
C S I R O P U B L I S H I N G

AUSTRALIAN JOURNAL OF PLANT PHYSIOLOGY

Volume 26, 1999
© CSIRO Australia 1999

AJPP

An international journal of plant function

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Foliar $\delta^{15}\text{N}$ is negatively correlated with rainfall along the IGBP transect in Australia

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A comment on 'Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia' by E.-D. Schulze, R. J. Williams, G. D. Farquhar, W. Schulze, J. Langridge, J. M. Miller and B. H. Walker, *Aust. J. Plant Physiol.*, 1998, 25, 413–425.

The recent paper by Schulze *et al.* (1988) describes patterns of nitrogen content, and stable isotope ^{15}N and ^{13}C along the North Australian Tropical Transect. Along the transect, annual precipitation changes dramatically with latitude (between 11°S and 25°S). The authors found effects on community-averaged carbon isotope discrimination (Δ) in the low range of precipitation (below 475 mm), and they reported no relationship between the foliar $\delta^{15}\text{N}$ and the nitrogen-fixing status of the species across the gradient. In addition, the authors concluded that there was a positive relationship between the grazing intensity and foliar $\delta^{15}\text{N}$; that is, sites with high grazing intensity have more positive $\delta^{15}\text{N}$ values (enriched in the heavier isotope ^{15}N). An explanation for this pattern could be that, with increased grazing, there would be an acceleration in turnover of nitrogen through increased mineralization and hence increased ^{15}N -depleted gaseous losses together with the removal of ^{15}N -depleted plant material by herbivores. This hypothesis is logical based on our current understanding of potential effects of grazing on nitrogen cycling and the effects of various fractionation factors on plant and soil $\delta^{15}\text{N}$. (see Handley and Scrimgeour 1997; Höglberg 1997 for reviews). However, the patterns as they exist in the current literature are not clear—in one study, soil $\delta^{15}\text{N}$ became more positive in the more heavily grazed sites (Frank and Evans 1997), although in this same study foliar $\delta^{15}\text{N}$ of grazed species decreased with grazing. In another study, there was no demonstrated change in foliar or soil $\delta^{15}\text{N}$ between grazed and ungrazed pastures (Neilson *et al.* 1998). While stable isotopes of ^{13}C and ^{15}N are used in animal ecology for analyses of trophic interactions, dietary tracing, and animal movement patterns (see Gannes *et al.* 1998 for review), the relationship between grazing and ecosystem $\delta^{15}\text{N}$ has yet to be understood completely.

A simple correlative analysis between annual precipitation, rather than latitude, and foliar $\delta^{15}\text{N}$ (data from their Fig. 4, precipitation data from their Table 1) indicates a pattern distinct from the one suggested by the authors. This correlation indicates a highly significant ($P < 0.0001$, $r = -0.64$) negative linear relationship between foliar $\delta^{15}\text{N}$ and median annual precipitation (Fig. 1 of this comment). With increasing annual rainfall, there is a systematic decrease in the foliar $\delta^{15}\text{N}$ signatures. More than 40% of the variance in this data set is explained by the relationship of foliar $\delta^{15}\text{N}$ with annual precipitation.

First, there are many hard-to-measure variables in ecology while others are straightforward. The measurement of annual precipitation generally comes from long-term data collection (in the case of this study, a climate atlas and established

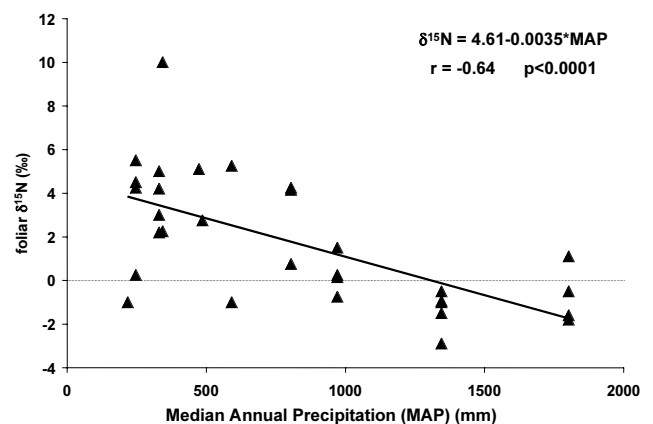


Fig. 1. Correlation of foliar $\delta^{15}\text{N}$ with median annual rainfall along the Australian IGBP transect. Each symbol represents average values of $\delta^{15}\text{N}$ for each species sampled (data from Schulze *et al.* 1998)

weather stations). In contrast, variables such as 'grazing intensity' are difficult to determine unless completed with very careful sampling over time (McNaughton *et al.* 1996). In Schulze *et al.* (1998), grazing intensity was 'qualitatively assessed from grass and weed cover, data not presented', rather than an objective measure of changes in species composition or cover compared to a similar non-grazed situation. The lack of objective assessment or historical data calls into question the validity of the conclusions that changes in $\delta^{15}\text{N}$ are related to changes in grazing intensity.

