

*Pedogenesis, nutrient dynamics, and  
ecosystem development: the legacy of T.W.  
Walker and J.K. Syers*

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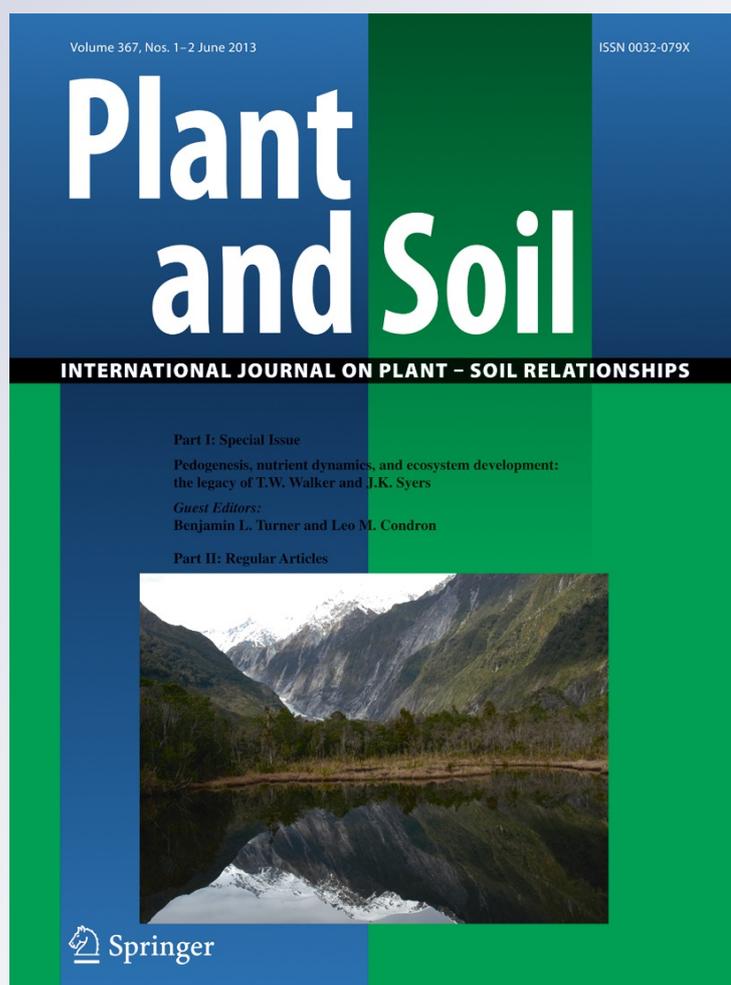
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## Pedogenesis, nutrient dynamics, and ecosystem development: the legacy of T.W. Walker and J.K. Syers

Benjamin L. Turner · Leo M. Condon

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Almost four decades ago, T.W. Walker and J.K. Syers published a paper in the journal *Geoderma* that transformed our understanding of nutrient availability and limitation in terrestrial environments. The paper, entitled *The fate of phosphorus during pedogenesis*, distilled data from four New Zealand soil chronosequences to show that soil nutrients followed predictable but fundamentally different patterns during long-term ecosystem development. Specifically, Walker and Syers observed that nitrogen is absent from most parent materials and enters ecosystems through biological nitrogen fixation. As a result, nitrogen concentrations are low in young soils but increase rapidly during the early stages of ecosystem development. In contrast, they argued that phosphorus is derived almost exclusively from the parent material, so phosphorus concentrations are greatest in young soils but decline continuously during pedogenesis as phosphorus is lost in runoff at a greater rate than it is replenished by bedrock weathering. Importantly, Walker and Syers also demonstrated that the decline in total phosphorus occurs

in parallel with chemical transformations of the phosphorus remaining in the soil. These changes include a decline in primary mineral phosphate (principally apatite) and an accumulation of phosphorus in organic and secondary mineral forms associated with metal oxides.

The changes in soil nutrients predicted by the Walker and Syers model have important ecological consequences, because nutrient availability shapes the productivity, composition, and diversity of biological communities (Vitousek 2004). A key prediction of the model, now supported by a number of different lines of evidence, is that the nutrient most limiting to primary production varies during ecosystem development, with nitrogen limitation on young, weakly weathered soils, co-limitation by nitrogen and phosphorus on moderately weathered soils, and phosphorus limitation on old, strongly weathered soils. Indeed, in the absence of rejuvenating disturbance, phosphorus limitation can be sufficiently strong on old soils to cause a decline in the biomass and productivity of the vegetation, termed 'retrogression' (Wardle et al. 2004; Peltzer et al. 2010). Long-term phosphorus depletion also has other important consequences for plant communities, including changes in species composition and an increase in vascular plant diversity as ecosystems age (Richardson et al. 2004; Wardle et al. 2008; Laliberté et al. 2013). The Walker and Syers model therefore provides a strong conceptual framework for investigating the causes and consequences of changes

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in nutrient availability during long-term ecosystem development, and provides one of the few theoretical models linking biogeochemical cycles with the ecology of biological communities.

