Modelling plant nutrition of horticultural crops: a review

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Abstract

In this review, studies in plant nutrition are classified according to their time scales and microscopic or macroscopic level of approach. Short-time scale studies are mostly dealt by plant physiologists with the prospect of building mechanistic models. They describe elementary plant functions implicated in, or dependent on, the mechanisms of plant nutrition, with the goal of explaining the mechanisms underneath the functions. The concept of ‘active ion transport’ across the root plasma membrane derives from precise analyses of uptake isotherms describing nutrition as a function of ion concentration in the root medium. Attempts to introduce feedback mechanisms, as required to model whole-plant response to the environment, are reviewed. Similarly, the response of plant photosynthetic capacity to leaf nitrogen status is extremely rapid and the role of nitrogen in regulating photosynthesis seems to hold for a large number of species. Therefore, it appears possible to introduce nitrogen regulation on leaf photosynthesis, thus allowing better simulations of plant growth under nitrogen limiting conditions. Long-time scale studies are dealt by agronomists and have long been the basis of fertilization advice. They attempt to predict crops’ mineral nutrient requirements over the entire cycle from the empirical knowledge of general laws governing crop growth. Recent advances propose to manage nutrition on the basis of crop structure independently from species and give opportunities to develop mechanistic concepts at this time scale. For nitrogen, this has been formalized extensively in crops such as cereals and grasses. It deserves to be carefully looked at for horticultural crops. These models also provide a sound basis to diagnosis through plant analysis. In horticultural agrosystems, such as those used for hydroponic cultures under commercial glasshouses, the use of on-line sensors is currently an alternative to crop models, since fertilization is induced by the immediate response of the sensors. This practice made
possible by technological breakthrough is meant to correct drifts but lacks anticipation. © 1998 Elsevier Science B.V.

**Keywords:** Efflux; Functional equilibrium; Influx; Mineral ions; Model; Nitrogen; Photosynthesis; Plant growth; Regulation; Uptake rates

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### 1. Introduction

Plants acquire from their aerial and root environments all constituents of their tissues. In particular, soil fertility governs plant growth and thereby the quantities of mineral nutrients taken up by the roots. In natural ecosystems, the minerals absorbed by growing organisms return to the soil after organic matter decomposition, and soil fertility is more or less maintained through nutrient cycling. In cultivated ecosystems, however, all
harvested biomass withdrawn from the field contains nutrients that no longer return to the soil. Hence, maintenance of soil fertility and plant yield production depend on counterbalancing fertilizer inputs. Considering all the nations in the world, grain yield increases linearly with the doses of (N + P + K) fertilizers applied to cereals and this accounts for more than 80% of the variance in yield (Greenwood, 1990). From the viewpoint of agricultural productivity, it means that mineral nutrition is the main factor limiting growth and therefore high fertilizer inputs are necessary to produce large quantities of biomass. This idea explains the peculiarity of horticulture where fertilization is extremely intensive: although nitrate concentration in the soil solution of a fertile field ranges between 2 to 20 mol m\(^{-3}\) (Mengel and Kirkby, 1987; p. 365), the nutrient solution used to grow tomatoes in soilless cultures is maintained in between 15–25 mol m\(^{-3}\) NO\(_3\)\(^-\). Meanwhile, 1 ha of fertile wheat field yielding 8 tonnes of grains produces around 14 tonnes of aerial dry biomass, whereas 1 ha of greenhouse yielding 450 tonnes of tomatoes produces around 40 tonnes of total aerial dry biomass.

Since the XIXth century, it is well known that plant growth is always limited by the first factor whose availability in the environment starts missing. This fundamental concept has guided research to render modern agriculture more efficient. The contemporary research in crop physiology has identified the factors limiting plant growth (Table 1), tempted to delay their upcoming limitation or change their order of appearance, and quantified their potential productivity increase when economically profitable.

These lines of research resulted in increasingly more complex models of plant growth processes and yields which offer today the operational bases for strategic (long-term) and tactical (short-term) crop management. Meanwhile, industrialization and breakthrough in technology have given growers powerful and sophisticated tools to manipulate these factors. Moreover, for highly profitable potential productivity increases, new agrosystems have been developed to manipulate the naturally fixed limiting factors. For instance, the development of horticulture in protected environments proceeds from this technical breakthrough and growers use in their greenhouses CO\(_2\) enrichment, soilless cultural techniques, artificial lighting and heating and cooling to increase productivity.

It may seem a paradox to trace the first reports on plant water and mineral nutrition back to the XVIIth century and state that today there is still controversy about the mechanisms of ion uptake, and moreover, the use of mineral nutrition in crop models (Fig. 1; Table 2).

### Table 1
Factors limiting plant yield. For non-fixed factors, the names expensive and cheap refer to the cost in energy required to set-up the desired factor (modified after Mohr and Schopfer, 1995)

<table>
<thead>
<tr>
<th>Fixed factors</th>
<th>Non-fixed factors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Expensive factors</td>
<td>Cheap factors</td>
</tr>
<tr>
<td>CO(_2) concentration</td>
<td>Irrigation</td>
</tr>
<tr>
<td>Light integral</td>
<td>Fertilization</td>
</tr>
<tr>
<td>Temperature</td>
<td>Crop protection</td>
</tr>
<tr>
<td>Type of soil</td>
<td>Nutritional value</td>
</tr>
<tr>
<td></td>
<td>External yield quality</td>
</tr>
</tbody>
</table>
Agronomists and plant physiologists have developed a dual approach to characterize the uptake of a mineral nutrient [X] by a plant. A ‘mechanistic’ approach describes uptake as successive steps: uptake per se (i.e. the entrance of [X] inside the root), assimilation (if any) and/or transport in the plant and at last utilisation in plant metabolism (Fig. 1; groups 1, 2 and 3). Research along these lines aims at explaining the ‘proximate’ factors controlling mineral uptake. Hence, modelling is set at fine spatio-temporal scales: short-time studies at the cellular and molecular levels. The uppermost important question concerns the identification of uptake regulatory processes likely to happen in one or several successive steps. In the end, only the integration of these successive steps will simulate adequately the behaviour of a whole plant. The second ‘statistic’ approach has anteriority and proceeds from higher levels of integration. This research focus on the ‘ultimate’ factors governing the equilibrium between mineral uptake and plant demand considered through growth (Fig. 1; groups 4 and 5). From this viewpoint, modelling is set at a broad spatio-temporal scale: long-time studies (months, year) at the whole plant or field levels. This approach has resulted in the actual fertilization practices, which attempt simultaneously to maintain soil fertility (by a ‘maintenance’ fertilization) and to fulfil the crop-growth demand (by a ‘growth’ fertilization). Table 2 is a non-exhaustive compilation of the authors which have developed the main concepts used as starting points for models dealing with plant mineral nutrition.

This review will concentrate on the main models of plant mineral nutrition published in the literature with an attempt to explicate the hypotheses underneath the concepts. It reflects our view of agronomists seeking for a leading thread in the plentiful literature on plant nutrition. Thereby, we have tried here to organize the current hypotheses into a logical conceptual frame suitable for whole-plant physiologists and agricultural engi-
Table 2: A brief history of plant nutrition modelling. In the ‘model’ column, (s) and (m) refer to statistic and mechanistic models. The ‘group’ column refers to the place of the models in Fig. 1.

<table>
<thead>
<tr>
<th>Explained factor/function</th>
<th>Explicative factors</th>
<th>Model</th>
<th>Group</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth: final yield</td>
<td>dose of one element</td>
<td>law of minimum (s)</td>
<td>4</td>
<td>von Liebig (1841)</td>
</tr>
<tr>
<td></td>
<td>dose of one element</td>
<td>diminishing return (s)</td>
<td>4</td>
<td>Mitscherlich (1909)</td>
</tr>
<tr>
<td></td>
<td>plant nutrient content</td>
<td>critical concentration (s)</td>
<td>5</td>
<td>Ulrich (1952)</td>
</tr>
<tr>
<td></td>
<td>dose of two or more elements</td>
<td>nutrient equilibrium (s)</td>
<td>4</td>
<td>Homès and van Schoor (1982)</td>
</tr>
<tr>
<td></td>
<td>dynamic rate of supply of one element</td>
<td>relative addition rate (m)</td>
<td>4</td>
<td>Ingestad and Ågren (1992); Larsson (1994)</td>
</tr>
<tr>
<td></td>
<td>plant N, P, K contents</td>
<td>critical concentration (s)</td>
<td>5</td>
<td>Burns (1990)</td>
</tr>
<tr>
<td>Nutrient content: K + Ca + Mg</td>
<td>thermodynamic activity ratio</td>
<td>selectivity constant (m)</td>
<td>14</td>
<td>Hansen (1972); Nielsen and Hansen (1984); Nielsen and Sørensen (1984)</td>
</tr>
<tr>
<td></td>
<td>N total aerial biomass</td>
<td>diminishing N demand (s)</td>
<td>68</td>
<td>Greenwood et al. (1990); Lemaire and Gastal (1997)</td>
</tr>
<tr>
<td></td>
<td>N plant compartments</td>
<td>2 compartments (m)</td>
<td>68</td>
<td>Caloin and Yu (1984)</td>
</tr>
<tr>
<td></td>
<td>N plant compartments</td>
<td>core-skin (m)</td>
<td>68</td>
<td>Hardwick (1987)</td>
</tr>
<tr>
<td>Uptake rate: K, Na, Cl, SO$_4$,$^{\text{a}}$, NO$_3$,$^{\text{a}}$, NH$_4$</td>
<td>solution ion content</td>
<td>Michaelis–Menten (m)</td>
<td>1</td>
<td>Epstein (1972)</td>
</tr>
<tr>
<td></td>
<td>K, Cl plant and solution contents</td>
<td>feedback/Michaelis (s)</td>
<td>17</td>
<td>Siddiqi and Glass (1982); Cram (1983)</td>
</tr>
<tr>
<td></td>
<td>NO$_3$ plant NO$_3$ content</td>
<td>pump–leak–buffer (m)</td>
<td>17</td>
<td>Scaife (1989)</td>
</tr>
<tr>
<td></td>
<td>NO$_3$ plant NO$_3$ content</td>
<td>feedback/Michaelis (s)</td>
<td>17</td>
<td>Buyse et al. (1996)</td>
</tr>
<tr>
<td></td>
<td>NO$_3$ root respiration</td>
<td>C–N interaction (m)</td>
<td>18</td>
<td>Le Bot (1991); Andriolo (1995)</td>
</tr>
<tr>
<td></td>
<td>PO$_4$ root length</td>
<td>C–N interaction (s)</td>
<td>18</td>
<td>Sanders (1993)</td>
</tr>
<tr>
<td>H$^+$/OH$^-$ excretion</td>
<td>NO$_3$, NH$_4$ and SO$_4$ assimilation</td>
<td>cytoplasmic pH-stat (m)</td>
<td>1238</td>
<td>Djikshoorn et al. (1968); Ben Zion et al. (1971)</td>
</tr>
<tr>
<td>Root respiration</td>
<td>anion uptake</td>
<td>energy requirement (m)</td>
<td>8</td>
<td>Veen (1980); Lambers et al. (1983); van der Werf et al. (1988)</td>
</tr>
<tr>
<td>Photosynthesis</td>
<td>specific leaf N</td>
<td>C–N interaction (s)</td>
<td>3</td>
<td>Sinclair and Horie (1989)</td>
</tr>
</tbody>
</table>
neers interested by the subject. The scheme of this paper is set on the description of the dual spatio-temporal approach mentioned above, which is in our view the most interesting for horticulture. For reasons of conciseness, we will not develop extensively the role of each nutrient in plant metabolism, information on the implication of mineral nutrition in crop production being reviewed elsewhere (Le Bot et al., 1994). At last, this paper aims to unify different modelling approaches by exploring the diversity of species and environments studied so far. This is a reason why we will not confine our analysis to horticultural plants. Moreover, modelling in this field is too scarce to justify a separate study from other agrosystems.

