
Integrated approach to nutrient cycling monitoring

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There are two issues of social importance in relation to nutrient cycling. The first is the *depletion* of nutrients in croplands and rangelands. The second is the *overabundance* of nutrients through the enhancement of inputs, particularly in freshwater bodies and coastal systems, which results in loss of biodiversity and ecosystem services through eutrophication. Nutrient cycling encompasses 15 or so elements, each with multiple chemical forms and phases, four media (air, soil, biomass and water) and many transformation and transport processes. It is not cost-effective to monitor them all, even in intensive research sites. The two key elements involved in both fertility loss and eutrophication are nitrogen and phosphorus; thus their changes in nutrient pools and fluxes need to be monitored. Key anthropogenic nitrogen contributions are through atmospheric deposition and liquid waste streams. A sensitive impact indicator is the nitrogen saturation index, which rises abruptly when the absorptive capacity of the landscape is exceeded. Key anthropogenic phosphorus inputs are agriculture and, in certain locations, mining and industry. Monitoring phosphorus fertilizer application rates and local-to-regional nutrient balances is useful because phosphorus is highly conserved in ecosystems. Measurement of nutrients associated with sediment fluxes in rivers is important for both nitrogen and phosphorus, as well as for carbon balance. To place current fluxes and perturbations in perspective, historical records have to be established. Additionally, tools such as isotopic tracers,

which can be used unequivocally to differentiate between the natural and anthropogenic components of nutrient cycles, need to be explored.

Introduction

Element interactions have been studied since the middle of the nineteenth century. Von Liebig was one of the early pioneers investigating the role of soil crop nutrition. He stated that 'by the deficiency or absence of one necessary constituent, all others being present, the soil is rendered barren for all those crops to the life of which the one constituent is indispensable'.¹ This concept, termed the 'law of the minimum', has been central in biology since the 1840s even despite some awareness of multiple resource limitation. An oceanographer, Redfield, proposed a stoichiometric model in 1958, which required the elements carbon, nitrogen, phosphorus, sulphur and some others to be available in distinct proportions for the formation of organic compounds in biological processes. This concept of stoichiometry is now widely applied to explain the basic principles of element interactions and to explore the consequences of human perturbations for the main element cycles. It is believed that there are 31 elements essential for the functioning of animals, microbes and plants.² Of these, the macronutrients, carbon, hydrogen, oxygen, nitrogen, phosphorus and sulphur, are the principal constituents of living tissue and comprise 95% of the living biosphere.³ The productivity of many ecosystems is limited by the supply of biologically available nitrogen (N) and phosphorus (P).^{4,5} The mandate of SAEON is to develop and sustain a dynamic South African observation and research network that provides the understanding, based on long-term information, needed to address environmental issues. Six scientific themes have been chosen as key areas by the SAEON Technical Steering Committee. Five of these, namely, carbon/nutrient cycles, water,

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Table 1. The effect of human activity on global biogeochemical cycles, particularly nitrogen and phosphorus.⁷

Cycle	Percentage change [100 × (perturbed – natural)/natural]
Carbon	+13
Nitrogen	+108
Phosphorus	+400
Sulphur	+113
Water	+16
Sediments	+200

soils, biodiversity, and climate/atmosphere, all impinge on the need to have an integrated approach to nutrient cycling monitoring.

Nutrients are held in ecosystems in a variety of chemical forms that are constantly being cycled through the atmosphere, the biosphere and the soil. Two concepts are needed for understanding the cycling of nutrients. Nutrients can either be stored in pools or they can be moved between pools, this process being referred to as a nutrient flux. The size of the pools and the rate of the flux are what determine the extent of nutrient cycling in an ecosystem. These two processes require a different monitoring approach. Factors controlling these flux rates, such as soil moisture, temperature and species diversity, have formed the basis of many global ecosystem studies. Very limited nutrient cycling research has been conducted in South Africa linking terrestrial and aquatic environments, as these research communities do not often work together; SAEON can play a key role in facilitating new research, especially in the area of understanding and monitoring the impact of phosphorus sediment fluxes.

