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Analysis of Nutritional Interactions in Cropping Systems

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1. Introduction

Successful management of crop production systems requires design of cultural practices that enhance yield by ensuring that growth limiting factors are minimized or eliminated altogether. Together with moisture, light, competition, diseases and pests, availability and efficient utilization of soil nutrients is one of the major determinants of healthy plant growth and realization of optimum yield returns. Thus, assessment of nutrient availability, uptake and utilization by plants is critical for optimization of crop productivity. It is also important to note that these factors and other physiological processes characteristically involve complex relationships and interactions among many factors, some of which are of non-nutritional in nature. Traditionally, diagnoses of these nutritional responses and interactions have involved chemical analysis of soil and plant samples, while different approaches have been employed for the interpretation of the analytical results. These interpretations have been derived from empirical studies related to plant responses to specific nutrients in terms of visual symptoms, nutrient uptake and use, nutrient ratios, and soil, biochemical, physiological tests. Unfortunately, most of these techniques have focused on causes of nutrient deficiencies in an attempt to identify nutrients that are most limiting rather than in trying to optimize their availability, uptake and utilization by the crops. Also, interactions among different nutrients and other growth limiting factors such as moisture and light are seldom considered. Moreover, most of these interpretative approaches are only known to scientists in terms of their power and limitations, while land managers seldom use them to diagnose simple conditions in their farms.

Most of the diagnostic methods use chemical analysis of plants or plant parts to determine the qualitative or quantitative nutritional status since the plant itself is the subject of interest, thus its nutrient composition reflects most of the factors affecting its nutrition. These plant chemical analyses often use three plant parameters in interpretations of crop responses (growth and yield, nutrient concentration, and nutrient uptake also measured as nutrient content) to evaluate plant response to soil nutrient supply and fertilization. Unfortunately, overwhelming majority of studies on crop response to nutrient supply often express their results using only one or two of these parameters at a time, but not all of them combined. Our past research experience and review of other literature has clearly identified this glaring gap. Similar problems associated with excessive use of concentration data alone and improper use of terminology have been detected in plant nutrient studies several decades

ago (e.g. Timmer and Stone 1978; Smith *et al.* 1981), which unfortunately is still common in current literature. There is now strong evidence to demonstrate that conclusions derived from such results may be misleading if any one of these plant parameters is excluded from the interpretation of plant nutrient analysis.

Current trends towards precision agriculture with intensive fertilization to achieve optimum nutrition is likely to lead to more complex nutritional disorders that will be more difficult to detect, thus the need for interpretative techniques that provide more comprehensive and precise plant nutritional status with the capacity to identify single and multiple nutrient deficiencies, sufficiency, imbalances, toxicity and interactions. The objective of this Chapter is to highlight the pitfalls associated with relying solely on concentration of nutrients only when interpreting results of plant responses to nutrient availability. The Chapter demonstrates that more insight into the mechanisms behind changes in plant nutritional status under changing soil nutrient conditions can be achieved by simultaneous examination of changes and interrelationships between all the three plant nutritional parameters i.e. growth or yield, nutrient concentration and nutrient uptake or content using a graphical approach called "Plant Nutrient Vector Analysis". Although this method has been used extensively in forestry research, little applications in evaluating nutritional status in agricultural crops have been. It is strongly suggested that agricultural scientists involved in intensive fertilizer management systems utilize the enormous potential of this method.

2. Background

2.1 Defining plant nutrient status

Plant nutrient status is often defined by either nutrient concentration or absolute content. By definition, the term nutrient *concentration* refers to the amount of a compound present in a unit amount of plant tissue and is expressed as a ratio (e.g. %, ppm, mg g⁻¹, or mg cm⁻¹ etc.), while nutrient *content* is the total amount of a compound present in a specific amount of plant tissue (e.g. whole plant, leaf, shoot, root etc.) and is expressed in any unit of mass such as mg, g, kg, and tons (Farhoomand and Peterson, 1968). Clearly, while concentration is *intensive* and *non-additive* (i.e. does not depend on the size of the sample but simply an indicator of plant quality), content on the other hand is *extensive* and *additive* (i.e. depends on the size of the plant or plant part and is an indicator of production and growth allocation). Further, it is good to note that concentration is simply a ratio between content and biomass (or area) in which content has been measured. Thus, the discussion on when to use concentration or content really is a matter to be determined by the objective of the analysis between variables; whether original or derived variables, a question that has been debated extensively in biological (e.g. Jackson and Somers, 1991) and statistical literature (e.g. Sokal and Rohlf, 1995) in the past.

In statistics for example, part of the drawbacks in the use of ratios (i.e.. concentration) is because these ratios are often derived from two independently measured variables, thus often resulting in inaccuracy and non-normal distribution (Sokal and Rohlf, 1981). Fortunately in the case of plant nutrient concentrations, they are not derived variables even though they are ratios since they are primary variable measured directly as a result of biochemical analyses. This is probably one of the reasons why most researchers prefer using concentration data directly since to obtain content requires multiplying concentration by the weight of the plant sample, which is rarely done. Statistically therefore, using content is

likely to be more prone to error since it is derived from two independent variables i.e. concentration and biomass.

Koricheva (1999) has pointed out the major problems associated with the use of ratios and concentrations in interpreting changes in plant allelochemistry. The problem with the use of ratios is that they do not give any indications on the relationships between the two variables from which they are derived. This means that changes in a ratio can be caused by changes in the numerator, the denominator or both, and there is no way of distinguishing the mechanism responsible for the observed changes in the ratios. However, this would not be a problem if the ratio itself is the primary variable of interest, and the researcher is interested only on the implications of the shift in the ratio rather than in the mechanisms which brought about the change. If the biological process being investigated operates on the ratio of variables studied, then one must study the variables affecting the ratio in order to understand the mechanisms involved.

In terms of interpretations of plant responses to nutrient availability, the major problem often arises when researchers try to elucidate the mechanisms causing the observed changes in concentrations. Given the above definition, such changes can be brought about by either changes in plant growth (biomass accumulation), nutrient uptake (nutrient accumulation or content), or both. While changes in nutrient concentration due to changes in content can be considered as “*active*” since the plant altered nutrient uptake, synthesis or transport of the specific nutrient, changes in concentration due to changes in biomass can be considered as “*passive*” responses because they are simply by-products of plant growth and there is no specific effect on the metabolism of the compound analyzed.

It is important to distinguishing between these passive and active responses in order to enable establish the mechanisms that lead to observed changes in plant nutrient concentrations. This is important in enabling predictions of the effects of varying nutrient variability on plant physiological responses. When the focus of the study is on the mechanisms behind the changes in concentration, more can be achieved by studying the variables singly first and then examining their relationship to each other i.e. analysis of changes in content and plant biomass in addition to analysis of concentrations. Unfortunately, most research papers reporting plant nutrient data have not taken this message seriously probably because of the belief that concentrations do reflect changes in nutrient content but remove the effects of biomass, thus are superior indicators of plant nutrient status.

2.2 Problems with the use of plant nutrient concentrations alone

Although many researchers have often preferred using nutrient concentration (C) over nutrient content (U) by assuming that the former removes the effect of plant biomass (W) on nutrient content, and therefore good for standardizing data to allow for comparison between different plant individuals or plant parts by adjusting for differences due to biomass using the function $C = U/W$ i.e. concentration does not depend on the size of the plant (Jackson and Somers, 1991), there are many inherent problems with this approach. First, mathematically such a ratio can only remove the effect of W on U if and only if the relationship U/W is linear and passes through the origin (Raubenheimer and Simpson, 1992). Any nonlinearity of the function increases the probability of differences between the ratios calculated for the different parts of the curve, while non-zero intercept diminishes the statistical power to detect small differences between treatments. These assumptions are

unlikely to hold for the U/W relationship, which is presumably non-linear and non-zero intercept may arise, for example, the rate of nutrient uptake is not equal to the rate of growth and biomass accumulation. As such, concentration is unlikely to remove the effect of plant weight from content, and analysis of covariance with content as the dependent variable and biomass as a covariate is a better option (Raubenheimer and Simpson, 1992).

