prize in chemistry had been awarded to Melvin Calvin ‘for his research on the carbon dioxide assimilation in plants’.

The 50th anniversary of the first papers detailing the C4 pathway was marked in 2016, and during that year several overviews of the discovery as well as surveys of the status of the C4 pathway were published (Furbank 2016; Gartner 2016; Hibberd & Furbank 2016; Sage 2016a,b). These both provide an historical perspective and refer to earlier memoirs written by Hatch and Slack. They also provide an analysis of the significance of C4 pathway plants from agricultural, historical, evolutionary and ecological perspectives.

The discovery of the C4 photosynthetic pathway came shortly after the C3 pathway was regarded as an established and finalized pathway (Bassham 1964) and so was a surprise to the scientific community. The C4 pathway of photosynthesis has evolved independently more than 66 times (Sage et al. 2012) over the last 15 million years in response to falling CO2 concentrations over millions of years. Many of the major crops are C4, including corn, sorghum, sugar cane and various sub-tropical and tropical pasture species. The advantage lies in the ability of C4 plants to grow faster than C3 plants under low-CO2 (i.e. historic less than 300 ppm preindustrial concentrations) and high-temperature conditions by significantly enhancing photosynthesis. This is achieved by pumping CO2 to high concentrations at the site of RuBisCO, thus stimulating CO2 fixation, strongly reducing the direct oxygen inhibition of photosynthesis and the competing oxygenase activity where O2 reacts with RuBP instead of CO2 to produce phosphoglycolate (PG), a C2 compound, as well as PGA. The PG is recovered through photorespiration, a pathway to convert PG back to PGA with the release of one molecule of CO2 for every two molecules of PG produced (Bowes et al. 1971; Ogren & Bowes 1971). As the initial CO2-fixing enzyme, PEP carboxylase, has a higher affinity for CO2 (lower $K_M(CO_2)$) and higher maximum velocity ($V_{max}$) than RuBisCO, and is not inhibited by oxygen, C4 plants can photosynthesize more efficiently at low CO2 than C3 plants and need less protein (nitrogen) to do it.
In an excellent summary of the discovery of C4 photosynthesis and the significance of the work, Hibberd and Furback pointed out the importance of C4 plants in agriculture and in the natural environment, especially in hot dry conditions, and that C4 plants out-yield C3 plants significantly under these conditions (Hibberd & Furbank 2016). For this reason, efforts are being made to improve the efficiency of rice (C3) by converting it to C4 photosynthesis.

A personal account of the events surrounding the discovery of the C4 pathway was written by Hatch and Slack in 1998 (21). This is of special interest as it describes their thinking and the processes leading up to these major discoveries.

**Transition to New Zealand**

After the elucidation of the C4 pathway, in the late 1960s Roger and Hal were directed by CSR management to concentrate on problems of sugar production. Coca Cola® had complained that sugar from Townsville caused a haze to appear in bottles of their drink. This was due to a dextran produced by bacteria that infected juice exuding from cane stalks damaged in the burning before harvest. Roger searched for a dextranase to remove the haze, but the problem was solved by not burning the cane field prior to harvest. However, he did find a use for the dextranase in toothpaste to reduce dental plaque formation.

Roger was looking for new jobs after the David North Research Centre owners, CSR, closed down research into C4 photosynthesis. The small Plant Physiology Division (PPD) of the DSIR in Palmerston North, New Zealand, was recruiting prominent scientists to take up short-term National Research Advisory Council fellowships to celebrate the opening of their new climate laboratory facility (a 24-room phytotron, since demolished in 2020). During his sabbatical at the David North Research Centre, Dr Grattan Roughan, a PPD staff member, proposed Roger be one of these fellows, and Roger arrived in Palmerston North to start his fellowship on 14 October 1970. He then joined the permanent staff of PPD on 14 April 1971 (figure 4).