Increasing public awareness of the impact of anthropogenic change on ecosystem function will increase demands to improve the interface between scientific findings and policy intervention. This has already followed the release of the Southern African Millennium Ecosystem Assessment in 2004.⁶ Human activity has altered all global biological cycles, notably those of nitrogen and phosphorus (Table 1),⁷ with the degree of change being dependent on the nature of the alteration at any particular location. Data shown in Table 1 indicate the percentage change in nutrient stocks as a result of industrialization. The productivity of many ecosystems is limited by the supply of biologically available (or reactive) nitrogen.^{4,5} For many years now, anthropogenic activities have been altering the nitrogen cycle in the atmosphere, on land and in water, locally and globally.^{8,9} Over the last 100 years, there has been a doubling of the rate of nitrogen transferred from the mostly biologically inaccessible, atmospheric pool to biologically available pools. This doubling is largely as a result of human activities, especially the production of food and energy.⁹ Important processes in which nitrogen is transformed include the cultivation of nitrogen-fixing crops, the production of fertilizer and the combustion of fossil fuel.⁴

Increased nitrogen in many ecosystems has numerous ecological consequences, since it contributes to many environmental phenomena, such as the greenhouse effect, atmospheric smog, the production of tropospheric ozone, the depletion of stratospheric ozone, acid deposition, nutrient loading and eutrophication processes in fresh water and coastal ecosystems, and changes in the productivity and species composition of ecosystems. These effects have also led to an increase in respiratory illnesses due to ozone and the inhalation of particulate matter.⁹ One of the important characteristics of reactive nitrogen molecules is their linked effects along the continuum from the atmosphere, through the biosphere, to the soil and back to the atmosphere.

For example, nitrogen can increase ozone in the troposphere, augment particulate matter in the atmosphere, alter the productivity of terrestrial ecosystems, acidify surface water, enhance the productivity of coastal ecosystems, increase coastal eutrophication and raise the greenhouse potential of the atmosphere.¹⁰

While many of these environmental impacts are global, they may vary regionally. Many parts of the industrialized, developed world are experiencing nitrogen saturation, whereas the main nitrogen issues for the African region can be briefly listed as follows:

- 1) The low use of mineral nitrogen fertilizer inputs on small-holder farms (less than 5 kg N ha⁻¹yr⁻¹), compared with the average fertilizer use on commercial farms in the developed world of between 150–300 kg N ha⁻¹yr⁻¹.
2. Nutrient mining, which results in unsustainable agricultural production. The low productivity of African soils has an effect on food security and poverty in the region.
3. The production and deposition of atmospheric trace gases, which lowers air quality. The production of atmospheric trace gases results from large-scale biomass burning across vast areas of the continent, biogenic emissions from soil and vegetation, and from industry in South Africa and other localized areas in Africa.¹¹
4. Eutrophication, caused by excessive contributions of nitrogen through atmospheric deposition, leaching and runoff from areas of human habitation and agricultural lands. Eutrophication also results from phosphorus inputs from a variety of sources, including industrialization, dust deposition, leaching and runoff.

In contrast to the many papers published on changes in plant species diversity as a result of nitrogen enrichment,^{12,13} much less emphasis has been placed on the impacts of phosphorus additions or depletions and the measurement of phosphorus in ecosystems. Some studies, however, show that plant species that have become adapted to limited phosphorus availability may be much more sensitive to increased phosphorus levels than those species lost as a consequence of elevated nitrogen levels.¹⁴ A review of techniques for measuring soil phosphorus pools and fluxes, which focused specifically on Africa, was last published by Tiessen and Frossard in 1991.¹⁵ The situation in South Africa is particularly interesting because it reflects a combination of the problems listed above: many of the rural areas show nutrient depletion due to agricultural activities, acidic deposition from coal-burning power stations and increased sediment loading of rivers following overgrazing and droughts. The use of integrated spatial information, provided by SAEON through its agreement with Collaborative Geographical Information Services, will facilitate the creation of a novel map of the country detailing areas of nitrogen depletion versus parts which may become saturated with nitrogen.

While nitrogen and phosphorus limitations are one of the main drivers of food insecurity in Africa, research in this area does not fall within the scope of SAEON. However, estimates of nitrogen deposition, which do fall within the SAEON mandate, should be incorporated into the agricultural database, because deposition may offset nitrogen depletion due to mining from the majority of African soils.¹⁶ Large-scale deposition of anthropogenically liberated sulphur and nitrogen, over the eastern regions of South Africa, has been occurring over almost a century. This can lead to increased acidity of soils and water, as well as enhanced salt export, which may, in turn, impact negatively on ecosystem function with further declines in plant species diversity, water quality, plant growth rates and soil health. The effects are insidious and cumulative, only becoming

evident over periods of decades, and are difficult to reverse. The deterioration in water quality also impacts negatively on industrial and domestic water use, necessitating additional water treatment and water transfer schemes. This has implications for supply costs, as well as having direct and indirect environmental consequences. Acidic deposition has affected ecosystems in South Africa to varying extents. This mosaic of impacted lands provides SAEON with an interesting template with which it can conduct monitoring studies. In addition, SAEON can play a key role in making databases available which, to date, were difficult to access for instance, information from the agricultural database on fertilizer usage and from the water quality database.