Secondly, changes in nutrient concentration does not always reflect changes in nutrient content since changes in biomass are not due exclusively to changes in nutrient content since biomass production is a function complex interactions among many factors of plant growth including nutrients, light, water, temperature, cultural practices, weeds, pests and diseases (Jarrell and Beverly, 1981). Moreover, plant biomass (W) is the sum of the total contents of all plant constituents such as nutrients, carbon and other plant chemical compounds (i.e. W_1, W_2, W_3, W_n , where n is the number of plant constituents). The concentration of a specific nutrient C_1 can then be derived as $C_1 = U_1 / (W_1 + W_2 + W_3 + \dots + W_n)$. Therefore, any change in any of the plant constituents will result in change in concentration of nutrient C_1 even if its content remains the same. Decrease in concentration of a compound as a result in increase in content of other plant constituents is known as *dilution effect*, while increase in concentration of a compound due to decrease in content of another constituent is called *concentration effect*.

Although dilution and concentration effects will have relatively small impacts on the concentration of the major plant constituents such as carbon-based compounds, most nutrients are present in relatively very low concentrations making them potentially very sensitive to dilution and concentration effects. The dependence of concentration of a specific nutrient on the levels of other nutrients and plant constituents as well as environmental conditions has important implications on interpretation of concentration data with respect to active uptake e.g. in response to amelioration of nutrient deficiency, or passive uptake in response to accelerated or suppressed growth by other non-nutritional factors. Separation of these nutritional response mechanisms (active vs. passive) using only nutrient concentration data is seldom possible. To date, only a few studies have presented both nutrient concentration and content results demonstrating these distinct nutritional responses directly as for example using isotope techniques.

Thirdly, the use of nutrient concentration as a measure of nutrient uptake has no biological meaning since plants absorb molecules (content) of nutrients – concentration simply reflects distribution of these molecules within a given amount of plant biomass. Biologically, therefore, this distribution is not of any strategic importance but simply an inevitable consequence of plant growth (Timmer 1991). It has often been interpreted that higher nutrient concentration in young tissue is a strategy for resource allocation for higher productivity, while decline in nutrient concentration with leaf age may be largely a result of dilution due to accumulation of other metabolites as leaves expand. One alternative to using concentrations for assessing changes in allocation to nutrients in growing tissues is to plot nutrient content in the plant or plant part against plant biomass and to examine changes in the slope over time. Increase in slope indicates increased allocation to growth while decrease in slope indicates reduced allocation to growth

Fourthly, it is often assumed that plant resources are limited and thus plant preferential investment in certain organs of specific functions depending on prevailing environmental conditions. For example, increased root growth for increased drought resistance necessarily reduces investments in other plant organs such as shoot growth resulting in higher

root/shoot ratio (Herms and Mattson 1992). Such trade-offs can only be examined in terms of the correlations between nutrient concentration and plant biomass that can demonstrate either positive or negative correlations. If a negative correlation is detected, then uptake of a given nutrient can be considered costly, while a positive correlation may be interpreted to be cheap or luxury uptake.

The problem however is whether two or more physiological processes jointly consume the same resource. Moreover, negative correlation between nutrient concentration and plant biomass may arise because biomass is a denominator in the ratio defining concentration. Thus, plotting nutrient concentration against biomass is the same as plotting a ratio against its denominator, which causes a negative relationship by default (Herms and Mattson 1992). Furthermore, the sign of correlation between nutrient concentration and plant biomass may depend on the timing of the compound synthesis during plant development. If uptake of a nutrient occurs early plant development and later metabolised or retranslocated to other plant parts, its concentration in the plant or old leaf will decrease with age, first due to dilution effect and later due to reduced nutrient content. Consequently, concentration of such nutrient would be negatively correlated with plant biomass. If however nutrient uptake equals growth demand and no retranslocation occurs, nutrient concentration will remain the same throughout the plant development stages, and will show no correlation with changes in plant biomass.

2.3 Reducing impacts of dilution and concentration effects

As discussed above, interpretation of concentration data is often confounded by dilution and concentration effects. Several methods have been developed to reduce the impacts of these dilution and concentration effects on the results of bioassays.

2.3.1 Concentration on a free-biomass basis

In cases where applied treatments are known to cause large changes in specific plant constituents (e.g. carbon), which may lead to dilution of other plant constituents (e.g. nitrogen), concentration of the other compounds (i.e. nitrogen) may be calculated on a carbon-free basis. For example, since elevated CO₂ usually causes large accumulation of carbon in plant tissue (Korner *et al.*, 1995), then nutrient concentration can be calculated on carbon-free basis. According to Poorter *et al.* (1997), if the effect of CO₂ disappears when concentrations are compared on carbon-free basis, changes in concentration were due to dilution by the accumulated carbohydrates, while more pronounced differences when calculated on carbon-free basis means the CO₂ enrichment had real effect on the synthesis of the compound in question but this difference is obscured by larger changes in carbohydrate levels increased.

2.3.2 Concentration on a unit area basis

Expression of chemical concentrations on a unit area basis may also be an alternative to conventional expression on mass basis if the aim of the study is to assess the effects of non-seasonal environmental factors. Leaf area is usually more sensitive than leaf biomass to environmental changes hence less affected by seasonal variation and leaf age (Gholz 1978). Expressing nutrient concentration on area basis might be especially relevant for determination of large scale fertilizer prescriptions.

2.3.3 Concentration on fresh weight basis

Expressing concentration on fresh weight basis may also reduce impacts of dilution and concentration effects since fresh water-saturated plant material in mature organs is a more constant property than dry weight (Tamm, 1964). Unfortunately, this approach is based on the assumption that no difference in water content exists between the samples, which can only be tested by comparing water content among the treatments, sampling dates etc.

2.3.4 Comparison of nutrient concentration in similar plant developmental stages

As stated earlier, dilution effects are an integral part of plant development, thus nutrient concentrations of most plant constituents change during the plant life cycle if no environmental factors or cultural practices interfere with plant growth and nutrient uptake and concentration during the growing season. Therefore, assessing the effects of treatments at different dates during the season may result in confounding of environmental effects. This might be avoided if plants of the same the same development stage or age are compared between the treatments (Roumet *et al.* 1996). This approach may require changing the experimental design to facilitate comparisons between treatments through growth and developmental stages over time (Coleman *et al.*, 1994). Thus, disappearance of treatment effects when plants of the same biomass are compared means that differences in nutrient concentrations were due to growth dilution, while similar effects on nutrient concentrations would suggest that the examined factor has an effect on plant nutrient status which is independent of developmental changes. Unfortunately, all these methods are inadequate for comprehensive analysis of plant responses to plant nutrient status. These are described in detail in the following sections.

3. Theoretical foundations

3.1 Nutrient uptake and growth relationships

3.1.1 Nutrient uptake

Uptake of mineral nutrients by higher plants occurs mainly through absorption of mineral elements from the soil environment by the roots, although leaves of some plants are also known to absorb limited amounts of mineral elements. Once absorbed, these elements accumulate in plant tissue. Although analyses of plant tissues often show accumulation of almost all elements found in the root environment, only a small number has been demonstrated to be essential for plant growth. Since nutrients accumulate in plant tissue during growth, and nutrient content of a plant gives an integrated estimate of both total uptake and use by a plant, studying the relationships between the two fundamental processes involved (nutrient accumulation and biomass production) can provide insight into the mechanisms involved. This can be achieved by studying the relationships between biomass, uptake and concentration. The following section discusses these fundamental relationships in terms of tissue nutrient composition, and its usefulness in elucidating mechanisms of plant nutrient interactions.

3.1.2 Plant nutrient composition

Chemical analysis of plants is frequently used to diagnose the nutritional status of plants since the plant itself is the object of interest, and its nutrient composition reflects many of the factors affecting its nutrition. Traditionally, plant nutrient composition is expressed

either in relative terms (i.e. concentration [C], the amount of nutrient present per unit amount of biomass) or on total mass basis (i.e. absolute content [U], the total amount of nutrient present in a specific amount of plant tissue [W]) (see for example Imo 1999). Total content is obtained by multiplying concentration by dry mass of the sample, thus $U = C(W)$. Timmer (1991) has argued that using concentration alone does not reveal the mechanism on how nutrient content and dry mass are related, since changes in concentration may be caused by changes in either biomass or nutrient uptake or both, and there is no way of distinguishing between these mechanisms. Changes in concentration as a result of changes in content implies that the plant itself altered nutrient uptake and synthesis, while changes in concentration due to changes in biomass can be regarded as a growth response without any specific effects on metabolism of the nutrient.