Roger was seen by Ken Mitchell, the director of PPD, as a key researcher to recruit to PPD. The focus at PPD was on developing tropical and sub-tropical grasses as crops for the temperate New Zealand environment. These grasses could resist summer drought but would not survive the cool winters of temperate New Zealand. Resistance to chilling injury was a major focus for the biochemists at PPD, and it was realized that these sub-tropical species had C4 photosynthesis! Roger joined the effort in 1970. The aim was to discover why these plants were chilling-sensitive. Initially working on biochemically focused chilling injury in these species (15, 16), Ken Mitchell insisted that his staff contribute to field work, and Roger and others also assisted in field trials (18, 19).

**Fatty acid biosynthesis with Grattan Roughan**

Around this time, the consensus was reached that lipid domains in cell membranes were critical in chilling injury, and that lipid composition determined whether the membrane underwent phase changes that affected membrane permeability: the hypothesis suggested more desaturated lipids would aid to protect the membrane.

At this time (early 1970s), how plants synthesized desaturated lipids was only a hypothesis. Roger worked with Grattan Roughan to understand the detailed pathway of desaturated lipid
biosynthesis. As was evident from Roger’s work on the C4 pathway, they also followed the same principles in studying lipid metabolism: ‘Much useful information can be obtained by carefully studying the kinetics of incorporation of specifically labelled precursors into lipids in vivo. Indeed, it could be argued that a knowledge of the metabolism occurring within the
intact cell is essential before a meaningful interpretation can be made of results obtained using cell-free preparations. This is a quote from their review of their work in 1982 (20). Grattan Roughan writes of his time working closely with Roger in the online obituary.

The theory of plant cold tolerance developed during the 1970s was that membrane properties determined chilling tolerance and membrane properties were determined by fatty acid composition. Unsaturated fatty acids were critical to membrane properties, but how these unsaturated fatty acids were synthesized was unknown. Grattan Roughan had observed earlier that fatty acids synthesized de novo within chloroplasts of pumpkin leaves were exported to the endoplasmic reticulum, incorporated into phosphatidylcholine, desaturated there and transported to the chloroplasts for assembly particularly of the major chloroplast membrane lipids. Grattan Roughan persuaded Roger to join him in studying plant fatty acid metabolism, and together the pair confirmed and extended these results using maize leaves and published in the Biochemical Journal in 1975 (17). They established that fatty acid desaturation required cooperation of both the chloroplasts and the cytoplasmic endoplasmic reticulum and that oleate was only desaturated after being incorporated into glycerolipids.

This work established the key role of phosphatidyl choline in the endoplasmic reticulum in the formation of linolenic acid and largely explained how the characteristic acyl composition of the different plant lipids is determined. Roger’s work with Grattan Roughan on fatty acid synthesis established that cooperation occurred between the chloroplast and the cytoplasm, and oleate desaturation occurred after it was incorporated into glycerolipids. They established a new scheme for leaf glycerolipid synthesis that included those synthesized in the prokaryotic pathway entirely within chloroplasts, while a second set of lipid species were synthesized through the eukaryotic pathway, involving cooperation between different cell compartments. This work resulted in a second major review (20).

**Malting barley breeding with Roger Haslemore**

From about 1980, Roger—with his strong views on the necessity for applicability of research—focused on practical research to improve the processing quality of malting barley varieties bred for the New Zealand environment. He established methods to measure malting and brewing quality via screening larger numbers of barley breeding lines, and later used greenhouse and climate laboratory facilities to accelerate the production of early generation lines through single seed descent. He also measured grain and wort β-glucan levels, and identified proanthocyanidin-free barleys. Roger also worked on bread wheats using polyacrylamide gel electrophoresis to separate wheat glutenin and gliadin proteins to identify varieties as potential parents.

In the early 1990s, Roger and his colleagues became part of the newly formed Crown Research Institute of Crop & Food Research, and Roger’s focus changed yet again as he decided to take a more active role in breeding high quality malting barley varieties. This included making crosses from parents selected from the laboratory testing and using glasshouses and controlled environment rooms in the climate laboratory at Palmerston North to accelerate the small-scale production of early and middle generation lines. From the mid-1990s through to his retirement in 2000, he distanced himself somewhat from the laboratory testing and concentrated on becoming a full-time barley breeder, which included all of the physical work involved with planning, sowing and harvesting of trials plus the labour-intensive work of evaluating agronomic and disease attributes during their growth cycles.
Roger was focused on practical, applied research later in his career, and using his biochemical knowledge and understanding to develop new barley cultivars was a logical progression. His strong scientific focus upon the underlying biochemical characterization of quality is also a lasting legacy that is still applied within all crop breeding programmes.