2. Proximate functions

2.1. Nutrient uptake

In productive agrosystems, ion concentration at the root surface level is determined both by the properties of the rooting medium and by the plant ion uptake kinetics. Clarkson (1985) reviewed these interface aspects ‘between plant physiology and soil science’. For example, he reported on the work of Silberbush and Barber (1983) showing that root elongation rate and soil diffusion coefficient are the main determinants of phosphorus uptake rate by roots. Thus, although these aspects are not dealt with in this paper, it is important to stress that the knowledge of nutrient distribution and mobility in soils or substrates, as well as uptake capacity distribution and architecture of roots (for review, see Habib et al., 1991) are required to model nutrition. Furthermore, these determine the root units that plant physiologists should prefer. However, although for phosphorus most works relate uptake to root surface or length, for other nutrients only more accessible units such as root dry or fresh weights are commonly used, which may be a limit for models.

Plants regulate their tissue mineral composition against electrochemical gradients through active and passive processes. This explains why mineral concentrations are sometimes lower (e.g. Ca, Na, and toxic elements) or higher (e.g. N, P, S, K) in the plant than in the soil solution. Extensive research on ion uptake has been dedicated to characterizing plant ability to extract nutrients from the soil solution. In particular, uptake velocity has been related to external nutrient concentration, thus, yielding the so-called ‘uptake isotherms’, most of the time using young plants grown in well defined environmental conditions or excised roots. While results have proven useful in defining sound ecological properties of the transport systems, they are questionable in the context of rich soil environments, typical of intensive horticultural systems. In fact, technical difficulties seriously limit the accuracy of uptake rate measurements when the nutrient concentration is elevated, and (or) with older plants.

For most ions (K\(^+\), Na\(^+\), Ca\(^{2+}\), Cl\(^-\), NH\(_4\)\(^+\), NO\(_3\)\(^-\), PO\(_4\)\(^{3-}\), SO\(_4\)\(^{2-}\)), uptake is the net result between simultaneous influx from the solution to the roots and efflux from the roots to the solution, these processes being considered independent (Clarkson, 1986; Aslam et al., 1996a). Many studies are concerned with net uptake or influx, but since
high values of efflux have been reported, it influences significantly net uptake and should be considered in its regulation.

Influx of anions being mostly ATP-dependent, the existence of a significant amount of efflux is puzzling, as it may be seen as an energy-wasting process. Indeed, due to efflux, net anion uptake could require 25 to 100% more energy than expected from theoretical values (van der Werf et al., 1988; Bouma and De Visser, 1993). As a consequence, in addition to growth and biomass maintenance, Johnson (1990) proposed two supplemental specific components for root respiration, one being the energy cost of ion uptake and the other the energy cost of ion re-uptake (i.e. the uptake needed to balance efflux). Some data also suggest that efflux occurs through specialized specific systems requiring both RNA and protein synthesis (Aslam et al., 1996a). To date, the physiological role of efflux, if any, is unclear. It might be an essential process, the most direct way to regulate internal ion concentration (Miller and Smith, 1996), and the respiration re-uptake component would be the cost of homeostasis.

2.1.1. Influx isotherms

Influx kinetics are established by measuring the accumulation rate of an isotope (e.g. $^{13}$N or $^{15}$N for nitrogen) or an analogue (e.g. $\text{ClO}_3^-$ for nitrate, $\text{Rb}^+$ for potassium) in plant tissues. To minimize efflux, the shorter the experiments the better, experiments shorter than 10 min being preferable (Clarkson, 1986; Nissen, 1991). However, due to sensitivity limits, many published data were obtained over 30 min to 1 h periods, leading to large influx rate underestimation.

For low concentrations (e.g. under 1 mol m$^{-3}$ for $\text{NO}_3^-$, $\text{NH}_4^+$ or $\text{K}^+$) influx rate increases with ion concentration following an hyperbola. Since the early work of Epstein and Hagen (1952), the mechanistic enzyme kinetic formula of Michaelis and Menten (Table 3 is widely accepted as best describing this behaviour. Two parameters, $I_{\text{m}}$ (also notated $V_{\text{m}}$) and $K_{\text{m}}$ (also notated $K$ or $C_{\text{m}}$) characterize this model. The former, the maximal rate of influx, is a capacity parameter which can be approached at high external concentrations. Its value is related both to the number of transporters per root unit and to their intrinsic characteristics. The latter is the ion concentration (mol m$^{-3}$) for which influx rate is half the maximum. The lower its value the higher is the affinity of the transporter for a particular ion. It does not depend on the root units but it is determined only by intrinsic characteristics of the transporter.

Table 3
Formulas used for ion influx ($I$) into roots. $I_{\text{m}}$, $I_{\text{m1}}$ and $I_{\text{m2}}$ maximum influx, $K_{\text{m}}$, $K_{\text{m1}}$ and $K_{\text{m2}}$ Michaelis–Menten constants, $x_s$ nutrient solution concentration of ion X

<table>
<thead>
<tr>
<th>Formula</th>
<th>Type</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>$I = I_{\text{m}} \times \frac{x_s}{x_s + K_{\text{m}}}$</td>
<td>Michaelis–Menten</td>
<td>Epstein and Hagen (1952)</td>
</tr>
<tr>
<td>$I = I_{\text{m1}} \times \frac{x_s}{x_s + K_{\text{m}}}$ + $I_{\text{m2}} \times \frac{x_s}{x_s + K_{\text{m2}}}$</td>
<td>Dual Michaelis–Menten</td>
<td>Epstein et al. (1963)</td>
</tr>
<tr>
<td>$I = I_{\text{m}} \times \frac{x_s}{x_s + K_{\text{m}}}$ + $\beta \times x_s$</td>
<td>Michaelis–Menten + Linear</td>
<td>Kochian and Lucas (1982)</td>
</tr>
</tbody>
</table>
If kinetic measurements are made at higher concentrations (above 1 mol m\(^{-3}\) for \(\text{NO}_3^-, \text{NH}_4^+\) or \(\text{K}^+\)), influx rate increases again and reaches much higher values than predicted by \(I_m\). Such a complex pattern has been described for \(\text{K}^+, \text{Na}^+, \text{Cl}^-, \text{Mg}^{2+}, \text{PO}_4^{3-}, \text{SO}_4^{2-}, \text{NO}_3^-, \text{NH}_4^+\) and most micro nutrients (Berlier et al., 1969; Laties, 1969; Epstein, 1972; Hodges, 1973; Nissen, 1974; Rao and Rains, 1976). The molecular interpretation of influx kinetics over a wide range of concentration has led to considerable debate (Laties, 1969; Epstein, 1972; Hodges, 1973; Nissen, 1974, 1991; Borstlap, 1981; Smart et al., 1996), but the dual transport mechanism of Epstein (1972) is the most widely accepted. Mechanism I (or HATS for high affinity transport system) operates in the low concentration range, obeys simple Michaelis–Menten kinetics and shows very low \(K_m\) values. Reported \(K_m\) and \(I_m\) values are greatly variable with plant age, species or varieties and growth conditions (Glass and Siddiqi, 1984a; Clarkson, 1985; Schenk, 1996), but also due to resolution of the measurement set-up. For nitrate, ammonium and potassium, most \(K_m\) values lay between 5 and \(100 \times 10^{-3}\) mol m\(^{-3}\) (Glass and Siddiqi, 1984a; Peuke and Kaiser, 1996), but values as high as \(985 \times 10^{-3}\) mol m\(^{-3}\) have also been reported for nitrate (Pace and McClure, 1986). Mechanism II (or LATS for low affinity transport system) operates mostly in the higher concentration range and its kinetic is not clearly characterized. There are reports that influx rate fits the saturable Michaelis–Menten kinetics with lower affinity (i.e. higher \(K_m\) and higher \(I_m\) than HATS (Peuke and Kaiser, 1996). Observed \(K_m\) values for LATS reach 25 mol m\(^{-3}\) for nitrate (Peuke and Kaiser, 1996) and 3 to 19 mol m\(^{-3}\) for potassium (Benlloch et al., 1989; Maathuis and Sanders, 1996; Smart et al., 1996). However, most published data on \(\text{NO}_3^-; \text{NH}_4^+; \text{PO}_4^{3-}\), and \(\text{K}^+\) describe a linear influx in the high range of external ion concentration. According to Bielecki (1973) when experimental concentrations are far below the \(K_m\) value of LATS, a linear expression is an adequate approximation of a Michaelis–Menten hyperbola. Only one parameter characterizes the linear LATS kinetics (i.e. the slope between uptake rate and nutrient concentration) and it should be expressed in m\(^3\) h\(^{-1}\) per root unit. Reported values, in m\(^3\) h\(^{-1}\) g\(^{-1}\) of fresh root, range from \(150 \times 10^{-6}\) (Kronzucker et al., 1995a) to \(14 \times 10^{-3}\) (Peuke and Kaiser, 1996) for nitrate, from \(670 \times 10^{-6}\) to \(1.3 \times 10^{-3}\) (Wang et al., 1993b) for ammonium, and from \(160 \times 10^{-6}\) (Kochian and Lucas, 1982) to \(540 \times 10^{-6}\) (Kochian et al., 1985) for potassium.