Distinguishing between these processes is important to test hypotheses related to the effect of changing nutrient supply on plant growth and nutrient composition. One way of solving this problem is by first studying the effects of nutrient supply on each of the individual plant response variables (biomass, nutrient concentration and content), and then examining their interrelationships. Timmer (1991) presented a classic generalized interpretation of the relationship between these nutritional parameters diagrammatically (Fig. 1), which shows the possible relationships between increasing nutrient supply with plant growth, nutrient concentration and nutrient content. This diagram shows that growth responses to

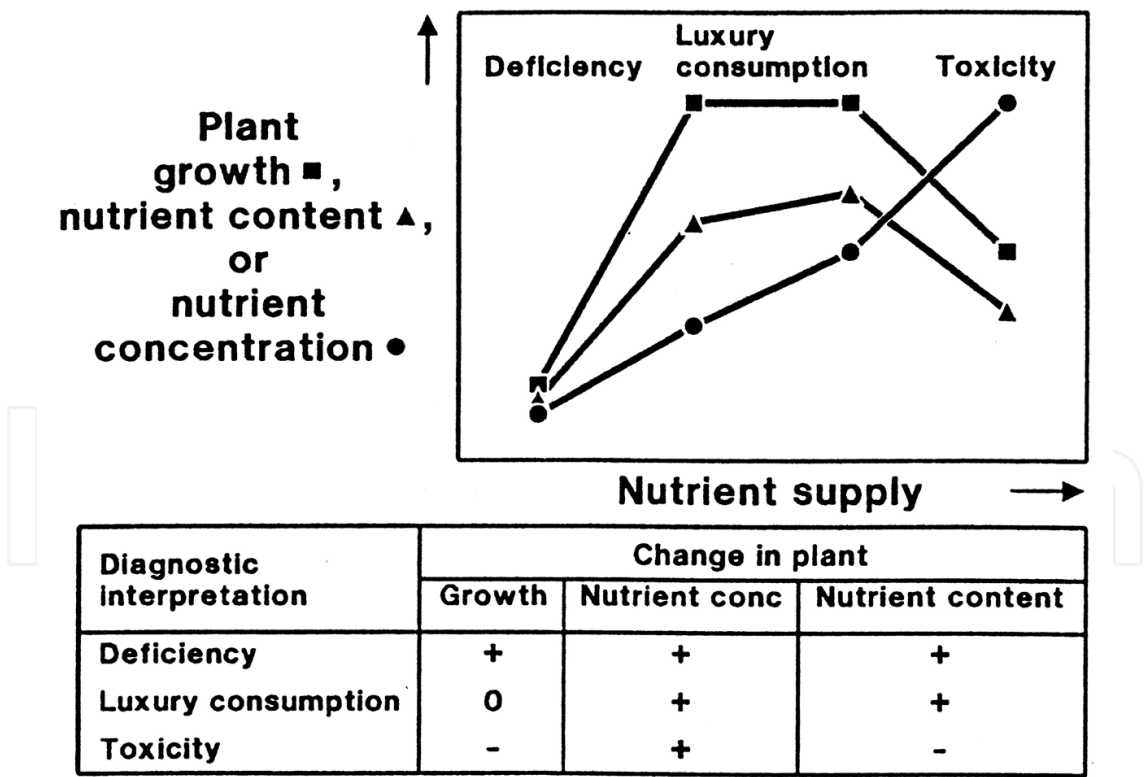


Fig. 1. Generalized interpretation of the relationships between plant growth, nutrient concentration and nutrient content with increasing nutrient supply. The lower box shows the expected direction of change (0, +, or -) in growth, nutrient concentration and nutrient content in the three phases. Adapted from Timmer (1991).

increasing supply of a limiting nutrient follows a curvilinear relationship that can be divided into three distinct nutritional phases: deficiency, luxury uptake, and toxicity (Timmer 1991). At each phase, changes in growth, nutrient concentration and uptake can be identified as either increasing (+), no change (0), or declining (-) as shown in Fig. 1. Notice that growth is restricted at low nutrient levels, increases sharply with increasing nutrient supply until sufficiency is reached, it levels off when nutrient supply is at luxury levels, and then declines gradually as nutrient concentrations become toxic (Fig. 1).

Nutrient content follows a similar curvilinear pattern as biomass, except that it continues to increase as a result of luxury uptake until toxicity occurs (Fig. 1). In contrast, nutrient concentration will continue to rise throughout the whole range of nutrient supply (Fig. 1), slowly in the deficiency range because of growth dilution, and more rapidly in the toxicity range because of accumulation. Thus, interpretation of concentration data alone is often confounded by dilution and concentration effects, and nutrient content data is often confounded by effects of total plant biomass.

One way of avoiding this problem is by examining all the three parameters simultaneously using vector diagnosis as discussed in the following section.

3.1.3 Nutrient interactions

While in general the term “interaction” is defined the mutual or reciprocal effects, it has been used in soil fertility evaluation in agriculture and forestry to mean both quantitative and qualitative responses to fertilizer nutrients in plant-soil systems, which involve both single or multi elements interactions as well other non-nutritional factors that may be occurring in these systems. These interactions often occur when the level of one factor of biological production influences the response of an intended product to another factor, resulting in mutual or synergistic (positive), reciprocal (compensatory) or antagonistic (negative) effects. For example, if the supply of one nutrient affects the absorption, distribution or function of other nutrients and thus modifies growth response then interactions can be said to occur. These interactions can occur in the soil as biochemical reactions, in the soil-plant interface due to uptake processes, or interactions within the plant itself due to varying requirements for nutrients by plants of varying phenotypes and life cycles. Inevitably, other non-nutritional factors that affect plant growth and development, and nutrient availability, uptake and utilization also influence the nature of nutrient interactions in soil-plant systems. Although management practices always strive to achieve positive interactions, methods for ascertaining achievement of the desired objectives are hardly explicit. A positive interaction occurs when the influence of the combined practices exceeds the sum of the influences of the individual practices. Such positive interactions have served as the science-based justification for development of a “balanced” plant nutrition program.

These interpretations often involve plant responses such as steady-state nutritional effects, synergistic or antagonistic dilution effects and induced toxicities are often quite complex and multi-factored. Detection of such interactions therefore requires specialized and comprehensive techniques and approaches for their quantification, especially in intensively managed cropping systems. Several methods and approaches have been proposed to detect these interactions in cropping systems including visual symptoms, critical nutrient approach, optimum nutrient ratios, factorial experiments, mathematical modeling and

graphical nutrient analysis. Unfortunately, questions still arise especially when dealing with nutritional elements of different biochemical nature, varying requirements and quantities by plants, multiple factors affecting their availability, prioritizing nutrient limitations, and making practical recommendations for optimum crop production. Separation of all these interaction effects in terms of site-specific fertilizer nutrient recommendation is seldom reported in research papers.

3.1.4 Steady state nutrition

Steady state nutrition refers to a condition whereby plants grow with constant internal nutrient concentration, free from stress (Ingestad and Lund 1986). This condition can be achieved by adding fertilizer nutrients at exponential rather than conventional (or constant) rates, which corresponds closer to the desired relative growth rates of the plants during their exponential phase of growth as has been demonstrated by Imo and Timmer (1992a; Imo and Timmer 1997). These studies also showed that although and nutrient accumulation of conventionally fertilized plants normally increases as the season progresses, internal nutrient concentration usually declines due to growth dilution, which suggests excess fertilization at the start but nutrient stress at the end of the growing season. In contrast, Plants growing at steady-state nutrition were growing relatively free of nutrient stress since it was characterized by stable internal nutrient concentration. Long term experiments are required to demonstrate achievement of this condition under field conditions, which would greatly improve nutrient use efficiency of applied fertilizers while reducing environmental pollution.

4. Vector analysis of plant nutritional responses

4.1 Diagnostic approach

Vector nutrient analysis is based on the biological dependence of plant growth on nutrient uptake. Fundamentally, the technique is a multivariate approach of examining changes in nutrient concentration (C) in relation to functional processes that cause these changes, namely nutrient uptake (U) and biomass accumulation (W), where $C = U/W$. This relationship is then compared graphically by plotting C on the y-axis and U on the x-axis (Fig. 2). Since concentration is a ratio between content and biomass, biomass is the inverse of the slope factor, and C and U values for each plant sample will follow a diagonal line (z-axis) corresponding to biomass (W) (Fig. 2). These diagonals also serve to separate biomass of various samples being compared. Changes in C, U and W can be plotted as absolute values (thus allowing standard error of the means to be shown on the diagram) or relative values (thus enabling multiple treatment, nutrients and inter-site comparisons by eliminating inherent differences in plant size and nutrient status).

