NITROGEN BALANCES IN NATURAL GRASSLANDS AND EXTENSIVELY-MANAGED GRASSLAND SYSTEMS

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SUMMARY: An approach is outlined for synthesising current understanding of nitrogen dynamics in natural grasslands and extensively managed grassland systems. The increasing complexity of models is illustrated from recent literature, first conceptualising and eventually process-simulating the dynamics of nitrogen, especially in the soil sub-systems of grasslands. Some comparisons are made between New Zealand and North American grasslands in the magnitude of some N pools and fluxes and some of the principal features of soil biological studies are noted.

Natural environmental variations in N balances are reviewed, especially with regard to climatic influences on organic N pools, mineral N pools and nitrification. The role of nitrogen fixation is related to ecological succession and is presented as sometimes a facultative response of natural systems to natural and some cultural perturbations. Attention is redirected at symbiotic nitrogen fixers in New Zealand tussock grasslands.

The effects of management factors on N balances are reviewed. The special susceptibility of New Zealand tall tussock grasslands to large N losses from fire is indicated. Grazing is especially examined for its influence on mineral N pools and losses as well as for its N redistribution effects.

A summary assessment of the understanding of nitrogen regimes of New Zealand tussock grasslands is made in terms of higher plant uptake and transfers, litter accumulation and decomposition, and soil biology and biochemistry. Special attention is directed to the possible effects of pastorally-induced changes in these regimes.

The review ends with an indication of the likely significance of model-guided, co-ordinated research into the dynamics of nitrogen and other biogeochemical transformations, as of phosphorus and sulphur, in both natural grasslands and the culturally developed grasslands and forests which may now replace many of them.

This paper should be regarded as an approach to the topic, not as an adequate review of various approaches. Rather it is a personal statement of my own present understanding of the essentials of nitrogen accounting in grasslands, natural and extensively-managed for pastoral purposes. It does not arrive at a factual statement of nitrogen accounts valid for New Zealand natural grasslands. Instead, it serves to show the variety in balances of natural grassland systems. While it attempts to keep detailed process studies in perspective, it also indicates their value for warning of the pitfalls of summary generalization.

The pattern adopted in this paper is to present a general outline of the main topics identified in turn and to comment on New Zealand work in the context of each topic. 'A summary statement on New Zealand natural grassland concludes the paper.

THE CONCEPT OF BALANCE AND REALITY

It should be emphasised that use of the word balance in the title does not imply that an ecosystem is, of necessity, in balance. Equilibrating features may indeed be present within grassland ecosystems as in other sectors of the biosphere. My use of the word balance emphasises its meaning in accounting - a statement of the difference between debits and credits. We need to know not only the volume of nitrogen accounts but whether an ecosystem is in positive or negative nitrogen balance. This need arises from the economic and ecologic requirements of resource management. Scientific curiosity and the need to know where to apply management effort alike require that we be interested in the processes of gain and loss and of transfer within the system as we conceive it.

I should emphasise that the systems we deal with are changing, open systems, dynamic not only in their internal transfers but also in the changes of the balance direction or magnitude with time, and often in relatively short time. Some changes in balance are seasonal, but even in annual balances there may be marked changes in magnitude that may constitute secular trends, discernible over comparatively short spans of years. As Woodmansee, Vallis and Mott (1981) indicate, if prolonged imbalance occurs in utilizable nitrogen, ecosystem succession may result. I shall comment further on the relationships between nitrogen balance and grassland succession.

Grassland nitrogen may vary spatially in landscapes. Some of these variations may derive from abiotic features such as the movement of groundwater or the varying thickness of soil material. Others may arise from variation in the distribution of plants and especially from the behaviour of animals. I shall comment further on the significance of such factors of spatial variation.

MODELS AND PROCESSES OF THE NITROGEN CYCLE

The Concepts of Pools and Pathways

At anyone location in a grassland, a graphic representation may be made of nitrogen flow into, through and out of the system. That of O'Connor (1974) (Fig. 1) represented major pools as rectangular boxes, intermediate states as oval shapes and pathways through different levels from atmosphere to groundwater as distinct losses, gains and transfers. Each scientist, as Clark (1981) notes, represents the nitrogen cycle according to his own biases. In his parlance, my 1974 model represented the "process and compartmental" stage of model development. Its biases are those of a New Zealand agronomist concerned with pastoral influence on natural grasslands and the transformation of such grasslands by legume introduction and intensive grazing management. For more valid general use of the figure in natural grasslands, even in New Zealand, some modifications of its concepts are necessary. Livestock as animal N should be referred to as herbivores, legumes should be shown as nitrogen-fixing systems. What is represented as an intermediate state, decay of plant material, should be considered as a distinct pool, litter.

What are represented here as pools may be further partitioned. For' example, Woodmansee et al. (1978) partitioned their plant pools into living and dead tops, crowns and roots to represent the short grass prairie of Colorado. What is shown in Figure 1 as a composite "soil and organic matter" was partitioned by Woodmansee et al. (1978) into "soil organic nitrogen" and several sub-compartments of soil animals and microbes in a budgeted nitrogen cycle. A simple version of the flows and compartments of a natural grassland cycle is shown in Figure 2, adapted from Woodmansee and Wallach (1981).
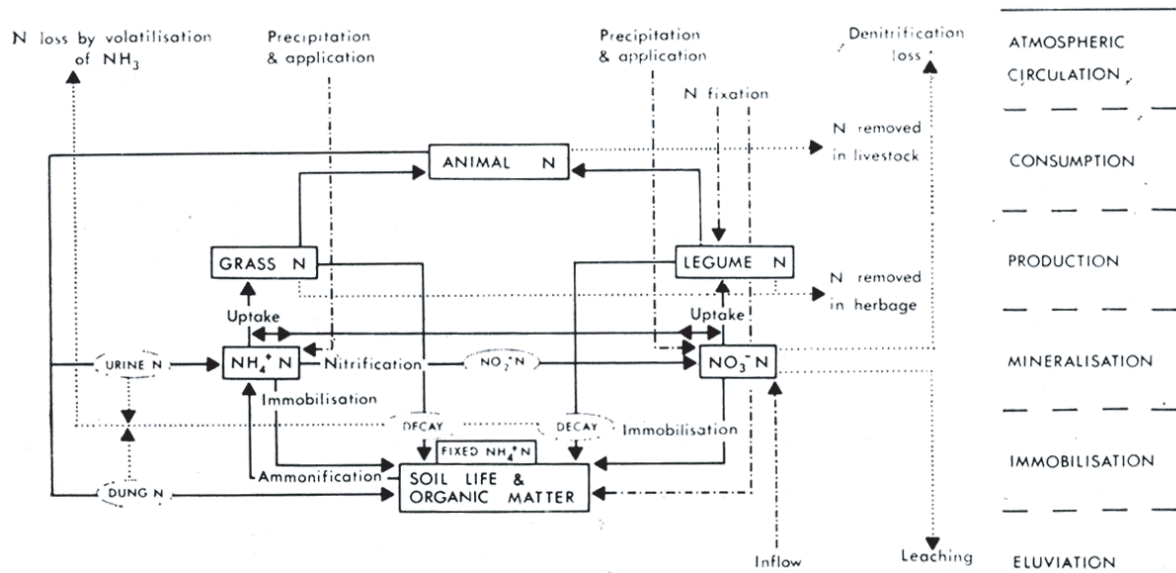