Overall influx is usually computed as the sum of HATS and LATS components (Table 3), referring either to the dual Michaelis–Menten kinetics with four parameters (two for maximum influx and two for affinity) or single Michaelis–Menten plus a linear component, with three parameters (\(I_m\) and \(K_m\) of HATS, and slope of LATS).

2.1.2. Efflux measurements

The use of isotopes in influx studies allows the determination of efflux by monitoring the accumulation of natural isotope (originating from the roots) into the nutrient solution (Morgan et al., 1973). As for influx, experiments should be as brief as possible but due to low analytical sensitivity, nitrate efflux determinations for concentrations above 0.1 mol m\(^{-3}\) last for about 1 h, thus resulting in underestimated values. To overcome this problem, efflux is usually computed rather than measured, either by subtracting net uptake from influx (Deane-Drummond, 1986; Macduff and Jackson, 1992), or through
compartmental analysis (Cram, 1968; Pitman, 1971; Devienne et al., 1994a) which may appear too cumbersome a procedure. Therefore, little information is available on efflux in the high concentration range, above 1 mol m\(^{-3}\) for nitrate and ammonium (Macklon et al., 1990; Devienne et al., 1994b). It should also be emphasized that efflux values may be largely artefactual. Usually, experimental set-ups require the transfer of the plants from their cultivation medium prior measurements. In some cases, the resulting transplant shock has been shown to inhibit net uptake for several hours (Bloom and Sukrapanna, 1990), due to a dramatic enhancement of efflux, while influx remained unchanged (Delhon et al., 1995a; Aslam et al., 1996b).

Depending on growth conditions and species, efflux rates (mol h\(^{-1}\) g\(^{-1}\) root fresh weight) range from \(4 \times 10^{-9}\) (Kronzucker et al., 1995b) to \(10 \times 10^{-6}\) for nitrate (Deane-Drummond and Glass, 1983), and from \(100 \times 10^{-9}\) to \(4 \times 10^{-6}\) for ammonium (Wang et al., 1993a). Expressed in percentage of influx, efflux ranges from 5% (Siddiqi et al., 1991; Kronzucker et al., 1995b) to 93% (Devienne et al., 1994b) for nitrate, from 9–10% (Wang et al., 1993a; Kronzucker et al., 1995c) to 33–35% (Macklon et al., 1990; Kronzucker et al., 1995c) for ammonium, and values of 30% have also been reported for phosphate and sulphate (Lee, 1993). Efflux is mostly seen as an unidirectional leak, depending only on the root ion content, but independent of the external ion concentration (Breteler and Nissen, 1982; Mackown, 1987; Teyker et al., 1988).

2.1.3. Net uptake isotherms

Under near constant ion concentrations, net uptake is measured by the difference between initial and final ion content in the nutrient medium. Some experimental set-ups allow the continuous monitoring of ion concentrations and solution volume which are maintained at set points through automatic additions (Clement et al., 1974; André et al., 1979; Blom-Zandstra and Lupijn, 1987; Alloush and Sanders, 1990; Freijsen et al., 1990). Plant ion and water uptake are computed as the added amounts. Depending on the sensitivity of the experimental set-ups and ion concentrations, their time-scale ranges from a few minutes to 3 h. Accumulation of an isotope in plant tissues during a long time of exposure (1 h at least) can also be used as an estimate of net ion uptake (Macduff and Jackson, 1992; Ourry et al., 1996). Uptake isotherms are usually obtained under variable ion concentrations, following the depletion method of Claassen and Barber (1974). Plants are transferred to a small solution volume and are allowed to deplete a particular ion until its concentration becomes constant. Manual or automatic (Goyal and Huffaker, 1986) ion titration allows to compute net uptake rate against ion concentration. However, the time necessary to complete an experiment increases with increasing initial ion concentrations, which seriously limits isotherm studies to a very low range. Experiments may last for about 10 h for nitrate and phosphate at respective initial concentrations of \(250 \times 10^{-3}\) mol m\(^{-3}\) and \(30 \times 10^{-3}\) mol m\(^{-3}\) and 4 h for potassium at initial concentration of \(200 \times 10^{-3}\) mol m\(^{-3}\). However, since net uptake shows diurnal variations even under constant ion concentrations, we believe that these isotherms probably happen to be distorted.

Net uptake characteristics are mostly the same as those deduced from the influx studies, i.e. existence of two uptake mechanisms, the first being saturable. The Michaelis–Menten kinetics have been adapted to take efflux into account (Table 4).
Claassen and Barber (1974) proposed a model where net uptake is the mere difference between influx, following simple Michaelis–Menten kinetics, and efflux, considered as a constant. The model of Nielsen (1976) does not include efflux explicitly, but considers that the ion concentration necessary for null net uptake, as measured at the end of depletion experiments, is an ion compensation point. Both models are currently used to fit the data, but in view of the stated mechanistic independence of influx and efflux (Clarkson, 1986; Aslam et al., 1996a), the formulation of Claassen and Barber should be preferred.

2.2. Feedback regulation of uptake

Evidence has accumulated showing that uptake characteristics of both HATS and LATS are not fixed values, but are closely dependent on experimental conditions and plant growth demand. Under near constant ion concentrations, net uptake of nitrate (Clement et al., 1978; Tribó-Blondel, 1979; Pearson et al., 1981; Le Bot and Kirkby, 1992; Delhon et al., 1995a; Andriolo et al., 1996; Ourry et al., 1996), ammonium (Wild et al., 1987; Ourry et al., 1996) and potassium (Wild et al., 1987; Le Bot and Kirkby, 1992; Macduff and Dhanoa, 1996; Ourry et al., 1996) undergo continuous variations, the pattern being (roughly) an increase during the light period and a decrease during the night. For nitrate, these variations have been stated for concentrations as low as $20 \times 10^{-3}$ mol m$^{-3}$ (Ourry et al., 1996) and as high as 5 mol m$^{-3}$ (Pearson et al., 1981). Nitrate and ammonium net uptake rates are strongly reduced by defoliation (Wild et al., 1987; Macduff and Jackson, 1992) in less than 90 min, and reduction in nitrate uptake rate becomes significant within 20 min (Wild et al., 1987). These continuous and rapid variations in uptake rates cannot be explained by changes in the root system size or by synthesis of new transporters. In addition, different ions share common uptake patterns in these experiments. For these reasons, it has been suggested that uptake rates are controlled by a common, non-specific, mechanism, presumably transpiration or the flow of carbon compounds from leaves to roots, necessary to the respiration-dependent influx (Wild et al., 1987). Today, the former hypothesis is rejected (see Section 2.3) while the latter is not. However, as variations of uptake rate take place even when nutrient concentration is limiting, the second hypothesis seems also unlikely. What is more, homeostasis can hardly be explained by non-specific mechanisms, and underneath most studies, regulation lays on negative feedback from internal specific components.

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<tr>
<th>Formula</th>
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<tr>
<td>$\text{In} = \ln_{m} x - \ln_{m} \frac{x_{s}}{x_{i} + K_{m}} - E$</td>
<td>Influx minus efflux ($E$)</td>
<td>Claassen and Barber (1974)</td>
</tr>
<tr>
<td>$\text{In} = \ln_{m} x - \ln_{m} \frac{(x_{s} - x_{cp})}{(x_{s} - x_{cp}) + K_{m}}$</td>
<td>Compensation point ($x_{cp}$)</td>
<td>Nielsen (1976)</td>
</tr>
</tbody>
</table>
Given its relative importance and sensitivity to internal ion concentration, efflux might explain both homeostasis and net ion uptake regulation (Miller and Smith, 1996). Since the early work of Morgan et al. (1973) introduced efflux as a regulatory component of net nitrate uptake and Deane-Drummond and Glass (1983) suggested that it might be the main short-term regulator, experimental results have led to contradictory and much debated results. During the day–night cycle under constant ion concentrations, net nitrate uptake variations have been stated to be due only to efflux (Pearson et al., 1981), or mostly to influx (Delhon et al., 1995a). In experiments involving nutritional pre-treatments, net nitrate uptake regulation has also been explained by either efflux (Breteler and Nissen, 1982; Deane-Drummond and Glass, 1983; Mackown, 1987), influx (Lee and Drew, 1986; Lee, 1993) or both (Teyker et al., 1988; Devienne et al., 1994b; Kronzucker et al., 1995b). While different results may be explained by specific differences and experimental peculiarities, it remains that modelling both fluxes is a necessity. Successful incorporation of nutrition dynamics in a crop model requires correct and simultaneous simulation of homeostasis, energy cost and net uptake.

2.2.1. Influx

The simplest, most general and selective regulation mechanism lays on the sensitivity of the transport systems to the internal concentration of the particular transported ion (Glass and Siddiqi, 1984a). Indeed, inverse relationships between root (non-metabolized) ion concentration and influx rates have been stated for nitrate (Siddiqui et al., 1990; Delhon et al., 1995a), ammonium (Wang et al., 1993b), sulphate (Clarkson et al., 1983), phosphate (Lefebvre and Glass, 1982), chloride (Cram, 1983) and potassium (Siddiqui and Glass, 1987). Most studies focused on the HATS, for which \( I_m \) appears to be inversely related to root ion concentration. \( K_m \) has been found positively correlated to root ion concentration for ammonium (Wang et al., 1993b) and potassium (Siddiqui and Glass, 1987), or constant for sulphate (Clarkson et al., 1983), while reports are conflicting for nitrate (Lee and Drew, 1986; Siddiqui et al., 1990). For a linear LATS, it has also been reported, both for ammonium (Wang et al., 1993b) and nitrate (Siddiqui et al., 1990) that the slope parameter is lower when root ion concentration is high.

