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Concepts of nutrition in relation to cellular processes and environment

Introduction

Plants increase in mass and energy as they grow; carbon, mineral nutrients, absorbed in suitable form from the environment (Epstein, 1972; Marschner, 1986) and water provide the mass whilst energy is derived from the sun (Lawlor, 1987). As part of the growth process, cells with complex structures such as membranes and organelles are formed (Schnepf, 1983). This review aims to provide a conceptual framework of the relation between nutrition and cellular processes, of how the supply of chemical elements and energy are intimately related to the needs of the plants' cellular metabolism and thence to growth. One central theme is that the overall nutritional requirements of plants are determined by the biochemical and chemical components of cells and that these, in turn, are needed for biochemical function. Another theme is that the potential size of a plant and its organs is genetically determined (Strickberger, 1976) and thus the absolute amounts of nutrients required for growth are defined.

The growth process requires the synthesis of proteins, both structural and enzymatic, and it is a central tenet of biology that the production of proteins is genetically controlled by the information stored in DNA (Gerloff & Gabelman, 1983; Darnell, Lodish & Baltimore, 1986). This genetic control is strong, as shown by the fidelity with which the phenotypes of plant varieties and species are reproduced through generations (Strickberger, 1976). However, plant populations are genetically heterogeneous (Bradshaw, 1983; 1984) so variation occurs in phenotype, in structure and cellular and sub-cellular composition and in metabolic processes. The rates of growth and the size and composition of plants, as seen from this viewpoint, depend on the interaction between the genetic constitution, the needs of cellular metabolism and on the environmental supply of nutrients, energy and the conditions, such as temperature which determine growth. Genes regulate the rate of production of cellular components and therefore the potential rate of growth in different species

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(Stebbins, 1971; Grime & Hunt, 1975; Bradshaw, 1983). Hence, the forms, potential amounts and potential rates of demand for the nutrients and energy required for growth are also genetically determined (Fig. 1). This *potential* growth rate (Grime & Hunt, 1975) will be attained when the supply of materials necessary for full expression of the genotype under particular conditions is equal to the genetically determined demand. The *actual* growth rate will fall below the potential rate when the above conditions are inadequate (Hunt & Lloyd, 1987) or exceed the ability of the plants' metabolism and physiological systems to cope so that damage ensues.

These concepts are not simply theoretical, they provide a framework for analysing how plants of different genotypes respond to their environments (both aerial and edaphic) and for understanding how nutrition interacts with other features of the environment in determining the growth of particular species. Any conceptual framework to improve analysis of the links between processes in the plant and its environment must combine with a quantitative understanding of the biological and physiological mechanisms by which growth occurs (Grime, 1991, this volume). Better understanding of such mechanisms and their genetic control will aid prediction of the form, amounts, timing and rates of supply of nutrients and also the other resources and conditions required by plants for growth in natural and managed ecosystems (Ågren, 1988). Such understanding is needed if the maximum efficiency of plant growth is to be achieved either by altering the environment or by changing the plant by genetic engineering (Gasser & Fraley, 1989). Similarly, minimising the damage to ecosystems caused by human activities (Huettl & Fink, 1991, this volume) depends on understanding how plants respond to the coincidental impacts of nutrition and their aerial and edaphic environment.

Nutrients and biochemical composition

Autotrophic plants absorb their chemical constituents from the environment either as simple molecules or ions of molecular mass less than 100 (Epstein, 1972); energy is derived from photons of solar radiation (Lawlor, 1987). Water is also essential but its absorption follows rather than determines growth, unless the supply is inadequate and water stress restricts and slows metabolism (Kramer, 1969). Therefore, the role of water is not further considered. Fig. 1 illustrates the main pathways for the synthesis of cellular components and structures, which perform the metabolic functions and determine the links to the environment. Plants are composed predominantly of H, C and O which are derived from CO_2 and H_2O incorporated via photosynthesis. Additionally, plants contain 13 mineral elements (Table 1) which are essential for metabolism, growth and