In this article we present examples of nutrient cycling studies from South Africa and other regions in the world, and a framework suitable for SAEON in the investigation of biogeochemical questions. In so doing, we hope to make the links between terrestrial, aquatic and atmospheric processes clear. An evident national need exists for integrating ecological data with those from other disciplines. We also recognize the need to combine biogeochemical issues with those of other challenges within the emerging SAEON project; namely, land-use change, loss of biodiversity, spread of invasive species, impact of emerging diseases, and climate change.

South African studies

There have been several nutrient cycling studies in South Africa which have mostly focused on relationships between soils, plants and animals in the savannas, grasslands,^{17,18} Karoo (see Milton *et al.*³³ this issue) and fynbos biomes. Nitrogen and phosphorus were the elements examined in most detail, with phosphorus playing a more important role in the fynbos than in the other biomes. In the fynbos, low ecosystem nitrogen and phosphorus levels have resulted from frequent fires and erosion over extremely long periods of time, resulting in unique root modifications for phosphorus capture (e.g. cluster roots).^{19,20} Most of the research has focused on savanna systems, with the studies conducted at Nylsvley, the site of the Savanna Biome Programme, contributing extensively to the understanding of nutrient cycling.²¹ Nitrogen was a stronger limiting factor than phosphorus, probably due to the nitrogen losses which occur during fires. The process of mineralization, whereby nutrients are made available in ionic forms by the oxidation of organic compounds, dominates both the nitrogen and phosphorus cycles at Nylsvley, and is controlled by water availability and soil temperature. Nitrogen can accumulate as a result of landscape processes and the formation of sodic soils, which often have high nitrogen levels and elevated sodium to calcium and magnesium levels, or as a consequence of local processes, at scales of a few metres, through accumulation by trees and termites.²² Biogenic emissions occur as nitric oxide at the beginning of the rainy season and there is evidence from studies in the Kruger National Park that some of this nitrogen is returned through biological fixation taking place in the herbaceous legumes.^{23,24} There is significant deposition of nitrogen in Mpumalanga province as a result of fossil fuel-burning power stations.¹⁶ At the regional scale, nitrogen and phosphorus cycling is determined by the interactions of factors such as climate, parent material, biodiversity, herbivores, fires and anthropogenic effects.²⁵

Examples from other regions of the world

In the northern hemisphere, environmental problems exist, mostly due to excess fertilizer additions, resulting in eutrophication of water bodies, altered ecosystem biodiversity and changes in retention of nitrogen and carbon in ecosystems.^{26–28}

The examples below show that the contribution of nitrogen is an environmental problem with a wide range of consequences by causing changes in the structure and type of primary productivity. The extra input of nitrogen has multiple sources, distributed across many temporal and spatial scales, resulting from various different activities; for example, from local agriculture to Europe-wide industrial and vehicular emissions. It is, therefore, important to stress the importance of these different causes and effects; the relevant research and management should be multidisciplinary and cooperative.

Cedar Creek case study

Extensive work has been conducted by researchers at the University of Minnesota at the Cedar Creek research site, which is one of the long-term ecological study sites in the United States.^{29,30} The savanna/grassland systems in South Africa are similar to those studied at Cedar Creek. Net primary productivity is limited by nitrogen at the American site and research has focused on determining the influence of nitrogen on species abundance, composition and diversity, the relevant feedbacks and the mechanisms that control these effects. The deposition of nitrogen has increased worldwide, and is expected to continue rising. While the experiments at Cedar Creek do not explicitly determine the effects of nitrogen deposition, they do give insights into how nitrogen deposition will alter species composition. Nitrogen additions were made to 162 grassland plots in three nitrogen-limited Minnesota grasslands varying in successional age, total soil carbon and plant species composition. The youngest field (field A) was dominated by vegetation, with the C₃ photosynthetic pathway, primarily non-native cool season grasses and forbs, whereas the two older sites (fields B and C) were dominated by native C₄ 'warm season' prairie grasses. All other potentially limiting nutrients were supplied and soil pH was controlled.