A model of root ion concentration negative feedback on HATS has been introduced by Siddiqui and Glass (1982, 1986) for potassium uptake (Table 5). For this particular ion, the relationships of \( I_m \) and \( K_m \) with root potassium concentration are exponential with negative and positive parameters, respectively. Therefore, the original \( I_m \) and \( K_m \) values of the Michaelis–Menten model have been replaced by their statistical relationship with root potassium concentration so that \( I_m \) and \( K_m \) become, respectively, the maximum and minimum values reached for a null root potassium content. Cram (1983) compared various models involving feedback on the \( I_m \) component only (Table 5). They are of the proportional type, influx being greater when root concentration is either far from a set point concentration (error actuated feedback) or close to a minimum concentration (reciprocal feedback). Cram (1983) concluded that error-actuated feedback best simulated both influx and homeostasis for chloride. This choice has been criticized by Glass and Siddiqui (1984b, 1985), and indeed a molecular mechanism for sensing a set point concentration is hardly imaginable. However, a similar approach has been recently proposed for nitrate influx regulation by Buysse et al. (1996).
Table 5
Some feedback formulas used for ion influx ($I$) into roots. $I_m$, absolute or relative maximum influx, $K_m$ Michaelis–Menten constant, $x_i$, $x_{cyst}$, $x_s$ nutrient solution, cytoplasm and root concentrations of ion X, $x_{min}$ and $x_{sp}$ minimum and set point root concentrations of ion X

<table>
<thead>
<tr>
<th>Formula</th>
<th>Type</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>$I = I_m e^{b \times I_s} \times \frac{x_i}{x_s + K_m e^{b \times I_s}}$</td>
<td>feedback on $I_m$ and $K_m$</td>
<td>Siddiqi and Glass (1982, 1986)</td>
</tr>
<tr>
<td>$I = I_m (1 - \frac{x_{min}}{x_{sp}}) \times \frac{x_s}{x_i + K_m}$</td>
<td>error actuated feedback on $I_m$</td>
<td>Cram (1983)</td>
</tr>
<tr>
<td>$I = I_m \frac{x_{min}}{x_s} \times \frac{x_i}{x_s + K_m}$</td>
<td>reciprocal feedback on $I_m$</td>
<td>Cram (1983)</td>
</tr>
<tr>
<td>$I = I_m (x_{sp} - x_{cyst}) \times \frac{x_s}{x_i + K_m}$</td>
<td>error actuated feedback on $I_m$</td>
<td>Buysse et al. (1996)</td>
</tr>
</tbody>
</table>

From a mechanistic viewpoint, a direct negative feedback of internal potassium and chloride on their respective transporters is currently admitted. This is mostly supported by the absence of metabolism for these ions. Instead, other ions ($\text{NH}_4^+$, $\text{NO}_3^-$, $\text{SO}_4^{2-}$, $\text{PO}_4^{3-}$) are metabolized, and feedback from their assimilation products is under examination. Indeed, when plants are treated with L-cysteine (an S-containing amino acid), sulphate uptake is strongly depressed (Clarkson et al., 1983). Similarly, treatments with various amino acids reduce nitrate or ammonium uptakes (Lee et al., 1992; Müller and Touraine, 1992) while malate, a by-product of leaf nitrate and sulphate assimilation, stimulates nitrate uptake (Touraine et al., 1992, 1994). However, reports on correlation between root amino acid content and nitrate uptake rates remain conflicting (Delhon et al., 1995a,b; Lainé et al., 1995). As a matter of fact, the same problems arise to prove either a direct effect of the transported ion itself or an indirect effect by its assimilation products. Split-root experiments where part of the root system is deprived of a particular ion, result in an increase of ion uptake by normally fed roots. For nitrate, this enhancement is not correlated to root amino acid content (Lainé et al., 1995). For both nitrate (Lainé et al., 1995) and sulphate (Clarkson et al., 1983), uptake rate is usually better correlated with the non-metabolized ion content of shoots than roots. Interestingly, the same arises for potassium (Claassen and Barber, 1977), showing that such experiments are not decisive in proving a direct or indirect effect on the transporters. Even experiments involving the use of treatments affecting nitrogen assimilation, or nitrate reductase deficient mutants, do not prove decisive (Lee et al., 1992; King et al., 1993). Experimental uncertainties arise from the difficulty to devise experiments involving only short-term regulations, and from the analytical significance of root ion or amino acid content, as only the cytoplasmic content of cortical cells is expected to act on the transporters.

2.2.2. Efflux

Few experimental data are available for efflux. A positive linear relationship between root ion content and efflux has been demonstrated for nitrate (Breteler and Nissen, 1982;
Mackown, 1987; Teyker et al., 1988), and a correlation between cytoplasmic ion content and efflux have been reported for nitrate (Kronzucker et al., 1995b) and ammonium (Wang et al., 1993a; Kronzucker et al., 1995c). Efflux being considered as a passive leak, it is usually computed as the mere product of internal concentration and a permeability constant (Cram, 1983).

2.2.3. Net uptake

Net uptake can be modelled by subtracting efflux from influx in the above models (Cram, 1983; Siddiqi and Glass, 1986). However, an interesting endeavour to simulate nitrate uptake under constant ion concentrations should be mentioned here. Scaife (1989) showed realistic nitrate uptake rate patterns in the diurnal cycle using a model based on a constant influx rate, an efflux proportional to the plant nitrate content and a nitrogen assimilation rate proportional to photosynthesis. This model even predicted the time-lag usually observed between maximum photosynthesis and maximum nitrate uptake rate. Our own simulations (unpublished) showed that this time-lag is not constant, but increases from day to day when diurnal photosynthesis increases, or decreases on the reverse situation. This behaviour is consistent with published data (Clement et al., 1978). Furthermore, diurnal variations of plant nitrate concentration are also realistic. It should be emphasized that all these properties are typical of a capacitive model, where fluxes are controlled by the buffer content. In fact, Scaife proposed that net nitrate uptake be negatively correlated to plant nitrate concentration. His interpretation of parameters can be turned round in terms of regulated influx and constant efflux; eventually both fluxes can be regulated without changing the model’s behaviour. The energy cost of net uptake, however, should be strongly affected by these different options. Most important of all, models based on feedback from internal ion concentration (Cram, 1983; Siddiqi and Glass, 1986; Scaife, 1989; Buysse et al., 1996) are potentially able to simulate both ion uptake and homeostasis. However, they were formulated in a context of low ion concentration and further studies are needed in the high concentration range corresponding to horticultural practice.

2.3. Nutrient use efficiency

2.3.1. Nutrients and photosynthesis: a causal relationship?

There is an intimate relation between plant nitrogen or phosphorus status and the carbon metabolism. Hence, N and P deficiencies in plants induce changes in carbohydrate synthesis and degradation pathways (Rufty and Huber, 1983; Vesey and Layzell, 1987; Rufty et al., 1988; Fredeen et al., 1989; Paul and Stitt, 1993). For instance, nitrogen-deficient tomato plants accumulate starch in their leaves which decreases rapidly their SLA (specific leaf area in m$^2$ g$^{-1}$ leaf) (Suniaga Quijada, 1991; Gary and Bertin, 1992). Many observations made over a range of nitrogen availability in the environment suggest the existence of a compulsory balance between nitrogen and carbon nutrition. This explains why plants optimize their carbon gains in relation to nitrogen available for photosynthesis (Field, 1983; Hirose and Werger, 1987a,b; Lawlor, 1994). This optimization implies a tight relation between leaf nitrogen concentration ($N$) and its maximum photosynthetic activity ($A_{\text{max}}$), measured at saturating light intensity.
under optimum temperature and humidity conditions at ambient CO₂ levels. Similarly, phosphorus deficiency progressively stops aerial plant growth, decreases phosphorus concentration in the dry biomass \( P \) and diminishes leaf maximum photosynthetic activity (Brooks, 1986; Fredeen et al., 1989; Halsted and Lynch, 1996). The decrease in growth, however, results more from a lack of phosphorus for new tissue biosyntheses (leaf expansion for instance) than from a drop in photosynthesis. Thus, the observed close \( A_{\text{max}}-P \) relation (Lynch et al., 1991) comes from the indirect effect of phosphorus on leaf expansion, which in turn affects photosynthesis. Sanders (1993) discussed this argument and reckoned that a shortage in phosphorus affects growth via changes in the root:shoot ratio. Reference to photosynthesis is therefore not essential in modelling plant phosphorus nutrition. The \( A_{\text{max}}-N \) relationship has been investigated thoroughly, especially in ecological studies where nitrogen availability in the soil influences species adaptation to their ecosystems. At the present time, only statistical models account for the \( A_{\text{max}}-N \) relationships (Table 6). They are based on several hypotheses about the role of nitrogen in several photosynthesis-limiting reactions (Field and Mooney, 1986).

\( A_{\text{max}} \) could be regulated by one or several processes functioning at rates determined by leaf nitrogen content. For instance, the rate at which CO₂ is transported from gaseous to liquid phases depends on the activity of carbonic anhydrase and CO₂ fixation depends on the activity of the enzyme Rubisco, on RuBP, NADPH, ATP regenerations. All these steps require enzymes, in which the constitutive nitrogen may be the rate limiting factor. As a consequence, the optimization of nitrogen efficiency for photosynthetic use is made through the function of nitrogen distribution between plant organs and between classes of nitrogen compounds.