Walker and Syers died recently within a few months of each other. Professor Thomas William Walker passed away on the 8th of November 2010, aged 94 years. Professor John Keith Syers passed away a few months later on the 15th of July 2011, aged 72 years. Obituaries for both T.W. Walker and J.K. Syers have been published in the New Zealand Soil News, and we encourage readers to visit the following links:

[http://nzsss.science.org.nz/documents/soil\\_news/Feb%202011-%20print.pdf](http://nzsss.science.org.nz/documents/soil_news/Feb%202011-%20print.pdf)

[http://nzsss.science.org.nz/documents/soil\\_news/August%202011-%20print.pdf](http://nzsss.science.org.nz/documents/soil_news/August%202011-%20print.pdf)

This special issue celebrates the lives of T.W. Walker and J.K. Syers by bringing together a collection of reviews and original research articles on pedogenesis, nutrient availability, and ecosystem ecology. The special issue is devoted to the memory of these two scientists and their scientific legacy — our understanding of nutrient dynamics during long-term ecosystem development.

### **The development of the Walker and Syers model of phosphorus transformations during pedogenesis**

From his obituaries, it is clear that T.W. Walker was influenced profoundly by Hans Jenny's book *Factors of Soil Formation* (Jenny 1941). Jenny brought mathematical rigor to the science of pedology, and proposed that five factors interact to determine the nature of a soil: climate, organisms, relief, parent material, and time. This was captured in Jenny's iconic equation:  $s=f(cl, o, r, p, t)$ . Walker recognized the importance of isolating time as a factor of soil formation and deliberately pursued "those rare monosequences which, intensively studied, should indicate the most important trends and processes in pedogenesis" (Walker 1965).

The dynamic landscape of New Zealand provided fertile ground for this work, and a succession of chronosequences (and, indeed, several other types of sequence) was studied by members of Walker's group. For example, of the four key chronosequences

summarized in Walker and Syers (1976), Peter Stevens conducted MSc and PhD theses on the iconic Franz Josef chronosequence (Stevens 1963, 1968), Keith Syers's postdoctoral studies included the Manawatu sequence of coastal sand dunes (Syers and Walker 1969a, b; Syers et al. 1970), Alistair Campbell and Thian Tan studied the Reefton terrace chronosequence (Tan 1971; Campbell 1975), and Ranjit Shah studied a chronosequence in alluvial greywacke in the Canterbury region (Shah 1966; Shah et al. 1968; Syers et al. 1969). In addition, John Adams studied soil sequences on granitic parent material in the northern part of the South Island of New Zealand (Adams et al. 1975; Adams and Walker 1975), although his data were not included in Walker and Syers (1976). A list of graduate students supervised by T.W. Walker is given below.

Walker recognized early on the central importance of phosphorus in shaping patterns of other nutrients and plant communities during long-term ecosystem development. He noted that "In these studies [of soil chronosequences], phosphorus emerges as perhaps the key element in pedogenesis, because of its great ecological significance. It is the one major element in soil organic matter that must be supplied almost entirely from the parent material" (Walker 1965). Other elements were not neglected, however. Walker was a strong advocate of the importance of phosphorus in the promotion of nitrogen fixation in agricultural systems, for example, and his early models predicted changes in carbon, nitrogen, phosphorus, and sulfur, in organic matter during pedogenesis (Fig. 1a).

The development of the Walker and Syers model can be traced through a series of earlier published versions. For example, an initial model separated soil phosphorus into three operationally-defined pools, depicting the rapid accumulation of organic phosphorus at the expense of primary mineral phosphate, and the continual accumulation of occluded inorganic phosphate associated with secondary minerals (Fig. 1b). This reflects insight into the dynamics of inorganic phosphate during long-term pedogenesis, principally the switch from primary mineral phosphate in young soils to occluded secondary mineral phosphate in old soils. As the methodology for phosphorus fractionation was further refined, principally through the studies of Julian Williams, a graduate student under Walker's supervision, an additional pool of non-occluded secondary inorganic phosphate was

incorporated into the model, which followed a similar pattern to the organic phosphorus pool (Williams and Walker 1969). With the incorporation of new data from additional sequences, the now classic Walker and Syers (1976) model of phosphorus transformations emerged (Fig. 1c). The final model differed from the earlier models in a number of ways, including the initial rate of organic phosphorus accumulation, the relatively long period of high organic phosphorus, and the extension of the model to long time scales, predicting a “terminal steady state” at which point phosphorus outputs would be balanced by phosphorus inputs from the atmosphere. In the terminal steady state, soils would contain only organic and occluded inorganic phosphorus in similar amounts.