In this graphical model, vectors are drawn to depict changes in the relationship between C, U and W. Plant samples for comparison can either be for different treatments (Timmer 1991) or changes over time (Imo and Timmer 1997). Interpretation of the relationships between C, U and W are based on changes in vector direction and magnitude observed as an increase [+], decrease [-], or no change [0] in biomass, nutrient content, and nutrient concentration relative to the reference plant status, and help quantify treatment effects (Fig. 2). The direction and magnitude of the vectors quantify treatment effects relative to the reference status, and facilitate diagnoses of nutritional effects of growth dilution, sufficiency, deficiency, luxury uptake, toxicity (excess uptake) and antagonism. Vector nutrient analyses of these nutritional effects are discussed here below.

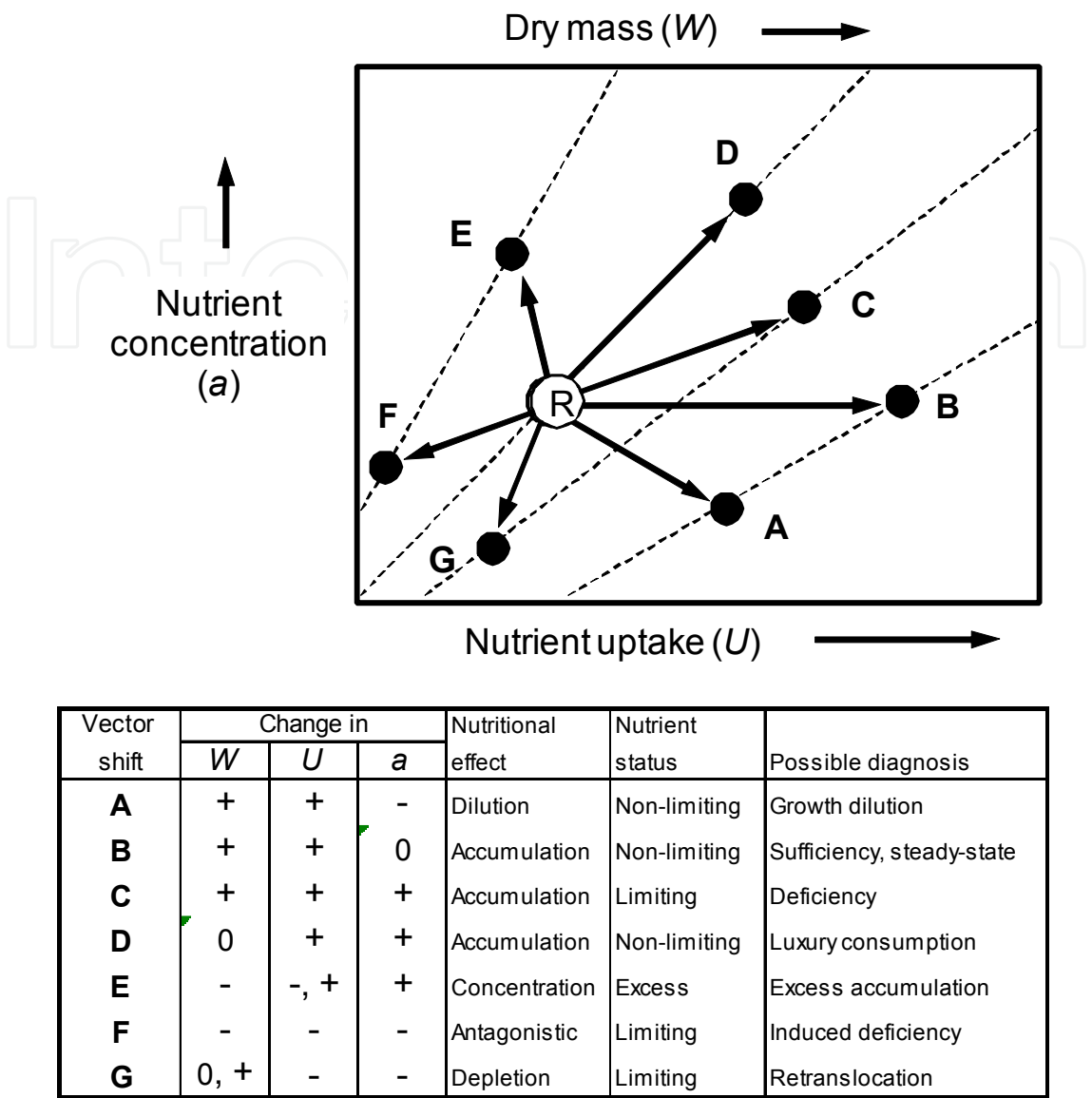


Fig. 2. Vector nutrient diagnosis of directional changes in relative dry mass (*W*), nutrient content (*U*) and concentration (*C*) of plants (or plant components) contrasting in growth and nutrient status. The reference status (*R*) is usually normalized to 100%. The dotted diagonal lines represent the biomass of samples being compared. Vector shifts (*A* to *G*) indicate increase [+], decrease [-], or no change [0] in dry mass and nutrient status relative to the reference status as summarized in the Box beneath. Vector magnitude reflects responsiveness of individual nutrients. From Imo (1999).

4.2 Diagnostic interpretations of nutritional responses, with examples

4.2.1 Growth dilution of nutrients

Growth dilution (Shift *A*, Fig. 2) occurs when nutrient concentration declines while growth and nutrient uptake increase (Armson 1977, Timmer 1991). Such dilution effects usually occur during periods of rapid plant growth when nutrient uptake cannot keep pace with the high rate of biomass accumulation (Ingestad and Ågren 1988; Jarrell and Beverly 1981). For

example, Imo and Timmer (1992a) used single dose and constant top dressing fertilization regimes to induce growth dilution of nutrients in mesquite (*Prosopis chilensis*) seedlings under greenhouse conditions. because seedling growth rate was higher than rate of nutrient uptake during the growing season. Interpretation of the growth dilution of nutrient effects by vector nutrient analysis during seedling development is illustrated in Fig. 3 using the single dose treatment (Imo and Timmer 1997).

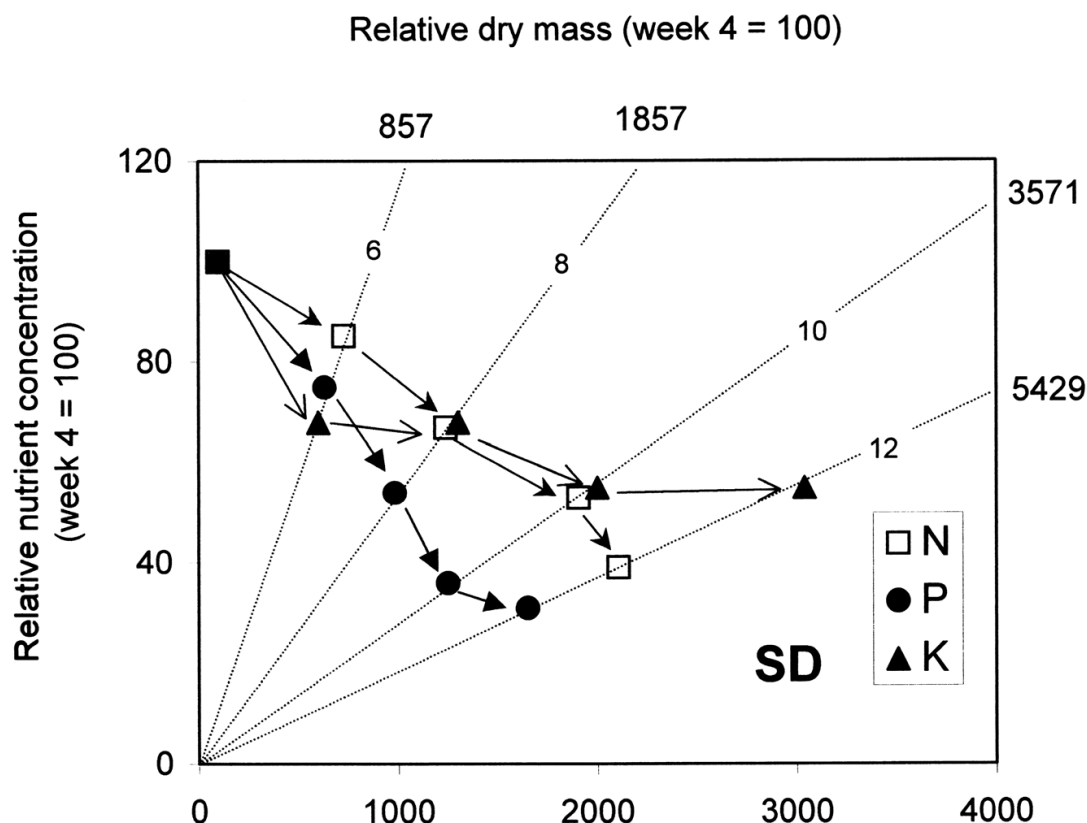


Fig. 3. Vector nomogram of relative changes in dry mass, nutrient content and nutrient concentration occurring at 2 week intervals of mesquite seedling shoots cultured under a single dose (SD) fertilization regime. Seedling status at week 4 was normalized to 100 for comparison with subsequent time intervals. Vectors reflect progressions in time from week 4 to 12. The downward-pointing vectors indicate growth dilution of nutrients (Shift A in Fig. 2) over time because nutrient uptake did not keep pace with growth demand by the seedlings (Imo and Timmer 1992 a; Imo and Timmer (1997).