Results were reported after 12 years of experimental nitrogen addition (Fig. 1).³⁰ Nitrogen loading greatly changed plant species composition, decreased diversity and increased above-ground productivity in these plots. Species richness declined by more than 50% across the nitrogen-addition gradient, with the greatest losses occurring at values similar to the depositional nitrogen levels of 1–5 g N m⁻² yr⁻¹ currently being experienced in North America. This loss of diversity was accompanied by major shifts in composition, with C₄ grasses declining and the weedy C₃ grass *Agropyron repens* becoming dominant at high nitrogen addition rates. Of the remaining C₄ species, one, *Schizachyrium scoparium*, contributed >95% of the C₄ biomass in the plots.

As the vegetation shifted with increasing nitrogen inputs from C₄ to C₃ species, the C:N ratios of above-ground and below-ground plant tissue decreased. Two analyses indicate that interspecific differences in tissue chemistry together with the observed species shifts can account for most of this shift in biomass C:N ratios across the experimental nitrogen gradient. The efficiency of nitrogen use by plants, soil nitrate levels, soil nitrogen retention and nitrogen mineralization rates all responded to high levels of nitrogen additions.³⁰

Kattegat case study

Coastal zones are a valuable resource that is extensively threatened by human activity. In Europe, high population densities and levels of industrial activity create acute pressure on coastal seas. One of the main problems is the rapid increase in the amounts of nitrogen-based contaminants entering the water, with resultant eutrophication. Rivers are frequently the dominant source of nitrogen to the coastal seas, but recent evidence

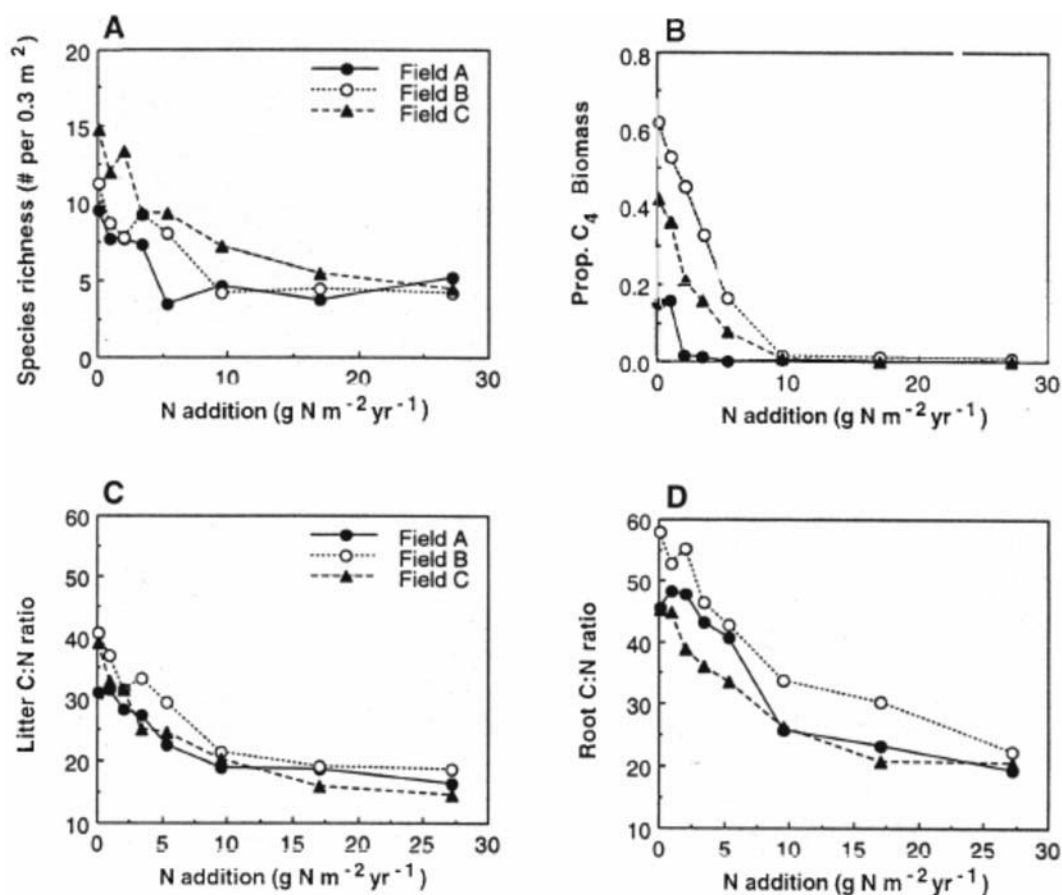


Fig. 1. Ecosystem responses of carbon, nitrogen and vegetation to 12 years of nitrogen addition in EOO1 (from Wedin and Tilman³⁰). Points represent treatment means (6 replicates per nitrogen addition level, 12 for controls) for each of three fields. (A) Number of vascular plant species found in 0.3-m² vegetation samples; (B) biomass of grasses with the C₄ photosynthetic pathway as a proportion of above-ground live biomass at mid-growing season; (C) C:N ratios of above-ground litter; and (D) C:N ratios of below-ground root biomass.