FIGURE 1. *Levels, major pools, intermediate states, and pathways of gain, loss and transfer for nitrogen circulation in a grazed legume-grass system (from O' Connor, 1974).*
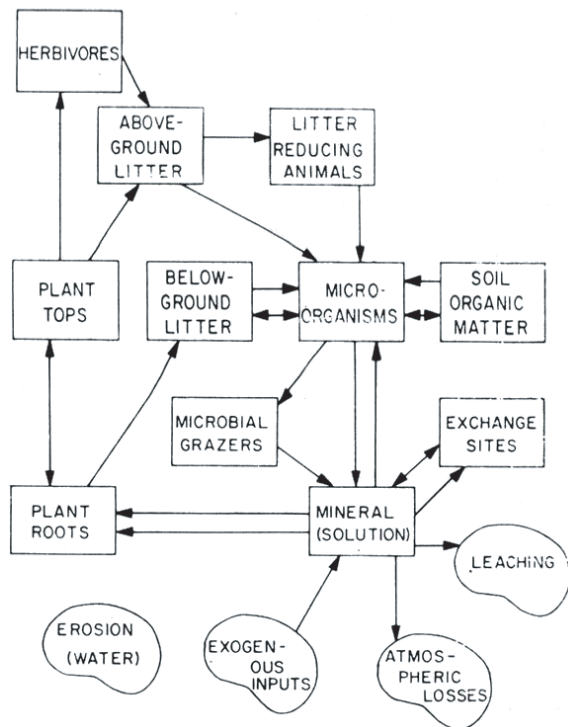
FIGURE 2. *Pathways of nitrogen movement in an undisturbed grassland ecosystem. (after Woodmansee and Wallach, 1981).*

FIGURE 3. *Basic flow diagram for a simple model stimulating nitrogen flow in a grassland ecosystem. (from Reuss and Innis, 1978).*

In summary, a natural or extensively-managed grassland is generally distinguished from intensively-grazed, improved grasslands by comparatively large numbers of fairly long retention pools or compartments, the comparatively small volume of herbivore N pools and, in consequence, comparatively slow total cycling mass flow rates. As will be seen, soil climate influences soil carbon levels in grassland and related systems and thereby affects the magnitude and proportion of soil organic nitrogen and mineral pools.

Simple Models of Nitrogen in Natural and Extensively Managed Grasslands

Most current attempts at assessing the volume and balance of nitrogen in grassland systems involve simulation models. A simple representation of the natural grassland system, taken from an early modelling exercise from the US IBP Grassland Biome, is presented as Figure 3, from Reuss and Innis (1978). This model simulating nitrogen flow was, as Van Veen et al. (1981) noted, a simple mathematical model which included no biological vector other than plants. It included 23 state variables comprising (a) soil nitrate nitrogen at four depths,
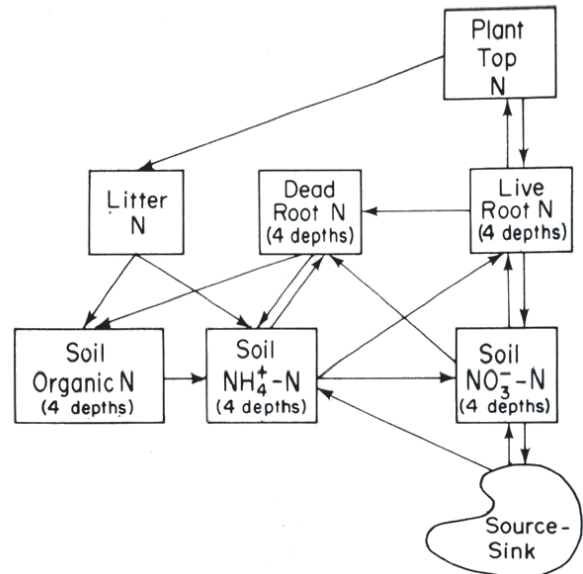
(b) soil ammonium nitrogen at four depths, (c) live root nitrogen at four depths, (d) dead root nitrogen at four depths, (e) soil organic nitrogen at four depths, (f) live plant top nitrogen, (g) nitrogen in aboveground dead plant parts and surface litter and (h) source or sink. For each of the internal pathways of that model, Reuss and Innis (1977, 1978) used precise mathematical formulations from known or presumed general relationships. Inputs tend to be site specific and were estimated at higher levels than free-living fixation. Symbiotic fixations also site specific are small and were omitted. They included fertilizer nitrogen, not generally applied to natural grasslands. Leaching and denitrification were considered to be significant only when substantial amounts of nitrate are present in wet soils. This was considered unlikely for arid and semi-arid conditions and the processes were not included in the model. Ammonia loss from animal excreta was indicated to be as much as half the rainfall input and was therefore omitted as negligible.

In consequence of these assumptions and estimations (which were not unreasonable for the Pawnee natural grassland), the output of the model demonstrates many interesting short run internal changes in nitrogen pools or state variables but, of course, negligible change in N balance. Additions of fertiliser nitrogen were also simulated. A noteworthy feature for the 109 N m-2 addition simulation was that, at peak live top biomass (240 days), the highest propor-

TABLE 1. *Distribution of plant nitrogen (N g m^{-2}) in North American grassland systems with comparative data from* Chionochloa *stands at Paddle Hill Creek, Canterbury.*

	Short grass prairie at Pawnee site, Colorado, U.S.A.[1]	Mixed prairie at Matador site, Saskatchewan, Canada[2]	C. *rigid a* Paddle Hill Creek, Canterbury, New Zealand [3]	C. *macro* Paddle Hill Creek, Canterbury, New Zealand [3]
All live shoots	5.2	2.2	5.0	2.1
All dead shoots	2.9	3.4	5.6	2.8
"Litter"	6.0	3.7	3.1	0.8
Dead roots	16.5			
Living roots	4.2			
Total roots	*20.7*	13.5	15.4	10.0

Note: For *Chionochloa* stands, shoot weights of other species present are not recorded.

Sources: 1. Woodmansee *et al.,* 1978
2. McGill *et al.,* 1974
3. Williams *et al.,* 1977

tions of the nitrogen increment were in the live tops and the dead roots, with comparatively small proportions in soil mineral or organic nitrogen. In contrast, a further increment of 109 N m^{-2} resulted in a similar proportion (just over one third) of the increment in the live tops and almost the same proportion in soil nitrate. This is the kind of situation which probably applied in Power's (1970) North Dakota study which had the soil nitrate pool building up from fertilizer addition, fluctuating in depth with seasons and taking three years or more before it ceased to affect grassland yield. Reuss and Innis (1978) also noted from the ELM nitrogen submodel that the pool with the longest turnover time is the soil organic matter.

Comparative Pool Sizes and Fluxes in *Grasslands*

Woodmansee et al. (1978) assessed, for the Pawnee short grass prairie, the quantities of nitrogen in the above-ground and below-ground pools, soil, plant and animal, including separately microflora and microfauna. They presented their empirical model as a budgeted nitrogen cycle, including their estimates of pool sizes. The total N in the system to a soil depth of 36 cm was 375g m^{-2}. Table 1 presents the principal plant N pools for the Pawnee site, with comparable values for the mixed prairie at Matador site, Saskatchewan (McGill, Paul and Sorensen, 1974) and the *Chionochloa* grasslands at Paddle Hill Creek, South Canterbury, New Zealand (Williams, Nes and O'Connor, 1977). It should be noted that for these New Zealand examples, only *Chionochloa* plant

material is included in the values recorded. If only blue gram a *(Bouteloua gracilis)* were included at Pawnee, Colorado, the value for living shoots would be reduced to 1.5g m^{-2} (Woodmansee, Vallis and Mott, 1981). All compartment values are from samples taken near mid-summer.

Table 2 presents, from the same sources, comparable N fluxes from root to live shoot and from live shoots to standing dead and litter in the Pawnee grassland and the two Paddle Hill Creek grasslands. Although it is not possible to make exact comparisons between these aggregated pools and fluxes of differently studied and differently structured grasslands, it can be readily recognized that for plant nitrogen parameters they are of similar magnitude.

TABLE 2. *Fluxes of nitrogen from root to live shoot and from live shoot to dead shoot and litter (N g m^{-2} y^{-1}) in Pawnee short grass prairie and* in *Paddle Hill Creek tall tussocks.*

	Short grass prairie[1]	C. *rigida*[2]	C. *macra*[2]
Root to live shoot	2.4	1.9	1.0
Live shoot to dead	2.9	1.3	1.0
Dead shoot to litter	2.8	?	?