### Table 6
Mathematical functions used for modelling the effect of nitrogen on photosynthesis

<table>
<thead>
<tr>
<th>Ref.</th>
<th>Model Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>( A_{\text{max}} = a \times N + b )</td>
</tr>
<tr>
<td>(2)</td>
<td>( A = \frac{a_0 \times N_s}{\text{SLA} \times T} )</td>
</tr>
<tr>
<td>(3)</td>
<td>( A_{\text{max}} = A_s \times \left( \frac{2}{1 + e^{-a(N-N_{0s})}} - 1 \right) )</td>
</tr>
<tr>
<td>(4)</td>
<td>( A_{\text{max}} = a \times N^2 + b \times N + c )</td>
</tr>
<tr>
<td>(5)</td>
<td>( A_{\text{max}} = A_s \times [1 - e^{-k(N-N_{0s})}] )</td>
</tr>
<tr>
<td>(6)</td>
<td>( A_{\text{max}} = A_s \times \frac{N^k}{K_p + N^k} )</td>
</tr>
</tbody>
</table>

(2) $A_{\text{max}}$ could be regulated independently from nitrogen (by stomata, CO$_2$ diffusion resistance, etc.) but leaf nitrogen content could be adjusted to maximum leaf photosynthetic activity. In case of nitrogen shortage, the plant would optimize nitrogen investment since any enzyme activity or nitrogen compound in excess of that strictly required for maximum rate would be useless, only the limiting factor being worth upraising. As a consequence, nitrogen use efficiency is highest when the distribution of nitrogen to all non-limiting plant growth processes is regulated towards the critical $N$ concentration.

(3) $A_{\text{max}}$ and $N$ could not be adjusted one to another but be both regulated by one or several leaf parameters. In this case, $A_{\text{max}}$ and $N$ would be invariant when expressed relative to the appropriate leaf unit but would vary proportionally based on other units.

Hypotheses (1) and (2) may be put forward since they are backed by a number of observations concerning nitrogen distribution and use in plant leaves. In a leaf, the fraction of nitrogen used in photosynthesis is determined by the orientation of assimilates towards compounds required by photosynthesis. The latter are numerous and almost identical in all plant cells. Hence, structural N is associated with the protection of cell walls against biotic or non-biotic attacks, and cells contain various nitrogen solutes such as vegetative storage proteins (VSP), peptides, polyamines, alkaloids, etc. (Lambers and Poorter, 1992). On the other hand, up to 75% of leaf nitrogen may be associated with the functioning of the chloroplast. Nitrogen is constitutive of proteins (16 to 18% N in average) involved in CO$_2$ fixation and CO$_2$ acceptor replacement (Field and Mooney, 1986). Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the CO$_2$ fixing protein, represents more than 50% of the chloroplast soluble proteins (Evans, 1983, 1989a; Makino and Osmond, 1991). Nitrogen is also constitutive of pigments associated with the light-harvesting machinery (50 mol N mol$^{-1}$ chlorophyll), proteins of the electron transport chain and proteins of the Calvin–Benson cycle (Abadia et al., 1987; Nishio et al., 1985; Wong et al., 1985). Moreover, nitrogen is found in nucleic acids, the peroxisome and in mitochondria enzymes responsible for the renewal of products during photorespiration. At last, according to environmental conditions (incoming radiation), nitrogen may be allocated in priority to compounds involved in the light phases of photosynthesis (pigments, photosystems, etc.) or those concerned with the dark reactions (Rubisco, Calvin–Benson cycle proteins, etc.). Acclimatization to shade induces a lower nitrogen investment in light harvest (Evans, 1989a).

2.3.2. Several models

In a comparison of a plentiful number of plant species characteristic of natural ecosystems, Field and Mooney (1986) observed a tight linear relationship between $A_{\text{max}}$ and $N$ when both parameters were expressed per unit of leaf dry matter. This could indicate a general ‘law’. However, expressing data per unit leaf area, which is more satisfactory from a physiological viewpoint, may result in differences which are attributed to SLA variations between plants of different leaf $N$ status. Several models have been proposed so far to account for the $A_{\text{max}}$–$N$ relation (Table 6). For several species, this relation is not linear but hyperbolic. Hence, for these species, from low leaf $N$ onwards, $A_{\text{max}}$ increases rapidly with increasing $N$ but reaches a plateau where $N$ accumulation is no longer beneficial to photosynthesis. According to Evans (1989a), the curvature of the relationship does not reflect an inactivation in Rubisco at high leaf $N$
but could result either from (1) an underestimation of $A_{\text{max}}$ or (2) a decrease in CO$_2$ partial pressure in the leaf between the intercellular space and the site of carboxylation because of an increase in the resistance of cell walls to CO$_2$ transport. According to Sage and Pearcy (1987b), the loss of linearity in the $A_{\text{max}}$–N relation proceeds from the appearance of nitrogen storage compounds in the leaves (nitrate, asparagine, etc.).

The ratio $A_{\text{max}}/N$ is called the photosynthetic nitrogen use efficiency (PNUE). It removes the effects of fluctuating SLA and allows the comparison between species to be carried out. Several studies have shown that the efficiency of C$_4$ species is higher than that of C$_3$ species, which has been interpreted as the result of a better acclimatization to environments low in nitrogen (Brown, 1978; Sage and Pearcy, 1987a,b). However, the reduced rates of photorespiration in C$_4$ species gives also these plants higher $A_{\text{max}}$ values than C$_3$ plants. In this case, higher PNUE may also proceed from a better use of carbon. The difficulty of interpreting PNUE data comes from the fact that in a ratio, similar data may result from equal changes either in the numerator or the denominator. Within a similar photosynthetic type, however, changes in PNUE have been reported (Field and Mooney, 1986; Lambers and Poorter, 1992). These could reflect interspecific differences in Rubisco activity or nitrogen allocation towards the functioning of this enzyme (Evans, 1989a) as well as intra-specific differences in nitrogen allocation towards compounds not involved in photosynthesis or involved but not limiting photosynthesis.

Most horticultural crops being fast growing species, it is reasonable to assume that their leaf nitrogen is invested in priority towards photosynthetic compounds. Therefore, leaf nitrogen analysis is a potential tool for assessing the limiting or non-limiting nature of nitrogen in crop photosynthesis using the $A_{\text{max}}$–N relationship typical of the species. Moreover the calculation of the PNUE index indicates the closeness of nitrogen supply to the demand of the crop. Any supra-optimal nitrogen availability results in nitrogen accumulation in plant tissues and thereby decreases PNUE compared with pre-defined optimal value. This index could therefore be used as an indicator for nitrogen fertilization decision making. This index, however, should be considered with care since a PNUE increase is not necessarily beneficial to plants. For instance a PNUE increase has been observed in nitrogen-deprived rose plants (Bellert, 1995) together with a decrease in $A_{\text{max}}$. In this case, the decrease in leaf N concentration more than offset the decrease in $A_{\text{max}}$, thus yielding higher PNUE. This was interpreted as the result of a greater remobilization of non-photosynthetic nitrogen under nitrogen shortage, hence, rendering the remaining nitrogen more efficient for photosynthesis.

2.3.3. Nutrients and water fluxes

Stomata are a compulsory passageway for CO$_2$ and H$_2$O gas exchanges between the plant and the atmosphere. Therefore, in order to fix carbon, the plant looses water to the atmosphere, the ratio being variable depending on species and growing conditions. This ratio is called the “water use efficiency” (WUE), i.e., the quantity of water transpired per unit carbon fixed in the dry matter. Plants under conditions of low water availability and/or great water demand have low stomatal conductance and low leaf CO$_2$ partial pressure. Therefore, these plants have low WUE because the decrease in their rate of transpiration is larger than the decrease in CO$_2$ fixation. Under such circumstances, the
low $A_{\text{max}}$ values associated with normal leaf nitrogen concentrations, also give these plants low PNUE indices. The measurement of the isotopic ratio $^{13}\text{C}/^{12}\text{C}$ is an assessment of plant WUE. It has been introduced as a tool for geneticists in breeding programs to select plants with low water use efficiency (Evans and Farquhar, 1991). Similarly, Masle et al. (1992) suggested that plant breeders use plant mineral concentration as an alternative measurement, simpler and economically more viable than isotopic ratio determinations. Hence, these authors observed positive correlation between WUE and mineral concentration in the dry matter of several $C_3$ and $C_4$ species.

2.3.3.1. Is there a causal relationship between PNUE or mineral concentrations and WUE? Is mineral uptake, in particular nitrogen, controlled by plant water fluxes? In a study made on several herbaceous species, Lambers and Poorter (1992) were able to observe the doubling of PNUE index in plants of constant WUE. Similarly, Field and Mooney (1986) measured the same isotopic ratio $^{13}\text{C}/^{12}\text{C}$ in $C_3$ species of markedly different PNUE index. Therefore, in light of the present evidences, we may seriously doubt a causal and general relation between PNUE and WUE. Moreover, Barthes et al. (1995) observed for two wheat species widely different rates of mineral accumulation in the whole plant, and concluded that the measurement of mineral concentration in the tissues could not be proposed as an alternative measurement to the $\delta^{13}\text{C}$ (isotopic ratio normalized against an absolute reference) and thereby to WUE. At last, Tanner and Beevers (1990) found that two lots of maize plants grown in controlled cabinets under two contrasting regimes of relative humidity (RH = 60 or $>$ 95%) had on the one hand a WUE differing by a factor 3.3 and on the other hand, a same dry matter yield production and a similar plant mineral content at the end of the crop cycle.

The questions addressed above are fundamental in horticulture. For instance, in the practice of soilless culture, the frequency of delivery of nutrient solution doses to the crop is determined almost solely by plant water demand estimated from incoming solar radiation. Underlying in this practice is the hypothesis that the requirements for water and for minerals are always intimately correlated. The experiments made over long periods of time (weeks, months) generally support such an hypothesis (Brun and Blanc, 1987; Schacht and Schenk, 1990; Bar-tal et al., 1994) and have led agronomists to empirical determinations of recipes for ideal ion mixtures adapted to plant growth stages. On the contrary, experiments made over short periods of time (hour, day/night cycle) demonstrate clearly that the ratio of water to nutrients taken up by the plants vary widely with time of the day (Triboõ-Blondel, 1979; Le Bot, 1991; Ferrario et al., 1992; Le Bot and Kirkby, 1992; Andriolo, 1995; Brun et al., 1997). Moreover, during summer, and in particular under Mediterranean conditions, growers observe frequently a sharp and rapid increase in the nutrient solution salinity, potentially at risks for both the plants and the environment. This happens because during such periods of time, plant water demand increases more than mineral requirement.