**PERSONAL LIFE**

Pam and Roger with the children explored New Zealand avidly. They were keen trampers (bush walkers) and completed several South Island scenic walks. I accompanied them with my daughter on a three-day hike on the Matemateāonga Track near the Whanganui River. Roger was also a keen fly fisherman, a skilful woodworker, home handyman and gardener. He involved himself in conservation work, improving the sand-stabilizing cover at the mouth of the Manawatu River, as well as bird watching throughout New Zealand. He took up sailing on Morton Bay and, on moving to Palmerston North in 1970, he built a sailing dinghy in spite of Palmerston North being 40 kilometres from the sea (Tasman Ocean).

Roger and Pam were actively involved in the study of birds, travelling extensively in New Zealand, Australia and the United Kingdom in their search. He was an active member of the Ornithological Society of New Zealand (now Birds New Zealand), specializing in Arctic waders. These shorebirds breed in the Arctic and high latitudes of the Northern Hemisphere and migrate to estuaries in the Southern Hemisphere for the austral summer. Following his retirement, Roger made regular fortnightly visits to the Manawatu River Estuary at Foxton to study these waders. He carefully observed and counted the bird numbers and details of leg bands, and sent his results to the authorities compiling nationwide counts for publication. He sighted two rare (for New Zealand) Arctic waders, greenshank and marsh sandpiper (both *Tringa* species), at the same time on 13 January 2013.

He also observed New Zealand’s native breeding waders. Wrybill numbers at Manawatu Estuary were carefully monitored and visits were made to gravel areas of the Manawatu River to observe the activities of dotterel species. He supported the Pukokoro Miranda Naturalist’s Trust located on the coast of the Firth of Thames, the major centre for the study of wading birds in New Zealand, and he visited their mudflats and wetlands whenever he could. Roger had a strong interest in the conservation and recovery of endangered native birds. To a friend and fellow bird watcher, an abiding memory is of ‘Roger at the estuary pushing forth into the near gale westerly with sand stinging his feet but determined to find the rare wader that was always going to be on the next shoreline’.

His health deteriorated as he got older, requiring a hip replacement in 1998, which was very successful and allowed resumption of many activities. However, replacement of the other hip in 2005 was not as successful. He had a mild heart attack in 2009 and was diagnosed with congestive heart failure and sub-optimal kidney function. Rejecting the chance to undergo dialysis, he eventually died from kidney failure.

**CONCLUSION**

Roger’s work in developing an understanding of the C4 photosynthesis pathway has resulted in a huge legacy of research papers on the C4 pathway. With rising temperatures, potential drought and pressure on food production, there is considerable effort being placed on
understanding the evolution of the C4 pathway and developing methods to convert current C3 plants such as rice into C4 plants. This is the ultimate practical application of his early work. When it is successful, the value of his early basic research will be huge.

Roger was an approachable and likeable man, with strong passions about hands-on science. He had little patience for administration, officialdom and committee work, and preferred to spend his time in the lab. Grattan Roughan, friend and colleague who worked alongside Roger for many years in New Zealand, writes:

Roger was an exceptional hands-on experimentalist, sharp as a tack and a most agreeable colleague to work alongside. He had co-authored two authoritative reviews on plant biochemistry in *Annual Reviews in Plant Physiology* (1970 and 1982) [12, 20] in totally different fields yet behaved as if unaware of his scientific reputation. Both the C-4 pathway of photosynthesis and the 2-pathways of lipid synthesis in plants are standard fare in modern textbooks where due credit is given. It could be argued that the original contentious discoveries only became respectable following Roger’s involvement. (From the online obituary.)