Note: For *Chionochloa* spp. net uptake to live shoots is for October *to* March inclusive.

Sources: 1. Woodmansee *et al.,* 1978
2. Williams *et al.,* 1977

Models Including Soil Biological Processes

From the intensive microbial process studies at Matador IBP grassland site in Saskatchewan (McGill, Paul and Sorensen, 1974), we learn several important lessons. First, although the mass of the nitrogen system is principally constituted by the nitrogen contained in soil organic matter, a comparatively small portion of that pool is actively involved in N transfers. At any time a small contribution to total N mass, of similar order to live plant N, is made by nitrogen in soil bacteria, fungi and fauna. A still smaller contribution is made by above-ground bacteria and fungi. Likewise at peak standing crop of a blue grama sward at Pawnee, Colorado, live shoot N comprised 1.5g m^{-2}, live root N 5.1g m^{-2}, bacterial N 1.5g m-2 and fungal N 2.lg m^{-2}, a total 'living' nitrogen content of 109 m^{-2} or 2.9 percent of total N mass (Woodmansee et al., 1981).

Despite these generally low proportions of microfloral N, both modelling and measurement studies in Saskatchewan demonstrated the importance of soil microbes in efficiently first immobilizing added or returned nitrogen, and then mineralizing different fractions of soil organic N in keeping with the amount of CO_2 evolved from the soil system (McGill et al., 1974). However, more recent carbon and nitrogen labelling and simulation studies (Paul and Juma, 1981) have clarified the relative contribu

FIGURE 4. *Compartment diagram for nitrogen flow in a complex model for a grassland ecosystem. Asterisks indicate that state variables are replicated by depth (0-2, 2-6, 6-14 and 14-30 cm) (from McGill et al., 1981).*

tions to the mineral N pool of organic-N fractions (principally biomass N, active-N, and stabilized-N), suggesting that no single active fraction dominates.

To explore the relationships between plant and microbial processes and their effects on plant production, microbial secondary production and nitrogen cycling in semi-arid grasslands, McGill et al. (1981) have developed a realistic N transformation simulation model "PHOENIX" of which the compartments are represented in Figure 4. Included in these compartments are distinct structural and metabolic compartments of standing dead and litter, differing in their assumed C/N ratios. The term humad is a contraction, representing materials stabilized by partial humification and adsorption. Results from operation of this simulation model seem generally satisfactory both for normal field performance and for cultural perturbations, in so far as field results are available for validation. Important features of the PHOENIX model are its provisions for the integration of microbial submodels and for the interdependence of the carbon and nitrogen submodels and for the interdependence of the carbon and nitrogen cycles, as well as the compartmentalization of the soil profile to describe transport processes and the use of multiplicative reduction factors to account for the influence of environmental variables on the several nitrogen transfer processes.

Complex models are often of more value for indicating research needs than they are for predicting outcomes. For example Van Veen et al. (1981), lament the lack of good methods to partition "stable soil nitrogen" and identify this as one of our most severe single deficiencies in our understanding of soil-N dynamics. They point out that, despite "our reasonably good understanding of what causes N to cycle, we do not understand the mechanisms, unique to soil systems, which prevent N from cycling." The experiments of Paul and Juma (1981) are a warning to us that simplified concepts of a dominant active fraction are inadequate. Jansson (1981), in commenting on their paper, argues for a new biologically-founded analytical technique for fractionation. In his view, "conventional humus chemistry, dealing with the extraction and purification of fulvic and humic acids has proved inadequate in this respect". In perspective, it is therefore appropriate to recognize our present understanding by integrating Jansson's model of the "universal nitrogen cycle" including its three partial cycles, the elemental, autotrophic and heterotrophic, with his representation of the somewhat pragmatic fractionation of dead organic matter as put forward by Paul and Juma (1981). This composite is presented as Figure 5.

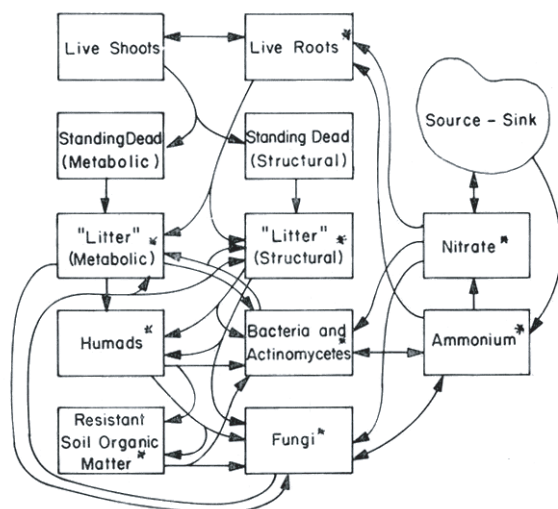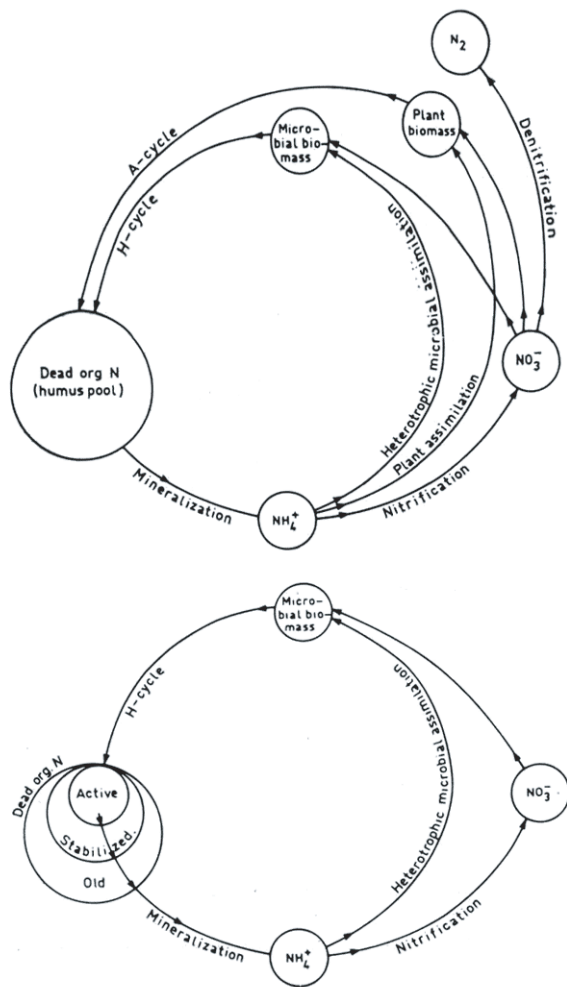Conceptual models such as Jansson's can lead to

FIGURE 5. *(Upper): Jansson's representation of a universal nitrogen cycle divided into its' three partial cycles, the elemental (E), the autotrophic (A), and the heterotrophic (H).*

(Lower): Jansson's representation of the fractionation proposed by Paul and Juma (1981) for the dead organic N pool, integrated into part of his universal nitrogen cycle. (from Jansson, 1981).

simulation models such as is illustrated from the PHOENIX of McGill et al. (1981) or they can lead to more precise and careful experimentation, such as that of Paul and Juma (1981), to quantify important processes. Ideally these two outcomes should follow in what might be recognized as a reciprocating pattern. What needs also to be noted is that the herbivory of large animals and biological dinitrogen

fixation are both unspecified for the PHOENIX model. Other factors of some importance are provided for implicitly rather than explicitly. For example, soil grazing populations are implied by McGill et al. (1981) by the death functions described for bacterial and fungal masses. Coleman et al. (1978) indicated from experiments that, in the absence of grazers, soil bacteria mineralize little nitrogen. Uncertainty remains as to whether such effects are conditioned by differential response of soils of different textures to such phenomena as wetting and drying, freezing and thawing. Anderson, Coleman and Cole (1981) propose a hypothesis of accelerated nutrient release in grazed bacterial systems, even though carbon substrate utilization may be similar to that of ungrazed bacterial systems.