suggests that atmospheric inputs are large and can equal, and in some cases exceed, those from the rivers.²⁷ Atmospheric inputs are dominated by nitric acid, nitrate, ammonia and ammonium through a combination of wet and dry deposition. The sources and atmospheric chemical characteristics of these compounds differ from one another and their differential rates impact on the amounts deposited.^{27,31}

Kattegat, the transitional area between the Baltic Sea and the North Sea, has been studied in detail because of extensive eutrophication occurring from high rates of atmospheric deposition. Algal blooms first devastated fish population, with large economic losses in 1988; since that time extensive studies have aimed at quantifying the full nitrogen budget for the Kattegat. The data (Fig. 2)³¹ indicate the complexity of the system, with atmospheric deposition contributing a major external input additional to a very large internal cycle of nitrogen that dominates the productivity of the system. An integrated, interdisciplinary project (MEAD) showed that atmospheric deposition on its own cannot induce algal blooms. Knowledge of the source of the nitrogen was essential for introducing policy and regulations to reduce the impact on fisheries. A 50% reduction in NH₃ and NO_x emissions resulted in only an 8.8% reduction in algal primary production. It was shown that some strategies need to be locally applied; for instance, emissions of ammonia from local agriculture had to be reduced, whereas other strategies required were more far-reaching; for example, reduction in nitrous oxide emissions across the whole of Europe.³¹ Transboundary pollution is an emerging environmental problem in southern Africa and an integrated study like that described from the Baltic would be

very valuable in southern Africa. SAEON could champion this type of regional study.

Scientific approach and infrastructure for SAEON

Approach

It is essential that SAEON embraces the living landscape and not only conserved areas as is clearly stated in their mandate. Nearly all nutrient cycling studies to date in South Africa have been conducted in conserved areas and this needs to change rapidly. SAEON can play a major role in facilitating the permissions needed for data collections across different land uses. There is a growing need to conduct studies across gradients from urban to rural areas where a variety of land uses are practised. Studies should be conducted within an integrated framework of research questions.

Possible research questions

1. How does the element residence time (the balance between sequestration and liberation) of carbon and other elements determine the level of human impact on natural ecosystems?
2. How will water management in the 21st century affect element interactions along a continuum from uplands to oceans?
3. What is the general theoretical framework linking plant and animal species interactions to element cycles? Can we go beyond strong but idiosyncratic effects of species changes on element interactions? How do the main plant photosynthetic and functional types react to changes in nitrogen and phosphorus availability?

4. What is the effect of climate forcing on element interactions?
5. What is the role of natural and anthropogenically-accelerated fire regimes on critical pools and fluxes?

Addressing these questions will require multidisciplinary teams to quantify the driving forces, develop an understanding and predictive ability of the processes and to apply tools to assess the present and likely impacts on the ecosystems and water supply. There have been many attempts to conduct multidisciplinary research in South Africa over the last 20 years and there have been successes (for example, see Milton *et al.*³³ this issue). However, SAEON could create a platform which would help establish a modelling framework in which multidisciplinary teams could use the data to test hypotheses and key questions. In addition, research and human capacity needs to be developed in some very specific areas, such as in the use of isotopes in environmental applications. A number of different scientific methods will be needed and will include working with existing networks as well as establishing new areas where critical mass is not achieved at any one institution in the country. Stable isotopes are very powerful tools and are used extensively in many studies to elucidate biogeochemical process and pathways and anthropogenic influences. Nitrogen isotopes, in combination with other isotopes, can be used to elucidate the contributing sources of nitrogen to the aqueous environment (Fig. 3).³² Such studies have proved particularly useful in the identification of fertilizer or human and animal waste sources. There are two stable isotopes of nitrogen: ¹⁴N and ¹⁵N. All nitrogen compounds contain both isotopes, but because of isotopic fractionation they are incorporated into compounds in differing ratios, depending on the nature of the reactions that produce the compounds. The dominant source of nitrogen in most forested ecosystems is the atmosphere ($\delta^{15}\text{N} = 0\text{‰}$); many plants fix nitrogen and organisms cycle this into the soil. The greater the amount of nitrogen fixed through the process of biological nitrogen fixation, the more negative is the isotopic signature. Other important sources of nitrogen include fertilizers, produced from atmospheric nitrogen, with compositions of $0 \pm 3\text{‰}$.

