A theoretical explanation of the Piper–Steenbjerg effect

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ABSTRACT

The relation between plant yield and plant nutrient concentration is sometimes found to be negative, a phenomenon called the Piper–Steenbjerg (PS) effect. A model was used to examine the underlying causes of the PS effect, and the conditions under which it is most likely to occur. The model uses the nutrient productivity concept for plant growth and a nutrient uptake equation in which root growth rate and external nutrient concentration determine the uptake rate. The study suggests that the PS effect occurs when the fast growth of plants grown in an initially higher nutrient medium eventually leads to a more rapid depletion of external nutrients than the slow growth of plants grown in an initially lower nutrient medium. The fast growth of plants combined with a rapid decrease of nutrient uptake leads to a fall in plant nutrient concentration. When these large plants with very low nutrient concentrations are compared with the smaller, slow-growing plants, a PS effect may be found depending on the time at which the plants are harvested, and on the range of initial values of the external nutrient content. When it occurs, the effect is greatest when the depletion volume per unit new root (Vd) is lowest, and when the mobility of nutrients in the medium is highest (α=1). The results are sufficiently general to apply to a variety of nutrients, plant species and growth media.

Key-words: growth; model; nutrient productivity; Piper–Steenbjerg; uptake.

INTRODUCTION

In search of the relationship between agricultural yield and fertilization, Piper (1942) and later Steenbjerg (1951) grew plants with different amounts of fertilizer (Cu). They expected to find a positive correlation between plant nutrient concentration and the amount of fertilizer applied, but found no such correlation. The yield increased in response to more fertilizer, but the plant nutrient concentration varied in both directions, as shown in Fig. 1. At the bottom left of the figure, increasing yield corresponds to decreasing plant nutrient concentration. The phenomenon has been observed in laboratory as well as in field experiments and for several nutrients and plant species (see reviews by Bates 1971 and Loneragan 1978) and continues to be reported (e.g. Maier, Dahlenburg & Twigden 1992). The negative relation between yield and plant nutrient concentration was later named the ‘Piper–Steenbjerg effect’ (Rosell & Ulrich 1964), and has caused considerable confusion.

The most frequent explanation of the Piper–Steenbjerg effect has been that the nutrient concentration in plant tissue changes with age. For example, old leaves might have a high nutrient concentration while the whole plant has a severe deficiency of the same nutrient. The Piper–Steenbjerg effect might then disappear if tissues of the same physiological age were compared instead of whole plants (Bates 1971; Spencer & Chan 1981). However, Rosell & Ulrich (1964) found a Piper–Steenbjerg effect in plants deficient in zinc despite a well-defined sampling of tissues. Today, the most common explanation seems to be the somewhat vague ‘nutrient dilution brought about by the higher production of plant material’ (Mengel & Kirkby 1987). Another possible explanation is that the nutrient element studied is not the one limiting growth; in experiments with micronutrients, for example, the internal micronutrient concentration that limits growth is extremely low (Göransson 1993a,b).

The purpose of Piper’s and Steenbjerg’s investigations was to relate yield to the nutrient status of the plant. However, yield and plant nutrient concentration are not directly related. The yield is a monotonically increasing function of time, but the nutrient concentration can change both upwards and downwards so that the relationship varies during the lifespan of a plant.

The objective of this paper is to demonstrate that the Piper–Steenbjerg effect can arise as a result of dynamic changes of plant nutrient concentration. In order to show this, I will use a simple model based on one equation for plant growth and one for nutrient uptake.

THE MODEL

Plant growth

Using a steady-state growth technique, a linear relationship between relative growth rate and plant nitrogen concentration was established when nitrogen was the growth-limiting
nutrient (Ingestad & Lund 1986). This relationship has subsequently been validated for a large range of nutrients in a number of plant species (e.g. Ericsson & Ingestad 1988; Oscarson, Ingemarsson & Larsson 1989a; Goransson 1993a,b). From these experiments, a theory for the relation between growth and plant nutrient concentration has been developed, with the 'nutrient productivity' as a key concept (Agren 1985, 1988; Ingestad & Agren 1988, 1992). For simplicity, I will use nitrogen as a model element, but the results are equally valid for other nutrients.