Walker and Syers were careful to predict that their model would apply only to stable surfaces under humid climates. They did not expect it to apply where relatively high rates of erosion promoted rejuvenation of the soil phosphorus pool, or in drier areas where leaching was insufficient to deplete the soil of phosphorus (e.g. semi-arid grasslands). The limits of the Walker and Syers model have been explored extensively, including along chronosequences under a variety of climates and on a variety of parent materials (Peltzer et al. 2010). Perhaps the most thorough assessment has been by Peter Vitousek and colleagues along the Hawaiian Island soil chronosequence, a series of volcanic islands differing in age from hundreds to millions of years where the state factors of soil formation can be constrained with a remarkable degree of accuracy (summarized in Vitousek 2004). However, despite a number of refinements and adaptations, the Walker and Syers model has proved remarkably robust and there is now evidence that the expected patterns in soil nutrients and associated plant communities occur consistently in a wide variety of soils and ecosystems (Tiessen et al. 1984; Crews et al. 1995; Cross and Schlesinger 1995; Peltzer et al. 2010). The effects can manifest over vastly different time scales, however: from a few thousand years under the warm and wet climate at Haast, New Zealand (Turner et al. 2012) to millions of years under the semi-arid climate of the volcanic chronosequence in northern Arizona, USA (Selmants and Hart 2010).

Although Walker and Syers were involved primarily in elucidating pedogenic changes in soil nutrients, they had a clear interest in the application of their findings to agricultural systems, and also recognized the ecological

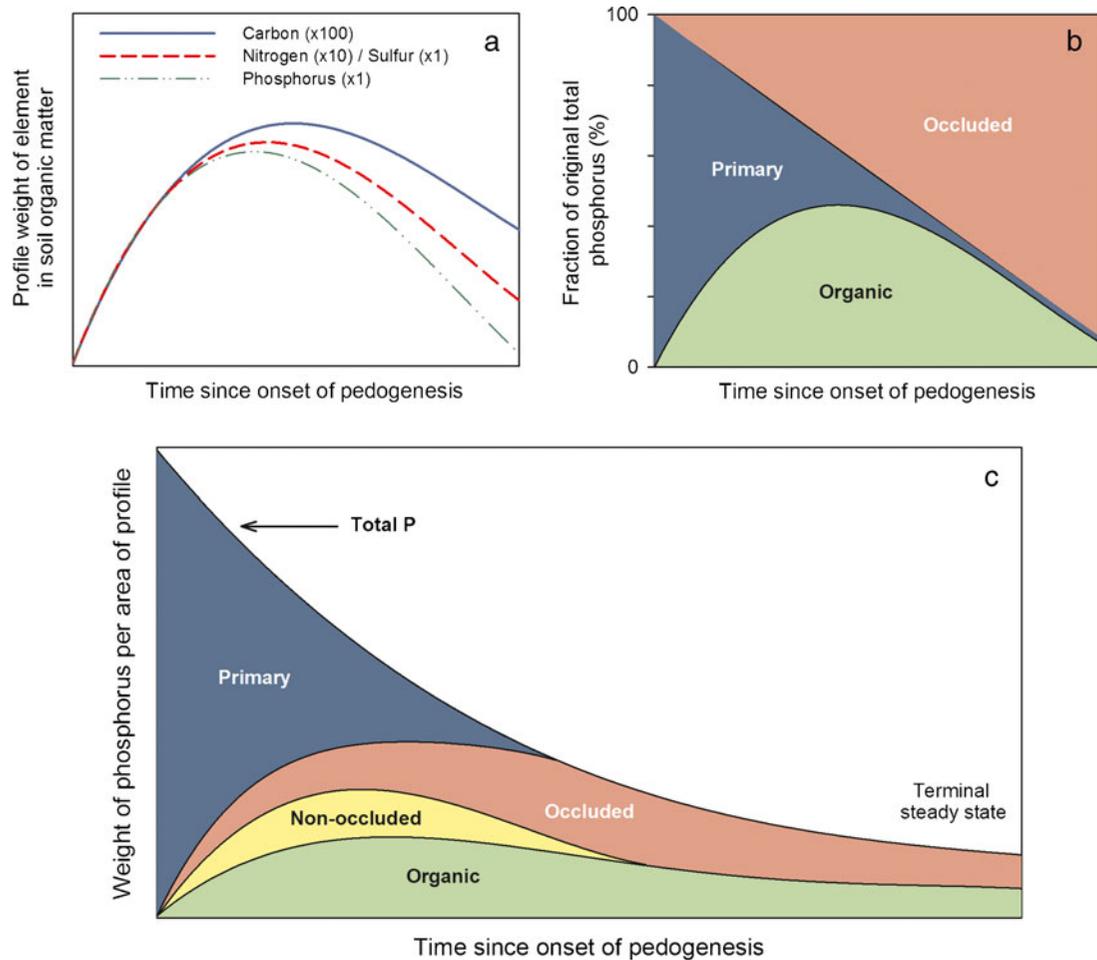
significance of their work. For example, Walker explained when phosphorus was most likely to limit nitrogen fixation and accumulation in the soil (when all available inorganic phosphate is converted to organic phosphorus in the rooting zone) and noted that these conditions favor plants with low phosphate requirements or adaptations that allow them to obtain phosphorus from recalcitrant forms (Walker 1965). In fact, the patterns of nutrient availability predicted by the model have profound ecological consequences, including for nutrient limitation (Vitousek 2004), forest retrogression (Wardle et al. 2004), plant nutrient acquisition strategies (Lambers et al. 2008), and vascular plant diversity (Wardle et al. 2008; Laliberté et al. 2013). Most work so far has investigated the implications for plant communities, but recent studies suggest that the below-ground consequences are equally as profound (Williamson et al. 2005; Tarlera et al. 2008; Jangid et al. 2013).