There are a number of tools identified by the North American Experimental Observation Network (NEON) shown in Table 2. Key areas which will need development through the SAEON network include the setting up of a Centre for Scaling and Modelling Studies. This centre could engage with colleagues specializing in complex-system analysis and together develop data sets for validation of predictive models to be used in scenario planning. The establishment of a few instrumented catchment studies in which soil, plant, animal, atmosphere and social studies could be conducted in an integrated way would be invaluable in addressing some of the key questions posed earlier in this article.

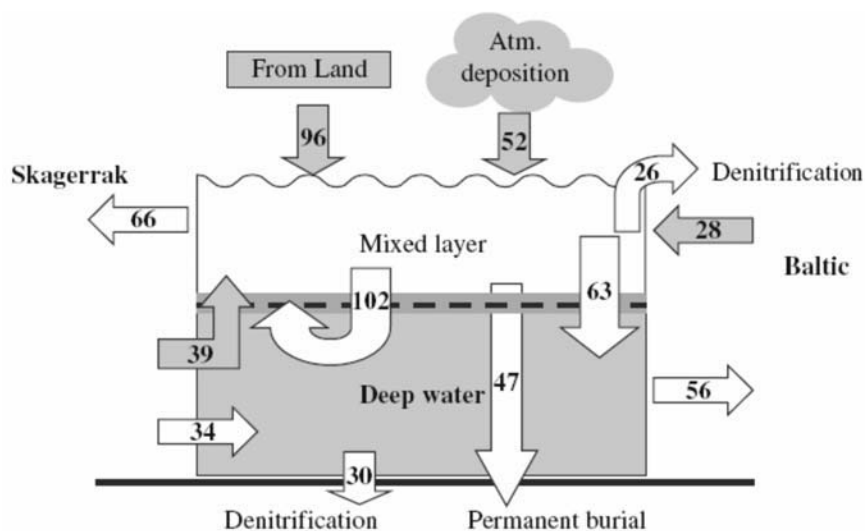


Fig. 2. Budget of biologically active nitrogen for the Kattegat (kt yr^{-1}) differentiated in terms of fluxes into the mixed layer and deep water.³¹

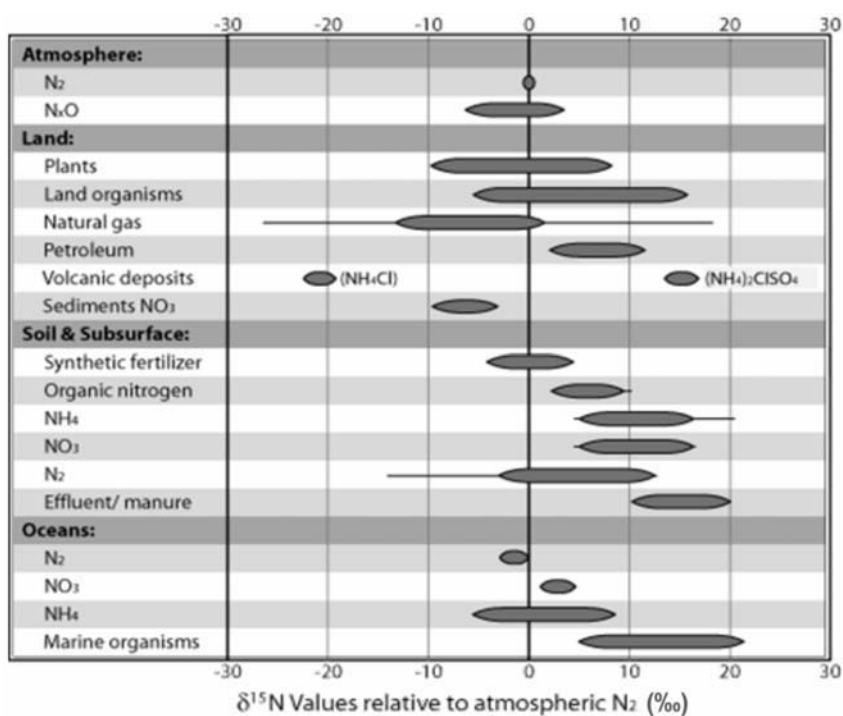


Fig. 3. $\delta^{15}\text{N}$ values for a variety of sources.³²

Concluding remarks

An integrated approach to terrestrial, aquatic and atmospheric monitoring must be conducted in South Africa to allow for an improved understanding of impacts. This can be done through the establishment of instrumented catchments in which nitrogen and phosphorus form part of the focus. This understanding will feed into adaptation strategies, which will be key to sustainable resource utilization. SAEON can play a number of useful roles in ensuring the success of an integrated programme, by: bringing academics from the terrestrial and aquatic communities together, conducting research over a wide range of eco-regions and land uses; linking data sets that are difficult to access, e.g. the national water quality data set and the atmospheric emissions data set; creating a Centre for Scaling and Modelling Studies; strengthening the capacity in key research areas, e.g. the use of stable isotopes for environmental studies;

Table 2. Tools identified by the North American Experimental Observation Network (NEON), and the associated approaches suggested for SAEON.