Roger was a committed experimentalist with high technical and analytical skills (figure 5). He made his experiments work the first time. He regarded time in the laboratory to be reserved for experimental work, with writing papers and reading to be done at home. He also wanted his work to be relevant to the end-users, to be able to see an application for the results.
Roger was awarded the Goldacre Award by the Australian Society of Plant Physiologists in 1970 for his work on discovering C4 photosynthesis. He then shared the Charles F. Kettering award in photosynthesis research from the American Society of Plant Physiologists in 1980 and the Rank Prize for Nutrition in 1981 with Hal Hatch and Hugo Kortschak (figure 6). The citation for the latter prize read: ‘For their outstanding work on the mechanism of photosynthesis which established the existence of an alternative pathway for the initial fixation of carbon dioxide in some important food plants. This work provided the basis for advances in plant physiology and biochemistry.’

He was elected Fellow of the Royal Society of New Zealand in 1983 and of the Royal Society of London in 1989. The citation for the Royal Society of London reads:

Dr Slack is distinguished for his contributions to the understanding of photosynthetic carbon assimilation and the mechanism of polyunsaturated fatty acid synthesis in higher plants. He contributed equally with Dr M.D. Hatch in establishing the basic principles of mechanism and function of an alternative photosynthetic carbon assimilation process now known as the C4 pathway. He was primarily responsible for identifying several of the key enzymes involved in C4 photosynthesis and determining their inter and intracellular location. Later, in collaboration with Dr P.G. Roughan, he demonstrated that oleoyl phosphatidylcholine rather than oleoyl-CoA is the major substrate for C18 polyunsaturated fatty acid synthesis in plants. These studies led to a novel hypothesis for the origin of the diacylglycerol moieties of different lipids.
In 2007 the New Zealand Society of Plant Biologists renamed their annual award for outstanding plant physiologists the Roger Slack Award. It is named after Dr Roger Slack in recognition of his outstanding contribution as a plant biologist.

Degrees
1958 BSc (Hons), School of Agricultural Science at the University of Nottingham
1962 PhD, University of Nottingham

Fellowships
1983 Royal Society of New Zealand Te Apārangi
1989 Royal Society London

Other distinctions
1970 Goldacre Award, the Australian Society of Plant Physiologists
1980 Charles F. Kettering award in photosynthesis research, the American Society of Plant Physiologists
1981 Rank Prize in Nutrition

Appointments
1962 Scientist, David North Plant Research Centre in Brisbane, Queensland, Australia
1970 Visiting Scientist, Plant Physiology Division, DSIR, Palmerston North, New Zealand
1971 Scientist, Plant Physiology Division, DSIR, Palmerston North
1992 Scientist, Crop and Food Research, Palmerston North

ACKNOWLEDGEMENTS

I would like to thank the various people who contributed to this memoir. These include Pam Slack, Grattan Roughan, Roger Haslemore, Bill Griffin and Lindsay Davies. Hal Hatch read an early version, and Ian Brooking and John Christeller constructed the bibliography.

The frontispiece portrait is from the Royal Society’s collection. All other photographs were kindly provided by Pam Slack.

REFERENCES TO OTHER AUTHORS

Bassham, J. A. 1964 Kinetic studies of the photosynthetic carbon reduction cycle. Annu. Rev. Plant Physiol. 15, 101–120. (doi:10.1146/annurev.pp.15.060164.000533)
Bassham, J. A., Benson, A. A. & Calvin, M. 1950 The path of carbon in photosynthesis: VII the role of malic acid. J. Biol. Chem. 185, 781–787.
Bjorkman, O. & Gauhl, E. 1969 Carboxydismutase activity in plants with and without beta-carboxylation photosynthesis. Planta 88, 197–203. (doi:10.1007/BF00385062)
Bowes, G., Ogren, W. L. & Hageman, R. H. 1971 Phosphoglycolate production catalyzed by ribulose diphosphate carboxylase. Biochem. Biophys. Res. Commun. 45, 716–722. (doi:10.1016/0006-291X(71)90475-X)
Ermakova, M., Danila, F. R., Furbank, R. T. & von Caemmerer, S. 2020 On the road to C4 rice: advances and perspectives. Plant J. 101, 940–950. (doi:10.1111/tpj.14562)
Furbank, R. T. 2016 Walking the C4 pathway: past, present, and future. J. Exp. Bot. 67, 4057–4066. (doi:10.1093/jxb/erw161)
Gartner, S. 2016 The discovery of C4 photosynthesis, *Achievements*. CSIROpedia. See https://csiropedia.csiro.au/the-discovery-of-c4-photosynthesis/ (accessed 31 March 2020).