All these evidences support the idea that the transpiration flux is not essential to ion uptake and transport in plants, and therefore in plant nutrient uptake modelling it is necessary to dissociate mineral fluxes from water fluxes. A model of ion uptake simply based on plant transpiration flux has no scientific grounds, neither does the calculation or use of ‘uptake concentrations’ (i.e., the ratio of ions to water taken up over time). In
spite of these statements, the actual practice of fertilization of soilless cultures grown under greenhouses with drainage-to-waste bases the supply of nutrients on plant water demand models (de Villèle, 1972). This modelling of nutrient supplies is successfully operative in most commercial greenhouses yet it has extremely poor predictive properties as proven by (1) the occurrence of the drifts in nutrient solution salinity requiring heavy washing of the rockwool slabs with diluted nutrient solution and (2) the poor coefficients of fertilizer use (i.e. the ratio of fertilizer taken up by the plants to that applied in the slabs), especially for nitrate (van Noordwijk, 1990), which are of serious environmental concern, especially in intensive areas of greenhouse production. These conclusions, however, should not hide the fact that in soil, the transpiration flux is the driving force for the transport of most mineral ions from the soil layers to the roots, and therefore, it is essential for modelling nutrient availability at the soil/root interface.

3. Ultimate functions

3.1. Nutrient uptake and functional equilibrium

Plant nutrient uptake rate is computed as the product of net uptake rate per root unit (Section 2.1.) by the size of the root system. The latter, usually characterized by the RSR (root:shoot ratio) or RWR (root:whole plant weight ratio), varies greatly between species, edaphic conditions and with plant age. For instance, Lainé et al. (1993) found a negative relationship between nitrate uptake capacity per root unit and RSR (from 0.1 to 1) in ten catch crop species grown under non-limiting constant nutrition. However, when we computed their data to express them per total plant fresh weight, uptake capacity was roughly the same for all these species, showing that a similar absorption rate can be achieved by various plant strategies. Similarly, it is commonly observed that most plants increase the size of their root system when water or nutrients particularly nitrate and phosphate are limiting, or decrease it under low light conditions. However, under non-uniform nutrient supplies, root growth is usually stimulated in the well-fed zone, while it can be depleted in the restricted zone (for review, see Habib et al., 1991; Robinson, 1994). From the nutritional viewpoint, the importance of these strategies depends upon if the root medium is homogeneous (e.g. hydroponics) or heterogeneous (e.g. natural soil). From a carbon utilization viewpoint, high RSR differences are necessarily important since roots represent from 1 (see Table 1 in the work of Marcelis and De Koning, 1995) to 50% (Lainé et al., 1993) of plant dry weight.

Mechanisms involved in RSR elaboration are unclear (for review of opinions, see the special issue of Plant and Soil, 185, 1996). They include specific root growth regulation by plant hormones (cytokinins and abscisic acid) or sucrose, and non-specific determination by the so-called functional equilibrium (Brouwer, 1962; see also Marcelis et al., this issue). In the latter, RSR may be seen as an emergent property, resulting from the balance between root and shoot growth necessary to acquire the limiting resources, nutrients and carbon, respectively. To achieve such models, it is necessary to formalize dry mass production under nutrient limitation, nutrient uptake under carbon limitation, and rules of carbon and nutrient exchanges between roots and shoots.
It is beyond the scope of this review to develop all these aspects but it should be stressed that existing models lay on unregulated root uptake activity. The latter is either expressed as only proportional to the size of the root system (Cheeseman, 1993; Reynolds and Chen, 1996), or following the Michaelis–Menten kinetics of Epstein and Hagen (Lim et al., 1990). Although such models do predict the right tendency of RSR variations, such oversimplified assumptions should result in exaggerated changes, as the only way to increase nutrient uptake rate is to increase the size of the root system. A more realistic approach requires the use of nutrient uptake feedback regulation (Section 2.2.), which implies, therefore, the modelling of nutrient accumulation and assimilation rates (Buysse et al., 1996). This should result in more realistic effects of nutrient limitation, i.e. increase of both RSR and SAR (specific absorption rate). Furthermore, more research is required on transport of resources between compartments. It is viewed as a purely diffusive process where flux is along a concentration gradient affected by a resistance parameter (Thornley, 1972, 1995), an active process following a Michaelis–Menten relationship whose substrate is the concentration in the source compartment (Cheeseman, 1993), or the much-controversial xylemic water transport process where flux is determined by transpiration (for review, see Tanner and Beevers, 1990). Choosing between these possibilities is uneasy, as nitrate concentration in the shoots of several species has been reported to be higher than, equal to or lower than that of roots (Laine et al., 1993). This might explain why less mechanistic approaches may be preferred. These include a simple partition coefficient where a constant proportion of the mineral is allocated to roots and shoots (Siddiqi and Glass, 1986), or sophisticated models of source–sink relationships, where flow between compartments is governed by the size of the source and growth rate of the sink (Ran et al., 1994).

3.2. Growth control by nutrients

The general idea that nutrient availability in the root medium determines plant growth arises from the general concepts of the limiting factor (von Liebig, 1841). An original use of this concept has been developed since the seventies by Ingestad and Cottorkers (for review, see Ingestad and Ågren, 1992): their technique consists in supplying nitrogen at constant relative addition rates (RAR) to hydro- or aeroponically grown plants. As long as nitrogen remains limiting, they show that the plant relative growth rate (RGR) equals RAR, and that whole-plant nitrogen concentration is nearly constant. On this ground, Ingestad introduced the term of ‘steady-state nutrition’. This technique has been used on a large number of plants and was shown to hold also for phosphorus (Ericsson and Ingestad, 1988), and is probably generalizable to other macronutrients.

On the one hand, there is no doubt that this technique is a valuable tool to monitor growth under controlled conditions. On the other hand, theoretical considerations have been derived to interpret the relationship between plant nutrient content and RGR (Ågren, 1985, 1988). Whether these have sound physiological background or not is under debate (for opinions, see Macduff et al., 1993; Burns, 1994; Wikström and Ågren, 1995; Hellgren and Ingestad, 1996; Burns, 1997) and their use for diagnostic procedure for crop nutrient management (Burns, 1997) or for modelling nutrient uptake by horticultural crops (Willits et al., 1992) are far from being straightforward. Hence, the
parameters of the relationship linking plant nutrient content to RGR are not unique, but vary according to plant species (Ågren, 1988), plant age and environmental conditions (Willits et al., 1992).

3.3. Growth demand of nutrients

3.3.1. Statistic approach

Minerals are taken up by the roots (and eventually assimilated) in order to fulfil plant growth requirements. For nitrogen, phosphorus and potassium it has been demonstrated at all times of the vegetative crop cycle, that a critical concentration is required in plant tissues to sustain 90% of the maximum growth rate potentially obtained by the amount of radiation intercepted by the crop (Ulrich, 1952; Burns, 1990). Below the critical concentration, growth is impaired. On the contrary, if nutrient availability is excessive, nutrients accumulate in the plant without concomitant increase in dry biomass. The implicit relationship between nutrient uptake and dry matter accumulation (= growth) during the vegetative development of a crop is particularly well expressed for nitrogen in the 'law' of progressive decline of %N (g total N 100 g dry matter) during crop growth (Lemaire and Salette, 1984; Justes et al., 1994):

\[
%N = a \times DM^{-b}
\]

where: DM (tonnes ha\(^{-1}\)) is the total dry aerial biomass, %N is the critical nitrogen concentration, coefficient \(a\) represents the nitrogen concentration in the dry biomass at the end of the exponential growth period, and \(b\) is a statistical parameter governing the slope of the relation.

This relation implies an allometry between nitrogen uptake by the crop (\(N\), kg ha\(^{-1}\)) and the dry matter biomass accumulation:

\[
N = (10 \times a) \times DM^{1-b}
\]

where: \((1 - b)\) is the ratio between the relative rates of N uptake and dry matter accumulation (allometric parameter) and \((10 \times a)\) is the amount of nitrogen (kg) taken up by 1 ha of the crop at the end of the exponential growth (i.e. about 1 tonne DM ha\(^{-1}\) for most crops).

The practical interest of such a relationship comes from the prediction of the minimum nitrogen fertilization required by the crop to produce a targeted dry matter yield. Greenwood et al. (1990) have established that critical N concentration of a great number of plant species fit one out of two possible relationships providing that they belong either to the C\(_3\) or C\(_4\) type of photosynthesis. Many authors agree on the idea that the parameter \(b\) is identical for C\(_3\) and C\(_4\) species while \(a\) is specific for the type of photosynthesis. Various estimates of the parameters have already been published in the literature but the later review on the subject (Lemaire and Gastal, 1997) proposes the following average relations:

for C\(_3\) species: %N = 4.8 \times DM^{-0.34}
for C\(_4\) species: %N = 3.6 \times DM^{-0.34}
These findings may be interpreted as an indication that under non-limiting nitrogen supplies, C_4 species are 25% more efficient than C_3 species in accumulating the same amount of dry matter with a same quantity of nitrogen taken up. This better nitrogen use efficiency determined at the large time scale supports the findings of higher PNUE index of C_4 species measured over short time scales, as already discussed in Section 2.3. However, the argumentation developed earlier of a higher carbon use in C_4 species because of low photorespiration also leads to the same conclusions. The finding of a unique parameter \( \alpha \) between C_3 and C_4 species grown on 1 ha of land suggests that nitrogen use is identical in all plants, irrespective of their carbon metabolism, and is essentially determined by light interception.