Soil Biological Studies in New Zealand Natural Grasslands

Two major phases of soil microbial and biochemical research have been carried out by Soil Bureau personnel of DSIR in the natural grasslands of New Zealand. The first, led by Dr R. H. Thornton in the late 1950s (e.g. Thornton, 1958; Stout, 1958; Ross 1958, 1960), dealt principally with short tussock grasslands and cultivated sites related to them. The second, introduced by Dr L. F. Molloy in the 1970s (e.g. Molloy and Blackmore, 1974; Ross and McNeilly, 1975), was focussed on a climosequence from Central Otago to South Westland and included many tall tussock grassland sites as well as modified and depleted tussock grasslands. More than forty research papers have resulted from these studies, dealing with micro-organism populations and comparisons of the soil life of different soils and also comparing the soils and organic fractions of different soils in microbial performance in common laboratory environments. Because of difficulties of access and lack of suitable facilities and equipment for field studies on a sustained basis, field performance studies have been confined to such exercises as litter incorporation measurements and other periodically assessible phenomena. As a result we have as yet little information that could be incorporated with confidence in a process simulation model such as that expounded by McGill et al. (1981). From the soil comparisons involved in these studies, however, and from more intensive studies at some localities (e.g. Hollings, Dutch and Stout, 1969; Robinson, 1963; Robinson and MacDonald, 1964a) and reviews of the ecology of soil biota (e.g. Stout, 1973, 1980; Stout and Lee, 1980) we are comparatively well furnished with the background information that would make intensive process studies highly fruitful. As well, we might expect such intensive process

studies to give a scientific basis in soil biology to the greatly expanded knowledge of plant nutrient status and primary productivity in the tussock grasslands (Williams et al., 1976, 1978; Meurk, 1978; Evans 1980).

NATURAL ENVIRONMENTAL VARIATIONS IN N BALANCES

I have indicated that the early investigators at the Pawnee site considered, for good reasons, that gains and losses from their semi-arid system would tend to be of small magnitude. As Woodmansee et al. (1981) indicate, both more humid and more arid systems may be characterised by greater exchanges with their environment. More humid systems may be subject to leaching, compensated by greater dinitrogen fixation. Atmospheric exchanges may be of some significance in at least some arid environments. Figure 6 is derived directly from West and Skujins' (1977) summary presentation of an annual static model for an *Atriplex confertifolia* dominated ecosystem in Utah. An important feature is the 2.5g N $m^{-2}y^{-1}$ nitrogen fixation by blue green algae in the cryptogamic crust which constitutes 17 % of the total above-ground biomass and directly contributes almost one third of the annual input to the soil mineral N pool. In these desert conditions, the soil mineral N pool is by far the largest N pool in the system, in contrast to more humid grasslands where the soil organic N pool is largest. The authors note that most of this large and apparently stable mineral N pool is fixed to clay and is only partially available for plant growth. Another important feature of this desert system is that dinitrogen fixation is approximately balanced by gaseous losses to the atmosphere, principally by denitrification, occurring in partially anaerobic microsites within the decaying wet cryptogamic crust where a carbon source is also available. Spatial and temporal variations in some important pools and processes are briefly reviewed.

Organic N Pools

Wide variations occur in organic N in grassland soils. Evidence from the studies of Molloy and Blackmore (1974) and Ross and McNeilly (1975) indicate generally increasing organic N pools, with increasing precipitation within the tussock grassland sequences. True deserts are not found in New Zealand but induced deserts in Central Otago are characterised by lower organic N pools than the natural grasslands.

Mineral N Pools

Other features of the nitrogen cycle characteristic of natural grasslands are also subject to environmental variation. As noted by Clark and Paul (1970),
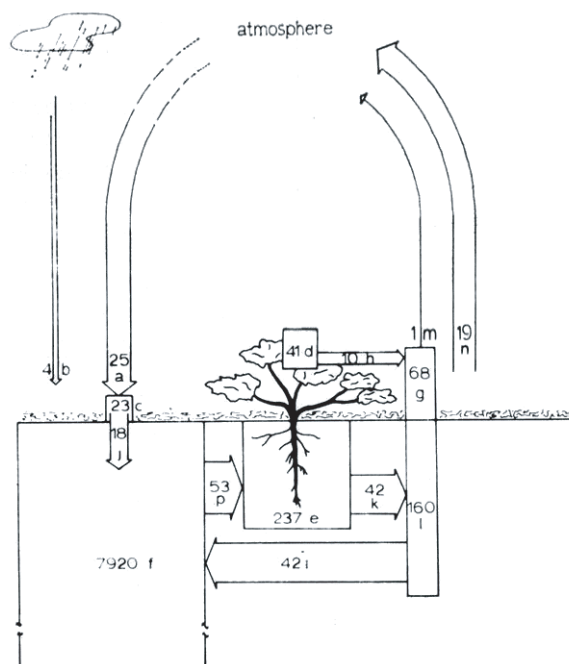

FIGURE 6. *A schematic representation of the main aspects of the annual nitrogen balance for a desert ecosystem dominated by* Atriplex confertifolia *in Curlew Valley, Utah. Arrows indicate annual fluxes in kg N ha^{-1} y^{-1}. Compartments show highest annual values as kg N ha^{-1}. Key is below. (from West and Skujins, 1977).*

a = *biological fixation, mainly by glue green algae in cryptogamic crust*
b = *input in wet and dry precipitation (including dust)*
c = *=total N in cryptogamic crust*
d = *total N content of above ground higher plant biomass*
e = *total N content of living below ground higher plant biomass*
f = *total N mineral content of soil, to 90 cm (rooting depth)*
g = *total N in above ground phanerogamic plant litter*
h = *total N in above ground higher plant litter production*
i = *mineralization rates of N in higher plant litter*
j = *mineralization of cryptogamic plant litter*
k = *below ground litter production*
l = *total N in below ground litter standing crop*
m = *volatilization*
n = *denitrification*
p = *plant uptake*

generally low levels of ,nitrifying activity and relatively small pools of mineral nitrogen are among such characteristic features. Substantial pools of fixed ammonium nitrogen or indeed of nitrate nitrogen are not uncommon in natural grasslands systems. Such pools are usually not long-lasting, except at depth, and their occurrence is generally associated with strong seasonal or secular climatic pulses. For example, Jones and Woodmansee (1979) found accumulation of nitrogen as nitrate in annual grasslands in low soil water conditions. Bate (1981) has noted transient high levels of nitrate in African savannas. Indeed, it was such transient phenomena in East African soils that encouraged H. F. Birch to begin the series of studies of the effects of alternate wetting and drying that are now central to our understanding of nitrogen mineralization in field conditions. Major flushes of mineralization and nitrification may occur in short periods of re-wetting of soil following drought in natural grasslands and savannas as well as deserts. It has been suggested (O'Connor, Robinson and Corke, 1966) that periodic nitrification and flushing of nitrate from *Prosopis* shrublands and Adesmia-containing grasslands may be responsible for the lower elevation nitrate deposits of northern Chile and the nitrate-richness of vegas of southern Chile. We should not conclude from merely annual summaries of water balances that drier grasslands and semi-desert systems are immune to short-term periodic losses of nitrogen by leaching or denitrification of nitrate. Nor should we infer, as I have tended to (O'Connor, 1974), that because mineral nitrogen pools are nearly always very small in natural grassland soils and nitrification little evident, plant nitrogen nutrition in such natural grass~ lands is almost universally ammonium nutrition. It is very easy to have a balance sheet with the net effect zero but it may fail to show the volume of external exchanges and the volume of short-term internal transformation.