Second, the implication that grazing is more intense in drier sites (or sites intermediate on this transect, in this case 329 and 590 mm) is not well supported by regional-scale analyses of the relationship between precipitation and herbivory. Herbivory is positively correlated with precipitation, with an increasing proportion of above-ground primary production consumed with increasing rainfall (McNaughton *et al.* 1989, 1991; Oesterheld *et al.* 1992). Even in ecosystems that are actively managed, stocking rate by land managers is correlated exponentially with mean annual precipitation (Oesterheld *et al.* 1998). Grazing intensity, described as the fraction of above ground net primary production (ANPP) being consumed, increases with increasing precipitation. Therefore, there is no reason to conclude that there is a decrease in grazing intensity with an increase in annual precipitation, causing a pattern of depleted $\delta^{15}\text{N}$ values with increasing rainfall.

In contrast, the correlation of $\delta^{15}\text{N}$ with annual precipitation is a pattern that appears to be robust across many different types of ecosystems. Very positive $\delta^{15}\text{N}$ values are often reported from arid sites (Lajtha and Schlesinger 1986; Fry 1991; Schulze *et al.* 1991), while negative values are reported from sites of high rainfall or cold and wet systems outside the mainland tropics (Vitousek *et al.* 1989; Nadelhoffer *et al.* 1996). In addition, a negative correlation of foliar and/or soil $\delta^{15}\text{N}$ with increasing mean annual precipitation has been observed in several studies: a soil survey in the continental United States by Shearer *et al.* (1978); by Heaton (1987) in South African ecosystems; in tropical forests sites on the island of Hawaii by Austin and Vitousek (1998); and by Austin *et al.* (unpublished data) along a contiguous precipitation gradient in Patagonia, Argentina. Most recently, an extensive global synthesis by Handley *et al.* (1999), demonstrates a negative linear relationship between foliar $\delta^{15}\text{N}$ and annual rainfall across a wide range of ecosystems. This current study by Schulze *et al.* (1998) is another example of the generality of the pattern of decreasing foliar $\delta^{15}\text{N}$ with increasing annual precipitation, independent of nitrogen-fixing status of species, or large differences in other climatic factors such as temperature.

The correlation of precipitation and $\delta^{15}\text{N}$ suggests that annual rainfall input may be an important component controlling ecosystem nitrogen cycling. There are a number of interrelated mechanisms at work that will determine the

ecosystem $\delta^{15}\text{N}$ signature—a net result of all factors affecting the inputs, outputs, and internal fractionations of ^{15}N over ^{14}N . In addition to the direct effects of precipitation on short-term turnover, long-term losses affecting ecosystem nitrogen pools are reflected in the $\delta^{15}\text{N}$ values. The increasingly depleted foliar ^{15}N in wetter sites suggests that, in spite of potentially more rapid turnover, accumulated losses of nitrogen relative to ecosystem nitrogen pools are greater in the drier sites. While the magnitude of both input and output will increase with increasing rainfall, the ratio of loss relative to intrasystem turnover will become smaller, such that increased water availability will result in a systematically less open cycle (Austin and Vitousek 1998). This pattern of decreasing $\delta^{15}\text{N}$ with rainfall suggests that the integrated effect of increased rainfall on nitrogen cycling is a decrease in the openness of the cycle itself. For every unit of nitrogen that moves through the plant–soil–microbial components of an ecosystem, the potential for loss from that system is greater in sites of lower rainfall.

Climatic variability is most pronounced in arid and semi-arid ecosystems, particularly the amounts and periodicities of rainfall between dry and wet years (coefficient of variation of precipitation) (Goudie and Wilkinson 1977; Jobbágy *et al.* 1995). This climatic variability enhances the mechanisms of loss in the drier ecosystems; build-up of inorganic nutrients in the soil due to wet–dry cycles or low plant demand in dry years will have a higher risk for loss during unusual storm events. The resulting expression of the net fractionation in the $\delta^{15}\text{N}$ of the nitrogen pool will be even greater due to the small pool size in these drier sites.