### Overview of the special issue

This special issue contains contributions grouped around three main themes:

1. Soil chronosequences and nutrient transformations during pedogenesis
2. The importance of the Walker and Syers (1976) model for plant community ecology
3. Changes in below-ground microbial communities during long-term ecosystem development

Given the apparent broad applicability of the Walker and Syers model, it is fitting that a wide range of soil chronosequences are represented in this special issue. These include the iconic Franz Josef chronosequence that was so central to the original Walker and Syers model (Atkin et al. 2013; Turner et al. 2013), as well as the Ecological Staircase chronosequence studied by Hans Jenny and colleagues (Jenny et al. 1969) at Mendocino, California, USA (Izquierdo et al. 2013). The special issue also contains articles describing research along the Swedish Island chronosequence (Hyodo et al. 2013; Jackson et al. 2013; Lagerström et al. 2013), the Haast dune chronosequence in New Zealand (Eger et al. 2013; Jangid et al. 2013), the Maluxa sand chronosequence in the Leningrad region of Northwest Russia (Celi et al. 2013), and terrace chronosequences in Oregon, USA (Lindeburg et al.



**Fig. 1** The development of the Walker and Syers (1976) conceptual model of phosphorus dynamics during long-term ecosystem development. Panel **a** shows T.W. Walker's early model of changes in carbon, nitrogen, and phosphorus in organic matter during pedogenesis (redrawn and modified from Fig. 2 in Walker 1965). Organic carbon continues to accumulate following the onset of the decline in soil organic phosphorus, because productivity continues to increase initially (before eventually declining) and decomposition is slowed by the increasingly acidic pH. Panel **b** shows an early depiction of changes in soil phosphorus pools during pedogenesis (redrawn and modified from Fig. 4 in Walker 1965). The three major pools of phosphorus were defined operationally by their mode of quantification. Thus, the primary mineral phosphorus pool (here "Primary" but " $P_a$ " in the original figure) was defined as the pool of inorganic phosphate extracted in 0.5 M  $H_2SO_4$  without prior ignition (Walker and Adams 1958); this acid-extractable pool included primary mineral phosphate (i.e. apatite) as well as some inorganic phosphate bound to metal oxides. The organic phosphorus pool (here "Organic" but " $P_o$ " in the original figure) was defined as the difference between phosphorus extracted in 0.5 M  $H_2SO_4$  from ignited and unignited samples (Saunders and Williams 1955). Although mainly consisting of organic phosphorus, this ignition pool can also include some inorganic phosphorus associated with

secondary minerals, especially in strongly-weathered soils (Williams and Walker 1967). The occluded pool (here "Occluded" but " $P_f$ " in the original figure) was defined as inorganic phosphate insoluble in 0.5 M  $H_2SO_4$  after ignition (i.e. the difference between total phosphorus determined by HF- $HNO_3$  digestion and phosphorus extracted in 0.5 M  $H_2SO_4$  after ignition). A subsequent development of this model (Williams and Walker 1969) incorporated non-occluded secondary inorganic phosphate, which followed a similar pattern to the organic phosphorus pool. Panel **c** shows the now classic conceptual model of changes in soil phosphorus fractions during pedogenesis (redrawn and modified from Fig. 1 in Walker and Syers 1976). As noted by Walker and Syers (1976), the conceptual model in panel **c** differs from earlier models (e.g. in panel **a**) by (i) the initial rate of organic phosphorus accumulation, (ii) the relatively long period of high organic phosphorus, and (iii) the extension of the model to a "terminal steady state", where losses of phosphorus are balanced by inputs from the atmosphere. In the original figure, a vertical line in the center indicated 22,000 years pedogenesis along the Franz Josef chronosequence, at which point the primary mineral phosphate pool was exhausted. The dates of the older stages of the Franz Josef chronosequence have now been re-evaluated, however, and the 22,000 year soils are now considered to be approximately 120,000 years old (Almond et al. 2001)