In this diagram, the right-pointing vectors indicate dry mass and nutrient uptake increased while the downward-pointing vectors indicate decline in concentration over time, thus growth dilution (Shift A, Fig. 2). Growth dilution may also occur due to imbalanced nutrition, resulting in a decline in concentration of a non-limiting nutrient as a result of increased availability of a limiting factor (Armson, 1977; Timmer and Stone 1978), as demonstrated by Munson and Timmer (1989) using vector nutrient analysis (Fig. 4). In this study, addition of a limiting nutrient (N) induced a rapid increase in growth of black spruce seedlings resulting in a decline in concentration of a non-limiting element (K). From interpretation of the vector directions and length, they concluded that the result was primarily a response to N deficiency since the N vector is longer than the K vector

4.2.2 Nutrient deficiency

Nutrient deficiency response (Shift C, Fig. 2) is associated with increases in growth, nutrient uptake and concentration (see for example Imo and Timmer 1992a, Fig. 5), indicating that nutrient uptake rate is higher than rate of biomass accumulation. Such a response is characteristic of addition of a limiting nutrient (Timmer and Stone 1978). Imo and Timmer (1999) also examined the effects of 5-year old *Leuceana* hedgerows on growth and nutrient uptake of a maize intercrop over one cropping season in a humid highland of western Kenya. In this experiment, three between-alley spacing (2, 4 and 8m) and two within-alley spacing (1.0 and 0.5m) treatments plus a treeless sole crop control were compared with or without fertilization. Fig. 6 shows some of the results after evaluation using vector analysis. This diagram shows that the sole maize crop planted without any *Leuceana* trees experienced N deficiency since mulch application resulted in increased N availability due to and deficiency response (Fig. 6).

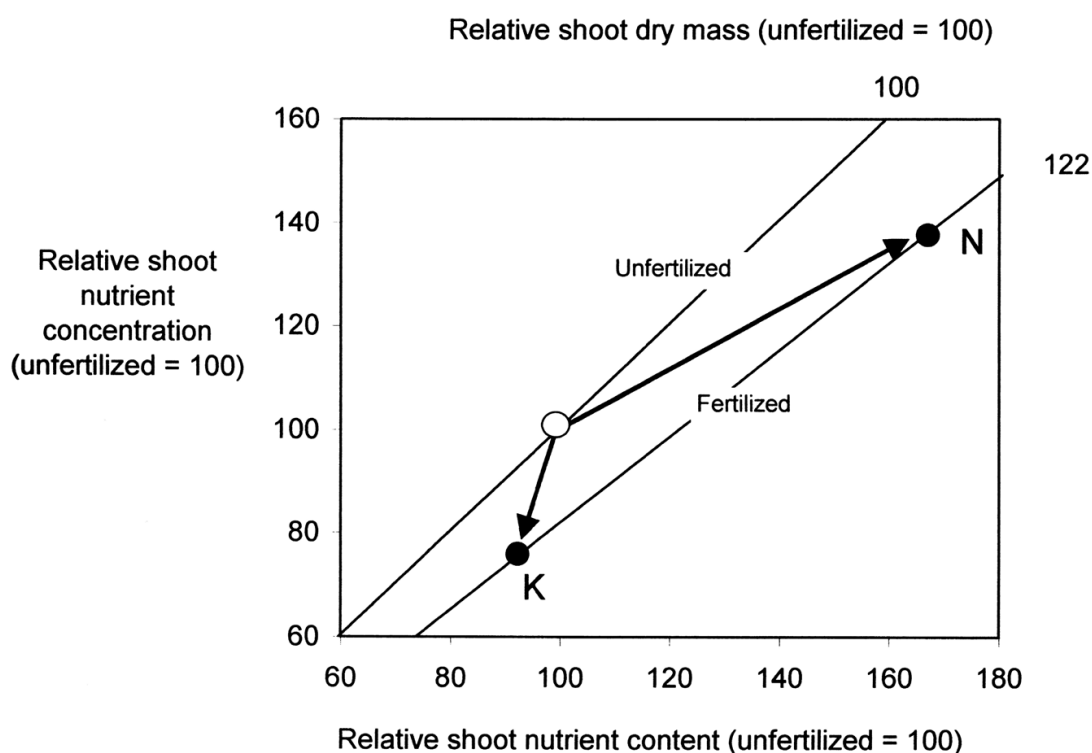


Fig. 4. Relative differences in nutrient content, concentration and shoot dry mass between unfertilized and fertilized black spruce seedlings and planted and grown for 5 months in potted, intact blocks of forest humus under nursery conditions with supplemental irrigation. The fertilized seedlings received 250 kg/ha NH_4NO_3 fertilizer. The seedling status of the unfertilized control was normalized to 100 for comparison with unfertilized treatment. Fertilization increased growth, and N content and concentration signifying N deficiency response (vector shift C in Fig. 2). Concentration of K, however, declined despite increase in growth and content indicating growth dilution (vector shift A in Fig. 2). This phenomenon is usually associated with growth dilution of non-limiting nutrients (e.g. K in this example) on addition of a limiting factor (e.g. N in this example) probably reflecting imbalanced nutrition Data from Munson and Timmer (1989).

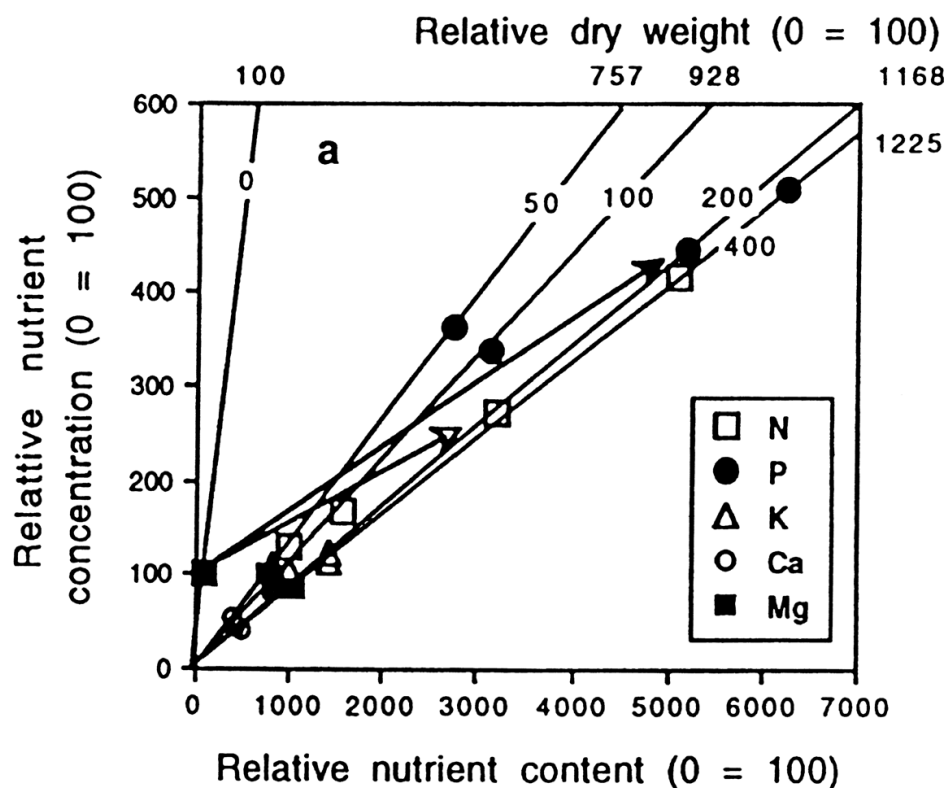


Fig. 5. Vector nomogram of relative shoot dry mass, nutrient concentration, nutrient content of mesquite seedlings grown at 0, 50, 100, 200 and 400 m g N seedling⁻¹ fertilized with complete fertilizer. The unfertilized control was norm alized to 100 (0 = 100) for comparison with the fertilized treatments. Vector lengths indicate P as the primary and N the secondary responsive nutrients, clearly reflecting the effect of fertilization. The positive shifts in dry mass, nutrient concentration and content after fertilizer addition signified P and N deficiency responses (Shift C in Fig. 2). Adapted from Imo and Timmer (1992).