The general relationship of progressive decline in %N in the dry biomass of plants has been verified for a large set of crop species which confers this relation the status of 'law', at least for non-ligneous plants free of storage organs. A more detailed analysis of the literature can be found in the work of Justes et al. (1994) and Lemaire and Gastal (1997). For horticultural crops, to our knowledge, only tomato has been evaluated. For this species, the progressive decline in %N has been shown to hold both for vegetative and fruiting plants (Andriolo, 1995; Le Bot et al., 1997a; Bellert et al., 1997), although for the time being, a precise relationship using critical nitrogen values has not yet been established. However, under non-limiting nitrogen supply, Andriolo (1995) determined the following relation: %N = 5.77 × DM^{−0.33}. For this particular species, it is interesting to note that the concept of progressive decline in %N values, which was first developed over the vegetative growth of field crops having a closed canopy structure, also holds for the entire cycle of a row crop with indeterminate growth.

3.3.2. Mechanistic approach

Two mechanistic models explain the progressive decline of %N in the dry biomass in terms of plant compartmentalization. For Caloin and Yu (1984) plant nitrogen content varies during growth according to the proportion of two conceptual compartments in the plant. The first compartment is physiologically active for growth; its dry mass \( M_1 \) is related to the rate of total dry mass increase \((\partial M / \partial t)\) by the following relation:

\[
\frac{\partial M}{\partial t} = \text{RGR}_{\text{max}} \times M_1
\]

\( \text{RGR}_{\text{max}} \) being measured during the exponential growth phase. Along growth, the proportion of \( M_1 \) in plant is:

\[
p_1 = \frac{M_1}{M} = \frac{1}{\text{RGR}_{\text{max}}} \times \frac{1}{M} \times \frac{\partial M}{\partial t} = \frac{\text{RGR}}{\text{RGR}_{\text{max}}}
\]

The second compartment has a mass \( (M_2 = M - M_1) \). It is involved in the other metabolic activities of the plant, including structures and storage. Caloin and Yu (1984) propose to give both compartments \( (M_1 \text{ and } M_2) \) different nitrogen concentrations although constant over time, i.e. \( n_1 \) and \( n_2 \) (g N 100 g^{-1} DM). At any time \( t \) of the crop growth, total plant nitrogen content \((N)\) may be calculated from the size of the two compartments:

\[
N(t) = n_1 \times M_1(t) + n_2 \times M_2(t)
\]
therefore, total nitrogen concentration ($n$) is:
\[
n(t) = \frac{N(t)}{M(t)} = n_1 \times p_1 + n_2 \times (1 - p_1) = n_1 \times RGR + n_2 \times \left(1 - \frac{RGR}{RGR_{\text{max}}}\right)
\]
that is,
\[
n(t) = \left(\frac{n_1 - n_2}{RGR_{\text{max}}}\right) \times RGR + n_2 = a \times RGR + b
\]

In contrast to other approaches (see Section 3.2.), in this model the relative growth rate is not a forcing variable for nitrogen uptake but its measurement gives a good determination of the sizes of the two compartments. From practical viewpoints, the linear relationship between RGR and plant nitrogen concentration has been verified in the case of several cultivated species. However, a generalization of the model parameters has not been established yet, which appears as a limitation compared with the statistical approach developed above (Section 3.3.1.).

A second model (Hardwick, 1987) has been developed from studies on woody plants. It assumes that plants are composed of an external ‘skin’ of energetically active tissues covering a three dimensional inner ‘core’ which does not engage in energy exchange. In a closed canopy structure, the mass of skin ($K$) is proportional to the area of light interception; it is therefore proportional to the square of plant’s length ($l$).

Moreover, the mass of the whole plant ($W$) is proportional to the volume of the plant, i.e. the cube of plant’s length:
\[
K = c \times l^2 \quad W = d \times l^3
\]
where $c$ and $d$ are constants of proportionality. Replacing $l$ in the first equation results in the following expression:
\[
K \propto W^{\frac{2}{3}}
\]

Some evidence supports the idea that the amount of skin is proportional to plant nitrogen content (Sylvester-Bradley et al., 1990; Le Bot et al., 1997b). In this case, for a young plant in which the mass of core is negligible, increase in the amount of skin is mirrored by a similar increase in plant nitrogen content ($N$):
\[
\frac{\partial N}{\partial W} = 1 \text{ that is, } N \propto W
\]

For an adult plant, however, the core becomes predominant. Therefore, the total plant mass is a good estimate of the mass of core, which implies that:
\[
\frac{\partial N}{\partial W} = \frac{2}{3} \text{ that is, } N \propto W^{0.66}
\]

According to Hardwick (1987), for a given species, there is a curvilinear relationship between the nitrogen content of a plant and its total biomass, the slope of the curve
varying between 1 and 0.66. Hardwick proposes the following mathematical formula to fit the relationship:

\[ y = p + (q \times x) + (r \times e^{-x}) \]

where: \( y \) = log (nitrogen mass per plant), \( x \) = log (total plant biomass), \( r, p \) and \( q \) are constants determined by the initial plant biomass and allometric parameters relating length to surface and volume plant dimensions. Rewriting this equation leads to:

\[ N = k \times e^{W^q} \times W^q \]

Therefore, when \( W \to \infty \), as is the case in an adult plant, this expression yields the same formula expressed by Lemaire and Salette (1984) and already developed above:

\[ N = k \times W^q \]

In conclusion, both models of Caloin and Yu (1984) and Hardwick (1987) explicate dynamically the reasons for the progressive decline of %N in the dry matter from the existence of two compartments having different physiological functions and biochemical compositions. In both models, however, the two compartments are virtual and remain to be studied further. Hardwick associates the skin with the tissues responsible for the ‘process of life’, which include the foliage, responsible for energy income, but also the fractions of roots, responsible for ion uptake, while the core is associated with tissues comprising cellulose, starch and lignin which do not require maintenance ‘costs’. In the model of Caloin and Yu, compartment \( M_1 \) presumably comprises foliage and root fractions while compartment \( M_2 \) should be composed of the structures holding the foliage in position and storage tissues. It is only if plant compartmentalization is associated with a more precise anatomical description of the appropriate tissues that a validation will be possible. More work is therefore required on that subject, although a first attempt to fit the model of Caloin and Yu to ageing tomato plants, led Bellert et al. (1997) to separate the foliage rich in nitrogen (4 g N 100 g DM) from the stems, petioles and fruits low in nitrogen (1.8 g N 100 g DM).

4. Operational approach of nutrition

4.1. Diagnostic of nutritional status

The appraisal of substrate fertility and the assessment of plant mineral requirements are fundamental for crop fertilization management. In practice, the cultural system should be optimized in accordance with expectations on yield, crop quality (of harvested or transformed organs) or environmental concerns (residues in the soil for instance). The estimation of nutrient availability for plant growth is generally achieved through soil (substrate) testing, which is more or less convenient depending on the agrosystem, or through plant or sap analysis. For soilless cultures, technology is providing on-line sensors (pH, electrical conductivity EC) to monitor ion concentrations, which make possible the short-term management of nutrition (see Section 4.2.). In orchards, the measurement of minute changes in stem diameter can be used to manage irrigation.
Whole-plant testing is also widely used because it gives a direct measurement of the actual quantities of nutrients taken up by the crop. When testing is not possible on the entire plant, analysis of individual organs (leaf, petiole, etc.) is often taken as a substitute. In such cases, the mineral concentration measured in plant tissue is compared to that of 'reference' material obtained from plants grown under non-limiting nutrient supply. The increasingly widespread use of leaf analysis since the fifties has resulted in exhaustive compilations of 'normal, deficient or toxic' nutrient concentrations in plants (Chapman, 1966; Martin-Prével et al., 1984). Following this approach, it seems that each tested plant has its own nutrient deficiency concentrations which may appear irrational considering the similitude in metabolism between different species. However, it is evident from the modelling approaches developed in Sections 3.2. and 3.3. that a sensible interpretation of analytical data for diagnostic purposes requires knowledge of the plants' critical nutrient concentrations over the whole growing cycle. For example, the diagnostic of nitrogen nutrition is an immediate and practical output of the critical N concentration model (see Section 3.3.). Hence, during plant growth, nitrogen concentration in the plant tissues may be compared to the critical nitrogen concentration thus allowing calculation of a nitrogen nutrition index (NNI):

\[
\text{NNI} = \frac{\%N}{\%N_{\text{critical}}}
\]

As long as NNI is greater than 1, crop growth is not limited by nitrogen availability in the root environment. When NNI is lower than 1, the rate at which the crop grows is limited by nitrogen uptake. Hence, increasing nitrogen availability in the root environment may increase the crop growth rate. In this case, NNI may be used as a decision-making indicator to provide the crop with an extra dressing of nitrogen fertilizer. This approach also provides an ubiquitous rationale for diagnostic that may probably be extended to minerals other than nitrogen. Hence, phosphorus and sulphur, which are also taken up as anions (\(\text{H}_4\text{PO}_4^-\) and \(\text{SO}_4^{2-}\)) and undergo a step of reduction in plants, should obey similar 'laws' of progressive decline in critical concentrations in the dry biomass. Moreover, due to similarities in their metabolisms, we may speculate that the parameters of the progressive decline of \%P and \%S should be similar to that of nitrogen. For cations, it is probable that potassium, which is the largest counterbalancing ion for nitrate uptake, also follows similar pattern. Calcium and magnesium, however, are likely to require different modelling approach due to the importance of plant cation exchange capacity (CEC) and water fluxes in uptake and transport of these two divalent cations.

4.2. Managing the cultural system: the greenhouse as an example

The actual development of protected cultural systems is characterized by an increase in soilless techniques and the automatic monitoring of climate and fertilization. Such systems are costly in respect to hand-power and energy inputs. Optimizing these high-tech systems requires the use of models describing fluxes of mass and energy in the plant in harmony with those described for the environment (Baille, 1997; Gary and Baille, 1997). In terms of fertilization, the widespread use of on-line programmable
fertilizer injectors gives growers an opportunity to apply the current scientific knowl-
edge to greenhouse crop 'fertigation', for instance the uncoupling between water and
nutrient supplies. The analysis of current practices reveals a dual approach for control-
ling plant nutrition, i.e. inductive or deductive regulations.