Nitrification

Nitrification has been reported in many grasslands of the world since the times when it was widely believed to be inhibited. Evidence of nitrification in New Zealand tussock grassland soils has been found by Robinson (1963), Than (1967), Ross and McNeilly (1975) and Ross and Bridges (1978). Differences occur between soils in nitrifier populations, nitrifying capacity and nitrate content at sampling, generally indicating greater nitrification in soils of the drier sites of the series studied. Robinson's (1963) study of the Craigieburn soil revealed that it was not necessary to postulate biological or chemical inhibition of nitrification in order to account for the low level of

nitrification activity. In accordance with Jansson's (1958) concepts of a NH_4 pool, illustrated in his universal cycle (Fig. 5), Robinson found that augmentation of the NH_4 pool led to effective nitrification. Recent studies using field extracts of soils under tall tussock grasslands (McSweeney, 1983) reveal a marked surge in mineralization and nitrification in late winter, a phenomenon escaping detection in annual late spring sampling. McSweeney (1983) attributes this late winter flush to freeze-thaw effects analagous to those of drying and wetting in other climates. Experimental freezing and thawing of tussock sods has given supporting evidence. Mineral nitrogen uptake by vegetation may soon follow this late winter mineralization. Williams, Nes and O'Connor (1977) and Williams et al. (1978) reveal high leaf sheath N. concentrations in *Chionochloa* in early spring and I have established from field observations that root development in tall tussocks at 900 m may begin as early as mid-winter while leaf elongation is delayed for as much as two months. Determinations of N concentrations in roots have not been carried out as frequently or in as many compartments as Williams et al. (1977) made for shoots. Clearly it is important to determine the fate of this cool-season nitrified nitrogen.

Both McSweeney (1983) and Ross et al. (1979) have found that these tall tussock grassland soils have low levels of mineral nitrogen and low numbers of ammonium-oxidizing and nitrite-oxidizing bacteria at other times of year. Some of the Otago climosequence sites demonstrate little or no mineralization in winter (McSweeney, 1983; Ross and Cairns, 1981). They appear to have low nitrification activity throughout the year, similar to the Craigieburn soil studied by Robinson (1963). It seems that the reasons for these variations between soils may also warrant investigation, whether they be of soil chemical, biological or climatic origin.

Dinitrogen Fixation

Natural grasslands are frequently characterised by a paucity of legumes. Fixation of nitrogen from symbiotic sources may be generally low but Paul (1978) noted that non-symbiotic N fixation by algae can be significant. Jones and Woodmansee (1979) found that in unimproved annual grassland, nitrogen fixation by legumes could fluctuate from almost zero to more than 5g 6 m^{-2} y^{-1}. Bate (1981) has reviewed evidence of dinitrogen fixation in tropical and subtropical savannas, indicating rates in excess of 3g N m^{-2} y^{-1}.

Two aspects may be important to consider here in regard to ecosystem strategies. First, we can acknowledge dinitrogen fixation as an obligate property of

a seral ecosystem. We might also recognize N-fixation as a facultative property of mature ecosystems, especially one in a strongly pulsing environment, allowing the ecosystem to restore nitrogen pools depleted as a consequence of natural environmental oscillations. Wet and dry deposition may account for up to 1g N m^{-2} y^{-1} but primary successional accumulation of nitrogen and possibly also secondary successional restoration of N frequently exceed this rate (Stevens and Walker, 1970; Reiners, 1981).

The second aspect which needs to be considered in relation to dinitrogen fixation is soil phosphorus regime in both primary and secondary successions. The foundation work of Jenny (1961), Walker (1964), Walker and Syers (1976) in establishing the role of phosphorus in quantitative pedogenesis is now firmly integrated into the nitrogen balance context by the review of Cole and Heil (1981). Relationships exist of phosphorus and nitrogen in virgin grasslands of the United States Great Plains (Haas, Grunes and Reichman, 1961) and in the Alaskan tundra (Chapin and Van Cleve, 1978). The significance of phosphorus availability to nitrogen fixation in at least primary succession is acknowledged by Reiners (1981). From the review of Gorham, Vitousek and Reiners (1979), we can identify the role of acid production by biota in determining mineral weathering, in turn governing the availability of phosphorus. I have already pointed to the role of acid production in the rhizosphere by *Rhizobia* as a factor apparently affecting the edaphic adaptation of some legumes to fresh soil material in which phosphorus occurs principally as apatite (O'Connor, 1969). In the same report I demonstrated that inoculation of white clover *(Trifolium repens)* with acid-producing strains of *Rhizobium* allowed it to overcome in part the acute phosphorus deficiency induced by reverting dihydrogen calcium phosphate with heavy dressings of lime. This depressive effect of lime was serious even in the presence of abundant mineral nitrogen, showing that in the short term, the bacterial inoculation effect was independent of any effect of nitrogen fixation.

In introducing, from Gorham, Vitousek and Reiners (1979), a casual loop diagram (Fig. 7), Reiners (1981) outlined the nitrogen-fixation / acid-generation/weathering-rate loop as a central principle affecting nitrogen cycling in relation to ecosystem succession. He also identified the core principle of both Jenny, Arkley and Schultz (1969) and Walker (1964) that "as substrate ages and in the absence of stripping of the weathered layers by erosion, weathering products will eventually be produced below the point at which they can be utilized by plants", with consequent adjustment of ecosystem structure and function to fit a tighter nutrient economy. Finally, he
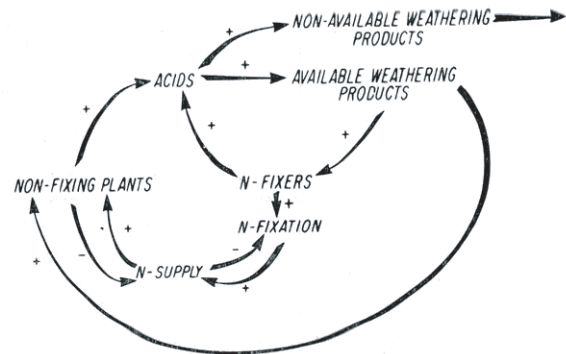

FIGURE 7. *A simplified causal loop diagram relating nitrogen fixation to rock weathering. An arrow marked + signifies that one process or component is connected with another such that increase in one leads to increase in the other. A negative influence of one on another is denoted with a negative-marked arrow. (from Reiners, 1981).*

pointed to the competition between non-fixing plants and N-fixing plants for such factors as light or weathering products including phosphorus, leading to the decline of N-fixation.

This convergence of thought between the doyens of pedology and of ecosystem succession may serve to remind those dealing with New Zealand grassland management that their traditional practice of applying superphosphate to promote legumes to fix nitrogen to grow grass has been succinctly described by Walker (1964) as "turning back the soil and ecologic clock." The widespread landscape instability and the abundant biocoenotic adaptation to the edaphic conditions resulting from such instability have been recently reviewed for the New Zealand mountains (O'Connor, 1980, 1983), suggesting a natural endemic precedent for our traditional rejuvenating land use practice.

With this perspective, some order and unity in the role of dinitrogen fixation can be seen across a wide range of natural grassland ecosystems, from early successional stages where N-fixers may be very prominent (Stevens and Walker, 1970) to mature stages where they are inconspicuous, except after disturbance, or where they flourish erratically as in some annual grasslands (Jones and Woodmansee, 1979). It follows as a corollary that as soils mature they may no longer support the N-fixing elements characteristic of their youth. If new N-fixing elements are present, having adapted to mature soils, the ecosystem may still have a capacity to restore N balances after disturbance. Savannas and other grassland associations of the tropics and sub-tropics, even in mature stages of successions, are frequently char

acterised by genera which Norris (1965) has shown to be adapted to acid-tolerant or alkali-producing *Rhizobia*. In many cases such legumes of mature soils may exist without an N -fixing function until disturbance occurs requiring balancing by fixation. Temperate grasslands may not always be as frequently characterized by such legumes although some are noteworthy adventives in New Zealand (e.g. *Ulex europaeus* and *Cytisus* spp.) while several genera, (e.g. *Hovea; Oxylobium)* are present in Australian alpine grasslands (Costin, 1970). If a facultative N-fixing association adapted to mature or post-mature soils does not exist in ecosystems of advanced successional stage, their disturbance may lead to lasting N loss, not compensated by N-fixation. Such situations may be so unfavourable to productivity that stability may be lost and erosion ensue.