4.2.3 Nutrient sufficiency and steady state nutrition

Nutrient sufficiency (Shift B, Fig. 2) is associated with increases in both nutrient uptake and growth, but no change in concentration indicating that the rate of nutrient uptake matched the rate of biomass accumulation, or steady state nutrition (Ingestad and Lund 1986). This response is characteristic of non-limiting nutrients that are present in sufficient amounts in the growing medium (Timmer 1991). In an experiment with mesquite seedlings (Imo and Timmer 1997) the model demonstrated the ability of exponentially based fertilization regimes to achieve steady state conditions in these seedlings (Fig. 7).

4.2.4 Luxury consumption

Luxury consumption occurs when there is no change in growth despite increased nutrient uptake, thus resulting in elevated concentration (Shift D, Fig. 2). This nutritional effect may signify nutrient loading (see for example Timmer and Munson 1991, Fig. 8).

4.2.5 Nutrient interactions

Both antagonistic dilution and nutrient toxicity are associated with reduced growth and nutrient content, often involving interaction of various factors. Antagonistic dilution (Shift

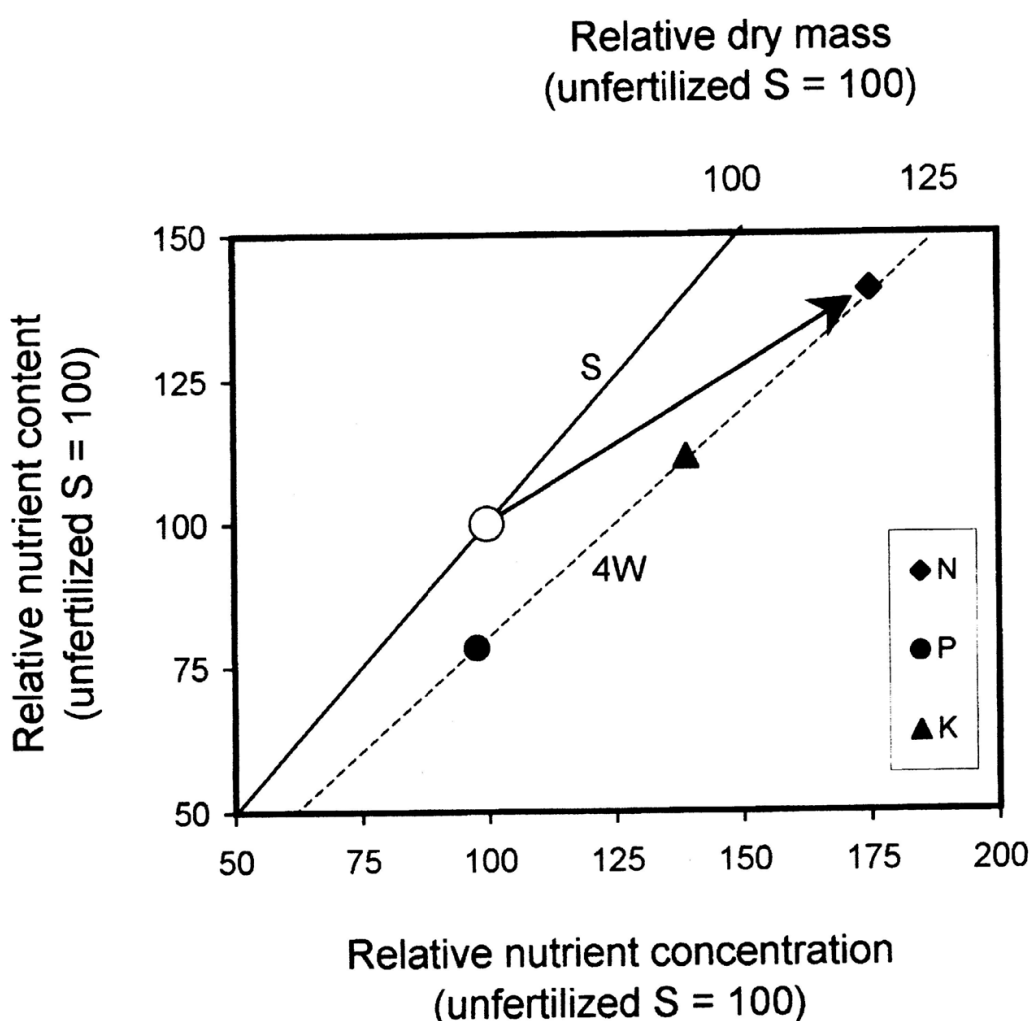


Fig. 6. Vector nutrient diagnosis of relative biomass and nutrient status of unfertilized maize grown in the *Leucaena* alleys (4W) and the treeless sole crop (S). The vector indicates a primary response of the maize crop to N deficiency (i.e. the largest vector is for N) in this treatment, presumably because of improved N availability.

Fin Fig. 2) occurs when a decline in nutrient concentration is associated with reduced growth and nutrient uptake. For example, Teng and Timmer (1990a, b) found antagonistic dilution (or induced deficiency) of Zn and Cu after fertilizing red pine seedlings with N and P (Fig. 9). Severe competition for a limiting nutrient may also cause antagonistic dilution as was found in *Pinus radiata* trees competing for nutrients with pasture in New Zealand (Mead and Mansur 1993). Nutrient toxicity (or excess uptake), on the other hand, is associated with reduced growth and nutrient uptake but elevated nutrient concentration (Shift E, Fig. 2), and occurs when growth declines more than corresponding reduction in nutrient uptake. This response, also referred to as concentration effect, often results from factors that stunt plant growth such as nutrient toxicity (Jarrell and Beverly 1981). For example in Fig. 9, P fertilization at high rates not only induced Zn and Cu deficiencies, but also resulted in P toxicity (Teng and Timmer 1990a, b).