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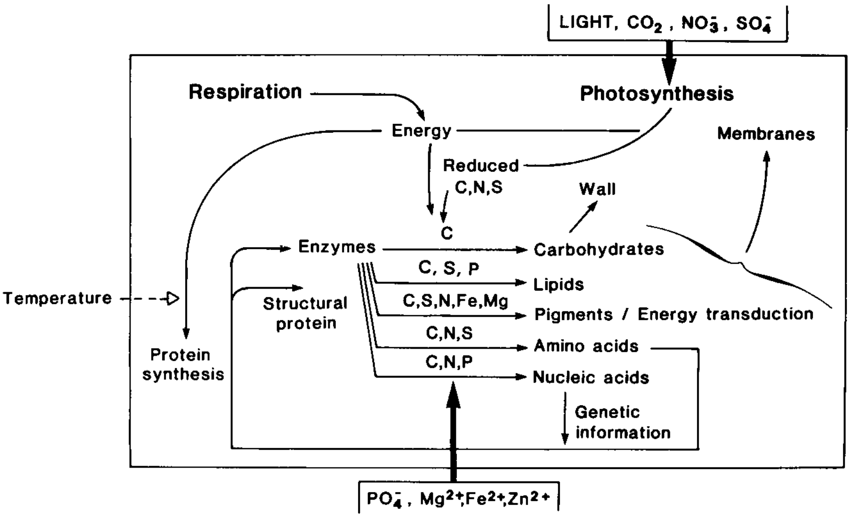

Fig. 1. Scheme of the interactions between the environment and plant metabolism. The synthesis of cell components and the role of the major environmental factors is illustrated to emphasise the cyclic nature of metabolic processes and how it is they generate structures which serve to capture nutrients and energy.

development and, ultimately for successful reproduction (Epstein, 1972; Rains, 1976; Marschner, 1986). These elements form either an integral part of the cellular structure (covalently or strongly bound) or are essential for providing the conditions needed for metabolism. An example of the former is nitrogen, which is a constituent of proteins; an example of the latter is potassium which is not covalently linked into organic molecules (Rains, 1976) but is essential for ionic and osmotic regulation in the cell (Leigh & Storey, 1991, this volume). Magnesium functions both as a constituent of molecules (e.g. chlorophyll) and in ionic regulation of enzyme activities.

Elements other than those in Table 1 may stimulate growth of particular species; Na is beneficial for sugar beet and Si for grasses but neither appear essential for growth. Substitution of one element is possible; for example, Na and K are partially interchangeable especially in halophytes. Also K may be replaced by Rb in regulation of stomatal activity (Rains, 1976). However, essential elements cannot be completely replaced by others, so growth depends on a supply of the required amounts of all essential components from the environment.

Mineral elements in plants are classified as macro- or micro- based on their proportion in tissues. There is a 10-fold difference in molar concentration per unit of dry matter between sulphur, the least abundant

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Table 1. *Chemical elements essential for growth and their average content in material from cultivated higher plants (from Epstein, 1972), and approximate concentration in the environment.*

Element	Mass conc. (g dry matter^{-1})	Molar conc. (mmol (kg dry matter)$^{-1}$)	No. of atoms relative to Mo	Conc. in environment (mol m^{-3})	Examples of function in cell
Macro-					
H	60	60000	60×10^6	$1–111 \times 10^3$	Oxidation/reduction structure in organic molecules
C	450	35000	35×10^6	14×10^{-3}	Structure of cell organic molecules, oxidation/reduction
O	450	30000	30×10^6	14×10^{-3}	Structure of cell organic molecules, oxidation/reduction
N	15	1000	1×10^6	1–3	Constituent proteins, nucleic acids, regulation
K	10	250	2.5×10^5	1–2	Ionic and osmotic regulation, medium for synthetic processes, e.g. protein synthesis
Ca	5	125	1.25×10^5	0.5–1.5	Cell walls, pectinates, regulation of cell metabolism, hormones, membrane stability
Mg	2	80	8×10^4	2–4	Constituent of chlorophyll, enzyme co-factor, control cell metabolism/enzymes