The nitrogen productivity $P_N$ (d$^{-1}$) is defined as the amount of plant dry mass produced per unit plant nitrogen and time. The relationship between the growth rate of plant mass, $W$ (g), and the amount of nitrogen in the plant, $N$ (g) (when nitrogen is the growth-limiting nutrient), is then formulated as

$$\frac{dW}{dt} = P_N (N - c_{N,\text{min}} W), \quad (1)$$

where $c_{N,\text{min}}$ is the minimum nitrogen concentration (mass of nitrogen per unit dry mass of tissue) required for growth. The relationship can also be expressed as relative growth rate, $R_g$, versus plant nitrogen concentration, by dividing Eqn 1 by $W$:

$$R_g = \frac{1}{W} \frac{dW}{dt} = P_N \left( \frac{N}{W} - c_{N,\text{min}} \right). \quad (2)$$

There is an upper plant nitrogen concentration, $c_{N,\text{opt}}$, above which no further growth increase is obtained. The relative growth rate is then constant ($= R_{g,\text{max}}$, the maximum relative growth rate) up to toxic concentrations (Fig. 2).

**Nutrient uptake**

Many models indicate that root elongation, or root growth rate, and the solution concentration of nutrients are the two most important factors determining nutrient uptake (cf. Clarkson 1985). The idea that root growth rate is an important determinant of nutrient uptake is supported by the results of Jensén & Pettersson (1980), who found that root tips had much higher nutrient uptake rates than other parts of the root system. In contrast, Chung & Kramer (1975) stressed that most uptake is associated with older roots because root tips are only a small fraction of the total root biomass.

I assume that root elongation and external nitrogen concentration are the two most important parameters, setting the nitrogen uptake rate ($dN/dt$) proportional to root growth rate ($dW/dt$) and to the nitrogen concentration ($N/V$) in the vicinity of the roots, or

$$\frac{dN}{dr} = \frac{dW}{dt} \frac{N}{V}, \quad (3)$$

where $V$ is the volume of the growth medium that is depleted of nitrogen by 1 g of new root, and $N$ (g) is the initial nitrogen content of the growth medium, the volume of which is $V$ (m$^3$). [The term $V$ has strong similarities with the root absorbing power formulated by Nye (1966), although it is not identical to it. The root absorbing power is the ratio between the nutrient flux into the root and the nutrient concentration at the root surface in an idealized uptake situation, whereas $V$ also includes nutrient movement to the root surface in the vicinity of the root.]

The uptake rate is also affected by the mobility of nitrogen in the growth medium. If there is low mobility, as in soil, a root growing into an undepleted volume, $V$, is not affected by any previous depletion of surrounding volumes. The root tips experience about the same local nitrogen concentration until the entire volume of the growth medium has been explored, after which the external nitrogen concentration seen by new roots falls rapidly. If the
mobility of nitrogen is high, as in a well-stirred aqueous solution, the amount of nitrogen remaining after uptake is mixed through the whole growth volume and the root tips experience a continuous decline in nitrogen concentration. The dependence of uptake rate on the nitrogen mobility can be described by a parameter $\alpha$:

$$\frac{dN}{dt} = \frac{dW}{dt} \frac{N_v - \alpha[N(t) - N(0)]}{V},$$

where the last equality holds as long as $f_r$ is constant ($f_r$ is the root fraction of plant mass, i.e. $W_r/W$).

The initial amount of nitrogen ($N_v$) in the growth medium decreases with the amount taken up by the plant $[N(t) - N(0)]$. $\alpha = 0$ corresponds to zero nitrogen mobility (i.e. the nitrogen uptake rate $dN/dt$ remains proportional to $N_v/V$) while $\alpha = 1$ corresponds to infinite mobility (i.e. $dN/dt$ is proportional to the decreasing nitrogen concentration in the medium), and $0 < \alpha < 1$ gives intermediate mobilities between the extremes.