2013), Waitutu, New Zealand (Coomes et al. 2013), and Väserbotten, Sweden (Vincent et al. 2013).

Several articles in the special issue deal with factors that influence the trajectory of ecosystem development. For example, the initial phosphorus content in the parent material has a profound effect on subsequent patterns of nutrient limitation, and this is assessed in detail for the first time in this issue (Porder and Ramachandran 2013). Temporal changes in soil phosphorus and its availability to plants are also influenced by rates of dust deposition (Eger et al. 2013) and fire (Hyodo et al. 2013; Jackson et al. 2013; Lagerström et al. 2013), while pan formation and consequent waterlogging can promote retrogression on old, strongly-weathered surfaces (Coomes et al. 2013). Paradoxically, the earliest stages of pedogenesis can be phosphorus limited, because most phosphorus is bound up in primary minerals (e.g. Schlesinger et al. 1998) and this earliest stage is examined in this issue along a young chronosequence of sand surfaces in Northwest Russia (Celi et al. 2013). As a state factor, climate profoundly influences rates of pedogenesis, and this is explored here for alluvial terrace sequences in the Oregon Coast Range, USA (Lindeburg et al. 2013).

One of the strengths of the Walker and Syers model is the detailed prediction of changes in the chemical nature of soil phosphorus during pedogenesis, which has been verified by a number of subsequent studies (e.g. Tiessen et al. 1984; Crews et al. 1995; Cross and Schlesinger 1995). This is extended in the special issue by a study of soil phosphorus chemistry along the Ecological Staircase chronosequence of marine uplift terraces at Mendocino, California, USA. This chronosequence and associated pygmy forest was studied intensively by Hans Jenny and colleagues and is considered to be a classic example of the influence of iron pan formation on forest retrogression (Jenny et al. 1969). Izquierdo et al. (2013) show here that phosphorus limitation also plays a key role, although the nature of the parent material means that even soils on relatively young terraces can be considered pedogenically old.

One significant development in soil phosphorus chemistry since the publication of the Walker and Syers model has been the ability to obtain much more detailed information on the organic phosphorus pool than was possible previously. Organic phosphorus has conventionally been considered to represent a homogenous pool of limited availability to plants, but in fact consists of a variety of chemical compounds that vary widely in their behavior and bioavailability in soil (Condon et al. 2005).

The application of solution phosphorus-31 nuclear magnetic resonance ( $^{31}\text{P}$  NMR) spectroscopy to soil chronosequences in New Zealand has revealed that the composition of the soil organic phosphorus varies markedly during pedogenesis (McDowell et al. 2007; Turner et al. 2007), which adds further complexity to the patterns of phosphorus transformations in the Walker and Syers model. Changes in soil organic phosphorus composition have been studied along only a limited number of sequences so far, but an article in this issue extends the available data to an additional chronosequence of uplift terraces in Scandinavia (Vincent et al. 2013).

The consequences of the Walker and Syers model for nutrient limitation of primary production (i.e., a switch from nitrogen limitation to phosphorus limitation during long-term ecosystem development) are widely accepted, yet have rarely been tested experimentally (Vitousek and Farrington 1997; Laliberté et al. 2012). Of particular interest is therefore an article in this issue describing a fertilization study along the Waitutu chronosequence of marine uplift terraces in New Zealand (Coomes et al. 2013), which yields results consistent with predictions of the Walker and Syers model. The physiological consequences of nutrient limitation for plant communities are examined in three studies in the special issue, including leaf respiration along the Franz Josef chronosequence (Atkin et al. 2013), root phosphatase activity along a phosphorus gradient under tropical montane forest on Mount Kinabalu (Kitayama 2013), and leaf traits along the Swedish Islands chronosequence (Lagerström et al. 2013). Two further studies on the Swedish Islands demonstrate the importance of this sequence for our understanding of factors influencing ecosystem development. First, stable nitrogen isotopes are used to assess patterns of nitrogen fixation and supply along the sequence (Hyodo et al. 2013), while a second study used experimental plant removal to quantify the influence of mosses on litter decomposition (Jackson et al. 2013).