Tools identified by NEON	Approaches suggested for SAEON
Pool and flux measurement networks	Industrial and agricultural databases
Deposition networks	Deposition of biogeochemically important trace species (wet and dry network)
Stable isotope networks	Natural abundance plus few experiments
Atmospheric transport network	South African Weather Service (University of Cape Town, University of the Witwatersrand, University of Pretoria, Council for Scientific and Industrial Research)
Aquatic transport networks	SA water quality and flow network
Analytical laboratories	Quality data for research and monitoring
Palaeobiogeochemical laboratories	Quaternary Dating Research Unit, iTemba Laboratory, CSIR, and the laboratories at the University of Cape Town.
Scaling and modelling centres	Not currently available
Coupling land-use change to cycling	Selected paired catchment studies

and, finally, by establishing instrumented catchment studies in key areas.

- Brady N.C. (1974). *The Nature and Properties of Soils*, 8th edn. Macmillan, New York.
- Sterner R. and Elser J.J. (2002). *Ecological Stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, NJ.
- Schlesinger W.H. (1997). *Biogeochemistry: An analysis of global change*, 2nd edn. Academic Press, New York.
- Vitousek P.M., Aber J.D., Howarth R.W., Likens G.E., Matson P.A., Schindler D.W., Schlesinger W.H. and Tilman D.G. (1997). Human alteration of the global nitrogen cycle: sources and consequences. *Ecol. Appl.* 7(3), 737–750.
- Vitousek P.M., Hattenschwiler S., Olander L. and Allison S. (2002). Nitrogen and nature. *Ambio* 31, 97–101.
- Scholes R.J. and Biggs R. (2004). *Ecosystem Services in Southern Africa: A regional assessment*. CSIR, Pretoria.
- Falkowski P., Scholes R.J., Boyle E., Canadell J., Canfield D., Elser J., Gruber N., Hibbard K., Höglberg P., Linder S., Mackenzie F.T., Moore B. III, Pedersen T., Rosenthal Y., Seitzinger S., Smetacek V. and Steffen W. (2001). The global carbon cycle: a test of our knowledge of earth as a system. *Science* 290, 291–296.
- Nosengo N. (2003). Fertilized to death. *Nature* 425, 894–895.
- Galloway J.N., Dentener F.J., Capone D.G., Boyer E.W., Howarth R.W., Seitzinger S.P., Asner G.P., Cleveland C.C., Green P.A., Holland E.A., Karl D.M., Michaels A.F., Porter J.H., Townsend A.R. and Vorosmarty C.J. (2004). Nitrogen cycles: past, present and future. *Biogeochemistry* 70, 153–226.
- Galloway J.N., Aber J.D., Erisman J.W., Seitzinger S.P., Howarth R.W., Cowling E.B. and Cosby B.J. (2003). The nitrogen cascade. *Bioscience* 53(3), 341–356.
- Galloway J.N., Bekunda M.A., Cai Z., Erisman J.W., Frenay J., Howarth R.W., Martinelli L.A., Scholes M.C. and Seitzinger S.P. (2004). *A preliminary assessment of 'changes in the global nitrogen cycle as a result of anthropogenic influences'*. International Nitrogen Initiative, Nanjing, China.
- Aber J.D., Nadelhoffer K.J., Steudler P. and Melillo J.M. (1989). Nitrogen saturation in northern forest ecosystems. *BioScience* 39(6), 378–386.
- Matson P.A., Lohse K.A. and Hall S.J. (2002). The globalization of nitrogen deposition: consequences for terrestrial ecosystems. *Ambio* 31, 113–119.
- Wassen M.J. (2005). Endangered plants persist under phosphorus limitation. *Nature* 437, 547–550.
- Tiessen H. and Frossard E. (eds) (1991). Phosphorus cycles in terrestrial and aquatic ecosystems. Regional workshop 4: Africa. In *Proceedings of a workshop at UNEP, Nairobi*. Saskatchewan Institute of Pedology, University of Saskatchewan, Saskatoon, Canada.
- Scholes M.C., Scholes R.J., Otter L.B. and Woghiren A. (2003). Biogeochemistry: the cycling of nutrients in the Kruger National Park. In *The Kruger Experience: Ecology and management of savanna heterogeneity*, eds J. du Toit, H. Biggs and K.H. Rogers, pp. 130–148. Island Press, Washington, D.C.