$V_d$ and $\alpha$ are not independent; for example, a high mobility of nitrogen increases $V_d$, the volume depleted per unit new root. However, we do not need to deal with this dependence further in this paper.

Nutrient uptake is often described by Michaelis–Menten kinetics. Oscarsson, Ingemarsson & Larsson (1989b) measured $V_{\text{max}}$ (mg g$^{-1}$ d$^{-1}$) in species of *Lemna* and *Pisum* and found a linear relation between $V_{\text{max}}$ and $c_N$ up to $c_{N,\text{opt}}$, i.e.

$$\frac{1}{N} \frac{dN}{dt} = k c_N = k \frac{N}{W},$$

where $k$ is a constant. Rearranging,

$$\frac{1}{N} \frac{dN}{dt} = k.$$

In other words the relative uptake rate, $R_u$, is constant up to $c_{N,\text{opt}}$ (but decreases above $c_{N,\text{opt}}$).

The nitrogen uptake rate in Eqn 4 has no upper limit because $dN/dt$ can be made arbitrarily large by increasing $N_v$. I have chosen to keep the model as simple as possible, and $R_u$ is limited only by

$$R_u \leq R_{u,\text{max}} = R_{g,\text{max}},$$

ignoring the uptake capacity above the capacity needed for maximal growth.

**Simulation method**

Using the growth rate (Eqn 1) and the nitrogen uptake rate (Eqn 4), the plant mass $W$ and plant nitrogen content $N$ are calculated from day 0 onwards with a daily time-step. If the calculated $R_u$ values exceed the maximal limit defined above, the rate is adjusted down to $R_{u,\text{max}}$.

**Parameter values**

I used parameters that are typical for birch seedlings (*Betula pendula* Roth.) with nitrogen-limited growth. Ågren (1988) reported values of $c_{N,\text{opt}} = 39$ mg g$^{-1}$, $c_{N,\text{min}} = 4.9$ mg g$^{-1}$, and a maximal exponential growth rate ($R_{g,\text{max}}$) of 0.22 d$^{-1}$, which corresponds to a weight increase of 25% on a daily time-step. Eqn 2 then gives $P_N = 0.25/0.039 = 7.33$ d$^{-1}$.

The initial plant dry mass $W$ was set to 1 g and the nitrogen concentration ($c_N = N/W$) to 25 mg g$^{-1}$. The volume $V$ of the growth medium was set to 5 dm$^3$. The root fraction $f_r$ is a function of the nitrogen concentration in the plant. At the optimum concentration $c_{N,\text{opt}}$, $f_r = 0.20$, while $f_r = 0.50$ at the minimum concentration. (Ingestad & Ågren 1991). For the sake of simplicity, I have chosen to use a fixed $f_r = 0.35$.

The value of $V_d$ is not experimentally known but can be calculated. At steady-state growth, the relative increases of plant nitrogen and biomass are equal, i.e.

$$\frac{1}{N} \frac{dN}{dt} = \frac{1}{W} \frac{dW}{dt} = \frac{1}{W_r} \frac{dW_r}{dt}.$$

If Eqn 8 is multiplied by $W_r$ and combined with Eqn 3, then

$$W_r \frac{dW_r}{dt} V_d \frac{N_v}{V} = \frac{dW_r}{dt},$$

or

$$V_d = \frac{N}{W_r} \frac{V}{N_v} = \frac{1}{f_r} \frac{N}{W} \frac{V}{N_v}.$$

If $f_r = 0.35$ and $N/W = c_{N,\text{opt}}$ are inserted in Eqn 10, $V_d$ is determined by the minimum external nitrogen concentration necessary for maximal relative growth rate. For nitrate, this minimum concentration has been reported to lie in the range 1–20 mmol m$^{-3}$ (Olsen 1950; Edwards & Barber 1976; Clement, Hopper & Jones 1978; MacDuff et al. 1993) but large variation has been reported. In a compilation by Asher & Edwards (1978), the nitrate concentration ‘just adequate for growth’ was in the range 20 000–50 000 mmol m$^{-3}$. As Asher & Edwards suggested, this variation is probably attributable more to differences in experimental conditions than to differences between species. Explanations for this variation include (i) insufficient control of nutrient concentration with time (Ingestad 1982), and (ii) differences in the transport rate of nutrients from the solution to the root surface because of low stirring rate and the build-up of a boundary layer around the root surface (Dalton 1984; Ingestad & Ågren 1988).