The long-term effects of the openness of the nitrogen cycle on the carbon-nutrient balance could be important. While water availability would continue to be the most frequent limitation to ecosystem production, nitrogen availability could become limiting in wet periods. The greater potential for losses would maintain these systems in a state of nitrogen limitation, in spite of relatively lower nitrogen demand. Thus, openness of nitrogen cycling may help to explain the persistence of nitrogen limitation in some terrestrial ecosystems (Vitousek and Howarth 1991).

Acknowledgments

Thanks to M. Aguiar and M. Oesterheld for critical review of the ideas presented here; support for A.T.A. comes from a National Science Foundation International Research Fellowship.

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Manuscript received 20 October 1998

The authors of the original paper respond on page 296.

Interpretation of increased foliar $\delta^{15}\text{N}$ in woody species along a rainfall gradient in northern Australia

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A response to the comment 'Foliar $\delta^{15}\text{N}$ is negatively correlated with rainfall along the IGBP transect in Australia' by A. T. Austin and O. E. Sala,
Aust. J. Plant Physiol., 1999, 26, 293–295.

Austin and Sala (1999) have re-evaluated the data published by Schulze *et al.* (1998) and claim that the pattern of $\delta^{15}\text{N}$ was not related to grazing, but was rather a linear function of mean annual rainfall. Although the regression line presented by Austin and Sala (1999) is statistically significant, we argue that the complexity of the nitrogen cycle under conditions of changing rainfall and grazing is unlikely to be encapsulated by a single linear regression. In fact, the $\delta^{15}\text{N}$ data show no response at high rainfall (in open forest communities) and an increasing variability at low rainfall, where the minimum $\delta^{15}\text{N}$ values were similar to those at high rainfall. Austin and Sala (1999) interpret the increasing site-averaged $\delta^{15}\text{N}$ under increasingly arid conditions as evidence of the increasing 'openness of the nitrogen cycle', but provide no mechanism for such interpretation.

The re-evaluation of Austin and Sala (1999) is based on site-average data, resulting in a r^2 of 0.41. If the regression is based on all measured data points and not on site averages, the r^2 decreases to 0.35 which indicates that other processes are just as significant. The regression line overestimates the values at high rainfall, and it is totally determined by the average response of highly variable data at low rainfall. Thus, factors in addition to aridity are likely to have influenced the observed pattern.

In the original paper, Schulze *et al.* (1998) stressed that the transect study provided observational data only, and that the sampling was not designed to investigate the nitrogen cycle in detail. Thus we wrote that 'we cannot rule out an interaction between aridity and grazing'. Here, we hypothesize that aridity *per se* cannot explain our observations, and emphasize the original hypothesis 'that grazing results in a loss of the light ^{14}N which over time leads to an accumulation of

heavy ^{15}N in the ecosystem'. The reasons for this opinion are outlined below and Fig. 1 summarizes the ways in which aridity and grazing could interact in the N-cycle to produce the observed patterns.

In order to discuss the effects of drought on $\delta^{15}\text{N}$ we may distinguish between direct and indirect effects of aridity. Water seepage will generally decrease with aridity, and this may lead to very tight nutrient cycling (Penning de Vries and Djiteye 1982). Seepage may occur along tree roots (Wetselaar 1980), but soil nitrate concentrations become minimal at 1.7 m soil depth even though nitrate may accumulate in higher levels of the profile under undisturbed conditions of bare fallow land. Thus the capacity to store nitrogen increases with aridity and the N-cycle is more closed under non-managed (undisturbed) arid conditions (Penning de Vries and Djiteye 1982). Decreasing seepage will also decrease the accumulation of ^{15}N in the top soil as is generally observed in humid climates (Gebauer and Schulze 1991). This equilibration of the ^{15}N distribution with soil depth will be enhanced by wind erosion of bare soil in arid regions. Also, denitrification, which increases $\delta^{15}\text{N}$ ratios (Durka *et al.* 1994) and which is a prime mechanism to increase $\delta^{15}\text{N}$ of soils in humid climates (Neilson *et al.*, 1998), will decrease with aridity, because waterlogging conditions will have a lesser probability. In summary, all these processes will tend to maintain, or decrease, rather than increase the $\delta^{15}\text{N}$ level at low rainfall. The main loss of ^{14}N from the soil will be by plant growth (Frank and Evans 1997) but, since net primary production decreases with aridity, this process (as the main possible leak of the N-cycle) will also decrease rather than increase with a decrease in precipitation.