Hatch, M. & Stumpf, P. 1961 Fat metabolism in higher plants. XVI: Acetyl coenzyme A carboxylase and acyl coenzyme A-malonyl coenzyme A transcarboxylase from wheat germ. *J. Biol. Chem.* 236, 2879–2885.

Hibberd, J. M. & Furbank, R. T. 2016 In retrospect: fifty years of C₄ photosynthesis. *Nature* 538, 177–179. (doi:10.1038/538177b)

Kortschak, H. P., Hartt, C. E. & Burr, G. O. 1965 Carbon dioxide fixation in sugarcane leaves. *Plant Physiol.* 40, 209–213. (doi:10.1104/pp.40.2.209)

Ogren, W. & Bowes, G. 1971 Ribulose diphosphate carboxylase regulates soybean photorespiration. *Nat. New Biol.* 230, 159–160. (doi:10.1038/newbio230159a0)

Sage, R. F. 2016a A portrait of the C₄ photosynthetic family on the 50th anniversary of its discovery: species number, evolutionary lineages, and Hall of Fame. *J. Exp. Bot.* 67, 4039–4056. (doi:10.1093/jxb/erw156)

Sage, R. F. 2016b Tracking the evolutionary rise of C₄ metabolism. *J. Exp. Bot.* 67, 2919–2922. (doi:10.1093/jxb/erw137)

Sage, R., Sage, T. & Kocacinar, F. 2012 Photorespiration and the evolution of C₄ photosynthesis. *Annu. Rev. Plant Biol.* 63, 19–47. (doi:10.1146/annurev-arplant-042811-105511)

von Caemmerer, S., Quick, W. P. & Furbank, R. T. 2012 The development of C₄ rice: current progress and future challenges. *Science* 336, 1671–1672. (doi:10.1126/science.1220177)

Weissbach, A., Horecker, B. L. & Hurwitz, J. 1956 The enzymatic formation of phosphoglyceric acid from ribulose diphosphate and carbon dioxide. *J. Biol. Chem.* 218, 795–810.

## Bibliography

The following publications are those referred to in the text. A full bibliography is available online at http://dx.doi.org/10.1098/rsbm.2019.0007.

1. 1966 (With M. Hatch) Photosynthesis by sugar-cane leaves: a new carboxylation reaction and the pathway of sugar formation. *Biochem. J.* 101, 103–111. (doi:10.1042/bj1010103)

2. 1967 (With M. D. Hatch) The participation of phosphoenolpyruvate synthetase in photosynthetic CO₂ fixation of tropical grasses. *Archiv. Biochem. Biophys.* 120, 224–225. (doi:10.1016/0003-9861(67)90618-2)

3. (With M. Hatch & H. Johnson) Further studies on a new pathway of photosynthetic carbon dioxide fixation in sugar-cane and its occurrence in other plant species. *Biochem. J.* 102, 417–422. (doi:10.1042/bj1020417)

4. (With M. Hatch) Comparative studies on the activity of carboxylases and other enzymes in relation to the new pathway of photosynthetic carbon dioxide fixation in tropical grasses. *Biochem. J.* 103, 660–665. (doi:10.1042/bj1030660)

5. 1968 (With M. D. Hatch) A new enzyme for the interconversion of pyruvate and phosphopyruvate and its role in the C₄ dicarboxylic acid pathway of photosynthesis. *Biochem. J.* 106, 141–146. (doi:10.1042/bj1060141)