Because it is impossible to determine a single value for the minimum external concentration for optimal growth, a range of values of $V_d$ is used in the simulations, corresponding to minimum external nitrogen concentrations for maximal uptake of 1.3, 2.6 and 5.2 mol m$^{-3}$ ($V_d = 6, 3$ and 1.5, respectively).

A summary of variables and parameters is given in Table 1.
be positive until $c^\text{N}$ approaches $c^\text{N} \text{min}$ in Eqn 2, resulting in a decrease of $\alpha$ and that of $\beta$g. When $R^\text{u}$, is zero, $P^\text{N}$, concentration and the root growth rate (Eqn 3). A high root growth rate can counteract a decrease in the external concentration, giving a high uptake rate until the external concentration approaches zero, and hence a more rapid depletion of nitrogen than that in a slowly growing plant. The internal concentration in the higher-N treatments may therefore fall below that in the low-N treatment (see point X in Fig. 3b) because the latter does not deplete the external nitrogen as quickly. This induces the Piper–Steenbjerg effect.

The plant mass and nitrogen concentration from Figs 3(a) and (b) on three different days are plotted in Fig. 3(c). The day of harvest determines whether or not a Piper–Steenbjerg effect is observed. As $t$ increases, the relation approaches a vertical line at $c^\text{N, min}$, which is the final stage in the model since plant death is not explicitly included. The pattern in Fig. 3c has often been reported (e.g. by Terman 1974, and Jones, Ruckman & Lawler 1972).

**Effect of $V_d$**

Most parameters in the model are fairly well known. However, the volume depleted by new roots, $V_d$, is a variable that has to be estimated indirectly (see above). Its importance can be seen in Fig. 4, where the results for three different values of $V_d$ are shown.

The Piper–Steenbjerg effect is amplified by lower values of $V_d$. If the external concentrations in the higher nitrogen treatments are so high that the calculated uptake is not limited by $V_d$ but is limited by $R^\text{u, max}$ (Eqn 7), a decrease in $V_d$ does not decrease uptake rates. In the low-nitrogen treatments, where the calculated uptake is not limited by Eqn 7, a decrease in $V_d$ decreases the uptake rate. Hence the differences in uptake rate between high- and low-nitrogen treatments are magnified by lower values of $V_d$, which amplify the Piper–Steenbjerg effect. If $R^\text{u, max}$ increases, the Piper–Steenbjerg effect is magnified for the same reason (data not shown).

Note that a change in parameters not only changes the possibility of seeing a Piper–Steenbjerg effect, but also changes the time of occurrence of the effect. The Piper–Steenbjerg effect becomes more pronounced earlier if $V_d$ is low.

**Effect of nutrient mobility in medium**

A low nitrogen mobility in the medium ($\alpha = 0$) will give a step decrease in nitrogen uptake, and result in a sharper response than in a medium with higher nitrogen mobility (Fig. 5). The small qualitative effects of $\alpha$ indicate that nitrogen mobility in the growth medium is of minor importance for occurrence of the Piper–Steenbjerg effect. This is supported by experimental reports of Piper–Steenbjerg effects in various growth media (Bates 1971).