Uniting this interpretation is the concept that direction of N balance affects successional change. Positive N balance leads to ecosystem succession towards maturity. Negative N balance in undisturbed mature systems may lead to succession to post-mature systems, if adaptive N-fixation does not exist to compensate for losses. Negative N balance arising from disturbance to early or immature stages generally leads to secondary succession with compensating N-fixation. Negative N balance arising from disturbance to mature or post-mature stages may not be compensated by N-fixation and new primary successions may eventually occur on new substrates exposed by erosion.

Nitrogen fixation in New Zealand grasslands and seral shrublands has been inadequately investigated. Silvester (1968, 1977) found from a biomass sample study that *Coriaria arborea* fixed 13 to 10 g N m^{-2} y^{-1}. No strictly comparable results have been reported from the other rhizomatous *Coriaria* spp. more characteristic of grassland associations, although Daly, Smith and Chua Siew (1972) have shown a wide range of performance in acetylene reduction. Silvester and Smith (1969) reported as much as 1 g N m^{-2} y^{-1} fixed by the *Gunnera arenaria-Nostoc* symbiosis. Daly (1969) demonstrated that stands of matagouri *(Discaria toumatu)* of from 25 to 110 years of age accumulated 6.7 g N m^{-2} y^{-1} in the soil-plant system. The widespread native legumes *Carmichaelia* spp., *Corallospartium crassicaule* and *Sophora* spp. and the more localised genera, *Notospartium, Chordospartium* and the herbaceous *Swainsona,* have not been quantitatively assessed for their dinitrogen fixation, although their rhizobial relationships have been examined by Greenwood (1969). Until their recent conspicuous recovery in the physiognomy of many tussock grasslands following sustained reduction in grazing from sheep and rabbits, these native

legumes were discounted from consideration in nitrogen budgets. All native legumes in New Zealand seem concentrated on, if not confined to, juvenile or somewhat immature soils (O'Connor, 1969; Greenwood, 1969). Where *Discaria* or *Coriaria* occurs in mature soil landscapes it is often found to be associated with a nutrient flush zone. *Discaria* may persist in old soils without N fixation function.

The possibility of other symbioses in the native flora contributing to N-fixation has been considered but explicit proof is lacking. Non-symbiotic fixation has been demonstrated by Line and Loutit (1971, 1973) in tussock grassland soils. No quantitative field studies have been published of fixation by other bacteria, *Azotobacter* and *Seierinckia,* sometimes reported from New Zealand tussock grasslands.

In their present modified condition the tussock grasslands doubtless receive substantial dinitrogen fixation from adventive legumes. Gorse and *Cytisus scoparius* (leafless broom) are especially common in a wide range of sites from raw riverbed sands and gravels to mature soils in the lowland and montane zones. White clover and other clovers (e.g. *T. campestre, T. dubium, T. arvense)* are now widely distributed in many environments in the tussock grasslands, especially those where phosphorus deficiency is not severe. In such situations they are often suffering from sulphur deficiency because of low atmospheric returns. Limited quantitative assessments of N-fixation from such volunteer or unfertilized associations have been reported (Nordmeyer, 1978). It is clear from the abundance of such annual species as *T. arvense* and *T. dubium* in the depleted grass lands of Central Otago that they are significant in the secondary or new primary successions of such landscapes. Other genera, notably *Lotus, Melilotus* and *Medicago,* are adventive in some localities, *Lotus nedunculatus* principally in flush sites, species of the last two genera in open areas of non-phosphorus-deficient soils of semi-arid regions.

MANAGEMENT AND MISMANAGEMENT EFFECTS ON NITROGEN BALANCES

Burning

Woodmansee and Wallach (1981) have reviewed the effects of fire on biogeochemical cycles in a wide range of ecosystems, principally forests. They point out that ecosystems such as grasslands which have comparatively small proportions of nutrients in aerial biomass are not likely to suffer as severely from fire as do forests and the like. They estimate that grasslands with up to 3 g N m^{-2} available for loss in gaseous form from fire might be expected to be restored to N balance from atmospheric deposition and low level fixation in from one to six years. They

acknowledge the importance of available fuel and fire intensity in affecting the proportion of N lost. Woodmansee et al. (1978) recorded a total of about 14 g N m^{-2} in litter, crowns and plant tops at Pawnee site in mid-summer, suggesting the possibility of gaseous nitrogen losses in excess of 3 g m^{-2}. Similar or greater potential N losses are indicated for savannas (Bate, 1981). In addition to direct losses from smoke and volatilized gaseous compounds, Woodmansee and Wallach (1981) noted the immediate biologic effects of increased mineralization, nitrification and uptake of nutrients by microorganisms with possible leaching or other losses if higher plant uptake of nutrients was much delayed by slow recovery.

Comparable values of above ground material at Paddle Creek, Canterbury were 14.3±0.9 g N m^{-2} for *Chionochloa rigida* and 6.4±0.8 g N m^{-2} for C. *macra* (Williams et al., 1977). Evans and Kelland (1982) reported phytomass and litter determinations for stands of C. *pallens* at 1440 m. and C. *macra* at 1200 m. on the Craigieburn range where the vegetation had not been burnt for several decades. In litter and above ground material there were some 33 g N m^{-2} and 18.5 g N m^{-2} at the respective sites. Induced *Festuca novae zelandiae*. severely-modified grassland at 1050 m. with much less litter, contained only 4.2 g N m^{-2} above ground. These data confirm the earlier indication (O'Connor, 1974) of substantial amounts of nitrogen available for loss to the atmosphere from burning of New Zealand tall tussock grasslands. Burning repeated at intervals of less than five years is likely to have severe debilitating effects on tall tussocks (Mark, 1969). Burning results in increased concentration of nutrients in the freshly grown tissue (Williams and Meurk, 1977). It has recently been suggested (Payton and Brasch, 1978) that burning of tall tussock grasslands may foster mineralization of soil organic matter, thereby contributing to the observed enhancement of flowering in the following season as well as increased tissue nutrient concentration. It can be speculated therefore, that frequent burning, uncompensated by nitrogen fixation, might accelerate nitrogen depletion from tall tussock ecosystems beyond the rates calculated from periodic fuel loads alone.

Grazing

Floate (1981) has reviewed the effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems and has pointed out that extensive range-grazing systems are characterised by the small proportion of the total dry matter production that is utilised by grazing animals. While this may be generally true, it may serve to conceal more severe

effects if grazing use reduces production substantially below potential levels by inducing changes in plant physiologic behaviour or in vegetation composition. In commenting on this paper (O'Connor, 1981), I have indicated that close defoliation in tall natural grassland, which is often found to reduce productivity, may also reduce nitrogen uptake. Temporary increases in soil ammonium pool resulting in this way from overgrazing may lead to increased nitrification and risk of nitrate loss. A further effect of a similar kind can result from more lasting changes to vegetation itself. In earlier papers (O'Connor, Robinson and Corke, 1966; O'Connor, 1966, 1974) I have pointed to evidence from S.E. Australia, southern Chile, Kansas and New Zealand of increased nitrifiers or nitrification with depletion. Table 3 presents additional evidence of a similar effect on nitrifier populations in autumn in western Canadian grassland soils under natural grasslands differently managed for several years. Samples were chilled and air-freighted within four days to the laboratory for immediate analysis, as was done by O'Connor et al. (1966) with soils from southern Chile. Mineral N levels were low, without always demonstrating the preponderance of NH_4-N which often characterizes natural grassland soils. Nitrifier populations were higher in grassland soils with moderate to severe grazing, than they were under ungrazed grassland or even, in most comparisons, in long-term cultivated soils. Incubation of soil samples for seven days resulted in ready mineralization of NH_4 + and NO_3-nitrogen from all grassland samples. In contrast. samples from the same soils maintained in arable culture for several years mineralized less additional nitrogen but a much higher proportion of that mineralized was nitrified, reflecting the NH_4 +-N / NO_3- -N ratios in fresh cultivated samples. For the 20 samples in Table 3 which were collected under grassland cover, log of most probable number of nitrifiers was found to be negatively correlated with index of grassland condition ($r = -0.64$, $P < 0.01$). Like the relationship in Kansas *Andropogon* prairie (O'Connor, 1974), as grassland condition deteriorated from a nominal 100 with progressive increases in grazing intensity, most probable numbers of nitrifying organisms tended to increase. These data suggest but do not themselves prove that nitrification is implicated in nitrogen loss from natural grassland ecosystems as they are degraded by overgrazing.