In contrast to the relatively well-understood patterns in plant communities during long-term ecosystem development, few studies have assessed the consequences of long-term pedogenesis for below-ground microbial communities. Four articles explore this in the special issue. First, a major review examines patterns of mycorrhizal community composition during ecosystem development (Dickie et al. 2013). A previous conceptual model

proposed that root symbiotic associations undergo broad shifts during long-term pedogenesis, from dominance by arbuscular mycorrhizal plants on young soils, ecto- and ericoid mycorrhizal plants on intermediate aged soils, to non-mycorrhizal plants on the oldest, most strongly-weathered soils (Lambers et al. 2008). However, Dickie et al. (2013) argue that mycorrhizal types do not demonstrate predictable patterns along soil chronosequences. A second article reveals the significance of the soil microbial biomass as a phosphorus pool and driver of phosphorus transformations during long-term ecosystem development (Turner et al. 2013). Soil microbial biomass contains approximately twice as much phosphorus as the above-ground biomass for the majority of the Franz Josef chronosequence, which is likely to have important consequences for plant–microbe competition in mature ecosystems. A third article examines the response of the soil microbial community to phosphorus stress in a tropical montane forest sequence on Mount Kinabalu, revealing a consistent physiological response to phosphorus stress in above and below-ground communities (Kitayama 2013). Finally, a fourth article reports detailed information on changes in bacterial community composition along the 6500 year Haast dune chronosequence (Jangid et al. 2013). Although only a handful of studies have examined changes in soil microbial communities over long-term ecosystem development, results suggest that bacterial taxa undergo patterns of change that are consistent with those observed in above-ground plant communities.

The Walker and Syers model enables us to understand and predict spatial and temporal patterns of nutrient availability and limitation, and provides a testable framework within which to examine factors regulating the productivity, distribution, and diversity of plants and microbes in the terrestrial environment. Indeed, the Walker and Syers model remains one of the only models to unite dynamic changes in biogeochemical cycles with the development of above and below ground biological communities. The model has important implications for the development of novel agricultural systems that seek to optimize inputs of nitrogen and phosphorus fertilizers, and is of increasing importance as we seek to understand the consequences of climate change, rising atmospheric carbon dioxide concentrations, increasing rates of atmospheric nitrogen deposition, and other anthropogenic disturbances of biological communities and biogeochemical cycles. We hope that the fifteen articles in this special

issue provide a fitting tribute to the lives and scientific legacy of T.W. Walker and J.K. Syers, and will inspire further research on this fascinating topic.

**Acknowledgments** We thank Hans Lambers, Editor-in-Chief of Plant and Soil, for his support for the Walker and Syers special issue and for comments on this introduction. We are grateful to Dr Philip Tonkin, Dr John Adams, and Dr Trish Fraser for their contributions, and we thank the New Zealand Soil News for providing photographs of T.W. Walker and J.K. Syers.

### Walker and Syers Bibliography

This bibliography contains journal articles and book chapters on soil chronosequences or soil phosphorus authored by T.W. Walker and/or J.K. Syers. It is not an exhaustive list of their scholarly output, but includes only those publications related to nutrient dynamics during long-term ecosystem development. The articles are listed in chronological order to illustrate the progress of research and development of the model of phosphorus transformations during pedogenesis. We also list MSc and PhD theses on soil chronosequences authored by students supervised by T.W. Walker (see below). Note that J.K. Syers also published a number of articles on phosphorus in lake sediments and the chemistry and transport of phosphorus in runoff that are not included here.

Walker TW, Adams AFR (1958) Studies on soil organic matter: I. influence of phosphorus content of parent materials on accumulations of carbon, nitrogen, sulfur, and organic phosphorus in grassland soils. *Soil Sci* 85: 307–318

Walker TW, Adams AFR (1959) Studies on soil organic matter: 2. Influence of increased leaching at various stages of weathering on levels of carbon, nitrogen, sulfur, and organic and total phosphorus. *Soil Sci* 87: 1–10

Walker TW, Thapa BK, Adams AFR (1959) Studies on soil organic matter: 3 Accumulation of carbon, nitrogen, sulfur, organic and total phosphorus in improved grassland soils. *Soil Sci* 87: 135–140

Walker TW (1965) The significance of phosphorus in pedogenesis. In: Hallsworth EG (ed) *Experimental Pedology*. Butterworths, London. p 295–315

Syers JK, Williams JDH, Campbell AS, Walker TW (1967) The significance of apatite inclusions in soil phosphorus studies. *Soil Sci Soc Am Proc* 31: 752–756