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P	2	60	6×10^4	0.0005–0.002	Constituent of nucleic acids, lipids, essential cellular energetics, co-enzyme regulation
S	1	30	3×10^4	0.3–0.7 0.001–10	Constituent of proteins, sulpholipids, energy transfer
Micro-					
Cl	0.1	3	3×10^3	0.001	Chloroplast photosystem II, metabolism, growth
B	0.02	2	2×10^3	0.001	
Fe	0.01	2	2×10^3	0.001	Energy transfer proteins, co-enzyme factor prosthetic groups
Mn	0.05	1	1×10^3	0.001	Co-factor in water splitting enzyme, aminopeptidase etc.
Zn	0.02	0.3	3×10^2	7×10^{-4}	Enzyme co-factor, carbonic anhydrase, alkaline phosphatase, enzyme regulation
Cu	0.06	0.1	1×10^2	3×10^{-4}	Constituent of plastocyanin, ascorbic acid oxidase etc.
Mo	0.0001	0.001	1	5×10^{-4}	Constituent of nitrate reductase

macro-element, and chlorine the most abundant micro-element (Rains, 1976). However, there is little physiological justification for the distinction. Macro-elements occur in large molar ratios in the more abundant molecules (e.g. N in proteins) and at high concentrations in the cell solution (e.g. K in vacuoles). Micro-elements often form prosthetic groups in enzymes (Table 1) and have specific, vital functions in metabolism (Marschner, 1983; 1986). For example, zinc is a component of the active catalytic centre of the enzyme carbonic anhydrase (6 Zn atoms per molecule) which increases the rate at which an equilibrium is achieved between CO_2 and bicarbonate ions in solution. The reaction is very fast (a turnover time of 10^{-6} s) and therefore the concentration of the enzyme and thus of Zn of this particular component of leaf tissue is very small (Poincelot, 1979). Another example is iron which is a component of electron transport molecules such as haem groups in iron sulphur centres. Terry & Rao (this volume) discuss the role of nutrition in the photosynthetic processes. In contrast, nitrogen occurs in all proteins at about 16% by mass (Bray, 1983; Rains, 1976).

Although the functions of nutrients are generally understood, details of the mechanisms of action and how they are incorporated into plant structures are often lacking. Manganese, for example, is essential for the water splitting and oxygen evolving processes in photosynthesis (Lawlor, 1987) but its location and mode of action in the photosystem II complex of chloroplast are uncertain (Rutherford, 1989).

Nutrient absorption

Plants obtain mineral nutrients mainly from the soil and the atmosphere is the source of CO_2. However, ammonia, oxides of nitrogen and sulphur dioxide as well as particulate materials, often pollutants produced by human activity, may contribute to the plant's mineral balance and also cause damage (Huettl & Fink, 1991, this volume). The forms, amounts and proportions of different nutrients in the environment vary greatly as does the timing and the rates of availability to plants. These depend on the type of soil and the biological activity of microorganisms and of the plants themselves (Marschner, 1986; 1991, this volume). Many plant strategies for exploitation of nutrient resources depend on matching the supply with plant demand (Grime & Hunt, 1975). The mineral nutrients exploited by plants are largely in ionic form, such as K^+, NO_3^- and SO_4^{2-}, and plants may exploit forms depending on the conditions, e.g. NO_3^-, NH_3 and NH_4^+ are sources of N for higher plants, ultimately and largely metabolised to amino acids (Bray, 1983) and used in protein synthesis. The total amount of a nutrient available to plants depends on the concentrations of usable forms of the nutrient in the environment, the efficiency of the plant in extracting the element, and the total volume of the medium exploited. This is very