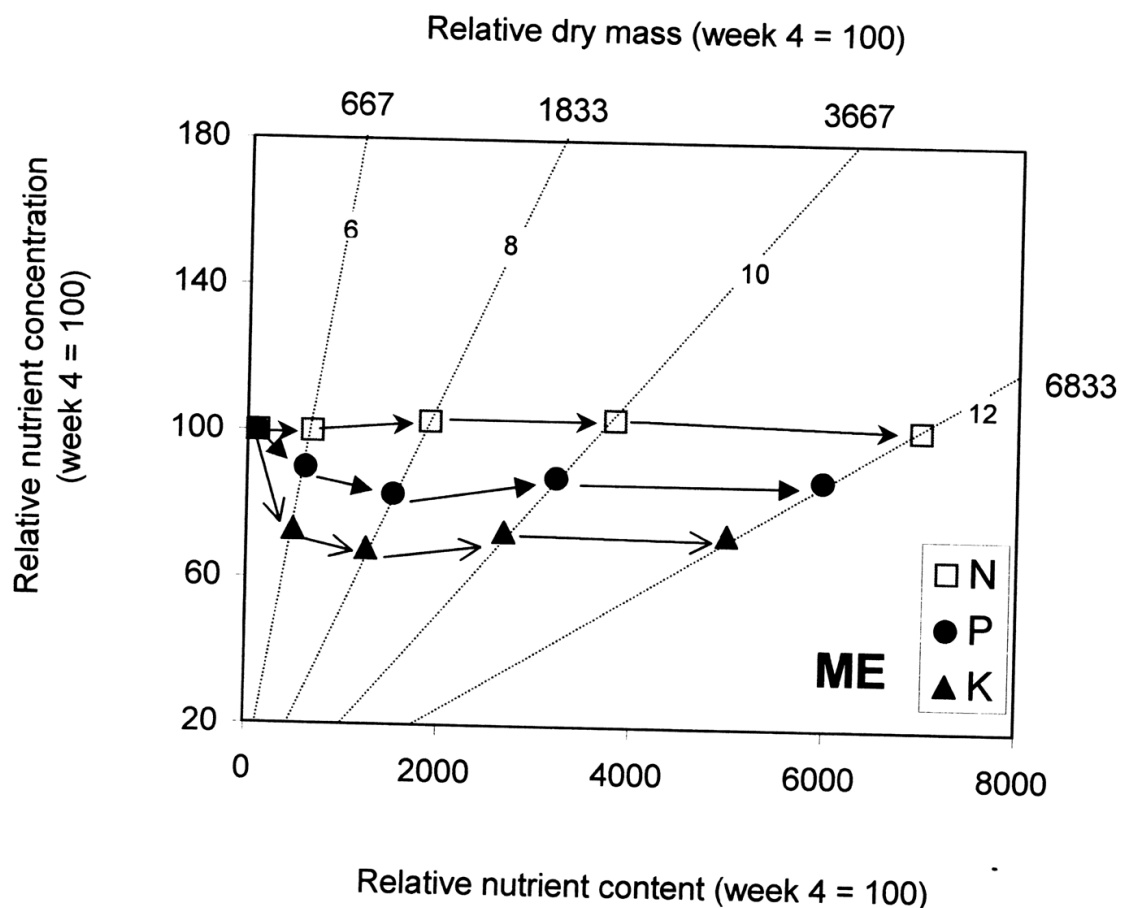


Fig. 7. Relative changes occurring at 2-week intervals in dry mass, and nutrient concentration and content of mesquite seedlings cultured under modified exponential (ME). The seedling status at week 4 was normalized to 100 for comparison with subsequent time intervals. Vectors reflect progressions in time from week 4 to 12. The near-horizontal vector (shift B in Fig. 2) associated with the modified exponential regime indicates that growth and nutrient uptake rates were equal, exemplifying nutrient sufficiency at steady-state nutrition (Ingstad and Lund 1986). Adapted from Imo and Timmer (1997).

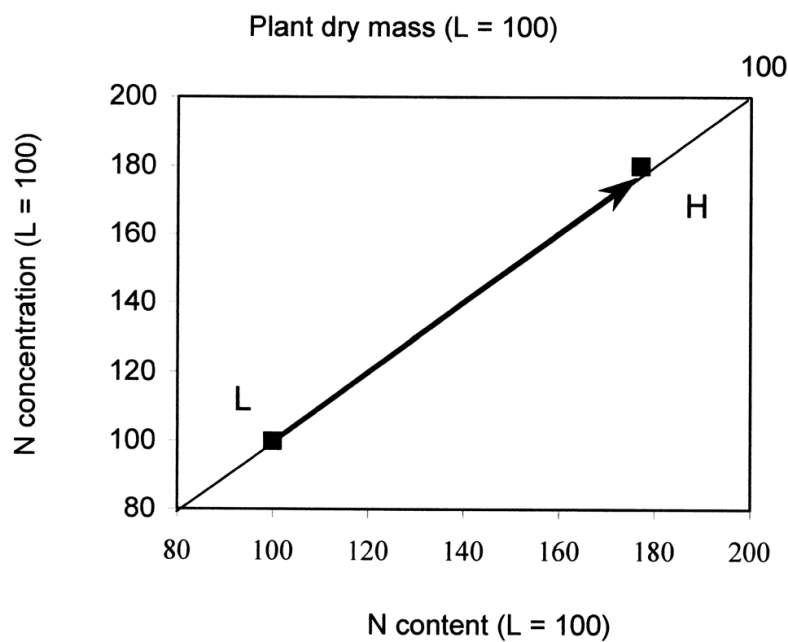


Fig. 8. Relative difference in dry mass, and N concentration and content of seedlings raised under a low (L) and high (H) N fertilization regime. L levels were normalized to 100. The higher N status of the fertilized treatment without dry mass increase reflects luxury consumption of N (shift D in Fig. 2) that characterizes nutrient loading. Adapted from Timmer and Munson (1991).

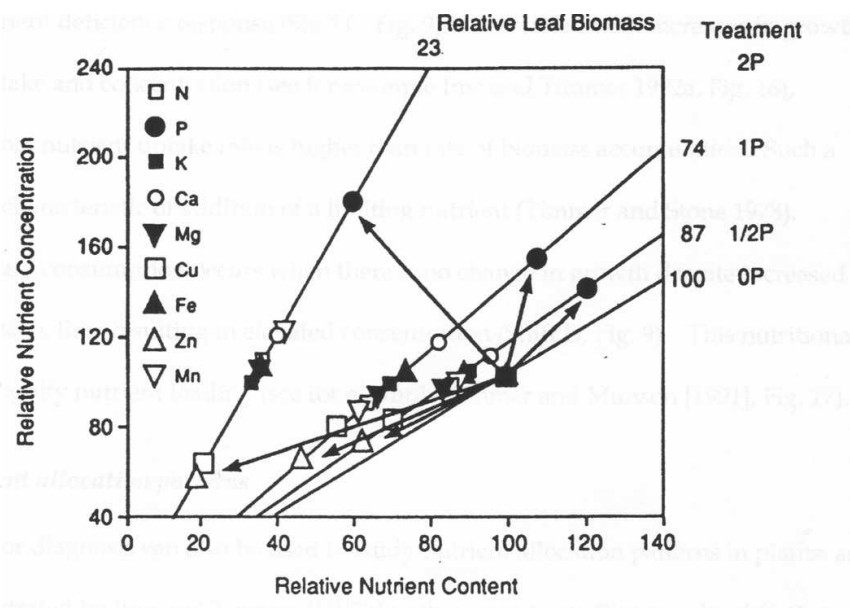


Fig. 9. Relative responses in nutrient concentration, nutrient content and biomass in hybrid poplar fertilized at various levels of P (0, 288, 576 and 1152 kg ha⁻¹, denoted as 0P, 1/2P, 1P and 2P, respectively). Status of the reference treatment (0P) was normalized to 100 to allow comparison on a common base. The downward-pointing vectors (Shift F in Fig. 2) indicate that addition of P induced Zn and Cu deficiency. The upward-pointing vectors (shift E in Fig. 2) indicate excess uptake of P at higher P dose levels presumably because of stunted growth (i.e. concentration effect). Adapted from Teng and Timmer (1990a).

4.2.6 Nutrient allocation patterns

Vector diagnosis can also be used to study nutrient allocation patterns in plants, as was demonstrated by Imo and Timmer (1992b) with mesquite seedlings under differing fertilization regimes (Fig. 10). In this trial, leaf N status was markedly higher than in roots and stem (downward-pointing vectors in Fig. 8) presumably because of the higher physiological importance of the leaves. Apparently, stem biomass increased while N content and concentration declined in stems (Fig. 10), indicating nutrient depletion (Shift G, Fig. 2) probably because of retranslocation to the leaves. Malik and Timmer (1998) also used this diagnostic approach to study nutrient retranslocation in nutrient loaded and non-loaded black spruce seedlings planted on competitive boreal mixedwood forest sites. Thus, vector diagnosis approach can be used to study effects of different management regimes on both plant nutrient allocation and retranslocation processes.