Williams JDH, Walker TW (1967) Comparison of 'ignition' and 'extraction' methods for the determination of organic phosphorus in rocks and soils. *Plant Soil* 27: 457–459

Williams JDH, Syers JK, Walker TW (1967) Fractionation of soil inorganic phosphate by a modification of Chang and Jackson's procedure. *Soil Sci Soc Am Proc* 31: 736–739

Shah R, Syers JK, Williams JDH, Walker TW (1968) The forms of inorganic phosphorus extracted from soils by *N* sulphuric acid. *NZ J Agric Res* 11: 184–192

Syers JK, Williams JDH, Walker TW (1968) The determination of total phosphorus in soils and parent materials. *NZ J Agric Res* 11: 757–762

Syers JK, Walker TW (1969) Phosphorus transformations in a chronosequence of soils developed on wind-blown sand in New Zealand. I. Total and organic phosphorus. *J Soil Sci* 20: 57–64

Syers JK, Walker TW (1969) Phosphorus transformations in a chronosequence of soils developed on wind-blown sand in New Zealand. II. Inorganic phosphorus. *J Soil Sci* 20: 318–324

Syers JK, Shah R, Walker TW (1969) Fractionation of phosphorus in two alluvial soils and particle-size separates. *Soil Sci* 108: 283–289

Syers JK, Williams JDH, Tyner EH, Walker TW (1969) Primary and secondary origin of “non-extractable” soil inorganic phosphorus. *Soil Sci Soc Am Proc* 33: 635–637

Williams JDH, Walker TW (1969) Fractionation of phosphate in a maturity sequence of New Zealand basaltic soil profiles: 1. *Soil Sci* 107: 22–30

Williams JDH, Walker TW (1969) Fractionation of phosphate in a maturity sequence of New Zealand basaltic soil profiles: 2. *Soil Sci* 107: 213–219

Williams JDH, Syers JK, Walker TW (1969) Apatite transformations during soil development. *Agrochimica* 13: 491–501

Stevens PR, Walker TW (1970) The chronosequence concept and soil formation. *Q Rev Biol* 45: 333–350

Syers JK, Adams JA, Walker TW (1970) Accumulation of organic matter in a chronosequence of soils developed on wind-blown sand in New Zealand. *J Soil Sci* 21: 146–153

Syers JK, Williams JDH, Walker TW, Chapman SL (1970) Mineralogy and forms of inorganic phosphorus in a graywacke soil-rock weathering sequence. *Soil Sci* 110: 100–106

Syers JK, Campbell AS, Walker TW (1970) Contribution of organic carbon and clay to cation exchange capacity in a chronosequence of sandy soils. *Plant Soil* 33: 104–112

Williams JDH, Syers JK, Walker TW, Rex RW (1970) A comparison of methods for the determination of soil organic phosphorus. *Soil Sci* 110: 13–18

Jackson ML, Gibbons FR, Syers JK, Mokma DL (1972) Eolian influence on soils developed in a chronosequence of basalts of Victoria, Australia. *Geoderma* 8: 147–163

Mokma DL, Jackson ML, Syers JK, Stevens PR (1973) Mineralogy of a chronosequence of soils from greywacke and mica-schist alluvium, Westland, New Zealand. *NZ J Sci* 16: 769–797

Walker TW (1974) Phosphorus as an index of soil development. *Trans 10th Int Congr Soil Sci* 6: 451–457

Runge ECA, Walker TW, Howarth DT (1974) A study of Late Pleistocene loess deposits, South Canterbury, New Zealand. Part 1. Forms and amounts of phosphorus compared with other techniques for identifying paleosols. *Quat Res* 4: 76–84

Adams JA, Walker TW (1975) Some properties of a chrono-toposequence of soils from granite in New Zealand, 2. Forms and amounts of phosphorus. *Geoderma* 13: 41–51

Goh KM, Rafter TA, Stout JD, Walker TW (1976) The accumulation of soil organic matter and its carbon isotope content in a chronosequence of soils developed on aeolian sand in New Zealand. *J Soil Sci* 27: 89–100

Walker TW, Syers JK (1976) The fate of phosphorus during pedogenesis. *Geoderma* 15: 1–19

#### List of graduate student theses supervised

The following is a list of MSc and PhD theses supervised by T.W.

Walker at Lincoln College, University of Canterbury (now Lincoln University), Canterbury, New Zealand. The theses are given in chronological order, to illustrate the progression of research on soil chronosequences and phosphorus chemistry. The theses are accessible through the Lincoln University Library (<http://library.lincoln.ac.nz/>).