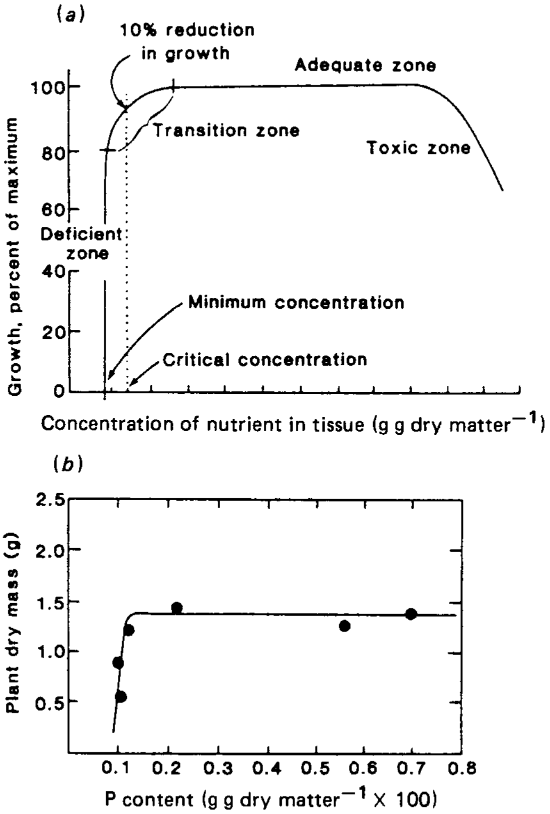

Fig. 2. Illustration of how growth of plants is related to the concentration of nutrients. (*a*) General response curve showing dependence of growth on external nutrient concentration and showing the 'critical' concentrations for a 10% reduction in growth, the minimum concentration for growth to occur, the zone of adequate nutrient supply and the concentration at which toxic symptoms appear. (*b*) Growth in mass of maize in relation to the phosphorus content (g g dry matter^{-1}) of the tissue (after Epstein, 1972).

dependent on the extent and efficiency of the root system (Epstein, 1972) which are genetically determined but depend also on the environment for expression.

The response of plants to nutrient concentrations in the environment and also to light, CO_2 and temperature generally takes the form shown in Fig. 2*a* which summarises experimental information of the type shown in Fig. 2*b*. Such a 'diminished returns' type of relationship is characteristic of plant responses to all essential resources and conditions. The response shows that to maintain a genetically determined growth rate (Grime & Hunt, 1975) at its maximum, all resources must be supplied at a rate equal to or greater than the potential demand (Ingestad, 1970*a*,*b*; 1982). If supply falls below demand, photosynthetic processes decrease and growth slows. At very small concentrations, growth ceases. At very large supply or concentration of a resource a plant's biochemical and physiological mechanism may be damaged, e.g. by large concentrations of ions which cannot be excluded by the roots (Marschner, 1986). Species have different requirements for nutrients and different abilities to acquire resources and to tolerate or avoid damage by particular conditions, so the quantitative details of Figs 2*a* or 2*b* are very species specific and therefore genetic.

In order to transport selected nutrients into cells against a concentration gradient 100 to 1000 times greater than that found in the soil solution (Table 1) and to maintain similar ratios of essential to non-essential elements in cells (Epstein, 1972; Marschner, 1986) efficient biochemical transport and accumulation mechanisms have evolved (Fromter, 1983). These are coupled to a supply of energy and to the intermediary metabolism which maintains cellular homeostasis and, at the same time, ensures that fluxes of nutrients are available for growth when required. However, these mechanisms may not completely regulate the entry of elements which may damage plant metabolism; sodium, for example, may be absorbed from saline soils. Heavy metals (Cd, Pb, Zn) from mine and industrial wastes may accumulate in plants and damage them and pose a threat to the animals, including man, that consume the plants (Bollard, 1983). There are great differences in the adaptation of species of genotypes of plants to the chemical composition of the environment. Some, such as *Agrostis tenuis* have populations that differ in susceptibility to heavy metals (Bradshaw, 1975, 1984). Similarly there are large differences between species and sub-populations in their tolerance in calcareous soils (Jefferies & Willis, 1964). *Caluna vulgaris* (an extreme calcifuge) cannot grow in such soils whereas *Scabiosa columbaria* (an extreme calcicole) is adapted to them (Grime, Hodgson & Hunt, 1988).

Nutrients and cell composition

Mineral nutrients absorbed by cells accumulate in particular cell compartments, where they may regulate metabolism or are stored before entering into metabolism. They are incorporated into about 10^5 types of organic molecules, synthesised in very different amounts (Lehninger, 1975). Half are of molecular mass less than 500 and are often metabolic intermediates in the synthesis of structural, large molecular mass components such as proteins (10^4–10^5 kD), nucleic acids (10^9 kD) and carbohydrate polymers such as cellulose. The main classes of components are given in Table 2. They are carbohydrates (cell walls, membrane glycolipids, starch) con-

Table 2. *Elemental composition (percent by mass) of the main classes of biochemical components and of a whole plant of maize (Zea mays) (after Epstein, 1972).*