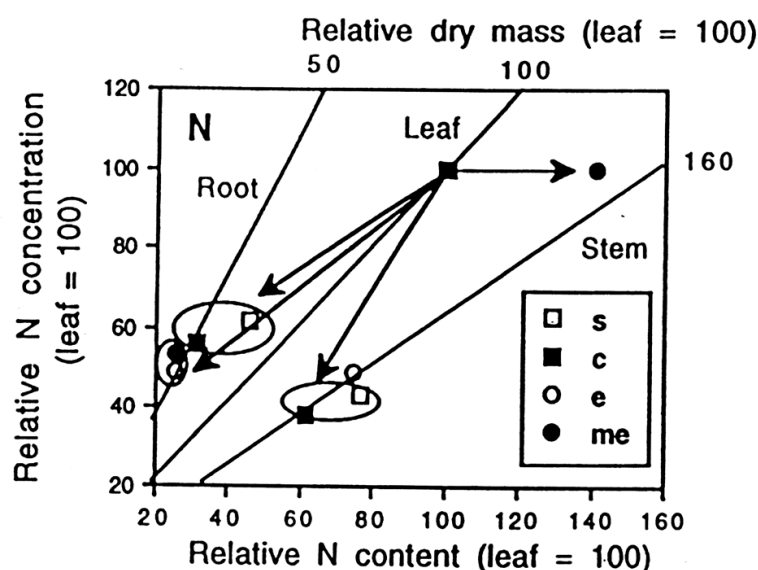


Fig. 10. Relative dry mass and N composition of components of mesquite seedlings cultured under single dose (s), constant top dressing (c), pure exponential (e), and modified exponential (me) fertilization schedules at final harvest. Leaf status for each treatment was normalized to 100. Vectors reflect relative change in dry mass and nutrient composition of the stem or root when compared to the leaf, and indicate N concentration and content were higher for leaf than both the stem (except 'me' treatment) and roots. Notice that both N content and concentration in the stem declined despite increase in growth (except 'me' fertility regime), indicating N depletion from the stem (Shift G, Fig. 2) that is usually associated with nutrient retranslocation (adapted from Imo and Timmer, 1992b).

5. Practical applications: characterization of soil fertility targets

As indicated at the start of this chapter, poor diagnosis of soil fertility and crop response to soil fertility changes has been identified a major cause of poor soil fertility management in many cropping systems. Although mineral nutrition is a critical aspect of crop production and quality, precise diagnosis of soil and plant nutrient status has received little attention in tropical agriculture. Current trends reflect increased interest to use fertilizers in cropping systems in order to improve the nutritional quality of field crops, but recommended

guidelines are relatively unavailable for quantifying and characterizing fertility targets in these systems.

Timmer (1997) proposed a conceptual fertilizer dose response model that can be used to quantify and characterize fertility targets in cropping systems, which has since been re-configured to indicate how plant growth and nutrient status will increase with increasing fertilization, and distinguishes nutrient deficiency, sufficiency, luxury consumption and toxicity responses in plants (Fig. 11; Salifu and Timmer 2003). Traditionally based on biomass or yield parameters alone, this model has been re-configured to include nutrient uptake and nutrient concentration as well in order to improve its diagnostic capacity, thus allowing precise diagnosis of crop responses to soil fertility regimes (Salifu and Timmer 2003, Fig. 11). The application of this model been validated across a broad spectrum of soil N fertility ranging from nutrient deficiency to toxicity in conifer production systems (Salifu and Timmer, 2003; Salifu and Jacobs, 2006). Although this model has yet to be tested under multi-element interaction scenarios and various cropping systems and environmental conditions, the theoretical foundations as elaborated in Section 3 above makes the model promising for general applications.

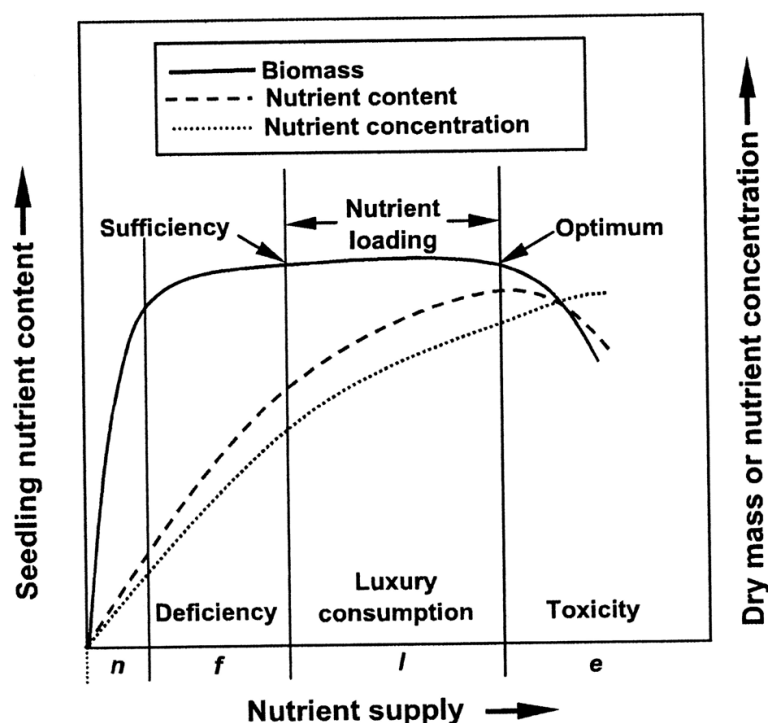


Fig. 11. Plant growth and nutrient status conform to a curvilinear pattern with increased fertilization, but partitioned here into phases to distinguish nutrient deficiency, sufficiency, luxury uptake and toxicity. Fertilizer (*f*) supplements native fertility (*n*) to avert nutrient deficiency to maximize growth at sufficiency. Extra high fertilization or nutrient loading (*l*) induces luxury uptake in excess of growth demand, which are stored as reserves for later utilization. Excess fertilization (*e*) may induce toxicity signified by diminished plant growth and N content at increasing tissue N concentration (adapted from Salifu and Timmer 2003a; Salifu and Jacobs, 2006).

Principally, this model can help quantify and define target rates (n , f , l and e , Fig. 11) for production of field crops (e.g. Cheaib *et al* 2005). The model shows that fertilizer (f) is usually added to supplement native fertility (n) in order to avert nutrient deficiency to maximize growth at sufficiency. Any extra higher fertilization induces luxury uptake in excess of growth demand and nutrients are stored as reserves (i.e. nutrient loading, $[l]$) for later utilization. Excess fertilization (e) may induce toxicity, often indicated by decreased plant growth and N content but elevated tissue nutrient concentration. Such higher internal nutrient reserves acquired during nutrient loading have been shown to correlate well with improved field performance of tree seedlings (Salifu and Timmer 2003b; Malik and Timmer 1998). This simple model has been used to adapt the concept of steady-state nutrition to soil-based seedling culture by developing fertilizer delivery models which effectively induce steady state nutrition (Marney *et al.* 2010)

6. Conclusions

Diagnosis of nutritional status in cropping systems is complex given the many biochemical, physiological, ecological, socio-cultural and economic factors that determine the productivity of the target systems. The often used visual and mathematical models may not be adequate to prescribe and recommend processes for and visual methods are unlikely to confirm nutritional status of any cropping system. Vector nutrient diagnosis is an insightful tool for elucidating plant growth and nutritional responses to different cultural treatments such as fertilization and irrigation. The method also allows detection and isolation of possible nutritional effects associated with growth responses, namely: dilution and concentration effects, nutrient imbalances and interactions, and nutrient allocation patterns and retranslocation.

Originally conceived by Timmer and Stone (1978), vector nutrient diagnosis has been used widely to diagnose nutrient limitations (e.g. Joslin and Wolfe 1994; Moran and Moran 1998; Labrecque *et al.* 1998), explain silvicultural responses (e.g. MacDonald *et al.* 1998), and to assess nutrient supply from added mulch to crops in agroforestry (e.g. Anthofer *et al.* 1997; Yobterik *et al.* 1994). Some authors have also used the technique in a modified graphical form at by plotting concentration on the y-axis and growth on the x-axis, following the same diagnostic interpretations shown in Fig. 2 (e.g. Binkley *et al.* 1995; Valentine and Allen 1990). The technique has been reviewed extensively (Haase and Rose 1995; Timmer 1991), and is also described as a standard tool for soil fertility evaluation and nutrient diagnosis in several text books (for example Binkley 1986; Black 1993; Fageria *et al.* 1991; Kimmins 1996; Pritchett and Fisher 1987; Weetman and Wells 1990). The general conclusion from these reviews is that the technique is relatively simple, reliable, comprehensive, flexible, and practical in application as compared to other diagnostic techniques.

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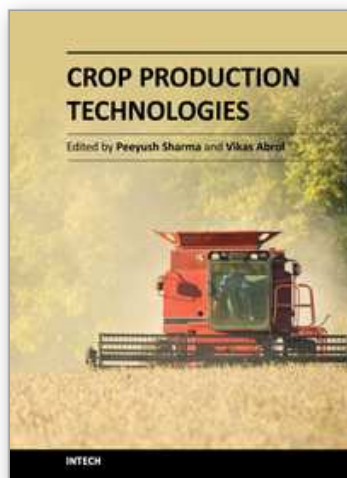
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