**DISCUSSION**

The model can produce a Piper–Steenbjerg effect, but can we trust it? The predictions of a model cannot be better

### Table 1. Variables used in the text

<table>
<thead>
<tr>
<th>Variable</th>
<th>Meaning</th>
<th>Unit</th>
<th>Value used</th>
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</thead>
<tbody>
<tr>
<td>$N$</td>
<td>Nitrogen mass in plant</td>
<td>mg</td>
<td>$N(0)=25*$</td>
</tr>
<tr>
<td>$W$</td>
<td>Plant dry mass</td>
<td>g</td>
<td>$W(0)=1.0*$</td>
</tr>
<tr>
<td>$W^\text{r}$</td>
<td>Root dry mass</td>
<td>g</td>
<td>-</td>
</tr>
<tr>
<td>$c^\text{N}$</td>
<td>Mass of nitrogen per unit dry mass of tissue</td>
<td>mg g$^{-1}$</td>
<td>$c^\text{N}(0)=25*$</td>
</tr>
<tr>
<td>$c^\text{N, min}$</td>
<td>Minimum $c^\text{N}$ for growth to occur</td>
<td>mg g$^{-1}$</td>
<td>4-9</td>
</tr>
<tr>
<td>$c^\text{N, opt}$</td>
<td>Minimum $c^\text{N}$ for maximal relative growth rate of tissue</td>
<td>mg g$^{-1}$</td>
<td>39</td>
</tr>
<tr>
<td>$f^\text{r}$</td>
<td>Root fraction (W/W)</td>
<td>-</td>
<td>0.35</td>
</tr>
<tr>
<td>$N^\text{v}$</td>
<td>Initial nitrogen mass in medium</td>
<td>g</td>
<td>0.2-2.0</td>
</tr>
<tr>
<td>$P^\text{N}$</td>
<td>Rate of increase in plant mass per unit plant nitrogen</td>
<td>d$^{-1}$</td>
<td>7.33</td>
</tr>
<tr>
<td>$V$</td>
<td>Volume of growth medium</td>
<td>dm$^3$</td>
<td>5</td>
</tr>
<tr>
<td>$V^\text{d}$</td>
<td>Volume of growth medium that is depleted by 1 g new root dry mass</td>
<td>dm$^3$ g$^{-1}$</td>
<td>1.5, 3.0, 6.0</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>Mobility of nutrients in medium</td>
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<td>0-1</td>
</tr>
<tr>
<td>$R^\text{u, max}$</td>
<td>Maximum relative uptake rate</td>
<td>d$^{-1}$</td>
<td>0.25</td>
</tr>
<tr>
<td>$R^\text{g, max}$</td>
<td>Maximum relative growth rate</td>
<td>d$^{-1}$</td>
<td>0.25</td>
</tr>
</tbody>
</table>

* Initial values in simulations.
Figure 3. The time development of (a) plant dry mass and (b) plant nitrogen concentration ($c_N$). The straight dotted line in (b) is the nitrogen concentration for maximal growth, $c_{N,\text{opt}}$. Three values for the amount of initial nitrogen, $N_v$, in the growth medium are shown: 0.2 g (solid line), 0.8 g (dashed line) and 1.5 g (dotted line). The relation between plant mass and nitrogen concentration as $N_v$ varies changes drastically with time, as can be seen in (c), where plant mass is plotted versus the nitrogen concentration on three different days: days 20, 25 and 30. Eventually, all points in (c) end up at the minimum plant nitrogen concentration for growth, $c_{N,\text{min}}$ (the dotted line). $R_{\text{g}}$ and $R_{\text{u}}$ for the simulation with $N_v=0.8$ g are shown in (d). $V_d$ is 1.5 dm$^3$ g$^{-1}$ and $\alpha=1$ (infinite mobility). Other parameters are as in Table 1.

than its underlying assumptions. This model is based on three basic assumptions: the growth equation, the uptake equation and the upper limits of $R_u$ and $R_g$. The relation between the mass of plant nitrogen and the absolute growth rate of plant mass, as well as the upper limit of $R_g$, is extremely well validated and has been extensively discussed elsewhere (e.g. Ingestad & Ågren 1992).