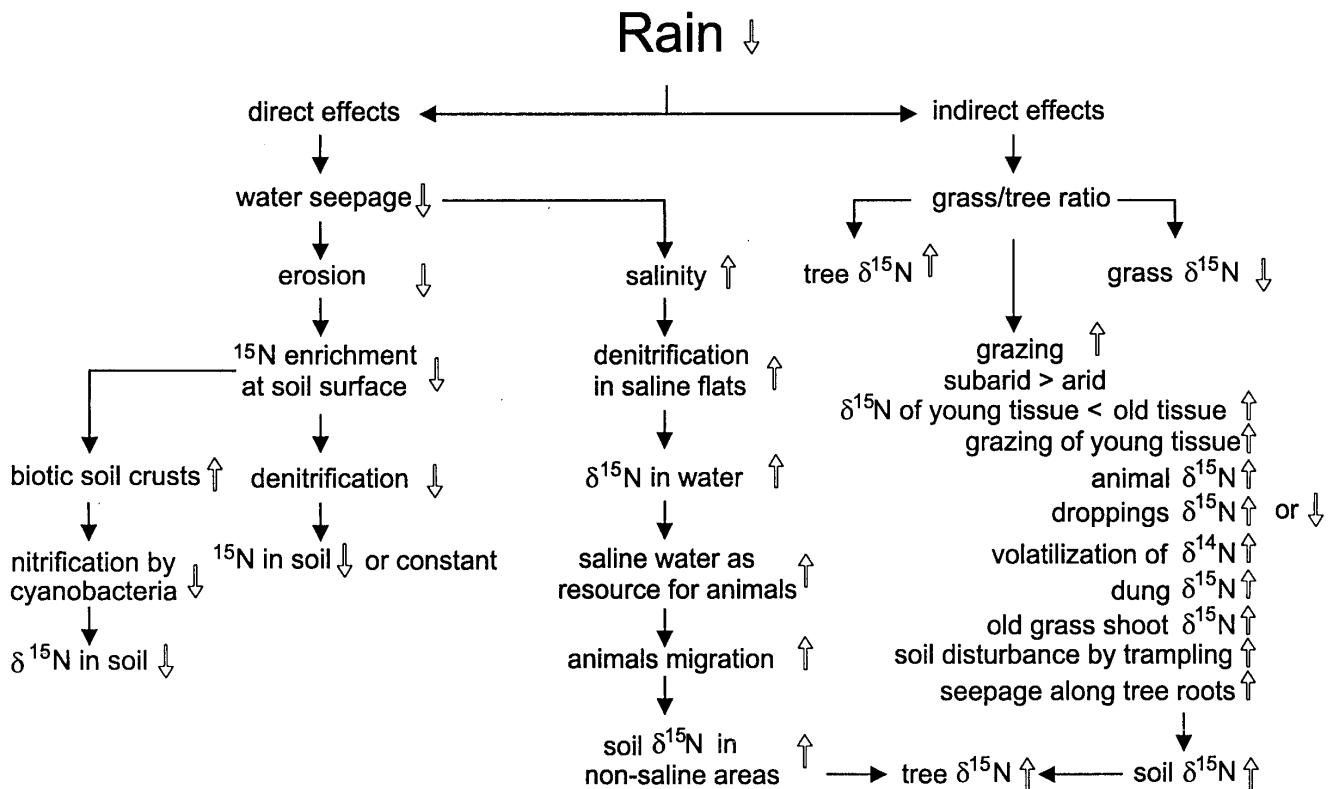


Fig. 1. Schematic presentation of some processes that affect $\delta^{15}\text{N}$ in foliage under arid conditions and grazing. The direction of the arrow after the process indicates the response of the process (increase or decrease) to a decrease in rainfall. For more explanations see text.

Three additional physico-chemical processes may indirectly increase the $\delta^{15}\text{N}$ level at low rainfall.

First, soil crusts may form on stable soils in arid climates and, due to the capacity of cyanobacteria for N_2 -fixation, this may result in a decrease rather than an increase in $\delta^{15}\text{N}$. Second, formation of salt on the surface may increase $\delta^{15}\text{N}$ level due to waterlogging and denitrification (Heaton 1987; Heaton *et al.* 1986).

Third, decreasing rainfall will also change the balance between grasses and trees. Grasses, due to a more shallow and intense root system, will have initial access to soil N and trees will receive the remaining N which is ^{15}N -enriched (Frank and Evans 1997). Thus, it is important to distinguish between what happens in herbaceous and woody species. The study of Schulze *et al.* (1998) focussed on woody species, while Austin and Sala (1999) used data from woody, as well as herbaceous species, as convenient. There is a lack of studies that investigate the effect of competition between woody and herbaceous species (e.g. Breymeyer *et al.*, 1996). In a humid climate, the study by Gebauer and Schulze (1991) showed that the $\delta^{15}\text{N}$ values of the grass cover of the forest floor was lower than same age tree foliage by 1–2%.