N losses may also result from grazing as a function of the partial herbivore separation of carbon from nitrogen with subsequent volatilization of ammonia from urine, as recognized by Floate (1981), O'Connor (1974, 1981), and Woodmansee et al. (1981). Ammonia volatilisation is probably the most impor-

TABLE 3. Indicators of nitrification potential of some western Canadian soils as affected by management

	Mineral nitrogen at sampling		Ratio NH₄-N/NO₃-N	MPN nitrifiers per g	Index of grassland condition	Additional mineralized nitrogen in 7 days at 35°C		
	NH$_4$-N ppm	NO$_3$-N ppm	$\frac{NH_4-N}{NO_3-N}$			NH$_4$-N ppm	NO$_3$-N ppm	Total ppm
MANITOBA *Andropogon* Prairie								
Shallow Newdale soil 0–10 cm								
Protected	1.2	1.4	0.9	2080	70	20.7	20.8	41.5
Moderate grazing	0.8	1.7	0.5	15670	40	31.8	30.0	61.8
Cultivated	0.9	2.6	0.3	9040		3.1	24.8	27.9
Harding Clay 0–10 cm								
Protected	0.4	0.4	1.0	244	80	31.2	27.8	59.0
Heavy grazing	0.3	1.6	0.2	10570	30	3.2	38.0	41.2
Cultivated	0.5	4.9	0.1	4390		1.0	26.3	27.3
Bede loamy coarse sand 0–10 cm								
Protected	2.1	1.2	1.8	300	90	20.6	26.8	47.4
Moderate grazing	7.2	2.9	2.5	10870	40	59.7	30.5	90.2
Heavy grazing	1.5	2.5	0.6	6680	25	44.9	25.5	70.4
Cultivated	0.7	9.3	0.1	2200		2.5	38.4	40.9
SASKATCHEWAN *Stipa-Agropyron* Grassland								
Weyburn soil 0–10 cm								
Protected	1.5	1.6	0.9	540	75	28.7	41.9	70.6
Heavy grazing	5.8	2.6	2.2	1940	40	23.4	48.9	72.3
Severe overgrazing	1.5	5.3	0.3	12640	20	28.4	46.2	74.6
Cultivated	1.3	6.4	0.2	2510		3.8	33.6	37.4
ALBERTA *Stipa-Bouteloua* Grassland								
Manyberries brown soil 0–10 cm								
Protected	1.4	2.5	0.6	360	80	21.7	22.6	44.3
Light grazing	1.8	2.5	0.7	690	60	20.4	24.4	44.8
Moderate grazing	1.1	1.9	0.6	360	50	26.7	25.0	51.7
Heavy grazing	1.7	1.6	1.1	1420	40	25.2	23.5	48.7
Severe grazing	1.0	2.2	0.5	1540	25	20.6	13.1	33.7
ALBERTA *Festuca scabrella* Grassland								
Stavely shallow black soil 0–10 cm								
Protected	3.9	4.5	0.9	510	90	58.6	39.8	98.4
Light grazing	4.7	3.3	1.4	20600	70	118.2	41.0	159.2
Moderate grazing	8.0	5.7	1.4	7280	60	63.6	31.5	95.1
Heavy grazing	6.2	7.6	0.8	51300	40	59.2	25.6	84.8
Severe overgrazing	4.5	3.8	1.2	23970	25	62.0	51.5	113.5
Cultivated	1.0	5.1	0.2	6860		8.6	50.2	58.8

tant pathway of N loss from drier grassdland soils (Watson and Lapins, 1969; Woodmansee and Duncan, 1980). It has been demonstrated for nearly 40 years (Thompson and Coup, 1940, 1943) that the urine patch is a microsite for nitrification as well as ammonia volatilisation. How much is lost by each pathway in extensively grazed grasslands is largely guesswork at the present time. Distribution in time and space is critical. In earlier reviews on this topic (O'Connor, 1974, 1981), I have pointed out the temporal and spatial significance of the grazing-excretion patterns of large herbivores. Woodmansee et al. (1981) have hypothesised six kinds of areas of differing nitrogen status that can be generated in a pasture as a result of such temporal and spatial variability. Although Woodmansee et al. (1981) conceded that these areas may shift in space over time, it is difficult outside of a particular landscape to formulate a valid definition of their distinct status. I prefer, therefore, the concepts of local, often short-term, N-donor and N-receptor sites within the longer-term trends of N-gaining and N-losing systems, as outlined in my commentary on Floate's review (O'Connor, 1981).

An important topic for further analysis in this field is that of defoliation influence on herbage productivity and its influence on nitrogen uptake. As indicated earlier there is considerable evidence both in North American range and in New Zealand tall tussock grassland that close defoliation may reduce productivity and thereby potentially reduce nitrogen uptake. The recent research of McNaughton (1979a, b) in Tanzanian savanna grasslands suggests that increase in productivity may result from defoliation of some natural grasslands by herbivores, mediated through nutrient cycling in normal herd behaviour.

The fate of nitrogen in senescent herbage tissue that remains uneaten is uncertain in many situations. Some may be lost by volatilisation of NH_3, while some may be retained in tissue, subjected to faunal and microbial attack, eventually to be incorporated in soil organic matter. As Floate (1981) indicates, consumption by herbivores may therefore accelerate the recycling of at least some such herbage N without inducing any reduction in productivity or in N uptake. These aspects warrant increased research, additional to that properly being given to the fate and effects of animal excretory N.

A SUMMARY ASSESSMENT OF THE NITROGEN REGIMES OF NEW ZEALAND NATURAL AND EXTENSIVELY MANAGED GRASSLAND SYSTEMS

It would be a happy occasion if one could, at this stage, present a synthesis of all relevant New Zealand research on tussock grasslands in a nitrogen budget,

after the manner of Woodmansee et al. (1978). That is not possible, in part because insufficient field work has been done on many of the key processes identified and also on many to which I have here given scant attention e.g. denitrification. A further reason arises from the fact that many of the studies have been done only in laboratory conditions with samples collected and stored from the field. Without more field studies, it is rash to assume that even comparisons between soils would remain valid when translated from laboratory conditions to field situations. There are some features of N budgets that we are beginning to understand.

Higher Plants

Compartments and fluxes of the within-plant sub-system have been investigated with some thoroughness at Paddle Hill Creek (Williams et al., 1977). The schema of that subsystem is outlined in Figure 8. Both carbon and other elements can now be approximated according to this schematic model. The intensive measurement and analytical programme on the Craigieburn Range, outlined by Evans (1980) extends this work, although in a somewhat different procedure. Likewise, the intensive biomass and productivity studies of Meurk (1978) in Otago, when coupled with the widespread mineral composition survey of Williams et al. (1978), may allow some approximations to be extended for the plant sub-model to the taxa and sites of that region.

Three caveats should be expressed. One is the real possibility of within-plant N-recycling, as discussed by Clark (1981). The second, related to this, has been earlier alluded to, the fact that root to shoot fluxes have been determined from net changes in shoots between early October and late March only, without attention to possible cool season root activity. The third is that no quantification has been made at Paddle Hill Creek sites of *non-Chionochloa* shoot material, although this has been done at the Craigieburn Range sites (Evans, 1980). The possible differences among *Chionochloa* species in nutrient frugality suggested by Williams et. al. (1977, 1978) would be clarified by attention to these three features as well as by further study of litter accumulation and decomposition, especially with careful attention to soil fauna effects.