Mouat MCH (1957) Competition for nutrients between grasses and white clover (MSc thesis)

Stevens PR (1963) A chronosequence of soils and vegetation near the Franz Josef Glacier (MSc thesis)

Williams JDH (1965) Forms of soil phosphate in some genetically-related New Zealand soils (PhD thesis)

Shah R (1966) The fractionation of phosphorus in two soils of different ages (MSc thesis)

Woon L-C (1967) Effect of particle size on the availability of phosphorus in Nauru rock phosphate, greywacke and basaltic rocks (MSc thesis)

Ritchie IM (1968) A study of forest ecosystem development (MSc thesis)

Stevens PR (1968) A chronosequence of soils near the Franz Josef Glacier (PhD thesis)

Adams JA (1970) A study of soil sequences in relation to the growth of *Pinus radiata* in Nelson (PhD thesis)

Tan TO (1971) Studies on a chronosequence of terrace soils near Reefton (MSc thesis)

Baker RT (1974) Chemical nature and distribution of soil organic phosphate in two chronosequences of soils (PhD thesis) O'Connor PW (1974) A study of a set of hydrosequences and chronosequences in Manawatu County (PhD thesis)

Campbell AS (1975) Chemical and mineralogical properties of a sequence of terrace soils near Reefton, New Zealand (PhD thesis)

Archer AC (1976) Pedogenesis and vegetation trends in the efulvic and eldefulvic zones of the north-east Ben Ohau Range, New Zealand (PhD thesis)

Williams MR (1978) Molecular weight distribution and chemical nature of organic matter in soil chronosequences (PhD thesis)

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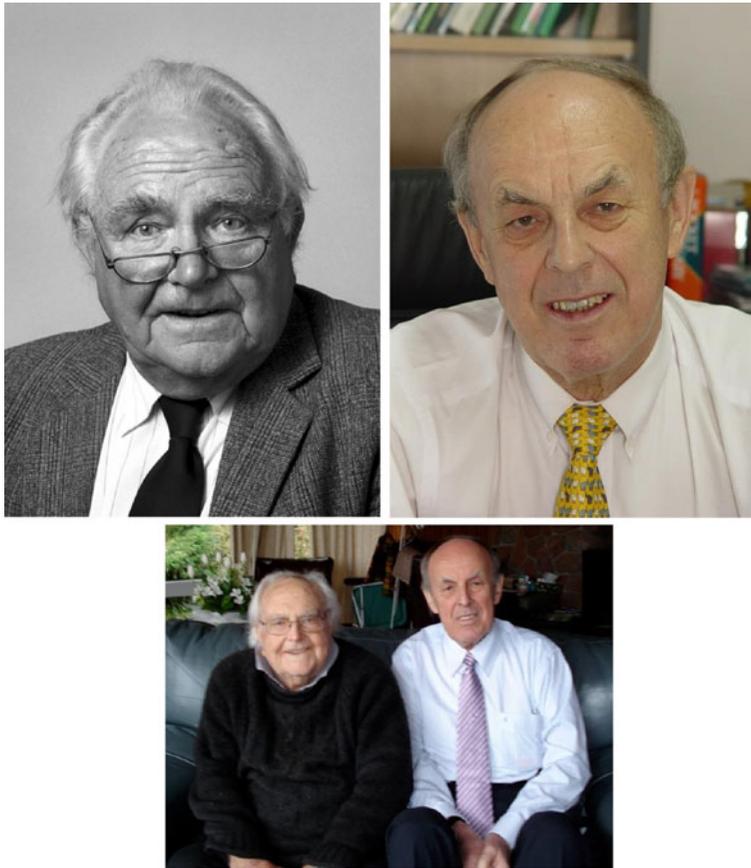
Almond PC, Moar NT, Lian OB (2001) Reinterpretation of the glacial chronology of South Westland, New Zealand. *N Z J Geol Geophys* 44:1–15

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Campbell AS (1975) Chemical and mineralogical properties of a sequence of terrace soils near Reefton, New Zealand. PhD thesis, Lincoln College, University of Canterbury, New Zealand

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- Coomes D, Bentley W, Tanentzap A, Burrows L (2013) Soil drainage and phosphorus depletion contribute to retrogressive succession along a New Zealand chronosequence. *Plant Soil*. doi:10.1007/s11104-013-1649-5
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Professor Thomas William Walker (left), who died on the 8th of November 2010, aged 94 years, and Professor John Keith Syers (right), who died on the 15th of July 2011, aged 72 years. The images show T.W. Walker on his retirement from Lincoln College, New Zealand, in

1979 and J.K. Syers at his desk at Naresuan University, Thailand. The third image (bottom) shows T.W. Walker and J.K. Syers together for the last time in 2010 in Christchurch, New Zealand. Photographs are reproduced by courtesy of the New Zealand Soil News.