We may interpret the initial increase in $\delta^{15}\text{N}$ of tree foliage with decreasing rainfall as it was observed by Schulze *et al.* (1998) between Melville island (1800 mm rainfall) and

Kidman Springs (650 mm rainfall) as related to competitive interactions between herbaceous and woody species. However, since grazing is closely associated with grass cover, one cannot easily separate the effects of competition between grasses and trees from associated effects due to grazing. More interesting, though, is the observation that the variation of $\delta^{15}\text{N}$ increased markedly at low rainfall (<600 mm rainfall), but was lumped into one block of data in the analysis of Austin and Sala (1999).

In order to understand the effects of grazing, one must recognize that, in arid regions, ungulates will concentrate on young shoots of grasses (Penning de Vries and Djiteye 1982). Young shoots tend to have lower $\delta^{15}\text{N}$ values than old tissues due to the process of remobilization of reserves (see Schulze *et al.* 1998). There are data that appear to show the opposite, such as those of Neilson *et al.* (1998), who observed a decrease in $\delta^{15}\text{N}$ in grasses between spring and summer and increasing $\delta^{15}\text{N}$ of the soil in England. However, in that case, no distinction was made between young and old tissues and, since grasses grow continually all year in England, these data may reflect the availability of N during the season and not necessarily an age effect. The age effect is, however, important in a seasonal climate such as in northern Australia.

With respect to grazing, we hypothesize that old tillers of grasses will be ^{15}N -enriched similar to old leaves on trees

(Schulze *et al.* 1998), and old leaves will contribute most to the decomposing litter. The overall effect on woody species will be an increase in $\delta^{15}\text{N}$, due to an increased consumption of ^{14}N from feeding by stock on fresh grasses. This process of ^{15}N -enrichment will be accelerated by disturbance of the soil by stock. It is mainly such disturbance that opens the N-cycle under these conditions (Vitousek 1980). The seepage of nitrogen by disturbance will be available to tree roots rather than to grasses at greater soil depth.

Heaton *et al.* (1986) described discrimination in favour of ^{15}N in herbivores under arid conditions (see also Neilson *et al.* 1998), because water is ^{15}N -enriched in arid environments. Dung and urine from such animals are ^{15}N -enriched (Livingston *et al.* 1962).

All these processes will tend to lead to a 'spiral' of ^{15}N -enrichment, and to higher $\delta^{15}\text{N}$ values in trees under conditions of grazing. We agree with Austin and Sala (1999) that the absolute amount of grazed material will decrease under very arid conditions. The North Australian Tropical Transect does not extend into areas as arid as those in the Sahara (Penning de Vries and Djiteye 1982), but our data suggest that there is a slight tendency of $\delta^{15}\text{N}$ to decrease again at the very arid sites. In fact, the highest $\delta^{15}\text{N}$ values were found in the intermediate rainfall range where the landscape is used primarily for cattle grazing.

From this observation alone we probably would not have drawn the conclusion about grazing. However the Tyler's Pass site, which appeared to be ungrazed by stock, and was potentially drier than average as it was on a slope, had the lowest foliar $\delta^{15}\text{N}$ values. We are aware that this single location is not a proof of our hypothesis, and it would be necessary to collect more data at ungrazed sites such as Tyler's Pass. However, in a similar transect study along Namibia (Schulze *et al.* 1991), an increase in $\delta^{15}\text{N}$ values was found under conditions where grazing pressure was very high (near a water hole) at the base of the escarpment. In that study, $\delta^{15}\text{N}$ values also decreased with increasing aridity and the associated decreasing grazing pressure.

In summary, we feel that the indirect effect of aridity on the competition between grasses and trees might increase $\delta^{15}\text{N}$ in woody species. This effect is likely to be enhanced by grazing through selective consumption of young shoots which are ^{15}N -depleted, by droppings that may be ^{15}N -enriched, and by disturbance of the soil surface that opens the N-cycle.

Thus, the openness of the N-cycle, as already discussed by Vitousek (1980) as a mechanism for N-enrichment under arid conditions, is not necessarily an effect of drought *per se*, but results from an interaction between aridity and grazing. We are aware of the limitations of our data in resolving this hypothesis, and it is clear that the N-cycle under arid conditions needs further attention and experimental investigation. Sampling along grazing gradients (Ludwig *et al.* 1999)

and/or replicated sampling of grazed and ungrazed sites under the same moisture regime, would be useful methodological approaches to the issue.

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Manuscript received 24 February 1999