Litter

Incorporation and decomposition of litter is slow. Turnover rates for nitrogen in tall tussock dead leaf compartments above ground were calculated by Williams et al. (1977) at 8.2 years for *C rigida* and 5.3 years for *C . macra*. Comparative values for dry matter were 6.7 years and 5.0 years respectively. Olson values for predicting 95 percent decay time
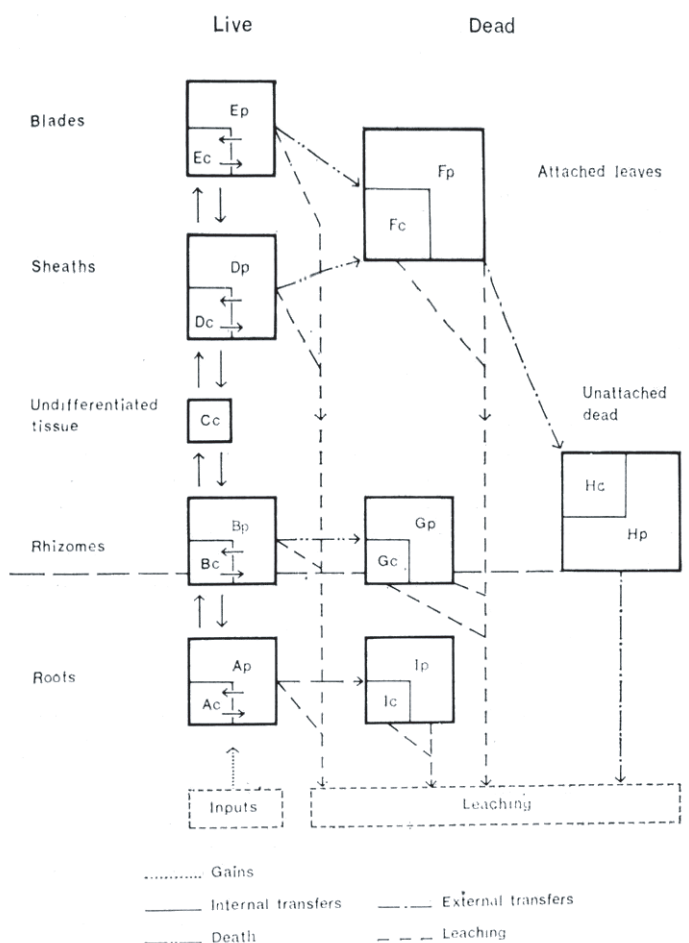
FIGURE 8. *Schematic model of tall tussock part of a grassland ecosystem. Within each compartment the subscript c refers to current season, the subscript p to previous season. (from Williams, Nes and O'Connor, 1977).*

for standard *C. rigida* leaf blade litters were found after 3.3 years at the Paddle Hill Creek *rigida* site to be 10.0 years. With similar material for two years only, Molloy, Bridger and Cairns (1978) found Olson values ranging from 13.6 to 42.8 years at seven Otago upland and mountain sites. With more extended exposure these values may have declined, for Williams et al. (1977) reported a rapid increase in decomposition rate after the initial two years. Comparative studies with other materals and IBP cellulose suggested that leaf litter orientation and leaf structure may be the principal reasons for their comparatively slow rate of disappearance (Molloy and Bridger, 1978; Ross et al., 1978). Site differences remain substantial in the Otago study. The large litter values of the Craigieburn sites (Evans, 1980; Evans and Kelland, 1982) raise many questions concerning significance of such factors as fire history and

microbial and soil fauna habitats. Few fescue tussock sites have been studied. There are many practical observations which suggest that decomposition there is no faster than in tall tussock sites and in some cases, it may be much slower.

Soil Biology and Biochemistry

As indicated earlier, a collaborative synthesis is called for to interpret and apply the work which has already been reported and that which is continuing. There is ample evidence in both the work of the Soil Bureau, D.S.I.R. personnel already discussed and that of McSweeney (1983), that the Otago sites do not constitute a simple climosequence with gradients of temperature or precipitation accounting for differences in organism populations or performance. In effect the great value of these studies for me has been to sharpen the focus on the possible effects of

pastorally-induced change within the pedological and climatic spectrum. The thesis has already been advanced (Williams et al., 1977) of a "pseudo-aging" process in soil-plant systems induced by destruction or substantial modification of the vegetation, as from forest or tall tussock to short tussock grassland. It is perhaps significant that in both the earlier series of studies (Thornton, 1958, 1960) and the more recent series (Molloy and Blakemore, 1974), the least biologically active soils, so far as mineralization was concerned, were those in which fescue tussock grassland had been induced by pastoral practices. It was this stage of ecosystem modification that I identified (O'Connor, 1966) as suffering the lowest "cyclic mass flow" of nitrogen. It was also this system which Robinson (1963) and Robinson and MacDonald (1964a, b) experienced in the Craigiebum soil as one where nitrification and soil respiration were both at minimal levels for lack of available substrate.

After years of field and glasshouse experiments with such "pseudo-aged" soils I do not underestimate the problems associated with phosphorus availability, aluminium, pH, and micro-nutrients. However, it is suggested that a *pastorally-induced* change in soil biology and biochemistry may also be implicated in the problems that so many of these modified soil-plant systems in the less-arid, montane and lower sub-alpine zone present.

CONCERNING THE FUTURE

We now have, for the varied tussock grasslands of New Zealand, a much clearer perspective of their suitability and unsuitability for different kinds of use. We have a large body of information on the vegetation, on the principal species, on the basic character of the soil body on different landscapes. We now have a not insignificant volume of information on their soil floras and faunas, on their comparative enzymology and biochemistry. We are now beginning to understand some of the space-time dimensions of these soil-and-vegetation landscape systems. We are also beginning to understand their pre-historic and historic behaviour. Perhaps more urgently, we are now technically equipped with the practical knowledge, materials and methods for transforming much of these lands into potentially highly productive pastures or forests, the sustainability of which may remain in some cases questionable. These doubts which we must hold are rooted in the fact that for both the natural and modified landscapes as well as the potential cultures which we might employ, the dynamics' of nitrogen and other biogeochemical transformations in the soil phase largely remain unquantified.

There are many apparent parallels and convergences between the microfloral, faunal, enzymic and organo-chemical processes indicated in Soil Bureau D.S.I.R. studies from Otago sites and those of Pawnee and Matador sites in North America. There are some apparent differences. A concerted effort would still be necessary in New Zealand to achieve a similar level of quantitative understanding and predictive power concerning carbon and nitrogen balances to what has been reached by the development and testing of successive ELM and PHOENIX models. A renewed and co-ordinated effort would be required to integrate such work with the dynamics of sulphur and phosphorus, as is currently being done in grassland, tundra and forest biomes in North America. It is unlikely that such action in concert and co-ordination will be inspired among research scientists in New Zealand without the promotion of greater exchange and without the guiding stimulus of models. It is unlikely that the full value of such model-guided research would be achieved unless it were applied to both natural and developmental cultural systems in the same landscapes. For that purpose, land must be reserved and used for science. The tussock grasslands and the potential intensive pastoral and forestry uses for which they seem suited offer an outstanding opportunity. There are probably few places in the world where there is equal likelihood that the results of research could be put so swiftly into profitable practice. Some of the profit may come from learning where not to attempt land development for pastoral farming or forestry. Some of it will clearly come from application of biochemical understanding to the development of land use technologies that adapt to endemic processes likely to persist in the soil-landscape systems which we have.

ence to his unpublished work. Dr Kwan Goh, Soil Science Department, Lincoln College and Dr Des Ross, Soil Bureau, D.S.I.R. have made valued comments on the manuscript. The late Dr John Stout gave repeated stimulus to the author to attempt such a synthesis.

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