6. The photoactivation of a phosphopyruvate synthase in leaves of *Amaranthus palmeri*. *Biochem. Biophys. Res. Commun.* 30, 483–488. (doi:10.1016/0006-291X(68)90077-6)

7. 1969 (With M. D. Hatch) Studies on the mechanism of activation and inactivation of pyruvate, phosphate dikinase: a possible regulatory role for the enzyme in the C₄ dicarboxylic acid pathway of photosynthesis. *Biochem. J.* 112, 549–558. (doi:10.1042/bj1120549)

8. (With M. D. Hatch & T. A. Bull) Light-induced changes in the content of some enzymes of the C₄ dicarboxylic acid pathway of photosynthesis and its effect on other characteristics of photosynthesis. *Phytochemistry* 8, 697–706. (doi:10.1016/S0031-9422(00)85841-0)

9. Localization of certain photosynthetic enzymes in mesophyll and parenchyma sheath chloroplasts of maize and *Amaranthus palmeri*. *Phytochemistry* 8, 1387–1391. (doi:10.1016/S0031-9422(00)85902-6)
(10) (With M. D. Hatch & D. J. Goodchild) Distribution of enzymes in mesophyll and parenchyma-sheath chloroplasts of maize leaves in relation to the C4-dicarboxylic acid pathway of photosynthesis. *Biochem. J.* **114**, 489–498. (doi:10.1042/bj1140489)

(11) 1970 (With D. Graham, M. D. Hatch & R. M. Smillie) Light-induced formation of enzymes of the C4-dicarboxylic acid pathway of photosynthesis in detached leaves. *Phytochemistry* **9**, 521–532. (doi:10.1016/S0031-9422(00)85683-6)

(12) (With M. D. Hatch) Photosynthetic CO2-fixation pathways. *Annu. Rev. Plant Physiol.* **21**, 141–162. (doi:10.1146/annurev.pp.21.060170.001041)

(13) (With M. Hatch) The C4-dicarboxylic acid pathway of photosynthesis. In *Progress in Phytochemistry* (ed. L. Reinhold & Y. Liwschitz), pp. 35–106. London, UK: Wiley-Interscience.

(14) 1971 The C4 pathway: assessment. In *Photosynthesis and photorespiration* (ed. M. Hatch, C. Osmond & R. Slatyer), pp. 297–301. New York, NY: Wiley-Interscience.

(15) 1974 (With P. G. Roughan & H. C. Bassett) Selective inhibition of mesophyll chloroplast development in some C4-pathway species by low night temperature. *Planta* **118**, 57–73. (doi:10.1007/BF00390503)

(16) (With A. O. Taylor & H. G. McPherson) Plants under climatic stress. VI: Chilling and light effects on photosynthetic enzymes of sorghum and maize. *Plant Physiol.* **54**, 696–701. (doi:10.1104/pp.54.5.696)

(17) 1975 (With P. G. Roughan) The kinetics of incorporation in vivo of [14C]acetate and [14C]carbon dioxide into the fatty acids of glycerolipids in developing leaves. *Biochem. J.* **152**, 217–228. (doi:10.1042/bj1520217)

(18) 1976 (With B. J. Forde, P. G. Roughan, R. M. Haslemore & M. N. McLeod) Growth of tropical and temperate grasses at Palmerston North. *N. Z. J. Agric. Res.* **19**, 489–498. (doi:10.1080/00288233.1976.10420980)

(19) (With B. J. Forde, P. G. Roughan & H. C. M. Whitehead) Growth of tropical and temperate grasses at Palmerston North. *N. Z. J. Agric. Res.* **19**, 135–142. (doi:10.1080/00288233.1976.10426759)

(20) 1982 (With P. G. Roughan) Cellular organization of glycerolipid metabolism. *Annu. Rev. Plant Physiol.* **33**, 97–132. (doi:10.1146/annurev.pp.33.060182.000525)

(21) 1998 (With M. D. Hatch) C4 photosynthesis: discovery, resolution, recognition and significance. In *Discoveries in plant biology*, vol. 1 (ed. S.-D. Kung & S.-F. Yang), pp. 175–196. Singapore: World Scientific: Singapore.