

Variability of inorganic nutrient concentrations in leaves

Nutrient supply and acquisition are two of the most important factors that control plant productivity and diversity, as growth is generally limited by the availability of inorganic nutrients in the soil. From a biochemical point of view, all plant species should need the same quantity of nutrients to construct a given amount of tissue. However, differences do exist in tissue concentrations because of heterogeneous distribution of nutrients in the soil and varying uptake efficiency. In addition, plants respond differently to environmental variability, including nutrient shortage, and have different physiological needs that cause differences in metabolism and constitution (Chapin, 1980). Adaptation to variation of nutrient availability in soils leads to nutrient concentrations that differ widely between organs, species and ecosystems. Alonso & Herrera (see pp. 629–640 in this issue) looked at nutrients in a novel way. They considered concentrations of leaf nutrients as traits that respond plastically to environmental variability and tested whether a consistent pattern of nutrient covariation among populations could be expected as a result of the plant's acclimation to a given environment.

The role of nutrients

Traditionally, agronomists looked for an equilibrium among nutrients to optimize yield and thereby establish basic values for optimal plant growth. Critical nutrient ratios (e.g. N : P,

N : K, P : K) were soon established that could increase the productivity of crops – nonspecific interactions among mineral nutrients can cause a deficient concentration of one nutrient to become sufficient as the concentration of other nutrients change. There are synergies and antagonisms among nutrients that could cause unexpected responses (Marschner, 1986).

Mineral nutrients have different functions within the plant, and their concentration in the leaves may differ by orders of magnitude – from nitrogen, which is the base of structural and soluble proteins (such as Rubisco) and is found in the range of 0.5–10 g g⁻¹ of leaf dry mass, to trace elements like molybdenum, which acts as an enzyme cofactor and is needed in minute amounts in the order of a few mg kg⁻¹ of leaf (Table 1). In addition to their different functions, nutrients also differ in their concentration with time. Mineral nutrient concentrations show seasonal changes – those with an active metabolic function (N, P and K) increase when the leaf is developing and decline afterwards, partly because of the increasing proportion of cell wall structures and partly because there is translocation of nutrients out of leaves before senescence (Chapin & Kedrowsky, 1983; Pugnaire & Chapin, 1993). By contrast, nutrients such as Ca and Mg are less mobile and monotonically increase with age.

Plants in natural systems show high inter- and intra-specific variability in nutrient concentrations and critical ratios have been used to analyse growth and predict which elements are limiting at the community level (Verhoeven *et al.*, 1996), although to a lesser extent than in agronomy. In spite of the natural variability of nutrient concentrations in the soil, plants from adverse environments (e.g. arid or cold regions) show more consistent tissue concentrations of nutrients and a conservative strategy in the use of resources (Valladares *et al.*, 2000).

Element	Symbol	Concentration			Relative number of atoms
		μmol g ⁻¹ dry mass	mg kg ⁻¹ dry mass	% mass mass ⁻¹	
Molybdenum	Mo	0.001	0.1	–	1
Copper	Cu	0.10	6	–	100
Zinc	Zn	0.30	20	–	300
Manganese	Mn	1.0	50	–	1 000
Iron	Fe	2.0	100	–	2 000
Boron	B	2.0	20	–	2 000
Chlorine	Cl	3.0	100	–	3 000
Sulphur	S	30	–	0.1	30 000
Phosphorus	P	60	–	0.2	160 000
Magnesium	Mg	80	–	0.2	80 000
Calcium	Ca	125	–	0.5	125 000
Potassium	K	250	–	1.0	250 000
Nitrogen	N	1000	–	1.5	1 000 000

Table 1 Average concentrations of mineral nutrients in plant shoot dry matter that are sufficient for adequate growth¹

¹Reproduced courtesy of E. Epstein, in Marschner (1986).

Nutrient variability

Originally interested in the potential consequences of variability of tissue nutrient concentration to habitat selection by herbivores, Alonso & Herrera (this issue) focused on the intraspecific patterns of nutrient covariation at the individual and population levels in *Prunus mahaleb*. They found no consistent pattern of relatedness among concentrations of different nutrients at the individual level; individual *P. mahaleb* shrubs living in the same site differed vastly in their tissue concentrations of nutrients with no apparent patterns of covariation. They did find, however, consistent pairwise correlations across all sites for Ca and Mg, but that other relationships, such as B–Ca or N–P, were significantly correlated in only one or a few populations. The latter result is striking because many reports over the years have consistently found positive correlations of N and P concentrations. In addition, correlations between nutrients did not hold among populations. Covariation of macronutrients (N, P, K, Ca and Mg) show that they were closely related, and responsible for the main gradients of variation observed across trees. The results show that covariance among nutrients was mutually independent and had no significant spatial trends. Differences between shrubs in some elements (N, K, Cu and Fe) were responsible for most of the intraspecific variation, while concentrations of other elements (P and Ca) caused the large variation among populations. Variability in nutrient concentration was generally greater among individual trees living in the same site than among populations from different sites.

Variations within a population could be attributable to microsite characteristics as much as genotype differences. The important high levels of variation across populations did not mirror within-population variation, and probably reflected different local soil characteristics (e.g. different proportions of dolomite and calcite under each population). Altogether, the data show that phenotypic integration of nutrient concentrations in *P. mahaleb* is weak, and blurred by plasticity in nutrient uptake and transport (Sultan & Bazzaz, 1993).

There seems to be no ecological reasons for the high intraspecific variation in the concentration of some elements, which often equals or exceeds interspecific variation (Ohlson, 1988). Nutrients frequently covary nonrandomly across species because they share functional similarities and/or chemical behaviour, though the ultimate reason for random covariance is not really known. Statistically significant patterns of nutrient covariation may also be strongly affected by the nature of the sampling units and by patterns of allocation so that environmental or sampling effects may conceal inherent physiological or chemical associations between elements.

Nutrient concentration has a strong effect on herbivory because feeding is affected by leaf quality (McNaughton, 1988). A nutrient imbalance may affect resistance or tolerance to herbivores (Hartley & Jones, 1997). Nonetheless, the paper by Alonso & Herrera shows that the predictability of

nutritive quality is low and, as the authors conclude, diffuse patterns of nutrient covariation show a lack of common ground for selective processes exerted by herbivores on plants, whereas local, specific factors provide ways of adaptive adjustment of herbivores to host plants.

Summary

Alonso & Herrera clearly show that the highly variable nutrient environment experienced by plants favours plasticity rather than genetic specialization, and that the ability to grow at both low and high nutrient supply may be an important aspect of adjustment of individual plants to the environment. Other factors such as irradiance, soil moisture, or herbivory similarly influence phenotypic responses in plants (Sultan & Bazzaz, 1993).

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