Element	Carbo-hydrates	Fats	Protein	Nucleic acid	Plant
O	51.4	11.3	24	30	44.4
C	42.1	76.5	52	39	43.6
H	6.5	12.2	7	3.5	6.2
N	—	—	16	17	1.5
S	—	—	0.1	—	1.2
K	—	—	—	—	0.9
P	—	—	—	10	0.2
Mg	—	—	—	—	0.2
Fe	—	—	—	—	0.1
Other	—	—	0.9	0.5	1.7
	100	100	100	100	100

taining only C, H and O; proteins (enzymes, cytoskeleton and membrane proteins) and nucleic acids containing C, H, O, N, P and S as well as many metallic mineral elements in prosthetic groups and as electron carriers (Lehninger, 1975; Marschner, 1986); and lipids (phospholipids, oils) with C, H, O, P and S. The amounts of N, S and P that occur in the major groups are known; although proteins have, on average, 16% by mass of N, particular proteins differ in their proportions of amino acids and therefore in elemental composition. However, the major differences in composition are *between* classes of biochemical components rather than *within* them. Of great significance in composition of tissues is the proportion of biochemical components which depends on the type of cell and its functions and thus differ in the proportion of constituents. For example, leaf mesophyll cells contain much protein, chlorophyll and lipid associated with the photosynthetic apparatus, whereas storage parenchyma cells contain much carbohydrate but little protein.

The important general principle, stated earlier and worthy of repetition, is that it is the biochemical components of tissues that determine the amounts of mineral and other elements in cells. Further, it is by biochemical processes that plant nutrition, composition and the influence of the environment are linked.

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Tissue and plant composition

Different tissues and organs of plants contain different amounts of nutrients (Epstein, 1972); for example, leaves contain more N than roots or stems per unit of dry matter. Differences in the gross nutrient composition of plants are often due to different amounts and proportions of organs and their age (Lawlor *et al.*, 1981). Young plants have proportionally more material in leaves than in stems and storage organs than old plants. The cellular proteins of older leaves may be broken down and used for growth of new leaves or of reproductive organs (Lawlor *et al.*, 1981; Lawlor, Kontturi & Young, 1989; Groot & Spiertz, 1991, this volume), so the C/N ratio of young plants is smaller than that of old plants. Nutrient requirements of plants may be estimated if the biochemical composition of the tissues and the proportions are known. Penning de Vries (1974, 1975) used this approach to estimate the costs of synthesising plant tissues. Stated very simply, the rate of dry matter production, D ($\mathrm{g\,s^{-1}}$) is a function of photosynthetic rate, Pn ($\mathrm{g\,m^{-2}\,s^{-1}}$), total leaf area, L ($\mathrm{m^2}$), respiration per unit of dry matter, Rd ($\mathrm{g^{-1}\,s^{-1}}$) and the mass of the respiring crop, W (g), all expressed as a mass of carbon. Thus:

$$D = (Pn \times L) - (Rd \times W) \tag{1}$$

To estimate D over a period, Pn must be summed over L and Rd summed over W; both L and W change with time. Pn is a well defined function of the photon flux, of CO_2 concentration in the atmosphere, and of temperature; it is also a function of nutrient supply. From such information the capacity of the leaf for photosynthesis may be estimated. Similarly the respiration of crops may be calculated if the relation between respiration and temperature is known in addition to the mass of the standing crop.

It is instructive to consider how assimilation rates and nutrient uptake rates are related for a barley crop growing under field conditions (Lawlor *et al.*, 1981). The aerial parts of the plant grew at a rate of 50 mg dry matter $\mathrm{day^{-1}}$; as the photosynthetically produced dry matter accumulating in the roots is *c.* 15% of the shoot mass and the equivalent of 30% of the total dry matter is lost as respiration (Mitchell & Lawlor, unpublished), the total daily demand for assimilates is equivalent to 74.8 mg. It is established that 1 g of dry matter contains an average of 0.5 g carbon, corresponding to 1.83 g of CO_2 (Penning de Vries, 1974, 1975) so the daily assimilation of CO_2 is 3.11 mmol. A typical photosynthetic rate is 10 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ and an average daily radiation flux of 600 $\mu\mathrm{mol}$ photons $\mathrm{m^{-2}\,s^{-1}}$. An average barley plant has a leaf area of 0.01 $\mathrm{m^2}$, so in a 10 hour day total photosynthesis would be 3.6 mmol CO_2 $\mathrm{day^{-1}}$, compared to the 3.11 mmol of dry matter accumulated. Experimental measurements show that a soluble protein content of *c.* 10 $\mathrm{g\,m^{-2}}$ is necessary to maintain such rates of