1) In open (run-through) or closed types of soilless cultures, the actual practice of
fertigation consists in providing the crop with doses of nutrient solution at pre-set pH
and electrical conductivity values (EC$_r$). As long as water and nutrients are taken up at
the same rates, EC in the drainage (EC$_{\text{meas}}$) remains close to a reference value (EC$_{\text{ref}}$).

In case of drifts, the nutrient solution concentration can be altered based on the
difference between the reference and measured EC in the drainage. Therefore at any
time (t), EC may be determined from the previous EC of the nutrient solution supplied
at (t - 1):

$$EC_t = EC_{t-1} \times \left(1 + \frac{EC_{\text{dr}} - EC_{\text{meas}}}{EC_{\text{ref}}^{\text{dr}}}ight)$$

However, EC measurement is partially relevant to the system since it provides only
limited control of fertigation. Indeed, it is an indiscriminate indicator of the overall
concentration of fertilizers in solution while the appropriate blending of several mixtures
of fertilizers requires a precise adjustment of individual ion concentration. Therefore, the
inductive (a posteriori) regulation exhibits two main limitations: (1) the absence of
specific sensors reliable in greenhouse conditions, and (2) the time-lag of the horticul-
tural systems (2–5 days for fertigation in rockwool slabs) is incompatible with the
hourly control of nutrient feed targeted by the regulator. In our view, the success of this
type of regulation is linked to a straight forward technological breakthrough in the
construction of reliable ion specific sensors, in particular for nitrate measurements in
drainage. Also required are changes in the root system environment. It will be necessary
to find a compromise between the current inertia of the system which is stable and
secure, and the regulation time-lag requirements on which depend the optimization of
the system.

2) The deductive (a priori) regulation is potentially ideal to optimize the control of
greenhouse crop mineral nutrition. It is based on the knowledge of plant responses to
varying its environment. Plant water supply based on calculation of potential evapotran-
spiration (ET$_p$) belongs to this type of approach. It allows the precise short-term
prediction of plant water demand based on the measurement of current environmental
parameters. For tomato plants growing under the greenhouse, de Villèle (1972) proposed
to estimate ET$_p$ from the measurement of global radiation and parameters typical of the
greenhouse and the crop growth stage. Using this approach in plant fertilization should
offer two main advantages: (1) the quality of the regulation is independent of the inertia
of the system and no compromise is required between security and efficiency; (2) the
needed climatic sensors already exist in most greenhouses since they provide inputs for
climate regulation. It is therefore possible to make use of the actual systems without any
more technological inputs. The success of this approach, however, is linked to the
prerequisite knowledge of the relevant parameters; thus, modelling plant response to
fluctuating environment is essential. For the time being, no knowledge-based plant
Table 7
Examples of deductive models used to control water or nitrogen supply to greenhouse crops

<table>
<thead>
<tr>
<th>Mathematical formulation</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\text{ET}_s = 0.67 \times R_g - 0.2$</td>
<td>de Villele (1972)</td>
</tr>
<tr>
<td>$N_f = N_i \times \left[ x_1 \frac{\text{SLI}_C - \text{SLI}_A}{\text{SLI}_A} + x_2 \frac{\text{DLI}_C - \text{DLI}_A}{\text{DLI}_A} + x_3 \frac{\text{DRH}_C - \text{DRH}_A}{\text{DRH}_A} + x_4 \frac{\text{DT}_C - \text{DT}_A}{\text{DT}_A} + \ldots + \text{CD} \right]$</td>
<td>Papadopoulos and Liburdi (1989)</td>
</tr>
<tr>
<td>$N_e = 0.796 \times 10^{-3} \times R_g \times \left( \frac{R_{\text{ET},s}}{R_{\text{ET},s}} \right) + 1.435 \times 10^{-2} \times T_{\text{nut}}$</td>
<td>Brun and Chazelle (1996)</td>
</tr>
</tbody>
</table>

Abbreviations: $\text{ET}_s$, potential evapotranspiration; $R_g$, total incident radiation; $N_f$ and $N_i$, final and initial nitrogen concentration in solution; $\text{SLI}_C$ and $\text{SLI}_A$, current and average seasonal light integrals; $\text{DLI}_C$ and $\text{DLI}_A$, current and average daily light integrals; $\text{DRH}_C$ and $\text{DRH}_A$, current and average daily relative humidity; $\text{DT}_C$ and $\text{DT}_A$, current and average daily air temperature; CD, overall growers rating of crop demand for Nitrogen; $x_i$, scalars; $N_e$, NO$_3$ uptake rate (mg N plant$^{-1}$ h$^{-1}$); $T_{\text{nut}}$, temperature of nutrient solution.
model is operational to optimize the practice of mineral nutrition. Nevertheless, research among these lines is active and most relevant parameters controlling ion uptake are known. Current deductive regulation of ion concentration in solution is simply based on statistical models (Table 7). For instance, Papadopoulos and Liburdi (1989) use numerous parameters influential for nutrient requirement (i.e. light, RH, fruit load, crop age, etc.) to adjust the base values of nutrient feed for tomatoes. Hence, for nitrogen as an example, the final concentration \( [N_f] \) in solution equals the initial value before adjustment \( [N_i] \) corrected by the difference between current (index C) and average (index A) values of seasonal light integral [SLI], daily light integral [DLI], daily relative humidity [DRH] and daily air temperature [DT]. The influence of each component is set by scalars \( [x_i] \) to \( [x_A] \) (%) and an overall grower’s rating of crop demand for nitrogen \( [CD] \). Another illustration is given by the work of Brun and Chazelle (1996) on roses. They described the kinetic of nitrate uptake \( [N_t] \) (mg N plant\(^{-1}\) h\(^{-1}\)) with a multiple regression using agroclimatic factors, i.e. global radiation \( [R_g, W m^{-2}] \), global radiation of the previous day \( [R_{g,i}] \), the expected global radiation of the day \( [R_{g,d}] \) and the temperature of the nutrient solution \( [T_{ew}] \). This relation was strong enough to fit successfully \( (r^2 = 0.71) \) hourly uptake rate data obtained under greenhouse conditions over a period of 5 consecutive days.

To summarize, the inductive regulation is set on a purely technological breakthrough and is rapidly operational while the deductive regulation depends on knowledge and requires models. The use of the former in mineral nutrition implicates that the agrosystem undergoes normal climatic fluctuations and that action takes place only after an alteration of the system has occurred. In other words, the regulator is set to ‘repair’ accidents. The application of the latter regulation, should prevent the occurrence of alteration in the agrosystem. Moreover, the use of climatic parameters to control plant nutrition should lead to a more integrated greenhouse management, in harmony with the regulation of water and carbon fluxes at the crop level. Since all physiological plant functions obey the same stimuli, a global model appears essential to understand truly the interactions and optimize the functioning of the greenhouse.

5. Conclusions

For the purpose of this review, we segregated nutrient uptake into proximate and ultimate functions. This was a mean to classify the concepts according to their spatio-temporal level of approach, as needed for modelling. Another prerequisite is knowledge of the agricultural system. For instance, in the present understanding of plant physiology, the role of water fluxes through plants is negligible for uptake of most nutrients. However, depending on the agrosystem, the flux of nutrients from the bulk substrate to root surface may be limited by water fluxes, i.e. plant transpiration. Therefore, in field conditions, diffusion barriers may overrule uptake kinetics, while in hydroponics, the solution stirring or circulation ensures nutrient availability at the root surface, and transpiration is clearly uncoupled from nutrient uptake. What is more, in intensive horticultural agrosystems, the technology allows, up to a certain extent, the monitoring of plant nutrition without reference to physiological knowledge. In this case,
models are concerned with optimizing the physical system itself (i.e. faster response time, sensors, etc.) rather than understanding plant functioning. This latter approach should not be neglected as it is probably the nearest to implementation.

Among proximate functions, most studies have been based on the concept of ion transporters and their response to low ion concentrations, which seriously limits their use in horticultural crop models dealing with a rich ionic environment. These studies generally do not take plant demand into account, and therefore, are unable to provide the necessary feedback regulation of uptake. As a consequence, they cannot make the link with environmental conditions (irradiance, CO₂ enrichment, etc.), nor predict nutrient accumulation, which is a weakness for diagnostic purposes and quality prediction. Furthermore, realistic estimations of respiratory costs of ion uptake, required by carbon models, will not be made without a better understanding of uptake mechanisms and regulation. Similarly, we may highlight the lack of models of nutrient transport and partitioning in tissues, which are required to understand the efficiency of their use for growth and RSR equilibrium.

Though plentiful, the literature on plant nutrition rarely serves modellers in the development of general concepts applicable to agronomic conditions. For instance, under different experimental conditions, i.e., steady-state vs. constant nutrition, the same formula relates nitrogen concentration in whole plant tissue to relative growth rate:

\[ n(t) = a \times RGR + b \]

The parameters of the relation, however, have different values and are interpreted in a distinct way according to the context: in terms of nutrient productivity (Ågren, 1985, 1988) or plant compartmentalisation (Caloin and Yu, 1984). The former concept explains growth by the plant nutrient content, while in the latter, the nutrient content is a result of growth. This underlines the weakness of these theories in formulating functionally the interaction between growth and nutrients. Nevertheless, the steady-state approach shows that at large-time scales, the amount of nutrients added to the medium is more determinant than their concentration, for growth. It thus turns out that a definition of plant demand is the relevant ultimate function for modellers. Mankin and Fynn (1996) proposed a general formulation of the demand approach:

\[ U_n = D_n \pm X_n \]

where \( U_n \) and \( D_n \) are the actual uptake and plant demand, respectively, while \( X_n \) is luxury consumption when positive, and storage mobilisation when negative. Plant demand, computed from growth rate and a critical nutrient concentration, may be seen as the basis for fertilisation policy. Interestingly, critical concentration has been shown to depend strongly on canopy structure in relation to light interception, and on photosynthetic metabolism, more than on other species-dependent characteristics (Hardwick, 1987; Lemaire and Gastal, 1997). It should thus be emphasized that plant nutrition borrows the concepts used in carbon models. However, in the present nutrition studies, growth is seen as a mere dry weight increase. We may speculate that further improvements could arise from the use of recent growth models, which introduced the concepts of structural and non-structural dry matter.
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