The weak point in the model is the formulation of nitrogen uptake. The uptake process is complex, and it is difficult to identify and measure key components in the process, especially for short-term dynamics. It is beyond the scope of this paper to review the research on uptake kinetics, but it seems plausible that uptake depends on the rate of root growth and the external nitrogen concentration, although there is no generally accepted formulation. The uptake equation remains unvalidated.

The description of $R_{g,\text{max}}$ probably does not affect initiation of the Piper–Steenbjerg effect. A higher uptake capacity only magnifies the effect, as discussed in the section ‘Effect of $V_d^*$’, and the lack of variable allocation is not likely to change the results significantly. Increased allocation to roots in slow-growing plants does increase the
uptake rate slightly, but the rapid decrease of plant nitrogen concentration in fast-growing plants, which is the reason for the Piper–Steenbjerg effect, is only accelerated by an allocation function.

There are no published measurements that allow direct comparison with the model, but a similar experiment for small birch is described by McDonald, Lohammar & Ericsson (1986). They decreased the relative addition rate of nitrogen from 0.20 to 0.05 d⁻¹, a situation similar to the exhaustion of nitrogen by fast-growing plants in the model simulations. A simulation was performed to test the model against their results. The two values of \( N_v/V \) required to obtain steady-state growth at 0.20 and 0.05 d⁻¹ in the model were found empirically. \( N_v/V \) was 61 g m⁻³ from day -5 to day 0, on which day it was decreased to 22 g m⁻³ (Fig. 6), this being the same day on which the relative addition rate was decreased in the experiment. Figs 6(a) and (b) show the time developments for \( c_N \) and \( R_g \), respectively. The decreases of \( R_g \) and \( c_N \) are quite similar in the model and in the experiment, both in magnitude and over time, although the decreases were slightly faster in the experiment. The time lag depends on the difference in nutrient uptake. Nitrogen flow to the roots is controlled in the experiment and allows a step decrease in relative uptake rate, but in the model the uptake is equally determined by root growth and external nitrogen concentration. Since root growth is higher in the transition period between the two steady states than at the lower steady state, the uptake predicted by the model is higher than that in the experiment.

The overshoot observed in the experimental values of \( R_g \) is a result of an imperfect steady state at 0.20 d⁻¹ (Fig. 6b). This comparison is not a validation of the uptake equation since the uptake formulation in the model is not directly applicable to the experimental set-up. The nitrogen productivity, \( P_N \), has previously only been tested against steady-state measurements but holds also for the step decrease in this comparison, as can be seen from the close relationship between \( c_N \) and \( R_g \).

The hypothesis presented states that the Piper–Steenbjerg effect is initiated by a rapid nutrient dilution in fast-growing plants. What then is the difference between this explanation and the ‘nutrient dilution’ cited in Mengel & Kirkby (1987)? Although not defined, these authors discuss a steady-state relation between nutrient availability, plant nutrient concentration and growth or yield. This is a very distinct difference from the hypothesis presented in this paper, where dynamic changes in time initiate the Piper–Steenbjerg effect. This difference is not obvious at first glance, but makes the two explanations and their underlying assumptions incompatible.

The result of the simulations imply that there are at least two conditions that must be fulfilled to obtain a Piper–Steenbjerg effect:

(i) the relative uptake rate must be lower in low-nutrient treatments than in high-nutrient treatments, and
(ii) harvest must occur at a time when the external nutrients have been depleted in the high-nutrient treatments but not in the low-nutrient treatments.

Despite some simplifications in the model formulation, it is concluded that the analysis gives a plausible explanation for the occurrence of the Piper–Steenbjerg effect.

Figure 4. The relation between plant dry mass and plant nitrogen concentration (\( c_N \)) at day 30 for three values of \( V_e \). Each line is generated by varying the initial amounts of nitrogen in the growth medium, from \( N_v = 0.2\) g (bottom) to 2.0 g (top). Other parameters are as in Fig. 3.

Figure 5. As Fig. 4 (\( V_e = 1.5 \)) except for the extremes of nutrient mobility, \( \alpha \), in the medium.
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