- Fynn R.W.S. and O'Connor T.G. (2005). Determinants of community organization of a South African mesic grassland. *J. Veg. Sci.* 16(1), 93–102.
- Snyman H.A. (2002). Short-term response of rangeland botanical composition and productivity to fertilization (N and P) in a semi-arid climate of South Africa. *J. Arid Environ.* 50(1), 167–183.
- Hawkins H.-J., Wolf G. and Stock W.D. (2005). Cluster roots of *Leucadendron lauratum* (Proteaceae) and *Lupinus albus* (Fabaceae) take up glycine intact: an adaptive strategy to low mineral nitrogen soils. *Ann. Bot.* 96(7), 1275–1282.
- Lambers H., Shane M.W., Cramer M.D., Pearse S.J. and Veneklaas E.J. (2006). Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Ann. Bot.* 98(4), 693–713.
- Scholes R.J. and Walker B.H. (1993). In *An African Savanna: Synthesis of the Nylsvley study*, pp. 81–110. Cambridge University Press, Cambridge.
- Grant C.C. and Scholes M.C. (2006). The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biol. Cons.* 130, 426–437.
- Parsons D., Scholes M.C., Scholes R.J. and Levine J.S. (1996). Biogenic NO emissions from savanna soils as a function of fire regime, soil type, soil nitrogen and water status. *J. Geophys. Res.* 101(D19), 23684–23688.
- Levine J.S., Winstead E.L., Parsons D., Scholes M.C., Scholes R.J., Cofer W.R. III, Cahoon D.R. Jr and Sebach D.I. (1996). Biogenic soil emissions of nitric oxide (NO) and nitrous oxide (N₂O) from savannas in South Africa: the impact of wetting and burning. *J. Geophys. Res.* 101(D19), 23689–23698.
- Augustine D.J., McNaughton S.J. and Frank D.A. (2003). Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecol. Appl.* 13(5), 1325–1337.
- Spokes L.J. and Jickells T.D. (2005). Is the atmosphere really an important source of reactive nitrogen to coastal waters? *Contl Shelf Res.* 25(16), 2022–2035.
- Jickells, T. (2006). The role of air–sea exchange in the marine nitrogen cycle. *Biogeochemistry* 3(3), 271–280.
- Dentener F., Drevet J., Lamarque J.F., Bey I., Eickhout B., Fiore A.M., Hauglustaine D., Horowitz L.W., Krol M., Kulshrestha U.C., Lawrence M., Galy-Lacaux C., Rast S., Shindell D., Stevenson D., Van Noije T., Atherton C., Bell N., Bergman D., Butler T., Cofala J., Collins B., Doherty R., Ellingsen K., Galloway J., Gauss M., Montanaro V., Müller J.F., Pitari G., Rodriguez J., Sanderson M., Solomon F., Strahan S., Schultz M., Sudo K., Szopa S. and Wild O. (2006). Nitrogen and sulfur deposition on regional and global scales: a multimodel evaluation. *Global Biogeochem. Cycl.* 20(4), 1–39.
- Tilman D. (1990). Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58, 3–15.
- Wedin D.A. and Tilman D. (1996). Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* 274, 720–723.
- Spokes L., Jickells T., Weston K., Gustafsson B.G., Johnsson M., Liljebladh B., Conley D., Ambelas-Skjødth C., Brandt J., Carstensen J., Christiansen T., Frohn L., Geernaert G., Hertel O., Jensen B., Lundsgaard C., Markager S., Martinsen W., Möller B., Pedersen B., Sauerberg K., Sørensen L.L., Hasager C.C., Sempreviva A.M., Pryor S.C., Lund S.W., Larsen S., Tjernström M., Svensson G. and Zagar M. (2006). MEAD: an interdisciplinary study of the marine effects of atmospheric deposition in the Kattegat. *Environ. Pollut.* 140, 453–462.
- Hoefs J. (1997). *Stable Isotope Geochemistry*, 4th edn. Springer, Berlin.
- Milton S.J., Dean W.R.J., O'Connor T.G. and Mills A.J. (2007). Scaling up from site-based research to a national research and monitoring network: lessons from Tierberg Karoo Research Centre and other design considerations. *S. Afr. J. Sci.* 103, 311–317.